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Tolerance of *Capsicum frutescens* L. (Solanales: Solanaceae) to the duration of waterlogging and impact on the post-waterlogging and recovery periods

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Abstract - Waterlogging is a shallow flooding in the area of the root and in some parts of the shoot. It is one of the most common types of flooding in agricultural areas. The duration of waterlogging affects plant growth and yield in response to stress by interacting with their ability to adapt. Plant adaptability during waterlogging affects their resilience to post-waterlogging and recovery conditions. In this research, we examined the tolerance of *Capsicum frutescens* to short (1 day), medium (3 days) and long (10 days) duration of waterlogging, as well as its implications on post-waterlogging, recovery, reproductive phase and harvest. Adaptability and growth rates were used to determine plant tolerance to waterlogging stress. The percentage of wilting, root damage, survival, stomatal response, formation of hypertrophic lenticels, adventitious roots, photosynthetic pigment content, height, leaf number, plant biomass, flower number, and fruit fresh weight were used to measure adaptability and growth. The results showed that a longer duration of waterlogging increased root damage and decreased plant growth, affecting photosynthetic pigment content, leaf number, root and shoot biomass. The ability to regulate the stomata opening, the formation of hypertrophic lenticels and adventitious roots enabled plants not to wilt permanently, surviving post-waterlogging conditions and during recovery, growing during reproductive phase and producing yields. The critical duration of waterlogging at the beginning of the vegetative phase occurred at 10 days, and pepper suffered a drastic reduction in vegetative and reproductive growth and yields. The maintenance of the root system and the development of adaptive mechanisms increased plant survival, thereby affecting yield.

Keywords: adventitious, flooding, hypertrophic lenticels, reproductive growth, vegetative growth.

Riassunto - Tolleranza di *Capsicum frutescens* L. (Solanales: Solanaceae) alla durata del ristagno idrico e impatto sui periodi di post-ristagno idrico e di recupero.

Il ristagno idrico (*waterlogging*) è un tipo di allagamento superficiale nella zona delle radici e in alcune parti del fusto. È uno dei tipi più comuni di allagamento nelle aree agricole. La durata del ristagno idrico influenza la crescita delle piante e la resa in risposta allo stress, interagendo con la loro capacità di adattamento. L'adattabilità delle piante durante il ristagno idrico influisce sulla loro capacità di riprendersi dopo l'allagamento e durante il periodo di recupero. In questa ricerca, abbiamo esaminato la tolleranza di *Capsicum frutescens* a brevi (1 giorno), medie (3 giorni) e lunghe (10 giorni) durate del ristagno idrico, nonché le implicazioni sul periodo di recupero dopo l'allagamento, sulla fase riproduttiva e sulla raccolta. Sono stati utilizzati tassi di crescita e adattabilità per determinare la tolleranza delle piante allo stress da ristagno idrico. La percentuale di appassimento, danni alle radici, sopravvivenza, risposta stomatica, formazione di lenticelle ipertrofiche, radici avventizie, contenuto di pigmenti fotosintetici, altezza, numero di foglie, biomassa delle piante, numero di fiori e peso fresco dei frutti sono stati utilizzati per misurare l'adattabilità e la crescita. I risultati hanno mostrato che una durata più lunga del ristagno idrico aumentava i danni alle radici e riduceva la crescita delle piante, influenzando il contenuto di pigmenti fotosintetici, il numero di foglie, la biomassa delle radici e del fusto. La capacità di regolare l'apertura degli stomi, la formazione di lenticelle ipertrofiche e radici avventizie ha consentito alle piante di non appassire permanentemente, sopravvivendo alle condizioni post-allagamento e durante il recupero, crescendo durante la fase riproduttiva e generando rese. La durata critica del ristagno idrico all'inizio della fase vegetativa è stata di 10 giorni, e il peperoncino ha subito una drastica riduzione della crescita vegetativa e riproduttiva e delle rese. Il mantenimento del sistema radicale e lo sviluppo di meccanismi adattativi hanno aumentato la sopravvivenza delle piante, influenzandone quindi la resa.

Parole chiave: avventizio, allagamento, lenticelle ipertrofiche, crescita riproduttiva, crescita vegetativa.

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INTRODUCTION

High rainfall causes groundwater availability to exceed plants requirements, when they are flooded. Therefore, flooding is a soil condition of water saturation. Waterlogging is one of the most common types of flooding in agricultural areas (Kaur *et al*., 2020). It is a shallow flooding in the area of the root and in some parts of the shoot (Ahmed *et al*., 2013; Fukao *et al*., 2019). Sasidharan *et al*. (2017) also stated that waterlogging is a type of flooding, occurring when there is a flooding in the area or a shallow flooding of the soil, resulting in the root system being inundated. The other types of flooding are partial submergence and submergence. This type of flooding results in poor oxygen diffusion to the roots, leading to hypoxia and more severe anoxic conditions (Herzog *et al*., 2016). The limited O_2 supplied to the roots results in aerobic respiration to turn into anaerobic respiration, with low ATP production (Ploschuk *et al*., 2018). The result is a decrease in the root function to absorb water and nutrients toward the shoot (Tong *et al*., 2021). The accumulation of ethylene and carbon dioxide during waterlogging also causes root damage, decreased aquaporin activity and root hydraulic conductance, thereby inhibiting root functions (Shaw *et al*., 2013; Voesenek & Bailey-Serres, 2015). Root malfunction causes leaves wilt and fall, damages chlorophyll thus reducing photosynthesis rate, and impacts vegetative growth, reproduction and crop yields in the future (Ploschuk *et al*., 2018).

Plant species (or cultivar) tolerance to waterlogging includes: the formation of adventitious roots equipped with aerenchyma structures, the formation of hypertrophic lenticels, the regulation of stomatal opening, the regulation of damage levels, the regulation of leaf chlorophyll content and antioxidant activity (Anee *et al*., 2019; Sharma *et al*., 2021; Ploschuk *et al*., 2018). Adventitious roots replace damaged ones, while aerenchyma can increase roots internal aeration until sufficient O_2 becomes available during waterlogging (Yamauchi *et al*., 2014; Zhang *et al*., 2015). The appearance of adventitious and aerenchyma roots as a response to waterlogging is shown in *Glycine max* (L.) Merr. (Ploschuk *et al*., 2022), *Nicotiana tabacum* L. (Al Habib *et al*., 2022), and *Momordica charantia* L. (Peng *et al*., 2020). Hypertrophic lenticels formation enhances internal root aeration in the stems (Yamauchi *et al*., 2013). The formation of hypertrophic lenticels is reported to occur in *Distylium chinense* (Franch. ex Hemsl.) Franch. ex Diels (Liu Z. *et al*., 2014), *Cajanus cajan* (L.) Millsp. (Hingane *et al*., 2015) and *Ormosia arborea* (Vell.) Harms (Junglos *et al*., 2018). Plant tolerance to decreased root function is carried out by closing the stomata until the plant withers (Bashar *et al*., 2019; Purnobasuki *et al*., 2021). Waterlogging also accumulates reactive oxygen species (ROS), resulting in membrane damage and chlorophyll degradation (Ren *et al*., 2016). Tolerant plants increase antioxidant activity, avoid oxidative damage and maintain chlorophyll content (Bansal *et al*., 2019). In *Sorghum bicolor* (L.) Moench, the increasing of the antioxidant system activity during waterlogging increases grana number and maintains leaf chlorophyll content (Zhang R.D. *et al*., 2019).

Capsicum frutescens L. is one of the most economically important cultivated plants in Indonesia (Yamamoto *et al*., 2013), because of its use as a raw material for medicines, cosmetics, pigments, and food (Sinaga, 2020). The bioactive compounds include flavonoids, capsaicinoids, phenolics, and several organic acids such as malic, citric, and ascorbic contained in pepper (Wijaya *et al*., 2020). Several cultivars are grown in Indonesia, such as Bara, Pelita I, Siung, Carica, Taruna, and Batari. *C. frutescens* grows well in soils with low water content (Sinaga, 2020), but it is generally cultivated during both dry and rainy seasons, due to the high market demand, which mainly occurs during religious festivals.

Climate change, prolonged high rainfall, and poor drainage cause waterlogging in growing areas (Manik *et al*., 2019). In Indonesia, extreme weather conditions and intense rainfall, which can occur from December to late February, cause flooding in pepper cultivation centers, including West Java, East Java, South Kalimantan, North Sumatra, West Sumatra, Central Sulawesi, West Kalimantan, Yogyakarta and Jambi (Sukarman & Purwanto, 2018). Waterlogging in pepper cultivation areas causes crops damage and harvest failure (Prasad & Chakravorty, 2015). Waterlogging conditions can occur during the early vegetative, late vegetative, reproductive, and harvest phases and can affect crops for a variable duration, threatening the productivity of *C. frutescens.* In riverine areas, flooding can submerge farmlands for several days, seriously affecting the local communities and damaging crops (including *C. frutescens*), houses, public facilities and social and economic activities, as in the case of the Bengawan Solo River (Java Island) with its annual floods (Rustinsyah *et al*., 2021). Waterlogging also occurs in peatlands of Kalimantan, Papua and Sumatra, where, among others, *C. frutescens* is grown (Sakuntaladewi *et al*., 2022).

The response and tolerance of plants to waterlogging depend on several factors: the susceptibility of the species or cultivar, the phase of development during waterlogging, and the duration of waterlogging (de San Celedonio *et al*., 2014). Based on the decrease in stomatal conductance and photosynthetic rate under waterlogging conditions, *C. frutescens* is more tolerant than *C. chinense* (Ou & Zou, 2012). Waterlogging for 24 *C. frutescens* cv. Pelita F1 h in the late vegetative phase of does not reduce growth, but causes damage to the root tips and decreases photosynthetic pigment content (Raras *et al*., 2021). According to Insani *et al*. (2021), increased duration of waterlogging during the early vegetative phase, decreases growth, and delays flower bud formation of *C. annuum*. Martínez-Acosta *et al*. (2020) reported that flooding *C. annuum* 20 days after planting impairs stomatal conductance, photosynthetic rate and transpiration, with significant effects occurring with submergence 120 days after planting. These studies had not included the adaptability of plants during waterlogging and their impact on plant resilience during post-waterlogging, recovery, reproductive and harvest phases. Plant tolerance to waterlogging stress includes their response after waterlogging and recovery period (Ploschuk *et al*., 2017). Since the adaptability of *C. frutescens* to waterlogging has not been widely reported, this study examines the tolerance of *C. frutescens* cv. Carica to the duration of waterlogging in the early vegetative phase, including adaptation during waterlogging, plant growth response in post-waterlogging, recovery, reproductive and harvest phases.

MATERIALS AND METHODS

Place and plant materials

The study was conducted in a greenhouse in East Ungaran (Semarang, Central Java, Indonesia) from July to November 2020. Observations of anatomical parameters were made at the Plant Structure and Function Laboratory, Department of Biology, Diponegoro University in Semarang. Photosynthetic pigment content was measured at the Integrated Laboratory, Diponegoro University. The plant material used in this study – *C. frutescens* cv. Carica seeds – were obtained from PT Trubus in Semarang. These seeds were later used in a germination experiment.

Treatments

C. frutescens seeds were soaked in water for approximately 12 hours, then spread in a bamboo container and kept moist until germination. Germinated seeds were then transferred to polybags (12×11 cm) containing a mixture of sand and compost (1:1 by vol.) until the seedling grew (32 days after planting - DAP). The seedlings were selected according to their uniformity of appearance and then transferred to treatment pots of 15 cm (height) × 20 cm (diameter), which were filled with planting media, a mixture of soil, sand, and compost (1:1:1 by vol.). Each treatment pot was added 2 g of NPK as the basic fertilizer (32-10-10) and 1 g of carbofuran to prevent infestations. Furthermore, plants were watered every day, and added 1 g of NPK fertilizer follow-up per pot once a week; plants were also sprayed with insecticides once a week.

Waterlogging treatment was applied in the early vegetative phase, when the plants were 40 days old. The hole in the bottom of the plastic pot was clogged with Dacron® to prevent leakage of the planting media during waterlogging. Also, treatment pots and pepper plants were placed in a plastic container of 30 cm (height) × 50 cm (diameter) and flooded with water, up to ±5 cm above the soil surface. The waterlogging treatment consisted of short-duration waterlogging (1 day), medium-duration waterlogging (3 days) and long duration waterlogging (10 days). The control group were plants that were not waterlogged. All treatments were dried by removing the Dacron® plug in the pots after the waterlogging period. Maintenance and watering were continued during the recovery period, 30 days after the longest duration of waterlogging. The reproductive phase began 10 days after the end of the recovery period, and fruit was harvested 31 days after the end of the recovery phase. In each treatment, 30 plant samples were used to measure various growth and productivity parameters. The research used a completely randomized design, with a single treatment being the duration of waterlogging.

Morphology and plant survival

The percentage of permanent wilting (plants wilted/whole plants), the visual percentage of root damage (damaged roots/total roots), the formation of hypertrophic lenticels and adventitious roots, and the percentage of survival (live plants/total plants) were measured as morphological and survival parameters. These measurements were taken after waterlogging (AW) and at the end of the recovery period (ER).

Stomata anatomy

The anatomy of stomata was used to determine the opening or closing of stomata pores after waterlogging and at the end of the recovery period. A thin incision was made on the underside of the marked leaf and then was fixed with 70% (v/v) ethylic alcohol and immersed in 1% safranin (aqueous solution). The preparation was closed in a microscope slide with 1% (v/v) glycerin and a cover glass. Observation of stomata anatomy was performed with a microscope (CX23, Olympus, Japan) connected to an advanced optical camera (OptiLab Miconos, Indonesia) and a laptop computer. Data were analyzed descriptively.

Content of Photosynthetic Pigments

The content of photosynthetic pigments included chlorophyll a, chlorophyll b, and carotenoids. Content measurements were carried out after waterlogging and at the end of the recovery period. Marked leaf samples were cleaned, then 0.1 g of leaf fragments were extracted with acetone at a concentration of 80 % (v/v). The sample was filtered, and the filtrate was measured for absorbance using a spectrophotometer (Hitachi Double Beam Spectrophotometer UH5300, Japan) at 663, 646 and 470 nm. The content of photosynthetic pigments (mg g^{-1} FW) was calculated using the formula of Wellburn (1994):

$$\text{Chlorophyll a (Ca)} = 12.21 \times (A663) - 2.81\,(A646)$$

$$\text{Chlorophyll b (Cb)} = 20.13 \times (A646) - 5.03\,(A663)$$

$$\text{Carotenoids (C)} = \frac{[(1000 \times A470) - (3.27 \times Ca) - (104 \times Cb)]}{198}$$

$$\text{Total chlorophyll} = [12.21 \times (A663) - 2.81 \times (A646)] + [20.13 \times (A646) - 5.03 \times (A663)]$$

Growth

Growth measurements included plant height, leaf number, and biomass before and after waterlogging and at the end of the recovery period. Growth patterns of plant height and leaf number were monitored every week (R1, R2, R3 and R4) during the recovery period. Root length and leaf area were determined at the end of the recovery period. The root length was determined by measuring the longest lateral root (Liu C. *et al*., 2020). The five largest leaves in each sample were chosen to calculate the total leaf area, using the Montgomery formula (Ren *et al*., 2016): leaf area = $L \times W \times 0.75$, where L is leaf length and W is leaf width. The number of flowers and fruit fresh weight were recorded during the reproductive phase and after harvest, respectively.

Statistical Analysis

After waterlogging, recovery, reproduction, and harvest, plant response was analyzed by regression analysis. A paired t-test was used to determine the differences in plant response after waterlogging and recovery period for each treatment (Fig. 1). All statistical tests were performed with SPSS 25.0 (SPSS, Chicago, USA) with a significance level of $p < 0.05$.

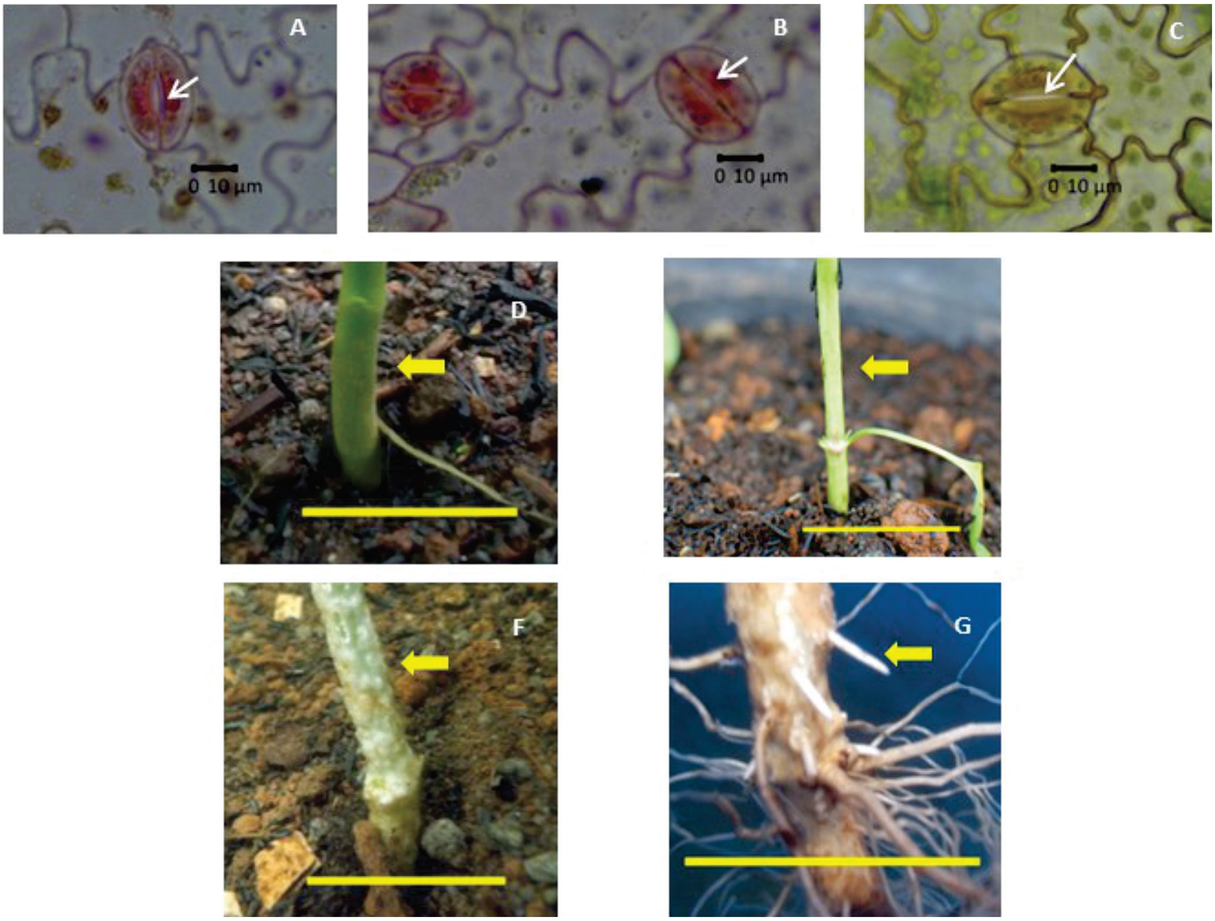

Fig. 1 - Plant response after waterlogging and the end of the recovery period. Stomata opened at the control (A), stomata closed after waterlogging AW (B), stomata opened at ER (C), there was no hypertrophic lenticels formation at the control (D), a whitish color marked the early formation of hypertrophic lenticels after waterlogging AW at the base of the stems that were flooded for three days (E), the development of hypertrophic lenticels on the seventh day of waterlogging (F), and adventitious root formation on the ninth day of waterlogging (G). The scale bars (yellow line) in D, E, F, and G are 5 cm. / Risposta delle piante dopo il ristagno d'acqua e alla fine del periodo di recupero. Gli stomi si sono aperti al controllo (A), gli stomi si sono chiusi dopo il periodo di ristagno idrico AW (B), gli stomi si sono aperti ER (C), non c'è stata formazione di lenticelle ipertrofiche al controllo (D), il colore biancastro ha indicato la formazione precoce di lenticelle ipertrofiche dopo il periodo di ristagno idrico AW alla base degli steli sommersi per tre giorni (E), lo sviluppo di lenticelle ipertrofiche al settimo giorno di ristagno idrico (F) e la formazione di radici avventizie al nono giorno di ristagno idrico (G). Le barre di scala (linea gialla) in D, E, F e G sono di 5 cm.

RESULTS

Morphology, stomata opening, and survival

The waterlogging duration influenced plant morphology, stomata opening, and survival (Tab. 1). Initial root damage occurred after a short waterlogging duration (1 d), reaching 2.6%. The root damage was characterized by the rotting of the root tip that radiates toward the base. The percentage of root damage increased with the increase in the waterlogging duration. Damage reached 88% with a longer waterlogging duration (10 d). The stomata pores visible on the anatomical preparations closed after waterlogging treatment, while they remained open in the control plants (no waterlogging). Plant adaptations included the formation of hypertrophic lenticels and the appearance of adventitious roots in medium- and long-term flooding. Hypertrophic lenticels began to appear 3 days after flooding, as evidenced by a whitish color of the surface of the flooded stems. Ripe hypertrophic lenticels formed on day 7, and adventitious roots formed on day 9. Root damage and stomata closure at all waterlogging durations were not followed by permanent wilting. At the end of the recovery period, no permanent wilting occurred, and all plants survived in all treatments.

Photosynthetic pigment content

Generally, the content of chlorophyll and carotenoid pigments decreased at AW as the duration of waterlogging increased (Fig. 2). Waterlogging reduced the content of photosynthetic pigments. At ER, there was an increase in chlorophyll and carotenoid content in all treatments. The histogram in Figure 3 shows that the highest increase in chlorophyll and carotenoids occurred in day 10 of waterlogging treatment. There was no significant increase in carotenoid content at days 1 and 3 of flooding.

Tab. 1 - Morphology, stomatal opening, and survival after waterlogging (AW) and at the end of the recovery period (ER). / Morfologia, apertura stomatica e sopravvivenza dopo il ristagno idrico (AW) e alla fine del periodo di recupero (ER).

Duration of waterlogging	Plant response	AW	ER
Control/not waterlogging	Wilting permanently	0%	0%
	Root damage	0%	0%
	Porus stomata	Open	Open
	Hypertrophied lenticels	Not formed	-
	Adventitious root	Not formed	-
	Survival	100%	100%
1 day	Wilting permanently	0%	0%
	Root damage	2,6% ± 0,9%; root tip transparent and wilting	0%
	Porus stomata	Close	Open
	Hypertrophied lenticels	Not formed	-
	Adventitious root	Not formed	-
	Survival	100%	100%
3 days	Wilting permanently	0%	0%
	Root damage	71% ± 4,2%; some root tips rot and break	0%
	Porus stomata	Close	Open
	Hypertrophied lenticels	Early formation	-
	Adventitious root	Not formed	-
	Survival	100%	100%
10 days	Wilting permanently	0%	0%
	Root damage	88% ± 2,7%; some of the root tips rot and were damaged	0%
	Porus stomata	Close	Open
	Hypertrophied lenticels	formed on the 7th day	-
	Adventitious root	formed on the 9th day	-
	Survival	100%	100%

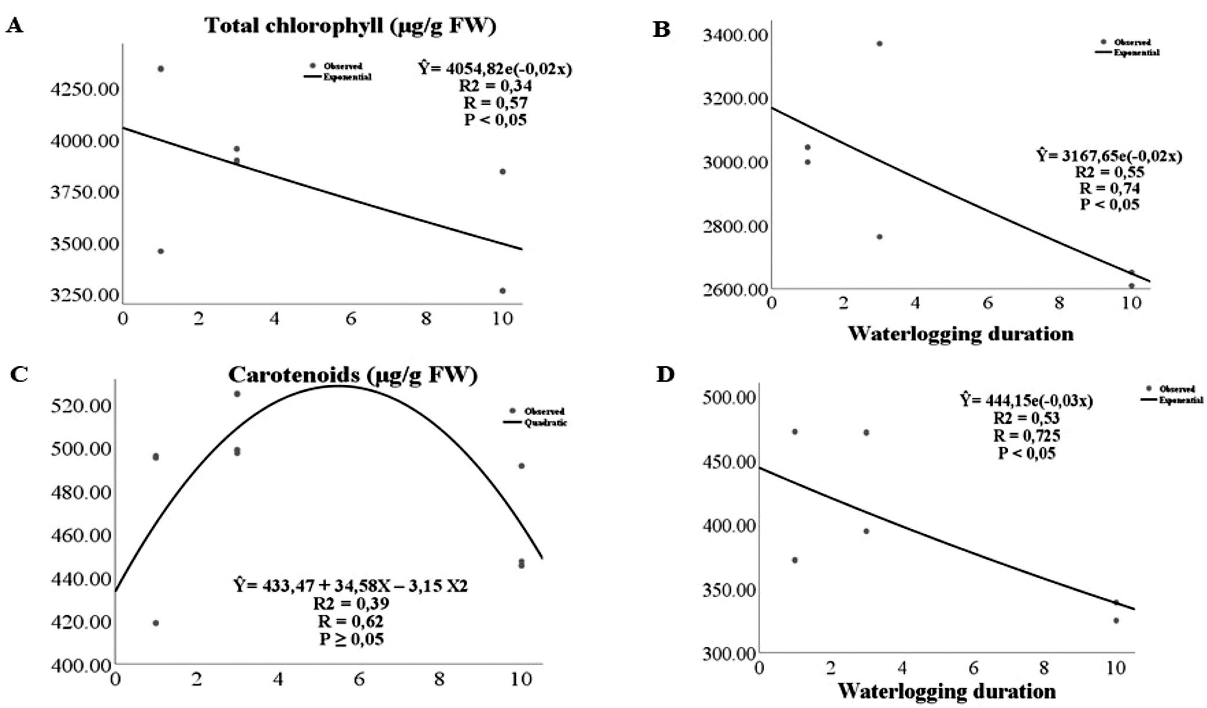

Fig. 2 - Relationship between total chlorophyll and carotenoid content with waterlogging duration. Measurements were made after the flooding ended. Total chlorophyll in control (not waterlogging) (A), and waterlogging duration treatment (B). Carotenoid content in control (C), and the treatment with increasing waterlogging duration (D). / Relazione tra il contenuto di clorofilla totale e carotenoidi con la durata del ristagno idrico. Le misurazioni sono state effettuate dopo la fine del periodo di allagamento. Clorofilla totale nel controllo (senza ristagno d'acqua) (A) e nel trattamento con l'aumento della durata del ristagno idrico (B). Contenuto di carotenoidi nel controllo (C) e nel trattamento con l'aumento della durata del ristagno idrico (D).

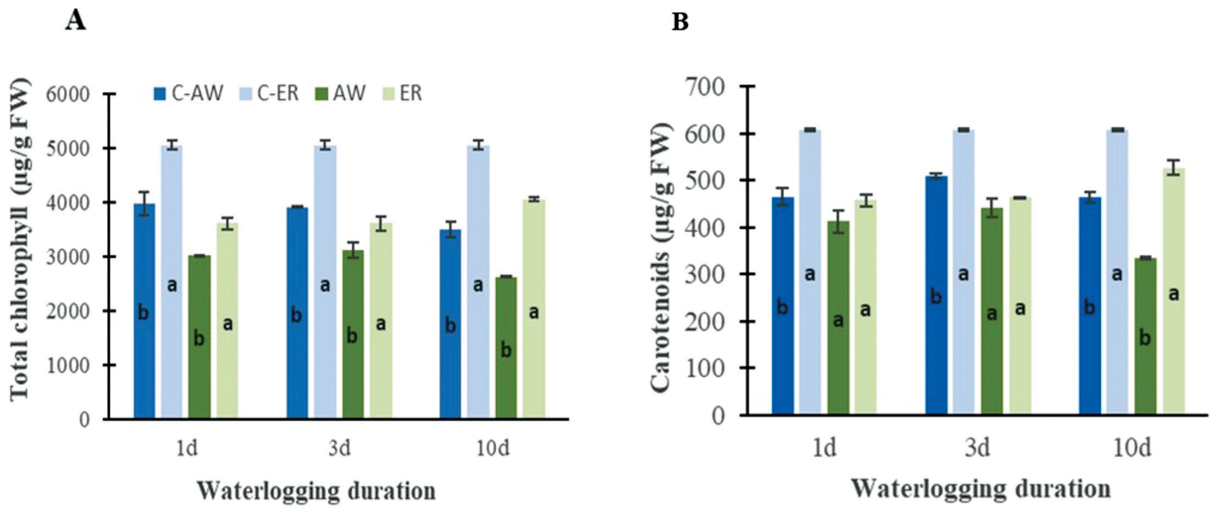

Fig. 3 - The content of total chlorophyll (A) and carotenoids (B) after waterlogging and the end of the recovery period. Means and standard errors were based on five replications. Bars with different letters under the same category indicated a significant difference ($p \leq 0,05$) with a paired t-test. C-AW: control after waterlogging, C-ER: control of the end recovery period, AW: after waterlogging, ER: the end of the recovery period. / Contenuto di clorofilla totale (A) e carotenoidi (B) dopo il ristagno idrico e al termine del periodo di recupero. Le medie e gli errori standard si basano su cinque repliche. Le barre con lettere diverse sotto la stessa categoria indicano una differenza significativa ($p \leq 0,05$) con un t-test a coppie. C-AW: controllo dopo il ristagno idrico, C-ER: controllo alla fine del periodo di recupero, AW: dopo il ristagno idrico, ER: alla fine del periodo di recupero.

Plant growth

Plant height showed an increasing pattern after waterlogging. In the 1-day waterlogging treatment (W-1d), the increase occurred 9 days after the end of waterlogging; the 3-days waterlogging treatment (W-3d) showed an apparent increase in the R1 period, and in the 10-days waterlogging treatment (W-10d) it occurred in the R2 period (Fig. 4). The pattern of increasing leaf number at W-1d occurred 9 days after waterlogging ended, at W-3d occurred in the R2 period, and at W-10d decreased towards the end of waterlogging but increased in the R3 period. The growth pattern in all waterlogging treatments remained under control until the end of the recovery period (Fig. 4). The lowest growth pattern of plant height and leaf number was found in the 10-day waterlogging treatment (W-10d).

The increased duration of waterlogging reduced shoot and root biomass, but this condition did not occur in the control group (Fig. 5). Here, there was a significant increase in shoot and root biomass after the recovery period (ER). The lowest increment occurred in the 10-day waterlogging treatment (Fig. 6).

Total leaf area and root length increased exponentially as the recovery duration increased. The lowest total leaf area and root length were found in 10-day waterlogging treatment with a recovery duration of 30 days. The highest was found in 1-day waterlogging with a recovery duration of 39 days (Fig. 7A-B). Flower number and fresh fruit weight also increased along with the increase in reproductive period and harvest (Fig. 7C-D).

DISCUSSION

Plant tolerance to flooding stress is the overall response of plants during flooding and during recovery period (Striker, 2012). Plant adaptation during waterlogging and

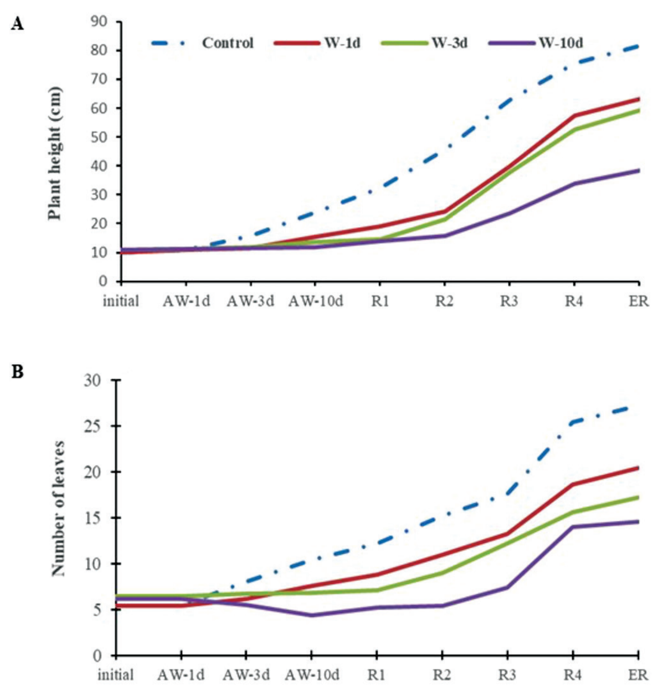

Fig. 4 - The pattern of plant height (A) and number of leaves (B) during waterlogging and recovery period. Initial: before waterlogging treatment, AW-1d: after waterlogging one day, AW-3d: after waterlogging three days, AW-10d: after waterlogging ten days, R1: one-week recovery period, R2: two-week recovery period, R3: three-week recovery period, R4: four-week recovery period, ER: end of the recovery period. / Andamento dell'altezza delle piante (A) e del numero di foglie (B) durante il periodo di ristagno idrico e di recupero. Iniziale: prima del trattamento di ristagno idrico, AW-1d: dopo un giorno di ristagno idrico, AW-3d: dopo tre giorni di ristagno idrico, AW-10d: dopo dieci giorni di ristagno idrico, R1: periodo di recupero di una settimana, R2: periodo di recupero di due settimane, R3: periodo di recupero di tre settimane, R4: periodo di recupero di quattro settimane, ER: fine del periodo di recupero.

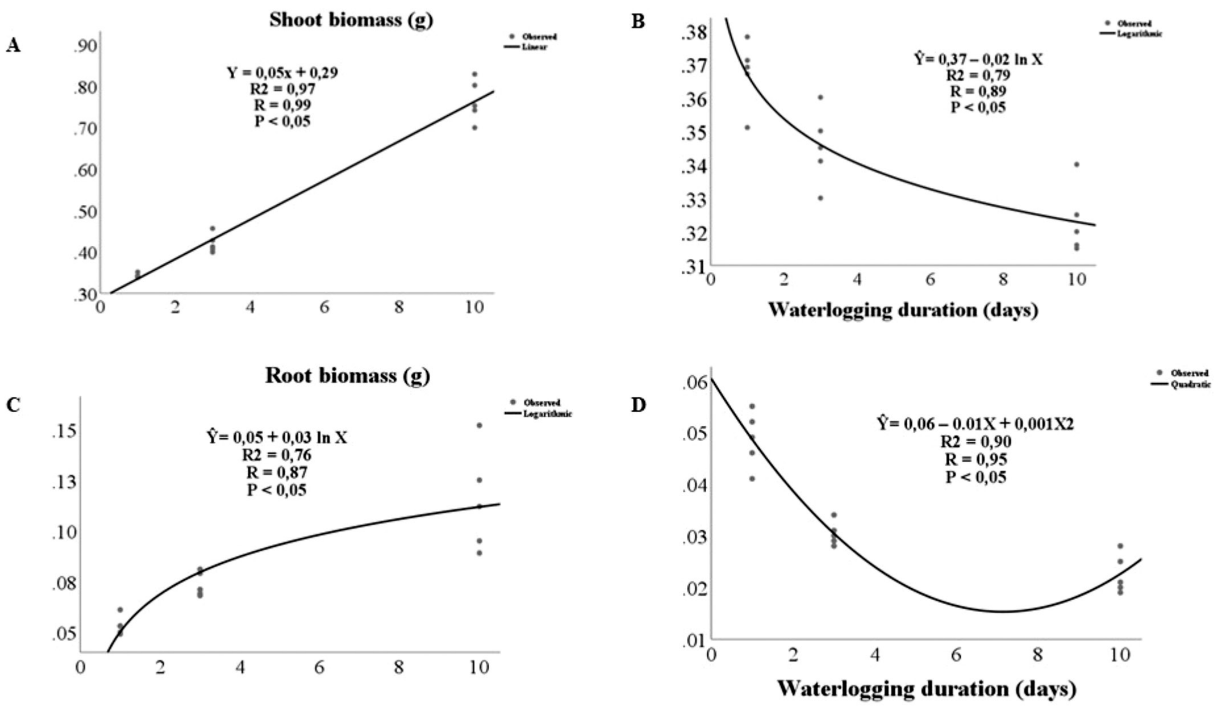

Fig. 5 - Relationship between shoot biomass and root biomass with waterlogging duration. Measurements were made after the flooding ended. Shoot biomass in control (A), Shoot biomass in waterlogging duration treatment (B). Root biomass in control (C), root biomass in the waterlogging duration treatment (B). / Relazione tra la biomassa dei germogli e la biomassa delle radici con la durata del ristagno idrico. Le misurazioni sono state effettuate dopo la fine dell'allagamento. Biomassa dei germogli nel controllo (A), biomassa dei germogli nel trattamento di durata crescente del ristagno idrico (B). Biomassa radicale nel controllo (C), biomassa radicale nel trattamento di durata crescente del ristagno idrico (B).

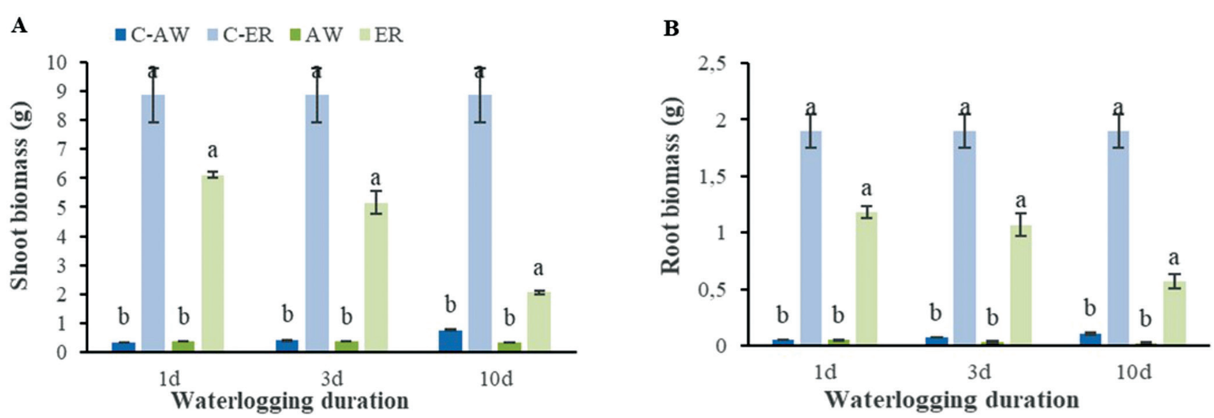

Fig. 6 - Shoot biomass (A) and root biomass (B) after waterlogging and the end of the recovery period. Means and standard errors were based on five replications. Bars with different letters under the same category indicated a significant difference ($p \leq 0{,}05$) with a paired t-test. C-AW: control after waterlogging, C-ER: control of the end recovery period, AW: after waterlogging, ER: the end of the recovery period. / Biomassa dei germogli (A) e delle radici (B) dopo il ristagno d'acqua e al termine del periodo di recupero. Le medie e gli errori standard si basano su cinque repliche. Le barre con lettere diverse sotto la stessa categoria indicano una differenza significativa ($p \leq 0{,}05$) con un t-test a coppie. C-AW: controllo dopo il ristagno idrico, C-ER: controllo alla fine del periodo di recupero, AW: dopo il ristagno idrico, ER: alla fine del periodo di recupero.

the ability to recover determined the performance of vegetative growth, reproduction, and harvest (Yuan *et al*., 2022). The results showed differences in plant response at AW and ER. Root damage occurred in all waterlogging treatments. Root damage included wilting at the root tips and root rot. An increase in the duration of waterlogging increased the percentage of root damage. Increasing root damage due to increasing waterlogging duration is reported in *Cajanus cajan* (L.) Millsp.) (Bansal & Srivastava, 2012), *Saccharum* spp. cv. NiF8 (Jaiphong *et al*., 2016), *Zea mays* L. (McDaniel *et al*., 2016), and *Sesamum indicum* L. cv. BARI Til-4 (Anee *et al*., 2019). Root damage is caused by reduced respiration rate, and accumulation of toxic compounds and ROS (Patel *et al*., 2014; Kaur *et al*., 2020). Root damage due to ROS accumulation is reported in *Pisum sativum* L. (Zhou *et al*., 2016), and *S. indicum* (Anee *et al*., 2019). In the present study, root damage was detected after 1 day of waterlogging, and the greatest da-

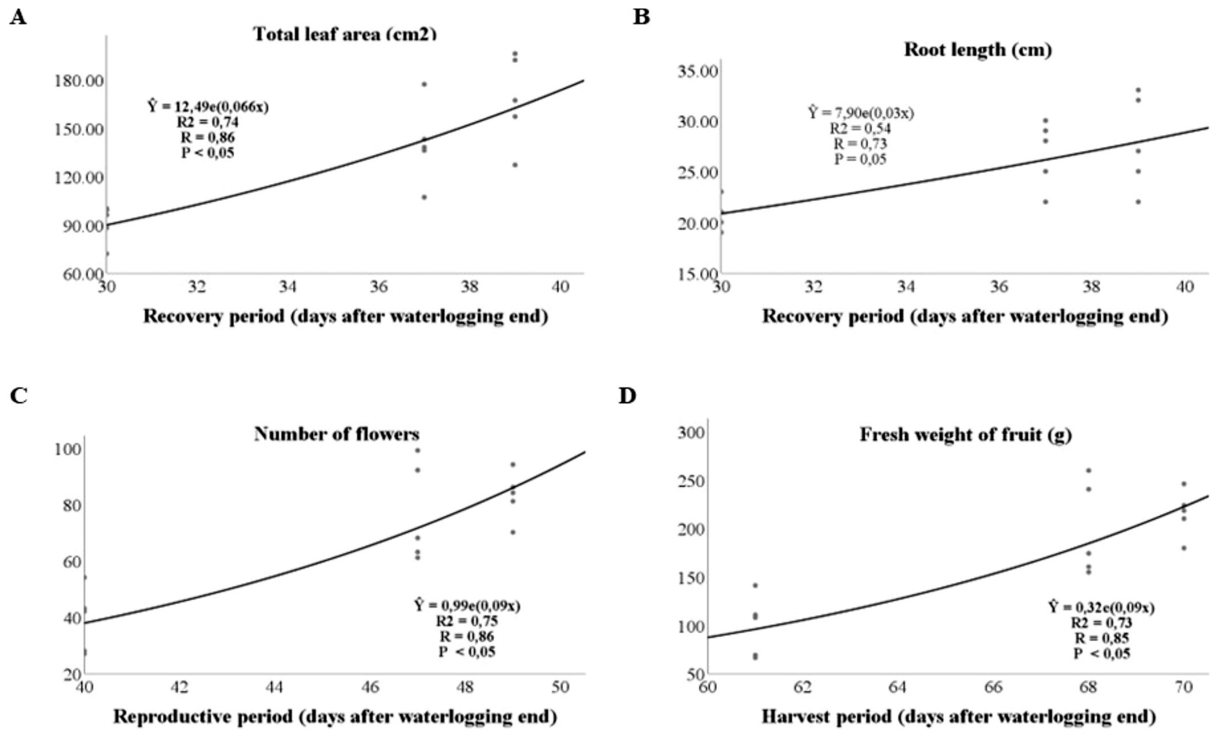

Fig. 7 - The relationship between total leaf area, root length, and recovery period (A, B). Measurements were taken at the end of the recovery period (30 days after the most prolonged duration of flooding). The relationship between the number of flowers and the reproductive period was determined ten days after the recovery period ended (C). The relationship between fresh-weight fruit and the harvest period was determined 31 days after the recovery period ended (D). / Relazione tra area fogliare totale, lunghezza delle radici e periodo di recupero (A, B). Le misure sono state effettuate alla fine del periodo di recupero (30 giorni dopo la durata più prolungata dell'inondazione). La relazione tra il numero di fiori e il periodo riproduttivo è stata determinata dieci giorni dopo la fine del periodo di recupero (C). La relazione tra il peso fresco dei frutti e il periodo di raccolta è stata determinata 31 giorni dopo la fine del periodo di recupero (D).

mage occurred at day 10 of waterlogging. Da-Silva & do Amarante (2020) recorded a similar condition in *G. max,* where the accumulation of ROS in roots occurred during a 24-h waterlogging and lipid peroxidation increased significantly up to a 240-h inundation duration. Changes at the molecular level were detected in tomato plants subjected to waterlogging after a 6-h flooding (Safavi-Rizi *et al*., 2020).

Root damage decreases root hydraulic conductance, resulting in stomatal closure and shoot wilting (Tan *et al*., 2018; Sauter, 2013). In the present study, stomatal closure occurred in all waterlogging treatments; however, no permanent wilting occurred and all plants survived. This can be explained by the formation of hypertrophic lenticels and adventitious roots that allowed continued water absorption by the roots. The formation of hypertrophic lenticel facilitates the diffusion of O_2 to internal tissues and the transportation of anaerobic metabolic products, including ethanol, CO_2, and CH_4 to the atmosphere (Hasanuzzaman *et al*., 2017). Internal aeration increased respiration rate, energy gain and active transport, while the formation of adventitious roots replaced the role of dead early roots and facilitated the absorption of water and nutrients (Jia *et al*., 2021). Tan & Zwiazek (2019) reported on *N. tabacum* the formation of adventitious root to maintain aquaporin expression and root hydraulic conductance during hypoxia. Some pepper species, such as *Capsicum pubescens* Ruiz & Pav. and *C. baccatum* L., increasing the number of adventitious roots during 3 days of waterlogging, enhanced water use efficiency compared to *C. chinense*, which forms a small number of adventitious roots (Ou *et al*., 2011). In *Vigna radiata* (L.) R. Wilczek, genes related to adventitious root development are highly expressed in tolerant cultivars during long-term waterlogging (7 days duration) (Sreeratree *et al*., 2022). In the present study, the early formation of lenticel hypertrophy was detected at 3 days of flooding and reached maturity at 7 days of flooding. In comparison, adventitious root formation was detected on the ninth day of waterlogging. This showed that after 3 days of flooding, it was necessary to increase internal aeration to balance metabolic processes and plant survival. Towards the end of the long period of waterlogging, the total roots were almost completely non-functioning and damaged. These conditions stimulated the formation of adventitious roots. At the end of the recovery period root growth, stomata opened, and plant growth occurred. Root system development is crucial for plant tolerance to waterlogging stress (Herzog *et al*., 2016).

The content of leaf photosynthetic pigments (chlorophyll and carotenoids) can indicate the susceptibility or tolerance of plants to abiotic stress, including waterlogging stress (Chávez-Arias *et al*., 2019). The photosynthetic electron transport chain becomes over-reduced during waterlogging, producing ROS and oxidative damage (Lal *et al*., 2019). Types of ROS, such as superoxide radicals and hydrogen peroxide, can damage lipid membranes (Candan & Tarhan, 2012). Damage to lipid membranes in chloroplasts is reported to occur in susceptible *Hordeum vulgare* L. (Luan *et al*., 2018), (*Zea mays* L.) hybrids Denghai 605 and Zhengdan 958 (Ren *et al*., 2016), and *Sorghum bicolor* L. (Zhang R.D. *et al*., 2019b). Damage to the chloroplast membrane indirectly resulted in damage to photosynthetic pigments. The most reactive ROS can also damage chlorophyll, namely hydroxyl radical (Candan & Tarhan, 2012). In the current study, the waterlogging duration reduced photosynthetic pigment content (total chlorophyll and carotenoids). There was a strong relationship between the decrease in photosynthetic pigment content and the duration of waterlogging, as shown by R=0.72 (total chlorophyll content) and R=0.725 (carotenoid content). The highest reduction in photosynthetic pigments occurred with a waterlogging duration of 10 days (Figs. 2B, 2D). In *S. indicum*, the increase in the duration of waterlogging to 8 days enhanced the content of malondialdehyde and hydrogen peroxide (Anee *et al*., 2019). This resulted in a reduction of total chlorophyll and carotenoid content (Anee *et al*., 2019). Anee *et al*.'s study reinforces the findings of the present paper that ROS accumulation and membrane damage cause a decrease in photosynthetic pigment content; other causes are nutrient deficiencies in the soil and damage to root function (Steffens *et al*., 2005; Board, 2008). On the other hand, in control plants a decrease in photosynthetic pigment also occurred, along with an increase in the duration of waterlogging (Figs. 2A, 2C). Plants were not fertilized during the waterlogging treatment, so leaf growth was not supported by the addition of plant nutrients. This resulted in a decrease of the content of photosynthetic pigments. In *S. indicum*, the control photosynthetic pigment content does not change significantly during waterlogging (Anee *et al*., 2019).

The increase in the content of photosynthetic pigments was one of the plant responses during the recovery period. Re-exposure to oxygen in the post-waterlogging period resulted in the accumulation of ROS, causing oxidative damage (Bashar, 2018). Reoxygenation in turn also resulted in unfavorable conditions for plants, including nutrient deficiency, decreased hydraulic conductance of roots, closure of stomata and damage to photosynthetic structures (Bashar, 2018; Yuan *et al*., 2022). The resilience of plants in coping with these conditions was determined by their performance, particularly their low damage levels and adaptability during waterlogging (Zhao *et al*., 2018; Liu K. *et al*., 2020). At ER, photosynthetic pigment content increased, especially during the 10-days waterlogging period. The level of root and leaf damage in the 1-day and 3-days waterlogging treatment was low, thus supporting the increase in total chlorophyll at ER. Optimization of photosynthesis during recovery in both treatments was achieved by increasing the chlorophyll content. Chlorophyll acts as the main reaction center and light harvester, while carotenoids act as accessory pigments (Lokstein *et al*., 2021). The high increase in photosynthetic pigment at the end of the recovery period in the 10-day waterlogging treatment was probably closely related to the lower number and area of leaves. *Capsicum frutescens* tolerance on the long duration of waterlogging could be increased by increasing photosynthetic pigment content to optimize the photosynthetic capacity. In general, the pattern of changes in the photosynthetic pigments after waterlogging and at the end of recovery in *G. max* (Da-Silva & do Amarante, 2020) and in some cultivars of *S. lycopersicum* (Mohanty *et al*., 2020) is similar to the results of the present study. Increased antioxidant enzyme activity, high photosynthetic pigment content, and adventitious root formation during waterlogging are important factors for the increase in photosynthetic pigment during recovery period in both plants.

In the present study, plants that were flooded for 10 days could form hypertrophied lenticels and adventitious roots, thereby supporting the optimization of photosynthesis during the recovery period. Root biomass decreased according to the quadratic equation (Fig. 5D) as the duration of flooding increased. In contrast, there was an increase in the control group. The decrease in root biomass was caused by root damage and decay (Fujita *et al*., 2020; Liu K. *et al*., 2020). That condition disrupted root functions related to the absorption of water and nutrients, thus impacting the metabolic processes in the shoot, one of which is photosynthesis (Herzog *et al*., 2016). Photosynthesis affected biomass accumulation during the vegetative, reproductive, and harvest phases (Kim *et al*., 2019; Honda *et al*., 2021). Our study showed a decrease in root biomass followed by a decrease in shoot biomass during the flooding. There was indeed a strong correlation between the decreased in root and shoot biomass and the duration of flooding, namely R=0.95 (root biomass) and R=0.89 (canopy biomass).

Plant height showed a stable pattern during waterlogging, while the number of leaves decreased during the 10 days of waterlogging, which showed that the leaf number determined a decrease in shoot biomass.

During long periods of waterlogging, photosynthetic-related enzyme activity was inhibited, chlorophyll synthesis decreased, photosynthetic structural damage increased, senescence occurred, and leaf drop and new leaf formation were inhibited (Pan *et al*., 2021). A similar result was reported for *Vigna unguiculata*: the leaves were damaged and fell off during 10 days of waterlogging (Olorunwa *et al*., 2022). In *Z. mays*, damage to leaf function was caused by harm to the chloroplast and mitochondrial membranes during 3 and 6 days of waterlogging (Ren *et al*., 2016). In contrast, in *Triticum aestivum*, cv. AGP FAST, the formation of adventitious roots and aerenchyma structures occurred after 14 days waterlogging, so that they were able to maintain low rates of photosynthesis, shoot biomass, root biomass, and leaf damage (Ploschuk *et al*., 2018). It seems that in *C. frutescens*, the formation of hypertrophied lenticels and adventitious roots during the 10 days of waterlogging was unable to fully maintain leaf function from damage, thus reducing shoot biomass. However, plants recovered and increased their growth during the recovery period.

Leaf number, plant height, shoot and root biomass increased during recovery. Other growth variables, such as the leaf area and root length also increased during recovery. The recovery period for waterlogging of 1, 3 and 10 days was 39, 37 and 30 days, respectively. It has been reported that several plants are able to overcome post-waterlogging stress and recover during this period. *Chrysanthemum morifolium* cv. Nannongxuefeng develops adaptation by regulating carbohydrate metabolism and ethylene production and maintaining high growth potential after waterlogging (Zhao *et al*., 2018). It can overcome post-waterlogging conditions through ROS-scavenging enzyme activities, ethylene production, and energy saving (Zhao *et al*., 2018). *Arabidopsis thaliana* activates the antioxidant pathway through the accumulation of jasmonates and increases the expression of jasmonic acid biosynthetic genes during reoxygenation (Yuan *et al*., 2017). In *Hylotelephium spectabile* cv. Carl, tolerance to waterlogging is achieved through the formation of adventitious roots, increased activity of antioxidant enzymes, and maintenance of root and shoot growth, to overcome oxidative damage during reoxygenation and better recover (Zhang J. *et al*., 2019). Liu & Zwiazek (2022) reported on *Brassica napus*, that increased activity of antioxidant enzymes in roots during recovery increase aquaporin activity, root hydraulic conductivity, transpiration, shoot water content, and photosynthesis.

The results of the present study indicated that plant performance after the recovery period was related to the degree of root damage, root biomass, and shoot during waterlogging. Root damage increased with the increasing duration of flooding, resulting in reduced plant biomass. Biomass regulation during waterlogging is closely related to energy saving, affecting plant resilience in post-waterlogging and recovery (Striker, 2012). *Vigna radiata* cv. Jade-AU and *Vigna mungo* cv. Onyx-AU maintain biomass after waterlogging and recover faster than susceptible genotypes (Kyu *et al*., 2021). The same pattern also occurs in *Trifolium subterranean* ssp. *yanninicum* (Enkhbat *et al*., 2021). In our paper, the highest plant growth after the recovery period was found in 1-day waterlogging, and the lowest was in 10 days. At 10 days of waterlogging, root damage was significant, and plant biomass was low, while during recovery period it was short. This resulted in low recovery and growth ability. However, plants flooded for 10 days were able to overcome post-waterlogging conditions and recover. The ability to develop lenticel hypertrophy and adventitious roots supported plant resilience in post-waterlogging. During the recovery period, adventitious roots continued to grow, and new roots were formed in lenticel hypertrophy areas. Plant recovery supported flower formation and fresh fruit weight. Flower number and fresh fruit weight increased with the length of the reproductive period and harvest. The highest number of flowers and fresh fruit weight were found in 1 day of flooding and the lowest in 10 days.

CONCLUSION

The tolerance of *C. frutescens* to the duration of waterlogging was determined by its ability to protect the root system from damage, the high content of photosynthetic pigments, maintenance of biomass, and the ability to form adventitious roots and hypertrophic lenticels. The performance of these plants determined their resilience during post-waterlogging and recovery period. The level of root damage and shoot wilt can be used as indicator of plant tolerance to short-term waterlogging. In comparison, the ability to develop lenticel hypertrophy and adventitious roots indicates plant tolerance to long-term flooding. *Capsicum frutescens* was tolerant to short and long-term flooding during the early vegetative phase, as evidenced by its ability to grow during the reproductive and harvest phases. Further studies should be conducted on antioxidant activity closely related to the level of oxidative damage. Hormonal and molecular studies related to the anatomical, morphological and physiological adaptations of *C. frutescens* in waterlogging tolerance should be also developed.

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