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Specific Leaf Area and Photosynthesis of Apple Trees Under a Dynamic Agrivoltaic System

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Abstract. It has been assumed that crops cultivated in agrivoltaics (AV) systems can produce enough carbohydrates through the process of photosynthesis because they are exposed to an excess of light. However, many studies have shown increases in specific leaf area (SLA) under shading that can be associated to reductions in the photosynthetic capacity of leaves. This study aimed to evaluate the impact of severe and fluctuating AV shading on apple leaf morphophysiological characteristics (SLA and photosynthesis). 10-year-old 'Golden Delicious' apple trees grown in a dynamic AV system were monitored over three consecutive seasons (2019 to 2021) along with a control without panels. From February 2019 until July 2021, the photovoltaic modules rotated to maximise tree shading (15 hours of shading per day in summer). From July 2021 onwards, a lighter shading strategy was tested (5.8 hours of shading per day in summer). SLA at several dates was always higher for trees in the AV system (bigger individual leaf area but thinner leaves). SLA was not modified when light availability was increased late in the season. Light response curves indicated a lower saturation point for leaves grown in the AV system and a linear negative relationship was found between SLA and maximal photosynthetic capacity. To avoid leaf morphology modifications due to shade acclimation, we propose to avoid severe shading during leaf development. We expect this study will provide a better understanding on how to modulate the light microclimate at specific times of the season in dynamic AV systems.

Keywords: Carbon Assimilation, Fruit Trees, Leaf Morphology, Low Light Environment, Shade Acclimation

1. Introduction

Agrivoltaic (AV) systems were developed based in the idea that cultivated plants only employ a small percentage of incident sunlight (between 3% and 6% of total solar radiation) to accomplish their maximum rate of photosynthesis [1]. Above a light saturation threshold, specific to each crop, the photosynthetic activity of the leaf saturates (light saturation point). Increases of light above the saturation point are not associated with increases in photosynthesis. Moreover, excessive radiation can even cause photoinhibition [2]. Shading crops with AV systems may not impact the photosynthetic activity of leaves and avoid photodamage. However, the reduction in incident radiation caused by AV systems has been sometimes associated with a decrease in yield [3],[4]. We hypothesised that this reduction could be partly explained by a reduction of the saturation point of leaves developed under AV systems among other factors. Shading experiments indicated that shade-grown leaves had

lower net photosynthetic rates [5] due to their larger specific leaf area [6]. This observation has been done under constant shading conditions during the day (e.g., shading nets), but it is not known if the fluctuating shade caused with AV systems may have the same effect on leaf specific leaf area and photosynthesis. This is even more relevant for dynamic AV systems because leaves can be exposed to fluctuating shading during the day (maximum shading or full sun during the same day) [7]. To propose shading strategies with dynamic AV systems that can guarantee commercial yields, it is first important to understand the consequences of fluctuating shading on leaf morphology (specific leaf area) and their maximum rate of photosynthesis. The objectives of this study in apple trees were: (1) to determine the impact of a dynamic AV system managed to produce the maximum shading during the whole season on SLA at several dates during two consecutive seasons (2019 and 2020), (2) to determine if a return to light once the leaves have reached their maturity can modify their SLA developed under maximum shading in an additional season (2021), and (3) to establish relationships between SLA and leaf photosynthetic capacity measured over the three experimental years.

2. Material and Methods

2.1 Experimental orchard

A dynamic AV system was constructed in February 2019 in a mature 'Golden Delicious' apple orchard located in Mallemort (south of France). The experimental orchard consisted of 735 m² for the AV (shade treatment) and 1482 m² for the control part without solar panels (control treatment) (Figure 1). This study include research from three consecutive seasons (2019, 2020 and 2021). From February 2019 until July 2021, the photovoltaic modules rotated following a 'Solar Tracking' approach to maximise tree shading (tree mean interception about 50-55 %) with a shading rate during the day fluctuating between 4% and 88% [7]. From July 2021 onwards, a lighter shading strategy was tested by shading the trees only during the sunniest and warmest hours of the day by reducing the number of hours with solar tracking. The average tracking time was reduced from 15 to 5.8 hours per day.



Figure 1. View of the dynamic agrivoltaic system in the apple orchard constructed by Sun'Agri in Mallemort (France).

2.2 Leaf morphology and photosynthetic activity

Between May (one month after full bloom) and August (canopy fully developed), 60 leaves of each treatment were destructively sampled in a monthly basis to determine the seasonal

patterns of specific leaf area (SLA, ratio of individual leaf area to leaf dry mass, $\text{m}^2 \text{kg}^{-1}$) for each treatment and season. Therefore, four SLA values (one per month) are available for each treatment and season. From ten experimental trees, six fully expanded leaves outside the canopy at a height of 1.50 m were collected to determine the SLA. Individual leaf area was first determined with a leaf area meter (LI-3100C, LI-COR Biosciences GmbH, Germany). Leaves were then dried to constant mass at 70 °C in an air-forced oven, and the dry weights were individually determined. In 2021, for each sampling date, an additional sampling of six fully expanded shaded leaves (leaves inside the canopy) was done to determine if there was an effect of leaf position on SLA (internal vs. external position within the canopy).

Leaf photosynthetic light responses were assessed in June between 10:00 and 12:00 h for each treatment and season. Measurements were made using a portable photosynthesis system (LICOR, LI-6400-XT, Lincoln, NE, USA). Sampled leaves were fully expanded, sun-exposed and located at a height of about 1.5 m (sampling like the one done for SLA determination outside the canopy). For each treatment, six leaves from three trees were chosen for the measurements. CO_2 concentration and the temperature of the leaves were maintained constant during the measurements at $400 \mu\text{mol mol}^{-1}$ and 25 °C, respectively. For each light response curve, the photon flux density ($\mu\text{mol m}^{-2} \text{s}^{-1}$) was initiated at zero values to determine the light compensation point (the minimum light intensity at which the leaves show a gain of carbon fixation). Then light was gradually increased from 0 to 60, 120, 250, 500, 1000 to a maximum of $2000 \mu\text{mol m}^{-2} \text{s}^{-1}$. Each leaf photosynthetic light response curve was performed in about 30 minutes.

In 2021, we studied the specific relationships between SLA and leaf maximal photosynthetic activity (P_{max}) at light values of $2000 \mu\text{mol m}^{-2} \text{s}^{-1}$ using the portable photosynthesis system and the same setting values of CO_2 and leaf temperature mentioned before. P_{max} and SLA were made first under maximal shading conditions (4 June, full tracking strategy) and three times after the increase in light availability (8 July, 19 July, and 20 August). For these measurements (P_{max} and SLA), an additional sampling of shaded leaves (leaves inside the canopy) was done to determine if there was an effect of leaf position on P_{max} and SLA (internal vs. external position within the canopy). SLA was determined for the leaves used for P_{max} determination and two additional close leaves (36 leaves in total for SLA and 12 leaves for P_{max}).

3. Results and Discussion

Growing trees under the maximum shading of an AV system increased SLA of external leaves by 22% in comparison with control (Figure 2). That means that leaves for apple trees in the AV system were thinner than for leaves of control trees. These results were obtained for leaves in the periphery of the canopy, i.e. for leaves that were punctually exposed to direct sun radiation (in particular near solar noon, when the panels only shade the central part of the row). These support the fact that SLA is very sensitive to changes in the availability of environmental resources such as light [6], even for large shading intensity variation during the day ranging between 4 to 88 % in this study [7]. From the two components of SLA, the leaf area is the one most impacted by AV with an average increase over the three years of 15% [7], as illustrated in Figure 3.

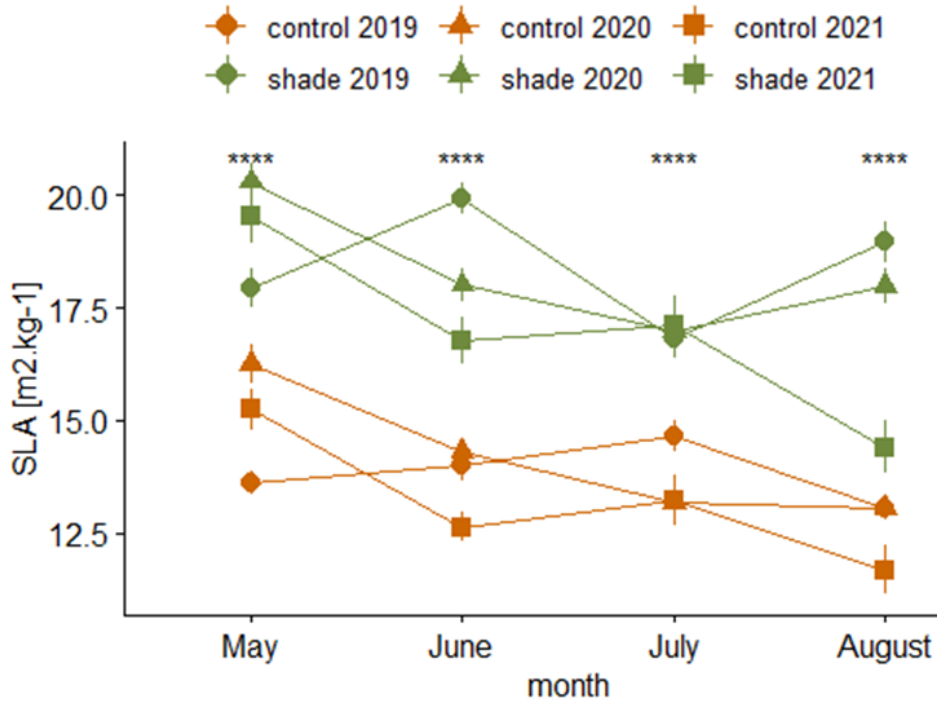


Figure 2. Mean specific leaf area [m²/kg] (\pm standard error) in May, June, July, August 2019, 2020, and 2021 for shaded and control leaves. Each point represents 60 measurements (six leaves for ten trees) (ns: $P > 0.05$; *: $P \leq 0.05$; **: $P \leq 0.01$; ***: $P \leq 0.001$; ****: $P \leq 0.0001$).

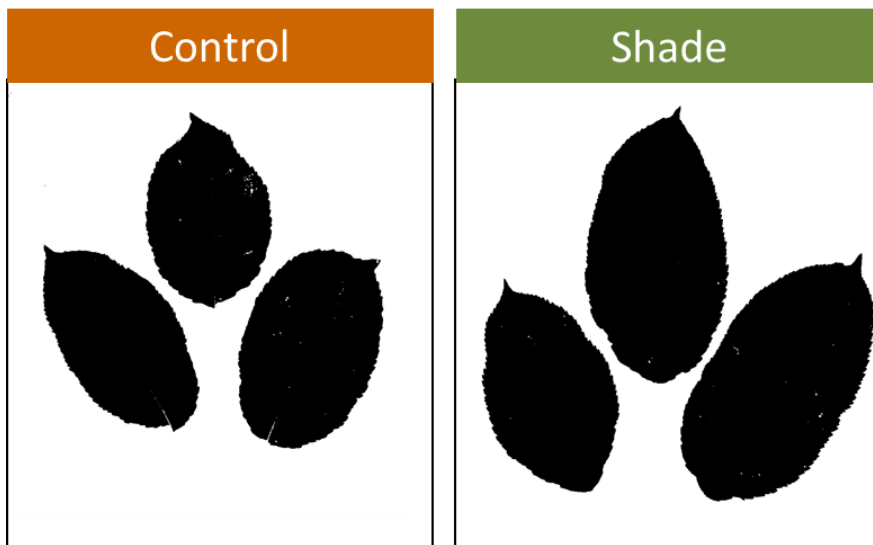


Figure 3. Photography of leaf area for control and AV leaves during 2019 season

Measurements on leaves under photovoltaic panels in the outside part of the canopy, which were fully exposed to saturating light radiation at the time of measurement, showed a P_{max} about 20% lower than the control leaves whatever the year (Figure 4).

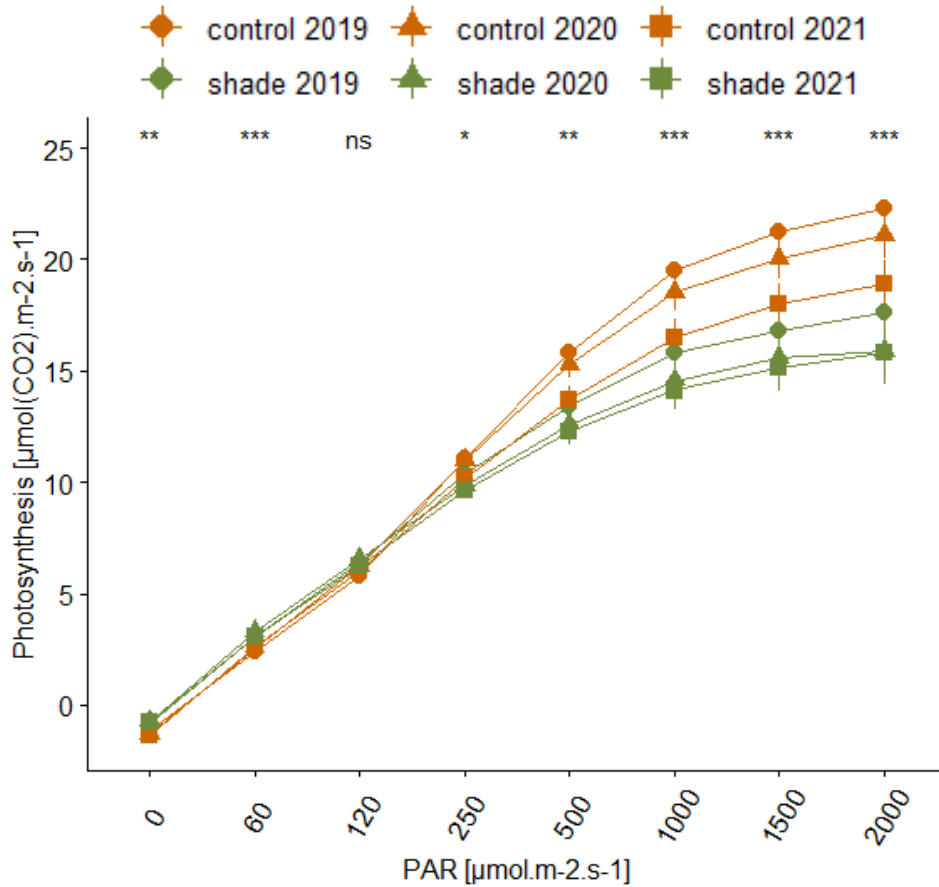


Figure 4. Net photosynthesis [$\mu\text{mol}(\text{CO}_2).\text{m}^{-2}.\text{s}^{-1}$] (\pm standard error) according to PAR [$\mu\text{mol}.\text{m}^{-2}.\text{s}^{-1}$] in June 2019, 2020, and 2021 for shaded and control leaves. Each point represents six measurements (one leaf for six trees) (ns: $P > 0.05$; *: $P \leq 0.05$; **: $P \leq 0.01$; ***: $P \leq 0.001$; ****: $P \leq 0.0001$).

While shading from the PV panels appears to impact leaf morphology and physiology, shading within the tree also had a strong influence on SLA and Pmax (Figure 5). Leaves in the inner canopy have an average 30% higher SLA than leaves in the outside part of the canopy (Figure 5, A). This distribution of SLA showed a gradation with the exposed leaves of the shaded treatment which had an SLA intermediate to the leaves of the control treatment. Considering Pmax, variations under AV is comparable to the variation observed within the tree between leaves inside and outside the canopy (Figure 5, B). These results indicated a strong heterogeneity within the apple tree in terms of leaf morphology and photosynthetic capacity. Moving from the leaf scale to the tree scale seems essential to understand the impact of the shading of agrivoltaic systems on carbon acquisition at the canopy level. Therefore, whole tree modelling seems to be an essential tool to optimise agrivoltaic structures and shading strategies. To integrate the complexity of the fruit tree canopy scale, several models describing a three-dimensional tree architecture have been developed. L-PEACH [8] and QualiTree [9] described the carbon acquisition and allocation of peach trees in response to agricultural practices. However, the effects of fluctuating shade have not been yet formalised in any of these models.

Despite a lighter shading strategy after July 2021 (from 15 hours of tracking per day to 6 hours per day for the same period), SLA and Pmax remained stable under the shading of the AV system with still higher values than control trees for SLA and lower values for Pmax (Figure 5). The pattern of shading intensity during the season seems important since SLA and Pmax are strongly correlated to light conditions during leaf development and does not seem to be highly affected by incident light when leaf development and growth are completed [10].

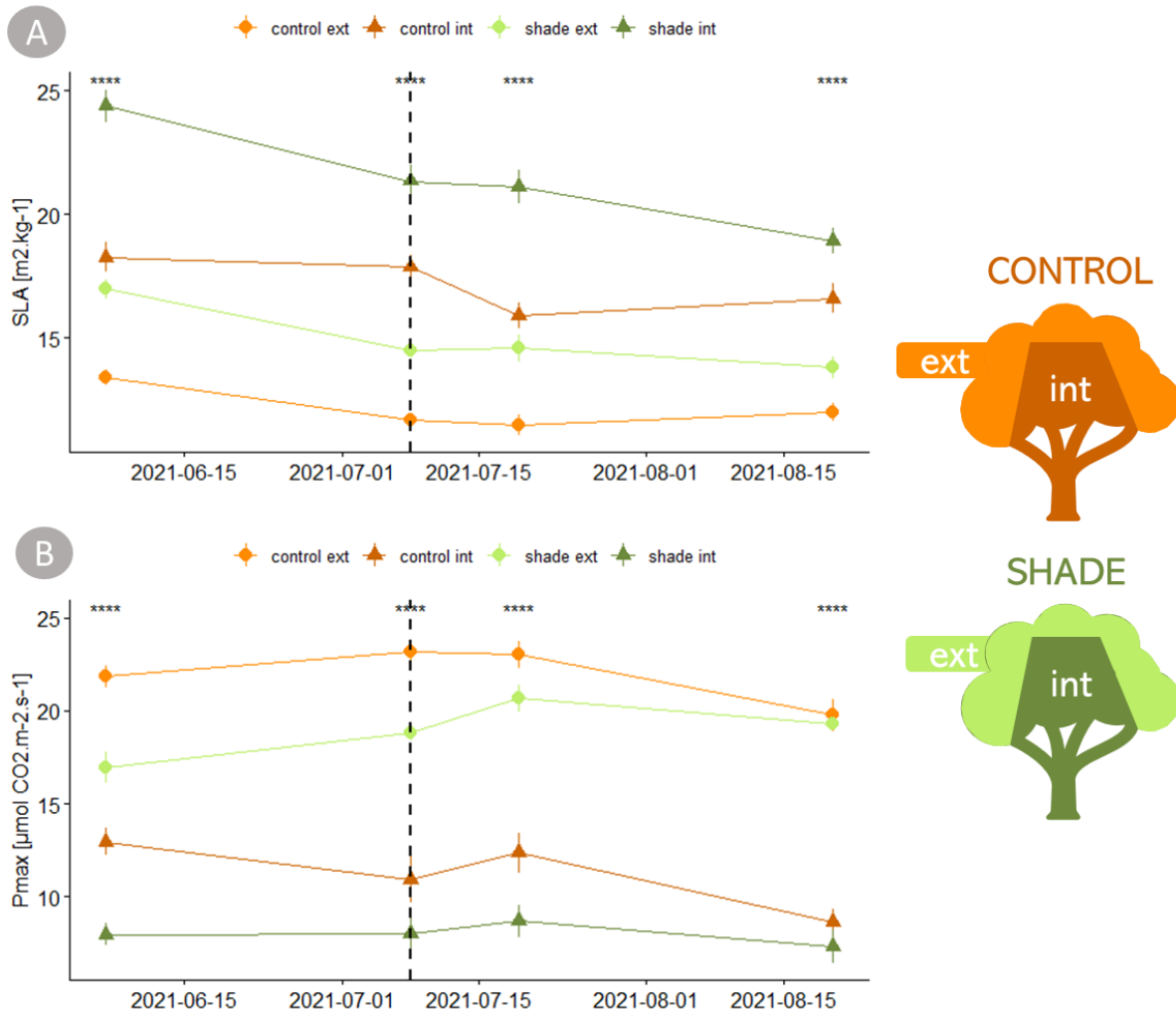


Figure 5. (A) Specific leaf area (SLA) [m².kg⁻¹] (\pm standard error) and (B) Maximal photosynthesis (Pmax) [μ mol CO₂ m⁻² s⁻¹] (\pm standard error) during 2021 season for shaded leaves outside (shade ext) and inside (shade int) the canopy and control leaves outside (control ext) and inside (control int) the canopy. Each point represents 36 measurements (six leaves for six trees) for SLA and 12 measurements for Pmax (2 leaves for six trees). Vertical line indicated changes in strategy from strong to lighter shading. (ns: P > 0.05; *: P \leq 0.05; **: P \leq 0.01; ***: P \leq 0.001; ****: P \leq 0.0001).

A negative correlation was observed between SLA and Pmax, directly influenced by shading rate as illustrated in Figure 6. Thus, the shading of the solar panels increased their individual leaf area but at the same time limited their photosynthetic capacity. It has been previously reported for apple that lowering light availability reduce the leaf palisade thickness [11]. During photosynthesis light energy enters through the cuticle and upper epidermis and filters through the palisade layers where the process of photosynthesis occurs. That may be one of the reasons why AV leaves had lower Pmax values.

An interesting research question to address in future analysis would be to determine to what extent the increase in individual leaf area for AV trees could compensate for the reduction of leaf carbon acquisition at the whole-canopy level.

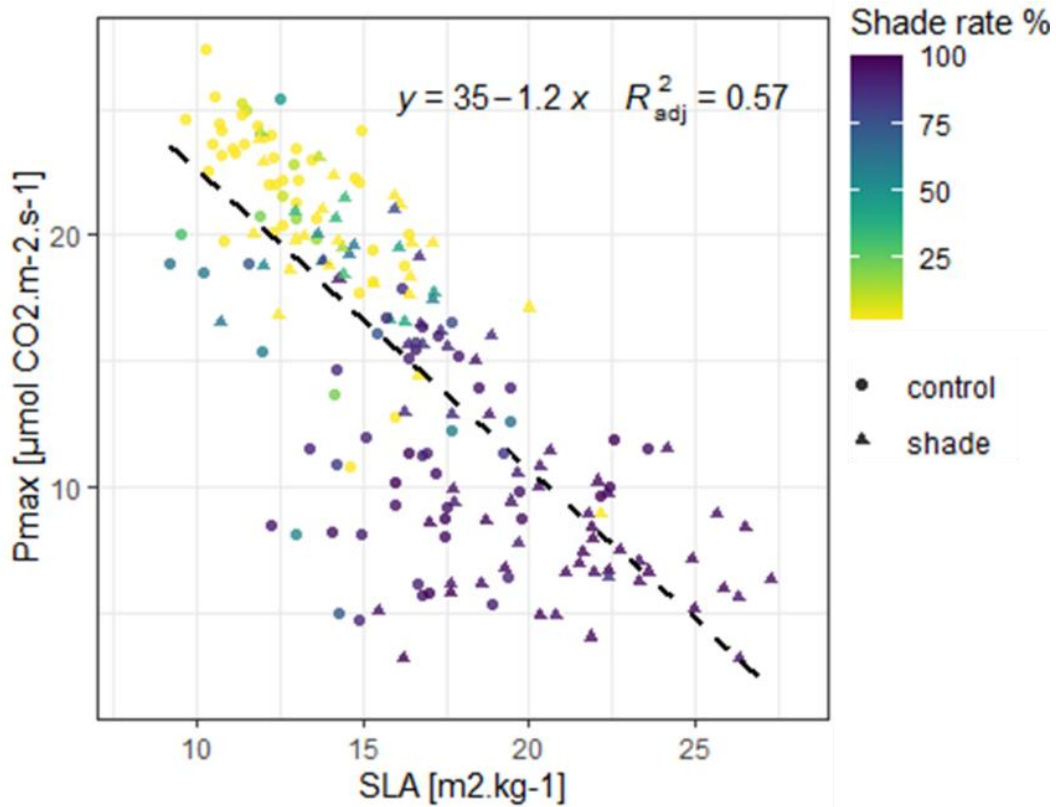


Figure 6. Linear regression between Pmax [µmolCO₂.m⁻².s⁻¹] and SLA [m².kg⁻¹]. Shape of the points representing treatment and colour representing the shade intensity rate [%] of the leaf at the time of measurement between June and August 2021.

4. Conclusions

Leaves of apples trees grown in a dynamic AV system had higher values of SLA in comparison with control trees when maximal shading was applied during their development. Higher SLA implies bigger individual leaf area but thinner leaves. SLA was determined early in the season, and it was not significantly modified even if light availability was increased late in the season. This confirm the idea that SLA is strongly correlated to light conditions during leaf development and does not seem to be highly affected by incident light when leaf development and growth are completed. Light response curves indicated a lower saturation point for leaves grown in the AV system and a linear relationship was found between SLA and maximal photosynthetic capacity. Photosynthesis capacity decreases with increases in SLA. Apple trees may have therefore a lower capacity to assimilate carbohydrates due to their leaf morphology. To avoid leaf morphology modifications due to shade acclimatation, we propose to avoid severe shading during leaf development. Once most part of the leaves in the canopy are fully developed, shading can be increased to photosynthetic photon flux density levels high enough to saturate carbon assimilation but low enough to reduce photoinhibition and leaf damage. To move from the leaf scale to the tree scale, the shading strategy should be decided considering the whole canopy, in which a strong light heterogeneity and photosynthetic capacity of leaves exists. To integrate the complexity of the canopy scale, whole tree modelling seems to be an essential tool.

Data availability statement

The data of this study is confidential.

Author contributions

PJ, GL, GV and MG: Conceptualization and Writing – original draft. PJ and VL: Investigation. DF: Supervision and Project administration.

Competing interests

The authors declare that they have no competing interests.

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