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Long Term Seasonal Variability on Litterfall in Tropical Dry Forests, Western Thailand

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Abstract: Nutrient recycling is one of the most important services that supports other processes in ecosystems. Changing litterfall patterns induced by climate change can cause imbalances in nutrient availability. In this study, we reported the long-term (28-year) interplay between environmental factors and variability among litterfall fractions (leaves, flowers, and fruit) in a tropical dry forest located in Kanchanaburi, Thailand. A long-term litter trap dataset was collected and analyzed by lagged generalized additive models. Strong seasonality was observed among the litter fractions. The greatest leaf and flower litterfall accumulated mostly during the cool, dry season, while fruit litterfall occurred mostly during the rainy season. For leaf litter, significant deviations in maximum temperature (Tmax), volumetric soil moisture content (SM), and evapotranspiration (ET) during the months prior to the current litterfall month were the most plausible factors affecting leaf litter production. Vapor pressure deficit (VPD) and ET were isolated as the most significant factors affecting flower litterfall. Interestingly, light, mean temperature (Tmean), and the southern oscillation index (SOI) were the most significant factors affecting fruit litterfall, and wetter years proved to be highly correlated with elevated fruit litterfall. Such environmental variability affects both the triggering of litterfall and its quantity. Shifting environmental conditions can therefore alter nutrient recycling rates through the changing characteristics and quantity of litter.

Keywords: long term ecological research; litterfall seasonality; interannual variation

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1. Introduction

Litterfall is a fundamental ecological process that influences carbon and nutrient cycling as a result of the decomposition of aboveground litter into soil [1,2]. Litter is considered essential for the maintenance of soil fertility in terrestrial ecosystems [3,4]. The seasonality of litterfall is tightly related to plant vegetative phenology (i.e., leaf emergence, development, aging, and abscission) because most of the litterfall necromass is composed of leaves [5]. Climate change is a major driving force of variability in litterfall production, its spatiotemporal patterns, and the dynamics of productivity and nutrient balance in forest ecosystems [6,7]. Significant variables that affect litterfall dynamics include temperature [8,9], precipitation [10,11], temperature-precipitation interactions [12], photoperiod [13,14], and topography, in conjunction with soil water retention capacity [15].

By reducing relative humidity, wind can dry the soil (especially at high temperatures) and increase the VPD [16]. These conditions can increase rates of leaf and branch fall, which can be seen as adaptations to avoid transpiration water losses and cope with water stress [17]. However, litterfall seasonality varies among forest ecosystems and tree species [18,19], and can display unimodal, bimodal, or irregular patterns through time [3,20]. Climate change can also affect tree phenology by stimulating the irregular production of flowers and fruits, which in turn can increase the variability of total leaf litterfall [21,22].

Tropical dry forests (TDFs) are characterized by prolonged dry seasons [23,24]. They experience high intra-annual variations in climate and usually experience less than 100 mm during the months of the dry season [25]. Tropical dry forests exhibit distinct differences in patterns of vegetative and reproductive phenology when compared to other biomes [26]. Moreover, phenological events in TDFs are mostly caused by seasonal variations in rainfall, rather than temperature [27,28]. Strong water deficits are a crucial trigger for leaf shedding, and their peak often occurs during the dry season [20,29]. Up to 95% of leaves may be lost from living trees during the dry season [30], which causes a massive accumulation of litter necromass on the soil surface [10]. In TDFs, leaf shedding by deciduous species usually peaks during the dry season, whereas litterfall in evergreen species does not generally show any obvious seasonal pattern [20,31].

Broad variations in resource acquisition and reproductive strategies among TDF tree species could be associated with interspecific differences in phenological responses to seasonal cycles and to phase changes in the southern oscillation index (SOI) [32]. The SOI is one measure of the large-scale fluctuations in air pressure occurring between the western and eastern tropical Pacific during El Niño and La Niña episodes. Recent studies have shown that litterfall seasonality is associated with climate seasonality [5,20,33,34]. Some seasonal features of litterfall can be captured through short-term (less than 1 year) datasets with a minimal variability of 10% [5], but long-term monitoring is necessary to detect spatiotemporal variations in litterfall that are caused by interannual climate variability. Moreover, identifying the factors that govern litterfall production can help us understand more fully the response of forest ecosystems to climate change [35,36]. Most studies on litterfall production conducted in TDFs have been short-term in nature [37,38], particularly in Southeast Asia, compared to Central Africa and South America [33]. Investigations of the long-term dynamics of litterfall fractions, such as the 30-year study by Detto et al. [32], have been relatively rare [39].

In this study, we investigated interannual variation in aboveground litterfall over a 28-year period in a tropical dry forest (TDF) in western Thailand. Our objectives were to clarify (1) what climatic variables determine the seasonal variation of litterfall production and (2) investigate whether litterfall production varies over the years during long-term monitoring.

2. Materials and Methods

2.1. Study Site

The study was conducted at Mae Klong Watershed Research Station (MKWRS) in Thong Pha Phum district, western Thailand (Figure S1). Litterfall data were collected between January 1993 and December 2021 in litter traps that were placed in a 4-ha (200 m × 200 m) forest dynamic plot (FDP) of TDF. The TDF was located between 14°30′ and 14°45′ N and from 98°45′ to 99° E. The mean monthly temperature is approximately 27.5 °C, with a maximum of 39.1 °C in April and a minimum of 14.6 °C in December. The climate is affected by monsoons, and annual rainfall usually exceeds 1650 mm, most of which falls during the rainy season from April to October. The altitude of the study site ranged from 150 to 350 m a.s.l. Soil was classified as an alfisol derived from sedimentary rock, gneiss, and limestone. Topsoil was approximately 20 cm deep, and its texture varied from sandy clay to sandy clay loam. The subsoil was approximately 2 m in depth and was composed of clay. The site was moderately well-drained [40].

On the permanent plot, it is mostly covered by mature MDF, nearly 30 m tall, with some patches of deciduous dipterocarp forest (DDF) on mountain ridges and dry evergreen forest (DEF) along the creeks. The tree density was 171 individuals ha^{-1}, and the basal area was 17.2 m^2 ha^{-1}. The dominant tree species were mostly deciduous and included *Pentacme siamensis*, *Xylia xylocarpa* var. *kerrii*, and *Pterocarpus macrocarpus*. Some evergreen species, such as *Dipterocarpus alatus*, grew on the valley floor [41]. In MDF, bamboos dominate the middle layer of the canopy profile and achieve heights of 10–15 m. Fires are frequent during the dry or summer seasons [42]. Three dominant species, *D. alatus* (Dipala), *P. macrocarpus* (Ptemac), and *P. siamensis* (Pansia), which are representative of DEF, MDF, and DDF, respectively [41], were analyzed to detect seasonal variations in litterfall.

2.2. Litterfall Collection

In 1993, a 1-ha (100 m × 100 m) area within the 4-ha plot was selected for the intensive monitoring of litterfall. One hundred litter traps were arranged in a regular matrix at 10 m × 10 m spacing. Each litter trap had an opening of 0.5 m^2 (0.7 m × 0.7 m) and was created from a stainless-steel net (mesh size, 2 mm) to ensure protection from fire. Traps were set approximately 1 m above the forest floor. Litter was collected monthly over a period of 28-year between January 1993 and December 2021. Litter samples were oven-dried at 70 °C for 48 h and sorted into leaves, flowers, fruits, and other components (bark, twigs, and branches), based on the methods of [43]. Dry biomass of each component was identified by species and weighed using an analytical balance with a resolution of 0.01 g. The sum of the component dry weights was referred to as the total litterfall.

2.3. Climate Data

The daily weather data during the study period was measured locally from the MKWRS weather station and included evaporation (Evap, mm), rainfall (Rain, mm), maximum temperature (Tmax, °C), mean temperature (Tmean, °C), minimum temperature (Tmin, °C), and relative humidity (RH, %). Vapor pressure deficit (VPD, kPa), windspeed (Vs, ms^{-1}), light (light, MJ m^{-2} day^{-1}), volumetric soil moisture content (SM, %), Palmer drought index (PI, unitless), and evapotranspiration (ET, mm) were collected from the TerraClim database (URL: https://www.climatologylab.org/terraclimate.html, assessed on 7 March 2023).

2.4. Data Analysis

To characterize the temporal variability in litterfall, excluding bamboo litterfall, we calculated monthly and annual means and standard deviations for the 28-year study period. To determine the contribution of every component (leaf, flower, fruit, and other components), the respective percentages were first calculated and were then averaged to generate monthly and yearly litterfall variations as a fractional contribution to the total litter pool. Additional exploratory analyses were conducted to determine whether trends in litterfall correlated with the values of the climate variables.

The determination of underlying links between litterfall and climatic variables can have both spatial and temporal components and requires a precise understanding of the estimated "instantaneous" values of the variables [44]. As mentioned above, the interest in modeling litterfall through a generalized additive model (GAM) was primarily to detect any significant effect of environmental variables on litterfall types and to determine the potential influence of lagged environmental variables. We investigated the environmental drivers influencing litterfall components using GAM. Over the linear models, GAM has the added advantage of capturing any nonlinear temporal features in a litterfall time series and can be used to model the relationship between the mean response variable and 'smoothed' functions of the explanatory variables [45,46]. In the current analysis, we used the monthly and annual scales of resolution as fixed factors, with the Gaussian distribution as the identity link function.

Similar GAM structures were used to model monthly litterfall components as a function of environmental variables. Collinear environmental variables were identified by calculating variance inflation factors between variable pairs and were removed from the analysis. Model fits were used to examine the effects of climate variables on each litter fraction, as indicated by significant p-values (at a 95% confidence interval). We also tested the explanatory power of environmental variables at various lags, ranging from zero (simultaneous with the current litterfall month) to five months before a given litterfall measurement using a lagged GAM approach.

The lagged GAM model was used to plot the temporal variability of statistically significant environmental variables and to test whether incremental changes in the values of these variables could increase or decrease the probability of litterfall (as quantified by the odds ratio). Environmental variables during the months leading up to and during litterfall have been reported to correlate with leaf phenology in tropical forests [34]. We therefore used a window spanning the current litterfall month to five months prior to current litter production to test for significant environmental forcing. All the analyses were performed using R statistical software version 3.6.1 [47], and GAMs were modeled using the "mgcv" package [48]. All analyses were performed using R statistical software version 3.6.1 [47], and GAMs were modeled using the "mgcv" package [48].

3. Results

3.1. Climate Regime

Twenty-eight years of climatic data (1993–2021) showed that MKWRS experiences a monsoon climate with marked seasonal variations in temperature and rainfall. The average annual rainfall was 1615 ± 236 mm, and no significant temporal rainfall trend was detected. Rainfall seasonality was distinct throughout the study period (Figure S2a,b), and the rainy period generally began in late April and extended until late October. Peak rainfall occurs from July to September and accounts for approximately 53% of the annual total. The rainfall was very low from November to March, although small rainfall events (<10 mm) occurred occasionally. Depending on the intra-annual variation in temperature, three seasons could be observed in the area, namely winter (November–January), summer (February–April), and the rainy season (May–October). The cold or winter season starts in November, lasts until February, and experiences lower temperatures (15–19 °C) and significantly less rainfall. During the summer, temperatures range from 35 to 38 °C (Figure S2b).

When considering the potential climate change signature, we found that maximum and mean temperatures displayed significant decreasing trends ($p < 0.001$) over the 28-year period (Figure 1a,b). A contrasting trend was found for evaporation (Figure 1c), indicating that increased evaporation might lead to droughts in the future.

3.2. Litter Production

Total annual litter production was 9.46 ± 1.56 Mg ha^{-1} yr^{-1} (range = 6.79–12.22 Mg ha^{-1} yr^{-1}). Annual litter production varied among study years, and a slightly decreasing trend was found ($p < 0.001$, Figure 2). The greatest litterfall was recorded in 2002 (12.22 Mg ha^{-1} yr^{-1}) and the lowest in 1999 (6.79 Mg ha^{-1} yr^{-1}). The monthly variation of litterfall components is shown in Figure 3. Peaks in leaf litter and other fractions were uniformly distributed during the 28-year study period and were distributed unimodally across seasons. Flower and fruit litter production decreased when the first 10-year period (1993–2003) and the last 20-year period (2004–2021) were compared, and leaf litter displayed a slightly decreasing trend (Figure 3b,c).

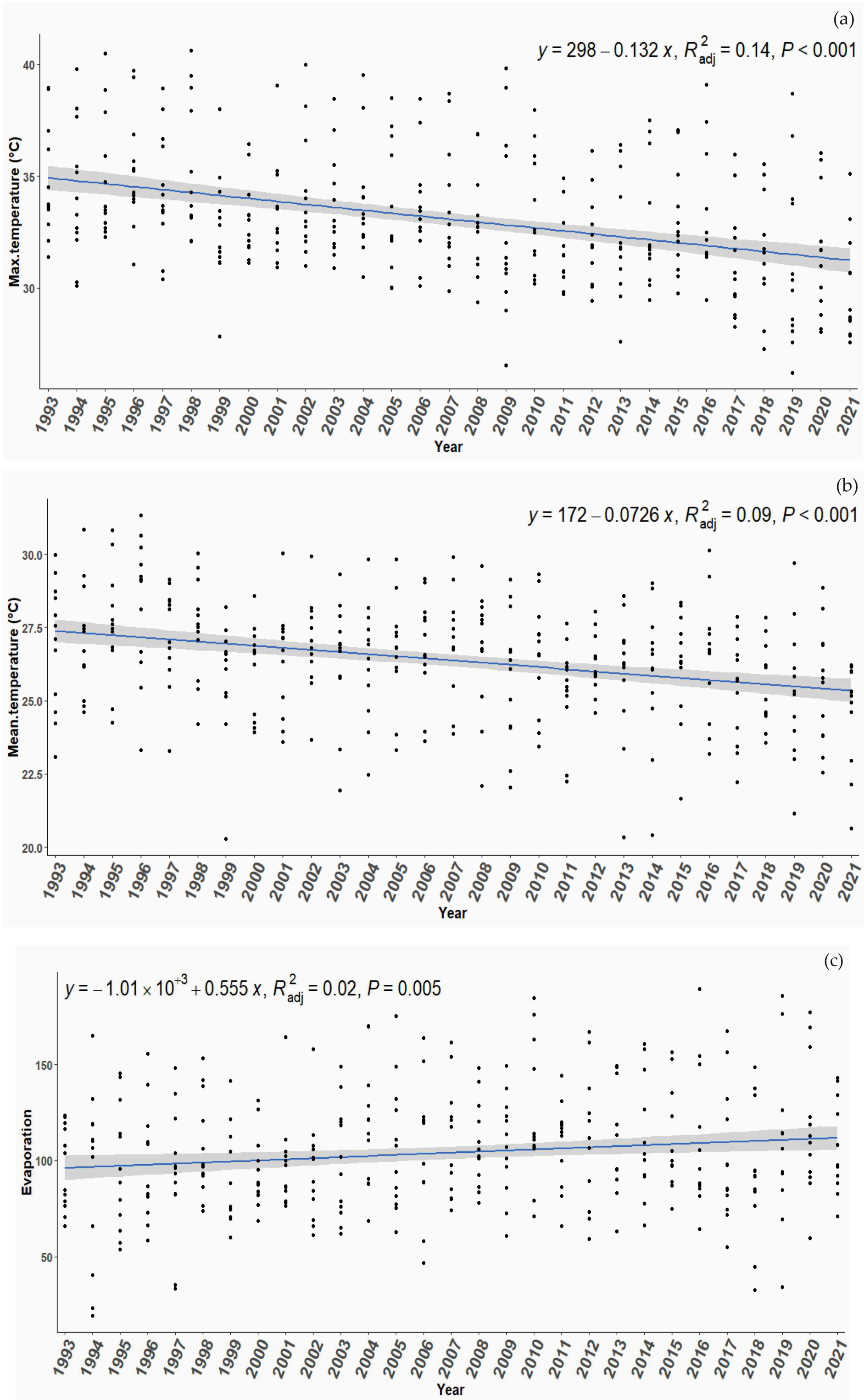

Figure 1. Trends in maximum and mean temperature (**a**,**b**) and evaporation (**c**) during 1992–2021 at MKWRS. Dots represent the monthly value of each variable.

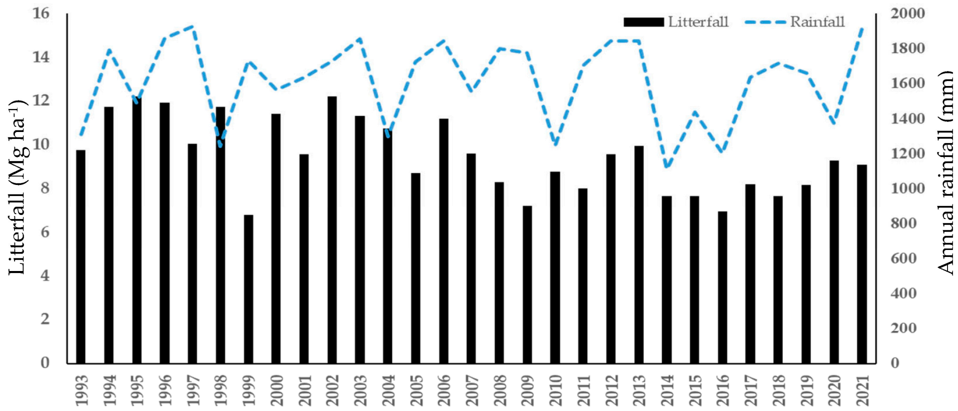

Figure 2. Annual litterfall production (bars) and rainfall (broken line) during 1993–2021 at MKWRS, western Thailand.

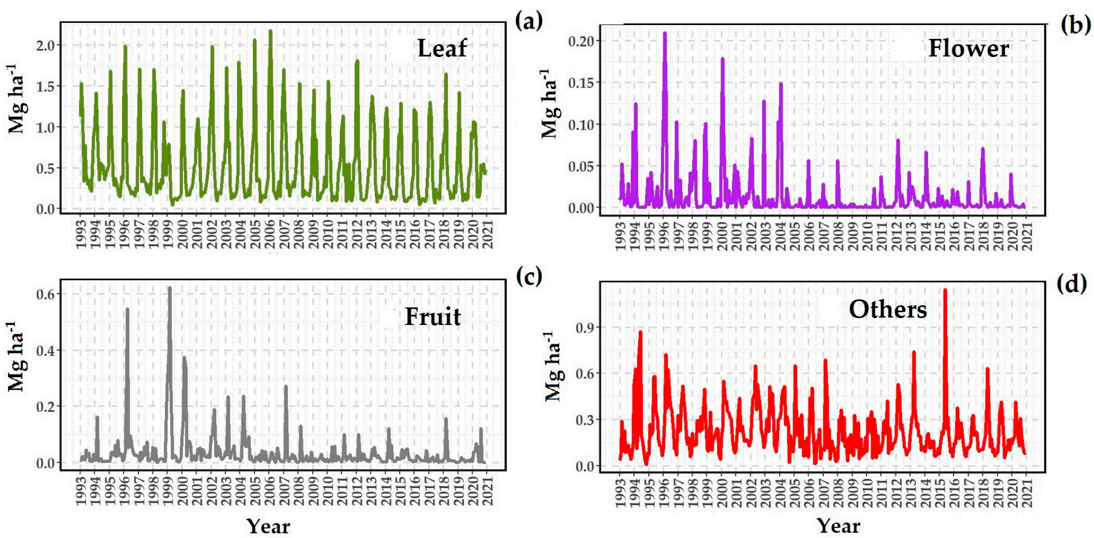

Figure 3. Variations in the four litter components (leaf, flower, fruit, and others measured in Mg ha^{-1}) during 1993–2021 in MKWRS, western Thailand.

When split into their litter components, mean leaf litterfall was 6.26 ± 1.14 Mg ha^{-1} yr^{-1}, mean flower litter was 0.16 ± 0.15 Mg ha^{-1} yr^{-1}, mean fruit litter was 0.41 ± 0.37 Mg ha^{-1} yr^{-1} for fruit litter, and other components (bark, twigs, and branches) contributed 2.63 ± 0.72 Mg ha^{-1} yr^{-1}. Leaf litter represented 67% of the total litterfall, while 26% was contributed by the category of other components. Fruit litterfall accounted for 5% of the total, and flower litterfall contributed the remaining 2%. Annual variations in the various litterfall components are shown in Figure 4a. In Figure 4b, leaf litter is shown to have reached its maximum during the cool dry season (November–February) and lowest during the rainy season (May–August). Flower litter followed a similar pattern, with peak contribution during November–February, while the contribution of fruit to the litter pool was highest between March and September, indicating that fruit fall followed flower and leaf fall. The "other" component of litter followed a similar trend to fruit fall.

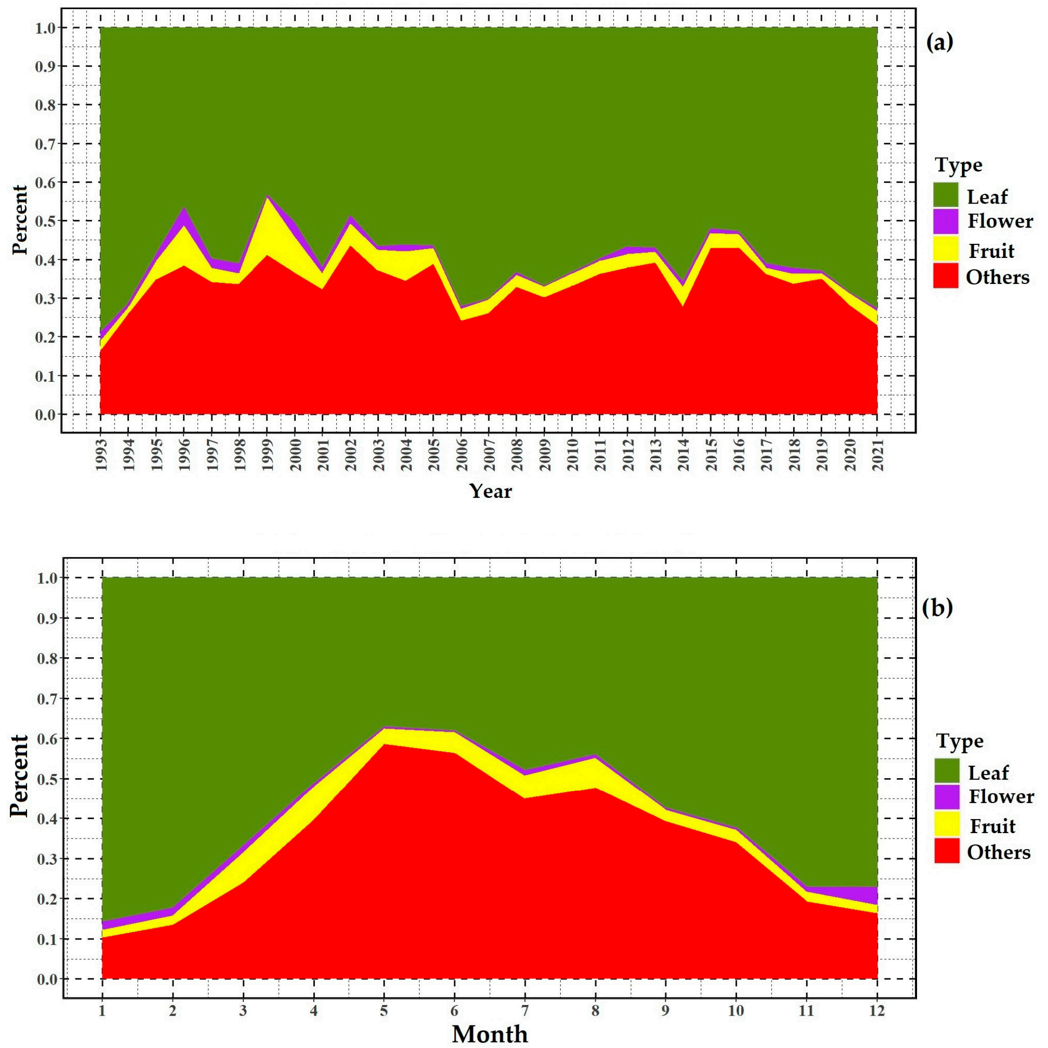

Figure 4. (**a**) Total annual and (**b**) mean monthly variations in the relative contribution to the litterfall pool by leaf, flower, fruit, and other/miscellaneous categories during 1993–2021 in TDF at MKWRS.

Litterfall trends among evergreen *D. alatus*, deciduous *P. macrocarpus*, and *P. siamensis* are plotted in Figure 5. Although temporal patterns of litterfall components varied among species, peak leaf fall for all three occurred during the cool, dry season, and only slight differences were recorded among them. Peak litterfall for *D. alatus* occurred in November, which was earlier than the peaks for other species, which took place in January (Figure 5a). Leaf litterfall was highest for *P. siamensis* (0.37 $\pm$ 0.11 Mg ha^{-1} yr^{-1}, 5.89% of total leaf litterfall), followed by *D. alatus* (0.22 $\pm$ 0.05 Mg ha^{-1} yr^{-1}. 3.58% of the total), and *P. siamensis* (0.11 $\pm$ 0.05 Mg ha^{-1} yr^{-1}, 1.77% of the total). Flowers and fruit litterfall were similar in magnitude (Figure 5b,c). Peak flower fall for *D. alatus* took place during the same period as leaf litterfall. However, fruit and flower peaks for the two deciduous species took place slightly after peak leaf fall during the hot, dry season. Fruit fall for all three species peaked during the hot, dry (March–April) season. The apparent peaks of leaf and flower fall for evergreen *D. alatus* occurred during the cool, dry season, with the fruit fall peaking two months later. However, in *P. siamensis* and *P. macrocarpus*, deciduous species, the peak leaf fall occurs two months before the flower and fruit fall.

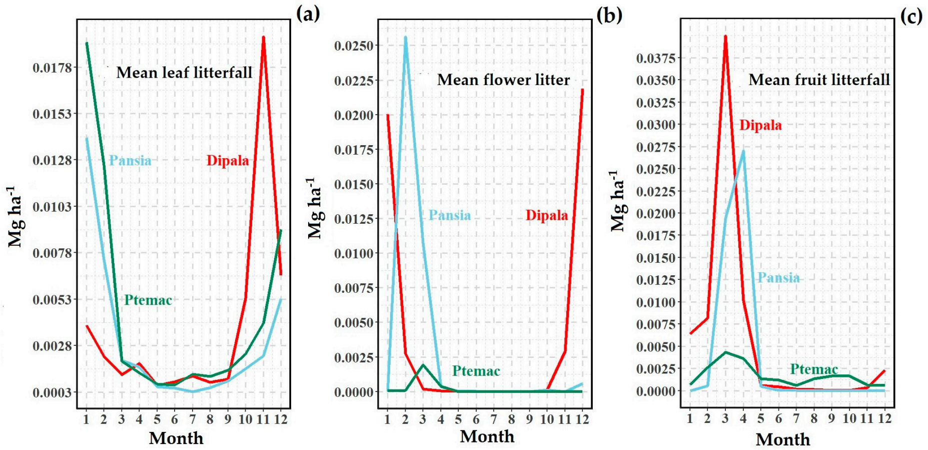

Figure 5. Mean monthly litterfall components: (**a**) leaf litter, (**b**) flower litter, and (**c**) fruit litter, for three dominant species (evergreen *D. alatus*, Dipala, and two deciduous species, *P. macrocarpus*, Ptema, and *P. siamensis*, Pansia).

3.3. Relationship between Litterfall Seasonality and Climate Change

A GAM was used to fit the litterfall components pooled across species. The major variables affecting the litterfall components are listed in Table 1, with only leaf, flower, and fruit fractions modeled. Model fits returned R^2 values between 0.64 and 0.82, with the overall deviance explained being greater than 67%. All the litterfall components displayed strong trends and seasonality, as indicated by statistically significant yearly and monthly variations.

Table 1. Results of GAM fits to litter components. The model structure includes the most significant variables indicated by the model, deviance, and R^2 values.

Litter Fraction	Model Structure	Deviance Explained [%]	R^2 [%]	Variable Significance
Leaf	Leaf.litter~f(Year) + f(Month) +f(Tmax) + f(SM) + f(ET)	83.6	82.1	Year [$p < 0.0001$ ***] Month [$p < 0.0001$ ***] Tmax [$p = 0.0293$ *] SM [$p < 0.0001$ ***] ET [$p = 0.0013$ **]
Flower	Flower.litter ~ f(Year) + f(Month) +f(VPD) + f(Light) + f(ET)	67.2	65	Year [$p < 0.0001$ ***] Month [$p = 0.03486$ *] VPD [$p = 0.00284$ **] Light [$p = 0.02393$ *] ET [$p < 0.0001$ ***]
Fruit	Fruit.litter ~ f(Year) + f(Month) +f(Light) + f(Tmean) + f(SOI)	67.2	64.9	Year [$p < 0.0001$ ***] Month [$p < 0.0001$ ***] Light [$p = 0.001668$ **] Tmean [$p < 0.0001$ ***] SOI [$p < 0.0001$ ***]

Significant codes: *** < 0.001; ** < 0.01; * < 0.05.

The lagged GAM showed that leaf litterfall was influenced by SM, ET, and Tmax (Figure 6 and Table 1). Figure 6 demonstrates how the effect of these significant environmental variables changed at lags of 0–5 months. The strongest influence was exerted by SM, which had a statistically significant positive effect on litterfall one and two months prior to collection (with a u-shaped functional relationship) for values between 0.25 and 0.35. However, SM measured four months before litter collection was associated with reduced leaf shedding. Other lags failed to exhibit statistically significant relationships with litter fractions, as indicated by odds ratios < 1. Elevated levels of ET at lags of 3–5 months were associated with greater litterfall. However, high ET values at lags of 1–2 months were associated with reduced leaf litterfall.

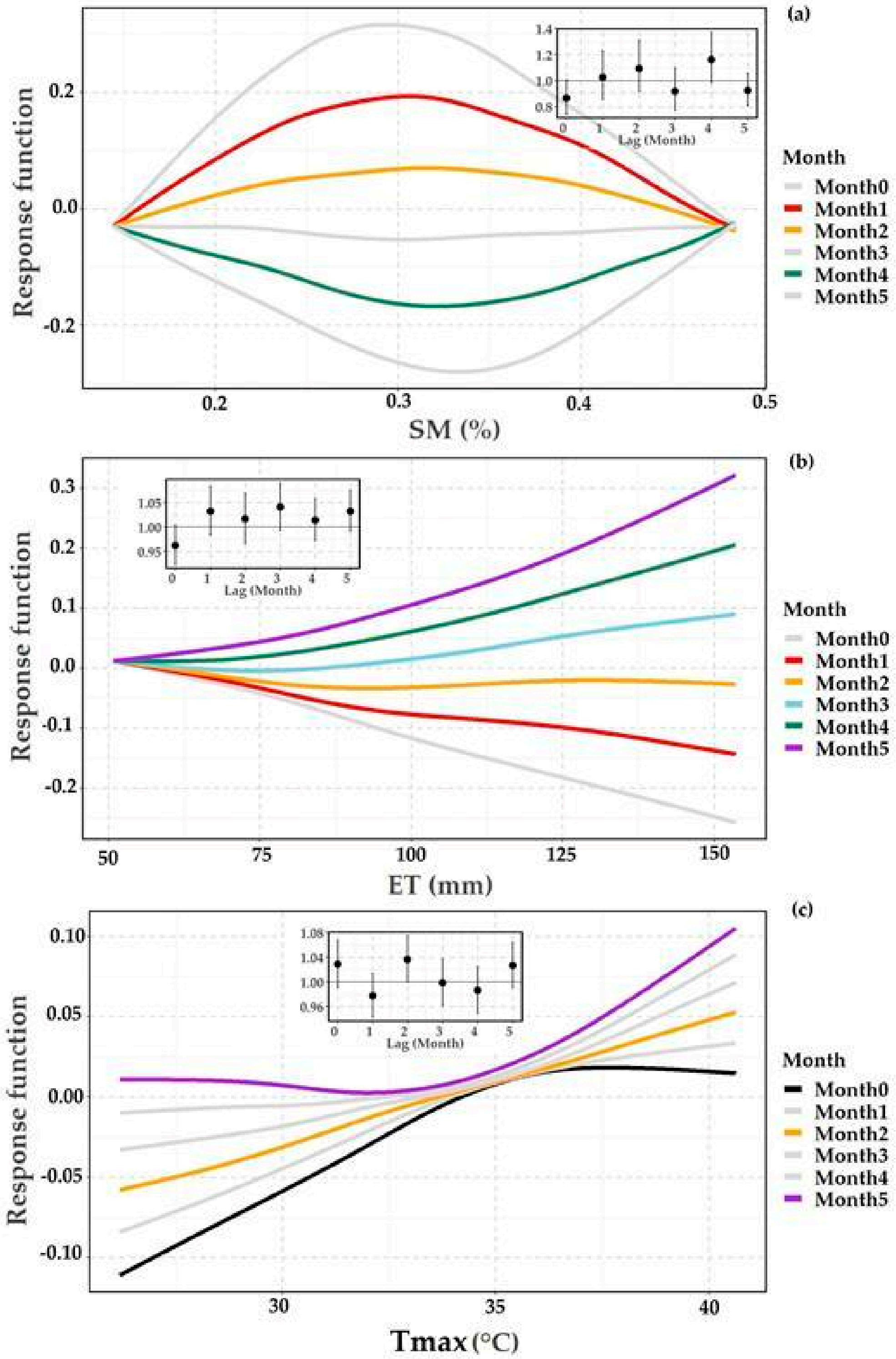

Figure 6. Estimated lag effect variations in the most significant environmental variables on leaf litterfall: (**a**) SM, (**b**) ET, and (**c**) Tmax. The inset indicates the effect of an incremental change in the respective environmental variable on either increasing or decreasing the chances of leaf litterfall. Incremental changes in 0.1, 10 mm, and 1 °C were used for SM, ET, and Tmax, respectively. The lagged variables plotted in gray on the larger graphs indicate nonsignificant changes in litterfall as determined by odds ratios in the inset graph.

The effects of Tmax at different lags were divided around temperatures above and below 35 °C. Lags over 1–4 months appeared to display a more linear relationship with litterfall. Tmax > 35 °C at lag zero did not cause significant litterfall, while the same temperatures at lags of five months may have increased litterfall. Values of Tmax at a lag of two months had a positive linear effect on leaf litterfall. Overall, Tmax > 35 °C appears to promote litterfall and high ET (>100 mm), which could be balanced by SM values between 0.25 and 0.35, which could ensure adequate water uptake.

Flower litterfall was influenced by ET, VPD, and light (Figure 7 and Table 1). Evapotranspiration exerted the strongest effect on litterfall and appeared to promote leaf litterfall at lags of 1–2 months. However, at ET values of 75–140 mm, lags of two months were associated with double flower fall. The effects of VPD were oscillatory, with lags of 3–4 months being different from lags of 1 month. Normal air dryness is characterized by VPD values of 0–2 kPa, with higher values indicating greater relative drought. We observed that VPD values of 0.8–1.1 kPa and >2 kPa were associated with increased flower litterfall, while VPD values of 1.3–1.6 kPa were associated with reduced flower litterfall. A VPD > 2 kPa would result in increased litterfall at all lags tested in the model. Available light between 17–21 MJ m^{-2} day^{-1} was associated with increased flower litterfall at lags of 1–3 months. Overall, flower litterfall in the study of the forest was associated with ET between 75 and 140 mm, VPD of 0.8–1.1 kPa, and light levels of 17–21 MJ m^{-2} day^{-1}. Such conditions are very specific relative to the leaf fall, given that peak leaf and flower falls occur during the cool, dry season.

The GAM analysis showed that fruit litterfall was influenced by SOI, Tmean, and light (Figure 8 and Table 1), with the effects of SOI having a highly cyclic pattern. Values of SOI > +8 (indicating wet years or La Niña) and −8 (indicative of dry years or El Niño) increased fruit litterfall at most lags, with most of the fruit litterfall promoted by La Niña (wet) events. The effect of Tmean was comparatively stable and monotonically increased fruit litterfall at temperatures of 20–35 °C at lags of 0–1 month. However, increasing Tmean at lags of 3–5 months tended to reduce fruit litterfall. The influence of light was also oscillatory in nature, with values between 16 and 21 MJ m^{-2} day^{-1} at lags of 0, 2, and 5 months tending to increase the fruit litterfall. A shift in the peak light intensity affecting litterfall was also observed at 19 MJ m^{-2} day^{-1} at a zero lag and 17.5 MJ m^{-2} day^{-1} at lags of 4–5 months. In summary, fruit litterfall was influenced by oscillatory SOI and light, accompanied by a monotonically increasing Tmean.

Yearly plots of SOI and fruit litterfall for individual species (Figure 9a) indicated that the peaks in fruit litterfall were significantly correlated ($p = 0.009$) with La Niña (>+8 or wet) and El Niño (<−8 or dry) events. Neither leaf nor flower litterfall responded in this way. The greatest values of peak fruit litterfall were found during La Niña, particularly the 1999–2000 and 1995–1996 events. Fruit production in the MDF was therefore promoted under wet conditions, while fruit formation may have been inhibited by dry conditions during La Niña events, particularly the dry years of 1997–1998. SOI apparently had no significant effects on fruit litterfall for selected species, however, some variational trends were found (Figure 9b). A high necromass of fruit litterfall in *D. alatus* was mostly found during the dry El Niño years of 2003 and 2007, which contrasted with the peak fruit litterfall in *P. siamensis*, which occurred during the La Niña years of 1996, 2000, and 2008. Contrasting with both of these species, *P. macrocarpus* exhibited a constant production of fruit litterfall.

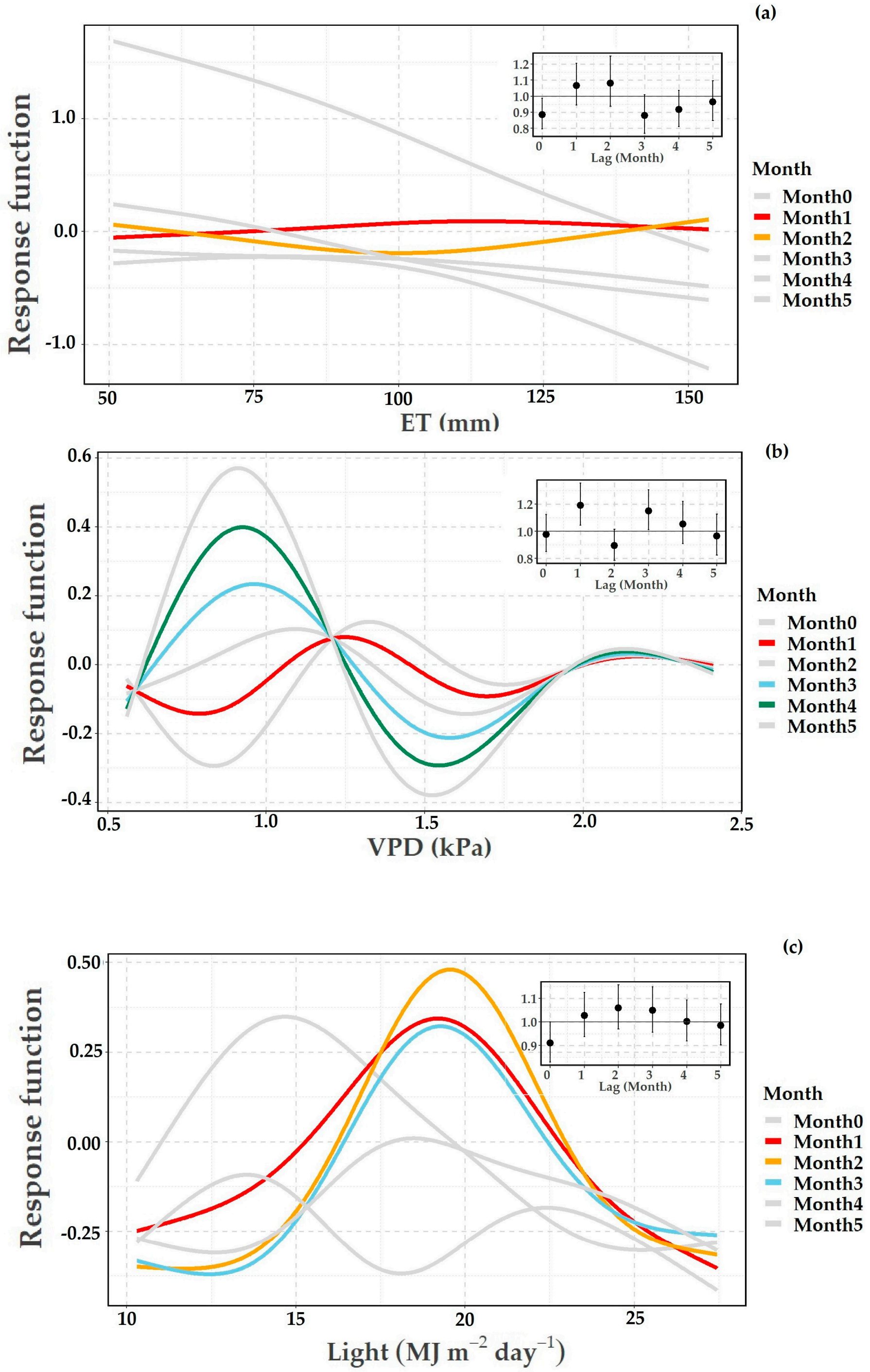

Figure 7. Estimated lag effect variations among statistically significant environmental effects on flower litterfall: (**a**) ET, (**b**) VPD, and (**c**) light. Insets indicate the effects of an incremental change in an environmental variable on the probability of flower litterfall. Incremental changes of 10 mm, 0.1 kPa, and 1 MJ m^{-2} day^{-1} mm were used for ET, VPD, and light, respectively. The lagged variables plotted in gray (in the main graph) indicate a nonsignificant change in litterfall, as determined through the odds ratios in the inset graph.

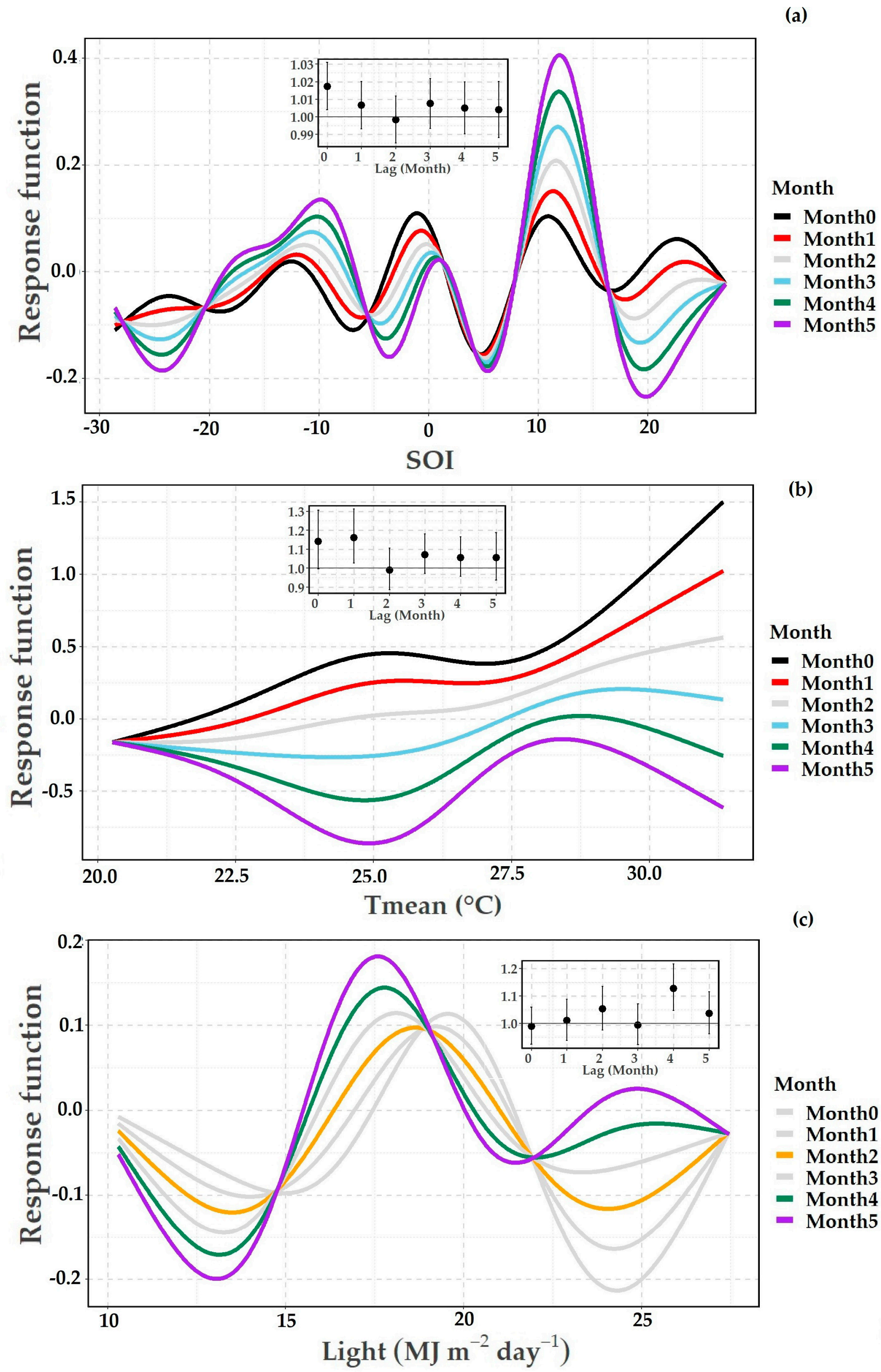

Figure 8. Estimated lag effects of the most significant environmental influences on fruit litterfall: (**a**) SOI, (**b**) Tmean, and (**c**) light. Insets indicate the effects of an incremental change in a given environmental variable on either increasing or decreasing the chances in fruit litterfall. Incremental changes of one unit, 1 °C, and 1 MJ m^{-2} day^{-1} mm were used for SOI, Tmean, and light, respectively. Lagged variables plotted in gray (in the main graph) indicate nonsignificant changes in litterfall, as determined through the odds ratios in the inset graph.

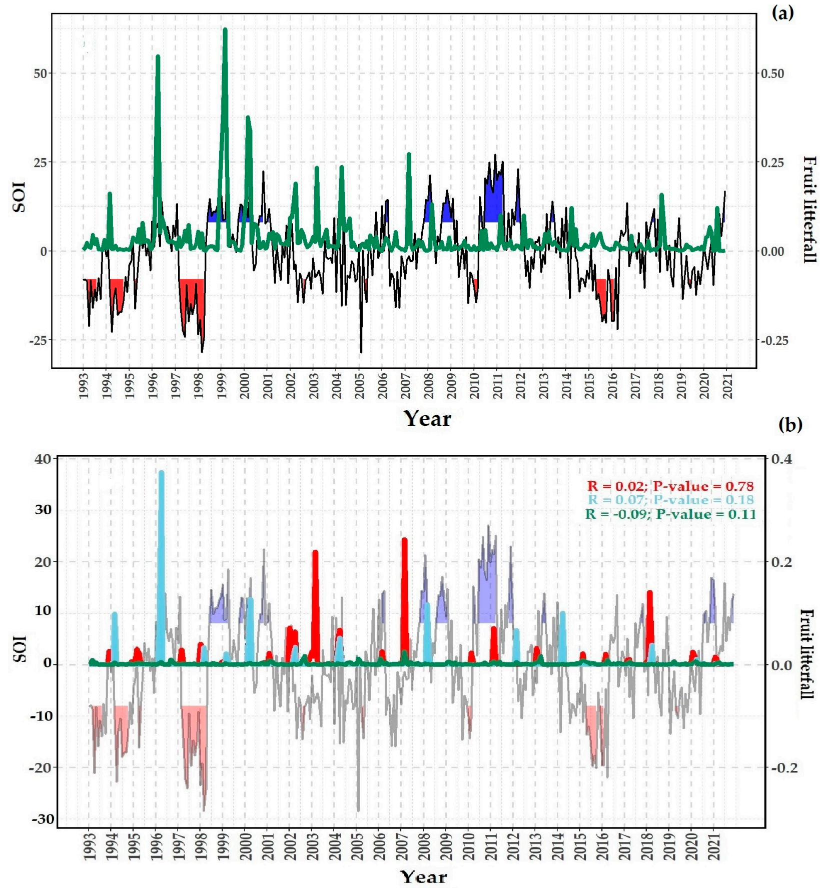

Figure 9. (**a**) SOI (black) and fruit litterfall (green) during the study period, and (**b**) fruit litterfall of *D. alatus* (red), *P. siamensis* (blue), and *P. macrocarpus* (green). The La Niña (>+8 or wet) and El Niño (<−8 or dry) events are shaded in blue and red, respectively.

4. Discussion

In this study, we studied the variability of litterfall components using 28 years of litter trap data in a TDF in western Thailand. We estimated litterfall necromass and the intra- and interannual distribution of necromass in leaf, flower, and fruit components, as well as seasonal patterns, together with a set of meteorological variables that had the potential to influence litter production. The use of such long-term datasets can help identify possible patterns of climatic influence over litterfall production [33,49].

4.1. Annual Litterfall Production and Seasonality

Tropical forests usually produce more litter than other terrestrial biomes [50]. In this study, we found that annual litterfall production ranged from 6.79 to 12.22 Mg ha^{-1} yr^{-1}, with an average value of 9.46 ± 1.56 Mg ha^{-1} yr^{-1}. These values are generally higher than litterfall production measured in other TDFs, which ranged from 3.8 to 7.7 Mg ha^{-1} yr^{-1} in previous studies [27,38,51–54]. However, our measurements were slightly lower than those reported for humid tropical forests, such as lower montane forest in Thailand (Marod et al. [8]; 9.43–12.22 Mg ha^{-1} yr^{-1}), primary humid forest in Amazonia (Barlow et al. [9]; 9.4–12.4 Mg ha^{-1} yr^{-1}), and old-growth upper montane forest in Costa Rica (Köhler et al. [55]; 12.27–13.49 Mg ha^{-1} yr^{-1}).

Relative to tropical moist forests, there is a distinct seasonality of litterfall production in TDFs, and most litterfall takes place during the dry season [9,22,55–57]. Overall litter production is similar in TDFs and tropical moist forests [58]. As in previous studies, our results demonstrated clear seasonal litterfall patterns with major peaks during the dry season and significant yearly and monthly variations (Table 1). The leaf litterfall fraction was the major component of litterfall production and comprised approximately 67% of the total (Figure 5). These values were broadly comparable to the 60%–76% reported for forests worldwide [50]. The maximum leaf contribution was found during the cool, dry season (November–February) and reached its minimum during the rainy season (May–August). A similar pattern was found in the flower litterfall, while fruit litterfall followed flower litterfall.

It is notable that deciduous tree species in a given habitat can differ dramatically in their timing of leaf emergence and abscission compared to evergreen species [59]. In our study, the temporal pattern of litterfall components varied among three selected species (Figure 5). Although the peak of leaf litterfall mostly occurred during the cool dry season (November–January), evergreen *D. alatus*, which was found along the banks of a creek running through the permanent plot, shed its leaves 1–2 months earlier than deciduous *P. macrocarpus* and *P. siamensis*.

4.2. Relationship between Litterfall Seasonality and Climate Change

Environmental factors can produce either delayed or instantaneous responses in actual litterfall, being influenced by a complex interaction of biotic and abiotic variables [60,61]. In addition, climate change may exert an important influence over litterfall dynamics, even in evergreen species [51,62]. Rainfall, temperature, wind speed, relative humidity, and light availability can all affect litterfall production [20,63]. Leaf fall occurs after the buildup of seasonal stresses, particularly water stress related to soil moisture and temperature during the dry season [64,65]. In this study, we found that the main driving variables differed among litterfall components (Table 1). Leaf litterfall was influenced by SM, ET, and Tmax (Figure 7 and Table 1), flower litterfall was influenced by ET, VPD, and light (Figure 8 and Table 1), and fruit litterfall was influenced by SOI, Tmean, and light (Figure 9 and Table 1).

Peak leaf and flower litterfall had lagged responses of 1–4 months to environmental forcing. Peak leaf litterfall occurred 1–2 months after the strongest influence of SM, and a similar trend was found for Tmax. The effects of ET were felt at lags of 3–5 months, with higher ET values resulting in higher litterfall. Peak litterfall, therefore, happened during the cool, dry period, just after the rainy season. The strongest association of ET with flower litterfall was observed at lags of 1–2 months. Peak flower litterfall occurred during the dry season in response to high evaporative demand and transpiration under elevated VPD and light levels (Figure 8). Such conditions are very specific relative to leaf litterfall, given that peak leaf and flower litterfall occur during the cool, dry season. A lag in litterfall response was observed by Zalamea and González [13], with peak total litterfall production occurring two weeks after rainfall. Detto et al. [32] reported lags that were related to seasonal and ENSO cycles. de Queiroz et al. [66] reported a four-month lag following the onset of the dry season in peak leaf deposition and observed flower fall, which occurred 2–3 months following the onset of rains.

In contrast to leaf and flower litterfall, fruit litterfall responds instantaneously to environmental conditions, such as lightning storms accompanied by winds [67–69]. Higher fruit litter production during the wet season could constitute a propagation strategy, as the increased soil water availability benefits seed germination and subsequent seedling growth [70]. Our results showed a response to fruit litterfall for individual species during the wet months (Figure 9a). In addition, fruit litterfall was influenced by cyclic patterns in the SOI. Fruit litterfall during ENSO events tended to increase at most of the lags and was enhanced by wet La Niña events, particularly in 1999–2000 and 1995–1996. The La Niña influence contrasted with that of El Niño, particularly with regard to the severe drought in 1997–1998. Fruit litterfall patterns also varied among selected species. In particular, fruit litterfall peaked in evergreen *D. alatus* under moderate El Niño conditions (Figure 9b).

Drought could therefore emerge as an important driver of fruiting phenomena by triggering mast flowering, particularly in species from the Dipterocarpaceae [21,71,72]. A contrasting pattern was found for *P. siamensis* (family Dipterocarpaceae, deciduous), for which fruit litterfall peaked under La Niña conditions. Comparable results have been reported from the wet tropics. Working at Barro Colorado Island, Panama, Wright et al. [73] found that high forest-wide fruit production occurred during El Niño events, with low fruit production following a mild dry season one year later. In peninsular tropical Malaysia, Ashton et al. [74] also found that El Niño drought years produced mass flowerings, particularly among Dipterocarpaceae, and induced mast fruiting on windward slopes. In the wet tropics, El Niño droughts could enhance light availability by reducing cloud cover [14,75]. This condition may stimulate mass flowering and fruiting production [73]. This knowledge can improve our understanding of the responses of tropical forest ecosystems to climate change [34,36], which may lead to the degradation of ecosystem services provided by such forests.

5. Conclusions

We investigated long-term (28-year) seasonal and annual patterns of litterfall production in a TDF in western Thailand. Our results showed that total annual litterfall varied from year to year across a range of 6.79–12.22 Mg ha^{-1} yr^{-1}, and that leaf litterfall was the main component of litter production. Strong seasonality was observed in all litter fractions, and the greatest leaf and flower litterfall accumulated principally during the cool, dry season, while fruit litterfall occurred mostly during the rainy season. Environmental variables associated with litterfall varied among the litterfall components. For leaf litter, significant deviations in maximum temperature (Tmax), volumetric soil moisture content (SM), and evapotranspiration (ET) during the months prior to litterfall collection were the strongest correlates of litterfall. The most significant factors affecting flower litterfall were VPD, light, and ET. Interestingly, light, Tmean, and the SOI were the most significant factors affecting fruit litterfall, and a high correlation was observed between the occurrence of wet La Niña events and elevated fruit production. Significant lags of up to five months between climatic variables and peak litterfall production were recorded. Variability in litterfall production could increase during climate change since interannual variation in climatic patterns affects both the triggering of litterfall and its quantity. Such changing patterns could potentially alter forest function and nutrient cycling. Our results can be used to monitor the future alleviation of climate change-related effects on litterfall.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/f14102107/s1, Figure S1: The location of permanent plot in the mixed deciduous forest of the Mae Klong Watershed Re-search Station (MKWRS), Kanchanaburi province, western Thailand; Figure S2: (a) Monthly rainfall variation (dots) and (b) total monthly rainfall with mean monthly maximum and minimum temperature for 1992–2021 at MKWRS, western Thailand.

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