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Decoupled Litterfall and Canopy Signals Reveal Species-Specific Leaf Phenology in a Wet Hawaiian Tropical Forest

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ABSTRACT

Leaf phenology in evergreen wet tropical forests reflects diverse life history strategies. Even as forest canopies maintain year-round cover, individual species undergo distinct, asynchronous cycles of leaf turnover. Understanding the timing and drivers of leaf turnover is essential for predicting climate change impacts and informing conservation. In a wet montane forest in Hawai'i dominated by *Metrosideros polymorpha* ('ōhi'a lehua), a resource-conservative species, and *Acacia koa* (koa), a resource-acquisitive species, we investigated species- and season-specific leaf turnover. We aimed to (a) determine whether leaf litterfall timing corresponds to leaf replacement; (b) compare leaf litterfall and chemistry across species and seasons; and (c) identify species-specific environmental drivers of litterfall. Using a 12-year litterfall record, litter chemistry, machine-learning classification of PhenoCam imagery, and local climate data, we show that *M. polymorpha* exhibits continuous leaf turnover and high green canopy cover during the wet season, and a discrete senescence-abscission event during the dry season followed by leaf flush at the wet season onset. Canopy greenness did not track *M. polymorpha* litterfall, likely due to these varied seasonal dynamics. In contrast, *A. koa* leaf turnover occurred primarily during the dry season and canopy signals were tightly coupled with litterfall. *A. koa* invested more nutrients in individual leaves than *M. polymorpha*. *M. polymorpha* litterfall was best predicted by temperature while *A. koa* litterfall was best predicted by precipitation. These contrasting phenologies reflect divergent strategies and climate sensitivities, with implications for how co-occurring tropical tree species mediate ecosystem function and respond to shifting temperature and precipitation regimes.

1 | Introduction

There is growing recognition of the complex and cryptic nature of leaf phenology in evergreen tropical wet forests, wherein species exhibit diverse temporal patterns of continuous, deciduous, and semi-deciduous leafing (Albert et al. 2019;

Detto et al. 2018; Frankie et al. 1974; Piao et al. 2019; Reich 1995; van Schaik et al. 1993). However, the extent to which these varied phenological patterns in tropical wet forests are associated with variation in climate is unclear (e.g., Abernethy et al. 2018; Cook et al. 2012; Menzel et al. 2006; Pau et al. 2020; Reich et al. 2004). In contrast to seasonally dry

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tropical forests, where decades of research have synthesized links between phenology and climate (Bullock et al. 1995), this knowledge gap in wet forests persists in part from the perception that wet tropical forests are “aseasonal” or uniformly “evergreen.” This assumption largely results from different scales of analyses and variation at the individual, population, and community levels. Particularly, high diversity and continuous dense canopy cover at the community scale has made it methodologically difficult to detect distinct seasonal variation at the individual or population scale (Albert et al. 2019; Malhado et al. 2009). Yet, understanding how tropical species’ phenologies respond uniquely to climatic variability provides critical insights into how they may or may not acclimate and adapt to changes in climate (Parmesan and Yohe 2003). Such responses, or lack thereof, at the species level have the potential to shift future forest composition, shape climate feedbacks (Peñuelas et al. 2009) and alter ecological function (Forrest and Miller-Rushing 2010; Morisette et al. 2009; Pau et al. 2011; Pugh et al. 2020).

Across ecosystems, environmental drivers of leaf productivity and phenology include temperature, precipitation, light availability (including photoperiod), and vapor pressure deficit (Forrest and Miller-Rushing 2010). In wet tropical forests, seasonal variation in rainfall and light, in particular, shape patterns of leaf phenology and productivity (Alberton et al. 2023; Huete et al. 2006; Jackson 2009; Vico et al. 2017; Wright and van Schaik 1994). Alberton et al. (2023) found strong synchrony between environmental conditions, PhenoCam-derived phenology, and GPP across forest types. Pau et al. (2020) linked temperature, rainfall, and PAR with species-specific seed production and with bulk (non-specific) leaf litterfall in a Hawaiian wet forest, with leaf litterfall increasing with increased precipitation and PAR and decreasing with lower minimum temperatures. Despite these advances, long-term phenological data in wet tropical forests remain limited, and how environmental drivers vary among species with different ecological strategies is not well understood (Abernethy et al. 2018; Morellato et al. 2016).

Western science observations and remote sensing technologies provide complementary insights into local phenology and seasonality. Satellite-based remote sensing, including long-standing platforms such as MODIS, has provided foundational phenology metrics derived from vegetation indices at regional to global scales (Justice et al. 1998). Proximate remote sensing tools, such as phenology cameras, combined with machine learning, now enable higher spatial and temporal resolution monitoring of tropical phenology than periodic in situ observations, with higher sensitivity to short-term and species-specific dynamics (de Moura et al. 2017; Lopes et al. 2016; Park et al. 2019; Richardson et al. 2009). Phenology cameras take repeat digital images that can be analyzed using metrics such as the Green and Red Chromatic Coordinates (Gcc and Rcc) to monitor canopy or leaf phenology (Alberton et al. 2014, 2017, 2019; Liu et al. 2020; Richardson et al. 2009; Richardson, Hufkens, Milliman, and Frolking 2018; Sonnentag et al. 2012). Despite the increased use of phenology cameras in tropical forests (Alberton et al. 2014, 2019; Lopes et al. 2016; Nagai et al. 2016), it is unclear how well resulting canopy-derived signals reflect in situ leaf litterfall measurements and other aspects of leaf turnover (Caldararu et al. 2012).

Commonly used indicators of leaf phenology, such as canopy greenness and leaf litterfall, each capture only part of the leaf turnover process (Caldararu et al. 2012; Malhado et al. 2009; Pugh et al. 2020). Leaf turnover describes the full life cycle of a leaf from its emergence (flushing) and growth (full expansion) to senescence (aging) and eventual abscission (shedding). The rate and pattern of leaf turnover can differ by species, reflecting differences in life history and/or resource-use strategy (Chuine et al. 2000; Cleland et al. 2007; Hikosaka 2005; Reich et al. 2004). While increased leaf litterfall may occur during dry periods, without concurrent measurements of leaf flushing it is unclear whether the higher leaf litterfall reflects a net loss of canopy leaves (Reich 1995; Abernethy et al. 2018). As such, litterfall alone may not fully capture what is occurring in the canopy (Lopes et al. 2016). Canopy activity is a function of total green foliage and the quality of that foliage (e.g., nutrient content) (Chavana-Bryant et al. 2017; Wu et al. 2017). Because leaf flush and senescence may not be synchronized (Reich et al. 2004), litterfall patterns may not directly align with canopy greenness or biomass.

Interspecific differences in leaf phenology and chemistry (e.g., carbon (C) and nitrogen (N) concentration) can indicate how species allocate resources into leaf construction and function (Escudero and Mediavilla 2003; Hikosaka 2005; Reich et al. 1992; Wright et al. 2004). Species with higher leaf N and lower C:N tend to prioritize rapid photosynthetic activity and growth, whereas species with higher leaf C and lower N concentrations tend to optimize for resource retention and structural integrity (Wright et al. 2004). These strategies can influence phenology, responses to environmental conditions, and ecosystem processes such as nutrient cycling and decomposition, as both the chemistry and timing of senesced leaves affects nutrient inputs to the forest floor (Litton et al. 2020; Reed et al. 2011; Vitousek 1998; Vitousek, Turner, and Kitayama 1995).

In this study, we investigate leaf turnover in a Hawaiian wet tropical forest, focusing on two dominant, co-occurring tree species that occupy similar positions in the upper canopy but have distinct ecological and physiological strategies. Despite co-occurrence, the species differ markedly in climatic distribution, abundance, and canopy structure. *Acacia koa* (koa) is a nitrogen-fixing, shade intolerant species that typically occurs across a wide elevation gradient in mesic to wet forests and is less common in dry environments. It typically forms more open and structurally heterogeneous crowns (Pasquet-Kok et al. 2010; Bayliss et al. 2025). In contrast, *Metrosideros polymorpha* (‘ōhi‘a lehua) occurs across diverse climatic and edaphic conditions, from early successional and dry habitats to mature mesic and wet forests and is a slower-growing species that forms dense canopies in wetter environment (Vitousek, Turner, and Kitayama 1995). While both species are considered evergreen, the denser canopies of *M. polymorpha* mean that high leaf litterfall is not necessarily expected to correspond to a large net loss of canopy leaves or reduction in canopy LAI. Specifically, the aims of our study were to: (a) determine whether leaf litterfall corresponds to canopy leaf replacement; (b) evaluate leaf litter chemistry (carbon and nitrogen) across species and seasons; and (c) determine the key environmental drivers of leaf litterfall by species.

We hypothesized that the strength of the relationship between leaf litterfall and green canopy biomass would vary by species and season, with *A. koa* canopy biomass showing a stronger negative relationship to litterfall and *M. polymorpha* canopies showing a weaker relationship with litterfall (i.e., a more continuous replacement of leaves). Furthermore, we hypothesized that *A. koa* leaf turnover would be more sensitive to changes in rainfall than *M. polymorpha* because of its nitrogen-fixing, resource-acquisitive strategy and higher investment in nutrient-rich foliage. To test these hypotheses, we combined repeat camera imagery (PhenoCam), ground-collected leaf litterfall and chemistry data, and local climate data.

2 | Methods

2.1 | Study Site, Species, and Leaf Litter Collection

Leaf litter was collected at Laupāhoehoe, a tropical montane wet forest site on the Island of Hawai'i. The forest is a 4-ha plot that is part of the Hawai'i Permanent Plot Network (HIPNET; Ostertag et al. 2014), and the Smithsonian ForestGEO Network (The Center for Tropical Forest Science and Forest Global Earth Observatories CTFS-ForestGEO). The plot exists at 1155–1170m elevation off the windward coast with a canopy dominated by *Metrosideros polymorpha* and *Acacia koa* (Figure 1), two species with different canopy densities (Bayliss et al. 2025). At this site, *M. polymorpha* contributes substantially more basal area ($25.2\text{ m}^2\text{ ha}^{-1}$) than *A. koa* ($5.49\text{ m}^2\text{ ha}^{-1}$) (Ostertag et al. 2014) – important context

for interpreting species-level litterfall rates within a mixed-species canopy. Forests dominated by *M. polymorpha*, or a mix of *M. polymorpha* and *A. koa*, represent 38% of the total forest cover on the Island of Hawai'i (Asner et al. 2011).

Within the 4-ha plot, sixty-four 0.5 m^2 litter traps were distributed approximately 10 m apart in a regular grid to monitor monthly reproductive and leaf phenology, following established protocols (Wright et al. 2005). Litter collection began in October 2009; however, sampling was not continuous throughout the full study period due to logistical and resource constraints. During the initial phase of the study, bulk leaf litter samples were collected and weighed without species-level identification (e.g., data presented in Pau et al. 2020). Subsequently, we conducted post hoc species sorting on as many collection dates as possible (all samples each month were always sorted), focusing on the two dominant canopy species, *M. polymorpha* and *A. koa*. For these, we recorded leaf litter mass for each species. In total, of 78 monthly litter collections spanning this period, approximately 30% of the original collections (23 of 78 months) could be post hoc sorted to species yielding 14 wet-season and 9 dry-season collections for each species.

The dry season was defined as May–October and the wet season as November–April (Giambelluca et al. 2013; Frazier and Giambelluca 2017). Despite its classification as a wet forest, there is still variability in precipitation across the year. From August 2009 through January 2023, mean annual cumulative precipitation was $3463\text{ mm} \pm 1559\text{ SD}$ during the wet season and $2074\text{ mm} \pm 1292\text{ SD}$ during the dry season, while mean air

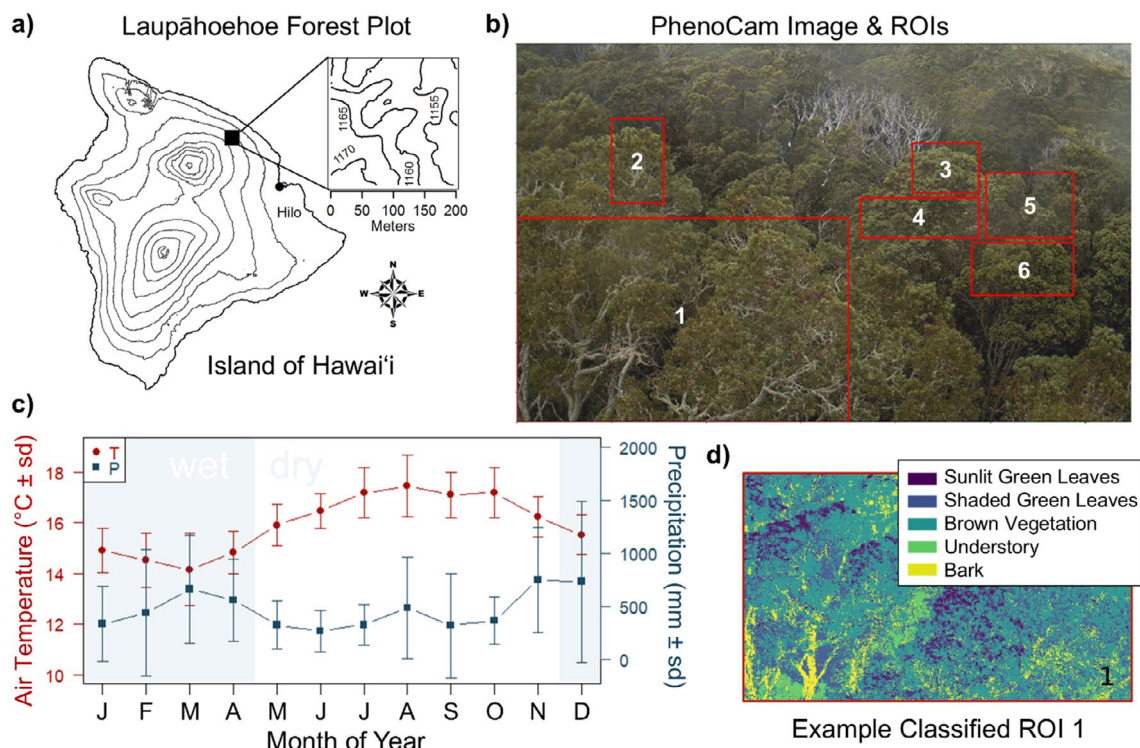


FIGURE 1 | Map of study location in Laupāhoehoe, Hawai'i (a); Cropped PhenoCam image example and six regions of interest (ROIs) used in study to represent *Acacia koa* (ROIs 1–2) and *Metrosideros polymorpha* (ROIs 3–6) (b); Average ($\pm 1\text{ SD}$) monthly air temperature ($^{\circ}\text{C}$) and monthly cumulative precipitation (mm) at Laupāhoehoe across wet and dry seasons $N=14$ except Feb, Mar, Apr $N=13$ (c); An example of classified ROI 1 from a PhenoCam image (d). The map in (a) was adapted from Ostertag et al. (2014).

temperature during the wet and dry seasons was $15.0^{\circ}\text{C} \pm 0.74$ SD and $16.9^{\circ}\text{C} \pm 0.58$ SD, respectively.

2.2 | Leaf Litterfall Rates

To estimate leaf litterfall rates ($\text{g m}^{-2} \text{day}^{-1}$) for the two dominant species, we only used intervals between consecutive collection months that had clearly recorded start and end dates. We calculated the litterfall rate as the mass of leaf litter (g) divided by the number of days between collections and total area of collected traps. Of the 23 species-sorted months, we were able to calculate 18 rates for each species, of which nine fell into the wet season, and nine fell into the dry season. For rates that were calculated over a time interval that spanned dry into wet or wet into dry seasons, we grouped those dates into the season when the litter was collected (e.g., April into May was categorized as “dry”). To compare litterfall rates between species and seasons we performed a fully factorial ANOVA test in R (version 4.4.2; “pile of leaves”).

2.3 | Elemental Analysis: Leaf Carbon and Nitrogen

We sampled a subset of 59 species-specific litter samples for %C and %N, though we ended with 58 records of %C for *A. koa*. The samples were ground, dried, and analyzed using elemental combustion and isotope ratio mass spectrometry at Florida State University as part of The National High Magnetic Field Laboratory (NHMFL). For %C, we used ANOVA to compare species and seasons, as the data met assumptions of normality and homogeneity of variance. For %N, which did not meet ANOVA assumptions, we ran a beta regression using the package *betareg* (Cribari-Neto and Zeileis 2010) in R (version 4.4.2).

2.4 | PhenoCam Green Leaf Classification

We applied a random forest model to classify green vegetation (both sunlit and shaded green leaves) from images captured by a phenology camera at the Climate Tower in Hawai‘i Experimental Tropical Forest, Laupāhoehoe, Hawai‘i (PhenoCam Network site *laupahoehoe*; Richardson, Hufkens, Milliman, Aubrecht, et al. 2018; Seyednasrollah et al. 2019). We cropped images to remove sky, horizon, and camera metadata to reduce the Fresnel effect (angular-dependent surface reflectance and glare that increases near scene boundaries) and Rayleigh scattering (atmospheric scattering of light) (Cao et al. 2021; Park et al. 2019). To preserve short-term variation while minimizing redundancy, we used a subset of images captured every 7 days (i.e., Mondays; ~12 images per day). The random forest classifier was trained using 4800 manually labeled pixels from 607 images, with a minimum of five training pixels per image. Pixels were classified into five canopy classes: (1) sunlit green leaf, (2) shaded green leaf, (3) brown (non-photosynthetically active) vegetation such as senesced leaves, fruit, or flowers, (4) bark, and (5) understory (Figure 1d). We ran the random forest classification using *scikit-learn* (Python 3.8.13), and optimized parameters with the package *hyperopt* (Version 0.2.7; Bergstra et al. 2013). The final model achieved an overall classification accuracy of

~77%, with accuracies for individual classes of 76% (sunlit green leaves), 84% (shaded green leaves), 85% (brown vegetation), 83% (understory), and 57% (bark) correctly identified (Figure S1). Misclassification rates were low between any two classes (< 5%; Figure S1c), with the most common misclassifications between sunlit and shaded leaves as bark (3.1% and 4.3%, respectively) (Figure S1c). Because bark constituted only a small fraction of total pixels (0.02%–2.0%), these misclassifications had minimal influence on results. “Sunlit” and “shaded” green leaves were combined to calculate the total number and percentage of green leaf pixels (hereafter “green canopy percentage”) within each of the six ROIs shown in Figure 1b.

ROIs were selected to capture spatial heterogeneity in canopy structure and species identity, while maintaining relatively consistent viewing geometry to minimize variability caused by illumination and distance from the lens. Because green canopy percentage was calculated relative to each ROI, values are normalized so that differences in ROI size do not bias seasonal (temporal) patterns. ROI1 was intentionally designated in the foreground to capture more canopy class variation. Visual examination of images revealed that unrealistically high percentages of green canopy (up to 100% within ROI1) were assigned to images that were less clear in misty conditions. To account for this, we examined the standard deviation of green canopy percentage for each day to identify days where images were susceptible to the issue. This allowed us to select a subset of images for each day in which ROI1 green canopy percentage fell at or below the daily median. We averaged the classification results from the remaining images and used linear regressions to evaluate relationships between green canopy percentage within each ROI and leaf litterfall rates.

2.5 | Environmental Drivers of Leaf Litterfall Rates

Climate data were collected from the climatological station at Laupāhoehoe Forest, which is maintained by Hawai‘i MESONET (<https://www.hawaii.edu/climate-data-portal/hawaii-mesonet/>). The climatological station and the plot are both situated on intermediate-aged volcanic substrates and share similar elevation, slope, and forest structure, with no evidence of major geological or edaphic discontinuities over the ~300 m separating the station and plot (Ostertag et al. 2014). The station records air temperature (Tair, °C), precipitation (P, mm), soil temperature (Tsoil, °C), net radiation (RN, W m^{-2}), soil moisture (SM, %), wind speed (WS, m s^{-1}), photosynthetically active radiation (PAR, $\mu\text{mol m}^{-2} \text{s}^{-1}$), soil heat flux (SHF, W m^{-2}), and relative humidity (RH, %). We aggregated all variables to monthly averages except rainfall, which we summed for each month. Three variable pairs were correlated with Pearson correlation coefficients above 0.70: SHF and PAR (0.74), P and PAR (−0.71), and SM and Tair (−0.74).

To investigate environmental influences on leaf litterfall rates, we fit random forest models separately for each species using the *randomForest* package in R (Liaw and Wiener 2002). We included all variables in the models for each species and assessed model performance using root mean squared error (RMSE) and variable importance using percent increase in

mean squared error (%IncMSE). Lower %IncMSE indicates that the variable has little to no impact on model accuracy, while higher %IncMSE indicates that the variable has a larger impact. We also constructed analogous linear models using stepwise AIC to identify the most parsimonious subset of environmental predictors of leaf litterfall rate using the function *stepAIC* from the package *MASS* in R (Venables and Ripley 2002) – which performed the stepwise regression in both forward and backward directions. We used both approaches to evaluate environmental influence because stepwise AIC provides interpretable coefficients, while random forest offers a flexible approach to capture nonlinear relationships, variable interactions, and to assess variable importance.

3 | Results

3.1 | Monthly and Seasonal Leaf Litterfall

The two species varied in leaf litterfall rates, with *M. polymorpha* shedding more leaf litter than *A. koa* overall (Figure 2a). *M. polymorpha* litterfall averaged $10.0 \pm 1.2 \text{ g/m}^2$ in the wet season and $15.0 \pm 2.6 \text{ g/m}^2$ in the dry season, while *A. koa* leaf litterfall averaged $3.1 \pm 0.38 \text{ g/m}^2$ in the wet season and $5.2 \pm 0.89 \text{ g/m}^2$ in the dry season (Figure 2b). Accordingly, *M. polymorpha* had a significantly higher litterfall rate than *A. koa* ($p < 0.001$), averaging $0.65 \text{ g m}^{-2} \text{ day}^{-1}$ ($237 \text{ g m}^{-2} \text{ year}^{-1}$) compared to $0.42 \text{ g m}^{-2} \text{ day}^{-1}$ ($153 \text{ g m}^{-2} \text{ year}^{-1}$) for *A. koa*. We detected no significant species $\times$ season interaction ($p = 0.20$), but both species had significantly higher rates of litterfall in the dry season ($p = 0.02$; Figure 2b,c; Table S1). After normalizing for basal area dominance (Ostertag et al. 2014), *A. koa* produces $\sim 3\times$ more litterfall per unit basal area annually than *M. polymorpha*, despite lower stand-level litterfall rates.

3.2 | Relationship Between Leaf Litterfall Rate and Green Canopy Percentage

The average green canopy percentage varied monthly and seasonally across all six ROIs, with lower values observed during the dry season months, particularly from July to September, and the highest values during the wet season, particularly in January and February (Figure 3a,b). We did not find the same relationship between the percentage of green canopy and leaf

litterfall rates for the two species. For *A. koa*, the relationship between litterfall rates and percentage green canopy was clear and consistent: the rate of litterfall was negatively related to the percentage of green canopy for both ROIs ($R^2 = 0.30$, $F(1, 16) = 6.9$, $p = 0.02$; and $R^2 = 0.29$, $F(1, 16) = 6.6$, $p = 0.02$) (Figure 3c). However, for *M. polymorpha*, only one of the four ROIs showed a significant negative relationship between the rate of litterfall and the percentage of green canopy (ROI 6; $p = 0.01$) (Figure 3d; Table S2).

3.3 | Annual Patterns of Leaf Turnover

Metrosideros polymorpha canopies exhibited peak green canopy cover in January and February, averaging about 90% across ROIs. The canopy had two large decreases in green canopy percentages across the year: one between February and March (-15.4%) and another between June and July (-9%). Despite the notable drop in February and March, the percentage of green canopy cover remained relatively high overall (above 75%) from December through May until the large decrease in June–July (Figure 4). After August, the percentage of green canopy increased again through February (Figure 4).

Despite the large drop in green canopy percentage in February and March for *M. polymorpha*, there was no simultaneous increase in brown canopy percentage. *M. polymorpha* maintained minimal brown canopy (less than 1%) from January through July (Figure 4b). There was, however, an increase in litterfall from February to March that coincided with the decrease in green canopy percentage (Figure 2a). These wet season dynamics contrast with the second large drop in green canopy percentage observed in the dry season (June–July). In this case, just following the decrease in green canopy percentage (June–July; Figures 3a and 4a), the percentage of brown canopy increases from below 1% to about 15% (brown increase: July–August; Figure 4b). This higher percentage of brown canopy remained through September before subsequently declining (Figure 4b). Immediately following peak canopy brownness, litterfall peaked in October (Figures 2a and 4) before decreasing over the wet season. These dry season dynamics mark a distinct period of leaf senescence followed by leaf flush beginning in September–October and continuing through the wet season, with the largest increase in green canopy percentage for *M. polymorpha* occurring

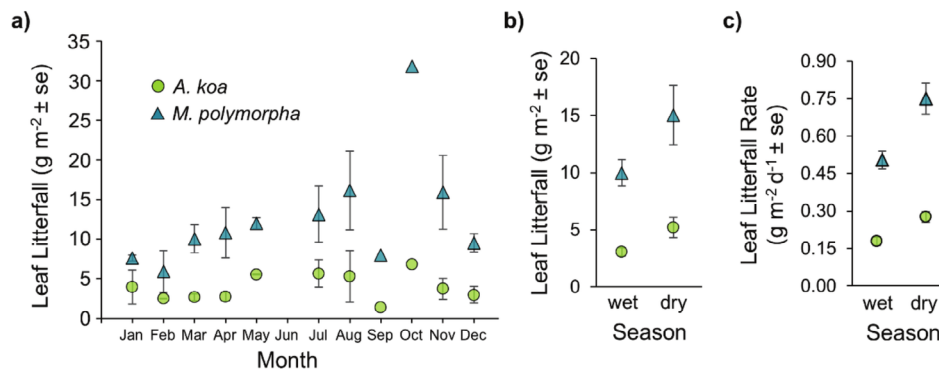


FIGURE 2 | Dominant species leaf litterfall (g/m^2) by month (a) and season (b). All months represent at least two collection years except October (based only on 2017) and September (based only on 2023); no data from June. (c) Leaf litterfall rate ($\text{g m}^{-2} \text{ day}^{-1}$) by species and season.

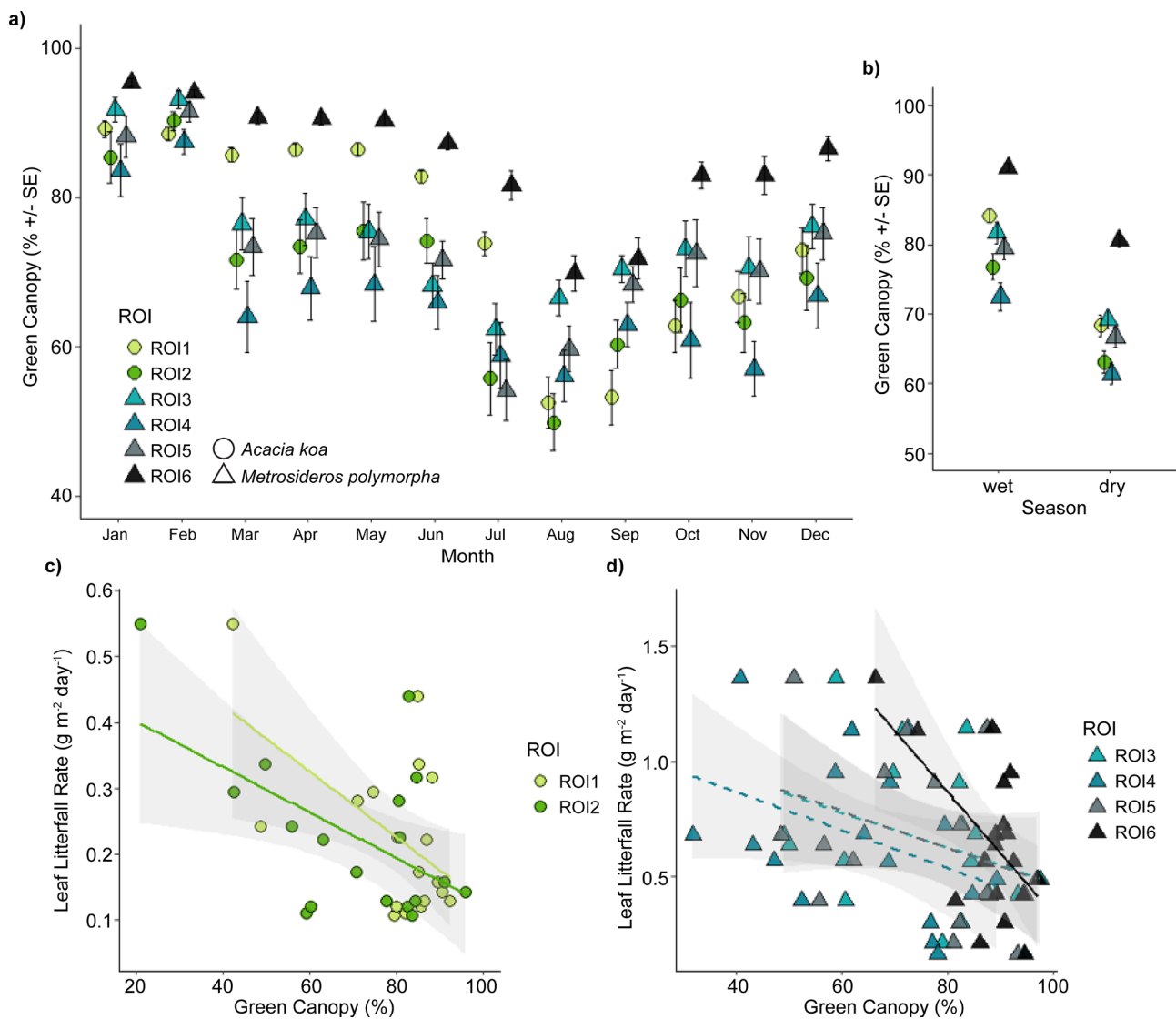


FIGURE 3 | Percent green canopy from PhenoCam images by month (a) and season (b) for *Acacia koa* and *Metrosideros polymorpha* ROIs; Relationship between green canopy percent from PhenoCam images and leaf litterfall ($\text{g m}^{-2} \text{day}^{-1}$) for *A. koa* ROIs (c) and *M. polymorpha* ROIs (d). Green canopy percentage included pixels classified as either sunlit or shaded green pixels. Points represent the average percentage of sunlit and shaded green pixels in each ROI per month (a) or per turnover period (c, d). In Figure (c, d), shaded gray regions represent a 95% confidence interval around the predicted lines, and dashed lines represent non-significant relationships.

between November and January (+22%; Figure 4). The different dynamics between leaf litterfall and canopy metrics between the two seasons for *M. polymorpha* explains the lack of a strong relationship between green canopy percentage and leaf litterfall rates (Figure 3d).

As expected, *A. koa* exhibited a strong negative relationship between leaf litterfall rates and green canopy percentage (Figure 3c). From January through June, *A. koa* maintained relatively high green canopy cover, minimal brown canopy, and steady but low rates of litterfall (Figure 4). Leaf litterfall reached an annual peak in the dry season from July through October (Figures 2a and 4c). The percentage of brown canopy increased from less than 1% to about 30% in July and August (Figure 4c), while green canopy percentage decreased sharply from about 79% in June to about 52% in August (Figures 2a and 4a). Percent green canopy peaked in February at around 89% and the largest increase occurred between December and January (+16.2%; Figure 4).

3.4 | Leaf Carbon and Nitrogen

Metrosideros polymorpha litter %C ranged from 22.5% to 54.2%, averaging 34.1% (± 5.8 SD; Figure 5a). *M. polymorpha* %C was 33.2% (± 0.88 SE) in the wet season and 35.4% (± 1.1 SE) in the dry season (Figure 5b). *A. koa* litter %C ranged from 20.4% to 47.9%, averaging 34.9% (± 5.7 SD; Figure 5a). *A. koa* litter %C was 36.3% (± 1.5 SE) in the wet season and 33.6% (± 0.9 SE) in the dry season (Figure 5b). We found a statistically significant species $\times$ season interaction in litter %C ($F(1, 113) = 4.23$, $p = 0.042$; Figure 5b). *M. polymorpha* litter %N ranged from 0.54% to 1.31%, averaging 0.87% (± 0.17 SD; Figure 5c). *A. koa* litter %N ranged from 1.0% to 6.2%, averaging 1.75% (± 0.70 SD; Figure 5c). The species differed significantly in litter %N, with *A. koa* consistently having higher %N than *M. polymorpha* ($p < 0.001$; Figure 5c,d). Seasonal differences in %N were small ($p = 0.012$) and not significantly different between species (species $\times$ season, $p = 0.22$), though monthly

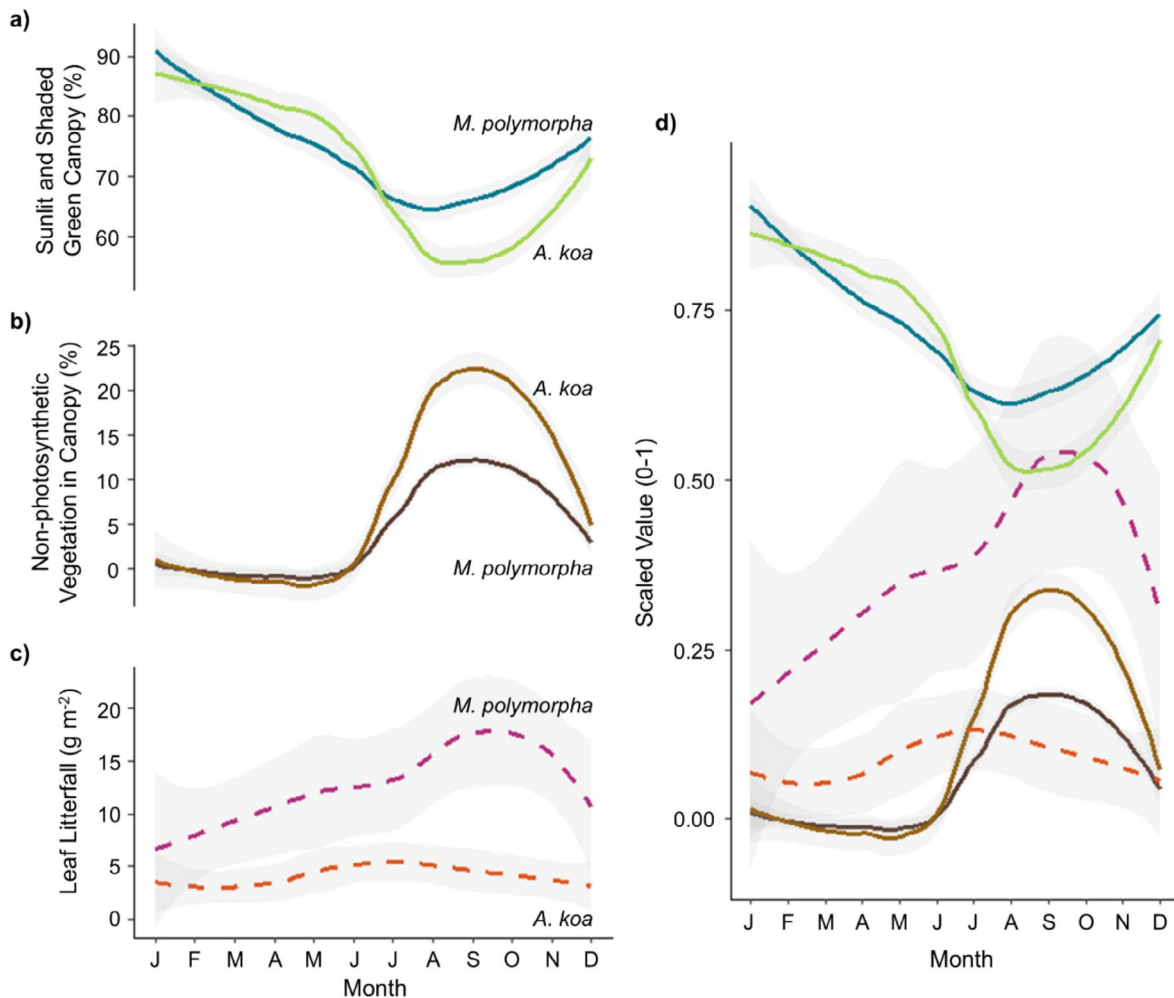


FIGURE 4 | Annual patterns of leaf turnover components including percent green canopy (a), percent “brown” (non-photosynthetic vegetation) canopy (b), and leaf litterfall (c) for *A. koa* and *M. polymorpha*. In Figure (a–c), lines represent loess-smoothed values. Shaded ribbons represent a 95% confidence interval around the loess line. In Figure (d), the same patterns from a to c are scaled from 0 to 1.

and interannual variation was evident for both %N and %C (Figure S3). Consistent with these patterns, *A. koa* litter had a lower average carbon to nitrogen ratio (C:N = 20.23 ± 0.40) than *M. polymorpha* (C:N = 39.90 ± 0.76).

3.5 | Environmental Predictors of Litterfall

Variable importance (%IncMSE) from the random forest model identified air temperature as the strongest predictor of litterfall rate in *M. polymorpha* (7.7 %IncMSE), with lower contributions from soil temperature and precipitation (3.1 and 3.4 %IncMSE, respectively) (Figure 6). Air and soil temperatures are positively correlated ($r=0.66$). Wind speed (Figure 6d), relative humidity (Figure 6e), and soil heat flux (Figure 6c) did not improve the model’s performance when included (Figure 6i). The linear regression model, selected via stepwise AIC, retained only air temperature which explained 36% of the variation in leaf litterfall rate ($R^2=0.36$; $F(1, 16)=8.93$; $p=0.009$), with a significant positive relationship between air temperature and litterfall ($\beta=0.13$, $p=0.009$; Figure 6a). The random forest model had an RMSE of 0.31 and R^2 of 0.10, and the linear model RSE was 0.28 (Table S3).

For *A. koa* leaf litterfall rate, the random forest model had a RMSE of 0.12 and an R^2 of 0.08, and the variable importance analysis showed that monthly precipitation (Figure 6b) had the highest percentage increase in mean squared error (12.2 %IncMSE; Figure 6e), followed by PAR (2.4 %IncMSE; Figure 6h,i). All other variables did not improve model performance and were not included in the final multiple linear regression model, which retained air temperature, precipitation, relative humidity, soil heat flux, and soil moisture, explaining 60% of the variation in *A. koa* leaf litterfall rate ($R^2=0.60$, $F(5, 12)=3.64$, $p=0.03$). *A. koa* leaf litterfall rate was positively related to mean air temperature ($\beta=0.067$, $p=0.01$) and soil moisture ($\beta=3.11$, $p=0.04$) and negatively related to total precipitation ($\beta=-0.0004$, $p=0.005$) (Table S3).

4 | Discussion

Our study revealed distinct species- and season-specific patterns of leaf litterfall and canopy phenology in a montane tropical wet forest in Hawai’i. Although *M. polymorpha* and *A. koa* are both considered evergreen, their leaf phenology varied in ways that were linked to different climatic factors and species-specific

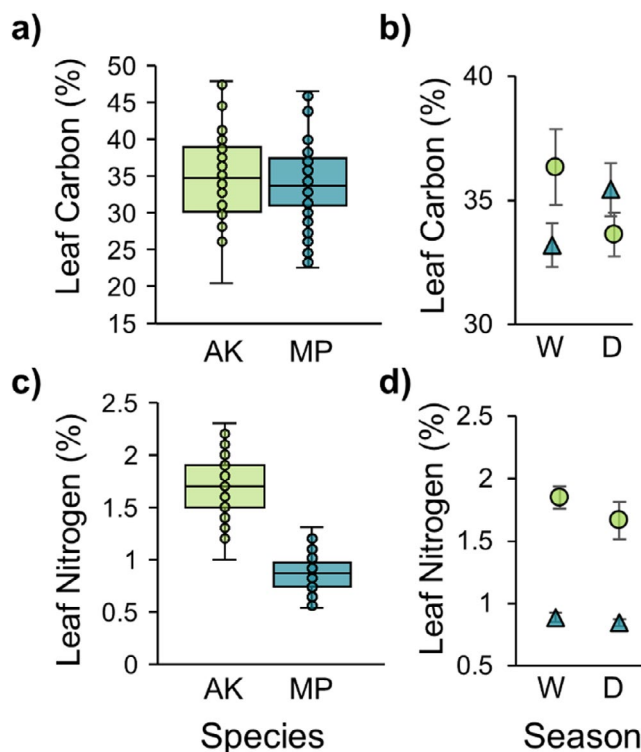


FIGURE 5 | Leaf litter carbon and nitrogen variation across species and seasons. Percent leaf litter carbon (%C) by species (a), and by species and season (b); percent leaf litter nitrogen (%N) by species (c) and species and season (d). In Figure (b) and (d), points represent averages and error bars represent standard error. In Figure (a) and (c), the box represents the interquartile range, the line inside the box represents the median.

ecological strategies. We also demonstrate that remotely sensed green and brown canopy dynamics do not consistently track leaf litterfall across species, indicating that canopy greenness alone may mask underlying turnover processes.

4.1 | Species- and Season-Specific Leaf Phenology

Metrosideros polymorpha and *A. koa* both exhibited seasonal leaf turnover patterns, shedding the most foliage during the late summer dry season. However, the timing and expression of canopy dynamics differed between species. *M. polymorpha* showed two distinct periods of green canopy decline across the year—one in the wet season and one in the dry season—whereas *A. koa* exhibited a single, more strongly expressed dry-season decline.

Despite the designation of a “dry” season, Laupāhoehoe remains perennially wet, receiving over 2000 mm of precipitation during the dry season, compared to approximately 3500 mm during the wet season. Seasonal differences are therefore better characterized by reduced rainfall combined with higher solar radiation and warmer temperatures rather than by strong water limitation. Recent work in this forest has shown that sunnier, warmer years can be more productive than cooler, wetter years, and that the temperature sensitivity of litterfall is greatest during the driest years, reinforcing the role of relatively warm conditions in amplifying canopy turnover (Lyu et al. 2021). This broader interannual climatic context is consistent with our observations that the most pronounced senescence-abscission event and subsequent leaf flush occur around the dry-wet seasonal transition.

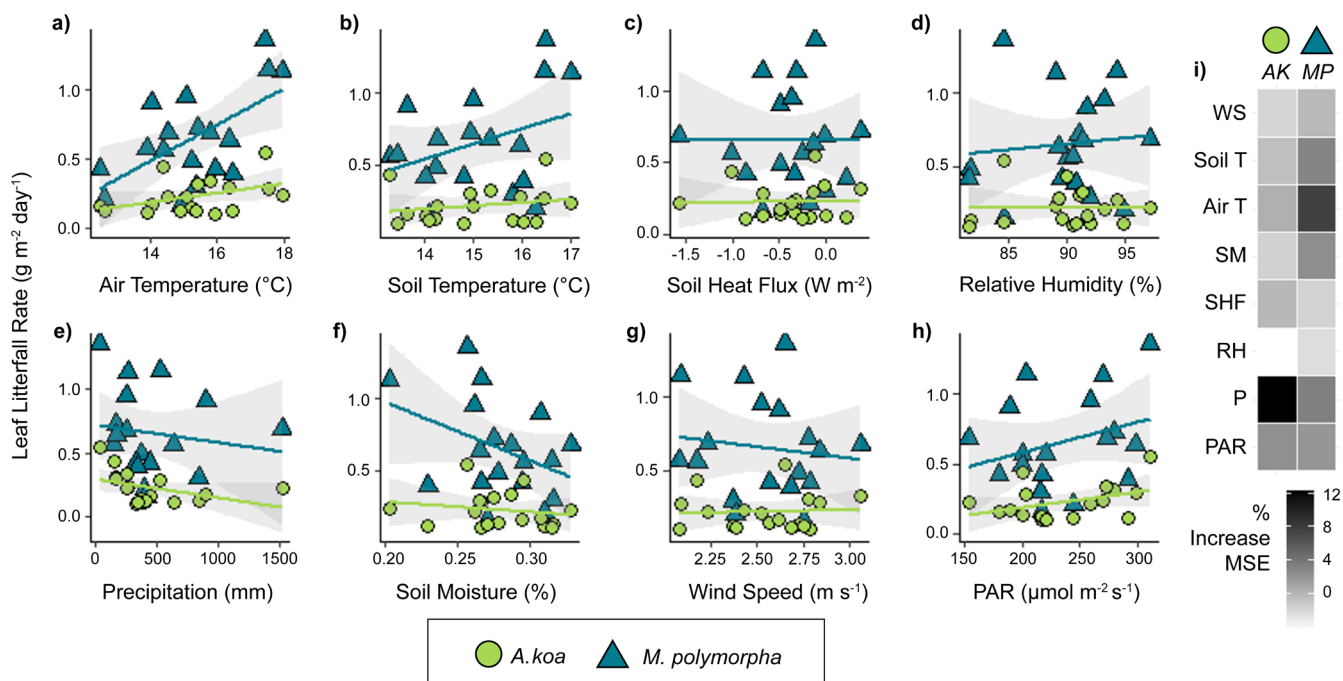


FIGURE 6 | Relationship between environmental parameters and leaf turnover by species for air temperature (°C) (a), soil temperature (°C) (b), soil heat flux (c), relative humidity (%) (d), precipitation (mm) (e), soil moisture (%) (f), wind speed (m/s) (g), and photosynthetically active radiation (PAR, μmol m⁻² s⁻¹) (h); predictor importance is measured as percent increase in MSE (%IncMSE) from random forest models for each species (i). Low or negative %IncMSE (light) indicates that the variable has little to no impact on model accuracy, and high relative %IncMSE (dark) indicates that the variable has a large impact on model accuracy.

For *M. polymorpha*, the wet-season decline in green canopy was not associated with detectable increases in brown canopy, nor did wet-season litterfall coincide with an influx of younger leaves into the canopy, suggesting little change in leaf-level photosynthetic capacity during this period (Albert et al. 2018; Wu et al. 2016). In contrast, the steeper dry season decline in green canopy was associated with a marked increase in brown canopy and subsequent litterfall peak, indicating a distinct senescence-abscission event followed by new leaf flush at the onset of the wet season. *A. koa* showed broadly similar dry-season dynamics—a decrease in green canopy with concurrent increases in brown canopy and litterfall, though peak litterfall occurred earlier than for *M. polymorpha*. Across the year *M. polymorpha* maintained a higher average rate and sharper increase in litterfall, while *A. koa* exhibited steeper changes in green and brown canopy.

4.2 | Linking Leaf Litterfall to Camera-Based Canopy Greenness

We show that peak leaf litterfall may not be synchronous with leaf flush and growth for all species in this forest. Our classification-based green canopy percentages captured *A. koa* leaf litterfall rates well (Figure 3c, Table S2), and peak litterfall occurred prior to canopy signals of leaf flush and growth (Figure 4). This coupling is consistent with expectations from the leaf economics spectrum: As a faster, more acquisitive species with shorter leaf lifespans, *A. koa* is likely to exhibit relatively rapid and seasonally coherent turnover of a large fraction of its canopy each year, producing clear canopy signals of senescence and subsequent leaf flush (Wright et al. 2004). By contrast, the relationship between canopy greenness and leaf litterfall was not as clear for *M. polymorpha* (Figure 4d). This species follows a more conservative strategy, with longer-lived leaves, such that a smaller fraction of the canopy turns over each year, leading to more diffuse canopy greenness signals despite substantial cumulative leaf litter inputs (Cordell et al. 2001). This type of variation in how leaf senescence, abscission, and flushing coincide makes it important to capture species-specific leaf turnover underlying community-level leaf phenology patterns.

4.3 | Leaf Litter Chemistry and Its Seasonal Coupling

We found distinct differences in leaf litter chemistry between *A. koa* and *M. polymorpha* that reflect their contrasting resource-use strategies. Consistent with its role as a nitrogen-fixer, *A. koa* exhibited higher litter N concentrations and lower C:N than *M. polymorpha*. Our estimates of *M. polymorpha* litter %N ($0.87\% \pm 0.17\%$) were slightly higher than those reported by Vitousek (1998) for control plots during a fertilization experiment near Laupāhoehoe ($0.73\% \pm 0.02\%$), but were still lower than *A. koa* %N. Island-wide remote sensing of *M. polymorpha* canopy traits showed a strong relationship between leaf mass per area and nitrogen, consistent with global leaf economics spectrum expectations (Seeley and Asner 2023; Wright et al. 2004). At Laupāhoehoe, increasing mean annual temperature has also been shown to alter nutrient availability and increase plant productivity (Litton et al. 2020).

Photosynthetic nitrogen use efficiency (PNUE) can decline with leaf age, particularly in species with shorter-lived leaves (Escudero and Mediavilla 2003). In *M. polymorpha*, longer leaf lifespans are associated with lower photosynthetic rates and higher C cost per C gain, suggesting a tradeoff between leaf construction cost and C uptake (Cordell et al. 2001). This pattern reflects the species' conservative position on the leaf economics spectrum, characterized by long-lived leaves with higher construction costs and lower mass-based N, in contrast with shorter-lived, N-rich leaves of more acquisitive species such as *A. koa* (Reich et al. 1992; Wright et al. 2004). In species with continuous leaf turnover, such as *M. polymorpha*, the %N of fallen leaves, together with soil N uptake rates, can further constrain new leaf production and photosynthetic capacity (Reich et al. 1992), contributing to species-specific patterns of canopy turnover and litter chemistry.

Although both species exhibited peak litterfall in the late dry season (Figure 4), the chemistry of abscised leaves varied by species and season. *A. koa* produced generally higher-quality litter, with peak litterfall coinciding with lower %C, indicating higher quality nutrient inputs into the soil in the dry season. In the wet season, *A. koa* shed lower quality leaves but dropped fewer (Figure 5). In contrast, *M. polymorpha* shed more carbon-rich, higher C:N leaves during its dry-season litterfall peak (Figure 5), potentially contributing to a denser and more persistent litter layer. These species- and season-specific shifts in litter chemistry highlight how phenological timing can alter nutrient inputs to the forest floor and, consequently nutrient cycling (Vitousek, Gerrish, et al. 1995; Litton et al. 2020). The consistently higher-quality litter of *A. koa* likely facilitates faster decomposition, consistent with previous studies showing more rapid decomposition rates for *A. koa* litter relative to *M. polymorpha* litter (Scowcroft 1986). Decomposition rates at Laupāhoehoe are also higher than many other Hawaiian forest sites (Hobbie and Vitousek 2000) and increase with higher mean annual temperatures and lower elevation for *M. polymorpha* (Bothwell et al. 2014; Giardina et al. 2014; Scowcroft et al. 2008). Together, these patterns indicate distinct tradeoffs between leaf structural investment, nutrient concentration, and leaf lifespan, with *A. koa* adopting a more nutrient-intensive, fast-acquisition strategy and *M. polymorpha* exhibiting a more conservative investment strategy paired with continuous leaf turnover (Figures 4 and 5; Hikosaka 2005; Reich et al. 1992; Wright et al. 2004).

4.4 | Environmental Drivers of Leaf Litterfall

We found that environmental drivers of leaf litterfall were both season- and species-specific, reflecting the complex ways that tropical forest species' phenology interacts with climate. Warmer conditions were associated with greater leaf litterfall rates for *M. polymorpha*—an increase of $0.13 \text{ g m}^{-2} \text{ day}^{-1}$ leaf litter per °C—suggesting temperature-driven metabolic or hydraulic limits to leaf lifespan (Table S3). These findings suggest that *M. polymorpha*, which forms denser crowns and reaches higher canopy temperatures than *A. koa* (Bayliss et al. 2025), may be particularly sensitive to temperature as a cue for leaf turnover. Our results support findings that showed *M. polymorpha* litterfall increased linearly with mean annual temperature (Litton et al. 2020) and decreased with increasing rainfall (Lyu et al. 2021). *A. koa* leaf

litterfall was best explained by precipitation: Warmer, drier conditions were associated with higher leaf litterfall (Table S3). Rather than indicating purely drought-deciduous behavior, these patterns may also reflect increased dry-season light and evaporative demand, which could promote the translocation of nutrients out of older shaded leaves, prompting senescence in favor of younger, more light-exposed leaves. Long-term climatic trends in the region provide some context for these patterns: Rainfall has decreased during the dry season at Laupāhoehoe (from 1983 to 2012; Frazier and Giambelluca 2017), such that *A. koa* may experience more frequent drought-induced leaf shedding events. In contrast, smaller decreases in precipitation have occurred in the wet season (Frazier and Giambelluca 2017).

Though we demonstrate abiotic controls on leaf phenology, biotic factors like herbivory, competition, and phenological coordination with reproductive events may also impact the timing of leaf phenology (Aide 1988, 1992; Pau et al. 2011; van Schaik et al. 1993). For instance, species may synchronize or stagger leaf flush to avoid competition or reduce herbivore pressure, as leaves produced during flushing peaks often sustain less herbivore damage than leaves produced out of synchrony (Aide 1988, 1992; van Schaik et al. 1993).

Understanding how turnover events align with these seasonal patterns is essential for predicting how future shifts in the length or intensity of wet and dry seasons will influence canopy dynamics, litter quality, and ecosystem function. The leaf flush during this time would shift the canopy towards having younger and more light-use efficient leaves going into the wet season. Other studies have shown this type of synchronization to correspond to large seasonal increases in ecosystem photosynthesis (Wu et al. 2018).

5 | Conclusions

We show that litterfall rates and canopy dynamics are not synchronous across two dominant co-occurring species, and that different climatological factors drive their phenological responses. Although both species are considered evergreen, their leaf phenology exhibited clear and distinct seasonality. In particular, *M. polymorpha* displayed a cryptic phenology that would be difficult to detect without integrating litterfall and canopy observations—a wet season decline in canopy leaves despite sustained greenness and a dry season senescence event associated with browning—both associated with increased leaf litterfall. In contrast, *A. koa* exhibited phenological patterns more closely aligned with expectations of increased litterfall corresponding to a less green canopy.

Although no “systematic phenological records” exist for tropical forests prior to the 20th century (Abernethy et al. 2018), Indigenous and local communities have long developed a deep understanding of place-based ecology, including species-specific phenologies (Hsu et al. 2023). Our findings align with Native Hawaiian (*Kanaka maoli*) traditions of observation, demonstrating that even evergreen-dominated Hawaiian wet forests exhibit clear and ecologically meaningful seasonality. *Kanaka maoli* knowledge challenges the assumption that wet forests lack seasonality, as careful observations of plant phenology and

environmental drivers are embedded in proverbs and sayings (*ōlelo no’eau*). For example, *Welehu ka malamā, liko ka ‘ōhi’a*, translates to “*Welehu* is the month [when] the ‘ōhi’a trees are putting forth leaf buds,” linking leaf flush of ‘ōhi’a lehua (*M. polymorpha*) to *Welehu* (approximately November), coinciding with the transition into the wet season (Pukui 1983; Pukui and Elbert 1986). Other sayings more directly describe seasonal environmental transitions between wet (*ho’oilo*) and dry seasons (*kauwela*), reinforcing that wet forests are not devoid of seasonality (Pukui 1983). By revealing cryptic, species-specific phenological patterns that are not always detectable through canopy greenness alone, our results support these long-held observations and underscore the value of integrating multiple ways of knowing to understand tropical forest dynamics.

Author Contributions

S.L.J.B. and S.P. conceived the study. S.L.J.B. led the data analysis and C.A. conducted image analysis. S.L.J.B. and S.P. processed samples and led laboratory analyses. All authors contributed to manuscript revisions and interpretation of results.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

Data that support the findings of this study are openly available in DRYAD at DOI: <https://doi.org/10.5061/dryad.sn02v6xmk>.

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- Regions of Interest for *M. polymorpha* (ROI 3; top) and *A. koa* (ROI 1; bottom) for each month of the year 2020. **Table S1:** 2-Way ANOVA testing effects of species and season on leaf litterfall rates ($\text{g day}^{-1} \text{m}^{-2}$). **Table S2:** Relationships between leaf litterfall rates ($\text{g day}^{-1} \text{m}^{-2}$) and percent green canopy (%). The percent green canopy includes sunlit and shaded green leaves for *Acacia koa* and *Metrosideros polymorpha* ROIs. **Table S3:** Results of stepwise regression models and random forest models of environmental variables predicting leaf litterfall. For the two stepwise regression models, if the predictor variable has a coefficient and standard error ($\text{EST} \pm \text{SE}$) in the cell, it was kept in the final model. Blank cells indicate the variable was not in the final model. Model R^2 , p -values, F values and degrees of freedom, and root squared error (RSE) are also presented. The percentage increase in mean squared error (%IncMSE) for each variable is recorded for each random forest model, along with the root mean squared error (RMSE).

Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Figure S1:** Confusion matrices and classification accuracy results for five canopy classes. (a) Per-class classification accuracies (%), calculated as the number of correct predictions for each class (true positives = diagonal values in plot (b) divided by the total number for that class (i.e., row totals from plot (b))). Darker colors and higher numbers represent higher accuracy. Confusion Matrices with (b) raw classification counts and (c) normalized to percentages. Each value represents the number or proportion of total classifications ($n = 974$) attributed to each predicted-true class pairing. Higher values and darker shading along the diagonal in (b) and (c) indicate better agreement between predicted and true. Off-diagonal values represent misclassifications, with larger values indicating more frequent confusion between the two class pairs. **Figure S2:** Whole forest leaf litterfall by month and season. (a) Whole forest leaf litterfall (g) by month; (b) whole forest leaf litterfall (g) by season. The shaded background represents the wet season, and the non-shaded background represents the dry season. Plots represent 77 months of litter collections (wet season $n = 35$ months, dry season $n = 42$ months). **Figure S3:** Yearly and monthly leaf carbon and nitrogen ($\% \pm$ standard error). Species: *M. polymorpha* (dark green triangles) and *A. koa* (lighter green circles). **Figure S4:** Example PhenoCam