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Coastal low cloudiness and fog enhance crop water use efficiency in a California agricultural system

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ABSTRACT

Impacts of climate change threaten California farmers in a number of ways, most importantly through a decline in freshwater availability, concurrent with a rise in water demand. In coastal California, the growing season of economically important crops, such as strawberries, overlap with the occurrence of summertime coastal fog, which buffers the summer dry season through shading effects and direct water inputs. The impacts of coastal fog on plant physiology have been extensively studied in natural ecosystems. Yet, very few studies have evaluated its direct effects on crop water use and demand, which has potential to curtail groundwater use. We established two sites on large, conventional strawberry farms along a coastal-inland gradient in the Salinas Valley, California, where we monitored variation in microclimate conditions and measured strawberry plant physiological responses to foggy and non-foggy conditions between June–September 2015. Spatial analysis of coastal low clouds and fog from satellite imagery was preformed to quantify and characterize fog events at seasonal and diel time scales. We found strong agreement between field and satellite-derived observations of coastal fog events. Canopy-level conductance and whole-plant carbon uptake were reduced by 60% and 30%, respectively, on foggy compared to clear-sky days. Leaf-level photosynthesis and stomatal conductance were 30% lower on foggy compared to clear-sky days, which was driven by reduced photosynthetically active radiation and cooler temperatures during fog events. Taken together, we found that whole-plant water use efficiency increased significantly during foggy periods, and these patterns were driven by changes in the radiation balance and atmospheric water stress. Our results provide evidence that the shading effect by fog is a primary influence on crop water use efficiency in coastal agricultural fields during summer. The outcome of our research can inform estimates of how much irrigation water may be reduced during foggy periods without sacrificing crop yields on coastal agricultural lands.

1. Introduction

California agriculture is a US$47 billion industry and consumes 80% of freshwater resources in the state (California Department of Food and Agriculture, 2015). Availability of freshwater resources is threatened by climate change and drought, in particular (Postel 1998; Green et al., 2011). The economic, social, and ecological impacts of drought are widespread, especially for the agricultural sector which is highly vulnerable to water scarcity and climate variability (Tanaka et al., 2006; Connell-Buck et al., 2011; Howitt et al., 2015). Between 2012–2015, California experienced the most severe drought in the past 1200 years (Griffin and Anchukaitis, 2014). While precipitation deficit is the primary driver of drought conditions, anthropogenic warming of the atmosphere increases the likelihood of more extreme droughts in California (Diffenbaugh et al., 2015; Williams et al., 2015a), which is a direct threat to water availability in agriculture (AghaKouchak et al., 2014; Thomas et al., 2017). Because freshwater utilization by agriculture far outpaces usage by any other sector, agricultural irrigation practices should be more water efficient for food production to be sustainable in the future (Marques et al., 2005; Schaible and Aillery, 2012).

Coastal California supports production of many economically important crops (i.e., strawberries, lettuce, and broccoli) that contribute significantly to the state's multibillion-dollar agricultural industry. For example, in crop-year 2015–16, strawberry production was valued at US$1.8 billion dollars and ranked fifth in agricultural commodities in the state (California Department of Food and Agriculture, 2015). Strawberry crops occupy nearly 20,000 hectares of coastal California farmland and are also one of the most water-intensive crops to grow. Coastal farms are threatened not only by water scarcity, but also by

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saltwater intrusion that contaminates groundwater supply, which effectively reduces the amount of arable land in this region. To curtail groundwater use, support tools have been developed to inform irrigation practices (amount and timing) based on daily estimates of evapotranspiration (ET) rates, known as 'ET-based irrigation' (Snyder and Pruitt, 1992; Melton et al., 2012; Snyder et al., 2015). Despite scientific evidence that ET-based irrigation would not negatively impact crop yield (Johnson et al., 2016), the pervasive narrative among farmers is that the economic risk of crop loss by reducing irrigation application is too great. However, the recently enacted Sustainable Groundwater Management Act (SGMA) requires that groundwater be regulated for the first time in California's history (Kiparsky et al. 2017), which incentivizes farmers to implement sustainable water use plans and rely more on ET-based irrigation systems.

In California, crop productivity peaks during the summer months (June-August) when the photoperiod is longest; however, this is also when rates of potential evapotranspiration (PET) are highest. Heat loading and evaporative demand in coastal California are partially relieved during summer due to the occurrence of low-level coastal stratus clouds and ground fog, which is when the cloud interacts with the land surface (hereafter, grouped together as "coastal fog"). Coastal fog forms when warm subsiding air interacts with cool air over the ocean that is driven by coastal upwelling. Water vapor condenses on condensation nuclei, such as salt spray, forming the marine layer offshore. Inland temperature drives a gradient that causes the marine layer to advect onshore (Koračin et al., 2005). Coastal fog influences the water and energy balance of ecosystems in a number of ways. Shading by fog reduces PET, which improves plant water status, supporting plant growth, especially during the otherwise dry time of year in Mediterranean climates (Williams et al., 2008; Fischer et al., 2009). Plants immersed in fog can benefit from direct water inputs because water droplets drip to the ground and increase soil moisture (Azevedo and Morgan, 1974; Harr 1982; Ingraham and Matthews, 1995; Dawson 1998; Corbin et al., 2005; Williams et al., 2008; Carbone et al., 2013; Fischer et al., 2016; Baguskas et al., 2016). Several studies have also demonstrated that transpiration rates decline during fog events across a wide-variety of plant species in natural ecosystems (Burgess and Dawson, 2004; Ritter et al., 2009; Berry and Smith, 2013; Alvarado-Barrientos et al., 2014; Gotsch et al., 2016) due to lower vapor pressure deficit and leaf-wetting events. Direct foliar absorption of fog water can reduce leaf water deficit and increase leaf gas-exchange rates (Burgess and Dawson 2004; Simonin et al., 2009; Limm et al., 2009; Goldsmith et al., 2013; Berry et al., 2014; Baguskas et al., 2016) and contribute to whole-plant rehydration (Eller et al., 2013). There are also potential tradeoffs between reduced plant water stress and reduced solar radiation on foggy days (Bai et al., 2012). Cloud shading can reduce plant productivity by reducing the total amount of light available to drive photosynthesis and growth (Knapp and Smith, 1990; Larcher, 2003). Alternatively, cloudy conditions can increase whole-plant productivity because diffuse, cloud-scattered light can irradiate otherwise shaded leaves in the plant canopy (Gu et al., 1999; Gu et al., 2002; Min 2005; Alton et al., 2007; Still et al., 2009; Mercado et al., 2009; Bai et al., 2012). Associated changes in atmospheric conditions (temperature, relative humidity, and vapor pressure deficit) during fog events can also have a significant impact on plant water use and productivity (Williams et al., 2008; Ritter et al., 2008, 2009; Still et al., 2009).

While the impacts of coastal fog on plant biology have been extensively studied in natural ecosystems, only a few studies have evaluated its direct effects on the water, carbon, and energy budgets of agroecosystems (Hunt et al., 2008; Moratiel et al., 2013). Moratiel et al. (2013) found that the deposition of water on leaves from dew, fog, and light rain increases the accuracy of modeled crop-ET in California farmlands because leaf-wetting from these events results in a discrepancy between soil water balance and crop-ET estimates. Similarly, Hunt et al. (2008) found that summertime coastal fog decreases actual ET from blueberry farms on the east coast of the U.S., which was attributed to the effects of both shading and direct water inputs through fog-drip to the soil. These studies provide evidence that coastal fog can significantly offset water loss from farms. Because peak growing season of highly valued crops in California overlaps with the occurrence of coastal fog, improving estimates of crop-scale ET rates based on mechanistic relationships between coastal fog and crop physiology has potential to increase irrigation efficiency on farms.

Characterizing fog events in ways that are ecologically significant has been a challenge because there are many ways to define fog, and these definitions vary in space and time (Torregrosa et al., 2014; Weathers et al., 2014; Piso et al., 2016). In the field, measuring fog-drip using passive or active fog collectors is a common method used to identify and quantify fog events (e.g., Ingraham and Matthews, 1995; Dawson 1998; Fischer and Still, 2007; Hiatt et al., 2012); however, relying on fog-drip alone to identify fog events can be problematic because often overcast conditions do not generate fog-drip, as in low elevation agricultural areas where ground fog is less common. Yet, fog shading and associated reduction in atmospheric water stress during fog events have significant effects on ecosystem function (Williams et al., 2008). Local micrometeorological conditions are usually monitored to assess the effect of fog on incoming solar radiation, leaf wetness, and vapor pressure deficit that impact plant function (Fischer et al., 2016). A limitation to field-based approaches for characterizing fog events is that they are spatially-limited; therefore, the more robust evaluations of fog on ecosystem function characterize the fog events at multiple spatial and temporal scales. Spatiotemporal patterns of coastal fog can be quantified using satellite imagery (Williams et al., 2008, Clemesha et al., 2016, Torregrosa et al., 2016, Rastogi et al., 2016), which is necessary for assessing landscape scale spatial patterns of fog inundation and frequency. Expanding our understanding of fog at landscape scales has many ecologically-relevant applications. For example, Baguskas et al. (2014) found that satellite-derived summertime cloud frequency was a significant predictor of the spatial extent of drought-induced tree mortality in a California coastal forest ecosystem. Parameterization of regional climate models with fog climatologies can advance our understanding of physical controls on fog formation (O'Brien et al., 2013). Integrating fog climatologies into water balance models can improve predictions of how climate change may impact water budgets of ecosystems, and to help identify suitable habitat for species (Johnstone and Dawson 2010; Fernández et al., 2015; McLaughlin et al., 2017). Developing mechanistic relationships between field and satellite observations of coastal fog is essential for scaling our ecological understanding of fog, especially for land managers and decision makers in government, industrial, and agricultural sectors of society.

The objectives of our study were to: 1) characterize fog events at an inland and coastal farm site by combining field and satellite observations, and 2) develop a mechanistic understanding of the relationships between coastal fog and the water and carbon balance of croplands. We hypothesized that: 1) Coastal fog decreases from the coast inland; therefore, the effects of fog on reducing crop transpiration rates will be stronger closer to the coast; 2) Through the effects of shading and reduced evaporative demand, coastal fog will increase water use efficiency of crops at the leaf and canopy scales.

2. Materials and methods

2.1. Study sites

We conducted a field investigation at two conventional strawberry farms located at the coastal and inland extent of the fog gradient in the Salinas Valley, California. The coastal farm was located approximately 1.5 km from the coastline while the inland farm was 30 km from the coast, and both sites were at sea level. The strawberry crops (*Albion* var.) were grown using conventional methods, and similar farming practices were applied at each farm. The peak strawberry growing and

Table 1
Characterizing 'foggy' and 'clear' conditions based on a combination of field observations, satellite imagery of coastal low clouds and fog (CLCF), and micrometeorological measurements at the coastal and inland farm sites. Field-satellite agreement were based on 75 data points between June and September, 2015. Field observations were made during canopy physiology measurements.

Site	Foggy or Clear	CLCF	% Time satellite agrees with field observation (satellite obs/field obs.)	Avg. midday solar radiation ($W m^{-2}$)	Avg. Ψ_{atm} (MPa)	Avg. RH (%)	Avg. ambient Temp (ºC)	Avg. leaf wetness (mV)	Sum fog-drip (mm)
Coast	Clear	0	91.7% (22/24)	721	−38	76	20.4	0	0
	Foggy	1	100% (22/22)	381	−6	95	15.6	5.5	0
Inland	Clear	0	100% (19/19)	758	−53	68	21.5	0	0
	Foggy	1	80% (8/10)	453	−28	81	17.6	0	0

harvest season began in May 2015 and the final harvest was in October 2015.

Strawberries were grown in parallel rows comprised of beds following conventional management practices for this region (USDA, 1999). Each strawberry bed was 52 cm wide and 30 cm tall with two rows of strawberry plants per bed. Beds were spaced 30 cm apart. Gray-colored plastic mulch was used to apply fumigants to the soil prior to planting and left on the beds for the entire growing season to retain soil moisture. Two drip irrigation tapes were placed in each bed beneath the plastic mulch close to the strawberry plants and were used during the entire growing season. Irrigation events varied in frequency and amount of water applied. At the coastal farm, each irrigation event usually occurred between 0830 h and 1030 h, and was applied at 9 psi for 1.5 h. Information about the irrigation application schedule for the inland farm was not made available to us.

2.2. Measuring coastal fog and local meteorology in the field

We used visual field-based observations to identify coastal fog events at our field sites on days when we measured leaf and canopy physiology. We refer to 'foggy' conditions as both ground fog (i.e., when the cloud base is at the ground level), and overcast conditions. Low stratus summertime clouds rarely reached ground level (two ground fog days observed during our 2015 field season) at our low elevation agricultural site durings the daytime when we collected plant physiological observations. We refer to 'clear' conditions as periods when there were no clouds overhead.

We installed a passive fog collector (Schemenauer and Cereceda, 1994; Hiatt et al., 2012) along with micrometeorological sensors at each site to characterize local meteorological conditions on 'foggy' and 'clear' days. The passive fog collector was constructed of a 1 m^2 mesh screen mounted 2 m off the ground surface perpendicular to the prevailing wind direction. Fog water droplets deposited on the mesh screen drip into a collection trough below that is angled towards a tipping bucket rain gauge (ECRN-100 high-resolution rain gauge, Decagon Devices Inc.). Each tip of the tipping bucket is equal to 0.2 mm of water. The total number of bucket tips was recorded every 15 min for the entire study period. We calculated the total fog water inputs (fog-drip) each hour of the day and also the total inputs from June through September. To quantify local meteorological variability, we measured leaf wetness (mV) (Leaf Wetness Sensor, Decagon Devices Inc.), temperature (°C) and relative humidity (%) (VP3, Decagon Devices Inc.), total solar radiation ($W m^{-2}$) (PYR, Decagon Devices Inc.), and wind speed, direction, and gusts (DS2-Sonic Anemometer, Decagon Devices Inc.). The average value for each environmental variable was recorded every 15 min over the study period. We summarized these data by calculating the hourly average value for each variable. To assess the degree of atmospheric stress and the driving gradient for transpiration, we calculated the atmospheric water potential (Ψ_{atm}, MPa) using temperature and relative humidity (Nobel, 2009; Vasey et al., 2012)

2.3. Remote sensing of coastal fog

We used an established algorithm to identify low-level coastal stratiform clouds (stratus, stratocumulus, and fog) in the satellite imagery, which was validated and optimized using airport observations (cloud cover and base height) at 7 coastal airports along the California coastline (Clemesha et al., 2016). We used the satellite derived coastal low cloudiness and fog (CLCF) as an index for coastal fog, which was calculated as a percent of time low cloud was present in a 24-hour day from a time series of GOES-15 imagery (NASA/NOAA Geostationary Operational Environmental Satellite Imager). While GOES imagery has relatively low spatial resolution (4 km), it has a high temporal resolution (every 30 min), which was crucial to this study for two reasons: 1) plants respond rapidly on the order of minutes to hours to changes in energy and water balance, and 2) the spatial extent of a fog event is subject to change hourly. We generated maps of average CLCF frequency for each month of the summer (May–August) in 2015. We also generated a binary dataset of half hourly observations of CLCF over the summer months, where a value of one indicated that low clouds were detected and zero indicated no low clouds. From this file, we could calculate seasonal and diel patterns in CLCF frequency at each farm site. We found a strong agreement between field and satellite observations of foggy and clear-sky conditions (Table 1 and Fig. 1S). In sum, for our analyses of micrometeorological and plant physiological datasets, we used detailed field observations to identify foggy and clear-sky days, which was confirmed by satellite observations.

2.4. Canopy and leaf-level physiology

We evaluated the physiological responses of strawberry plants at the leaf and canopy scales to foggy and clear-sky conditions at the coastal and inland farms. At each site, we measured leaf and canopy-level physiological function between 0900 h–1200 h, when gas exchange should be at maximum rates. To estimate net ecosystem exchange (NEE) and water loss at the field-scale, we measured canopy-level CO_2 and H_2O vapor fluxes using an open-path infrared gas analyzer (IRGA; Model LI-7500A, LI-COR) placed in an infrared-transparent Tefzel® chamber (DuPont, Wilmington, DE; 0.75 m wide × 0.75 m long × 0.75 m tall) over four plant canopies per flux measurement. Concentration of CO_2 and H_2O were recorded once per second over approximately 300 s (5 min) per sample. A small fan was used to mix the air to remove any boundary layer effects within the chamber. Change in concentration ($mg m^{-3} s^{-1}$) of gases measured in the chamber was converted to a flux ($\mu mol m^{-2}$ canopy area s^{-1}) (Patrick et al., 2007). Because of time required to move and set up between plots, we were able to collect approximately 10 canopy flux measurements per field day. Canopy area was determined for each plot from a digital photograph of the four plant canopies at 1 m overhead and quantified using digital imagery analysis (ImageJ) (Patrick et al., 2007). We counted the number of sun (top of canopy) and shade (within canopy) leaves from four plant canopies and estimate that the proportion of sun versus shade leaves within a canopy was approximately 80:20. Canopy-level water use efficiency (WUE_{canopy}) was calculated by

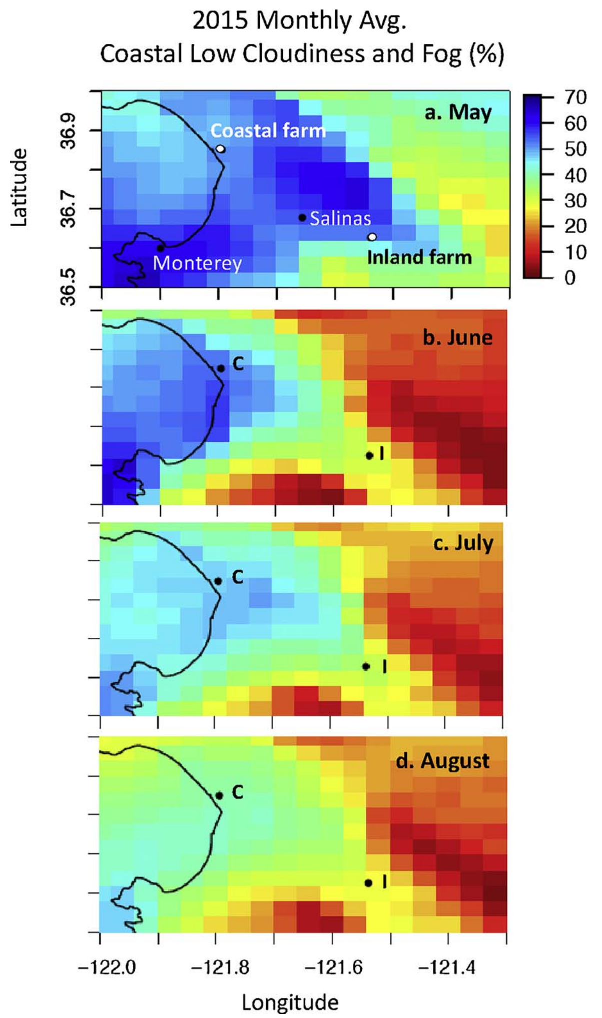

Fig. 1. Average monthly summertime fog climatology for Monterey Bay in 2015. Average coastal low cloudiness and fog (CLCF, %) was calculated for each month between May and August in 2015 from daily CLC values, which is the percent of time low cloud was present over a 24-hour period.

dividing NEE (μmol CO_2 $m^{-2}s^{-1}$) by conductance (mmol H_2O $m^{-2}s^{-1}$) (Patrick et al., 2007). Because strawberries are planted in raised beds covered with plastic mulch over the soil surface, soil evaporation and respiration were excluded from our canopy-level CO_2 and H_2O flux measurements. Between June and September, we measured canopy fluxes on six days at the coastal farm and three days at the inland farm. Establishment of the inland field site was delayed until early July, hence the reduced sample size compared to the coastal farm.

Leaf-level physiology was measured using a portable open-flow photosynthesis system (Model LI-6400, LI-COR, Lincoln, NE) under ambient conditions in the morning (0900–1200 h). Inside the leaf chamber, photosynthetically active radiation (PAR, 400–700 nm, μmol $m^{-2}s^{-1}$) tracked ambient light, CO_2 reference concentration was 400 μmol mol^{-1}, leaf temperature (T_{leaf}, °C), and relative humidity (RH, %) were allowed to vary naturally. On each sampling day, we measured leaf gas exchange rates from two leaves at the top of each plant canopy from 20 randomly selected plants at each site. Intrinsic water-use efficiency ($iWUE_{leaf}$) was calculated as maximum photosynthesis divided by stomatal conductance (A_{max} g_s^{-1}, Field et al., 1983), which is a measure of carbon gain per unit water lost by the leaf. We measured leaf physiology on seven days at the coastal farm and two days at the inland farm over the field season.

2.5. Data analysis

Using binary data of coastal low cloudiness and fog (CLCF) retrieved from GOES-15 satellite imagery, we calculated average monthly and diel CLCF values at the coastal and inland farm from May to August in 2015. We pooled daily CLCF observations recorded at 30 min intervals to calculate average daily CLCF, which we then used to calculate average percent monthly CLCF and the standard deviation. To compare the diel patterns of fog frequency at the coastal and inland farm, we pooled hourly CLCF values between June and September. We used a combination of detailed field observations and satellite-derived observations of CLCF to identify foggy and clear-sky periods in our micrometeorological and plant physiological response datasets. We then compared how local meteorology and crop responses differed between these conditions.

Micrometeorological observations were summarized on seasonal and diel time steps. For the seasonal patterns, we calculated average daily temperature (°C), relative humidity (%), midday solar radiation (W m^{-2}), leaf wetness (mV), and fog-drip (mm) for days when we also had personal field observations of conditions (n = 75 days between June and September 2015). For diel patterns, we compared representative foggy and clear-sky days at the coastal and inland farm, and calculated the integral to quantify the magnitude by which environmental variables differed between these conditions.

Plant physiological responses were analyzed at the canopy and leaf scales. A two-way analysis of variance was conducted to test for differences in canopy physiological responses between conditions (clear vs. foggy) and site (coastal vs. inland farm). We also performed a one-way analysis of variance to test for statistical differences in canopy and leaf-level physiological responses between clear and foggy conditions at each of the farm locations (coastal and inland). Sample size varied between the sites and conditions. We tested for assumptions of homogeneity of variance using the Bartlett Test, and found that this assumption was not violated in both the canopy and leaf datasets. These analyses were performed using the RStudio version 3.2.4 (R Development Core Team 2016) statistical software package.

A linear model was used to evaluate canopy-level water use efficiency at each site. A least-squares regression analysis was used to test for the correlation between canopy-level water-use efficiency (WUE_{canopy}) and solar radiation as well as atmospheric water stress, for both the coastal and inland farm sites. We also performed a least-squares regression analysis to test for the correlation between leaf-level physiological function (CO_2 assimilation and stomatal conductance) and environmental factors (PAR and leaf temperature). These analyses were performed using the 'lm' statistical package in R Development Core Team 2016.

To track changes in leaf-level condition and physiological function from a foggy morning (0930 h) to clear-sky afternoon (1400 h), we plotted leaf responses from a single leaf on an individual plant over time at the coastal farm in mid-summer (8 July 2015). We repeated sampling during the fog to clear transition for the same seven plants examined above throughout this field day.

3. Results

3.1. Fog climatology

Field observations of ground fog and overcast conditions were in strong agreement with half-hourly CLCF identification based on satellite imagery (Table 1, Fig. 1S). In 2015, the percent of days when CLCF was observed in the study area was higher in May and June compared to July and August (Fig. 1a–d). In the long-term monthly average CLCF (1996–2014), July and August had greater cloud cover than May and June (Fig. 2S), which is opposite to what we observed in 2015. Average monthly CLCF values were consistently greater at the coastal than inland farm from May through August, with the greatest

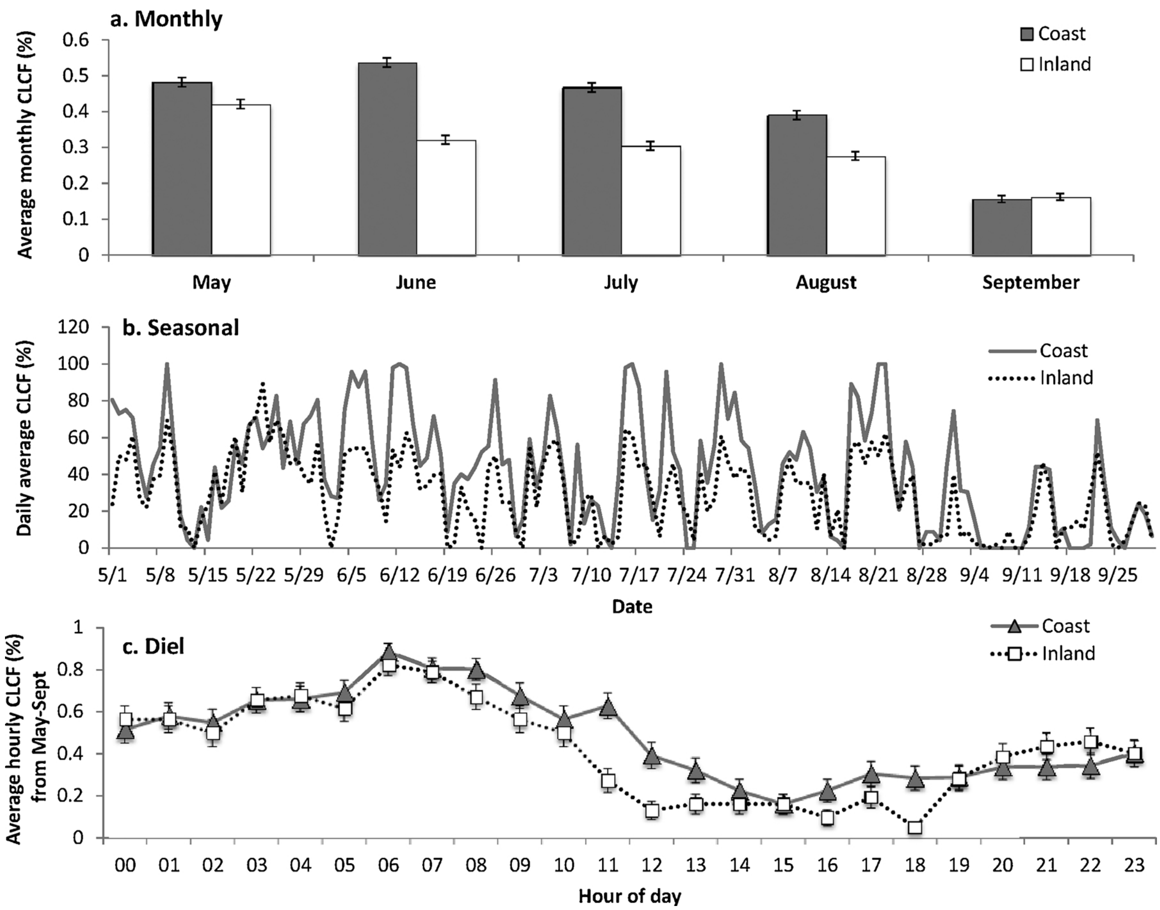

Fig. 2. Average (a) monthly, (b) seasonal, and (c) diel values of coastal low cloudiness and fog (CLCF, %) observations derived from satellite imagery at the coastal and inland farm locations in 2015. Monthly CLCF averages pool all 30 min. observations for each month (n = 1488 per month) and hourly CLCF averages pooled observations at each hour from May-August. Error bars indicate standard error.

difference between sites (40%) occurring in June (Fig. 2a). Seasonal patterns in CLCF were similar at each site; however, the magnitude of daily average CLCF was greater at the coast, indicating that the duration of fog events were longer at the coast than inland farm on days when it was foggy (Fig. 2b). We did not observe differences in average hourly CLCF values during night and predawn hours (2300 h–0400 h) between sites; however, CLCF values were greater at the coast than inland farm during the daytime and early evening (Fig. 2c). The dissipation of coastal fog occurred more quickly at the inland than coastal farm from morning (0700 h) to afternoon (1500 h) (Fig. 2c). We observed the greatest site difference in CLCF between 1000 h and 1300 h. Overall, the patterns of coastal fog captured in CLCF agreed with field observations at the diel timescale.

3.2. Seasonal microclimate variability

We observed midday incoming solar radiation reduced by 340 W m^{-2} at the coast and by 305 W m^{-2} inland between clear and foggy conditions, which is in agreement with the satellite-derived estimates of summertime coastal fog (Table 1, Fig. 1S). During foggy compared to clear conditions, atmospheric water potential (Ψ_{atm}) was 32 MPa higher at the coast and only 25 MPa higher inland, indicating that fog had a greater effect on reducing atmospheric water stress at the coastal than inland farm (Table 1). Between clear and foggy conditions, relative humidity increased by 19% at the coast and by 13% inland between clear and foggy conditions. At both sites, ambient temperature decreased by roughly 5 °C on foggy compared to clear days (Table 1). Leaf wetting events only occurred at the coastal farm, and increases in leaf wetness were relatively small during fog events (Table 1). Our observations of foggy periods, as indicated by fluctuations in CLCF values, were not coincident with fog-drip events (Fig. 3S). At the coastal farm, a total of 4 mm of fog water derived from fog-drip was collected from ten discrete overnight fog events between mid-June and early-September 2015 (Fig. 3S). Cumulative summer fog-drip was negligible at the inland farm (0.26 mm) (Fig. 3S).

3.3. Diel microclimate variability: foggy vs. clear-sky days

Integrated over a 24-hour period, we found that percent maximum incoming solar radiation was reduced by 27% during a foggy day compared to a clear-sky day at the coastal farm and by 14% at the inland farm (Fig. 3a and b; Table 1S). At both sites, the shading effect by fog was greatest in the late morning (0900–1100 h), and this difference decreased in the afternoon (~1200–1800 h), once the fog dissipated. Specifically, during a fog event, incoming solar radiation was reduced by as much as 500 W m^{-2} at the coastal farm at 0900 h and by 280 W m^{-2} at the inland farm at 1000 h. By midday (1300 h), the fog had evaporated and solar radiation reached a similar maximum value to a clear-sky day at each site (Fig. 3a and b).

The range of atmospheric water potential (Ψ_{atm}, MPa) values on a clear sky day at the inland farm indicates that there was greater water stress, i.e., Ψ_{atm} values were much more negative, compared to the coastal farm (Fig. 3c and d, Table 1S). At the coastal farm, integrated Ψ_{atm} over 24 h was 82% greater (more negative) on a clear than foggy day (Fig. 3c, Table 1S). By 0800 h on a clear-sky day, Ψ_{atm} reached −60 MPa; however, peak Ψ_{atm} was less negative (ca. −25 MPa) and did not occur until the later in the afternoon (~1430 h) on a foggy day at the coastal farm (Fig. 3c). Ψ_{atm} integrated over 24 h was 105%

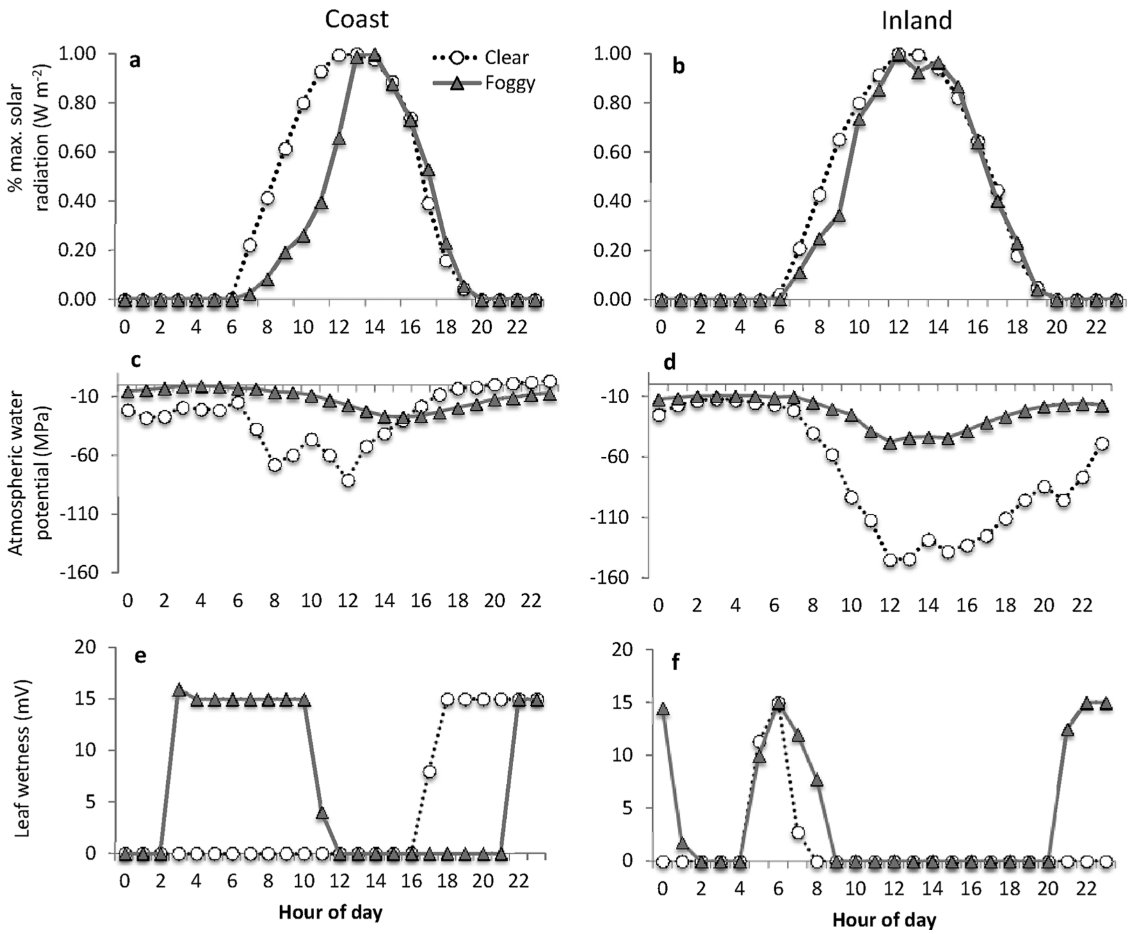

Fig. 3. Diel patterns in (a) % maximum solar radiation ($W\,m^{-2}$), (b) atmospheric water potential (MPa), and (c) leaf wetness (mV) between a clear-sky (open circles) and foggy day (gray triangles) at the coastal (left panel) and inland (right panel) farm. Days represented are different between the coastal (clear: 8/28/15, foggy: 9/1/15) and inland (clear: 7/31/15, foggy: 8/15/15) farms.

greater on a clear compared to foggy day at the inland farm, and the peak minimal Ψ_{atm} was close to noon on both the clear and foggy day (Fig. 3d and Table 1S). On foggy days, leaf wetness was greater than on a clear sky day at the coastal and inland farm (Fig. 3e and f; Table 1S). Moreover, leaves were wet for a longer duration at the coastal compared to the inland farm.

3.4. Effects of coastal fog on canopy-level physiology

During the peak-growing season, whole strawberry plants do not demand as much water during coastal fog events compared to clear-sky conditions (Fig. 4a). During fog events, canopy-level conductance, i.e., transpiration rate, was significantly reduced by approximately 60% at both the coast ($F_{1,44} = 42.1$, $P < 0.001$) and inland ($F_{1,27} = 21.5$, $P < 0.001$) farms relative to clear-sky conditions (Fig. 4a, Table 2S). Canopy-level photosynthesis, (i.e., net ecosystem exchange, NEE, where a more negative value indicates a greater uptake of CO_2 by the plant canopy), was significantly greater by about 30% on clear-sky compared to foggy days at the coastal farm site (Fig. 4b; $F_{1,44} = 16.5$, $P < 0.001$). At the inland farm, we observed an increase in NEE during clear-sky compared to foggy conditions, but this increase was only marginally significant (Fig. 4b; Table 2S, $F_{1,27} = 3.1$, $P = 0.09$). Canopy-level water use efficiency ($WUE_{canopy,}$ carbon gain per water loss) of strawberry plants increased significantly during foggy compared to clear-sky conditions at both the coastal ($F_{1,44} = 23.8$, $P < 0.001$) and inland ($F_{1,27} = 33.1$, $P < 0.001$) farm (Fig. 4c, Table 2S).

Atmospheric condition (clear vs. foggy) and site (coastal vs. inland farm) both had significant effects on canopy-level physiology, and we found no significant interaction between these main effects for any of the physiological response variables (Table 2S). Across sites, changes in solar radiation and atmospheric water stress (Ψ_{atm}) explained 73% of the variability in WUE_{canopy} (Table 2). Solar radiation had a negative effect on WUE_{canopy}, Ψ_{atm} had a positive effect on WUE_{canopy}, and location of the farm added to the explanatory power of the model, but the effect was weaker than the other predictor variables.

3.5. Effects of coastal fog on leaf-level physiology at the coastal farm

Leaf-level microenvironment and physiology differed significantly between foggy and clear-sky conditions at the coastal farm, where we had a greater number of leaf-level observations compared to the inland site (Fig. 5). In fact, the low sample size at the inland farm precluded statistical comparisons for leaf-level photosynthesis between sites. In any case, during foggy conditions, we observed a 65% reduction in photosynthetically active radiation (PAR, μmol photons $m^{-2}\,s^{-1}$), a 5.7 °C reduction in leaf temperature (T_{leaf}, °C), and a 28% reduction in leaf-level vapor pressure deficit (VPD_L, kPa) relative to clear-sky conditions (Fig. 5a–c). During fog events, leaf-level stomatal conductance (g_s, $mol\,m^{-2}\,s^{-1}$) was significantly reduced by 32% and photosynthesis (A, $\mu mol\,m^{-2}\,s^{-1}$) was reduced by 29% relative to clear-sky conditions (Fig. 5d and e). Unlike the canopy-level response during fog events, we found no significant difference in intrinsic water-use efficiency ($iWUE_{leaf}$) between clear and foggy conditions (Fig. 5f).

Increase in plant light availability drove higher rates of leaf-level photosynthesis ($R^2 = 0.70$, $P < 0.001$) and stomatal conductance ($R^2 = 0.28$, $P < 0.001$) (Fig. 4S). Leaf-level photosynthesis was

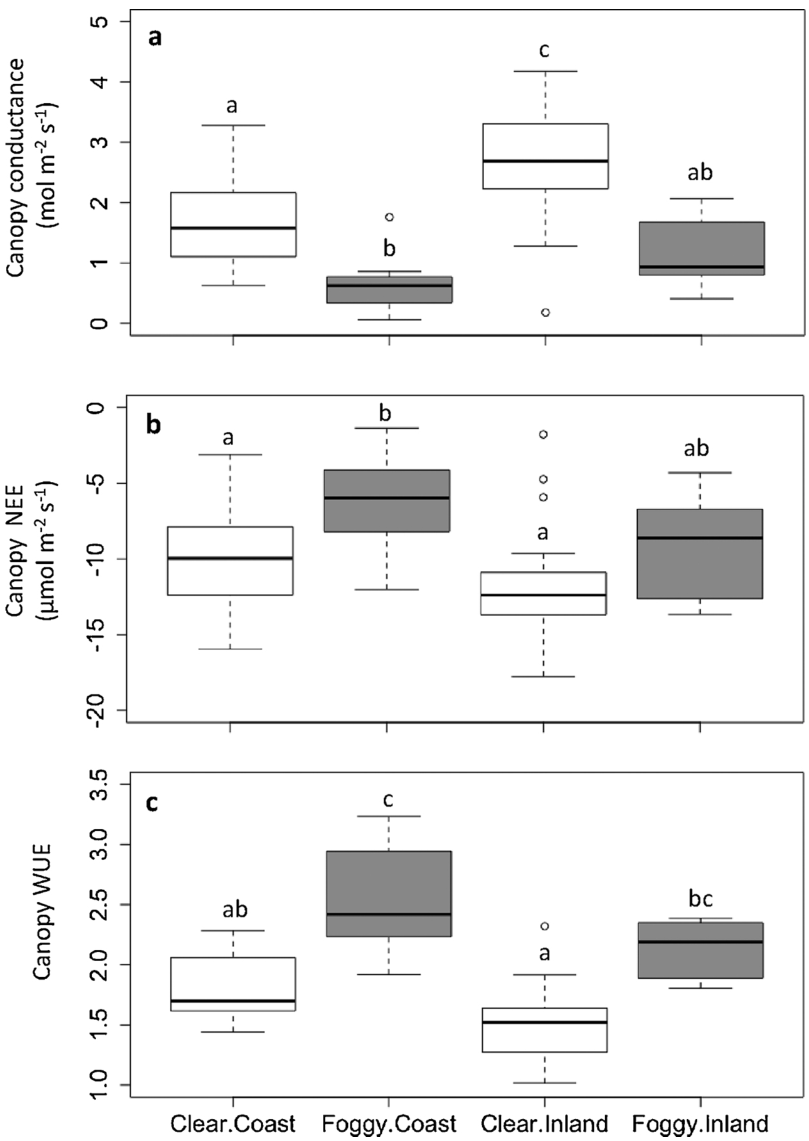

Fig. 4. Differences in average values of canopy-level conductance, net ecosystem exchange (i.e., canopy photosynthesis), and water use efficiency between foggy (grey) and clear-sky (white) conditions at the coast and inland farms. Observations were pooled over the sampling days between late June and early September and over hours that we sampled (approximately 0900 h and 1300 h) on each day. Sample size varied between the coastal farm (n = 24 clear-sky and n = 22 foggy observations) and the inland farm (n = 19 clear-sky and n = 10 foggy observations). For box plots, the horizontal line is the median and the edges of the box are the 25th and 75th percentiles. Different letters above boxplots indicate significant differences between average values (α = 0.05). Results from two-way analysis of variance are shown in Table 2S.

Table 2
A linear model to explain variation in canopy-level water use efficiency. Model parameters included incoming solar radiation ("solar", $W m^{-2}$), atmospheric water stress ("Ψ_{atm}" MPa), and farm location (coast or inland). There were no significant interactions between predictor variables.

Model parameter	Estimate	Standard error	P-value	R^2 (adj)
Intercept	2.97	0.095	< 0.001	0.73
solar	−0.001	0.002	0.001	
Ψ_{atm}	0.02	0.002	0.002	
location	−0.53	0.07	0.045	

negatively correlated with a decline in leaf temperatures associated with fog events ($R^2 = 0.63$, $P < 0.001$). Similarly, we observed a significantly negative relationship between stomatal conductance and leaf temperature on clear-sky days ($R^2 = 0.32$, $P = 0.001$) but not on foggy days ($R^2 = 0.02$, $P = 0.36$) (Fig. 4S).

3.6. A single fog event: Change in leaf microenvironment and physiology

We monitored leaf-level physiological function from a foggy morning (0930 h) to clear-sky afternoon (1400 h) at the coastal farm in mid-summer (8 July 2015) (Fig. 6). Between approximately 0930 h and 1130 h, PAR increased from 350 to 700 µmol photons $m^{-2} s^{-1}$ (Fig. 6a). On a clear-sky day, PAR at 1130 h is typically 1600–1800 µmol photons $m^{-2} s^{-1}$ during this time of year. As the fog dissipated close to noon, PAR increased to over 1000 µmol photons $m^{-2} s^{-1}$, and this was associated with significant changes in VPD_L and leaf temperature (Fig. 6a–c). Photosynthesis increased steadily between 0930 h and 1400 h while stomatal conductance peaked at 0930 h then declined through the late morning, and increased again by late afternoon when the fog had fully dissipated (Fig. 6d and e). Change in WUE_{leaf} was anti-phase with stomatal conductance (Fig. 6e and f).

4. Discussion

Our spatial analysis of variation in coastal low cloudiness and fog (CLCF) derived from satellite imagery showed that coastal fog is more prevalent in a band along the coast where it could potentially have a stronger influence on crop physiology (Figs. 1, 2 and Table 1), supporting our primary hypothesis. Furthermore, we found that there were many more days when coastal fog inundated the coast than there were days when fog-drip was produced by these events (Fig. 3S). In support of our second hypothesis, we found that whole-plant water use efficiency was significantly higher at the coastal and inland farm during fog events compared to clear-sky days, indicating that crops do not lose as much water while maintaining photosynthesis under foggy

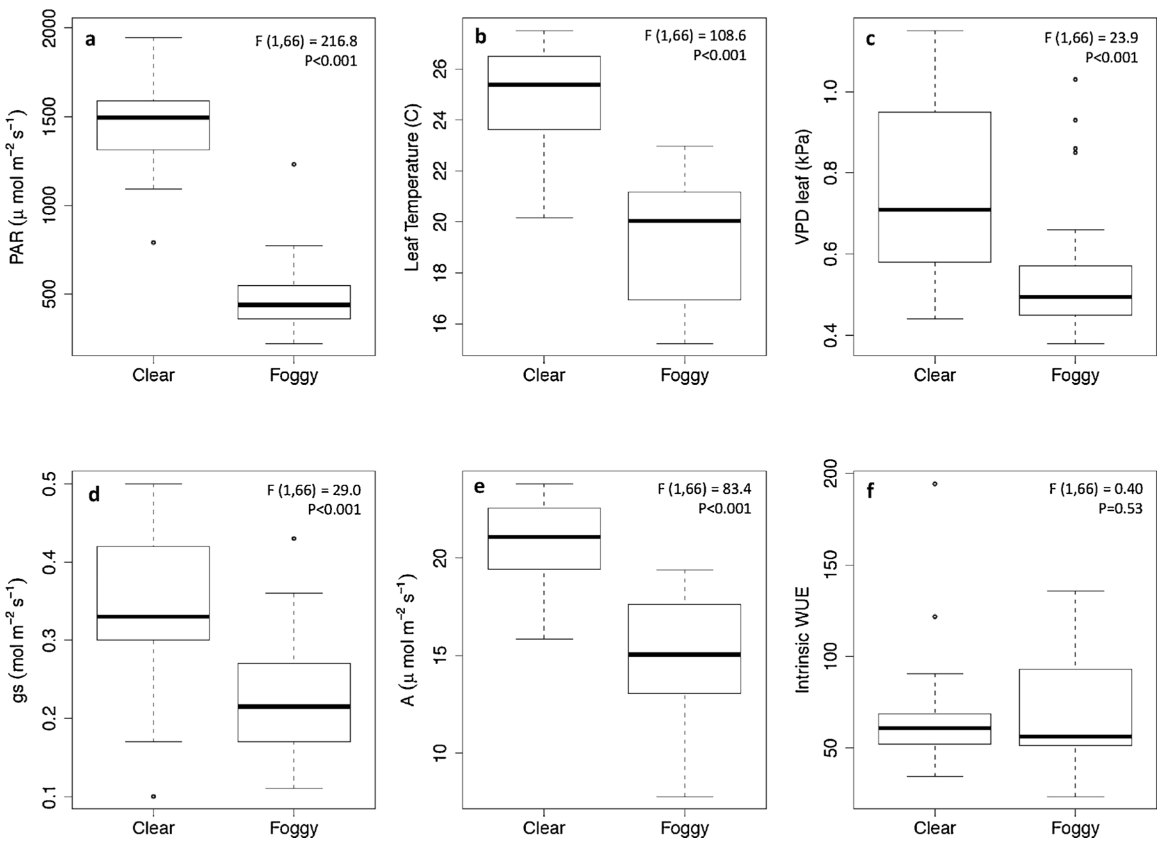

Fig. 5. Differences in average leaf-level condition and physiological function between foggy and clear-sky conditions at the coastal farm. Conditions include (a) photosynthetically active radiation (PAR, μmol photons $m^{-2}s^{-1}$), (b) leaf temperature (T_{leaf}, °C), and (c) leaf vapor pressure deficit (VPD_L, kPa). Physiological responses include (d) stomatal conductance (g_s, mol $m^{-2}s^{-1}$), (e) photosynthesis (A, μmol $m^{-2}s^{-1}$), and (f) intrinsic water-use efficiency ($iWUE_{leaf}$). Each average value pools plants sampled on four clear days and four foggy days between late June and early September, where n = 30 plants on clear-sky days and n = 38 on foggy days. For box plots, the horizontal line is the median and the edges of the box are the 25th and 75th percentiles. Significant differences between clear-sky and foggy conditions are shown by the P-value (α = 0.05) and F-statistic in each panel.

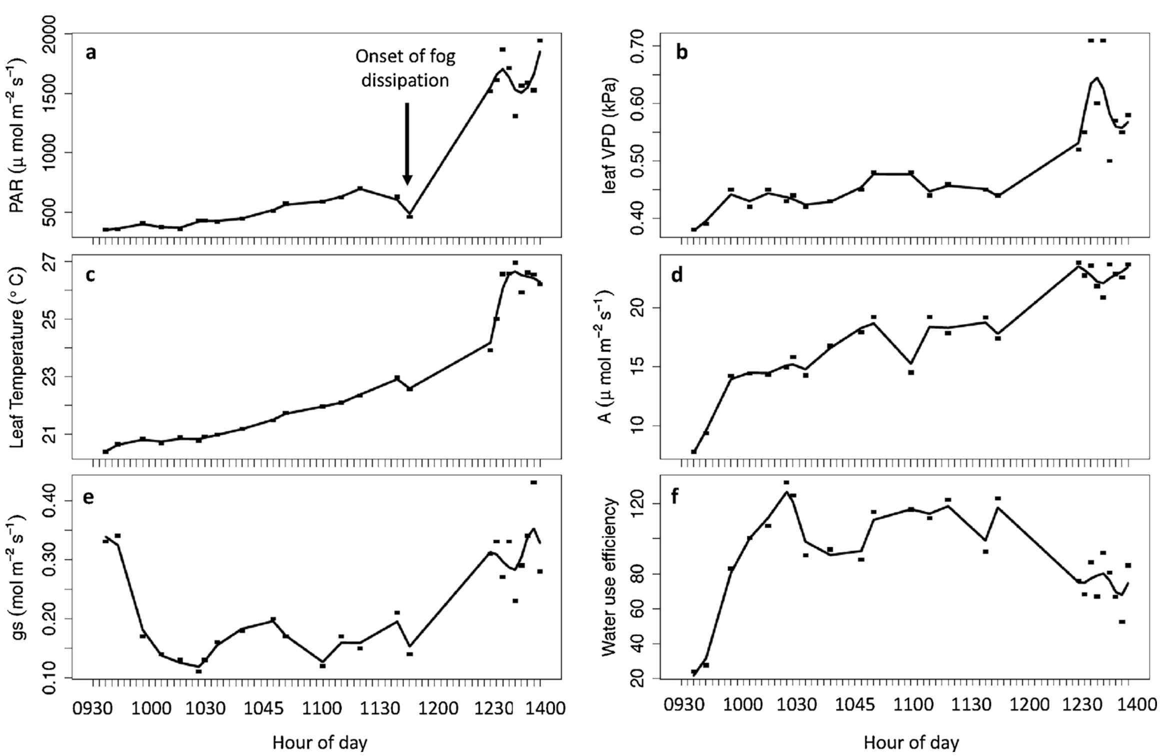

Fig. 6. Changes in leaf-level condition and physiological function from a foggy morning (0930 h) to clear-sky afternoon (1400 h) at the coastal farm in mid-summer (8 July 2015). Each point represents an observation from a single leaf on an individual plant. We repeated sampling from the same seven plants throughout the day.

conditions (Fig. 4). These patterns were best explained by changes in plant-available light and atmospheric water stress (Table 2). At the leaf scale, photosynthetic rates were negatively affected by reduced plant light availability and lower leaf temperatures associated with fog events (Fig. 4S). Stomatal conductance showed similar patterns, but was more sensitive to changes in leaf temperature (Fig. 4S). In contrast to canopy observations, we did not find a significant increase in leaf-level intrinsic WUE between foggy and clear sky conditions; however, the trend is in the direction we would expect (Fig. 5f). We hypothesize that this lack of significant difference in leaf WUE is attributed to our inability to capture the scattered nature of light (diffuse vs. direct). The instrument we used to measure leaf physiology could match ambient photon flux density, but not the many incident angles of the scattered light on foggy days. Yet, there is evidence that sun-adapted leaves that receive diffuse light will have lower rates of photosynthesis due to light focusing by epidermal tissue (Vogelmann et al., 1996); therefore, the effect of fog on leaf photosynthesis would likely have been even lower than we observed had we adequately captured the effect of diffuse cloud light on leaf gas exchange rates. The net effect would have been higher intrinsic WUE at the leaf scale on foggy days, which would have manifested in a significant difference to observations on a clear-sky day. Taken together, our results demonstrate that strawberry plants not only demand less water, but also use water more efficiently, during foggy compared to clear-sky periods; therefore, if our results were accurately captured in crop water use models, reductions in irrigation during fog events could be incentivized, especially on farms in the fog-belt close to the coast (Blanc et al., 2017).

4.1. Detecting and characterizing coastal fog events using satellite and field observations

Detecting fog events (here defined as both overcast and ground fog) at multiple spatial and temporal scales is an essential first step to understanding how coastal fog influences ecosystem function. Our satellite-derived index of summertime coastal low cloudiness and fog (CLCF) was a good indicator of coastal fog events in the Salinas Valley because it agreed strongly with field observations of ground fog and overcast conditions based on visual field observations and micrometeorological conditions (Table 1). While this is not the first fog climatology generated for this region of coastal California (Iacobellis and Cayan, 2013; Clemesha et al., 2016; Torregrosa et al., 2016), we have shown how coastal fog observed from satellite observations relates to environmental conditions that impact plant function. The few discrepancies (Table 1) between field and satellite observations can be attributed to differences in the temporal and spatial resolution of the observations. Field-based observations made by researchers were subhourly at point locations while satellite observations are made at 30-minute intervals over a more coarse 4 km × 4 km grid. Since the temporal and spatial resolution of field-based observations of coastal fog was finer, for comparison, the satellite-derived observations were matched to the closest grid cell and time of ground observations. For all discrepancies (Table 1), a directly neighboring satellite grid or time step was indeed in agreement with the field observations. This suggests the disagreement was purely due to the coarse nature of the satellite resolution during times of subtle changes in fog. Despite these discrepancies, combining satellite and ground observations of coastal fog resulted in a more robust analysis of how coastal fog events impact carbon gain and water loss from an agricultural system. Based on these results, we argue that spatial and temporal patterns of coastal fog should be better incorporated into landscape scale projections of evapotranspiration from fog-influenced agricultural areas. This should increase the model accuracy and improve irrigation management tools available to farmers that are based on ET-model outputs (Melton et al., 2012).

4.2. Coastal fog impact on crop water use efficiency

In support of our second hypothesis, we found that whole-plant crop water use efficiency increased significantly during foggy periods at both the coast and inland farms (Fig. 4) when atmospheric water stress and solar radiation were reduced compared to clear-sky days (Tables 1 and 2). These relationships were particularly pronounced at the coastal farm, which received more frequent fog events during the summertime months (Figs. 1 and 2). Based on these results, we hypothesize that canopy-level water use efficiency increased during fog events because diffuse radiation irradiated a greater fraction of the canopy, which engages more leaves in photosynthesis (Min, 2005; Mercado et al., 2009; Kanniah et al., 2013; Cheng et al., 2015; Tognetti, 2015; Reinhardt and Smith, 2016; Lu et al., 2017), while vapor pressure deficit is lower, which minimizes transpiration rates (Burgess and Dawson, 2004; Ritter et al., 2009). The effect of diffuse light on enhancing plant productivity has not only been observed in natural ecosystems, but in crop plants as well, which have smaller plant canopies (Li et al., 2014).

Our observations of higher plant water use efficiency on foggy compared to clear-sky days is in contrast to observations in certain natural ecosystems. For example, Vasey et al. (2012) found that maritime chaparral shrub species growing closer to the coast in central California, where summertime fog buffers the effects of soil drying and atmospheric water stress, had lower water use efficiency than the same plant species growing further inland. These inland shrubs minimized water loss through stomatal regulation as the soil dried and also exhibited morphological traits correlated with risk of xylem cavitation. Our strawberry plants were irrigated, which likely decoupled the patterns seen between WUE and coastal *vs.* inland location observed for native, long-lived, woody shrub species. In this well-irrigated agricultural system, the controls on whole-plant water use efficiency were not driven by stomatal response to soil water deficit, which is commonly observed in water-limited natural ecosystems (Naithani et al., 2012). Rather, controls on water-use efficiency of strawberries were top-down constraints imposed by PAR and VPD on CO_2 assimilation and transpiration. The discrepancy in WUE between strawberries and plants in natural systems may also be due to the outcome of selection for certain production traits in strawberries, or different ability to regulate biochemical controls on photosynthesis (i.e., V_{cmax} and J_{max}) such as through re-allocation of nitrogen or end-product inhibition (Woodrow and Berry, 1988). It would also be valuable to know how strawberry respiration responds to leaf temperature under foggy and clear conditions (Atkin and Tjoelker, 2003). Moreover, we note that photosynthetic CO_2 uptake and hydrologic responses of leaves are only two examples of traits that may differ in relation to the coastal-to-inland gradient, and trade-offs with other processes in native shrubs (e.g. production of defense compounds; Huot et al., 2014) may cause allocation patterns to be quite different than for the herbaceous strawberries.

4.3. Coastal fog impact on crop water loss

We demonstrate that crop water loss at the whole-plant and leaf-level was significantly reduced during fog events, which is consistent with findings from other fog-influenced natural and agricultural ecosystems. For example, tree transpiration rates in fog-influenced forests were 30 times lower on foggy compared to fog-free conditions in the Canary Islands (Ritter et al., 2009) and 40% lower in an Australian forest (Hutley et al., 1997). In California's coast redwood (*Sequoia sempervirens* D.Don) forest, a significant reduction in whole-plant transpiration rates during fog events ameliorates water stress for this drought-sensitive species (Burgess and Dawson, 2004). These studies attribute reduced transpiration rates to lower vapor pressure deficit and leaf wetting events during fog events.

Similar to patterns observed in forests, Hunt et al. (2008) found that blueberry crop ET rates were suppressed during summertime coastal fog events by as much as 13.5 cm during the growing season, which they attributed to a reduction in vapor pressure deficit and direct fog water deposition on leaves and to the soil. Likewise, Starr and Yarborough (2006), found that during nighttime and early morning coastal fog events, leaf and soil wetting events accounted for 28% of blueberry crop ET. Glenn et al. (1996) found that dew deposition on strawberry plants in an east coast farm in the United States accounted for 33% of daily ET rates. Similarly, Moratiel et al. (2013) show that the accuracy of modeled crop ET was significantly improved by incorporating a surface vaporization (i.e., evaporative loss of water from leaf surfaces) term driven by leaf-wetting events due to fog, dew, and light rain. In our study, we did not find any relationship between leaf-wetting from fog water deposition and crop physiology because there were fewer instances of ground fog compared to overcast days during our sampling times (Table 1, Fig. 3S). We hypothesize that leaf-wetting events would be a strong control over strawberry crop ET rates in coastal California by increasing surface vaporization, and minimizing transpiration rates, as observed in these previous studies, and should be integrated into future studies of coastal fog on crop water use. We did find that fog impacted crops in more indirect ways, i.e., not through direct fog-water inputs, and argue that indirect effects of fog (increased shading, diffuse light, and reduced atmospheric water stress) should also be included in future studies on crop-scale estimates of carbon and water fluxes on fog-influenced farms.

5. Conclusions

In our study, we demonstrate that strawberry crops growing in coastal California demand less water on foggy compared to clear-sky days, and that whole-plants are more efficient with their water use during fog events. By developing a mechanistic understanding of how crops respond to local meteorology during the peak-growing season for an economically important crop, the outcome of our study can be used to parameterize models that inform sustainable irrigation decisions now and in the future.

While there is still a high degree of uncertainty about how the coastal fog regime in California may change in the future, current projections suggest that fog frequency and duration are likely to decline with an increase in sea surface temperature (Johnstone and Dawson 2010). Moreover, cloud-base height has been shown to increase with urbanization of coastal areas of southern California (Williams et al., 2015b), and urbanized areas are only expected to increase with a growing population. Based on the results from our study, less fog would drive greater demand for groundwater on coastal farms because a decline in coastal fog would increase crop demand for water and decrease whole-plant water use efficiency. If farmers begin to implement adaptive irrigation management, e.g., ET-based irrigation systems, farmers will be more likely to sustain their farming practices in a future likely to become warmer, drier, and possibly less foggy.

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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:https://doi.org/10.1016/j.agrformet.2018.01.015.

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