Morphological and Physiological Changes of Hydroponic Lettuce Grown in Varying Potassium Concentrations and an Adaptive Lighting Control System

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Abstract. **We investigated the growth dynamics of hydroponic lettuce (*Lactuca sativa*) driven by the influence that potassium (K^+) has on crop growth. This study aimed to determine whether increased K^+ concentrations under different daily light integrals (DLIs) in a hydroponic system will boost growth of greenhouse lettuce. This study was conducted within a controlled glass greenhouse environment with varying DLIs achieved by integrating an adaptive lighting control system over a 16-hour photoperiod. We used three K^+ treatments of 200, 400, or 600 mg·L^{-1} K^+ and six DLI lighting treatments of 11.1, 12.9, 14.6, 15.9, 16.9, and 17 mol·m^{-2}·d^{-1}. We found that increasing K^+ did not increase shoot dry weight, leaf area, or specific leaf area with increasing DLIs. Although K^+ and DLI had an interacting effect on the root dry weight fraction, leaf chlorophyll content, and quantum yield of photosystem II, the K^+ treatments did not increase or decrease with increasing DLIs. The influencing factor was DLI, which led to increases in shoot dry weight and leaf area, whereas a decrease in specific leaf area was observed with increasing DLIs. Ultimately, adding supplemental concentrations of K^+ did not enhance lettuce growth, nor did these effects show any increase with increasing DLIs.**

In controlled environmental agriculture, the conventional role of natural sunlight is either replaced or supplemented by electric lighting to secure adequate photosynthesis levels and foster optimal growth (Palmer and van Iersel 2020). The extraordinary capabilities of programmable control systems and the integration of dimmable light-emitting diodes (LEDs) empower the precise regulation of the timing and intensity of horticulture lighting (Palmer and van Iersel 2020). The use of LED lighting has gained popularity because of its high efficiency and unique dimmability feature, thus allowing precise control (Nelson and Bugbee 2014; Weaver and van Iersel 2020). Using a dimmable LED lighting system within greenhouses regulates the photosynthetic photon flux density (*PPFD*) to which a plant is exposed and can achieve a target daily light integral (DLI) by the end of the photoperiod.

Dimmable LED lights can be interfaced with quantum sensors and control systems to create an automated system that responds to sunlight to achieve a desired light level, thus enabling adaptive lighting control (ALC) (Weaver and van Iersel 2020). The ALC constantly adjusts the supplemental lighting to ensure that the combined DLI from sunlight and supplemental lighting reaches a predefined DLI threshold. If the DLI from sunlight alone exceeds this predetermined threshold, then the supplemental lights are turned off to reduce electricity costs and potential photoinhibition (Mosharafian et al. 2021).

The process starts with the quantum sensor measuring sunlight intensity in *PPFD*, which is then sent to the datalogger. The datalogger calculates the amount of *PPFD* needed from the LEDs to reach the desired plant DLI threshold (Weaver and van Iersel 2020). The ALC system ensures precise light adjustments based on changing sunlight levels, with the LEDs brightening or dimming in response. Notably, this control is contingent on the sunlight that the plants receive, thus facilitating an adaptable and responsive lighting environment that can reach the programmed target DLI (Palmer and van Iersel 2020; Weaver and van Iersel 2020).

Potassium (K^+) is an essential macronutrient that is the most abundant inorganic cation in plant tissue (Jordan-Meille and Pellerin 2008; Wang et al. 2013; Xu et al. 2020). As a macronutrient, K^+ is needed in larger quantities for adequate plant growth and development (Taiz et al. 2015). Additionally, K^+ affects most biochemical and physiological processes that are essential for enzyme activation, photosynthesis, sugar transportation, stomatal regulation, protein and starch synthesis, and stress resistance (Jordan-Meille and Pellerin 2008; Prajapati and Modi 2012; Wang et al. 2013). Furthermore, K^+ reduces abiotic and biotic stresses and can be used to improve plant stress responses (Wang et al. 2013). Moreover, K^+ is essential for increasing turgor pressure, which drives plant cell expansion and leaf elongation of all plant organs (Taiz et al. 2015).

Notably, K^+ has a crucial and complex role in photosynthesis. It can activate enzymes that produce adenosine triphosphate (ATP), which is an energy-rich molecule created from the cellular respiration of glucose that is produced from sunlight, carbon dioxide, and water (Prajapati and Modi 2012). For most chemical reactions in plants, ATP is the primary source of energy. At the site of ATP production, K^+ ions help maintain the electrical balance, thus directly affecting the rate of photosynthesis, ATP production, and respiration (Prajapati and Modi 2012). When a plant lacks sufficient K^+, its photosynthesis and ATP production rates decrease, thereby slowing plant growth (Prajapati and Modi 2012). Additionally, K^+-deficient plants experience increased respiration rates, thus reducing their growth (Prajapati and Modi 2012). In essence, K^+ is vital to maintaining plant energy production and growth.

Additionally, K^+ is used to transport sugars created during photosynthesis. Sugars are carried through the phloem, where they can be used or stored. The AKT2 K^+ channel is a K^+ channel that plays a role in phloem loading and unloading (Dennison et al. 2001). This transportation process relies on energy in the form of ATP. If a plant lacks sufficient K^+, then its ATP levels decrease, leading to a breakdown in sugar transportation (Prajapati and Modi 2012). This, in turn, causes the rate of photosynthesis to decrease because photosynthates accumulate in the leaves (Prajapati and Modi 2012). The symptoms of K^+ deficiency have been observed in soybeans and maize plants with a reduced stature and canopy size as well as reduced numbers of leaves and leaf areas of those leaves (Oosterhuis et al. 2014).

Tipburn is a physiological disorder usually observed in the leaves of vegetable plants such as lettuce (*Lactuca sativa*) (Saure 1998). Tipburn symptoms are irreversible and can cause entire yield losses for growers. These losses are caused by a localized calcium (Ca^{2+}) macronutrient deficiency that causes necrosis on the tips of younger leaves (Saure 1998). Tipburn mainly occurs during the late stages of lettuce growth, when the growth rate rapidly increases and the plant is unable to transport enough Ca^{2+} to developing leaves (younger expanding leaves) during this period of rapid growth (Kirkby and Pilbeam 1984; Saure 1998). Excess K^+ can impact the movement of Ca^{2+} ions within leaves, leading to reduced absorption through the roots (Kirkby and Pilbeam 1984; Sustr et al. 2019). This creates competition between Ca^{2+} and K^+, thus hindering the efficient nutrient uptake of Ca, which could cause tipburn in lettuce (Sustr et al. 2019). Plants grown under high light intensity have severe tipburn or an increased risk of tipburn (Saure 1998). Plants grown in greenhouses are affected earlier and to a greater extent than plants grown in field production, even though they receive nearly half the amount of radiation (Saure 1998).

This study aimed to determine whether increased K^+ concentrations under different DLIs in a hydroponic system will boost the growth of greenhouse lettuce. We hypothesized that increasing the K^+ concentration in hydroponic nutrient solutions will enhance lettuce growth, and that this effect will further intensify with higher DLI. We also hypothesized that increasing K^+ concentrations would increase the chance of tipburn symptoms.

Materials and Methods

Growing conditions. This study was performed at the University of Georgia (CAES, Department of Horticulture, Controlled Environment Agriculture Laboratory) between 9 Jun and 10 Jul 2023, in Athens, GA, USA (lat. 33°57′26.676″ N, long. 83°22′36.48″ W). The average daily temperature, relative humidity, and vapor pressure deficit during the entirety of this study were 26.2 °C (±1.15 °C),
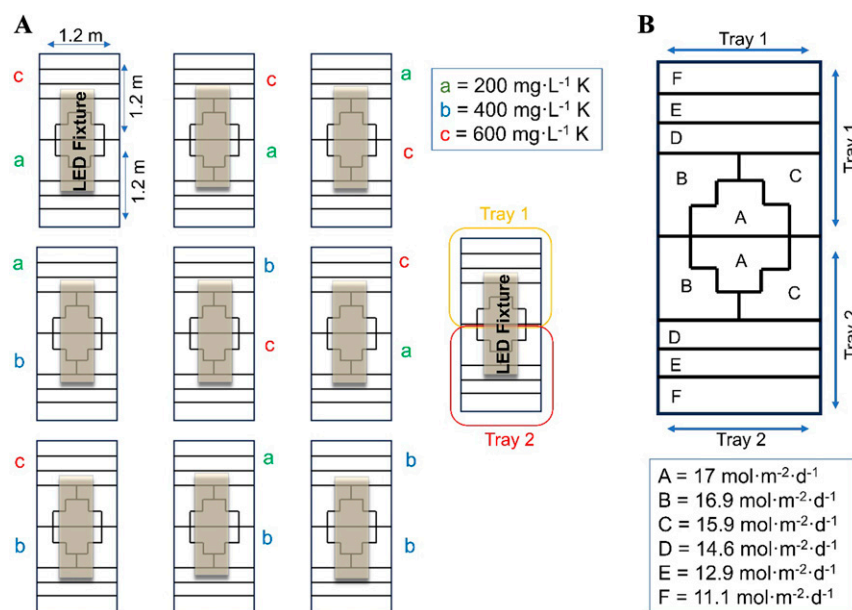

Fig. 1. (**A**) Two growing trays were placed on each bench. A total of nine benches were used. In the center of each tray, we installed one light-emitting diode (LED) lighting fixture that provided supplemental lighting to both trays on each bench. Eighteen trays were randomly filled with 200, 400, or 600 mg·L⁻¹ K^+ hydroponic solution. (**B**) The daily light integral (DLI) averages received from the supplemental LED fixtures were provided for each lighting treatment. The lighting treatments were divided into six sections based on the similarity of their received supplemental light, thus creating the six light treatments. The average total DLI was calculated by adding the DLI received from sunlight to the supplemental DLI of each lighting treatment at the end of the study.

87.1% (±3.3%), and 0.44 kPa (±0.11 kPa), respectively.

This study was conducted within a glass-enclosed greenhouse with nine deep water culture benches, with each measuring 2.4 × 1.2 m [length (L) × width (W)]. The layout of these benches followed a 3 × 3 configuration, as illustrated in Fig. 1. Each bench was furnished with two deep water trays, with each measuring 1.2 × 1.2 m × 10 cm [L × W × depth (D)], resulting in 18 trays distributed across six completely randomized locations within the greenhouse (with each considered a replication). The planting density was 25 plants/m², with 36 plants per tray, resulting in a total of 648 plants in the study. Each tray held 144 L of treatment fertilizer solution and water.

Nine 1.2-m-long dimmable LED light bars (Arize Element Top Light PPR; Current, Montreal, Canada) were centered between two trays and hung 1.4 m above the shared benches. To optimize the light distribution from the LED bars, aluminum reflectors were attached around the edges of each LED fixture. A 70% shade net was installed above the LED fixtures to reduce the sunlight entering the glass greenhouse. An extended photosynthetically active radiation (*PAR*) sensor (ePAR; covering 400–750 nm range; SQ-610-SS; Apogee Instruments, Logan, UT, USA) and *PAR* sensor (SQ500-SS; Apogee Instruments) connected to a datalogger (CR1000; Cambell Scientific, Logan, UT, USA) were used to monitor and log the amount of sunlight received by the plants. All the *PAR* sensors were placed above the LED fixtures and below the 70% shade net to record the light measurements accurately.

The datalogger was used to monitor the combined *PAR* of sunlight and target the extended DLI of 17 mol·m⁻²·d⁻¹ at the end of the 16-h photoperiod. This threshold was selected based on the recommendation provided by Weaver and van Iersel (2020) and is known as an ideal target DLI for lettuce (Mosharafian et al. 2021). The datalogger controlled and adjusted the output of the LED fixtures in real-time, continuously adapting to sunlight intensity variations throughout the day. This adjustment was achieved by delivering a 0- to 10-V direct current dimming signal, which was regulated using a four-channel analog output module (SDMAO4A; Campbell Scientific, Logan, UT, USA) (Weaver and van Iersel, 2020).

Lighting conditions. One day before transplanting on 20 Jun 2023, supplemental greenhouse lights were deliberately positioned to create variations in light intensity. In each supplementary lighting treatment, the LED lights and sunlight provided a maximum DLI of 17 mol·m⁻²·d⁻¹. The maximum output of the LED light bars used during this experiment targeted an intensity of 400 ± 34 μmol·m⁻²·s⁻¹; therefore, a DLI of at least 17 mol·m⁻²·d⁻¹ could be reached if there was a total absence of sunlight. These measurements were recorded directly beneath the center of two trays using a quantum sensor, with the maximum PPFD reading recorded at 434 μmol·m⁻²·s⁻¹, whereas the average was 393 μmol·m⁻²·s⁻¹.

To measure the supplementary light conditions, we created a system with 36 diodes attached to a foam board, and this configuration allowed us to efficiently capture all 36 light measurements simultaneously. The diodes

Table 1. Daily light integral (DLI) during the experiment. We used an adaptive lighting control system with a DLI target and the datalogger subtracted the amount provided by the sun from the thresholds by applying the difference needed using the light-emitting diodes (LEDs). The total DLI refers to the amount received by sunlight plus that provided by the LEDs. The DLI received each day from the sunlight and the supplemental LED fixtures were averaged over 19 d. The average total DLI received in each light treatment was calculated for each of the six lighting treatments.

				DLI received ($mol·m^{-2}·d^{-1}$)												
				17		16.9		15.9		14.6		12.9		11.1	
	DLI			Ratios											
	From sun + LEDs	From sun only	From LEDs only	1.00		0.99		0.89		0.76		0.59		0.41	
Day	($mol·m^{-2}·d^{-1}$)			LED DLI	Total DLI	LED DLI	Total DLI	LED DLI	Total DLI	LED DLI	Total DLI	LED DLI	Total DLI	LED DLI	Total DLI
1	17.0	7.0	10.0	10.0	17.0	9.9	16.9	8.9	15.9	7.6	14.6	5.9	12.9	4.1	11.1
2	17.0	7.2	9.8	9.8	17.0	9.7	16.9	8.7	15.9	7.5	14.7	5.8	13.0	4.0	11.2
3	17.0	8.7	8.3	8.3	17.0	8.2	16.9	7.4	16.1	6.3	15.0	4.9	13.6	3.4	12.1
4	17.0	9.0	8.0	8.0	17.0	8.0	16.9	7.2	16.1	6.1	15.1	4.7	13.7	3.3	12.3
5	17.0	8.7	8.3	8.3	17.0	8.2	16.9	7.4	16.1	6.3	15.0	4.9	13.6	3.4	12.1
6	17.0	7.8	9.2	9.2	17.0	9.2	16.9	8.2	16.0	7.0	14.8	5.4	13.2	3.8	11.6
7	17.0	3.0	14.0	14.0	17.0	13.9	16.9	12.5	15.5	10.7	13.7	8.3	11.2	5.8	8.7
8	17.0	8.1	8.9	8.9	17.0	8.9	16.9	8.0	16.0	6.8	14.9	5.3	13.3	3.7	11.7
9	17.0	6.8	10.2	10.2	17.0	10.1	16.9	9.1	15.9	7.8	14.6	6.0	12.8	4.2	11.0
10	17.0	6.8	10.2	10.2	17.0	10.1	16.9	9.1	15.9	7.7	14.6	6.0	12.8	4.2	11.0
11	17.0	5.6	11.4	11.4	17.0	11.3	16.9	10.2	15.8	8.7	14.3	6.7	12.3	4.7	10.3
12	17.0	4.1	12.9	12.9	17.0	12.8	16.9	11.5	15.6	9.8	13.9	7.6	11.7	5.3	9.4
13	17.0	7.1	9.9	9.9	17.0	9.8	16.9	8.8	15.9	7.5	14.7	5.8	12.9	4.1	11.2
14	17.0	6.1	10.9	10.9	17.0	10.8	16.9	9.7	15.8	8.3	14.4	6.4	12.5	4.4	10.6
15	17.0	7.3	9.7	9.7	17.0	9.7	16.9	8.7	15.9	7.4	14.7	5.7	13.0	4.0	11.3
16	17.0	7.7	9.3	9.3	17.0	9.2	16.9	8.3	16.0	7.1	14.8	5.5	13.2	3.8	11.5
17	17.0	4.6	12.4	12.4	17.0	12.3	16.9	11.1	15.7	9.5	14.1	7.3	11.9	5.1	9.7
18	17.0	8.9	8.1	8.1	17.0	8.0	16.9	7.2	16.1	6.1	15.1	4.8	13.7	3.3	12.2
19	17.0	8.8	8.2	8.2	17.0	8.1	16.9	7.3	16.1	6.3	15.1	4.8	13.6	3.4	12.2
Averaged DLI received ($mol·m^{-2}·d^{-1}$)				10.0	17.0	9.9	16.9	8.9	15.9	7.6	14.6	5.9	12.9	4.1	11.1

were interconnected and controlled using proprietary software (LoggerNet 4.1; Cambell Scientific, Logan, UT, USA) and measured using a datalogger (CR1000X; Cambell Scientific, Logan, UT, USA) hand-held quantum sensor (MQ-500; Apogee Instruments) to measure the PPFD provided by the LED fixtures when they were at maximum power. Importantly, these measurements were obtained exclusively under supplemental lighting conditions at night.

At the end of the study, we calculated the supplemental DLI provided during each day by subtracting the total DLI from the DLI of sunlight (Table 1). Using the PPFD ratios from Table 1, we calculated the DLI for each lighting treatment received from the supplemental lighting. For replication purposes, we aimed to calculate the average total DLI for each lighting treatment in the study. This involved adding the DLI received from sunlight to the supplemental DLI of each lighting treatment, which resulted in the average total DLI.

Hydroponic K^+ formulation. Three K^+ hydroponic nutrient solution treatments were randomly allocated to the 18 trays. Each tray was filled with 200, 400, or 600 $mg·L^{-1}$ K^+ hydroponic solution for six replications. The three fertilizer treatments differed in concentrations and potassium nitrate (KNO_3) ratios (Table 2). Regarding the 200-$mg·L^{-1}$ K^+ treatment, the nutrient solution contained 57.49 $mg·L^{-1}$ NO_3^- and 161.5 $mg·L^{-1}$ K^+ [pH = 6.48; electrical conductivity (EC) = 2.52 $mS·cm^{-1}$]. Regarding the 400-$mg·L^{-1}$ K^+ treatment, the levels were 128.8 $mg·L^{-1}$ NO_3^- and 361.5 $mg·L^{-1}$ K^+ (pH = 6.42; EC = 1.99 $mS·cm^{-1}$). Regarding the 600 $mg·L^{-1}$ K^+ treatment, the nutrient solution included 199.88 $mg·L^{-1}$ NO_3^- and 561.5 $mg·L^{-1}$ K^+ (pH = 6.39; EC = 1.37 $mS·cm^{-1}$). The initial pH of each K^+ treatment solution ranged from 6.39 to 6.48, with EC values ranging from 1.37 to 2.52 $mS·cm^{-1}$. To achieve a desired pH range of 5.5 to 6.5, we used a 1-M NaOH solution for pH adjustment. Approximately 1 week before the harvest, we observed an increase in the pH, thus prompting us to make corrections using a 2-M H_3PO_4 solution.

Treatments. Hydroponically cultivated lettuce was subjected to six DLIs of 11.1, 12.9, 14.6, 15.9, 16.9, and 17 $mol·m^{-2}·d^{-1}$ achieved by using an ALC system (sunlight + LED); it was also subjected to three K^+ concentrations of 200, 400, and 600 $mg·L^{-1}$. To calculate the DLI, we measured the PPFDs from the supplemental lighting across six treatments, with each offering varying light intensities at the beginning of the study. Then, we calculated the average PPFD ratios between these six treatments by dividing the DLI of each light treatment received from the supplemental LED fixture by the highest supplemental DLI (17 $mol·m^{-2}·d^{-1}$), resulting in ratios of 0.41, 0.59, 0.76, 0.89, 0.99, and 1.0, respectively (Table 1). The 36 collected light measurements were grouped into six treatments based on the similarity of their PPFD light levels. This grouping resulted in six distinct lighting treatments, each with an average maximum supplemental PPFD of 162, 233, 300, 353, 390, and 393 $μmol·m^{-2}·s^{-1}$, respectively.

Seedling management. The lettuce cultivar Casey (Johnny's Selected Seeds; Winslow, ME, USA) was selected because of its disease resistance, strong root system, and exceptional heat tolerance, thus making it an ideal choice for summer greenhouse growing conditions. For seedling production, approximately

Table 2. Nutrient formulation for the three potassium (K^+) treatments of 200, 400, and 600 $mg·L^{-1}$.

K^+	N	NO_3^-	NH_4^+	P	K	Ca	Mg	S	B	Cu	Fe	Mn	Mo	Zn
					($mg·L^{-1}$)									
200	149	139	10	31	200	24	32	0.25	1.8	0.02	1.8	0.1	0.02	0.2
400	212	202	10	31	400	24	32	0.25	1.8	0.02	1.8	0.1	0.02	0.2
600	283	274	10	31	600	24	32	0.25	1.8	0.02	1.8	0.1	0.02	0.2

B = boron; Ca = calcium; Cu = cooper; Fe = iron; Mg = magnesium; Mn = manganese; Mo = molybdenum; N = nitrogen; NH_4^+ = ammonium; NO_3^- = nitrate; P = phosphorus; S = sulfur; Zn = zinc.

1000 pelleted seeds were sown in rockwool plugs measuring 2.5 × 2.5 × 4 cm (L × W × D; A0 25/40; Grodan Rockwool BV, Roermond, the Netherlands). Before seeding, these rockwool plugs were thoroughly saturated with water; then, a single lettuce seed was placed within each rockwool plug (120 plugs were arranged per tray). Eight trays were seeded, and the rockwool was misted once more to ensure adequate moisture for seed germination. Transparent plastic domes were used to cover the trays for the initial 4 d, creating a conducive environment that could sustain high humidity levels during germination to ensure that the seeds would not dry out.

The seeded rockwool plugs were placed within double-stacked, black, rectangular plastic mesh flats measuring 50.8 × 12.7 × 5.08 cm in height. These flats were double-stacked to prevent seedling roots from growing into the black felt fabric lining the ebb-and-flow trays inside the growing room or vertical farm. The flats were positioned beneath 1.1-m-long white LED light fixtures (RAY with Physiospec indoor spectrum; Fluence Bioengineering, Austin, TX, USA). These light fixtures provided *PAR* of 250 μmol·m^{-2}·s^{-1} during a 16-h photoperiod. Daily ebb-and-flow subirrigation was performed for 5 min using a 15N–2.2P–12.45K water-soluble fertilizer solution containing 100 mg·L^{-1} nitrogen (N) (15–5–15 Ca-Mg Professional LX; J.R. Peters, Allentown, PA, USA).

Transplant management. At 12 d after the initial seedling on 9 Jun, we carefully selected the most uniform seedlings, randomly distributed them, and transplanted them into a deep water culture hydroponic system using 36 net pots on 21 Jun 2023. These net pots had dimensions measuring 4.8 × 4.5 × 3.3 cm (H × top diameter × bottom diameter; Teku G46; Pöppelmann GmbH & Co., Lohne, Germany).

To create an appropriate environment for the plants within each tray, we used foam lids that ensured buoyancy within the deep water hydroponic system. To achieve this, we positioned a 1.2-m × 1.2-m × 1.3-cm-thick square foam board on the top of the trays. These foam lids were drilled with 36 evenly spaced holes that were each 12.9032 cm^2 apart and had a diameter of 4.2 cm. Each of these holes held a net pot containing a single plant grown in rockwool. Subsequently, these prepared setups were placed into the deep water culture trays.

Clear plastic tubing with a diameter of 0.64 cm and six 2-cm-wide air stones (Aquarium Air Stone; Pawfly, Guangzhou, China) were positioned within each tray to ensure adequate aeration and oxygenation of the nutrient solution. The circulation of air and maintenance of optimal oxygen levels within the nutrient solution were facilitated using an air pump (0.48 bar, 3.0 A, 120 V, 12.7-mm-diameter tube inlet; EcoPlus-7; Hawthorne Gardening Company, Vancouver, WA, USA).

Measurements. On 10 Jul 2023 [31 d after sowing (DAS)], we harvested the plants and determined the fresh shoot and root weights on two randomly selected plants from all

replications, and these plants were also placed in a drying oven at 80 °C for 144 h (6 d) to determine dry weights. We also conducted various assessments of two randomly selected plants from three replications only to assess the total leaf area, specific leaf area (SLA), and projected canopy size (PCS). To assess the total leaf area, we separated individual leaves from the same two randomly selected plants and measured them using a leaf area meter (LI-3100; LI-COR, Lincoln, NE, USA). Subsequently, the shoots and roots for the same two plants were weighed to assess fresh weights; then, they were placed in a drying oven at 80 °C for 96 h (4 d) to determine the dry weights of each replication. The fresh and dry shoot and root weights were divided by the number of plants in each lighting treatment to calculate the average weights per plant. The SLA was calculated using the dry shoot weight and total leaf area (total leaf area/dry shoot weight). Additionally, the PCS was determined using a multispectral imaging system (Topview; Aris, Eindhoven, the Netherlands).

On 9 Jul 2023 (30 DAS), we assessed the quantum yield of photosystem II (ΦPSII) at nighttime exclusively under the illumination of supplemental lighting without sunlight using a pulse amplitude modulated fluorometer (Mini-PAM II; Heinz Walz, Effeltrich, Germany). We recorded the ΦPSII measurements of two randomly selected plants from each replication.

On 8 Jul 2023 (29 DAS) or 17 d after transplanting, using a gas analyzer (CIRAS-4; PP Systems, Amesbury, MA, USA), CO_2 assimilation of the upper-most fully expanded leaf of one randomly selected plant from each treatment combination in all replications was recorded. The leaf CO_2 assimilation measurements were obtained at nighttime exclusively under the illumination of supplemental lighting without sunlight.

Petiole sap samples were obtained from an additional two plants within each replication on 9 Jul 2023 (30 DAS). This involved extracting sap from two fully grown leaf petioles by squeezing them through cheesecloth

using a garlic press. Then, a small quantity of the collected sap was analyzed to determine K^+. The leaf chlorophyll content of two plants from each of the six treatment combinations in all replications was measured using a leaf chlorophyll meter (CCM-200 plus; Apogee Instruments Logan, UT, USA).

Notably, on 10 Jul, before the initial harvest, although we did not formally record tip-burn incidence among light treatments, the tip burn incidence of the K^+ treatments was recorded.

Experimental design and statistical analysis. The experiment was arranged using a complete randomized design with six lighting treatments and three K^+ concentrations with six replications. Each experimental unit had six plants, resulting in a total of 36 plants per tray.

Subsequent statistical analyses were conducted using a multiple regression analysis and statistical software (SigmaPlot 11.0; Systat Software, San Jose, CA, USA). To identify any interaction effects between DLI and K^+ concentrations, we performed a multiple stepwise regression analysis with backward selection using statistical software (JMP Pro 17; SAS Institute, Cary, NC, USA) at a significance level of 5%, meaning that nonsignificant components in the regression equation were eliminated during the selection procedure. This method was applied to investigate the potential interaction effects of DLI and K^+ on various parameters, including shoot fresh weight per plant, shoot dry weight per plant, root dry weight per plant, root dry weight fraction, leaf area per plant (LA), SLA, PCS, ΦPSII, CO_2 assimilation, K^+ petiole sap concentration, chlorophyll content, and tipburn.

Results

Fresh and dry weights. The average shoot fresh weight of each plant increased with the increasing DLI ($P < 0.0001$) (Fig. 2). Although each K^+ treatment may have seen a different level of increase in the shoot fresh weight, this was not attributed to the K^+
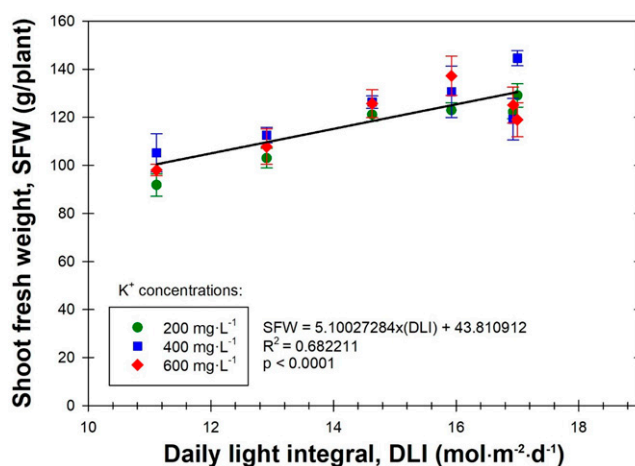

Fig. 2. Shoot fresh weight (SFW) of lettuce (*Lactuca sativa* 'Casey') plants grown at six daily light integrals (DLIs) and three K^+ concentrations in hydroponics solution. The black line shows the results of multiple regression analyses, which indicated a significant DLI interaction. K^+ and DLI × K^+ interactions were not significant. Each data point represents the average ± *SE* of six replications (n = 6).

treatment, but rather to the DLI. Similarly, for shoot dry weight, increasing the DLI from 11.1 to 17 $mol·m^{-2}·d^{-1}$ increased the average plant weight ($P < 0.0001$) (Fig. 3), and that K^+ did not affect the shoot dry weight. The average root dry weight of each plant increased with the increasing DLI ($P = 0.0002$) (Fig. 4), and the K^+ treatments comprising 200, 400, and 600 $mg·L^{-1}$ K^+ did not contribute to this increase in root dry weight. The root dry weight fraction was calculated by dividing the root dry weight by the total plant dry weight. The root dry weight fraction was affected by DLI and K^+ ($P = 0.0007$), but with an increasing DLI and without an effect of the K^+ treatment (Fig. 5).

Leaf area, specific leaf area, and projected canopy size. The total LA increased with the increasing DLI, whereas all K^+ treatments did not have an interacting effect on LA ($P = 0.0374$). The LA increased from 1934 to 2031 cm^2/plant when the DLI increased from 11.1 to 17 $mol·m^{-2}·d^{-1}$ (Fig. 6). With the increasing K^+, the total LA did not change. The SLA, calculated by dividing shoot dry weight by LA, decreased with the increasing DLI ($P = 0.0001$) (Fig. 7). The SLA decreased from 568 to 449 $cm^2·g^{-1}$ with the increasing DLI (from 11.1 to 15.9 $mol·m^{-2}·d^{-1}$), whereas an increase in the DLI from 16.9 to 17 $mol·m^{-2}·d^{-1}$ resulted in a decrease in the SLA from 480 to 443 $cm^2·g^{-1}$ (Fig. 7). The SLA did not change with the increasing K^+. The PCS for all plants were similar in size and decreased with the increasing DLI ($P = 0.0659$) (Fig. 8). However, K^+ did not change the PCS, and it was not significant.

ΦPSII and CO_2 assimilation. The ΦPSII was affected by DLI and K^+ ($P = 0.0011$); however, the ΦPSII for all K^+ treatments did not increase or decrease with the increasing DLI (from 11.1 to 17 $mol·m^{-2}·d^{-1}$) (Fig. 9). The DLI had an interacting effect on the CO_2 assimilation rate, which increased with increasing DLI ($P < 0.0001$) (Fig. 10).

Petiole K^+ concentration and leaf chlorophyll content. The DLI and K^+ interacted with the petiole K^+ concentration (0.0186) (Fig. 11). The petiole K^+ concentration for all K^+ treatments did not change with the increasing DLI. The leaf chlorophyll content interacted with the DLI and K^+ ($P = 0.0061$) (Fig. 12). The leaf chlorophyll content did not change with the increasing DLI.

Tipburn. Unfortunately, tipburn was only recorded for the K^+ treatments; it was not recorded for the DLI treatments. This was a mistake made during the harvest (Fig. 13). With the 200 $mg·L^{-1}$ K^+ treatment, the tipburn incidence was minimal at 0.92%. With the 400 $mg·L^{-1}$ K^+ treatment, the tipburn incidence increased to 4.62%, and the highest tipburn incidence was observed at 600 $mg·L^{-1}$ K^+ treatment, reaching 9.72%.

Discussion

When K^+ is supplied in a deficient amount, plants experience a decrease in biomass accumulation (Jordan-Meille and Pellerin 2008). In theory, increasing K^+ levels
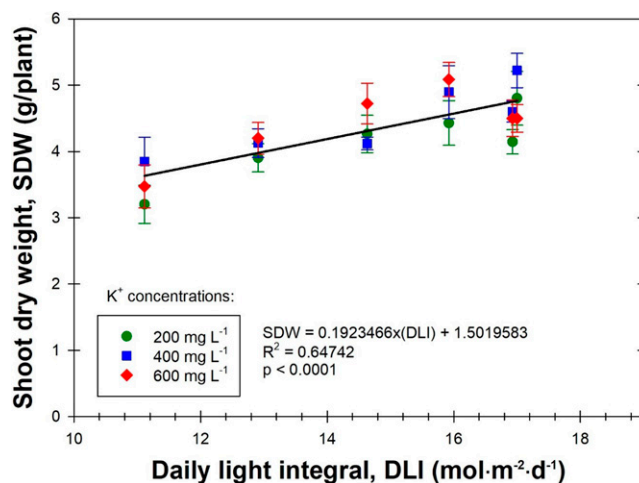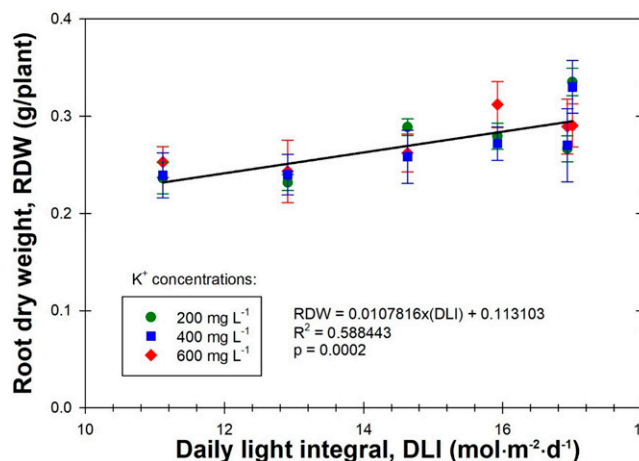

Fig. 3. Shoot dry weight (SDW) of lettuce (*Lactuca sativa* 'Casey') plants grown at six daily light integrals (DLIs) and three K^+ concentrations in hydroponics solution. The black line shows the results of multiple regression analyses, which indicated a significant DLI interaction. K^+ and DLI × K^+ interactions were not significant. Each data point represents the average ± *SE* of six replications (n = 6).

Fig. 4. Root dry weight (RDW) of lettuce (*Lactuca sativa* 'Casey') plants grown at six daily light integrals (DLIs) and three K^+ concentrations in hydroponics solution. The black line shows the results of multiple regression analyses, which indicated a significant DLI interaction. K^+ and DLI × K^+ interactions were not significant. Each data point represents the average ± *SE* of six replications (n = 6).
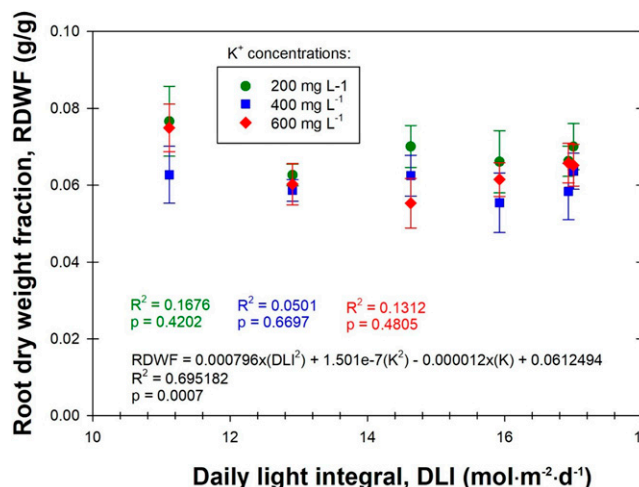

Fig. 5. Root dry weight fraction (RDWF) of lettuce (*Lactuca sativa* 'Casey') plants grown at six daily light integrals (DLIs) and three K^+ concentrations in hydroponics solution. Results of multiple regression analyses indicated no significant DLI × K^+ interaction ($P > 0.05$). Lines are not presented. The RDWF was calculated by dividing the root dry weight (RDW) by the total plant dry weight. Each data point represents the average ± *SE* of six replications (n = 6).
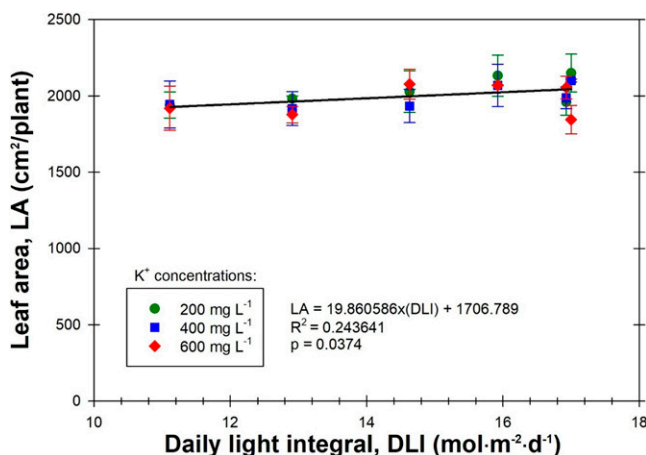
Fig. 6. Leaf area (LA) of lettuce (*Lactuca sativa* 'Casey') plants grown at six daily light integrals (DLIs) and three K^+ concentrations in hydroponics solution. The black line shows the results of multiple regression analyses, which indicated a significant DLI interaction. K^+ and DLI × K^+ interactions were not significant. Each data point represents the average ± *SE* of three replications (n = 3).
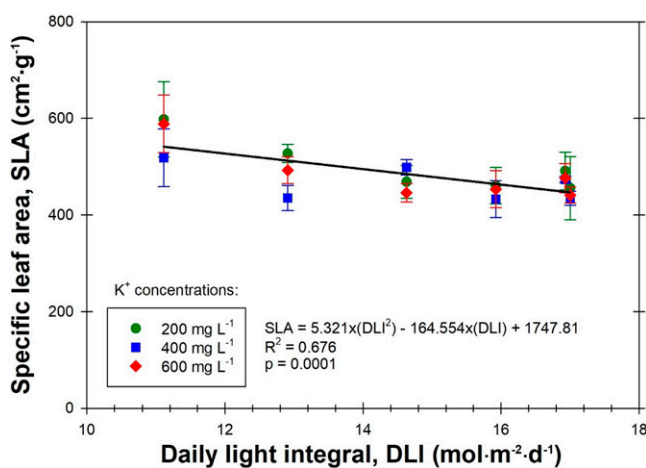

Fig. 7. Specific leaf area (SLA) of lettuce (*Lactuca sativa* 'Casey') plants grown at six daily light integrals (DLIs) and three K^+ concentrations in hydroponics solution. The black line shows the results of multiple regression analyses, which indicated a significant DLI interaction. K^+ and DLI × K^+ interactions were not significant. The SLA was calculated by dividing the leaf area (LA) by the shoot dry weight (SDW). Each data point represents the average ± *SE* of three replications (n = 3).
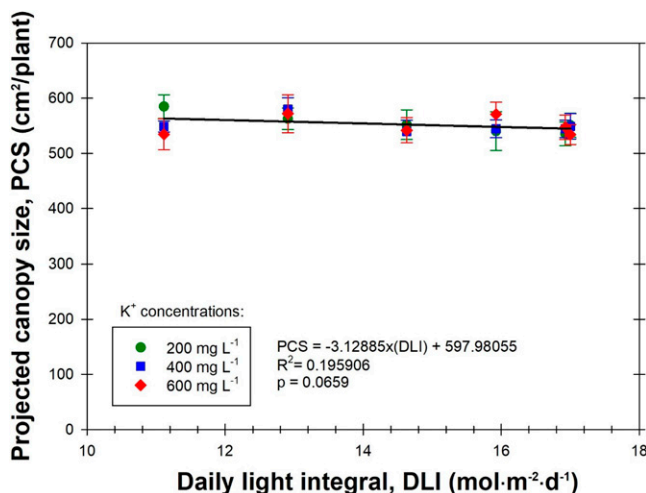

Fig. 8. Projected canopy size (PCS) of lettuce (*Lactuca sativa* 'Casey') plants grown at six daily light integrals (DLIs) and three K^+ concentrations in hydroponics solution. The line shows the results of multiple regression analyses, which indicated a significant DLI interaction. K^+ and DLI × K^+ interactions were not significant. Each data point represents the average ± *SE* of three replications (n = 3).

in plants should increase growth (Jordan-Meille and Pellerin 2008). However, K^+ did not affect the shoot fresh weight or shoot dry weight; rather, the increase was attributable to the increasing DLI (Figs. 2 and 3). This increases in the shoot fresh weight and shoot dry weight were most likely caused by the increased *PPFD* that the plants received, which caused an increase in photosynthesis activity. During other studies, increasing the DLI increased the fresh and dry shoot weights of lettuce cultivars (Kelly et al. 2020). When *PPFD* conditions increased, the PSII reaction centered close to minimize photodamage, and this protective mechanism resulted in greater dissipation of absorbed light energy as heat (nonphotochemical quenching). Consequently, a reduced proportion of the absorbed light energy remained excited, leading to a decline in the PSII efficiency under conditions of high DLI.

Previous studies showed that an increased *PPFD* decreased the PSII because of the partially closed PSII reaction centers and upregulation of nonphotochemical quenching (Elkins and van Iersel 2020). In this study, the ΦPSII did not decrease or increase with the increasing DLI, even though there was an interaction between DLI and K^+ (Fig. 9).

With the increasing DLI, we observed increased CO_2 assimilation (Fig. 10). This was also most likely attributable to the increase in the *PPFD* that the plants received to increase the DLI. Some studies also observed increased CO_2 assimilation because of the increasing *PPFD* (Weaver and van Iersel 2020; Zhen and van Iersel 2017). Therefore, the increased CO_2 assimilation with the increasing DLI could be attributed to plants allocating more carbon resources to biomass production. This reasoning could also explain why the shoot fresh weight and shoot dry weight were positively correlated with the increasing DLI, whereas K^+ did not influence the shoot fresh weight and shoot dry weight.

The root dry weight increased with the increasing DLI (Fig. 4) during this study. The increase in the DLI was most likely caused by the increase in *PPFD*, which primarily led to an increase in growth such as that of the shoot fresh weight and shoot dry weight. However, it could also explain the increase in the root dry weight. As biomass production increased, it would be expected that a portion of this increased biomass would be allocated to root growth for enhanced water and nutrient absorption. Although K^+ did not affect the root dry weight, an excess of K^+ and a deficiency of K^+ decreased root development and growth were observed in apple rootstock seedlings (Xu et al. 2020). Other studies reported a reduction in the root dry weight fraction (root dry weight/total plant dry weight) of hydroponic lettuce with the increasing DLI (Lin et al. 2018). However, there was no increase or decrease in the root dry weight fraction observed during our study (Fig. 5).

With the increasing DLI, we observed an increase in the LA (Fig. 6). As the DLI increased, the LA increased also; this was most likely attributable to the increasing DLI. The
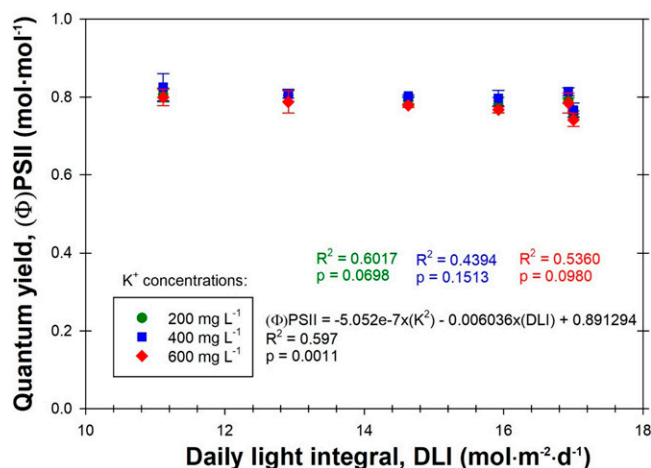
Fig. 9. The quantum yield of photosystem II (ΦPSII) of lettuce (*Lactuca sativa* 'Casey') plants grown at six daily light integrals (DLIs) and three K^+ concentrations in hydroponics solution. Results of multiple regression analyses indicated no significant DLI × K^+ interactions ($P > 0.05$). Lines are not presented. Each data point represents the average ± *SE* of six replications (n = 6).
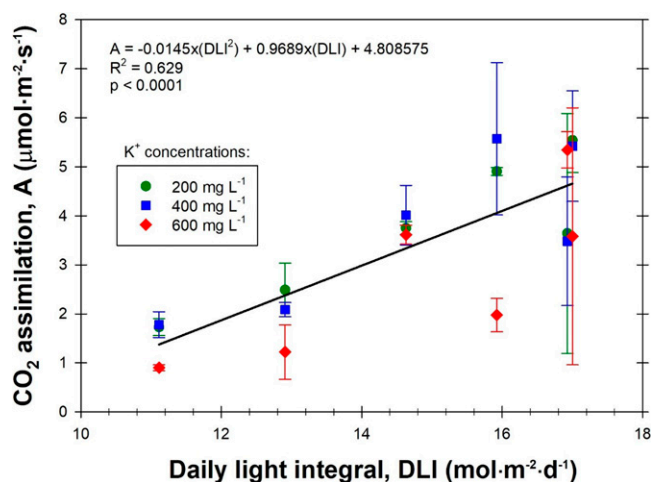

Fig. 10. Net CO_2 assimilation rate (**A**) of lettuce (*Lactuca sativa* 'Casey') plants grown at six daily light integrals (DLIs) and three K^+ concentrations in hydroponics solution. The black line shows the results of multiple regression analyses, which indicated a significant DLI effect. K^+ and DLI × K^+ interactions were not significant. Each data point represents the average ± *SE* of six replications (n = 6).
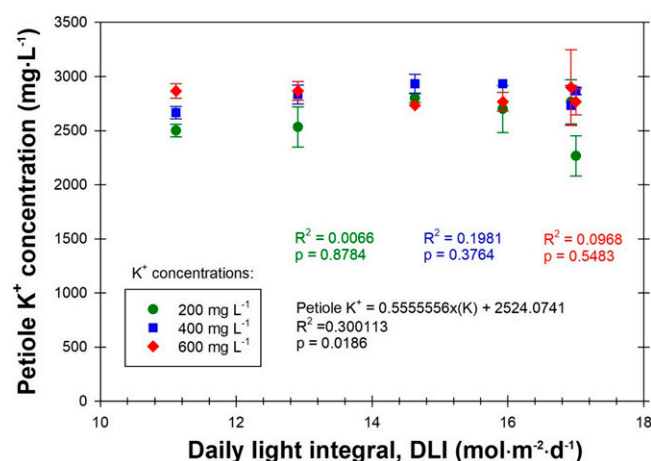

Fig. 11. Petiole K^+ concentration of lettuce (*Lactuca sativa* 'Casey') plants grown at six daily light integrals (DLIs) and three K^+ concentrations in hydroponics solution. Results of multiple regression analyses indicated no significant DLI × K^+ interaction ($P > 0.05$). Lines are not presented. Each data point represents the average ± *SE* of six replications (n = 6).

increasing DLI has increased the LA of lettuce more than that of kale (Baumbauer et al. 2019). Under low DLI conditions, the LA and growth of cucumber seedlings were reduced (Kitaya et al. 1998). Both studies showed results similar to those of our study, during which plants had a lower LA under low DLI and a higher LA under high DLI.

The SLA decreased with the increasing DLI (Fig. 7). A similar trend was observed during a study that evaluated increasing *PPFD*s of lettuce and found that the SLA decreased with the increasing *PPFD* (Jayalath and van Iersel 2021). The reduction in the SLA can be attributed to the increasing DLI. As the DLI increases, leaves can become thicker (based on our observations). Using the PCS imaging system, we also observed that leaves began to overlap under high DLI as the PCS decreased with the increasing DLI (Fig. 8).

Tipburn symptoms were only recorded for the K^+ treatments on the day of harvest, thus presenting a limitation. Nevertheless, it was observed that tipburn increased with increasing K^+ levels (Fig. 13). One potential reason for this observed phenomenon could be that an excess of K^+ may influence the movement of Ca^{2+} ions within leaves, resulting in reduced absorption through the roots (Kirkby and Pilbeam 1984; Sustr et al. 2019). This established competition between Ca^{2+} and K^+, thus hindering the effective nutrient uptake of Ca^{2+} and potentially contributing to tipburn in lettuce (Sustr et al. 2019).

Regarding the leaf petiole K^+ concentration, none of the K^+ treatments showed an increase with the increasing DLI (Fig. 11). During a study by Gent (2014), the K^+ levels in plants increased with the increasing daily integrated irradiance, and plants also exhibited a greater increase in the K^+ concentration when harvested during the afternoon rather than during the morning (Gent 2014). However, during our study, we observed a different trend. A potential explanation for these differing results may be the extended harvest period, which encompassed both morning and afternoon sessions, thus potentially affecting the leaf petiole K^+ concentrations.

A high leaf chlorophyll content can increase the CO_2 assimilation rate and potential growth rate of plants (Jayalath and van Iersel 2021); however, during this study, the leaf chlorophyll content did not increase or decrease with the increasing DLI in any of the K^+ treatments (Fig. 12). A different trend was observed for wax begonia (*Begonia semperflorens*): a small decrease in the leaf chlorophyll content was observed with the increasing DLI (Nemali and van Iersel 2004). The CO_2 assimilation rate increased with the increasing DLI (Fig. 10). Other studies have also reported that an increased DLI was correlated with an increased CO_2 assimilation rate and enhanced growth of tomato (*Solanum lycopersicum*) plants (Huber et al. 2021). These findings aligned with our findings; we observed the highest growth under high DLIs during our study. Overall, the K^+ treatments did not have much of an impact
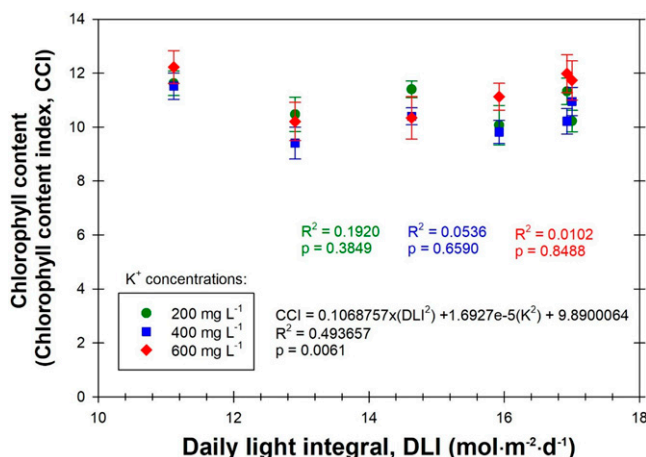
Fig. 12. Leaf chlorophyll content of lettuce (*Lactuca sativa* 'Casey') plants grown at six daily light integrals (DLIs) and three K^+ concentrations in hydroponics solution. Results of multiple regression analyses indicated no significant DLI × K^+ interaction. Each data point represents the average ± *SE* of six replications (n = 6).

on plant growth; however, this could have been attributable to the K^+ concentration we used, which approximately corresponded to 5, 10, and 15 mmol/L K^+. Such concentrations do not cause much stress to plants because 0.2 Murashige Skoog medium contains 4 mmol/L K^+, which is widely used as a plant growth medium in laboratories when cultivating plant cell cultures.

Conclusions

This study found that an increase in the K^+ concentration up to 600 mg/L did not affect the plant biomass and leaf development with increasing DLIs for greenhouse-grown lettuce. There was an interacting effect between K^+ and DLI on root development and photosynthetic performance. The increase in plant growth (biomass and leaf expansion) was mainly caused by the increase in the DLI, whereas elevated K^+ levels appeared to have minimal or no beneficial effects. Adverse outcomes, such as an increase in

tipburn, were observed with higher K^+ fertilization. Future studies should investigate whether the interaction between increasing light intensity and higher K^+ concentrations influences tipburn in lettuce. Ultimately, this study suggests that increasing K^+ is not useful for boosting the growth of hydroponic lettuce.

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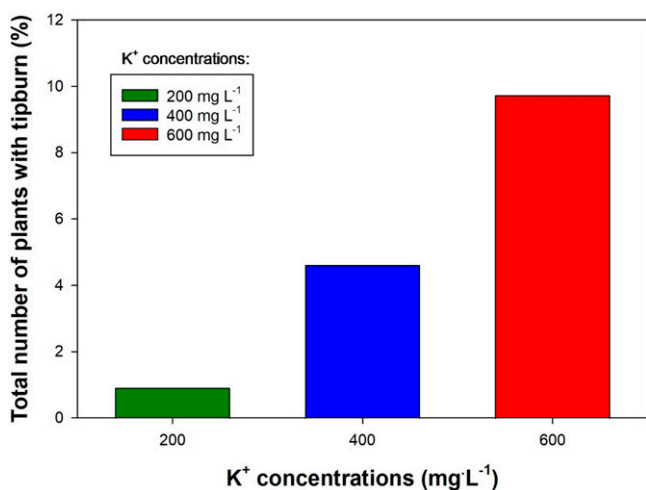
Fig. 13. Tipburn incidence according to each potassium (K^+) treatment. Each bar on the graph represents the percentage of plants with tipburn symptoms at the end of the study before the harvest of 216 plants for each K^+ treatment.

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