HortScience 60(8):1276–1281. 2025. https://doi.org/10.21273/HORTSCI18630-25

Photosynthetic Activity in Highbush Blueberry Plants: A Review

Md Zohurul Kadir Roni, Marlon Retana-Cordero, Sarah da Silva Benevenute, Cecilia Rubert Heller, Lauren Goldsby, Valentina Goles Varela, and Gerardo H. Nunez

Horticultural Sciences Department, Institute of Food and Agricultural Sciences, University of Florida, Gainesville, FL 32611-0690, USA

Keywords. CO_2 concentrations, light, photosynthesis activity, single leaf

Abstract. **This comprehensive review examined leaf photosynthetic rates, research methodologies, and existing knowledge gaps in highbush blueberry (*Vaccinium corymbosum* interspecific hybrids) research through a systematic and quantitative analysis of scientific literature spanning the past six decades. Studies of photosynthesis in northern and southern highbush blueberry were reviewed, revealing a lack of consensus on environmental set points for studying blueberry photosynthesis. Research of northern highbush blueberry has been more prevalent than that of its southern counterpart. According to the literature, northern highbush blueberry exhibits higher leaf photosynthetic rates than that of southern highbush blueberry, but both blueberry types exhibit lower photosynthetic rates than those of other fruit crops. Additionally, there is no evidence that selective breeding has increased blueberry leaf photosynthetic rates. Additional research is needed to understand and optimize highbush blueberry photosynthesis in agricultural settings.**

Photosynthesis is the source of all carbon available for plant growth, defense, and productivity. Thus, photosynthesis measurements represent an invaluable source of information for horticulturists, plant biologists, and plant breeders. Nevertheless, photosynthesis research is costly both in terms of time and resources. Therefore, little is known about the photosynthetic activity of several important crops. Highbush blueberry (*Vaccinium corymbosum* interspecific hybrids) is one of those crops. Despite the popularity of this fruit crop and its cosmopolitan cultivation (Fang et al. 2020), our understanding of the factors that affect blueberry photosynthesis is limited. This review aimed to explore photosynthesis research of highbush blueberry plants over the past six decades by drawing upon a systematic and quantitative analysis of literature.

Most blueberry P_n research focuses on plant responses to environmental factors or agronomic practices. For example, nitrogen nutrition (Cárdenas-Navarro et al. 2024), light intensity, carbon dioxide (CO_2) concentration (Reyes-Díaz et al. 2016; Wen et al. 2022), temperature (Hao et al. 2019), soil pH (Jiang et al. 2019), pathogen attacks (Hilário et al. 2023), growing substrates (Viencz et al. 2021; Yang and Lin 2025), and water stress (Rho et al. 2012) affect blueberry P_n. Nevertheless, there is no consensus about instrumentation set points used for this research. Therefore, this review also aimed to provide a set of recommendations to standardize blueberry photosynthesis research and allow aggregation and meta-analyses in the future.

Received for publication 27 Mar 2025. Accepted for publication 16 May 2025.

Published online 11 Jul 2025.

The authors declare no conflict of interest.

The authors are not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

G.H.N. is the corresponding author. E-mail: g.nunez@ufl.edu.

Materials and Methods

Methodology of literature collection. We surveyed peer-reviewed articles available in Clarivate's Web of Science. Two sets of keywords were used: ["blueberry" AND "photosynthesis"] and ["blueberry" AND "photosynthetic"]. Literature data were collected from Aug 1965 to Dec 2024. This review focused on the primary literature of studies of highbush blueberry. Both northern highbush blueberry (NHB) and southern highbush blueberry (SHB) were included. Publications that focused on lowbush, rabbiteye, and wild blueberry were excluded. This search returned 243 publications; of these, 56 duplicate articles were removed (Fig. 1). A total of 68 relevant peer-reviewed articles were selected to be discussed in this review. When comparisons were made, the Kruskal-Wallis nonparametric analysis of variance ($\alpha = 0.05$) was used. Analyses and illustrations were performed in R (version 4.4.2; R Cor Development Team 2021).

Leaf P_n Range for Healthy Plants

Blueberry P_n measurements between 1986 to 2000 were available (Fig. 2). Notably, no published literature between 2000 and 2010 was found. However, from 2010 to 2023, a substantial increase in reports of blueberry P_n occurred (Fig. 2). From 1986 to 2016, research of blueberry photosynthesis focused on NHB cultivars, but few studies reported SHB (Fig. 2). After 2017, however, research of SHB photosynthesis became more prevalent, likely because of the increasing cultivation of this blueberry type in tropical and subtropical regions (Fang et al. 2020).

With the exception of one report, all highbush blueberry P_n was less than 20 $\mu mol \cdot m^{-2} \cdot s^{-1}$ (Supplemental File 1), which is lower than that of other fruit crops like apple (Fu et al. 2015), pear (Zhao et al. 2022), peach (Jiménez et al. 2020), strawberry (Lalk et al. 2023), and citrus (Nebauer et al. 2013) (Supplemental Fig. 1). In general, NHB exhibited higher leaf P_n than that of SHB, with maximum and minimum P_n values of 27.0 $\mu mol \cdot m^{-2} \cdot s^{-1}$ ('Brigitta') and 0.9 $\mu mol \cdot m^{-2} \cdot s^{-1}$ ('Gulfcoast') for NHB and 16.0 $\mu mol \cdot m^{-2} \cdot s^{-1}$ ('Jewel') and 2.0 $\mu mol \cdot m^{-2} \cdot s^{-1}$ ('Camellia') for SHB (Fig. 2). Blueberry leaf P_n measurements were typically conducted at 400 $\mu mol \cdot mol^{-1}$ CO_2, photosynthetic photon flux density (PPFD) of 800 to 1000 $\mu mol \cdot m^{-2} \cdot s^{-1}$, air temperature of 25 to 30 °C, and 60% to 70% relative humidity (Hao et al. 2019; Smrke et al. 2023).

Blueberry P_n in the literature is almost exclusively obtained from single-leaf measurements of young, fully expanded, and healthy leaves (usually in the second to fifth node) that are fully exposed to solar radiation (Petridis et al. 2020). This practice is consistent with research that suggested blueberry leaf age affects P_n. Older leaves exhibit P_n that is lower than that of recently matured ones (Forsyth and Hall 1965; Long et al. 2024).

Photosynthetic measurements of branches or groups of leaves are still rare in this crop (Retana-Cordero and Nunez 2025). Research of low bush blueberry (*V. angustifolium*) identified chamber size effects that can lead to underestimation of leaf P_n when large cuvettes are used for these measurements (Tasnim and Zhang 2021). It is unknown if this issue is also present in highbush blueberry branches.

Highbush blueberry P_n measurements usually were performed in the morning or at mid-day. Daily P_n curves for several SHB cultivars suggest that steady-state mid-day measurements can be performed between 12:00 and 2:00 PM (Li et al. 2009; Salazar-Gutiérrez et al. 2023) when PPFD is highest. However, mid-day P_n rates might not be the highest daily rate of blueberry (Osorio et al. 2020; Salazar-Gutiérrez et al. 2023). For example, 'Bluecrop' NHB exhibited mid-day photosynthesis depression, which is a phenomenon primarily attributed to stomatal limitations caused by high temperatures and high vapor pressure deficits (Kim et al. 2011; Li et al. 2009). Therefore, researchers should conduct daily response curves before settling on a time of day for survey P_n measurements. The time of the year when P_n measurements are made also appears to be relevant because changes in the timing of seasonal peak photosynthetic activity have been previously reported (Park et al. 2019).

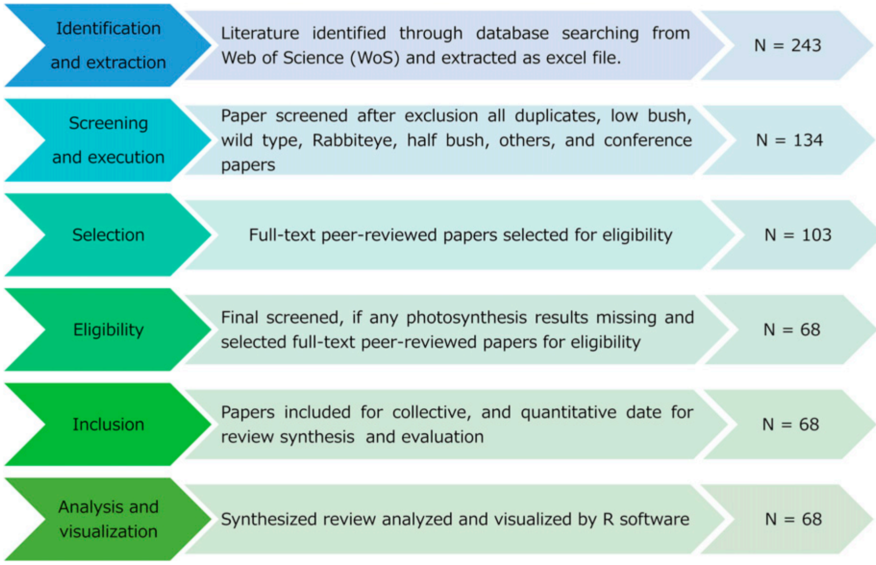

Fig. 1. Overview of the article selection process. N = the number of published literatures. See Supplemental File 1 for data and metadata.

Despite the well-known challenges encountered when performing P_n measurements when cuvette conditions are different from ambient (Haworth et al. 2018), there are no reports of blueberry leaf acclimation times. Therefore, currently, the duration of the necessary leaf acclimation to cuvette conditions in blueberry is unknown. Petridis et al. (2018) and da Silva Benevenute et al. (2025) reported slow stomatal conductance (g_s) responses to a step change in PPFD in several NHB and SHB cultivars. Thus, it is possible that some of the reported instantaneous measurements represent leaves that are not fully acclimated to cuvette conditions, especially if stomata are closed at the start of the measurement. This may explain the wide range of P_n reported for some cultivars (for example, Brigitta NHB). This knowledge gap should be addressed to ensure that accurate P_n measurements are made.

Blueberry leaf P_n varies depending on genotype and environmental factors. Some cultivars exhibited higher P_{nmax} than that of others (Salazar-Gutiérrez et al. 2023), but high leaf P_n rates are not directly reflected in agronomic performance. Additionally, environmental factors like high temperature (Hancock et al. 1992; Lobos and Hancock 2015), water deficit (Ribera-Fonseca et al. 2019), and plant-to-plant competition for light (Strik and Buller 2005) can lead to lower P_n. However, optimal nitrogen fertilization (Swain

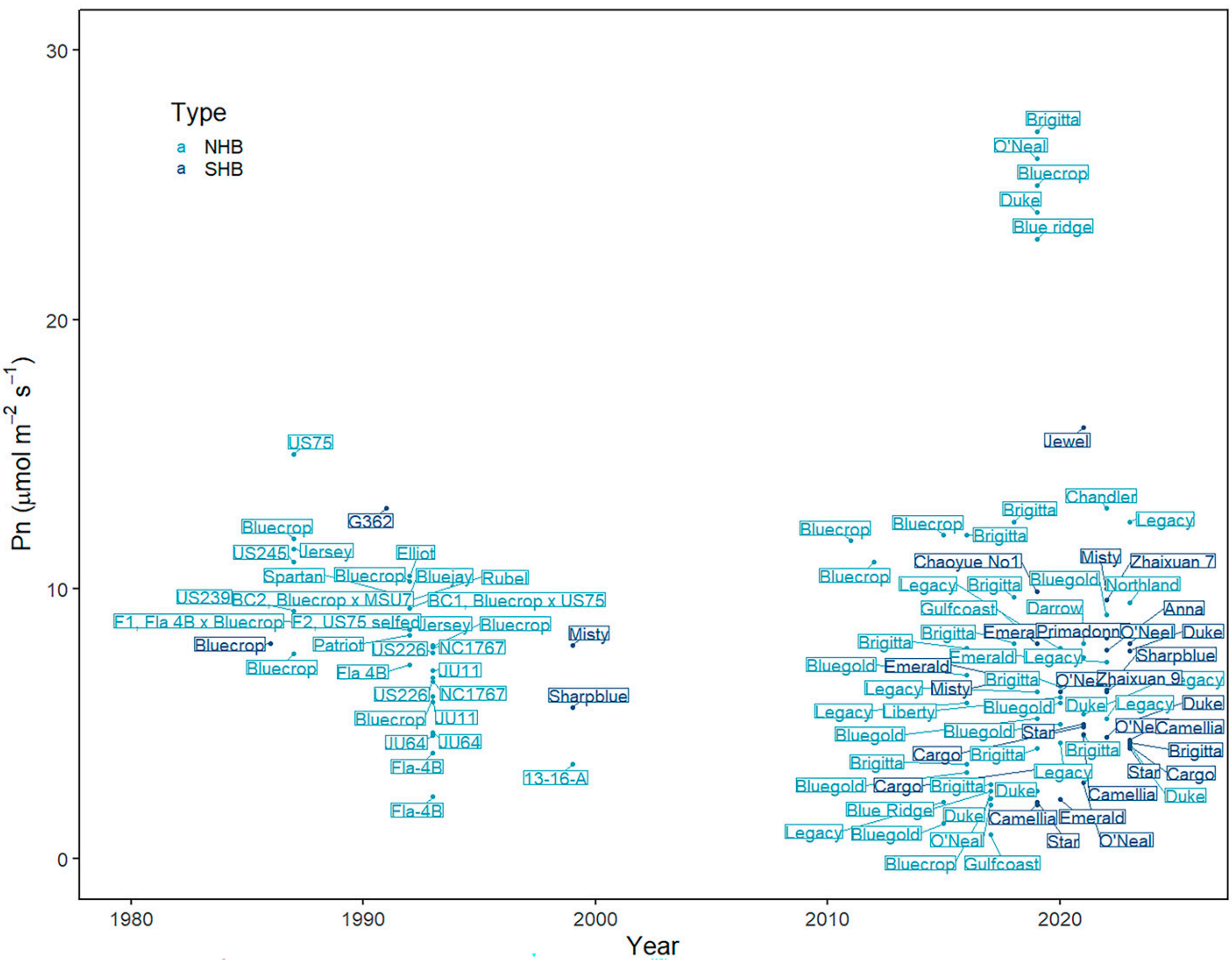

Fig. 2. Single-leaf photosynthetic rates (P_n) of northern highbush blueberry (NHB) and southern highbush blueberry (SHB) cultivars. No study of highbush blueberry P_n was published between 2000 and 2010.

and Darnell 2001), reflective plastic mulches (Muneer et al. 2019; Petridis et al. 2021), and selective pruning (Lee et al. 2015) can increase P_n. Understanding these dynamics is crucial to optimizing blueberry production and enhancing overall photosynthetic efficiency.

Environmental Effects on Leaf P_n

CO_2 effects. Blueberry steady-state P_n measurements are usually conducted with infrared gas analyzers set at CO_2 concentrations of 400 $\mu mol \cdot mol^{-1}$ (Fig. 3A). The P_n correlates linearly with the ambient CO_2 concentration in the range of 150 to 400 $\mu mol \cdot mol^{-1}$ (Davies and Flore 1986). Whenever measurements were made at higher CO_2 concentrations, P_n rates were inflated; therefore, they are not comparable with the literature. High ambient CO_2 concentrations lead to high P_n, especially in crops that perform C3 photosynthesis such as blueberries. Studies that related cuvette CO_2 concentrations to leaf P_n responses indicated that blueberry plants could benefit from cultivation in controlled environments with CO_2 enrichment. In several NHB cultivars, P_n increased rapidly as the intercellular CO_2 concentration increased. However, the rate of P_n increase tapered at intercellular CO_2 concentrations above 250 $\mu mol \cdot mol^{-1}$, presumably because of limitations in the maximum carboxylation (Vc_{max}) efficiency of ribulose 1,5-bisphosphate carboxylase oxygenase (RuBisCO) (Moon et al. 1987; Petridis et al. 2018). The Vc_{max} of blueberry is lower than that of other fruit crops ($P = 0.06$), including apple (Hassan and Ito 2023; Yang et al. 2021), citrus (Hussain et al. 2024; Ribeiro et al. 2009), raspberry (Fernandez 1994), peach (Walcroft et al. 2002), and strawberry (Yu et al. 2023). The Vc_{max} is an important indicator used to determine the photosynthetic capacity and overall productivity of the plant (Lu et al. 2020), including blueberry (Rho et al. 2012; Wu et al. 2022).

Blueberries, like many crops, are experiencing the impacts of a changing planet. Human activity is increasing ambient CO_2 concentrations, especially in urban and peri-urban settings. Single leaf P_n of blueberry plants is likely to increase under CO_2 concentrations higher than 400 $\mu mol \cdot mol^{-1}$. Nevertheless, CO_2 enrichment will likely lead to different higher-order constraints that will hinder productivity, like water or mineral nutrient limitations. Research that examined whole plant responses to CO_2 enrichment is necessary to predict impacts and devise mitigation strategies for sustainable blueberry production in the future.

Light effects. Light plays a crucial role in affecting P_n, plant growth, and survival. The infrared gas analyzer settings ranged between 0 and 2000 $\mu mol \cdot m^{-2} \cdot s^{-1}$ (Fig. 3B). The relationship between light intensity and P_n (light response curves) of only a few blueberry cultivars has been studied. 'Bluecrop' NHB, 'Liberty' NHB, 'Darrow' NHB, 'Duke' NHB, and 'Misty' SHB reach single-leaf light saturation points between 500 $\mu mol \cdot m^{-2} \cdot s^{-1}$ and 600 $\mu mol \cdot m^{-2} \cdot s^{-1}$ (Kim et al. 2011; Petridis et al. 2018, 2020; Rho et al. 2012). Leaf light saturation points of 'Bluecrop' NHB and 'O'Neal' SHB were higher and lower than this range, respectively (Li et al. 2012; Long et al. 2024). Blueberry light saturation points are lower than those of other cultivated soft fruits ($P < 0.001$) such as apple (Yang et al. 2021), peach (Quilot et al. 2004), strawberry (Choi et al. 2016), raspberry (Qiu et al. 2017), and citrus (Wang et al. 2020). The low light saturation points of blueberry invite close examination of infrared gas analyzer settings for instantaneous P_n measurements because settings far above 600 $\mu mol \cdot m^{-2} \cdot s^{-1}$ might cause photoinhibition.

While single leaves reach light saturation at relatively low photosynthetically active radiation intensities, research of other fruit crops suggested that whole plant photosynthesis benefits from light intensities above the light saturation point. Polyethylene and Mylar film chambers have been previously used to measure whole canopy gas exchange in apple (Corelli-Grappadelli and Magnanini 1993; Lakso et al. 1996) and grapevine (Miller et al. 1996). Modeling tools have also been used to estimate canopy gas exchange (Kaneko et al. 2022; Luo et al. 2018). Neither approach has been applied to highbush blueberry research. However, research suggested that light is a yield-limiting factor in blueberry production in some locations (Petridis et al. 2018). As a result, reflective plastic mulch has been used to increase irradiance within the plant canopy, positively impacting blueberry crop production (Muneer et al. 2019; Petridis et al. 2018).

Rapid fluctuations in light intensity caused by changes in cloud cover, the angle of the sun, and shading by neighboring plants affect blueberry and other crops (Assmann and

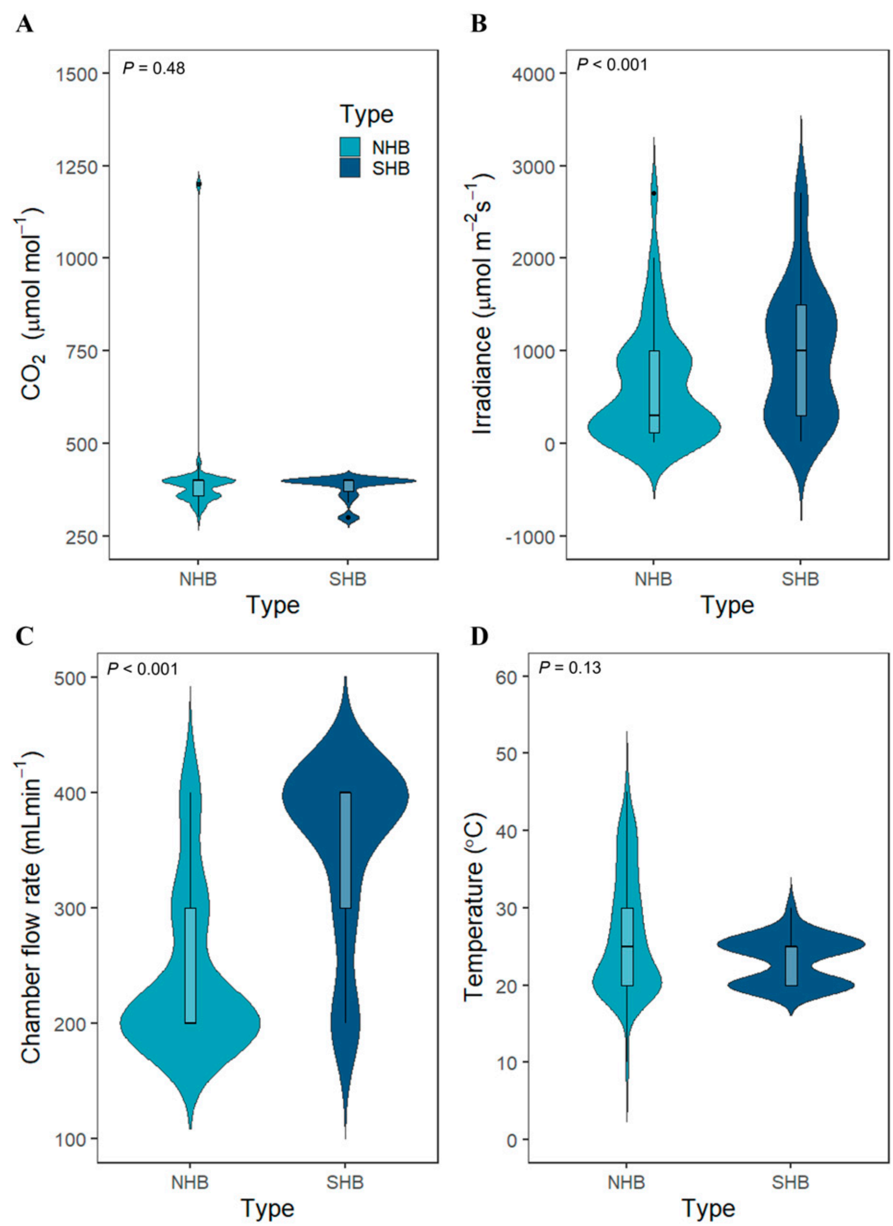

Fig. 3. Infrared gas analyzer setpoints used for blueberry research during 1986 to 2025. A Kruskal-Wallis nonparametric analysis of variance was performed to compare infrared gas analyzer setpoints between northern highbush blueberry (NHB) and southern highbush blueberry (SHB).

Wang 2001; McAusland et al. 2016; Pearcy 1990; Petridis et al. 2021). However, the fluctuations might be particularly detrimental for highbush blueberry plants because of their slow stomatal responses (da Silva Benevenute et al. 2025; Petridis et al. 2018). Thus, NHB and SHB plants might be better suited for locations with constant diffuse light. Understanding these light interactions is crucial for optimizing growing conditions and improving the productivity of both NHB and SHB cultivars.

Chamber flow rate effects. The chamber flow rate is a critical parameter in leaf gas exchange measurements because it significantly influences the accuracy of photosynthesis estimates. In other fruit crops and model plants, high flow rates ($>$400 mL$\cdot$min^{-1}) can lead to rapid removal of CO_2 from the chamber, potentially underestimating photosynthetic rates. Low flow rates ($<$200 mL$\cdot$min^{-1}) lead to CO_2 accumulation within the chamber, potentially overestimating photosynthetic rates. Low flow rates can also result in condensation in the chamber as water vapor from transpiration accumulates. The P_n measurements are stable and consistent between 200 to 300 mL$\cdot$min^{-1} (Adnew et al. 2021; Busch et al. 2024; Keeley et al. 2022; Le et al. 2021). Crop-specific research of chamber flow rates is not available for highbush blueberry. In the surveyed literature, chamber flow rates in the blueberry literature range from 200 mL$\cdot$min^{-1} to 395 mL$\cdot$min^{-1} (Fig. 3C).

Temperature effects. Temperature plays a crucial role in the photosynthetic efficiency of blueberry plants. Blueberry P_n is influenced by temperature through its effects on enzymatic activities and physiological processes. Chamber temperature setpoints in the blueberry literature range between 20 and 40 °C (Fig. 3D). In NHB, the optimal temperature range for photosynthesis is 20 to 25 °C (Hancock et al. 2008; Lobos et al. 2018). Exposure to temperatures exceeding 30 °C can lead to photosynthetic decline caused by enzyme deactivation (e.g., RuBisCO) and increased photorespiration (Hancock et al. 1992; Lobos et al. 2018). Increased leaf temperature can decrease stomatal conductance and intercellular CO_2 concentrations, inducing photorespiration in highbush blueberry (Ru et al. 2024). Additionally, extremely high temperatures can increase transpiration rates, leading to water deficit stress and further inhibiting photosynthesis (Long et al. 2024).

In SHB, the optimal temperature for photosynthetic activity has not been established because most research has focused on the research conditions established for NHB (Long et al. 2024). Based on the distribution range of SHB (Fang et al. 2020), it is possible that SHB exhibits a higher optimum temperature range for P_n. Future research should address this knowledge gap.

Other effects. Several factors beyond CO_2, light, chamber flow rate, and temperature influence blueberry P_n. Fungal infections like septoria leaf spot (caused by *Septoria albopunctata*) can severely reduce photosynthetic rates. Studies have shown that as the severity of septoria leaf spot increases, P_n decreases exponentially (Roloff et al. 2004). This reduction is primarily caused by damaged leaf tissues and disrupted chlorophyll production. Fertilization also impacts the blueberry P_n by influencing nutrient availability and overall plant health. Nitrogen is a key component of chlorophyll, which is the pigment responsible for capturing light energy. Studies have shown that nitrogen fertilization can enhance P_n by increasing the chlorophyll content and augmenting the leaf area (Viencz et al. 2021). Larger leaf areas generally lead to increased photosynthetic capacity because of more light being absorbed and more sites for gas exchange, but there are also tradeoffs with transpiration and the efficiency of photosynthesis (Funnell et al. 2002; Hao et al. 2019; Wang et al. 2019). Phosphorus is vital for energy transfer within the plant (Guo et al. 2021). Phosphorus deficiency reduced SHB photosynthetic rates (Retana-Cordero and Nunez 2025). The specific effects of other nutritional deficiencies of blueberry P_n are unknown at this time.

Conclusion and Future Prospects

This review explored photosynthesis research of highbush blueberry (Supplemental File 1). Blueberry eco-physiology is inherently heterogenous because of the recent and frequent interspecific crosses used for highbush blueberry breeding (Lobos and Hancock 2015; Lyrene and Olmstead 2012). Thus, large-scale studies that use multiple genotypes and environments are necessary to build a thorough and nuanced understanding of the photosynthetic diversity in this crop. While some authors have claimed that blueberry breeding programs improved photosynthesis efficiency (Lobos and Hancock 2015), our bibliographic research suggested that this goal has not been accomplished or reported yet. Our overarching impression at the conclusion of this review is that more research is necessary to understand blueberry photosynthesis and optimize blueberry cultivation. Additional research is also necessary to integrate blueberry single-leaf P_n measurements, which comprise the majority of what is known of this crop, into canopy modeling, carbon budgeting, and the future of controlled environment agriculture. In this context, this review offers a baseline of existing research and a list of potential research avenues for the future.

References cited

Adnew GA, Hofmann ME, Pons TL, Koren G, Ziegler M, Lourens LJ, Röckmann T. 2021. Leaf scale quantification of the effect of photosynthetic gas exchange on Δ47 of CO2. Sci Rep. 11(1):14023. https://doi.org/10.1038/s41598-021-93092-0.

Assmann SM, Wang XQ. 2001. From milliseconds to millions of years: Guard cells and environmental responses. Curr Opin Plant Biol. 4(5):421–428. https://doi.org/10.1016/s1369-5266(00)00195-3.

Busch FA, Ainsworth EA, Amtmann A, Cavanagh AP, Driever SM, Ferguson JN, Kromdijk J, Lawson T, Leakey ADB, Matthews JSA, Meacham-Hensold K, Vath RL, Vialet-Chabrand S, Walker BJ, Papanatsiou M. 2024. A guide to photosynthetic gas exchange measurements: Fundamental principles, best practice and potential pitfalls. Plant Cell Environ. 47(9): 3344–3364. https://doi.org/10.1111/pce.14815.

Cárdenas-Navarro R, Luna-Béjar JA, Castellanos-Morales VdC, Bravo-Hernández NL, López-Pérez L. 2024. Effect of the concentration and ionic form of nitrogen (N) on photosynthesis, growth and fruit production of blueberry (*Vaccinium corymbosum* L.). BIOTECNIA. 26:e2325–e2325. https://doi.org/10.18633/biotecnia.v26.2325.

Choi HG, Moon BY, Kang NJ. 2016. Correlation between strawberry (*Fragaria ananassa* Duch.) productivity and photosynthesis-related parameters under various growth conditions. Front Plant Sci. 7:1607. https://doi.org/10.3389/fpls.2016.01607.

Corelli-Grappadelli L, Magnanini E. 1993. A whole-tree system for gas exchange studies. HortScience. 28(1):41–45. https://doi.org/10.21273/HORTSCI.28.1.41.

da Silva Benevenute S, Adunola PM, Nunez GH. 2025. Diversity in stomata morphology among cultivated blueberry genotypes and its influence on irradiance response dynamics. J Am Soc Hortic Sci. 150(1):42–51. https://doi.org/10.21273/JASHS05458-24.

Davies FS, Flore JA. 1986. Flooding, gas exchange and hydraulic root conductivity of highbush blueberry. Physiol Planta. 67(4):545–551. https://doi.org/10.1111/j.1399-3054.1986.tb05053.x.

Fang Y, Nunez GH, Silva MND, Phillips DA, Munoz PR. 2020. A review for southern highbush blueberry alternative production systems. Agronomy. 10(10):1531. https://doi.org/10.3390/agronomy10101531.

Fernandez GE. 1994. Carbon assimilation and partitioning in ‘titan’ red raspberry: An analysis of canopy, whole-plant, leaf and biochemical factors. Cornell University, Ithaca, NY, USA. https://login.lp.hscl.ufl.edu/login?url=https://www.proquest.com/dissertations-theses/carbon-assimilation-partitioning-titan-red/docview/304112550/se-2.

Forsyth FR, Hall IV. 1965. Effect of leaf maturity, temperature, carbon dioxide concentration, and light intensity on rate of photosynthesis in clonal lines of the lowbush blueberry, *Vaccinium angustifolium* Ait. under laboratory conditions. Can J Bot. 43(8):893–900. https://doi.org/10.1139/b65-099.

Fu C, Li M, Zhang Y, Zhang Y, Yan Y, Wang YA. 2015. Morphology, photosynthesis, and internal structure alterations in field apple leaves under hidden and acute zinc deficiency. Sci Hortic. 193:47–54. https://doi.org/10.1016/j.scienta.2015.06.016.

Funnell KA, Hewett EW, Plummer JA, Warrington IJ. 2002. Acclimation of photosynthetic activity of Zantedeschia ‘Best Gold’ in response to temperature and photosynthetic photon flux. J Am Soc Hortic Sci. 127(2):290–296. https://doi.org/10.21273/JASHS.127.2.290.

Guo X, Li S, Wang D, Huang Z, Sarwar N, Mubeen K, Shakeel M, Hussain M. 2021. Effects of water and fertilizer coupling on the physiological characteristics and growth of rabbiteye blueberry. PLoS One. 16(7):e0254013. https://doi.org/10.1371/journal.pone.0254013.

Hancock JF, Haghighi K, Krebs SL, Flore JA, Draper AD. 1992. Photosynthetic heat stability in highbush blueberries and the possibility of genetic improvement. HortScience.

27(10):1111–1112. https://doi.org/10.21273/HORTSCI.27.10.1111.
Hancock JF, Lyrene P, Finn CENV, Lobos GA. 2008. Blueberry and cranberry, p 115–149. In: Hancock JF (ed). Temperate fruit crop breeding: germplasm to genomics. Kluwer Academic Publishers, Dordrecht, the Netherlands.
Hao L, Guo L, Li R, Cheng Y, Huang L, Zhou H, Xu M, Li F, Zhang X, Zheng Y. 2019. Responses of photosynthesis to high temperature stress associated with changes in leaf structure and biochemistry of blueberry (*Vaccinium corymbosum* L.). Sci Hortic. 246:251–264. https://doi.org/10.1016/j.scienta.2018.11.007.
Hassan MR, Ito D. 2023. Down-regulation of photosynthesis in apple leaves under elevated CO2 concentration: A long-term field study with different fruit load. J Agric Meteorol. 79(1):49–57. https://doi.org/10.2480/agrmet.D-22-00021.
Haworth M, Marino G, Centritto M. 2018. An introductory guide to gas exchange analysis of photosynthesis and its application to plant phenotyping and precision irrigation to enhance water use efficiency. J Water Clim Chang. 9(4):786–808. https://doi.org/10.2166/wcc.2018.152.
Hilário S, Pinto G, Monteiro P, Santos L, Alves A. 2023. The impact of two Diaporthe species on *Vaccinium corymbosum* physiological performance under different water availability scenarios. Eur J Plant Pathol. 166(2):161–177. https://doi.org/10.1007/s10658-023-02651-w.
Hussain SB, Stinziano J, Pierre MO, Vincent C. 2024. Accurate photosynthetic parameter estimation at low stomatal conductance: Effects of cuticular conductance and instrumental noise. Photosynth Res. 160(2-3):111–124. https://doi.org/10.1007/s11120-024-01092-8.
Jiang Y, Zeng Q, Wei J, Jiang J, Li Y, Chen J, Yu H. 2019. Growth, fruit yield, photosynthetic characteristics, and leaf microelement concentration of two blueberry cultivars under different long-term soil Ph treatments. Agronomy. 9(7):357. https://doi.org/10.3390/agronomy9070357.
Jiménez S, Fattahi M, Bedis K, Nasrolahpour-Moghadam S, Irigoyen JJ, Gogorcena Y. 2020. Interactional effects of climate change factors on the water status, photosynthetic rate, and metabolic regulation in peach. Front Plant Sci. 11:43. https://doi.org/10.3389/fpls.2020.00043.
Kaneko T, Nomura K, Yasutake D, Iwao T, Okayasu T, Ozaki Y, Mori M, Hirota T, Kitano M. 2022. A canopy photosynthesis model based on a highly generalizable artificial neural network incorporated with a mechanistic understanding of single-leaf photosynthesis. Agric For Meteorol. 323:109036. https://doi.org/10.1016/j.agrformet.2022.109036.
Keeley M, Rowland D, Vincent C. 2022. Citrus photosynthesis and morphology acclimate to phloem-affecting huanglongbing disease at the leaf and shoot levels. Physiol Planta. 174(2):e13662. https://doi.org/10.1111/ppl.13662.
Kim SJ, Yu DJ, Kim TC, Lee HJ. 2011. Growth and photosynthetic characteristics of blueberry (*Vaccinium corymbosum* cv. Bluecrop) under various shade levels. Sci Hortic. 129(3):486–492. https://doi.org/10.1016/j.scienta.2011.04.022.
Lakso AN, Mattii GB, Nyrop JP, Denning SS. 1996. Influence of European red mite on leaf and whole-canopy carbon dioxide exchange, yield, fruit size, quality, and return cropping in ‘Starkrimson Delicious’ apple trees. J Am Soc Hortic Sci. 121(5):954–958. https://doi.org/10.21273/JASHS.121.5.954.
Lalk GT, Bi G, Stafne ET, Li T. 2023. Fertilizer type and irrigation frequency affect plant growth, yield, and gas exchange of containerized strawberry cultivars. Technology in Horticulture. 3(1):1–8. https://doi.org/10.48130/TIH-2023-0003.
Le LT, Dinh HT, Takaragawa H, Watanabe K, Kawamitsu Y. 2021. Whole-plant and single-leaf photosynthesis of strawberry under various environmental conditions. Environ Control Biol. 59(4):173–180. https://doi.org/10.2525/ecb.59.173.
Lee SG, Cho JG, Shin MH, Oh SB, Kim HL, Kim JG. 2015. Effects of summer pruning combined with winter pruning on bush growth, yields, and fruit quality of ‘Misty’ southern highbush blueberry for two years after planting. Hortic Environ Biotechnol. 56(6):740–748. https://doi.org/10.1007/s13580-015-0101-6.
Li X, Chen W, Li Y. 2012. Study on photosynthetic characteristics of blueberry in greenhouse. Acta Hortic. 926:315–319. https://doi.org/10.17660/ActaHortic.2012.926.43.
Li Y, Wei C, Zhidong Z, Wulin L. 2009. Study on the influence of three production methods on blueberry photosynthesis. Acta Hortic. 810:521–526. https://doi.org/10.17660/ActaHortic.2009.810.69.
Lobos GA, Hancock JF. 2015. Breeding blueberries for a changing global environment: A review. Front Plant Sci. 6:782. https://doi.org/10.3389/fpls.2015.00782.
Lobos GA, Bravo C, Valdés M, Graell J, Ayala IL, Beaudry RM, Moggia C. 2018. Within-plant variability in blueberry (*Vaccinium corymbosum* L.): Maturity at harvest and position within the canopy influence fruit firmness at harvest and postharvest. Postharvest Biol Technol. 146:26–35. https://doi.org/10.1016/j.postharvbio.2018.08.004.
Long J, Tan T, Zhu Y, An X, Zhang X, Wang D. 2024. Response of blueberry photosynthetic physiology to light intensity during different stages of fruit development. PLoS One. 19(9):e0310252. https://doi.org/10.1371/journal.pone.0310252.
Lu X, Ju W, Li J, Croft H, Chen JM, Luo Y, Yu H, Hu H. 2020. Maximum carboxylation rate estimation with chlorophyll content as a proxy of Rubisco content. JGR Biogeosciences. 125(8):e2020JG005748. https://doi.org/10.1029/2020JG005748.
Luo X, Chen JM, Liu J, Black TA, Croft H, Staebler R, He L, Arain MA, Chen B, Mo G, Gonsamo A, McCaughey H. 2018. Comparison of big-leaf, two-big-leaf, and two-leaf upscaling schemes for evapotranspiration estimation using coupled carbon-water modeling. JGR Biogeosciences. 123(1):207–225. https://doi.org/10.1002/2017JG003978.
Lyrene PM, Olmstead JW. 2012. The use of intersectional hybrids in blueberry breeding. Int J Fruit Sci. 12(1-3):269–275. https://doi.org/10.1080/15538362.2011.619429.
McAusland L, Vialet-Chabrand S, Davey P, Baker NR, Brendel O, Lawson T. 2016. Effects of kinetics of light-induced stomatal responses on photosynthesis and water-use efficiency. New Phytol. 211(4):1209–1220. https://doi.org/10.1111/nph.14000.
Miller DP, Howell GS, Flore JA. 1996. A whole-plant, open, gas-exchange system for measuring net photosynthesis of potted woody plants. HortScience. 31(6):944–946. https://doi.org/10.21273/HORTSCI.31.6.944.
Moon JW, Jr. Flore JA, Jr. Hancock JF. 1987. A comparison of carbon and water vapor gas exchange characteristics between a diploid and highbush blueberry. J Am Soc Hortic Sci. 112(1):134–138. https://doi.org/10.21273/JASHS.112.1.134.
Muneer S, Kim JH, Park JG, Shin MH, Cha GH, Kim HL, Ban T, Kumarihami HMPC, Kim SH, Jeong G, Kim JG. 2019. Reflective plastic film mulches enhance light intensity, floral induction, and bioactive compounds in ‘O’Neal’ southern highbush blueberry. Sci Hortic. 246:448–452. https://doi.org/10.1016/j.scienta.2018.10.042.
Nebauer SG, Arenas C, Rodríguez-Gamir J, Bordón Y, Fortunato-Almeida A, Monerri C, Guardiola JL, Molina RV. 2013. Crop load does not increase the photosynthetic rate in citrus leaves under regular cropping conditions. A study throughout the year. Sci Hortic. 160:358–365. https://doi.org/10.1016/j.scienta.2013.06.008.
Osorio R, Cáceres C, Covarrubias JI. 2020. Vegetative and physiological responses of “Emerald” blueberry to ammoniacal sources with a nitrification inhibitor. J Soil Sci Plant Nutr. 20(2):507–515. https://doi.org/10.1007/s42729-019-00135-7.
Park T, Chen C, Macias-Fauria M, Tømmervik H, Choi S, Winkler A, Bhatt US, Walker DA, Piao S, Brovkin V, Nemani RR, Myneni RB. 2019. Changes in timing of seasonal peak photosynthetic activity in northern ecosystems. Glob Chang Biol. 25(7):2382–2395. https://doi.org/10.1111/gcb.14638.
Pearcy RW. 1990. Sunflecks and photosynthesis in plant canopies. Annu Rev Plant Physiol Plant Mol Biol. 41(1):421–453. https://doi.org/10.1146/annurev.pp.41.060190.002225.
Petridis A, van der Kaay J, Archibald IW, McCallum S, Graham J, Hancock RD. 2021. Reflective mulch increases fruit yield of highbush blueberry (*Vaccinium corymbosum* L. cv. Darrow) grown in a northern maritime environment while maintaining key fruit quality traits. J Sci Food Agric. 101(8):3376–3385. https://doi.org/10.1002/jsfa.10967.
Petridis A, van der Kaay J, Sungurtas J, Verrall SR, McCallum S, Graham J, Hancock RD. 2020. Photosynthetic plasticity allows blueberry (*Vaccinium corymbosum* L.) plants to compensate for yield loss under conditions of high sink demand. Environ Exp Bot. 174:104031. https://doi.org/10.1016/j.envexpbot.2020.104031.
Petridis A, van der Kaay J, Chrysanthou E, McCallum S, Graham J, Hancock RD. 2018. Photosynthetic limitation as a factor influencing yield in highbush blueberries (*Vaccinium corymbosum*) grown in a northern European environment. J Exp Bot. 69(12):3069–3080. https://doi.org/10.1093/jxb/ery118.
Qiu C, Ethier G, Pepin S, Dubé P, Desjardins Y, Gosselin A. 2017. Persistent negative temperature response of mesophyll conductance in red raspberry (*Rubus idaeus* L.) leaves under both high and low vapour pressure deficits: A role for abscisic acid? Plant Cell Environ. 40(9):1940–1959. https://doi.org/10.1111/pce.12997.
Quilot B, Génard M, Kervella J. 2004. Leaf light-saturated photosynthesis for wild and cultivated peach genotypes and their hybrids: A simple mathematical modelling analysis. J Hortic Sci Biotech. 79(4):546–553. https://doi.org/10.1080/14620316.2004.11511803.
R Core Development Team. 2021. R: A Language and Environment for Statistical Computing, 2021. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/.
Retana-Cordero M, Nunez GH. 2025. Southern highbush blueberry (*Vaccinium corymbosum* interspecific hybrids) responses to phosphorus deficiency. Sci Hortic. 342:114057. https://doi.org/10.1016/j.scienta.2025.114057.
Reyes-Díaz M, Meriño-Gergichevich C, Inostroza-Blancheteau C, Latsague M, Acevedo P, Alberdi M. 2016. Anatomical, physiological,

and biochemical traits involved in the UV-B radiation response in highbush blueberry. Biologia plant. 60(2):355–366. https://doi.org/10.1007/s10535-015-0580-4.

Rho H, Yu DJ, Kim SJ, Lee JJL. 2012. Limitation factors for photosynthesis in 'Bluecrop' highbush blueberry (*Vaccinium corymbosum*) leaves in response to moderate water stress. J Plant Biol. 55(6):450–457. https://doi.org/10.1007/s12374-012-0261-1.

Ribera-Fonseca A, Jorquera-Fontena E, Castro M, Acevedo P, Parra JC, Reyes-Diaz M. 2019. Exploring VIS/NIR reflectance indices for the estimation of water status in highbush blueberry plants grown under full and deficit irrigation. Sci Hortic. 256:108557. https://doi.org/10.1016/j.scienta.2019.108557.

Ribeiro RV, Machado EC, Santos MG, Oliveira RFD. 2009. Seasonal and diurnal changes in photosynthetic limitation of young sweet orange trees. Environ Exp Bot. 66(2):203–211. https://doi.org/10.1016/j.envexpbot.2009.03.011.

Roloff I, Scherm H, Van Iersel MW. 2004. Photosynthesis of blueberry leaves as affected by Septoria leaf spot and abiotic leaf damage. Plant Dis. 88(4):397–401. https://doi.org/10.1094/PDIS.2004.88.4.397.

Ru S, Sanz-Saez A, Leisner CP, Rehman T, Busby S. 2024. Review on blueberry drought tolerance from the perspective of cultivar improvement. Front Plant Sci. 15:1352768. https://doi.org/10.3389/fpls.2024.1352768.

Salazar-Gutiérrez MR, Lawrence K, Coneva ED, Chaves-Córdoba B. 2023. Photosynthetic response of blueberries grown in containers. Plants. 12(18):3272. https://doi.org/10.3390/plants12183272.

Smrke T, Vodnik D, Veberic R, Sircelj H, Lenarcic D, Jakopic J. 2023. Growing highbush blueberries (*Vaccinium corymbosum* L.) in a protected environment—How much does a microclimate matter? S Afr J Bot. 160:260–272. https://doi.org/10.1016/j.sajb.2023.07.023.

Strik B, Buller G. 2005. The impact of early cropping on subsequent growth and yield of highbush blueberry in the establishment years at two planting densities is cultivar dependent. HortScience. 40(7):1998–2001. https://doi.org/10.21273/HORTSCI.40.7.1998.

Swain PAW, Darnell RL. 2001. Differences in phenology and reserve carbohydrate concentrations between dormant and nondormant production systems in southern highbush blueberry. J Am Soc Hortic Sci. 126(4):386–393. https://doi.org/10.21273/JASHS.126.4.386.

Tasnim R, Zhang YJ. 2021. Are wild blueberries a crop with low photosynthetic capacity? Chamber-size effects in measuring photosynthesis. Agronomy. 11(8):1572. https://doi.org/10.3390/agronomy11081572.

Viencz T, Santana K, Ayub RA, Botelho RV. 2021. Development, photosynthesis and yield of blueberry cultivar 'Climax' growth with different substrates and nitrogen fertilization under protected cultivation. Cienc Rural. 51(6). https://doi.org/10.1590/0103-8478cr20190367.

Walcroft A, Le Roux X, Diaz-Espejo A, Dones N, Sinoquet H. 2002. Effects of crown development on leaf irradiance, leaf morphology and photosynthetic capacity in a peach tree. Tree Physiology. 22(13):929–938. https://doi.org/10.1093/treephys/22.13.929.

Wang C, He J, Zhao TH, Cao Y, Wang G, Sun B, Yan X, Guo W, Li MH. 2019. The smaller the leaf is, the faster the leaf water loses in a temperate forest. Front Plant Sci. 10:58. https://doi.org/10.3389/fpls.2019.00058.

Wang T, Xiong B, Tan L, Yang Y, Zhang Y, Ma M, Xu Y, Liao L, Sun G, Liang D, Xia H, Zhang X, Wang Z, Wang J. 2020. Effects of interstocks on growth and photosynthetic characteristics in 'Yuanxiaochun' citrus seedlings. Funct Plant Biol. 47(11):977–987. https://doi.org/10.1071/FP20079.

Wen X, Xu L, Wei R. 2022. Research on control strategy of light and co2 in blueberry greenhouse based on coordinated optimization model. Agronomy. 12(12):2988. https://doi.org/10.3390/agronomy12122988.

Wu Y, Huang Z, Zhang C, Shi C, Lyu L, Li W, Wu W. 2022. Comparative analysis of the morphological, physiological, proteomic, and metabolic mechanisms of the "Biloxi" blueberry response to shade stress. Front Plant Sci. 13:877789. https://doi.org/10.3389/fpls.2022.877789.

Yang JL, Lin SY. 2025. Evaluating sustainable media mixes using local agricultural and forestry wastes for enhancing the early establishment of container-grown southern highbush blueberry in subtropical climates. Sci Hortic. 339:113845. https://doi.org/10.1016/j.scienta.2024.113845.

Yang X, Chen LS, Cheng L. 2021. Leaf photosynthesis and carbon metabolism adapt to crop load in 'Gala' apple trees. Horticulturae. 7(3):47. https://doi.org/10.3390/horticulturae7030047.

Yu M, Sun P, Huang X, Zha Z, Wang X, Mantri N, Lou H, Jiang B, Shen Z, Sun Y, Lu H. 2023. Interacting effects of CO2, temperature, and nitrogen supply on photosynthetic, root growth, and nitrogen allocation of strawberry at the fruiting stage. Agronomy. 13(5):1353. https://doi.org/10.3390/agronomy13051353.

Zhao M, Sun W, Li H, Wang W, Cao G, Wang F. 2022. The effects of the tree structure of Zaosu pear on the transport and distribution of photosynthetic assimilates and fruit quality under desert-area conditions. Agronomy. 12(10):2440. https://doi.org/10.3390/agronomy12102440.