Agriculture and Food

AIMS Agriculture and Food, 7(4): 750–761.
DOI: 10.3934/agrfood.2022046
Received: 07 July 2022
Revised: 15 August 2022
Accepted: 06 September 2022
Published: 19 September 2022

http://www.aimspress.com/journal/agriculture

Research article

Effect of salinity on growth, physiology, and production of groundcherry (*Physalis angulata* L.)

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Abstract: This study investigated the response of *Physalis angulata* L. to salt stress in terms of its growth, physiology, and production using a randomized block design with three replicates. For greenhouse cultivation, 21-day-old seedlings were cultivated in polybags containing Mediterranean soil and subjected to salinity treatments at concentrations set at 0, 20, 40, 60, 80, 100, 120, 140, 160, and 180 mM. Growth, physiology, and production parameters were measured 90 d after planting. Growth, stomatal density, yield, and fruit physical attributes were reduced at 80 mM and higher salinity. Salinity also increased the physiological responses and chemical features of the fruit. However, *P. angulata* grew faster and exhibited better yield and fruit quality at a salinity of 20 mM (2.25 dS m^{-1}). Therefore, *P. angulata* can be cultivated in moderately saline soils, allowing for efficient land use.

Keywords: antioxidant activity; climate change; *Physalis*; salt stress; soil; yield

1. Introduction

Land conversion due to increase in population has reduced the availability of agricultural land. Sub-optimal land use is an alternative solution but one of the main challenges is soil salinity, which

results in low productivity [1]. Increased salinity can occur in irrigated land due to poor water quality and drainage [2]. Salinization further occurs because of climate change due to global warming. Low rainfall and high daily temperatures in tropical areas trigger increased evaporation and evapotranspiration, thereby inhibiting salt leaching from the soil [3,4].

Salt accumulation in the soil limits water absorption by plant roots, causes osmotic stress, and leads to salt accumulation in cells, resulting in nutrient imbalance; this significantly influences the growth, yield, and quality of crops produced in high salinity soils [5,6]. Consequently, most plants develop adaptation strategies in the form of morphological responses and physiological mechanisms, such as stomatal plasticity, osmotic adjustment, and antioxidant responses, to prevent salt damage [7]. Moreover, soil salinity causes oxidative stress in plants by generating superoxide radicals that alter plant metabolism [8].

Using salt-tolerant varieties of plants is a practical and cost-effective way to optimize suboptimal land compared to chemical amendment-based reclamation technologies. Thus, identifying plants that are tolerant to salinity, especially those with medicinal and nutritional value, is crucial [1]. For this study, we chose the ground cherry (*Physalis angulata* L.) because of its medicinal properties and high nutraceutical value. This plant grows in semi-warm humid and tropical sub-humid climates at altitudes ranging from 0–2400 m asl [9]. *P. angulata* is considered a highly tolerant species because of its ability to adapt to various local environmental conditions, including dry land with insufficient availability of resources, and has consequently been reported as an invasive species in several countries [10,11].

P. angulata is also beneficial commercially because it produces abundant fruits in all seasons, with a long shelf life of up to eight weeks, making it valuable to the fresh fruit market. Production of this plant in North America can yield up to 8–13 tons ha^{-1} in outdoor fields and up to 40 tons ha^{-1} in greenhouses [9]. Furthermore, *P. angulata* contains physalin, phenolics, and glycosides as its primary compounds and medicinally valuable for anti-inflammation, immunostimulant, antibacterial, and antineoplastic [12]. Overall, *P. angulata* is an ideal crop for small- and medium-scale farmers in rural areas because of its high yield and increasing market potential [9].

In recent years, the focus of plant screening has shifted from growth response and productivity to particular physiological features involved in salt tolerance [13]. The screening mainly focuses on food crops and other commercial commodities, such as fruits and aromatic plants [1]. Understanding salt-tolerant strategies are essential for crop improvement in the salt-affected environment through morphological, physiological, and biochemical processes. This study aims to evaluate the growth, physiology, and yield of *P. angulata* under salt stress.

2. Materials and methods

2.1. Plant material and experimental management

Plants were grown in a private greenhouse in Madura Island, Indonesia, at 5 m asl. The study took place in May–July 2021 with average temperature ranged between 33.7–35.7 ℃, average relative humidity ranged between 52.5–61.2 % and light intensity ranged between 10560–19260 lux.

This study was conducted using a randomized block design with three replicates. Each replicate consisted of four plant samples. The *P. angulata* genotype was chosen based on previous observations in drylands [10]. Seedlings (21-day-old) were planted in polybags and cultivated for 90 d. The planting medium used was Mediterranean soil. Table 1 represents the physical and chemical properties of the

medium. A compound fertilizer containing 2 g NPK i.e., nitrogen, phosphorus, and potassium (16:16:16) was supplemented twice for each plant. The first supplementation was one day after the planting date, and the second supplementation followed seven weeks later.

Table 1. Physical and chemical properties of the soil used as a growing medium.

Physical properties				Chemical properties				
Sand (%)	Silt (%)	Clay (%)	Texture	pH	N (%)	P Olsen (ppm)	K (Me $100g^{-1}$)	Organic carbon (%)
46.96	28.72	24.32	Loam	7.40	0.50	40.86	0.28	1.99

Table 2. Electrical conductivity of the saline solution used for the treatment.

Salinity level (mM)	pH	EC (dS m^{-1})
0	6.13	0,69
20	6.16	2.25
40	6.20	4.12
60	6.50	5.59
80	6.60	7.42
100	6.60	9.20
120	6.53	10.51
140	6.49	11.81
160	6.46	13.32
180	6.46	14.61

Ten different salinity concentrations were used to test the salinity tolerance for this study. The salinity levels of the solutions were adjusted to 0, 20, 40, 60, 80, 100, 120, 140, 160, and 180 mM, respectively. The electrical conductivities (EC) for each concentration are shown in Table 2. The saline solution consisted of salt collected from local farmers and dissolved in tap water. The applied volume was adjusted to field capacity by measuring the weight reduction of the growing medium after irrigation. Polybags were irrigated with saline solution every 3 d, with the first irrigation 10 d after transplanting. Observations were recorded 90 d after planting.

2.2. Measurement of growth performance

The influence of salt on growth was determined by measuring plant height, stem diameter, number of leaves and flowers, total leaf area per plant, and fresh weight. A measuring tape was used to measure the height of the plant from the primary stem base to the apical growth point. Digital calipers were used to measure the diameter of the stem above the cotyledons. The plants that had been uprooted and cleaned were weighed to determine their fresh weight. The method of Pandey and Singh (2011) [14] was used to measure total leaf area per plant, with some modifications. Measurements were taken on 100 leaves from each plant. The leaf picture was cut off and weighed. The number of leaves was determined by counting the leaves on the plants under study.

2.3. Determination of physiological response

Physiological responses, including proline content, catalase activity, antioxidant capacity, and stomatal density, were determined by analyzing fresh leaves. Proline content was determined using a previously reported method [15] with slight adjustments. Fresh leaves (weighing 500 mg) were homogenized in 10 mL of 3% 5-sulphosalicylic acid; 2 mL of this mixture was dissolved in 2 mL of ninhydrin reagent and 2 mL of glacial acetic acid and incubated in a water bath at 100 ℃ for 1 h. After cooling for 15 min, the reaction mixture was eluted using toluene (4 mL). The absorbance of chromophore-containing toluene was measured at 520 nm using a UV-visible spectrophotometer (Shimadzu UVmini-1240).

Catalase activity was measured using the modified method described by Tahjib-Ul-Arif et al. (2019) [16]. The catalase assay mixture (3 mL) comprised 0.05 mL leaf extract, 1.5 mL phosphate buffer (100 mM buffer, pH 7.0), 0.5 mL H_2O_2, and 0.95 mL distilled water. The reduction in the absorbance was measured at 240 nm.

Antioxidant capacity was determined based on the method described by Molyneux (2004) [17]. The leaf extract (1.0 $mg \cdot mL^{-1}$) was dissolved into a series of five solution concentrations. Each solution in the series of concentration (2.4 mL) was mixed with 0.6 mL 50 M DPPH (2,2-diphenyl-1-picrylhydrazyl). After 30 min of incubation in the dark, the absorbance of the solution was recorded at 517 nm and converted to percentage antioxidant activity using a previously described formula [17]. IC_{50} values were determined using linear regression of two variables, namely the concentration of the tested plant extracts and the average percentage of antioxidant activity from three distinct tests. The lower the value, the greater the antioxidant activity.

Stomatal density was measured as described by Yan et al. (2012) [18]. Stomatal density was measured on three representative planes of three leaves of the same age per treatment using a clear nail polish mold and expressed as the number of stomata per surface unit ($n \cdot mm^{2\ -1}$).

2.4. Determination of fruit yield and characteristics

The yield was determined by measuring the number of fruits per plant during cultivation. Fruit characteristics were recorded for each treatment by collecting five randomly selected fruits from each plant in each replicate. Physical characteristics of fruit included fruit size and weight. The fruit length and diameter (mm) were measured using a digital caliper. The fruit weight (mg) was measured using an analytical balance.

The chemical characters of fruit include total soluble solids, vitamin C, flavonoid and antioxidant activity. Total soluble solids (°Brix) were measured in a drop of fruit juice obtained using a refractometer. Vitamin C analysis was performed according to Arayne et al. (2009) with several modifications [19]. The fruit extract was first filtered, and 0.5 mL of the filtrate was added to distilled water to obtain a total volume of 100 mL. The absorption was measured at a maximum wavelength of 265 nm. Flavonoid assay was performed according to the method described by Chang et al. (2002) [20] with modifications. The fruit extract was dissolved in 10 mL of methanol, and 1 mL of this solution was further mixed with 3 mL of methanol, 0.2 mL of 10% aluminum chloride ($AlCl_3$), 0.2 mL of potassium acetate, and 5.6 mL of aquabidestilata. The mixture was then stored in the dark at room temperature for 30 min, and the absorbance was measured at 415 nm using UV-Vis spectrophotometry. The total flavonoid levels were expressed in grams of quercetin equivalent (QE) per gram of extract.

2.5. Statistical analysis

Data were analyzed using the Statistical Tool for Agricultural Research (STAR) 2.0.1. from International Rice Research Institute (IRRI) for analysis of variance to test the significance of the differences among treatments at a 95% confidence level and Least Significant difference (LSD) for post hoc comparison.

3. Results and discussion

3.1. Growth performance under salinity

The effects of salinity are the resultant of intricate interactions between morphological, physiological, and biochemical processes that affect plant growth and other critical functions [21]. The results obtained in our study, as presented in Table 3, revealed that the administration of salt at a low dose of 20 mM led to the highest growth and fresh weight. Plants utilizing sodium and chloride require sufficient concentrations of these compounds to meet the basic metabolic requirements for several major cellular processes [8,22]. These ions are involved in photosynthesis, turgor regulation, and growth elongation. The uptake of such ions is advantageous as long as the supply concentration remains below the osmotically challenging level [22,23].

Table 3. The growth of *P. angulata* as affected by salinity.

Salinity level (mM)	Plant height (cm)	Stem diameter (mm)	Number of leave/plant	Number of flower/plant	Fresh weight (g)
0	130.03^{a}	10.94^{abc}	750.25^{b}	87.58^{ab}	219.98^{bc}
20	136.36^{a}	11.88^{a}	893.75^{a}	100.67^{a}	287.76^{a}
40	125.22^{ab}	11.50^{ab}	708.83^{b}	74.42^{bc}	252.10^{ab}
60	124.37^{ab}	11.06^{abc}	693.83^{bc}	71.75^{bc}	241.62^{ab}
80	115.02^{bc}	10.74^{abcd}	608.25^{c}	64.00^{cd}	200.44^{bc}
100	110.49^{cd}	10.34^{bcd}	477.83^{d}	56.67^{cde}	178.44^{cd}
120	106.28^{cde}	9.89^{cde}	472.50^{d}	49.00^{def}	168.78^{cd}
140	106.15^{cde}	9.62^{def}	466.92^{d}	43.25^{efg}	137.21^{de}
160	99.23^{de}	8.94^{ef}	408.33^{de}	35.42^{fg}	90.92^{e}
180	96.02^{e}	8.44^{f}	360.00^{e}	27.08^{g}	83.28^{e}

Note: Distinct letters in the row indicate significant differences according to LSD ($P \leq 0.05$).

Salinities higher than 20 mM (Figure 1) decreased the growth variables, which were significantly different from those at 0 mM. The decrease of it occurred at different concentrations. This indicates differences in the salinity response according to the metabolic pathways of each organ [24]. The decreases in height, number of leaves, and number of flowers showed statistical significance at a concentration of 80 mM and higher, compared with 0 mM. Stem diameter and fresh weight were significantly different at a concentration of 140 mM and higher compared with 0 mM. The decrease in growth varied between 22.9% for stem diameter and 69% for the number of flowers. These findings corroborate the moderate salt tolerance of *P. angulata,* in accordance with previous studies [16]. Salt stress suppresses the growth of *P. angulata* because of limitations in water supply, the emergence of

ionic toxicity, and nutritional imbalance due to excessive buildup or reduction of a particular ion. Reduced concentration of ions, such as phosphorus and potassium, in plant cells may decrease the number of flowers [25]. Reduced leaf number and total leaf area in response to salt stress are morphological responses that prevent water stress [26].

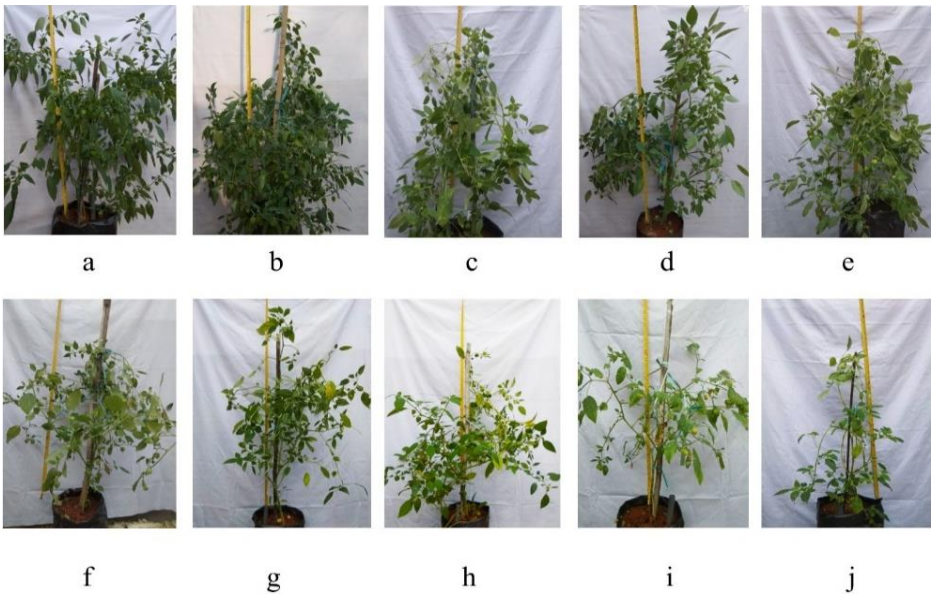

Figure 1. The growth declining of *P. angulata* under salinity stress. (a) 0 mM, (b) 20 mM, (c) 40 mM, (d) 60 mM, (e) 80 mM, (f) 100 mM, (g) 120 mM, (h) 140 mM, (i) 160 mM, (j) 180 mM.

3.2. Physiological response under salinity

Physiological responses of *P. angulata* to a varying range of salinity are shown in Table 4. Our results revealed that salinity affects osmotic balance, antioxidant activity, and stomatal plasticity.

We observed that the proline content increased in response to increased salinity. Elevated proline accumulation is an essential plant physiological response for maintaining the osmotic balance of cells with respect to the extracellular environment of salinity-associated osmotic stress [16]. In addition to this primary function, proline may counteract reactive oxygen species (ROS) excess effect and maintain enzyme, protein, and membrane stability [24].

Catalase aids in neutralization, removes excess H_2O_2, and protects plants from oxidative stress [16]. The extent of catalase production in plants in response to salt stress varies. Under salt stress, catalase activity decreased in *B. papyrifera* leaves [27], increased in maize cultivars [28], and remained unchanged in wheat cultivars [29]. Salt stress affects the expression of antioxidant enzyme isoforms, thereby stimulating or inhibiting the resulting enzyme response [27]. In this study, we observed that catalase levels increased gradually with increasing salinity but decreased in the 180 mM salinity treatment. This reduction indicates an imbalance in ROS production and catalase defense, which causes oxidative stress in plants [30].

Table 4. The average value of proline, catalase, antioxidant activity, and stomatal density of *P. angulata* as affected by salinity.

Salinity concentration (mM)	Proline ($mg \cdot g^{-1}$)	Catalase ($U \cdot mL^{-1}$)	IC_{50} DPPH Inhibition (ppm)	Stomatal density ($n \cdot mm^{-1}$)
0	4.07^{d}	9.91^{d}	276.97^{a}	90.79^{a}
20	2.70^{e}	10.58^{d}	219.83^{b}	87.20^{ab}
40	4.82^{d}	11.08^{cd}	209.03^{b}	90.42^{a}
60	7.02^{c}	12.71^{abcd}	181.30^{c}	86.45^{ab}
80	7.83^{c}	13.13^{abcd}	131.93^{d}	84.75^{b}
100	8.27^{c}	12.85^{abcd}	114.40^{e}	77.95^{c}
120	9.81^{b}	14.02^{abc}	106.13^{ef}	76.82^{c}
140	10.79^{b}	14.73^{ab}	103.50^{ef}	65.50^{d}
160	11.08^{ab}	15.52^{a}	100.33^{f}	63.42^{d}
180	12.15^{a}	11.79^{bcd}	98.20^{f}	55.49^{e}

Note: Distinct letters in the row indicate significant differences according to LSD ($P \leq 0.05$).

Salinity causes oxidative damage mainly through increased ROS formation and damage to proteins, lipids, DNA, and carbohydrates. Antioxidants are generated in cells to detoxify ROS [31]. In this study, the antioxidant activity of the plants increased, as indicated by the decline in the IC_{50} of DPPH inhibition with increasing salinity. The highest antioxidant activity of 98.20 ppm was obtained at 180 mM. In previous studies, an increase in catalase levels was followed by an increase in the antioxidant activity of rice and *Hyssopus officinalis* under osmotic [32] and drought stress [33], respectively. Notably, the decrease in catalase activity at a concentration of 180 mM did not reduce antioxidant activity due to the synergistic effect of other components that may have direct or indirect antioxidant effects [34].

Salinity concentration affected the stomatal density of *P. angulata*. A salinity concentration of 80 mM and higher decreased stomatal density significantly compared with the 0 mM. The stomatal density decreased up to 38.88% at the highest salinity concentration of 180 mM. However, salinity treatments in other studies generally increased stomatal density along with leaf area reduction [35]. Another study in quinoa demonstrated a similar reduction in stomatal density, comparable to our finding, to prevent excessive water loss and achieve optimal plant water-use efficiency [18,36].

3.3. Fruit characteristics

Salinity stress affected fruit yield and physical characteristics (Table 5). A salinity concentration of 20 mM resulted in the highest fruit yield and physical characteristics. The decrease in fruit number, weight, and size were statistically significant beginning from 80, 100, and 120 mM salinity concentrations, respectively, compared to 0 mM. The number of fruits showed the largest decrease of 67.36%, while the decreases in fruit weight, length, and diameter were 12.09%, 15.57%, and 14.31%, respectively. The reduction in yield and physical characteristics may be due to a decrease in growth and stomatal density, which is an essential physiological response under salt stress. However, decreased yield under salinity may increase fruit quality indicators [32,37]. The fruits of *P. angulata* grown under saline conditions are shown in Figure 2.

Table 5. Yield and physical characteristics of *P. angulata* fruit under salinity.

Salinity level (mM)	Number of fruit/plant	Fruit Weight (g)	Fruit length (mm)	Fruit diameter (mm)
0	87.58^{ab}	1.24^{b}	14.06^{ab}	12.37^{ab}
20	100.67^{a}	1.33^{a}	14.57^{a}	12.81^{a}
40	74.42^{bc}	1.23^{bc}	14.00^{b}	12.20^{abc}
60	71.75^{bc}	1.21^{bc}	13.63^{b}	12.23^{abc}
80	60.67^{cd}	1.21^{bc}	13.60^{b}	11.91^{bcd}
100	57.83^{cd}	1.20^{c}	13.74^{b}	11.89^{bcd}
120	51.17^{de}	1.15^{d}	12.92^{c}	11.53^{cde}
140	41.58^{def}	1.14^{d}	12.34^{d}	11.34^{de}
160	35.75^{ef}	1.15^{d}	12.26^{d}	11.04^{ef}
180	28.58^{f}	1.09^{e}	11.87^{d}	10.60^{ef}

Note: Distinct letters in the row indicate significant differences according to the LSD ($P \leq 0.05$).

The levels of flavonoids and vitamin C increased with increasing salinity, as shown in Table 6. The highest flavonoid and vitamin C levels of 1.67 mg QE·g extract^{-1} and 15.25 mg·100 g^{-1}, respectively, were found at the highest salt concentration of 180 mM. Plants exposed to stress tend to accumulate higher amounts of secondary metabolites than their non-stressed peers as part of their physiological response to salt stress [38]. According to recent findings, some of these compounds, such as flavonoids and vitamin C, act as non-enzymatic antioxidants with ROS scavenging and redox properties [39]. The variations in the antioxidant activity of honey were a result of differences in the levels of antioxidant compounds, such as flavonoids and vitamin C [34,40]. Highly active antioxidant activity is also related to the flavonoid and vitamin C content in grapes [41] and saline-stressed *Amaranthus tricolor* [42]. Accumulation of these metabolites in plants is beneficial as human complementary medicine to prevent degenerative and cardiovascular diseases [39].

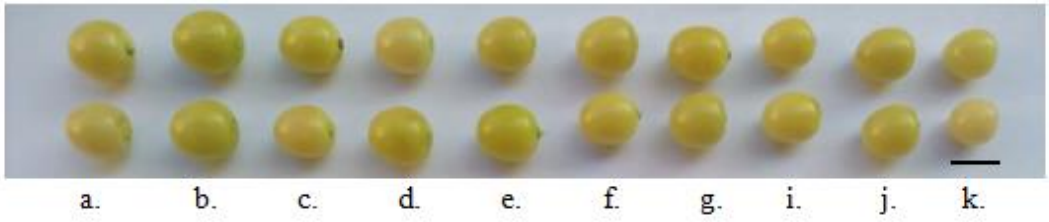

Figure 2. Fruit of *P. angulata* under salinity stress. (a) 0 mM, (b) 20 mM, (c) 40 mM, (d) 60 mM, (e) 80 mM, (f) 100 mM, (g) 120 mM, (h) 140 mM, (i) 160 mM, (j) 180 mM. Bar = 1 cm.

Similar to the other chemical contents of the fruit, the total soluble solids decreased at a particular salinity concentration. The highest average total soluble content was 13.23 °Brix at a concentration of 60 mM. The decrease in total soluble solids was statistically significant at a concentration of 140 mM and higher compared to the 0 mM. This indicator may reflect the sweet taste of the fruits. The increase in total soluble solids in various plants might be an adaptive response to osmotic stress due to salinity [25]. However, according to Rouphael et al. (2018) [43], this response is specific to certain

genotypes and species; for example, as observed in this study, the enhancement in fruit taste appears only in mild salinity with an increase in total soluble solids.

Table 6. The average Chemical contents of *P. angulata* fruit under salinity.

Salinity level (mM)	Flavonoid (mg QE·g extract^{-1})	Vitamin C (mg·100 g^{-1})	Total soluble solids (°Brix)	IC_{50} of DPPH Inhibition (ppm)
0	0.65^{f}	7.00^{g}	13.00^{ab}	155.97^{a}
20	0.66^{f}	7.38^{f}	13.15^{ab}	130.83^{b}
40	0.79^{ef}	8.39^{e}	13.13^{ab}	129.53^{b}
60	0.94^{de}	8.70^{de}	13.23^{a}	124.37^{bc}
80	1.00^{cd}	8.69^{de}	13.03^{ab}	117.43^{cd}
100	1.14^{c}	8.84^{d}	13.05^{ab}	108.03^{de}
120	1.37^{b}	8.83^{d}	12.79^{b}	104.57^{e}
140	1.38^{b}	10.08 ^{c}	12.25^{c}	91.53^{f}
160	1.65^{a}	10.57^{b}	12.08^{c}	89.23^{f}
180	1.67^{a}	15.25^{a}	11.89^{c}	76.93^{g}

Note: Distinct letters in the row indicate significant differences according to LSD ($P \leq 0.05$).

4. Conclusions

This study investigated the effect of salinity on the growth, physiology, production, and fruit quality of *P. angulata*. Our results indicate that the growth, yield, stomatal density, and fruit physical characteristics of *P. angulata* decreased from 80–140 mM salinity treatment, whereas the catalase activity decreased at 180 mM. However, salinity increased concentrations of proline (osmoregulator), flavonoids, and vitamin C (non-enzymatic antioxidant), as well as antioxidant activity. Salinity treatment at a concentration of 20 mM (2.25 dS m^{-1}) stimulated growth, yield, and fruit quality. Based on these results, we suggest that the salinity threshold for *P. angulata* is 80 mM NaCl. Thus, *P. angulata* can be considered tolerant to moderate salinity and a potential crop for cultivation in saline-affected lowland and coastal areas.

Acknowledgments

This work was supported by The Ministry of Education and Culture - Research and Technology for the Republic of Indonesia under the Postgraduate Research Grants - Doctoral Dissertation Research which Airlangga University manages. The Postgraduate Research Grants - Doctoral Dissertation grant number is 454/UN3.15/PT/2021.

Conflict of interest

The authors declare no conflict of interest.

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