



## **Final Report**

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### **Student Project No.**

**Title:** Engineering Blue Light Responses to Break the Carbon Water Trade Off and Approaches for Climate Resilient Plant Improvement

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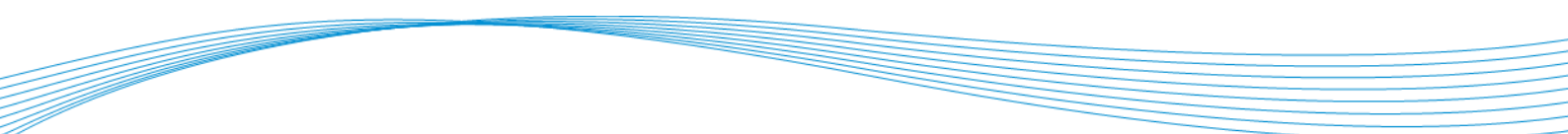
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### **Report No:**

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## 1. Industry Summary

Plants continually juggle a fundamental trade-off: opening stomata to assimilate carbon while losing water. This PhD project converted that trade-off into a set of actionable levers for protected cropping and arable cereals by engineering blue light responses, quantifying previously inaccessible spatial stomatal traits, and testing naturalistic light regimes that expose hidden performance penalties under real world dynamics. Collectively, the work shows how modest, precisely targeted manipulations can lift daily carbon gain without increasing photon input and enhance water use characteristics without sacrificing responsiveness to light.

Three practical advances underpin these outcomes. First, we established robust infrared thermography workflows that turn canopy or leaf surface temperature into a reliable index of stomatal conductance with correct emissivity calibration, reference standards, boundary layer determination, and time-series analysis which enabled high throughput screening of stomatal traits and dynamics in glasshouse and field settings. These methods allow phenotyping of fast blue light driven stomatal movements at scale, far beyond the throughput of cuvette gas exchange. Second, we introduced a simple, non-destructive imaging pipeline that uses chlorophyll autofluorescence to map stomata over very large leaf areas ( $>18\text{ cm}^2$ ), enabling the quantification of  $>1,000,000$  stomata with validated 95% detection accuracy. In barley, this revealed strong spatial heterogeneity and demonstrated that overexpressing EPIDERMAL PATTERNING FACTOR 1 (EPF1) reduces stomatal density (SD) far more on the abaxial surface ( $-59.5\%$  base;  $-64.9\%$  tip) than on the adaxial surface ( $-19.9\%$  base;  $-40.1\%$  tip) a pattern with direct consequences for water use and gas exchange. Third, we show two complementary routes to operational gains. In strawberry, early life blue light priming transiently boosts photosynthetic capacity ( $J_{\max} +35.4\%$ ;  $V_{c,\max} +15.9\%$ ) and induces

lasting structural shifts (SD +53.1%), though most biochemical gains revert ~30 days post priming, indicating plastic but short lived memory for capacity. In parallel, a pulsed blue strategy targeted to the abaxial surface increases daily carbon gain by >8% without adding photon dose by exploiting stomatal blue light sensitivity and leaf optical geometry. A random forest model trained on thousands of measurements predicted the quantum yield of CO<sub>2</sub> assimilation ( $\Phi_{CO_2}$ ) with  $R^2 = 0.922$  and identified stomatal conductance as the dominant predictor, guiding pulse timing to the mid late photoperiod when conductance naturally wanes. At the genetic level, moderate EPF1 driven reductions in SD in wheat do not blunt blue light responsiveness, in fact, blue supplementation on red backgrounds induced amplified stomatal opening and water use effects, while maintaining lower baseline conductance under red light. This indicates scope to combine density engineering for water savings with spectral control for dynamic responsiveness. Under truly naturalistic fluctuating light (not square waves), guard cell AHA2 overexpression (GC> AHA2) reduced transition penalties by ≈40% and revealed a reduced dependence on blue vs red signals which are performance traits invisible under conventional step protocols but decisive under canopy like dynamics.

**What growers and controlled-environment operators can use now:**

(i) validated thermography protocols for fast, large-scale stomatal phenotyping; (ii) a high throughput stomatal mapping method enabling spatially representative SD measurement and better WUE inference; (iii) lighting regimes applying periodic abaxial blue pulses (≈10-min pulse cadence, mid–late photoperiod emphasis) to lift daily carbon gain without extra photons; and (iv) genetic strategies (e.g., moderate EPF1 overexpression) that retain dynamic blue light responsiveness while lowering background water loss. Together, these

tools chart a path toward climate resilient production systems that integrate spectral control, anatomy, and guard cell bioenergetics.

## **2. Introduction**

Improving crop carbon gain while containing transpiration is a central challenge for resilient production under intensifying heat, light variability, and water limitation. Blue light signalling is uniquely positioned at the intersection of development (stomatal patterning), guard cell ion transport, and rapid photosynthetic regulation. Yet industry ready methods to measure these traits at scale and to operationalise them in lighting/management strategies have been limited. This project developed and integrated three classes of innovations: (i) scalable phenotyping of stomatal function via infrared thermography with rigorous calibration; (ii) large area, in-situ stomatal mapping using chlorophyll autofluorescence; and (iii) spatiotemporal manipulation of blue-light delivery (priming and abaxial pulsing), assessed under naturalistic fluctuations that expose transition penalties missed by steady state or square wave protocols.

Objectives of this project are 1) Establish validated thermographic workflows that convert thermal imagery into indices of conductance and kinetics suitable for screening and research in CE and field settings; 2) quantify spatial stomatal heterogeneity at the scale relevant to leaf function and link it to gas exchange; 3) test whether early spectral priming (blue percentage) produces durable improvements in photosynthetic induction and capacity; 4) design abaxial-targeted pulsed blue regimes that raise diurnal carbon gain without added photon cost; 5) assess whether SD engineering (EPF1) compromises or complements dynamic blue responsiveness; and 6) evaluate whether boosting guard-cell H<sup>+</sup>-ATPase

(AHA2) mitigates transition penalties under realistic, stochastic light profiles based on the conceptual premise as natural canopies impose rapid, irregular fluctuations where photosynthesis requires minutes to reequilibrate. Steady state data therefore overestimate real carbon gain. The project's "naturalistic fluctuation" approach identical growth and measurement programs with tunable coefficients of variation and frequent transitions can resolve this discrepancy and tests traits under the regimes that matter agronomically.

### **3. Materials and methods**

#### **3.1. Infrared thermography for stomatal function and kinetics (Chapter 2; published)**

Methods for camera selection, emissivity determination (thermocouple and water-bath approaches), wet/dry reference standards, index of stomatal conductance ( $I_g$ ), derivation of leaf conductance to water vapour ( $g_w$ ), snapshot vs time-series acquisition, boundary-layer determination, and kinetic analysis under fluctuating light are fully described. **Published as:** Fan, M., Nemali, K., Lawson, T. (2024) *Using Infrared Thermography for High-Throughput Plant Phenotyping*. *Methods in Molecular Biology*. DOI: 10.1007/978-1-0716-3964-1\_20.

#### **3.2. Large-area stomatal mapping by chlorophyll autofluorescence (Chapter 3; published)**

Confocal/epifluorescence imaging of the intact leaf using the negative contrast of chlorophyll (stomata appear as local minima), automated segmentation, and validation against manual counts. Imaging spans  $>18$  cm<sup>2</sup> per leaf, enabling quantification of  $>1,000,000$  stomata, surface-specific (adaxial/abaxial) and positional (base/tip) gradients, and spatial statistics of heterogeneity. **Publication:** *New Phytologist*. DOI: 10.1111/nph.70514.

### 3.3. Plant materials and growth

**Barley (EPF1-OE).** Transgenic barley lines overexpressing *TaEPF1* under rice actin promoter (with azygous WT controls) grown under controlled environment (23 °C, 65% RH, 14-h photoperiod; PPFD ~250  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ). Sampling at base/tip and both surfaces.

**Wheat (TaEPF1-OE).** Lines characterised for red vs blue responses and surface specificity (adaxial vs abaxial) under controlled spectral treatments.

**Strawberry (blue-light priming).** Gradient blue-percentage priming during early development; post-priming growth under natural light. *Fragaria ananassa* cv. Malling Champion (everbearing strawberry) plants were received as potted individuals in cold storage from RW Walpole (United Kingdom) and transplanted into 1.4-liter pots containing coconut coir moistened with Hoagland nutrient solution (electrical conductivity 1.7 mS/cm, pH 5.8 at 20°C). Following transplantation, plants were randomly allocated to compartmentalized sections within a controlled climate room (Aralab, Portugal) maintained at 20°C during the photoperiod and 16°C during the dark period, with relative humidity controlled between 60–70%.

### 3.4. Measurement protocols

Newly developed, fully expanded leaves were used for all gas exchange measurements. Leaves were clamped inside the leaf chamber of infrared gas analyser systems (Li-6800, LI-COR Biosciences, NE, USA) equipped with 6 cm<sup>2</sup> cuvette and multiphase fluorometer (6800-01A, LI-COR). The fluorometer light source provided peak wavelengths of 625 nm (red) and 475 nm (blue) for actinic illumination. Standard measurement conditions included a flow rate of 500  $\mu\text{mol s}^{-1}$ , leaf temperature controlled at 20°C, vapor pressure deficit

regulated at 1.2 kPa, and a reference CO<sub>2</sub> concentration fixed at 400 μmol mol<sup>-1</sup> (except during A/C<sub>i</sub> response measurements).

### Photosynthesis light response curve

Leaves were acclimated to a saturating light intensity of 1500 μmol m<sup>-2</sup> s<sup>-1</sup> PPFD for a minimum of 15 minutes. Subsequently, light intensity was sequentially decreased using the following PPFD levels: 1500, 1300, 1100, 900, 700, 550, 400, 250, 150, 100, 50, and 0 μmol m<sup>-2</sup> s<sup>-1</sup>. A minimum stabilization period of 1 minute was allowed before logging each measurement point. Data were fitted to a non-rectangular hyperbola function following Von Caemmerer (2000):

$$A_n = \frac{\Phi \cdot I + A_{max} - \sqrt{((\Phi \cdot I + A_{max})^2 - 4k \cdot \Phi \cdot I \cdot A_{max})}}{2\Phi} - R_d \quad \text{Equation 1}$$

where  $A_n$  represents net CO<sub>2</sub> assimilation rate (μmol m<sup>-2</sup> s<sup>-1</sup>),  $\Phi$  denotes the quantum yield of CO<sub>2</sub> assimilation under light-limiting conditions (mol CO<sub>2</sub> mol<sup>-1</sup> photons),  $I$  indicates incident PPFD (μmol m<sup>-2</sup> s<sup>-1</sup>),  $A_{max}$  denotes the light-saturated assimilation rate (μmol m<sup>-2</sup> s<sup>-1</sup>),  $k$  represents the curve convexity (dimensionless), and  $R_d$  is the dark respiration rate (μmol m<sup>-2</sup> s<sup>-1</sup>).

**Photosynthetic Induction Kinetics:** Leaves were first dark-adapted overnight and then in the measurement chamber for another 20 min and minimum fluorescence was obtained, before they were exposed to a saturating light pulse (8000 μmol m<sup>-2</sup> s<sup>-1</sup> for 960 ms) to determine  $F_m$  and calculate the maximum quantum efficiency of PSII ( $F_v/F_m = F_m - F_o/F_m$ ). Plants with  $F_v/F_m$  value higher than 0.78 were used for subsequent gas exchange measurements. Leaves were then acclimated to low light (50 μmol m<sup>-2</sup> s<sup>-1</sup> PPFD) for a minimum of 15 minutes. The induction protocol comprised further acclimation at 100 μmol

$\text{m}^{-2} \text{s}^{-1}$  PPFD for 15 minutes, followed by a step increase to  $1000 \mu\text{mol m}^{-2} \text{s}^{-1}$  PPFD for 60 minutes, and subsequently a step decrease to  $100 \mu\text{mol m}^{-2} \text{s}^{-1}$  PPFD. Gas exchange parameters were recorded at 2 second intervals throughout the measurement period. Stomatal conductance ( $g_{sw}$ ) responses to changing light intensity were characterized using a modified exponential sigmoid function (McAusland *et al.*, 2016):

$$g_{sw} = (g_{smax} - g_{smin})e^{-e^{\left(\frac{\lambda-t}{k}+1\right)}} + g_{smin}$$

where  $g_{smax}$  represents the steady-state stomatal conductance at  $1000 \mu\text{mol m}^{-2} \text{s}^{-1}$  PPFD ( $\text{mol m}^{-2} \text{s}^{-1}$ ),  $g_{smin}$  denotes the minimum stomatal conductance during acclimation at  $100 \mu\text{mol m}^{-2} \text{s}^{-1}$  PPFD ( $\text{mol m}^{-2} \text{s}^{-1}$ ),  $\lambda$  indicates the initial lag time before stomatal response (minutes),  $K$  is the time constant for the stomatal response (minutes).

### Estimation of Photosynthetic Biochemical Parameters

Dynamic  $\text{CO}_2$  Responses ( $A/C_i$ ) (Experimental Phase 1) was conducted following Salter *et al.* (2019). For selected treatments (5%, 25%, and 45% blue light), temporal changes in biochemical capacity were quantified by measuring photosynthetic induction across eight  $\text{CO}_2$  concentrations. Leaves were exposed to a step increase in PPFD from  $100$  to  $1000 \mu\text{mol m}^{-2} \text{s}^{-1}$  measured at eight reference  $\text{CO}_2$  concentrations ( $50, 150, 250, 400, 550, 700, 900,$  and  $1200 \mu\text{mol mol}^{-1}$ ) in randomized order to minimize hysteresis effects. A minimum one hour recovery period under low light conditions was used between successive measurements to ensure complete reequilibration of photosynthetic and stomatal processes. Net  $\text{CO}_2$  assimilation rate ( $A$ ), intercellular  $\text{CO}_2$  concentration ( $C_i$ ), and leaf temperature ( $T_{leaf}$ ) were recorded at 2-second intervals. The resulting time-resolved  $A/C_i$  curves were used to estimate three biochemical parameters: maximum carboxylation rate

of Rubisco ( $V_{cmax}$   $\mu\text{mol m}^{-2} \text{s}^{-1}$ ), maximum electron transport rate for RuBP regeneration ( $J_{max}$ ,  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ), and mitochondrial respiration in the light ( $R_d$ ,  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ).

Parameter estimation was based on the Farquhar–von Caemmerer–Berry model for  $C_3$  photosynthesis:

$$A = \min \left( \frac{V_{cmax}(C_i - \Gamma)}{C_i + K_c \left(1 + \frac{O}{K_o}\right)}, \frac{J(C_i - \Gamma)}{4.5C_i + 10.5\Gamma^*} \right) - R_d$$

Where  $K_c$  and  $K_o$  denote the Michaelis–Menten constants for  $\text{CO}_2$  and  $\text{O}_2$ , respectively ( $\mu\text{mol mol}^{-1}$  and  $\text{mmol mol}^{-1}$ ), and  $O$  indicates the ambient  $\text{O}_2$  concentration ( $210 \text{ mmol mol}^{-1}$ ). Temperature dependencies of  $K_c$  and  $K_o$  were accounted for using Arrhenius functions (temperature dependent exponential relationships describing enzyme kinetics) with reference values at  $25^\circ\text{C}$ :  $K_c = 336 \mu\text{mol mol}^{-1}$ ,  $K_j = 262 \text{ mmol mol}^{-1}$ . Activation energies were  $79.43 \text{ kJ mol}^{-1}$  for  $K_c$ ,  $36.38 \text{ kJ mol}^{-1}$  for  $K_o$ .

Model fitting used the Levenberg–Marquardt algorithm for non-linear least squares optimization in R, with initial parameter values were set to 60, 100, and  $1 \mu\text{mol m}^{-2} \text{s}^{-1}$  for  $V_{cmax}$ ,  $J_{max}$ , and  $R_d$ , respectively, with bound constraints for  $V_{cmax}$ ,  $J_{max}$  in  $[0, 300]$ , and  $R_d$  in  $[0, 5]$ . To analyze temporal dynamics, sequential  $A/C_i$  curves were fitted across the induction period. The resulting  $V_{cmax}(t)$  and  $J_{max}(t)$  time series were segmented into an activation phase (0.5–15 minutes post-induction) and a stabilization phase (15.5–60 minutes), following Salter *et al.* (2020) for quantitative characterization of the dynamic activation processes for both carboxylation and electron transport capacities following increases in irradiance.

**Steady-State A/C<sub>i</sub> Responses:** steady state A/C<sub>i</sub> curves were measured under assumed saturating light (1200  $\mu\text{mol m}^{-2} \text{s}^{-1}$  PPFD) using the following sequence of reference CO<sub>2</sub> concentrations: 400, 250, 150, 100, 50, 400, 550, 700, 850, 1000, 1200, 1500, and 400  $\mu\text{mol mol}^{-1}$ . All other environmental conditions (temperature 20°C, VPD 1.2 kPa, flow rate 500  $\mu\text{mol s}^{-1}$ ) remained constant as described above.

### **Dynamic Photosynthetic Response to Illumination on different leaf surfaces**

Photosynthetic responses to light were measured using eight LI-6800 infrared gas exchange systems (LI-COR Biosciences, Lincoln, NE, USA) with Li6800-01A fluorometer. To evaluate the effects of light intensity and light quality on both the adaxial and abaxial leaf surfaces. Plants were randomly divided into two groups. Measurements for Group A were conducted on the adaxial surface, while Group B's measurements were conducted on the abaxial surface. Initially, leaves were positioned in the 6 cm<sup>2</sup> leaf chamber of the LI-6800 gas exchange system. Baseline measurements were taken under low light conditions set at 50 PPFD (photosynthetic photon flux density) using 100% red light for a duration of 15 minutes. Following this, the light intensity was increased to 500 PPFD with 100% red light and maintained for 45 minutes. Subsequently, the light composition was altered to 90% red and 10% blue at 500 PPFD, and measurements were taken for an additional 30 minutes. After completing these measurements, the plants were adapted to 50 PPFD for 2 hours before flipping the leaves and repeating the measurements on the opposite surfaces. Photosynthesis rates and stomatal conductance were recorded at each stage of light intensity and composition.

## Randomized Diurnal Light Response

Gas exchange measurements were performed using eight LI-6800 Portable Photosynthesis Systems (LI-COR Biosciences, Lincoln, NE, USA). To ensure unbiased and randomized light conditions, the LI-6800 machines were programmed using a Python-based control program that randomized light intensity and spectral composition for each measurement event. The photosynthetic photon flux density (PPFD) was set to vary randomly between 200 and 900  $\mu\text{mol m}^{-2} \text{s}^{-1}$ , while the fractions of red and blue light were randomized within a range of 0 to 100%. Due to the limitations of the LED light source in the LI-6800 fluorometer, the far-red light fraction was constrained to values between 0 and 5%. The Python script used the `random.randint()` function to generate unique parameter combinations for measurement points throughout the day.

Measurements were only logged after stability was achieved based on pre-defined criteria. Stability was determined by continuously monitoring the slope and standard deviation of the changes in  $\text{CO}_2$  concentration ( $\Delta\text{CO}_2$ ) and  $\text{H}_2\text{O}$  concentration ( $\Delta\text{H}_2\text{O}$ ). Stability was defined as  $|\Delta\text{CO}_2| < 0.5 \mu\text{mol mol}^{-1} \text{min}^{-1}$  and  $|\Delta\text{H}_2\text{O}| < 0.5 \text{mmol mol}^{-1} \text{min}^{-1}$ , with standard deviations of  $< 0.1 \mu\text{mol mol}^{-1}$  and  $< 0.5 \text{mmol mol}^{-1}$ , respectively. Each machine waited a minimum of 30 seconds and a maximum of 300 seconds to achieve stability for any given parameter set. If stability was not achieved within this time window, the machine proceeded to the next randomized parameter set without recording a log point to thereby minimizing potential artifacts from unstable conditions. After logging a measurement, the program adjusted the chamber conditions to a new set of randomized light parameters for the next step. Environmental conditions were maintained consistently throughout the experiment, with leaf temperature set to 23°C, a reference  $\text{CO}_2$  concentration of 400  $\mu\text{mol mol}^{-1}$ , and a leaf-to-air vapour pressure deficit (VPD) of 1.2 kPa.

## **Diurnal Photosynthetic Measurements with Blue Light Pulses to the abaxial surface**

To measure diurnal photosynthetic rates, a customized dual-chamber system connected to two LI-6400XT gas analysers (LI-COR Biosciences, Lincoln, NE, USA) was utilized for simultaneous measurement of both leaf surfaces. Plants were randomly assigned to either a red-light control treatment at  $500 \mu\text{mol m}^{-2} \text{s}^{-1}$  PPFD or a treatment with periodic blue light pulses ( $100 \mu\text{mol m}^{-2} \text{s}^{-1}$  PPFD) applied to the abaxial leaf surface. In the blue light pulse treatment, the adaxial surface was illuminated with red light at  $500 \mu\text{mol m}^{-2} \text{s}^{-1}$  PPFD. Every 10 minutes, blue light at  $100 \mu\text{mol m}^{-2} \text{s}^{-1}$  PPFD was pulsed to the abaxial surface for a duration of 10 minutes. During the blue light pulse, the illumination on the adaxial surface was reduced by  $100 \mu\text{mol m}^{-2} \text{s}^{-1}$  PPFD to maintain a constant total PPFD at the leaf surface. The red light only treatment served as a control, with treatments applied in random order (red first then blue, or vice versa). Measurements were conducted continuously over a 10-hour period, with photosynthetic rates and stomatal conductance data recorded every 10 seconds.

## **Spectral Reflectance Measurement**

Spectral reflectance measurements were conducted using the PolyPen RP 410 instrument (Photon Systems Instruments, Drásov, Czech Republic), which measured reflectance across wavelengths from 380 to 1,050 nm. These measurements were performed on both the adaxial and abaxial surfaces of the leaves previously used for gas exchange measurements. The collected reflectance spectra were analysed to determine leaf optical properties, which were subsequently modelled against gas exchange-derived parameters to evaluate relationships between leaf optical properties and photosynthetic performance.

## Feature Engineering and Predictive modelling

Raw data were processed to calculate additional spectral ratios and derived features. Red/blue ( $r/b$ ), red/far-red ( $r/fr$ ), and blue/far-red ( $b/fr$ ) light ratios were calculated from the raw light intensity data ( $Q_{red}$ ,  $Q_{blue}$ ,  $Q_{far-red}$ ). Extreme outliers were capped at the 95th percentile of each variable's distribution to minimize the influence of anomalies. Additional interaction and polynomial features were generated, including the product of blue light intensity and time of day ( $Q_{blue} \times t$ ), squared blue light intensity ( $Q_{blue}^2$ ), and squared time of day ( $t^2$ ). A random forest regression model was trained to predict the quantum yield of  $CO_2$  assimilation ( $\Phi$ ) as a function of gas exchange parameters and light spectral features. The model formula included gas exchange variables ( $g_{sw}$ ), light intensities ( $Q_{red}$ ,  $Q_{blue}$ ,  $Q_{far-red}$ ), spectral ratios ( $r/b$ ,  $r/fr$ ,  $b/fr$ ), and derived features ( $Q_{blue} \times t$ ,  $Q_{blue}^2$ ,  $t^2$ ). The dataset was split into training (80%) and test sets (20%), and the model was trained with 100 trees. The mean squared error (MSE) and coefficient of determination ( $R^2$ ) were calculated to evaluate model performance. Feature importance was determined based on the percentage increase in mean squared error (%IncMSE) and to identify key predictors of  $\Phi$ .

## Analysis of Photon Energy and Flux Density

Photon energy ( $E\lambda$ ) for red ( $\lambda = 625$  nm), blue ( $\lambda = 475$  nm), and far-red ( $\lambda = 735$  nm) light was calculated using Planck's equation ( $E\lambda = hc/\lambda eV$ ) where eV is the energy conversion factor ( $1.602 \times 10^{-19}$  J/eV). Energy flux density ( $EFD\lambda$ ) for each wavelength was calculated as:  $EFD\lambda = Q\lambda \times E\lambda \times 10^{-6}$ , where  $Q\lambda$  is the photon flux density ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ ).

## Transgenic Plant Materials Generation

Transgenic *Nicotiana tabacum* L. lines were generated using Golden Gate cloning for modular assembly. The *Arabidopsis thaliana*  $H^+$ -ATPase gene (AT4G30190) was codon optimized for *Nicotiana tabacum* and synthesized by Twist Bioscience (CA, United States),

was assembled with the guard cell-specific potato *KST1* promoter and HSP18.2 terminator sequence (Plesch *et al.*, 2001; de Felippes *et al.*, 2022). This expression cassette was then cloned into the pAGM4723 binary vector containing the *NPTII* kanamycin resistance marker driven by the CaMV 35S promoter. Following *Agrobacterium tumefaciens* mediated transformation, transgene copy number was determined by quantitative PCR of the *NPTII* gene to identify single copy insertion events, and T1 plants exhibiting single copy insertions were self-pollinated and leaf discs submitted to iDNA Genomics (Norwich, UK) for segregation analysis using the same qPCR method on DNA for the *NPTII* marker. Plants identified as homozygous in the T2 generation (2 copies) were established as stable transgenic lines. From this population of homozygous lines, A31 and A32 were selected for detailed physiological characterization in this study. Azygous segregants (AZ) from the same transformation event served as genetically matched negative controls.

Functional expression of the H<sup>+</sup>-ATPase transgene was validated through quantitative RT-PCR analysis using a tissue specific normalization. Total RNA was extracted from whole leaf discs using the RNeasy Plant Mini Kit (Qiagen) with DNase I treatment, followed by integrity verification and purity assessment through spectrophotometric analysis (NanoDrop 2000, Thermo Scientific). First strand cDNA synthesized using the UltraScript cDNA Synthesis Kit (PCR Biosystems) with integrated RNase inhibitor. Quantitative PCR was performed on a CFX96 Touch Real-Time PCR Detection System (Bio-Rad, CA, United States) using qPCRBIO SyGreen Mix Lo-ROX (PCR Biosystems Ltd, London, UK), with thermal cycling parameters of 95°C for 2 minutes initial denaturation followed by 40 cycles of 95°C for 5 seconds and 60°C for 20 seconds. Critically, AHA gene specific primers AHA2-F (5'-ATGGCTGCTGAAGCTGAAGA-3') and AHA2-R (5'-TCACTTGGCAGCATCAGAGA-3') were designed to exclusively amplify the codon optimized *AtAHA2* transgene without cross amplification of endogenous tobacco *AHA* genes to ensure specificity for transgene

derived transcripts. Expression normalization was achieved using *NtGORK* which encodes a guard cell-specific outward rectifying potassium channel, amplified with primers NtGORK-F (5'-TCCGTGTTTGTGAACTCTGC-3') and NtGORK-R (5'-ACTCCACTTGCTTCACACGA-3'), as this housekeeping gene choice enabled quantification of transgene expression relative to guard cell abundance within whole leaf samples. Melt curve analysis (65-95°C, 0.5°C increments) was used to confirm single product amplification for all primer pairs. Seeds of selected lines were surface sterilized with 70% ethanol (1 min) followed by 10% sodium hypochlorite (10 min), then research grade potting media. After days post germination, uniform seedlings were transplanted to 96L pots and grown in walk-in controlled environment chambers (Aralab, Portugal) for four weeks. Environmental parameters were maintained at 25 °C (day/night), 60 ± 8% relative humidity and with no CO<sub>2</sub> concentration enrichment. Plants were grown under our generated natural fluctuating light program (described below) using HelioSpectra DYNA LED arrays with programmable spectral (5700k) and intensity control.

### **Natural Fluctuating Light Program Generator**

We developed a simple biologically informed algorithm to generate naturalistic light fluctuation patterns while maintaining user determinable daily light integrals (DLI). The algorithm uses a temporal modulation function that mimics diurnal solar patterns with superimposed stochastic variation. We have also developed a web based interface for generating custom natural light programs and is available as [Natural Light Generator v3](#) hosted on Streamlit. The temporal modulation function  $M(\tau)$  for normalized time  $\tau \in [0, 1]$  was defined as:

$$M(\tau) = \begin{cases} 2\tau, & 0 \leq \tau < 0.5, \\ [4pt]2(1 - \tau), & 0.5 \leq \tau \leq 1. \end{cases}$$

This function generates a symmetric triangular profile peaking at solar noon ( $\tau = 0.5$ ) with  $M(0.5) = 1.0$ . Therefore, the instantaneous photosynthetic photon flux density (PPFD) values were generated stochastically:

$$PPFD_i \sim U[I_{min}, I_{max}M(\tau_i)]$$

where  $U[a,b]$  denotes a uniform random distribution over interval  $[a,b]$ . For example, the light program generated and used for this study has  $I_{min} = 16 \mu\text{mol m}^{-2} \text{s}^{-1}$  (twilight conditions),  $I_{max} = 1384 \mu\text{mol m}^{-2} \text{s}^{-1}$  (peak sunlight), and  $\tau_i = i/N$  represents the normalized time for step  $i$  out of  $N$  total steps.

To achieve the target DLI that is representative of typical species habitats (i.e., shade-tolerant, sun-like) and is user customizable, a normalization factor  $\alpha$  was applied:

$$\alpha = \frac{DLI_{target}}{DLI_{initial}}, \quad PPFD_{final,i} = \min(\alpha PPFD_i, I_{max})$$

where  $DLI_{initial}$  was calculated via trapezoidal integration with  $\Delta t = 300 \text{ s}$  (5 minutes) set as default.

The generated light program used in this study consisted of 133 sequential PPFD steps (5 minutes each, 11.08-hour photoperiod) executed using HelioSpectra DYNA LED growth modules (Text file downloadable from our web based interface). Light uniformity across the growth area was verified by quantum sensor grid measurements. The light program used in this study has a PPFD range of 16-1,384  $\mu\text{mol m}^{-2} \text{s}^{-1}$  and has a coefficient of variation of 87.6% with a total daily light integral of 17.1  $\text{mol m}^{-2} \text{d}^{-1}$ . The kinetics of the light program has an average transition of 8.2 significant changes ( $>100 \mu\text{mol m}^{-2} \text{s}^{-1}$ ) per hour.

### Diurnal Gas Exchange Measurement

Leaf gas exchange was measured using 9 LI-6800 Portable Photosynthesis Systems (LI-COR Biosciences) equipped with a 6  $\text{cm}^2$  chamber head and multiphase flash fluorometer. Chamber conditions were controlled at 25°C leaf temperature, 400  $\mu\text{mol mol}^{-1} \text{CO}_2$ , 70%

relative humidity, and 500  $\mu\text{mol s}^{-1}$  flow rate. During diurnal measurements, the LI-6800 light source replicated the same intensity patterns from the growth fluctuating light program using compatible Light generator's exported JSON file in an "AutoGen-Loop" program. Each leaf was measured twice on separate days under identical PPFD sequences but different spectral compositions: pure red light (625 nm) or a red:blue mixture (90% red at 625 nm, 10% blue at 475 nm). Measurement order was randomized across genotypes and days to minimize systematic bias. Data were logged at 5-second intervals throughout the photoperiod (7,990 data points per leaf measurement).

#### **4. Results**

This PhD project contains 7 data chapters and has demonstrated that blue light signalling serves as a multiscale regulatory mechanism in plants for controlling carbon and water balance. This mechanism operates through a hierarchical cascade beginning with photoreceptor activation and progressing through to overall plant performance. The integration of methodological innovations in imaging temperature response and anatomical characterization (Chapters 2 and 3), developmental plasticity analysis (Chapter 4), spectral delivery optimization (Chapter 5), the discovery of a blue light compensatory mechanism (Chapter 6), and molecular enhancement of natural fluctuating light response (Chapter 7) has yielded novel methods and insights into the mechanisms governing light perception and photosynthetic gas exchange coordination across multiple species (i.e., wheat, barley, tobacco, strawberry), with some critical to global food security.

The thermographic framework standardized in Chapter 2 standardised infrared imaging from a qualitative observation tool into a quantitative phenotyping platform at scale. The technical

rigor established here aligns with recent advances showing that thermal imaging can detect genotypic variation in dynamic stomatal behaviour (McAusland et al., 2014) with heritabilities comparable to destructive biochemical assays (Ferguson *et al.*, 2021; Pignon *et al.*, 2021). Our standardization protocols provide reproducible calibration methods, thereby establishing thermography as a legitimate high throughput phenotyping tool for stomatal traits. This method, along with the findings from the remaining chapters, will be highly useful in developing future climate resilient crops with altered gas exchange response patterns, such as optimized stomatal responses to blue light.

In chapter 3 the discovery of differential EPF1 effects between leaf surfaces represents more than anatomical curiosity, as it reveals fundamental constraints on how plants optimize gas exchange. The 59.5% reduction in abaxial stomatal density versus 19.9% adaxially in barley EPF1 overexpressors demonstrates that developmental signalling pathways exhibit surface specific sensitivities. The method innovation of using chlorophyll autofluorescence confocal microscopy has enabled, for the first time, large scale and high resolution quantification of over a million stomata, making spatial analysis relevant to physiological functions possible. The spatial heterogeneity analysis revealed 55% increased variance in stomatal distribution on EPF1 abaxial surfaces, which has important implications for water use efficiency under field conditions (Bertolino *et al.*, 2019).

Longitudinal tracking of blue light priming effect (Chapter 4) revealed that blue light operates through distinct temporal hierarchies of plant memory. The immediate biochemical responses with 35.4%  $J_{max}$  enhancement and 15.9%  $V_{cmax}$  increase under 35% blue light both dissipate within 30 days post priming. However, structural modifications persist; the 53.1% increase in stomatal density in high-blue-primed plants represents developmental commitments that might result in drought resilience months later. The drought protection

mechanism appears multifaceted. While low blue primed plants showed 16%  $V_{cmax}$  reduction under water limitation, and high blue primed plants maintained capacity (2% reduction), suggesting persistent metabolic adaptation beyond visible structural changes. Furthermore, the preferential enhancement of  $J_{max}$  over  $V_{cmax}$  aligns with recent discoveries that blue light specifically upregulates cyclic electron flow components (Degen & Johnson, 2024; Woodford *et al.*, 2024), providing photoprotection during stress episodes through enhanced ATP generation without accumulating excess NADPH (Ermakova *et al.*, 2024).

The finding within Chapter 5 demonstration that abaxial illumination maintains 77-79% of adaxial photosynthetic capacity represents a paradigm shift in our understanding of leaf optical properties and gas exchange optimization. The 8% enhancement in daily carbon assimilation through periodic 10 minute blue pulses to the abaxial surface, without increasing total photon input suggesting a fundamental advance in photon use efficiency. The temporal optimization of maximum benefit during mid to late photoperiod when baseline conductance naturally declines aligns with circadian regulation of guard cell metabolism. Our modelling analysis further revealed stomatal conductance as the dominant predictor of  $CO_2$  quantum yield (68.4% feature importance) and thus provides the computational framework for predicting optimal pulse timing under diverse environmental conditions.

Chapter 6 resolves the critical question of whether water use efficiency gains from reduced stomatal density compromise dynamic light responsiveness particularly to red and blue light. The wheat EPF1 overexpression lines demonstrated that despite 20-30% lower baseline conductance under red light, blue light supplementation induced amplified responses with 90% relative conductance increases from steady state value under red light in EPF1 plants versus 49% in wild type on abaxial surfaces (Figure 6.2). It was postulated that this compensation mechanism operates through altered  $C_i$  to stomatal aperture relationships.

The chronically lower intercellular CO<sub>2</sub> in reduced density leaves (180-200 μmol mol<sup>-1</sup> versus 240-260 μmol mol<sup>-1</sup> in wild type) creates a primed state for blue light responsiveness. Recent discoveries that CBC1/CBC2 kinases link blue light and CO<sub>2</sub> signals in guard cells by inhibiting S-type anion channels provide the molecular framework support for this compensation (Hiyama *et al.*, 2017a), with lower baseline C<sub>i</sub> enhances sensitivity to blue light triggered CBC signalling. The surface specific nature of these responses, with stronger compensation abaxially where EPF1 effects were greatest, demonstrates that developmental modifications and physiological responses are spatially coupled. This coupling ensures that genetic interventions targeting stomatal density need not sacrifice the dynamic control essential for fluctuating field conditions which can be a major concern in crop engineering work for water use efficiency (Hepworth *et al.*, 2015; Caine *et al.*, 2019).

The enhancement of H<sup>+</sup>-ATPase transcript in guard cells (Chapter 7) reduced transition penalties from 17.3% to 6.9% under fluctuating light addresses the fundamental constraint limiting photosynthetic efficiency in nature. The preservation of photosynthetic biochemistry ( $V_{cmax}$ : 57-61 μmol m<sup>-2</sup> s<sup>-1</sup> across genotypes) while dramatically altering stomatal kinetics validates the strategy of targeting actuator capacity rather than sensor sensitivity. The unexpected abolishment of blue light enhancement during photosynthetic induction in AHA2 lines could suggest system level saturation, with vastly expanded H<sup>+</sup>-ATPase pools, even partial activation through red light driven metabolism generates sufficient proton motive force for rapid opening. This finding aligns with recent structural work showing sequential phosphorylation at Thr948 followed by Thr881 creates a molecular coincidence detector (Fuji *et al.*, 2024; Hayashi *et al.*, 2024), where excess AHA2 protein reduces the requirement for full dual phosphorylation. Furthermore, the matched growth and measurement conditions using our stochastic light program with 133 transitions over 11 hours proved critical for isolating engineered effects from acclimation artifacts. Previous studies conflating steady

light growth with fluctuating measurements likely underestimated potential gains from enhanced stomatal kinetics.

## **5. Discussion**

This project establishes blue light as a multiscale regulatory axis for coordinating carbon acquisition with water loss by linking photoreceptor level signalling to stomatal physiology, canopy gas exchange under realistic light fluctuations, and ultimately biomass formation. The combined methodological, anatomical, physiological, and genetic strands show how spectral information can be engineered and deployed to minimise transition penalties and increase daily carbon gain without incurring adverse biochemical trade-offs. In doing so, the work moves beyond steady state characterisations to the dynamic regimes in which crops actually operate, and provides a practical route for immediate gains in controlled environments while outlining genetic levers for field translation. A central conceptual advance is that blue light responses form a hierarchical cascade, from phototropin activation and H<sup>+</sup>-ATPase phosphorylation through to leaf-surface specific stomatal behaviour with system level consequences under fluctuating irradiance. The thesis conclusion articulates this as a multiscale mechanism validated across species (wheat, barley, tobacco, strawberry), integrating new tools (Ch.2–3), induced plasticity (Ch.4), targeted light delivery (Ch.5), compensation under architectural constraint (Ch.6), and guard cell molecular enhancement (Ch.7).

## **5.1. Methodological foundations: turning “qualitative” optics into quantitative physiology**

Two enabling contributions underpin the biological findings. First, Chapter 2 turns infrared thermography from an indicative, qualitative technique into a calibrated, high throughput phenotyping platform for stomatal traits with explicit guidance on emissivity determination, boundary layer characterisation, and protocol design for dynamic kinetics. These standardisations allow reproducible estimation of stomatal conductance indices and water status at scale, which aligned with recent demonstrations that thermal traits carry robust heritability and track dynamic stomatal behaviour. Second, Chapter 3 establishes leaf surface resolved, million cell scale stomatal mapping using chlorophyll autofluorescence confocal imaging, enabling spatial statistics previously inaccessible. In barley lines overexpressing EPF1, abaxial density was reduced by 59.5% whereas adaxial density fell by 19.9%, revealing strong surface-specific sensitivity of the developmental pathway. Variance in stomatal spatial distribution increased by ~55% on the abaxial surface, highlighting that density changes are accompanied by altered heterogeneity which is a factor with direct implications for diffusional supply and local boundary layer coupling. The dataset encompasses >1,000,000 stomata and >18,000 mm<sup>2</sup> of leaf area, providing the statistical power to connect anatomy to gas-exchange function. These method advances matter because the subsequent chapters quantify processes that are intrinsically variable in space and time. Without calibrated thermal imaging and large N stomatal maps, it would be easy to overinterpret small, nongeneralizable effects. Here, the foundations support the more ambitious claims that follow.

## **5.2. Developmental plasticity and spectral memory: blue light as a programming signal**

Chapter 4 shows that elevating blue light fraction drives a temporally stratified plasticity. Immediately, photosynthetic biochemistry is enhanced ( $J_{\max}$  +35.4%,  $V_{\max}$  +15.9%), but these gains wash out within ~30 days post-priming. Structurally, however, a 53.1% increase in stomatal density persists, indicating a “slow memory” in developmental programs even after biochemical acclimation relaxes. This temporal decoupling implies at least two memory systems: a labile biochemical state set by current irradiance history, and a committed architectural state reflecting earlier spectral cues. The practical consequence is that blue light can be used both as a short term performance lever and as a developmental programming signal but the two timescales must be managed differently in cultivation strategies.

## **5.3. Targeted light delivery: exploiting surface asymmetry to raise daily carbon gain**

With these anatomical and memory constraints characterised, Chapter 5 turns to spectral delivery. Using an unbiased, high-throughput gas-exchange protocol to discover response structure, the work identifies a pragmatic tactic: pulsing a small blue fraction at the abaxial surface where stomata predominate superimposed on red light. This approach increased daily  $\text{CO}_2$  assimilation by  $8.2 \pm 1.3\%$  while minimising energy input, demonstrating that targeted, temporally structured blue application can harvest “free” dynamic efficiency otherwise lost in transition penalties. This is a diurnal integrated gain, not a transient spike, and therefore agronomically meaningful. Mechanistically, the benefit reflects the rapid phototropin– $\text{H}^+$ -ATPase pathway’s capacity to accelerate stomatal opening during up-steps, coupled to abaxial stomatal dominance. By synchronising stomatal kinetics with incident

PPFD on the surface where diffusional control is strongest, the pulsed blue tactic reduces the lag between light availability and CO<sub>2</sub> supply. In other words, it narrows the classic “dynamic mismatch” between biochemistry and diffusion that can erode 10–40% of theoretical daily carbon gain under fluctuating light.

#### **5.4. Genetic constraint and compensation: EPF1 lines reveal adaptive blue sensitivity**

Chapter 6 examines how architectural constraints feed back into light sensitivity. In wheat EPF1 overexpressors with 11–20% lower stomatal density (abaxial reduction stronger), abaxial blue illumination elicited up to ~90% increases in stomatal conductance compared to ~49% in wild type under the same spectral conditions. The lines also maintained 15–20% higher water use efficiency across light regimes. The interpretation advanced is that diffusional limitation under red light (lower intercellular CO<sub>2</sub>) “primes” the guard cell signalling apparatus, heightening responsiveness to blue light and compensating for reduced pore number, a surface specific compensation that would be invisible without directional illumination. This shows that breeding for lower density need not inevitably reduce dynamic capacity if blue-light pathways are concurrently leveraged. This chapter has been structured as a journal article, readers can refer to Chapter 6 for the published version details as included in the thesis table of contents.

#### **5.5. Molecular enhancement under realistic light: guard-cell AHA2 overexpression**

Chapter 7 tests whether boosting the guard cell H<sup>+</sup>-ATPase, which is the effector at the end of the blue-light cascade can relieve dynamic limitations under a naturalistic light regime. Two independent transgenic tobacco lines (A31, A32) achieved ~150-fold higher AHA2 transcript abundance in guard cells, yet mesophyll biochemistry remained unchanged. This

decoupling is crucial: the manipulation isolates diffusional control without perturbing photosynthetic enzyme capacity, avoiding a common confound in whole plant overexpression studies. The fluctuating light program used here mimicked canopy dynamics over an 11.08 hour photoperiod, with a daily light integral of  $\sim 17.1 \text{ mol m}^{-2} \text{ d}^{-1}$  and 78 major transitions ( $|\Delta\text{PPFD}| > 100 \text{ } \mu\text{mol m}^{-2} \text{ s}^{-1}$ ;  $\sim 7$  significant transitions per hour), spanning low ( $< 200$ ), medium (200–800), and high ( $\geq 800 \text{ } \mu\text{mol m}^{-2} \text{ s}^{-1}$ ) zones representative of semi open canopies. Under this regime, azygous plants forfeited 17.3% of potential daily carbon to transition performance deficits (TPD), whereas an AHA2 line reduced this penalty by  $\sim 60\%$ . Network analyses showed tighter  $A-g_{\text{sw}}$  coupling and a reversal of the typical negative  $g_{\text{sw}}-WUE$  relationship in one line, consistent with re-optimised stomatal behaviour under transients. Growth over four weeks under the same program produced 31–41% higher dry biomass (numerically; one line significant in one-tailed tests), with an integrated phenotype index  $\sim 18.7\text{--}18.8\%$  above controls which showed convergent across independent lines. Two system level insights arise. First, matching growth and measurement light regimes is decisive: prior dynamic studies often exposed constant light grown plants to sudden fluctuations, confounding acclimation state with response capacity. Using the identical 133-step program for both growth and measurement avoids this artefact and likely explains the clarity with which TPD and its determinants were resolved. Second, purely diffusional enhancement via guard cell AHA2 can shift the entire trait network into a more favourable operating space without “pulling” on biochemical capacity which is a cleaner lever than whole plant overexpression, and one immediately compatible with crop pipelines given tissue-specific promoters.

## 5.6. Synthesis: a practical route to higher daily carbon gain

Collectively, Chapters 4–7 outline a progression from environmental programming (blue fraction and priming), through delivery optimisation (abaxial blue pulses), to architectural constraints (density and heterogeneity), and finally to molecular reinforcement (H<sup>+</sup>-ATPase). The central practical message is that transition costs — the “tax” plants pay when light changes — are both measurable and reducible. In absolute terms, tactics demonstrated here recovered on the order of 8–10% of daily CO<sub>2</sub> assimilation (abaxial pulses), with further reductions in TPD via molecular enhancement. These effects compound: a plant with faster blue-driven stomatal kinetics will benefit more from directed blue pulses; a genotype with lower density can maintain dynamic capacity if abaxial blue sensitivity is harnessed; and a canopied crop operating under frequent sunflecks will benefit disproportionately from any reduction in TPD.

## 5.7. Limitations and boundary conditions

The work is explicit about scope. Dynamic performance benefits depend on the frequency and magnitude of irradiance transitions; under very stable light, the gains diminish, while in highly intermittent canopies they can be substantial. The fluctuating program used here is moderate (DLI ~17.1 mol m<sup>-2</sup> d<sup>-1</sup>; CV ~87.6%) and representative of semi-open conditions, but translation to dense field canopies will require spectrum-aware modelling of within-canopy blue flux and leaf orientation. The EPF1 compensation result is surface-specific and depends on abaxial stomatal dominance; species with more amphistomaty or inverted distributions may respond differently. Finally, while guard-cell AHA2 overexpression preserved J<sub>max</sub> and V<sub>cmax</sub> at wild-type levels, long-season, deficit-irrigated conditions

could reveal trade-offs not captured here; water-use optimisation under heat and VPD extremes should be tested before widescale deployment. The thesis conclusion discusses these systemic limitations and the importance of matching growth and assay regimes when assessing dynamics.

## **5.8. Implications for controlled environments and field breeding**

For controlled environments (greenhouses, vertical farms), the immediate recommendation is to use red-dominant spectra supplemented with modest, temporally pulsed blue directed toward the abaxial surface (via intercanopy or reflective delivery), tuned to periods of rising PPFD to pre-empt induction lags. This is compatible with energy constraints because blue duty cycles can be low while still delivering rapid stomatal signalling, as demonstrated by the day-integrated gains. Integration with dynamic lighting control systems should use leaf-surface aware sensors and short-horizon forecasts of PPFD transitions to schedule blue pulses just ahead of up-steps.

For field breeding, two complementary levers emerge. First, developmental programming via spectral priming could set stomatal density trajectories and leaf surface distributions early in ontogeny, potentially interacting with natural amphistomaty patterns; the persistence of density changes after biochemical acclimation fades suggests room for durable architectural tuning. Second, guard-cell targeted enhancement of H<sup>+</sup>-ATPase is a clean, mechanistically grounded way to accelerate stomatal kinetics without perturbing

photosynthetic enzyme stoichiometry, reducing TPD under sunfleck-rich conditions. Moreover, density reduced genotypes can retain dynamic capacity if abaxial blue sensitivity is leveraged — an important message for water-saving breeding that fears trading away responsiveness.

## 6. References

### Published chapters with links:

- **Chapter 2** — Fan, M., Stamford, J., & Lawson, T. (2024). Using Infrared Thermography for High-Throughput Plant Phenotyping. In *Photosynthesis: Methods and Protocols* (pp. 317-332). New York, NY: Springer US. DOI: [https://doi.org/10.1007/978-1-0716-3790-6\\_16](https://doi.org/10.1007/978-1-0716-3790-6_16).
- **Chapter 3** — Fan, M., Moss, K. A., Jindal, P., Kasznicki, P., Davey, P., Laissue, P. P., & Lawson, T. (2025). Large-scale quantification of stomatal patterning in barley leaves overexpressing epidermal patterning factor 1 reveals differential stomatal density between the adaxial and abaxial surfaces and spatial heterogeneity that impact stomatal function. *New Phytologist*. DOI: <https://doi.org/10.1111/nph.70514>.
- **Chapter 6** — Fan, M., Dorussen, D., Gherli, H., & Lawson, T. (2025). Reduced stomatal density in wheat overexpressing EPIDERMAL PATTERNING FACTOR1 differentially affects red and blue light responses. *Plant Physiology*, 199(1), kiaf379. DOI: <https://doi.org/10.1093/plphys/kiae423>.

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