

Research Paper

Genotypic differences in the growth and mineral uptake of passion fruit vines and roots under different soil environments

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ABSTRACT

The preferable soil pH for purple passion fruit (*Passiflora edulis*), yellow passion fruit (*P. edulis* f. *flavicarpa*), and their hybrids, has been reported to range 4–8, but the optimal pH remains unclear. In this study to evaluate and compare the vine and root growth among the parent species and hybrids, we cultivated cutting-propagated young plants of one purple passion fruit (PK), one yellow passion fruit (MQ), and three hybrid cultivars (RS, SQ, and SS) in 4 different pH (4–8) soils using acidic (pH ≈5) and calcareous (pH ≈8) soils. Then, rhizosphere pH trends were monitored, and dry matter production, photosynthetic rate, and mineral content were recorded after 11 weeks. PK showed a preference for acidic soil and grew vigorously only in pH ≈5, but exhibited severe chlorosis and growth inhibition at pH ≥ 6. MQ showed broad tolerance to soil pH, maintaining high root dry matter production, photosynthetic rates, root and leaf mineral content even in calcareous soils. Among hybrids, RS showed a soil preference similar to PK and highest tolerance to extremely acidic conditions (pH ≈4), but was susceptible at higher pH; SQ showed high-pH tolerance similar to MQ; SS was intermediate. In acidic soils, elevated exchangeable Al coincided with reduced Mg content, except for RS. Whereas, chlorosis emerged as a critical limitation under high pH, causing reduced leaf photosynthesis. Our results demonstrated RS as the most tolerant hybrid cultivar for growing in extremely acidic soils, while SQ as a feasible one like yellow passion fruit in calcareous alkaline soils.

1. Introduction

Purple passion fruit (*Passiflora edulis* Sims), yellow passion fruit (*P. edulis* Sims f. *flavicarpa* Deg.), and their hybrids are commercially significant fruit crops cultivated widely from temperate to tropical regions. The native habitats of purple passion fruit include the tropical highlands and plateaus of Brazil, Paraguay, and Argentina (Morton, 1987; Ulmer and MacDougal, 2004), where acidic soils are prevalent. Various soil pH ranges have been reported to be suitable for passion fruit cultivation, including pH levels around 4.5 (Niwayama and Higuchi, 2019), 5.5–6.5 (Sale, 1988), 5.5–6.8 (Nakasono and Paull, 1998), and 6.5–7.5 (Morton, 1987). Hybrid passion fruit cultivars have been found to prefer strongly acidic conditions around their roots. For example, ‘Ruby Star’ exhibited optimal fruit quality under nutrient solution pH levels of 4–5 (Nakayama and Matsuda, 2022), and ‘Summer Queen’

roots showed the best elongation even in excessively acidic soils with a pH of 3.5 (Niwayama and Higuchi, 2018). Additionally, the best quality of ‘Summer Queen’ fruits was obtained from acidic soils with pH around 4.5 (Niwayama and Higuchi, 2019). Root elongation of ‘Summer Queen’ was significantly restricted in soils with a pH above 5.5 (Niwayama and Higuchi, 2018), and plant growth was further inhibited in alkaline soils (Kondo et al., 2017). Conversely, Knight and Sauls (1994) reported that yellow passion fruit can tolerate alkaline soils. Despite these reports, no comprehensive studies have examined the growth responses of these species to different soil environments from acidic to alkaline.

Purple passion fruit thrives in cooler mid- to high-elevation subtropical regions and is particularly suitable for fresh consumption due to the lower acidity of its juice. However, it is susceptible to high temperatures and several diseases (Fischer and Rezende, 2008; Morton, 1987; Ortiz et al., 2014; Thokchom and Mandal, 2017). In contrast,

Abbreviations: (Al), Aluminum; (NH₄NO₃), Ammonium nitrate; ((NH₄)₂SO₄), Ammonium sulfate; (B), Boron; (Ca), Calcium; (CaCl₂), Calcium chloride; (Ca(NO₃)₂), Calcium nitrate; (Cu), Copper; (K₂HPO₄), Dipotassium hydrogen phosphate; (Fe), Iron; (MgSO₄), Magnesium sulfate; (Mn), Manganese; (Mo), Molybdenum; (N), Nitrogen; (P), Phosphorus; (K), Potassium; (KNO₃), Potassium nitrate; (K₂SO₄), Potassium sulfate; (Zn), Zinc.

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Table 1Soil properties of original acidic and calcareous soils (*Kunigami-Mahji* and *Shimajiri-Mahji*, respectively) used in the present study.

Soil name	pH		TC ^z (gC/kg)	TN ^z (gN/kg)	Water holding capacity ^y (%)	Particle size distribution (%) ^x			Exchangeable cations ^w (cmol(+)/kg)						CEC pH 7 ^v (cmol (+)/kg)
	(H ₂ O)	(KCl)				Sand	Silt	Clay	Ca ²⁺	Mg ²⁺	Na ⁺	K ⁺	Al ³⁺	H ⁺	
<i>Kunigami-Mahji</i>	5.10	4.96	3.77	0.36	36.00	40.2	19.0	40.8	1.60	1.05	0.40	0.21	1.17	0.91	6.05
<i>Shimajiri-Mahji</i>	8.06	8.02	5.89	0.34	26.80	58.2	26.0	15.8	22.06	0.67	0.15	0.22	0.10	0.00	2.44

^z : The dry combustion method using an EA isolink™ CN analyzer (IRMS System, Thermo Fisher Scientific Co. Ltd., Tokyo, Japan) was used to determine total carbon and nitrogen (TC and TN, respectively).

^y : The saturation and drainage method was used to determine water holding capacity.

^x : Following removal of organic matter with H₂O₂, soil texture was determined by dry sieving for sand (0.05–2 mm) and by the pipette method (Stokes' law) for silt (2–50 μm) and clay (<2 μm) at 25 °C, following ISO 11,277 and Gee and Or (2002).

^w : Exactly 5 g of soil was extracted with ammonium acetate solution and analyzed with an atomic absorption spectrophotometer (AA-660, Shimadzu, Kyoto, Japan) to determine exchangeable Ca²⁺, Mg²⁺, Na⁺, and K⁺; the titration method was used to determine exchangeable Al³⁺ and H⁺.

^v : Cation exchange capacity (CEC) was determined by flow injection analysis (FIA) for CEC method with 0.1 M NaCl as the background solution.

yellow passion fruit, in addition to its tolerance of alkaline soils, adapts well to warmer lowland tropical areas, tolerates high temperatures and diseases, and produces larger fruits, though it is less ideal for fresh consumption due to the high acidity of its juice (Akamine et al., 1974; Morton, 1987; Nakasone et al., 1967). To consistently produce high-quality fruits for fresh consumption, hybrids with desirable traits from both purple and yellow passion fruits have been developed in several regions, including Australia (Menzel et al., 1987), Florida (Knight, 1972), Japan and Taiwan (Matsuda and Ogata, 2020), India (Thokchom and Mandal, 2017), Israel (Nave et al., 2010), and Kenya (Matheri et al., 2016). These broad cultivation areas cover diverse soil environments, suggesting wide adaptability mechanisms of hybrid cultivars.

Calcareous soils, characterized by a pH range of 7–9 and containing >15 % calcium carbonate or lime, possibly including sodium carbonate (Leytem and Mikkelsen, 2005), may present some challenges, e.g. limitation of nutrient availability (George et al., 2012; Marschner and Rengel, 2012), for the cultivation of hybrid passion fruit cultivars. The high pH and calcium concentrations in these soils can inhibit root elongation and photosynthetic activity (Kondo et al., 2017; Niwayama and Higuchi, 2018), cause leaf necrosis (Kondo and Higuchi, 2020), and increase juice acidity (Niwayama and Higuchi, 2019), leading to inferior fruit quality for fresh consumption. Kondo et al. (2017) also observed a significant decrease in Mn and Zn content in hybrid passion fruit leaves grown in alkaline soils, noting that the uptake of these micronutrients may be hindered under high pH conditions.

Calcareous soils make up approximately 30 % of global soils (Chen and Barak, 1982) and are commonly found in arid and semi-arid subtropical regions, as well as subtropical and tropical islands. For example, on Japan's southern subtropical islands, in addition to acidic *Kunigami-Mahji* soils which occupy 31.4 % of arable land (Kuba, 1993), calcareous *Shimajiri-Mahji* soils occupy 41 % (Hamazaki, 2005), which limits the areas suitable for passion fruit cultivation and production. To expand cultivation and improve productivity in such regions, it is crucial to elucidate the growth characteristics of each cultivar under different soil environments, helping growers select suitable cultivars. Furthermore, understanding the mineral uptake tendencies can provide recommendations for cultivation management strategies to mitigate growth disorders, such as chlorosis, necrosis and leaf fall, caused by calcareous soils.

In this study, focusing on the growth and mineral uptake of young passion fruit plants, i.e. from transplanting to the completion of the main stem before flowering, cuttings of purple and yellow passion fruits, as well as hybrid cultivars, were grown in soils with pH levels ranging from 4 to 8, using locally sourced acidic *Kunigami-Mahji* soils and high-pH calcareous *Shimajiri-Mahji* soils. We determined genotypic differences in vegetative growth and mineral uptake under these different soil environments.

2. Materials and methods

The greenhouse cultivation trial using various genotypes of passion fruit was conducted at the Tropical Agriculture Research Front (TARF) of Japan International Research Center for Agricultural Sciences (JIRCAS) in Ishigaki Island (24.4 °N, 124.2 °E), Okinawa, Japan as follows.

2.1. Plant material, cultivation management, and soil pH treatments

Twenty-five young plants were used for each of five passion fruit genotypes: one purple passion fruit (*P. edulis*) Kagoshima Strain (PK), one cultivar of yellow passion fruit (*P. edulis* f. *flavicarpa*) 'MaQuatro' (MQ), and three cultivars of hybrid passion fruit (*P. edulis* × *P. edulis* f. *flavicarpa*) 'Ruby Star' (RS), 'Summer Queen' (SQ), and 'Sunny Shine' (SS). These plants were propagated by cuttings in December 2021 and induced their roots in river sand until April 2022. Then, using local acidic soils, *Kunigami-Mahji* (initial pH ≈5), and calcareous soils, *Shimajiri-Mahji* (initial pH ≈8) (Table 1), four soil treatments were prepared: 1) extremely acidic conditions using *Kunigami-Mahji* adjusted with sulfuric acid to pH 4 (K4); 2) strongly acidic conditions using unadjusted *Kunigami-Mahji* (K5); 3) mildly acidic conditions using *Shimajiri-Mahji* adjusted with sulfuric acid to pH 6 (S6); and 4) alkaline conditions using unadjusted *Shimajiri-Mahji* (S8). Based on sand–silt–clay percentages, the acidic *Kunigami-Mahji* soil (40.18 %, 19.04 %, 40.78 %) classifies as clay, while the calcareous *Shimajiri-Mahji* soil (58.23 %, 26.02 %, 15.75 %) classifies as sandy loam (USDA NRCS, 2017).

On 27 April 2022, five cuttings from each genotype were transplanted into 3-L plastic pots filled with 2.5 kg of air-dried K4, K5, S6, or S8 soils (5 plants × 5 genotypes × 4 soils). Additionally, four other RS plants were propagated and transplanted into each soil as well, and the pH trends of four different soils were monitored biweekly as follows: Approximately 10 g each of soil was sampled using a spatula from 5 to 6 cm depth at three evenly spaced positions along the inner pot wall to minimize root damage, and the soil samples from these three positions were mixed for each of four RS plants. After air-drying, each 5 g of air-dried soil sample was mixed with 25 mL of distilled water and gently shaken for ≈60 min, and allowed to rest for ≈30 min. Then the electrode of a pH/EC meter (D-220 PC-S, HORIBA, Ltd., Kyoto, Japan) was soaked into the mixture for 3 min to record the value. Considering these pH trends (Fig. S1), if the pH values dropped below the target level, the pH of the soils for the relevant RS plant and the other experimental plants in the same soil treatment was adjusted by mixing calcium hydroxide into daily irrigation water. Conversely, if the pH values rose above the target, pH was adjusted with sulfuric acid as well. The necessary amounts of 0.1 M sulfuric acid and calcium hydroxide for each soil pH adjustment were determined using the buffering curves generated from the original and acidified soils from each acidic and calcareous soil type (Fig. S2). In

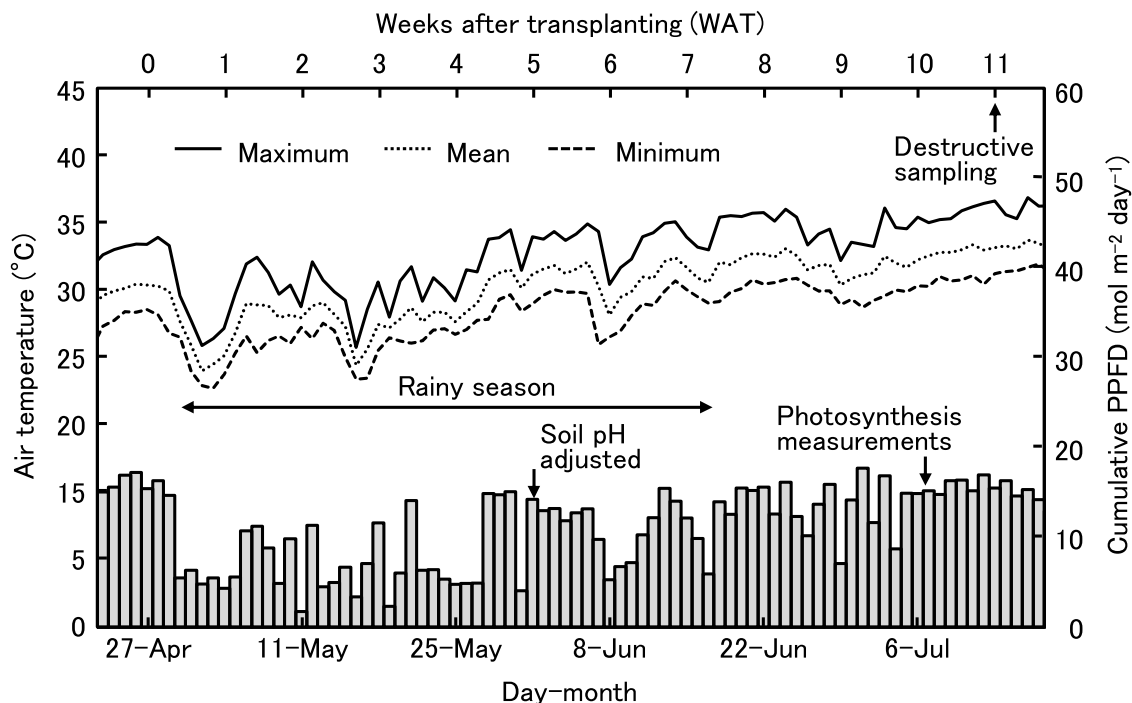


Fig. 1. Daily maximum, mean, minimum air temperatures and cumulative photosynthetic photon flux density (PPFD) in the greenhouse from late April–mid July 2022. Rooted cuttings of passion fruit were transplanted into acidic and calcareous soils on 27 April. Soil adjustment was carried out once on 31 May at 5 weeks after transplanting (WAT). Photosynthetic-rate measurements were conducted on 7 July under sunny and high mean temperature ($\geq 30^\circ\text{C}$) conditions between 0930 and 1430 h. Destructive sampling of all plants were conducted at 11 WAT for the growth and mineral uptake analysis.

addition to the four RS plants used for pH monitoring, pH measurements were carried out as well for each genotype and treatment at 0 (26 April), 5 (31 May), 9 (2 June), and 11 (14 July) weeks after transplanting (WAT) to track the trends in soil pH conditions for each genotype and treatment.

A nutrient solution (pH ≈ 7) of 6.0 mM NH_4NO_3 , 6.0 mM $(\text{NH}_4)_2\text{SO}_4$, 2.0 mM KNO_3 , 1.0 mM $\text{Ca}(\text{NO}_3)_2$, 1.5 mM K_2HPO_4 , 3.0 mM CaCl_2 , 2.0 mM MgSO_4 , 1.0 mM K_2SO_4 , 57 μM Fe, 0.6 μM Cu, 0.9 μM Zn, 9.9 μM Mn, 47.2 μM B, and 0.08 μM Mo (Kondo and Higuchi, 2012; Niwayama and Higuchi, 2019) was applied at a rate of 800 mL per week to each plant. The timing and amount of irrigation and nutrient solution application were determined daily using a water content reflectometer (HydroSense CS620/CD620, Campbell Scientific Inc., Utah, U.S.A) to monitor soil moisture, prevent percolation, drought stress, and waterlogging, and minimize pH drift caused by irrigation water; the amount of irrigation was determined using equations for soil water content (Fig. S3) and fixed at 70 % of the deficit between the soil water capacity and the calculated values. A pair of 12-cm sensor rods were inserted into the soils of several representative pots multiple times a day for measurements to avoid drought stress. Each pot was placed on a 10-cm-thick concrete block to prevent external contamination from the drainage hole at the bottom. The main stem of each plant was trained vertically up to a height of about 140 cm from its base and then trained horizontally until three axillary buds emerged. The terminal buds of the stem were pinched, and the three axillary buds were allowed to grow downward from the horizontally trained portion, while all other axillary and flower buds were removed.

2.2. Measurements

Shoot lengths, the number of leaves, and the leaf area were monitored at 1, 4, 6, 8, and 11 WAT for each plant. The leaf area was estimated using the formula by Kondo and Higuchi (2011):

$$A = 0.85L^2 - 2.39L + 3.37$$

where A represents the leaf area, and L represents the leaf costa length. For each plant, mature and fully-expanded five leaves were selected randomly from the stem and the leaf costa lengths were recorded. The SPAD value (indicating relative chlorophyll content) of each leaf was measured using a chlorophyll meter (SPAD-502Plus, Konica Minolta Sensing Inc., Tokyo, Japan) at 4, 6, 8, and 11 WAT.

The photosynthetic rates of two fully expanded leaves, located at the midpoint of each stem, were measured on a sunny day (7 July). Photosynthesis measurements were conducted using a rapid, closed gas-exchange system (MIC-100 system, Masa International Corp., Tokyo, Japan) between 0930 and 1430 h in a randomized plant order. The light intensity inside the leaf chamber was $1200 \mu\text{mol m}^{-2} \text{s}^{-1}$ PPFD, and photosynthetic rates were calculated based on the time required for the CO_2 concentration inside the chamber to decrease from 400 ppm to 380 ppm. The stabilization time before measurement was set to 10 s. After the measurements, the SPAD values of each two leaves were recorded in the same manner as described above.

On 14 July (11 WAT), incidence of chlorosis was evaluated visually using three plants, randomly selected from each genotype under each soil treatment. Five fully expanded leaves were selected randomly from the top to bottom stem sections of each plant. Leaves were classified as chlorotic (showing interveinal chlorosis; Fig. S4) or healthy, and incidence was calculated as the percentage of chlorotic leaves relative to the total number of leaves examined per treatment. Severity of chlorosis was recorded visually at three levels: Mild (1–50 %), Moderate (51–75 %), and Severe (76–100 %).

All leaves, stems, and roots were separately sampled in 11 WAT. The fresh samples were weighed and then oven-dried at 70°C for >3 days, then dry-matter weight was recorded separately in aboveground vine (leaf and stem) and root. During the extraction of each root sample from the soil, approximately 500 g of soil was collected in plastic bags. These soil samples were air-dried at room temperature in the laboratory for 1 week, and the pH (H_2O) of approximately 5 g of each air-dried soil sample was measured in the same manner as described above.

Air temperatures in the greenhouse were recorded using a data

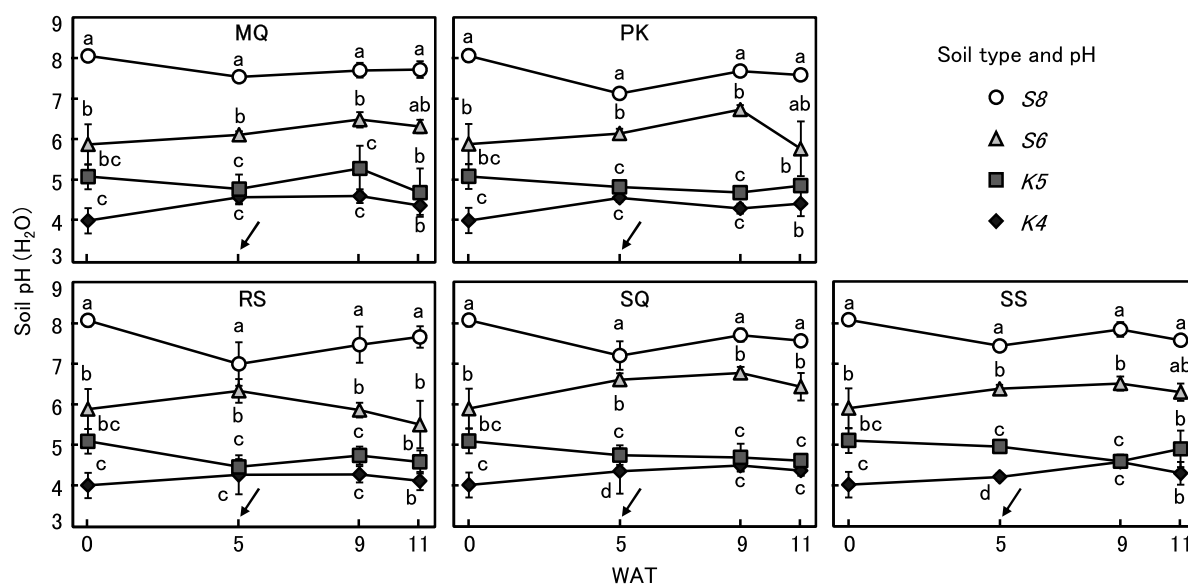


Fig. 2. Soil pH (H₂O) trends during 0–11 weeks after transplanting (WAT), i.e. from 27 April to 14 July 2022, for yellow passion fruit (*Passiflora edulis* f. *flavicarpa*) ‘MaQuatro’ (MQ), purple passion fruit (*P. edulis*) Kagoshima strain (PK), and three cultivars of hybrid passion fruit (*P. edulis* × *P. edulis* f. *flavicarpa*) ‘Ruby Star’ (RS), ‘Summer Queen’ (SQ), and ‘Sunny Shine’ (SS). The arrows indicate the day of pH adjustment at 5 WAT with Ca(OH)₂ and H₂SO₄ using pH buffering curves shown in Fig. S2. Soil types are indicated by K4 (pH 4), K5 (pH 5), S6 (pH 6), and S8 (pH 8). Different letters in the same measurement week in each graph indicate significant differences by Tukey’s multiple comparison test at $P < 0.05$.

logger connected to a copper-constantan thermocouple. The thermocouple was covered by a forced-ventilation and heat-insulating pipe and installed at a height of 1.5 m above the ground near the plants. Photosynthetic photon flux density (PPFD) in the greenhouse was recorded using a quantum sensor (LI-190SA, LI-COR, Inc., Lincoln, Nebraska) installed at a height of 2.5 m above the ground as well. Data was recorded every 15 min by averaging values for every 15 s.

2.3. Mineral analysis

The mineral contents of all leaves and roots were determined using the wet digestion method. Approximately 100 mg of oven-dried leaves or root samples from each plant were placed in a boiling tube and

decomposed with 2 mL of concentrated 60 % nitric acid (1.38 g mL^{-1}) heated to 100°C in a draft chamber until the thick brown bubbles faded away. Three glass beads and 0.2 mL of concentrated sulfuric acid were then added, and the sample was heated until it became transparent, which took about 8–12 h. Two independent digestion batches were prepared, and the samples were filtered with 0.1 M hydrochloric acid into 50 mL flasks. The filtrate of each digest was then analyzed in triplicate using an inductively coupled plasma atomic emission spectrometer (ICPE 9000, Shimadzu, Kyoto, Japan) for precision element analysis. Each plant sample was digested once per batch, and corresponding values from batch A and batch B were averaged to obtain a single dataset for each replicate. The elements measured included Al, K, Ca, Fe, Mn, Mg, and P.

Table 2

The effect of four treatments of soil type and pH, i.e. acidic *Kunigami-Mahji* soils (K4 and K5) and calcareous *Shimajiri-Mahji* soils (S6 and S8), on the vegetative growth of yellow passion fruit (*Passiflora edulis* f. *flavicarpa*) ‘MaQuatro’ (MQ), purple passion fruit (*P. edulis*) Kagoshima strain (PK), and three hybrid (*P. edulis* × *P. edulis* f. *flavicarpa*) cultivars ‘Ruby Star’ (RS), ‘Summer Queen’ (SQ), and ‘Sunny Shine’ (SS), and the results of two-way analysis of variance (ANOVA).

		Aboveground dry weight ^z (ADW, g)		Root dry weight (RDW, g)		Stem length (SL, cm)		Leaf area (LA, cm ²)		Leaf number (LN)		Root/aboveground ratio ^y (RAR)	
Genotype													
	MQ	18.5 ± 2.6	B	1.7 ± 0.3	C	140.6 ± 15.9	A	83.8 ± 6.9	BC	19.8 ± 2.6	C	0.09 ± 0.01	C
	PK	5.8 ± 1.9	C	0.9 ± 0.4	C	57.7 ± 20.1	B	59.0 ± 13.9	C	9.7 ± 2.1	D	0.13 ± 0.02	BC
	RS	19.9 ± 1.8	B	1.9 ± 0.4	C	146.5 ± 14.2	A	93.1 ± 8.2	AB	23.0 ± 1.7	BC	0.09 ± 0.01	C
	SQ	29.8 ± 1.1	A	5.6 ± 0.6	A	174.4 ± 7.1	A	107.0 ± 6.7	A	31.4 ± 1.8	A	0.19 ± 0.01	A
	SS	21.3 ± 2.2	B	3.7 ± 0.7	B	165.3 ± 17.7	A	81.0 ± 7.1	BC	24.8 ± 2.9	B	0.17 ± 0.02	AB
Soil													
	K4	18.5 ± 1.8	a	3.0 ± 0.5	ab	144.5 ± 16.3		88.3 ± 9.8	b	21.3 ± 2.1	b	0.15 ± 0.02	
	K5	23.4 ± 1.6	a	3.6 ± 0.5	a	152.4 ± 13.9		110.4 ± 7.4	a	27.7 ± 2.7	a	0.14 ± 0.01	
	S6	19.4 ± 1.6	a	2.3 ± 0.4	bc	137.0 ± 9.8		92.2 ± 9.1	ab	23.8 ± 1.6	ab	0.12 ± 0.01	
	S8	14.9 ± 2.6	b	2.1 ± 0.5	c	116.8 ± 19.7		81.9 ± 9.0	b	21.8 ± 3.2	b	0.12 ± 0.01	
Two-way ANOVA													
Effect of genotype [G]		***		***		***		***		***		***	
Effect of soil [S]		***		***		ns		***		***		ns	
[G] × [S] interaction		**		**		ns		**		ns		ns	

Data are shown as means ± SE. *** and ** represent statistical significance at $P < 0.001$ and $P < 0.01$, respectively. “ns” indicates no significance. Different upper and lowercase letters within the same column indicate statistical differences among genotype and soils, respectively by Tukey’s multiple comparison test at $P < 0.05$.

^z : Above-ground dry weight is the sum of stem and leaf dry weight.

^y : Root/aboveground ratio was calculated using the dry weight values of root and aboveground plant body.

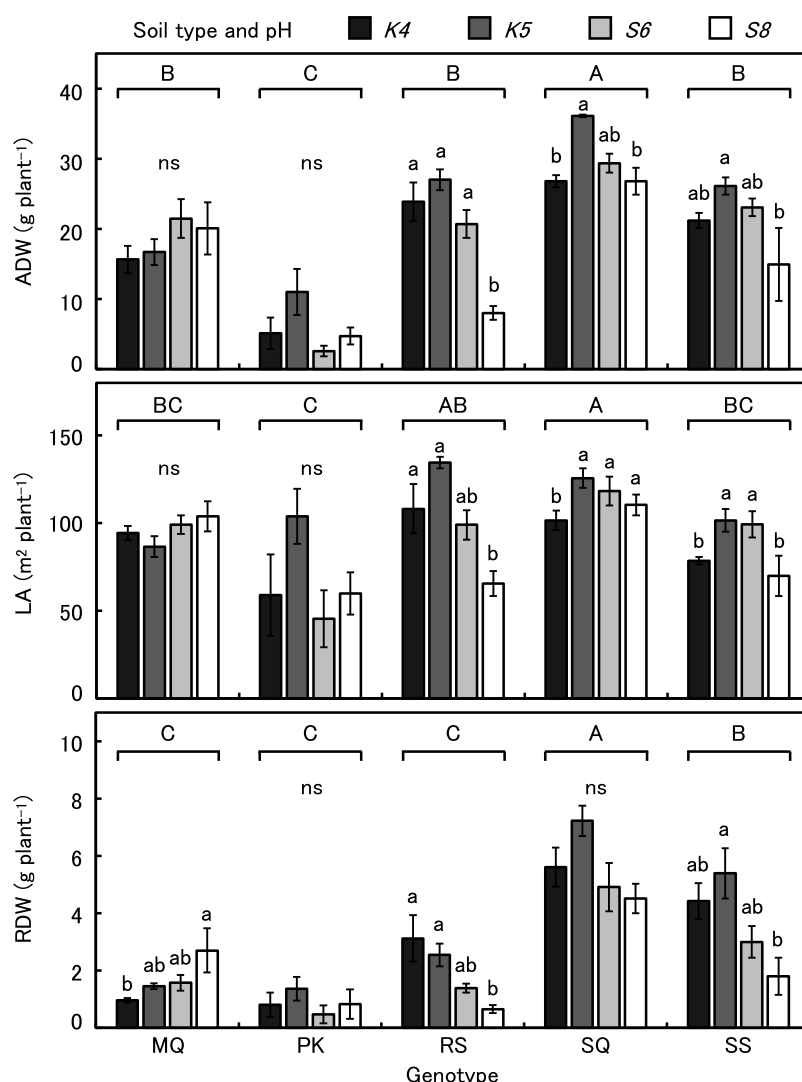


Fig. 3. The effects of acidic *Kunigami-Mahji* (K), calcareous *Shimajiri-Mahji* (S) soils and pH on the aboveground dry weight (ADW), leaf area (LA), and root dry weight (RDW) at 11 weeks after transplanting of five passion fruit genotypes: yellow passion fruit (*Passiflora edulis* f. *flavicarpa*) ‘MaQuatro’ (MQ), purple passion fruit (*P. edulis*) ‘Kagoshima Strain’ (PK), and three cultivars of hybrid passion fruit (*P. edulis* × *P. edulis* f. *flavicarpa*) ‘Ruby Star’ (RS), ‘Summer Queen’ (SQ), and ‘Sunny Shine’ (SS). Vertical bars indicate SE. Different capital letters in each graph and small letters for each genotype indicate significant differences by Tukey’s multiple comparison test at $P < 0.01$. “ns” indicates no significance.

2.4. Data analysis

The cultivation experiment followed a randomized block design with four soil treatments (K4, K5, S6, and S8) and five passion fruit genotypes (MQ, PK, RS, SQ, and SS). For the growth and mineral content data at 11 WAT, two-way analysis of variance (ANOVA) was performed to analyze genotype, soil, and their interaction effects, followed by Tukey’s multiple comparison test ($P < 0.05$). For chlorosis incidence data, incidence percentage value was calculated for each plant, arcsine-transformed, and then analyzed in the same manner as described above. All analyses were carried out using OriginPro 2023 (version 10.0.0.154; Lightstone Corp., Tokyo, Japan).

3. Results

The mean air temperatures in the greenhouse were maintained between 25 and 30 °C from April to June, peaking at 32 °C in July after the end of the rainy season (Fig. 1). Daily maximum/minimum temperatures ranged from 25–35/20–28 °C until early June and rose constantly above 35/25 °C thereafter. Daily cumulative PPFD was above 15 mol

$\text{m}^{-2} \text{day}^{-1}$ on sunny days and decreased below 5 $\text{mol m}^{-2} \text{day}^{-1}$ on rainy days. Rainy season was from the beginning of May to mid-June. Throughout the experimental period, although the four levels of pH conditions were not perfectly maintained at the target values, their relative levels ($K4 < K5 < S6 < S8$) were generally maintained (Figs. 2 and S1). At 5 WAT, the pH of K4 and S6 soils increased to 4.2–4.6 and 6.1–6.6, respectively, and adjustment using 0.1 M sulfuric acid was conducted to prevent the pH values from increasing. Conversely, the pH of K5 and S8 soils decreased to 4.5–4.8 and 7.0–7.5, respectively, and adjustment with calcium hydroxide was conducted.

The growth parameters at 11 WAT and the results of the two-way ANOVA are presented in Table 2. The hybrid cultivar SQ showed the most vigorous growth among all genotypes, with an average aboveground dry weight (ADW) of 29.8 g. Yellow passion fruit (MQ) and the hybrid cultivars RS and SS exhibited similar ADW values, ranging from 18.5 to 21.3 g. In contrast, the purple passion fruit PK had the weakest growth, with an average ADW of 5.8 g. On average, SQ had the highest root dry weight (RDW) at 5.6 g, stem length (SL) at 174.4 cm, leaf area (LA) at 107.0 cm^2 , leaf number (LN) at 31.4, and root/aboveground ratio (RAR) at 0.19. SS had the second-highest values for all parameters,

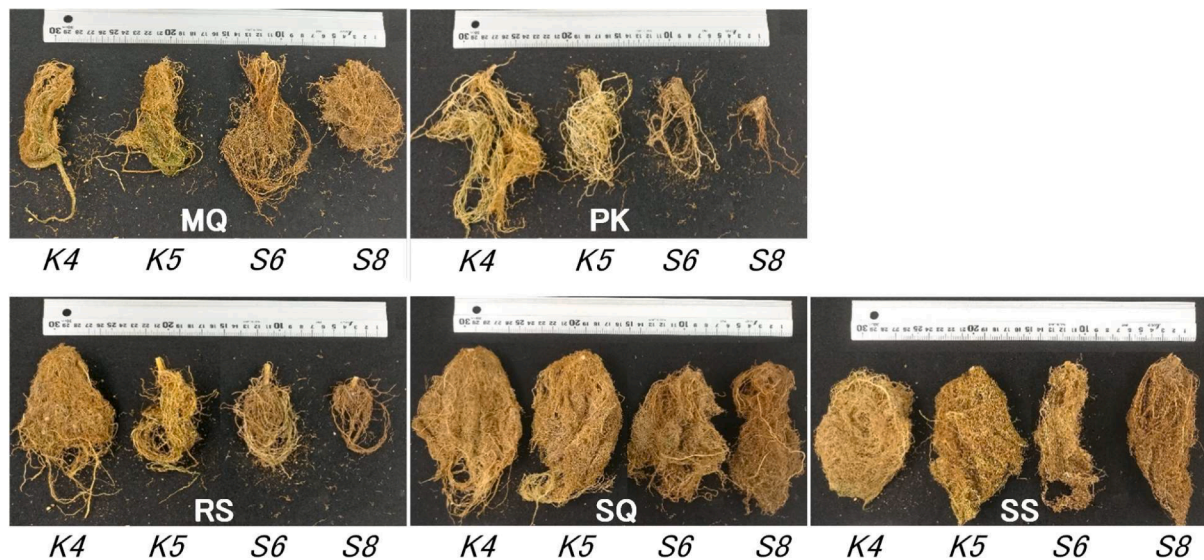


Fig. 4. Typical root appearances at 11 weeks after transplanting on four different soils in five passion fruit genotypes: yellow passion fruit (*Passiflora edulis* f. *flavicarpa*) ‘MaQuatro’ (MQ), purple passion fruit (*P. edulis*) Kagoshima strain (PK), and three cultivars of hybrid passion fruit (*P. edulis* × *P. edulis* f. *flavicarpa*) ‘Ruby Star’ (RS), ‘Summer Queen’ (SQ), and ‘Sunny Shine’ (SS). These plants were cultivated in acidic Kunigami-Mahji soils of pH 4 (K4) and 5 (K5), and calcareous Shimajiri-Mahji soils of pH 6 (S6) and 8 (S8).

although no significant differences were observed between SQ and SS for SL and RAR. RS and MQ had similar values for all parameters. PK tended to have the lowest values, except for RAR, which was comparable to those of SQ and SS. Strongly acidic soil conditions (K5) generally yielded the highest values for all parameters. ADW significantly decreased under alkaline conditions (S8), and RDW also decreased in higher pH soil conditions (S6 and S8). Both LA and LN were reduced under extremely acidic (K4) and alkaline (S8) conditions. No significant differences were found between soil conditions for SL and RAR. Chronological changes in SL, LN, and LA at 1–11 WAT are shown in Figs. S5–S7.

Interaction between the effect of genotype and soil was significant ($P < 0.01$) for ADW, LA, and RDW, and the detailed results for each treatment and genotype are shown in Fig. 3. For SQ, ADW was highest (36.1 g) in K5 soil and significantly decreased to around 26 g under both lower and higher pH conditions, i.e., K4 and S8, respectively. For RS and SS, ADW was also highest (27.0 g and 26.0 g, respectively) in K5, though no significant differences were found between K4, K5, and S6. ADW generally decreased in S8 compared to K5. For PK, ADW also peaked in K5, similar to the hybrid cultivars, but no significant differences were observed among soil conditions, with values generally remaining under 11 g. For MQ, ADW remained around 20 g with no significant differences among soil conditions, similar to PK, although ADW tended to increase in higher pH soils. For the hybrid cultivars, LA showed a similar tendency to ADW, i.e., it peaked ($> 100 \text{ cm}^2$) in K5. For SQ, LA significantly decreased to around 100 cm^2 under the lower pH condition of K4, while for RS, it decreased below 100 cm^2 in the higher pH S8. For SS, LA significantly decreased in both K4 and S8. For PK and MQ, LA showed similar trends to ADW, with no significant differences among soil conditions.

For SQ, RDW also tended to peak around 7 g in K5, though no significant differences were observed among soil conditions. For SS, RDW was highest (5.4 g) in K5 and significantly decreased below 2 g in the higher pH S8. For RS, RDW was generally lower than that of SQ and SS and tended to decrease under higher pH conditions, with a significant decline in S8 compared to K4 and K5. PK showed a similar downward trend in RDW as SQ and SS, but with generally lower values, and no significant differences across soil conditions. MQ showed a distinct pattern in RDW, similar to its ADW and LA trends, with the highest RDW (2.7 g) in S8. The RDW of MQ decreased in acidic pH conditions, with a significant reduction in K4 (1.0 g) compared to S8. The external

appearance of typical roots from each genotype and treatment is shown in Fig. 4.

For incidence of chlorosis, i.e., yellowing of leaves, the effects of genotype and soil were both significant ($P < 0.01$ and $P < 0.001$, respectively), and interaction between them was also significant ($P < 0.001$). Chlorosis leaves tended to be frequently observed in RS, PK, and SS, with incidences of 93 %, 80 %, and 60 %, respectively, under the high-pH condition of S8 (Table 3). Leaves of RS and PK exhibited severe chlorotic symptoms in S8, while SS leaves occasionally exhibited yellow spots in S8; typical external appearances of each severity level leaf are shown in Fig. S4. In hybrid cultivars, leaves generally maintained a dark green coloration and mild incidences (≤ 40 %) in acidic soil pH conditions. SQ leaves displayed slight yellowing, with a 47 % incidence even in S8, although the incidence was significantly low in K5. Chlorosis was mild in MQ under all soil conditions, with only a 7 % incidence in S8 soil and rather increasing tendency at lower pH conditions.

Leaf K concentrations were highest in MQ and SQ (≈ 0.20 %) and in calcareous S8 soil (Table 4) but was significantly lower in other genotypes (0.12–0.14 %) and K5 soil. Leaf P concentrations differed significantly only among genotypes, with MQ and SS showing the highest levels (0.12–0.14 %) and RS the lowest (0.08 %). Leaf Ca concentrations did not differ significantly among genotypes but increased in calcareous soils S6 and S8 (0.36–0.38 %). Whereas, in the case of leaf Al and Fe, concentrations were not significantly different between genotypes and soil with concentrations ranging 79.0–105.1 ppm for Al, and 226.9–424.6 ppm for Fe, across genotypes and soil type. Most mineral concentrations in roots were significantly influenced by soil type and genotype. The highest concentrations of root Al and Mn were observed in acidic K5 soil, with 2.42 % Al and 993.0 ppm Mn, while the lowest concentrations occurred in calcareous S8 soil, with 0.69 % Al and 320.9 ppm Mn. However, unlike other minerals, root Al and Mn did not differ significantly among genotypes. Root K and P concentrations were highest in MQ (1.03 % and 0.18 %, respectively) and lowest in PK (0.39 % and 0.12 %, respectively), with peak root K and P concentrations observed in calcareous S8 soil and acidic K5 soil, respectively. Root Fe and Mg concentrations were highest in SQ (1.23 % and 0.48 %, respectively), both peaking in K5 soil. Root Ca concentration was highest in RS (2.60 %), with its peak in calcareous S8 soil.

Interaction between the effect of genotype and soil was significant for leaf Mn and Mg concentrations, and the detailed results are shown in

Table 3
The incidence of plant showing chlorotic leaves in yellow passion fruit (*Passiflora edulis* f. *flavicarpa*) ‘MaQuatro’ (MQ), purple passion fruit (*P. edulis*) Kagoshima strain (PK), and three hybrid (*P. edulis* × *P. edulis* f. *flavicarpa*) cultivars ‘Ruby Star’ (RS), ‘Summer Queen’ (SQ), and ‘Sunny Shine’ (SS), under four treatments of soil type and pH, i.e. acidic *Kunigami-Mahji* soils (K4 and K5) and calcareous *Shimajiri-Mahji* soils (S6 and S8) soils.

Soil type	Incidence (severity of chlorosis)											
	MQ			PK			RS			SQ		
K4	46.7	%	a	(Mild)	40.0	%	b	(Mild)	13.3	%	b	(Mild)
K5	40.0	%	a	(Mild)	26.7	%	b	(Mild)	13.3	%	b	(Mild)
S6	26.7	%	ab	(Mild)	53.3	%	ab	(Moderate)	33.3	%	a	(Mild)
S8	6.7	%	b	(Mild)	80.0	%	a	(Severe)	93.3	%	a	(Moderate)

Two-way ANOVA^y
Effect of genotype [G]
Effect of soil [S]
[G] × [S] interaction

z : Severity was determined visually in three levels: Mild (< 50 %), Moderate (50 %–75 %), and Severe (> 75 %); see Fig. S4 for typical external appearances of each level.
y : For each genotype and soil, 5 leaves were randomly surveyed from the top to bottom stem sections of each 3 plants, then incidence percentage values from each plant was arcsine-transformed. *** and ** represent statistical significance at $P < 0.001$ and $P < 0.01$, respectively. Different letters within the same column indicate statistical differences between the arcsine-transformed values of each soil type in each genotype by Tukey’s multiple comparison test at $P < 0.05$.

Fig. 5. The highest Mn concentrations, ranging from 315 to 399 ppm, were recorded in MQ and SS in acidic K4 soil. Mn decreased with a rise in pH, and the concentration was less than optimal values from literature in S8 soil for all genotypes; RS and SQ in addition to S8, also had less than optimal Mn concentrations in S6. The highest Mg concentrations, approximately 0.3 %, were observed in SS, SQ, and MQ in calcareous S6 soil. Mg concentrations were less than optimal values in extremely acidic soil K4 for all genotypes, and in high pH calcareous soil S8 for PK and SS, while RS had no significant difference in Mg among soil types. On average, PK and RS had the lowest Mn and Mg concentrations.

As shown in Fig. 6, the photosynthetic rate of SS peaked in extremely acidic soil (K4) at $10.3 \mu\text{mol m}^{-2} \text{s}^{-1}$, and there was a significant downward trend as pH increased across soil types. The photosynthetic rate of MQ and SQ also peaked (10.1 and $7.7 \mu\text{mol m}^{-2} \text{s}^{-1}$, respectively) in K4 soil, but there was a downward trend as pH increased, although with no significant difference across soil types. PK and RS had similar trends under acidic soil conditions, with peaks of 8.4 and $6.2 \mu\text{mol m}^{-2} \text{s}^{-1}$ in K5, but exhibited very low photosynthetic rates ranging 1.3 – $1.9 \mu\text{mol m}^{-2} \text{s}^{-1}$ for PK and 0.7 – $2.4 \mu\text{mol m}^{-2} \text{s}^{-1}$ for RS, in high-pH soils. SPAD values of most genotypes (PK, RS, SQ, and SS) peaked in K5 and significantly lowered in S8, with the exception of PK which also decreased in S6. In contrast, MQ was unaffected by soil. Chronological changes in SPAD value at 1–11 WAT are shown in Fig. S8.

4. Discussion

In this study, both original soils had relatively low CEC (Table 1), all plants received the same amount of liquid fertilizer under sufficient irrigation, and soil solution was kept from leaching to minimize texture-related differences in water availability. Artificial pH adjustment was performed only once, resulting in the similarly regulated soil pH gradient and range in all genotypes (Fig. 2), although the measured pH values were not completely uniform among genotypes and overlapped during some periods in the acidic-soil treatments for each genotype. These cultivation operations can be considered to subject each passion fruit plant to almost the same nutrient supply. Consequently, the observed change patterns of physiological responses generally corresponded to the soil pH gradient (Tables 2, 3, Figs. 3–6). Therefore, we considered that the effects of pH levels in two soil types (acidic and calcareous) were detected, while the effects of physical properties of original soils and artificial pH adjustment operations can be negligible.

The growth responses to soil pH corresponded to biogeographical origins for purple passion fruit: PK grew vigorously in acidic soil of pH ≈ 5 but was inhibited in slightly acidic to alkaline conditions (Figs. 3 and 6). The tropical highlands of Brazil–Paraguay–Argentina, the indigenous region for purple passion fruits (Morton, 1987; Ulmer and MacDougall, 2004), typically have acidic soils. Purple passion fruit generally has a smaller plant body than yellow passion fruit and hybrids. Nevertheless, PK produced noticeably lower biomass than the other genotypes in all soil conditions, both aboveground and root (Table 2; Figs. 3 and S5), although leaf area from K5 conditions were comparable with other genotypes in the same soil (Fig. S7). Besides acidic soils, the cool temperatures of tropical highlands are important for purple passion fruit growth (Akamine et al., 1974; Morton, 1987). Thus, the relatively reduced vegetative growth of PK after 6 WAT in mid-June (Figs. S5–S7) can be ascribed to daily maximum temperatures of above 35°C (Fig. 1). This was higher than 33°C at which Utsunomiya (1992) reported the maximum vegetative growth of purple passion fruit.

In contrast, yellow passion fruit MQ performed best in calcareous soil (pH ≥ 6), with higher aboveground biomass and especially root biomass (Fig. 3). Although yellow passion fruit, a mutant form of purple passion fruit (Akamine et al., 1974; Morton, 1987), is sensitive to cool weather, it is comparatively tolerant of high temperatures, some soilborne pathogens, and alkaline soils (Knight and Sauls, 1994; Morton, 1987). The growth of MQ was modest during the cooler period ($< 30^\circ\text{C}$; 1–6 WAT) but increased markedly when daily maximum temperatures rose to

Table 4

The effect of four treatments of soil type and pH, i.e. acidic *Kunigami-Mahji* soils (*K4* and *K5*) and calcareous *Shimajiri-Mahji* soils (*S6* and *S8*), on shoot and root mineral contents of yellow passion fruit (*Passiflora edulis* f. *flavicarpa*) 'MaQuatro' (MQ), purple passion fruit (*P. edulis*) Kagoshima strain (PK), and three hybrid (*P. edulis* × *P. edulis* f. *flavicarpa*) cultivars 'Ruby Star' (RS), 'Summer Queen' (SQ), and 'Sunny Shine' (SS), and the results of two-way analysis of variance (ANOVA).

		Leaf													
		Al (mg kg ⁻¹)		Fe (mg kg ⁻¹)		Mn (mg kg ⁻¹)		K (%)		Ca (%)		Mg (%)		P (%)	
Genotype	MQ	105.09		424.58		180.30	AB	0.20	A	0.35		0.20	A	0.14	A
	PK	79.03		328.46		132.90	C	0.14	B	0.28		0.17	B	0.11	BC
	RS	104.40		285.33		103.20	C	0.12	B	0.20		0.16	B	0.08	C
	SQ	89.81		226.85		149.10	B	0.21	A	0.27		0.19	A	0.10	BC
	SS	102.88		374.83		217.10	A	0.14	B	0.23		0.22	A	0.12	B
Soil	K4	98.07		245.90		286.20	a	0.13	bc	0.21	b	0.16	b	0.10	
	K5	95.92		364.83		246.90	a	0.09	c	0.11	b	0.20	b	0.12	
	S6	92.71		374.15		86.90	b	0.20	ab	0.38	a	0.25	a	0.13	
	S8	98.27		327.17		6.00	c	0.23	a	0.36	a	0.17	b	0.12	
Optimal Range ^z				116–233		100–500		1.60–3.20		1.75–2.75		0.19–0.24		0.15–0.25	
Two-way ANOVA															
Effect of Genotype [G]		ns		ns		***		*		ns		***		***	
Effect of Soil [S]		ns		ns		***		***		***		***		ns	
[G] × [S] interaction		ns		ns		*		ns		ns		***		ns	
		Root													
		Al (%)		Fe (%)		Mn (mg kg ⁻¹)		K (%)		Ca (%)		Mg (%)		P (%)	
Genotype	MQ	1.34		0.72	BC	852.0		1.03	A	1.94	AB	0.22	CD	0.18	A
	PK	1.20		0.64	C	685.5		0.39	B	1.02	C	0.14	D	0.12	C
	RS	1.26		0.99	AB	512.5		0.83	AB	2.60	A	0.34	AB	0.13	BC
	SQ	2.13		1.23	A	692.3		0.76	AB	1.54	B	0.48	A	0.15	AB
	SS	2.10		1.05	AB	828.6		0.59	AB	1.30	BC	0.34	BC	0.16	AB
Soil	K4	2.24	a	1.05	ab	859.4	ab	0.33	c	0.75	c	0.29	b	0.15	ab
	K5	2.42	a	1.22	a	993.0	a	0.50	bc	0.87	c	0.35	a	0.18	a
	S6	1.09	b	0.78	bc	683.4	abc	0.92	ab	1.79	b	0.23	b	0.14	b
	S8	0.69	b	0.66	c	320.9	c	1.12	a	3.31	a	0.34	ab	0.13	b
Two-way ANOVA															
Effect of Genotype [G]		ns		***		ns		**		***		***		**	
Effect of Soil [S]		***		**		**		**		***		*		***	
[G] × [S] interaction		ns		ns		ns		ns		ns		ns		ns	

***, **, and * indicate statistical significance at $P < 0.001$, $P < 0.01$, and $P < 0.05$, respectively. "ns" represents no significance. Different capital and small letters within the same column indicate significant differences in genotypes and soil treatments, respectively by Tukey's multiple comparison test at $P < 0.05$.

^z Optimal Range for leaf mineral content was determined following Haag et al. (1973) for Fe and K; Menzel et al. (1993) for Mn, Ca and P; and Marchal et al. (1978) for Mg.

around 35 °C after mid-June (Fig. 1; Figs. S5–S8). These results correspond with a previous study in which yellow passion fruit MQ maintained high photosynthetic activity even at temperatures > 35 °C (Matsuda and Takaragawa, 2023).

In hybrid cultivars, significant genotypic differences in response to environmental conditions, such as temperature, have been reported. Menzel et al. (1987) noted that the three cultivars, 'Lacey', 'E-23', and 'Purple Gold', showed clear differences in their response to temperature during vegetative growth and flowering. For the cultivars SQ and RS, which were also used in the present study, clear differences were reportedly observed in the high-temperature response of photosynthesis (Matsuda and Takaragawa, 2023; Shimada et al., 2017) and the thermal response of pollen germination (Matsuda and Ogata, 2020). Matsuda and Takaragawa (2023) and Matsuda and Ogata (2020) reported that the patterns of physiological responses to temperature conditions in hybrid cultivars varied widely between those of their parent species, i.e., purple passion fruit and yellow passion fruit.

Similarly, in the present results, among the three hybrid genotypes, the patterns of vegetative growth (Figs. 3 and 6) and leaf mineral content (Table 4; Fig. 5) in response to soil environmental conditions tended to vary between those of the parent species genotypes, i.e. PK and MQ. Considering the patterns of change in aboveground and root growth, photosynthetic rates, and SPAD values (which correlate with leaf nitrogen content), RS can be considered a cultivar with a similar response

to that of purple passion fruit PK, SQ with a similar response to yellow passion fruit MQ, and SS intermediate between RS and SQ.

In this study, the higher vegetative growth of the hybrid cultivars RS, SS, and SQ in *K5* soil (Table 2; Fig. 3) suggests a preference for strongly acidic conditions, consistent with the pH range of 4.7–6.8 sufficient for growth in *Kunigami-Mahji* soils reported by Kondo et al. (2017). Niwayama and Higuchi (2018) reported that root growth and photosynthesis of SQ were highest in weathered granite soils and bark compost mixture at pH 3.5. Niwayama and Higuchi (2019) also observed high photosynthesis in the same soil mixtures at pH 3.5, and the highest dry matter production of both aboveground and root at pH 4.5, similar to our results for *K4* and *K5* (Figs. 3 and 6). For SQ and SS, dry matter production tended to decrease in extremely acidic *K4*, while RS maintained similar levels in both *K4* and *K5*. Nakayama and Matsuda (2022) reported that RS exhibited higher dry matter weight in soilless sand culture at pH 4–5, consistent with our results in acidic *Kunigami-Mahji* soil. Accordingly, RS can be considered the most tolerant to extremely acidic soil (*K4*) conditions among the three hybrid cultivars.

Al solubility increases under acidic conditions, where its toxicity typically inhibits plant root elongation (Kochian, 1995). However, plant roots exude acids and absorb acid-soluble nutrients for growth (e.g. Jones, 1998; Rovira, 1969; Ström et al., 1994; Walker et al., 2003), and such root exudation, together with other apex-protective mechanisms, can sustain root growth under Al stress (Delhaize and Ryan, 1995;

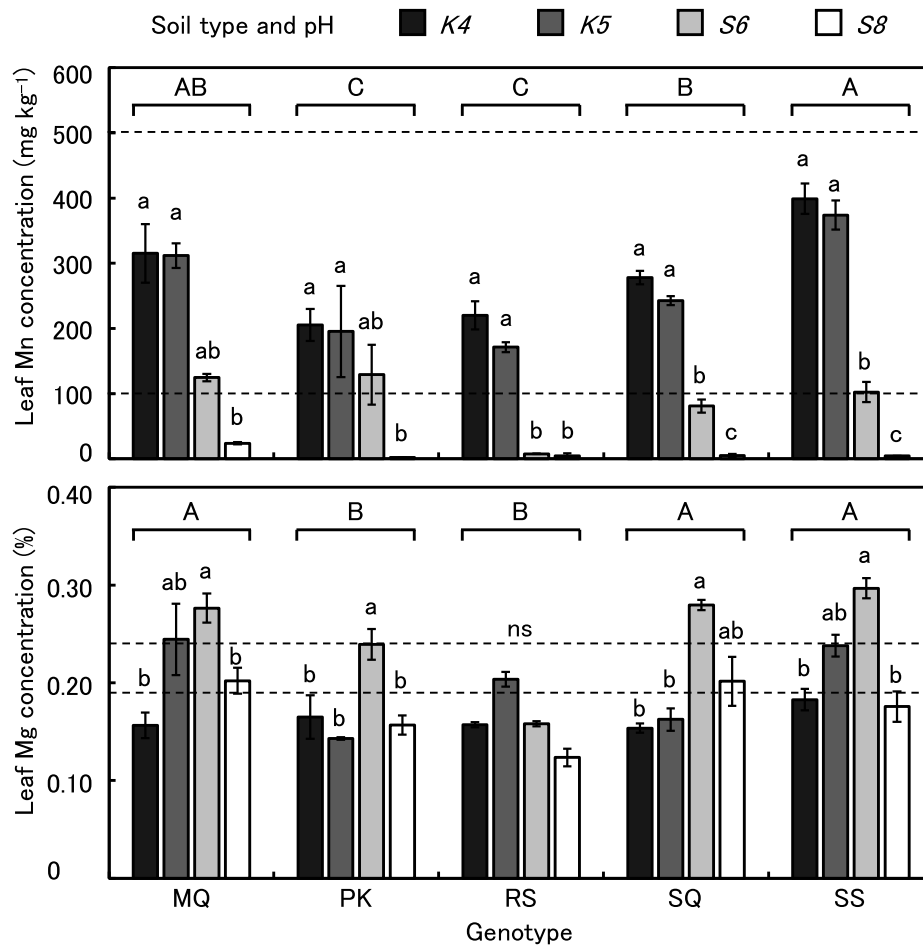


Fig. 5. The effects of acidic *Kunigami-Mahji* (K), calcareous *Shimajiri-Mahji* (S) soils and pH on leaf Mn and Mg content at 11 weeks after transplanting of five passion fruit genotypes: yellow passion fruit (*Passiflora edulis* f. *flavicarpa*) 'MaQuatro' (MQ), purple passion fruit (*P. edulis*) Kagoshima strain (PK), and three cultivars of hybrid passion fruit (*P. edulis* × *P. edulis* f. *flavicarpa*) 'Ruby Star' (RS), 'Summer Queen' (SQ), and 'Sunny Shine' (SS). Different capital letters in each graph and small letters for each genotype indicate significant differences by Tukey's multiple comparison test at $P < 0.01$. Vertical bars indicate SE. "ns" indicates no significance. The horizontal dashed lines in both graphs indicate upper and bottom limits of optimal range according to literature for Mn (Menzel et al., 1993) and Mg (Marchal et al., 1978).

Kochian et al., 2015; Matsumoto, 2000). Leaf and root Al accumulation was reported as concentrations in the 10^3 to 10^4 mg kg⁻¹ range in Al accumulator plants, such as tea plant (Matsumoto et al., 1976) and *Melastoma malabathricum* (Watanabe et al., 1997). Whereas in our results, leaf and root Al content under acidic conditions were ≈ 100 mg kg⁻¹ and 1–2 %, respectively, in all passion fruit genotypes (Table 4). These were similar to those reported for SQ by Niwayama and Higuchi (2018); they noted a possible mechanism in passion fruit involving root exudation acids to detoxicate and exclude Al from root symplast, like reported such as in wheat (Delhaize et al., 1993) and maize (Pellet et al., 1995).

Leaf Ca and K in our results (Table 4) were comparatively lower than the sufficiency ranges according to literature (Haag et al., 1973; Menzel et al., 1993), in which measurements were conducted in reproductive stages. Leaf Ca and K increases due to transpiration and phloem loading as reproductive development progresses (Hawkesford et al., 2012). Therefore, the lower contents of Ca and K in our results likely reflect the measurements in young and vegetative growth stage. Additionally, leaf disorders were not observed in passion fruit even after three months without application of K (Kondo and Higuchi, 2013) and Ca (Kondo and Higuchi, 2020), suggesting not much K and Ca requirements.

Yellow passion fruit MQ exhibited the highest content of K, P, Ca, and Fe in leaves, despite relatively high Al content (Table 4). MQ also

accumulated greater amounts of these nutrients in roots compared with purple passion fruit PK. This is consistent with Haag et al. (1973), who reported greater cumulative K absorption in yellow passion fruit compared with purple passion fruit but smaller differences for P, Ca, and Fe. These minerals are essential for sustaining high vegetative growth of plants through enzyme activation and photosynthesis: K regulates stomatal conductance and activates photosynthetic enzymes (Evans and Sorger, 1966; Wang and Wu, 2017); P supports ATP/NADPH production and carbon metabolism (Bieleski, 1973; Carstensen et al., 2018); Ca stabilizes thylakoid membranes and supports photosystem II function (Marschner, 1995; Rocha and Vothknecht, 2012); Fe is indispensable for electron transport and redox enzymes (Briat et al., 2015; Terry and Low, 1982). The vigorous growth of MQ across a wide range of soil environments (Figs. 3 and S7) suggested efficient root-to-shoot delivery of these key nutrients, in contrast to PK, which shows clear limitations.

Compared with yellow passion fruit MQ, purple passion fruit PK, and hybrids RS and SS showed steep vegetative declines in calcareous soil S8 (Fig. 3), coinciding with lowered root growth (Fig. 4). In calcareous soils, P reacts with Ca²⁺ and precipitates as sparingly soluble calcium phosphates (Lindsay, 1979), making P less available to plants than total P content. MQ's root dry weight increased with rising pH (Figs. 3, 4), possibly due to enhanced lateral root growth under P limitation (Drew and Saker, 1978; Péret et al., 2011; Wiersum, 1958), which is a common

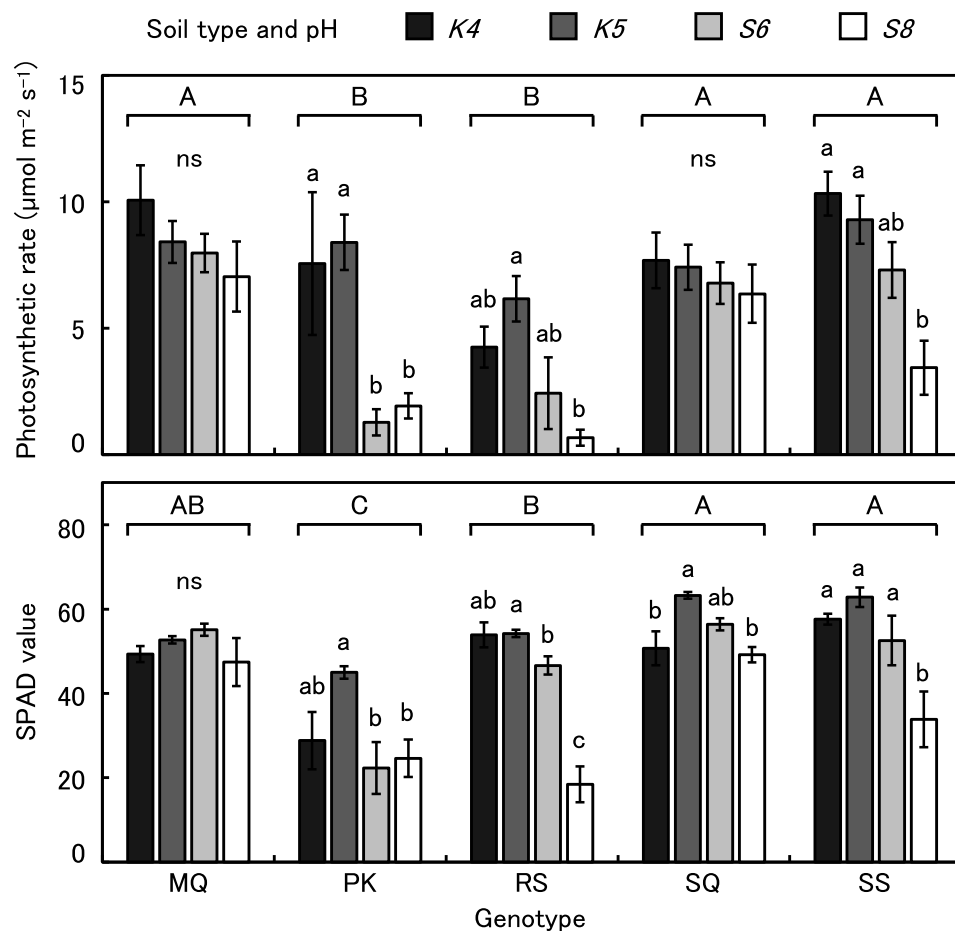


Fig. 6. The effects of acidic *Kunigami-Mahji* (K), calcareous *Shimajiri-Mahji* (S) soils and pH on the photosynthetic rates and SPAD values of five passion fruit genotypes: yellow passion fruit (*Passiflora edulis* f. *flavicarpa*) ‘MaQuatro’ (MQ), purple passion fruit (*P. edulis*) Kagoshima strain (PK), and three cultivars of hybrid passion fruit (*P. edulis* × *P. edulis* f. *flavicarpa*) ‘Ruby Star’ (RS), ‘Summer Queen’ (SQ), and ‘Sunny Shine’ (SS). For both photosynthetic-rate and SPAD values, the measurements were conducted using two fully expanded leaves located at the midpoint of main stem for each plant at 10 weeks after transplanting (7 July 2022, a sunny day). Different capital letters in each graph and small letters for each genotype indicate significant differences by Tukey’s multiple comparison test at $P < 0.01$. Vertical bars indicate SE. “ns” indicates no significance.

adaptive response in high-pH soils (López-Bucio et al., 2003; Lynch, 2007). The greater root biomass of MQ was considered to prevent P fixation in high pH soil, that possibly resulted in the higher P uptake (Table 4).

The photosynthetic rates of MQ and SQ were relatively stable across soils, whereas those of the other genotypes declined with rising pH (Fig. 6). MQ maintained higher photosynthetic activity with higher SPAD (chlorophyll content) and leaf Mg and Mn in high pH soil S8 (Fig. 5), despite leaf Mn below the sufficiency range in previous reports (100–500 mg kg⁻¹; Menzel et al., 1993). Similarly, SQ maintained higher photosynthetic rates, SPAD, and content of Mg at high pH, although the Mn content did not differ from PK and other hybrids (Fig. 5). Mg is essential as the central atom of chlorophyll and for Mg-ATP formation, photophosphorylation, and carbon metabolism in plants (Gerendás and Führes, 2013; Hawkesford et al., 2012). The high leaf Mg likely enabled these two genotypes to maintain higher photosynthetic rates even in high pH soils. Mn is also essential as the catalytic metal of the PSII oxygen-evolving complex and as a cofactor for multiple enzymes (Broadley et al., 2012; Schmidt et al., 2016), but leaf Mn did not clearly affect photosynthesis reduction of passion fruit in the present study.

Severe interveinal chlorosis (yellow-white leaves; Fig. S4) is typically associated with Fe or Mn imbalances (Borges and Lima, 2007). Mn uptake has antagonism with Fe uptake in plants (Olson and Carlson, 1950; Somers and Shive, 1942). Although such antagonism was not directly

assessed in our study, leaf Mn content declined at higher pH and became less than the reference range in S8 soils (Fig. 5; Menzel et al., 1993). In contrast, leaf Fe exceeded the 116–233 ppm reference range in all genotypes except SQ (Table 4; Haag et al., 1973), with no clear soil or genotype effect. The observed chlorosis was likely caused by Mn deficiency, possibly intensified by high leaf Fe; accordingly, Fe concentration in our liquid fertilizer may be too high for passion fruit grown in high-pH soils.

Even for MQ and SQ, though the severity was lower, typical Mn deficiency symptoms, shown as interveinal chlorosis (Table 3; Fig. S4), indicate slight disruptions in chlorophyll formation (Wilkinson and Ohki, 1988) and in N assimilation processes (Rengel, 2000). Such impairments ultimately constrain photosynthesis and growth (Roosta et al., 2018; Schmidt et al., 2016). In higher pH calcareous soils, leaf Mg of MQ and SQ were within and above the previously reported sufficiency threshold of 0.19–0.24 % (Fig. 6; Marchal et al., 1978), and SPAD values were kept relatively high (Figs. S7 and S8). Accordingly, the high assimilation capacity of MQ and SQ even in alkaline soils can be attributed to their high ability of Mg uptake. These genotypes may be a good candidate rootstock for cultivation of susceptible cultivars such as RS in calcareous soils.

Exchangeable Mg was higher in acidic K5 (1.05 cmol(+) kg⁻¹) than in calcareous S8 (0.67 cmol(+) kg⁻¹) (Table 1). Nevertheless, leaf Mg for most genotypes was lowest in extremely acidic K4 and peaked in slightly

acidic calcareous S6, except for RS (Fig. 6), indicating that plant Mg status did not directly reflect soil exchangeable Mg. In acidic soil conditions, exchangeable Al was also high (Table 1), and root Al content was significantly higher in acidic soils of pH below 5 (Table 4). Al ions inhibit nutrient uptake of plants, particularly Mg (Gransee and Führs, 2013; Rengel and Robinson, 1989). Therefore, an increase of exchangeable Al may be associated with the reduction of leaf Mg in acidic soils in the present results.

5. Conclusion

Our results demonstrated clear genotypic differences in the growth and leaf/root nutrient status of passion fruits under different soil environments, i.e. acidic and calcareous soils with pH ranging 4–5 and 5–8, respectively. Purple passion fruit (PK) showed a preference for acidic soils, consistent with the environment of its original habitat, but limited to a narrow range with peak performance in strongly acidic soils of pH $\approx$ 5. Whereas its growth, photosynthesis, and uptake of Mg and Mn were severely inhibited at pH $\geq$ 6. In contrast, yellow passion fruit (MQ) exhibited broad pH tolerance, growing vigorously in calcareous soils of pH $\approx$ 8 while maintaining high photosynthetic rates and higher Mg uptake. The three hybrid cultivars showed varied responses, with RS resembling purple passion fruit in its preference for acidic soils but with overall greater vegetative growth, SQ showing the second-highest tolerance to high pH similar to yellow passion fruit, and SS being intermediate. Therefore, yellow passion fruit and the hybrid cultivar SQ can be feasible options for cultivation in calcareous-soil-dominant areas, particularly due to their resilient root systems. These differences indicate the importance of root vigor as a critical mechanism in passion fruit genotypes for overcoming Mg uptake limitations across both acidic and calcareous soils. Further studies are needed in passion fruit vines to elucidate the physiological mechanisms of soil-to-root and root-to-shoot nutrient dynamics, such as the effects of soil texture, rhizosphere acidification, and mineral antagonisms, and to examine soil environmental effects on flowering and fruit quality.

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CRediT authorship contribution statement

Kingston Tochukwu Obike: Writing – original draft, Visualization, Validation, Investigation, Formal analysis, Conceptualization. **Hiroshi Matsuda:** Writing – review & editing, Writing – original draft, Methodology, Investigation, Formal analysis, Conceptualization. **Hitoshi Shinjo:** Writing – review & editing, Methodology, Formal analysis, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Supplementary materials

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Data availability

Data will be made available on request.

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