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Assessing the cross-site and within-site response of potential production to atmospheric demand for water in *Eucalyptus* plantations

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ABSTRACT

Plant water deficits arise from low soil water and high atmospheric demand for water (expressed as vapor pressure deficit; VPD). Soil water and VPD often covary making it difficult to examine the effect of only VPD on biomass production. We used four Eucalyptus plantation sites where one treatment maintained high soil water with irrigation to evaluate the response of forest production to VPD independent of soil water. We used two approaches: an empirical test and simulations with the 3-PG model. For the empirical test, we examined the VPD response of gross primary production (GPP), net primary production of aboveground wood biomass ($ANPP_W$), photosynthesis per unit of light absorbed (GPP per unit of intercepted photosynthetically active radiation (APAR)), and wood growth per unit of light absorbed ($ANPP_W\ APAR^{-1}$). For modeling, we compared 3-PG model predictions of these variables using a constant VPD and VPD that varied with data from the sites. Photosynthesis per light absorbed and wood growth per light absorbed both decreased exponentially as VPD increased, but neither GPP nor $ANPP_W$ varied with VPD. Across sites, photosynthesis per light absorbed increased with VPD, but the other variables had no relationship with it; wood growth per light absorbed, flux to $ANPP_W$, and partitioning of GPP to aboveground and $ANPP_W$ decreased with site mean annual temperature. Results from the 3-PG model simulations were similar to those in the data. Two factors explain the response of photosynthesis per light absorbed and wood growth per light absorbed to VPD and the lack of response of GPP and $ANPP_W$ to VPD. First, VPD is strongly correlated with APAR—clear days yield high APAR and high VPD. Second, the extra light absorbed when APAR is high cannot be used for GPP because leaf stomata are closed when VPD is high. We expect that similar results would apply across the wet tropics, and future studies linking aboveground production to water in the wet tropics should focus on soil water status, not VPD.

1. Introduction

Ecophysiological assessments of production of Eucalyptus plantations have focused on factors that constrain stem wood production (Laclau et al., 2013). Among biotic and abiotic factors, water deficits can be very important, as irrigation increases production (Pereira et al., 1989; Stape et al., 2010), and rainfall removal lowers production (Binkley et al., 2020). Tree responses of production to water supply involve several mechanisms, including alterations of photosynthesis and partitioning (Ryan et al., 2010). Atmospheric demand for water (expressed as vapor pressure deficit, VPD) can also alter production by affecting stomata conductance and photosynthesis (Lange et al., 1971; Oren et al., 1999). If VPD is high and water fluxes to leaves are too low to sustain the water-conducting pathway, stomata close to maintain leaf water potential and to reduce extreme water loss even if soil water is available. High temperatures increase VPD as the partial pressure of water in the atmosphere remains constant, further underscoring the importance of stomatal control relative to soil water supply in determining growth. A VPD response has been incorporated in ecosystem production models (Landsberg and Waring, 1997; Huth et al., 2001) even though empirical tests that separate the effects of soil water supply and VPD remain scarce.

In a light-use efficiency framework, biomass production is determined at several branching points: (1) the amount of photosynthetically active radiation absorbed by canopy (APAR), (2) photosynthesis per unit of APAR, net primary production (NPP) per unit

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photosynthesis or gross primary production (GPP) (carbon use efficiency, determined by the amount of autotrophic respiration), and (3) partitioning the NPP to wood biomass production (Monteith, 1977; Linder, 1985; Landsberg and Waring, 1997). Photosynthesis per unit of light absorbed is dependent on VPD, CO_2, soil water and nutrient availabilities, and temperature. Carbon Use Efficiency is roughly constant (Ryan et al., 1997; Waring et al., 1998; Litton et al., 2007) and partitioning patterns are mainly determined by site fertility (Haynes and Gower, 1995; Litton et al., 2007; Lim et al., 2015), soil water (Stape et al., 2008; Ryan et al., 2010) and temperature (Litton and Giardina, 2008). This implies that if no other limitation occurs, the response of biomass production to VPD will be mediated through reduced photosynthesis per light absorbed.

Manipulating VPD in the field condition is costly for a free air humidity manipulation (Tullus et al., 2016) and temporal variation of VPD is often used in field experiments (Tor-ngern et al., 2015; Novick et al., 2016; Sulman et al., 2016; Zhang et al., 2019). This requires daily or sub-daily measurements to decouple VPD and soil water content, as an averaged VPD for weekly or monthly periods is often correlated with soil water availability. The eddy covariance technique allows an evaluation of the VPD response with high frequency measurements, and has shown a greater response for VPD than for soil water across a range of sites (Novick et al., 2016). Many studies evaluated the effect of VPD indirectly using process-based models (Almeida et al., 2004; Stape et al., 2004a) and empirical growth models (Campoe et al., 2016). Field data on VPD response from controlled experiments that manipulate soil water supply can provide insight and validation for eddy covariance and modeling studies by constraining abiotic factors.

In the early 2000s, the Brazil Eucalyptus Potential Productivity Project (BEPP, www.ipef.br/bepp) investigated responses of intensively managed plantations to high rates of addition of nutrients and water across eight sites in Brazil. The whole-rotation results for four of these sites showed that water supply limited growth more than then-current operational rates of fertilization (Ryan et al., 2010; Stape et al., 2010). Related work also indicated that VPD might limit the ability of Eucalyptus plantations to respond to high supplies of water (Stape et al., 2004a, 2008). These insights from the BEPP project led to the larger TECHS Project (Binkley et al., 2017, Tolerance of Eucalyptus Clones to Hydric, Thermal and Biotic Stresses, www.ipef.br/techs/en). In this paper we examined the influence of VPD on the production in the original four BEPP sites using a combination of empirical statistical analyses and modeling with 3-PG (Landsberg and Waring, 1997).

We expected that a VPD response is important for biomass production because of the physiological responses for canopy stomata conductance and photosynthesis. We explored the four BEPP sites, where extensive field measurements were made monthly or quarterly to estimate aboveground NPP, total belowground carbon flux, leaf area and biomass, aboveground respiration and GPP, based on the sum of the compartment fluxes. Soil nutrient and water availabilities were manipulated, providing the opportunity to separate the influence of VPD from that of water supply. The irrigation treatment coupled with existing rainfall provided soil water that matched potential evapotranspiration (PET) and increased GPP by 18% across the four sites (Ryan et al., 2010).

Given soil water that matched PET, how important was VPD in determining the productivity of these stands? We hypothesized that VPD plays a large role in determining growth of Eucalyptus within a site and across sites because VPD will close leaf stomata and reduce photosynthesis per unit of light absorbed. Based on this hypothesis, we made three predictions for the within-site response (P1 – 3) and one for the cross-sites response (P4):

P1) photosynthesis per unit of light absorbed will decrease with increasing VPD;
P2) the sensitivity of photosynthesis per unit of light absorbed to VPD will be greater than that of biomass production;
P3) 3-PG model simulations match observed production better when VPD varies with measured VPD than with a constant VPD; and
P4) cross-site variation of photosynthesis per unit of light absorbed in irrigate treatments will be related to cross-site differences in VPD.

We tested these predictions with four response variables: GPP, NPP of aboveground wood biomass ($ANPP_W$), gross primary production per unit of photosynthetically active radiation (APAR) absorbed (photosynthesis per unit of light absorbed; GPP $APAR^{-1}$)), and wood growth per unit APAR ($ANPP_W$ $APAR^{-1}$).

2. Materials and methods

2.1. Description of sites and data collection

This paper analyzes data from the Brazil Eucalyptus Potential Productivity (BEPP) project (for more detail see Stape et al. (2010) and Ryan et al. (2010)). Four sites were used in the analyses: Aracruz (ARA), International Paper (IPB), Suzano (SUZ), and Veracel (VER). All sites were supplied with two fertilization regimes, best practices, where application varied by site and non-limiting, where fertilizer was applied quarterly (see Stape et al. (2010) for nutrients and amounts applied). An irrigation treatment, where irrigation plus rainfall equaled PET, removed soil water limitations on growth along with an unirrigated treatment. An additional stand structure treatment manipulated stand heterogeneity by planting the same clone either all at once or in three stages 40 days apart to allow the first stage to establish dominance (Binkley et al., 2010). Only the irrigation treatment led to a strong production response, so in our assessment we combined the fertilization and stand structure treatments to examine the overall effect of irrigation.

Gross primary production was estimated between age three to five based on the mass-balance method, summing aboveground compartmental production, total belowground carbon flux and aboveground wood respiration (24 h) and foliar respiration (night only). Aboveground production was estimated using a combination of repeated tree measurements every third month along with site specific allometric equations and litterfall. Stem CO_2 efflux (respiration) was estimated using age dependent respiration functions and foliar respiration was estimated using canopy foliar N content. Both wood and foliar respiration were adjusted for monthly site temperature. Soil CO_2 efflux was measured monthly. Litterfall was collected monthly using six 0.25 m^2 traps, and corrected for within-month decomposition. Details of measurements of carbon fluxes and pools, optical light measurements and leaf area index (LAI) are described in Ryan et al. (2010)). Monthly estimates of fluxes for this study were estimated using linear interpolation between quarterly measurements.

2.2. Meteorological data

Climate data were recorded at automatic weather stations near each experimental site. The hourly meteorological variables were minimum and maximum air temperature, minimum and maximum relative humidity, accumulated rainfall, average wind speed, average rate of incoming global radiation, and average rate of photosynthetically active radiation (PAR). In addition to the BEPP weather stations, we used at least two more weather stations in the trial region to validate and fill any data gap of site meteorology. Hourly VPD was estimated based on air temperature and relative humidity (Allen et al., 1998). Sunrise and sunset times and day length were calculated using latitude and longitude for each site. Monthly VPD was calculated as monthly averaged daily daytime VPD (Fig. 1).

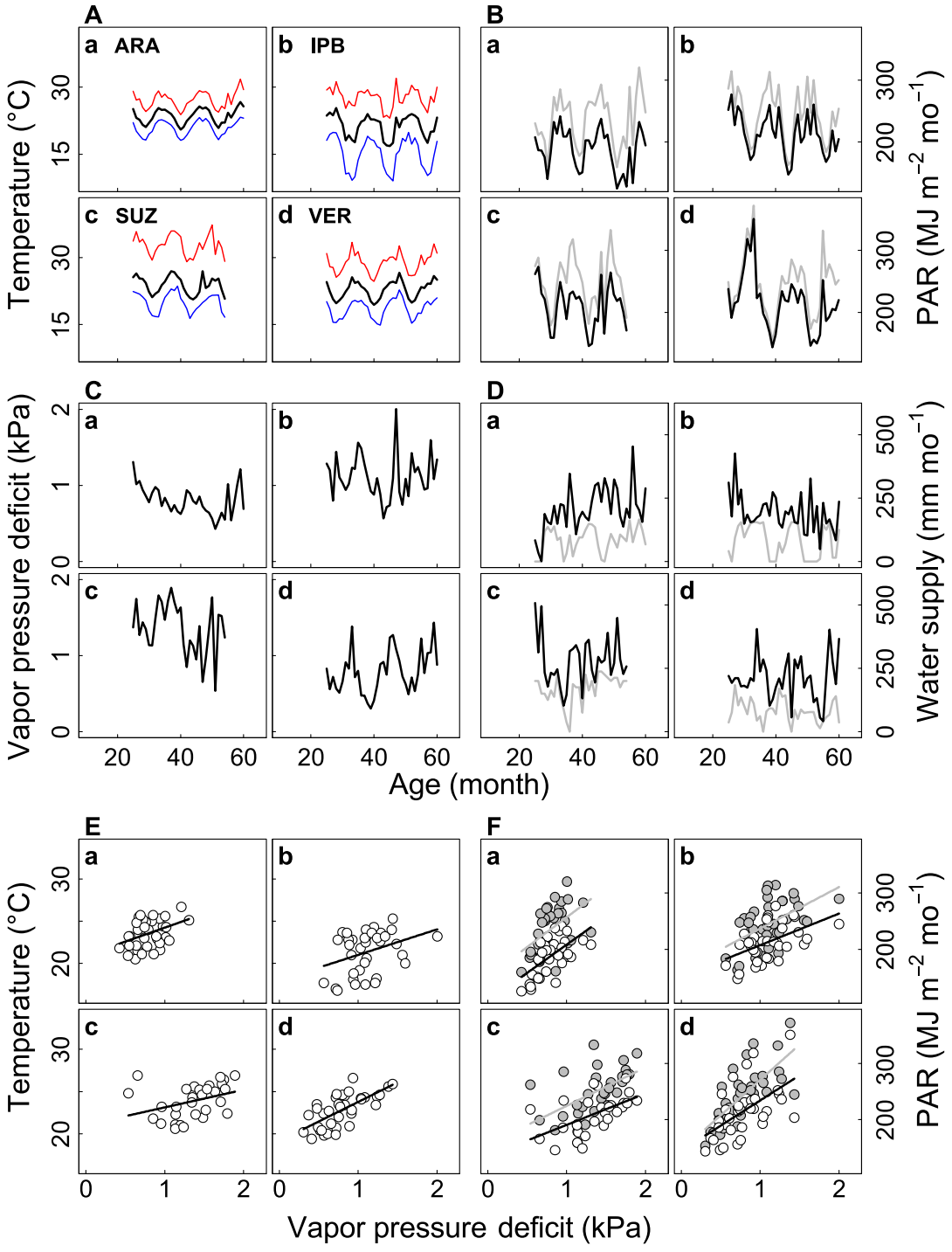

Fig. 1. Environmental conditions throughout study periods. Temperature and PAR were both strongly correlated with daytime vapor pressure deficit (VPD). (A) Monthly averaged daily mean (black), maximum (red), and minimum temperature (blue); (B) photosynthetically active radiation (PAR; grey) and intercepted PAR by canopy (black); (C) monthly averaged daily daytime VPD; (D) soil water supply by rainfall (grey) and by rainfall + irrigation (black); (E) correlation between the mean temperature and daytime mean VPD; (F) correlation between daytime mean VPD and PAR (grey) and intercepted PAR by canopy (open).

2.3. Data analyses

2.3.1. Analysis of the within-site VPD response

The daytime VPD was used to analyze the effect on photosynthesis per unit of light absorbed (GPP $APAR^{-1}$), and wood growth per unit of light absorbed ($ANPP_W$ $APAR^{-1}$) for each site. This allowed us to use effective VPD during the periods of photosynthesis. The 3-PG model employs an exponential function for the VPD response of photosynthesis per light absorbed that extrapolates the maximum photosynthesis per light absorbed at VPD = 0 (Landsberg and Waring, 1997). Because we did not observe photosynthesis per light absorbed at VPD = 0, we used a modified relationship between photosynthesis per light absorbed and VPD following Oren et al. (1999), using a linear mixed model after log-transformation of VPD (Eq. (1)).

$$v_{ijk} = -(\alpha_0 + \alpha_T)\cdot\ln(VPD_k) + \beta_0 + \beta_T + \varepsilon_{jk} + \varepsilon_{ijk} \quad (1)$$

where v_{ijk} is the response variable in ith plot of jth block in age k (month), α is the coefficient and β is the intercept to be estimated, and

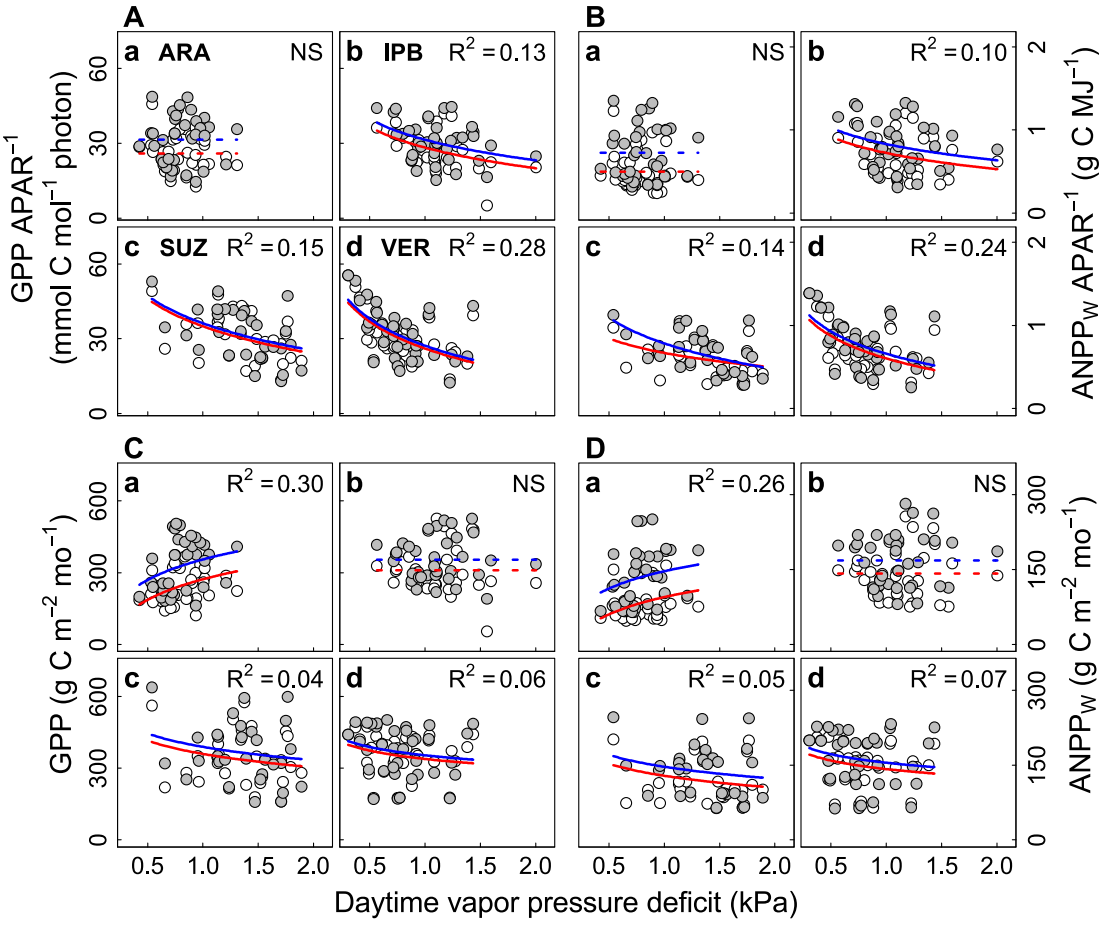

Fig. 2. Relationship between daytime vapor pressure deficit (VPD) and (A) photosynthesis per absorbed light (GPP $APAR^{-1}$), (B) wood growth per APAR ($ANPP_W$ $APAR^{-1}$), (C) gross primary production (photosynthesis, GPP), and (D) net primary production of aboveground wood biomass (wood growth, $ANPP_W$) for four Eucalyptus plantation sites showed that the light efficiency terms (GPP $APAR^{-1}$ and $ANPP_W$ $APAR^{-1}$) generally decreased with VPD while GPP and $ANPP_W$ did not. Sites are: (a) ARA, (b) IPB, (c) SUZ, and (d) VER. Unirrigated (open circles and red lines) and irrigated plots (grey circles and blue lines). Each data point represents mean value across replicated plots in each month. The NS indicates no significant slope of the relationship. Statistical results of the model are given in Table S1.

ϵ_{jk} is the block associated residual and ϵ_{ijk} is the final residual. The effect of irrigation was examined by the significance of αT and βT, and when no significance of α_T was detected at $p < 0.05$, then the term was removed. Eq. (1) was fitted using R (v. 3.6.1) with the *lme* function in the nlme package.

2.3.2. Analysis of the cross-site VPD response

Monthly estimated APAR, GPP, and $ANPP_W$, and precipitation were summed, and temperature and VPD were averaged by year for each block in each site. Photosynthesis per light absorbed and wood growth per light absorbed were estimated using annual GPP, $ANPP_W$, and APAR. To examine the effect of VPD on the response variables, we used a general linear model (Eq. (2)),

$$v_{ij} = \alpha \bullet VPD_j + \beta + \varepsilon_{ij} \quad (2)$$

where v_{ij} is the response variable in ith block of site j, α is the coefficient and β is the intercept to be estimated, and ε_{ij} is the residual. Coefficients were estimated using R (v. 3.6.1) with the *lm* function.

2.4. Parameterization of the 3-PG model

Parameters for biomass partitioning and turnover were derived from observations from each site, except that monthly root turnover ratio was taken from literature (0.025; Sands and Landsberg, 2002). Temperature, frost, atmospheric CO_2, and age modifiers followed literature values (Stape et al., 2004b). Because no fertilization effect was observed in this study and only data from the irrigated plots were used to constrain the other factors, soil water availability and fertility modifiers were set to non-limiting (1). Parameters for specific leaf area were from observations, and maximum canopy quantum efficiency (photosynthesis per light absorbed) from the literature (0.8; Stape et al., 2004b) was adjusted by observed canopy quantum efficiency for each site. After setting these parameters, stomatal response to VPD was tuned for each site using VPD from the site measurements, based on minimum normalized sum of squares (Eq. (3)).

$$\frac{1}{v}\sum_{i=1}^{v} n_i \sum_{j=1}^{n_i} (P_j - O_j)^2 / \left(\sum_{j=1}^{n_i} (O_j)^2\right) \quad (3)$$

where P is predicted and O is the observed value in jth variable. Monthly LAI and aboveground wood biomass (AWB), and GPP, and $ANPP_W$ were used as the variables. The best parameter for the stomatal response to VPD was used for modeling with a constant VPD (the site average for the three years). Model performance between variable and fixed average VPD inputs were compared with Eq. (3). Parameters are presented in the supplementary information.

3. Results

3.1. Empirical assessment of the within-site VPD response

The daytime vapor pressure deficit (VPD) varied from 0.3 to 2.0 kPa across the sites, and variation of VPD was greatest in the VER site (0.36

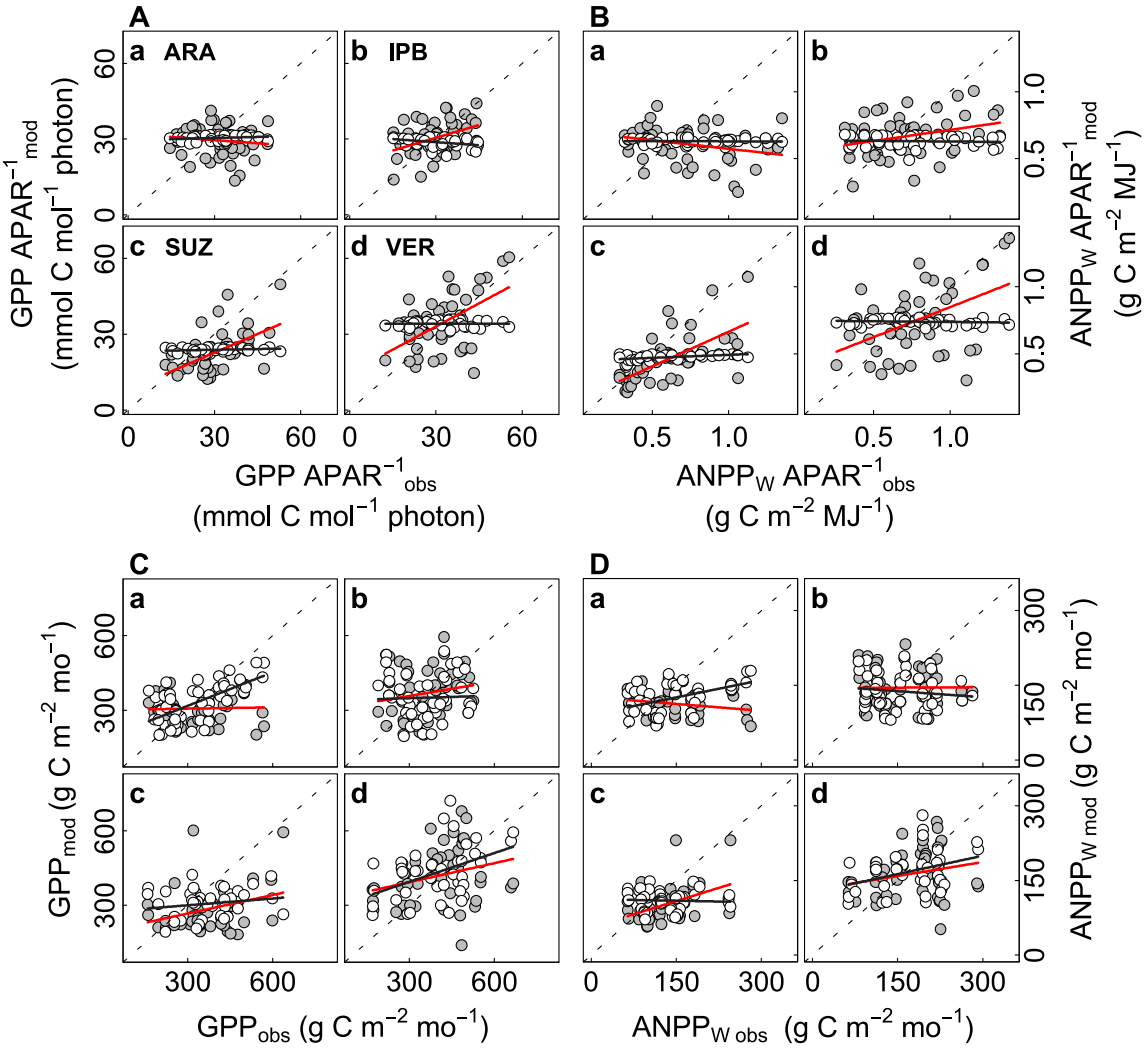

Fig. 3. Comparisons between observations and 3-PG model predictions showed that using site vapor pressure deficit (VPD, variable) in the 3-PG model generally matched the data better for photosynthesis per absorbed light (GPP APAR^{-1}, A) and wood growth per APAR (ANPP$_W$ APAR^{-1}, B) than using a constant VPD in the 3-PG model. White circles and black lines are predictions using a constant VPD, and grey circles and red lines are predictions using site VPD. (A) GPP APAR^{-1}, (B) ANPP$_W$ APAR^{-1}, (C) gross primary production (photosynthesis, GPP), (D) net primary production of aboveground wood biomass (wood growth, ANPP$_W$); (a) ARA, (b) IPB, (c) SUZ, and (d) VER; dotted lines are 1:1 line. Slopes between observations and predictions for each variable were averaged across sites, and presented in Fig. 4B.

of coefficient of variation; 0.79 ± 0.29 kPa, mean ± SD), followed by IPB, SUZ, and ARA sites (0.26, 1.11 ± 0.29 kPa; 0.25, 1.36 ± 0.34; 0.24, 0.80 ± 0.19, respectively) (Fig. 1C). At all sites, temperature and APAR were positively correlated with VPD (Fig. 1E, F).

Photosynthesis per unit of light absorbed (GPP APAR^{-1}) decreased with increasing VPD at the IPB, SUZ, VER sites, but not at the ARA site ($P = 0.157$; Fig. 2A, Table S1). VPD explained 13–28% of the variation in photosynthesis per light absorbed. The response did not change with irrigation. Wood growth per unit light (ANPP$_W$ APAR^{-1}) also responded to VPD in a similar manner as the response of photosynthesis per light absorbed (Fig. 2B). GPP and ANPP$_W$ showed very little or no response to VPD (Fig. 2C, D).

3.2. Model-based assessment of the within-site VPD response

Our parametrization of 3-PG successfully predicted outcomes and temporal variations (Fig. S1; Table S2). Using VPD from the site measurements, photosynthesis and wood growth per light absorbed, 3-PG model estimates responded to the changing VPD, while those for a constant VPD did not (Fig. 3; Fig. S1). GPP and ANPP$_W$ estimates from the 3-PG model were similar for both the constant VPD and the VPD from the site measurements.

3.3. Synthesis of the within-site VPD responses

For the empirical analysis, we compared the impact of VPD on each variable by normalizing the response by a reference response at VPD = 1 for the irrigated plots. Photosynthesis and wood production per unit light responded to VPD, while fluxes (GPP and ANPP$_W$) generally did not (Fig. 4A). For the modeling results, photosynthesis and wood production per unit light responded to VPD that varied with site values, while fluxes (GPP and ANPP$_W$) generally did not (Fig. 4B). Higher sensitivity was recorded using variable VPD for light normalized variables (photosynthesis and wood production per light absorbed), whereas no sensitivity was observed for predictions using a constant VPD.

3.4. Assessment of the cross-site VPD response

Photosynthesis per light absorbed increased across sites as VPD increased (Fig. 5A), but the other variables showed no response to VPD. Mean annual temperature, on the other hand, did explain ~80% of variability of wood production per light absorbed, ANPP$_W$, and aboveground C partitioning, with no effect on photosynthesis per light absorbed and GPP (Fig. 5B).

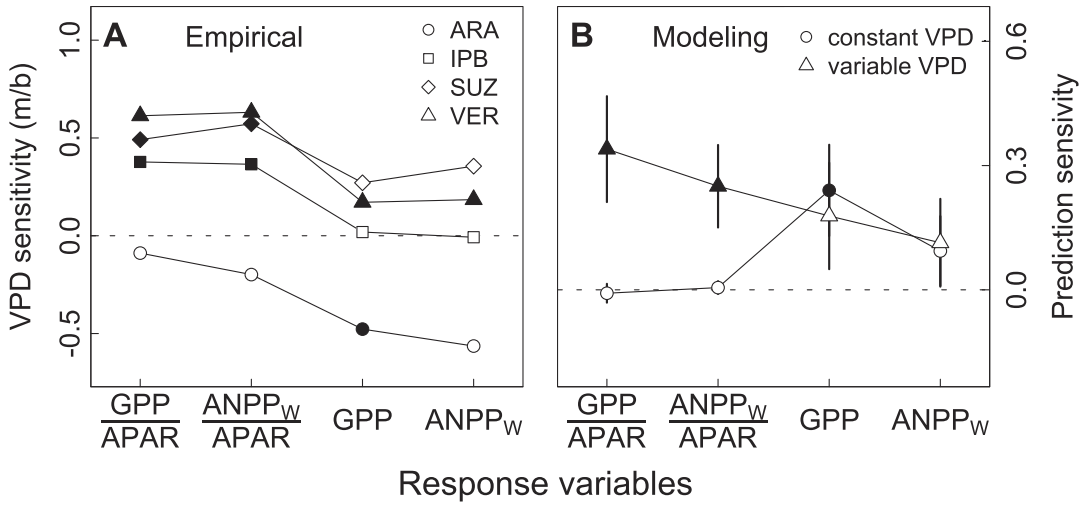

Fig. 4. Assessment of the vapor pressure deficit (VPD) sensitivity for each variable based on (A) empirical and (B) model-based analyses shows that the light efficiency terms (GPP APAR^{-1} and ANPP$_W$ APAR^{-1}) are sensitive to VPD, while the fluxes (GPP and ANPP$_W$) generally are not. (A) Normalized sensitivity of response variables to VPD for irrigated plots. Sensitivity was normalized to the reference value at VPD = 1 kPa (Eq. (1), Table S1). Error bars are standard deviations among blocks. (B) VPD sensitivity is the slope between observation and prediction from Eq. (2) and Fig. 3. Error bars are standard errors across sites that were propagated based on standard errors of the coefficient estimates (Eq. (2)). Filled symbols indicate that the sensitivity is significantly different from 0.

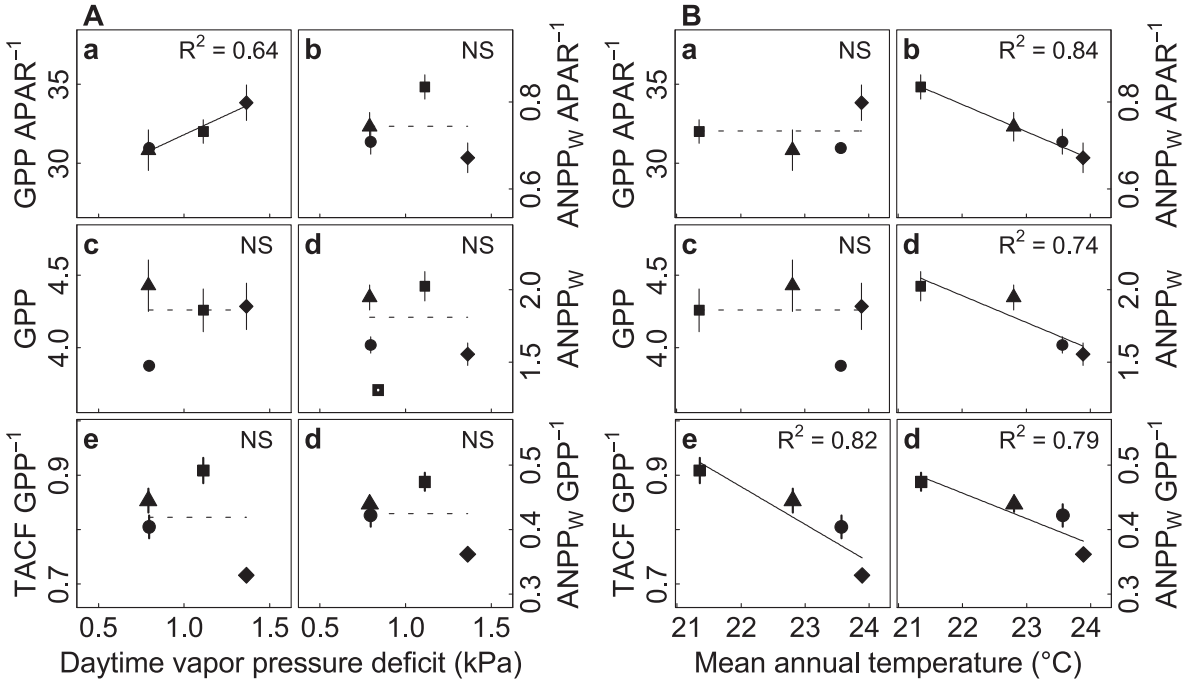

Fig. 5. Cross-site relationships show that photosynthesis per absorbed light (GPP APAR^{-1}) increased with vapor pressure deficit (VPD), while wood growth per APAR (ANPP$_W$ APAR^{-1}), flux to wood growth, and partitioning of GPP to wood and belowground decreased with site mean annual temperature. Response to D (A) and temperature (B). (a) photosynthesis per absorbed light (GPP APAR^{-1}; mmol C mol^{-1} photon), (b) wood growth per APAR (ANPP$_W$ APAR^{-1}; g C MJ^{-1}), (c) gross primary production (photosynthesis, GPP; g C m^{-2} month^{-1}), (d) net primary production of aboveground wood biomass (wood growth, ANPP$_W$; g C m^{-2} month^{-1}), (e) ratio of total aboveground carbon flux (TACF; production + respiration) to GPP, and (f) ratio of ANPP$_W$ to GPP. Error bars are standard deviations among blocks and only irrigated plots were analyzed. circle: ARA; square: IPB; diamond: SUZ; triangle: VER.

4. Discussion

We found that VPD strongly affected photosynthesis per light absorbed in the experimental data regardless of soil water availability, consistent with canopy photosynthesis theory and models (Prediction 1, Fig. 2). Increasing VPD also reduced wood production per light absorbed, but to a lesser extent. This negative impact of VPD on photosynthesis per unit light absorbed and on wood production per unit light absorbed had little or no effect on carbon fluxes (GPP and ANPP$_W$) within sites (Prediction 2, Fig. 2).

Simulations with the 3-PG model generally agreed with the data and the parameter for stomata sensitivity to VPD was greater than that of other studies on Eucalyptus (0.83–1.24 kPa^{-1} in this study; 0.45–0.50, Almeida et al., 2004; 0.324, Stape et al., 2004b), providing a clear test for a VPD response. The 3-PG model estimates were generally similar to the results for the experimental data, where the model simulated reductions in photosynthesis per light absorbed and wood production per light absorbed, but not a reduction in fluxes to GPP and ANPP$_W$ within sites. 3-PG simulations matched the data more closely when using VPD measured on the sites compared to simulations with a constant VPD

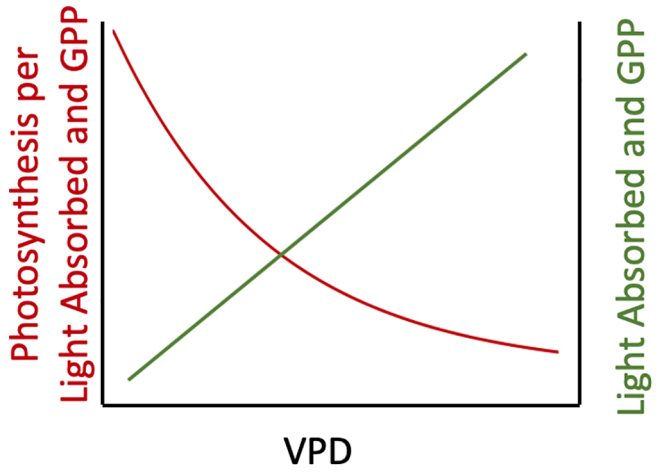

Fig. 6. Conceptual diagram for the effect of vapor pressure deficit (VPD) on photosynthesis per unit of light absorbed and GPP (red) and the correlation of VPD with absorbed light (green) and gross primary production (GPP). Since VPD covaries with light, then the VPD response of GPP is confounded by the light response.

(Prediction 3, Fig. 3).

We predicted that VPD would account for the variability in production across the sites, but GPP and wood production did not vary with VPD across sites, refuting Prediction 4 (Fig. 5A). Also, at this larger scale, photosynthesis per unit light absorbed was positively related to VPD, likely because of a strong correlation of APAR with VPD. Differences in temperature across sites did explain cross-site patterns in wood production per unit light absorbed, $ANPP_W$ and partitioning of GPP to aboveground and to $ANPP_W$, with all four factors decreasing as temperature increased (Fig. 5B). These patterns with temperature suggest that a shift in carbon partitioning is an important mechanism for biomass production in these plantations (Litton et al., 2007; Litton and Giardina, 2008; Ryan et al. 2010).

Using data from 38 Ameriflux eddy covariance sites in the continental United States, Novick et al. (2016) showed that VPD limited surface conductance more than soil moisture in many biomes, especially in temperate mesic forests. This study disentangled VPD from soil moisture effects on conductance by using half-hour values, where the correlation between VPD and soil moisture is low. Surface conductance in mesic forests largely comes from stomatal conductance because high leaf area and the soil organic layer limit soil evaporation. So, the Novick et al. (2016) finding of a large VPD effect on surface conductance would translate into a large effect on photosynthesis through stomatal conductance. Our results show that wet tropical plantations do not follow this pattern of a strong VPD effect.

This study's results also contradict an earlier conclusion by Stape et al. (2008) that VPD was an important limiting factor in the production of Eucalyptus plantations even when water supply was not limiting: well-irrigated plots grew 19% less during a year of higher VPD than in the prior year with lower VPD. Monthly VPD at the site for the Stape et al. (2008) study was comparable to that at the SUZ site in this study, so this study's results should apply. If VPD did not account for the difference in growth in well-watered plots between years, what other factor might have been response? The observed pattern could have related to temperatures, as Eucalyptus plantation growth responds strongly to temperature (Fig. 5; Binkley et al., 2020) and a year with high VPD might be hotter. However, the higher VPD year was only 0.1 °C warmer on average than the low VPD year (Stape, 2002), which would lead to a growth decline of only about 2% (Binkley et al., 2020). The growth of Eucalyptus stands declines with age after canopy closure, and the plantation was 3.8 years old in the middle of the lower VPD year and 4.8 years old in the middle of the higher VPD year. The TECHS Project for tropical sites would predict a decline of 24% across this age interval, giving a null expectation of declining growth in succeeding years. This decline would be sufficient to account for the observed decline of 19%, so we conclude that the large difference in growth between years observed by Stape et al. (2008) in irrigated plots likely resulted from a typical pattern of age-related decline rather than VPD.

Why was there no clear VPD response in the measured and modeled fluxes in this study? Two factors explain the VPD response of photosynthesis per unit light absorbed and wood production per unit light absorbed and the lack of response of GPP and $ANPP_W$ to VPD. First, VPD is strongly correlated with APAR—clear days yield high APAR and high VPD. This relationship is shown in Fig. 6, which our data in Fig. 1F supports. Despite decoupling VPD from soil moisture through the irrigation treatment, we have shown that the correlation of VPD and radiation confound interpretation of the VPD response. Eucalyptus do respond to VPD as shown by the 3-PG model, but the response is masked by co-occurring high VPD and radiation both in the data and in the model. Changes in intrinsic water-use efficiency, defined as the ratio of photosynthesis to stomatal conductance, may also lower a response of GPP to VPD (Zhang et al., 2019). Second, as shown by decrease in photosynthesis per unit light absorbed and wood production per unit light absorbed with VPD coupled with no change in GPP and wood production, the extra light absorbed when APAR is high cannot be used for GPP because leaf stomata are closed when APAR and VPD are high. Wet tropical forests are often limited by light because of cloud cover, and VPD is low compared with many temperate forests. Therefore, we expect that VPD and radiation would be correlated across the wet tropics, and we expect that a similar lack of a clear VPD response for photosynthesis would apply across the wet tropics. For Eucalyptus plantation production, soil moisture is more important than atmospheric water demand.

CRediT authorship contribution statement

Hyungwoo Lim: Formal analysis, Investigation, Writing - original draft, Visualization. **Clayton Alcarde Alvares:** Formal analysis, Data curation. **Michael G. Ryan:** Conceptualization, Validation, Writing - review & editing. **Dan Binkley:** Conceptualization, Validation, Writing - review & editing.

Declaration of interests

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2020.118068.

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