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Climate Change Effects on Long-Term Leafing Activity of a Tropical Rainforest Tree Species, *Davidsonia pruriens*

Nara O. Vogado[1] | Michael J. Liddell[2]

[1]Department for the Ecology of Animal Societies, Max Planck Institute for Animal Behaviour, Konstanz, Germany | [2]Centre for Tropical Environmental and Sustainability Science, College of Science and Engineering, James Cook University, Cairns, Queensland, Australia

Correspondence: Nara O. Vogado (vogado.nara@gmail.com)

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ABSTRACT

Leafing activity is a crucial part of the tree life cycle and is tightly linked to photosynthesis, gas exchange and biomass accumulation, among other processes. Despite this, many aspects of leafing phenology, such as climate drivers of community and species-level temporal patterns, are poorly understood in tropical rainforest species. Here, we present 18 years of above-canopy phenological observations of leafing phenology for *Davidsonia pruriens*, an important endemic species in the Wet Tropics, from January 1997 to December 2014. We assessed changes in leafing patterns through time and how they are being affected by climate drivers. We found that, while the tropical rainforest region is considered to have low seasonality in leaf production, leafing in this species was seasonal with a peak in the wet season. Analysis of climate drivers showed that increased leaf production was correlated with increased daily rainfall and decreased solar radiation. Interannual activity responded similarly to changes in annual rainfall and solar radiation but was also significantly impacted by cyclones and El Niño events. Our results show that *Davidsonia pruriens* has seasonal leafing patterns which are strongly influenced by climate drivers. Our study is the first to present field-based measurements of long-term leafing phenology in Australia, which clearly demonstrate climate change sensitivity of leafing in an endemic plant, a plant that is a significant bush tucker species to Aboriginal traditional custodians of the rainforest region of Northern Australia.

1 | Introduction

Leaves are an essential organ of plants, being responsible for photosynthesis and gas exchange. The arrangement of leaves in time and space is, as a result, a key element in plant strategies for carbon gain (Kikuzawa 1995). Leaf exchange, that is, the process of dropping senescent leaves and producing new ones, is important for maintaining the plant's water and carbon balance. Carbon and water cycling at an ecosystem level are strongly influenced by the length and timing of the growing season (Parmesan 2006; Polgar and Primack 2011). The timing of leaf production affects photosynthesis rates, which in turn have a big influence on biomass accumulation (Polgar and Primack 2011). Leaves, in addition, are subjected to biomass loss from insects or intense herbivory from vertebrate animals. It is known that many herbivores have a preference for eating young rather than mature leaves, likely because some plant species produce younger leaves that contain less fibre and more protein compared to mature leaves (Milton 1979). Yoneyama and Ichie (2019) studied the relationship between leaf phenology and defences against herbivores in five dipterocarp species in Malaysia. They found that species with high annual leaf flushing frequency had greater chemical defences, while those with lower annual flushing frequency had tougher leaves with greater photosynthetic capacity. As producing new leaves represents a cost to the tree, through the resources required for leaf construction and chemical defences, there is likely a complex set of trade-offs between fibre, leaf protein, photosynthetic capacity, chemical defences and tree survival (Kursar and Coley 1992).

To avoid damage from herbivores, plants have adopted several phenological strategies. One leafing strategy that protects young leaves is synchronising the timing of leaf production to the period with the lowest insect density or activity (Aide 1988; Aide 1993). Alternatively, trees may produce large synchronic amounts of new leaves that will satiate herbivores (Lamarre et al. 2014). Finally, it is common in some species that there is production of leaves in colours that are not easily seen by herbivores, the so-called 'delayed greening' (Kursar and Coley 1992). It is thought that young leaves with delayed greening are less likely to be eaten by herbivores, which may be beneficial for species where leaves take longer to fully develop. The hypothesis that young leaves with delayed greening would be more protected against herbivory has been tested and corroborated in various tropical lowland species in Peninsular Malaysia (Numata et al. 2004), Ecuador and Panama (Queenborough et al. 2013) and the Bahamas (Agrawal and Spiller 2004). Changes to the timing and length of leaf production and growth through these different phenological strategies directly affect the tree physiological processes and hence impact forest community ecology.

Tropical forests are highly valued for their unique biodiversity; in addition, they play important roles in carbon storage and climate regulation. Despite their importance, relatively little is known about the relationships between leafing phenology and climate drivers, and hence, how this process will be impacted by climate change in tropical forests. Changes to climate drivers of leafing activity could cause shifts that would lead to an imbalance between phenological strategies and herbivory. Species that start leaf flushing with the first rains of the rainy season could suffer increased herbivory damage if prolonged dry seasons delay leaf production (Aide 1993). Changes in climate drivers, such as rainfall, temperature and solar radiation, which lead to a reduction in the synchronicity of leaf production across the community, could lead to a decrease in herbivore satiation (Morellato et al. 2016). Climate drivers of leafing phenology are, therefore, an essential aspect of tropical forest ecology that needs to be considered, not only because they directly affect the carbon balance of forests, but also because they may impact tight plant–herbivory relationships. Responses to climate drivers may be dependent on species (de Camargo et al. 2018). The majority of leafing studies in tropical rainforests rely on indirect methods such as litter traps or satellite imagery. These methods capture the pattern for the whole community but are not detailed enough to disentangle patterns at a population level that can be buffered by the high diversity of tropical forests.

Leafing phenology is understudied in the Wet Tropics of Australia. We did not find any long-term (> 10 years) field-based study of leafing phenology in Australian rainforests. In other tropical rainforests, leafing has been correlated with photoperiod (Morellato et al. 2000; Wright and van Schaik 1994) and rainfall (Jones et al. 2014). Since the major climate driver is often the limiting resource, in tropical rainforests, rainfall is less expected to be the main influence. However, in the Amazon rainforest, Jones et al. (2014) found that forest leafing activity temporally adjusted to either water availability or solar radiation, depending on the resource that is less available, reducing drought susceptibility.

The rainforests found in the Wet Tropics of Australia are a hotspot of biodiversity, with a high level of endemism, and they are highly threatened by climate change (Williams et al. 2009). The climate in the region has been getting warmer, but changes in rainfall patterns are still uncertain (IPCC 2021). The forests in the region are subjected to climate extremes, such as El Niño events and cyclones. *Davidsonia pruriens* is an endemic species, an important source of fruit for frugivores, such as the Southern Cassowary (*Casuarius casuarius johnsonii*) Australia's heaviest bird (Stocker and Irvine 1983). Here, we present 18 years of fortnightly phenological observations in the wet tropics rainforest conducted by the same observer. We aimed to investigate: (i) what is the leafing phenological pattern of the species and how it is changing through time; (ii) what are the climate drivers of leafing phenology; and (iii) how leafing seasonality is being affected by climate change. To our knowledge, this is the first long-term (> 10 years) study of leafing in Australia. We discuss the results in light of expected leafing patterns at the community level and relate them to possible effects on the species ecology.

2 | Methods

2.1 | Study Site and Climate Variables

The study site is characterised by a wet season that spans from November to May, with a peak around February, often reaching more than 400 mm/month (Figure 1A). The wet season is also characterised by an increase in mean daily temperature and solar radiation (Figure 1B). The maximum rainfall amount is often found in February (565.2 ± 377.3 mm), while the lowest rainfall amount is found in Sep (45.7 ± 50.2 mm). The peak of mean temperature occurs in Nov (27.3°C ± 0.9°C), while the coolest month is usually May (22.8°C ± 1.3°C), while Dec (22.8 ± 2.0 MJ/m^2) was the month with the highest solar radiation, with the month with the least solar radiation being June (15.6 ± 1.3 MJ/m^2) (Figure 1A,B). The study region is particularly susceptible to the effects of climate change, as it experiences cyclones, El Niño weather events and heatwaves (Hughes et al. 2003; Turton 2012).

Barron Gorge National Park is located within the Wet Tropics World Heritage Area of Australia (16.84°S, 145.64°E), and is a recognised hotspot of plant and animal biodiversity (Williams et al. 2011). The park is located on traditional lands of the Djabugandji people (traditional owners), and has a vegetation composed of a closed-canopy mesophyll/notophyll vine forest (Tracey 1982). *Davidsonia pruriens*, commonly called the Davidson's Plum, is an evergreen rainforest species endemic to Northeast Queensland, Australia. It is a cauliflory species that presents pink flowers and blue fruits when ripe. Young leaves exhibit delayed greening, with leaves flushing pink. The species is a source of nutrients for frugivores, such as the flightless Southern Cassowary and the Spectacled Flying Fox.

For the analyses between phenology and climate, we used mean monthly rainfall (mm), temperature (°C), solar radiation (MJ/m^2) and photoperiod (hours of daylight). For interannual

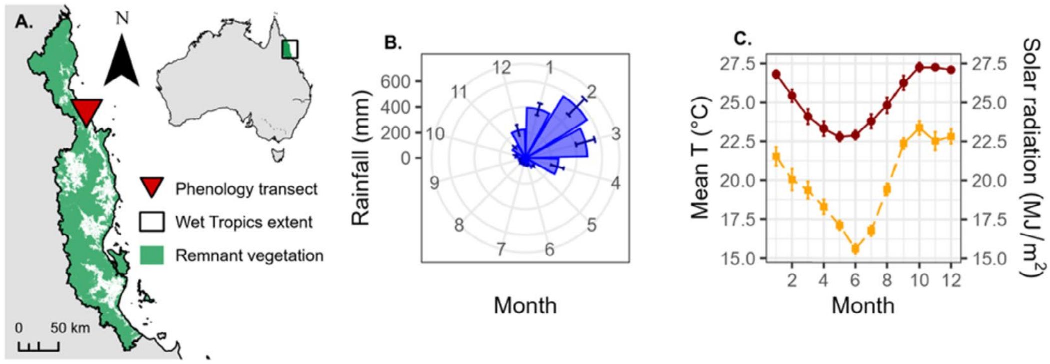

FIGURE 1 | A) Location of the study site and its cllimate data showing (B) monthly total Rainfall (mm) and (C) monthly mean temperature and solar radiation from January 1997 to December 2014 in Barron Gorge National Park, Queensland, Australia.

analyses, we also used the Multivariate El Niño/Southern oscillation (ENSO) Index (MEI) and the presence of cyclones. Climatic information for the study area was obtained from the Australian Bureau of Meteorology (BOM) for the Kuranda Railway Station weather station (BOM, Station Numbers 031036 and 031011). The weather station is located at the end of the transect. MEI was obtained from https://psl.noaa.gov/enso/mei/ (accessed in August 2024).

2.2 | Phenological Observations

Phenological observations were conducted from 1997 to 2014 using the Skyrail Rainforest Cableway gondola on a fortnightly basis, by the same observer. The Skyrail Rainforest Cableway spans a 7.5 km transect and provides unimpeded vision over the forest canopy from a distance of around 5–15 m above the canopy. The transect is divided into towers, and each tower is further divided into around 10 subtransects (depending on the distance between towers), for a total of 320 subtransects. The observer noted, for each subtransect, whether individuals of *Davidsonia pruriens* were presenting leaf flushing activity. *Davidsonia pruriens* was observed in a total of 93 subtransects. The data are part of a long-term project monitoring the reproductive phenology of the plant community, including over 200 species of trees and lianas, on a weekly basis (Vogado et al. 2022). Vogado et al. (2022) provide details on how the observer was trained to distinguish and confirm the different species.

2.3 | Statistical Analyses

All statistical analyses were conducted in R (R Core Team 2023; 12.1 + 402).

First, to better visualise the phenological behaviour of the raw rime series, we used a Savitzky–Golay smoothing filter (Figure 1A). To analyse temporal patterns, both seasonal and long-term trends, in leafing activity from January 1997 to December 2014, we used generalised additive models (GAMs) with count of observations as the response variable and week of year and total week (date) as independent variables (smoothers). GAMs are highly suitable for phenology analyses as they are able to accommodate nonlinear and nonmonotonic relationships (Wood 2017; Alberton et al. 2019; Vogado et al. 2024). We developed the models using a negative binomial family (link='logit') as the response variable is count data with a strong bias to zeros and low values. To build the GAMs, we used the package 'mgcv' (Wood 2004).

To calculate the mean date and circular parameters for the phenology, we used circular statistics. To do so, we first converted each fortnight into an angle ranging from 0° (representing the first fortnight of January) to 345° (representing the last fortnight of December). Because the season of peak leafing activity was in the wet season, in the transition between years, we rearranged the angles to start in July and end in June. We converted the angles in the results to the original dates. We calculated the following circular statistical parameters: mean angle, circular standard deviation (SD) and vector length (r), which indicates the degree of seasonality, varying from 0 (aseasonal) to 1 (seasonal) (Zar 1999; Morellato et al. 2010; please see Vogado et al. 2020; Vogado et al. 2022 for the use of circular statistics in other studies from Australia). We consider the circular standard deviation as a proxy for season length (Ting et al. 2008). To determine if phenological patterns were significantly seasonal, we used Rayleigh tests (Zar 1999). Circular analyses did not include the Year 2014 due to the leafing season being between years. We have also deleted the Year 1998 from the circular analysis due to missing data in the wet season.

To test for the relationship between leafing activity and climate drivers, we created a generalised linear model (GLM, family = negative binomial) with maximum monthly number of individual observations as the response variable, and rainfall, mean temperature, solar radiation, photoperiod and MEI as the independent variables. The negative binomial model family was chosen as the response variable is count data with a strong bias to zeros and low values. We used monthly climate variables from the current month, as well as the previous month (lag 1) and 2 months before (lag 2), since trees can take some time to respond to climate cues (Seghieri et al. 2012). We used the package 'MASS' (Venables and Ripley 2002) for these analyses. Model selection was conducted comparing the significance of variables, model fit and Akaike information criteria (AIC). All combinations of the climate variables were tested, and the full model included all abiotic variables and time lags (Table S1). To extract the marginal effects of each fixed variable, we used the package 'emmeans' version 1.10.0 (Lenth 2024). Residuals were tested using the package 'DHARMa' version 0.4.6 (Hartig 2022).

To assess the interannual influence of climate variables on phenological activity, as well as the possible influence of climatic disturbance events, such as ENSO variation and cyclones, we conducted cross-correlation analyses that allow us to test the relationship between two time series and the most significant lag (best point match) between them. Using the 'stl' function in base R, we first decomposed the phenological activity time series (split the time series into its long-term [trend], seasonal and residual components) and removed the seasonal component. We then conducted cross-correlation analysis using the 'timeSeries' R package version 4032.109 (Wuertz 2020). The influence of ENSO was modelled using the multivariate ENSO index (MEI), and cyclones were treated as a discrete event with values of 1 for months when cyclones occurred and 0 when they did not occur. Storms and heatwaves were not added as discrete events, as it was assumed that their influence would be captured by rainfall and temperature patterns, respectively.

To test for the influence of seasonality, we assigned 1 for years where there was seasonality (Rayleigh test was significant at $p<0.05$), and 0 to years where seasonality was not statistically significant. We then conducted general linear model (GLM) analysis using the binomial family (link logit) of models with seasonality as the binomial response variable and mean annual rainfall, solar radiation, temperature and MEI as the independent variables. All annual averages were calculated considering the year beginning in July and ending in June of the following year.

We calculated the length of the wet (rainy) season by counting the number of months with above 60 mm of cumulative rainfall in a sequence of more than 2 months (Van Schaik et al. 1993; Boulter et al. 2006); the first month of the wet season was taken as the first month in the previously selected sequence. We then tested for the relationship between the first month of the wet season and the length of the wet season, and the length of the leafing period (using circular standard deviation as a proxy) through linear regressions. Finally, we calculated the relationship between the annual mean leafing activity date and the leafing coefficient of variation (CV), and between the leafing coefficient of variation (CV) and year, using linear regressions. To test for changes in timing through years, we used circular–linear regressions (Pabon-Moreno et al. 2019). For the circular analyses, we used the packages 'circular' version 0.5–0 (Agostinelli and Lund 2023) and 'Directional' version 7.0 (Tsagris et al. 2024).

3 | Results

Leaf flushing was seasonal in most of the study years (1997–2014), with the exception of the Years 1998, 2005, 2008, 2009 and 2012 (Table 1). Seasonality of leafing occurred with peak activity in the wet season, with the mean date ranging from November 30th (2005) to March 26th (1999) (Figure 2A,B and Table 1). Temporal GAMs showed a peak of activity from November to February (Figure 2C). The long-term trend showed an increase in activity up until the middle of the study period (2005), but then decreased again from 2008 until the end of the study (Figure 2D).

Results from GLMs showed flushing activity had a significant positive relationship with rainfall from the 2 previous months (z-value = 2.261, $p<0.05$), mean temperature from the current month (z-value = −2.864, $p<0.01$), mean temperature from 2 months before (z-value = 4.073, $p<0.0001$) and photoperiod from the current month (z-value = 2.858, $p<0.01$) (Figure 3). Similar to the results from the GLMs, the relationship between interannual flushing activity and rainfall was significant (lag 0, $r=0.213$). The interannual cross-correlation indicates that periods with increased rainfall lead to an increase in leafing activity. The relationship between interannual solar radiation was negative (lag 0, $r=-0.314$), which is likely related to the increase in cloudiness during particularly rainy years (Figure 4). Flushing activity decreased 1 month after a cyclone (lag −1, $r=-0.147$) (Figure 4) and almost 2 years after an increase in MEI (lag −22, $r=-0.196$) (Figure 4), suggesting a negative response to El Niño events.

The GLM with binomial distribution, which tested the relationship between the probability of seasonality and annual mean climate variables, showed no significant relationship. Finally, the investigated relationship between mean annual leafing activity and the leafing coefficient of variation (CV), through linear regression, was significant. We found a significant linear negative relationship between mean annual leafing activity and year (t-value = 14.173, $p<0.01$) (Figure 5A), and a negative polynomial (two terms) significant relationship between CV and year (t-value = 14.173, $p<0.01$) (Figure 5B). There was a significant circular–linear relationship between leafing mean dates and year (estimate = −0.015, t-value = 2.01, $p<0.05$), indicating an advancement in the timing of leaf production.

4 | Discussion

This is the first study presenting a long-term (> 10-year) leafing phenology analysis in the wet tropics of Northern Australia. We found that *Davidsonia pruriens*, an important endemic species in the coastal tropical rainforest belt, has seasonal leaf production, which is tightly related to rainfall, mean temperature and photoperiod; in addition, leafing is affected by interannual extreme events, such as cyclones and El Niño events.

Davidsonia pruriens, although evergreen, presented seasonal leafing activity peaking in the wet season. In this study, we have focused on leafing activity in terms of flushing, which in this species is very characteristic due to the pink new leaf growth. This region of the Wet Tropics is classed as tropical broadleaf evergreen forest, and there should be very little seasonality in leafing activity, but our results have demonstrated that for this species in particular, the leafing activity is seasonal. A previous study (Frith and Frith 1985) over 2 years in notophyll rainforest in the southern area of the Wet Tropics also found peak leaf production in the wet season at the community level using a different method of measurement. Thus, an increase in leafing activity in the wet season does not seem to be an artefact of the phenological methods of observation being used in our study. Contrasting with this, in rainforests of Southeast Asia, leafing

TABLE 1 | Results of circular analysis of yearly leafing activity of *Davidsonia pruriens* in Barron Gorge National Park, Australia.

Year	1997	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011	2012	2013
Number of observations	16	14	51	32	48	84	89	42	74	78	67	57	74	41	16	39
Mean vector (μ)	218.232	264.614	254.166	226.895	258.209	232.553	209.211	149.81	262.62	210.153	188.946	259.357	177.62	241.312	240.202	206.513
Mean date	8th Feb	26th Mar	16th Mar	17th Feb	20th Mar	23rd Feb	30th Jan	30th Nov	24th Mar	30th Jan	10th Jan	21st Mar	28th Dec	03rd Mar	02nd Mar	27th Jan
Length of mean vector (*r*)	0.303	0.791	0.434	0.353	0.506	0.377	0.387	0.053	0.275	0.44	0.143	0.117	0.478	0.485	0.351	0.468
Concentration	0.636	2.197	0.963	0.754	1.168	0.814	0.839	0.107	0.571	0.98	0.29	0.235	1.086	1.107	0.749	1.058
Circular variance	0.697	0.209	0.566	0.647	0.494	0.623	0.613	0.947	0.725	0.56	0.857	0.883	0.522	0.515	0.649	0.532
Circular standard deviation	88.521	39.222	74.005	82.701	66.922	80.009	78.94	138.751	92.125	73.374	112.903	118.785	69.62	68.915	82.934	70.569
Rayleigh test (*Z*)	1.471	8.762	9.617	3.984	12.268	11.951	13.335	0.119	5.578	15.131	1.38	0.775	16.905	9.649	1.969	8.556
Rayleigh test (*p*)	0.233	<0.00001	<0.00001	<0.05	<0.00001	<0.00001	<0.00001	0.889	<0.01	<0.00001	0.252	0.461	<0.00001	<0.00001	0.14	<0.00001

has been found to peak in the dry season in Sumatra (van Schaik et al., 199: X. Zhang, editor, 3) or after dry spells in a bimodal pattern in Malaysia (Ichie et al. 2004). In the Brazilian Atlantic rainforest, however, leafing activity was found to also occur in the wettest period and was influenced by temperature and photoperiod in three study sites (Morellato et al. 2000). Against this backdrop, the drivers of leafing activity of *Davidsonia pruriens* sit closer to the behaviour observed in the Atlantic rainforest of Brazil.

Moore et al. 2016 investigated the EVI (enhanced vegetation index, MODIS) patterns of the Daintree tropical rainforest region located in a more northern area of the Wet Tropics; this is the same lowland forest type that occurs in the Barron Gorge. They found that the studied region in the Daintree has a constant pattern of greening, with little variation throughout the year. However, when selecting six individual tree crowns to be analysed in detail using PhenoCam imagery, they found a more dynamic variability in greening, which showed fluctuation of leaf flush and leaf fall in two of the six species. Although they did not study multiple trees of each species, the individual trees' greening pattern differed from the pattern found for the forest, supporting the idea that at forest level, population variability in leaf production might not be visible. The high richness of species in tropical rainforests may buffer patterns at the species level (Reich et al. 2004; Wright and van Schaik 1994), which may also happen with reproductive phenology (Vogado et al. 2022).

Davidsonia pruriens presents pink leaf flushes that are not expected to be photosynthetically active as they are newly formed (Vogado et al. 2020). Vogado et al. (2020) studied the delayed greening of some species from the Wet Tropics and found that species that flush in pink/red/purple have higher levels of nitrogen and use stored carbon to develop the leaves until they are photosynthetically autonomous. This might allow the species to produce new leaves when herbivores are around and active. In the Wet Tropics, herbivory is higher in the wet season, with multiple species of insect folivores reaching peak activity in the wettest months (Frith and Frith 1985). Itioka and Yamauti (2004) analysed changes in lepidopteran and leafing in Bornean tropical rain forest for 1 year and found that increased abundances of lepidopterans, both larval and adult, and herbivory damage occurred simultaneously with increases in the community-level leafing. Another study on leafing phenology and herbivory in different rainforests of Australia also found an increase in herbivory during periods of higher leafing activity (Lowman 1992). Producing large, synchronous pulses of leaves during periods of higher insect activity is a strategy presented by trees to satiate herbivores (Lamarre et al. 2014). Future climate scenarios may increase the overlap between insect and plant activity. It is expected that changes to climate patterns will disrupt leafing synchrony, preventing plants from satiating insect herbivores, which will have a great impact on plant productivity (Van Asch et al. 2007).

Our results show clear seasonality in leafing and, therefore, species seem to present a diversity of leafing patterns across the Oceania–Asia–Pacific tropical rainforest region. With peak activity in the wet season, *Davidsonia pruriens* seems to benefit from delayed greening, since it would decrease the risk of herbivory at a time when herbivores present higher activity. A

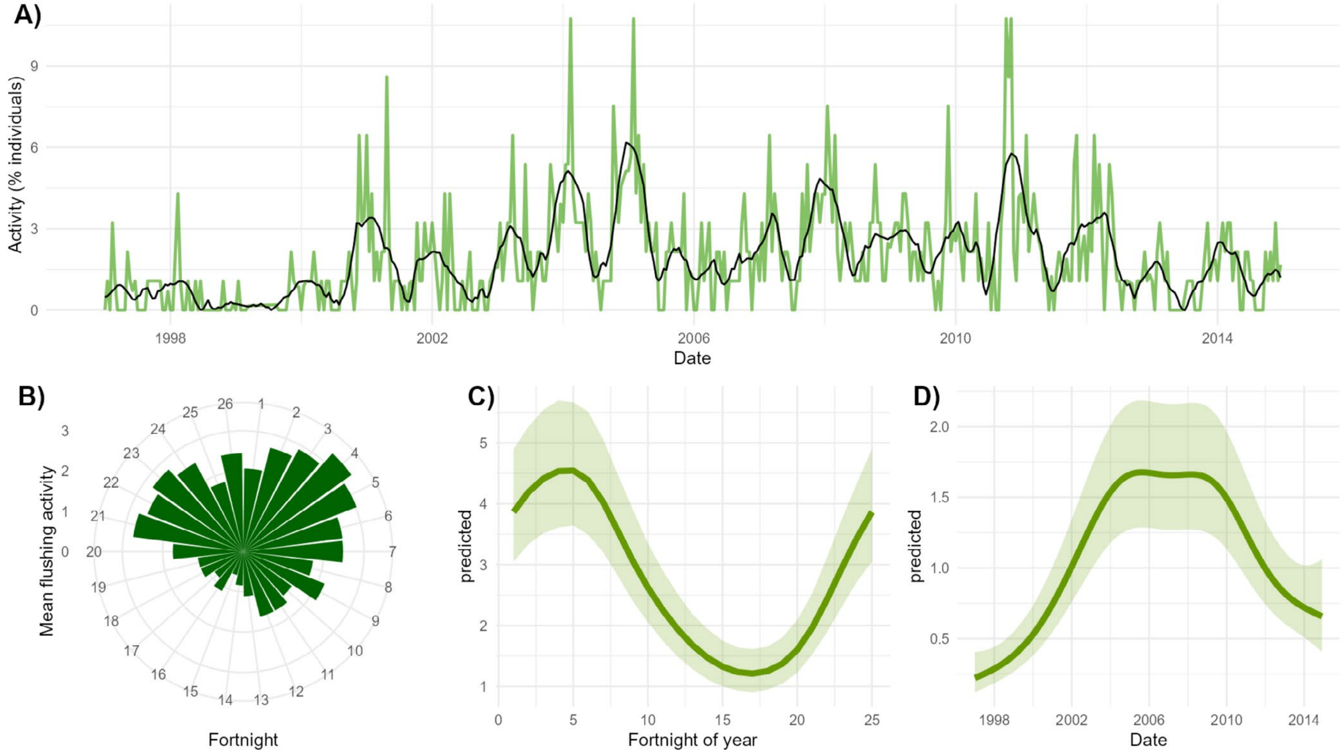

FIGURE 2 | Leafing pattern of *Davidsonia pruriens*. (A) Raw time series of fortnightly leafing activity from January 1997 to December 2014 (green) and Savitzky–Golay smoother (black); (B) Circular plot showing the mean leafing activity for the whole study period, (C) predicted GAM smoother for fortnightly leafing activity and (D) predicted GAM smoother for long-term trend in leafing activity (in fortnights).

study comparing leaf defence mechanisms and insect activity along an altitude gradient in Australian rainforests found that an increase in temperature is leading to an increase in herbivorous insects, but not to an increase in defence against herbivory found in the leaves (de Puigdollers i Balle and Martínez Vilalta 2009). At the community level, they observed an increase in the rate of herbivory of 1.3% for the mean leaf area loss and 3.7% for the damaged leaves, both per increase of 1°C. This will likely lead to an increase in leaf damage by herbivory with the warming expected in the region, therefore affecting the trees' physiology and fitness. In addition, an increase in herbivory due to increased temperature and CO_2 has been presented by Currano et al. (2008), who analysed 5062 fossil leaves from five sites positioned before, during and after the Palaeocene–Eocene Thermal Maximum. The Palaeocene–Eocene Thermal Maximum was an event of abrupt global warming connected to an increase in CO_2. The magnitude of modern anthropogenic climate change is considered to be comparable to this event (Currano et al. 2008). It is expected, therefore, that *Davidsonia pruriens*, although adapted to avoid excessive damage by herbivores through delayed greening, might still be threatened by changes in herbivory patterns resulting from increased temperatures occurring in the Wet Tropics since the region is expected to experience increasing temperatures (IPCC 2021).

Climate change may have a direct effect on the leafing activity of the species as well, since the species was significantly influenced by seasonal changes in climate. The model results showed that the species increases the leafing activity 2 months after the peak of rainfall, temperature and photoperiod, with a current decrease in temperature. The timing and level of activity of *Davidsonia pruriens* are expected to change if climate patterns change in the wet season, since our results show that the timing of leafing is tightly related to rainfall and temperature. On the interannual activity, extreme weather events are also predicted to impact the level of leafing activity. *Davidsonia pruriens* responded to cyclones, decreasing leaf production 1 month after the event. It is well known that canopy species suffer significant leaf loss after cyclones as a result of intense wind damage in this region (Turton and Dale 2007). The species also decreased leaf production after a period of almost 2 years following an El Niño event, which in Northern Queensland is correlated with decreased rainfall and increased temperature (Dyez et al. 2024). This is an interesting result as it suggests that the species could be investing in reproductive activity immediately after drought. Some species produce new leaves soon after drought, as it provides the best cost–benefit for the tree. However, some species respond to El Niño events by producing flowers in large quantities, which can cause a trade-off between reproduction and growth. This behaviour has been more often seen in forests from Southeast Asia, including Dipterocarp forests (Miyazaki 2013; Ichie et al. 2005). Because the studied species has cauliflorous flowering, it was not possible to observe flowering events from the gondola, and so we could not evaluate this relationship. Further phenology studies on the species would be warranted to further investigate these relationships.

Newly flushed leaves rely mainly on carbon uptake from other leaves, in the case of evergreen species, or stored carbon, in the case of deciduous species, to grow (Cernusak 2020). How these processes are in turn influenced by changes in timing and level

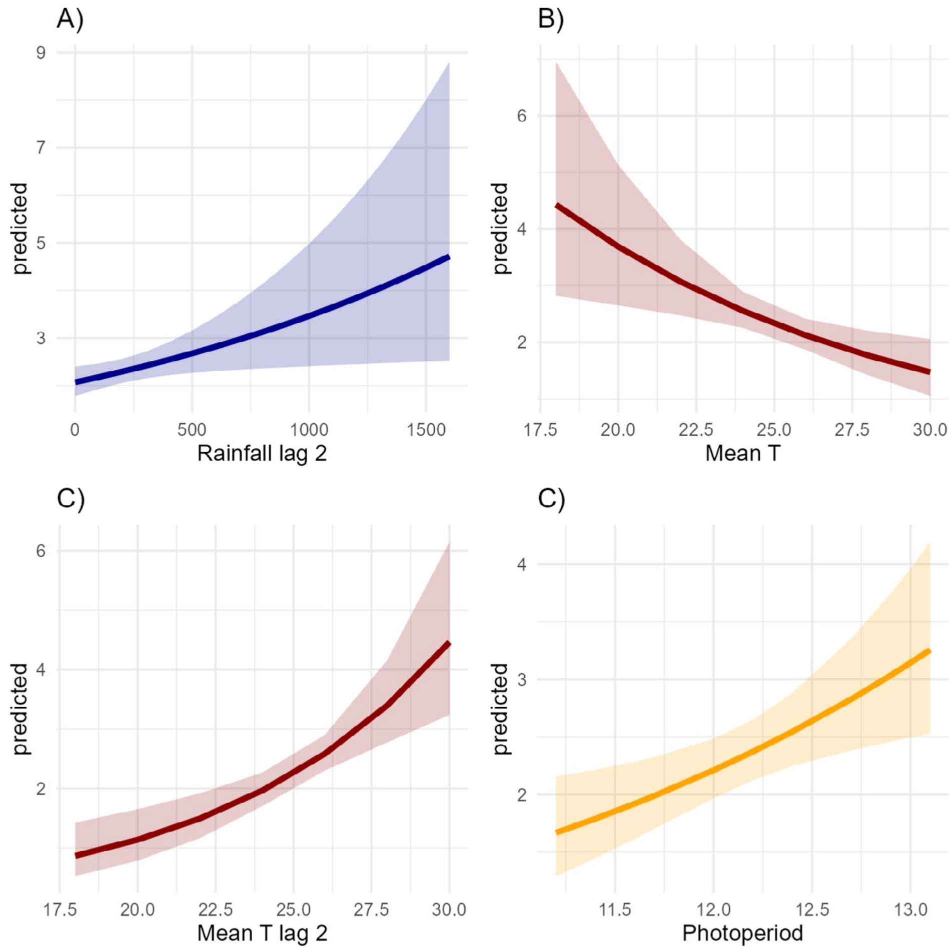

FIGURE 3 | Results of GLM testing of climate drivers of leafing activity in *Davidsonia pruriens*. Significant drivers were (A) increased rainfall from 2 months before, (B) mean temperature from current month, (C) mean temperature from 2 months before and (D) photoperiod from current month.

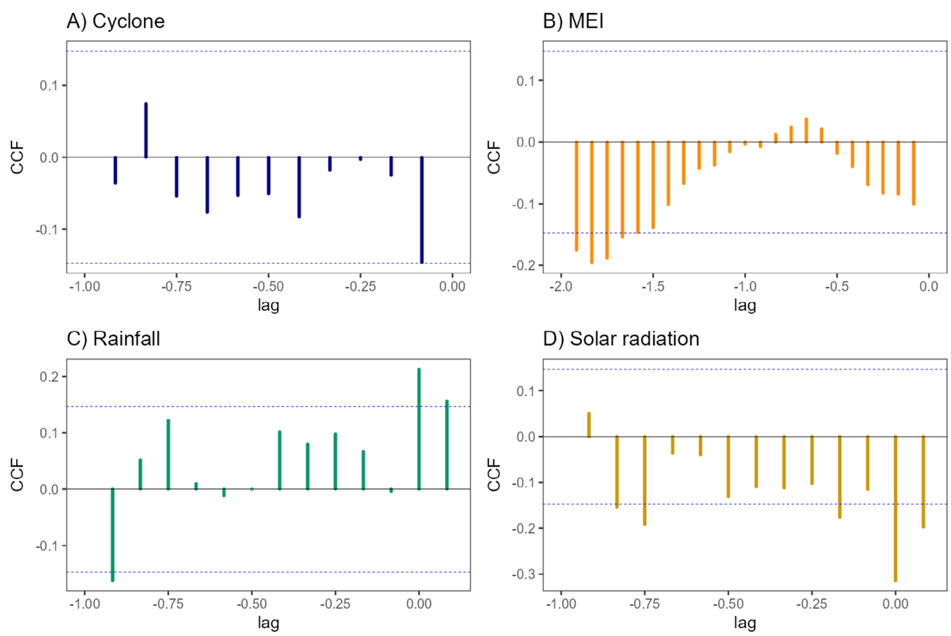

FIGURE 4 | Results of cross-correlation between long-term monthly aseasonal leafing and (A) cyclones, (B) MEI, (C) rainfall and (D) solar radiation, from January 1997 to December 2014 in the Wet Tropics of Australia, Queensland. CCF is the cross-correlation function; lag is in months.

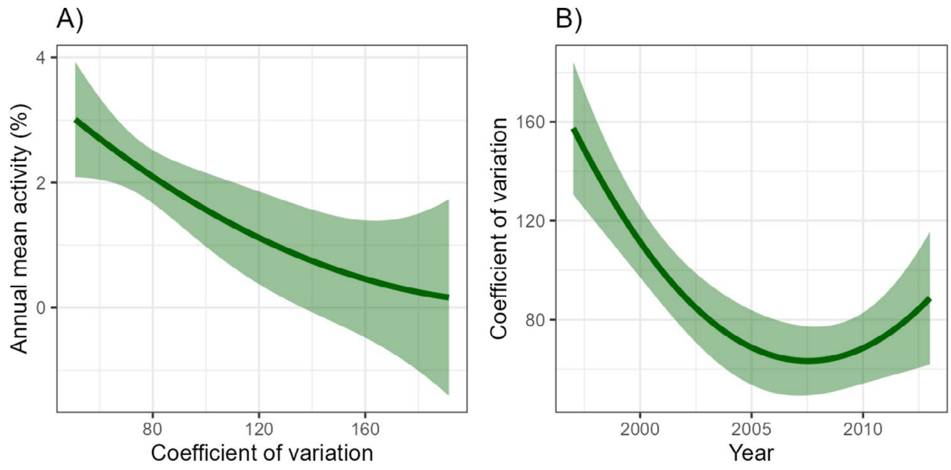

FIGURE 5 | Linear models showing significant relationships ($p < 0.05$) between (A) annual mean leafing activity and leafing coefficient of variation (CV) and between (B) leafing CV and years.

of flushing activity is unknown. Being strongly influenced by climate, *Davidsonia pruriens* appears to be susceptible to climate change effects in the Wet Tropics. Climate change effects for this region beyond increased temperature are not particularly well constrained due to the complex topography in the Wet Tropics. How changes in leafing phenology would subsequently affect the species' physiological and reproductive processes is unknown. Changes to reproductive phenology will be particularly important as this is a significant fruit resource for species such as species of flying foxes and the vulnerable Southern cassowary *(Casuarius casuarius)*.

5 | Conclusions

Without an understanding of leafing phenology at the species and population level, it is not possible to understand the detailed processes influencing tree growth and physiological processes in a forest community. The climate sensitivity of the seasonal leafing phenology that we have reported for just one species, *Davidsonia pruriens*, in the biodiverse lowland rainforest of the Barron Gorge highlights the need for more long-term phenological studies. The studied species was found to present seasonal leafing activity, peaking in the wet season, and a long-term increase in activity up until the middle of the study period, followed by a decrease. Flushing activity was significantly influenced by rainfall, temperature and photoperiod. Similarly, interannual behaviour was significantly influenced by climate variables, such as rainfall, solar radiation, cyclones and El Niño events. The seasonality was also correlated with mean dates from climate variables. As the species' leafing patterns are tightly related to climate, the species is vulnerable to climate change. Studying the relationships between leafing phenology and climate drivers may be used to identify which species' photosynthetic capabilities, and hence growth and survival, are likely to be impacted by climate change.

Author Contributions

Nara O. Vogado: conceptualization, data curation, formal analysis, investigation, writing – original draft, writing – review and editing. **Michael J. Liddell:** funding acquisition, investigation, methodology, supervision, writing – review and editing.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

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

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.