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# Partial shade effects of dual land use systems: Harnessing plant acclimation to drive sustainable farming solutions

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ABSTRACT

Dual land-use systems such as agroforestry (AFS) and agrivoltaics (APV) are increasingly proposed as climate-resilient agricultural strategies, yet concerns remain regarding reduced light availability and its impact on crop performance. We conducted a multi-site field study across AFS and APV systems in Germany to assess photosynthetic acclimation in five arable crops (barley, beans, potatoes, cabbage, maize) using light response curves derived from leaf gas-exchange measurements using a portable photosynthesis system (LI-6800, LI-COR Biosciences, Lincoln, NE, USA). Across sites, crops consistently exhibited reduced dark respiration (Rd; 12–46%) and light compensation point (LCP; 20–54%) under shaded conditions relative to full sun, indicating acclimation that lowers respiratory costs and the irradiance threshold for positive carbon balance. In contrast, light-saturated assimilation (Asat) and apparent quantum yield (AQY) showed variable responses depending on crop type and system. These results demonstrate that commonly cultivated, typically sun-adapted crops exhibit physiological plasticity under heterogeneous field shading, particularly through reductions in Rd and LCP, challenging the assumption that such crops are inherently limited in shaded agricultural systems. While these responses do not directly translate to yield outcomes, they suggest that crops can maintain carbon balance under moderate shading and provide field-based evidence of photosynthetic acclimation and plasticity in these dual land-use systems.

## 1. Introduction

The global food system is at a critical juncture, facing unprecedented challenges of climate change causing decreasing yields that threaten future food security. In Europe, warm season droughts are increasing both in occurrence and severity, while spring precipitation shows higher uncertainty and snow water equivalent in the Alps is at historical lows, all causing a widespread decrease in groundwater (Brás et al., 2021; Hari et al., 2020; Ionita et al., 2020; Markonis et al., 2021; Toreti et al., 2023). Yield patterns in Central Europe are already experiencing declines due to such increased impacts of climate change-induced water shortage (Brás et al., 2021; Lüttger and Feike, 2018), leading to increased uncertainty for farmers and the agricultural sector at large.

Addressing these mounting pressures urgently requires innovative solutions that integrate sustainability with crop resilience that will guarantee adequate production for the future. Agroforestry (AFS), the integration of trees with agriculture, and agrivoltaics (APV), the combination of crop cultivation with photovoltaic panels, have emerged as promising dual land-use approaches that optimize resource utilization and promote resilience, offering transformative potential. The microclimate changes provided by the panels and trees are known to ameliorate some of the negative climate change effects by reducing temperature extremes, windspeed, and evapotranspiration (Jacobs et al., 2022; Schoeneberger et al., 2012) thereby also increasing soil moisture and water availability (Barron-Gafford et al., 2019; Marrou et al., 2013; Pataczek et al., 2023; Weselek et al., 2021). Beyond their agronomic and microclimatic benefits, agrivoltaic systems also contribute directly to renewable energy generation while maintaining agricultural production on the same land area, thereby addressing competition between food and energy production and improving overall land-use efficiency. This dual-function approach has been highlighted as a key pathway for simultaneously advancing agricultural sustainability, energy security, and climate-change mitigation while alleviating concerns regarding land-use conflicts associated with large-scale solar

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energy deployment (Chopdar et al., 2025; Giri and Mohanty, 2026). However, plant physiological responses within these systems remain insufficiently understood. The feasibility of arable crops, typically bred for open-field conditions, to acclimate to these altered systems remains insufficiently understood.

Both systems introduce new complexities by changing light availability patterns – a crucial driver of growth and yield (Croce et al., 2024). As the cornerstone of photosynthesis, light is often considered the most limiting factor in these systems (Ehret et al., 2015). The efficiency of photosynthesis, an ultimate driver of organic matter production (Croce et al., 2024), depends on multiple factors, including the interception of photosynthetic active radiation (PAR) and the plant's ability to adapt its metabolic processes (Farquhar et al., 1980; Valladares and Niinemets, 2008). Shade-tolerant plants have evolved strategies to optimize their light-use efficiency in order to perform better in low light conditions and minimize $CO_2$ losses. These strategies include morphological adaptation of leaf surface, reduced respiration, stomatal adaptations, etc. (Martinez-Garcia and Rodriguez-Concepcion, 2023; Valladares and Niinemets, 2008). Although much is already known about shade acclimation within crop canopies, the shading imposed by agroforestry and agrivoltaic systems is qualitatively different from forest canopies and crop self-shading, therefore requiring direct study. Tree canopies in AFS create heterogeneous, temporally stable shade that varies with crown architecture and seasonality (Arenas-Corraliza et al., 2019; Reynolds et al., 2007). In contrast, APV systems generate more structured and dynamic shading, characterized by alternating sunflecks and open gaps as panels track the sun or cast regular shadows (Semeraro et al., 2024; Weselek et al., 2021). These distinct light regimes mean that crops may face either gradual, diffuse shading (AFS) or temporal fluctuations in PAR (APV), with implications for light interception and carbon gain (Murchie et al., 2018; Wang et al., 2020). These systems therefore expose crops to light patterns and microclimatic conditions not experienced under their own leaf canopies. These differences directly impact key photosynthetic parameters, which are central to evaluating plant acclimation to shading. Additionally, shade acclimation is highly species-specific: while some cereals like barley or wheat have been observed to exhibit physiological plasticity traits that allow sustained productivity under shade (Arenas-Corraliza et al., 2019), others, such as legumes or C4 crops, may rely on entirely different strategies or struggle under the same conditions (Chen et al., 2014; Gong et al., 2015). Furthermore, the capacity of arable crops, bred for full-sun, open-field conditions, to acclimate to the partial and often heterogeneous shading imposed by these systems remains poorly, if at all, understood (Ehret et al., 2015; Weselek et al., 2021). In this study we focus specifically on photosynthetic parameters derived from light response curves (light--saturated assimilation, apparent quantum yield, light compensation point and dark respiration) to elucidate how arable crops adjust photosynthesis under the unique heterogeneous light conditions of these systems.

Phenotypic plasticity, the ability to optimize metabolic demands and photosynthetic efficiency under variable conditions, has been pinned as a critical trait for survival in variable environments that may hold the key to mitigating climate impacts on agriculture (Gibbin et al., 2017). Existing studies on field-level metabolic responses under AFS and APV systems are lacking, as many current shading studies rely on controlled environments or uniform shading methods like netting, which fail to replicate the complex microclimatic pattern of real-world field conditions (Laub et al., 2022; Stallknecht et al., 2023). While shading effects on photosynthesis have been widely studied in controlled environments and within crop canopies, less is known about how arable crops typically grown in full sun respond to the heterogeneous and dynamic light conditions imposed by agroforestry and agrivoltaic systems under field conditions. In particular, field-based assessments of key photosynthetic parameters across diverse sites and crops remain limited. Therefore, current growth models do not produce accurate predictions (Frantz and Bugbee, 2005). This gap underscores the need for multi-site investigations that encompass diverse soil types, crop species, and environmental conditions to unravel how plants adapt to heterogeneous light availability. In this study we use 'acclimation' to describe short-term and reversible physiological or morphological changes and 'plasticity' as the capacity of an organism to alter its phenotype in response to variations in the environment. Together, these processes contribute to what we broadly refer to as 'adaptation.' Elucidating the intricacies of how plant species respond to variable light conditions under these systems, especially on the field level, is crucial to understanding the potential for acclimation of arable crops in dual land use settings.

In this study we address the knowledge gap by conducting a multi-site field study across AFS and APV systems, directly quantifying photosynthetic acclimation to five arable crops under real-world heterogeneous light environments. This approach allows us to evaluate whether acclimation patterns observed under controlled or uniform shading conditions translate to complex field environments and varying arable crop species. Light response curves, a fundamental tool for quantifying how photosynthesis responds to changing light levels (Farquhar et al., 1980), are used as the central diagnostic tool to evaluate the key photosynthetic parameters. We focus on four key parameters derived from light response curves: the light-saturated net assimilation rate (Asat), representing the maximum $CO_2$ assimilation under non-light-limited conditions; the apparent quantum yield of $CO_2$ fixation (AQY), which quantifies the efficiency of $CO_2$ assimilation under low-light conditions; the light compensation point (LCP), defined as the light intensity at which net $CO_2$ exchange is zero; and dark respiration (Rd), the rate of $CO_2$ release in the absence of photosynthesis (Busch et al., 2024). These metrics provide insights that allow for assessing crop photosynthesis and light use efficiency that underpin crop resilience in shaded environments. Furthermore, the five studied crops represent both C3 (barley, beans, potatoes, cabbage) and C4 (maize) photosynthetic pathways, which are known to differ fundamentally in their responses to light limitation. This diversity also allows us to assess whether the shading imposed by agroforestry and agrivoltaic systems elicits similar or divergent responses between C3 and C4 crops.

By compiling data across diverse conditions in a temperate climate, our research aims to uncover trends in photosynthetic acclimation that contribute to understanding crop responses within AFS and APV systems. Beyond advancing fundamental plant physiology knowledge, our findings provide a basis for improving the integration of arable crops in these systems under changing environmental conditions, contributing to ongoing efforts to develop more sustainable and resilient agricultural systems under escalating climate challenges.

## 2. Materials and methods

### 2.1. Study sites

Field experiments were conducted across five distinct sites in Germany (Fig. 1) during the 2023 and 2024 growing seasons. The Eckartsweier (EW) and Heidfeldhof (HFH) sites represent agroforestry systems, while Strasskirchen (STR), Bürgewald (BW), and Heggelbach (HG) are agrivoltaic (APV) systems with solar modules mounted at varying heights and orientations. The soils range from sandy to loam textures, and management practices vary from biodynamic to conventional. Altitudes range from 122 to 656 m asl, with average annual temperatures between 8.8 and 10.7°C and precipitation from 685 to 1022 mm. The crops investigated in this study were barley (*Hordum vulgare*), maize (*Zea mays*), cabbage (*Brassica oleracea*), potatoes (*Solanum tuberosum*), and field beans (*Vicia faba*), all widely grown and agronomically important varieties commonly used by farmers in Germany, ensuring relevance for regional agricultural practice. Operationally, APV shade in these sites is structured and tracking (regular sunflecks/open gaps as panels move or cast periodic shadows), whereas AFS shade is heterogeneous and temporally stable, governed by crown

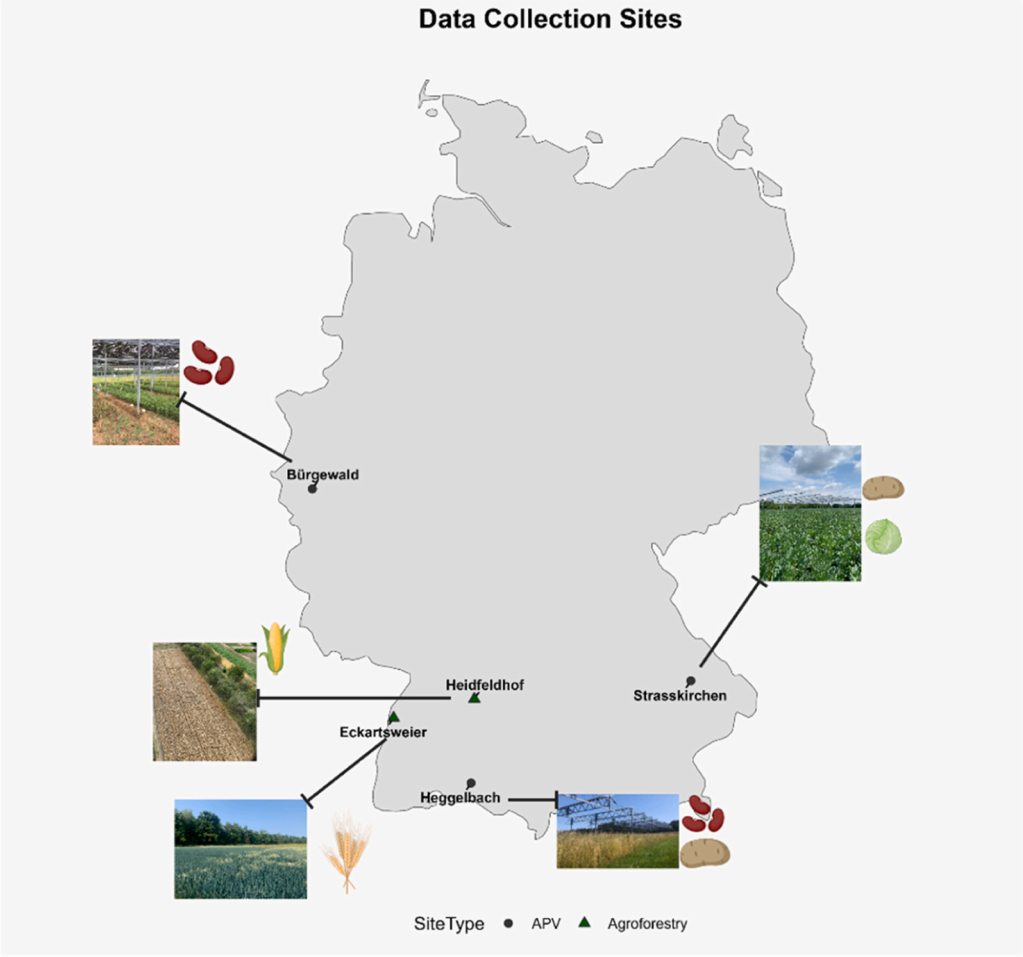


**Fig. 1.** Map of site locations and their crops (Note: site markings are not to scale). Photos of Bürgewald, Eckartsweier, Heggelbach, and Strasskirchen are by authors. Photo of Heidfeldhof by Zoe Schindler. All photographs are original and reproduced with permission.

architecture and seasonality; this distinction underpins our system comparisons. A more complete summary of the site characteristics, including geographic coordinates, elevation, climatic data, soil types, cultivars, management practices, and system specifics are presented in Appendix B.

### 2.2. Gas exchange measurements

This study assessed the effects of varying light conditions on photosynthetic responses using light response curves (LRCs) generated with a portable photosynthesis system (LI−6800, LI-COR Biosciences, Lincoln, NE, USA). Light response curves were selected as they provide a robust and widely applied approach for quantifying key photosynthetic parameters (Asat, AQY, Rd, LCP) and allow direct assessment of plant responses to varying irradiance, which is central to evaluating acclimation under heterogeneous shading conditions. In situ measurements of leaf gas exchange were performed during the primary growth season, June–August, on the flag leaf or outermost viable leaf. Measurements were taken according to time availability and therefore range in developmental stages. In APV fields measurements were taken directly under the panel, between the panels, and in a reference field. At all APV sites, the reference field plots are adjacent to the plots under the panels and share the same design and crop growth conditions, but are exposed to full open sunlight. The EW agroforestry field is oriented north-south, with the tree stand located on the east side, resulting in morning shade. Measurements were taken at two data points: 3–5 m into the field under morning shade, and 12–15 m into the field where the plants receive full sunlight. In the HFH field, which is positioned east-west, a shading gradient (imposed by the tree row) was measured using the LI−250A Light Meter (LI-COR Biosciences, Lincoln, NE, USA). Light intensity levels are reported as percent PAR in figures and text, following common convention in agroforestry and shading studies. In this study, % PAR denotes percent PPFD relative to the open-field reference (400–700 nm, $\mu$mol photons $m^{-2}s^{-1}$), measured in situ with the LI−250A; thus, “55% PAR” indicates a 45% reduction from the paired open-field PPFD at the same site/date. Monitoring at HFH took place in early June 2024 over the course of several hours and days in order to establish the shading gradient at 30% PAR, 55%, 70%, and 100%. This is represented at meters 1, 3, 8, and 15. Due to differences in site design and measurement approaches, light environments are interpreted as relative categories within each site rather than directly comparable quantitative values across all systems. Accordingly, analyses focus on within-site comparisons of photosynthetic responses across defined light environments. Further details on the field sites and systems can be found in Table 1.

Each light response curve represents an independent biological replicate measured on a different plant within a given treatment. Treatments were defined based on light environment (e.g., PAR level or spatial position relative to panels or tree rows), and replicate plants were selected within each treatment area. Sampling points were spatially distributed to avoid repeated measurements on neighboring individuals and to capture within-treatment variability. Due to the constraints of multi-site field experiments, full randomization of treatments was not feasible. However, measurements were conducted across representative

**Table 1**
Measurement details per site. Note: BBCH stage refers to the BBCH scale, a standardized coding system for the phenological development stages of plants (Hack et al., 1992). BBCH growth stages were recorded in situ by visual assessment of crop developmental characteristics according to the standardized BBCH scale (Hack et al., 1992). Representative photographs of the field sites and cropping systems are provided in Fig. 1, and further photos are provided in Appendix B.".

| Site | System | Crop | Measurement period | BBCH (growth) stage at collection | Leaf position |
|---|---|---|---|---|---|
| **Heidfeldhof (HFH)** | Agroforestry | Maize | July 2024 | 30 | last fully developed leaf<br>n = 42 |
| **Eckartsweier (EW)** | Agroforestry | Summer barley | June 2023 | 80 | flag leaf<br>n = 10 |
| **Strasskirchen (STR)** | Agrivoltaic | Potatoes | July 2024 | 60–65 | uppermost, fully developed leaf<br>n = 24 |
| | | Cabbage | July 2024 | 40–42 | outer, healthy leaf<br>n = 12 |
| **Bürgewald (BW)** | Agrivoltaic | Field beans | July 2023 | 70 | fully developed, healthy leaf<br>n = 12 |
| **Heggelbach (HG)** | Agrivoltaic | Potatoes | July 2023 | 60–63 | last fully developed leaf<br>n = 12 |
| | | Field beans | May 2023 | 32–34 | last fully developed leaf<br>n = 22 |

positions within each treatment, and all replicates were treated as independent observations for statistical analysis.

Photosynthetic activity was measured using light response curves, recorded at 10 light intensities (Qin = 2000, 1500, 1000, 750, 500, 250, 100, 50, 0, 2000 μmol $m^{-2}$ $s^{-1}$ PPFD). The protocol followed the automated light response curve program of the LI−6800, with each value recorded after stabilization criteria were met, defined as consistent values with minimal fluctuation in net $CO_2$ assimilation. Leaves underwent an initial acclimation to saturating light intensity (2000 μmol $m^{-2}$ $s^{-1}$) for 3–5 min after clamping before the measurement commenced. This time allows the leaves to reach a photosynthetic steady state, when net assimilation and stomatal conductance stabilize to a low standard deviation. Initial $CO_2$ matching to sample ambient $CO_2$ was performed before setting the $CO_2$ reference to 410 μmol $mol^{-1}$ during light response measurements. Environmental parameters were controlled and maintained at the following reference setpoints during measurements: $CO_2$ concentration at 410 μmol $mol^{-1}$ , leaf temperature at 24°C, relative humidity at 50%, fan speed at 10,000 rpm, and flow setpoint at 750 μmol $s^{-1}$ . Measurements were conducted from late morning to early afternoon to minimize diurnal variation.

Where available, grain yield, bean yield, and thousand kernel weights were also recorded. These metrics were used as crop-specific indicators of agricultural production, representing the harvested or harvest-relevant portion of biomass. Because yield data were not available for all site × crop combinations and photosynthetic acclimation was the primary focus of the study, these measurements were included only to provide context for physiological responses and were not treated as primary response variables.

### 2.4. Data analysis

Upon compilation of data, all statistical analyses were completed using R software (version 4.3.0; R Development Core Team, 2008). Specific R packages photosynthesis (Stinziano et al., 2023) and readLicorData (McClain, 2023) were used for the analysis of Licor data in the creation of light response curves, using the versions available at the time of analysis. Model fitting was performed using nonlinear regression and photosynthetic parameters were extracted from the resulting fitted curve. These packages fit measured $CO_2$ assimilation rates to the non-rectangular hyperbola model of Marshall and Biscoe (Marshall and Biscoe, 1980):

$$A = \frac{AQY * Q_{abs} + A_{sat} - \sqrt{(AQY * Q_{abs} + A_{sat})^2 - 4\theta * AQY * Q_{abs} * A_{sat}}}{2\theta} - R_d$$

### 2.3. Yield data

Yield data were collected at harvest for each site and crop, wherever feasible. For some field sites and crops, complete yield measurements (total biomass, grain yield, and thousand kernel weight) were unavailable due to logistical constraints or incomplete harvest records. Analysis therefore refers to the subset of sites/crops for which reliable data exists, and is included as an indicator of crop production rather than as a primary response variable. The sites/crops HG (field beans), BW (field beans), HFH (maize), and EW (barley) have general yield and biomass data available. However, due to the initial study design or other limitations, the potatoes at HG and STR do not have yield data. There is, however, wheat data available from STR for the same year, grown under the same conditions as the cabbage and potatoes, and therefore interesting also for relative information.

Aboveground biomass was determined from 0.25 $m^2$ plots (0.5 m × 0.5 m) collected at crop maturity (or peak biomass production, depending on crop and site), oven-dried at 70°C for 72 h, and weighed.

where A is net $CO_2$ assimilation, $Q_{abs}$ is absorbed photosynthetic photon flux density (PPFD), AQY is the apparent quantum yield, $A_{sat}$ is the light-saturated assimilation rate, theta θ is the curvature parameter, and $R_d$ is dark respiration. AQY was estimated as the initial slope of the fitted curve at low irradiance, $A_{sat}$ as the asymptotic maximum assimilation rate, $R_d$ as the respiration rate at zero irradiance, and the light compensation point (LCP) as the PPFD at which net $CO_2$ assimilation equals zero.

Light compensation point (LCP) was calculated from the fitted Marshall–Biscoe parameter estimates as:

$$LCP = \frac{R_d\,(R_d\theta - A_{sat})}{AQY(R_d - A_{sat})}$$

All parameter estimates were obtained using built-in functions within the package. Assumptions of normality and homogeneity of variance were evaluated prior to analysis; Levene's test indicated no significant deviation from homoscedasticity. While sample sizes differed

among treatments due to field constraints, one-way ANOVA is robust to moderate imbalance when variance assumptions are met. Statistical comparisons were therefore conducted using one-way analyses of variance (ANOVA) followed by Tukey post hoc tests. All tests were two-tailed, and statistical significance was set at $p < 0.05$. Post hoc comparisons (Tukey) did not reveal consistent significant differences among treatments for most parameters.

## 3. Results

Due to differences in site design and data availability, light conditions are interpreted as relative categories rather than directly comparable quantitative values across all sites. Analyses therefore focus on within-site comparisons between shaded (and a gradient at HFH) and full-light conditions. The absolute values of parameters are not directly comparable between crops due to variations in developmental stages; thus, only relative trends are discussed. Extended data visualizations and tables, including light response curves, are provided in Appendix A.

Overall, the data showed a surprising yet coherent acclimation of dark respiration ($R_d$) and light compensation point (LCP) across all locations, sampling years and crops. Despite being bred for full sun conditions, these crop varieties consistently exhibited decreased $R_d$ and LCP under shade, irrespective of soil conditions, management practices, crop type (including $C_4$ crops, i.e., maize), shading system, and shading level (see Appendix B for individual site information). While the magnitude of acclimation varied among crops, the overarching trend was clear: all species showed a recurring acclimatory response of reduced respiration and compensation point under shaded conditions (Fig. 2).

Statistical analyses confirmed significant reductions in LCP for the agroforestry system EW with Barley ($p = 0.037$) and the agrivoltaic system STR with Potatoes ($p = 0.0002$ for under-panel and interpanel shading, respectively, compared to the reference). For Heidfeldhof maize, a significant effect of light level was detected (ANOVA, $p = 0.04$). However, post hoc comparisons (Tukey HSD) did not reveal statistically significant differences among individual light levels, although some comparisons approached significance ($p \approx 0.07$–$0.10$). Similarly, significant reductions in Rd were detected in EW with barley ($p = 0.029$), BW with beans ($p = 0.046$ between under-panel and reference), STR Potatoes ($p = 0.006$ for under-panel and interpanel

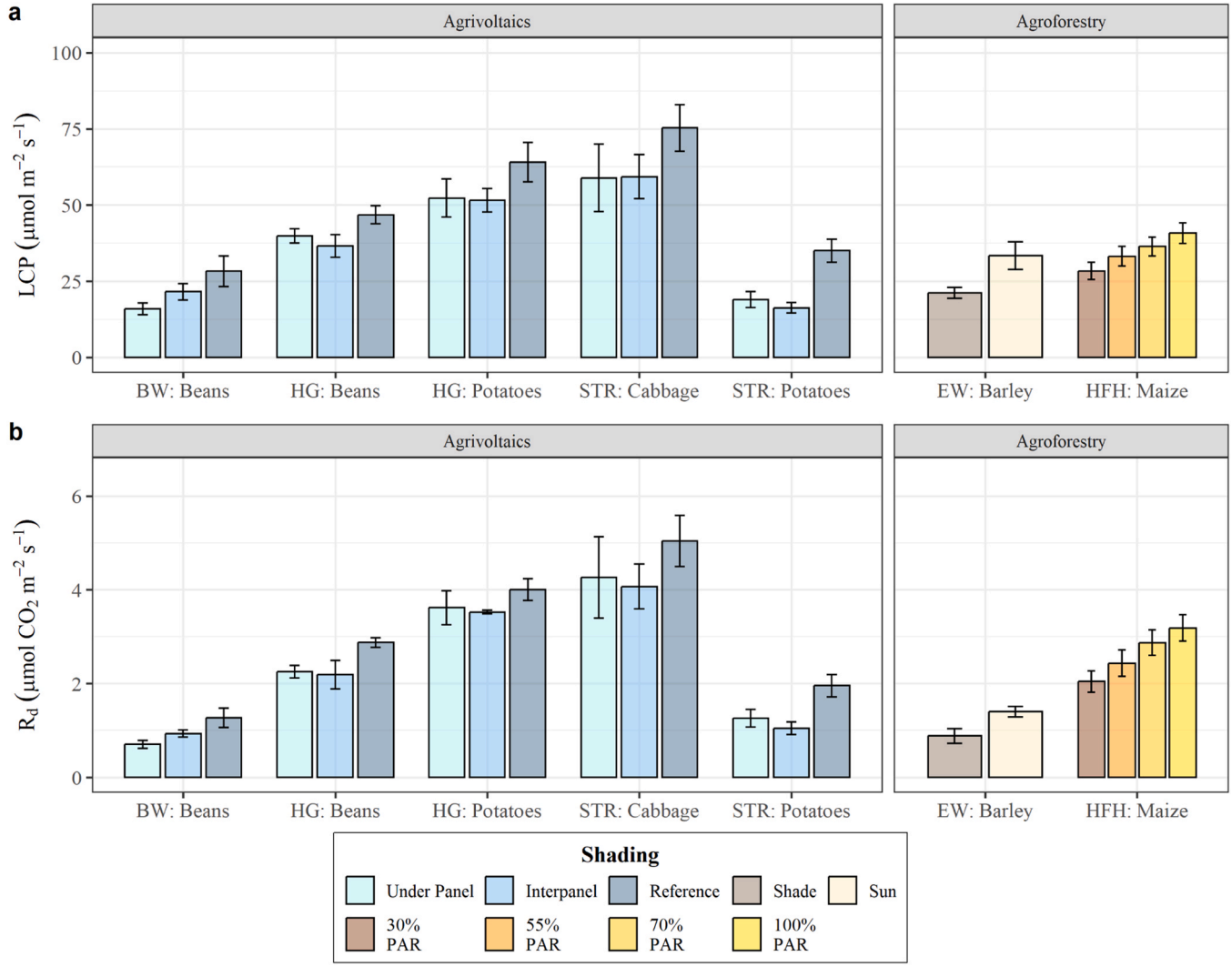


**Fig. 2.** Impact of shading on light compensation point (LCP) and dark respiration ($R_d$) for the different arable crops and the different agrivoltaic (APV) and agroforestry systems. Fields are represented by the abbreviations HG (Heggelbach), BW (Bürgewald), STR (Straßkirchen), EW (Eckartsweier), and HFH (Heidfeldhof). APV fields were measured directly under the solar panel, between the solar panel rows in the APV field (Interpanel) and in the reference field with no shading effect. At EW shade is representative of barley under the shading of the tree canopy, at 3–5 m in the field. 'Sun' measurements are representative of barley in the same field which receives no shading from the trees. At Heidfeldhof a gradient is set up according to various levels of photosynthetic active radiation (PAR) experienced across the field. Error bars represent standard deviation. %PAR is expressed relative to open-field PPFD. Statistical significance is reported in Table 4, Appendix A.

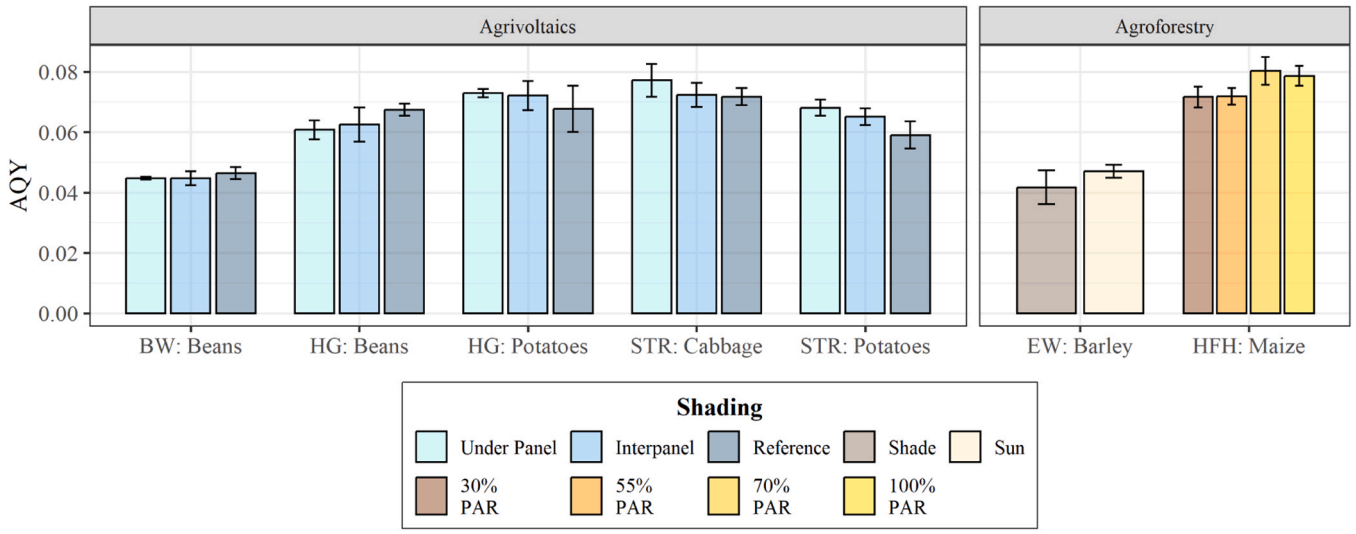


**Fig. 3.** Impact of shading on apparent quantum yield (AQY) for the different arable crops and the different agrivoltaic and agroforestry systems. Fields are represented by the abbreviations HG (Heggelbach), BW (Bürgewald), STR (Straßkirchen), EW (Eckartsweier), and HFH (Heidfeldhof). APV fields were measured directly under the solar panel, between the solar panel rows in the APV field (Interpanel) and in the reference field with no shading effect. At EW shade is representative of barley under the shading of the tree canopy, at 3–5 m in the field. 'Sun' measurements are representative of barley in the same field which receives no shading from the trees. At Heidfeldhof a gradient is set up according to various levels of photosynthetic active radiation (PAR) experienced across the field. Error bars represent standard deviation. %PAR is expressed relative to open-field PPFD. Statistical significance is reported in Table 4, Appendix A.

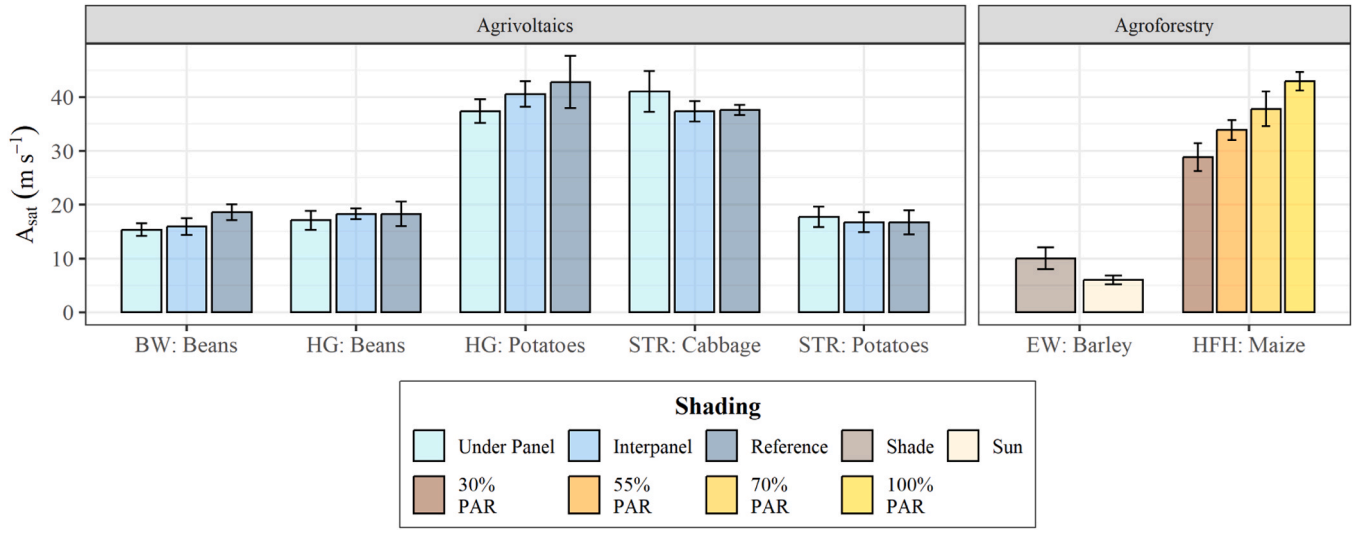


**Fig. 4.** Impact of shading on light saturated assimilation ($A_{sat}$) for the different arable crops and the different agrivoltaic and agroforestry systems. Fields are represented by the abbreviations HG (Heggelbach), BW (Bürgewald), STR (Straßkirchen), EW (Eckartsweier), and HFH (Heidfeldhof). APV fields were measured directly under the solar panel, between the solar panel rows in the APV field (Interpanel) and in the reference field with no shading effect. At EW shade is representative of barley under the shading of the tree canopy, at 3–5 m in the field. 'Sun' measurements are representative of barley in the same field which receives no shading from the trees. At Heidfeldhof a gradient is set up according to various levels of photosynthetic active radiation (PAR) experienced across the field. Error bars represent standard deviation. Statistical significance is reported in Table 4, Appendix A.

shading,u respectively, compared with the reference) and HFH with maize ($p = 0.002$ across 30%−100% PAR).

In contrast, the parameters apparent quantum yield (AQY) and light-saturated photosynthetic rate ($A_{sat}$) displayed system- and species-dependent responses with variable trends (Figs. 3 and 4). The AQY responses (Fig. 3) differed between systems and crops, which, with the exception of beans, showed general observable patterns within each system. In agrivoltaic systems, AQY was slightly lower in reference plots compared to shaded conditions, whereas in agroforestry systems AQY increased with higher PAR levels. Beans (both BW and HG), however, showed a deviation from the patterns both in their comparable responses to each other as well as the other APV crops. There were no significant differences.

Responses of $A_{sat}$ also diverged between systems (Fig. 4). In APV setups, $A_{sat}$ remained relatively stable across shading levels, indicating an acclimation response where shaded plants maintained their photosynthetic capacity rather than experiencing reductions. Conversely, in AFS fields, $A_{sat}$ exhibited stronger variance between shading conditions, with HFH and maize displaying the expected pattern of higher $A_{sat}$ under greater light availability.

Harmonized yield was not collected across all site × crop combinations; we therefore confine inference to physiology and summarize any available harvest notes in Appendix B. Statistical analyses (ANOVA and Tukey post hoc tests) were conducted for all parameters, including Asat

and AQY, and results are summarized in Tables 3–5 of Appendix A. Differences in Asat and AQY were not consistently significant across sites and treatments and are therefore interpreted as variable trends rather than consistent acclimation responses.

## 4. Discussion

Across multiple sites in Germany using locally relevant cultivars, we observed consistent physiological acclimation to partial shading in crops grown under mixed light environments representative of agrivoltaic and agroforestry systems. Given the heterogeneous and site-specific nature of shading in APV and AFS systems, light environments were evaluated as categories rather than continuous gradients. Accordingly, the findings reflect comparative crop responses across defined light environments rather than explicit functional relationships with irradiance. This approach captures plant responses under realistic field conditions, where light availability is spatially structured and temporally variable, and reflects system-driven shading scenarios rather than modeled or experimentally imposed gradients. Across all studied fields, crops, soil types, and management practices, a conserved acclimation pattern emerged in two key physiological variables: dark respiration rate (Rd) and light compensation point (LCP), both of which were reduced under shaded conditions, ranging from approximately 10–45% for Rd and 15–55% for LCP depending on crop and system.

The responses observed here indicate a shift in leaf-level carbon balance that supports carbon assimilation under reduced irradiance and reflect a consistent physiological adjustment across diverse field settings. Notably, this pattern was observed in crops typically cultivated under full-sun conditions, suggesting a broader capacity for acclimation to heterogeneous light environments than is often assumed. This convergence in response suggests that arable crops - even those typically grown in full sun - possess an inherent capacity to alter their metabolism under changing light availability. Photosynthetic plasticity is a key component of plant responses to variable environments, enabling rapid adjustment to changing light conditions and contributing to adaptation and performance under stress, which underpins crop resilience (Laitinen, 2024; Valladares and Niinemets, 2008). Within this framework, photosynthetic acclimation represents a central component of plant stress responses and has been linked to improved performance under variable environmental conditions, although whole-plant outcomes depend on the integration of multiple physiological processes.

Common assumptions are that arable crops developed for full-sun conditions will struggle under these shaded systems, suffering and expressing traits associated with shade avoidance – an expectation that frames the discussion as a trade-off between microclimatic advantages and shading constraints. Plants are typically classified as responding to chronic low irradiance via shade avoidance (elongation, thinner leaves, maintenance of higher light requirements) or via shade tolerance (efficient use of low light characterized by lower light-compensation point and reduced dark respiration). Across sites, the dominant pattern was a reduction in LCP and Rd under shade, pointing to an acclimation in these field conditions. Such adjustments are consistent with maintaining a positive carbon balance as the plants adapt to perform better in low light by minimizing $CO_2$ losses (Valladares and Niinemets, 2008). The reduced $R_d$ reflects an acclimation strategy that reduces respiratory cost in the shade. This response is well documented in shade tolerant plants as part of an energy-consuming strategy that allows them to survive longer in light deprived environments (Chen et al., 2014; Valladares and Niinemets, 2008). A higher $R_d$ is associated with overall reduced photosynthetic efficiency and yield, while plants with lower $R_d$ tend to allocate more energy towards growth and storage rather than maintaining basal metabolism (Arenas-Corraliza et al., 2019; Wang et al., 2020). The presence of this mechanism in open-field crops, however, offers a unique and unexpected revelation of the plasticity in respiratory acclimation, suggesting that even plants adapted to high light can employ what were previously characterized as shade-tolerant strategies under reduced light conditions. The energy-saving strategy allows the plants to minimize excessive and unnecessary energy loss.

The conserved decreases in Rd and LCP under shade mean that common cultivars can remain carbon-positive at lower irradiance. Practically, this enables two actions: to screen cultivars by measuring LCP and Rd under site-typical shade to identify shade-compatible lines; and to design layouts to minimize persistent deep-shade zones (e.g., panel/tree spacing, row orientation) so that most plants experience moderate %PAR where carbon balance remains favorable. In our sites, APV produced more structured shade (Asat relatively stable), whereas AFS produced heterogeneous shade (greater between-condition variance), suggesting different design levers in each system. These steps operationalize leaf-level physiology for field decisions.

Similarly, a reduced LCP indicates a physiological acclimation response that lowers the light threshold required to achieve a positive carbon balance. In a shaded environment, plants with a lower LCP can maintain net photosynthesis at lower light intensities, ensuring that they continue to assimilate carbon even under suboptimal light conditions (Arenas-Corraliza et al., 2019; Cavanagh and Kubien, 2014; Craine and Reich, 2005). A reduction in LCP allows for improved light capture (Frantz and Bugbee, 2005; Wang et al., 2020), an advantageous acclimation capability for crops in shaded agricultural systems. A lower LCP thus represents a critical acclimation for plants in shaded systems that enables them to sustain photosynthesis and growth at reduced light levels that would have traditionally been considered disadvantageous for sun-demanding species. The reductions in $R_d$ and LCP observed here represent key components of photosynthetic efficiency, as they allow plants to optimize their metabolic processes under reduced-light conditions.

This mechanistic response of sun crops to reduce $R_d$ and/or LCP in response to reduced light availability has been observed in a small handful of other studies (Arenas-Corraliza et al., 2019; Chen et al., 2014; Lombardini et al., 2009). In alignment with our findings here, Gong et al. (Gong et al., 2015) observed that while some soybean seedlings displayed typical shade-avoidance responses, many exhibited characteristics of what is typically considered shade tolerance. Similarly, Arenas-Corraliza et al. (Arenas-Corraliza et al., 2019) found that barley grown in Mediterranean conditions significantly reduced its Rd and LCP under shading, demonstrating sufficient plasticity for growth in Mediterranean agroforestry systems. The findings in this study therefore align with this underrecognized concept that there is much more nuance and room to move along a broad continuum of light acclimation strategies, challenging rigid classifications and thus underscoring the complexity of predicting physiological acclimation behaviors in crops. The consistent patterns we observed here suggest that arable crops possess the ability to physiologically optimize their baseline metabolic demands, enhancing their survival and growth potential in shaded environments. This raises the possibility that such crops – while bred for full sun - may have more capacity for acclimation to the shade of these systems than previously assumed and is currently represented in models (Frantz and Bugbee, 2005).

It is important to note that partial shading in APV and AFS systems not only reduces light availability but may also alleviate excess irradiance and associated stress. Under high light conditions, photoinhibition and photoprotective energy dissipation can reduce the efficiency of carbon assimilation, leading to suboptimal photosynthetic performance (Long et al., 1994; Murchie and Niyogi, 2011). In field environments characterized by fluctuating irradiance, these constraints can be particularly pronounced (Murchie et al., 2018; Wang et al., 2020). In this context, moderate shading may improve the balance between light capture and carbon fixation by reducing excess energy load and thermal stress (Niinemets, 2010; Valladares and Niinemets, 2008). Similar effects have been reported in agrivoltaic systems, where partial shading can mitigate heat and radiation stress and influence plant physiological performance (Barron-Gafford et al., 2019). It is possible that the observed responses in $R_d$ and LCP may also partly reflect improved

photosynthetic efficiency under reduced stress conditions. In particular, enhanced efficiency at low irradiance and reduced metabolic costs associated with stress responses could contribute to lowering the light compensation point. These mechanisms are not mutually exclusive and may operate simultaneously under heterogeneous field conditions.

In contrast to the consistent patterns of $R_d$ and LCP, the other key photosynthetic parameters – quantum yield and light-saturated photosynthetic rate – were more variable, showing situational trends rather than a uniform acclimation across situations. These inconsistencies drive us towards understanding the complexity of mechanisms that are species and environmental dependent, while solidifying the primary role of $R_d$ and LCP in shading acclimation. They also highlight the influence of shading heterogeneity effects in AFS versus the more structured shading of the APV systems. An important dimension of this variability is the distinction between C3 and C4 crops. In our study, maize (C4) exhibited a decline in AQY under shade, consistent with earlier findings that C4 species often show maladaptive responses to shading (Collison et al., 2020; Pignon et al., 2017). In dense canopies or shaded agroecosystems, C4 photosynthesis can be disproportionately constrained due to limited efficiency at low light. By contrast, the beans, potatoes, and cabbage in our study generally maintained or slightly improved AQY under shade, reflecting their greater capacity to enhance light-use efficiency through known shade-acclimation strategies. These results emphasize that while $R_d$ and LCP reductions represent a universal acclimation strategy, the resilience of photosynthesis under shading is also pathway-dependent, with C3 crops better positioned to sustain carbon gain in heterogeneous light environments than C4 crops such as maize.

While the $A_{sat}$ parameter displayed high variation in the AFS fields, it remained relatively stable across the APV sites, indicating another acclimation response. Typical expectations would have been a down-regulation of $A_{sat}$ so that levels are decreased with decreased light availability (as seen in the pattern of HFH: Maize). Stability suggests that plants under the panels optimize their light use efficiency without significant shifts, potentially due to physiological plasticity in response to altered light environments (Semeraro et al., 2024; Weselek et al., 2021). It suggests that plants in the APV set-up are able to maintain their photosynthetic capacity, a practical measure of resilience. The differences between AFS and APV suggest that $A_{sat}$ may be more sensitive to species-specific traits and environmental conditions.

Apart from the beans (in both HG and BW), where values are relatively static, the trend for AQY appears slightly lower in the reference fields of APV sites. Some plants optimize their quantum yield under moderate shading when light levels are sufficient but not excessive, indicating potential photosynthetically active radiation (PAR) thresholds where light saturation is avoided (Cavanagh and Kubien, 2014; Marshall and Biscoe, 1980). The ability to increase AQY under shaded conditions suggests additional acclimation, as we know that shade-tolerant species tend to enhance their quantum yield to maximize light-use efficiency (Frantz and Bugbee, 2005; Valladares and Niinemets, 2008). Therefore, while AQY patterns are not uniform or pronounced, the limited differences and occasional increases under shaded conditions indicate plasticity traits that warrant further study. This aligns with the idea that crops possess a broader capacity for light acclimation than previously assumed, particularly in agroforestry and agrivoltaic systems where shading is a key factor in productivity trade-offs (Laub et al., 2022; Wang et al., 2020).

It is widely accepted that photosynthetic efficiency translates to yield projections (Keller et al., 2024; Taylor and Long, 2017; Schweiger and Pataczek, 2023; Wang et al., 2020). While direct integration with yield was not possible in this study, photosynthetic acclimation represents a key mechanistic component of plant responses to variable light environments and has been widely used to interpret crop performance under field conditions (Murchie et al., 2018; Valladares and Niinemets, 2008). Similarly, agrivoltaic research has highlighted the importance of plant physiological responses to altered microclimates in shaping system performance (Barron-Gafford et al., 2019). Yield results for AFS and APV sites are shown to be both site-specific and crop-specific. Shading studies in temperate climates are still very limited, with yield results fluctuating widely from positive, to negative, to dependent (Amaducci et al., 2018; Laub et al., 2022; Reynolds et al., 2007; Semeraro et al., 2024; Swieter et al., 2019; Weselek et al., 2021). Mixed yield results were also evident for our study fields. At the STR site in 2024, wheat plants showed no significant difference between the APV and reference fields in total biomass, grain size, or thousand kernel counts. Nonetheless, the reference field exhibited a trend towards increased grain yield per plant – a higher grain/plant biomass ratio. Yield data for HG beans showed no significant difference in the total biomass, but nearly double the amount of bean yield in the reference fields (a 54–60% reduction under the panels). The BW beans, on the other hand, produced significantly greater biomass in the reference area (a 58% increase over the panel area), yet no significant difference for bean production between APV and reference ($p = 0.23$). Similar observations were made at EW barley where fully sun-exposed barley had an increased total biomass of 31%, but the thousand kernel count was nearly identical for each field. At HFH maize significant difference became apparent at the 55% PAR level and below; there was otherwise no significant difference between 70% and 100%, with an even slightly higher total biomass and kernel yield at 70% versus 100% PAR.

This information therefore leads us to conclude that while these acclimation responses are critical to understanding the capacity of crops to adjust to shaded environments and maintain photosynthetic activity in reduced light, they do not translate directly to improved yields under all conditions at this time. Although we did not observe consistent yield advantages across our study sites, the importance of shade acclimation should not be understated. As climate change continues to intensify drought and heat stress, the capacity of crops to acclimate photosynthetically to reduced light becomes increasingly valuable when combined with the microclimatic benefits of agroforestry and agrivoltaic systems, such as improved soil moisture and moderated temperatures (Jacobs et al., 2022; Pataczek et al., 2023). In this context, shade acclimation represents an essential foundation for resilience: while it may not always boost yields under current conditions, it provides the physiological capacity for crops to maintain productivity under future climates where water limitation and heat stress are greater constraints than light availability.

The more we understand the plasticity possibility of plants, the better we can select for traits that will promote photosynthetic efficiency under variable light conditions, as suggested by Keller et al. (Keller et al., 2024). The parameters discussed here not only complement parameters like max assimilation rate (Amax) and net photosynthetic rate ($P_n$) which are commonly utilized in photosynthetic studies, but also provide a deeper mechanistic understanding of how crops optimize photosynthesis under challenging environmental conditions. Therefore, due to the observations here, $A_{sat}$, AQY, $R_d$, and LCP should be considered in more studies moving forward as we continue to expand our understanding of the acclimation possibilities of arable crops typically bred for open-field conditions.

Several considerations provide important context for interpreting our findings and highlight opportunities for future research. The 30% PAR measurements in HFH: Maize may have been influenced by an edge effect that is often observed in maize fields. Differences in absolute values between sites (e.g., HG: potatoes versus STR: potatoes) likely reflect variation in BBCH stages, soils, or climatic conditions. Rather than detracting from the results, these differences emphasize the value of testing acclimation responses under diverse real-world conditions that can then be widely applicable across conditions. While our study successfully identified conserved acclimation traits across sites, it also opens the door to further work disentangling site- and crop-specific effects. A particularly promising next step would be to account for spectral quality differences between agroforestry and agrivoltaic shading, as variation in red:far-red ratios is known to influence plant acclimation (Casal, 2012; Smith, 2000). Including shade-tolerant reference species

would also provide benchmarks for gauging the relative plasticity of crops. These considerations highlight how targeted follow-up studies could build on this work to refine our understanding of shade acclimation in these alternative cropping systems.

Furthermore, these results substantiate the need to re-evaluate agricultural research frameworks for plants in dynamically shaded systems like APV and AFS. In their study on the effects of decreased PPFD on tomatoes and lettuce, Frantz and Bugbee (2005) also realized that predictions from the most widely used growth models did not match the outcomes of acclimation. While there are shading characteristics involved, the plants did not necessarily always exhibit typical shade avoidance characteristics, assumably due to the dynamic shading patterns and microclimatic changes. Emerging studies indicate that the shading patterns of these systems emulate sunfleck regimes, triggering a distinctly different response as compared to static shading (Heitz et al., 2023). This research leads us to re-examine our notions of considering APV and AFS shading scenarios as light-depleted systems where plants suffer from decreased PAR. Compounded by microclimate mediation and resource allocation trade-offs, these systems have their own eco-physiological contexts requiring their own frameworks. Therefore, specifically adapted models based on in situ studies, with such data as presented here, are necessary moving forward. Future studies integrating continuous light measurements across sites would further strengthen these comparisons.

Beyond these physiological and agronomic implications, agrivoltaic and agroforestry systems also offer broader sustainability benefits by supporting food production, renewable energy generation, and more efficient land use. As such, they are relevant to several United Nations Sustainable Development Goals (SDGs), including: SDG 2 (Zero Hunger) through the development of more resilient agricultural systems that will maintain adequate production, SDG 7 (Affordable and Clean Energy) through agrivoltaic energy and agroforestry biofuel production, SDG 12 (Responsible Consumption and Production) through more efficient land and resource use, SDG 13 (Climate Action) through improved adaptation to heat and water stress, and SDG 15 (Life on Land) through supporting biodiversity and ecosystem functions within agricultural landscapes. While the present study does not directly quantify progress toward these SDGs, it does provide mechanistic evidence that arable crops are capable of physiological acclimation to partial shading, supporting the further development of APV and AFS as more sustainable agricultural systems.

The well-documented benefits of shading in mitigating heat and drought stress (Jacobs et al., 2022; Pataczek et al., 2023; Swieter et al., 2019), an increasing threat across Europe's temperate climates, combined with the evidence of photosynthetic acclimation observed in this study, support the potential relevance of APV and AFS systems under future environmental conditions. Our findings align with emerging recognition of phenotypic plasticity as a central adaptation strategy for survival in heterogenous environments (Gibbin et al., 2017). Therefore, utilizing this knowledge in breeding strategies moving forward could be especially beneficial for stabilizing and improving yields to mitigate the negative impact of changing environmental factors. Both universal acclimation strategies and complex, context-dependent responses observed here allow us to distinguish between broadly applicable mechanisms ($R_d$ and LCP) and those that are specific to particular environmental conditions ($A_{sat}$ and AQY). This provides mechanistic insight into general metabolic responses associated with optimization under reduced light. These results further support the potential compatibility of APV and AFS systems as dual-purpose land-use strategies and emphasize their role in enhancing global food security through capacity for crop resilience, especially in consideration of future breeding strategies. This plasticity may be leveraged or enhanced to support resilience under heterogeneous field conditions. Future research should prioritize identifying acclimation mechanisms consistently expressed across arable crops to target traits amenable to breeding for enhanced plasticity. By leveraging the inherent resilience and plasticity of crops, APV and AFS systems represent not just an agricultural innovation but also a promising pathway toward more sustainable and resilient production systems under increasing environmental variability.

## CRediT authorship contribution statement

**Jennifer Moore:** Writing – review & editing, Writing – original draft, Visualization, Formal analysis, Data curation, Conceptualization. **Christoph Jedmowski:** Writing – review & editing, Data curation. **Andreas Schweiger:** Writing – review & editing, Supervision, Conceptualization. **Lisa Pataczek:** Writing – review & editing, Data curation. **Onno Muller:** Writing – review & editing, Data curation.

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## Declaration of generative AI and AI-assisted technologies in the writing process

During the preparation of this work the author(s) used ChatGPT (OpenAI), Language Tool, and Citavi version 7 in order to review literature, generate sources, and conduct a final language check of the manuscript. After using this tool/service, the author(s) reviewed and edited the content as needed and take(s) full responsibility for the content of the publication.

## Author Contribution

A.H.S. and J.M. conceptualized and designed the study. Data preparation, analysis and visualization were performed by J.M. The manuscript was written by J.M. Data contributions were made by L.P, O.M., and C.J. A.H.S. supervised the study. All authors read and approved the final manuscript.

*Representative photographs of field conditions and measurement campaigns at the agroforestry and agrivoltaic study sites*

Photographs are provided to illustrate the cropping systems and field measurement conditions. BBCH growth stages reported in Table 1 were determined independently by direct in situ assessment at the time of gas-exchange measurements according to the standardized BBCH scale.

*Harvest notes*

Yield outcomes varied across sites and crops. Data availability was limited for some field sites, and yield results are reported for those with complete measurements only. At the STR site (2024), wheat (grown on the same site with identical methods, but no LRC data here) showed no significant difference in total biomass or kernel count between APV and reference fields, though the grain/plant biomass ratio trended higher in the reference field. HG beans exhibited no significant difference in total biomass, but a 54–60% reduction in bean yield under panels versus reference plots. In BW, beans yielded 58% greater biomass in reference plots but showed no statistical difference in total bean production ($p = 0.23$). EW barley produced 31% more biomass in full sun, with similar thousand kernel weights in both treatments. At HFH maize, significant differences emerged at PAR $\leq$ 55% but not at higher light

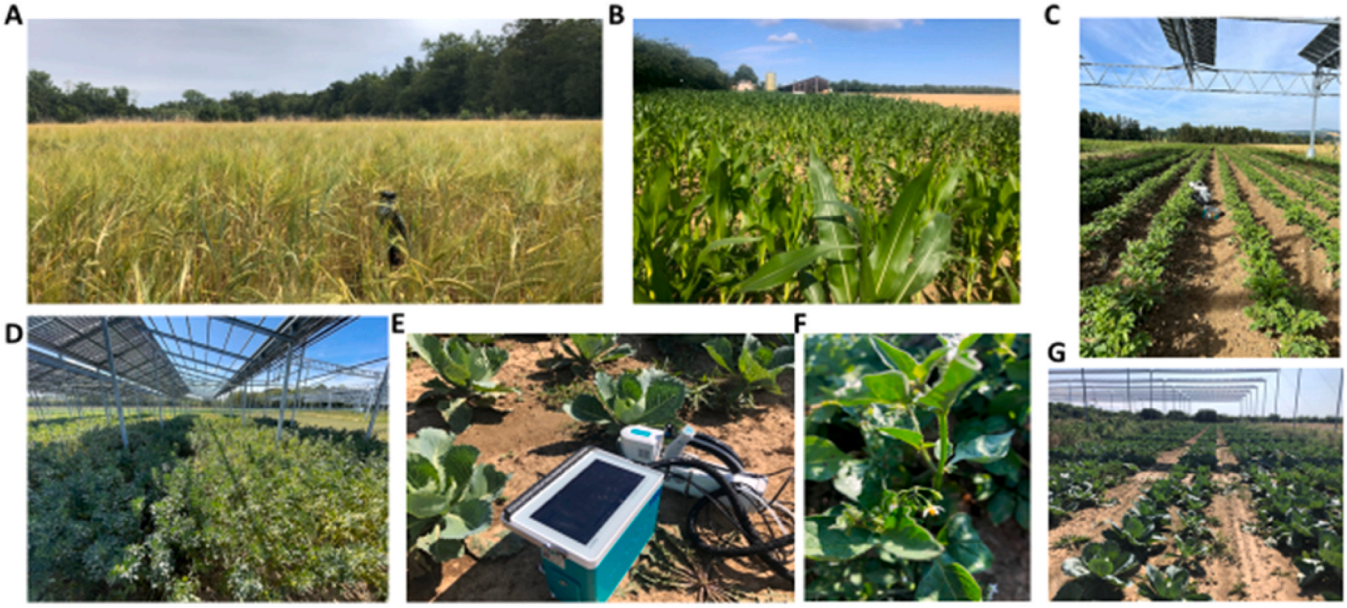


**Fig. B1.** Representative photographs illustrating field conditions and gas-exchange measurements across the agroforestry and agrivoltaic study sites. (A) Barley at Field site Eckartsweier (B) maize at Heidfeldhof (c) potatoes at Heggelbach (d) Beans at bürgewald (d) cabbage at straßkirchen (e) potatoes at straßkirchen (g) the straßkirchen system

levels. Yield data for other crops/sites were unavailable and are not included in comparative analysis.

## Declaration of Competing Interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Jennifer Moore reports financial support was provided by BMLEH (German Federal Ministry of Agriculture and Food). Onno Muller, Christoph Jedmowski2 reports a relationship with German Federal Ministry of Education and Research that includes: funding grants. Lisa Pataczek reports a relationship with SynAgri-PV project that includes: funding grants. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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## Appendix A

**Table A1**
Mean and SD of photosynthetic parameters for each arable crops and field

| | Location | Crop | Condition | Asat ($\mu mol\ CO_2\ m^{-2}\ s^{-1}$) | AQY | Rd ($\mu mol\ CO_2\ m^{-2}\ s^{-1}$) | LCP ($\mu mol\ m^{-2}\ s^{-1}$) |
|---|---|---|---|---|---|---|---|
| Agroforestry | Eckartsweier (EW) | Barley | Sun | 5.99 ± 1.80 | 0.05 ± 0.00 | 1.40 ± 0.26 | 33.36 ± 10.16 |
| | | | Shade | 9.97 ± 4.51 | 0.04 ± 0.01 | 0.88 ± 0.35 | 21.16 ± 4.07 |
| | Heidfeldhof (HFH) | Maize | 30% PAR | 28.81 ± 7.80 | 0.07 ± 0.01 | 2.04 ± 0.69 | 28.35 ± 8.43 |
| | | | 55% PAR | 33.84 ± 6.34 | 0.07 ± 0.01 | 2.43 ± 0.97 | 33.16 ± 11.12 |
| | | | 70% PAR | 37.78 ± 10.23 | 0.08 ± 0.01 | 2.87 ± 0.87 | 36.38 ± 9.79 |
| | | | 100% PAR | 42.91 ± 6.00 | 0.08 ± 0.01 | 3.19 ± 0.98 | 40.79 ± 11.56 |
| Agrivoltaic | Straßkirchen (STR) | Potatoes | Under panel | 17.70 ± 5.42 | 0.07 ± 0.01 | 1.26 ± 0.53 | 19.01 ± 7.39 |
| | | | Interpanel | 16.72 ± 5.64 | 0.07 ± 0.01 | 1.05 ± 0.40 | 16.26 ± 5.27 |
| | | | Reference | 16.65 ± 5.89 | 0.06 ± 0.01 | 1.96 ± 0.63 | 35.02 ± 9.94 |
| | | Cabbage | Under Panel | 41.06 ± 6.55 | 0.08 ± 0.01 | 4.26 ± 1.50 | 58.89 ± 19.15 |
| | | | Interpanel | 37.32 ± 3.22 | 0.07 ± 0.01 | 4.07 ± 0.82 | 59.29 ± 12.47 |
| | | | Reference | 37.56 ± 1.88 | 0.07 ± 0.01 | 5.04 ± 1.09 | 75.28 ± 15.13 |
| | Heggelbach (HG) | Potatoes | Under Panel | 37.34 ± 4.37 | 0.07 ± 0.00 | 3.62 ± 0.73 | 52.31 ± 12.51 |
| | | | Interpanel | 40.54 ± 4.72 | 0.07 ± 0.01 | 3.52 ± 0.08 | 51.55 ± 7.61 |
| | | | Reference | 42.78 ± 9.67 | 0.07 ± 0.02 | 4.01 ± 0.46 | 64.10 ± 12.89 |
| | | Beans | Under Panel | 17.07 ± 6.01 | 0.06 ± 0.01 | 2.26 ± 0.47 | 39.88 ± 8.20 |
| | | | Interpanel | 18.25 ± 2.41 | 0.06 ± 0.01 | 2.19 ± 0.74 | 36.58 ± 9.21 |
| | | | Reference | 18.26 ± 4.63 | 0.07 ± 0.00 | 2.88 ± 0.20 | 46.80 ± 5.90 |

(*continued on next page*)

**Table A1** (*continued*)

| | Location | Crop | Condition | Asat ($\mu mol\ CO_2\ m^{-2}\ s^{-1}$) | AQY | Rd ($\mu mol\ CO_2\ m^{-2}\ s^{-1}$) | LCP ($\mu mol\ m^{-2}\ s^{-1}$) |
|---|---|---|---|---|---|---|---|
| | Bürgewald (BW) | Beans | Under Panel | 15.31 ± 2.31 | 0.04 ± 0.00 | 0.70 ± 0.16 | 15.89 ± 3.83 |
| | | | Interpanel | 15.92 ± 3.12 | 0.04 ± 0.00 | 0.93 ± 0.15 | 21.56 ± 5.39 |
| | | | Reference | 18.57 ± 2.94 | 0.05 ± 0.00 | 1.27 ± 0.41 | 28.27 ± 9.94 |

**Table A2**
Summary of statistical analyses (one-way ANOVA) for photosynthetic parameters across sites and treatments. P-values are reported for each parameter, with significant differences indicated at $p < 0.05$*. Post hoc comparisons were conducted using Tukey's HSD test to assess pairwise differences among treatments

| Location | Crop | Parameter | ANOVA p-value |
|---|---|---|---|
| Eckartsweier (EW) | Barley | LCP | 0.0373* |
| | | $R_d$ | 0.0294* |
| | | AQY | 0.4053 |
| | | $A_{sat}$ | 0.1039 |
| Heidfeldhof (HFH) | Maize | LCP | 0.0461* |
| | | $R_d$ | 0.0183* |
| | | AQY | 0.1380 |
| | | $A_{sat}$ | 0.0007* |
| Bürgewald (BW) | Beans | LCP | 0.0874 |
| | | $R_d$ | 0.0442* |
| | | AQY | 0.7661 |
| | | $A_{sat}$ | 0.2690 |
| Straßkirchen (STR) | Potatoes | LCP | 0.0002* |
| | | $R_d$ | 0.0065* |
| | | AQY | 0.1939 |
| | | $A_{sat}$ | 0.9179 |
| | Cabbage | LCP | 0.3378 |
| | | $R_d$ | 0.5262 |
| | | AQY | 0.6017 |
| | | $A_{sat}$ | 0.4802 |
| Heggelbach (HG) | Potatoes | LCP | 0.2309 |
| | | $R_d$ | 0.8111 |
| | | AQY | 0.5554 |
| | | $A_{sat}$ | 0.9952 |
| | Beans | LCP | 0.1767 |
| | | $R_d$ | 0.1111 |
| | | AQY | 0.5883 |
| | | $A_{sat}$ | 0.8634 |

**Table A3**
Percent decrease in photosynthetic parameters across light environments. Percent decrease in dark respiration (Rd) and light compensation point (LCP) across light environments relative to reference or full-sun conditions (100% PAR). Values represent percent reduction from higher light to lower light conditions

| System | Comparison | Rd % decrease | LCP % decrease |
|---|---|---|---|
| EW Barley | Sun → Shade | 37.1 | 36.6 |
| HFH Maize | 100% → 30% | 36.1 | 30.5 |
| | 100% → 55% | 23.8 | 18.7 |
| | 100% → 70% | 10 | 10.8 |
| BW Beans | Reference → Under panel | 44.9 | 43.8 |
| | Reference → Interpanel | 26.8 | 23.7 |
| HG Beans | Reference → Under panel | 21.5 | 14.8 |
| | Reference → Interpanel | 24.0 | 21.8 |
| HG Potatoes | Reference → Under panel | 9.7 | 18.4 |
| | Reference → Interpanel | 12.2 | 19.6 |
| STR Cabbage | Reference → Under panel | 15.5 | 21.8 |
| | Reference → Interpanel | 19.2 | 21.2 |
| STR Potatoes | Reference → Under panel | 35.7 | 45.7 |
| | Reference → Interpanel | 46.4 | 53.6 |

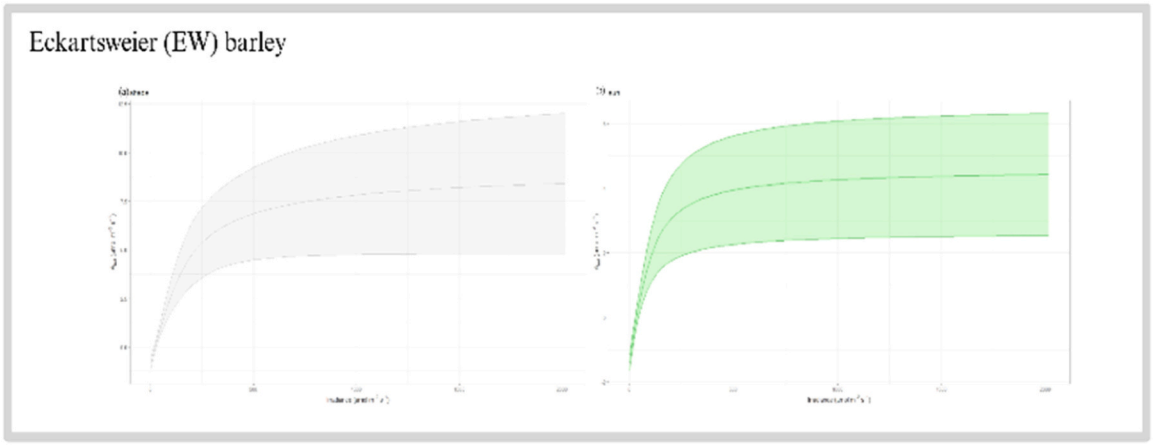


**Fig. A1.** Light response curves for $CO_2$ assimilation of Summer barley (*Hordeum vulgare* L.) leaves measured at two field positions (plants exposed to moring shade (a) and plants located in full sun) at Eckartsweier (EW) agroforestry site in June 2023. Curves represent means ± SE (n = 5 per position); shaded areas are 95% confidence intervals. Fitted curves are non-rectangular hyperbolae Created with R package photosynthesis (Stinziano et al., 2023) based on the Marshall-Biscoe model

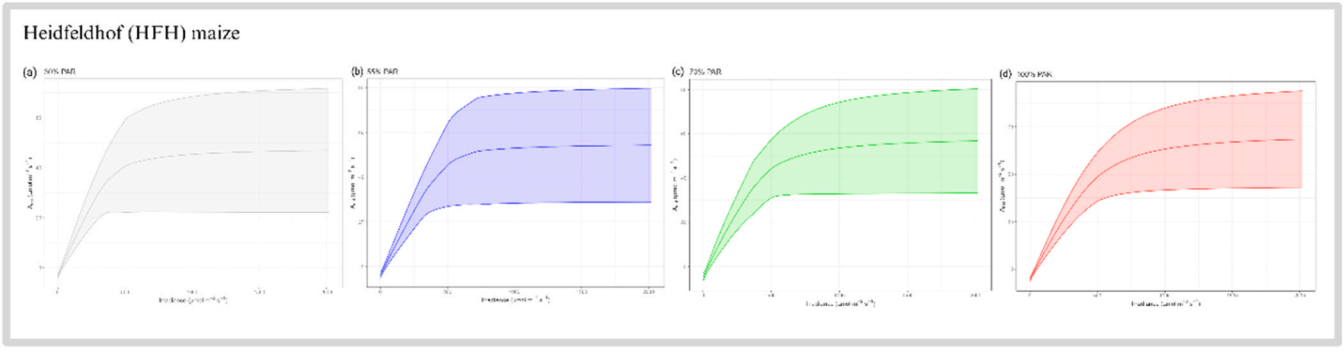


**Fig. A2.** Light response curves for $CO_2$ assimilation of Maize (*Zea mays L.*) leaves measured at four field positions (30% PAR (a), 55% PAR (b) 70% PAR (c) and full sun (d)) at Heiedfeldhof (HFH) agroforestry site in July 2024. Curves represent means ± SE (n = 8, 12, 10 and 12 per position); shaded areas are 95% confidence intervals. Fitted curves are non-rectangular hyperbolae Created with R package photosynthesis (Stinziano et al., 2023) based on the Marshall-Biscoe model

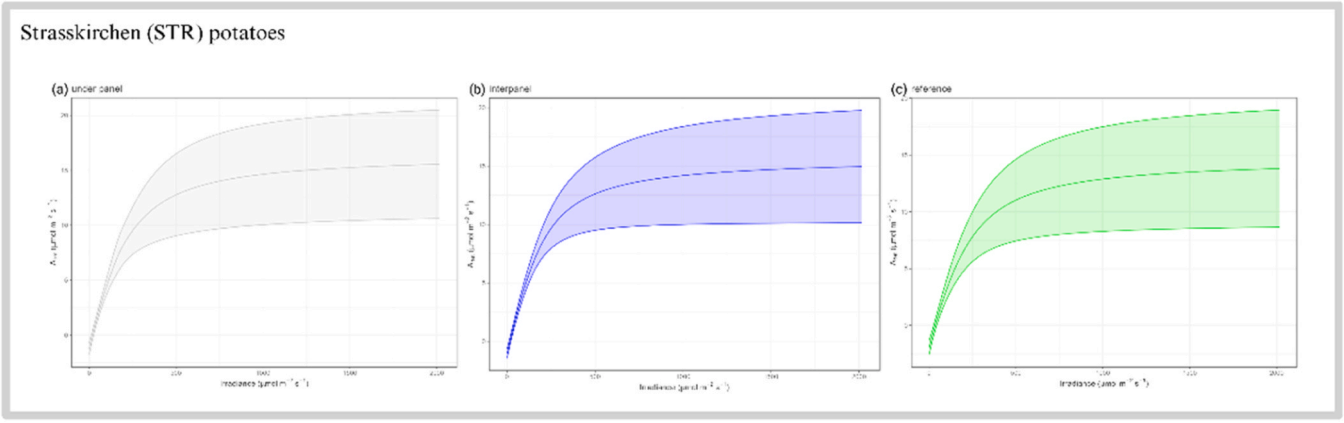


**Fig. A3.** Light response curves for $CO_2$ assimilation of Potatoes (*Solanum tuberosum*) leaves measured at three field positions (directly under the panel (a), between the panels (b) and the reference field (c)) at Strasskirchen (STR) agrivoltaic site in July 2024. Curves represent means ± SE (n = 8, 9, and 7 per position); shaded areas are 95% confidence intervals. Fitted curves are non-rectangular hyperbolae Created with R package photosynthesis (Stinziano et al., 2023) based on the Marshall-Biscoe model

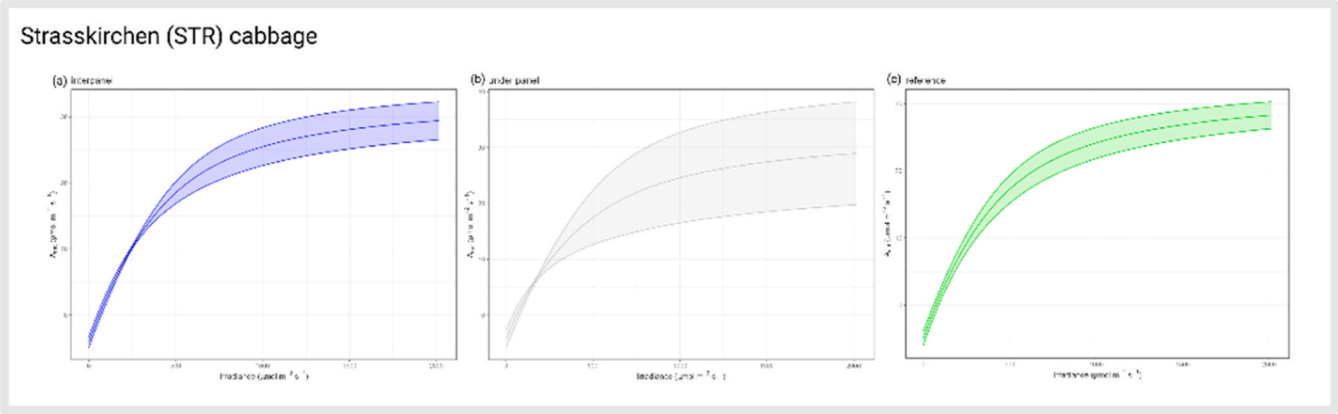


**Fig. A4.** Light response curves for $CO_2$ assimilation of White cabbage (*Brassica oleracea*) leaves measured at three field positions (directly under the panel (a), between the panels (b) and the reference field (c)) at Strasskirchen (STR) agrivoltaic site in July 2024. Curves represent means ± SE (n = 4 per position); shaded areas are 95% confidence intervals. Fitted curves are non-rectangular hyperbolae Created with R package photosynthesis (Stinziano et al., 2023) based on the Marshall-Biscoe model

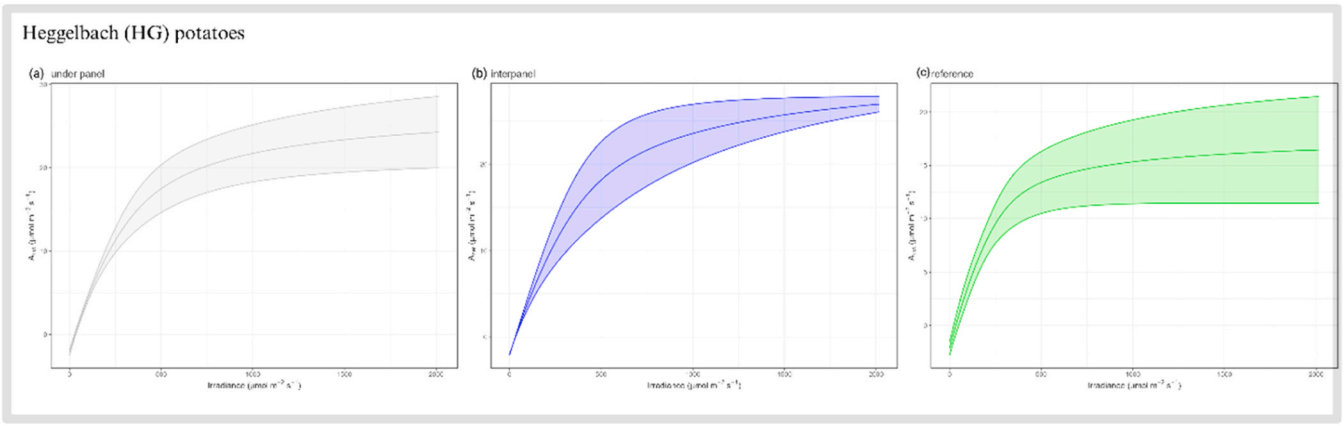


**Fig. A5.** Light response curves for $CO_2$ assimilation of Potatoes (*Solanum tuberosum*) leaves measured at three field positions (directly under the panel (a), between the panels (b) and the reference field (c)) at Heggelbach (HG) agrivoltaic site in July 2023. Curves represent means ± SE (n = 4 per position); shaded areas are 95% confidence intervals. Fitted curves are non-rectangular hyperbolae Created with R package photosynthesis (Stinziano et al., 2023) based on the Marshall-Biscoe model

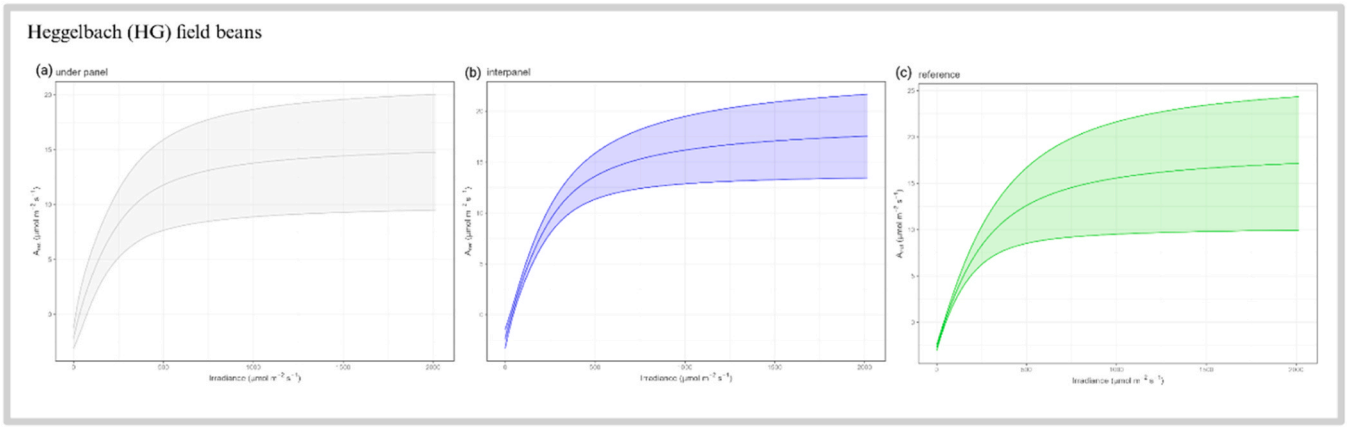


**Fig. A6.** Light response curves for $CO_2$ assimilation of field bean (*Vicia faba*) leaves measured at three field positions (directly under the panel (a), between the panels (b) and the reference field (c)) at Heggelbach (HG) agrivoltaic site in may 2023. Curves represent means ± SE (n = 12, 6, and 4 per position); shaded areas are 95% confidence intervals. Fitted curves are non-rectangular hyperbolae Created with R package photosynthesis (Stinziano et al., 2023) based on the Marshall-Biscoe model

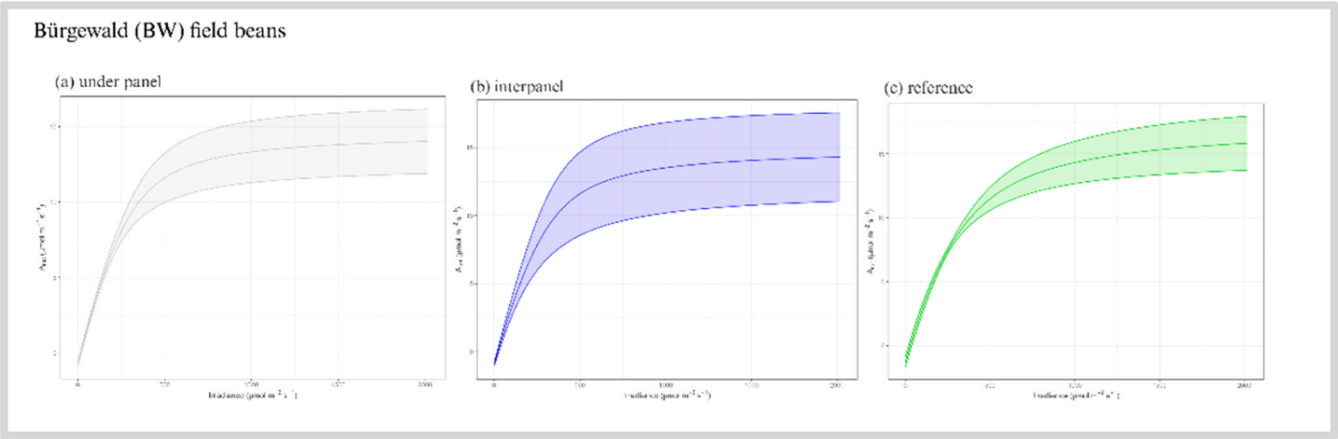


**Fig. A7.** Light response curves for $CO_2$ assimilation of field bean (*Vicia faba*) leaves measured at three field positions (directly under the panel (a), between the panels (b) and the reference field (c)) at Heggelbach (HG) agrivoltaic site in July 2023. Curves represent means ± SE (n = 4 per position); shaded areas are 95% confidence intervals. Fitted curves are non-rectangular hyperbolae Created with R package photosynthesis (Stinziano et al., 2023) based on the Marshall-Biscoe model

## Appendix B

**Table B1**
Site specifics for each location (DWD; Universität Hohenheim)

| Site | System | Crop | Soil | Latitude, Longitude | Elevation (m asl) | Annual mean temperature (°C) | Precipitation (mm/year) | Management |
|---|---|---|---|---|---|---|---|---|
| **Heidfeldhof (HFH)** | Agroforestry | Maize (*Zea mays L.*, KWS Arturello with Redigo M) | Haplic luvisol (loess-derived, sandy loam) | 48°42'54" N 9°11'24" E | 400 | 8.8 | 685 | Conventional treatments, with additions of compost and biochar |
| **Eckartsweier (EW)** | Agroforestry | Summer barley (*Hordeum vulgare* L., Avalon) | Sandy loam | 48°31'45.6"N, 7°51'23.3"E | 140 | 9.9 | 726 | Conventionally managed |
| **Strasskirchen (STR)** | Agrivoltaic | Potatoes (*Solanum tuberosum)*, White cabbage (*Brassica oleracea*) | Gleyic soil (sandy) | 48.7615° N, 12.5645° E | 322 | 9.5 | 750 | Conventional with biochar additions |
| **Bürgewald (BW)** | Agrivoltaic | Beans (*Vicia faba,* Tiffany*)* | Parabrown earth (loam) | 50°51'49.14"N, 6°31'50.15"E | 122 | 10.7 | 668 | Conventionally managed |
| **Heggelbach (HG)** | Agrivoltaic | Potatoes (*Solanum tuberosum,* Amanda*)*, Beans (*Vicia faba,* Birgit*)* | Sandy loam | 47° 51' 12.83"N 9° 8′ 11.436"E | 656 | 9 | 1022 | Biodynamic |

**Table B2**
Field specifics for each field

| Site | System specifics |
|---|---|
| **Heidfeldhof** | The agroforestry field consists of arable land lined with an alley of trees: *Prunus avium L.* (wild cherry). Trees were planted in 1995. They stand at an average height of 10.18 m (status: 23.02.2023), an average stem diameter (at height 1.3 m) of 37.18 cm and featured a crown width of ca. 10.95 m. Distance from tree row to field is approximately 4 m. |
| **Eckartsweier** | The agroforestry field consists of forested land next to the arable field (forest margin). The forest is composed of mixed broadleaf species, and is dominated by beech (*Fagus sylvatica)* and hornbeam (*Carpinus betulus*). The distance from forest to the west field is 6–18 m (3 single trees at 6 m, with the remainder of the trees at 12–18 m distance). The tree height reaches a maximum of 26 m. |
| **Strasskirchen** | The agrivoltaic system cover 0.5 ha. The modules are bifacial solar modules, mounted at 6 m above ground. They are oriented on an east-west tracking system (single axis). Row spacing allows for four, 12 m wide and 91 m long strips covered by the panels (HyPErFarm Project, 2023). |
| **Bürgewald** | The agrivoltaic field covers a total area of 4000 $m^2$ with two both a high and low system. The fields for this data set include an area of 520 $m^2$ in the lower system and 600 $m^2$ reference area. The modules are bifacial silicon modules. Their orientation is south-facing and tilted at 20°. The system is elevated at 2.5 m above ground with 4.4 m row spacing. |
| **Heggelbach** | The agrivoltaic field consists of a total area of 2.5 h, of which 2500 m2 are built with solar panels and the remaining area serves as a reference. The modules are bifacial glass-glass solar modules mounted 6 m high with an inclination angle of 20o and a southwest orientation. The modules are mounted at 5 m height and a row spacing of 6.4 m. |

## Data availability

Data will be made available on request.

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