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Leaf Defoliation Tolerance of Root-Cutting Chili Varieties (*Capsicum annum* L.) Planted in Lowland Areas Related to Improve Yield and Physiological Activity

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Abstract

Lowland chili (*Capsicum annum* L.) cultivation in Indonesia has lower productivity than highlands. Root-shoot growth increment can enhance chili yield. Leaf defoliation with root cutting is modification technique to optimize root-shoot growth. This research aims to determine improving physiological activity and yield of root-cutting chili varieties tolerant to leaf defoliation in lowland areas. The factorial treatments were arranged in randomized complete block design with 3 replications. The first factor was lowland chili varieties (Kencana, Lembang-1, Tanjung-2, and Ungara). The second factor was leaf defoliation on root-cutting chili, consisting of 0, 20, 40, 60 %, and control (0 % leaf defoliation without root-cutting). Analysis of variance was used to determine effect of leaf defoliation on physiological activity and chili yield. The grouping chili varieties were analyzed through principal component and cluster analysis based on yield, stress selection indices, and physiological activity. The result identified Lembang-1 and Ungara as tolerant varieties to leaf defoliation, while Kencana and Tanjung-2 were intolerant. Ungara and Lembang-1 could increase fresh weight of fruit by 39.26 and 29.30 %, respectively under 40 and 60 % leaf defoliation compared to control. The increased chili yield and root-shoot growth in tolerant varieties were caused by improving physiological activity. Root growth was driven by increased invertase activity, reducing sugar, indole acetic acid, and kinetin hormones, while shoot growth was influenced by increased sucrose, invertase activity, reducing sugar, gibberellin, and kinetin hormones. Leaf defoliation until 60 % on intolerant varieties (Tanjung-2 and Kencana) decreased chili yield by 9.53 and 19.64 %, respectively. It was concluded that 40 and 60 % leaf defoliation treatment were toleranted by root-cutting chili varieties of Ungara and Lembang-1, which increased chili yield in lowland areas.

Keywords: Chili yield, Invertase activity, Kinetin, Reducing sugar, Sucrose

Introduction

Chili (*Capsicum annum* L.) is one of horticultural commodities that is cultivated in lowland and highland areas with tropical climates such as Indonesia. The productivity of lowland area was lower than highlands in Indonesia by 6.33 and 11.79 tons ha^{-1}, respectively [1]. Increasing chili plant productivity in lowland areas is necessary to meet the high demand for chili yield. In Indonesia, chili varieties which were adapted in lowland area, namely Lembang-1, Ungara, Kencana, and Tanjung-2. The chili varieties were classified as open-pollinated with diverse morphological traits. Ungara has wider leaves but smaller plant height. Lembang-1 has longer petioles, taller plant height, and small fruit diameter. Tanjung-2 has shortest harvest time, largest fruit diameter, and wider leaves. Kencana has longest harvest time, longer petioles, and small fruit diameter [2]. Kusumaningrum *et al.* [3] reported that increment of lowland chili yield can be obtained by root cutting at 8 weeks after transplanting (8 WAT). Moreover, Lembang-1, Ungara, and Kencana were classified as tolerant varieties while Tanjung-2 was classified as intolerant varieties. The root cutting at 8 WAT in tolerant varieties (Lembang-1, Ungara, and Kencana) could increase fresh weight of fruit by 33.76, 31.74, and

30.66 %, respectively, compared without root cutting. The root cutting treatment causes plants to mainly allocate assimilates to roots for growth after root biomass loss [4]. Mechanism involved changes in assimilate translocation from leaves to roots in chili plants [5]. Root cutting increases the need for root assimilates as a result of dry weight root loss, as had been observed in raspberries [6]. Not only root cutting, plant yield can be increased by regulating leaf composition through defoliation. Defoliation applied by removing below leaves in plant shoot. It could increase sunlight exposure and suppress leaf mutual shading [7]. According to Iseki *et al.* [8] mutual shading of leaf can inhibit tomato growth. High leaf plant density can result low penetration sunlight into canopy, and low carbon partitioning to fruit yield. Wang *et al.* [9] suggested the compensatory mechanisms of defoliation, e.g., enhance photosynthesis rate, and changing biomass allocation to maintain plant growth. Therefore, plant production in lowland areas can be increased by root-shoot growth modification through root cutting and/or leaf defoliation.

Leaves are main organ for production of organic matter and source of carbohydrates. According to Islam *et al.* [10] greater source capacity leads to poor crop performance because it produces greater foliage. It means instead of optimum source capacity increase potential sink size. Leaf defoliation be useful to suppress excessive vegetative growth, encourage reproductive growth, and promote fruit production. After defoliation, sugar allocation to new leaves increases. Sugar and starch are the main components of mobile carbon pools in plants. Starch functions as a storage compound and could be depleted in plants under stress conditions. Large carbon reserves can mobilize reserves for osmotic adjustment to maintain normal physiological activities under stress conditions. Plants could recover by up-regulating photosynthesis, and enhancing leaf biomass ratio [11]. In previous research, Islam *et al.* [10] showed that leaf defoliation at 37.5 % on tomato before initial flowering increased fruit yield compared to control. Raza *et al.* [12] reported that in soybean, the 15 % leaf defoliation from top of canopy could increase seed yield by 9 % compared to control. On maize, Liu *et al.* [13] informed that leaf defoliation 15.38 % from top of plant after silking increased kernel weight and grain yield compared to control. Leaf regeneration under defoliation requires carbohydrates supply from photosynthetic. During photosynthesis, 3-phosphoglyceric acid (3-PGA) and glyceraldehyde-3-phosphate (G3P) are produced by carbon fixation (CO_2+Ribulose-1,5-bisphosphate carboxylase/ oxygenase), which act as precursors of sucrose biosynthesis [14]. Sucrose is a non-structural carbohydrate which an important energy supply in metabolism processes. Sucrose acts as signaling molecule that produced in source and translocated to sink for growth [15]. In sink organ, sucrose is hydrolyzed into reducing sugar using invertase enzyme for metabolism. Invertase activity plays an important role in this hydrolysis process and has been reported in many plant species such as Arabidopsis [16], rice [17], petunia [18], pepper [19]. Previous research showed that defoliation in *A. fruitoca* can compensate leaf growth due to increased carbohydrates accumulation on shoot [20]. Hoidal *et al.* [21] reported after 50 % leaf defoliation in *Lolium parenne*, the utilization of reserve carbon is needed for leaf regeneration. In *Amarantus vruentus*, *A hypochondriacus* and *A caudatus* spinach, defoliation treatment had an effect reallocation of carbohydrates to shoot for leaf regeneration [22]. Wang *et al.* [15] also reported 50 % defoliation in leguminosae increased carbon allocation to shoot for leaf regeneration.

Leaf defoliation changes in carbon fixing and biomass production by changes in hormonal status. Plant hormones modify canopy and controlling crop growth through increase in redistribution of photosynthate [23]. In maize, increase shoot dry mass in defoliation treatment can be attributed to phytohormones, such as gibberellin (GA), indoleacetic acid (IAA), indolebutyric acid (IBA), and zeatin. Gibberellins play roles in stem cell elongation, leaf expansion, development of new leaf primordia, and plant adaptation to stress condition. Auxins are mainly produced in shoots and play a key role in regulating plant root development, shaping root system in response to variations environment, and conferring an adaptive advantage [24]. Cytokinin regulates growth, metabolism, nutrient absorption, and transport, all of which appear to be linked with regrowth vigor upon defoliation. Generally, cytokinin increases shoot cell growth, chlorophyll accumulation, and photosynthetic activity. It is anticipated that the role of cytokinin in shoot growth and physiology is determined by cell phases at which cytokinin accumulation is promoted. When cytokinins were induced in the cell expansion phase through upregulation of the isopentenyl transferase gene and downregulation of cytokinin oxidase/dehydrogenase gene (HvCKX2), this effect changes in leaf size, chlorophyll content, and photosynthetic activity [25,26].

Leaf defoliation tolerance to root-cutting chili varieties planted in lowland areas related to improve yield and physiological activity such as phytohormone, sucrose, invertase activity, reducing sugar in root and shoot was not reported yet. The lowland chili varieties including Lembang-1, Tanjung-2, Kencana, and Ungara are used in this research to evaluate root-cutting chili varieties under leaf defoliation tolerant through physiological activity and yield. Therefore, chili varieties tolerant under leaf defoliation can be identified in lowland areas. Increasing lowland root-cutting chili yield under leaf defoliation is expected to contribute improving chili yield. Yield improvement impacts the economy of chili farmers by optimizing root and shoot growth to support chili yield.

Materials and methods

Experimental site and research design

This experiment was performed at Tridharma Field, Faculty of Agriculture, Yogyakarta, Indonesia (latitude: 7°50′24.87″S and longitude: 110°24′29.99″E). The experiment was arranged in factorial randomized complete block design with 3 blocks as replications. The first factor was lowland chili varieties (Kencana, Lembang-1, Tanjung-2, and Ungara). The second factor was leaf defoliation on root-cutting chili, consisting of 0, 20, 40, 60 %, and control (0 % leaf defoliation without root cutting). Root cutting was applied at 8 weeks after transplanting (WAT) to all chili plants with leaf defoliation treatments based on research results of Kusumaningrum *et al.* [3]. Lembang-1, Kencana, and Tanjung-2 originated from Indonesia vegetable crops research institute, while Ungara originated from Bogor Agricultural University, Indonesia. In the experimental design, a single block consisted of 20 experimental units. Each experimental unit, measuring 700×100 cm, contained 28 plants. Three samples were observed in each experimental unit for physiological activity and yield measurement. Lowland environmental conditions were observed during research. Air temperature ranged from 29 to 35 °C, relative humidity ranged from 52 to 63 %, while light intensity ranged from 123,366 to 164,200 lux. Soil texture in the field was classified as regosol. The composition of sand, silt, clay fractions was 51:27:22 %.

Experimental procedure

The chili seedbed was prepared using 1:1:1 of organic fertilizer, soil, and husk charcoal. The planting medium was placed into 50 g nursery plastic, each containing chili seed, which were arranged in germination tray (30×30×15 cm^3) under alternating light and dark conditions. After 7 days, chili seedling with 4 fully opened were ready for transplanting. For transplanting, planting medium was prepared using mixture soil, husk, cow manure in 3:1:1 ratio. Organic fertilizers sourced from livestock waste were environmentally sustainable. Organic fertilizers contained essential macro and micronutrients, enhance nutrient availability, and promote root uptake. Rice husk produced through pyrolysis process. It was sterile, neutral, and porous when added into soil. It helped retain moisture and improve soil water holding capacity. Combination soil, husk and organic fertilizers in planting media offered significant benefits for plant productivity and long-term quality soil [26]. The plants were arranged with interspacing of 35×20 cm in field. Seedlings with 4 open leaves were transplanted at a depth of 5 cm until the base of stem was covered with soil based on procedure reported by Kusumaningrum *et al.* [3]. Fertilization during vegetative phase at 2 WAT, included applying 300 kg ha^{-1} of urea, 600 kg ha^{-1} of SP-36, and 300 kg ha^{-1} of KCl. During generative phase (6 WAT), P_2O_5 and $CaCO_3$ + B were applied at 3 - 5 and 3 g L^{-1}, respectively. Weed control was managed manually in field. Pest control was performed using contact insecticide containing 135 g L^{-1} of pyridaben and 18 g L^{-1} of abamectin, applied every 7 days. Yellow traps with 800 g L^{-1} of eugenol were used in field. Harvesting was conducted gradually, starting the chili reached 80 % ripe and continued until fruit were suitable for consumption.

Leaf defoliation treatments

Root-cutting was carried out at 8 WAT as much as 50 % planting distance (0.5×35 cm) in both side until 10 cm soil depth based on reported by Kusumaningrum *et al.* [3]. Leaf defoliation intensity was treated at 9 WAT until chili plants already had third branch. The number of leaves was counted that had third branch before defoliation. The number of leaves were calculated based on defoliation intensity treatment. For instance, if total number of leaves was 60, then number of leaf defoliation at 0, 20, 40, and 60 % would be 0, 12, 24, 36 leaves, respectively. Defoliation was started from bottom leaves (1st branch), then continued in middle (2nd branch) and upper leaves (3rd branch) by prioritizing shaded leaves (**Figure 1**). For example, Tanjung-2 has 40 leaves with defoliation treatment of 40 %, so number of leaves that must be defoliated at 16 leaves. Defoliation started from 1st branch. If there were only 6 leaves on 1st branch, then defoliation was continued on 2nd branch at 8 leaf defoliation by prioritizing shaded leaves, then 2 leaves defoliated on the 3rd branch.

Figure 1 Lowland chili used in research Kencana (a), Lembang-1 (b), Tanjung-2 (c), Ungara (d).

Chili yield and stress selection indices

Chili yield can be observed through fresh weight of fruit (g) up to 19 WAT. The fresh weight of fruit was used to calculate stress selection indices under leaf defoliation treatment. The chili tolerant under leaf defoliation was measured using stress tolerance level (TOL), stress tolerant index (STI), and yield stability index (YSI). TOL was used to describe yield reduction under stress condition [27] using Eq. (1).

$$\text{Stress tolerance level (TOL)} = Y_s - Y_c \quad (1)$$

Stress tolerant index (STI) was used to determine relative performance under stress condition [27] using Eq. (2).

$$\text{Stress tolerant index (STI)} = \frac{Y_S \text{ x } Y_C}{Y_C^2} \quad (2)$$

Yield stability index (YSI) was indicate stability under stress condition [27] using Eq. (3).

$$\text{Yield stability index (YSI)} = \frac{Y_S}{Y_C} \quad (3)$$

where Ys was fresh weight of fruit under stress condition (leaf defoliation with root-cutting), and Yc was fresh weight of fruit under control condition (0 % leaf defoliation without root cutting). TOL level > 1, STI < 1, and YSI > 1 was classified as tolerant varieties under leaf defoliation.

Dry weight and leaf number increment

The root and shoot dry weight were determined at 15 WAT by drying in oven with 80 °C temperature for 24 h until constant weight. These were calculated using analytical scales to obtain dry weight roots and shoot in grams (g). The leaf number increment was calculated between leaf number at 9 WAT (before defoliation) and leaf number at 14 WAT (after defoliation).

Physiological activity

Physiological activity including sucrose, invertase activity, reducing sugar, and phytohormones were analyzed at 14 WAT. Fresh weight leaf and fresh weight root were taken from 3 plant samples for physiological analysis. Samples were stored at 5 °C temperature to maintain freshness organ. Physiological analysis preparation was initiated by crushed 10 g leave and root using liquid nitrogen. Homogeneous 0.50 g sample used extraction buffer. The supernatant was produced by centrifugation at 10,000 rpm, temperature 4 °C for 10 min [28]. Sucrose was analyzed using resorcinol method [29] by added 15 µl supernatant and 70 µl of NaOH 1M, then vortex until homogeneous. The supernatant mixture was heated at 100 °C for 10 min. After cold, it was reacted with 250 µl of 0.1 % resorcinol (in 95 % ethanol) and 750 µl HCl 30 %. Re-vortex and incubated supernatant used temperature at 80 °C for 8 min. After cold, it was observed using spectrophotometer Genesys 10S UV-Vis λ 520 nm.

Reducing sugar was analyzed using dinitro salicylic acid reagent (DNS) method [30]. The 50 µl supernatant + 450 µl H_2O was inserted into tube, and was added 500 µl of DNS reagent. The tube was heated at 100 °C for 10 min for reaction between glucose in sample and DNS. The tube was cooled to room temperature. After cold, it was observed using spectrophotometer Genesys 10S UV-Vis λ 560 nm.

Invertase activity was analyzed using Arai method [31]. The reagent solution contained 25 mM MOPS-Na-OH (pH 5.5) and 100 mM sucrose was used to measure activity of enzyme acid invertase (AI). A 250 µL buffer was incubated at 30 °C for 5 min. After adding 50 µL of buffer, the enzyme sample was vortexed and incubated. After 0 and 20 min of incubation at 30 °C, 500 µL of DNS reagent was added. Boiling water was used for 10 min to boil it. It was measured using spectrophotometer Genesys 10S UV-Vis λ 560 nm.

Phytohormone analysis measurement, including indole acetic acid, gibberellin and kinetin were determined by linsken & jackson method [32]. Crushed 10 g leave and root using liquid nitrogen. The smooth sample was added 20 mL of 65 % MeOH solvent. Then supernatant was centrifuged at 4,000 rpm for 30 min, and filtered using Whatman 42. The pH of the solution was maintained in acidic condition by adding HPLC grade glacial acetic acid (Merck, USA) to prevent protonation of phytohormones [33]. The upper organic phase was collected and dried using vacuum rotary evaporator (Biobase Inc., China). The isocratic mobile phase used for this analysis consisted of HPLC grade methanol (Hi-media, India) and HPLC grade water (Merck, USA) in a 55:45 ratio, acidified with 1 % glacial acetic acid (Merck, USA), and was flowed at rate of 1 mL/min for 20 min. The supernatant was injection 5-10 µL to high-performance liquid chromatography (HPLC, thermo fisher scientific, USA 254 UV-VIS) column C18 (1.8 lm, 50 9 2.1 mm internal diameter) (Macherey–Nagel, Du¨ren, Germany) at temperature of 40 °C.

Statistical analysis

All data were analyzed using analysis of variance (ANOVA) (α = 5 %) factorial followed honestly significant difference (α = 5 %). The grouping chili variety were analyzed through principal component and cluster analysis based on yield, stress selection indices, physiological activity. Pearson correlation was used to determine relationship of fresh weight of fruit and physiological activity on chili group. SAS version 9 software and OriginPro 2023 were used in analyses.

Results and discussion

Fresh weight of fruit

Fresh weight of fruit chili varieties to leaf defoliation treatment (leaf defoliation with root-cutting) and control (0 % leaf defoliation without root-cutting) showed different responses. Lembang-1, Ungara, and Kencana could increase fresh weight of fruit by 10.59, 15.07, and 10.24 %, respectively under 0 % leaf defoliation (with root-cutting) compared to control (0 % leaf defoliation without root-cutting) (**Table 1**). While, 0 % leaf defoliation (with root-cutting) in Tanjung-2 could not increase fresh weight of fruit compared to control (0 % leaf defoliation without root-cutting). Similar to previous research which reported that root cutting at 8 WAT increased fresh weight of fruit on tolerant varieties, namely Lembang-1, Ungara, and Kencana [3]. The leaf defoliation on root-cutting chili up to certain limit on chili plant had positive response. Lembang-1 and Ungara could produce higher fresh weight of fruit under leaf defoliation increment. The leaf defoliation at 60 % in Lembang-1 could increase fresh weight of fruits by 20.93 % compared to 0 % leaf defoliation (**Table 1)**. In Ungara, fresh weight of fruit increased by 28.48 under 40 % leaf defoliation compared to 0 % leaf defoliation (**Table 1**). Therefore, it showed that leaf defoliation up to 60 and 40 % on Lembang-1 dan Ungara could increase fresh weight of fruit compared to 0 % leaf defoliation. Increasing fresh weight of fruit under leaf defoliation in Lembang-1 and Ungara indicated that chili varieties were adaptive to lowland environments. Chili preferred well-drained, moisture-holding loamy soil, with optimal growth and fruit production temperatures ranging from 18 to 30 °C [34]. Leaf defoliation increment up to 60 % decreased fresh weight of fruit on Kencana by 19.64 % compared to 0 % leaf defoliation (**Table 1**). Leaf defoliation at 60

% in Tanjung-2 not increased fresh weight of fruit compared to 0 % defoliation (with root-cutting) and control (0 % leaf defoliation without root-cutting) (**Table 1**). Therefore, leaf defoliation up to 60 % intensity on Kencana and Tanjung-2 could decrease fresh weight of fruit. After defoliation, plants required more assimilates for regrowth. Compensatory growth occurred through the synthesis of carbohydrates, allocation of assimilates, and remobilization of carbon storage compounds to recovery of photosynthetic capacity. Priority allocation of carbon resources to active shoot sinks was the main adaptive response to regrowth after defoliation [35]. Increased translocation of assimilates to shoot affected the growth of chili fruit. According to Marcelis & Heuvelink [36] fruit growth is influenced by sink ability to receive photoassimilate which depends on sink activity and assimilate availability at source. Chili yield increment in lowland areas under leaf defoliation could result higher chili productivity and improved farmer income. This means that high-income farmers due to effective use of land resulting increased chili production [37].

Table 1 Fresh weight of fruit, dry weight of shoot, and dry weight of roots under leaf defoliation.

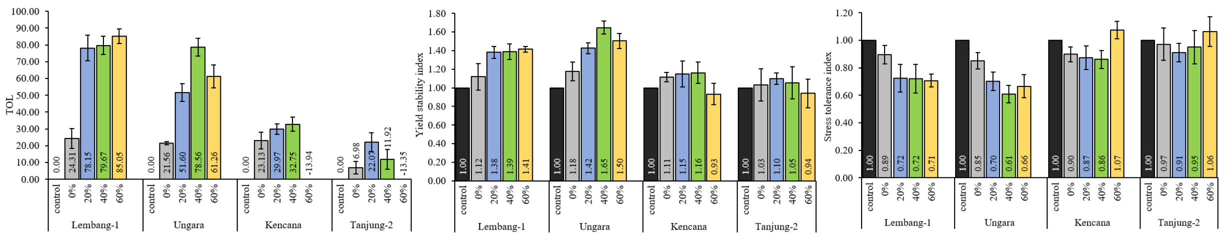
Varieties	Leaf defoliation	Fresh weight of fruit (g)		Dry weight of shoot (g)		Dry weight of roots (g)	
Lembang-1	Control	205.19	c	19.72	c	1.57	c
	0 %	229.50	b	26.83	b	2.27	bc
	20 %	283.34	a	28.12	b	2.50	b
	40 %	284.86	a	31.08	a	2.67	b
	60 %	290.24	a	32.01	a	3.77	a
Ungara	Control	121.55	d	18.47	b	1.47	c
	0 %	143.11	c	19.81	b	1.90	b
	20 %	173.15	b	20.72	b	2.01	b
	40 %	200.11	a	29.94	a	2.74	a
	60 %	182.81	b	19.33	b	2.18	b
Kencana	Control	202.71	b	22.18	b	1.14	a
	0 %	225.84	a	38.05	ab	1.23	a
	20 %	232.68	a	28.56	ab	1.31	a
	40 %	235.46	a	41.63	a	1.55	a
	60 %	188.77	b	24.81	b	1.28	a
Tanjung-2	Control	226.71	a	22.27	a	1.79	a
	0 %	233.69	a	23.87	a	1.26	a
	20 %	248.78	a	25.02	a	1.70	a
	40 %	238.63	a	22.83	a	1.56	a
	60 %	213.36	b	18.65	b	1.36	a
Sig.		*		*		*	

Note: The numbers followed by different letters in the same column and the same variety were significantly different at honestly significant difference test level at α = 5 % (*) levels.

Stress selection indices

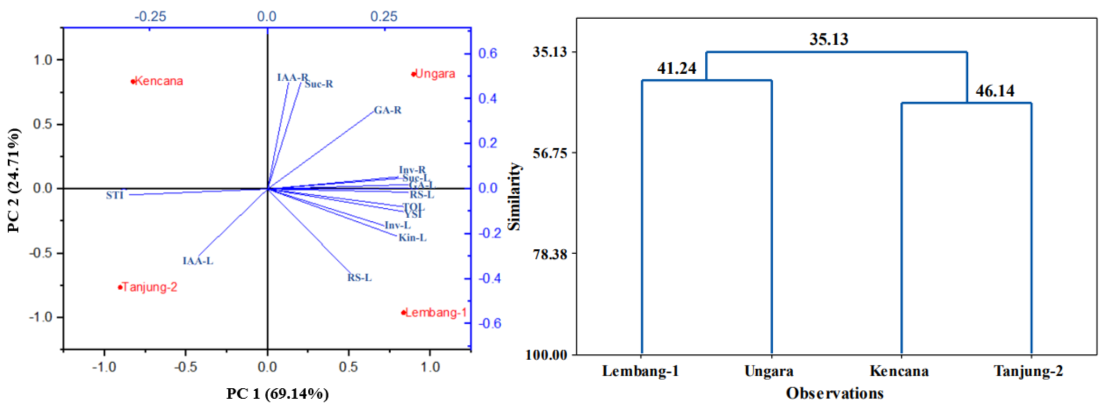
Stress selection indices on chili yield could be identified through fresh weight of fruit under leaf defoliation compared to control. Thus, root-cutting chili varieties could be identified as tolerant and intolerant to leaf defoliation. Tolerance level indicates plant adaptation under stress which can still increase fresh weight of fruit. Chili varieties with tolerance level greater than 0 indicated tolerant to leaf defoliation, while less than 0 was classified as intolerant varieties.

Lembang-1 and Ungara increased tolerance level (TOL) value 85.05 and 78.56 under 60 and 40 % leaf defoliation compared to control (**Figure 2(a)**). Lower value of TOL in Kencana and Tanjung-2 by −37.07 and −20.33 under 60 % leaf defoliation indicated high stress. The effectiveness and adaptability of plant tolerance under leaf defoliation can be evaluated through stress tolerance index (STI). An increase STI values indicates tolerant variety [38]. Chili varieties with stress tolerance index less than 1 indicated tolerant varieties, while greater than 1 was classified as intolerant to leaf defoliation. All leaf defoliation treatment on Lembang-1 and Ungara had STI values < 1 compared to control (**Figure 2(c)**). Conversely, leaf defoliation at 60 % on Kencana and Tanjung-2 resulted STI value > 1 compared to control (**Figure 2(c)**). Yield stability index (YSI) is useful for distinguishing tolerant and susceptible genotypes. Chili varieties with yield stability index greater than 1 indicated tolerant varieties, while less than 1 was classified as intolerant to leaf defoliation. Lembang-1 and Ungara had YSI values > 1 under 20, 40, 60 % leaf defoliation (**Figure 2(b)**). Kencana and Tanjung-2 had YSI value < 1 under 60 % leaf defoliation (**Figure 2(b)**). This showed that Kencana and Tanjung-2 at 60 % leaf defoliation had YSI < 1, STI > 1, TOL < 0. Conversely, Lembang-1 and Ungara had YSI > 1, STI < 1, TOL > 0 under leaf defoliation compared to control. Based on stress tolerance, Lembang-1 and Ungara were tolerant under leaf defoliation, whereas Kencana and Tanjung-2 were intolerant.



Note: The numbers presented mean ± standard error, (n = 3).

Figure 2 (a) Stress tolerant level (TOL), (b) Yield stability index (YSI), and (c) Stress tolerance index (STI), of four chili varieties planted in lowland at 19 WAT.



Note: TOL = Tolerance, STI = Stress tolerant index, YSI = Yield stability index, Suc = sucrose, AI = activity of invertase, RS = reducing sugar, IAA = indole acetic acid, GA = gibberellin, Kin = Kinetin R = root, L = leaf.

Figure 3 (a) Principal component analysis, and (b) cluster analysis based on stress selection indices and physiological activity.

Principal component and cluster analysis

The grouping of tolerant and intolerant chili varieties under leaf defoliation was determined through principal component analysis (PCA) and cluster analysis (**Figures 3(a) - 3(b)**). Analysis was conducted based on yield, stress tolerance indices, phytohormones, sucrose, invertase activity, and reducing sugar in root and shoot. PCA uses vector to reduced dimensionality of large data sets by transforming into uncorrelated principal component (PC). The main purpose was retaining variation possible, while simplifying data. Computation of principal components reduces to solution of an eigenvalue-eigenvector problem for a positive-semi-definite symmetric matrix. It is a way of identifying patterns in data, and expressing data to highlight their similarities and differences [39]. The results of principal component analysis could explain total diversity by 100 % through stress tolerance indices and physiological activity. The first component variant (PC1) contributed to 69.14 % of the total variability, and the second component variant (PCA 2) contributed to 24.71 % of the total variability. The variable that had eigenvalue (+) on PC1 such as TOL, YSI, sucrose of leaf, invertase activity of leaf, reducing sugar of leaf, gibberellin of leaf, kinetin of leaf, and invertase activity of root, while variable that had eigenvalue (-) on PC1 such as indole acetic acid of leaf and STI (**Figure 3(a)**). Based on the PC1 grouping Lembang-1 and Ungara were classified as tolerant varieties, while Tanjung-2 and Kencana as intolerant varieties under leaf defoliation. Grouping on tolerant varieties based on characters tolerance level, yield stability, sucrose, invertase activity, reducing sugar, and phytohormones. The similarity level into tolerant and intolerant group were analyzed using cluster. Tolerant varieties had similarity of 41.24 %, while intolerant had similarity of 46.14 % (**Figure 3(b)**). The similarity of 4 lowland chili varieties by 35.13 % through stress tolerance indices and physiological activity under leaf defoliation.

Dry weight of shoot and dry weight of root

Dry weight is accumulation of assimilate from photosynthesis process which is used for plant growth. The dry weight of shoot-roots in tolerant varieties under leaf defoliation had different response. The dry weight of shoot on Lembang-1 and Ungara could increase by 16.18 and 33.83 %, respectively under 60 and 40 % leaf defoliation compared to 0 % leaf defoliation. Conversely, Kencana and Tanjung-2 could reduce dry weight of shoot by 34.80 and 21.87 % under 60 % leaf defoliation compared to 0 % leaf defoliation. The dry weight of root on Lembang-1 and Ungara could increase by 39.78 and 30.65 %, respectively under 40 and 60 % leaf defoliation compared to 0 % leaf defoliation (**Table 1**). The response of tolerant varieties under leaf defoliation treatment can be shown through dry weight shoot and dry weight root increment. The increased shoot growth indicated that there was competition between vegetative and reproductive organs on assimilate demand [40].

Physiological activity in plant roots

The root regeneration mechanism of tolerant varieties under leaf defoliation through hormones and sugars. Leaf defoliation increment until 60 and 40 % in Lembang-1 and Ungara could increase invertase activity in plant roots by 26.93 and 14.41 %, respectively, and increased reducing sugar in plant roots by 59.00 and 33.82 %, respectively compared to 0 % leaf defoliation (**Table 2**). The hormones mechanism in tolerant variety under leaf defoliation in plant root through increased indole acetic acid and kinetin hormone. In Lembang-1 and Ungara, 60 and 40 % leaf defoliation could promote indole acetic acid by 26.94 and 29.71 % respectively, and increased kinetin by 36.87 and 30.79 %, respectively compared to 0 % defoliation (**Table 2**). Leaf defoliation until 60 % on intolerant varieties could decrease dry weight of root (**Table 1**) because decreased reducing sugar in root compared to 0 % leaf defoliation (**Table 2**). Leaf defoliation caused changes sugar metabolism in root on tolerant variety. Leaf defoliation increased sucrose translocation from shoot to root to provide energy for root growth. Sucrose is translocated from mesophyll to sieve element in phloem tissue, then it is transported to sink tissue through phloem loading. Sucrose in sink tissue is converted into reducing sugar by invertase activity for growth [41]. The root regeneration was influenced by endogenous hormones that contribute to plant growth and development. Root growth can be initiated through increased indole acetic acid synthesis by apical meristem and transported basipetal to root tip. This is achieved through the regulation of various cellular processes such as cell wall relaxation, cell membrane permeability, and vascular bundles differentiation [42]. On the other hand, many studies have shown that higher cytokinin promotes root growth. Cytokinin is responsible for cell elongation, increased turgor cell, and endoreduplication during cell expansion. Meanwhile, auxin is involved in cell expansion through cell wall loosening encouragement. Cell expansion in root is mainly determined by crosstalk between cytokinin and indole acetic acid as occurs in tolerant variety under leaf defoliation [43].

Table 2 Sucrose content, invertase activity, reducing sugar, and hormone content in root under leaf defoliation.

Varieties	Leaf defoliation	Sucrose ($mg\ g^{-1}$)		Invertase activity (mg protein μg^{-1} glucose)		Reducing sugar ($mg\ g^{-1}$)		Indole acetic acid ($mg\ kg^{-1}$)		Gibberellin ($mg\ kg^{-1}$)		Kinetin ($mg\ kg^{-1}$)	
Lembang-1	Control	4.53	a	5.19	c	20.49	c	4.11	c	5.03	a	1.87	c
	0 %	3.41	a	5.48	c	23.61	c	4.53	c	4.99	a	2.26	b
	20 %	4.19	a	6.07	b	33.69	bc	5.15	b	5.34	a	2.56	b
	40 %	4.14	a	6.66	b	41.38	b	5.39	b	6.39	a	3.15	a
	60 %	4.31	a	7.50	a	57.58	a	6.20	a	6.37	a	3.58	a
Ungara	Control	3.33	b	3.84	a	16.63	c	4.01	b	5.99	a	2.11	b
	0 %	5.36	a	4.10	a	26.79	bc	4.85	b	6.43	a	2.72	b
	20 %	5.70	a	4.61	a	30.25	b	4.25	b	6.56	a	3.21	ab
	40 %	6.14	a	4.79	a	40.48	a	6.90	a	6.63	a	3.93	a
	60 %	5.81	a	4.01	a	22.40	c	6.16	a	6.57	a	3.06	ab
Kencana	Control	5.26	a	3.48	a	9.65	ab	2.05	b	4.29	a	1.20	a
	0 %	4.26	a	3.32	a	9.05	ab	2.29	b	4.13	a	1.05	a
	20 %	5.87	a	3.57	a	10.15	ab	3.69	a	4.21	a	1.64	a
	40 %	5.30	a	3.78	a	11.18	a	4.26	a	4.80	a	1.96	a
	60 %	5.98	a	2.78	b	8.56	b	2.60	b	4.63	a	1.59	a
Tanjung-2	Control	2.98	a	3.76	a	10.96	ab	2.18	b	4.56	a	2.05	a
	0 %	2.64	a	3.29	a	10.85	ab	2.74	b	4.71	a	2.21	a
	20 %	3.20	a	3.81	a	11.55	a	3.96	a	4.59	a	2.22	a
	40 %	2.87	a	4.29	a	12.95	a	4.36	a	4.49	a	2.45	a
	60 %	2.37	a	3.41	a	9.86	b	2.24	b	4.56	a	2.07	a
Sig.		*		*		*		*		ns		*	

Note: The numbers followed by different letters in the same column and the same variety were significantly different at honestly significant difference test level at α = 5 % (*) levels and non-significance (ns).

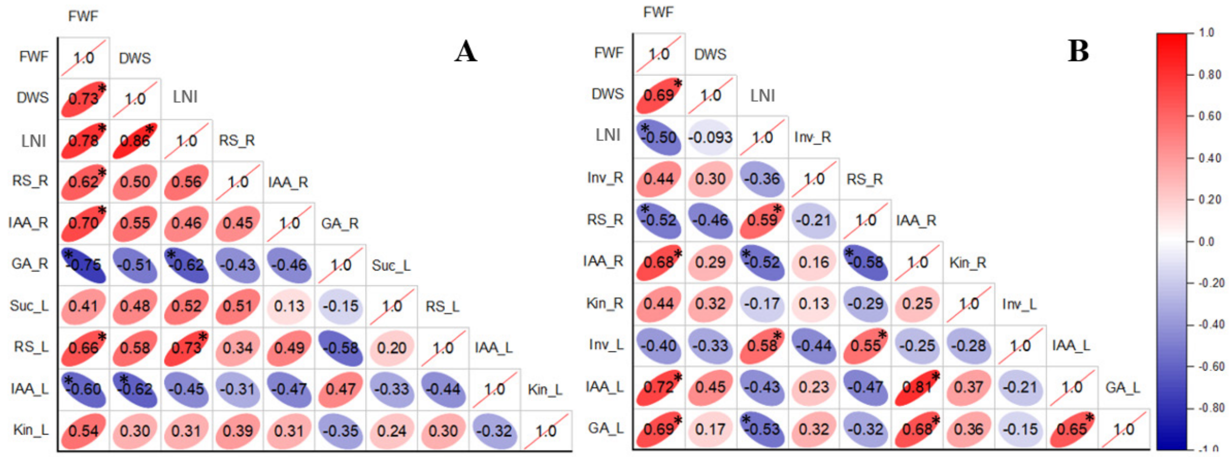
Physiological activity in plant shoot

The increased dry weight of shoot and chili yield in tolerant varieties could be associated with sugar and hormone activities. Leaf defoliation increment until 60 % in Lembang-1 and 40 % leaf defoliation in Ungara could increase sucrose by 42.18 and 49.15 %, respectively, increased invertase activity by 22.73 and 60.74 %, respectively, and increase reducing sugar by 60.23 and 40.69 %, respectively compared to 0 % leaf defoliation (**Table 3**). The hormone mechanism in shoot on tolerant variety can be seen on increasing gibberellin and kinetin. Gibberellin was found increment by 25.85 and 21.85 %, respectively under 60 and 40 % leaf defoliation in Lembang-1 and Ungara. The kinetin hormone increased by 23.30 and 25.51 %, respectively under 60 and 40 % leaf defoliation in Lembang-1 and Ungara compared to 0 % leaf defoliation (**Table 3**). The accumulation of sucrose, invertase activity, and reducing sugar increment in tolerant varieties could increase dry weight of shoot (**Table 3**). The shoot growth mechanism through changes carbon formation balance under stress condition [44]. During photosynthesis, CO_2 can be efficiently converted into 3-phosphoglyceric acid and glyceraldehyde-3-phosphate, which act as precursor for starch and sucrose biosynthesis. As much as 80 % of CO_2 is assimilated during photosynthesis and it is converted to sucrose [45]. Sucrose is dynamic process that degradation and synthesis simultaneous during stress conditions. Sucrose as soluble sugar not only serve as source metabolism and structural of cells, but also as primary messengers that control gene expression involved in biomass production, growth and metabolism [46]. Higher sucrose accumulation in tolerant varieties was associated with better plant resistance to stress condition and provides information about energy status of plant [47]. Sucrose was rapidly hydrolyzed into reducing sugar with invertase activity. In many cases, invertase activity have been confirmed to perform crucial physiological functions, such as in reproductive development, cell elongation, and stress responses. Furthermore, invertase activity are involved in cross-talk with most phytohormones, since carbohydrate metabolism is usually necessary for hormone-promoted plant development [43]. Invertase activity was associated with high sink activity [48]. Increasing invertase activity resulted higher reducing sugar in shoot. Reducing sugar is related to synthesis of secondary metabolites and signaling molecule that controls plant growth [49]. In general, lower sugar concentration in shoot promotes photosynthesis process, mobilization assimilate, and translocation assimilate, whereas higher sugar concentration promotes growth and storage carbohydrate [46]. Increasing reducing sugar can be converted to starch for shoot growth and increase shoot biomass on tolerant varieties.

Table 3 Sucrose content, invertase activity, reducing sugar, and hormone content in leaf under leaf defoliation.

Varieties	**Leaf defoliation**	**Sucrose ($mg\ g^{-1}$)**		**Invertase activity (mg protein μg^{-1} glucose)**		**Reducing sugar ($mg\ g^{-1}$)**		**Indole acetic acid ($mg\ kg^{-1}$)**		**Gibberellin ($mg\ kg^{-1}$)**		**Kinetin ($mg\ kg^{-1}$)**	
Lembang-1	Control	10.81	b	7.23	b	5.07	c	7.07	a	7.22	b	2.62	b
	0 %	11.20	b	7.48	b	9.87	b	7.51	a	7.83	b	3.72	ab
	20 %	17.53	a	8.02	b	9.34	b	8.29	a	9.26	a	4.78	a
	40 %	18.98	a	8.95	a	14.06	b	7.42	a	9.58	a	4.70	a
	60 %	19.37	a	9.68	a	24.82	a	8.33	a	10.56	a	4.85	a
Ungara	Control	12.70	c	3.55	b	6.28	b	8.99	a	7.51	b	4.24	b
	0 %	11.09	c	2.01	b	6.75	b	8.58	a	8.30	b	4.00	b
	20 %	18.48	b	3.91	b	10.54	a	8.49	a	10.19	a	4.25	b
	40 %	21.81	a	5.12	a	11.38	a	8.63	a	10.62	a	5.37	a
	60 %	13.64	c	3.52	b	7.88	b	9.47	a	8.92	b	4.24	b
Kencana	Control	7.53	b	3.82	a	4.10	b	3.68	b	5.15	b	2.81	ab
	0 %	11.14	a	3.66	a	6.44	a	5.76	a	6.58	a	3.29	a
	20 %	11.98	a	3.67	a	7.19	a	5.50	a	7.11	a	3.21	a
	40 %	12.64	a	3.39	a	7.60	a	5.25	a	6.60	a	3.81	a
	60 %	8.92	b	3.27	a	4.79	b	5.71	a	5.87	b	1.75	b
Tanjung-2	Control	13.59	b	2.53	a	4.73	b	8.70	a	6.81	b	4.26	a
	0 %	14.70	ab	3.88	a	7.91	a	7.52	a	9.68	a	4.42	a
	20 %	15.64	a	3.26	a	8.37	a	7.85	a	10.35	a	4.80	a
	40 %	13.64	b	3.37	a	6.13	ab	8.61	a	11.49	a	4.50	a
	60 %	13.03	b	2.66	a	5.91	b	8.72	a	6.99	b	4.00	a
Sig.		*		*		*		*		*		*	

Note: The numbers followed by different letters in the same column and the same variety were significantly different at honestly significant difference test level at α = 5 % (*) levels.



Note: FWF = fresh weight fruit, DWS = dry weight shoot, LNI = leaf number increment, Suc = sucrose, AI = activity of invertase, RS = reducing sugar, IAA = indole acetic acid, GA = gibberellin, Kin = Kinetin R= root, L = leaf. * indicates statistically significant correlations at $p < 0.05$. Variable displayed have correlation coefficient > 0.40 with FWF in each group.

Figure 4 Pearson correlation analysis of tolerant (a) and intolerant varieties (b).

Correlation analysis

Based on correlation analysis in the tolerant varieties showed that there was relationship between fresh weight of fruit with dry weight of shoot (r = 0.73*) and leaf number increment (r = 0.78*) (**Figure 4(a)**). The fresh weight of fruit positively related to indole acetic acid concentration of root (r = 0.70*) and reducing sugar (r = 0.62*) (**Figure 4(a)**). This showed that root growth under leaf defoliation caused by indole acetic acid and accumulation reducing sugar in root. Meanwhile, fresh weight of fruit associated with leaf reducing sugar (r = 0.66*) and indole acetic acid of leaf (r = −0.60*) (**Figure 4(a)**). The shoot growth in tolerant varieties can be associated with leaf invertase activity increment and leaf indole acetic acid decrement.

In the intolerant varieties showed that fresh weight of fruit was associated with shoot dry weight (r = 0.69*) and leaf number increment (r = −0.50*). Root regeneration positive related to indole acetic acid of root (r = 0.68*) but negative related to reducing sugar of root (r = −0.52*) (**Figure 4(b)**). The low accumulation reducing sugar of root on intolerant varieties encouraged shoot growth and chili yield. Fresh weight of fruit was positively associated with leaf indole acetic acid (r = 0.72*) and leaf gibberellin (r = 0.69*) **(Figure 4(b))**. This showed that on intolerant varieties under leaf defoliation could increase indole acetic acid and gibberellin as shoot regeneration mechanism.

Conclusions

The response of lowland root-cutting chili varieties under leaf defoliation was classified into 2 groups, namely tolerant and intolerant based on chili yield, stress selection, and physiological activity. The tolerant varieties Lembang-1 and Ungara could increase fresh weight of fruit by 29.30 and 39.26 %, respectively under 60 and 40 % leaf defoliation compared to control. The increased chili yield and root-shoot growth were due to physiological activity. Root growth was driven by increased invertase activity, reducing sugar, indole acetic acid, and kinetin hormones, while shoot growth was influenced by increased sucrose, invertase activity, reducing sugar, gibberellin, and kinetin hormone. Defoliation require more assimilates for regrowth. Compensatory re-growth occurred through synthesis of carbohydrates, allocation of assimilates, and remobilization of carbon storage compounds to recovery of photosynthetic capacity. Increased translocation of assimilates to shoot affected growth of chili fruit. It was concluded that 60 and 40 % leaf defoliation treatment were toleranted by root-cutting chili varieties of Lembang-1 and Ungara, which increased chili yield in lowland areas. The implication of this research, leaf loss until 60 % under unfavorable biotic and abiotic environmental conditions in tolerant varieties when third branching phase in lowland areas could increase chili yield. Treatment should be approached with caution for intolerant varieties like Kencana and Tanjung-2, which showed yield reduction until 9.53 and 19.64 %, respectively at high defoliation intensities. The limitation of this research used lowland environmental conditions to evaluate yield potential of root-cutting chili varieties under leaf defoliation. The lowland conditions affected reduction of chili leaves under intolerance to environment. Leaf defoliation had positive impact on tolerant chili varieties to increased chili yield in lowland areas.

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References

[1] AD Irjayanti, AS Wibowo, DA Khairunnisa, H Stiyaningsih, IM Putri, SK Areka and Z Nurfalah. *Statistics of horticulture 2022*, BPS Statistics Indonesia, Jakarta, Indonesia, 2023.

[2] R Kirana, N Carsono, Y Kusandriani and D Liferdi. Improvement of yield potency of pure line pepper with heterosis fenomenon at highland on dry season. *Jurnal Hortikultura* 2024; **24(1)**, 10-15.

[3] S Kusumaningrum, E Sulistyaningsih, R Harimurti and K Dewi. Identification of chili varieties (*Capsicum annum)* tolerance to root cutting based on stress selection indices and morphological traits planted in lowland area. *Biodiversitas* 2024; **25(5)**, 2063-2073.

[4] E Magana-Hernandez, S Zuloaga-Aguilar, R Cuevas-Guzman and JG Pausas. Variation in plant belowground resource allocation across heterogeneous landscapes: implications for post-fire resprouting. *American Journal of Botany* 2020; **107(8)**, 1114-1121.

[5] NI Zakaria, MR Ismail, Y Awang, PEM Wahab and Z Berahim. Effect of root restriction on the growth, photosynthesis rate, and source and sink relationship of chili (*Capsicum annuum* L.) grown in soilless culture. *BioMed Research International* 2020; **(1)**, 2706937.

[6] RL Darnell, HE Alvarado-Raya and JG Williamson. Root pruning effects on growth and yield of red raspberry. *HortScience* 2008; **43(3)**, 681-684.

[7] P O'brien, C Collins and RD Bei. Leaf removal applied to a sprawling canopy to regulate fruit ripening in cabernet sauvignon. *Plants* 2021; **10(5)**, 1017.

[8] K Iseki, O Olaleye and R Matsumoto. Effect of leaf thinning on shoot growth and tuber yield of white Guinea yam. *Plant Production Science* 2022; **25(1)**, 2022.

[9] N Wang, T Ji, X Liu, Q Li, K Sairebieli, P Wu, H Song, H Wang, N Du, P Zheng and R Wang. Defoliation significantly suppressed plant growth under low light conditions in two leguminosae species. *Frontiers in Plant Science* 2022; **12**, 777328.

[10] AFMS Islam, MM Haque, R Tabassum and MM Islam. Effect of defoliation on growth and yield response in two tomato (*Solanum lycopersicum* mill.) varieties. *Journal of Agronomy* 2016; **15(2)**, 68-75.

[11] Y Luo, C Zohner, TW Crowther, J Feng, G Hoch, P Li, AD Richardson, Y Vitasse and A Gessler. Internal physiological drivers of leaf development in trees: understanding the relationship between non-structural carbohydrates and leaf phenology. *Functional Ecology* 2024; **00**, 1-14.

[12] MA Raza, H Gul, F Yang, M Ahmed and W Yang. Growth rate, dry matter accumulation, and partitioning in soybean (*Glycine max* L.) in response to defoliation under high-rainfall conditions. *Plants* 2021; **10(8)**, 1497.

[13] T Liu, R Huang, T Cai, Q Han and S Dong. Optimum leaf removal increases nitrogen accumulation in kernels of maize grown at high density. *Scientific Reports* 2017; **7**, 39601.

[14] OO Aluko, C Li, Q Wang and H Liu. Sucrose utilization for improved crop yields: A review article. *International Journal of Molecular Sciences* 2021; **22(9)**, 4704.

[15] N Wang, Q Li, X Liu, S Yi, M Zhao, X Sun, H Song, X Peng, P Fan, Q Gao, Y Wang, L Yu, H

Wang, N Du and R Wang. Plant size plays an important role in plant responses to low water availability and defoliation in two woody leguminosae species. *Frontiers of Plant Science* 2021; **12**, 643143.

[16] ML Martin, L Lechner, EJ Zabaleta and GL Salerno. A mitochondrial alkaline/neutral invertase isoform (A/N-InvC) functions in developmental energy-demanding processes in Arabidopsis. *Planta* 2013; **237(3)**, 813-822.

[17] X Xu, Y Ren, C Wang, H Zhang, F Wang, J Chen, X Liu, T Zheng, M Cai, Z Zeng, L Zhou, S Zhu, W Tang, J Wang, X Guo, L Jiang, S Chen and J Wan. OsVIN2 encodes a vacuolar acid invertase that affects grain size by altering sugar metabolism in rice. *Plant Cell Reports* 2019; **38(10)**, 1273-1290.

[18] Y Klopotek, P Franken, H Klaering, K Fischer, B Hause, M Hajirezaei and U Druege. A higher sink competitiveness of the rooting zone and invertases are involved in dark stimulation of adventitious root formation in *Petunia hybrida cuttings*. *Plant Science* 2016; **243**, 10-22.

[19] L Shen, Y Qin, Z Qi, Y Niu, Z Liu, W Liu, H He, Z Cao and Y Yang. Genome-wide analysis, expression profile, and characterization of the acid invertase gene family in pepper. *International Journal of Molecular Sciences* 2019; **20(1)**, 15.

[20] N Wang, M Zhao, Q Li, X Liu, H Song, X Peng, H Wang, N Yang, P Fan, R Wang and N Du. Effects of defoliation modalities on plant growth, leaf traits, and carbohydrate allocation in *Amorpha fruticosa* L. and *Robinia pseudoacacia* L. seedlings. *Annals of Forest Science* 2020; **77**, 53.

[21] N Hoidal, S Jacobsen, A Odone and G Alandia. Defoliation timing for optimal leaf nutrition in dual-use amaranth production systems. *Journal of the Science of Food and Agriculture* 2020; **100(13)**, 4745-4755.

[22] I Cisneros-Hernandez, E Vargas-Ortiz, ES Sanchez-Martinez, N Martinez-Gallardo, D Soto Gonzalez and JP Delano-Frier. Highest defoliation tolerance in *Amaranthus cruentus* plants at panicle development is associated with sugar starvation responses. *Frontiers Plant Science* 2021; **12**, 658977.

[23] NA Khan, M Khan, HR Ansari and Samiullah. Auxin and defoliation effects on photosynthesis and ethylene evolution in mustard. *Scientia Horticulturae* 2002; **96(1)**, 43-51.

[24] JP Ferreira, DM Marques, D Karam, E Borghi, PC Magalhaes, KRDD Souza, SD Arantes and TCD Souza. How does early defoliation influence the morphophysiology and biochemical characteristics of maize? *Plant Growth Regulator* 2024; **103**, 747-761.

[25] Y Sakashita, H Kurashima, M Fukuda, H Hirano, S Lamsal, N Katayama and T Fukao. Possible roles of carbohydrate management and cytokinin in the process of defoliation–regrowth cycles in rice. *International Journal of Molecular Science* 2024; **25(10)**, 5070.

[26] SIH Putri and M Fitriana. Growth and yield of green eggplant applied to various compositions of growing media. *Journal of Suboptimal Lands* 2023; **12(2)**, 139-151.

[27] RA Fischer and R Maurerac. Drought resistance in spring wheat cultivars grain yield responses. *Australian Journal of Agricultural Research* 1978; **29(5)**, 897-912.

[28] ESH Dewi, P Yudono, ETS Putra and BH Purwanto. Physiological and biochemical activities of cherelle wilt on three cocoa clones (*Theobroma cacao*) under two levels of soil fertilities. *Biodiversitas* 2020; **21(10)**, 187-194.

[29] Miswar, B Sugiharto, T Handoyo and SA Made. The role of sucrose phosphate synthase (SPS) and acid invertase (AI) in sugarcane (Saccharum officinarum L.) in sucrose accumulation. *Jurnal Ilmu-Ilmu Pertanian* 2007; **26(4)**, 187-193.

[30] GL Miller. Use of dinitrosalicylic acid reagent for determination of reducing sugar. *Analytical Chemistry* 1959; **31(3)**, 426-528.

[31] M Arai, H Mori and H Imaseki. Roles of sucrose-metabolizing enzymes in growth of seedlings. Purification of acid invertase from growing hypocotyls of mung bean seedlings. *Plant and Cell Physiology* 1991; **32(8)**, 1291-1298.

[32] HF Linskens and JF Jackson. *High performance liquid chromatography in plant sciences*. Springer Nature, Berlin, Germany, 1987.

[33] S Das, KW Sultana and I Chandra. *In vitro* micropropagation of *Basilicum polystachyon* (L.)

Moench and identification of endogenous auxin through HPLC. *Plant Cell, Tissue and Organ Culture* 2020; **141**, 633-641.

[34] TL Olatunji and AJ Afolayan. The suitability of chili pepper (*Capsicum annuum* L.) for alleviating human micronutrient dietary deficiencies: A review. *Food Science and Nutrients* 2018; **6(8)**, 2239-2251.

[35] N Iqbal, A Masood and NA Khan. Analyzing the significance of defoliation in growth, photosynthetic compensation and source-sink relations. *Photosynthetica* 2012; **50(2)**, 161-170.

[36] LFM Marcelis and E Heuvelink. *Concepts of modelling carbon allocation among plant organs*. Springer Natrue, Dordrecht, Netherlands, 2007.

[37] J Mariyono and S Sumarno. Chilli production and adoption of chili-based agribusiness in Indonesia. *Journal of Agribusiness in Developing and Emerging Economies* 2015; **5(1)**, 57-75.

[38] K Lamba, M Kumar, V Singh, L Chaudhary, R Sharma, S Yashveer and MS Dalal. Heat stress tolerance indices for identification of the heat tolerant wheat genotypes. *Scientific Reports* 2023; **13**, 10842.

[39] SP Mishra, U Sarkar, S Taraphder, S Datta, DP Swain, R Saikhom, S Panda and M Laishram. Principal component analysis. *International Journal of Livestock Research* 2017; **7(5)**, 60-77.

[40] A Rosati, A Paoletti, RA Hariri, A Morelli and F Famiani. Resource investments in reproductive growth proportionately limit investments in whole-tree vegetative growth in young olive trees with varying crop loads. *Tree Physiology* 2018; **38(9)**, 1267-1277.

[41] CH Foyer and MJ Paul. *Source-sink relationships*. Rothamsted Research, Harpenden, 2001.

[42] J Li, Y Guan, L Yuan, J Hou, C Wang, F Liu, Y Yang, Z Lu, G Chen and S Zhu. Effects of exogenous IAA in regulating photosynthetic capacity, carbohydrate metabolism and yield of *Zizania latifolia*. *Scientia Horticulturae* 2019; **253**, 276-285.

[43] X Wang, S Wang, Y Xue, X Ren, J Xue and X Zhang. Defoliation, not gibberellin, induces tree peony autumn reflowering regulated by carbon allocation and metabolism in buds and leaves. *Plant Physiology and Biochemistry* 2020; **151**, 545-555.

[44] Y Li, H Sun, TDP Protasio, PRG Hein and B Du. The mechanisms and prediction of non-structural carbohydrates accretion and depletion after mechanical wounding in slash pine (*Pinus elliottii*) using near-infrared reflectance spectroscopy. *Plant Methods* 2022; **18**, 107.

[45] W Liu, J Su, S Li, X Lang and X Huang. Non-structural carbohydrates regulated by season and species in the subtropical monsoon broad-leaved evergreen forest of Yunnan province, China. *Scientific Reports* 2018; **8**, 1083.

[46] RM Rosa, C Prado, G Podazza, R Interdonato, JA Gonzalez, M Hilal and FE Prado. Soluble sugars-metabolism, sensing and abiotic stress, review. *Plants Signaling & Behavior* 2009; **4(5)**, 388-393.

[47] A Thomas, R Beena, G Laksmi, KB Soni, A Swapna and MW Viji. Changes in sucrose metabolic enzymes to water stress in contrasting rice genotypes. *Plant Stress* 2022; **5**, 100088.

[48] SS Sung, WJ Sheih, DR Geiger and CC Black. Growth, sucrose synthase, and invertase activities of developing *Phaseolus vulgaris* L. fruits. *Plant, Cell and Environment* 1994: **17(4)**, 419-426.

[49] N Fabregas and AR Fernie. The interface of central metabolism with hormone signaling in plants. *Current Biology* 2021; **31(23)**, 1535-1548.