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Growth and Physiological Responses of Strawberry (*Fragaria* × *Ananassa* Duch.) to Waterlogging Stress

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ABSTRACT

Changes in strawberry vegetative growth, carbon assimilation, tissue hydration and membrane integrity caused by waterlogging limit strawberry performance. Secondary analysis of the strawberry response data was used to investigate growth and physiological response for 5 durations of waterlogging. The treatments were freely drained control and root-zone waterlogging for 2, 4, 6 or 8 days with 8 plants per treatment and common day 8 endpoint. Growth, biomass, gas exchange, chlorophyll, fluorescence, relative water content, electrolyte leakage, malondialdehyde and proline were estimated. Finally, statistical approaches included one-way analysis of variance, Tukey comparisons, Benjamini–Hochberg adjustment and duration regressions with HC3 uncertainty estimates. After adjustment, 22 out of 23 outcomes had significant effects of the treatments, except for final plant height. Waterlogging for 8 days resulted in 61.6% reduction in net photosynthesis, 30.3% reduction in leaf area, 29.8% shorter root, and 25.0% reduction in total dry weight when compared with the control. The RWC decreased from 91.21% to 75.14%, while the electrolyte leakage increased from 14.84% to 45.60%. There was a significant rise in the concentrations of malondialdehyde (2.84-fold) and proline (3.76-fold). Fv/Fm did not change after 2 days but after longer exposure it dropped to lower levels like in the control. The overall results show good linear lack of fit for Fv/Fm and relative water content, indicating that the response did not fit constant daily changes. The results reveal a synergic performance reduction in strawberry growth related to time of exposure and show the importance of combining growth, photosynthetic, hydration and membrane parameters in the assessment of waterlogging responses.

INTRODUCTION

To grow strawberry plants, it is essential to balance the ability to supply water to the plants and allow gas exchange in the root environment. Even if water is seemingly available, excess water retention can result in a production constraint. Waterlogging is inundation of the root zone, water submergence is inundation of aerial tissues. The difference impacts interpretation as the main exposure in a root-zone treatment is below ground but the leaves are still available for exchange in the atmosphere. In essence, interactions between metabolic, developmental and environmental processes are involved in flooding responses and experimental definitions must be made with greater precision than a statement of excess irrigation (Rokosa *et al.*, 2025).

In strawberry, the correlation between the conditions in the root zone and the responses above ground is especially important when assessing vegetative establishment. A plant can maintain about the same external height while assimilation ability decreases; leaf surface area diminishes or roots become non-functional. A study based on only the visible dimensions could therefore underestimate the stress (Geng *et al.*, 2026). Morphological, biomass and physiological measurements can provide more solid evidence of the effects of waterlogging on short-term functioning or of the occurrence of wider injury. The utility of such an evaluation is in determining the useful response variables and if the sensitivity varies by the duration of exposures.

Research on flooding adaptation supports the physiological considerations for proposing multiple responses. Limited oxygen can change the way that energy is produced and make more sense of the control of resources or for better internal aeration. There is wide variation among species in the traits that allow survival in these conditions and tolerance does not necessarily imply a presence of a single stress response (Ploschuk *et al.*, 2025). This framework provides an impetus for considering both growth restriction and tissue damage and for considering potential adjustment separately. A reduction in growth could indicate that resources are being conserved but if the reduction is also associated with a corresponding leak in water status and increase in leakage then this must be interpreted with caution.

Strawberry evidence also shows direct effects of root-zone flooding in modulating stomatal behaviour, without matching all the drought impacts. Blanke and Cooke 2004 showed that stomatal closure was fast although the delivery of abscisic acid was reduced in flooded strawberry and leaf water potential was not affected in the experiment. They found their results showed that responses to excess water cannot be simply compared to responses to soil drying. They also give an opportunity to compare gas exchange with independent measures of hydration, rather than assuming that a reduction in gas exchange means that the leaf is dehydrated. It is a

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question for every experimental data set whether the relationships are positive or negative and how strong they may be (Xu *et al.*, 2023).

A molecular view is complementary. Strawberry FaSnRK1α has been shown to regulate anaerobic respiratory metabolism, and waterlogging tolerance, accompanied by the alteration of respiratory enzymes and antioxidant capacities. The results offer a physiological background to the relationship between the energy regulation of roots and plant performance. The present analysis explores the equivalent response domains at morphological and physiological levels (Hung *et al.*, 2025). It focuses on the interconnectedness of growth, photosynthesis, tissue hydration, and biochemical responses over a progressive time sequence of exposures.

For an integrated interpretation several measurement differences are required. Net photosynthesis reflects carbon exchange at the moment of measurement and dry mass reflects what has been accumulated in growth and what has been spent through respiration in the past. The concentration of chlorophyll is a measure of the pigment pool, fluorescence is a measure of the photochemical performance (Kasture *et al.*, 2024). The Fv/Fm measurements are subject to correct measurement procedures and should be analyzed in conjunction with other parameters as an indication of the efficiency of the photosystem II, but not as a comprehensive indicator of photosynthesis. Agreement in these areas can add weight to a descriptive assessment, but in individual plants doesn't indicate which component altered first.

The biochemical indicators need to be kept in check in the same way. Membrane leakage is an indication that cells were not properly contained during the assay. Although malondialdehyde is often regarded as a measurement of lipid peroxidation, spectrophotometric measurements may be influenced by interfering compounds if appropriate corrections are not made. Proline is also involved in various physiological roles and alone is unable to differentiate successful acclimations from severe responses to stress. A rise of one of the stress related compounds thus must be interpreted in the context of retained growth, water status and photochemical function (Iqbal *et al.*, 2026).

The goal was to describe growth and physiological response patterns for five waterlogging durations with the strawberry waterlogging response data. The analysis included testing to see if duration influenced vegetative performance, if photosynthetic variables were different in their apparent sensitivity to water deficit, and if membrane and biochemical indicators of water deficit were progressive as the tissues became more hydrated. An additional goal was to examine if the selected responses had simple linear duration trends that were good representations (Ananth *et al.*, 2025). It was hypothesized that there should be a coordinated physiological dysfunction and biomass reduction that would correspond with the duration of waterlogging. Immediate functional response from cross treatment differences in accumulated growth and condition of tissue are separated by the analysis.

MATERIALS AND METHODS

Analytical Design and Source of Data

A secondary analytical design was used for analyzing the plant response of the strawberry to the greater amounts of time spent water-logged in the root zone. Analytical material consisted of seven tables of statistics, three composite response figures and residual diagnostic plots. Treatment definitions, descriptive summaries, overall significance tests, pairwise comparisons, selected duration regressions were made available in the tables. These analytical outputs were drawn on for statistical estimates. The presented treatment means were used to calculate percentages changes.

Waterlogging Treatments

There were 5 treatments (WL0, WL2, WL4, WL6, and WL8). These were equal to 0, 2, 4, 6 and 8 days of

Table 1: Overall treatment tests

Outcome	F(4, 35)	Adjusted p	Descriptive η^2
Final height (cm)	0.94	0.453	0.097
Height change (cm)	19.31	< .001	0.688
Final leaf number	21.91	< .001	0.715
Leaf area (cm^2/plant)	32.81	< .001	0.789
Root length (cm)	28.01	< .001	0.762
Shoot fresh mass (g/plant)	14.66	< .001	0.626
Root fresh mass (g/plant)	39.06	< .001	0.817
Shoot dry mass (g/plant)	14.28	< .001	0.620
Root dry mass (g/plant)	27.63	< .001	0.759
Total dry mass (g/plant)	22.59	< .001	0.721
Root to shoot dry mass	3.55	0.016	0.289
SPAD	69.24	< .001	0.888
Photosynthesis ($\mu mol\ CO_2\ m^{-2}\ s^{-1}$)	90.52	< .001	0.912
Conductance (mol $H_2O\ m^{-2}\ s^{-1}$)	65.33	< .001	0.882

Transpiration (mmol H_2O m^{-2} s^{-1})	52.62	< .001	0.857
Fv/Fm	242.74	< .001	0.965
Chlorophyll a (mg/g FW)	49.83	< .001	0.851
Chlorophyll b (mg/g FW)	33.15	< .001	0.791
Total chlorophyll (mg/g FW)	56.51	< .001	0.866
Relative water content (%)	132.20	< .001	0.938
Electrolyte leakage (%)	189.23	< .001	0.956
Malondialdehyde (nmol/g FW)	65.95	< .001	0.883
Proline (µmol/g FW)	145.18	< .001	0.943

Note: N = 40 for every reported test. Adjusted p values use the supplied Benjamini–Hochberg correction across 23 outcomes. The photosynthesis residual normality test was significant (p = .0011). All Brown–Forsythe tests were nonsignificant.

waterlogging. Eight plants were recorded per treatment (40 plants analysed). WL0, WL1, WL2, and WL3 were the freely drained control, and the waterlogged groups, respectively. A common end point was reached on day 8 for all groups. Waterlogging started on day 6 for WL2, day 4 for WL4, day 2 for WL6 and day 0 for WL8. The results of overall tests are summarised in Table 6. The treatment structure is shown in Table 1.

Duration was considered as an exposure variable at the treatment level. So comparisons refer to different groups of plants measured at the same end-point and not repeated measurements of the same plants over the course of each day. The control was the control used for relative response calculations. Group differences were analysed categorically and selected regression models were used to summarise the relationship between exposure duration (0–8 days) and plant response.

Growth and Biomass Assessment

The growth variables measured were plant height initial, plant height final, change in plant height, number of leaves initial, number of leaves final, leaf area and root length. Change in height was used as an ancillary measure of growth over the period of observation. Initial measurements were taken to help interpret endpoint differences. The size at the end of the experimental period and the amount of increase in height were treated separately, since the two are not necessarily correlated and are separate aspects of vegetative performance. Above- and below-ground expansion were characterised by leaf area or recorded root dimension, respectively (Lili Jiang *et al.*, 2022).

Biomass parameters included fresh weight and dry weight of the shoots and roots as well as total dry weight and the root-to-shoot dry-weight ratio. Both fresh weight and dry weight were considered in order to separate out any differences in hydrated tissue mass from any differences in accumulated dry material (Maofu Li *et al.*, 2021). Total dry weight and allocation ratio were considered derived supporting outcomes. The basic evaluation of shoot and root responses was done on absolute component masses.

Photosynthetic and Stress Indicators

Photophysiological parameters measured included SPAD, net photosynthesis, stomatal conductance, transpiration, Fv/Fm, Chlorophyll a, Chlorophyll b, and total chlorophyll. Net photosynthesis was calculated in µmol CO_2 m−2 s−1, stomatal conductance was expressed in mol H_2O m−2 s−1 and transpiration was expressed in mmol H_2O m−2 s−1. Chlorophyll content was calculated as mg g fresh weight. Combination of gas exchange and pigment status data with Fv/Fm was interpreted as an index of maximum photosystem II (PSII) photochemical efficiency.

Biochemical variables included were relative water content, electrolyte leakage (EL), malondialdehyde (MDA), and proline. The relative water content and electrolyte leakage were calculated as percentages. Malondialdehyde content was represented in nmol g−1 of fresh weight while proline content was represented in µmol g−1 of fresh weight. These parameters were used in conjunction with growth and photosynthetic performance. The methodological approach to evaluate biochemical responses and interpret the physiological changes under waterlogging stress was based on established analytical methods for proline determination and malondialdehyde assessment (Fischer *et al.*, 2023).

Statistical Analysis

The data were analyzed in a statistical platform to determine the effects with 23 outcomes using one-way analysis of variance. For each model, there were five treatment groups and four degrees of freedom for treatment and 35 degrees of freedom for error. Tukey honestly significant difference comparisons were used to interpret pairwise differences. Multiple testing within the overall outcome analyses was controlled for by Benjaminini–Hochberg adjusted probabilities. Statistically significant adjusted probabilities were those that were < .05. Those probabilities which were zero numerically are shown as p < .001.

The proportion of variation in the sample associated with treatment was quantified with descriptive eta squared. Diagnostic plots were considered in conjunction with Brown–Forsythe tests and Shapiro–Wilk residual tests. Means and their accompanying plus–minus quantities were reproduced as reported dispersion. Comparison letters remained in their original groupings and

alphabetical order was not used as a relative measure of treatment effectiveness (Yenni *et al.*, 2022).

Waterlogging duration was associated with the plant response by selected regression models. Slopes, HC3 standard errors, 95% confidence intervals, coefficients of determination, and linear lack of fit tests were provided for these models. A significant lack-of-fit result meant that it was not sufficient to describe the response with one slope. The relative changes were expressed in percentages as 100 × (treatment mean- control mean) / control mean. The differences between percentage valued outcomes were represented in percentage points. Means displayed were rounded, causing calculations to be approximate (Benukar Biswas *et al.*, 2024).

RESULTS AND DISCUSSION

Overall Treatment Effects

After Benjamini–Hochberg adjustment, there was a significant difference for waterlogging treatment with 22 out of 23 outcomes. There was no significant difference among the four treatments in the final plant height, $F(4, 35) = 0.94$, adjusted $p = .453$. By contrast there were differences among treatments in height change, $F(4, 35) = 19.31$, adjusted $p < .001$. This is a distinction between the recorded growth increment and only its final height, and it demonstrates that the recorded growth increment was more informative. Table 6 summarises the overall tests. The treatment design is shown in Table 1 and the descriptive growth responses are shown in Table 2.

Table 2: Waterlogging treatment structure

Treatment	Duration (days)	Start day	Endpoint day	Plants
WL0	0	Not applicable	8	8
WL2	2	6	8	8
WL4	4	4	8	8
WL6	6	2	8	8
WL8	8	0	8	8

Note: WL0 represents the freely drained control; all other treatments represent root-zone waterlogging. The dataset records eight plants per treatment and a common day-eight endpoint.

Table 3: Waterlogging treatment structure

Outcome	WL0	WL2	WL4	WL6	WL8
Initial height (cm)	17.13 ± 1.42	16.58 ± 1.36	17.25 ± 1.33	17.32 ± 1.41	17.51 ± 0.92
Final height (cm)	19.62 ± 1.67 a	18.87 ± 1.36 a	18.80 ± 1.28 a	18.86 ± 1.44 a	18.32 ± 0.97 a
Height change (cm)	2.49 ± 0.45 a	2.29 ± 0.33 a	1.55 ± 0.24 b	1.54 ± 0.60 b	0.82 ± 0.45 c
Initial leaf number	7.62 ± 0.52	6.50 ± 1.07	7.00 ± 0.76	7.12 ± 0.64	7.25 ± 0.46
Final leaf number	9.75 ± 1.16 d	8.50 ± 0.76 a	8.00 ± 0.53 ab	7.25 ± 0.46 b	6.00 ± 1.07 c
Leaf area (cm^2/plant)	388.28 ± 31.64 a	370.38 ± 13.69 a	356.16 ± 31.70 a	306.41 ± 22.86 b	270.55 ± 12.85 c
Root length (cm)	23.35 ± 1.40 b	21.43 ± 1.52 ab	20.19 ± 1.54 ac	18.79 ± 1.26 c	16.40 ± 1.29 d

Note: Values are means ± reported dispersion; n = 8 per treatment. Within a row, means sharing a letter were not significantly different in the reported Tukey comparisons at .05; letter order has no ranking meaning. FW = fresh weight.

The effect sizes for each outcome reported were highly variable. Final height had a descriptive eta squared of .097, the root-to-shoot ratio had a descriptive eta squared of .2887, and Fv/Fm had a descriptive eta squared of .9652. The relative water content and electrolyte leakage were also significantly variable with eta squareds of .9379 and .9558, respectively. These values are for the analytical sample and not for population level predictive accuracy (Biswas *et al.*, 2024). These represent the relative strength of treatment separation in the analytical sample. These measures add to the importance of the significance tests in the sense that they differentiate between rather pronounced physiological responses and relatively weak structural responses (Tahjib-Ul-Arif *et al.*, 2023).

Vegetative Growth

Final-height groups were not significantly different from each other according to Tukey comparison letter, and initial means ranged between 16.58 and 17.51 cm and final means ranged between 18.32 and 19.62 cm. Height change, however, declined from 2.49 cm in WL0 to 2.29, 1.55, 1.54, and 0.82 cm in WL2, WL4, WL6, and WL8. The WL0 increment was ~67.1% larger than the WL8 increment. The height change was not significantly different between the control and WL2, but decreased in WL4 and WL6 and lowest in WL8.

Final leaf number decreased from 9.75 in WL0 to 8.50 in WL2, 8.00 in WL4, 7.25 in WL6, and 6.00 in WL8. Tuckey analysis, adjusted pairwise $p = .041$, indicated the WL2 versus control was significant. But at the start, the mean leaf number was 7.62 in Wl 0 and 6.50 in Wl 2. The difference is a baseline one and makes interpretation of the earliest final count contrast difficult. Changes of the number of leaves at the group level that were calculated from the rounded means for the five treatments were approximately +2.13, +2.00, +1.00, +0.13, and −1.25

leaves for the five treatments, respectively, but these are not new test results (Kim *et al.*, 2023).

After two and four days the leaf area decreased to 370.38 and 356.16 cm2plant-1 respectively from control value of 388.28 cm2plant-1. The Tukey comparisons indicated that there were no significant differences between these shorter-duration groups and the control. Leaf area was lower at six days, 306.41 cm^2 $plant^{-1}$, and at eight days, 270.55 cm^2 $plant^{-1}$. This was equivalent to an approximate reduction of 30.3% in the eight day's value. A different trend was observed for root length: WL4 was already significantly lower than the control while WL2 was still not significantly different from the control. There was a reduction of about 29.8% in mean root length from WL0 to WL8 (from 23.35 to 16.40 cm).

It can also be seen that the magnitude of the responses and the statistical sensitivity to them were not the same in the structural endpoint contrast. The change in height was 1.67 cm different between the control and eight-day groups although numerically the difference in final height was only 1.30 cm. The latter difference amounted to about two thirds of control increment. Both leaf area and root length had the same proportional endpoint reduction at eight days, and different units and comparison patterns, if any, at shorter durations (Adhikari *et al.*, 2026). Therefore, the highest duration contrast resulted in the lowest vertical growth rate, canopy leaf area and the lowest recorded root dimension. These changes reflect a general decrease in vegetative growth of the treatment series evaluated.

Biomass Accumulation and Allocation

The shoot fresh weight was 40.70 g plant-1 in WL0 and 31.26 g plant-1 in WL8 and the root fresh weight decreased from 12.21 to 8.20 g plant-1. These are equivalent to the reductions by around 23.2% and 32.8%, respectively. Control, 2-day and 4-day shoot fresh weights

Table 4: Biomass responses across waterlogging durations

Outcome	WL0	WL2	WL4	WL6	WL8
Shoot fresh mass (g/plant)	40.70 ± 2.63 a	37.39 ± 3.23 a	37.55 ± 3.30 a	32.91 ± 2.94 b	31.26 ± 1.72 b
Root fresh mass (g/plant)	12.21 ± 0.74 b	11.22 ± 0.50 ab	10.43 ± 0.76 ac	9.54 ± 0.88 c	8.20 ± 0.54 d
Shoot dry mass (g/plant)	7.26 ± 0.38 b	6.62 ± 0.64 ab	6.66 ± 0.51 ab	6.15 ± 0.44 ac	5.61 ± 0.25 c
Root dry mass (g/plant)	2.21 ± 0.14 a	2.03 ± 0.18 a	2.01 ± 0.17 a	1.78 ± 0.10 b	1.50 ± 0.13 c
Total dry mass (g/plant)	9.47 ± 0.42 c	8.64 ± 0.74 a	8.67 ± 0.55 a	7.93 ± 0.52 a	7.10 ± 0.33 b
Root to shoot dry mass	0.305 ± 0.021 a	0.308 ± 0.032 a	0.303 ± 0.033 ab	0.289 ± 0.015 ab	0.267 ± 0.022 b

Note: Values are means ± reported dispersion; n = 8 per treatment. Within a row, means sharing a letter were not significantly different in the reported Tukey comparisons at .05; letter order has no ranking meaning. FW = fresh weight.

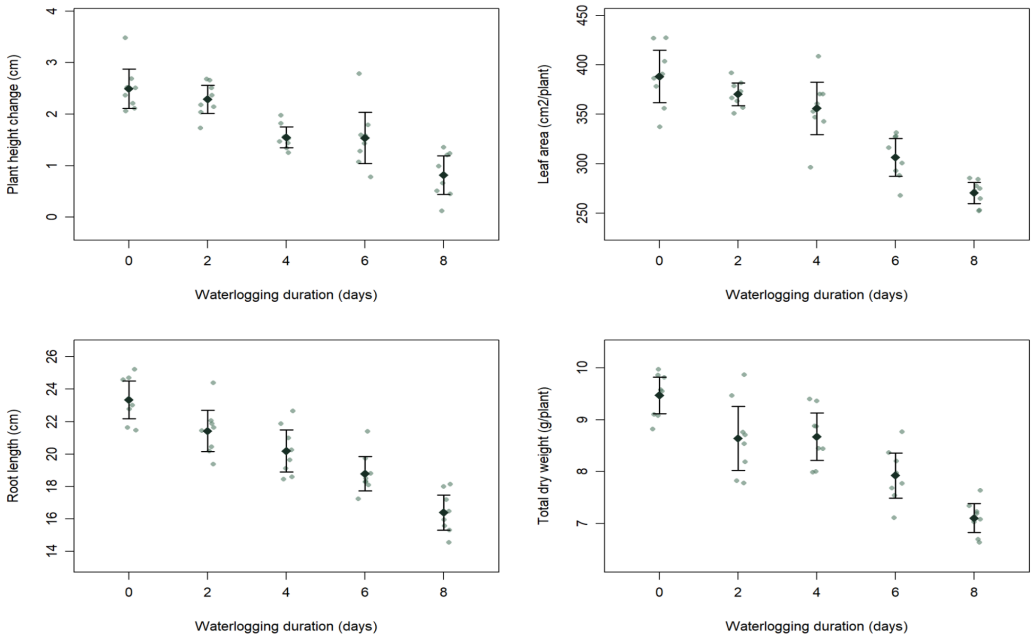


Figure 1: Growth and biomass responses

Note: Panels show height change, leaf area, root length, and total dry weight. Points show individual observations, and diamond markers indicate treatment means. Error bars are reproduced from the source figure. Each treatment contains eight recorded plants.

did not differ and received a common comparison letter; the values for 6-day and 8-day were lower. There was a significant control contrast in root fresh weight after four days. Root and shoot fresh-weight patterns are similar and consistent with the higher degree of relative restriction of the belowground portion of this dataset (Table 3).

Dry-weight responses agreed with this, as the fresh-weight reductions were not necessarily only due to decreased tissue water content. The control and WL8 were ~22.7% different in shoot dry weight (7.26 vs. 5.61 g plant^{-1}). The dry weight of roots decreased by about 32.1% from 2.21 to 1.50 g per plant. There was no difference in root dry weight at two and four days while root dry weight was lower at six and eight days. Root-to-shoot dry-weight ratio was decreased from 0.305 to 0.267, and there was a larger proportional decrease in root DW than shoot DW (Sherpa *et al.*, 2024).

Total dry weight was 9.47, 8.64, 8.67, 7.93, and 7.10 g plant^{-1} across WL0 through WL8. The WL8 reduction, compared to control, was ~25.0%. The comparison letter for the two day, four-day and six day groups was similar in spite of the different means, which shows that there was no significant separation between the adjacent treatments in a visually ordered series. In contrast, the root-to-shoot ratio showed a relatively small overall effect (adjusted p = .016) with intermediate groups overlapping at both the extremes. Figure 1 shows growth and biomass patterns.

Gas Exchange and Pigment Status

Net photosynthesis declined from 14.51 µmol CO_2 m^{-2} s^{-1} in WL0 to 11.15, 10.22, 7.51, and 5.57 µmol CO_2 m^{-2} s^{-1} with increasing duration. The two day value

Table 5: Photosynthetic responses across waterlogging durations

Outcome	WL0	WL2	WL4	WL6	WL8
SPAD	43.24 ± 1.53 d	41.02 ± 1.07 a	39.55 ± 1.83 a	36.51 ± 1.63 b	32.26 ± 1.02 c
Photosynthesis (µmol CO_2 m^{-2} s^{-1})	14.51 ± 1.62 d	11.15 ± 1.09 a	10.22 ± 0.84 a	7.51 ± 0.81 b	5.57 ± 0.21 c
Conductance (mol H_2O m^{-2} s^{-1})	0.269 ± 0.037 d	0.203 ± 0.024 a	0.183 ± 0.023 a	0.132 ± 0.013 b	0.093 ± 0.011 c
Transpiration (mmol H_2O m^{-2} s^{-1})	3.23 ± 0.29 c	2.83 ± 0.33 a	2.51 ± 0.34 a	1.89 ± 0.15 b	1.60 ± 0.10 b
Fv/Fm	0.809 ± 0.008 a	0.806 ± 0.006 a	0.777 ± 0.006 b	0.749 ± 0.011 c	0.708 ± 0.005 d
Chlorophyll a (mg/g FW)	1.511 ± 0.104 d	1.365 ± 0.109 a	1.332 ± 0.080 a	1.119 ± 0.056 b	0.968 ± 0.070 c
Chlorophyll b (mg/g FW)	0.523 ± 0.040 b	0.494 ± 0.028 ab	0.472 ± 0.024 a	0.413 ± 0.031 c	0.370 ± 0.027 c
Total chlorophyll (mg/g FW)	2.034 ± 0.132 d	1.860 ± 0.124 a	1.804 ± 0.097 a	1.532 ± 0.075 b	1.337 ± 0.079 c

Note: Values are means ± reported dispersion; n = 8 per treatment. Within a row, means sharing a letter were not significantly different in the reported Tukey comparisons at .05; letter order has no ranking meaning. FW = fresh weight.

was already well below the control in the Tukey analysis. Reductions relative to WL0 were approximately 23.2%, 29.6%, 48.2%, and 61.6%. The two-day group was not significantly different from the four-day group, both of which were higher than the six-day and eight-day groups. The overall analysis revealed a highly significant treatment association, $F(4, 35) = 90.52$, adjusted $p < .001$ (Table 4). Stomatal conductance declined from 0.269 mol H_2O m^{-2} s^{-1} in WL0 to 0.093 mol H_2O m^{-2} s^{-1} in WL8, approximately 65.4%. The amount of transpiration has reduced from 3.23 to 1.60 mmol H_2O m^{-2} s^{-1} which is reduced by ~50.5%. There was a significant difference between the six day and eight day groups for Conductance but not for transpiration. So, not the same pair-wise pattern was retained for different gas-exchange components (Modgil & Talekar, 2024). This overall direction is common for both of them which provides a link between increased exposure duration and decreased leaf exchange rate, but does not specify the causal part of stomatal limitation to assimilation.

After eight days the progression of changed SPAD was down from 43.24 in the control to 32.26, about 25.4% decrease. The levels of chlorophyll a decreased from 1.511 to 0.968 mg g-1 fresh weight and chlorophyll b reduced from 0.523 to 0.370 mg g-1 fresh weight. The total chlorophyll decreased by approximately 34.3% from 2.034 mg g-1 fresh weight to 1.337 mg g-1 fresh weight. After 2-days total-chlorophyll and chlorophyll a levels were significantly decreased compared with the control. The chlorophyll b did not change from the control at 2 days but was significantly lower after 4 days. Consequently, there was a difference in the earliest time when a difference was observed between the pigment fractions.

The loss in gas exchange at the longest period was more closely coupled to the loss in total dry weight. Net photosynthesis was about 38.4% of the control mean and the total dry weight was about 75.0%. This is a comparison on the basis of different response scales: photosynthesis is a description of endpoint function per unit leaf area, dry weight is a description of accumulated material per plant. The difference in their retained fractions thus does

not mean that there is a contradiction (Attar *et al.*, 2025). Rather, it means that there was a greater proportional difference at the end points in physiological performance than in accumulated mass. Leaf area was decreased as well, thus providing an additional structural difference in addition to the decrease of assimilation at the leaf level.

Photochemical Efficiency

The Fv/Fm was unchanged between WL0 and WL2 with the mean values being 0.809 and 0.806. It decreased to 0.777 at WL4; to 0.749 at WL6 and to 0.708 at WL8 with different Tukey comparison groups at the longer durations. The gap between WL8 and the control was 0.101, which falls to approximately 12.5% relative loss. The treatment effect was $F(4, 35) = 242.74$, adjusted $p < .001$. The two response measures, early fluorescence and assimilation, were not equally sensitive across the duration groups recorded (Figure 2); stable early fluorescence with reduced assimilation suggests that this might not be the case.

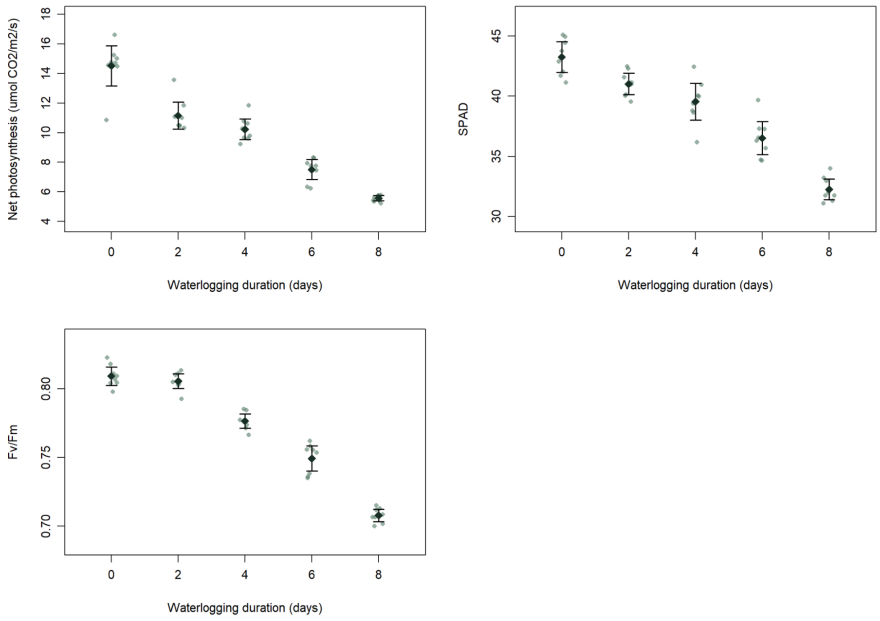


Figure 2: Photosynthetic performance

Note: Panels show net photosynthesis, SPAD, and Fv/Fm. Points show individual observations, and diamond markers indicate treatment means. Error bars are reproduced from the source figure. Each treatment contains eight recorded plants.

Water Status and Biochemical Indicators

Relative water content decreased from 91.21% in WL0 to 89.34%, 86.51%, 80.87%, and 75.14% with increasing exposure. The first appreciable level of control contrast was at 4 days. WL8 showed a 17.6% relative decrease (~16.07 percentage points) compared with the control.

Table 6: Water status and biochemical responses

Outcome	WL0	WL2	WL4	WL6	WL8
Relative water content (%)	91.21 ± 2.06 a	89.34 ± 1.62 a	86.51 ± 0.71 b	80.87 ± 1.56 c	75.14 ± 1.81 d
Electrolyte leakage (%)	14.84 ± 2.21 a	17.73 ± 3.06 a	25.98 ± 2.25 b	34.26 ± 1.67 c	45.60 ± 3.36 d
Malondialdehyde (nmol/g FW)	7.01 ± 0.71 a	8.76 ± 0.98 a	12.23 ± 1.70 b	14.83 ± 2.53 c	19.89 ± 2.24 d
Proline (µmol/g FW)	0.80 ± 0.11 a	1.02 ± 0.12 a	1.54 ± 0.19 b	2.17 ± 0.25 c	3.01 ± 0.32 d

Note: Values are means ± reported dispersion; n = 8 per treatment. Within a row, means sharing a letter were not significantly different in the reported Tukey comparisons at .05; letter order has no ranking meaning. FW = fresh weight.

This is due to the difference between percentage points and relative percentage change, since they report different amounts. Although the recorded root environment was saturated, the leaf-water indicator value was lower at the longer durations, indicating that water availability around the root and water availability in the tissues were not the same in this data set (Table 5).

Electrolyte leakage increased from 14.84% in WL0 to 17.73% in WL2, 25.98% in WL4, 34.26% in WL6, and 45.60% in WL8. The value of the two-day treatment was not significantly different from the control treatment, but the values of the other treatments were. The eight-day rise was equal to 30.76 percentage points and was about 207.3% above the control. Malondialdehyde rose from 7.01 to 19.89 nmol g-1 fresh weight (about 183.7%) while the level of proline increased from 0.80 to 3.01 µmol g-1

fresh weight (about 276.3%). Significant control contrasts were detected for both indicators after four days (Yin *et al.*, 2023).

At the longer times, the coordinated rise of leakage, MDA and proline, was accompanied by a decrease of water content and reduction in fluorescence. That the two concur lends support to an integrated description of an increasing stress burden, but does not make a statement as to whether any biochemical variable caused the morphological decline. No correlation between proline accumulation and maintenance of control level growth or photosynthetic performance was observed at eight days. As such, its rise alone cannot be considered as proof of effective tolerance based on assessed endpoints. This is depicted in Figure 3.

The variables of water status and biochemicals also varied

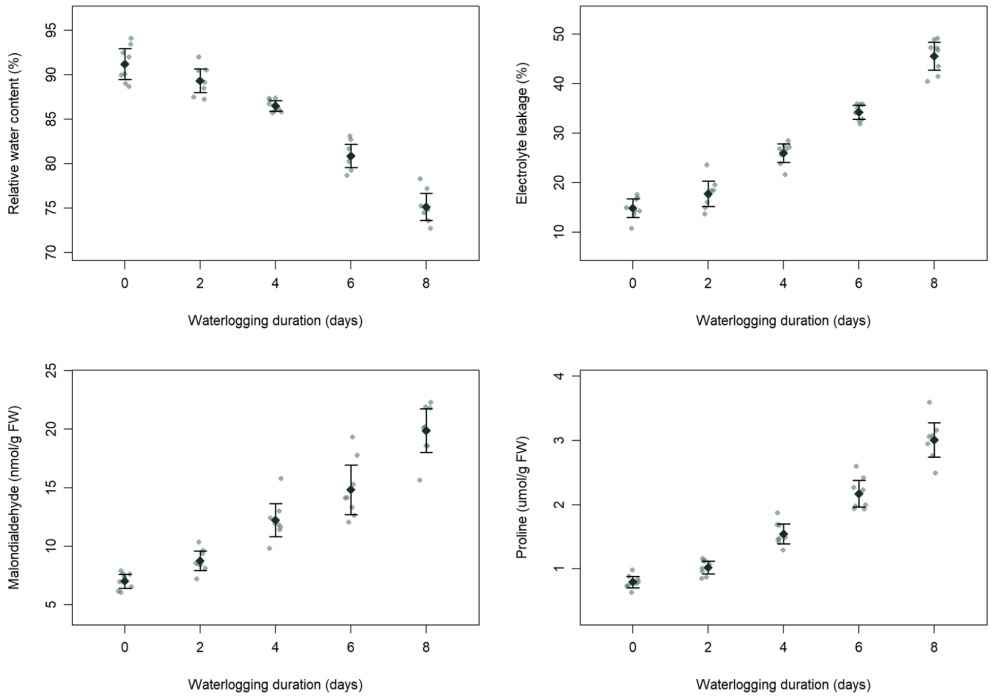


Figure 3: Water status and biochemical stress indicators

Note: Panels show relative water content, electrolyte leakage, malondialdehyde, and proline. Points show individual observations, and diamond markers indicate treatment means. Error bars are reproduced from the source figure. Each treatment contains eight recorded plants.

in the proportional response magnitude. The relative water content at four days was ~ 5.2% lower than that of the control; and the electrolyte leakage was ~ 75.1% higher. Malondialdehyde and proline were around 74.5% and 92.5% more respectively. The leakage, malondialdehyde and proline increased by about 130.9%, 111.6% and 171.3% respectively at six days. These percentages reflect changes from the individual control of each variable. They do not use a common physiological severity scale to indicate severity, and they do indicate that there was a high responsiveness of biochemical concentrations and permeability as the treatment groups separated in hydration.

Brand New for the Single Room 2016 - Duration Relationships and Diagnostics

The durations of the reported regressions were negative for height change, total dry weight, net photosynthesis,

Table 7: Associations with waterlogging duration

Outcome	Slope per day	95% CI	R^2	Lack of fit p
Height change (cm)	-0.205	-0.259 to -0.152	0.644	0.197
Total dry mass (g/plant)	-0.273	-0.326 to -0.220	0.674	0.137
Photosynthesis (µmol CO_2 m^{-2} s^{-1})	-1.076	-1.212 to -0.941	0.892	0.069
Fv/Fm	-0.013	-0.015 to -0.011	0.907	< .001
Relative water content (%)	-2.031	-2.298 to -1.764	0.893	< .001
Malondialdehyde (nmol/g FW)	1.591	1.369 to 1.813	0.858	0.079

Note: N = 40 for each reported regression. Confidence intervals use the supplied HC3 uncertainty estimates. All supplied adjusted slope probabilities were < .001. Significant lack of fit for Fv/Fm and relative water content means a linear slope is an incomplete description. Units follow the outcome label in Tables 2–5. Slopes describe between-group duration associations within 0–8 days, not observed daily losses within individual plants.

Fv/Fm, and relative water content, but positive with malondialdehyde (Table 7). For total dry weight, the slope was −0.273 g plant^{-1} per additional day, with a 95% confidence interval from −0.326 to −0.220 and R^2 = .674. The photosynthesis slope was −1.076 μmol CO_2 m^{-2} s^{-1} per day, with a confidence interval from −1.212 to −0.941 and R^2 = .892. These estimates reflect association for each duration between the groups and not repeated losses on the same plants day after day.

The linear lack of fit was significant for both Fv/Fm ($p < .001$) and relative water content ($p < .001$). They thus did not form good linear descriptions with their high R2 values. Lack of fit was not detected at .05 for height change, total dry weight, photosynthesis or malondialdehyde, though this does not establish linearity. None of the reported outcomes were significant in Brown–Forsythe tests. The normality probability of the photosynthesis residual was .0011 and the diagnostic plots exhibited a strong lower tail observation and deviations from the reference line. The other (residual) normality tests were not significant. The findings add to the specific caution of this statistics analysis of photosynthesis and the specific pairing probabilities: do not say that all of the assumptions were met.

The height-change model was y = −0.205 x plus another 1 cm per additional day; 95% CIs were −0.259 cm per day, −0.152 cm per day; R^2 = .644. It was the opposite for malondialdehyde which increased by a fitted 1.591 nmol g^{-1} fresh weight per additional day (1.369 to 1.813; R^2 = .858). The values in both intervals were positive. The parallel reduction in growth increment and biochemical stress indicator are summarised in their contrasting signs. These estimates can be used to describe the direction and magnitude of the fitted association over the entire exposure series and complement the categorical comparisons.

Discussion

Integrated Interpretation of the Response Pattern

The main result is the concentration of growth and physiological responses to increasing waterlogging period. This reduction in the total dry weight was accompanied by a decrease in the leaf area, a decrease in root length, a decrease in assimilation, a decrease in tissue hydration and an increase in membrane leakiness. The presence of both structural and functional abnormalities along with biochemical abnormalities suggests that the response was both morphological and functional (Scott & Villouta, 2026). The behaviour of the integrated pattern is more indicative than that of the final plant height that did not differ statistically between treatments. Physiological data and the growth increment were better able to differentiate exposure groups than was the final height alone in the data set (Jiang *et al.*, 2024).

The order of the group differences was detected could indicate that functional measures might detect stress earlier that all the structural endpoints are clearly discernible. Photosynthesis, conductance, SPAD, chlorophyll a and total chlorophyll differed from the control at two days, while the values for height change, leaf area, Fv/Fm, RWC, leakage, MDA and proline remained statistically similar. Several signs of hydration and injury were also significantly different at 4 days. Apparent differences in the sensitivity of different treatment groups. It is not designed to show a time-series within the same plant, as all endpoint measurements were present at day eight (Yin *et al.*, 2023).

The response profile can be explained in the general context of flooding adaptation, where the diversity of morphological, physiological, and biochemical traits associated with plant survival in flooded environments is stressed. The lowered growth and raised injury indicators in the current analysis focus on maintaining function, as opposed to just the presence of a stress response (Haverroth *et al.*, 2024). Small plant size or high biochemical levels do not necessarily represent good adjustment. The interpretation will depend on whether or not carbon assimilation, hydration and integrity of tissues are maintained at the same exposure.

The two day and eight day groups seem to be especially representative times for understanding breadth of response. Several photosynthetic indicators were distinct from the control at 2 days, although measures of fluorescence, hydration and membrane overlap. The response at eight days involved both a decrease of dry mass of the root and shoot and marked physiological differences (Sherpa *et al.*, 2024). It is not a simple classification of one group as unaffected, but with regard to the number and type of response domains involved. It indicates that a brief exposure is enough to produce functional changes even when the number of indicators of structure injuries are close to controls. Higher exposure resulted in a greater response throughout the measured plant system (Geng *et al.*, 2026).

Growth Assessment and Baseline Differences

There is methodologically important difference between nonsignificant final height, and the height change which is significant. Final height is a combination of the existing size and growth from the observation period. The apparent endpoint separation, however, might be smaller in the longest duration group because the mean height was a little higher than the control although the growth increment was also less (Geng *et al.*, 2026). The data thus shows why a final dimension should not automatically be considered as an absolute measure of growth related to treatment. Height change is more indicative of the interval reported but is still dependent on the regularity and timing of the measured heights.

This difference in end-point early and subsequent growth restriction is partially explained by initial leaf number. The two-day group started with a lesser number of leaves than the control and the approximate mean increase was similar to the mean increase for the control (Ploschuk *et al.*, 2025). This initial size component is thus part of the early final count contrast. The magnitude of the gains became progressively smaller with increasing duration and at eight days there was a lower than initial mean for

the groups. These differences cause the number of leaves to be most useful in combination with leaf area and height change. The combined growth indicators identify endpoint size as well as the ability to sustain vegetative spread during the growth period (Hung *et al.*, 2025).

Root length and leaf area are complementary structural information. By four days root length was found to be significantly reduced compared to the control while leaf area was not significantly different until six days after treatment. This pattern suggests varying sensitivity of the root and canopy size recorded in the range of time evaluated (Kasture *et al.*, 2024). Root length is a measure of one dimension of root development and leaf area accounts for the number and size of the photosynthetic surfaces. They both decrease at the longest duration, suggesting a lower structural capacity for resources to be acquired both above ground and below ground. Thus, taking both traits together offers a more comprehensive evaluation than can be obtained from each dimension taken separately.

This treatment setup also allows for duration to be interpreted as an integrated exposure variable. The under waterlogging period was different for each group, but the final assessment day was the same for all groups. Consequently, the contrasts are a combination of the amount of exposure to root-zone and the condition of the plant when exposed to the root-zone. They are not intended to be a series of observations of a single population but comparisons of treatment history. This separation maintains the significance of the ordered series of treatments and provides the regression slopes with the appropriate biological significance. Slopes are the mean fitted contrast across exposure groups of one more day (Iqbal *et al.*, 2026).

Biomass Distribution and Accumulated Performance

Results from the dry weight show that the plant waterlogging response was not only an instantaneous function but also accumulated plant material. The total dry weight loss after 8 days is significant on the analytical scale but should not be interpreted as a quarter loss in growth rate. Endpoint mass is the mass of material that was already there before the interval of exposure and mass of material that was added during the interval of exposure. The data is not of the change in total dry weight of each plant over time, but rather of a difference in total dry weight among groups, conditional on the analysis (Lili Jiang *et al.*, 2022).

Since this proportional reduction in dry weight was greater for the roots than for the shoots, this accounts for the decreased root to shoot ratio at 8 days. However, the ratio cannot show diversion of assimilates to shoots if it is active. The decrease in the root fraction may be due to differential growth inhibition, root tissue loss or variation in the initial allocation of the root fraction. These possibilities would need to be discerned from repeated or staged biomass sampling and more measures of tissue turnover. Even the intermediate ratio groups were not statistically distinct, so more precise claims of a smooth progression in the allocation cannot be made. There is therefore a need to maintain the focus of interpretation of the absolute amounts of the components and use the ratio as a summary.

Allocation response was less than absolute biomass loss. The change in root-to-shoot ratio from 0.305 to 0.267 represents about a 12.5% decline in root mass, compared to the shoot mass. Root and shoot dry weight, on the contrary, dropped by about 32.1% and 22.7% respectively. The ratio thus characterises a decrease between two decaying parts. Combining the ratio with those components prevents using relative shoot predominance as an indicator of increased shoot growth. Results from the combined experiment suggest a reduction in mass in both fractions with a greater relative decrease in mass of the root fraction and little change in the root:shoot ratio (Quiñones Martorello *et al.*, 2023).

Gas Exchange and Photochemical Responses

The early decline in assimilation with relatively stable Fv/Fm indicates different sensitivities of carbon exchange and maximum photochemical efficiency. The decrease of conductance is concurrent, thereby suggesting the notion of stomatal restriction, and the subsequent decline in fluorescence, which can be related to the changes in photochemical performance of the process. Fluorescence as described by Maxwell and Johnson (2000) is a valuable source of physiological information if treated as such based on the basis of the measurement. The current gas exchange and fluorescence setup allow to distinguish between an initial decrease in carbon uptake and the more widespread carbon uptake response at the longer timepoints. These indices are not equivalent measures of the same process but complementary indices of photosynthetic performance.

The reduction in Fv/Fm later on was correlated with lower SPAD and chlorophyll concentration. The general photosynthetic impairment confirmed by the agreement among the indicators suggests that during four to eight days a general photosynthetic impairment was present. Pigment status and photochemical efficiency are different properties of the leaf, but are co-directional, and this enhances the integrated response pattern. The lower pigment concentration represents a smaller measured pigment pool per unit fresh mass and less maximum photochemical efficiency (Fv/Fm) at the endpoint. These changes, in conjunction with the large decrease in assimilation, indicate that the longer duration response included several leaf-function components (Iqbal *et al.*, 2026).

A comparison with Blanke *et al.* Cooke (2004) also warns against the use of a unique hydraulic explanation for stomatal behavior. Their inundated strawberry plants showed stomatal responses but did not show any changes in leaf water potential. The variable of relative water content was seen to decrease with increasing time in the data set but is not the same as the water potential. These studies thus argue for a focus on root-to-shoot regulation but do not require the presence of identical hydraulic

responses. When comparing physiological meaning of the two indicators, differences in tissue, exposure, cultivar, and measurement procedure should be taken into consideration, accordingly (Fischer *et al.*, 2023).

Water Status and Membrane Integrity

Root-zone waterlogging and decreased RWC of the lower leaves was the factor that separated environmental water availability from plant hydration. Longer durations resulted in reduced conductance, reduced transpiration and reduced tissue water content. Thus, the decrease of water loss was not followed by a normalization of the control condition but it was followed by a decrease in hydration. This is in line with a mismatch in water supply to leaf versus demands of living tissues (Jiang *et al.*, 2024). RWC as a measure of tissue state thus provides a complementary view to the gas exchange measure: they measure aspects of the exchange with the atmosphere and with the tissue, respectively.

A good coincidental indicator of disturbed membrane integrity was electrolyte leakage. The higher up trend from ~15% to 46% coincided with a decrease in relative water content and Fv/Fm. At 4 days there was a significant difference from the control, and several other stress indicators significantly deviated from the control at this time (Yin *et al.*, 2023). This agreement facilitates interpretation of the longer-duration treatments as a coordinated physiological response to the treatment and not growth restriction only. Leakage is kept as an assay based index of permeability and the percentage leakage is not considered as percentage of dead cells. Its major use here is because of the obvious difference between exposure groups and its agreement with other, independent assessments of plant condition (Haverroth *et al.*, 2024).

Malondialdehyde and electrolyte leakage were biochemical and physical indices of tissue status, respectively. They both increased at the same time, especially on days six and eight, when photosynthesis was also decreased and relative water content was reduced. The interpretation was decided not on any single concentration but taking all the different indicators of physiological and biochemical trends into account. When using spectrophotometric estimates of malondialdehyde, care needs to be taken with analytical procedures and appropriate measurements (Sherpa *et al.*, 2024). Therefore, the measured concentration values were compared with the changes in the permeability of the membrane and the water content in the tissue. These indicators in this integrated assessment show the deterioration of the tissue condition on stress and the fact that all indicators represent different physiological and biochemical processes.

Proline Accumulation and Potential Adjustment

Among the biochemical indicators, the increase in proline was the largest relative to the other indicators. This increase could be biologically relevant, but it is not yet known whether their size alone provide protection. Proline has various functions in plant metabolic processes, such as osmotic regulation, cellular homeostasis and physiological changes in response to the environment (Biswas *et al.*, 2024). Within the current data set, high proline levels were correlated with low biomass, lowered photosynthetic assimilation and high electrolyte leakage. These results suggest that it is not the proline level per se that is directly linked to increased waterlogging stress tolerance, but instead, exposure to the stress was related to increased levels of proline. The evidence presented would need to indicate that higher levels of proline build-up help to sustain the physiological function in similar stress situations to give proline a protective role. These associations might be further explored by applying controlled experimental treatments or contrasting waterlogging tolerance of strawberry germplasm (Adhikari *et al.*, 2026).

Physiological Integration and Duration Relationships

Molecular and physiological studies of strawberry plants have shown that FaSnRK1α is related to anaerobic metabolism and antioxidant responses to a waterlogging stress. Important mechanistic information for whole-plant responses to prolonged flooding conditions is provided by root respiration, fermentation enzyme activities, carbohydrate metabolism, antioxidant defense mechanisms, and gene expression. The physiological and molecular processes help elucidate the interplay between energy regulation, cellular protection and plant growth during oxygen deficiency (Kasture *et al.*, 2024). The growth reductions observed were accompanied by a reduction in photosynthetic capacity which could be linked to alterations in root energy metabolism and related stress response pathways. More extensive studies with direct assessment of respiratory activity, enzyme activity and molecular response would be useful to better understand the mechanisms associated with the waterlogging tolerance of strawberry plants.

The trend regressions and the model adequacy regressions need to be separated. The direction of the association fitted is determined by the significant negative slopes, and Fv/Fm and relative water content displayed significant lack of linear fit. They cannot thus support constant daily rates of decline, because their R^2 values are high. The means imply rather modest early adjustments and subsequently larger cuts, whereas the design doesn't identify the exact point of the turnaround. Four days is more like the first sampled period of time with some important differences, than it is like the universal four-day physiological threshold.

Careful interpretation of nonsignificant comparisons is needed as well. Non-significant difference between two day waterlogging and control was not a proof of equivalence or non-injury for several traits. Biological acceptability would have to be prespecified and analysis would have to be tailored to measuring it. Similarly, commonalities in the comparison letters cannot be equated with commonalities in meaning, and the sequence of the letters does not reflect a quantitative aspect in biology. The comparison letters are only included to indicate Tukey comparisons made (Yin *et al.*, 2023). Thus, interpretation considers

magnitude of effect, as well as the intervals available and probabilities, instead of simply categorizing all of the treatments as unaffected and affected.

Derived variables add further dependence to the set of outcomes. Allocation ratio, total chlorophyll (including pigment fractions) and total dry weight (root + shoot dry weight) are all reliant on both root and shoot dry weight. Their agreement is helpful for the internal pattern but not to duplicate the same conclusion. The statistical conditions of FDR adjustment must be satisfied by one aspect of multiple testing, but not by these biological outcomes. Future analysis might consider a prespecified primary outcome; calculated sums then could serve as secondary outcomes, which would have the benefit of clearer interpretation but would still allow for a broad physiological evaluation (Scott & Villouta, 2026).

The results from the diagnostic questions emphasize the need for a prominent focus on a large treatment contrast as opposed to a description of form of response. The direction of separation of groups was straightforward for photosynthesis; however, the substantial residual normality test results should be remembered when interpreting exact model probabilities. Significant lack of fit for Fv/Fm and relative water content meant that a constant-rate model was not able to explain the whole group pattern. These considerations do not undo the actual means ordering (Yin *et al.*, 2023). They make a distinction between evidence of description, testing of the treatment, and model adequacy in the interpretation. Need for more appropriate description of the shape of a strong physiological contrast may exist.

Implications for Physiological Assessment

Results provide a supplementary list of indicators to evaluate strawberry reactions to root-zone waterlogging. The gas exchange and pigment status separated shorter exposures, and hydration, fluorescence and leakage gave better separation at longer exposures. These functional responses were related to vegetative performance by growth increments and dry mass (Haverroth *et al.*, 2024). Thus a combined assessment can be used to make these separations within one analytical context. This will give a starting point for choosing primary and secondary outcomes in future strawberry studies and the physiological responses will be measured alongside growth, rather than as stand-alone measures.

The total evidence also indicates a difference between detection and explanation. A sensitive indicator can be used to identify the difference between treatment groups, but not to specifically identify the process causing the difference. Net photosynthesis discriminated the two-day group from the control, for instance, and combined with conductance, fluorescence and pigments, became more informative physiologically (Benukar Biswas *et al.*, 2024). Likewise, an increase in proline could easily be distinguished at the longer times but would have limited biological relevance unless it was coupled with a corresponding decrease in tissue condition and growth. So integrated assessment enhances interpretation in ways that transcend choosing a single universally diagnostic variable by using complementary measurements.

CONCLUSION

There was a coordinated decrease in strawberry growth and physiological performance with the increase of the waterlogging duration. Exposure for eight days resulted in about 25.0%, 30.3%, and 61.6% reduction, respectively, in the total dry weight, leaf area, and net photosynthesis of the plants in comparison with the freely drained plants. The shoot dry weight decreased at a lesser rate than the root dry weight. Electrolyte leakage, malondialdehyde and proline increased with decreasing relative water content and Fv/Fm. Several physiological indicators and height change were better able to discriminate among the duration groups, whereas an overall treatment effect was not observed for final plant height.

The response pattern is conducive to an integrated assessment of growth, gas exchange, photochemistry, hydration and membrane integrity. The earliest significant control contrast difference shows that there are differences in the sensitivity of individual indicators. This lack of linear fit between Fv/Fm and relative water content also clearly shows that there is sometimes no constant daily decline when considering duration associated stress. The analysis results in identification of shorter and longer exposure groups who have contrasting physiological components; recovery, yield responses, and more precise biological thresholds are questions for experimental investigations.

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