# Improving Indoor Strawberry Production in Vertical Farming

# Through Enhanced Lighting and Fertilization Strategies

by

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ABSTRACT

There is increasing interest in growing strawberries (*Fragaria ×ananassa*) in indoor environments such as vertical farms, as the continued sustainability of outdoor production is threatened due to reductions in arable land, labor shortages, and an increased frequency of drought. However, the optimal conditions for growing strawberries hydroponically in sole-source lighting conditions have yet to be established. The objectives of this research were to investigate the optimal lighting conditions and nutrient concentrations for strawberry production in vertical farming. In the first study, bare-root plants of two strawberry cultivars, 'Albion' and 'Monterey', were grown in an indoor vertical farm under a 22 °C air temperature and an 18-h photoperiod with 90 $\mu mol \cdot m^{-2} \cdot s^{-1}$ of blue light and 250 $\mu mol \cdot m^{-2} \cdot s^{-1}$ of red light with and without 50 $\mu mol \cdot m^{-2} \cdot s^{-1}$ of additional far-red light from light-emitting diodes. Adding far-red light increased the fruit number per plant by 36%, total fruit fresh mass by 48%, and total soluble solids content by 12% in 'Albion', but not 'Monterey'. In the second study, bare-root plants of strawberries 'Monterey' and 'San Andreas' were grown under a 23 °C air temperature and an 18-h photoperiod with an extended photosynthetic photon flux density of 350 $\mu mol \cdot m^{-2} \cdot s^{-1}$. Plants were subjected to four potassium to nitrogen ratios (K:N) of 1.5:1, 2.5:1, 3.5:1, and 4.5:1 in a deep-water culture hydroponic system. Increasing K:N from 1.5:1 to 4.5:1 increased the root dry mass of 'Monterey', but generally had little to no effect on vegetative growth in either cultivar. In addition, in both cultivars, increasing K:N from 1.5:1 to 4.5:1 decreased individual fruit size and increased titratable acidity. These results suggest that for indoor strawberry production,

including far-red light in sole-source lighting can improve fruit production in some strawberry cultivars. However, increasing K:N in the hydroponic nutrient solution generally does not benefit plant growth, fruit production, and fruit quality.

# DEDICATION

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TABLE OF CONTENTS

Page

LIST OF TABLES

Table Page

Table Page

LIST OF FIGURES

Figure Page

Figure Page

Figure Page

Figure Page

# CHAPTER 1

# LITERATURE REVIEW

# LITERATURE REVIEW

## Vertical farming

Strawberries (*Fragaria ×ananassa*) are widely known for their desirable taste and a variety of health benefits, which in part led to a 300% increase in strawberry consumption between 1980 and 2013 in the US (Giampieri et al., 2014; USDA, 2014). While California has historically produced most strawberries in the US, 91% in 2017 (USDA, 2018), labor shortages, increases in land value, and higher prevalences of drought have led to a recent decline in overall acreage used for strawberry production in California (Samtani et al., 2019). In addition, with the advancements in technologies such as artificial lighting and the increased efficiency and sustainability of greenhouses and controlled environments such as vertical farms, growing strawberries in indoor environments is increasingly feasible (Kouloumprouka Zacharaki et al., 2024). In vertical farms, plants are typically grown in hydroponic systems where nutrients and light are delivered artificially, often using light-emitting diodes (LEDs) (Mitchell and Sheibani, 2020). In the case of sole-source lighting using LEDs, as in vertical farms, the entirety of lighting conditions, including wavelength, intensity, and photoperiod, can be fine-tuned to bring about desired outcomes for crop production (Mitchel and Stutte, 2015). Establishing the optimal environmental, nutrient, and lighting conditions will be crucial to bringing indoor strawberry crop production to the next phase as a sustainable and profitable endeavor.

Sole-source lighting

In sole-source lighting, particular wavelengths of light can be directed to plants, which can produce specific outcomes on photomorphogenesis and photosynthesis (Guiamba et al., 2022). The influence of blue (B, 400–500 nm) and red light (R, 600–700 nm) on the productivity of indoor strawberries have been studied extensively. 100 $\mu mol \cdot m^{-2} \cdot s^{-1}$ of monochromatic B light (peak = 436 nm) produced a 10% increase in petiole length, a 32% increase in flower stem length, earlier flower initiation, a 25% higher fruit set, and an 84% increase in yield over 100 $\mu mol \cdot m^{-2} \cdot s^{-1}$ of monochromatic R light (peak = 666 nm) in strawberry 'Elsanta' (Nadalini et al., 2017). Similarly, Yoshida et al. (2012) reported that 150 $\mu mol \cdot m^{-2} \cdot s^{-1}$ of B light (peak = 470 nm) reduced the time to initiate flowering in strawberry 'HS138' compared with 150 $\mu mol \cdot m^{-2} \cdot s^{-1}$ of R light (peak = 630 nm). While B light can improve strawberry growth and development over R light, a combination of B and R light can further enhance strawberry growth. For example, 'Daewang' strawberries were grown under 200 $\mu mol \cdot m^{-2} \cdot s^{-1}$ of B+R light, B light (peak = 448), or R light (peaks = 634 nm and 661 nm), and B+R light produced the highest yield and sucrose content of fruits (Choi et al., 2015). Similarly, Samuolienė et al. (2010) reported that combining 175 $\mu mol \cdot m^{-2} \cdot s^{-1}$ of R light with 26 $\mu mol \cdot m^{-2} \cdot s^{-1}$ of B light improved vegetative growth and increased fruit size by 53% compared with 200 $\mu mol \cdot m^{-2} \cdot s^{-1}$ of R light (peak = 640 nm).

Far-red light

Further improvements to the vegetative growth and flowering of strawberries and other horticultural crops have been achieved by adding far-red (FR, 700–750 nm) light to photosynthetically active radiation (PAR), which has traditionally been defined as photons between 400 and 700 nm that plants are able to use for photosynthesis (McCree, 1971). While falling outside of that spectrum, FR light can elicit photomorphogenic responses such as promoting flowering in some long-day plants, expanding leaf area, and increasing plant height as a shade-avoidance response (Tan et al., 2022). FR light is perceived in plants by phytochromes, which are photoreceptor proteins that exist in two interconvertible forms. Upon absorbing FR light, a phytochrome molecule undergoes a structural change from the biologically active $P_{fr}$ form to the inactive $P_r$ form. Conversely, the absorption of R light converts $P_r$ back to $P_{fr}$. The relative proportions of $P_r$ and $P_{fr}$ forms determine some physiological responses in plants. When plants are exposed to FR light, the balance of the phytochrome pool shifts away from the $P_{fr}$ form, the reduction of which can promote stem elongation, leaf expansion, and flowering. For example, adding 154 $\mu mol \cdot m^{-2} \cdot s^{-1}$ of FR light to 150 $\mu mol \cdot m^{-2} \cdot s^{-1}$ of B+R light in tomatoes (*Solanum lycopersicum*) increased leaf area by 26%, plant height by 92%, and overall plant dry mass by 33% over only B or R light (Kalaitzoglou et al., 2019). Similarly, in strawberry ‘Paros’, 32 days of treatments providing 15 $\mu mol \cdot m^{-2} \cdot s^{-1}$ of end-of-day FR light for 6 hours increased leaf area by 17% and petiole length by 20% (Zahedi and Sarikhani, 2016). Adding FR light to B+R light during the seedling stage also

increased the petiole length of strawberry ‘Yotsubushi’ by 185% (Tsuruyama and Shibuya et al., 2023).

When added to R light, FR light hastens flower initiation in some long-day plants, including snapdragon (*Antirrhinum majus*) and petunia (*Petunia* × *hybrida*) (Craig and Runkle, 2016; Park and Runkle 2017, 2018, 2019; Zhang et al., 2020). Recent strawberry research has shown that adding FR light to B+R light can promote flowering as well. For example, an end-of-day FR lighting treatment reduced the flowering time of long-day strawberry accession (*Fragaria vesca*) ‘Hawaii-4’ by a month over R or B light alone (Rantanen et al., 2014). In another strawberry accession (*F. vesca*) ‘Yellow Wonder’, 71 $\mu mol \cdot m^{-2} \cdot s^{-1}$ of FR light for 24-h + 300 $\mu mol \cdot m^{-2} \cdot s^{-1}$ of PAR for 16 h accelerated flower bud emergence over 16-h of 300 $\mu mol \cdot m^{-2} \cdot s^{-1}$ of PAR + 8-h of 100 $\mu mol \cdot m^{-2} \cdot s^{-1}$ of PAR radiation at night (Prisca et al., 2022). Adding 63 $\mu mol \cdot m^{-2} \cdot s^{-1}$ of FR light to B+R light for 24 h decreased the time to bud emergence in long-day strawberry ‘Elan’ compared with B or R light alone (Tsuruyama and Shibuya, 2023).

Nutrient management in hydroponics

In hydroponic systems, because the nutrients used for plant growth are provided solely via the nutrient solution, nutrient management is critical to crop outcomes (Ali Al Meselmani, 2023). As strawberries are especially sensitive to high nutrient concentrations and high salinity, nutrient management in hydroponic strawberry production can be particularly challenging (Barroso and Alvarez, 1997). The responses of different

strawberry cultivars to hydroponic culture are also varied, with some cultivars performing better in certain hydroponic systems than others (Richardson et al., 2022). As a result, determining the optimal nutrient concentrations in hydroponic strawberry production will be an important aspect of improving its viability as a crop in vertical farming and other controlled environments.

## Potassium in hydroponic crop production

Besides nitrogen (N), potassium (K) is often the nutrient most used by plants for growth (Zörb et al., 2014). Additionally, K and N have a complementary relationship in terms of their use in photosynthesis. K is responsible for regulating the osmotic potential of cells within plants, which ultimately facilitates water and nutrient transport (Mengel and Ameke, 1982). In fruiting crops, increasing the K concentration can increase yield and improve quality parameters such as fruit size, fruit color, soluble solids, and shelf life (Asaduzzaman and Asao, 2019). Increasing the K concentration from 0.5 to 7 mM in hydroponically grown bell pepper (*Capsicum annuum*) improved fruit firmness, increased total soluble solids content, and improved overall yield. In addition, improvements to total soluble solids content in bell pepper (Mardanluo et al., 2018) and tomato (Almeselmani et al., 2009) have been achieved by increasing the K concentration from 150 $mg \cdot L^{-1}$ and 200 $mg \cdot L^{-1}$, respectively, to 400 $mg \cdot L^{-1}$ in hydroponic systems.

## Potassium and nitrogen balance

N is responsible for a wide range of functions within plants, while the effective conversion of N into different compounds is often dependent on the presence of K, like in the case of the formation of glutamic acid, an amino acid used for nitrogen assimilation and plant growth (Blevins, 1985). As a result, the relative levels of K and N influence crop growth and yield (Pedrosa et al., 2011; Xu et al., 2024). Kaur et al. (2017) found that a K:N ratio of 2.1:1 (300- $mg \cdot L^{-1}$ K : 140- $mg \cdot L^{-1}$ N) in the vegetative stage and 2.1:1 (350 $mg \cdot L^{-1}$ K, 170 $mg \cdot L^{-1}$ N) in the reproductive stage of tomato increased fruit yield per plant and improved titratable acidity and total soluble solids content compared with providing K:N ratios of 1.4:1 (200 $mg \cdot L^{-1}$ K, 140 $mg \cdot L^{-1}$ N) in the vegetative stage and 1:1.5 (250 $mg \cdot L^{-1}$ K, 170 $mg \cdot L^{-1}$ N) in the fruiting stage.

Potassium research in hydroponically grown strawberries

In strawberries, research surrounding nutrient concentrations in hydroponic production has focused on K:N. K uptake can often exceed the uptake of N in strawberries, as K is a crucial aspect of the cell expansion process required for fruit growth (Tagliavini et al., 2005). Due to its importance in cellular processes such as osmotic potential regulation, enzyme activation, and facilitation of photosynthesis, the concentration of K within plants can indirectly promote fruit yield by enhancing overall plant growth and have a direct impact through promoting cell enlargement by maintaining turgor pressure (Kumar et al., 2006). For example, increasing the K concentration from 200 $mg \cdot L^{-1}$ to 300 $mg \cdot L^{-1}$ in strawberries ‘Camarosa’, ‘Parus’, and

‘Silva’ improved leaf area, fruit number, and total plant yield (Ebrahimi et al., 2012). Similarly, Tohidloo et al. (2018) increased leaf area, shoot dry mass, and fruit yield per plant in strawberry ‘Camarosa’ by raising the K concentration from 235 $mg \cdot L^{-1}$ to 350 $mg \cdot L^{-1}$ in a hydroponic system. In strawberries ‘Fortuna’, ‘Sabrina’, and ‘San Andreas’, a K:N of 2.6:1 before fruiting followed by a low K:N of 1.0:1 during fruiting increased fruit yield and total soluble solids content over a K:N of 1.3:1 before fruiting and a K:N of 2.0:1 during fruiting (Nakro et al., 2023).

REFERENCES

Almeselmani, M. (2023). Nutrient Solution for Hydroponics. IntechOpen. doi: 10.5772/intechopen.101604

Almeselmani, M., Pant, R. C., Singh, B. (2009). Potassium level and physiological response and fruit quality in hydroponically grown tomato. *International Journal of Vegetable Science, 16*(1), 85-99. https://doi.org/10.1080/19315260903271526.

Asaduzzaman, M., Asao, T. (2019). Introductory Chapter: Potassium in quality improvement of fruits and vegetables. Improvement of Quality in Fruits and Vegetables Through Hydroponic Nutrient Management, 1.

Barroso, M. M., Alvarez, C. E. (1997). Toxicity symptoms and tolerance of strawberry to salinity in the irrigation water. *Scientia horticulturae, 71*(3-4), 177-188. https://doi.org/10.1016/S0304-4238(97)00082-4.

Blevins, D. G. (1985). Role of potassium in protein metabolism in plants. *Potassium in Agriculture*, 413-424. https://doi.org/10.2134/1985.potassium.c17.

Botella, M. Á., Arévalo, L., Mestre, T. C., Rubio, F., García-Sánchez, F., Rivero, R. M., Martínez, V. (2017). Potassium fertilization enhances pepper fruit quality. *Journal of Plant Nutrition*, *40*(2), 145-155. https://doi.org/10.1080/01904167.2016.1201501.

Choi, H. G., Moon, B. Y., & Kang, N. J. (2015). Effects of LED light on the production of strawberry during cultivation in a plastic greenhouse and in a growth chamber. *Scientia Horticulturae*, 189, 22-31. https://doi.org/10.1016/j.scienta.2015.03.022.

Craig, D. S., Runkle, E. S. (2016). An intermediate phytochrome photoequilibria from night-interruption lighting optimally promotes flowering of several long-day plants. *Environmental and experimental botany*, *121*, 132-138. https://doi.org/10.1016/j.envexpbot.2015.04.004.

Ebrahimi, R., Souri, M. K., Ebrahimi, F., Ahmadizadeh, M. (2012). Growth and yield of strawberries under different potassium concentrations of hydroponic system in three substrates. *World Applied Sciences Journal*, *16*(10), 1380-1386. Retrieved from https://citeseerx.ist.psu.edu/document?repid=rep1&type=pdf&doi=49ca83af6746a1ac81b5ecf1192a2923e5e1afed

Giampieri, F., Alvarez-Suarez, J.M., Battino, M., (2014). Strawberry and human health: effects beyond antioxidant activity. J. Agric. Food Chem. 62, 3867–3876. https://doi.org/10.1021/jf405455n.

Guiamba, H. D. S. S., Zhang, X., Sierka, E., Lin, K., Ali, M. M., Ali, W. M., Lamlom, S.F., Kalaji, H.M., Telesiński, A., Yousef, A.F., Xu, Y. (2022). Enhancement of photosynthesis efficiency and yield of strawberry (Fragaria ananassa Duch.) plants via LED systems. Frontiers in Plant Science, 13, 918038. https://doi.org/10.3389/fpls.2022.918038.

Kaur, H., Bedi, S., Sethi, V. P., & Dhatt, A. S. (2018). Effects of substrate hydroponic systems and different N and K ratios on yield and quality of tomato fruit. *Journal of Plant Nutrition*, *41*(12), 1547-1554. https://doi.org/10.1080/01904167.2018.1459689.

Kouloumprouka Zacharaki, A., Monaghan, J. M., Bromley, J. R., & Vickers, L. H. (2024). Opportunities and challenges for strawberry cultivation in urban food production systems. Plants, People, Planet. https://doi.org/10.1002/ppp3.10475.

Kumar, A. R., Kumar, N., Kavino, M. (2006). Role of potassium in fruit crops-a review. *Agricultural Reviews*, *27*(4), 284-291. Retrieved from https://www.indianjournals.com/ijor.aspx?target=ijor:ar&volume=27&issue=4&article=006.

Mardanluo, S., Souri, M. K., Ahmadi, M. (2018). Plant growth and fruit quality of two pepper cultivars under different potassium levels of nutrient solutions. Journal of Plant Nutrition, 41(12), 1604-1614. https://doi.org/10.1080/01904167.2018.1463383.

Mengel, K., & Arneke, W. W. (1982). Effect of potassium on the water potential, the pressure potential, the osmotic potential and cell elongation in leaves of Phaseolus vulgaris. *Physiologia Plantarum*, *54*(4), 402-408. https://doi.org/10.1111/j.1399-3054.1982.tb00699.x.

Mitchell, C. A., & Sheibani, F. (2020). LED advancements for plant-factory artificial lighting. In *Plant factory* (pp. 167-184). Academic Press. https://doi.org/10.1016/B978-0-12-816691-8.00010-8.

Mitchell, C., Stutte, G. (2015). Sole-source lighting for controlled-environment agriculture. *Light Management in Controlled Environments*; Lopez, R., Runkle, ES, Eds, 119-134. Retrieved from https://www.spring-lake.net/pdfs/gh-tech/ch5-sole-source-Agriculture.pdf

Nadalini, S., Zucchi, P., Andreotti, C. (2017). Effects of blue and red LED lights on soilless cultivated strawberry growth performances and fruit quality. *European Journal of Horticultural Science, 82*(1), 12–20. https://doi.org/10.17660/eJHS.2017/82.1.2.

Nakro, A., Bamouh, A., Bouslama, H., San Bautista, A., Ghaouti, L. (2023). The effect of potassium–nitrogen balance on the yield and quality of strawberries grown under soilless conditions. Horticulturae, 9(3), 304. https://doi.org/10.3390/horticulturae9030304.

Park, Y., Runkle, E. S. (2017). Far-red radiation promotes growth of seedlings by increasing leaf expansion and whole-plant net assimilation. *Environmental and Experimental Botany, 136*, 41–49. https://doi.org/10.1016/j.envexpbot.2016.12.013.

Park, Y, Runkle, E. S. (2018). Far-red radiation and photosynthetic photon flux density independently regulate seedling growth but interactively regulate flowering. *Environmental and Experimental Botany, 155*, 206–216. https://doi.org/10.1016/j.envexpbot.2018.06.033.

Park, Y, Runkle E. S. (2019). Blue radiation attenuates the effects of the red to far-red ratio on extension growth but not on flowering. *Environmental and Experimental Botany, 168*, 103871. https://doi.org/10.1016/j.envexpbot.2019.103871.

Pedrosa, A. W., Martinez, H. E. P., Matiello, E. M., Fontes, P. C. R., & Pereira, P. R. G. (2011). Influence of the N/K ratio on the production and quality of cucumber in hydroponic system. *Revista Ceres, 58*, 619-624. https://doi.org/10.1590/S0034-737X2011000500012.

Richardson, M. L., Arlotta, C. G., Lewers, K. S. (2022). Yield and nutrients of six cultivars of strawberries grown in five urban cropping systems. *Scientia Horticulturae, 294*, 110775. https://doi.org/10.1016/j.scienta.2021.110775.

Samtani, J. B., Rom, C. R., Friedrich, H., Fennimore, S. A., Finn, C. E., Petran, A., Bergefurd, B. (2019). The status and future of the strawberry industry in the United States. HortTechnology, 29(1), 11-24. https://doi.org/10.21273/HORTTECH04135-18.

Samuolienė, G., Brazaitytė, A., Urbonavičiūtė, A., Šabajevienė, G., Duchovskis, P. (2010). The effect of red and blue light component on the growth and development of frigo strawberries. *Zemdirbyste-Agriculture*, *97*, 99–104. Retrieved from http://zemdirbyste-agriculture.lt/97(2)tomas/97_2_tomas_str11.pdf.

Tagliavini, M., Baldi, E., Lucchi, P., Antonelli, M., Sorrenti, G., Baruzzi, G., & Faedi, W. (2005). Dynamics of nutrients uptake by strawberry plants (Fragaria× Ananassa Dutch.) grown in soil and soilless culture. *European Journal of Agronomy*, *23*(1), 15-25. https://doi.org/10.1016/j.eja.2004.09.002.

Tohidloo, G., Souri, M. K., Eskandarpour, S. (2018). Growth and fruit biochemical characteristics of three strawberry genotypes under different potassium concentrations of nutrient solution. Open Agriculture, 3(1), 356-362. https://doi.org/10.1515/opag-2018-0039.

Tan, T., Li, S., Fan, Y., Wang, Z., Raza, M. A., Shafiq, I., Yang, W. (2022). Far-red light: A regulator of plant morphology and photosynthetic capacity. *The Crop Journal*, *10*(2), 300-309. https://doi.org/10.1016/j.cj.2021.06.007.

U.S. Department of Agriculture (USDA) 2014a U.S. strawberry consumption continues to grow. 28 Nov. 2018. <https://www.ers.usda.gov/data-products/chart-gallery/gallery/chart-detail/?chartId=77884>.
U.S. Department of Agriculture (USDA) 2018a Vegetables 2017 summary (February 2018). 28
Nov. 2018. http://usda.mannlib.cornell.edu/usda/current/VegeSumm/VegeSumm-02-13-2018.pdf

Xu, X., Zhang, X., Ni, W., Liu, C., Qin, H., Guan, Y., Liu, J., Feng, Z., Xing, Y., Tian, G. and Zhu, Z (2024). Nitrogen–potassium balance improves leaf photosynthetic capacity by regulating leaf nitrogen allocation in apple. *Horticulture Research*, *11*(1), uhad253. https://doi.org/10.1093/hr/uhad253.

Yoshida, H., Hikosaka, S., Goto, E., Takasuna, H., Kudou, T. (2012). Effects of light quality and light period on flowering of everbearing strawberry in a closed plant production system. *Acta Horticulturae*, *956*, 107–112. https://doi.org/10.17660/ActaHortic.2012.956.9.

Zahedi, S. M., Sarikhani, H. (2016). Effect of far-red light, temperature, and plant age on morphological changes and induction of flowering of a 'June-bearing' strawberry. *Horticulture, Environment, and Biotechnology*, *57*, 340-347. https://doi.org/10.1007/s13580-016-0018-8.

Zhang, M., Park, Y., Runkle, E. S. (2020). Regulation of extension growth and flowering of seedlings by blue radiation and the red to far-red ratio of sole-source lighting. *Scientia Horticulturae*, *272*, 109478. https://doi.org/10.1016/j.scienta.2020.109478.

Zörb, C., Senbayram, M., Peiter, E. (2014). Potassium in agriculture–status and perspectives. *Journal of Plant Physiology*, *171*(9), 656-669. https://doi.org/10.1016/j.jplph.2013.08.008.

# CHAPTER 2

# FAR-RED LIGHT IN SOLE-SOURCE LIGHTING CAN ENHANCE THE GROWTH AND FRUIT PRODUCTION OF INDOOR STRAWBERRIES

ABSTRACT

Strawberries (*Fragaria ×ananassa*) are being produced increasingly in indoor vertical farms, where the light quality of sole-source lighting is a primary factor that influences the outcomes of crop production. Far-red (FR, 700–750 nm) light has been shown to promote plant responses like leaf expansion, biomass accumulation, and flowering in some long-day plant species. However, the impacts of including FR light in sole-source lighting on strawberries have not been fully understood. This study investigated the impacts of FR light on the growth and development of long-day strawberries 'Albion' and 'Monterey' in an indoor vertical farm. We hypothesized that the addition of FR light under a long photoperiod would promote leaf expansion, biomass accumulation, flowering, and fruit production in ever-bearing strawberries. Bare-root strawberry plants were grown in a deep-water culture hydroponic system under a 22 °C air temperature and an 18-h photoperiod using 90 $\mu mol \cdot m^{-2} \cdot s^{-1}$ of blue (peak = 455 nm) + 250 $\mu mol \cdot m^{-2} \cdot s^{-1}$ of red (peak = 660 nm) light-emitting diodes (LEDs) with or without adding 50 $\mu mol \cdot m^{-2} \cdot s^{-1}$ of FR (peak = 730 nm) LEDs. After five weeks of lighting treatments, additional FR light increased the leaf area and shoot dry mass of strawberry 'Monterey' by 74% and 73%, respectively, and the number of crowns per plant of strawberry 'Albion' by 33%. However, FR light did not influence flowering time in either cultivar. Adding FR light increased the number of fruits harvested per plant by 36%, the total fruit yield by 48%, and the total soluble solids of fruits by 12% in strawberry 'Albion', but not in 'Monterey'. In both cultivars, FR light did not impact the

individual fruit mass but decreased the fruit diameter by 3-4%. Our results suggest that the addition of FR light in sole-source lighting can promote leaf expansion, biomass accumulation, fruit yield, and fruit quality in at least some ever-bearing strawberry cultivars.

*Keywords*: controlled environment agriculture, fruit yield, indoor, light quality, vertical farming

*Abbreviations*: B, Blue; EC, Electrical Conductivity; ePPFD, Extended Photosynthetic Photon Flux Density; FR, Far-Red; iPPE, Internal Phytochrome Photoequilibria; LD, Long-Day; LED, Light Emitting Diodes; PAR, Photosynthetically Active Radiation; PPE, Phytochrome Photoequilibria; PPFD, Photosynthetic Photon Flux Density; R, Red; SPAD, Soil-Plant Analysis Development; TSS, Total Soluble Solids; W, White

## Introduction

Strawberries (*Fragaria ×ananassa*) are a highly valued specialty food crop, valued at over $3.1 billion in 2022 in the U.S. (USDA 2022). However, outdoor growers are facing an increasing number of challenges, including more variable weather conditions, a shrinking labor supply, tightening environmental regulations, and increases in land value (Samtani et al., 2019). In response, cultivating strawberry crops in indoor vertical farms is increasingly appealing. With proper cultural practices, strawberry crops

can remain compact and respond well to hydroponic growing conditions and indoor growing environments, making them suitable for production in indoor vertical farms (Richardson et al., 2022). As a result, many established and startup indoor vertical farming companies are beginning to produce strawberries at a commercial level (Lore 2022; Marston 2023).

Because crop production in indoor vertical farming is highly energy-intensive and costly, it is critical to optimize the environmental conditions to improve crop productivity and quality (Bantis et al., 2018). In indoor vertical farms, the sole-source lighting strategy applied is among the most important environmental factors that affect crop yield and productivity. Sole-source lighting supplies light completely artificially, typically using light-emitting diodes (LEDs), which allow growers to deliver unique combinations of light wavebands for each specific crop. Given that light quality can impact a wide range of plant traits, such as plant height, leaf size, and flowering time, and that these responses can vary across plant species and cultivars (Rahman et al., 2021), determining the optimal light spectrum specifically for strawberries is crucial for their effective production in indoor vertical farms.

In strawberries, light quality studies in sole-source lighting have primarily focused on blue (B, 400–500 nm) and red (R, 600–700 nm) light. Monochromatic B light can improve the vegetative, flowering, and fruiting stages of strawberries compared with monochromatic R light. For example, monochromatic B (peak = 436 nm) light increased petiole length, flower stem length, fruit set, fruit yield, and accelerated flowering

compared with monochromatic R (peak = 666 nm) light in strawberry ‘Elsanta’ (Nadalini et al., 2017). The time to flower initiation was reduced by 17 days using B (peak = 470 nm) light over R (peak = 630 nm) light in everbearing strawberry ‘HS138’ (Yoshida et al., 2012). However, different combinations of B+R lighting have enhanced growth and fruiting parameters compared with B or R light alone. For example, B+R LED light produced the highest yield in ‘Daewang’ strawberries compared with B (peak = 448 nm) or R (peaks = 634 nm and 661 nm) light alone in a growth chamber, and a higher sucrose content was produced using B+R light compared with B light alone (Choi et al., 2015). Additionally, a combination of B+R light increased the total chlorophyll content compared with B or R light individually (Choi et al., 2015). Combining R (peak = 640) light with B (peak = 455) light improved vegetative growth and increased individual fruit fresh mass in strawberry ‘Elkat’ compared with only R (peak = 640 nm) light in a phytotron chamber (Samuolienė et al., 2010). In strawberry ‘Daewang’, a combination of B and R light increased overall fruit yield and fructose content over monochromatic B (peak = 448 nm) or R (peak = 661 nm) light.

Recently, including far-red (FR, 700–750 nm) light in sole-source lighting has received attention due to its positive effects on photosynthesis and photomorphogenesis (Tan et al., 2022). Although the traditionally defined range of photosynthetically active radiation (PAR, 400–700 nm) excludes FR light, FR light elicits comparable photosynthetic activity when combined with PAR photons (Zhen and van Iersel 2017; Zhen et al., 2021). On the other hand, FR light influences plant development through

phytochromes, which are photoreceptor proteins present in plants. Phytochromes exist in two forms: $P_r$ (inactive) and $P_{fr}$ (active). The absorption of R light causes a structural change in the phytochrome molecule, converting the $P_r$ form to the $P_{fr}$ form, the relative proportions of which can determine plant physiological processes such as stem elongation, leaf expansion, and, in some cases, flowering. The balance of $P_{fr}$ to $P_r$ can be estimated by measuring the spectral distribution of photons received by plants and using photoconversion coefficients to obtain a value that represents the ratio of $P_{fr}$ to ($P_r$ + $P_{fr}$), known as the phytochrome photoequilibria (PPE) (Sager et al., 1988). An improvement to this calculation has been suggested by Kusuma and Bugbee (2021), which incorporates the scattering and absorbance of photons within leaves to better predict phytochrome responses, known as internal PPE (iPPE). In tomato (*Solanum lycopersicum*), adding FR light to B+R light increased plant height, leaf area, and plant dry mass over plants receiving only B+R light (Kalaitzoglou et al., 2019). The promotive effects of including FR in sole-source lighting on stem elongation, leaf expansion, and biomass accumulation have also been observed in many horticultural crops, including geranium (*Pelargonium* × *hortorum*), petunia (*Petunia* × *atkinsiana*), snapdragon (*Antirrhinum majus*), impatiens (*Impatiens walleriana*), marigold (*Tagetes erecta*), zinnia (*Zinnia elegans*), dianthus (*Dianthus barbatus* × *chinensis*), geranium (*Pelargonium* × *hortorum*), sunflower (*Helianthus annuus*), lettuce (*Lactuca sativa*), and cucumber (*Cucumis sativus*) (Kurepin et al., 2007; Park and Runkle 2017; Zhen and Bugbee 2020; Kusuma and Bugbee 2023). Furthermore, in long-day (LD) plants snapdragon and petunia, adding ≥ 20

μmol·m−2·s−1 of FR light in sole-source lighting has been shown to accelerate flowering (Park and Runkle 2017, 2018; Zhang et al., 2020).

The inclusion of FR light has shown promotive effects on flowering in some LD strawberry cultivars and accessions. For example, a LD strawberry accession (*F. vesca* 'Hawaii-4') flowered a month earlier under end-of-day lighting from FR LEDs or incandescent lamps, which also emit FR light, than under R light (Rantanen et al., 2014). Similarly, flower induction was promoted in a LD strawberry accession, *F. vesca* 'Yellow Wonder', by supplying FR (peak = 740 nm) light for 24-h (Prisca et al., 2022). Flower bud emergence was accelerated in seedlings of LD strawberry cultivars 'Elan' and 'Yotsuboshi' by adding FR (peak = 730 nm) light to B (peak = 470 nm) +R (peak = 625 nm) light for 24-h (Tsuruyama and Shibuya et al., 2023). Collectively, the promotive effects of FR light on flowering in some LD plants are applicable to at least some LD or everbearing strawberries. However, previous strawberry studies focused on flowering responses to FR light, with a lack of emphasis on analyzing vegetative growth and fruit yield and quality. The objective of this study was to investigate the impacts of including FR light in sole-source lighting on plant morphology, biomass accumulation, flowering, and subsequent fruit yield and quality in everbearing strawberries. We postulated that additional FR light would promote leaf expansion, biomass accumulation, and flowering, thereby increasing fruit yield and quality in everbearing strawberries.

## Materials and Methods

### *Plant materials and transplanting*

We obtained bare-root plants of two ever-bearing strawberry cultivars, ‘Albion’ and ‘Monterey’, from a commercial nursery (Lassen Canyon Nursery Inc., Redding, CA, USA) on 24 August 2022. In each cultivar, we selected 100 bare-root plants with crown diameters of 10–13 mm for experimental use on 26 August 2022. The average crown diameters of the bare-root plants for ‘Albion’ and ‘Monterey’ were 11.2 mm and 11.3 mm, respectively. We washed the bare-root plants with tap water to remove residual media and sanitized them in a solution made with Zerotol (27.1% hydrogen peroxide and 2.0% peroxyacetic acid; Biosafe Systems, East Hartford, CT, USA) and deionized water (1:100 mL/mL) for 15 min.

We then moved the plants to a temperature-controlled indoor vertical farm and transplanted them into foam rafts (28 cell lettuce raft; Beaver Plastics Ltd., Acheson, Alberta, Canada) floating in deep-water-culture hydroponic growing trays (1.12 m × 0.66 m × 0.18 m; GT24X44X7B; Botanicare, Vancouver, WA, USA). Four growing racks were used, each of which contained three vertically stacked tiers that held a growing tray in each tier, totaling 12 growing trays. At the bottom of each rack, there were two reservoirs with recirculating water (0.80 m × 0.53 m × 0.37 m, 94 Liter Latch and Stack Tote; Husky, Atlanta, GA, USA), which connected to the growing trays. Each foam raft (growing area = 0.74 $m^2$) held 25 plants (planting density = 27 plants·$m^{-2}$), which were of

the same cultivar in each tier, and the cultivars were arranged identically between replications and treatments on each rack. The experiment was carried out using a randomized complete block design with each replication as a block, each reservoir as the experimental unit for the lighting treatment, and the individual plant of each cultivar as a subsample. The vertical location of each floating raft in the growing rack was cycled every two weeks for the duration of the experiment to reduce any positional effects in the growing trays in the growing rack, with the top raft moved to the bottom, the bottom raft moved to the middle, and the middle raft moved to the top.

The air temperature was maintained at 22 °C and logged on an hourly basis with a sensor placed in the center of each growing tray (Smart Thermo-Hygrometer H5075; Govee, Shenzen, China). A nutrient solution made with deionized water and the Yamazaki recipe provided (in $mg \cdot L^{-1}$) 77 N, 23 P, 116 K, 48 S, 40 Ca, 12 Mg, 2 Fe, 0.6 Mn and Zn, 0.3 B, 0.05 Cu, and 0.01 Mo (Jack's Strawberry Part A/B; JR Peters, Inc., Allentown, PA, USA) for the entire growing period. The nutrient solution within each rack was continuously circulated with water pumps (396 GPH Fixed Flow Water Pump; Sunlight Supply Vancouver, WA, USA) and oxygenated with an air pump (Vivosun Electrical Magnetic Air Pump ACO-050; Ontario, CA, USA) and air stones (ASD-200; Pawfly Guangzhou City, Guangdong, China). Daily measurements of the nutrient solution pH and electrical conductivity (EC) were taken with a portable meter (HI9814: Hanna Instruments, Smithfield, RI, USA), and the pH was adjusted to 5.8 if outside 5.5-

6.0, using 50% sulfuric acid to lower the pH and potassium bicarbonate to increase the pH, while EC was kept below 2.0 $mS \cdot cm^{-1}$ by adding deionized water.

*Lighting treatments*

After transplanting, the bare-root plants were grown under B (peak = 455 nm) + R (peak = 660 nm) or B (peak = 455 nm) + R (peak = 660 nm) + FR (peak = 730 nm) LED lamps (T8 Double-Row LED Indoor Grow Light; Homer Farms, Inc., Mesa, AZ, USA) (Fig. 1 and Table 1) as sole-source lighting treatments with an 18-h photoperiod. Each growing tray had seven or eight LED lamps for B+R or B+R+FR treatments, respectively, positioned 25.5 cm above the growing area. At plant height, the B+R treatment delivered 90 $\mu mol \cdot m^{-2} \cdot s^{-1}$ of B light and 250 $\mu mol \cdot m^{-2} \cdot s^{-1}$ of R light, whereas the B+R+FR treatment delivered 90 $\mu mol \cdot m^{-2} \cdot s^{-1}$ of B light, 250 $\mu mol \cdot m^{-2} \cdot s^{-1}$ of R light, and 50 $\mu mol \cdot m^{-2} \cdot s^{-1}$ of FR light. Photon flux densities were measured using a spectroradiometer (PS-300; StellerNet, Inc., Tampa, FL) at nine equally spaced locations in each growing tray at plant height (Fig. 1). With the spectra in Fig. 1, the percent FR (%FR) was calculated as the percentage of the photon flux density of FR (700–750 nm) light in the extended photosynthetic photon flux density (ePPFD) (400–750 nm), PPE was calculated as described in Sager et al. (1988), and the estimated iPPE was calculated according to Kusama and Bugbee (2021) (Table 1). Photon flux densities of $\geq 300$ $\mu mol \cdot m^{-2} \cdot s^{-1}$ and an 18-hour photoperiod were chosen based on a previous finding (Park

et al, 2023) that a longer photoperiod at a photosynthetic photon flux density (PPFD) of ≥ 300 µmol·m$^{-2}$·s$^{-1}$ promoted flowering and fruit yield.

*Data collection and analysis*

The experiment was replicated in independent growing racks during the same experimental period. In each replication, during the initial 5-week period after transplanting, all flowers and runners were removed daily to promote vegetative growth. Five weeks following transplanting, 10 representative plants of each cultivar, treatment, and replication were randomly chosen for vegetative growth data collection. At the time of collecting vegetative growth data, each plant was not in contact with another (leaf area index <1). For each plant, we recorded the number of fully formed trifoliate leaves, SPAD index [using a portable chlorophyll meter (SPAD-502; Konica Minolta Sensing, Inc., Chiyoda, Tokyo, Japan)], crown number, crown diameter [using a caliper (B07DFFYCXS; Adoric)], leaf area [using a leaf area meter (LI-3100; LI-COR Inc., Lincoln, Nebraska, USA)], root length, shoot and root fresh and dry mass [using a scale (PB602-S; Mettler Toledo, Columbus, OH, USA)]. Shoot and root dry mass were measured after plants were sufficiently dried at ≥ 70 °C for ≥ 5 days in a drying oven (Hafo 1600; VWR International, LLC, Aurora, CO, USA).

Following the vegetative growth data collection, each plant was allowed to develop flowers and fruits. For each plant, we recorded the date of the first open flower and the date of the first fruit harvest (at the visual appearance of the first fully red fruit).

Fruit harvesting started 66 days following transplanting, with subsequent fruit data collected for all ripened fruit twice weekly for the remainder of the experiment. In addition, 11 weeks after transplanting, the number of unopened flowers, fully opened flowers, fruits, and inflorescences were counted for all remaining plants, as well as the length of the peduncles for inflorescences with harvestable fruit. Once each fruit was harvested, we measured the fruit diameter at its largest width and vertical length using a caliper (B07DFFYCXS; Adoric), and fruit fresh mass using an analytical balance (PB602-S; Mettler Toledo, Columbus, OH, USA). For each plant, we measured the total soluble solids (TSS), reported as °Brix, of the first harvested fruit at room temperature. The largest fruit was chosen if the plant had multiple harvestable fruits. Once a fruit was selected for TSS measurement, we removed its pedicle and placed it in a plastic bag, where it was compressed by hand until reaching a consistent pulp state. A TSS reading was then taken using a digital refractometer (HI 96801; Hanna Instruments), which also recorded ambient temperature.

Data were analyzed using a Student's t-test in SAS (version 9.4; SAS Institute, Inc., Cary, NC) using PROC TTEST with a significance level of $P < 0.05$. The experiment was replicated, and data from each replication were pooled for the t-test since the experimental conditions remained consistent across replications, each replication was conducted independently, lighting treatments were randomly assigned within each replication, and pooling data from multiple replications can enhance the power of the analysis. The sample sizes for the analysis of vegetative growth (n = 20), days to flower

and fruit harvest (n = 24), peduncle length (n = 16), and fruit production and characteristics (n = 24) varied.

## Results

### *Vegetative growth*

The addition of FR light increased the number of crowns in ‘Albion’ by 33% but not in ‘Monterey’ (Table 2). Leaf number, crown diameter, and SPAD index for both ‘Albion’ and ‘Monterey’ were unaffected by FR light. In ‘Monterey’, additional FR light increased leaf area by 74%, shoot fresh mass by 59%, and shoot dry mass by 73%, whereas FR light did not influence these parameters in ‘Albion’. In ‘Monterey’, FR light also increased root fresh mass by 62%, root dry mass by 47%, and root length by 17%; however, root growth of ‘Albion’ was unaffected by FR light.

### *Flowering and fruit production*

FR light had little to no effect on days to flowering in both cultivars and days to fruit harvest in ‘Monterey’ (Table 3). In ‘Albion’, FR light hastened fruit harvest by 5 d. At fruit harvest, FR light increased the peduncle length by 62% in ‘Monterey’, but not ‘Albion’ (Fig. 2). FR light increased the number of fruits and total fruit fresh mass produced per plant by 36% and by 48%, respectively, in ‘Albion’, but not in ‘Monterey’ (Figs. 3 and 4). Individual fruits produced in both cultivars had similar fresh mass and fruit length regardless of FR light; however, FR light decreased the fruit diameter by 3-

4% (Table 4). FR light increased the TSS value of ‘Albion’ fruits by 12% but did not influence that of ‘Monterey’ fruits.

## Discussion

In this study, when 50 μmol·m$^{-2}$·s$^{-1}$ of FR light (or decreasing PPE from 0.88 to 0.84) was added to 90 μmol·m$^{-2}$·s$^{-1}$ of B + 250 μmol·m$^{-2}$·s$^{-1}$ of R light, both shoot dry mass and leaf area of strawberry ‘Monterey’ increased by 73% and 74%, respectively, showing a similar magnitude of change. Adding FR to sole-source lighting promotes leaf expansion and biomass accumulation of many horticultural crops, such as lettuce, petunia, and geranium (Park and Runkle 2017, 2018, 2019; Kusuma and Bugbee 2023). In addition, as leaf expansion significantly contributes to the rate of biomass accumulation, the increase in shoot dry mass was comparable to the increase in leaf area with the addition of FR light. For example, in lettuce, adding 52 μmol·m$^{-2}$·s$^{-1}$ of FR light to 24 μmol·m$^{-2}$·s$^{-1}$ of B light and 194 μmol·m$^{-2}$·s$^{-1}$ of R light increased leaf area by 61% and leaf dry mass by 63% (Jin et al. 2021). In *Crepidiastrum denticulatum*, adding 108.3 μmol·m$^{-2}$·s$^{-1}$ of FR light to 32.5 μmol·m$^{-2}$·s$^{-1}$ of B light and 97.5 μmol·m$^{-2}$·s$^{-1}$ of R light (decreasing PPE from 0.88 to 0.71) increased shoot dry mass by 90% and leaf area by 96% (Bae et al. 2017).

The extent of the increase in leaf area and shoot dry mass observed in ‘Monterey’ (73% and 74%, respectively) is greater than what has been reported in other shade-avoiding horticultural crops receiving FR light, given the relatively small amount of

additional %FR light supplied here (12% FR). For example, adding 40% FR light increased the leaf area and shoot dry mass of petunia by 65% and 50%, respectively (Park and Runkle 2018). In geranium, adding 10% FR light led to a 2% increase in leaf area and a 17% increase in shoot dry mass (Park and Runkle 2017). Similarly, a 6% FR light addition in geranium increased leaf area and shoot dry mass by 6% and 16%, respectively (Park and Runkle 2019). Leaf length was increased by 33% and shoot dry mass by 47% in lettuce ‘Rouxai’ with a 17% FR addition (Meng and Runkle 2019). Considering that plants may display varying sensitivity to FR light depending on whether they exhibit shade-avoiding or shade-tolerant traits (Roig-Villanova and Martínez-García 2016), the increases in leaf area and shoot dry mass observed in strawberries in this study indicate a high sensitivity to FR light in certain strawberry cultivars during the vegetative stage.

In contrast to ‘Monterey’, FR light did not affect leaf expansion or biomass accumulation in strawberry ‘Albion’. Leaf expansion responses to FR light may depend on the overall ePPFD supplied and crop species (Kusuma and Bugbee 2023). For example, in lettuce, increasing the %FR light promoted leaf expansion only under an ePPFD of 500 $\mu mol \cdot m^{-2} \cdot s^{-1}$, but not 100 or 200 $\mu mol \cdot m^{-2} \cdot s^{-1}$ (Kusuma and Bugbee 2023). Comparing the effects of R:FR ratios of 0.8, 1.4, and 4.5 at a low PPFD (157 $\mu mol \cdot m^{-2} \cdot s^{-1}$) and a high PPFD (421 $\mu mol \cdot m^{-2} \cdot s^{-1}$) in sunflower, increased leaf expansion by lowering the R:FR ratio (or adding FR light) was more pronounced at the higher PPFD than at the lower PPFD (Kurepin et al. 2007). Hidaka et al. (2013) found that the photosynthetic rate of strawberries increased by increasing the PPFD up to 400

μmol·m$^{-2}$·s$^{-1}$, at which point the response was nearly saturated, and Park et al. (2023) observed a linear increase in shoot dry mass through increasing the PPFD from 200 to 450 μmol·m$^{-2}$·s$^{-1}$. Considering the high light requirement for strawberries (Hidaka et al. 2013; Park et al. 2023), the ePPFD of 390 μmol·m$^{-2}$·s$^{-1}$ in this study might not have been sufficiently high to fully induce the pronounced effects of FR on promoting leaf expansion and dry mass accumulation in some strawberry cultivars.

In many LD plants, adding FR light to R light to elicit an intermediate PPE promotes flowering. For example, as 4-h night-interruption, R+FR light at an intermediate PPE (0.63–0.80) was most effective at inducing the flowering of snapdragon and petunia compared with a PPE of 0.46 or 0.16 (Craig and Runkle 2016). Under sole-source lighting conditions, adding ≥ 16 μmol·m$^{-2}$·s$^{-1}$ of FR light to B+R light (PPE=0.65–0.85) during an 18-h photoperiod decreased flowering time in snapdragon and petunia (Park and Runkle 2017, 2018, 2019; Zhang et al. 2020). Similarly, in the LD strawberry ‘Elan’, adding 63 μmol·m$^{-2}$·s$^{-1}$ of FR light (PPE=0.66) to the background of B+R light during 16-h or 24-h of sole-source lighting decreased the number of days to budding when compared to conditions solely under B+R light (PPE=0.88) (Tsuruyama and Shibuya 2023). In the current study, adding 50 μmol·m$^{-2}$·s$^{-1}$ FR light to the B+R light background decreased PPE from 0.88 to 0.84, making the PPE levels aligned within the range that has previously been reported as effective for stimulating flower initiation in some LD plants. However, the time to flower was not impacted by the addition of FR light or intermediate PPE in either cultivar in the current study. In addition to FR light, B

light can also regulate photoperiodic flowering responses in some LD plants (Meng and Runkle 2017; Lopez et al. 2020). For example, in calibrachoa (*Calibrachoa* × *hybrida*), petunia, and snapdragon, 30 μmol·m$^{-2}$·s$^{-1}$ of B light as night-interruption was as effective for promoting flowering as end-of-day or night-interruption treatments providing 2 μmol·m$^{-2}$·s$^{-1}$ of combined R+W+FR light (Meng and Runkle 2017). In LD strawberry accession *F. vesca* 'Hawaii-4', 6-h of day-extension lighting with 7–15 μmol·m$^{-2}$·s$^{-1}$ of B light promoted flowering over a 12-h short-day or 6-h of day-extension lighting with 7–15 μmol·m$^{-2}$·s$^{-1}$ of R light (Rantanen et al. 2014). In addition, flowering responses in some LD plants were saturated when day-extension or night-interruption lighting included ≥ 15 μmol·m$^{-2}$·s$^{-1}$ of B light (Lopez et al. 2020). Given the involvement of B light in photoperiodic flowering in LD plants and the observed saturation of B light-mediated photoperiodic flowering responses at a relatively low photon flux density, the application of 90 μmol·m$^{-2}$·s$^{-1}$ of B light for an 18-h photoperiod in both treatments in the current study may have exceeded the threshold necessary to induce a flowering response in the everbearing strawberry cultivars 'Monterey' and 'Albion', mitigating any potential effects from FR light.

In this study, the addition of 50 μmol·m$^{-2}$·s$^{-1}$ FR light (or adding 12% FR light) resulted in a 62% increase in peduncle length in strawberry 'Monterey'. Peduncles are specialized stems that can support either flowers or inflorescences in flowering plants or fruit in many fruiting crops. The promotive effects of FR light on the extension growth of peduncles were reported in other flowering crops. For instance, 50 μmol·m$^{-2}$·s$^{-1}$ of

localized FR irradiation to peduncles increased the peduncle length of geranium (*Pelargonium zonale*) by 30% compared with B or R light at the same intensity (Fukuda and Nishimura 2000). In pansy (*Viola* × *wittrockiana* Gams), increasing the percentage of FR light from 19% to 27% (or decreasing PPE from 0.77 to 0.72) by using a greenhouse spectral filter increased the peduncle length by 33% (Runkle and Heins 2003). In strawberries, the peduncle length determines the amount of space between the vegetative part of the plant and where the fruit is harvested (Darrow, 1929). Many robotic harvesting prototypes for strawberries have reported peduncle detection as one of the major limiting factors for successful strawberry harvesting, a problem that would be remedied by consistent increases in peduncle length (Xiong et al. 2020). The increases in peduncle length using FR light in strawberries could prove useful for the successful application of machine harvesters to reduce labor costs, which can account for significant expenses in indoor vertical farms (Lubna et al. 2022).

Although the addition of 50 $\mu mol \cdot m^{-2} \cdot s^{-1}$ FR light (or decreasing PPE from 0.88 to 0.84) did not affect flowering time in both everbearing strawberry cultivars, it decreased the time to harvest the first fruit in ‘Albion’. Also, in ‘Albion’, the addition of FR light increased the number of fruits, total fruit fresh mass, and the TSS content of fruits. Similar responses were reported in tomatoes (Ji et al. 2020; Kim et al. 2020). When tomato plants received 50–80 $\mu mol \cdot m^{-2} \cdot s^{-1}$ of FR light in addition to 150–170 $\mu mol \cdot m^{-2} \cdot s^{-1}$ of combined B and R light, the additional FR light reduced fruit ripening time by 4 d, increased the dry mass of fruits by 33%, and increased the fructose and

glucose content of ripened fruits by 32% and 42%, respectively (Ji et al. 2020). Increases of 50% in fresh yield, 26% in TSS content, and 77% in the dry mass of tomato fruits were also reported by Kim et al. (2020) by adding 95.5 $\mu mol \cdot m^{-2} \cdot s^{-1}$ of FR light to 234 $\mu mol \cdot m^{-2} \cdot s^{-1}$ of light provided by high-pressure sodium lamps, attributed to increases in dry mass partitioning to fruits and overall fruit sink strength. Fruit sink strength, a measure of the ability for plants to assimilate sugars and other organic compounds synthesized during photosynthesis into fruits, plays a pivotal role in the regulation of fruit development and ripening (Herbers and Sonnewald 1998; Marcelis 1996; Marcelis and Heuvelink 1999). Ji et al. (2020) observed that the additional FR light upregulated the genes responsible for fruit sugar transport and sugar metabolism and increased dry mass partitioning to fruits, and the promotive effects of FR light on tomato fruit growth and quality were attributed to an increase in fruit sink strength. Increased fruit sink strength may also explain the increase in fruit yield, accelerated harvest, and improved quality of strawberries ‘Albion’ with FR light observed in this study.

In conclusion, for strawberry ‘Monterey’, leaf expansion was promoted with the additional FR light, which culminated in a parallel increase in shoot dry mass. Also, the addition of FR light extended the peduncle length in strawberry ‘Monterey’, suggesting a potential practical application of FR light to improve harvesting practices in indoor vertical farms, particularly for machine harvesters facing challenges in peduncle detection. In strawberry ‘Albion’, the addition of FR light had minimal impact on vegetative growth but increased fruit yield and TSS. In both ‘Albion’ and ‘Monterey’, FR

light did not affect flowering time. Our findings indicate that the addition of FR in sole-source lighting can increase vegetative growth, fruit yield, and quality in some everbearing strawberry cultivars. However, further research on a wider range of cultivars is needed to fully comprehend how the effects of adding FR light may differ across different strawberry cultivars.

Table 1.1. Spectral Characteristics of the Blue + Red ($B_{90}+R_{250}$) and Blue + Red + Far-Red ($B_{90}+R_{250}+FR_{50}$) LEDs Used in the Sole-Source Lighting Treatments. The Number After Each LED Type is Its Photon Flux Density in $\mu mol \cdot m^{-2} \cdot s^{-1}$.

| Lighting treatments | PPFD[i] (400-700 nm) | ePPFD[ii] (400-750 nm) | %FR[iii] | PPE[iv] | iPPE[v] |
|---|---|---|---|---|---|
| $B_{90}+R_{250}$ | 345.7 | 349.0 | 0.9 | 0.876 | 0.846 |
| $B_{90}+R_{250}+FR_{50}$ | 338.5 | 388.0 | 11.9 | 0.841 | 0.660 |

[i]Photosynthetic photon flux density (PPFD): The photon flux density between 400 and 700 nm in $\mu mol \cdot m^{-2} \cdot s^{-1}$.

[ii]Extended photosynthetic photon flux density (ePPFD): The photon flux density between 400 and 750 nm in $\mu mol \cdot m^{-2} \cdot s^{-1}$.

[iii]Percent FR (%FR): The percentage of FR (700-750 nm) photon flux density relative to ePPFD.

[iv]Phytochrome photoequilibria (PPE): The estimated $P_{FR}/P_{R+FR}$ following Sager et al., (1988).

[v]Internal phytochrome photoequilibria (iPPE): The estimated $P_{FR}/P_{R+FR}$ within a leaf following Kusama and Bugbee (2021).

Table 1.2. Growth Characteristics of Strawberry ‘Albion’ and ‘Monterey’ Plants Grown for 5 Weeks Under Blue + Red ($B_{90}+R_{250}$) or Blue + Red + Far-Red ($B_{90}+R_{250}+FR_{50}$) LED Lighting Treatments. The Number After Each LED Type is Its Photon Flux Density in $\mu mol \cdot m^{-2} \cdot s^{-1}$. Data Represents the Mean of Two Replications With 10 Plants Per Replication (n = 20). Means Followed by Different Letters Within Columns for Each Cultivar Are Significantly Different by T-test at $P < 0.05$. NS, *, or ** Nonsignificant or Significant at $P < 0.05$ or 0.01, Respectively.

| Cultivar | Treatments | Leaf number | Leaf area ($cm^2$) | SPAD index | Crown number | Crown diameter (mm) | Shoot fresh mass (g) | Root fresh mass (g) | Shoot dry mass (g) | Root dry mass (g) | Root length (cm) |
|---|---|---|---|---|---|---|---|---|---|---|---|
| ‘Albion’ | $B_{90}+R_{250}$ | 3.6 | 237.2 | 46.4 | 1.5 a[i] | 11.8 | 18.1 | 24.9 | 4.0 | 1.9 | 27.3 |
| | $B_{90}+R_{250}+FR_{50}$ | 3.7 | 242.8 | 45.3 | 2.0 b | 12.2 | 18.7 | 23.4 | 4.3 | 1.9 | 27.2 |
| Significance | | NS[ii] | NS | NS | * | NS | NS | NS | NS | NS | NS |
| ‘Monterey’ | $B_{90}+R_{250}$ | 3.2 | 120.1 a | 41.1 | 1.8 | 11.6 | 10.8 a | 14.6 a | 2.1 a | 1.3 a | 26.0 a |
| | $B_{90}+R_{250}+FR_{50}$ | 4.0 | 209.2 b | 39.9 | 2.1 | 11.6 | 17.3 b | 23.6 b | 3.6 b | 1.9 b | 30.4 b |
| Significance | | NS | ** | NS | NS | NS | ** | ** | ** | ** | ** |

[i]Means followed by different letters within columns for each cultivar are significantly different by t-test at $P < 0.05$.

[ii]NS, *, or ** nonsignificant or significant at $P < 0.05$ or 0.01, respectively.

Table 1.3. Days to Flower and Fruit Harvest (After Transplanting) of Strawberry 'Albion' and 'Monterey' Plants Grown Under Blue + Red ($B_{90}+R_{250}$) or Blue + Red + Far-Red ($B_{90}+R_{250}+FR_{50}$) LED Lighting Treatments. The Number After Each LED Type is Its Photon Flux Density in $\mu mol \cdot m^{-2} \cdot s^{-1}$. Data Represents the Mean of Two Replications With 12 Plants Per Replication (n = 24). Means Followed by Different Letters Within Columns for Each Cultivar Are Significantly Different by T-test at $P < 0.05$. NS, *, or ** Nonsignificant or Significant at $P < 0.05$ or 0.01, Respectively.

| Cultivar | Treatments | Days to flower | Days to fruit harvest |
|---|---|---|---|
| 'Albion' | $B_{90}+R_{250}$ | 50 | 79 a[i] |
| | $B_{90}+R_{250}+FR_{50}$ | 51 | 74 b |
| Significance | | NS[ii] | ** |
| 'Monterey' | $B_{90}+R_{250}$ | 49 | 77 |
| | $B_{90}+R_{250}+FR_{50}$ | 49 | 74 |
| Significance | | NS | NS |

[i]Means followed by different letters within columns for each cultivar are significantly different by t-test at $P < 0.05$.

[ii]NS, ** nonsignificant or significant at $P < 0.01$, respectively.

Table 1.4. Individual Fruit Characteristics of Strawberry ‘Albion’ and ‘Monterey’ Plants Grown Under Blue + Red ($B_{90}+R_{250}$) or Blue + Red + Far-red ($B_{90}+R_{250}+FR_{50}$) LED Lighting Treatments. Data Represents the Mean of Two Replications with 12 Plants Per Replication (n = 24). Means Followed by Different Letters Within Columns For Each Cultivar Are Significantly Different by T-test at $P < 0.05$. NS, *, or ** Nonsignificant or Significant at $P < 0.05$ or 0.01, Respectively.

| Cultivar | Treatment | Fruit fresh mass (g) | Fruit diameter (mm) | Fruit length (mm) | Total soluble solids (°Brix) |
|---|---|---|---|---|---|
| Albion | $B_{90}+R_{250}$ | 10.8 | 27.1 a[i] | 31.1 | 6.9 a |
| | $B_{90}+R_{250}+FR_{50}$ | 10.3 | 26.3 b | 30.2 | 7.9 a |
| Significance | | NS[ii] | * | NS | NS |
| Monterey | $B_{90}+R_{250}$ | 11.2 | 27.4 a | 30.7 | 7.7 b |
| | $B_{90}+R_{250}+FR_{50}$ | 10.5 | 26.3 b | 30.9 | 8.6 a |
| Significance | | NS | * | NS | ** |

[i]Means followed by different letters within columns for each cultivar are significantly different by t-test at $P < 0.05$.

[ii]NS, *, or ** nonsignificant or significant at $P < 0.05$ or 0.01, respectively.

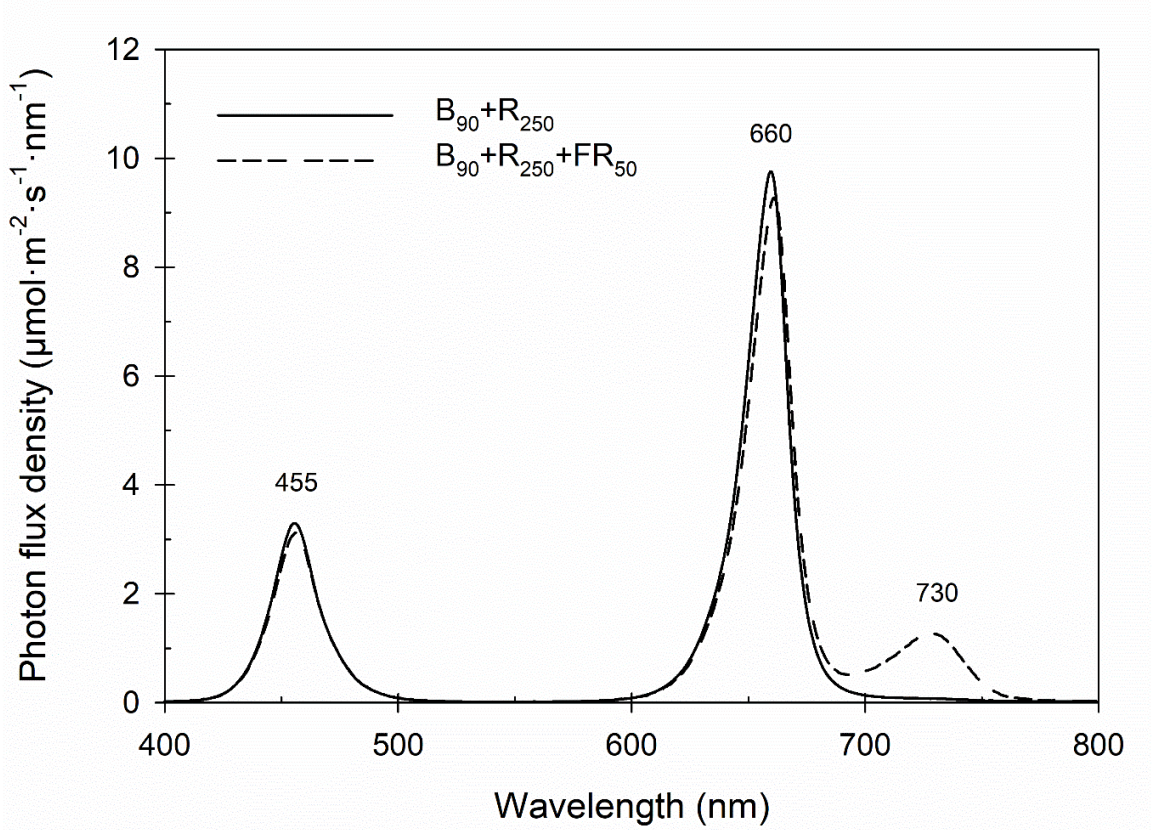


Figure 1.1. The Spectral Distribution of the Blue + red ($B_{90}$+$R_{250}$) and Blue + Red + Far-Red ($B_{90}$+$R_{250}$+$FR_{50}$) LEDs Used in the Sole-Source Lighting Treatments. The Number After Each LED Type is Its Photon Fux Density in $\mu mol \cdot m^{-2} \cdot s^{-1}$. The Numbers Above the Spectral Distribution Curves Represent the Peak Wavelengths.

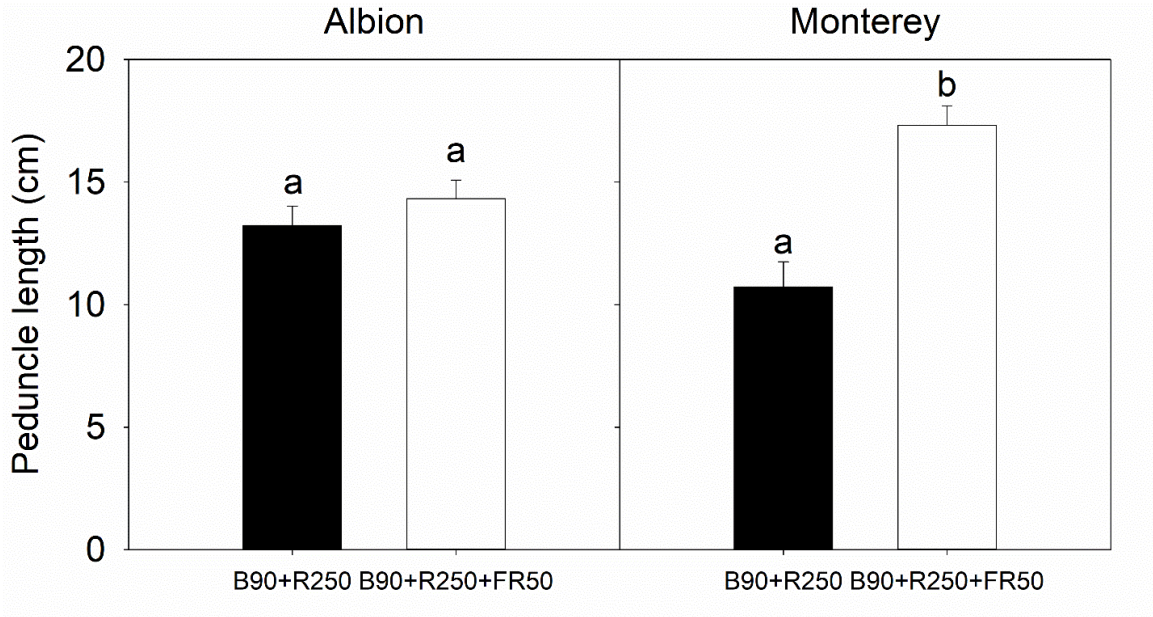


Figure 1.2. Peduncle Length of Strawberry ‘Albion’ and ‘Monterey’ Plants with Ripened Fruit Grown Under Blue + Red ($B_{90}+R_{250}$) or Blue + Red + Far-Red ($B_{90}+R_{250}+FR_{50}$) Led Lighting Treatments. The Number After Each Led Type Is Its Photon Flux Density in $\mu mol \cdot m^{-2} \cdot s^{-1}$. Data Represents the Mean and Standard Error of Two Replications With 8 Plants per Replication (N = 16). Means Followed by Different Letters for Each Cultivar Indicates Statistically Significant Differences Between Lighting Treatments at $P < 0.05$.

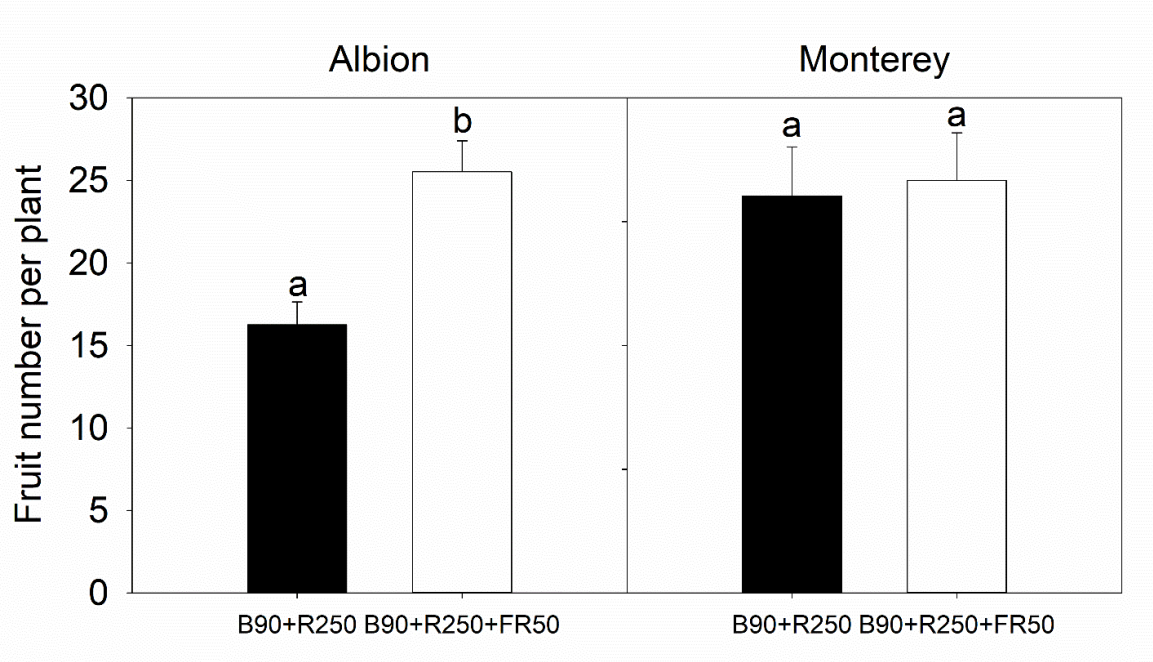


Figure 1.3. Number of Fruits Produced per Plant of Strawberry ‘Albion’ and ‘Monterey’ Grown Under Blue + Red ($B_{90}$+$R_{250}$) or Blue + Red + Far-Red ($B_{90}$+$R_{250}$+$FR_{50}$) Led Lighting Treatments. The Number After Each Led Type Is Its Photon Flux Density in $\mu mol \cdot m^{-2} \cdot s^{-1}$ Data Represents the Mean and Standard Error of Two Replications With 12 Plants per Replication (N = 24). Means Followed by Different Letters for Each Cultivar Indicates Statistically Significant Differences Between Lighting Treatments at $P < 0.05$.

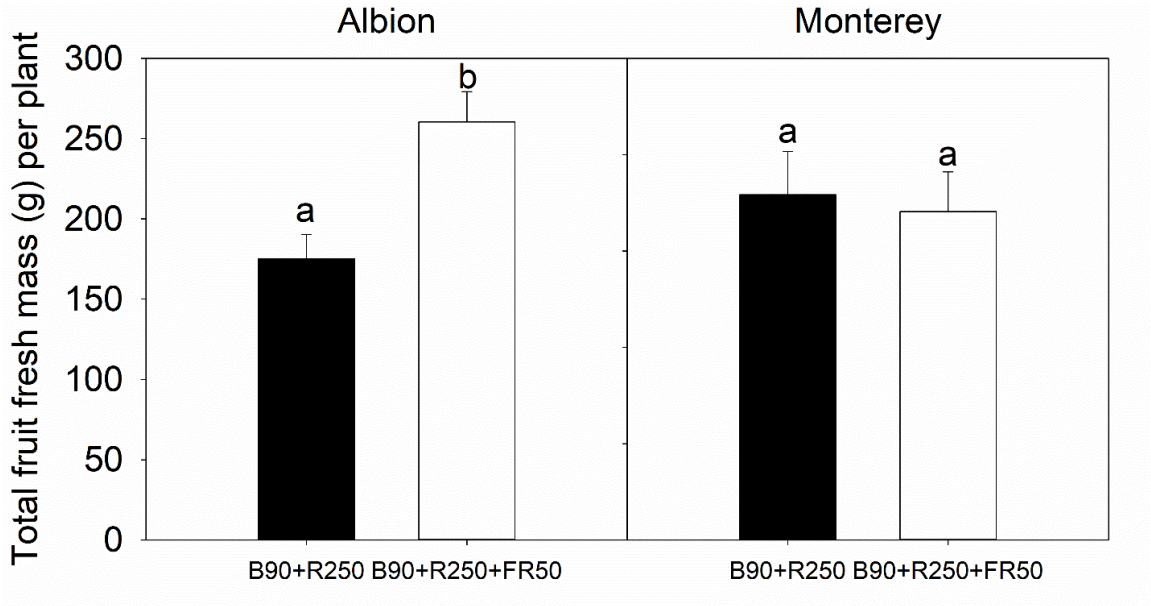


Figure 1.4. Total Fresh Mass of Fruits Produced per Plant of Strawberry 'Albion' and 'Monterey' Grown Under Blue + Red ($B_{90}+R_{250}$) or Blue + Red + Far-Red ($B_{90}+R_{250}+FR_{50}$) Led Lighting Treatments. The Number After Each Led Type Is Its Photon Flux Density in $\mu mol \cdot m^{-2} \cdot s^{-1}$. Data Represents the Mean and Standard Error of Two Replications With 12 Plants per Replication (N = 24). Means Followed by Different Letters for Each Cultivar Indicates Statistically Significant Differences Between Lighting Treatments at $P < 0.05$.

REFERENCES

Bae, J. H., Park, S. Y., Oh, M.M. (2017). Supplemental irradiation with far-red light-emitting diodes improves growth and phenolic contents in *Crepidiastrum denticulatum* in a plant factory with artificial lighting. *Horticulture, Environment, and Biotechnology, 58,* 357–366. https://doi.org/10.1007/s13580-017-0331-x.

Bantis, F., Smirnakou, S., Ouzounis, T., Koukounaras, A., Ntagkas, N., Radoglou, K. (2018). Current status and recent achievements in the field of horticulture with the use of light-emitting diodes (LEDs). *Scientia Horticulturae, 235,* 437–451. https://doi.org/10.1016/j.scienta.2018.02.058.

Choi, H. G., Kwon J. K., Moon B. Y., Kang N. J., Park K. S., Cho M. W., Kim Y. C. (2013). Effect of different light emitting diode (LED) lights on the growth characteristics and the phytochemical production of strawberry fruits during cultivation. *Horticultural Science and Technology, 31*(1), 56–64. https://doi.org/10.7235/hort.2013.12100.

Choi, H. G., Moon B. Y., Kang N. J. (2015). Effects of LED light on the production of strawberry during cultivation in a plastic greenhouse and in a growth chamber. *Scientia Horticulturae, 189,* 22–31. https://doi.org/10.1016/j.scienta.2015.03.022.

Craig, D. S., Runkle E. S. (2016). An intermediate phytochrome photoequilibria from night-interruption lighting optimally promotes flowering of several long-day plants. *Environmental and Experimental Botany, 121,* 132–138. https://doi.org/10.1016/j.envexpbot.2015.04.004.

Darrow, G. M., (1929). Inflorescence types of strawberry varieties. *American Journal of Botany, 16,* 571–585. https://doi.org/10.2307/2435912.

Fukuda, N., Nogi M, Sase, S., Nishimura, S., (2002). Effects of localized light quality from light-emitting diodes on geranium peduncle elongation. *Acta Horticulturae, 580*:151–156. https://doi.org/10.17660/ActaHortic.2002.580.18.

Garcia, K., Kubota C. (2017). Flowering responses of north american strawberry cultivars. *Acta Horticulturae, 1156*:483–490. https://doi.org/10.17660/ActaHortic.2017.1156.71.

Herbers, K., Sonnewald, U. (1998). Molecular determinants of sink strength. *Current Opinion in Plant Biology, 1*(3), 207–216. https://doi.org/10.1016/S1369-5266(98)80106-4.

Hidaka, K., Dan, K., Imamura, H., Miyoshi, Y., Takayama, T., Sameshim, K., Kitano, M., Okimura, M. (2013). Effect of supplemental lighting from different light sources on growth and yield of strawberry. *Environmental Control in Biology, 51*(1), 41–47. https://doi.org/10.2525/ecb.51.41

Ji, Y., Nuñez Ocaña, D., Choe, D., Larsen, D. H., Marcelis, L. F. M., Heuvelink, E. (2020). Far-red radiation stimulates dry mass partitioning to fruits by increasing fruit sink strength in tomato. *New Phytologist, 228*(6), 1914–1925. https://doi.org/10.1111/nph.16805.

Jin, W., Urbina, J. L., Heuvelink, E., Marcelis, L. F. (2021). Adding far-red to red-blue light-emitting diode light promotes yield of lettuce at different planting densities. *Frontiers in Plant Science, 11*, 609977. https://doi.org/10.3389/fpls.2020.609977.

Kalaitzoglou, P., van Ieperen, W., Harbinson, J., van der Meer, M., Martinakos, S., Weerheim, K., Nicole, C. C. S., Marcelis, L. F. M. (2019). Effects of continuous or end-of-day far-red light on tomato plant growth, morphology, light absorption, and fruit production. *Frontiers in Plant Science, 10*, 322. https://doi.org/10.3389/fpls.2019.00322.

Kim, H. J., Yang, T., Choi, S., Wang, Y. J., Lin, M. Y., Liceaga, A. M. (2020). Supplemental intracanopy far-red radiation to red LED light improves fruit quality attributes of greenhouse tomatoes. *Scientia Horticulturae, 261*, 108985. https://doi.org/10.1016/j.scienta.2019.108985.

Kurepin, L. V., Emery, R. N., Pharis, R. P., Reid, D. M. (2007). Uncoupling light quality from light irradiance effects in *Helianthus annuus* shoots: putative roles for plant hormones in leaf and internode growth. *Journal of Experimental Botany, 58*(8), 2145–2157. https://doi.org/10.1093/jxb/erm068.

Kusuma, P., Bugbee, B. (2021). Improving the predictive value of phytochrome photoequilibrium: consideration of spectral distortion within a leaf. *Frontiers in Plant Science, 12*, 596943. https://doi.org/10.3389/fpls.2021.596943.

Kusuma P., Bugbee, B. (2023). On the contrasting morphological response to far-red at high and low photon fluxes. *Frontiers in Plant Science, 14*, 1185622. https://doi.org/10.3389/fpls.2023.1185622.

Lopez, R. G., Meng, Q., Runkle, E. S. (2020). Blue radiation signals and saturates photoperiodic flowering of several long-day plants at crop-specific photon flux densities. *Scientia Horticulturae, 271*, 109470. https://doi.org/10.1016/j.scienta.2020.109470.

Lore, K. (2022) Driscoll's heads to virginia to grow strawberries in world's largest indoor vertical farm. The Packer. Retrieved from: https://www.thepacker.com/news/packer-tech/driscolls-heads-virginia-grow-strawberries-worlds-largest-indoor-vertical-farm.

Lubna, F. A., Lewus, D. C., Shelford, T. J., Both, A. J. (2022). What you may not realize about vertical farming. *Horticulturae, 8*(4), 322. https://doi.org/10.3390/horticulturae8040322.

Marcelis, L. F. M. (1996). Sink strength as a determinant of dry matter partitioning in the whole plant. *Journal of Experimental Botany, 47*, 1281–1291. https://doi.org/10.1093/jxb/47.Special_Issue.1281.

Marcelis, L. F. M., Heuvelink, E. (1999). Modelling fruit set, fruit growth and dry matter partitioning. *Acta Horticulturae, 499*, 39–50. https://doi.org/10.17660/ActaHortic.1999.499.3.

Marston, J. (2023). Learning from Japan's mistakes, Oishii CEO "hasn't spent a dime" on leafy greens as ultra-premium strawberries thrive. AFN. Retrieved from: https://agfundernews.com/learning-from-japans-mistakes-oishii-ceo-hasnt-spent-a-dime-on-leafy-greens-as-ultra-premium-strawberries-thrive.

Meng, Q., Runkle, E. S. (2017). Moderate-intensity blue radiation can regulate flowering, but not extension growth, of several photoperiodic ornamental crops. *Environmental and Experimental Botany, 134*, 12–20. https://doi.org/10.1016/j.envexpbot.2016.10.006.

Nadalini, S., Zucchi, P., Andreotti, C. (2017). Effects of blue and red LED lights on soilless cultivated strawberry growth performances and fruit quality. *European Journal of Horticultural Science, 82*(1), 12–20. https://doi.org/10.17660/eJHS.2017/82.1.2.

Park, Y., Runkle, E. S. (2017). Far-red radiation promotes growth of seedlings by increasing leaf expansion and whole-plant net assimilation. *Environmental and Experimental Botany, 136*, 41–49. https://doi.org/10.1016/j.envexpbot.2016.12.013.

Park, Y, Runkle, E. S. (2018). Far-red radiation and photosynthetic photon flux density independently regulate seedling growth but interactively regulate flowering. *Environmental and Experimental Botany, 155*, 206–216. https://doi.org/10.1016/j.envexpbot.2018.06.033.

Park, Y, Runkle E. S. (2019). Blue radiation attenuates the effects of the red to far-red ratio on extension growth but not on flowering. *Environmental and Experimental Botany, 168*, 103871. https://doi.org/10.1016/j.envexpbot.2019.103871.

Park, Y, Sethi R., Temnyk, S. (2023). Growth, flowering, and fruit production of strawberry 'albion' in response to photoperiod and photosynthetic photon flux density of sole-source lighting. *Plants*, *12*(4), 731. https://doi.org/10.3390/plants12040731.

Prisca, M., Maarten, V., Jan, V. D., Bart, N., Wouter, S., Timo, H., Barbara, D. C., Bram, V. de P. (2022). Blue and far-red light control flowering time of woodland strawberry (*Fragaria vesca*) distinctively via CONSTANS (CO) and FLOWERING LOCUS T1 (FT1) in the background of sunlight mimicking radiation. *Environmental and Experimental Botany*, *198*, 104866. https://doi.org/10.1016/j.envexpbot.2022.104866.

Rahman, M. M, Field, D. L., Ahmed, S. M., Hasan, M. T., Basher, M. K., Alameh, K. (2021). LED illumination for high-quality high-yield crop growth in protected cropping environments. *Plants*, *10*(11), 2470. https://doi.org/10.3390/plants10112470.

Rantanen, M., Kurokura, T., Mouhu, K., Pinho, P., Tetri, E., Halonen, L., Palonen, P., Elomaa, P., Hytönen, T. (2014). Light quality regulates flowering in FvFT1/FvTFL1 dependent manner in the woodland strawberry *Fragaria vesca*. *Frontiers in Plant Science*, *5*, 271. https://doi.org/10.3389/fpls.2014.00271.

Richardson, M. L., Arlotta, C. G., Lewers, K. S. (2022). Yield and nutrients of six cultivars of strawberries grown in five urban cropping systems. *Scientia Horticulturae*, *294*, 110775. https://doi.org/10.1016/j.scienta.2021.110775.

Roig-Villanova, I., Martínez-García, J. F. (2016). Plant responses to vegetation proximity: a whole life avoiding shade. *Front in Plant Sci*, *7*, 236. https://doi.org/10.3389/fpls.2016.00236.

Sager, J. C., Smith, W. O., Edwards, J., Cyr, K. L. (1988). Photosynthetic efficiency and phytochrome photoequilibria determination using spectral data. *Transactions of the ASAE, 31*(6), 1882–1889. https://doi.org/10.13031/2013.30952.

Samtani, J. B., Rom, C. R., Friedrich, H., Fennimore, S. A., Finn, C. E., Petran, A., Wallace, R. W., Pritts, M. P., Fernandez, G., Chase, C. A., and Kubota, C. (2019) The status and future of the strawberry industry in the United States. *Horttechnology*, *29*(11), 11–24. https://doi.org/10.21273/HORTTECH04135-18.

Samuolienė, G., Brazaitytė, A., Urbonavičiūtė, A., Šabajevienė, G., Duchovskis, P. (2010). The effect of red and blue light component on the growth and development of frigo strawberries. *Zemdirbyste-Agriculture*, *97*, 99–104.

Tan, T., Li, S., Fan, Y., Wang, Z., Ali Raza, M., Shafiq, I., Wang, B., Wu, X., Yong, T., Wang, X., Wu, Y., Yang, F., Yang, W. (2022). Far-red light: A regulator of plant morphology and photosynthetic capacity. *Crop Journal*, *10*, 300–309. https://doi.org/10.1016/j.cj.2021.06.007.

Tsuruyama, J., Shibuya, T. (2018). Growth and flowering responses of seed-propagated strawberry seedlings to different photoperiods in controlled environment chambers. *Horttechnology*, *28*(4), 453–458. https://doi.org/10.21273/HORTTECH04061-18.

Tsuruyama, J., Shibuya, T. (2023). Effects of far-red light and photoperiod during early growth stages on flower bud development of seed-propagated strawberry seedlings. *Scientia Horticulturae*, *317*, 112051. https://doi.org/10.1016/j.scienta.2023.112051.

USDA - National Agricultural Statistics Service – Retreieved from: https://www.nass.usda.gov/Statistics_by_Subject/result.php?59DFD141-00B1-3EDE-B526-7FDEFCD859A7&sector=CROPS&group=FRUIT%20%26%20TREE%20NUTS&comm=STRAWBERRIES [accessed 6 Sep 2023].

Xiong, Y., Ge, Y., Grimstad, L., From, P. J. (2020). An autonomous strawberry-harvesting robot: design, development, integration, and field evaluation. *Journal of Field Robotics*, *37*(2), 202–224. https://doi.org/10.1002/rob.21889.

Yoshida, H., Hikosaka, S., Goto, E., Takasuna, H., Kudou, T. (2012). Effects of light quality and light period on flowering of everbearing strawberry in a closed plant production system. *Acta Horticulturae, 956*, 107–112. https://doi.org/10.17660/ActaHortic.2012.956.9.

Zhang, M., Park, Y., Runkle, E. S. (2020). Regulation of extension growth and flowering of seedlings by blue radiation and the red to far-red ratio of sole-source lighting. *Scientia Horticulturae, 272*, 109478. https://doi.org/10.1016/j.scienta.2020.109478.

Zhen, S, Bugbee, B. (2020). Far-red photons have equivalent efficiency to traditional photosynthetic photons: Implications for redefining photosynthetically active radiation. *Plant, Cell & Environment, 43*(5), 1259–1272. https://doi.org/10.1111/pce.13730.

Zhen, S., van Iersel, M., Bugbee, B. (2021). Why far-red photons should be included in the definition of photosynthetic photons and the measurement of horticultural fixture efficacy. *Frontiers in Plant Science, 12*. https://doi.org/10.3389/fpls.2021.693445.

Zhen, S., van Iersel, M. W. (2017). Far-red light is needed for efficient photochemistry and photosynthesis. *Journal of Plant Physiology, 209*, 115–122. https://doi.org/10.1016/j.jplph.2016.12.00.

# CHAPTER 3

# WHAT IS THE OPTIMAL BALANCE OF POTASSIUM TO NITROGEN IN HYDROPONIC STRAWBERRY PRODUCTION?

ABSTRACT

The production of strawberries (*Fragaria ×ananassa*) in hydroponic systems has been increasing. In hydroponic systems, the precise management of nutrients delivered to crops is one of the major factors that determines their yield and quality. Among the nutrients provided, the concentration of potassium is among the most important to control, as potassium is crucial for many vital plant processes. Further, the concentration of potassium relative to nitrogen can also bring about changes in crop productivity. Here, we tested the effects of potassium to nitrogen ratios (K:N) on strawberry growth and development. We hypothesized that an increase in the K:N ratio would improve vegetative growth, increase fruit size and yield, and enhance fruit quality. Bare-root plants of strawberry 'Monterey' and 'San Andreas' were planted in a deep-water culture hydroponic system and grown with K:N ratios ranging from 1.5:1 to 4.5:1. The experiment was conducted inside an indoor vertical farm at a 23 °C air temperature with extended photon flux densities of 350 $\mu mol \cdot m^{-2} \cdot s^{-1}$ under an 18-h photoperiod. Three weeks after treatments, K:N ratios ranging from 1.5:1 to 4.5 had little to no effect on crown number, crown diameter, leaf number, leaf area, and shoot dry mass in both cultivars. However, root dry mass increased linearly in 'Monterey' but not in 'San Andreas' as K:N ratios increased from 1.5:1 to 4.5:1. Increasing the K:N ratio from 1.5:1 to 4.5:1 reduced the individual fruit mass, fruit length, and fruit diameter in 'Monterey' and 'San Andreas', although it did not affect the number of fruits produced per plant and total fruit fresh mass per plant. While there was a linear increase in the titratable acidity

with an increasing K:N ratio from 1.5:1 to 4.5:1 in both ‘Monterey’ and ‘San Andreas’, the total soluble solids linearly increased only in ‘San Andreas’ and was unaffected in ‘Monterey’. These results suggest that increasing the K:N ratio from 1.5:1 to 4.5:1 in hydroponic strawberry production using deep-water culture systems can improve root growth but reduce fruit size and fruit quality.

*Keywords*: controlled environment agriculture, hydroponics, strawberry, fruit quality

*Abbreviations*: B, Blue; EC, Electrical Conductivity; ePPFD, Extended Photosynthetic Photon Flux Density; FR, Far-Red; K, Potassium, LED, Light Emitting Diodes; N, Nitrogen; NFT, Nutrient Film Technique, PPFD, Photosynthetic Photon Flux Density; R, Red; SPAD, Soil-Plant Analysis Development; TSS, Total Soluble Solids

## Introduction

The use of hydroponic vertical farming systems to produce strawberries (*Fragaria ×ananassa*) is increasing as reductions in arable land, increased labor costs, and tightening regulations are making outdoor production more challenging for growers (Samtani et al., 2019). In hydroponic systems, the nutrient solution is the only source of the nutrients provided to plants, and the concentration of nutrients is one of the major factors that influences plant development and ultimately crop yield (Wada, 2019; Ali, 2023). Strawberries require precise management of nutrients to effectively produce

quality harvestable fruit in a timely manner, as they are particularly sensitive to nutrient concentrations (Barroso and Alvarez, 1997).

Potassium (K) is involved with a wide variety of plant growth processes, and the yield and quality of crops require K to be available to facilitate processes involved in plant growth (Zörb et al., 2014). K allows for the opening and closing of stomata to facilitate gas exchange during photosynthesis, contributes to regulating turgor pressure within cells, and is necessary for the activation of over 60 enzymes critical for plant growth (Johnson et al., 2022). In addition, as K facilitates cell expansion, increasing the concentration of K can promote leaf expansion and subsequent biomass accumulation (Oosterhuis et al., 2019). For example, in melon (*Cucumis melo*), leaf area and shoot fresh mass increased by 46% and 52%, respectively, by increasing the K concentration in a hydroponic system from 59 to 176 $mg \cdot L^{-1}$ (Pourranjbari Saghaiesh and Souri, 2018). Increasing the K concentration from 235 to 350 $mg \cdot L^{-1}$ increased the leaf area and shoot fresh mass by 6% and 16%, respectively, in strawberry ‘Camarosa’ in a hydroponic pot experiment (Tohidloo et al., 2018). K also promotes root development and influences the partitioning of biomass between shoots and roots (Sustr et al., 2019). Root growth has been inhibited in K-deficient conditions using hydroponic systems in tobacco (*Nicotiana tabacum* L.), strawberry, and tomato (*Solanum lycopersicum*) (Song et al., 2015; Cao et al., 2016; Naciri et al., 2022).

K is a primary nutrient in determining the size of fruits and ultimately yield by controlling the movement of nutrients into fruits (Kumar et al., 2006; Çalişkan and

Çalişkan, 2018). Many enzymes involved in fruit development, including sucrose phosphate synthase, invertase, and phosphofructokinase, depend on the sufficient availability of K (Sardans and Peñuelas, 2021). In hydroponic systems, improvements to fruit yield have been achieved by increasing the K concentration in the nutrient solution. For example, fruit yield was increased by 147% by increasing the K concentration from 150 to 300 $mg \cdot L^{-1}$ in a pot experiment growing bell pepper (*Capsicum annuum*) with cocopeat and perlite as a substrate (Mardanluo et al., 2018). K has also been considered a "quality element" in fruiting crops as its presence at optimal levels improves fruit quality parameters, such as total soluble solids (TSS) (Usherwood, 1985). For example, TSS content was linearly increased in bell pepper by raising the K concentration from 150 to 400 $mg \cdot L^{-1}$ (Mardanluo et al., 2018). Additionally, in tomato 'Pant T-3', increasing the concentration of K from 200 to 400 $mg \cdot L^{-1}$ using a nutrient film technique (NFT) increased TSS content by 39% (Almeselmani et al., 2009).

Research on K in strawberries has focused on its impact on fruit yield and quality. Strawberry yield and quality have been increased by raising the concentration of K to between 300 and 350 $mg \cdot L^{-1}$ in the nutrient solution while keeping N constant (Tohidloo et al., 2018; Nakro et al., 2023). Additionally, as K is crucial for the cell expansion process essential to strawberry fruit growth, studies have indicated that K uptake often exceeds that of nitrogen (N) (Kumar et al., 2006). It has been suggested that the optimum ratio of K to N in hydroponic strawberry fertilization is between 1.5:1 (K:N) and 2.5:1 (Morgan 2006). In a recent study, providing a high ratio of K:N (2.6:1 with 290 $mg \cdot L^{-1}$

K) in the vegetative stage increased total fruit yield by 42% and TSS content by 16% over a 1.3 K:N ratio in strawberries ‘Fortuna’, ‘San Andreas’, and ‘Sabrina’ (Nakro et al., 2023).

However, previous research focusing on the effects of K on strawberries has primarily explored fruit production with few analyses of vegetative growth. Investigations into the impact of K:N ratios beyond 3:1 in hydroponic systems remain unexplored. Increasing K:N ratios to higher ranges could potentially further enhance vegetative growth, fruit yield, and fruit quality. This study aims to determine the optimal K:N ratios for enhancing vegetative growth, fruit yield, and fruit quality in hydroponic strawberry production. We hypothesize that increasing the K:N ratio above 3:1 will improve root and vegetative growth, consequently enhancing fruit yield and quality.

## Materials and Methods

### *Plant materials*

Two ever-bearing strawberry cultivars, ‘Monterey’ and ‘San Andreas’, were obtained as bare-root plants from a commercial nursery (Lassen Canyon Nursery Inc., Redding, CA, USA) on March 17, 2023. From each cultivar, 130 bare-root plants were selected with crown diameters between 10 and 13 mm. The crown diameters for ‘Monterey’ and ‘San Andreas’ bare-root plants averaged 12.0 mm and 11.7 mm, respectively. After selection, the bare-root plants were thoroughly washed with tap water,

and all remaining substrate was removed before being soaked in a 1:100 Zerotol (27.1% hydrogen peroxide and 2.0% peroxyacetic acid; Biosafe Systems, East Hartford, CT, USA) and deionized water solution for 15 minutes so that any pathogens were removed.

*Growing environment*

After being cleaned and sanitized, the plants were moved to a temperature-controlled vertical farm on the Arizona State University Polytechnic Campus. The plants were then transplanted into styrofoam rafts (32 cell lettuce raft; Beaver Plastics Ltd., Acheson, Alberta, Canada), which were floating in deep water culture hydroponic growing trays (1.12 m × 0.66 m × 0.18 m; GT24X44X7B; Botanicare, Vancouver, WA, USA). Four growing racks with two tiers each holding a growing tray per rack were used, with four treatments and two replications, totaling eight growing trays. 15 plants of each cultivar were planted in each tray, with each tray holding 30 plants total. The cultivars were arranged in the same way for each replication, and the treatments were arranged differently between replications to remove any positional effects.

Sole-source lighting was supplied using blue (peak = 457 nm) + red (peak = 660 nm) + far-red (peak = 732 nm) light-emitting diode (LED) lamps (T8 Double-Row LED Indoor Grow Light; Homer Farms Inc., Mesa, AZ, USA) with an 18-hour photoperiod. On the surface of the floating raft, the photon flux densities of blue (400–500 nm), red (600–700 nm), and far red (700–750 nm) were measured at 80, 270, and 50 $\mu mol \cdot m^{-2} \cdot s^{-1}$, respectively, based on an average of nine measurements taken from a

spectroradiometer (PS-300; Apogee Instruments, Logan, UT, USA) made at predetermined horizontal positions. The air temperature was maintained at 23 °C, which was monitored continuously and recorded hourly with a sensor (Smart Thermo-Hygrometer H5075; Govee, Chung, NT, Hong Kong, China) that was placed in the middle of the growing tray.

The nutrient solutions were circulated continuously using a water pump (396 GPH Fixed Flow Water Pump; Sunlight Supply Vancouver, WA, USA) in a single reservoir connected to the individual growing trays. The reservoir was oxygenated using an air pump (ACO-050; Vivosun, Ontario, CA, USA) supplying air that moved through air stones (ASD-200; Pawfly Guangzhou City, Guangdong, China.), and each individual growing tray was also fixed with 2 additional air stones (Aquarium Air Stone 8-in; PawFly Inc., Tamil Nadu, India) connected to a separate air pump (EcoPlus Air 8 Outlet Air Pump HGC728350; Sunlight Supply Inc., Vancouver, WA, USA) for increased oxygenation. The pH and EC of the nutrient solutions were monitored daily using a pH and EC meter (HI9814: Hanna Instruments, Smithfield, RI, USA), and the pH was kept at 5.8 using 50% sulfuric acid ($H_2SO_4$) to lower the pH and potassium bicarbonate ($KHCO_3$) to increase the pH, and deionized water was added alone to keep the electrical conductivity (EC) below 2.0 $mS \cdot cm^{-1}$, which was added in equal amounts in every reservoir for the duration of the experiment. The average EC for the 1:5:1, 2.5:1, 3.5:1, and 4.5:1 K:N treatments were 1.0 ± 0.0, 1.3 ± 0.0, 1.6 ± 0.0, and 1.9 ± 0.0 for the

duration of the experiment (Table 2.1). The average pH for the duration of the experiment in each treatment was 5.8 ± 0.1.

*Nutrient treatments*

For the first three weeks after transplanting, the nutrient solution was mixed using a Yamazaki formula nutrient solution (Lee et al., 2017) that provided (in $mg \cdot L^{-1}$) 77 N, 23 P, 116 K, 48 S, 40 Ca, 12 Mg, 2 Fe, 0.6 Mn and Zn, 0.3 B, 0.05 Cu, and 0.01 Mo (Jack's Strawberry Part A/B; JR Peters Inc., Allentown, PA, USA) combined with deionized water. After the three-week period following transplanting, we tested four K:N nutrient treatments (1.5:1, 2.5:1, 3.5:1, and 4.5:1) (Table 2.1). The initial K:N ratio of Yamazaki solution was 1.5:1, and higher K:N ratios were created by adding potassium sulfate ($K_2SO_4$). Starting the nutrient treatments three weeks after transplanting, prior to flower or fruit development, enabled plants to store K for later use during the fruiting stage without inducing toxicity symptoms in the early stages before root initiation.

*Data collection and analysis*

The first and second replications of the experiment were carried out concurrently in separate growing trays for the same 17-week period. Runners and flowers were removed daily for the first five weeks of plant growth to promote vegetative growth. Five weeks after transplanting, a vegetative data collection was performed. Five representative plants of each cultivar, treatment, and replication were chosen for the data collection, one

of which was photographed to demonstrate the visual results (Fig. 2.1). For each plant chosen, the leaf number (based on the number of fully formed trifoliate leaves), SPAD index [using a chlorophyll meter (SPAD-502; Konica Minolta Sensing Inc., Chiyoda, Tokyo, Japan)], crown number, crown diameter [using a caliper (B07DFFYCXS; Adoric, Des Moines, IA, USA)], leaf area [using a leaf area meter (LI-3100; LI-COR Inc., Lincoln, Nebraska, USA)], root length, and the fresh and dry shoot and root mass [using a scale (PB602-S; Mettler Toledo, Columbus, OH, USA)] were recorded. The dry mass of the shoot and root were recorded after plants were dried at ≥70°C for ≥5 days in a drying oven (Hafo 1600; VWR International LLC, Aurora, CO, USA).

Five weeks after transplanting, plants were allowed to flower and produce fruits. The date on which the first flower bud opened and the date on which the first fruit fully ripened and was harvested were recorded for each plant. For each fruit harvested for the 51 days of the harvesting period, the diameter at its largest width and length from top to bottom were measured using a caliper (B07DFFYCXS; Adoric) and weighed using an analytical balance (PB602-S; Mettler Toledo). For each fruit harvest, which occurred twice a week after fruits began to fully ripen, the five largest fruits from each treatment, replication, and cultivar were selected for quality analysis. Each fruit selected had its pedicle removed, and the juice from all five fruits was combined using a pestle and mortar and filtered through a mesh screen to remove any pulp or seeds. The fruit juice was then analyzed for titratable acidity using a miniature titrator, which performed a titration on the fruit juice to determine acid content (HI 84532; Hanna Instruments), TSS

using a digital refractometer (HI 96801: Hanna Instruments), and the temperature of the fruit juice was recorded.

This experiment was conducted as a randomized complete block design using the replications as a block, the growing reservoir as an experimental unit for the nutrient solution treatments, and each plant of each cultivar as a subsample. The data from each replication was pooled, and linear regression analyses were performed using SAS (version 9.4; SAS Institute, Inc., Cary, NC, USA) using a PROC REG at $P<0.05$.

## Results

### *Vegetative growth*

In strawberries ‘Monterey’ and ‘San Andreas’, the K:N ratio did not influence crown number, crown diameter, leaf number, leaf area, fresh and dry mass of shoot, and root fresh mass (Figs. 2.1–2.3). Increasing the K:N ratio from 1.5:1 to 4.5:1 linearly increased root dry mass in strawberry ‘Monterey’, but not in ‘San Andreas’ (Fig. 2.3).

### *Flowering and fruiting*

Increasing the K:N ratio from 1.5:1 to 4.5:1 had no effect on the time to initiate flowering or the time to harvest the first fruit in both strawberry ‘Monterey’ and ‘San Andreas’ (Fig. 2.4). The K:N ratio also did not affect the fruit number or total fresh mass of fruits produced by each plant. However, there was a linear reduction in individual fruit fresh mass in strawberries ‘Monterey’ and ‘San Andreas’ through increasing the K:N

ratio from 1.5:1 to 4.5:1 (Fig. 2.5). Similarly, individual fruit length and diameter linearly decreased with increasing the K:N ratios from 1.5:1 to 4.5:1 in strawberries 'Monterey' and 'San Andreas'. In strawberry 'San Andreas', but not 'Monterey', the TSS value was linearly increased with the increasing K:N ratio from 1.5:1 to 4.5:1 (Fig. 2.6). The titratable acidity linearly increased in strawberries 'Monterey' and 'San Andreas' under increased K:N from 1.5:1 to 4.5:1. The maturity index, calculated as the ratio of TSS to titratable acidity, decreased linearly in strawberry 'Monterey' and was unaffected in strawberry 'San Andreas' under the K:N ratios between 1.5:1 and 4.5:1.

## Discussion

Shoot growth, including leaf area, was unaffected by raising the K:N ratio from 1.5:1 to 4.5:1 or K concentrations from 116 $mg \cdot L^{-1}$ to 347 $mg \cdot L^{-1}$ (Figs. 2.1–2.3). In previous studies, it has been observed that increasing K concentrations promoted leaf expansion, although plant responses saturated at higher K concentrations. For example, increasing the K concentration from 0 $mg \cdot L^{-1}$ to 118 $mg \cdot L^{-1}$ in hydroponically grown melon seedlings increased the leaf area by 46%, and further raising the K concentration to both 176 $mg \cdot L^{-1}$ and 235 $mg \cdot L^{-1}$ showed no additional increase in leaf area (Pourranjbari Saghaiesh and Souri, 2018). In addition, the leaf area of chili pepper was increased by raising the K concentration from 150 $mg \cdot L^{-1}$ to 235 $mg \cdot L^{-1}$, and additional increases to 300 $mg \cdot L^{-1}$, 400 $mg \cdot L^{-1}$, and 500 $mg \cdot L^{-1}$ did not further increase leaf area (Mardanluo et al., 2018). An increase in K concentration from 19 $mg \cdot L^{-1}$ to 58 $mg \cdot L^{-1}$

increased the leaf area of spinach (*Spinacia oleracea*), and an additional increase of the K concentration to 244 mg·L$^{-1}$ did not increase leaf area compared with 58 mg·L$^{-1}$ of K (Levine and Mattson, 2021). These results suggest that, in this study, the promotive effects of K concentration on leaf expansion in strawberries may reach a saturation point, either below or at a K:N of 1.5:1 or a K concentration of 116 mg·L$^{-1}$. Similarly, in a separate study, the leaf area of strawberry 'Selva' was similar between K concentrations of 235, 350, 450, and 600 mg·L$^{-1}$ (Tohidloo et al., 2018), suggesting that the effects of K on leaf area in strawberries were saturated at or below 235 mg·L$^{-1}$.

Root dry mass linearly increased with increasing K:N from 1.5:1 to 4.5:1 in strawberry 'Monterey' (Fig. 2.3). Similarly, in strawberry 'Camarosa' and 'Selva', root dry mass was increased by 7% and 16%, respectively, by increasing the K concentration from 235 mg·L$^{-1}$ to 350 mg·L$^{-1}$ (Tohidloo et al., 2018). The root dry mass and root length of strawberries were increased by 34% and 13%, respectively, by increasing the K concentration from 200 mg·L$^{-1}$ to 300 mg·L$^{-1}$ in a hydroponic system (Ebrahimi et al., 2012). Together, these results indicate that increasing K can promote root growth in strawberries, and compared to leaf expansion, which showed a saturating response, it appears that the saturation point for root growth may occur at a higher K concentration.

Increasing the K:N ratio from 1.5:1 to 4.5:1 linearly decreased the individual fruit fresh mass (Fig. 2.5). Our findings contrast with previous studies indicating that increasing K leads to an increase in individual fresh mass (Nakro et al., 2022). In this study, the increase in the K:N ratio from 1.5:1 to 4.5:1 was accompanied by a concurrent

rise in EC from 1.0 mS $cm^{-1}$ to 1.9 mS $cm^{-1}$. The elevated EC might have contributed to the reduction in fruit fresh mass. At a higher EC, the individual strawberry fruit fresh mass can decrease, which has been attributed to decreased water uptake, which can inhibit the transport of water into fruits (Keutgen and Pawelzik, 2008). In strawberry 'Albion', increasing the EC from 0.7 mS $cm^{-1}$ to 2.5 mS $cm^{-1}$ decreased the percentage of marketable-sized fruits (typically considered fruits weighing 10 g in fresh mass) by 40%, indicating a reduction in individual fruit size (Ferreira et al., 2019). In alpine strawberries, when plants were grown under an EC ranging from 1.3 to 2.2 mS $cm^{-1}$, the highest fruit fresh mass per plant and fruit number were obtained at an EC of 1.3 mS $cm^{-1}$ (Caruso et al., 2011). Thus, in this study, while the increase in the K:N ratio from 1.5:1 to 4.5:1 led to higher potassium availability, the concurrent rise in EC could potentially diminish fruit fresh mass.

The overall fruit fresh mass produced per plant was unaffected by K:N ratios from 1.5 to 4.5 (Fig. 2.4). This result is also not consistent with other studies. For example, the fruit fresh yield per plant was increased by 16% and 24% in strawberries 'Camarosa' and 'Selva', respectively, by increasing the K concentration from 235 mg·$L^{-1}$ to 350 mg·$L^{-1}$ in a hydroponic pot experiment using cocopeat and perlite as a substrate (Tohidloo et al., 2018). Reducing the K:N ratios from 2.6:1 during the vegetative stage to 1.0:1 during the fruit production stage increased overall fruit yield by 42% compared with a K:N ratio of 1.3:1 during the vegetative stage and 2.0:1 in the fruit production stage in a pot experiment using coarse river sand (Nakro et al., 2023). The reduced individual fruit size

in the current study at ECs above 1.0 mS $cm^{-1}$ may be a result of salt stress due in part to the lack of a substrate used in the deep-water culture system, which differs from similar studies on K concentration in strawberry fertilization that used cocopeat and perlite (Tohidloo et al., 2018) or coarse river sand (Nakro et al., 2023), both of which possess a high cation exchange capacity, which can act as a buffer against salt stress (Othman et al., 2019).

In each cultivar, a linear increase in titratable acidity was observed by increasing the K:N ratios from 1.5:1 to 4.5:1 (Fig. 2.6). Consistent findings regarding the impact of increased K on titratable acidity have been documented in several studies. For instance, raising the K concentration from 235 $mg \cdot L^{-1}$ to 450 $mg \cdot L^{-1}$ in strawberry 'Parus' increased titratable acidity by 23% (Tohidloo et al., 2018). The titratable acidity in tomato 'Avinash-2' was increased by 23% by increasing the K concentration in a hydroponic system from 200 $mg \cdot L^{-1}$ to 300 $mg \cdot L^{-1}$ (Almeselmani et al., 2009). A linear increase in titratable acidity was also observed by increasing the K concentration from 150 $mg \cdot L^{-1}$ to 500 $mg \cdot L^{-1}$ in both bell pepper and chili pepper (*Capsicum annuum* Avicolare) in a hydroponic pot experiment (Mardanluo et al., 2018). K is crucial for maintaining cellular homeostasis and regulating the balance of ions between and within plant cells, both of which are necessary for the effective synthesis of acids (Kumar et al., 2020). The linear increase in acid content here suggests that the strawberry plants provided with higher K concentrations were able to synthesize acids more effectively, subsequently leading to their enhanced accumulation in fruits.

TSS content increased linearly with increasing K:N ratios from 1.5:1 to 4.5:1 in ‘San Andreas’, although this trend was not observed in ‘Monterey’ (Fig. 2.6). The beneficial effects of increasing K on TSS have been reported in fruiting crops, including strawberries. For example, the TSS content was increased by 4% in strawberries ‘Camarosa’ and ‘Selva’ by increasing the K concentration from 235 $mg \cdot L^{-1}$ to 350 $mg \cdot L^{-1}$ (Tohidloo et al., 2018). The TSS content has been increased in bell pepper and tomato by raising the K concentration to 400 $mg \cdot L^{-1}$ (Mardanluo et al., 2018; Almeselmani et al., 2009). K enhances the expression of enzymes used to transport sugars produced during photosynthesis through the phloem and into fruits (Shah et al., 2024). Here, increasing K concentration from 116 $mg \cdot L^{-1}$ to 347 $mg \cdot L^{-1}$ may have facilitated the movement of more sugars into strawberry fruits, increasing the TSS content in ‘San Andreas’.

An established metric for evaluating the overall fruit flavor of strawberries is the maturity index, which is the ratio of the TSS content to titratable acidity (Nakro et al., 2023; Rahim Doust et al., 2023). In this study, increasing the K:N ratio from 1.5:1 to 4.5:1 linearly decreased the maturity index in strawberry ‘Monterey’ but not in ‘San Andreas’ (Fig. 2.6). Increasing the K:N ratio from 0.6:1 to 1.0:1 produced an increasing trend in the maturity index of strawberries ‘Fortuna’, ‘Sabrina’, and ‘San Andreas’, and further increasing the K:N ratio to 2.0:1 showed a decreasing trend in the maturity index, both of which coincided with the same trend in TSS content and had no effects on acid content (Nakro et al., 2023). By raising the K:N ratio in the current study, the magnitude of increases in titratable acidity in ‘Monterey’ and ‘San Andreas’ was greater than the

slight increase in TSS in ‘San Andreas’ and little changes in TSS in ‘Monterey’. The changes to TSS content may have been offset by the increase in titratable acidity, which could have led to a decrease in the maturity index in ‘Monterey’ and no effects observed in ‘San Andreas’.

In conclusion, K:N ratios between 1.5 and 4.5 did not impact shoot growth parameters, including leaf area, shoot dry mass, and crown number and diameter in both ‘Monterey’ and ‘San Andreas’. Raising the K:N concentration from 1.5 to 4.5 improved the root dry mass of strawberry ‘Monterey’, but it had no significant effect on the root dry mass of ‘San Andreas’. An increasing K:N ratio from 1.5 to 4.5 linearly increased the fresh mass, diameter, and length of individual fruits in strawberry ‘Monterey’ and ‘San Andreas’. However, K:N ratios did not influence the number of fruits produced per plant or the total fruit fresh mass per plant in both cultivars. As the K:N ratio increased from 1.5:1 to 4.5:1, ‘San Andreas’ showed a slight increase in TSS, while both ‘Monterey’ and ‘San Andreas’ showed greater increases in titratable acidity. These results suggest that in deep-water culture systems, increasing K:N ratios from 1.5:1 to 4.5:1 offers few benefits and may have negative effects on individual fruit size and quality.

Table 2.1. Potassium to Nitrogen (K:N) Ratios, Concentrations of K and N, and the Electrical Conductivity of Nutrient Treatments.

| K:N ratios | K ($mg \cdot L^{-1}$) | N ($mg \cdot L^{-1}$) | EC ($mS \cdot cm^{-1}$) |
|---|---|---|---|
| 1.5 | 116 | 77 | 1.0 |
| 2.5 | 193 | 77 | 1.3 |
| 3.5 | 270 | 77 | 1.6 |
| 4.5 | 347 | 77 | 1.9 |

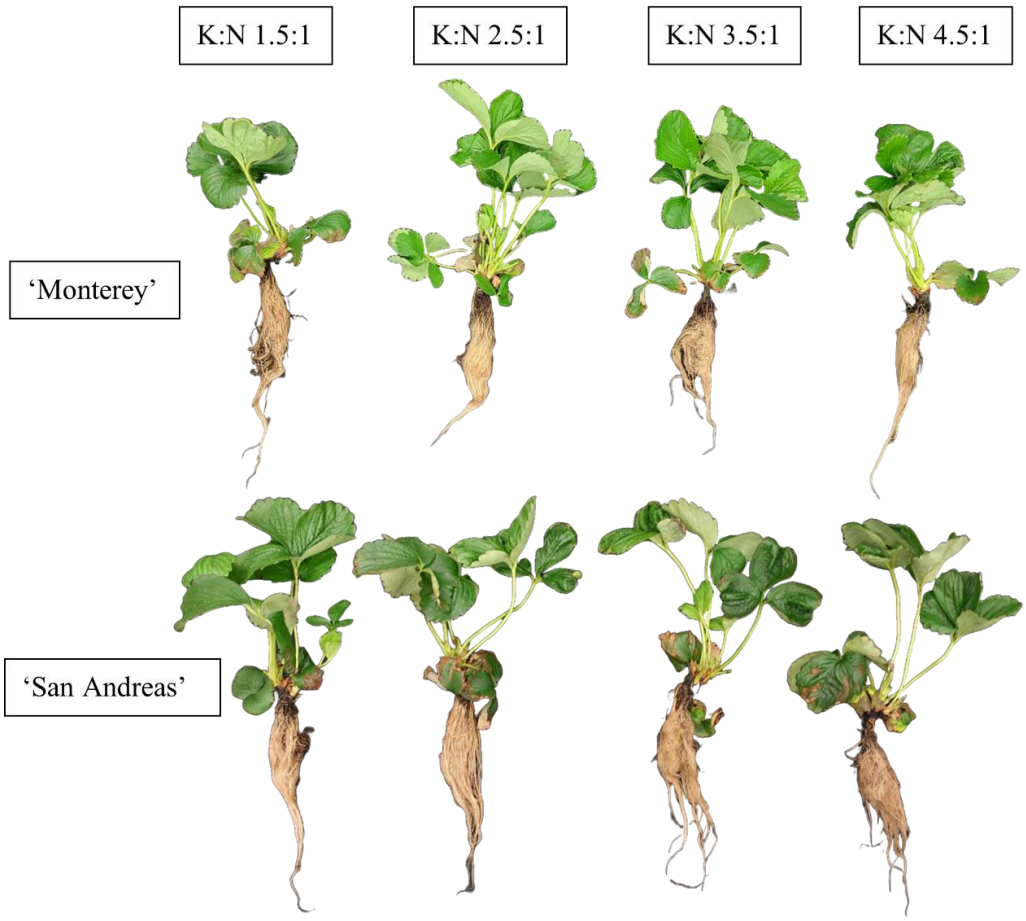


Figure 2.1. Strawberry 'Monterey' (Top) and 'San Andreas' (Bottom) Plants Grown for Three Weeks Under Four Potassium to Nitrogen Ratios of (From Left to Right) 1.5:1, 2.5:1, 3.5:1, and 4.5:1.

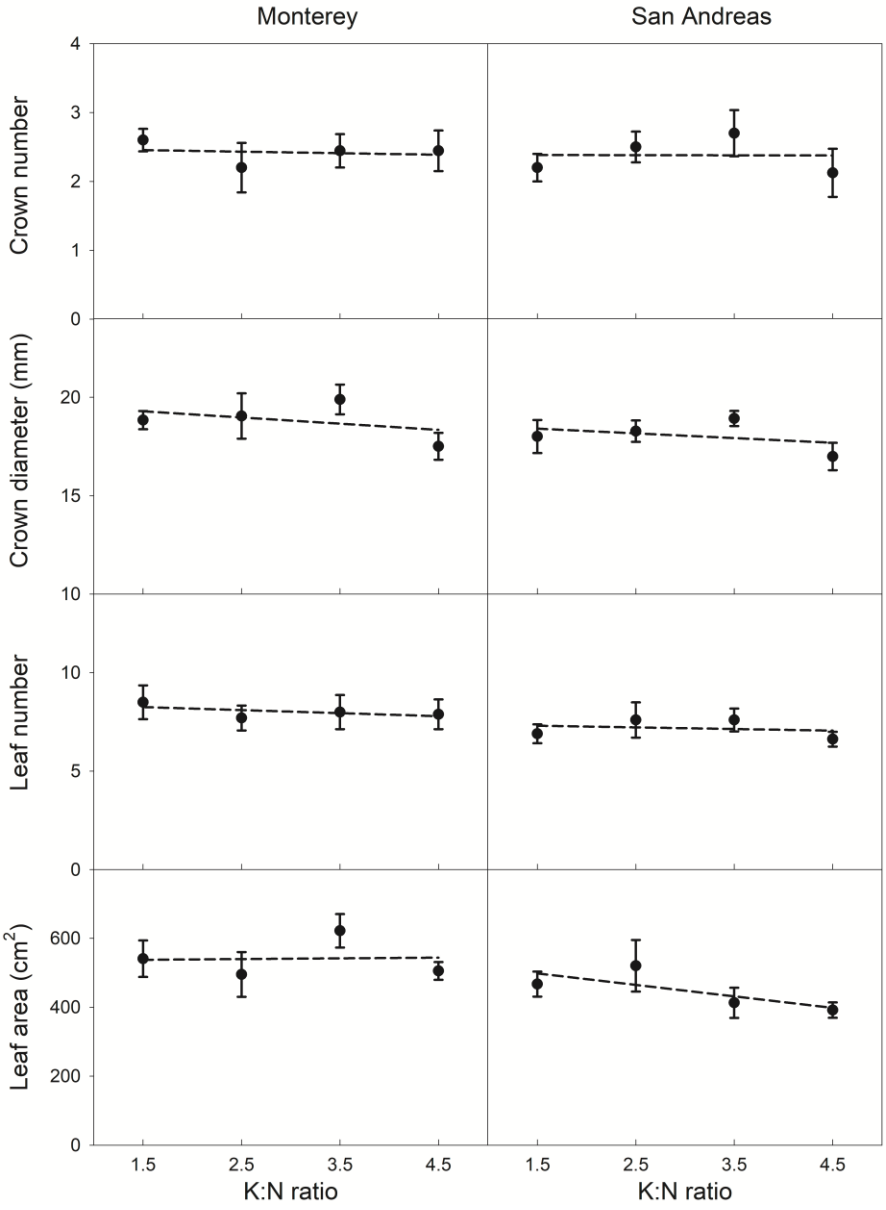


Figure 2.2. Crown Number, Crown Diameter, Leaf Number, and Leaf Area of Strawberry 'Monterey' and 'San Andreas' Grown Under Potassium to Nitrogen Ratios of 1.5:1, 2.5:1, 3.5:1, and 4.5:1 for Three Weeks. Each Data Point Represents the Mean and Standard Error of Two Replications with Five Plants per Replication. Correlation Coefficients ($r^2$) and Regression Equations Are Shown as a Solid Line When Statistically Significant and a Dotted Line When Not Significant. *, **, *** Indicate Significant at $P < 0.05$, 0.01 or 0.001, Respectively.

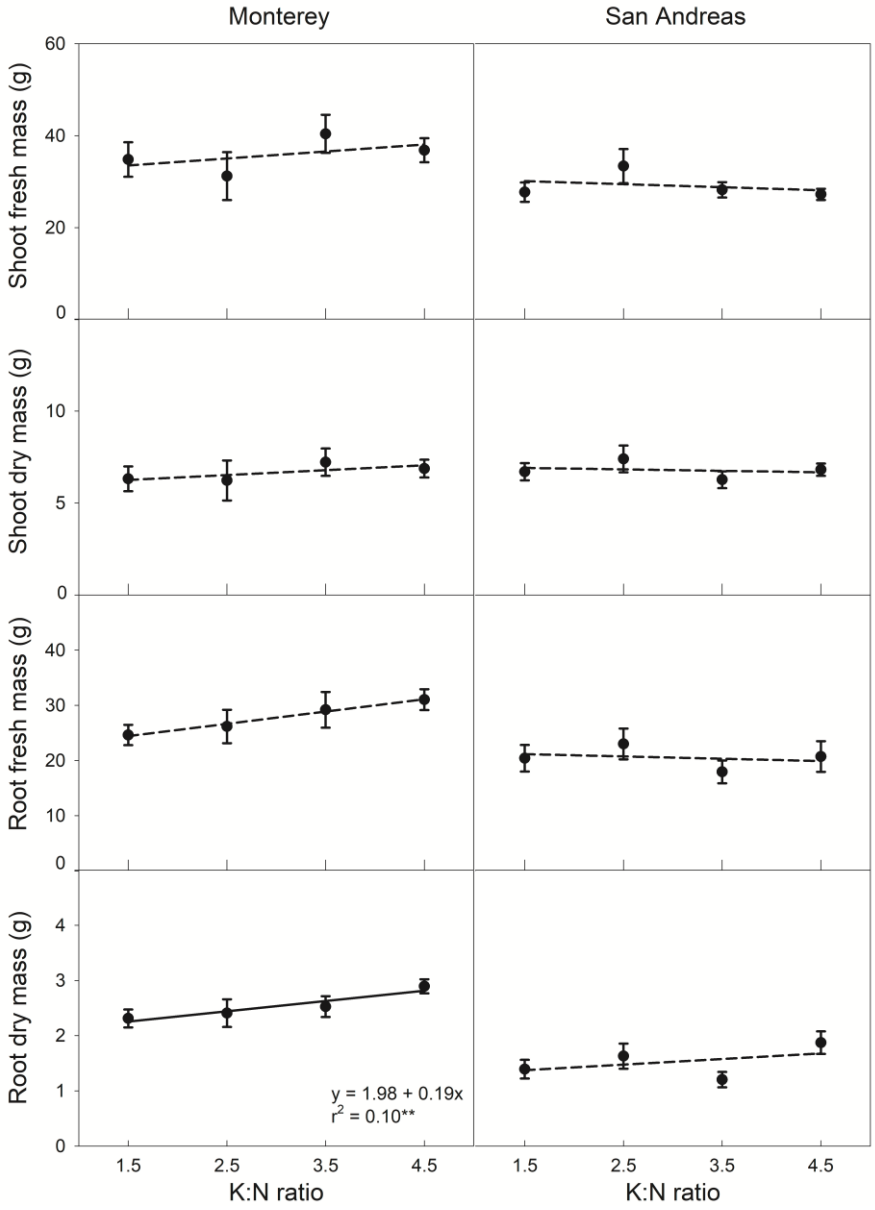


Figure 2.3. Fresh and Dry Mass of Shoot and Root of Strawberry 'Monterey' and 'San Andreas' Grown Under Potassium to Nitrogen Ratios of 1.5:1, 2.5:1, 3.5:1, and 4.5:1 for Three Weeks. Each Data Point Represents the Mean and Standard Error of Two Replications with Five Plants per Replication. Correlation Coefficients ($r^2$) and Regression Equations Are Shown as a Solid Line When Statistically Significant and a Dotted Line When Not Significant. *, **, *** Indicate Significant at $P < 0.05$, 0.01 or 0.001, Respectively.

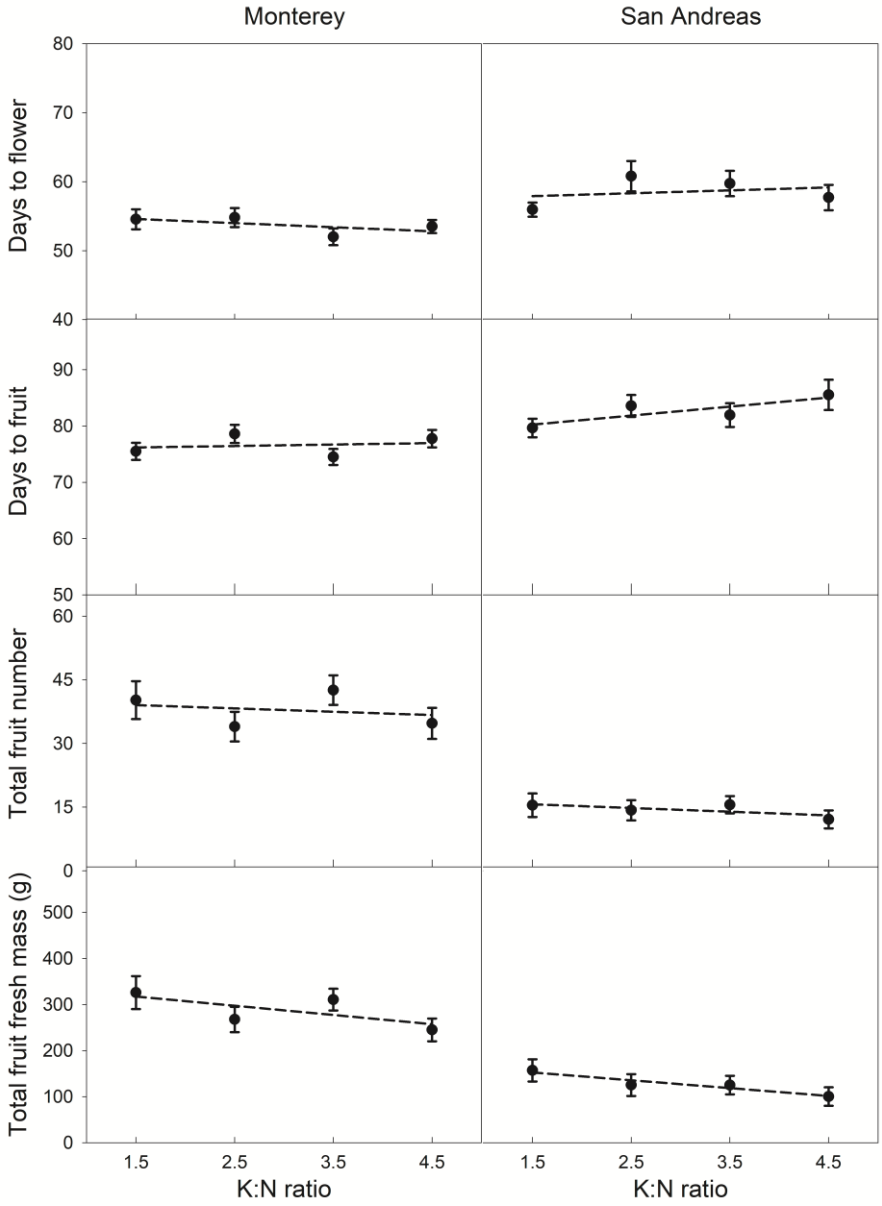


Figure 2.4. Days to Flower, Days to First Fruit Harvest, Total Number of Fruits Per Plant, and Total Fruit Fresh Mass Per Plant of Strawberry 'Monterey' and 'San Andreas' Grown Under Potassium to Nitrogen Ratios of 1.5:1, 2.5:1, 3.5:1, and 4.5:1. Each Data Point Represents the Mean and Standard Error of Two Replications with Ten Plants per Replication. Correlation Coefficients ($r^2$) and Regression Equations Are Shown as a Solid Line When Statistically Significant and a Dotted Line When Not Significant. *, **, *** Indicate Significant at $P < 0.05$, 0.01 or 0.001, Respectively.

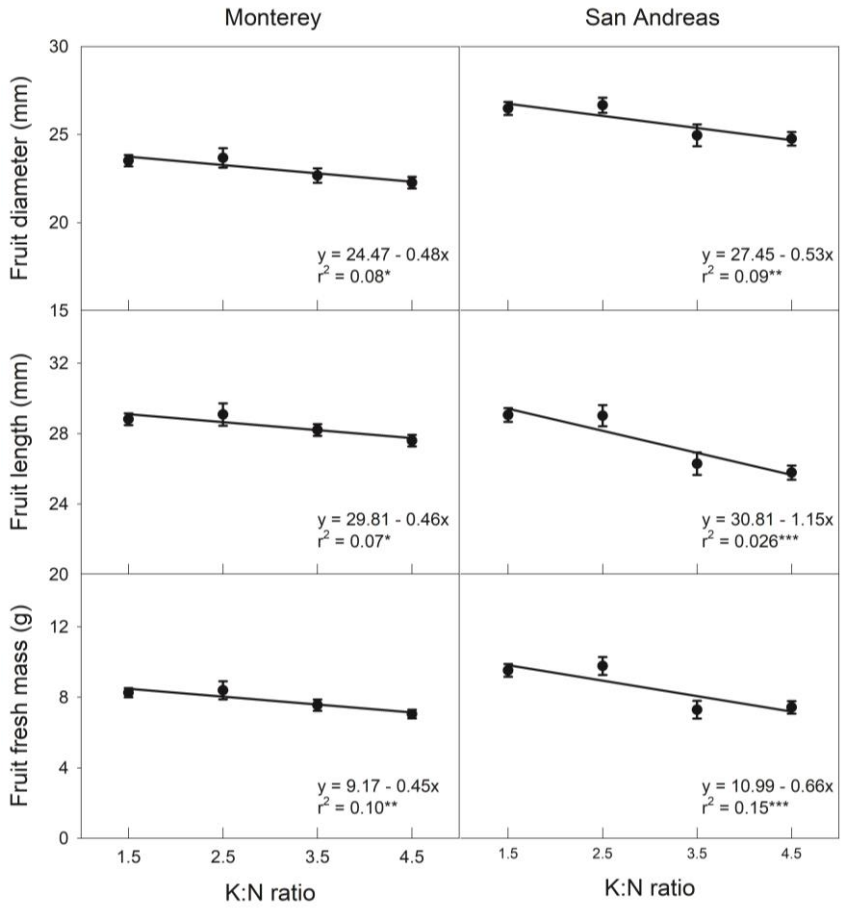


Figure 2.5. Diameter, Length, and Fresh Mass of Individual Fruits from Strawberry 'Monterey' and 'San Andreas' Grown Under Potassium to Nitrogen Ratios of 1.5:1, 2.5:1, 3.5:1, and 4.5:1. Each Data Point Represents the Mean and Standard Error of Two Replications with Ten Plants per Replication. Correlation Coefficients ($r^2$) and Regression Equations Are Shown as a Solid Line When Statistically Significant and a Dotted Line When Not Significant. *, **, *** Indicate Significant at $P < 0.05$, 0.01 or 0.001, Respectively.

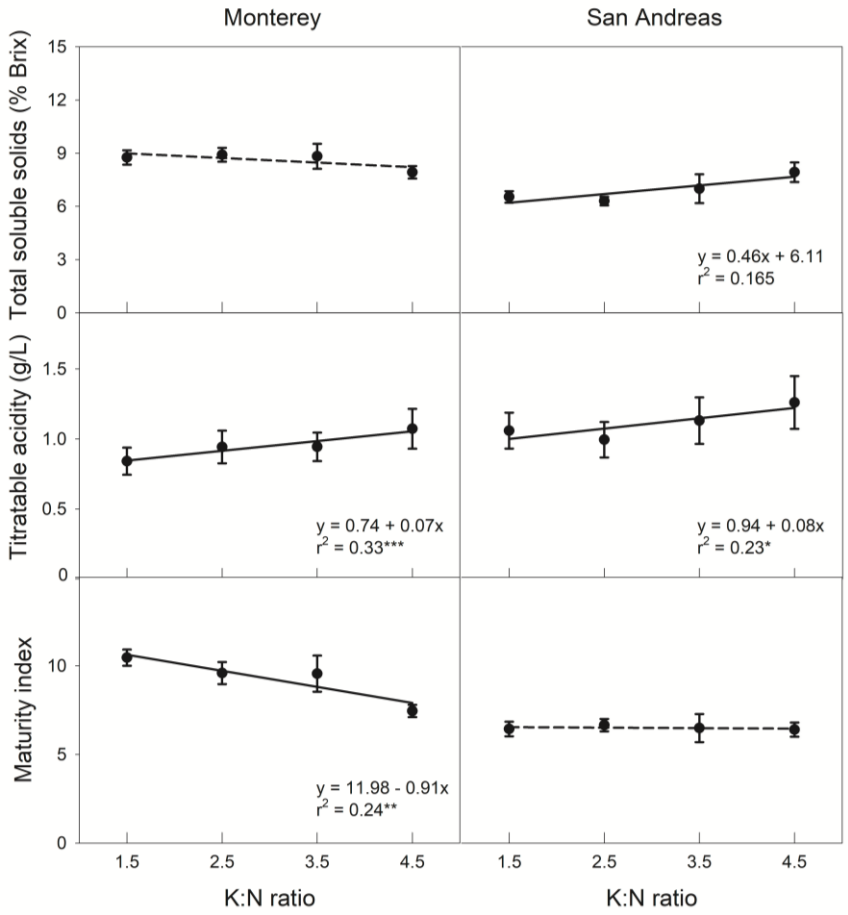


Figure 2.6. Total Soluble Solids, Titratable Acidity, and Maturity Index of Fruits of Strawberry 'Monterey' and 'San Andreas' Fruits Grown Under Potassium to Nitrogen Ratios of 1.5:1, 2.5:1, 3.5:1, and 4.5:1. Each Data Point Represents the Mean and Standard Error of Two Replications with Ten Plants per Replication. Correlation Coefficients ($r^2$) and Regression Equations Are Shown as a Solid Line When Statistically Significant and a Dotted Line When Not Significant. *, **, *** Indicate Significant at $P < 0.05$, 0.01 or 0.001, Respectively.

REFERENCES

Almeselmani, M. A. (2022). Nutrient solution for hydroponics. In Recent Research and Advances in Soilless Culture. *IntechOpen*. doi:10.5772/intechopen.101604.

Almeselmani, M., Pant, R. C., Singh, B. (2009). Potassium level and physiological response and fruit quality in hydroponically grown tomato. *International Journal of Vegetable Science, 16*(1), 85-99. https://doi.org/10.1080/19315260903271526.

Azeezahmed, S. K., Dubey, R. K., Kukal, S. S., Sethi, V. P. (2016). Effect of different nitrogen-potassium concentrations on growth and flowering of chrysanthemum in a drip hydroponic system. *Journal of Plant Nutrition, 39*(13), 1891-1898. https://doi.org/10.1080/01904167.2016.1187749.

Barroso, M. M., Alvarez, C. E. (1997). Toxicity symptoms and tolerance of strawberry to salinity in the irrigation water. *Scientia horticulturae, 71*(3-4), 177-188. https://doi.org/10.1016/S0304-4238(97)00082-4.

Çalişkan, B., Çalişkan, A. C. (2019). Potassium nutrition in plants and its interactions with other nutrients in hydroponic culture. *Improvement of Quality in Fruits and Vegetables Through Hydroponic Nutrient Management, 9*. doi:10.5772/intechopen.71951

Cao, Z. Q., Fan, T. F., Bi, Y. M., Tian, G. L., Zhang, L. S. (2016). Potassium deficiency and root exudates reduce root growth and increase Fusarium oxysporum growth and disease incidence in continuously cultivated strawberry. *New Zealand Journal of Crop and Horticultural Science, 44*(1), 58-68. https://doi.org/10.1080/01140671.2016.1146306.

Caruso, G., Villari, G., Melchionna, G., Conti, S. (2011). Effects of cultural cycles and nutrient solutions on plant growth, yield and fruit quality of alpine strawberry (Fragaria vesca L.) grown in hydroponics. *Scientia Horticulturae, 129*(3), 479-485. https://doi.org/10.1016/j.scienta.2011.04.020.

Ebrahimi, R., Souri, M. K., Ebrahimi, F., Ahmadizadeh, M. (2012). Growth and yield of strawberries under different potassium concentrations of hydroponic system in three substrates. *World Applied Sciences Journal, 16*(10), 1380-1386. Retrieved from https://citeseerx.ist.psu.edu/document?repid=rep1&type=pdf&doi=49ca83af6746a1ac81b5ecf1192a2923e5e1afed

Ferreira, J. F., Liu, X., Suarez, D. L. (2019). Fruit yield and survival of five commercial strawberry cultivars under field cultivation and salinity stress. *Scientia Horticulturae, 243*, 401-410. https://doi.org/10.1016/j.scienta.2018.07.016.

Hou, W., Yan, J., Jákli, B., Lu, J., Ren, T., Cong, R., Li, X. 2018. Synergistic effects of nitrogen and potassium on quantitative limitations to photosynthesis in rice (Oryza sativa L.). *Journal of Agricultural and Food Chemistry*, *66*(20), 5125-5132. https://doi.org/10.1021/acs.jafc.8b01135.

Johnson, R., Vishwakarma, K., Hossen, M. S., Kumar, V., Shackira, A. M., Puthur, J. T., Gholamreza Abdi, M.S. Hasanuzzaman, M. (2022). Potassium in plants: Growth regulation, signaling, and environmental stress tolerance. Plant Physiology and *Biochemistry*, *172*, 56-69. https://doi.org/10.1016/j.plaphy.2022.01.001.

Keutgen, A. J., Pawelzik, E. (2008). Quality and nutritional value of strawberry fruit under long term salt stress. *Food Chemistry*, *107*(4), 1413-1420. https://doi.org/10.1016/j.foodchem.2007.09.071.

Kumar, A. R., Kumar, N., Kavino, M. (2006). Role of potassium in fruit crops-a review. *Agricultural Reviews*, *27*(4), 284-291. Retrieved from https://www.indianjournals.com/ijor.aspx?target=ijor:ar&volume=27&issue=4&article=006.

Kumar, P., Kumar, T., Singh, S., Tuteja, N., Prasad, R., Singh, J. (2020). Potassium: A key modulator for cell homeostasis. *Journal of Biotechnology*, *324*, 198-210. https://doi.org/10.1016/j.jbiotec.2020.10.018.

Lee, J. H., Lee, Y. B., Choi, K. Y. (2017). Effect of Various Composition of Nutrient Solution on Growth and Yield of Strawberry 'Maehyang' in Coir Substrate Hydroponics. *Journal of Bio-Environment Control*, *26*(3), 227-234. https://doi.org/10.12791/KSBEC.2017.26.3.227.

Levine, C. P., Mattson, N. S. (2021). Potassium-deficient nutrient solution affects the yield, morphology, and tissue mineral elements for hydroponic baby leaf spinach (Spinacia oleracea L.). *Horticulturae*, *7*(8), 213. https://doi.org/10.3390/horticulturae7080213.

Mardanluo, S., Souri, M. K., Ahmadi, M. (2018). Plant growth and fruit quality of two pepper cultivars under different potassium levels of nutrient solutions. *Journal of Plant Nutrition*, *41*(12), 1604-1614. https://doi.org/10.1080/01904167.2018.1463383.

Morgan, L. (2006). *Hydroponic strawberry production*. Suntec (NZ).

Naciri, R., Rajib, W., Chtouki, M., Zeroual, Y., Oukarroum, A. (2022). Potassium and phosphorus content ratio in hydroponic culture affects tomato plant growth and nutrient uptake. *Physiology and Molecular Biology of Plants*, *28*(4), 763-774. https://doi.org/10.1007/s12298-022-01178-4.

Nakro, A., Bamouh, A., El Khatib, O., Ghaouti, L. (2022). Effect of potassium source and dose on yield and quality of strawberry fruit. *American Journal of Plant Sciences*, *13*(9), 1196-1208. https://doi.org/10.4236/ajps.2022.139081.

Nakro, A., Bamouh, A., Bouslama, H., San Bautista, A., Ghaouti, L. (2023). The effect of potassium–nitrogen balance on the yield and quality of strawberries grown under soilless conditions. *Horticulturae*, *9*(3), 304. https://doi.org/10.3390/horticulturae9030304.

Nazarideljou, M. J., Haghshenas, M., Jaberian Hamedan, H., Ferrante, A. (2019). Growth, yield and antioxidant capacity of strawberry under various K+: Ca++ ratios in hydroponic culture. *Acta Agriculturae Scandinavica, Section B—Soil & Plant Science*, *69*(2), 105-113. https://doi.org/10.1080/09064710.2018.1506500.

Oosterhuis, D. M., Loka, D. A., Kawakami, E. M., Pettigrew, W. T. (2014). The physiology of potassium in crop production. *Advances in agronomy*, *126*, 203-233. https://doi.org/10.1016/B978-0-12-800132-5.00003-1.

Othman, Y., Bataineh, K., Al-Ajlouni, M., Alsmairat, N., Ayad, J., Shiyab, S., Al-Qarallah, B., St Hilaire, R. (2019). Soilless culture: Management of growing substrate, water, nutrient, salinity, microorganism and product quality. *Fresenius Environmental Bulletin*, *28*(4), 3249-3260. Retrieved from https://www.cabidigitallibrary.org/doi/full/10.5555/20203439358.

Rahim Doust, J., Nazarideljou, M. J., Arshad, M., Ferrante, A. (2023). Comparison of the Growth, Physio-Biochemical Characteristics, and Quality Indices in Soilless-Grown Strawberries under Greenhouse and Open-Field Conditions. *Horticulturae*, *9*(7), 774. https://doi.org/10.3390/horticulturae9070774.

Samtani, J. B., Rom, C. R., Friedrich, H., Fennimore, S. A., Finn, C. E., Petran, A., Wallace, R.W., Pritts, M.P., Fernandez, G., Chase, C.A., Kubota, C., Bergefurd, B. (2019). The status and future of the strawberry industry in the United States. *HortTechnology*, *29*(1), 11-24. https://doi.org/10.21273/HORTTECH04135-18.

Saghaiesh, S. P., Souri, M. K. (2018). Root growth characteristics of Khatouni melon seedlings as affected by potassium nutrition. *Acta Scientiarum Polonorum - Hortorum Cultus*, *17*(5), 191-198. https://doi.org/10.24326/asphc.2018.5.1.

Sardans, J., Peñuelas, J. (2021). Potassium control of plant functions: Ecological and agricultural implications. *Plants*, *10*(2), 419. https://doi.org/10.3390/plants10020419.

Shah, I. H., Jinhui, W., Li, X., Hameed, M. K., Manzoor, M. A., Li, P., Zhang, Y., Niu, Q., Chang, L. (2024). Exploring the role of nitrogen and potassium in photosynthesis implications for sugar: Accumulation and translocation in horticultural crops. *Scientia Horticulturae*, *327*, 112832. https://doi.org/10.1016/j.scienta.2023.112832.

Song, W., Liu, S., Meng, L., Xue, R., Wang, C., Liu, G., Dong, J., Zhang, Y. (2015). Potassium deficiency inhibits lateral root development in tobacco seedlings by changing auxin distribution. *Plant and Soil*, *396*, 163-173. https://doi.org/10.1007/s11104-015-2579-1.

Sustr, M., Soukup, A., Tylova, E. (2019). Potassium in root growth and development. *Plants*, *8*(10), 435. https://doi.org/10.3390/plants8100435.

Tohidloo, G., Souri, M. K., Eskandarpour, S. (2018). Growth and fruit biochemical characteristics of three strawberry genotypes under different potassium concentrations of nutrient solution. *Open Agriculture*, *3*(1), 356-362. https://doi.org/10.1515/opag-2018-0039.

Usherwood, N. R. (1985). The role of potassium in crop quality. *Potassium in agriculture*, 489-513. https://doi.org/10.2134/1985.potassium.c21.

Wada, T. (2019). Theory and technology to control the nutrient solution of hydroponics. In Plant factory using artificial light. *Adapting to Environmental Disruption and Clues to Agricultural Innovation*. 5-14. https://doi.org/10.1016/B978-0-12-813973-8.00001-4.

Zörb, C., Senbayram, M., Peiter, E. (2014). Potassium in agriculture–status and perspectives. *Journal of Plant Physiology*, 171(9), 656-669. https://doi.org/10.1016/j.jplph.2013.08.008.

REFERENCES

Almeselmani, M. A. (2022). Nutrient solution for hydroponics. In Recent Research and Advances in Soilless Culture. *IntechOpen*. doi:10.5772/intechopen.101604.

Almeselmani, M., Pant, R. C., Singh, B. (2009). Potassium level and physiological response and fruit quality in hydroponically grown tomato. *International Journal of Vegetable Science, 16*(1), 85-99. https://doi.org/10.1080/19315260903271526.

Asaduzzaman, M., Asao, T. (2019). Introductory Chapter: Potassium in quality improvement of fruits and vegetables. *Improvement of Quality in Fruits and Vegetables Through Hydroponic Nutrient Management*, 1.

Azeezahmed, S. K., Dubey, R. K., Kukal, S. S., Sethi, V. P. (2016). Effect of different nitrogen-potassium concentrations on growth and flowering of chrysanthemum in a drip hydroponic system. *Journal of Plant Nutrition*, *39*(13), 1891-1898. https://doi.org/10.1080/01904167.2016.1187749.

Bae, J. H., Park, S. Y., Oh, M.M. (2017). Supplemental irradiation with far-red light-emitting diodes improves growth and phenolic contents in *Crepidiastrum denticulatum* in a plant factory with artificial lighting. *Horticulture, Environment, and Biotechnology, 58,* 357–366. https://doi.org/10.1007/s13580-017-0331-x.

Bantis, F., Smirnakou, S., Ouzounis, T., Koukounaras, A., Ntagkas, N., Radoglou, K. (2018). Current status and recent achievements in the field of horticulture with the use of light-emitting diodes (LEDs). *Scientia Horticulturae, 235*, 437–451. https://doi.org/10.1016/j.scienta.2018.02.058.

Barroso, M. M., Alvarez, C. E. (1997). Toxicity symptoms and tolerance of strawberry to salinity in the irrigation water. *Scientia horticulturae, 71*(3-4), 177-188. https://doi.org/10.1016/S0304-4238(97)00082-4.

Blevins, D. G. (1985). Role of potassium in protein metabolism in plants. *Potassium in Agriculture*, 413-424. https://doi.org/10.2134/1985.potassium.c17.

Botella, M. Á., Arévalo, L., Mestre, T. C., Rubio, F., García-Sánchez, F., Rivero, R. M., Martínez, V. (2017). Potassium fertilization enhances pepper fruit quality. *Journal of Plant Nutrition*, *40*(2), 145-155. https://doi.org/10.1080/01904167.2016.1201501.

Çalişkan, B., Çalişkan, A. C. (2019). Potassium nutrition in plants and its interactions with other nutrients in hydroponic culture. *Improvement of Quality in Fruits and Vegetables Through Hydroponic Nutrient Management, 9*. doi:10.5772/intechopen.71951.

Cao, Z. Q., Fan, T. F., Bi, Y. M., Tian, G. L., Zhang, L. S. (2016). Potassium deficiency and root exudates reduce root growth and increase Fusarium oxysporum growth and disease incidence in continuously cultivated strawberry. *New Zealand Journal of Crop and Horticultural Science*, *44*(1), 58-68. https://doi.org/10.1080/01140671.2016.1146306.

Caruso, G., Villari, G., Melchionna, G., Conti, S. (2011). Effects of cultural cycles and nutrient solutions on plant growth, yield and fruit quality of alpine strawberry (Fragaria vesca L.) grown in hydroponics. *Scientia Horticulturae, 129*(3), 479-485. https://doi.org/10.1016/j.scienta.2011.04.020.

Choi, H. G., Kwon J. K., Moon B. Y., Kang N. J., Park K. S., Cho M. W., Kim Y. C. (2013). Effect of different light emitting diode (LED) lights on the growth characteristics and the phytochemical production of strawberry fruits during cultivation. *Horticultural Science and Technology*, *31*(1), 56–64. https://doi.org/10.7235/hort.2013.12100.

Choi, H. G., Moon B. Y., Kang N. J. (2015). Effects of LED light on the production of strawberry during cultivation in a plastic greenhouse and in a growth chamber. *Scientia Horticulturae, 189*, 22–31. https://doi.org/10.1016/j.scienta.2015.03.022.

Craig, D. S., Runkle E. S. (2016). An intermediate phytochrome photoequilibria from night-interruption lighting optimally promotes flowering of several long-day plants. *Environmental and Experimental Botany, 121*, 132–138. https://doi.org/10.1016/j.envexpbot.2015.04.004.

Darrow, G. M., (1929). Inflorescence types of strawberry varieties. *American Journal of Botany, 16*, 571–585. https://doi.org/10.2307/2435912.

Ebrahimi, R., Souri, M. K., Ebrahimi, F., Ahmadizadeh, M. (2012). Growth and yield of strawberries under different potassium concentrations of hydroponic system in three substrates. *World Applied Sciences Journal*, *16*(10), 1380-1386. Retrieved from https://citeseerx.ist.psu.edu/document?repid=rep1&type=pdf&doi=49ca83af6746a1ac81b5ecf1192a2923e5e1afed.

Ferreira, J. F., Liu, X., Suarez, D. L. (2019). Fruit yield and survival of five commercial strawberry cultivars under field cultivation and salinity stress. *Scientia Horticulturae, 243*, 401-410. https://doi.org/10.1016/j.scienta.2018.07.016.

Fukuda, N., Nogi M, Sase, S., Nishimura, S., (2002). Effects of localized light quality from light-emitting diodes on geranium peduncle elongation. *Acta Horticulturae, 580*:151–156. https://doi.org/10.17660/ActaHortic.2002.580.18.

Guiamba, H. D. S. S., Zhang, X., Sierka, E., Lin, K., Ali, M. M., Ali, W. M., Lamlom, S.F., Kalaji, H.M., Telesiński, A., Yousef, A.F., Xu, Y. (2022). Enhancement of photosynthesis efficiency and yield of strawberry (Fragaria ananassa Duch.) plants via LED systems. *Frontiers in Plant Science*, *13*, 918038. https://doi.org/10.3389/fpls.2022.918038.

Herbers, K., Sonnewald, U. (1998). Molecular determinants of sink strength. *Current Opinion in Plant Biology, 1*(3), 207–216. https://doi.org/10.1016/S1369-5266(98)80106-4.

Hidaka, K., Dan, K., Imamura, H., Miyoshi, Y., Takayama, T., Sameshim, K., Kitano, M., Okimura, M. (2013). Effect of supplemental lighting from different light sources on growth and yield of strawberry. *Environmental Control in Biology, 51*(1), 41–47. https://doi.org/10.2525/ecb.51.41.

Hou, W., Yan, J., Jákli, B., Lu, J., Ren, T., Cong, R., Li, X. 2018. Synergistic effects of nitrogen and potassium on quantitative limitations to photosynthesis in rice (Oryza sativa L.). *Journal of Agricultural and Food Chemistry*, *66*(20), 5125-5132. https://doi.org/10.1021/acs.jafc.8b01135.

Ji, Y., Nuñez Ocaña, D., Choe, D., Larsen, D. H., Marcelis, L. F. M., Heuvelink, E. (2020). Far-red radiation stimulates dry mass partitioning to fruits by increasing fruit sink strength in tomato. *New Phytologist*, *228*(6), 1914–1925. https://doi.org/10.1111/nph.16805.

Jin, W., Urbina, J. L., Heuvelink, E., Marcelis, L. F. (2021). Adding far-red to red-blue light-emitting diode light promotes yield of lettuce at different planting densities. *Frontiers in Plant Science, 11*, 609977. https://doi.org/10.3389/fpls.2020.609977.

Johnson, R., Vishwakarma, K., Hossen, M. S., Kumar, V., Shackira, A. M., Puthur, J. T., Gholamreza Abdi, M.S. Hasanuzzaman, M. (2022). Potassium in plants: Growth regulation, signaling, and environmental stress tolerance. Plant Physiology and *Biochemistry*, *172*, 56-69. https://doi.org/10.1016/j.plaphy.2022.01.001.

Kalaitzoglou, P., van Ieperen, W., Harbinson, J., van der Meer, M., Martinakos, S., Weerheim, K., Nicole, C. C. S., Marcelis, L. F. M. (2019). Effects of continuous or end-of-day far-red light on tomato plant growth, morphology, light absorption, and fruit production. *Frontiers in Plant Science, 10*, 322. https://doi.org/10.3389/fpls.2019.00322.

Kaur, H., Bedi, S., Sethi, V. P., & Dhatt, A. S. (2018). Effects of substrate hydroponic systems and different N and K ratios on yield and quality of tomato fruit. *Journal of Plant Nutrition*, *41*(12), 1547-1554. https://doi.org/10.1080/01904167.2018.1459689.

Keutgen, A. J., Pawelzik, E. (2008). Quality and nutritional value of strawberry fruit under long term salt stress. *Food Chemistry*, *107*(4), 1413-1420. https://doi.org/10.1016/j.foodchem.2007.09.071.

Kim, H. J., Yang, T., Choi, S., Wang, Y. J., Lin, M. Y., Liceaga, A. M. (2020). Supplemental intracanopy far-red radiation to red LED light improves fruit quality attributes of greenhouse tomatoes. *Scientia Horticulturae, 261*, 108985.

Kouloumprouka Zacharaki, A., Monaghan, J. M., Bromley, J. R., Vickers, L. H. (2024). Opportunities and challenges for strawberry cultivation in urban food production systems. *Plants, People, Planet*. https://doi.org/10.1002/ppp3.10475.

Kumar, A. R., Kumar, N., Kavino, M. (2006). Role of potassium in fruit crops-a review. *Agricultural Reviews*, *27*(4), 284-291. Retrieved from https://www.indianjournals.com/ijor.aspx?target=ijor:ar&volume=27&issue=4&article=006

Kumar, P., Kumar, T., Singh, S., Tuteja, N., Prasad, R., Singh, J. (2020). Potassium: A key modulator for cell homeostasis. *Journal of Biotechnology*, *324*, 198-210. https://doi.org/10.1016/j.jbiotec.2020.10.018.

Kurepin, L. V., Emery, R. N., Pharis, R. P., Reid, D. M. (2007). Uncoupling light quality from light irradiance effects in *Helianthus annuus* shoots: putative roles for plant hormones in leaf and internode growth. *Journal of Experimental Botany, 58*(8), 2145–2157. https://doi.org/10.1093/jxb/erm068.

Kusuma, P., Bugbee, B. (2021). Improving the predictive value of phytochrome photoequilibrium: consideration of spectral distortion within a leaf. *Frontiers in Plant Science, 12*, 596943. https://doi.org/10.3389/fpls.2021.596943.

Kusuma P., Bugbee, B. (2023). On the contrasting morphological response to far-red at high and low photon fluxes. *Frontiers in Plant Science, 14*, 1185622. https://doi.org/10.3389/fpls.2023.1185622.

Lee, J. H., Lee, Y. B., Choi, K. Y. (2017). Effect of Various Composition of Nutrient Solution on Growth and Yield of Strawberry 'Maehyang' in Coir Substrate Hydroponics. *Journal of Bio-Environment Control*, *26*(3), 227-234. https://doi.org/10.12791/KSBEC.2017.26.3.227.

Levine, C. P., Mattson, N. S. (2021). Potassium-deficient nutrient solution affects the yield, morphology, and tissue mineral elements for hydroponic baby leaf spinach (Spinacia oleracea L.). *Horticulturae*, *7*(8), 213. https://doi.org/10.3390/horticulturae7080213.

Lopez, R. G., Meng, Q., Runkle, E. S. (2020). Blue radiation signals and saturates photoperiodic flowering of several long-day plants at crop-specific photon flux densities. *Scientia Horticulturae, 271*, 109470. https://doi.org/10.1016/j.scienta.2020.109470.

Lore, K. (2022) Driscoll's heads to virginia to grow strawberries in world's largest indoor vertical farm. The Packer. Retrieved from: https://www.thepacker.com/news/packer-tech/driscolls-heads-virginia-grow-strawberries-worlds-largest-indoor-vertical-farm.

Lubna, F. A., Lewus, D. C., Shelford, T. J., Both, A. J. (2022). What you may not realize about vertical farming. *Horticulturae*, *8*(4), 322. https://doi.org/10.3390/horticulturae8040322.

Marcelis, L. F. M. (1996). Sink strength as a determinant of dry matter partitioning in the whole plant. *Journal of Experimental Botany, 47*, 1281–1291. https://doi.org/10.1093/jxb/47.Special_Issue.1281.

Marcelis, L. F. M., Heuvelink, E. (1999). Modelling fruit set, fruit growth and dry matter partitioning. *Acta Horticulturae, 499*, 39–50. https://doi.org/10.17660/ActaHortic.1999.499.3.

Mardanluo, S., Souri, M. K., Ahmadi, M. (2018). Plant growth and fruit quality of two pepper cultivars under different potassium levels of nutrient solutions. *Journal of Plant Nutrition*, *41*(12), 1604-1614. https://doi.org/10.1080/01904167.2018.1463383.

Meng, Q., Runkle, E. S. (2017). Moderate-intensity blue radiation can regulate flowering, but not extension growth, of several photoperiodic ornamental crops. *Environmental and Experimental Botany, 134*, 12–20. https://doi.org/10.1016/j.envexpbot.2016.10.006.

Mengel, K., & Arneke, W. W. (1982). Effect of potassium on the water potential, the pressure potential, the osmotic potential and cell elongation in leaves of Phaseolus vulgaris. *Physiologia Plantarum*, *54*(4), 402-408. https://doi.org/10.1111/j.1399-3054.1982.tb00699.x.

Mitchell, C. A., Sheibani, F. (2020). LED advancements for plant-factory artificial lighting. In *Plant factory* (pp. 167-184). Academic Press. https://doi.org/10.1016/B978-0-12-816691-8.00010-8.

Mitchell, C., Stutte, G. (2015). Sole-source lighting for controlled-environment agriculture. *Light Management in Controlled Environments*; Lopez, R., Runkle, ES, Eds, 119-134. Retrieved from https://www.spring-lake.net/pdfs/gh-tech/ch5-sole-source-Agriculture.pdf

Morgan, L. (2006). *Hydroponic strawberry production*. Suntec (NZ).

Naciri, R., Rajib, W., Chtouki, M., Zeroual, Y., Oukarroum, A. (2022). Potassium and phosphorus content ratio in hydroponic culture affects tomato plant growth and nutrient uptake. *Physiology and Molecular Biology of Plants*, *28*(4), 763-774. https://doi.org/10.1007/s12298-022-01178-4.

Nadalini, S., Zucchi, P., Andreotti, C. (2017). Effects of blue and red LED lights on soilless cultivated strawberry growth performances and fruit quality. *European Journal of Horticultural Science, 82*(1), 12–20. https://doi.org/10.17660/eJHS.2017/82.1.2.

Nakro, A., Bamouh, A., El Khatib, O., Ghaouti, L. (2022). Effect of potassium source and dose on yield and quality of strawberry fruit. *American Journal of Plant Sciences*, *13*(9), 1196-1208. https://doi.org/10.4236/ajps.2022.139081.

Nakro, A., Bamouh, A., Bouslama, H., San Bautista, A., Ghaouti, L. (2023). The effect of potassium–nitrogen balance on the yield and quality of strawberries grown under soilless conditions. *Horticulturae*, *9*(3), 304. https://doi.org/10.3390/horticulturae9030304.

Nazarideljou, M. J., Haghshenas, M., Jaberian Hamedan, H., Ferrante, A. (2019). Growth, yield and antioxidant capacity of strawberry under various K+: Ca++ ratios in hydroponic culture. *Acta Agriculturae Scandinavica, Section B—Soil & Plant Science*, *69*(2), 105-113. https://doi.org/10.1080/09064710.2018.1506500.

Oosterhuis, D. M., Loka, D. A., Kawakami, E. M., Pettigrew, W. T. (2014). The physiology of potassium in crop production. *Advances in agronomy*, *126*, 203-233. https://doi.org/10.1016/B978-0-12-800132-5.00003-1.

Othman, Y., Bataineh, K., Al-Ajlouni, M., Alsmairat, N., Ayad, J., Shiyab, S., Al-Qarallah, B., St Hilaire, R. (2019). Soilless culture: Management of growing substrate, water, nutrient, salinity, microorganism and product quality. *Fresenius Environmental Bulletin*, *28*(4), 3249-3260. Retrieved from https://www.cabidigitallibrary.org/doi/full/10.5555/20203439358.

Park, Y., Runkle, E. S. (2017). Far-red radiation promotes growth of seedlings by increasing leaf expansion and whole-plant net assimilation. *Environmental and Experimental Botany, 136*, 41–49. https://doi.org/10.1016/j.envexpbot.2016.12.013.

Park, Y, Runkle, E. S. (2018). Far-red radiation and photosynthetic photon flux density independently regulate seedling growth but interactively regulate flowering. *Environmental and Experimental Botany, 155*, 206–216. https://doi.org/10.1016/j.envexpbot.2018.06.033.

Park, Y, Runkle E. S. (2019). Blue radiation attenuates the effects of the red to far-red ratio on extension growth but not on flowering. *Environmental and Experimental Botany, 168*, 103871. https://doi.org/10.1016/j.envexpbot.2019.103871.

Park, Y, Sethi R., Temnyk, S. (2023). Growth, flowering, and fruit production of strawberry ‘albion’ in response to photoperiod and photosynthetic photon flux density of sole-source lighting. *Plants*, *12*(4), 731. https://doi.org/10.3390/plants12040731.

Pedrosa, A. W., Martinez, H. E. P., Matiello, E. M., Fontes, P. C. R., & Pereira, P. R. G. (2011). Influence of the N/K ratio on the production and quality of cucumber in hydroponic system. *Revista Ceres*, *58*, 619-624. https://doi.org/10.1590/S0034-737X2011000500012.

Prisca, M., Maarten, V., Jan, V. D., Bart, N., Wouter, S., Timo, H., Barbara, D. C., Bram, V. de P. (2022). Blue and far-red light control flowering time of woodland strawberry (*Fragaria vesca*) distinctively via CONSTANS (CO) and FLOWERING LOCUS T1 (FT1) in the background of sunlight mimicking radiation. *Environmental and Experimental Botany*, *198*, 104866. https://doi.org/10.1016/j.envexpbot.2022.104866.

Rahim Doust, J., Nazarideljou, M. J., Arshad, M., Ferrante, A. (2023). Comparison of the Growth, Physio-Biochemical Characteristics, and Quality Indices in Soilless-Grown Strawberries under Greenhouse and Open-Field Conditions. *Horticulturae*, *9*(7), 774. https://doi.org/10.3390/horticulturae9070774.

Rahman, M. M, Field, D. L., Ahmed, S. M., Hasan, M. T., Basher, M. K., Alameh, K. (2021). LED illumination for high-quality high-yield crop growth in protected cropping environments. *Plants*, *10*(11), 2470. https://doi.org/10.3390/plants10112470.

Rantanen, M., Kurokura, T., Mouhu, K., Pinho, P., Tetri, E., Halonen, L., Palonen, P., Elomaa, P., Hytönen, T. (2014). Light quality regulates flowering in FvFT1/FvTFL1 dependent manner in the woodland strawberry *Fragaria vesca*. *Frontiers in Plant Science*, *5*, 271. https://doi.org/10.3389/fpls.2014.00271.

Richardson, M. L., Arlotta, C. G., Lewers, K. S. (2022). Yield and nutrients of six cultivars of strawberries grown in five urban cropping systems. *Scientia Horticulturae*, *294*, 110775. https://doi.org/10.1016/j.scienta.2021.110775.

Roig-Villanova, I., Martínez-García, J. F. (2016). Plant responses to vegetation proximity: a whole life avoiding shade. *Front in Plant Sci*, *7*, 236. https://doi.org/10.3389/fpls.2016.00236.

Sager, J. C., Smith, W. O., Edwards, J., Cyr, K. L. (1988). Photosynthetic efficiency and phytochrome photoequilibria determination using spectral data. *Transactions of the ASAE*, *31*(6), 1882–1889. https://doi.org/10.13031/2013.30952.

Saghaiesh, S. P., Souri, M. K. (2018). Root growth characteristics of Khatouni melon seedlings as affected by potassium nutrition. *Acta Scientiarum Polonorum - Hortorum Cultus*, *17*(5), 191-198. https://doi.org/10.24326/asphc.2018.5.1.

Samtani, J. B., Rom, C. R., Friedrich, H., Fennimore, S. A., Finn, C. E., Petran, A., Wallace, R. W., Pritts, M. P., Fernandez, G., Chase, C. A., and Kubota, C. (2019) The status and future of the strawberry industry in the United States. *Horttechnology*, *29*(11), 11–24. https://doi.org/10.21273/HORTTECH04135-18.

Samuolienė, G., Brazaitytė, A., Urbonavičiūtė, A., Šabajevienė, G., Duchovskis, P. (2010). The effect of red and blue light component on the growth and development of frigo strawberries. *Zemdirbyste-Agriculture*, *97*, 99–104.

Shah, I. H., Jinhui, W., Li, X., Hameed, M. K., Manzoor, M. A., Li, P., Zhang, Y., Niu, Q., Chang, L. (2024). Exploring the role of nitrogen and potassium in photosynthesis implications for sugar: Accumulation and translocation in horticultural crops. *Scientia Horticulturae*, *327*, 112832. https://doi.org/10.1016/j.scienta.2023.112832.

Song, W., Liu, S., Meng, L., Xue, R., Wang, C., Liu, G., Dong, J., Zhang, Y. (2015). Potassium deficiency inhibits lateral root development in tobacco seedlings by changing auxin distribution. *Plant and Soil*, *396*, 163-173. https://doi.org/10.1007/s11104-015-2579-1.

Sustr, M., Soukup, A., Tylova, E. (2019). Potassium in root growth and development. *Plants*, *8*(10), 435. https://doi.org/10.3390/plants8100435.

Tagliavini, M., Baldi, E., Lucchi, P., Antonelli, M., Sorrenti, G., Baruzzi, G., & Faedi, W. (2005). Dynamics of nutrients uptake by strawberry plants (Fragaria× Ananassa Dutch.) grown in soil and soilless culture. *European Journal of Agronomy*, *23*(1), 15-25. https://doi.org/10.1016/j.eja.2004.09.002.

Tan, T., Li, S., Fan, Y., Wang, Z., Ali Raza, M., Shafiq, I., Wang, B., Wu, X., Yong, T., Wang, X., Wu, Y., Yang, F., Yang, W. (2022). Far-red light: A regulator of plant morphology and photosynthetic capacity. *Crop Journal*, *10*, 300–309. https://doi.org/10.1016/j.cj.2021.06.007.

Tohidloo, G., Souri, M. K., Eskandarpour, S. (2018). Growth and fruit biochemical characteristics of three strawberry genotypes under different potassium concentrations of nutrient solution. *Open Agriculture*, *3*(1), 356-362. https://doi.org/10.1515/opag-2018-0039.

Tsuruyama, J., Shibuya, T. (2018). Growth and flowering responses of seed-propagated strawberry seedlings to different photoperiods in controlled environment chambers. *Horttechnology*, *28*(4), 453–458. https://doi.org/10.21273/HORTTECH04061-18.

Tsuruyama, J., Shibuya, T. (2023). Effects of far-red light and photoperiod during early growth stages on flower bud development of seed-propagated strawberry seedlings. *Scientia Horticulturae, 317*, 112051. https://doi.org/10.1016/j.scienta.2023.112051.

U.S. Department of Agriculture (USDA) - National Agricultural Statistics Service – Retreieved from: https://www.nass.usda.gov/Statistics_by_Subject/result.php?59DFD141-00B1-3EDE-B526-7FDEFCD859A7&sector=CROPS&group=FRUIT%20%26%20TREE%20NUTS&comm=STRAWBERRIES [accessed 6 Sep 2023].

U.S. Department of Agriculture (USDA) 2014a U.S. strawberry consumption continues to grow. 28 Nov. 2018. <https://www.ers.usda.gov/data-products/chart-gallery/gallery/chart-detail/?chartId=77884>.
U.S. Department of Agriculture (USDA) 2018a Vegetables 2017 summary (February 2018). 28 Nov. 2018. http://usda.mannlib.cornell.edu/usda/current/VegeSumm/VegeSumm-02-13-2018.pdf

Usherwood, N. R. (1985). The role of potassium in crop quality. *Potassium in agriculture*, 489-513. https://doi.org/10.2134/1985.potassium.c21.

Wada, T. (2019). Theory and technology to control the nutrient solution of hydroponics. In Plant factory using artificial light. *Adapting to Environmental Disruption and Clues to Agricultural Innovation*. 5-14. https://doi.org/10.1016/B978-0-12-813973-8.00001-4.

Xiong, Y., Ge, Y., Grimstad, L., From, P. J. (2020). An autonomous strawberry-harvesting robot: design, development, integration, and field evaluation. *Journal of Field Robotics, 37*(2), 202–224. https://doi.org/10.1002/rob.21889.

Xu, X., Zhang, X., Ni, W., Liu, C., Qin, H., Guan, Y., Liu, J., Feng, Z., Xing, Y., Tian, G. and Zhu, Z (2024). Nitrogen–potassium balance improves leaf photosynthetic capacity by regulating leaf nitrogen allocation in apple. *Horticulture Research, 11*(1), uhad253. https://doi.org/10.1093/hr/uhad253.

Yoshida, H., Hikosaka, S., Goto, E., Takasuna, H., Kudou, T. (2012). Effects of light quality and light period on flowering of everbearing strawberry in a closed plant production system. *Acta Horticulturae, 956*, 107–112. https://doi.org/10.17660/ActaHortic.2012.956.9.

Zahedi, S. M., Sarikhani, H. (2016). Effect of far-red light, temperature, and plant age on morphological changes and induction of flowering of a ‘June-bearing’ strawberry. *Horticulture, Environment, and Biotechnology*, *57*, 340-347. https://doi.org/10.1007/s13580-016-0018-8.

Zhang, M., Park, Y., Runkle, E. S. (2020). Regulation of extension growth and flowering of seedlings by blue radiation and the red to far-red ratio of sole-source lighting. *Scientia Horticulturae*, *272*, 109478. https://doi.org/10.1016/j.scienta.2020.109478.

Zhen, S, Bugbee, B. (2020). Far-red photons have equivalent efficiency to traditional photosynthetic photons: Implications for redefining photosynthetically active radiation. *Plant, Cell & Environment*, *43*(5), 1259–1272. https://doi.org/10.1111/pce.13730.

Zhen, S., van Iersel, M., Bugbee, B. (2021). Why far-red photons should be included in the definition of photosynthetic photons and the measurement of horticultural fixture efficacy. *Frontiers in Plant Science, 12*. https://doi.org/10.3389/fpls.2021.693445.

Zhen, S., van Iersel, M. W. (2017). Far-red light is needed for efficient photochemistry and photosynthesis. *Journal of Plant Physiology, 209*, 115–122. https://doi.org/10.1016/j.jplph.2016.12.00.

Zörb, C., Senbayram, M., Peiter, E. (2014). Potassium in agriculture–status and perspectives. *Journal of Plant Physiology*, 171(9), 656-669. https://doi.org/10.1016/j.jplph.2013.08.008.