Ecophysiological adjustments of a pine forest to enhance early spring activity in hot and dry climate

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Abstract

Climate change can impose large offsets between the seasonal cycle of photosynthesis and that in solar radiation and temperature which drive it. Ecophysiological adjustments to such offsets in forests growing under hot and dry conditions are critical for maintaining carbon uptake and survival. Here, we investigate the adjustments that underlie the unusually short and intense early spring productive season, under suboptimal radiation and temperature conditions in a semi-arid pine forest.

We used eddy covariance flux, meteorological, and close-range sensing measurements, together with leaf chlorophyll content over four years in a semi-arid pine forest to identify the canopy-scale ecophysiological adjustments to the short active season, and long seasonal drought.

The results reveal a range of processes that intricately converge to support the early spring peak (March) in photosynthetic activity, including peaks in light use efficiency, leaf chlorophyll content, increase in the absorption of solar radiation, and high leaf scattering properties (indicating optimizing leaf orientation). These canopy-scale adjustments exploit the tradeoffs between the yet increasing temperature and solar radiation, but the concurrently rapidly diminishing soil moisture. In contrast, during the long dry stressful period with rapidly declining photosynthesis under high and potentially damaging solar radiation, physiological photoprotection was conferred by strongly relaxing the early spring adjustments.

The results provide evidence for canopy-scale ecophysiological adjustments, detectable by spectral measurements, that support the survival and productivity of a pine forest under the hot and dry conditions, which may apply to large areas in the Mediterranean and other regions in the next few decades due to the current warming and drying trends.

1. Introduction

The seasonality of ecosystem photosynthetic activity is characterized by the time of peak activity and reflects the integration of plant response to variations in temperature, radiation, and water availability (Garonna et al. 2018, Park et al. 2016, 2019, Xia et al. 2015, Yang et al. 2019). Such analyses indicate, in turn, that the timing of peak photosynthesis can display offset of days to months relative to the seasonality in the physical climate parameters, such as solar radiation and temperature. For example, the peak in gross primary productivity (GPP) can be delayed by ∼45 d with respect to the seasonal peak in radiation, or precede it by up to ∼75 d in the transitions from the arctic to the temperate climate zones (Park et al. 2019).

Another study found that peak GPP in pine forests advanced by 7 d for each increase of 10 W m⁻² in annual mean radiation across Europe (Rotenberg and Yakir 2010). Consequently, while peak solar radiation in the Northern Hemisphere is around the day of year 172 (DOY; June 21), peak GPP in northern Finland was around DOY 205 (delayed by low temperatures) and around DOY 85 in Israel (advanced due to rapid
drying). Similar shifts in seasonality were also associated with biome type, with peak activity in early May in savannas and mid-July in crops (Xia et al. 2015). It was recently estimated that global warming results in gradual advance in the photosynthesis seasonality estimated at 1.66 d decade⁻¹ across the Northern Hemisphere (Park et al. 2019). Such trends are likely associated with a considerable increase in the relative influence of moisture constraint in determining the timing of peak photosynthesis (Garonna et al. 2018).

The changes in the seasonality of photosynthesis can enhance forest productivity in some cases (Menzel et al. 2006, Keenan et al. 2014, Park et al. 2019), but exceeds the ecosystem adjustment capabilities in other cases resulting in enhanced mortality (Allen et al. 2015, Klein 2015, Anderegg et al. 2019). These studies provide information on the spatial patterns of plant GPP and tree mortality. Much less information is available, however, on the ecophysiological processes that underlie the plant adjustments to changes in these forcing (McDowell et al. 2008, Anderegg et al. 2019). This is particularly so in the dry climates, including the Mediterranean and the semi-arid regions where ecophysiological adjustments are key to survival (Peñuelas et al. 2017, Biederman et al. 2017, Roby et al. 2019, Sperlich et al. 2019, Maseyk et al. 2019, Tarin et al. 2020), and could provide predictors for the future of ecosystems in currently wetter climates (Dai 2013).

Hot and dry regions, such as the sub-humid Mediterranean, are characterized by short mild winters and rainfall periods followed by rapidly drying soils and long dry summers with high radiation intensity (Joffre and Rambal 2001, Deitch et al. 2017). These strong environmental forcing result in a large shift in the time of peak activity from July-August in temperate forests to March in semi-arid Mediterranean forests (Rotenberg and Yakir 2010). Furthermore, the peak productivity season (period with GPP within 15% of the peak level) can also be as short as 1.5 months (Helman et al. 2017) and subject to sub-optimal conditions because of the limitation by low temperature and radiation at one end of the productive season, and the rapidly drying soil at the other end. However, detailed information is still scarce on ecophysiological adjustments that enable the exploitation of such short and time-shifted productive period and, in turn, sustain the long stress period, especially at the canopy and ecosystem scales.

Physiological stress can be enhanced during drought periods due, for example, to stomatal closure, reduced ET, and CO₂ exchange, together with the excessive incoming radiation, and can result in photo-damage, carbon starvation, and hydraulic failure (Ogaya and Peñuelas 2003, Asensio et al. 2007, McDowell et al. 2008, Sala et al. 2012, Klein et al. 2014, 2016, Rowland et al. 2015, Li et al. 2018). At the leaf scale, studies show a range of strategies that can help in dealing with the excessive absorbed light (Ruban 2009, 2016, Cazzaniga et al. 2013, Xu et al. 2015). This includes a reduction in chlorophyll and an increase in carotenoids and xanthophyll concentrations that reduce the solar radiation channeled to photosynthesis (Demmig-Adams and Adams 2006, Scartazza et al. 2016) or enhanced photorespiration (Wingler et al. 2000, Voss et al. 2013, Eisenhut et al. 2017). A recent study on pine needles in a semi-arid forest showed that a combination of reduced radiation absorption, a relative increase in photorespiration, and enhanced xanthophyll cycle, conferred resilience and full recovery from stress on the diurnal time scale (Maseyk et al. 2019). Some adjustments to drought are also identified at the tree scale, such as the response to the combined effects of drought and increased vapor pressure deficit (Grossiord et al. 2017), and a shift in carbon allocation from stem to root growth, together with tighter stomata and hydraulic functioning (Klein et al. 2011, Fernández-De-Uña et al. 2017).

At the canopy scale information often relies on eddy covariance (EC) flux measurements of CO₂, ET, and energy (Baldocchi 2003). Some EC-based studies have demonstrated that forests adjustment to long-term drought by shifting to efficient canopy cooling through enhanced sensible heat flux, substituting for the evaporative cooling common in temperate forests where soil water is available (Rotenberg and Yakir 2011). Evaluating a wide range of EC sites in the semi-arid regions of North America demonstrated a predictable link between variations in net ecosystem productivity (NEP) and the actual water availability for ET (Biederman et al. 2016). Another study in these regions identified a precipitation threshold where NEP switches from carbon sink to source (Liu et al. 2018). Canopy-scale EC measurements also demonstrated high ecosystem resilience to short-term heatwaves superimposed on the seasonal drought stress in dry forest sites (Tatarinov et al. 2016).

Remote sensing (RS) could extend and supplement ecosystem-scale studies (Kerr and Ostrovsy 2003, Mulla 2013, Lausch et al. 2016, Xiao et al. 2019). For example, the chlorophyll/carotenoid index (CCI) showed an increase in the fraction of carotenoids in leaf pigments in an evergreen forest as a biochemical response to the drought conditions. Another study about the ecosystem response to heatwaves used sun-induced fluorescence (SIF) measurements and showed stomatal closure in the early stages, intrinsic damage to the photosynthetic system at the height of the stress, and rapid recovery following the event (Wohlfahrt et al. 2018). Remote sensing includes satellite observations, aerial or ground level (close-range sensing) measurements at different temporal and spatial scales (White et al. 2016, Toth and Józıkow 2016). While satellite remote sensing is widely used it is often associated with limited spatial and temporal resolution and with caveats such as partitioning vegetation and soil, which is particularly relevant in sparse
dryland vegetation. Close-range sensing from flux towers, drones, or mobile masts provides the opportunity of obtaining direct and continuous canopy scale spectral information at high spatial resolution (Tittebrand et al 2009, Clasen et al 2015, Mikita et al 2016).

The limitations on forest productivity and survival associated with hot and dry climates are particularly significant in light of the predictions of warming and drying trends and increasing tree mortality in the Mediterranean and other regions (Allen et al 2015, Dai 2013). However, global terrestrial productivity is still increasing (Keenan et al 2014, Mao et al 2016, Park et al 2019, Menzel et al 2020), and some semi-arid ecosystems show surprisingly high productivity and resilience to stress (Grünzweig et al 2003, Cleverly et al 2013, Tagesson et al 2015, Yan et al 2019). This seems to indicate that while in certain cases trees succumb to the increasing intensity and frequency of drought stress (Hogg et al 2008, Hoffmann et al 2011, Aleixo et al 2019), in other cases trees and ecosystems can acquire ecophysiological adjustments to cope with the harsh conditions. Here, we use tower-based sensing and flux measurement methodologies to address the questions: (1) What are the ecophysiological adjustments that support forest productivity in the early spring despite the decoupling from the seasonal cycle in solar radiation and operation in suboptimal temperatures; (2) what are the canopy scale adjustments that provide photoprotection when productivity is suppressed by drought while radiation increases. We hypothesize that seasonal changes in the light absorption capability and light use efficiency, which can enhance productivity in the low radiation and temperature but high soil moisture season, and their relaxations that provide photoprotection in the hot and dry period.

2. Materials and methods

2.1. Study site and period

This work was conducted in Yatir forest (31° 20’ N; 35° 30’ E; 600–900 m above sea level; 2800 ha), which is located at the northern edge of the Negev desert in southern Israel. The forest is dominated by Aleppo pine (Pinus halepensis Mill.), with smaller proportions of other pine species and cypress and little understory vegetation. Stand density is about 300 trees per hectare, mean tree height is 11 m and Leaf Area Index (LAI) is about 1.70 (Sprintsin et al 2011). The native background vegetation is sparse shrubs with a total vegetation height of 0.30–0.50 m (Grünzweig et al 2003). The annual mean solar radiation load is 238 Wm−2. The annual mean air temperature is 17.7 ± 0.5 °C. Mean air temperature in January (the coldest month) and July (the hottest month) is 10 °C and 25 °C, respectively. The annual mean precipitation is 279 ± 90 mm.

2.2. EC and meteorological measurements

A 19 m high flux tower at the center of the Yatir forest is operated since 2000, continuously measuring fluxes of CO₂ (net ecosystem exchange, NEE), water vapor (evapotranspiration, ET), as well as other meteorological parameters such as incoming photosynthetic active radiation (PAR; 400–700 nm), air temperature, vapor pressure deficit (VPD) and soil water content (SWC) (Rotenberg and Yakir 2010, Tatarinov et al 2016), using the Euroflux methodology and data quality control (Aubinet et al 1999). The ecosystem gross primary production (GPP) was calculated from NEE measurements after correction for nighttime respiration (Tatarinov et al 2016).

2.3. Reflectance measurements

Since May 2012 two close-range radiometers (SKR 1850, Skye Instruments LTD, U.K.) were installed on the flux tower, facing the atmosphere and the ecosystem. With A diffuse cap, the sensors had a 90° viewing angle, which captured ~90% of the incoming radiation and allowed focusing on the canopy with the minimal signal from the soil. The sensors measured downwelling and upwelling irradiance in three visible (530 ± 1.5 nm, 570 ± 10.1 nm, 659.4 ± 11.3 nm) and one NIR (858 ± 10.7 nm) bands and the data were integrated over 30 min intervals to be compatible with flux measurements. The canopy reflectance ρ, was calculated as the ratio of the upwelling to downwelling irradiance at each spectral band. Based on the reflectance measurements, we used two approaches to estimate the fraction of absorbed PAR (fAPAR) and, in-turn, the actual absorbed photosynthetic radiation as APAR = fAPAR × PARp.

Firstly, the widely used Normalized Difference Vegetation Index (NDVI) was calculated as (Rouse et al 1974):

\[ \text{NDVI} = \frac{(\rho_{\text{NIR}} - \rho_{\text{red}})}{(\rho_{\text{NIR}} + \rho_{\text{red}})} \]  

(1)

where ρNIR and ρred refer to the reflectance at spectral bands centered at 858 nm and 659 nm, respectively.

NDVI is strongly correlated with leaf area, which is one of the main factors influencing canopy light absorption, and is linearly correlated with fAPAR (Ruimy et al 1994, Fensholt et al 2004). Therefore, APAR could be estimated as:

\[ \text{APAR}_{\text{NDVI}} = \text{PAR}_{\text{in}} \times \text{NDVI}(\mu\text{mol m}^{-2}\text{s}^{-1}) \]  

(2)

Light use efficiency (LUE) was derived from APARNDVI and GPP (Monteith 1972):

\[ \text{LUE} = \frac{\text{GPP}}{\text{APAR}_{\text{NDVI}}} \quad \text{(mol/mol)} \]  

(3)

Secondly, the canopy chlorophyll absorption

\[ \text{CHL} = \frac{\text{GPP}}{\text{APAR}_{\text{NDVI}}} \quad \text{(mol/mol)} \]  

(4)
coefficient in the green range was calculated as (Gitelson et al 2019):

\[
\alpha_{chl} = \rho_{NIR}/\rho_{green} - 1 \quad \text{(unitless ratio)} \quad (4)
\]

where \( \rho_{green} \) is the reflectance in the spectral band centered at 570 nm. Since \( \alpha_{chl} \) indicates the ability of light absorption by chlorophyll, its product with PAR\(_{in} \) could be used to estimate APAR:

\[
\text{APAR}_{\alpha_{chl}} = \text{PAR}_{in} \times \alpha_{chl} \left( \mu\text{mol m}^{-2}\text{s}^{-1} \right) \quad (5)
\]

Note that NDVI and \( \alpha_{chl} \) are both empirical indices and we used the more common approach to obtain NDVI-based LUE (equation (3)) and compared to published values. But we took advantage of the higher sensitivity of the newer index \( \alpha_{chl} \) (figures 1(d), S2 (available online at https://stacks.iop.org/ERL/15/114054/mmedia)) and its direct relationships to chlorophyll absorption (Gitelson et al 2019) to follow the seasonal variation and better identify the timing of its seasonal peaks and minima.

Leaf reflectance at the NIR 780 nm (775–785 nm) and red-edge 742 nm (736–747 nm) bands were measured monthly by Polypen UVIS spectrometer (PSI spol. s r.o., Drásov, Czech Republic) during 2018–2019. Leaf chlorophyll content (LCC) was estimated non-destructively from the red-edge chlorophyll index (\( CI_{re} = \rho_{NIR}/\rho_{red} - 1 \)) (Gitelson et al 2003, Gigandet et al 2009), after calibration with two sets of needles sampled on April 23 and May 30, 2018. During the calibration, the LCC of the two sets of the sampled needles was measured analytically. For each sample, 1 cm\(^2\) needle tissue (about 50 mg) were immersed in 1 ml of 80% acetone, then ground using a ball mill (two 3 mm balls; Retsch, Hann, Germany) at a frequency of 25 s\(^{-1}\) for about 5 min, and followed by centrifuge (5424 R, Eppendorf AG, Hamburg, Germany) at 14000 rpm for 10 min. The supernatant was transferred into a 96 well plate (300 \( \mu l \)), where its absorbance was measured at 663.6 nm and 646.6 nm by a microplate reader (Molecular Devices, Sunnyvale, CA, USA). After subtraction of the absorbance of a blank sample, the concentration of chlorophyll \( a + b \) was calculated (Porra et al 1989).

The detailed relationship between the \( CI_{re} \) and the analytical LCC can be found in supplementary materials (figure S1), from which LCC can be estimated as:

\[
\text{LCC} = 883.33 \times CI_{re} - 2.25
\]

With determination coefficient \( R^2 = 0.92 \) and RMSE of 3.7 \( \mu g \text{ cm}^{-2} \).

2.4. Evaluation of seasonal trends and statistical analysis
Canopy scale fluxes of CO\(_2\) were computed from the high-resolution EC measurements using EddyPro software 7.0.5 (LICOR Biosciences, Lincoln, Nebraska) and averaged over 30 min interval.

All canopy flux measurements were processed at a daily scale in two steps: Firstly, to eliminate the bias from the diurnal variations, the average of the daytime measurements were obtained. Secondly, a moving average was applied to the multiannual set of daily scale data to identify season peaks and minima. A 7 d running average provided the optimal representation of the seasonal changes.

To evaluate the seasonal cycle in the radiation and CO\(_2\) uptake (GPP) data, daily sum (daytime only) of the PAR\(_{in}\), APAR, and GPP data were used.

The period of peak productivity was determined, for each year, as the period during which photosynthetic CO\(_2\) uptake (GPP) was above 85% of its annual maximum values. The same threshold was also used to define the peak period for other variables.

Statistical analysis and visualization were carried out using R software (version R-3.4.1) and the ‘ggplot2’ package.

3. Results
In the results below we report on the seasonal offset between the peak in photosynthesis and its main driving forces, such as radiation and temperature. Afterward, we proceed to report on the factors that could help sustain high GPP despite such offset (including chlorophyll content and light absorption efficiency).

The seasonal variations in the meteorological and ecophysiological parameters for the study period 2013–2016 are reported in figure 1. In general, more than one distinct seasonal cycles are observed. One cycle includes the meteorological parameters dominated by solar radiation, such as PAR, APAR, temperature, and VPD, peaking in July, with a minimum in January. In contrast, the ecophysiological parameters showed clear offsets to the climatic parameters. SWC, NDVI, \( \alpha_{chl} \), \( \rho_{NIR} \) reached a peak in late winter (January–February), and decreased with the onset of the dry period. GPP and LUE peaked together about one month later in March, while \( \rho_{red} \) was at its minimum. The productive period where GPP was higher than 85% of its peak values, was only about 60 d. Precipitation occurred only from November to April, with annual precipitation of 323 mm, 358 mm, and 352 mm for the three hydrological years (1st October–31st September, 2013–2016). Notably, GPP and LUE were strongly coupled and were characterized by a sharp and narrow peak at the end of March, followed by a rapid decrease, from 0.5 mol m\(^{-2}\) d\(^{-1}\) at peak season to 0.05 mol m\(^{-2}\) d\(^{-1}\) around July (i.e. a 10-fold decrease), with the low values remaining through the long dry season.

Chlorophyll absorption coefficient \( \alpha_{chl} \) showed a seasonal cycle synchronously with GPP and with similarly narrow peak, but about 1–2 months in advance
Figure 1. Seasonal variation of daily climatic and biophysical variables in 2013–2016 after applying 7 d moving average. Red lines indicate the variables on the right axis. (a) Incoming photosynthetically active radiation (PAR) and canopy-absorbed PAR (APAR) derived from NDVI. (b) Mean air temperature at canopy height (7–13 m) and vapor pressure deficit (VPD). (c) Mean soil water content (SWC) at the top 50 cm and daily precipitation. (d) Canopy chlorophyll absorption coefficient ($\alpha_{chl}$) and NDVI. (e) Canopy reflectance at 660 nm ($\rho_{red}$) and 860 nm ($\rho_{NIR}$). (f) Gross primary production (GPP) and light use efficiency (LUE).

Maximal $\alpha_{chl}$ occurred around February while maximal GPP around the end of March. Such offset was less clear during the time of the minima in these parameters at the end of the dry season in October.

The APAR$\alpha_{chl}$ [$\alpha_{chl} \times \text{PAR}_{in}$] was tightly coupled with GPP during the December-March buildup period leading to the seasonal maximum in GPP, but with a time delay and slower decrease from around July to December (figure 2(b)). The slope of GPP as a
function of $[\alpha_{chl} \times \text{PAR}_{in}]$ represents an estimate of mean LUE (figure 3). Differences among slopes indicated that in the winter of the year 2013–2014 LUE was lower on average than in the following two years.

Canopy reflectance in NIR, $\rho_{\text{NIR}}$, decreased with increasing incident irradiance $\text{PAR}_{in}$ showing strong negative linear correlation ($R^2 = 0.74$) across the seasonal cycle (figure 4). This relationship was particularly strong as PAR levels increased in summer.

LCC showed a clear seasonal cycle with the minimal value in October (15 $\mu$g cm$^{-2}$) and the peak in March–April (45 $\mu$g cm$^{-2}$) (figure 5).

4. Discussion

The results reported above demonstrate two main components: First, the result of the photosynthetic CO$_2$ uptake fluxes (GPP) show the unusually early (March) and short (>60 d) peak activity period in the study ecosystem, as compared with the commonly observed peak time (June to August) and length (often >120 d) in temperate forests where it coincides with high solar radiation and temperature. This represents a shift from radiation-dominated to moisture-dominated ecosystems along the latitudinal and climatic gradient (Rotenberg and Yakir 2010, Park et al 2019). Second, the additional measurements provide evidence that while the early productivity period under suboptimal conditions is imposed by the water limitations, it is facilitated by synchronizing multiple factors, such as increased chlorophyll content, enhanced light use efficiency, and adjusted leaf inclination at just the right time.

We focus on canopy-scale adjustments, which address two key requirements: Optimizing productivity in the unusually narrow productive window, when soil moisture is still sufficient and radiation and temperature are least limiting, and providing photoprotection in the long dry and hot summer. The adjustments to these contrasting requirements are clearly reflected in the sequence of the seasonal cycles of key ecophysiological parameters as summarized in figure 6.

Optimizing offseason productivity (the Goldilocks effect): The unusually narrow peak in photosynthetic activity (GPP) in spring (figure 1(e)) seems to reflect environmental and ecophysiological evolution: (1) As the limitation of soil moisture is reduced at the end of winter, photosynthesis (GPP) increases synchronously with the increase in temperature and incoming solar radiation ($\text{PAR}_{in}$) into the early spring. (2) While $\text{PAR}_{in}$ and temperature continue to increase into the early summer, the rapid soil drying and high evaporation demands (VPD), quickly suppress the photosynthetic activities. This results in the observed narrow productivity peak in March (figure 2(a)). (3) To exploit this imposed narrow window of opportunities to optimize productivity, the results show that a range of ecophysiological resources are mobilized and are well synchronized to form what can be termed a ‘Goldilocks effect’ that underlies the high productivity of the dry forest.

One of the distinct aspects that supports the observed GPP seasonality is the temporal change in light use efficiency (LUE; figure 1(e)). While in temperate sites the highest LUE coincides with the lowest GPP in winter (e.g. Garbulsky et al 2008), here it coincides with the maximum GPP in spring. This is followed by a decrease in LUE to low values in the dry season that seems to reflect downregulation of biochemical activities, associated with the near-zero stomatal conductance (Maseyk et al 2008, 2019). Irrespective of the changes in the seasonal patterns, the magnitude of the observed LUE values (ranging between 0.002 and 0.02) was consistent with published estimates from different biomes (Garbulsky et al 2011).

Leaf development in Yatir has previously been shown to begin in spring and occur throughout the
dry and stressful summer, allowing to maximize the contribution of the new fully developed leaves, with peak concentrations of leaf nitrogen (Maseyk et al. 2008), to maximize GPP in the following short active season. The seasonality of leaf development was composed of two components. The first was reflected in the seasonal patterns of LAI that reached a maximum already in the fall (Sprintsin et al. 2011). However, as LAI reached its seasonal maximum, LCC was still at its minimum and only then started to increase, reaching a seasonal maximum in spring (~3-fold increase; figure 5), such that the combined effects of high LAI times LCC coincided with the peak of photosynthetic activity.

LAI and LCC, together with structural effects influence the canopy absorption coefficient (Gitelson et al. 2019), which was estimated here as $\alpha_{\text{chl}}$. We observed temporally synchronous behavior of GPP and $\alpha_{\text{chl}}$ but with the increase in $\alpha_{\text{chl}}$ leading GPP by 1–2 months (figure 2(a)). Note that although NDVI
Figure 5. Mean LCC retrieved from leaf reflectance using red edge chlorophyll index CI_{re}. Measurements in 2018 were with new needles and that in 2019 with both new and one-year-old needles. The dashed line is the two-period moving average.

Figure 6. A conceptual presentation of the sequence of key seasonal cycles in (a) soil moisture, the rate of photosynthetic activity, solar radiation, and temperature; and in ecophysiological adjustments in (b) light absorption coefficient, light use efficiency, leaf chlorophyll content, and canopy NIR reflectance. It highlights the large offset (several months) between photosynthetic activities and its driving forces (light and temperature), which is imposed by the water availability (soil moisture). The ecosystem’s ability to adjust the timing of peak photosynthesis requires the convergence of a range of ecophysiological adjustments (termed here the Goldilocks effect). The lines are a fit to mean data at the study site. The table indicates the peak timing of the above and additional parameters, which are discussed in more detail in the text.

| Month | Jan | Feb | Mar | Apr | May | Jun | Jul | Aug | Sep | Oct | Nov | Dec |
|-------|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|
| Max.  | $\rho_{PE}$ | SWC | NDVI | $\alpha_{chl}$ | GPP | LUE | Temp. | VPD | $\rho_{PE}$ | PAR | APAR | Temp. |
| Min.  | PAR, APAR | Temp., VPD | $\rho_{PE}$ | $\rho_{PE}$ | GPP, LUE, LCC | SWC, NDVI, $\alpha_{chl}$ |
Indeed, the product of $\alpha_{\text{chl}}$ and PAR$_{\text{in}}$, which provided an intrinsic measure of APAR$_{\text{in}}$ in the system showed a tight coupling with GPP during the early increasing phase in late winter to early spring (figure 2(b)). The linear GPP vs. $[\alpha_{\text{chl}} \times \text{PAR}_\text{in}]$ relationship is consistent with the Monteith model which assumes that productivity must be positively dependent on absorbed radiation (Monteith 1972), as has been observed in other ecosystems (Turner et al 2003, Lagergren et al 2005, Garbulsky et al 2011). The seasonal-scale slope of the linear regressions indicated the seasonal mean LUE (figure 3). The lower LUE observed in winter 2013–2014, was associated also with lower maximum values of GPP and $[\alpha_{\text{chl}} \times \text{PAR}_\text{in}]$. This is consistent with the lower annual precipitation (30 mm, and over 10% less than other study years), and lower minimum SWC at the end of winter in that year compared with the following two years (17% vs 20%), providing confidence in our APAR$_{\text{in}}$ and LUE estimates.

**Photoprotection under stress:** While the importance of increasing $\alpha_{\text{chl}}$ in the low PAR period is evident, the overall relationships of $\alpha_{\text{chl}}$ and GPP are more complex (see figure S2). The strong correlation between these parameters noted above also indicated a strong seasonal hysteresis with both low and high GPP values associated with similar $\alpha_{\text{chl}}$ before or after the March GPP peak, respectively. It seems that variations in $\alpha_{\text{chl}}$ are part of the canopy-scale adjustments to seasonal changes in ambient conditions, enhancing absorption when PAR$_{\text{in}}$ is low, but depressing absorption and providing some photoprotection when PAR$_{\text{in}}$ is high and GPP is in decline as the summer drought develops.

Structural changes can also enhance absorption or provide photoprotection, and reflectance in the NIR range, $\rho_{\text{NIR}}$, where chlorophylls do not absorb, roughly represents canopy scattering coefficient that related to canopy structural properties such as LAI, and leaf inclination angle (Gitelson et al 2019). This notion is supported by the strong positive correlation between PAR$_{\text{in}}$ and canopy $\rho_{\text{NIR}}$ (figure 4), with $\rho_{\text{NIR}}$ peaking in winter during the lowest annual PAR$_{\text{in}}$ and decreasing to a minimum in summer during the highest PAR$_{\text{in}}$. These changes do not coincide with those in LAI discussed above (Sprintsin et al 2011), and seasonal changes in solar angles are expected to have a small effect (Hinojo-Hinojo and Goulden 2020). We, therefore, suggest that the observed seasonal changes in $\rho_{\text{NIR}}$ are related to some changes in leaf orientation to a more horizontal angle in winter to maximize absorption, resulting in enhanced NIR scattering despite low PAR$_{\text{in}}$ at that time. In contrast, more vertical leaf orientation in summer reduces absorption and $\rho_{\text{NIR}}$ and, in turn, reduces over-excitation and photodamage during the high PAR$_{\text{in}}$-low GPP period.

Finally, we note that besides the structural changes, the large reduction in LCC observed in the summer (figure 5) provides additional photoprotection by reducing $\alpha_{\text{chl}}$ and minimize excessive light absorption. This is supported by canopy reflectance in the visible (red) range that was about 1.5-fold higher during the dry period (figure 1(e)). Additional photoprotection mechanisms at the leaf-scale at the same site have also been recently reported (Maseyk et al 2019).

The results discussed above have important implications for the future of forests in large parts of the world. This is because evolutionary-based genetic modifications are too slow to adapt to the rate of the warming and drying underway in many regions. In contrast, the phenotypic plasticity we report here in common Mediterranean pine trees, clearly shows that such trees can make large adjustments to off-season productivity and provide photoprotection under stress, to offer an effective basis for forest survival and continued productivity under increasingly stressful environments.

**5. Conclusion**

As global climate change is expected to expose large land areas to increasing hot and dry conditions, our results provide evidence for canopy-scale eco-physiological adjustments that boost the resilience and productivity of pine forests under harsh conditions. These adjustments reflect a combination of avoidance by a shift in the timing of activity, balanced by enhancing productivity under the sub-optimal temperature and PAR conditions through optimizing chlorophyll content, LAI, and LUE.

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**Author contributions**

D Y and E R conceived the study and carried out the flux and sensing measurements, and H W carried out pigment analyses; A G, M S and H W analyzed the data. H W drafted the manuscript with discussions and support from all co-authors that contributed to the final manuscript.
Data availability statement

The data that support the findings of this study are available upon reasonable request from the authors.

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