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Nutrient dynamics in agrivoltaics: Understanding plant responses to altered microclimates

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ABSTRACT

Agrivoltaics systems, integrating solar energy generation with agricultural production, offer a promising solution to escalating global demands for food, energy, and sustainable land use. While research has extensively explored yield impacts and system design, a critical knowledge gap persists regarding nutrient dynamics within these modified microclimates. This review bridged this gap by examining how agrivoltaics systems influence plant nutrient uptake, allocation, as well as overall physiology under altered conditions of light, temperature, and soil moisture. Species-specific responses for key nutrients were examined: nitrogen assimilation can be limited by shade, phosphorus dynamics often exhibit variable translocation, potassium and magnesium uptake may be enhanced or impaired depending on shade intensity and crop species, and calcium uptake tends to increase under shading, albeit with potential trade-offs in internal distribution as well as risk of physiological disorders. These changes are accompanied by adjustments in biomass partitioning and nutrient allocation as plants acclimate to the modified light environment. By synthesizing current knowledge and identifying research gaps, this review underscored the need for targeted crop selection, nutrient management, and system optimization to fully harness the potential of agrivoltaic systems for sustainable food-energy co-production.

Keywords: macronutrients, elements, plant mineral nutrition, dual land use, crop physiology.

INTRODUCTION

The escalating global demand for food, energy, and sustainable land use has driven innovation in agricultural practices. Agrivoltaic systems, which integrate photovoltaic panels with agricultural production on the same land, represent a promising approach to reconcile competing interests for land use (Al Mamun et al., 2022). By enabling dual land use, agrivoltaic systems offer potential benefits across the food-energy-water nexus, including enhanced land productivity, improved water use efficiency, and increased renewable energy generation (Barron-Gafford et al., 2019). Research has demonstrated that agrivoltaic systems modify the microclimate beneath solar panels, creating conditions that may benefit certain crops, particularly in the regions experiencing high temperatures and water scarcity (Adeh et al., 2018). These modifications include reduced solar radiation, altered temperature profiles, and changes in soil moisture dynamics (Marrou et al., 2013), all of which can significantly influence plant physiological processes.

While much research has focused on yield impacts and system design (Weselek et al., 2019), there remains a critical gap in understanding nutrient dynamics in agrivoltaic systems, particularly from a plant physiological perspective. Essential macro and micronutrients, including nitrogen (N), phosphorus (P), potassium (K), calcium (Ca), magnesium (Mg), sulfur (S), iron (Fe), manganese (Mn), zinc (Zn), copper (Cu), boron (B), molybdenum (Mo), and chlorine (Cl), must be available in adequate concentrations and balanced ratios for optimal plant health and yield (White and Brown, 2010). Mineral nutrition plays a fundamental role in plant growth, development, and stress responses (Tripathi et al., 2022). The availability, mobility, and uptake of essential minerals are influenced by multiple environmental factors, including light intensity, soil temperature, moisture content, and microbial activity (Marschner, 2012), all of which can be modified under agrivoltaic systems. Recent studies have begun to explore the effects of agrivoltaic systems on soil properties and nutrient dynamics. Luo et al. (2024) found that agrivoltaic systems significantly improved soil moisture, organic carbon, N, P, and K nutrients, microbial biomass, as well as urease activity. However, comprehensive studies specifically examining the interactions between agrivoltaic systems and plant mineral nutrition remain scarce, representing a critical research gap. Hence, this review examined the impact of agrivoltaic systems on plant nutrient dynamics, focusing on how the modified microclimate affects nutrient uptake, allocation, and overall plant physiology. Also, the potential effects on individual nutrients were examined, discussing crop specific considerations, as well as identify key knowledge gaps and research opportunities in this emerging field.

IMPACT OF AGRIVOLTAIC MICROCLIMATE ON NUTRIENTS UPTAKE

Water productivity can sometimes increase underneath AV systems as the panels can reduce evapotranspiration by 14–29% and save up to 20% on irrigation water as a result of shading (Marrou et al., 2013). This water conservation aspect is particularly significant for nutrient uptake, as water availability directly influences nutrient mobility in soil and absorption by plant roots (Marschner, 2011). The altered soil moisture regime under agrivoltaic systems can enhance the diffusion of nutrients to the root surface, particularly for mobile nutrients like nitrate (Fageria et al., 2008; Dobermann et al., 2007). In addition, soil microbial biomass represents the living component of soil organic matter and plays a vital role in nutrient cycling and soil fertility; agrivoltaic systems have been shown to enhance microbial biomass carbon, nitrogen, and phosphorus, indicating improved microbial activity as well as soil health under these systems, which may ultimately contribute to increased nutrient uptake by plants (Luo et al., 2024). On the other hand, the shading provided by solar panels typically reduces maximum daytime temperatures while having minimal effects on minimum temperatures (Thum et al., 2025). The reduced temperature extremes under agrivoltaic systems can prevent stress induced disruptions to nutrient transport systems within plants, maintaining more efficient uptake even during challenging weather conditions. Several studies report that high temperatures reduce nutrient uptake in plants by impairing root function and disrupting the expression as well as activity of key mineral transporter proteins, leading to decreased concentrations of essential nutrients (Giri et al., 2017; Mishra et al., 2023). A study on 58 cacao genotypes grown under 50% and 80% shade showed that the concentrations of most macronutrients such as nitrogen, calcium, and magnesium as well as all micronutrients increased under 80% shade, while phosphorus and potassium concentrations decreased under the same conditions. However, the microclimate impacts are not easily generalizable, as they can vary significantly between different agrivoltaics configuration of agrivoltaics, even within the same climate. Panel height, density, orientation, and transparency all influence the microclimate created beneath them, resulting in complex interactions with plant nutrient acquisition mechanisms (Dupraz et al., 2011).

IMPACT OF AGRIVOLTAIC MICROCLIMATE ON NUTRIENT AND BIOMASS ALLOCATION

Shading induced by agrivoltaic systems may result in yield reductions for some crops; however, under specific climatic conditions, it can offer protective benefits that enhance crop performance or improve quality attributes (Asa'a et al., 2024). The altered light environment in agrivoltaic systems significantly impacts how plants allocate nutrients within their tissues. Plants plastically modify how they distribute biomass between leaves and roots (L/R, g g^{-1}), as well as adjust leaf mass per area (LMA, g m^{-2}) and leaf nitrogen content per unit area (N_{area}, g N m^{-2}), in response to environmental factors like light intensity and nutrients supply such as nitrogen (poorter et al., 2012) by altering these allocation patterns to optimize their relative growth rate (RGR, g g^{-1} d^{-1}) (Sugiura and Tateno, 2011). Light intensity not only directly affects plant morphology, but also acts as a regulatory signal that interacts with endogenous plant hormones involved in resource allocation. Endogenous levels of cytokinins (CKs) and gibberellins (GAs) are influenced by nitrogen availability, while GAs also respond to environmental variables such as light intensity, and are transported from the leaves to the shoot apex to regulate how plants allocate biomass between roots and shoots, as well as alter leaf mass per area (LMA) and the leaf area ratio (LAR), ultimately affecting nitrogen uptake, Rubisco production, and the net assimilation rate (NAR) (Sugiura et al., 2016). While nutrient allocation refers to how plants distribute absorbed nutrients among organs and tissues to support metabolic processes and development, biomass allocation such as the distribution of growth between roots and shoots can be considered a structural outcome and one component of overall nutrient allocation strategies. In parallel with these internal physiological adjustments, agrivoltaic systems have also been shown to significantly impact soil organic carbon (SOC) content and overall soil quality. Studies in dry-hot valley eco-fragile areas have demonstrated a noteworthy enrichment in SOC within agrivoltaic systems. For instance, under-panel ryegrass cultivation showed a 14.94% increase in SOC compared to control areas (Luo et al., 2024). Similarly, in degraded grassland ecosystems, PV array areas exhibited a 17.93% increase in soil carbon storage (Zhang et al., 2024). This enrichment is often attributed to the deposition of higher-assimilation products into the soil through enhanced plant growth and biomass production under favorable microclimatic conditions (Nie et al., 2012). However, the impact on SOC can vary depending on the specific environmental context and duration of the AV system's operation. Contrasting results have been reported, with some studies indicating no significant changes in physicochemical properties. Conversely, a study in a natural grassland ecosystem in coastal Italy found a significant decrease of 61% in soil organic matter and 50% in total nitrogen beneath PV panels after 7 years, alongside reduced soil enzyme activity (Moscatelli et al., 2022). These varied outcomes underscore the complex interplay between shading, crop type, and long-term ecological processes. On the other hand, soil moisture under intense light restricts the vertical growth of seedlings, ultimately impacting their development and survival, thus, seedlings allocate a greater proportion of photosynthetic products to their root systems, promoting enhanced root development that facilitates water and nutrient absorption; in contrast, the seedlings exposed to low light conditions allocate biomass to aboveground structures, thereby improving their capacity for light capture (Walters et al., 1993; Kaelke et al., 2001; Kelly et al., 2015; Tang et al., 2015). Plants adaptively allocate more biomass to shoots under limited above ground resources like light or CO_2, and to roots when nutrients or water are scarce, in order to optimize access to the most limiting resource (Poorter and Nagel, 2000). Similarly, under low light conditions, freshwater macrophytes Myriophyllum spicatum and Elodea canadensis allocated more biomass to shoots over roots, showed lower carbon-to-nitrogen ratios, reduced nitrogen use efficiency, and shifted carbon away from secondary metabolites toward growth, reflecting a coordinated adjustment in nutrient allocation to optimize performance in shaded environments (Cronin and Lodge, 2003), and in line with that, mono seedlings grew taller and had larger stems, more leaves, greater leaf area, and higher dry weight under 75% light, while A. pseudosieboldianum performed better at 55% light (Zhang et al., 2022). This approach recognizes that nutrient allocation is influenced by light intensity, which is altered by the presence and configuration of solar panels in agrivoltaic systems.

THE IMPACT OF MINERALS ON PHOTOSYNTHESIS AS INFLUENCED BY AGRIVOLTAIC MICROCLIMATE

One key element that influences plant growth is light (Hatamian and Salehi, 2017; Khawlhring et al., 2012). Light is absorbed by chlorophylls and other pigments that are present in leaves and different part of plants as well as used for photosynthesis to produce glucose and oxygen. Low light levels cause insufficient ATP production for the biosynthesis of carbohydrates and fixation of carbon, which inhibits plant development (Shao et al., 2014). As light intensity rises, photosynthesis proceeds at a linear pace. The expansion of the absorption rate levels off as light intensity increases until a specific light saturation point is reached (Trommsdorf et al., 2022). The rate of photosynthesis remains constant despite additional increases in light intensity because light harvesting reactions have a limited capacity (Chapin et al., 2011). The underlying premise of all these techniques is that plants have an internal light saturation threshold that photosynthesis stabilizes at, and that they only utilize a portion of the solar spectrum to develop (Honsberg et al., 2021; Riaz et al., 2022). This suggests that agrivoltaic systems could be compatible with certain crop species that do not require high light intensities and can reach their light saturation point even under the reduced irradiance beneath solar panels. Yamori, (2016) reported that C4 pathway plants are typically less efficient in low light conditions, as an additional ATP for the C4 cycle cannot be sufficiently supplied, causing C4 plants to perform worse than C3 species under such environments. Such crops may continue to photosynthesize efficiently under partial shading, making them suitable candidates for cultivation within agrivoltaic setups.

Photosynthesis, the process by which plants convert light energy into chemical energy, is intricately linked with nutrient uptake and utilization. Both macronutrients (e.g., nitrogen, phosphorus, potassium, calcium, magnesium, sulfur) and micronutrients (e.g., iron, zinc, manganese) are indispensable for overall plant growth and development, playing vital roles in physiological functions such as photosynthesis, respiration, and general growth (Ferreira et al., 2023). Plants require macronutrients in large quantities and micronutrients in lower quantities to perform vital physiological functions like photosynthesis, respiration, and growth, ensuring an adequate and balanced availability of these nutrients in the soil is crucial for supporting healthy plant development (Karthika et al., 2018). This strong integration implies a direct causal link: the efficiency and capacity of the photosynthetic machinery are fundamentally constrained by the adequate supply and proper balance of these specific mineral nutrients. When soil nutrient availability is low, plants exhibit distinct visible symptoms. For instance, shortages of N, K, Mg, and Fe often cause leaves to turn yellow, whereas deficiencies in nitrogen, P, and Mg can lead to a reddish-purple coloration (Nam et al., 2021; De Bang et al., 2021; Jezek et al., 2023; Lu et al., 2020; Bell, 2023). Without them, the very structures and enzymes required for photosynthesis cannot function optimally. Any environmental alteration, such as the modified light environment in agrivoltaic systems, that affects a plant's ability to acquire or utilize these essential nutrients will inevitably have a profound impact on its photosynthetic efficiency and overall productivity. This underscores the critical need to meticulously monitor and manage the nutritional status of crops within agrivoltaic setups to ensure optimal plant performance, extending beyond merely managing light conditions.

IMPACT OF SHADING ON PLANT ELEMENTAL COMPOSITION

While partial shading in agrivoltaic systems provides beneficial microclimatic conditions, it also significantly affects how plants absorb, process, and allocate essential mineral nutrients. These effects are complex and depend on the specific nutrient, plant species, as well as the unique environmental changes created by the configuration of agrivoltaics. Given the limited number of studies directly addressing nutrient-specific responses to shading under agrivoltaic systems, this section focuses on the potential effects of altered light conditions on the uptake and dynamics of selected essential mineral elements.

NITROGEN

Nitrogen (N) is a vital mineral nutrient for plants, serving as a fundamental building block of proteins, nucleic acids, phospholipids, chlorophyll, hormones, vitamins, and alkaloids (Wand et al., 2024). Its uptake and distribution can vary under shaded environments, with responses influenced by light intensity, plant species, and growing conditions. Studies on soybeans indicate that shade can lead to reduced nitrate reductase activity and chlorophyll concentration in leaves, thereby limiting nitrogen assimilation and potentially affecting overall plant growth and seed nitrogen accumulation (Nacer et al., 2011). This suggests that prolonged or intense shading may further impair the plant's capacity to process and translocate nitrogen efficiently, ultimately constraining overall productivity. Within an agrivoltaic microclimate, lettuce plants grown under higher light exposure accumulated more nitrate compared to those grown under shaded conditions. The lowest nitrate concentration (29.47 mg/kg) was recorded in plants that received initial fertilization, were grown in shade, and irrigated at 100%, while the highest value (31.23 mg/kg) was found in plants with the same fertilization level, exposed to more light, and irrigated at 50% (Khudhair et al., 2024).

PHOSPHORUS

Shading has been shown to influence phosphorus dynamics in plants, though its effects can vary depending on the cropping system and plant-microbe interactions. In intercropping systems, the wheat grown under shaded conditions exhibited elevated shoot phosphorus concentrations, possibly due to reduced growth rates and dilution effects, or altered root competition and uptake dynamics (Whitehead and Isaac, 2012). Conversely, in mycorrhizal plants such as Medicago truncatula, short-term shading led to a sharp reduction in phosphorus translocation to the shoots, accompanied by phosphorus accumulation in the roots, likely within fungal tissues (Konvalinková et al., 2015). This contrast suggests that while shading may enhance phosphorus concentration in some plants under specific systems, it can also disrupt phosphorus allocation in the plants reliant on mycorrhizal symbiosis.

POTASSIUM

Potassium (K) is a vital nutrient involved in numerous biochemical and physiological processes that regulate plant development and metabolic activity (Wang et al., 2013). Potassium supports NADPH production for photosynthesis as well as facilitates the transport of metabolites, minerals, hormones, and water; thus, its deficiency can severely impair the vascular transport in plants (Kumari et al., 2015). Light intensity influences both the uptake and utilization of potassium in plants (Song et al., 2020). For instance, in greenhouse grown cucumber, higher light intensities (e.g., 240 $\mu mol\ m^{-2}\ s^{-1}$) have been shown to increase potassium content compared to lower intensities (120 $\mu mol\ m^{-2}\ s^{-1}$) (Grygoray et al., 2015). Cucumber and corn show increased potassium uptake with longer periods of light exposure (Xiong-song et al., 2004; Li and Liu, 2013). The uptake and accumulation of potassium in plants are influenced not only by light intensity but also by light wavelength; however, these effects can differ among plant species (Kim et al., 2020). In a study on ten leafy vegetables including green and red lettuce, lamb's lettuce, mizuna, swiss chard, red chard, spinach, rocket, chicory, and tatsoi plants grown under lower light intensity (200–400 $\mu mol\ m^{-2}\ s^{-1}$) exhibited higher leaf potassium content and greater dry matter accumulation compared to those exposed to higher light levels (800–1200 $\mu mol\ m^{-2}\ s^{-1}$) (Colonna et al., 2016). These findings suggest that agrivoltaic shading can influence potassium accumulation, potentially benefiting leafy greens, though these species specific effects necessitate tailored optimization of crop selection and management within such systems.

MAGNESIUM

Magnesium (Mg) is the second most prevalent cation in plants and plays a critical role in various physiological and biochemical functions, such as photosynthesis, enzyme activation, as well as the synthesis of nucleic acids and proteins (Chen et al., 2018). Magnesium serves as the central atom in the chlorophyll molecule and acts as a cofactor for many enzymes essential to photosynthesis and metabolic processes (de Sousa Ferreira et al., 2023). Under shaded conditions, leaves contain more chlorophyll per unit leaf weight than sun-exposed leaves; however, at equal magnesium concentrations, the proportional reduction in chlorophyll due to magnesium deficiency is similar in both, resulting in a higher percentage of leaf magnesium being bound to chlorophyll in shade leaves (up to 57%) compared to sun leaves (up to 37%) (Dorenstouter et al., 1985). Studies on *Phyllanthus niruri* have shown that moderate shading (60%) enhances magnesium uptake, while heavy shading (95%) significantly reduces it, indicating that excessive shade can impair magnesium acquisition (Hanudin et al., 2012). Similarly, in *Boesenbergia stenophylla* (jerangau merah), magnesium and potassium uptake were higher under 70% shade than under 90% shade, despite higher chlorophyll levels being observed at the greater shading level. Notably, the plants under 70% shade were taller and accumulated more dry matter, suggesting that moderate shading supports better overall growth and nutrient absorption (Saptu et al., 2021). This evidence indicates that while extreme light reduction from agrivoltaic systems can hinder magnesium uptake, moderate shading levels appear to either maintain or even enhance magnesium absorption in certain plant species.

CALCIUM

Calcium (Ca^{2+}), an essential macronutrient for plant growth, yield, and quality, is transported with water through root channels to the xylem via apoplastic or symplastic pathways, then moves to shoots driven by transpiration and organ growth (Kabir and Díaz-Pérez, 2025). Increased transpiration rates in leaves and fruits may enhance their Ca^{2+} uptake (De Freitas et al., 2013). However, high light intensity raises vapor pressure deficit, boosting leaf transpiration more than fruit transpiration, which reduces plant water potential and limits the fruit Ca^{2+} uptake (de Freitas et al., 2011). Hence, shading the canopy to lower light intensity can offset the adverse impact of high light and temperature on Ca^{2+} uptake (Montanaro et al., 2006). In cacao, shading significantly increased shoot calcium concentration, with plants grown under 80% shade exhibiting higher Ca levels than those under 50% shade, although this was accompanied by reduced calcium uptake efficiency due to lower biomass accumulation (Arévalo-Gardini et al., 2021). Similarly, 50% shading in 'Greensleeves' apple increased fruit Ca^{2+} uptake by improving plant water potential and enhancing Ca^{2+} transport to the low-transpiring fruit (de Freitas et al., 2011). These findings suggest that the specific light reduction implemented in agrivoltaic systems could be a viable strategy to enhance calcium accumulation in certain crops, provided that the balance between increased uptake and potential impacts on biomass or physiological disorders is carefully considered.

CONCLUSIONS

In conclusion, agrivoltaic systems present a transformative approach to land use, but their success hinges on a comprehensive understanding of their effects on plant physiology, particularly nutrient dynamics. This review has highlighted that the modified microclimate under solar panels can significantly influence nutrient uptake, allocation, and utilization, with effects varying widely depending on the specific nutrient, crop species, and system design. While moderate shading can enhance the uptake of certain nutrients and improve water use efficiency, it can also pose challenges for nutrient assimilation and biomass allocation. Future research should focus on long-term, field-based studies across diverse climatic conditions and crop types to unravel the complex interactions between agrivoltaic systems and plant mineral nutrition. A deeper understanding of these dynamics is essential for developing best practices for nutrient management in agrivoltaic systems, ultimately s of both food and energy production on the same land.

REFERENCES

1. Al Mamun, M. A., Dargusch, P., Wadley, D., Zulkarnain, N. A., Aziz, A. A. (2022). A review of research on agrivoltaic systems. *Renewable and Sustainable Energy Reviews*, *161*, 112351.
2. Arévalo-Gardini, E., Farfán, A., Barraza, F., Arévalo-Hernández, C. O., Zúñiga-Cernades, L. B., Alegre, J., Baligar, V. C. (2021). Growth, physiological, nutrient-uptake-efficiency and shade-tolerance responses of cacao genotypes under different shades. *Agronomy*, *11*(8), 1536.
3. Asa'a, S., Reher, T., Rongé, J., Diels, J., Poortmans, J., Radhakrishnan, H. S.,... Daenen, M. (2024). A multidisciplinary view on agrivoltaics: Future of energy and agriculture. *Renewable and Sustainable Energy Reviews*, *200*, 114515.
4. Barron-Gafford, G. A., Pavao-Zuckerman, M. A., Minor, R. L., Sutter, L. F., Barnett-Moreno, I., Blackett, D. T.,... Macknick, J. E. (2019). Agrivoltaics provide mutual benefits across the food–energy–water nexus in drylands. *Nature Sustainability*, *2*(9), 848–855.
5. Bell, R. (2023). Diagnosis and prediction of deficiency and toxicity of nutrients. In *Marschner's mineral nutrition of plants* 477–495. Academic Press.
6. Chapin III, F. S., Matson, P. A., Vitousek, P. M. (2011). The ecosystem concept. In *Principles of terrestrial ecosystem ecology* 3–22. New York, NY: Springer New York.
7. Chen, Z. C., Peng, W. T., Li, J., Liao, H. (2018, February). Functional dissection and transport mechanism of magnesium in plants. In *Seminars in cell & developmental biology 74*, 142–152. Academic Press.
8. Cronin, G., Lodge, D. M. (2003). Effects of light and nutrient availability on the growth, allocation, carbon/nitrogen balance, phenolic chemistry, and resistance to herbivory of two freshwater macrophytes. *Oecologia*, *137*(1), 32–41.
9. De Bang, T. C., Husted, S., Laursen, K. H., Persson, D. P., Schjoerring, J. K. (2021). The molecular–physiological functions of mineral macronutrients and their consequences for deficiency symptoms in plants. *New Phytologist*, *229*(5), 2446–2469.

10. De Freitas, S. T., do Amarante, C. V., Dandekar, A. M., Mitcham, E. J. (2013). Shading affects flesh calcium uptake and concentration, bitter pit incidence and other fruit traits in "Greensleeves" apple. *Scientia Horticulturae*, *161*, 266–272.
11. de Freitas, S. T., Shackel, K. A., Mitcham, E. J. (2011). Abscisic acid triggers whole-plant and fruit-specific mechanisms to increase fruit calcium uptake and prevent blossom end rot development in tomato fruit. *Journal of Experimental Botany*, *62*(8), 2645–2656.
12. de Sousa Ferreira, L., de Souza Oliveira, V., de Paula Marchiori, J. J., Ferreira, T. C., Bernabé, A. C. B., Boone, G. T. F.,... Carriço, E. (2023). The nutrient magnesium in soil and plant: a review. *Int. J. Plant Soil Sci*, *35*(8), 136–144.
13. Dobermann, A. (2007). Nutrient use efficiency–measurement and management.
14. Dorenstouter, H., Pieters, G. A., Findenegg, G. R. (1985). Distribution of magnesium between chlorophyll and other photosynthetic functions in magnesium deficient "sun"; and "shade"; leaves of poplar. *Journal of Plant Nutrition*, *8*(12), 1089–1101.
15. Fageria, N. K., Baligar, V. C., Li, Y. C. (2008). The role of nutrient efficient plants in improving crop yields in the twenty first century. *Journal of plant nutrition*, *31*(6), 1121–1157.
16. Giri, A., Heckathorn, S., Mishra, S., Krause, C. (2017). Heat stress decreases levels of nutrient-uptake and-assimilation proteins in tomato roots. *Plants*, *6*(1), 6.
17. Grygoray, E. E., Tabalenkova, G. N., Dalke, I. V., Golovko, T. K. (2015). Mineral nutrition and productivity of the greenhouse cucumber crop depending on lighting. *Agrokhimiya*, *4*, 74–79.
18. Hanudin, E., Wismarini, H., Hertiani, T., Sunarminto, B. H. (2012). Effect of shading, nitrogen and magnesium fertilizer on phyllanthin and total flavonoid yield of *Phyllanthus niruri* in Indonesia soil. *Journal of Medicinal Plants Research*, *6*(30), 4586–4592.
19. Hassanpour Adeh, E., Selker, J. S., Higgins, C. W. (2018). Remarkable agrivoltaic influence on soil moisture, micrometeorology and water-use efficiency. *PloS one*, *13*(11), e0203256.
20. Hatamian, M., Salehi, H. (2017). Physiological characteristics of two rose cultivars (*Rosa hybrida* L.) under different levels of shading in greenhouse conditions.
21. Honsberg, C. B., Sampson, R., Kostuk, R., Barron-Gafford, G., Bowden, S., Goodnick, S. (2021, June). Agrivoltaic modules co-designed for electrical and crop productivity. In *2021 IEEE 48th Photovoltaic Specialists Conference (PVSC)* 2163–2166. IEEE.
22. Jezek, M., Allan, A. C., Jones, J. J., Geilfus, C. M. (2023). Why do plants blush when they are hungry?. *New Phytologist*, *239*(2), 494–505.
23. Kabir, M. Y., Díaz-Pérez, J. C. (2025). Calcium route in the plant and blossom-end rot incidence. *Horticulturae*, *11*(7), 807.
24. Kaelke, C. M., Kruger, E. L., Reich, P. B. (2001). Trade-offs in seedling survival, growth, and physiology among hardwood species of contrasting successional status along a light-availability gradient. *Canadian Journal of Forest Research*, *31*(9), 1602–1616.
25. Karthika, K. S., Rashmi, I., Parvathi, M. S. (2018). Biological functions, uptake and transport of essential nutrients in relation to plant growth. In *Plant nutrients and abiotic stress tolerance* 1–49. Singapore: Springer Singapore.
26. Kelly, J. W. G., Landhäusser, S. M., Chow, P. S. (2015). The impact of light quality and quantity on root-to-shoot ratio and root carbon reserves in aspen seedling stock. *New Forests*, *46*(4), 527–545.
27. Khawlhring, N., Thanga, J. L., Lalnunmawia, F. (2012). Plant performance of Anthurium andreanum as affected by shade conditions and different conventional nutrient sources. *J. Hortic. For*, *4*(2), 22–26.
28. Khudhair, M. A., Sahib, M. R., AL-Agele, H. A. (2024). Interactive effects of agrivoltaic shading, irrigation, and biofertilizers on the chemical composition of Lettuce Leaves (*Lactuca sativa* L.): Pengaruh Interaktif Peneduh Agrivoltaic, Irigasi, dan Pupuk Hayati terhadap Komposisi Kimia Daun Selada (*Lactuca sativa* L.). *Indonesian Journal on Health Science and Medicine*, *1*(3), 10–21070.
29. 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.
30. Konvalinková, T., Püschel, D., Janoušková, M., Gryndler, M., Jansa, J. (2015). Duration and intensity of shade differentially affects mycorrhizal growth-and phosphorus uptake responses of Medicago truncatula. *Frontiers in plant science*, *6*, 65.
31. Kumari, A., Das, P., Parida, A. K., Agarwal, P. K. (2015). Proteomics, metabolomics, and ionomics perspectives of salinity tolerance in halophytes. *Frontiers in Plant Science*, *6*, 537.
32. Li, H. Y., Liu, H. H. (2013). Effects of supplementary illumination at night on hormones content and nutrient absorption of cucumber seedlings. *Chin. Agric. Sci. Bull*, *29*, 74–78.
33. Lu, Z., Ren, T., Li, J., Hu, W., Zhang, J., Yan, J.,... Lu, J. (2020). Nutrition-mediated cell and tissue-level anatomy triggers the covariation of leaf photosynthesis and leaf mass per area. *Journal of experimental botany*, *71*(20), 6524–6537.

34. Luo, J., Luo, Z., Li, W., Shi, W., Sui, X. (2024). The early effects of an agrivoltaic system within a different crop cultivation on soil quality in dry–hot valley eco-fragile areas. *Agronomy*, *14*(3), 584.
35. Gorjian, S., Campana, P. E. (Eds.). (2022). *Solar energy advancements in agriculture and food production systems*. Academic Press.
36. Marrou, H., Dufour, L., Wery, J. (2013). How does a shelter of solar panels influence water flows in a soil–crop system?. *European Journal of Agronomy*, *50*, 38–51.
37. Marrou, H., Guilioni, L., Dufour, L., Dupraz, C., Wery, J. (2013). Microclimate under agrivoltaic systems: Is crop growth rate affected in the partial shade of solar panels?. *Agricultural and Forest Meteorology*, *177*, 117–132.
38. Marschner, H. (2012). *Marschner's mineral nutrition of higher plants*. Academic press.
39. Mishra, S., Spaccarotella, K., Gido, J., Samanta, I., Chowdhary, G. (2023). Effects of heat stress on plant-nutrient relations: An update on nutrient uptake, transport, and assimilation. *International Journal of Molecular Sciences*, *24*(21), 15670.
40. Montanaro, G., Dichio, B., Xiloyannis, C., Celano, G. (2006). Light influences transpiration and calcium accumulation in fruit of kiwifruit plants (*Actinidia deliciosa* var. deliciosa). *Plant Science*, *170*(3), 520–527.
41. Moscatelli, M. C., Marabottini, R., Massaccesi, L., Marinari, S. (2022). Soil properties changes after seven years of ground mounted photovoltaic panels in Central Italy coastal area. *Geoderma Regional*, *29*, e00500.
42. Nacer, B., James R, S., Anne M, G., Daniel K, F., Alemu, M. (2011). Effect of shade on seed protein, oil, fatty acids, and minerals in soybean lines varying in seed germinability in the early soybean production system. *American Journal of Plant Sciences*, *2012*.
43. Nam, H. I., Shahzad, Z., Dorone, Y., Clowez, S., Zhao, K., Bouain, N.,... Rouached, H. (2021). Interdependent iron and phosphorus availability controls photosynthesis through retrograde signaling. *Nature Communications*, *12*(1), 7211.
44. Nie, S. A., Zhou, P., Ge, T. D., Tong, C. L., Xiao, H. A., Wu, J. S., Zhang, Y. Z. (2012). Quantifying rice (*Oryza sativa* L.) photo-assimilated carbon input into soil organic carbon pools following continuous 14C labeling. *Huan Jing ke Xue= Huanjing Kexue*, *33*(4), 1346–1351.
45. Poorter, H., Nagel, O. (2000). The role of biomass allocation in the growth response of plants to different levels of light, CO_2, nutrients and water: a quantitative review. *Functional Plant Biology*, *27*(12), 1191–1191.
46. Poorter, H., Niklas, K. J., Reich, P. B., Oleksyn, J., Poot, P., Mommer, L. (2012). Biomass allocation to leaves, stems and roots: meta-analyses of interspecific variation and environmental control. *New phytologist*, *193*(1), 30–50.
47. Riaz, M. H., Imran, H., Alam, H., Alam, M. A., Butt, N. Z. (2022). Crop-specific optimization of bifacial PV arrays for agrivoltaic food-energy production: The light-productivity-factor approach. *IEEE Journal of Photovoltaics*, *12*(2), 572–580.
48. Saptu, T., Abdullah, N. A. P., Kundat, F. R., Toyat, A. J., Endawie, C. G., Saleh, G. (2021). Accumulation of total nutrients, dry matter and phytochrome content in Boesenbergia stenophylla RM Smith as affected by different light conditions. *Journal of Plant Stress Physiology*, *7*, 10–16.
49. Shao, Q., Wang, H., Guo, H., Zhou, A., Huang, Y., Sun, Y., Li, M. (2014). Effects of shade treatments on photosynthetic characteristics, chloroplast ultrastructure, and physiology of *Anoectochilus roxburghii*. *PloS one*, *9*(2), e85996.
50. Song, J., Huang, H., Hao, Y., Song, S., Zhang, Y., Su, W., Liu, H. (2020). Nutritional quality, mineral and antioxidant content in lettuce affected by interaction of light intensity and nutrient solution concentration. *Scientific reports*, *10*(1), 2796.
51. Sugiura, D., & Tateno, M. (2011). Optimal leaf-to-root ratio and leaf nitrogen content determined by light and nitrogen availabilities. *PloS one*, *6*(7), e22236.
52. Sugiura, D., Kojima, M., Sakakibara, H. (2016). Phytohormonal regulation of biomass allocation and morphological and physiological traits of leaves in response to environmental changes in Polygonum cuspidatum. *Frontiers in Plant Science*, *7*, 1189.
53. Tang, H., Hu, Y. Y., Yu, W. W., Song, L. L., Wu, J. S. (2015). Growth, photosynthetic and physiological responses of Torreya grandis seedlings to varied light environments. *Trees*, *29*(4), 1011–1022.
54. Thum, C. H., Okada, K., Yamasaki, Y., Kato, Y. (2025). Impacts of agrivoltaic systems on microclimate, grain yield, and quality of lowland rice under a temperate climate. *Field Crops Research*, *326*, 109877.
55. Tripathi, R., Tewari, R., Singh, K. P., Keswani, C., Minkina, T., Srivastava, A. K.,... Sansinenea, E. (2022). Plant mineral nutrition and disease resistance: A significant linkage for sustainable crop protection. *Frontiers in Plant science*, *13*, 883970.
56. Walters, M. B., Kruger, E. L., Reich, P. B. (1993). Growth, biomass distribution and CO_2 exchange of northern hardwood seedlings in high and low light: relationships with successional status and shade tolerance. *Oecologia*, *94*(1), 7–16.
57. Wang, M., Zheng, Q., Shen, Q., Guo, S. (2013). The critical role of potassium in plant stress response. *International journal of molecular sciences*, *14*(4), 7370–7390.

58. Wang, Q., Li, S., Li, J., Huang, D. (2024). The utilization and roles of nitrogen in plants. *Forests*, *15*(7), 1191.
59. Weselek, A., Ehmann, A., Zikeli, S., Lewandowski, I., Schindele, S., Högy, P. (2019). Agrophotovoltaic systems: applications, challenges, and opportunities. A review. *Agronomy for sustainable development*, *39*(4), 35.
60. White, P. J., Brown, P. (2010). Plant nutrition for sustainable development and global health. *Annals of botany*, *105*(7), 1073–1080.
61. Whitehead, M., Isaac, M. E. (2012). Effects of shade on nitrogen and *phosphorus acquisition* in cereal-legume intercropping systems. *Agriculture*, *2*(1), 12–24.
62. Xiong-song, S. U. N., Xiao-liang, L. U., Zhao-xia, D. O. N. G. (2004). Effects of photopenod on growth and nutrient uptake in silage corn. *Journal of South China Agricultural University*, *25*(Z2).
63. Yamori, W. (2016). Photosynthetic response to fluctuating environments and photoprotective strategies under abiotic stress. *Journal of Plant Research*, *129*(3), 379–395.
64. Zhang, B., Zhang, R., Li, Y., Wang, S., Zhang, M., Xing, F. (2024). Deploying photovoltaic arrays in degraded grasslands is a promising win-win strategy for promoting grassland restoration and resolving land use conflicts. *Journal of Environmental Management*, *349*, 119495.
65. Zhang, J., Ge, J., Dayananda, B., Li, J. (2022). Effect of light intensities on the photosynthesis, growth and physiological performances of two maple species. *Frontiers in plant science*, *13*, 999026