Data-Driven Phsyiological Modeling of Canopy Photosynthesis for Precision Irrigation Management

Project No.:   **HORT37.Buckley**

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Grantee(s) of the Almond Board are REQUIRED to address sections A through G. These should be **submitted in PDF**, using Arial font size 12 for the main text, and be five to seven pages in length.

A. Summary *(In laymen's terms – emphasize key findings and recommendations)*

We sought to determine how canopy photosynthesis is affected by irrigation, to test the hypothesis that irrigation scheduling could be improved to increase total carbon gain for a given total irrigation input. The rationale is that growth and yield require carbohydrates from photosynthesis, which can be decoupled from water loss by variations in VPD, temperature and water deficit effects on the biochemistry of photosynthesis. Photosynthesis also typically sees "diminishing returns" from increasing transpiration, such that under heavy irrigation, it may be possible to reduce water applications with no detrimental impact on photosynthesis.

To test these ideas, we used sap flow and meteorological measurements to determine canopy conductance, and combined that data with measurements of the response of leaf photosynthesis to CO_2 and light to simulate canopy photosynthesis over a summer growing season, in two varieties (Aldrich and Nonpareil) in a research orchard in the northern Sacramento Valley near Arbuckle. Half of the study trees were stressed by withholding water for 7-10 days at two times during the season. Control trees were moderately stressed prior to harvest by reducing irrigation by 20%. Otherwise, all trees were irrigated to ETc.

We found that (1) photosynthetic biochemistry was unaffected by soil drought; (2) photosynthesis was tightly related to transpiration; (3) in this orchard, photosynthesis was nowhere near saturated with respect to water loss, such that (3a) yield declined in the stress treatment approximately in proportion to the estimated reduction in canopy photosynthesis caused by stomatal closure during stress, and (3b) optimal redistribution of a fixed total amount of irrigation over the season would have little benefit; and (4) even mild water stress such as associated with 20% reduction in irrigation prior to harvest may cause substantial decline in water transport capacity (hydraulic conductance), which has the potential to suppress photosynthesis even after resumption of full irrigation.

We conclude that irrigating to ETc during the main growing season is fairly efficient in terms of carbon gain, but that withholding water around harvest may substantially harm tree health and reduce current-year and future yield. The latter issue requires more intensive study.

B. Objectives *(300 words max.)*

1. Specify the goal(s) and specific objectives of the proposal – if a collaborative effort, identify who is the lead for each objective
2. Identify annual outputs or milestones for each of the objectives

Main Goal: Develop and deliver a method for irrigation scheduling based on physiological modeling of canopy photosynthesis. (*Note: these objectives were written in anticipation that funding would be extended beyond July 2020, which it was not. Items thus obviated are shown in strikethrough font.*)

Objective(s)	Date to be accomplished	Milestones and deliverables associated to the objective
(1) Parameterize a canopy photosynthesis model in Nonpareil and Aldrich and drive it with continuous measurements of canopy conductance from sap flow.	31 Dec 2020	31 Dec 2019: parameterization for Nonpareil, Aldrich. 31 March 2020: model for Nonpareil, Aldrich. ~~31 Dec 2020: 2nd year of parameters.~~
(2) To help scale the model from leaf to orchard level, quantify variation in PAR within tree crowns, and in intrinsic water use efficiency (iWUE, the ratio of photosynthesis to stomatal conductance) among trees.	30 July 2020	30 July 2019: proof of concept for Nonpareil (PAR [1 tree], iWUE [10 trees]). ~~30 July 2020: full results for Nonpareil, Aldrich (PAR [4 trees], iWUE [10 trees]).~~
(3) Determine how changes in irrigation affect modeled canopy photosynthesis and measured SWP as environmental conditions vary across a growing season.	31 July 2021	30 July 2020: analysis of 2019 season. ~~31 July 2021: analysis of 2020.~~
(4) To allow canopy photosynthesis to be modeled without sap flow data, parameterize and test a physiological model for canopy conductance in Nonpareil and Aldrich.	31 Dec 2020	31 Dec 2019: parameterization for Nonpareil, Aldrich. 30 July 2020: model for Nonpareil, Aldrich. ~~31 Dec 2020: 2nd year of parameters.~~
(5) To determine guidelines for more effective irrigation scheduling, use the model to simulate the impact of a range of potential irrigation strategies.	30 July 2021	30 July 2020/2021: Simulation~~s~~ for 2019~~/2020~~ season~~s, respectively~~.
~~(6) Develop a stand-alone package, including a user-friendly app, to provide irrigation advice to growers based on modelling canopy photosynthesis.~~	~~30 July 2021~~	~~31 Dec 2019: Prototype datalogger.~~ ~~31 Dec 2020: Demonstration version of app.~~ ~~30 July 2021: Final version.~~

C. Results and Discussion *(This is the core function of this report)*
1. Describe activities and outputs for each objective
2. Discuss significance of these in terms of progress toward goals, change in approach, next steps or other conclusions based on the overall results

This was originally designed to be a 2-year project (2019-2021), and the objectives and milestones described in Section B were organized accordingly. It was subsequently announced that all current projects would terminate in 2020. We therefore sought to gather as much knowledge as we could within the available timeline.

Objective (1): Parameterize a canopy photosynthesis model in Nonpareil and Aldrich and drive it with continuous measurements of canopy conductance from sap flow.

We <u>completed this objective</u> and the first two milestones in November 2019. We will be unable to complete a 2nd year of parameter estimation (the third milestone originally listed for this objective) due to early termination of the project.

We parameterized a canopy photosynthesis model for both Nonpareil and Aldrich and validated it with leaf-level measurements (Fig 1). We found no differences in photosynthetic parameters between the two varieties, so we combined data across varieties. and drove the model using continuous measurements of canopy conductance from sap flow (see Fig 3 under Objective 3).

Objective (2): To help scale the model from leaf to orchard level, quantify variation in PAR within tree crowns, and in intrinsic water use efficiency (iWUE, the ratio of photosynthesis to stomatal conductance) among trees.

We had planned to collect sapwood cores to quantify variation in intrinsic water use efficiency among trees at the Nickels orchard using isotopic techniques, but due to the COVID shutdown we were unable to complete this work. We had also to deploy handmade light sensors in summer 2020 to measure variation in PAR, but could not do so due to the early termination of the project.
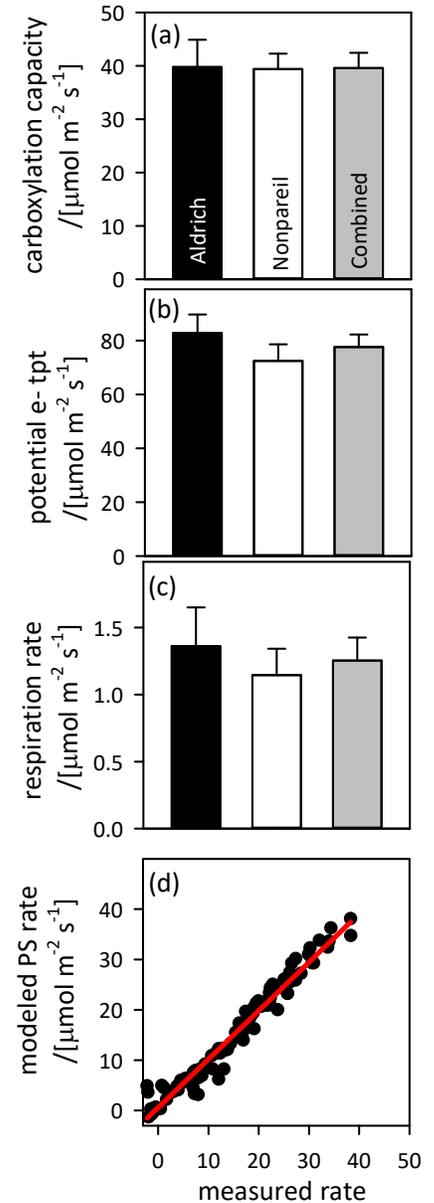

Fig 1. (a-c) Photosynthetic parameters (avg +/- SE, n=10). Variety differences were not significant. (d) Measured vs modeled leaf photosynthesis rate.

Objective (3): Determine how changes in irrigation affect modeled canopy photosynthesis and measured SWP as environmental conditions vary across a growing season.

We <u>completed this objective</u> in November 2019. We were unable to complete a 2nd year of measurements in 2020 (the second milestone originally listed) due to early termination of the project.
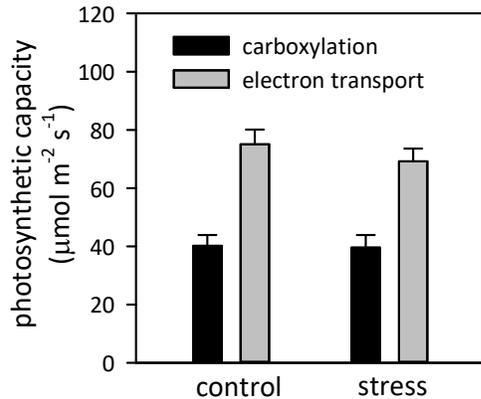

Fig 2. Water stress did not affect photo-synthesis biochemically (i.e., independently of stomatal closure).

We hypothesized that water stress would reduce canopy photosynthesis by two mechanisms: (i) by reducing photosynthetic capacity (photosynthesis in the absence of any limitations by stomatal opening) and (ii) by causing stomatal closure (reductions in canopy conductance) in response to declines in water potential. We found no evidence for the first hypothesis (Fig 2), but clear evidence for the second hypothesis (Fig 3). Canopy conductance (Fig 3a) and mid-day stem water potential (SWP, Fig 3b) both declined progressively during water stress, driving large declines in canopy photosynthesis (Fig 3a). The recovery of photosynthesis after resumption of irrigation to ETc was slow, taking more than two weeks to catch up with the control. Notably, SWP was not a reliable indicator of the occurrence of water stress during this period of lagging recovery: canopy conductance and photosynthesis remained depressed by ~20% for a week after watering, despite full recovery of SWP.

We also found evidence of strong decline in hydraulic conductance (the rate of water transport and hence transpiration that can be sustained for a given water potential gradient between the soil and canopy), during even moderate drought (Fig 3a). Our evidence suggests, although inconclusively, that hydraulic decline exacerbated the negative influence of drought on both stomatal opening and photosynthesis.
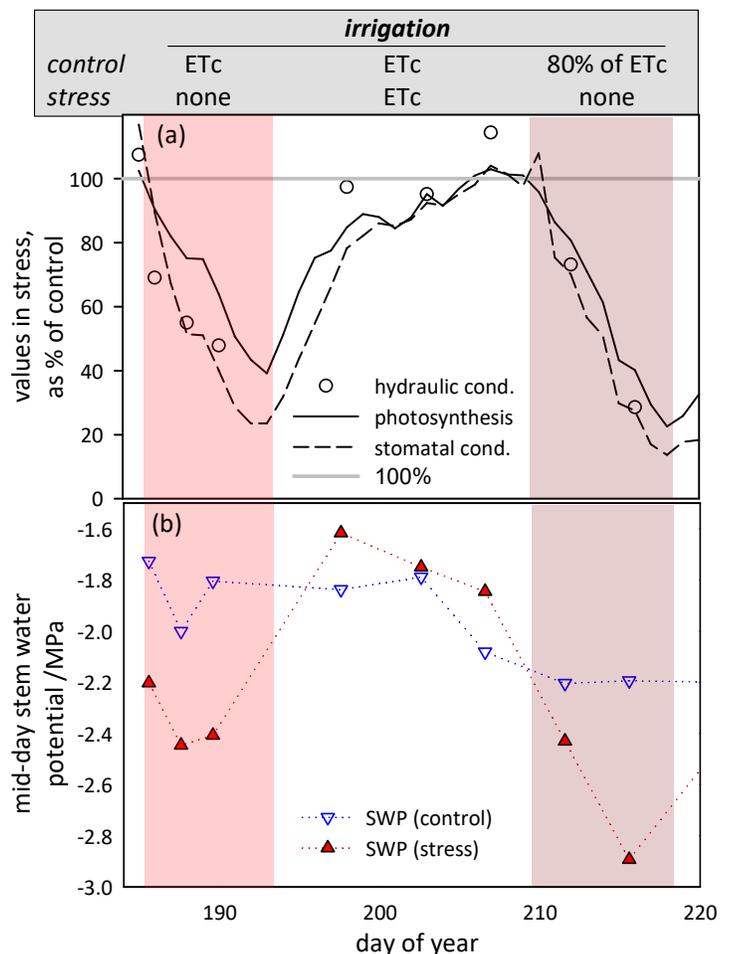

Fig 3. Effects of water stress on (a) canopy photosynthesis, stomatal conductance, & hydraulic conductance, and (b) SWP.

Consistent with these effects of water stress on canopy photosynthesis, we found that yield declined substantially in the stress treatment, and approximately in proportion to the estimated reduction in total photosynthesis caused by the stress treatment (Figure 4, left). We also estimated that mild harvest stress <u>in the control treatment</u> reduced total photosynthesis for July-August by approximately 23% (Fig 4, right).
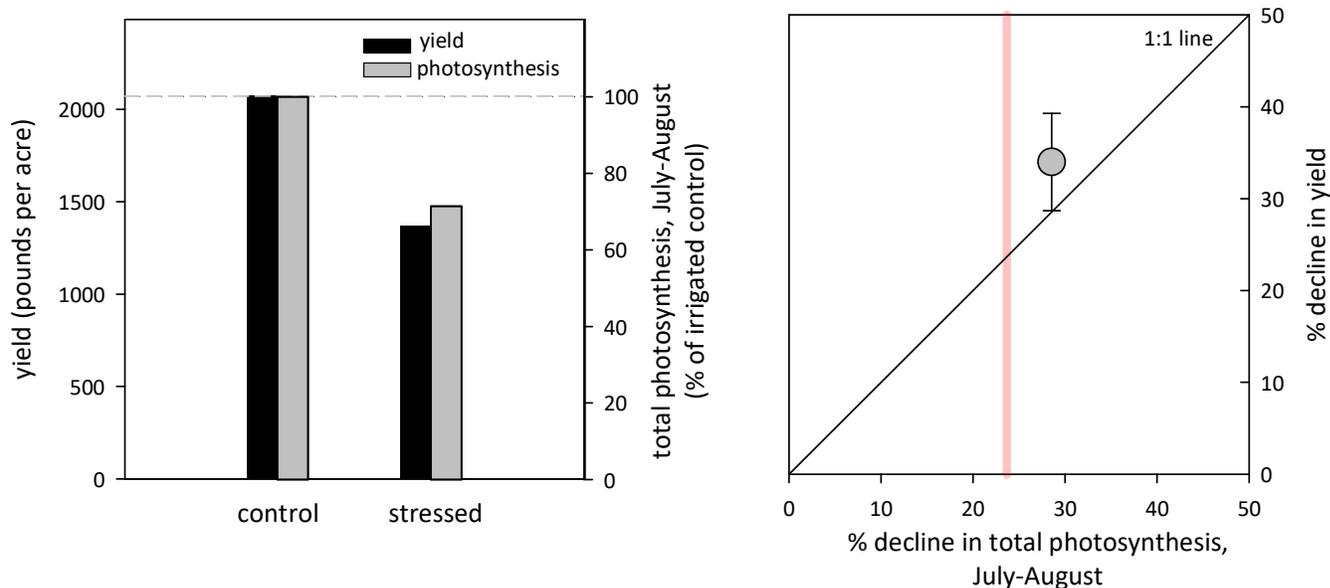

Figure 4. Yield and photosynthesis for control and stressed treatments (left; grey symbol at right), and the estimated decline in photoynthesis caused by reduction of irrigation prior to harvest in the control treatment (red line at right).

Objective (4): To allow canopy photosynthesis to be modeled without sap flow data, parameterize and test a physiological model for canopy conductance in Nonpareil and Aldrich.

We found that the physiological model was not capable of adequately reproducing dynamics of sap flow with soil water potential interpolated linearly between measurements of pre-dawn stem water potential taken every 4-5 days (Figure 5). This was likely due to the frequent fluctuations in soil moisture caused by periodic (every 3-4 days) pulses of irrigation, with significant drying occurring rapidly after each pulse due to the site's poor sandy/gravel soils. Changes in soil moisture could be incorporated in the model if they could be converted to soil water potential; however, when we attempted to simulate soil water potential from soil water content, we found that the inferred pre-dawn water potentials were invariably far higher than measured (e.g.,> -0.002 MPa simulated, vs. -0.5 to -1.2 MPa measured). This likely indicates that soil drying affected the soil-to-root hydraulic interface rather than the water potential of the bulk soil per se
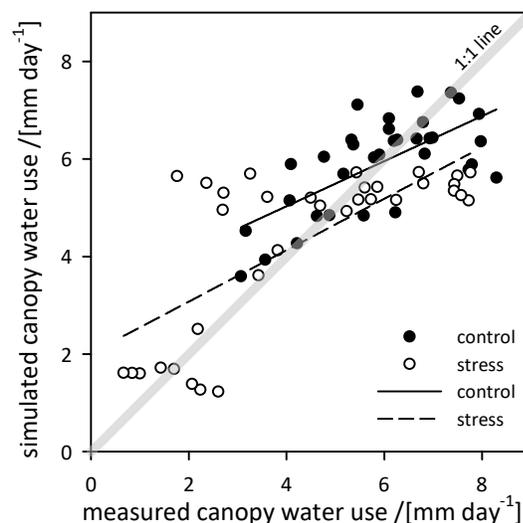

Fig 5. Performance of physiological model for canopy conductance. Lines = best fit (control: $y = 0.46x + 3.18$, $r^2 = 0.46$; stress: $y = 0.53x + 2.02$, $r^2 = 0.52$). Thick grey line is 1:1.

until soil water content was close to the permanent wilting point. To account for these effects would require much more intensive characterization of the plant hydraulic vulnerability curve (the response of hydraulic conductance to water potential, and particularly the soil-root interface component), which was beyond the scope of this study.

Objective (5): To determine guidelines for more effective irrigation scheduling, use the model to simulate the impact of a range of potential irrigation strategies.

Although this objective was planned to be carried out using two seasons of data, we completed it using 2019 season's data, due to the early termination of the project. Because this objective also depended upon the physiological conductance model from Objective (4), which we found to be inadequate, we used a different approach. We characterized the overall relationship between canopy photosynthesis and canopy transpiration, and then used that relationship to simulate the impact of redistributing water loss in time over the growing season in the manner that would maximize simulated whole-season canopy photosynthesis.

The rationale behind this objective was that it is less efficient to irrigate under some conditions than others. Our hypothesis was that, if water loss could be reduced during periods when photosynthesis was "expensive" in terms of water, and increased when photosynthesis was "cheap" in terms of water, then whole-season photosynthesis could be increased with no overall change in water use (or equivalently, water could be saved with no loss of total photosynthesis). The "cost" of photosynthesis in units of water is the slope of the relationship between canopy photosynthesis (on the y-axis) and canopy transpiration (on the x-axis). Generally, this slope decreases as water loss increases: that is, water earns diminishing returns in terms of carbon gain. We also hypothesized that differences in temperature would decouple carbon gain from water loss by negatively impacting photosynthetic biochemistry, increasing respiration rates (carbon loss), and increasing VPD.

Our results partially these ideas, but only partially and qualitatively. Water loss did earn diminishing returns of carbon gain (Figure 6a). However, deviations from this relationship were not strongly related to temperature (Fig 6b). Moreover, when we simulated a redistribution of
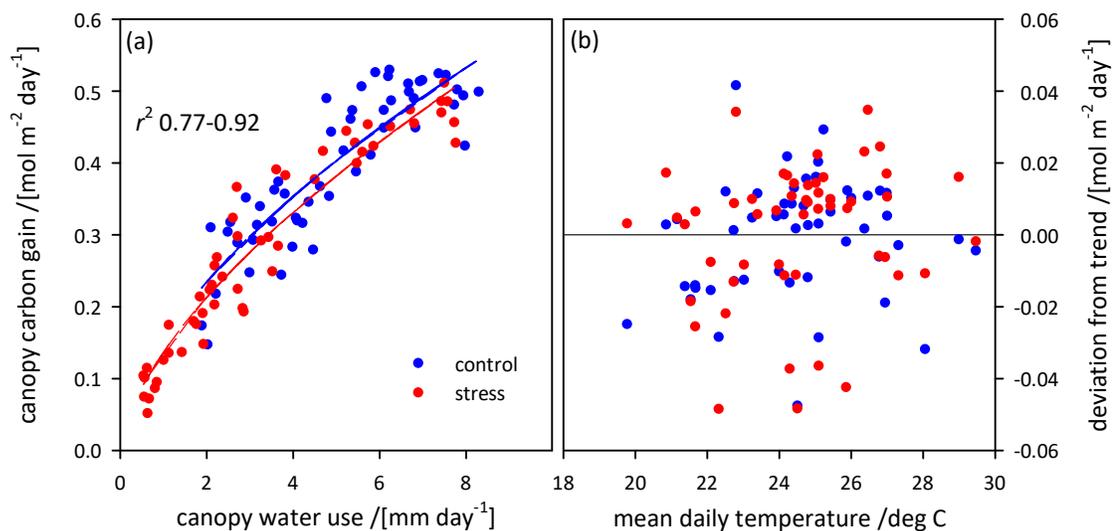

Figure 6. (a) Relationship between canopy water use and photosynthesis, and (b) deviations from that relationship, as a function of mean daily temperature.

water loss over the season in order to identify the "optimal" distribution, the benefits in terms of seasonal photosynthesis were minimal: we found that redistributing water use could, at best, improve whole-season carbon gain by about 5%. Even that small benefit was possible only under rather unrealistic assumptions. For example, it required assuming that that an irrigation strategy to achieve this goal could be designed and implemented with perfect precision, and that the resulting shifts in plant water status would have no other detrimental impacts.

There are two important conclusions from this result. Firstly, managing canopy transpiration by irrigating to ETc is actually quite efficient with respect to canopy photosynthesis. The factors that we expected to decouple photosynthesis from transpiration were much less important than we had anticipated. Secondly, even mild stress such as that experienced during a typical harvest period (in this case, the farm managers imposed a 20% decline in irrigation inputs beginning three weeks before harvest) may lead to damaging loss of water transport capacity, which would impact late-season photosynthesis and growth and possibly performance in subsequent years. We suggest that future research in this area should aim to rigorously quantify the effect of harvest stress on photosynthesis and yield, and that further study is required to understand the role of hydraulic decline in the effects of water stress on tree health and yield in almond.

D. Outreach Activities
  1. Please describe outreach activities including the event description (date, location, topic of the presentation, aprox number of participants and type of audience)

Results of this project to date were presented at the Almond Conference in Sacramento on 12 December 2019, to approximately 100 participants of varying backgrounds. We also presented a poster summarizing the results at the Almond Conference. Outreach efforts planned for 2020 (presentations at field days and academic conferences) were cancelled due to COVID.

E. Materials and Methods *(500 word max.)*:
  1. Outline materials used and methods to conduct experiment(s)
  2. Note any challenges or unforeseen developments that were encountered resulting in change of methodogy, timeline, or scope of project

Setting and treatments. We studied 20 individual trees at the Nickels Soil Laboratory near Arbuckle, CA, of which 10 were Nonpareil and 10 Aldrich. Trees were irrigated to ETc once every 3-4 days unless otherwise noted. Irrigation was withheld from 5 trees of each variety ("stress" treatment) at each of three times during the season, for 7-10 days (early June, early July and early August 2019). The remaining 5 trees of each variety (the "control" treatment) were irrigated normally until three weeks prior to harvest, when irrigation was reduced to 20% below ETc, and then withheld entirely from 4 days before to 6 days after shaking.

Sap flow. We measured sap flux (sapwood water flow per unit of cross-sectional sapwood area) in each tree using the double-ratio method (DRM). Four needles (one heated needle and three temperature sensors, located 7.5 mm below, 7.5 mm above and 22.5 mm above the heater, respectively; each needle was 1.27 mm in diameter and 30 mm in length) were installed in each tree trunk approximately 60 cm above the ground and underneath the bark,

and then insulated by wrapping the tree with batting insulation and mylar-coated bubble wrap (Reflectix). The DRM method was described in previous project reports for the ABC, and has been validated by lysimetry and tube flow experiments.

Canopy conductance. We calculated canopy conductance by dividing sap flow by estimated leaf to air water vapor mole fraction gradient (computed from air VPD) and then empirically adjusting the result to match mid-day values of stomatal conductance measured directly on each tree in early July.

Canopy photosynthesis. We measured photosynthetic parameters in each tree before and after the July dry-down, by recording the response of leaf net CO_2 assimilation rate to intercellular CO_2 concentration and fitting the biochemical photosynthesis model of Farquhar et al. (1980) to the results. We used previously published temperature responses for these parameters in almond. We combined these parameters with measurements of light intensity and temperature from an adjacent tower and canopy conductance to calculate leaf photosynthesis of sunlit leaves, and then scaled those values to the canopy used the sun/shade scaling method of de Pury and Farquhar (1997), based on leaf area index inferred from canopy light penetration measurements from Bruce Lampinen's mobile light bar.

Water re-distribution modeling. We generated a polynomial relationship between daily canopy photosynthesis and transpiration for July-August 2019 from the measurements and modeling described above, and then used this relationship to predict seasonal photosynthesis with daily transpiration adjusted while maintaining seasonal transpiration constant. The adjustments consisted of reducing water loss on days of high water loss (which are associated with lower marginal efficiency with respect to photosynthesis) and increasing it on days of low water loss.

F. Publications that emerged from this work
      1. List peer review publications in preparation, accepted or published
      2. Other publications (e.g. outreach materials)

Nothing to report.