Physiological Adaptation Capacities of Three Southern Highbush Blueberry (*Vaccinium corymbosum* L.) Cultivars to Çukurova Conditions

Eser ÇELİKTOPUZ[1]*, Erhan TURAN[2]

ABSTRACT

This study investigated the physiological performance of three highbush blueberry cultivars ('Star', 'Legacy', 'Biloxi') grown under the climate of the Çukurova region in southern Türkiye. Plants were grown in 30 L containers under a hail-net structure, and measurements were made at flowering, early fruit set and peak harvest. Principal physiological characteristics such as net photosynthesis, stomatal conductance, transpiration, leaf temperature, SPAD chlorophyll index and maximum PSII efficiency (Fv/Fm) were measured to identify cultivar specific responses to progressive increases in temperature and VPD. A consistent separation among cultivars emerged as environmental demand increased. 'Star' kept the highest photosynthetic activity, strongest stomatal response, and lowest leaf temperatures, with relatively stable Fv/Fm through the season. 'Legacy' had moderate resilience, largely through sustained chlorophyll levels, while 'Biloxi' was sensitive, reflected in higher leaf temperatures, lower PSII efficiency, and accelerated pigment decline. Overall, this study underlines the key role of cultivar choice in maintaining physiological stability in warm blueberry growing regions, pointing out 'Star' as a particularly suitable genotype for environments facing increasing thermal and evaporative stress.

Keywords: Physiological stress, vapor pressure deficit, photosynthesis, heat tolerance, climate change

Üç Güneyli Maviyemiş (*Vaccinium corymbosum* L.) Çeşidinin Çukurova Koşullarına Fizyolojik Uyum Kapasiteleri

ÖZ

Bu çalışma, Çukurova ikliminin altında üç güneyli maviyemiş çeşidinin ('Star', 'Legacy', 'Biloxi') fizyolojik performansını karşılaştırmak amacıyla yürütülmüştür. Deneme, dolu tülü altında 30 L saksılarda yetiştirilen üç yaşlı bitkilerde gerçekleştirilmiş ve ölçümler çiçeklenme, meyve başlangıcı ve yoğun hasat dönemlerinde yapılmıştır. Fotosentez hızı, stomatal iletkenlik, terleme, yaprak sıcaklığı, klorofil yoğunluğu (SPAD) ve PSII maksimum kuantum verimliliği (Fv/Fm) gibi temel fizyolojik değişkenler ayrıntılı biçimde değerlendirilmiştir. Bulgular, çevresel koşullar sertleştikçe çeşitler arasında belirgin bir ayrışma oluştuğunu göstermiştir. 'Star', artan sıcaklık ve buhar basıncı açığına rağmen daha yüksek fotosentetik aktiviteyi, daha güçlü stomatal tepkiyi ve daha düşük yaprak sıcaklığını korumuş; Fv/Fm değerleri de yüksek kalmıştır. 'Legacy' orta düzeyde dayanım gösterirken, 'Biloxi' yüksek yaprak sıcaklığı, düşen Fv/Fm ve hızlanan klorofil kaybıyla belirgin bir duyarlılık sergilemiştir. Bulgular, sıcak iklimlerde çeşit seçiminde fizyolojik dayanımın belirleyici bir unsur olduğunu ve özellikle 'Star' çeşidinin Çukurova gibi hızla ısınan üretim alanları için güçlü bir aday olduğunu ortaya koymaktadır.

Anahtar Kelime: Fizyolojik stres, buhar basıncı açığı, fotosentez, sıcaklık toleransı, iklim değişikliği

ORCID ID (Yazar sırasına göre)
0000-0002-5355-1717, 0000-0002-2953-2698

[1] Çukurova Üniversitesi, Ziraat Fakültesi, Tarımsal Yapılar ve Sulama Bölümü, Adana
[2] Osmaniye Üniversitesi, Mühendislik ve Doğa Bilimleri Fakültesi, Bilgisayar Mühendisliği Bölümü, Osmaniye
* E-posta: eceliktopuz@cu.edu.tr

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Introduction

The cultivation of highbush blueberry (*Vaccinium corymbosum L.)* has expanded globally in recent years, propelled by increasing consumer demand for nutrient dense "super-fruit" berries and the search for new high value crops under shifting agro climatic regimes. Nevertheless, as climate change advances, key physiological constraints, especially elevated temperatures and altered vapor pressure deficit (VPD) regimes, pose formidable challenges to blueberry productivity and quality in warm-climate production zones such as the Çukurova plain of southern Türkiye. Among those Mediterranean-type environments, growers are often faced with a combination of abiotic stresses such as high irradiance, heat loads, limited root-zone cooling, and episodic events of hail/drought. Moreover, cultivar selection and adaptive management are required for sustainable production (Çeliktopuz 2024a).

Understanding cultivar-specific physiological responses under such stressors is of great importance. Recent studies emphasize that blueberry photosynthesis, stomatal conductance, chlorophyll fluorescence efficiency, and intercellular CO_2 concentration are all highly sensitive to supraoptimal temperatures and increased VPD (Roni et al., 2025; González-Villagra et al., 2024). For instance, Roni et al. (2025) found that in the case of northern highbush blueberry, the optimal leaf temperature range for Pn was between 20-25 °C and that temperatures beyond ~30 °C led to steep declines in Pn and Fv/Fm as a result of enzyme deactivation and photorespiration enhancement. Meanwhile, González-Villagra et al. (2024) showed that the 'Legacy' variety of V. corymbosum exposed to a modest +5 °C treatment during fruit set under field conditions exhibited significant declines in stomatal conductance and photosystem II photochemical efficiency, which negatively impacted fruit quality.

In this context of global warming, adaptive and mitigative strategies will be highly necessary not only for yield stability but also for eco-efficient use of water/energy. The interrelations between plant physiology and agronomic interventions, like shading, substrate thermal buffering, and cultivar choice, are increasingly framed within the dual umbrella of adaptation and mitigation strategies: physiological/acclimative change and resource use optimization strategies, respectively. Indeed, blueberry plants have latent acclimation capacity under low light intensity through the up regulation of chlorophyll and carotenoid content (Long et al., 2024), yet much less is documented about tolerance thresholds and adaptive phenology in elevated VPD/temperature regimes in warm regions.

Climate change will also have adverse effects on Türkiye. Its detailed analysis, together with the projection for 2040-2059 under the SSP3-7.0 scenario, projects variable increases in the average temperature over Türkiye, with much more pronounced impacts in the south and west of the country (Çeliktopuz 2024b). The same study emphasizes that this warming trend could pose imminent threats to agriculture and alter crop yields, and that adaptive measures are urgently needed in this context. This necessitates cultivar selection strategies that can adapt to climate change, particularly in species such as blueberries, which are sensitive to water. Similarly, Çeliktopuz (2004c) reported that under different emission scenarios, Türkiye, especially under high-emission scenarios, initially exhibited a trend toward longer growing seasons due to global warming, but this trend would decline, particularly as a result of insufficient climate change mitigation efforts. Specifically for the Çukurova region, the unique combination of high summer irradiance (often >1 200 µmol m^{-2} s^{-1}), frequent day-time leaf zone temperatures exceeding 30 °C, and

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occasional hail net microclimates introduces a complex stress matrix. Under these conditions, even so-called "southern" cultivars may exhibit varietal differences in root-zone cooling, stomatal sensitivity, and photoinhibition resilience. To date, the literature remains remarkably thin on systematic comparative physiological assessments of multiple blueberry cultivars under such warm Mediterranean conditions with soilless culture, even though these conditions are projected to intensify with climate change.

The present study therefore aims to evaluate the seasonal physiological performance of three commercially important highbush blueberry cultivars ('Biloxi', 'Legacy', and 'Star') under soilless culture in the Paşaköy／Yüreğir-Adana region, using detailed leaf-level measurements of Pn, stomatal conductance (g_s), transpiration (E), internal CO_2 concentration ($IntCO_2$), PAR, leaf temperature (T_{leaf}), VPD, SPAD chlorophyll index and F_v/F_m at three phenological stages (mid-January, mid-March, mid-May). By doing so, we test the hypothesis that cultivar differences in physiological resilience under heat/VPD stress translate into measurable performance divergence in this region. The outcomes of this work are expected to inform cultivar ranking for warm-climate blueberry production, refine fertigation and climate-buffering strategies, and provide a framework for adaptation and mitigation in subtropical berry systems.

Materials and Methods

Study Site and Climatic Characterization
The experiment was conducted in Paşaköy (Yüreğir, Adana, Türkiye; 36.97° N, 35.23° E; 23 m a.s.l.), a region representing a typical eastern Mediterranean climate. Winters are mild and short, while spring transitions rapidly into high temperature and high radiation conditions. Long-term meteorological records indicate mean annual temperature of ~20 °C, summer maxima frequently exceeding 34–36 °C, and a mean annual precipitation of ~670 mm, largely concentrated between November and March.

Table 1. Monthly climatic conditions in Adana (January–May 2025) during the experimental period

Month	Mean Temp. (°C)	Max Temp. (°C)	Min Temp. (°C)	Mean RH (%)	Max RH (%)	Min RH (%)	Total Rainfall (mm)	Mean Wind Speed (m s⁻¹)	Total Sunshine Duration (h)	Mean Sunshine (h day⁻¹)
January	11.9	22.1	5.2	61.3	95	16	0.6	1.2	201.0	6.5
February	9.3	20.4	–2.8	62.4	98	11	40.8	1.4	197.0	7.0
March	16.7	33.3	4.4	56.5	95	8	6.8	1.3	268.4	8.7
April	18.2	33.9	5.6	60.4	98	13	25.5	1.5	244.0	8.1
May	23.2	36.6	13.3	63.5	98	14	27.9	1.6	298.8	9.6

Table 1 summarizes the monthly climatic conditions recorded in Adana during the experimental period ranging from January to May 2025 (TMS, 2025). The climate of the region is Mediterranean, characterized by mild, relatively humid winters and rapidly increasing temperatures toward the late spring. Accordingly, mean temperatures rose from 11.9 °C in January to 23.2 °C in May, while maximum temperatures as high as 36.6 °C were reached in early summer. Mean relative humidity was characterized by broad

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fluctuations; the monthly maxima were regularly above 95%, reflecting the presence of moist air masses during nighttime and early mornings. Notably, rainfall mostly occurred in February and April, and the sunshine duration increased markedly toward May, reaching nearly 300 total hours. Such climatic conditions represent the typical environmental gradient blueberry plants experience in Çukurova from cool flowering conditions to progressively warmer and drier phases during fruit set and peak harvest.

Plant Material and Experimental Design

Three commercially important southern highbush blueberry (Vaccinium corymbosum L.) cultivars were selected for their contrasting chilling requirements, phenological patterns, and reported variability in heat/VPD resilience: 'Biloxi', 'Legacy', and 'Star'. All plants were 3 year old container grown individuals, uniform in size and canopy structure, established in 30 L pots.

'Star' is a low–medium chill cultivar requiring approximately 300–400 chill hours, making it well suited for warm subtropical and Mediterranean climate. 'Legacy', although classified as southern highbush, has a relatively higher chilling requirement of 800–1000 hours, which may limit its vegetative vigor and early season performance under mild winters (Bañados, 2006). 'Biloxi' is among the lowest chill southern highbush cultivars currently available, typically requiring < 200–300 hours, and is widely recommended for low-latitude environments (Retamales and Hancock, 2018). These cultivar-level differences in winter chill accumulation strongly influence bloom timing, canopy development, and subsequent physiological resilience under increasing spring and summer heat loads, providing important context for interpreting the results of this study.

Substrate pH was maintained at 5.5 ± 0.1, which is within recommended ranges for blueberry root physiology (Gallegos-Cedillo et al., 2018; Glonek and Komosa., 2013; Çeliktopuz, 2024a). A completely randomized design was adopted with four biological replicates per cultivar. Plants were grown under a hail net structure providing approximately 25–30 % shading (black monofilament net; 8 × 4 mm mesh). Pots were arranged with 2.5 m between rows and 0.5 m between plants to ensure minimal shading and adequate air circulation.

Substrate Composition and Fertigation Management

All plants were cultivated in a standardized soilless substrate composed of %60 white peat, %10 cocopeat (washed, low EC) and %30 perlite, chosen to maintain a root-zone pH near the crop optimal value. Electrical conductivity (EC) and pH of the substrate solution were monitored once a week using a portable EC/pH probe (Hanna HI9814). Irrigation and fertigation were given by a pressure compensated drip system equipped with 2 L h^{-1} emitters, managed by a programmable fertigation unit to maintain drainage ratios between %20–25 during peak evaporative periods. The water used in fertigation programs is passed through reverse osmosis and has an Ec value of 0.027 ds m^{-1}. Nutrient solutions followed customized southern highbush requirements, with an emphasis on nitrate based N forms and low bicarbonate buffering to prevent pH drift. The fertigation regime was carefully controlled throughout the trial. The electrical conductivity (EC) of the nutrient solution was initiated at 0.7 dS m^{-1} early in the season and gradually increased to 1.5 dS m^{-1} toward the end of the experiment to match the plants nutrition demand. Solution pH was maintained at a constant 5.0, ensuring an optimal root zone environment for blueberry physiology. Irrigation timing and frequency were regulated according to the drainage fraction, with

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adjustments made daily to maintain a consistent leaching ratio appropriate for soilless blueberry production.

Phenological Stages and Measurement Schedule

Physiological measurements were performed at three key phenological stages representing seasonal transitions:

a) Mid-January: Flowering stage,
b) Mid-March: Early fruit set,
c) Mid-May: Peak harvest, high temperature period

All measurements were conducted between 11:00 and 13:00 h on fully expanded, sun exposed leaves located in the upper third of the canopy to minimize diurnal and positional variability (Figure 1). Plants were randomly selected for measurements from different periods.

Leaf-Level Physiological Measurements

Leaf gas-exchange parameters were recorded using a CID Bio-Science CI-340 Handheld Photosynthesis System. The instrument was calibrated before each measurement session. For each replicate plant, four leaves were measured and averaged. Parameters recorded included:

a) Net photosynthetic rate (Pn; μmol CO_2 m^{-2} s^{-1}),
b) Stomatal conductance (C; mol H_2O m^{-2} s^{-1}),
c) Transpiration rate (E; mmol H_2O m^{-2} s^{-1}),
d) Intercellular CO_2 concentration (IntCO2; μmol mol^{-1}),
e) PAR incident on the leaf (μmol m^{-2} s^{-1}),
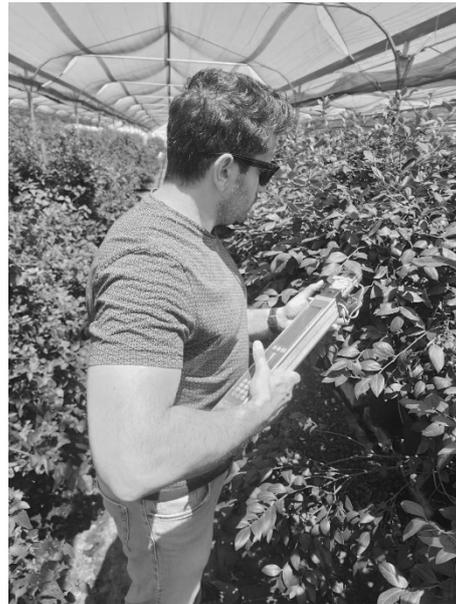f) Vapor Pressure Deficit (VPD; kPa),
g) Leaf temperature (°C)

Figure 1. Field measurement of gas-exchange parameters using a CI-340 portable photosynthesis system in the experimental blueberry plot located in Paşaköy (Yüreğir, Adana)

Fluorescence and Chlorophyll Metrics

Chlorophyll fluorescence was assessed using a Fluorpen FP-100 fluorometer (PSI, Czech Republic) following 20 min dark adaptation. Maximum PSII quantum efficiency (Fv/Fm) was calculated as:

$$\text{Eq. 1} \qquad F_v/F_m = \frac{F_m - F_0}{F_m}$$

Chlorophyll concentration was determined using a SPAD-502 plus (Konica Minolta) meter. Four readings per leaf were averaged.

Statistical Analysis

In the experiment, 10 plants were used for each replication, and a total of 120 plants were used with 4 replications and 3 varieties. All raw data were processed in Python (v3.11). Prior to analysis, normality and homoscedasticity were assessed using Shapiro Wilk and Levene's tests. A two-way ANOVA was performed for each parameter with:

Factor A: Cultivar (3 levels)

Factor B: Phenological Stage (3 levels)

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A×B interaction

When ANOVA indicated significance ($p < 0.05$), Tukey's HSD was applied for post-hoc comparison. Grouping letters (a, b, ab) were assigned for each period–cultivar combination. The final heatmaps presented in the Results section integrate:

A) Mean values,
B) Tukey grouping letters,
C) Minimum adjusted p-values across pairwise contrasts

All statistics were computed using statsmodels and scipy libraries.

Results And Discussion

Results
Gas-exchange and microclimatic responses
Stomatal conductance (C)

Stomatal conductance showed a clear seasonal and cultivar-dependent shift. In general, conductance was low throughout all genotypes during Flowering (0.28–0.33 mol H_2O m^{-2} s^{-1}), with limited statistical separation beyond a slight elevation in 'Star' (p(min)=0.002). Conductance increased in all genotypes at Fruit Set, but the magnitude varied: 'Legacy' and 'Star' reached 0.45–0.50 mol H_2O m^{-2} s^{-1} while 'Biloxi' remained significantly lower (0.41; p(min)=0.005), reflecting early stomatal restriction given increasing atmospheric demand. The greatest divergence occurred during peak Harvest measurements. 'Star' showed a particularly high C of 0.92 mol H_2O m^{-2} s^{-1} nearly a threefold increase over its early-season values-whereas 'Biloxi' and 'Legacy' had more modest gains of 0.32–0.39 mol H_2O m^{-2} s^{-1}, which suggests dramatically greater evaporative cooling potential in 'Star' during periods of high temperature (Figure 2).

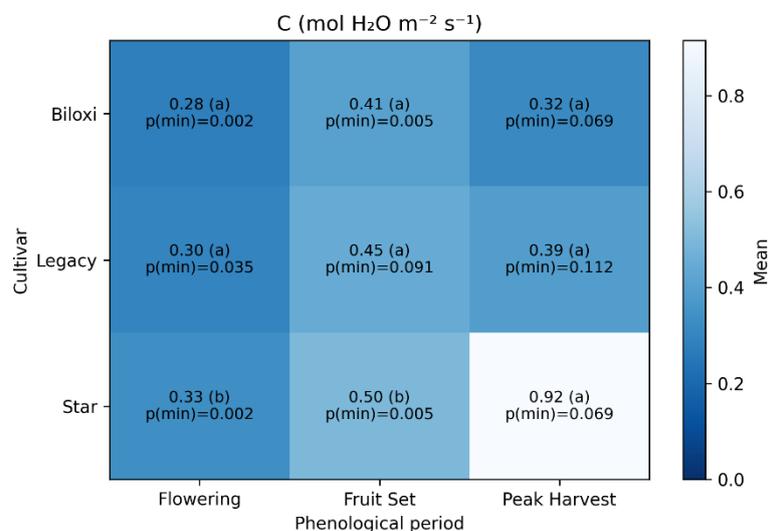**Figure 2.** Heatmap illustrating cultivar and phenology driven variation in stomatal conductance (C, mol H_2O m^{-2} s^{-1}) across flowering, fruit set and peak harvest periods. Values represent treatment means accompanied by Tukey group letters and corresponding minimum p-values.

Transpiration rate (E)

Transpiration followed a trend broadly parallel to stomatal conductance. At Flowering, values ranged from 1.68 to 1.95 mmol H_2O m^{-2} s^{-1}, again with 'Star' displaying slightly higher fluxes. Seasonal intensification was pronounced: at Fruit Set, E increased to 2.45–3.05 mmol m^{-2} s^{-1}, with 'Star' showing the highest transpiration (p(min)=0.009). The divergence reached its peak during Peak

Harvest, when transpiration climbed sharply in all cultivars, but in very different magnitudes: 'Star' reached 4.28 mmol m^{-2} s^{-1}, significantly higher than both 'Legacy' (3.65) and 'Biloxi' (3.40). Tukey groupings and p(min) values show that these differences were statistically robust (p(min)=0.001), matching the cultivar gradient observed in C and Pn (Figure 3).
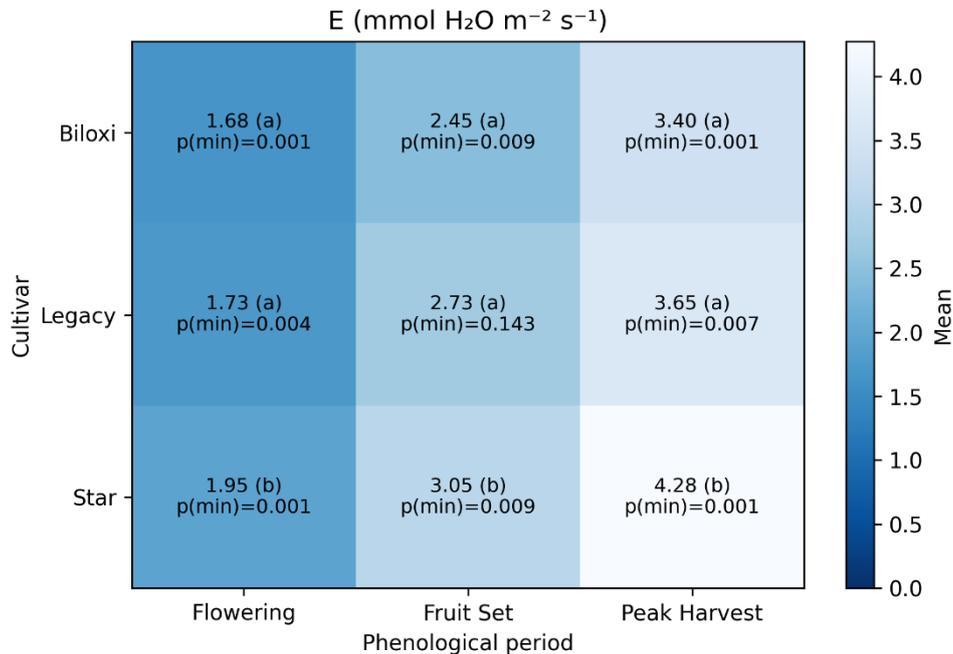

Figure 3. Heatmap illustrating cultivar and phenology driven variation in transpiration rate (E, mmol H$_2$O m^{-2} s^{-1}) across flowering, fruit set and peak harvest periods. Values represent treatment means accompanied by Tukey group letters and corresponding minimum p-values.

Internal CO$_2$ concentration (IntCO$_2$)

At Flowering, IntCO$_2$ was lowest in 'Star' at 243 µmol mol^{-1}, significantly lower than both 'Legacy' at 286 and 'Biloxi' at 263 (p(min)=0.000). During Fruit Set, IntCO$_2$ of 'Star' increased to 268.75 µmol mol^{-1} but remained significantly below that of 'Legacy' and 'Biloxi', consistent with greater carboxylation demand under higher assimilation rates. By Peak Harvest, IntCO$_2$ increased in 'Biloxi' to 284.75 µmol mol^{-1} while remaining comparatively lower in 'Star' (247), reinforcing the pattern of diffusional and biochemical limitation in 'Biloxi' versus maintained metabolic demand in 'Star' (Figure 4).

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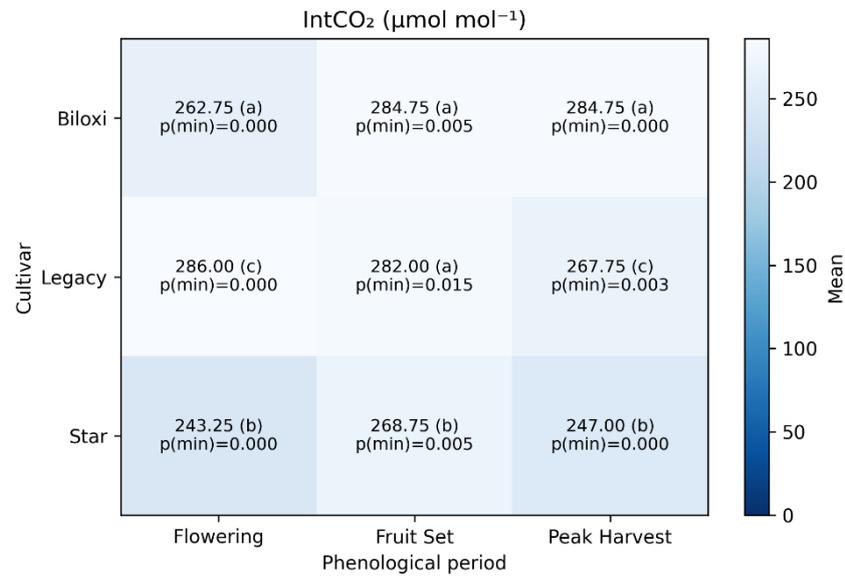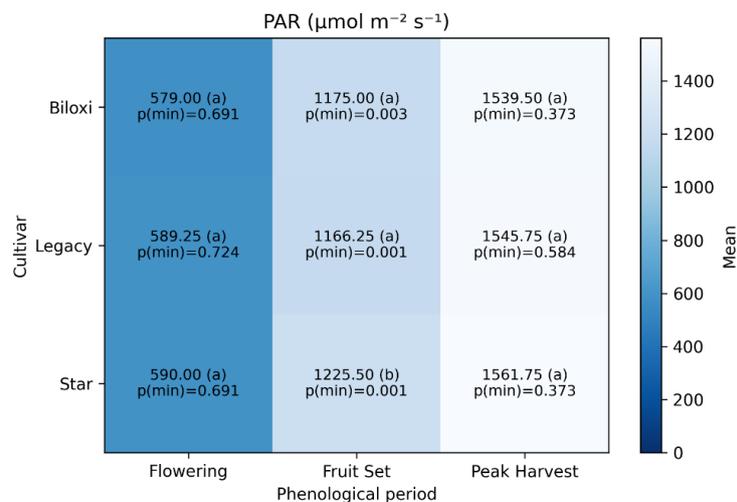

Figure 4. Heatmap illustrating cultivar and phenology driven variation in Internal CO_2 concentration (IntCO$_2$, µmol mol^{-1}) across flowering, fruit set and peak harvest periods. Values represent treatment means accompanied by Tukey group letters and corresponding minimum p-values.

Photosynthetically active radiation (PAR)

PAR increased markedly over the season regardless of cultivar, reflecting the regional solar trajectory. Flowering PAR values ($\approx$580–590 µmol m^{-2} s^{-1}) rose two-fold by Fruit Set and nearly tripled by Peak Harvest, reaching ~1550–1560 µmol m^{-2} s^{-1}. While cultivar effects were minimal, 'Star' received slightly higher PAR during Fruit Set (1225 µmol m^{-2} s^{-1}; p(min)=0.001), likely due to subtle positioning or canopy structure differences, but not to a treatment effect. Importantly, despite similar PAR loads at Peak Harvest, physiological responses diverged strongly among cultivars implying that differences were biological, not radiative, in origin (Figure 5).

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Figure 5. Heatmap illustrating cultivar and phenology driven variation in Photosynthetically active radiation (PAR, μmol m⁻² s⁻¹) across flowering, fruit set and peak harvest periods. Values represent treatment means accompanied by Tukey group letters and corresponding minimum p-values

Vapor pressure deficit (VPD)

VPD dynamics illustrate the environmental intensification underlying the physiological patterns. Mean VPD rose from ~0.70–0.72 kPa at Flowering to 1.35 kPa at Fruit Set, doubling the atmospheric evaporative demand. By Peak Harvest, VPD reached ~2.08–2.10 kPa. No cultivar differences were occurred, but the shared trajectory provides the environmental framework in which stomatal and photosynthetic differences emerged (Figure 6).

Net Photosynthetic Rate (Pn)

Across phenological stages, cultivar differences in Pn were consistent (Figure 6). At Flowering, mean Pn values clustered between ~8.45–9.32 $\mu mol\ CO_2\ m^{-2}\ s^{-1}$, with 'Biloxi' slightly higher than 'Star' and 'Legacy' (Tukey letters: b vs a; p(min) ≈ 0.002–0.051), indicating a small but significant advantage for Biloxi under cool, low VPD conditions. By Fruit Set, the ranking inverted decisively: 'Star' (14.52; letter b) > 'Legacy' (12.45; a) > 'Biloxi' (11.22; c), with all pairwise contrasts highly significant (p(min) ≈ 0.000). At Peak Harvest, the separation persisted under heat/VPD stress: 'Star' (12.10; b) > 'Legacy' (10.65; a) > 'Biloxi' (9.62; c), again with strong pairwise significance (p(min) ≈ 0.000) (Figure 7). Two patterns emerge. First, seasonal amplification: cultivar gaps widen from Flowering to Fruit Set and remain wide at Peak Harvest, implying differential resilience as thermal/evaporative load rises. Second, Star's dominance under stress: 'Star' converts rising irradiance into higher assimilation during Fruit Set and sustains the highest Pn at Peak Harvest, whereas 'Biloxi' loses ground as conditions intensify, and 'Legacy' sits intermediate.
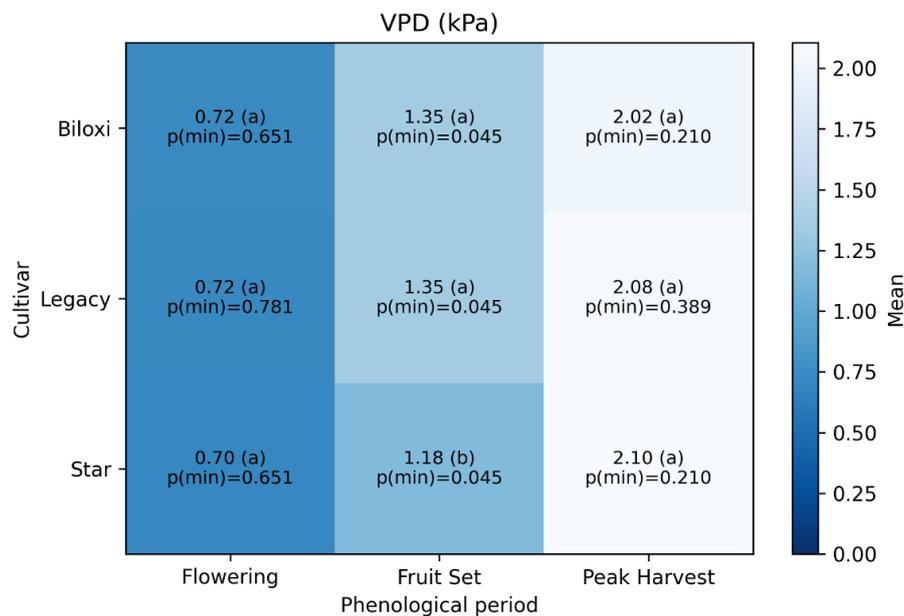

Figure 6. Heatmap illustrating cultivar and phenology driven variation in Vapor pressure deficit (VPD, kPa) across flowering, fruit set and peak harvest periods. Values represent treatment means accompanied by Tukey group letters and corresponding minimum p-values.

Figure 7. Heatmap illustrating cultivar and phenology driven variation in Net Photosynthetic Rate (Pn, μmol CO_2 m^{-2} s^{-1}) across flowering, fruit set and peak harvest periods. Values represent treatment means accompanied by Tukey group letters and corresponding minimum p-values.

Photochemical efficiency, chlorophyll status, and leaf thermal responses

PSII (Fv/Fm)

Maximum quantum efficiency of PSII (Fv/Fm) exhibited clear cultivar and period specific shifts. During Flowering, all genotypes sustained values within the optimal physiological range (0.80-0.84), but with statistically significant differences (p(min)=0.000). 'Biloxi' had the highest photochemical efficiency at 0.837, while 'Legacy' recorded the lowest at 0.805. At Fruit Set, Fv/Fm slightly declined in all cultivars (0.795-0.818), but statistical groupings narrowed, with all genotypes clustering within the "a-b" Tukey groups, indicating comparable PSII functionality under the more moderate spring light loads. By Peak Harvest, values decreased further, most notably in 'Biloxi' (0.748; p(min)=0.000), while 'Star' (0.802) maintained the highest PSII efficiency in the face of intense heat and radiation. This pattern indicates that 'Biloxi' underwent the most intense photochemical down-regulation late in the season, whereas 'Star' maintained stability in PSII despite the sharpened environmental conditions (Figure 8).

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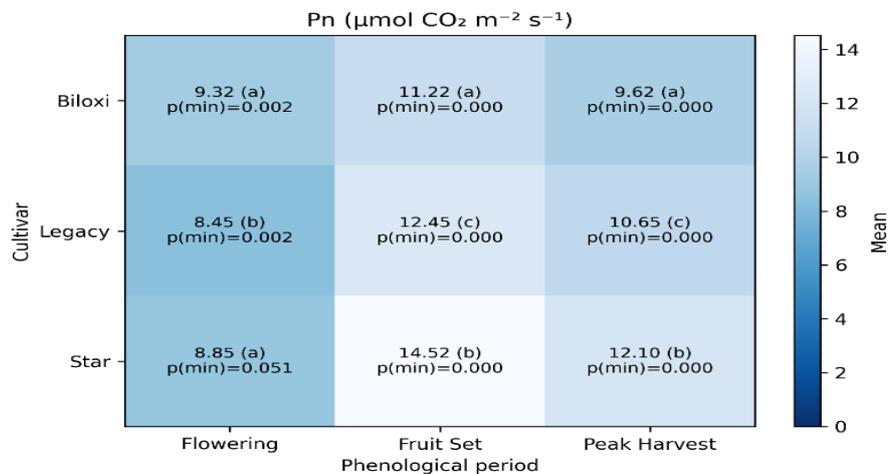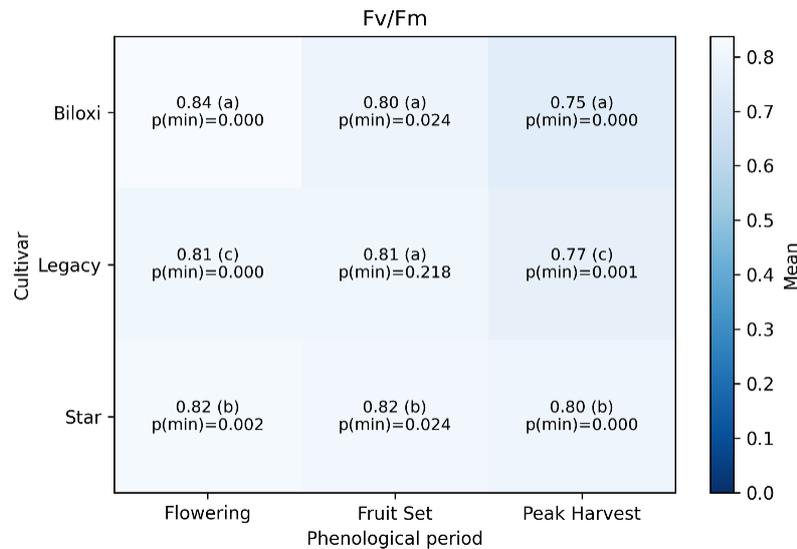**Figure 8.** Heatmap illustrating cultivar and phenology driven variation in PSII (Fv/Fm) across flowering, fruit set and peak harvest periods. Values represent treatment means accompanied by Tukey group letters and corresponding minimum p-values.

Chlorophyll content

SPAD was characterized by clear cultivar contrasts in all of the phenological periods under study. During Flowering, SPAD ranged from 44.5 ('Biloxi') to 46.7 ('Legacy'), where 'Legacy' was significantly higher than the remaining cultivars (p(min)=0.001). At Fruit Set, this trend is more pronounced: in 'Legacy', the highest chlorophyll density was found at 47.48, while in 'Biloxi' and 'Star', it was lower but statistically similar (~45-46) (Figure 9).

Tleaf

Leaf temperature rose sharply across phenological periods, reflecting the seasonal intensification of the environmental load. During Flowering, Tleaf remained cool at 19-20 °C and cultivar differences were small with the exception of higher values in 'Biloxi' (20.27; p(min)=0.000). At Fruit Set, temperatures rose to ~25°C and remained closely aligned across cultivars. However, by Peak Harvest, cultivar differentiation became substantial: 'Biloxi' reached the highest leaf temperatures (35.42 °C), significantly outpacing both 'Legacy' (34.88 °C) and 'Star' (34.08 °C). This is indicative of a reduced capacity for evaporative cooling in 'Biloxi', while 'Star', conversely, maintained the coolest leaves consistent with its elevated transpiration rates in the E dataset (Figure 10).

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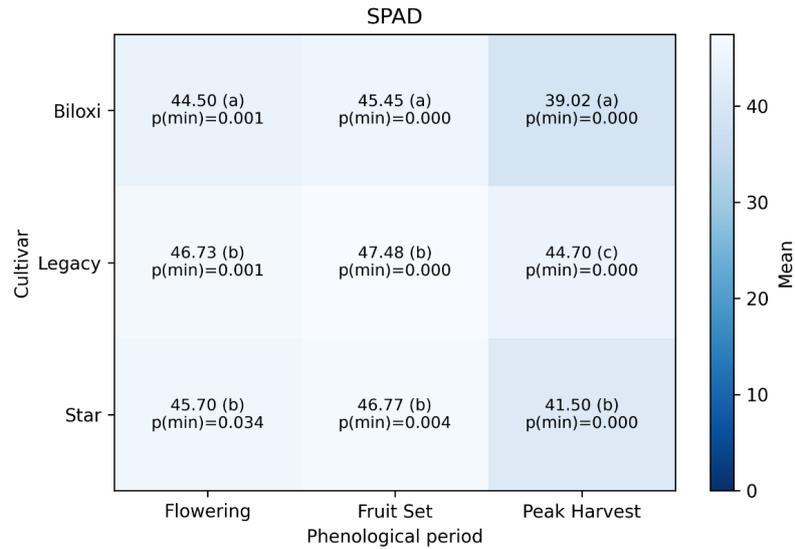

Figure 9. Heatmap illustrating cultivar and phenology driven variation in Chlorophyll content (SPAD) across flowering, fruit set and peak harvest periods. Values represent treatment means accompanied by Tukey group letters and corresponding minimum p-values.

Figure 10. Heatmap illustrating cultivar and phenology driven variation in Leaf temperature (°C) across flowering, fruit set and peak harvest periods. Values represent treatment means accompanied by Tukey group letters and corresponding minimum p-values.
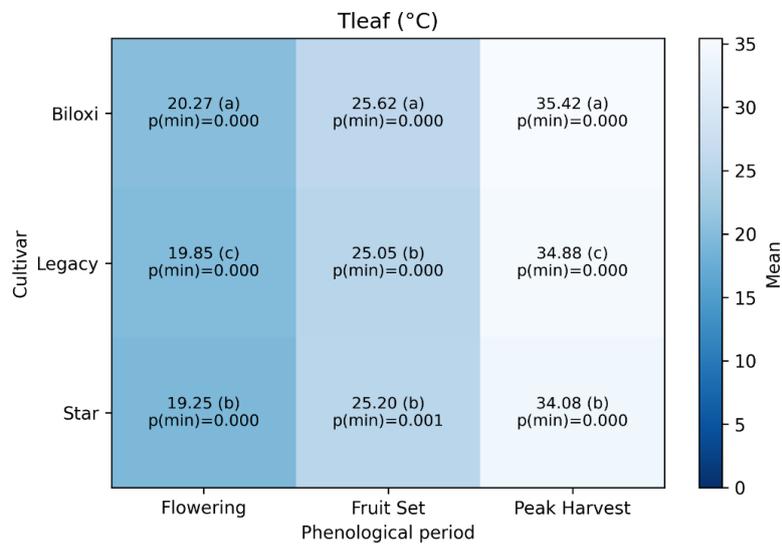
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Discussion

The relationships observed across Pn, C, E, IntCO$_2$, PAR, VPD, Fv/Fm, SPAD, and Tleaf collectively depict a coherent physiological differentiation among the three cultivars that are tightly coupled to the seasonal environmental gradient typical of the Çukurova region.

Stomatal behavior under rising evaporative demand

The shift from cool winter conditions (VPD <0.7 kPa) to a high spring evaporative load (VPD >2.0 kPa) enhanced the stomatal conductance response in different cultivars. The sharper increase of C in 'Star', especially at Peak Harvest, indicates a more responsive and heat-tolerant stomatal characteristic. This is consistent with studies which have found that heat-resilient highbush genotypes maintain stomatal aperture to sustain evaporative cooling when VPD increases (González-Villagra et al., 2024; Carella et al., 2023). The relatively flat conductance profile of 'Biloxi' points to early stomatal closure. Such an approach has been considered conservative, thus preventing excessive water loss while restricting CO$_2$ diffusion, and eventually depressing Pn. Similar stomatal restriction has been reported in many southern highbush cultivars, above the VPD threshold of 1.0 kPa (Petridis et al., 2018; Roni et al., 2025).

Transpiration and thermal buffering capacity

Higher transpiration in 'Star' at both Fruit Set and Peak Harvest points to strong evaporative cooling, which likely contributes to its lower leaf temperatures and higher Pn/Fv/Fm observed in the accompanying datasets. This pattern matches reports where high-performing blueberry cultivars exhibit enhanced water flux to maintain leaf temperatures near metabolic optima under warm, high radiation conditions (Smrke et al., 2023; Retamal-Salgado et al., 2017). The relatively small increase in 'Biloxi's

E further supports its heat sensitivity trait because less transpiration leads to less heat buffering around biochemical reactions.

Internal CO$_2$ as a signal of carboxylation competence

The fact that 'Star' maintained lower IntCO$_2$ with increased PAR and VPD is indicative of increased carboxylation demand, which matches its enhanced Pn. On the other hand, 'Biloxi's high IntCO$_2$ values suggest diffusional limitation (low C), in addition to metabolic suppression typical for heat-stressed species like Vaccinium (Wu et al., 2022). Legacy's intermediate values for IntCO$_2$ suggest its medium level of resilience.

Light environment and physiological differentiation

While PAR rose strongly across the season from ~600 to >1500 μmol m^{-2} s^{-1}, cultivars did not differ in incident light at Peak Harvest, reinforcing that light was not the driver of between cultivar divergence. Rather, there seems to be a connection between the discontinuity in terms of intrinsic properties related to stomatal regulation mechanisms, heat tolerance, and photoprotection. Similar findings under shade nets and high light field conditions show that cultivar-specific responses, not micro light differences, drive variation in gas exchange and fluorescence under Mediterranean climates (Smrke et al., 2024; Retamales et al., 2014).

Environmental intensification (VPD) as the overarching driver

The climb in VPD from Flowering to Peak Harvest forced stomatal and biochemical systems toward their tolerance limits. Importantly, the cultivar performance gradient (Star > Legacy > Biloxi) across all parameters C, E, IntCO$_2$, and Pn became most pronounced at the highest VPD values (~2.0 kPa). This corresponds to mechanism-based models explaining exponential stomatal sensitivity to

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increases in VPD (Miner et al., 2017), with direct downstream effects to photosynthesis.

Interpreting Pn dynamics in a warm Mediterranean system

The sharp stratification observed around Fruit Set and Peak Harvest corroborates observations that highbush blueberry has a small thermal amplitude for photosynthesis (~20-25 °C), with steep losses above 30 °C, which are cultivar dependent ('Legacy') (Roni et al., 2025; González-Villagra et al., 2024). Under warm conditions like Çukurova's high VPD environment, generally related increases in VPD are associated with stomatal closure and Pn suppression; but cultivars vary in how long diffusion or carboxylation capacities are maintained before decline (Smrke et al., 2023). Our data show 'Star' maintains higher Pn precisely where heat/VPD intensify, consistent with a wider operational window and delayed stomatal/biochemical limitation (Roni et al., 2025; González-Villagra et al., 2024).

Diffusional vs. biochemical limitation

The seasonal rise of Pn in 'Star' through Fruit Set, followed by a moderated decline at Peak Harvest, suggests that diffusional constraints (C-linked) are buffered by stronger evaporative cooling or stomatal control, while biochemical capacity (Rubisco-limited carboxylation, electron transport) remains comparatively intact under heat. On the other hand, 'Biloxi' exhibits the most severe Pn late decline, indicating both stomatal limitation and biochemical constraint due to heat. Both stomatal limitation and biochemical closure due to heat have been considered major contributors to yield instability in blueberry. As a result of environmental stress-induced limitation in the photosynthetic window, carbon fixation to fulfill fruit growth requirements remains inadequate (Petridis et al., 2018; Wu et al., 2022).

Our trial ran under hail netting, which typically reduces peak irradiance and can temper leaf temperature, thereby softening photoinhibition and stabilizing gas exchange. Even so, late spring PAR in the region often still exceeds ~1200 $\mu mol\ m^{-2}\ s^{-1}$. Literature from photo selective and neutral nets shows improved microclimate and, in some cases, preserved photosynthetic performance and fruit quality under warm conditions, effects that dovetail with the high Pn of 'Star' at Fruit Set and its maintained lead at Peak Harvest (Retamales et al., 2014; Smrke et al., 2024; Retamal-Salgado et al., 2017). These findings support the interpretation that 'Star's advantage is physiological rather than radiative, because incident PAR was comparable across cultivars while Pn diverged strongly (Smrke et al., 2024).

Under rising heat/VPD, three mechanisms likely underlie 'Star's Pn stability:

(i) Delayed stomatal closure sustaining CO_2 diffusion;

(ii) Efficient evaporative cooling that constrains leaf temperature near the enzyme-friendly range; and

(iii) Photoprotective capacity (NPQ/antioxidant systems) that preserves electron transport and carboxylation demand, thereby avoiding the $IntCO_2$ accumulation pattern typical of heat stressed leaves (as shown for Legacy under HT) (González-Villagra et al., 2024). The convergence of these traits yields the Star > Legacy > Biloxi ranking we observed when thermal/evaporative loads peak (González-Villagra et al., 2024).

In warm climate blueberry, variety first represents a managerial lever for 'Star' to resist heat/VPD pulses through its natural physiology, 'Legacy' to moderately tolerate heat incidents, or 'Biloxi' to more precisely regulate its microclimate (irrigate earlier or with pulses,

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potentially increasing shading coefficients for heat waves). Netting use and irrigation planning must coordinate to keep leaf surface temperatures around mid 20s °C (to avoid lowering photosynthetic nitrogenase tolerance to plant overheating conditions in highbush blueberry reported in numerous studies at süper optimal heat regimes (Smrke et al., 2023; Roni et al., 2025).

Fv/Fm: Photochemical resilience and cultivar-specific PSII stability

The decline in Fv/Fm values across winter flowering to late-spring harvest represents both the progressive increase in photochemical stress induced by increasing PAR and VPD conditions found in Çukurova. Although values did not fall into severe photoinhibition (≈0.70), the decline measured in 'Biloxi' plants at Peak Harvest (0.748) clearly indicated PSII photoinhibition, which occurs due to high temperature and high-light conditions found in blueberry plants (González-Villagra et al., 2024).

In contrast to this, 'Star' had the relatively high value of Fv/Fm ratios when subjected to maximum stress. It shows resilience to photoprotection. Many similar instances in cultivars are found in scientific literature. Those tolerant to solarization show relatively less degradation of 'Fv/Fm' ratios (Retamal-Salgado et al., 2017; Smrke et al., 2023).

Combined interpretation between Fv/Fm and Pn from previous sections indicates that photoinhibition in 'Biloxi' plants occurs both functionally (reduced PSII efficiency) and biochemically (reduced Pn but increased $IntCO_2$). These sources are in line with 'Biloxi' susceptibility to spring conditions in a Mediterranean climate (Petridis et al., 2018).

Chlorophyll stability as an indicator of stress tolerance

The fact that there are generally higher SPAD values for 'Legacy' than 'Biloxi' and the dramatic decrease for 'Biloxi' near Peak Harvest illustrates differences between varieties. Chlorophyll degradation is accelerated by heat and oxidative stress, especially when photoinhibition reduces electron transport balance (Smrke et al., 2024). The decline in SPAD value recorded in 'Biloxi' blueberry plants correlates well with its lower values of Fv/Fm recorded at almost the same time.

'Legacy' has shown to possess the highest SPAD value across all growing periods. It seems to retain a relatively more stable level of chlorophyll. Somehow, these traits agree with past studies focusing on 'Legacy' that utilized chlorophyll retention as a highly sensitive indicator for heat resistance in berries grown in the southern European and Chilean climate (Retamales et al., 2014; González-Villagra et al., 2024).

On the other hand, "Star" showed intermediate SPAD values but was high in Pn and had a consistently high value for Fv/Fm. This suggests that its tolerance to stress conditions does not lie in its pigments but rather in its stomatal control or evaporative cooling mechanisms.

Tleaf: Thermoregulation and evaporative cooling capacity

The leaf temperature patterns mirror gas exchange differences discussed previously. 'Star' had the coolest canopy temperature values throughout Peak Harvest, which aligns with 'Star's high stomatal conductance and transpiration values. Furthermore, this shows efficient evaporative cooling, which is a characteristic preferred in varieties grown in warm areas (Smrke et al., 2023; Carella et al., 2023).

'Biloxi', because of its limited stomatal conductance and lower transpiration rate, experienced a huge accumulation of heat in its leaf tissue. High leaf temperatures above 35°C are nearing values that cause inhibition to Rubisco function and promote chlorophyll

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losses in blueberries (Wu et al., 2022). It fits well with SPAD value decline and Fv/Fm ratios observed in 'Biloxi'.

'Legacy' demonstrated relatively intermediate leaf temperature values along with gas exchange because of its intermediate heat resistance reported in previous studies (Petridis et al., 2018; González-Villagra et al., 2024).

Conclusion

The physiological responses of the three blueberry cultivars grown under Çukurova's climate reveal a clear and consistent resilience gradient. Across all measured indicators including photosynthetic activity, stomatal regulation, internal CO_2 dynamics, photochemical efficiency, chlorophyll stability and leaf thermal load 'Star' consistently outperformed 'Legacy', while 'Biloxi' exhibited the strongest sensitivity to environmental intensification. Rising VPD, elevated PAR and increasing leaf temperatures magnified these differences from flowering through peak harvest.

'Star' had the highest Pn value, maximum stomatal conductance and transpiration rate, and lowest leaf temperature. These characteristics made 'Star' superior to other accessions in maintaining PSII functionalities against both heat and light stresses. 'Legacy' stood moderately stable due to its intermediate stability in chlorophyll content and resistance to photosynthesis. 'Biloxi' was found to possess lower stomatal conductivity, leaf temperature elevation, photoinhibition, and accelerated chlorophyll loss against warm spring conditions prevailing in mediterranean environments.

These results demonstrate that cultivar choice is the primary driver of physiological stability and productivity potential in warm region blueberry production. Integrating gas exchange parameters, chlorophyll contents, and fluorescence analysis offers a reliable platform to select heat resistant genotypes to grow in climate challenged sites.

From a practical point of view, some important implications for management are provided. Heat-tolerant cultivars like 'Star' are to be preferred in zones receiving high irradiance and high VPD values, whereas sensitive cultivars like 'Biloxi' are to be grown in conditions with more moderated microclimates. As heat tolerant cultivars make extensive use of evaporative cooling to regulate leaf temperature or PSII functions, water supply needs to be managed according to values of VPD to ensure that water supply to plants occurs before peak demand. For sensitive genotypes, photoselective shading or moderate netting can reduce thermal and radiative stress during critical phenological stages. Finally, monitoring Pn, gs, IntCO₂, SPAD value, Fv/Fm ratios, and leaf temperature data according to a standard schedule can create a system that will warn or indicate when plant condition starts to deteriorate.

In general, there are presented physiologic guidelines concerning cultivars' selection based on microclimate characteristics for warm blueberry cultivars' cultivating systems to improve resistance to climate warming.

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