DOI : 10.58993/ijh/2023.80.1.13

Indian J. Hortic. 80(1), March 2023: 86-92

Thermal stress-induced physiological and biochemical alterations in papaya genotypes

Naveen Kumar Maurya, Amit Kumar Goswami*, S. K. Singh, Jai Prakash, Suneha Goswami[1], Viswanathan Chinnusamy[2], S. K. Jha[3], Deepak Singh Bisht[4] and Satyabrata Pradhan
Division of Fruits and Horticultural Technology, ICAR-Indian Agricultural Research Institute, New Delhi-110 012, Delhi, India.

ABSTRACT

Low-temperature stress significantly affects physiological processes inducing plant growth hindrance and reducing crop productivity. The present study aimed to understand the low-temperature stress-induced physio-chemical behaviour of five papaya genotypes such as Pusa Nanha, Red Lady, P-9-5, P-7-9 and one wild relative species *Vasconcellea cundinamarcensis*). Low-temperature stress significantly decreased the canopy gas exchange parameters, relative water content (RWC), membrane stability index (MSI) and chlorophyll content in all the papaya genotypes while tending to increase the total soluble sugars, proline and total soluble proteins, although the alterations were genotype-specific. *V. cundinamarcensis* showed greater tolerance to low-temperature stress, followed by P-9-5 and P-7-9, than other genotypes by maintaining the highest RWC, MSI, total soluble proteins, chlorophyll and proline contents. Our results showed that the chlorophyll content, membrane lipid peroxidation, and MSI could be used as the indices for screening potential papaya genotypes against cold tolerance.

Keywords: *Carica papaya* L., low temperature, MSI, RWC, Proline.

INTRODUCTION

Papaya (*Carica papaya* L.) has now become a naturalized species in several tropical and subtropical areas worldwide. India is the largest papaya producer (5.98 million tonnes), and its world production share is expected to rise from 59 to 61% against only 2.1% of the world (up to 16.6 million tonnes) by 2029 (FAO, 6). In 2017 and 2018, the export of *C. papaya* declined due to adverse climatic conditions such as low-temperature stress. Low temperature is the major limiting factor causing chilling and freezing damage, which affects the plant in two ways (i) poor plant growth due to low temperature and (ii) by turning the cell membrane into a solid gel and dehydrating the cells, causing ice crystallization in the intercellular gaps, leading to osmotic stress. Photosynthesis is a highly synchronized process, and vulnerable to any fluctuation in environmental conditions, as it needs to balance the absorbed light energy of photosystems with the energy consumed by the plants' metabolic processes. The low-temperature stress producing reactive oxygen species (ROS) exacerbates an imbalance between the energy supply and the metabolic processes resulting in oxidative damage. To combat the oxidative damage, plants evolve a sophisticated antioxidant system that includes both enzymatic and non-enzymatic antioxidants such as proline and protein (Erdal *et al.*, 5). *Vasconcellea cundinamarcensis*, one of the remote cousins of cultivated papaya (*C. papaya* L.), is resistant to frost. However, practically all commercial varieties of papaya are susceptible to low-temperature stress, restricting their commercial cultivation in subtropical locations. The papaya thrives best in temperature range of 21° to 33°C, however, winter temperatures below 12° to 14°C severely impedes the plant growth and fruit production (Ram, 14). Despite the facts mentioned above, neither the genetic makeup nor the physiology behind papaya's ability to withstand cold stress has been thoroughly investigated. So the current study was planned to understand the low temperature induced alterations in different papaya genotypes, and to establish the criteria to be taken for the screening of papaya genotypes against the low-temperature stress.

MATERIALS AND METHODS

The four genotypes of *Carica papaya* L. (Pusa Nanha, Red Lady, P-9-5 and P-7-9) and one cold-tolerant wild species (*Vasconcellea cundinamarcensis*) were tested for low-temperature stress in a controlled condition at the National

---

*Corresponding author: amit.tkg@gmail.com
[1]Division of Biochemistry, ICAR-Indian Agricultural Research Institute, New Delhi -110 012, Delhi, India
[2]Division of Plant Physiology, ICAR-Indian Agricultural Research Institute, New Delhi 110 012, Delhi, India
[3]Division of Genetics, ICAR-Indian Agricultural Research Institute, New Delhi 110 012
[4]ICAR-National Institute of Plant Biotechnology, New Delhi 110 012, Delhi, India

Phytotron Facility, ICAR-IARI, New Delhi during 2020-2021. The seeds of these genotypes were sown in PVC trays containing a potting mixture of perlite, vermiculite, coco-peat, and vermicompost (1:1:1:1) and germinated seedlings were transplanted into plastic pots (8˝) after eight weeks. The transplanted seedlings were irrigated at three days interval with regular sterilized tap water. The plants at growth chamber was maintained at a temperature of 28°C (and 26°C for *V. cundinamarcensis*) during the day and 18°C at night, with a photoperiod of 12 h 30 min, relative humidity of 70% during the day and 85-90% during the night, under the irradiance of 700-800 mol $m^{-2} s^{-1}$, and subsequently the growing chamber's temperature was lowered by 2°C in every two days interval as part of the temperature treatment. The experiment was planned in Randomized Block design and replicated thrice. Twenty-seven plants were taken of each genotype were taken in a replication. Three plants were kept in the control at 28°C days and 18°C night. The details of treatment are given in Table 1. For each treatment, the data on various physiological and biochemical parameters were recorded.

Internal CO_2 content (*Ci*), photosynthetic rate (*A*), transpiration rate (*E*) and stomatal conductance (g_s) of five mature leaves on three different plants were measured using an infrared gas analyzer. The leaf relative water content (RWC) was estimated using the method of Barrs and Weatherley (1). The membrane stability index (MSI) was estimated using the procedure outlined by Sairam *et al.* (16), whereas total soluble sugars were estimated using the anthrone reagent method (Sadasivam and Manickam, 15). The total chlorophyll content was recorded as SPAD value with the help of a portable chlorophyll meter (Konica Minolta SPAD-502). Membrane lipid peroxidation was measured in terms of malondialdehyde (MDA, a product of lipid peroxidation) content using thiobarbituric acid (TBA) reaction with minor modifications (Heath and Packer, 7). Colorimetric method was followed for the estimation of total proline (Bates *et al.*, 2), while total soluble proteins content in the leaf tissue was estimated as per the method of Bradford (4). The data recorded were analysed using software SAS package (9.3 SAS Institute Inc, USA), followed by t-test (LSD). P values ≤ 0.05 were considered as significant.

RESULTS AND DISCUSSION

The low-temperature regime (T), papaya genotype (G), and their interaction (T ×G) substantially impacted the *Ci*, *A*, *E* and g_s (Fig. 1 A-D), which were reduced significantly with the decreasing temperature from T_0 to T_6. The highest *Ci* was observed in control (608.66 µmol CO_2 mol^{-1}), followed by T_1 (567.46 µmol CO_2 mol^{-1}) and was lowest in the T_6 (323.79 µmol CO_2 mol^{-1}). Of the five genotypes, P-9-5 was found to have the highest *Ci* (494.76 µmol CO_2 mol^{-1}), having similarity statistically with *V. cundinamarcensis* (491.61 µmol CO_2 mol^{-1}), while it was lowest in Pusa Nanha (433.09 µmol CO_2 mol^{-1}). The interactions (G × T) showed that P-9-5 × T_0 had the highest *Ci* value (658.33 µmol CO_2 mol^{-1}), while it as lowest in Red Lady × T_6 (301.66 µmol CO_2 mol^{-1}). In the present study, the highest reduction in leaf internal CO_2 concentration due to low temperature stress (from 28°C day/18°C night to 16°C day/06°C night) was recorded in Red Lady (68.37%), while it was lowest in P- 9 -5 (46.78%) (Fig 1 A).

Table 1. Details of temperature regimes maintained under controlled growth chambers.

Treatment	Day temp. (°C)	Night temp. (°C)
Control	28± 0.1	18 ± 0.1
T_1	26± 0.1	16 ± 0.1
T_2	24± 0.1	14 ± 0.1
T_3	22± 0.1	12 ± 0.1
T_4	20 ± 0.1	10 ± 0.1
T_5	18 ± 0.1	08 ± 0.1
T_6	16 ± 0.1	06 ± 0.1

The photosynthetic rate (*A*) of temperature-treated plant was lower than that of control plants (Fig. 1 B), being lowest in T_6 (0.84 mol $m^{-2}s^{-1}$), and highest in control (3.04 mol $m^{-2}s^{-1}$). Amongst the interactions (G × T), P-9-5 × T_0 (3.35 µmol $m^{-2}s^{-1}$) showed the highest *A*, while it was lowest in Red Lady × T_6 (0.68 µmol $m^{-2}s^{-1}$). Overall, a severe decline in the *A* was observed in the papaya genotypes Red Lady (79.33%) under the cold stress, while the lowest decline (65.37%) was observed in P-9-5. The low-temperature stress alters the normal rates of photosynthesis and other gas exchange attributes in crop plants (Hussain *et al.*, 9). The low-temperature stress causes crop plants to have low photosynthetic rates, which contributes to poor CO_2 conductance in stomatal and mesophyll cells, impaired chloroplastic development, restricted metabolite transport, decreased quantum efficiency, and lower quantum yield for CO_2 assimilation. It has been observed that low temperatures affect different aspects of the photosynthetic process. It reduces the activity of different enzymes involved in the Calvin cycle and ROS-scavenging systems resulting in ROS generation in PSI and PSII. The change in redox poise imposed by ROS accumulation reduced the *A* (Jiao *et al.,* 10). Huang *et al.* (8) also reported the reduced *A* in the albino tea cultivar, while exposed to low temperature significantly.

The untreated (control) papaya plants showed the highest *E* (2.16 mol $m^{-2}s^{-1}$) statistically (Fig.1 C), while the lowest *E* was observed in T_6 (0.41 mol m^{-2} s^{-1}). Amongst the interactions (G × T), the untreated plants of Red Lady exhibited the highest *E* (2.57 mol $m^{-2}s^{-1}$), while it was lowest in P-7-9 × T_6 (0.29 mol $m^{-2}s^{-1}$), which was statistically at par with *V. cundinamarcensis* × T_6 (0.33 mol $m^{-2}s^{-1}$). Earlier, Xu *et al*. (18) also reported the low *A* and severely suppressed *E*, in strawberry under low temperature stress. The *gs* of papaya leaves was significantly influenced by low-temperature regimes, individually as well as collectively (Fig. 1 D). The untreated plants of papaya had the highest g_s (0.286 mol m^{-2} s^{-1}), while it was lowest in T_6 (0.021 mol m^{-2} s^{-1}). Amongst the interactions (G × T), the untreated plants of *V. cundinamarcensis* maintained the highest g_s (0.316 mol m^{-2} s^{-1}), while P-7-9 × T_6 proved worse to have the lowest g_s (0.013 mol m^{-2} s^{-1}) closely followed by Red Lady × T_6 (0.016 mol $m^{-2}s^{-1}$). A reduction in g_s (15-40%) was observed under low-temperature regimes, compared to the control. A similar reduction in the stomatal conductance in strawberry seedlings under the low-temperature stress was also reported earlier by Xu *et al*. (18).

The temperature, genotypes and their mutual interactions significantly influenced the leaf RWC (Table 2). Low temperature-treated plants showed the lower RWC than the control plants. The lowest RWC was observed in T_6 (74.12%), while it was highest in control (91.62%) plants, followed by T_1 (89.20%). Of the six genotypes, *V. cundinamarcensis* maintained the highest RWC (86.19%), which is statistically similar to the RWC of P-9-5 plants. The lowest RWC was noted in the leaves of Red Lady (79.97%). Amongst the interactions (G × T), the untreated plants of *V. cundinamarcensis* showed the highest RWC (93.43%) registered the highest content, followed by P-9-5 × T_0 (92.36%), while the lowest RWC (70.01%) was observed in Red Lady × T_6. Beheshti *et al*. (3) in grapes and Pradhan *et al*. (12) in papaya also reported a significant decrease in RWC under low-temperature stress.

Plants exposed to low temperatures had lower MSI values than the control plants (Table 3), and as a result, MSI was lowest (48.35%) at T_6 level of temperature plants and the highest (74.88%) was note in in control plants. Amongst the G × T interactions, the untreated plants of *V. cundinamarcensis* showed the highest MSI (79.49%), which was followed by P-9-5 x T_0 (76.27%). The lowest MSI was observed in Red Lady × T_6 (37.09%). Significant depression in the MSI under cold stress was also reported in in papaya plants by Pradhan *et al*. (12).

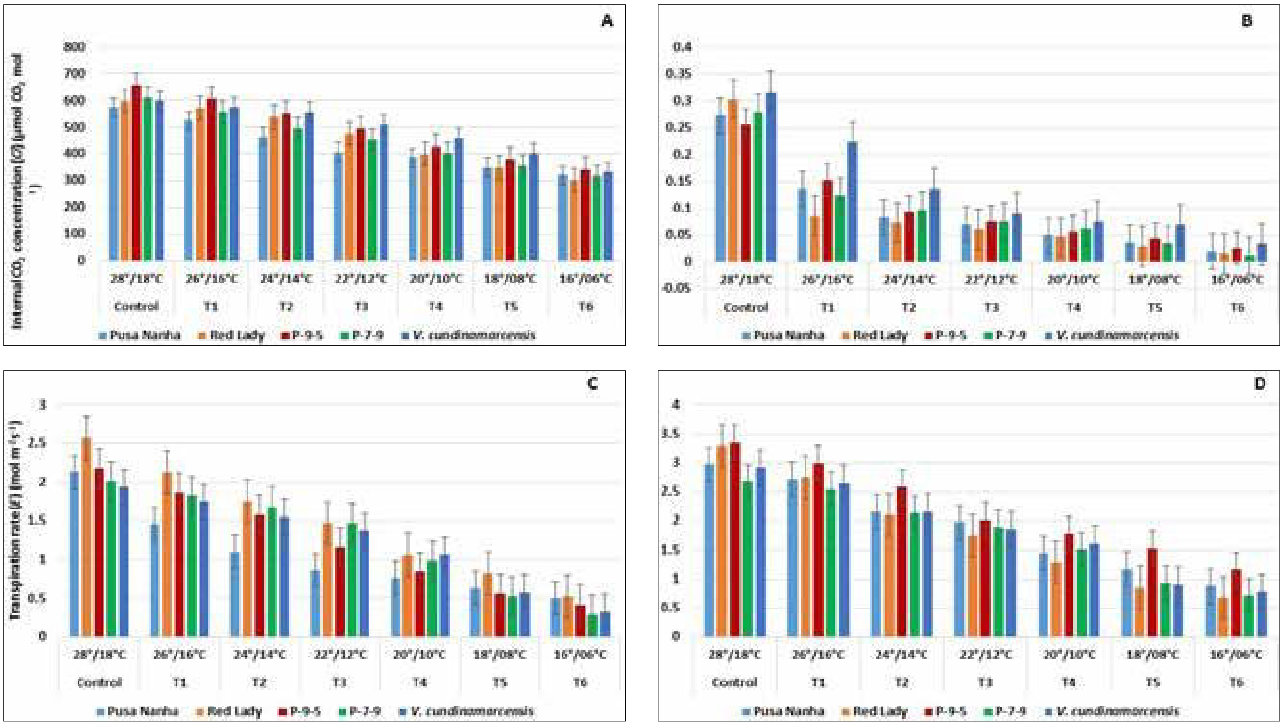

Fig. 1. Effect of different temperature regimes on internal CO_2 concentration (*Ci*), stomatal conductance (g_s), transpiration rate (*E*), and photosynthetic rate (*A*) of papaya genotypes grown under controlled phytotron conditions; Vertical bars indicate ± SE mean.

Table 2. Influence of different temperature regimes on relative water content (%) of papaya genotypes grown under Phytotron conditions.

Genotype	Control	T_1	T_2	T_3	T_4	T_5	T_6	Mean
	(28°/18°C)	(26°/16°C)	(24°/14°C)	(22°/12°C)	(20°/10°C)	(18°/08°C)	(16°/06°C)	
Pusa Nanha	91.57^{bc}	89.42^{de}	85.46^{hg}	82.59^{jk}	79.06^{nm}	77.57^{po}	72.99^{s}	82.66^{c}
Red Lady	90.48^{dc}	86.39^{g}	82.65^{j}	79.35^{m}	76.58^{pq}	74.36^{r}	70.01^{t}	79.97^{d}
P-9-5	92.36^{ba}	90.02^{d}	87.67^{f}	86.32^{g}	83.68^{ji}	80.53^{l}	75.57^{q}	85.16^{b}
P-7-9	90.25^{d}	88.51^{fe}	85.84^{g}	83.36^{ji}	80.72^{l}	77.49^{po}	74.01^{sr}	82.88^{c}
V. cund.	93.43^{a}	91.68^{b}	88.24^{f}	86.02^{g}	84.43^{hi}	81.50^{lk}	78.06^{no}	86.19^{a}
Mean	91.62^{a}	89.20^{b}	85.97^{c}	83.53^{d}	80.89^{e}	78.29^{f}	74.12^{g}	
LSD ($P \leq 0.05$)								
Genotype (G)								0.41
Temp. (T)								0.49
G × T								1.10

Table 3. Influence of different temperature regimes on membrane stability index (%) of papaya genotypes grown under Phytotron conditions.

Genotype	Control	T_1	T_2	T_3	T_4	T_5	T_6	Mean
	(28°/18°C)	(26°/16°C)	(24°/14°C)	(22°/12°C)	(20°/10°C)	(18°/08°C)	(16°/06°C)	
Pusa Nanha	74.36^{d}	73.76^{ed}	70.61^{gf}	65.42^{i}	61.45^{kl}	57.26^{n}	51.65^{q}	64.93^{c}
Red Lady	71.55^{f}	67.07^{h}	63.49^{j}	59.44^{m}	55.54^{o}	46.61^{s}	37.09^{u}	57.26^{e}
P-9-5	76.27^{b}	74.53^{cd}	71.33^{f}	66.44^{ih}	61.10^{l}	57.11^{n}	53.81^{p}	65.79^{b}
P-7-9	72.74^{e}	69.74^{g}	66.22^{ih}	61.24^{l}	56.65^{n}	49.83^{r}	42.78^{t}	59.89^{d}
V. cund.	79.49^{a}	75.47^{cb}	71.16^{f}	67.02^{h}	62.47^{kj}	59.51^{m}	56.46^{on}	67.36^{a}
Mean	74.88^{a}	72.11^{b}	68.56^{c}	63.91^{d}	59.44^{e}	54.06^{f}	48.35^{g}	
LSD ($P \leq 0.05$)								
Genotype (G)								0.39
Temp. (T)								0.46
G × T								1.04

The control plants had the highest SPAD value (50.61), whereas T_6 plants had the lowest (42.47) (Fig. 2 a). Amongst the six genotypes, *V. cundinamarcensis* exhibited the highest chlorophyll content (47.54 SPAD value), followed by P-7-9 (47.41 SPAD value). In G × T interactions, the control plants P-7-9 exhibited the highest SPAD value (52.45), having similarity statistically with the control plants of *V. cundinamarcensis* × T_0 (52.40), while the lowest SPAD value was observed in Red Lady × T_6 (40.96). The similar reduction in the eight melon genotypes was also reported, while the plants were exposed to a low-temperature regime (15° day/10°C night) for 5 days (Li *et al.*, 11) also, chlorophyll was significantly reduced in the melon. Huang *et al.* (8) too reported the significant reduction in the chlorophyll content in the albino tea cultivar, while subjected to a low temperature.

Low temperature-treated plants showed the higher leaf total sugars content than the control plants (Fig. 2 b). The highest content of total sugars was observed in T_6 (61.54 mg g^{-1}), while the control plants showed the lowest total sugars content (39.76 mg g^{-1}). Amongst the six genotypes, P-9-5 accumulated the highest total sugars content (61.77 mg g^{-1}), followed by P-7-14 (60.43 mg g^{-1}), which was statistically at par with *V. cundinamarcensis* (61.35 mg g^{-1}). Red Lady proved to show the lowest accumulation of total sugar content (32.95 mg g^{-1}). In G × T interactions, *V. cundinamarcensis* × T_6 showed the highest total sugar content (74.87 mg g^{-1}), followed by P-9-5 (73.26 mg g^{-1}) and P-7-9 × T_6 (69.70 mg g^{-1}). Wei *et al.* (17) also reported a rapid increase in soluble sugars concentration in watermelon seedlings, grown at low temperatures. The decrease in soluble sugars

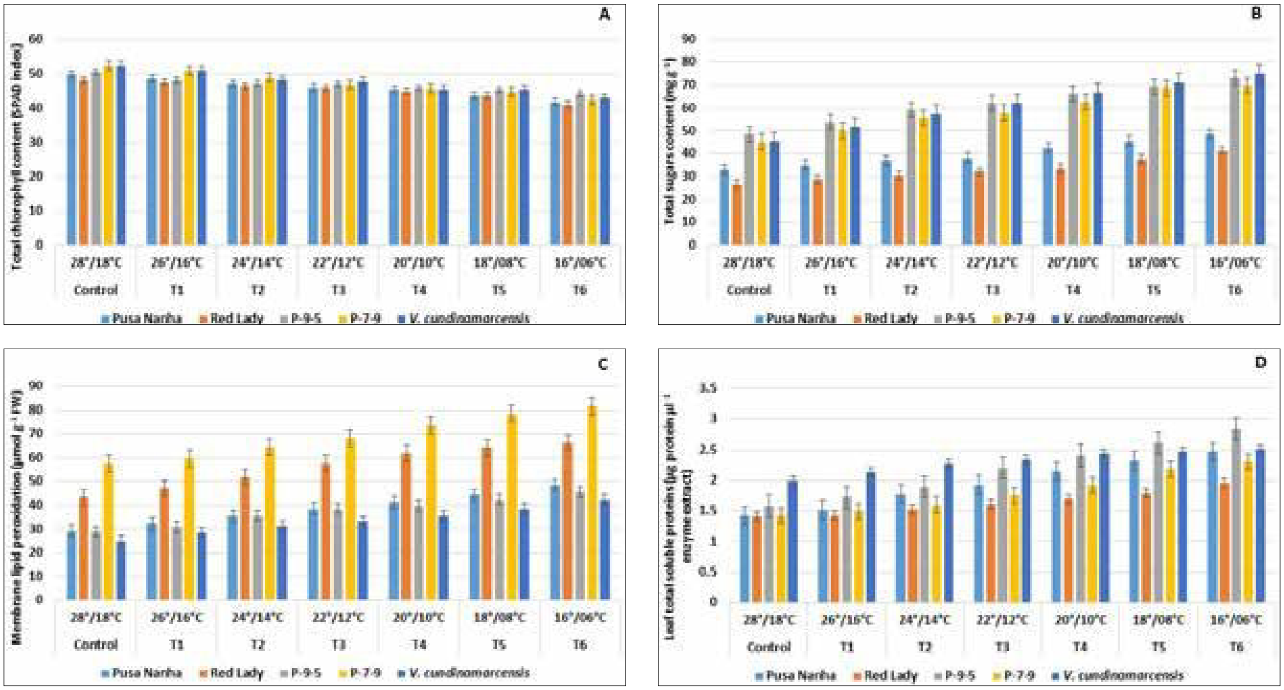

Fig. 2. Effect of different temperature regimes on total chlorophyll content, total sugars, membrane lipid peroxidation and leaf total soluble proteins of papaya genotypes grown under controlled phytotron conditions; Vertical bars indicate ± SE mean.

concentration in leaves may also be associated with a reduction in photosynthetic activity under low light conditions.

Malondialdehyde (MDA) content was used to indicate the amounts of lipid peroxidation in papaya leaves. Temperature-treated plants showed a higher value of lipid peroxidation in the leaves than the control plants, and the highest was observed in T_6 (56.85 µmol g^{-1}FW) significantly, while it was the lowest in control (36.77 µmol g^{-1}FW) plants (Fig 2 c). The MDA content increased within the papaya genotypes due to exposure to decreasing temperature regimes. Of the six genotypes, P-7-9 exhibited the highest MDA content (69.05 µmol g^{-1}FW), which was statistically different from all other genotypes. Erdal *et al*. (5) reported a significant increase in MDA content in chickpea seedlings, exposed to 10°/5°C (day/night) for two days as compared to control 25±1°C plants. The rise in MDA content measured in the low-temperature treated plants in the present study indicated an increased rate of oxidation of membrane lipids, presumably leading to membrane injury. Similarly, Xu *et al*. (18) reported the increased MDA concentration in strawberry on exposure to chilling stress. The plants in treatment regime T_6 had significantly higher total soluble protein content (2.41 µg protein µl^{-1}) followed by T_5 (2.27 µg protein µl^{-1}) than other treatment (Fig 2 d). The control plants had the lowest protein content (1.56 µg protein µl^{-1}). Among the genotypes, the highest accumulation of soluble proteins content was recorded in the plants of *V. cundinamarcensis* (2.31 µg protein µl^{-1}) significantly, while it was the lowest in Red Lady (1.63 µg protein µl^{-1}) plants. Amongst the G × T interactions, the total soluble proteins content was registered in the plants of P-9-5 × T_6 (2.83 µg protein µl^{-1}), followed by *V. cundinamarcensis* × T_6 (2.51 µg protein µl^{-1}). The lowest total soluble proteins content was observed in the untreated plants of Red Lady (1.41 µg protein µl^{-1}). The similar observations have also been reported in fruit crops by Beheshti *et al*. (3) and Pradhan *et al*. (13). Beheshti *et al*. (3) also reported that the concentrations of leaf soluble protein in all studied grapevine cultivars increased noticeably under cold stress (0-4°C). The higher soluble protein concentration in 'Red Sultana' leaves confirmed lower membrane damage in this cold hardy grapevine cultivar.

The proline concentration in papaya leaves increased with decreasing temperature regimes (Table 4), registering its highest accumulation in T_6 (0.41 µM proline g^{-1} FW) plants, while it was lowest in control (0.14 µM proline g^{-1} FW) plants. The genotype *V. cundinamarcensis* exhibited the highest proline content (0.32 µM proline g^{-1} FW), followed by P-9-5 (0.31 µM proline g^{-1} FW), while the lowest value (0.23

Table 4. Effect of different temperature regimes on proline content (μM proline g^{-1} FW) of papaya genotypes grown under phytotron conditions

Genotype	Control	T_1	T_2	T_3	T_4	T_5	T_6	Mean
	28°/18°C	26°/16°C	24°/14°C	22°/12°C	20°/10°C	18°/08°C	16°/06°C	
Pusa Nanha	1.42^{r}	1.51^{proq}	1.78^{kl}	1.93^{j}	2.15^{i}	2.32^{fe}	2.45^{c}	1.94^{c}
Red Lady	1.41^{r}	1.43^{rq}	1.53^{poq}	1.61^{mon}	1.69^{mln}	1.79^{kl}	1.95^{j}	1.63^{e}
P-9-5	1.58^{po}	1.72^{ml}	1.88^{kj}	2.21^{igh}	2.42^{cd}	2.61^{b}	2.83^{a}	2.18^{b}
P-7-9	1.43^{rq}	1.49^{prq}	1.61^{on}	1.75^{l}	1.92^{j}	2.19^{ih}	2.30^{fg}	1.81^{d}
V. cund.	1.99^{j}	2.14^{i}	2.27^{fgh}	2.34^{fde}	2.44^{cd}	2.47^{c}	2.51^{cb}	2.31^{a}
Mean	1.56^{g}	1.65^{f}	1.81^{e}	1.97^{d}	2.12^{c}	2.27^{b}	2.41^{a}	
LSD ($P \leq 0.05$)								
Genotype (G)								0.04
Temp. (T)								0.05
G × T								0.11

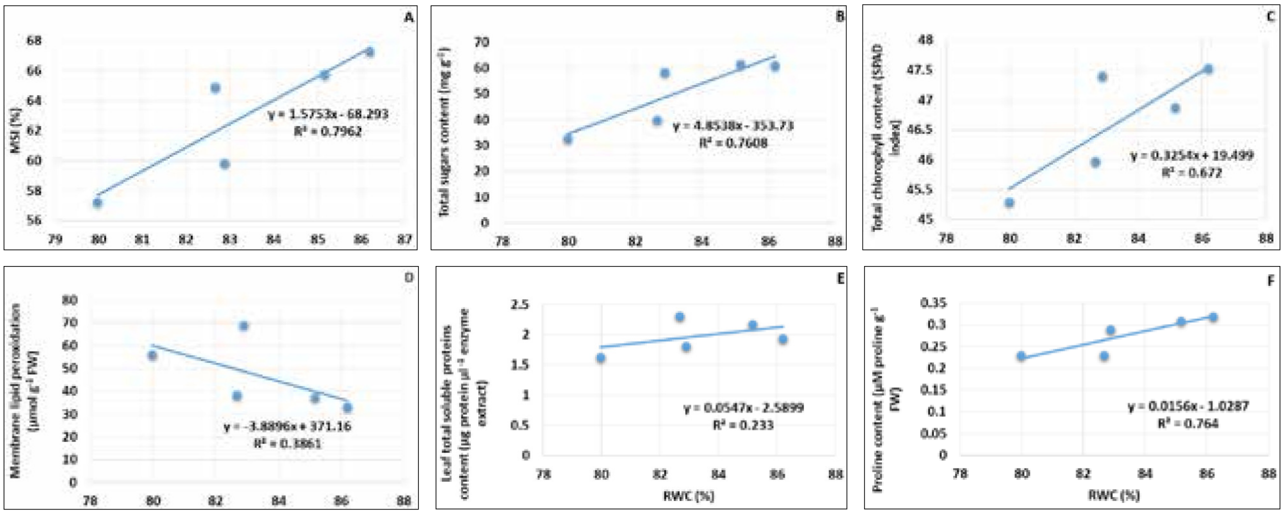

Fig. 3. Regression analysis of physiological and biochemical parameters with relation to relative water content (%) as affected by low temperature regime of 16°/06°C (day/night) in papaya genotypes. A, MSI; B, Total sugars content; C, Chlorophyll content ; D, MDA content; E, Total soluble proteins; and F, Proline. X-axis corresponds to RWC (%), while Y-axis to physiological and biochemical parameters at 06°/06°C (day/night) temperature regime.

μM proline g^{-1} FW) was observed in Pusa Nanha, which was statistically at par with Red Lady (0.23 μM proline g^{-1} FW). Amongst the G × T interactions, *V. cundinamarcensis* × T_6 (0.48 μM proline g^{-1} FW) accumulated the highest proline content, followed by P-9-5 × T_6 (0.46 μM proline g^{-1} FW), while the lowest accumulation was observed in the untreated plants of Red Lady (0.12 μM proline g^{-1} FW). Proline plays a vital role in maintaining the osmotic balance in plant tissue, as it protects seedlings against the adverse effects of low temperatures. The similar increase in proline was also reported in the melon genotypes, while exposed to low-temperature regime (15° day/10°C night) for 5 days (Li *et al.*, 11).

The regression analysis between relative water content (%) and different parameters at the 16°/06°C temperature regime revealed a higher R_2 value for MSI (0.796) followed by proline (0.764) and total sugars content (0.7608) (Fig. 3 A, F & B). The SPAD value was found to have the lowest (0.672) R_2 value, followed by membrane lipid peroxidation (0.3861) and total soluble proteins content (0.233) (Fig. 3 C, D & E). A positive value was found for the coefficient of x variable in all the regression equations.

It can be concluded from the present study that low-temperature exposure of seedlings of papaya genotypes showed distinct changes in physiological and biochemical parameters. Amongst the cultivated papaya genotypes screened, P-9-5 and P-7-9 were found tolerant to low-temperature stress, as noted in the cold-tolerant wild species *V. cundinamarcensis*.

AUTHORS' CONTRIBUTION

Conceptualization of research (AKG); Designing of the experiments (AKG, NKM); Contribution of experimental materials and execution of field/lab experiments and data collection (NKM, AKG, JP, SKS, SG); Analysis of data and interpretation (NKM, AKG, SKS); Preparation of the manuscript (NKM, AKG, SKS, JP, SG, VC, SKJ, DSB, SP)

DECLARATION

The authors declare that there is no conflict of interest.

REFERENCES

1. Barrs, H. D. and Weatherley, P. E. 1962. A re-examination of the relative turgidity technique for estimating water deficits in leaves. *Aust. J. Biol. Sci.* **15:** 413-28.
2. Bates, L. S., Waldren, R. P. and Teare, I. D. 1973. Rapid determination of free proline for water-stress studies. *Plant and Soil*, **39:** 205-207.
3. Beheshti, Rooy. S. S., Hosseini, Salekdeh, G., Ghabooli, M., Gholami, M. and Karimi, R. 2017. Cold-induced physiological and biochemical responses of three grapevine cultivars differing in cold tolerance. *Acta Physiol. Plant.* **39:** 1-13.
4. Bradford, M. M. 1976. A rapid and sensitive method for the quantitation of microgram quantities of protein utilizing the principle of protein-dye binding. *Anal. Biochem*. **72:** 248-54.
5. Erdal, S., Genisel, M., Turk, H., Dumlupinar, R. and Demir, Y. 2015. Modulation of alternative oxidase to enhance tolerance against cold stress of chickpea by chemical treatments. *J. Plant Physiol*. **175**: 95-101.
6. FAO, 2021. *Major Tropical Fruits*: *Preliminary Results* 2020. Rome.
7. Heath, R. L. and Packer, L. 1968. Photoperoxidation in isolated chloroplasts: I. Kinetics and stoichiometry of fatty acid peroxidation. *Arch. Biochem. Biophys*. **125:** 189-98.
8. Huang, S., Zheng, X., Yao, L., Luo, L., Zuo, T., Hou, Q. and Ni, W. 2022. Glycine betaine facilitates the photosynthesis of albino tea under low temperature by regulating related gene methylation. *Sci. Hortic*. **303:** 111235.
9. Hussain, H. A., Hussain, S., Khaliq, A., Ashraf, U., Anjum, S. A., Men, S. and Wang, L. 2018. Chilling and drought stresses in crop plants: implications, cross talk, and potential management opportunities. *Front. Plant Sci*. **9:** 393-413.
10. Jiao, X., Yu, X., Ding, J., Du, Q., Zhang, J., Song, X. and Li, J. 2022. Effects of rising VPD on the nutrient uptake, water status and photosynthetic system of tomato plants at different nitrogen applications under low temperature. *Sci. Hortic.* **304**: 111335.
11. Li, M., Duan, X., Liu, T. and Qi, H. 2022. Short-term suboptimal low temperature has short-and long-term effects on melon seedlings. *Sci. Hortic.* **297:** 110967.
12. Pradhan, S., Goswami, A. K., Singh, S. K., Prakash, J., Goswami, S., Chinnusamy, V. and Maurya, N. K. 2019. Low temperature stress induced physiological and biochemical alterations in papaya genotypes. *S. Afr. J. Bot.* **123:** 133-41.
13. Pradhan, S., Goswami, A.K., Singh, S.K., Prakash, J., Goswami, S., Chinnusamy, V. and Kumar, A. 2017. Physiological and biochemical alterations due to low temperature stress in papaya genotypes. *Indian J. Hortic.* **74:** 491-97.
14. Ram, M. 2005. *Papaya*, Indian Council of Agricultural Research, New Delhi, 78 p.
15. Sadasivam, S. and Manickam, A. 1992. In: *Biochemical Methods for Agricultural Science*, Wiley Eastern Limited, New Delhi, 11.
16. Sairam, R. K. 1994. Effect of moisture-stress on physiological activities of two contrasting wheat genotypes. *Indian J. Exp. Biol.* **32:** 584-93.
17. Wei, H., Ai, H. S., Fu, S. Y., Yuan, F. Z., Shan-Zhen, L. and Zhao, D. Z. 2015. Effects of sub-optimal temperatures and low light intensity on growth and anti-oxidant enzyme activities in watermelon (*Citrullus lanatus*) seedlings. *J. Hortic. Sci. Biotechnol.* **90:** 92-98.
18. Xu, C., Wang, M. T., Yang, Z. Q. and Zheng, Q. T. 2020. Low temperature and low irradiation induced irreversible damage of strawberry seedlings. *Photosynthetica* **58:** 156-64.

Received : August, 2022; Revised : February, 2023;
Accepted : February, 2023