

Article

Substrate Moisture Management Strategies for Optimizing Quality in Lettuce and Tomato Seedling Production

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Abstract

Proper substrate moisture management is essential for producing high-quality seedlings in nurseries. This study aimed to evaluate the morphological and physiological quality of lettuce (*Lactuca sativa* L.) and tomato (*Solanum lycopersicum* L.) seedlings subjected to different substrate moisture levels, monitored by weighing lysimetry under protected environment conditions. Four experiments were conducted over two growing seasons (2019 and 2020) using six irrigation treatments corresponding to 80, 70, 60, 50, and 40% of the substrate water-holding capacity, in addition to the conventional irrigation management adopted by the grower (Control). Water consumption, morphological traits, root architecture, gas exchange, chlorophyll fluorescence, and photosynthetic pigments were assessed. Cumulative irrigation water applied ranged from 77 to 92 mm in lettuce and from 91 to 132 mm in tomato. Reducing substrate moisture to 40% negatively affected seedling growth, root development, and physiological performance in both species. In tomato, stomatal conductance decreased by up to 90%, accompanied by a decline in Fv/Fm from 0.78 to 0.70. Both lettuce and tomato tolerated moderate reductions in substrate moisture (60–70% holding capacity) without significant losses in growth or gas exchange performance. However, the highest seedling quality was achieved under the grower-managed Control and the 80% substrate moisture treatment, although the traits contributing to this response differed between species. In lettuce, favorable performance was associated with growth, pigment-related traits, and photochemical efficiency, whereas in tomato superior seedling quality was linked to shoot growth, root development, and gas exchange characteristics. These findings support the use of species-specific irrigation strategies to improve seedling quality in nursery production.



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1. Introduction

Environmental conditions are key determinants of horticultural productivity, influencing the incidence of pests, diseases, nutrient imbalances, and abiotic stresses [1,2].

This is especially critical during the seedling stage, when plants are highly susceptible to environmental fluctuations. To mitigate environmental constraints during the seedling stage, growers commonly adopt protected cultivation systems [3], which reduce evapotranspiration, enhance water use efficiency, and facilitate year-round production [4]. In nursery production systems, where transplant quality largely determines final crop performance, precise water management is critical not only for water conservation but also for maintaining plant health and vigor [5].

Water is often applied in excess to nursery crops, with leaching fractions ranging from 30 to 50% [6]. Despite the recognized importance of substrate moisture management, nursery practitioners have historically relied on empirical criteria (visual inspection or fixed irrigation schedules) [7]. Substrate and container characteristics play a crucial role in irrigation management and seedling quality [8]. The balance between water retention and aeration determines water availability to roots and influences plant growth [9]. The shallow depth of the cells restricts gravitational drainage and increases water retention compared with larger containers, making the substrate more prone to waterlogging and oxygen deficiency under excessive irrigation [10]. These conditions require frequent irrigation with relatively small water applications. However, fluctuations in environmental demand can rapidly deplete water stored in the substrate, exposing seedlings to transient water deficits and compromising their growth [11]. Therefore, establishing appropriate upper and lower substrate moisture thresholds is critical to minimizing drainage losses, avoiding root-zone hypoxia, and ensuring optimal water availability throughout seedling production.

This challenge is often exacerbated by the lack of reliable substrate moisture monitoring systems [12–14]. An alternative for quantifying water inputs and outputs is the use of electronic weighing lysimeters [15,16]. Although initially developed to measure soil water percolation [17], lysimeters are now widely used in agricultural research to quantify water balance components and evaluate water dynamics in production systems. For example, the integration of weighing lysimeters into containerized nursery environments offers a physically rigorous alternative, enabling continuous gravimetric monitoring of water consumption and direct estimation of crop evapotranspiration (ET_c) [18], without the constraints associated with in-substrate sensor installation [19,20]. Currently, advances in electronics have facilitated both their use and construction through the availability of more precise and cost-effective sensors on the market, including load cells with different capacities [21,22]. However, the application of lysimeters in vegetable seedling production remains limited, particularly regarding the integrated assessment of morphological and physiological responses under varying substrate water availability.

Lettuce (*Lactuca sativa* L.) and tomato (*Solanum lycopersicum* L.) are among the most economically significant horticultural species globally. Lettuce is among the most economically important leafy vegetables worldwide, with China, India, and the United States accounting for nearly 75% of global production and cultivated area [23]. Likewise, tomato is the world's most important horticultural crop, with annual production exceeding 180 million tonnes cultivated on nearly 5 million hectares worldwide [24]. Lettuce and tomato are commonly established through containerized seedling systems owing to the high cost of hybrid seeds, the need to maximize stand establishment, and the limitations of direct sowing, which often result in poor and uneven emergence [25,26]. In lettuce, high-quality seedlings are characterized by a compact shoot, short stem, broad non-etiolated leaves, and a well-developed root system, traits associated with earlier establishment and greater biomass accumulation [27]. Similarly, high-quality tomato seedlings exhibit compact growth, stem diameters greater than 3 mm, fully developed green leaves, and a well-branched root system that occupies the entire substrate volume [28]. Characterizing the specific moisture thresholds that optimize seedling development in these species is therefore of considerable

practical and scientific interest, particularly in the context of increasing water scarcity in production regions.

Substrate water availability influences seedling quality through physiological and morphological mechanisms [29,30]. Water deficit usually reduces transpiration and constrains net photosynthesis, although the magnitude of these responses varies among species and genotypes [31]. For example, some tomato genotypes maintain photosynthesis even under high evaporative demand [32]. In contrast, maximum PSII efficiency is relatively stable and typically declines only under severe and prolonged water stress [33], as observed in *Arabidopsis* after 15 days of stress [34]. Root system architecture also responds to substrate water availability, with fine-root traits often declining under severe drought, although moderate irrigation levels may preserve or enhance root development [35]. Together, these differences in physiological and morphological sensitivity highlight the need for an integrated assessment of seedling responses to substrate moisture conditions.

The present study aimed to evaluate the quality of vegetable seedlings of lettuce and tomato as a function of substrate moisture levels maintained within commercial substrates, monitored by weighing lysimetry under protected environment conditions. The novelty of this work lies primarily in generating new knowledge on the relationship between substrate moisture thresholds and seedling physiological and morphological quality in containerized nursery systems.

2. Materials and Methods

2.1. Characterization of the Experimental Area, Planting and Crop Management

Four experiments were conducted from October to November 2019 and from October to December 2020 at IBS Mudás, located in Piracicaba, São Paulo State, Brazil (22°36′36.6″ S, 47°35′36.6″ W; 575 m above sea level; Figure 1A). The regional climate is classified as Cwa according to the Köppen classification, characterized as humid subtropical with dry winters and wet summers [36].

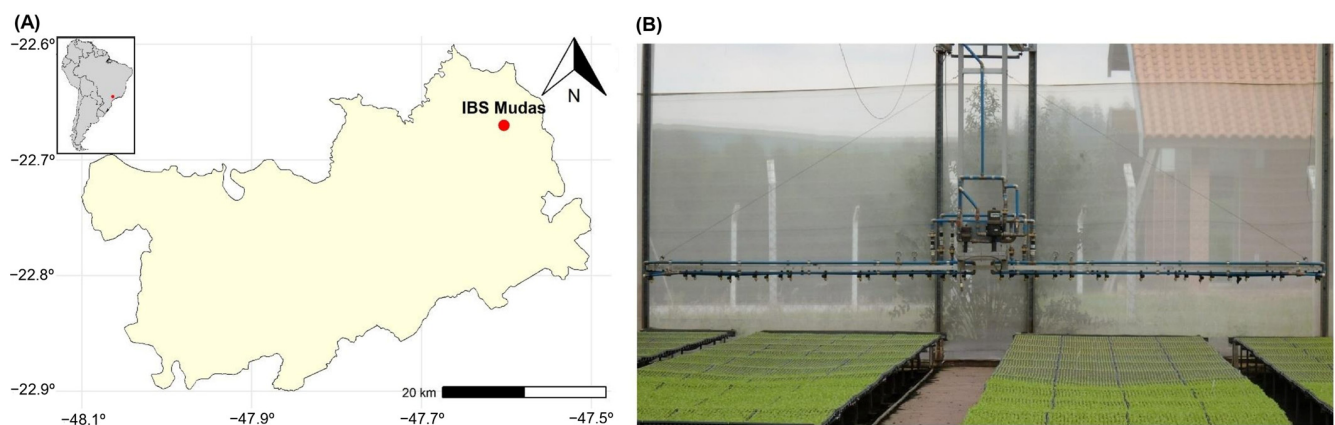


Figure 1. Geographic location of IBS Mudás (A) and overview of the experimental area (B).

The greenhouse structure consisted of galvanized steel with an arched roof, a height of 4.5 m (from ground level to the roof base), and dimensions of 8 m in width and 100 m in length (Figure 1B). The structure was covered with a 150 µm anti-static polyethylene film with UV protection, providing 88% photosynthetically active radiation transmission and 58% light diffusion. A 50% thermoreflective shade screen was installed beneath the roof. Environmental conditions inside the greenhouse were regulated using a cooling system to control air temperature and relative humidity, programmed to maintain temperatures below 28 °C. Daily solar radiation, minimum and maximum air temperatures, and relative humidity were recorded at 10 min intervals using an automatic station installed inside

the experimental area connected to a CR1000 data logger (Campbell Scientific, Logan, UT, USA) (Figure 2).

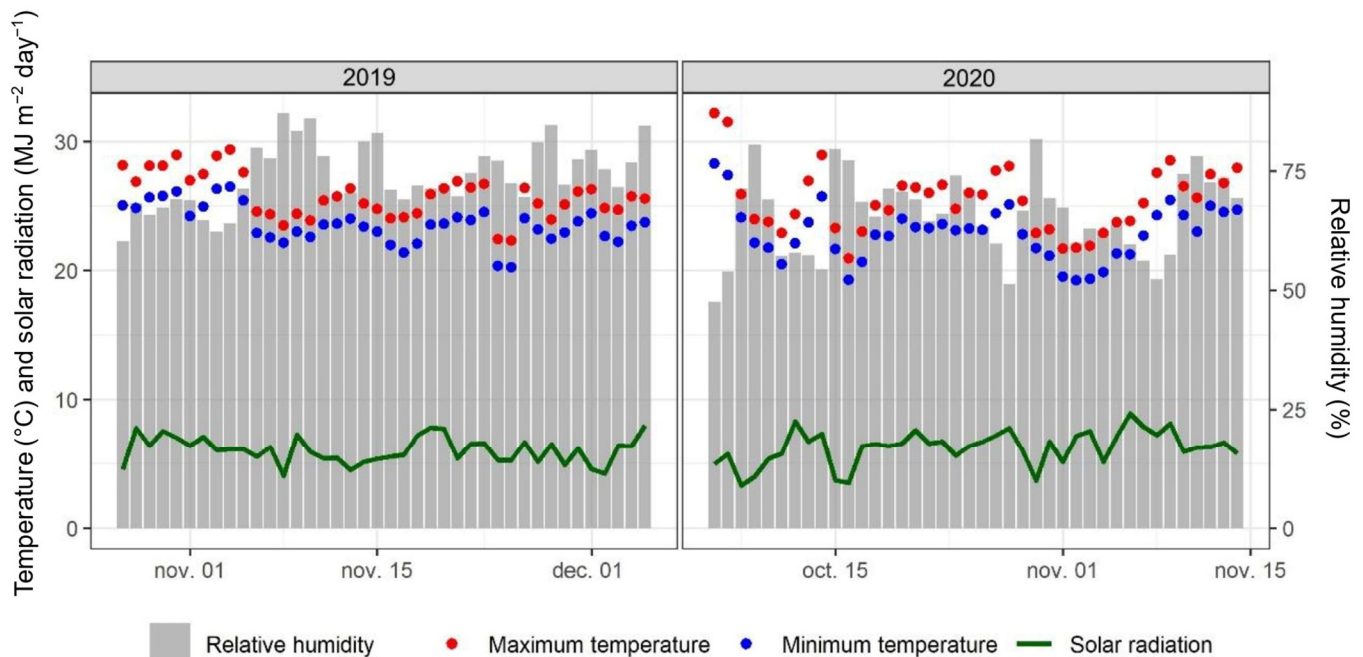


Figure 2. Maximum and minimum temperatures ($^{\circ}\text{C}$), total solar radiation ($\text{MJ m}^{-2} \text{ day}^{-1}$) and relative humidity (%) during the experimental period in 2019 and 2020.

Seeds of crisphead lettuce (*Lactuca sativa* L. cv. Vanda) and tomato (*Solanum lycopersicum* L. cv. Santa Cruz Kada) were sown in polyethylene trays containing 200 and 128 cells, respectively. Both cultivars are widely grown in Brazil and are commonly used as reference genotypes in studies of vegetable seedling quality [37]. Cell volumes were 10 cm^3 for lettuce and 18 cm^3 for tomato, and tray dimensions were $27 \times 54 \text{ cm}$. The trays were filled with a sphagnum peat-based substrate composed of 85% peat and 15% wood fiber, with a water-holding capacity of 40% (v/v , manufacturer-reported, EN 13041 method), electrical conductivity of 0.3 dS m^{-1} (without added fertilizers), and pH 5.6. Following sowing, seeds were covered with a thin layer of vermiculite and moistened to 50% gravimetric water content. The trays were then covered with black polyethylene film and transferred to a dark chamber maintained at $80 \pm 2\%$ relative humidity and $22 \pm 2^{\circ}\text{C}$ to promote germination. Germination occurred after 24 h for lettuce and 48 h for tomato.

2.2. Experimental Design and Irrigation Treatments, and Moisture Monitoring System

Two growing seasons were conducted for each species using a completely randomized design with four replications. Each replication consisted of two seedling trays, resulting in a total of 24 experimental units. Treatments consisted of five substrate moisture thresholds for irrigation scheduling corresponding to 80, 70, 60, 50, and 40% of the substrate water content at holding capacity (gravimetric basis), together with a Control treatment representing the nursery's conventional irrigation management. In the Control treatment, irrigation was applied zero to three times per day according to the grower's criteria.

Substrate moisture levels were determined by randomly selecting three trays from each production batch in each season. The trays were irrigated to saturation and weighed after free drainage had ceased to obtain the mass at container capacity. Subsequently, the trays were oven-dried to constant weight to determine dry mass [38]. All trays were maintained at 60–70% substrate moisture until complete seedling emergence, which occurred five days after sowing (DAS). Thereafter, the treatments were imposed and maintained until

the end of the production cycle, corresponding to 35 and 42 DAS for lettuce and tomato, respectively. The gravimetric substrate water content (SWC) at container capacity was calculated following the approach proposed by Minami and Salvador [39] as follows:

$$\text{SWC}(\%) = \frac{\text{STM} - \text{SDM} - \text{ETM}}{\text{STM} - \text{ETM}} \times 100 \quad (1)$$

where STM is the total mass of the tray at the time of measurement (g), SDM is the dry substrate mass (g), and ETM is the mass of the empty tray (g).

Irrigation was applied using a mechanized overhead microsprinkler system equipped with a linear-moving boom (Figure 1B). Irrigation frequency was kept constant across treatments, while the applied irrigation depth was adjusted by varying boom travel speed according to the target substrate moisture threshold. Average application depths were 1.69, 1.52, 1.23, 1.06, 0.81, and 0.68 mm, enabling adequate water replenishment from the critical tray mass to the target mass associated with each treatment. On average, two to three irrigation events were applied per day.

Irrigation water pH ranged from 7.0 to 7.5, while electrical conductivity (EC) varied between 0.23 and 0.29 dS m⁻¹ throughout seedling production. Fertigation was applied three times per week using a nutrient solution with pH 6.5 and EC 1.7 dS m⁻¹. The solution consisted of an NPK fertilizer supplemented with Micromaster® (3:11:38), containing 3% N, 11% P₂O₅, 38% K₂O, 2.5% Mg, and 10% S. Nutrients were supplied from potassium sulfate, potassium nitrate, magnesium sulfate, and monopotassium phosphate.

2.3. Moisture Monitoring System

Twelve weighing lysimeters were constructed using single-point load cells and arranged in pairs, resulting in six monitoring and control units. Each unit was based on an Arduino Nano microcontroller (ATmega328P, 5 V) and incorporated two HX711 analog-to-digital converter modules connected to two galvanized steel weighing platforms (27 × 54 cm, matching the tray dimensions), each equipped with a 10 kg load cell. The lysimeters were randomly distributed across the experimental bench. Each weighing lysimeter was individually calibrated before and during the experimental period using standard reference masses ranging from 5 to 5000 g, following the procedure described by Fernandes et al. [40].

Real-time tray mass was displayed using a 16 × 2 LCD screen, while measurements were recorded at 10 min intervals using a data logging system consisting of a microSD module with a 16 GB memory card and a DS3231 real-time clock module. Visual indicators (LEDs) were programmed to signal whether tray mass was within, below, or above the target range established for each treatment. All electronic components were mounted on a perforated phenolic board and powered by a regulated 12 V power supply.

Water replenishment was managed manually using gravimetric measurements obtained from the lysimeters, following the target moisture levels established for each treatment. The weighing system incorporated LED indicators linked to predefined lower and upper weight thresholds, providing real-time guidance for irrigation decisions. LEDs signaled when irrigation was required and when the target substrate moisture range had been reached. Crop evapotranspiration (ET_c) was estimated from the daily water consumption of the trays. Water use (L) was calculated as the difference between tray mass immediately after irrigation and the mass recorded before the subsequent irrigation event. The cumulative daily water consumption was then divided by the tray surface area (m²) and expressed as ET_c (mm day⁻¹).

2.4. Morphological Parameters

At the end of each experiment, 20 seedlings per replication were sampled at 35 and 42 DAS for lettuce and tomato, respectively. Shoot and root fresh mass, shoot and root dry mass, plant height, stem diameter (tomato only), and leaf area were assessed. Leaf area was measured using a leaf area meter (LI-3100C, LI-COR Biosciences, Lincoln, NE, USA). Shoot dry mass was determined by drying plant samples to a constant weight in an oven with forced air circulation for 72 h.

2.5. Root System Architecture

Root system architecture was evaluated using 10 plants per replication to ensure the precision and reliability of the results. Roots were carefully washed and preserved in a 20% ethanol solution prior to analysis. Root samples were scanned using an Epson scanner coupled to the WinRHIZO[®] image analysis software, version 4.1 (Regent Instruments Inc., Quebec, QC, Canada). The following root traits were quantified: total root length (cm), projected area (cm²), surface area (cm²), average diameter (mm), and root volume (cm³).

2.6. Physiological Parameters

Physiological measurements were conducted at the end of each experiment during the 2020 growing season in three plants per replication, due to technical issues with the measuring equipment in 2019. Gas exchange parameters were assessed using a portable gas exchange system (Li-6400 XT, IRGA/Li-COR Inc., Lincoln, NE, USA). Net photosynthesis, stomatal conductance, and transpiration rate were measured between 09:00 and 11:00 h on clear-sky days. Intrinsic water use efficiency (iWUE) was calculated as the ratio of A to g_s. The equipment was set to use concentrations of 400 µmol CO₂ mol⁻¹ air in the leaf chamber. Photosynthetic photon flux density (PPFD) was set at 1200 µmol [quanta] m⁻² s⁻¹ for lettuce and 1400 [quanta] µmol m⁻² s⁻¹ for tomato. In addition, the chlorophyll index (unitless) was measured using a handheld chlorophyll meter (Falker, Porto Alegre, Brazil) that uses photodiode emitters at three wavelengths: two emit within the red band, close to the peaks of each chlorophyll type (λ = 635 and 660 nm), and another in the near-infrared (λ = 880 nm).

Chlorophyll fluorescence-based technology was applied to obtain information in seedlings using a SeedReporter[™] (PhenoVation B.V., Wageningen, The Netherlands). This system allows the imaging of photosynthetic parameters of whole plants within a short time interval (≈800 ms). Chlorophyll fluorescence imaging was performed using a high-intensity LED illumination system composed of 36 amber LEDs (peak emission at 620 nm), generating a saturating flash of 6320 µmol m⁻² s⁻¹ according to the Kautsky induction curve methodology [41]. Prior to image acquisition, seedlings were dark-adapted for 30 min to ensure that all photosystem II reaction centers were fully open.

Leaves were positioned 25 cm from the LED source. A 730 nm interference filter blocked the excitation light and transmitted chlorophyll fluorescence emitted by the plant tissue to a CCD sensor. High-resolution images (2448 × 2448 pixels) were acquired and analyzed to assess photosynthetic performance through chlorophyll fluorescence parameters. Using the SeedReporter[™] software version 5.4.6, each pixel of the fluorescence image was used to calculate F_v/F_m, where F_v is the variable fluorescence and F_m is the maximum fluorescence, which correlates with the quantum yield of photosystem II (PSII) photochemistry.

2.7. Chlorophyll and Carotenoid Pigments

Chlorophyll and carotenoid contents were determined at 35 and 42 DAS for lettuce and tomato, respectively, following the non-maceration chlorophyll extraction method described by Hiscox and Israelstam [42]. Briefly, 20 mg of fresh leaf tissue was placed in test tubes containing 5 mL of dimethyl sulfoxide (DMSO). Samples were incubated in the dark at room temperature for 48 h to allow pigment extraction.

After extraction, 3 mL of the supernatant was transferred to a glass cuvette, and absorbance was measured using a spectrophotometer (Libra S22, Biochrom Ltd., Cambridge, UK). Absorbance readings were recorded at 665, 649, and 480 nm for the determination of chlorophyll a, chlorophyll b, and total carotenoids, respectively. Pigment concentrations were calculated using the equations proposed by Wellburn [43] and expressed as $\mu\text{g g}^{-1}$ fresh weight (FW).

2.8. Statistical Analysis

All statistical analyses were conducted using R software v4.5.1 [44]. Data were subjected to analysis of variance (ANOVA) using the package ‘ExpDes’ [45]. Shapiro–Wilk and Levene tests were used to estimate normality and homogeneity of variance. The effects of irrigation treatments were evaluated using the F-test at the 0.05 probability level. The means of variables with a significant F-test value were compared using the Tukey test.

Principal Component Analysis (PCA) was used to generate biplots to show the relationship between the assessed variables and the irrigation treatments using the FactoMineR package [46]. Data for lettuce and tomato seedlings were obtained from the 2020 growing season, as gas exchange measurements were performed only during this experimental period. To evaluate the appropriateness of the data for PCA, Bartlett’s test of sphericity was applied to assess multicollinearity among the variables.

3. Results

3.1. Irrigation Water Applied

The cumulative water consumption for lettuce and tomato subjected to irrigation treatments is shown in Figure 3. The total irrigation water consumption of lettuce seedlings ranged from 78 to 92 mm during the 2019 growing season and from 77 to 88 mm during the 2020 growing season. The 40% treatment diverged from the other treatments after 25 DAS in both growing seasons, consistently exhibiting lower irrigation water use. In contrast, the 80% treatment and the Control accumulated the greatest cumulative irrigation depths throughout the experimental period.

Across treatments, the total irrigation water consumption of tomato seedlings ranged from 91 to 97 mm during the 2019 growing season and from 111 to 132 mm during the 2020 growing season. In season 1, all treatments followed very similar irrigation depths despite the different moisture thresholds. In season 2, treatment separation became more apparent after 27 DAS. The 80% treatment accumulated the highest irrigation depth, whereas the 40% treatment accumulated the lowest.

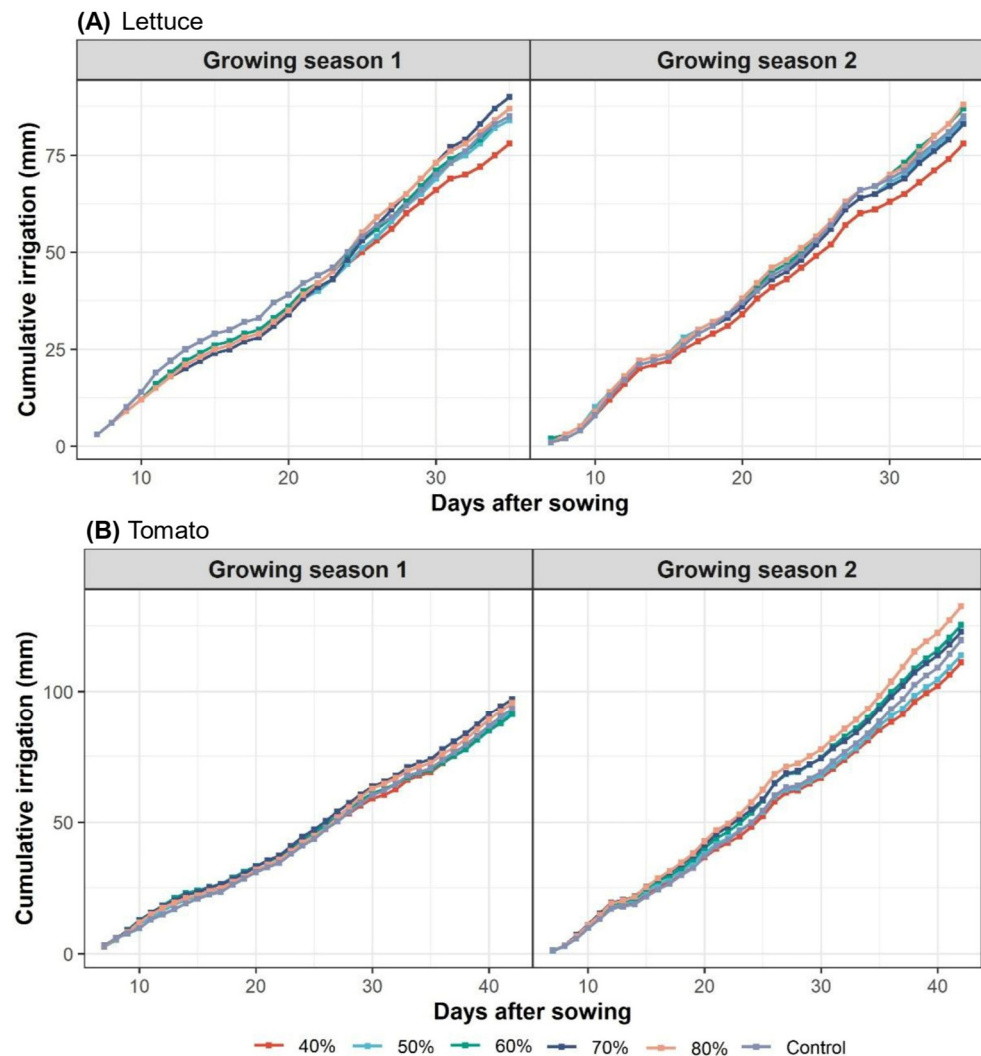


Figure 3. Irrigation water applied in lettuce (A) and tomato (B) subjected to different irrigation treatments.

3.2. Morphological Responses

Irrigation treatment affected all measured growth parameters in lettuce and tomato seedlings in both experimental years (Figure 4 and Table 1). In lettuce, leaf area per plant ranged from 22.9 to 29.2 cm² in 2019 and from 20.3 to 24.5 cm² in 2020. In 2019 and 2020, plants under 70 and 60% treatments produced significantly larger leaf areas than those at 40%. The Control and intermediate treatments (70 and 60%) did not differ significantly from one another. Plant height was the most sensible variable to irrigation reduction in both years. The general trend was that plants under the 60% treatment were the tallest plants compared to the other treatments (>12 cm in both seasons). In contrast, the 40% treatment resulted in the shortest plants (<8 cm in both seasons). Shoot and root fresh mass followed a similar pattern, with significant reductions concentrated in the most severe deficit treatments. Shoot fresh mass decreased by approximately 21% under the 40% irrigation treatment compared with the Control in 2019 and with the 70% irrigation treatment in 2020. Root fresh mass was significantly reduced under the 40% irrigation treatment, decreasing by 30.4% in 2019 and 18.2% in 2020 relative to the highest-irrigation treatment. Dry mass accumulation mirrored fresh mass trends, with shoot dry mass approximately 27% lower under the 40% irrigation treatment in 2019 compared to the 70% irrigation treatment, whereas in 2020 only root dry mass was significantly reduced (26%) under the same treatment.

Table 1. Lettuce and tomato morphological parameters under different irrigation treatments for two growing seasons.

Treatments	Lettuce							Tomato					
	Leaf Area (cm ²)	Plant Height (cm)	Shoot Fresh Mass (mg plant ⁻¹)	Root Fresh Mass (mg plant ⁻¹)	Shoot Dry Mass (mg plant ⁻¹)	Root Dry Mass (mg plant ⁻¹)	Leaf Area (cm ²)	Plant Height (cm)	Shoot Fresh Mass (mg plant ⁻¹)	Root Fresh Mass (mg plant ⁻¹)	Shoot Dry Mass (mg plant ⁻¹)	Root Dry Mass (mg plant ⁻¹)	Stem Diameter (mm)
2019													
Control	25.8 ± 0.7 ab	10.4 ± 0.4 bc	888.8 ± 26.1 a	362.7 ± 16.8 a	75.5 ± 3.26 ab	27.0 ± 0.9 ab	26.6 ± 1.6 a	11.8 ± 0.3 ab	1581.7 ± 104.2 a	610.0 ± 49.5 ab	152.2 ± 9.1 a	54.3 ± 2.7 a	2.6 ± 0.1 a
80%	25.2 ± 1.4 ab	10.7 ± 0.3 b	816.8 ± 37.6 ab	325.5 ± 17.7 ab	67.1 ± 4.23 b	29.2 ± 1.9 ab	23.0 ± 0.6 a	10.9 ± 0.7 bc	1282.0 ± 43.2 b	729.0 ± 81.0 a	116.7 ± 6.7 bc	48.0 ± 4.0 ab	2.2 ± 0.0 b
70%	29.2 ± 1.4 a	9.0 ± 0.4 cd	886.8 ± 39.8 ab	351.0 ± 25.7 ab	84.6 ± 3.39 a	32.7 ± 0.9 a	23.4 ± 1.4 a	11.4 ± 0.4 ab	1257.5 ± 70.0 b	641.0 ± 68.4 ab	139.7 ± 8.3 ab	43.8 ± 1.4 ab	2.4 ± 0.1 ab
60%	28.3 ± 0.8 a	12.8 ± 0.3 a	864.8 ± 62.6 ab	364.0 ± 33.1 a	78.4 ± 4.95 ab	31.5 ± 0.7 a	25.2 ± 0.7 a	12.8 ± 0.3 a	1369.7 ± 46.7 ab	731.5 ± 55.6 a	153.8 ± 6.3 a	45.9 ± 2.0 ab	2.6 ± 0.0 a
50%	26.2 ± 1.1 ab	7.3 ± 0.3 e	748.0 ± 40.0 ab	302.5 ± 20.2 ab	67.3 ± 2.42 b	30.0 ± 1.9 ab	17.9 ± 0.6 b	10.3 ± 0.3 bc	929.8 ± 26.4 c	657.5 ± 54.1 ab	102.8 ± 2.9 c	50.4 ± 2.1 ab	2.3 ± 0.0 ab
40%	22.9 ± 0.9 b	7.8 ± 0.3 de	705.8 ± 57.3 b	252.5 ± 11.8 b	62.0 ± 4.27 b	24.2 ± 2.1 b	17.4 ± 0.9 b	9.2 ± 0.4 c	1166.1 ± 52.2 bc	458.0 ± 12.2 b	130.2 ± 7.3 abc	40.8 ± 1.4 b	2.4 ± 0.1 ab
2020													
Control	21.8 ± 1.3 ab	11.0 ± 0.3 ab	823.3 ± 34.7 ab	443.0 ± 14.4 ab	63.8 ± 1.8 ab	42.5 ± 1.3 a	26.4 ± 1.1 a	13.6 ± 0.4 a	1491.9 ± 24.9 a	679.0 ± 40.9 a	204.0 ± 6.6 a	68.5 ± 2.9 a	2.4 ± 0.1 ab
80%	22.5 ± 1.0 ab	10.1 ± 0.3 bc	874.8 ± 38.9 ab	448.5 ± 15.6 a	66.3 ± 4.1 ab	41.5 ± 1.5 a	23.8 ± 0.5 ab	12.2 ± 0.4 ab	1537.2 ± 122.9 a	683.5 ± 22.2 a	205.5 ± 7.7 a	64.0 ± 2.5 ab	2.3 ± 0.1 ab
70%	24.5 ± 0.8 a	11.0 ± 0.7 ab	932.8 ± 18.3 a	458.5 ± 18.0 a	68.3 ± 1.4 ab	39.5 ± 1.0 a	22.5 ± 0.2 b	12.3 ± 1.1 ab	1391.6 ± 16.2 a	651.5 ± 18.7 ab	204.5 ± 3.5 a	63.0 ± 1.9 ab	2.5 ± 0.1 a
60%	24.4 ± 1.0 a	12.0 ± 0.1 a	932.5 ± 41.7 a	424.5 ± 19.8 ab	70.0 ± 4.2 a	40.0 ± 0.8 a	24.1 ± 0.9 ab	11.7 ± 0.3 ab	1460.9 ± 25.2 a	639.0 ± 19.8 ab	204.0 ± 11.2 a	69.5 ± 2.6 a	2.5 ± 0.1 a
50%	20.9 ± 0.4 ab	8.8 ± 0.1 cd	851.3 ± 22.5 ab	476.0 ± 15.2 a	70.0 ± 1.5 a	42.0 ± 1.4 a	22.4 ± 0.9 b	9.9 ± 0.5 bc	1351.9 ± 29.4 a	631.5 ± 17.8 ab	185.5 ± 9.7 a	57.0 ± 1.3 bc	2.2 ± 0.1 b
40%	20.3 ± 0.4 b	8.0 ± 0.3 d	774.0 ± 18.2 b	367.0 ± 19.0 b	57.5 ± 1.9 b	31.5 ± 2.2 b	22.8 ± 1.7 ab	8.7 ± 0.3 c	1370.9 ± 46.4 a	543.0 ± 21.9 b	176.5 ± 13.3 a	47.0 ± 2.4 c	2.2 ± 0.2 b

Means ± standard error followed by distinct letters within a column are different based on the Tukey test at 0.05 significance.

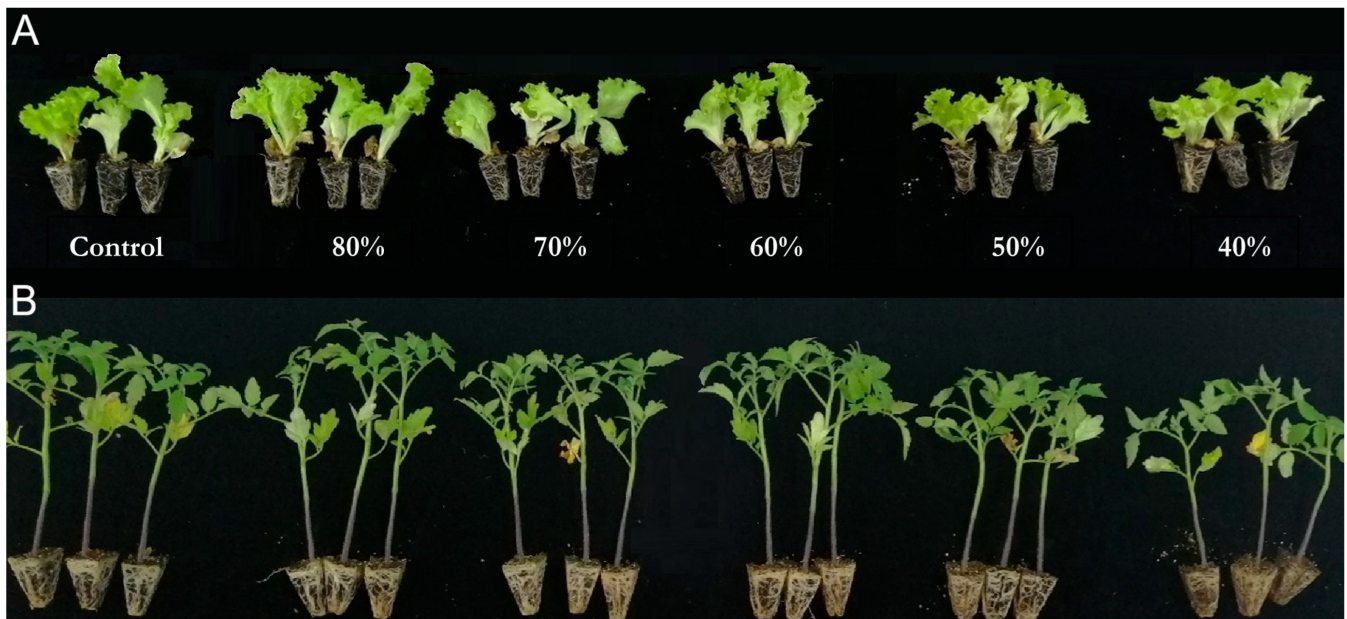


Figure 4. Representative plants of lettuce (A) and tomato (B) at the end of the 2020 growing season under the different irrigation treatments (Control, 80, 70, 60, 50, and 40% holding capacity).

In tomato, leaf area varied between 17.9 and 26.6 cm² in 2019 and between 1351.9 and 1537.2 cm² in 2020. In 2019, the Control treatment produced the largest leaf area, while the 50% irrigation treatment showed the lowest values. Furthermore, leaf area was significantly lower under the 80 and 70% irrigation treatments than under the Control. In 2020, however, no significant differences in leaf area were detected among treatments. Plant height responded differently to irrigation than leaf area. In 2019, the 60 and 80% irrigation treatments produced taller plants than the Control, whereas the most severe water deficit (40% irrigation) reduced plant height by 28%. Stem diameter was significantly reduced under the 80% irrigation treatment compared with the Control in 2019 and compared with the 50 and 40% irrigation treatments in 2020. Shoot fresh mass was greater under the 60% and Control irrigation treatments than under the 40% irrigation treatment. Interestingly, shoot fresh mass was reduced under the 80% irrigation treatment. Root fresh mass was reduced in both seasons, being lower under the 40% irrigation treatment compared to the Control and 80% irrigation treatments. Shoot dry mass was reduced under the 50% irrigation treatment in 2019 (102.8 mg) and under the 40 and 50% treatments in 2020 (176.5–185.5 mg). Root dry mass was consistently lower under the 40 and 50% treatments in both years.

3.3. Root System Architecture

The effects of irrigation on root architecture varied between species, revealing contrasting patterns of root development in lettuce and tomato (Table 2). In lettuce, the 80% irrigation treatment consistently promoted root development, producing the greatest total root length, projection area, total surface area, and root volume in both seasons. Relative to the 80% treatment, the 40% irrigation treatments reduced total root length by 30–39%, projection area and total surface area by 26%, and root volume by 11–21%. In contrast, root average diameter varied between years, increasing under 50 and 40% irrigation treatments in 2019 but showing no significant treatment effects in 2020.

Table 2. Lettuce and tomato root system architecture under different irrigation treatments for two growing seasons.

Treatments	Lettuce					Tomato				
	Root Total Length (cm)	Root Projection Area (cm ²)	Root Total Surface Area (cm ²)	Root Average Diameter (mm)	Volume (cm ³)	Root Total Length (cm)	Root Projection Area (cm ²)	Root Total Surface Area (cm ²)	Root Average Diameter (mm)	Volume (cm ³)
2019										
Control	245.88 ± 7.61 bc	9.23 ± 0.38 b	29.00 ± 1.20 b	0.38 ± 0.01 b	0.27 ± 0.01 b	334.28 ± 9.16 a	16.98 ± 0.52 ab	53.35 ± 1.66 ab	0.51 ± 0.01 ab	0.68 ± 0.02 ab
80%	317.32 ± 7.42 a	11.97 ± 0.25 a	37.60 ± 0.79 a	0.38 ± 0.02 b	0.36 ± 0.02 a	305.33 ± 20.00 ab	16.05 ± 0.86 ab	50.43 ± 2.76 ab	0.53 ± 0.01 a	0.67 ± 0.03 ab
70%	266.48 ± 12.63 ab	9.48 ± 0.38 b	29.77 ± 1.21 b	0.36 ± 0.01 b	0.27 ± 0.01 b	308.48 ± 14.65 ab	15.55 ± 0.62 b	48.85 ± 1.89 b	0.51 ± 0.01 ab	0.62 ± 0.03 bc
60%	265.79 ± 19.80 ab	9.89 ± 0.48 b	31.06 ± 1.51 b	0.38 ± 0.01 b	0.29 ± 0.01 ab	370.18 ± 17.58 a	18.65 ± 0.74 a	58.63 ± 2.28 a	0.51 ± 0.01 ab	0.74 ± 0.03 a
50%	203.40 ± 12.62 c	8.87 ± 0.48 b	27.86 ± 1.50 b	0.44 ± 0.01 a	0.31 ± 0.02 ab	313.55 ± 13.14 ab	14.70 ± 0.67 bc	46.15 ± 2.08 bc	0.47 ± 0.01 c	0.54 ± 0.03 cd
40%	203.46 ± 9.54 c	9.05 ± 0.29 b	28.42 ± 0.92 b	0.45 ± 0.01 a	0.32 ± 0.01 ab	254.25 ± 10.63 b	12.10 ± 0.43 c	37.98 ± 1.35 c	0.48 ± 0.01 bc	0.45 ± 0.01 d
2020										
Control	354.51 ± 14.70 ab	14.52 ± 0.48 ab	45.63 ± 1.52 ab	0.41 ± 0.01 a	0.47 ± 0.01 ab	413.29 ± 16.26 a	18.77 ± 1.28 ab	58.97 ± 1.28 ab	0.41 ± 0.01 a	0.67 ± 0.01 a
80%	372.87 ± 35.69 a	15.76 ± 1.23 a	49.50 ± 3.88 a	0.43 ± 0.01 a	0.53 ± 0.01 a	405.26 ± 21.06 a	18.52 ± 1.03 ab	58.19 ± 3.24 ab	0.42 ± 0.01 a	0.67 ± 0.04 a
70%	337.02 ± 22.42 ab	15.05 ± 1.00 ab	47.26 ± 3.15 ab	0.45 ± 0.01 a	0.53 ± 0.01 a	394.40 ± 11.71 a	19.58 ± 0.50 a	61.50 ± 1.58 a	0.45 ± 0.02 a	0.64 ± 0.02 a
60%	286.41 ± 16.22 ab	12.54 ± 0.60 ab	39.39 ± 1.88 ab	0.44 ± 0.01 a	0.43 ± 0.01 ab	387.40 ± 22.17 a	18.38 ± 0.47 ab	57.74 ± 1.49 ab	0.43 ± 0.01 a	0.69 ± 0.03 a
50%	261.31 ± 21.65 b	11.72 ± 0.66 b	36.81 ± 2.09 b	0.46 ± 0.02 a	0.42 ± 0.02 b	348.62 ± 12.78 ab	15.95 ± 0.28 bc	50.11 ± 0.86 bc	0.42 ± 0.01 a	0.58 ± 0.01 ab
40%	267.46 ± 17.73 b	12.19 ± 0.37 b	38.29 ± 1.16 b	0.46 ± 0.02 a	0.44 ± 0.02 ab	292.68 ± 13.27 b	13.69 ± 0.78 c	43.02 ± 2.45 c	0.43 ± 0.01 a	0.51 ± 0.04 b

Means ± standard error followed by distinct letters within a column are different based on the Tukey test at 0.05 significance.

In tomato, root development was maintained or enhanced under moderate irrigation deficit (80–60% irrigation treatments), whereas the 40% treatment consistently reduced root growth. Across both seasons, the 40% treatment decreased total root length by 20–31%, projection area and total surface area by 18–35%, and root volume by 21–39%, relative to the best-performing treatments. In contrast, root average diameter showed less sensitivity to irrigation, differing among treatments only in 2019, where the 50% irrigation treatment was reduced by 11% compared to the 80% treatment.

3.4. Physiological Responses

Physiological responses also revealed the contrasting responses of lettuce and tomato to the applied irrigation treatments (Table 3). For lettuce, net photosynthesis ranged from 2.57 to 4.83 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$, with the 80% treatment producing the highest value, significantly greater than the 40% treatment. Stomatal conductance and transpiration followed a similar trend, with the 80% treatment producing the highest values (0.17 $\text{mol m}^{-2} \text{ s}^{-1}$ and 3.93 $\text{mmol m}^{-2} \text{ s}^{-1}$, respectively), significantly higher than the 50 and 40% treatments, which presented the lowest stomatal conductance (0.05 and 0.03 $\text{mol m}^{-2} \text{ s}^{-1}$) and transpiration (1.32 and 0.86 $\text{mmol m}^{-2} \text{ s}^{-1}$). Intrinsic water use efficiency (iWUE) increased progressively as irrigation was reduced, from 33.97 in the 80% treatment to 92.16 in the 40% treatment. Irrigation treatment had no significant effect on F_v/F_m or the chlorophyll index.

For tomato, net photosynthesis was affected by irrigation treatments, ranging from 2.35 to 14.31 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$. Photosynthesis was highest under the 70 and 80% irrigation treatments (14.31 and 13.19, respectively), remaining comparable to the Control but exceeding the 60% treatment by 31–57% and the 50–40% treatments by 364–509%, which exhibited severely reduced photosynthetic rates. Stomatal conductance and transpiration exhibited an analogous pattern, with the 70 and 80% treatments showing the highest values (0.18–0.19 $\text{mol m}^{-2} \text{ s}^{-1}$ and 3.02–3.63 $\text{mmol m}^{-2} \text{ s}^{-1}$), while the 50 and 40% treatments presented values close to zero (0.02 $\text{mol m}^{-2} \text{ s}^{-1}$ and 0.39–0.40 $\text{mmol m}^{-2} \text{ s}^{-1}$). Intrinsic water use efficiency showed an increase under the most restrictive treatments, with the 50% and 40% treatments significantly exceeding all other treatments. F_v/F_m declined with increasing water deficit, from 0.78 in the Control to 0.70 in the 50 and 40% irrigation treatments. The chlorophyll index did not differ significantly among treatments.

3.5. Photosynthetic Pigments

Photosynthetic pigment concentrations differed significantly among irrigation treatments and seasons for both lettuce and tomato (Table 4). For lettuce, in 2019, chlorophyll *a* increased under severe water deficit, reaching its highest value under the 40% treatment, whereas chlorophyll *b* and carotenoids were greatest under the 70–80% irrigation treatments. In 2020, chlorophyll *a* and carotenoid contents were highest under the 80% treatment and lowest under the 70% treatment, while chlorophyll *b* was higher under the 50 and 40% treatments. Overall, irrigation effects on leaf pigment composition were inconsistent across seasons.

For tomato, in 2019, only chlorophyll *a* was affected by the irrigation treatment, with lower concentrations under the 80% treatment than under the remaining irrigation treatments, whereas chlorophyll *b* and carotenoids were similar among treatments. In 2020, chlorophyll *a*, chlorophyll *b*, and carotenoid concentrations were higher with increasing water deficit, reaching their highest values under the 40% treatment and their lowest values under the 80% treatment.

Table 3. Lettuce and tomato physiological responses under different irrigation treatments for two growing seasons.

Treatments	Lettuce						Tomato					
	Photosynthesis ($\mu\text{mol CO}_2$ $\text{m}^{-2} \text{s}^{-1}$)	Stomatal Conductance ($\text{mol m}^{-2} \text{s}^{-1}$)	Transpiration ($\text{mmol m}^{-2} \text{s}^{-1}$)	iWUE	Fv/Fm	Chlorophyll Index	Photosynthesis ($\mu\text{mol CO}_2$ $\text{m}^{-2} \text{s}^{-1}$)	Stomatal Conductance ($\text{mol m}^{-2} \text{s}^{-1}$)	Transpiration ($\text{mmol m}^{-2} \text{s}^{-1}$)	iWUE	Fv/Fm	Chlorophyll Index
2020												
Control	4.30 $\pm$ 0.79 ab	0.10 $\pm$ 0.02 ab	2.64 $\pm$ 0.35 ab	43.00 $\pm$ 3.00 bc	0.73 $\pm$ 0.00 a	12.85 $\pm$ 0.31 a	10.52 $\pm$ 0.96 bc	0.14 $\pm$ 0.02 ab	2.47 $\pm$ 0.49 ab	75.14 $\pm$ 6.85 b	0.78 $\pm$ 0.01 a	33.90 $\pm$ 0.81 a
80%	4.83 $\pm$ 0.38 a	0.17 $\pm$ 0.04 a	3.93 $\pm$ 0.82 a	28.41 $\pm$ 7.25 c	0.73 $\pm$ 0.01 a	11.05 $\pm$ 1.28 a	13.19 $\pm$ 1.07 ab	0.18 $\pm$ 0.04 a	3.02 $\pm$ 0.20 ab	73.28 $\pm$ 12.24 b	0.73 $\pm$ 0.01 ab	31.37 $\pm$ 0.49 a
70%	3.93 $\pm$ 0.29 ab	0.09 $\pm$ 0.01 ab	2.43 $\pm$ 0.22 ab	43.66 $\pm$ 3.10 bc	0.72 $\pm$ 0.01 a	11.10 $\pm$ 0.86 a	14.31 $\pm$ 0.47 a	0.19 $\pm$ 0.01 a	3.63 $\pm$ 0.22 a	75.32 $\pm$ 3.19 b	0.73 $\pm$ 0.01 ab	32.78 $\pm$ 1.74 a
60%	4.51 $\pm$ 0.65 ab	0.09 $\pm$ 0.02 ab	2.37 $\pm$ 0.48 ab	50.11 $\pm$ 6.27 abc	0.73 $\pm$ 0.00 a	12.63 $\pm$ 0.27 a	9.13 $\pm$ 0.61 c	0.12 $\pm$ 0.02 b	2.31 $\pm$ 0.29 b	76.08 $\pm$ 10.9 b	0.73 $\pm$ 0.01 ab	33.17 $\pm$ 0.91 a
50%	3.20 $\pm$ 0.31 ab	0.05 $\pm$ 0.01 b	1.32 $\pm$ 0.27 b	64.00 $\pm$ 16.88 ab	0.73 $\pm$ 0.01 a	11.98 $\pm$ 0.70 a	2.84 $\pm$ 0.72 d	0.02 $\pm$ 0.00 c	0.40 $\pm$ 0.06 c	142.00 $\pm$ 19.39 a	0.70 $\pm$ 0.00 b	34.07 $\pm$ 0.29 a
40%	2.57 $\pm$ 0.47 b	0.03 $\pm$ 0.01 b	0.86 $\pm$ 0.16 b	85.66 $\pm$ 7.35 a	0.74 $\pm$ 0.01 a	12.40 $\pm$ 0.52 a	2.35 $\pm$ 0.57 d	0.02 $\pm$ 0.00 c	0.39 $\pm$ 0.12 c	117.50 $\pm$ 14.01 a	0.70 $\pm$ 0.00 b	34.36 $\pm$ 0.22 a

Means $\pm$ standard error followed by distinct letters within a column are different based on the Tukey test at 0.05 significance.

Table 4. Lettuce and tomato photosynthetic pigments under different irrigation treatments for two growing seasons.

Treatment	Lettuce			Tomato		
	Chlorophyll <i>a</i>	Chlorophyll <i>b</i>	Carotenoids	Chlorophyll <i>a</i>	Chlorophyll <i>b</i>	Carotenoids
2019						
Control	0.23 $\pm$ 0.02 d	0.05 $\pm$ 0.01 b	0.10 $\pm$ 0.01 bc	2.01 $\pm$ 0.03 a	0.42 $\pm$ 0.01 a	0.71 $\pm$ 0.01 a
80%	0.32 $\pm$ 0.02 bc	0.06 $\pm$ 0.01 ab	0.13 $\pm$ 0.01 a	1.39 $\pm$ 0.06 b	0.53 $\pm$ 0.11 a	0.65 $\pm$ 0.05 a
70%	0.36 $\pm$ 0.01 b	0.08 $\pm$ 0.01 a	0.15 $\pm$ 0.01 a	1.80 $\pm$ 0.09 a	0.55 $\pm$ 0.07 a	0.74 $\pm$ 0.05 a
60%	0.29 $\pm$ 0.01 cd	0.05 $\pm$ 0.01 b	0.13 $\pm$ 0.01 ab	1.97 $\pm$ 0.07 a	0.41 $\pm$ 0.03 a	0.70 $\pm$ 0.02 a
50%	0.30 $\pm$ 0.01 bc	0.06 $\pm$ 0.01 ab	0.13 $\pm$ 0.01 ab	1.93 $\pm$ 0.09 a	0.35 $\pm$ 0.06 a	0.66 $\pm$ 0.02 a
40%	0.48 $\pm$ 0.01 a	0.06 $\pm$ 0.01 ab	0.09 $\pm$ 0.01 c	1.85 $\pm$ 0.03 a	0.41 $\pm$ 0.02 a	0.67 $\pm$ 0.01 a
2020						
Control	0.20 $\pm$ 0.01 bc	0.06 $\pm$ 0.01 bc	0.07 $\pm$ 0.01 b	1.76 $\pm$ 0.04 bc	0.38 $\pm$ 0.02 ab	0.65 $\pm$ 0.02 bc
80%	0.32 $\pm$ 0.04 a	0.08 $\pm$ 0.01 ab	0.10 $\pm$ 0.01 a	1.20 $\pm$ 0.08 d	0.25 $\pm$ 0.02 b	0.47 $\pm$ 0.03 d
70%	0.13 $\pm$ 0.01 c	0.05 $\pm$ 0.01 c	0.05 $\pm$ 0.01 c	1.51 $\pm$ 0.08 c	0.42 $\pm$ 0.08 ab	0.59 $\pm$ 0.03 c
60%	0.25 $\pm$ 0.02 ab	0.07 $\pm$ 0.01 abc	0.07 $\pm$ 0.01 b	2.03 $\pm$ 0.04 ab	0.44 $\pm$ 0.01 ab	0.79 $\pm$ 0.02 a
50%	0.25 $\pm$ 0.01 ab	0.09 $\pm$ 0.01 a	0.09 $\pm$ 0.01 ab	1.98 $\pm$ 0.03 ab	0.42 $\pm$ 0.01 ab	0.72 $\pm$ 0.01 ab
40%	0.28 $\pm$ 0.02 ab	0.09 $\pm$ 0.01 a	0.09 $\pm$ 0.01 ab	2.21 $\pm$ 0.10 a	0.54 $\pm$ 0.09 a	0.83 $\pm$ 0.03 a

Means $\pm$ standard error followed by distinct letters within a column are different based on the Tukey test at 0.05 significance.

3.6. Principal Component Analysis for Assessed Variables

For lettuce, the first two principal components explained 73.8% of total variance (PC1 = 54.2% and PC2 = 19.6%) (Figure 5A). The 80% treatment was positioned in the upper right quadrant, associated with high values of Fv/Fm, chlorophyll *a*, and carotenoids, as well as several growth-related variables, while the 70 and 60% treatments were positioned in the lower right quadrant, associated with high values of plant height, leaf area, shoot fresh mass, and shoot dry mass but lower values of root diameter (RD) and pigment-related variables. The 50 and 40% treatments were positioned on the negative side of PC1, associated with high iWUE and, in the case of the 40% treatment, elevated chlorophyll *a*. The Control treatment was positioned near the origin, close to the vector cluster of root architecture and gas exchange variables.

For tomato, the first two principal components explained 81.6% of the total variance (PC1 = 69.1% and PC2 = 12.5%) (Figure 5B). The Control and 60% treatments were positioned on the positive side of PC1, associated with high values of leaf area, plant height, and pigment-related variables, while the 80 and 70% treatments were positioned in the lower right quadrant, associated with high values of root architecture variables and gas exchange parameters but low root average diameter. The 50 and 40% treatments were positioned on the negative side of PC1, associated with high iWUE and low values of growth, root, and gas exchange variables.

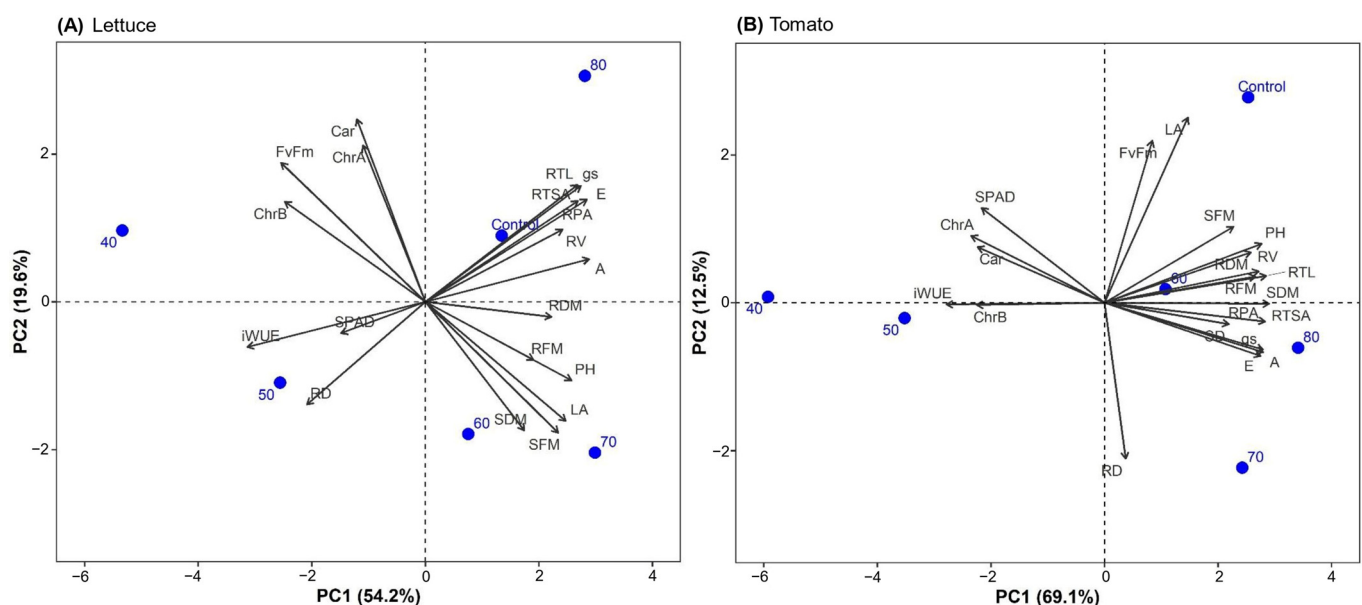


Figure 5. PCA biplots of the studied variables and irrigation treatments. Blue dots represent the centroids for each irrigation treatment. Black arrows represent the loading vectors of the studied traits. The angles between the vectors derived from the middle point of biplots exhibit the positive or negative interactions of the studied traits. LA, leaf area; PH, plant height; SFM, shoot fresh mass; RFM, root fresh mass; SDM, shoot dry mass; RDM, root dry mass; SD, stem diameter; RTL, root total length; RPA, root projection area; RTSA, root total surface area; RDM, root average diameter; RV, root volume; A, net photosynthesis; gs, stomatal conductance; E, transpiration rate; iWUE, intrinsic water use efficiency; Fv/Fm, maximum quantum yield of photosystem II; SPAD, chlorophyll index; ChrA, chlorophyll *a*; ChrB, chlorophyll *b*; Car, carotenoids.

4. Discussion

Seedling quality is linked to substrate moisture conditions, making irrigation management a critical component of nursery production. Although irrigation management for lettuce and tomato throughout the crop growing season has been widely studied [47–50],

little attention has been given to irrigation management during the nursery stage. The responses observed in the present study highlight the importance of identifying irrigation levels that maximize seedling growth and physiological activity.

4.1. Water Savings and Growth Responses During Seedling Production

Cumulative irrigation depth decreased progressively with increasing irrigation restrictions, with the highest values observed in the Control and 80% treatments and the lowest in the 40% treatment. Although water savings during the seedling stage were small (6–22 mm) compared with those achieved through deficit irrigation during later growth stages [51–53], their importance may be greater than suggested by water use alone because irrigation at this stage strongly influences subsequent crop development [54].

The results of this study demonstrate that both lettuce and tomato seedlings tolerate moderate reductions in irrigation supply, without significant losses in total biomass accumulation or leaf area development under 60 and 70% irrigation treatments. In contrast, the 40% irrigation treatment suppressed growth across both species. These findings are consistent with the concept of a linear response of crop growth to soil water availability [55]. This could be because plant growth is maintained near potential rates until a critical soil water fraction is reached [56], beyond which stomatal and non-stomatal limitations restrict photosynthetic activity [57], as discussed below. Interestingly, in both species, the 60% holding capacity treatment occasionally exceeded the Control in parameters such as plant height and shoot dry mass. This response at moderate deficit has been observed in other vegetable crops and is generally attributed to the moderate water stress-induced accumulation of proline and soluble sugars [58].

Root fresh and dry mass were significantly reduced by severe deficit (40% irrigation treatment) in both species, which is consistent with the studies of M'hamdi [59] and Tufail [60]. However, contrary to the commonly reported increase in root biomass under moderate water deficits [51], plants subjected to moderate deficit irrigation did not differ significantly from well-watered plants in the present study. The lack of increased root biomass under moderate deficit may be attributed to the short seedling growth period and sufficient substrate moisture [6]. While root biomass responses were limited, root architectural traits revealed clear responses to irrigation. Root architectural plasticity is a major adaptive response to water deficit [61] and may explain the contrasting patterns observed between species. In lettuce, the 80% irrigation treatment maximized root development, likely by maintaining substrate moisture near holding capacity, which is considered optimal for lettuce root growth [62]. The former treatment likely exceeded this optimum, and the 40–50% irrigation treatments fell below the threshold at which water itself becomes limiting for root elongation and surface expansion as observed in several lettuce genotypes [63]. In tomato, it is likely that root systems under nursery conditions tolerate a wide moisture range (60–80% and Control treatments). This may be attributed to the reduced root hydraulic conductivity and associated anatomical changes induced by water deficit in tomato [64]. Across both species, root system development declined under the 40% irrigation treatment, suggesting that this level approaches the lower limit of water availability required during seedling production.

4.2. Physiological Responses

Lettuce and tomato exhibited contrasting physiological responses to equivalent reductions in substrate moisture during the seedling stage. In lettuce, stomatal conductance and transpiration decreased progressively as irrigation was restricted, suggesting that stomatal regulation preceded significant reductions in carbon assimilation [31]. This is further supported by the stable F_v/F_m values across treatments, suggesting that photosyn-

thetic limitations were primarily stomatal rather than non-stomatal [57]. From a practical perspective, these results suggest that the capacity for post-transplant photosynthetic recovery is largely preserved, even under the most severe irrigation deficit evaluated in this study. Another practical implication concerns the interpretation of iWUE in nursery production systems. Although iWUE increased under water deficit, this response primarily reflected stomatal regulation and reduced water loss rather than improved photosynthetic performance [65].

In tomato, the superior gas exchange performance of the 70–80% treatments suggests that adequate substrate moisture is essential for maintaining stomatal aperture and ensuring sufficient CO₂ supply to the mesophyll [66]. The Control, despite reflecting standard nursery practice, performed similarly to the 60% treatment in terms of gas exchange. This finding suggests that conventional irrigation management did not provide substrate moisture conditions optimal for stomatal opening in tomato seedlings. Unlike lettuce, tomato exhibited an abrupt decline in photosynthetic activity between the irrigation treatments below 50% (stomatal conductance = 0.02 mol H₂O m^{−2} s^{−1}). The low stomatal conductance observed under the 50–40% treatments is consistent with reports linking near-zero conductance values to damage on stomatal and biochemical components of the photosynthetic apparatus during early plant development [67,68]. This interpretation is further supported by the decline in Fv/Fm, indicating the onset of photoinhibitory stress [69] that persisted as stomatal conductance reached minimum values under the 50% and 40% irrigation treatments. Carotenoid responses provide additional evidence of stress-induced photoprotection. In tomato, carotenoid concentrations peaked under the 40% irrigation treatment in 2020. Given their antioxidant and energy-dissipating functions, this accumulation likely represents an adaptive response to PSII stress under severe water deficit [70].

4.3. Implications for Seedling Production

This study not only contributes crop-specific insights into deficit irrigation during seedling production but also highlights the importance of appropriate irrigation scheduling to maintain substrate moisture within physiologically optimal ranges, thereby ensuring superior morphological development before transplanting. This finding reinforces the broader concept that successful irrigation management depends on maintaining adequate root-zone moisture conditions, regardless of whether scheduling is based on soil-, plant-, or atmosphere-based approaches [71]. In addition, the weighing lysimeter approach used in this study offers practical advantages for commercial nurseries, as it can be readily installed and in the future automated within seedling production facilities, allowing accurate irrigation scheduling and substrate moisture management.

Although water use under standard nursery management was similar to that of the less restrictive irrigation treatments, significant differences in physiological and morphological performance were observed among treatments. The species-specific responses observed in lettuce and tomato indicate that irrigation management during seedling production should be tailored to the requirements of each species. In both species, the grower-managed Control and the 80% substrate moisture treatment were associated with favorable seedling performance; however, the traits underlying this response differed. In lettuce, the 80% treatment was more closely associated with growth, photochemical efficiency, and pigment-related variables, whereas the Control was linked to root architecture and gas exchange traits. In tomato, the Control was associated with shoot growth and pigment accumulation, while the 80% treatment was more closely related to root development and gas exchange characteristics. These contrasting responses suggest that a single irrigation strategy may not maximize all aspects of seedling quality across species. From a practical standpoint, current nursery irrigation practices produced high-quality seedlings, although maintaining

substrate moisture near 80% of the water-holding capacity may further enhance seedling vigor characteristics [72]. Therefore, species-specific irrigation management offers an opportunity to improve seedling quality while avoiding the negative effects observed under more restrictive substrate moisture conditions.

5. Conclusions

Proper irrigation management is essential for vegetable seedling production, as different substrate moisture levels differentially affect seedling morphological and physiological traits. Both lettuce and tomato performed best at 80% of the substrate holding capacity, while tolerating moderate reductions in substrate moisture (60–70% holding capacity) without significant losses in growth or gas exchange performance. In contrast, the 40% irrigation treatment consistently restricted root development, biomass accumulation, and photosynthetic activity in both species. However, lettuce maintained stable F_v/F_m across treatments, indicating preserved photochemical efficiency, whereas tomato exhibited reduced F_v/F_m under severe deficit. These contrasting patterns indicate that irrigation thresholds for nursery seedling production should be defined on a species-specific basis rather than applying a uniform strategy across species.

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