Effects of Fertilization and Dry-Season Irrigation on Litterfall Dynamics and Decomposition Processes in Subtropical *Eucalyptus* Plantations

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Nutrient management in *Eucalyptus* plantations is critical for wood production and sustainable development. The biogeochemical mechanisms in *Eucalyptus* plantations are not fully understood due to changes in the spatiotemporal pattern of precipitation and plantation management. The nutrients released from litterfall are important sources of soil nutrition. We measured the seasonal production of various litterfall types and the proportions of their released nutrients in *Eucalyptus urophylla* × *E. grandis* plantations under compound fertilization, dry-season irrigation, and a combined compound fertilization and dry-season irrigation treatment. Our results showed that fertilization increased aboveground biomass and annual litterfall production (except leaf), and that the peak of litterfall production occurred in the rainy season. We found that the decomposition rates of leaf were significantly higher than that of twig, which were mainly controlled by stoichiometric characteristics, followed by soil enzyme activity (β-glucosidase, urease, and polyphenol oxidase). Fertilization decreased the carbon: nitrogen ratio and carbon: phosphorus ratio in litter, and increased soil enzyme activities, which accelerates litter decomposition and nutrient release. Dry-season irrigation increased litter decomposition and only affected the proportion of released potassium by changing the carbon: potassium ratio. Fertilization and dry-season irrigation accelerated the nutrient cycle to enhance compensatory growth. These results help to comprehend the effects of forest management on litterfall dynamics and decomposition processes in *Eucalyptus* plantations with seasonal drought.

Keywords: fertilization, irrigation, *Eucalyptus*, litterfall production, decomposition rate, nutrient release

GRAPHICAL ABSTRACT 1 | Response of litterfall production and decomposition to fertilization and dry-season irrigation.
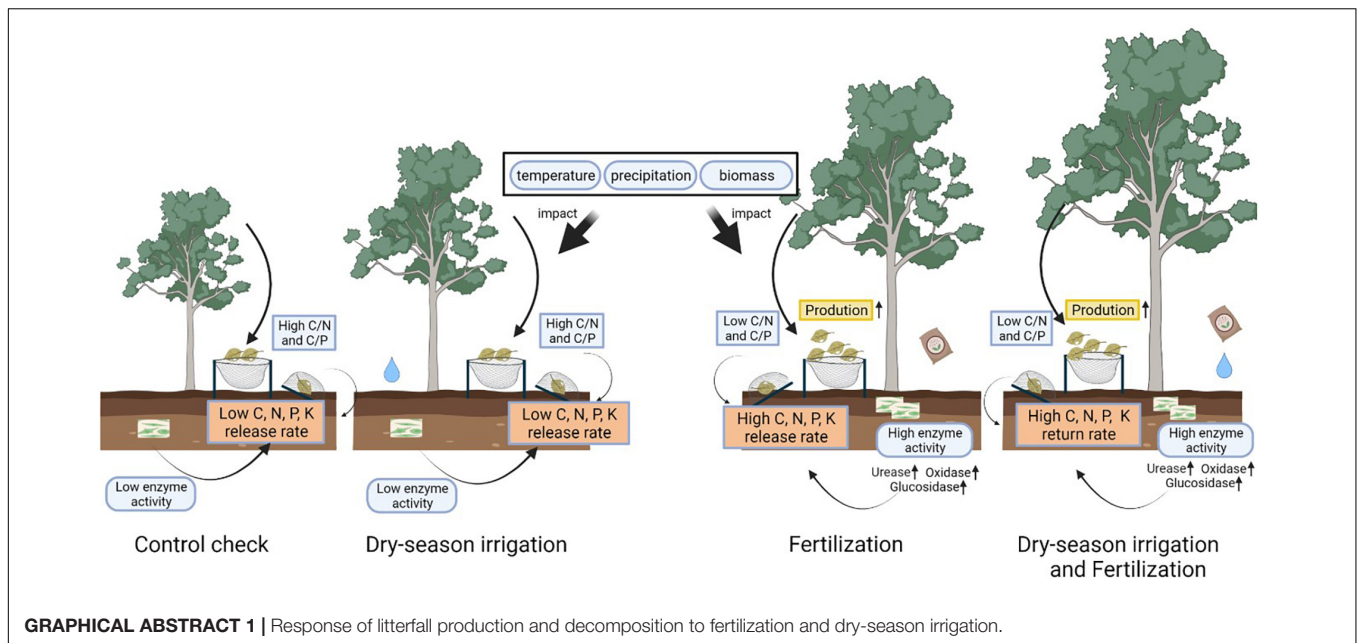
INTRODUCTION

Litterfall periodically falls to the forest floor and transfers carbon (C) and nutrients into the soil, providing an important biogeochemical process in forest ecosystems (Da Silva et al., 2018; Ni et al., 2021). In tropical forests, over 50% of aboveground net primary productivity is converted to litterfall which transfers nutrient resources to the forest floor, which is beneficial to the sustainable development of forest ecosystems (Camargo et al., 2015; Yin et al., 2019). Additionally, litter in the soil surface can maintain soil fertility by mitigating erosion (Wang et al., 2020) and providing an active environment for soil animals and microorganisms (Cajaiba et al., 2017; Dong et al., 2021). Global climate change has impacted the global hydrological cycle by changing the spatiotemporal pattern of precipitation, water availability, air temperature, air humidity, etc. (Dai, 2013; Dubreuil et al., 2019). Drought can change the nutrient cycle by increasing litterfall production and inhibiting its decomposition rate (Paudel et al., 2015; Yu et al., 2019b). The seasonal drought caused by changes in precipitation pattern (Zhou et al., 2011) in southern China has affected the ecosystem nutrient cycle (Dawoe et al., 2010; Yu et al., 2019b).

Numerous studies show that the shedding process of the aboveground parts of vegetation is affected by vegetation type, species composition, topography, climate, and the physical and chemical properties of soil (Blanco et al., 2008; Tang et al., 2010; Camargo et al., 2015; Kamruzzaman et al., 2019; Gonzalez et al., 2020; Zhu et al., 2021). In the tropical/subtropical forest with seasonal drought, the peak of litterfall production generally occurs in the dry season, which is highly correlated with precipitation (Chave et al., 2010; Paudel et al., 2015). Falling leaves are an important part of litterfall and respond rapidly to environmental changes (Liu et al., 2004). In order to avoid the risk of drought, plants will increase litter production to

decrease the loss of water, especially *via* leaf removal (Liu et al., 2015). In addition, nutrient deficits limit plant growth, resulting in the reduction of litterfall production (Wright et al., 2011). After falling from the plant, litter decomposes in the surface soil and releases nutrients to form organic matter, which is vital to maintaining soil fertility (Cotrufo et al., 2015). Litter decomposition is primarily determined by litter quality, decomposer biodiversity, decomposer activity, and environmental factors. Firstly, different indicators of litter quality determine the decomposability of substrate. The easily decomposed litter is characterized by high nutrient content [nitrogen (N) and/or phosphorus (P)], low stoichiometric characteristics (C:N and/or C:P), and lower recalcitrant polymer content (lignin or holocellulose) (Adair et al., 2008; Mora-Gómez et al., 2020; Hou et al., 2021). Generally, higher contents of soil nutrients were accompanied with high litter quality (Ge et al., 2013). Secondly, environmental factors affect litter decomposition through biodiversity and the activity of soil decomposers. For example the decrease of soil water content caused by drought can reduce the litter decomposition rates by changing the composition of the microbial community and decreasing microbial activity (Petraglia et al., 2019; Liu et al., 2021). Therefore, climate change and forest management (fertilization) not only change the nutrient input from litterfall production, but also affect the released nutrient proportions through litterfall decomposition. Combining litter production and decomposition to assess the nutrient return from litterfall would further realize the variations of soil fertility under the environmental changes.

With its fast growth and high yield, *Eucalyptus* is widely planted in southern China, covering an area of 4.5 million ha (Xie et al., 2017). Due to the soil in southern China being impoverished (Zhen et al., 2005), compound fertilizers have been applied to meet the fast-growing requirements in

the conventionally managed *Eucalyptus* plantations (Lu et al., 2020). Affected by the fast-growing characteristics and short rotation, the harvesting of *Eucalyptus* plantations leads to high nutrient export, and results in the decrease of soil fertility (Menegale et al., 2016; Lu et al., 2020). As defined by Li et al. (2020), compensatory growth refers to an organism's accelerated growth following a disturbance or a period of slow growth caused by unfavorable environmental conditions, such as low temperature or nutrient deprivation. After alleviating nutrient deprivation, compensatory growth caused by fertilization leads to an increase in litterfall production by increasing aboveground biomass (Wright et al., 2011). Moreover, increased litter quality under fertilization positively governs the litter decomposition rates (Hou et al., 2021). Due to *Eucalyptus*' high transpiration, fertilizing its plantation will increase transpiration, which reduces soil water content (Hua et al., 2021). The decrease of soil water content has negative effects on aboveground biomass and soil microbial community in *Eucalyptus* plantations, increasing the litterfall production and reducing the litterfall decomposition (Ribeiro et al., 2002; Nouvellon et al., 2012). Consequently, the reduced growth, increased litterfall production, and decreased decomposition rate are offset or reversed under sufficient water supply. Aboveground biomass is subjected to decreases *via* drought stress and increases *via* fertilization. These changes in aboveground biomass can affect the light environment and litter decomposition under the canopy, resulting in further alterations in plantation nutrient cycles (Wright et al., 2011; Liu et al., 2015; Almagro et al., 2017). Nevertheless, the effects of seasonal drought and variations in growth patterns under fertilization on litter deposition are not fully understood. Therefore, exploring the effects of dry season irrigation on nutrient inputs from litterfall in the early growth stage can provide better supporting data for improving nutrient management to ensure healthy growth in the early stage of *Eucalyptus* plantations under seasonal drought.

In this study, *Eucalyptus urophylla* × *E. grandis*, the high-productivity genotypes mainly planted in southern China, was selected to examine the variations of litterfall patterns and decomposition processes under dry-season irrigation and fertilization. The following hypotheses are proposed: (1) the peak of litterfall production occurs in the dry season; (2) fertilization increases the litterfall production, and irrigation decreases the litterfall production; (3) fertilization and irrigation accelerate litter decomposition by increasing litter quality and enzyme activity; (4) fertilization and irrigation promote nutrient release through enhancing soil enzyme activity; and (5) fertilization and irrigation enhance compensatory growth. This research aims to improve forest productivity in *Eucalyptus* plantations through the enhancement of water and fertilizer management.

MATERIALS AND METHODS

Study Site

The experimental site is located at the Zengcheng Teaching and Research Bases of South China Agricultural University, Guangzhou (23°14′48N, 113°38′20E), which belongs to a subtropical monsoon climate. According to the data of the Zengcheng meteorological observatory from 1981 to 2010, the annual average temperature is 21.91°C and the annual average precipitation is 2004.4 mm. The seasonal drought in the study site is obvious as its rainfall between October and March only is accounted for 14% of the whole year. The monthly precipitation and the mean air temperature during the experiment are shown in **Figure 1**.

Experimental Design

Eucalyptus urophylla × *E. grandis* was selected as experimental materials and its seedlings (approx. 20 – 35 cm tall) were planted in April 2017 at a density of 3 × 2 m. The forestland was 0.536 ha in total and divided into five terraces with horizontal terraced land preparation method. Each terrace had four treatments (one plot per treatment), which were randomly arranged from 20 to 92 trees for each plot. A total of 20 plots were employed in the present study, and their shapes were described in Yu's study (Yu et al., 2019a). The experiment was set up as a completely random block design of water and fertilizer. There were four treatments in total: (1) no dry-season irrigation and no fertilizer (CK), (2) dry-season irrigation but no fertilizer (W), (3) no dry-season irrigation but fertilizer (F), and (4) dry-season irrigation and fertilizer. Dry-season irrigation was carried out only from October to March with drip irrigation equipment. Following Yu's observation (Yu et al., 2019a), the irrigation was given 8 h/week at 4 L/h to ensure the soil relative water content of the soil from 40 cm depth and 40 cm away from the trees was maintained at 90% for 3 days. The fertilizer addition refers to the added amount of *Eucalyptus* production in southern China (Ministry of Forestry of the People's Republic of China, 2015). As of July 2020, fertilizer was applied 4 times: base fertilizer, first extra fertilizer, second additional fertilization, and third additional fertilization. The base fertilizer was applied at 400 g/hole in March 2017, which includes N: 24 g, P_2O_5: 72 g, and K_2O: 24 g. The first extra fertilizer was applied at 400 g/hole
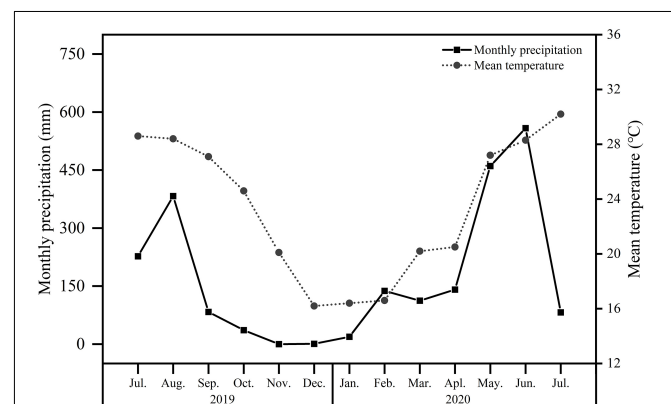
Figure 1 | Monthly precipitation and mean temperature during the experimental period from July 2019 to July 2020. The dot with the broken line represented the mean temperature and the square with solid line indicated the monthly precipitation.

for F and WF treatments in July 2017, including N: 45 g, P_2O_5: 21 g, and K_2O: 24 g. The second and third additional fertilization for F and WF treatments were, respectively, carried out at 400 g/hole in July 2018 and July 2019, each of which included N: 60 g, P_2O_5: 28 g, and K_2O: 32 g. The initial soil nutrient concentrations (40 cm) were total nitrogen (TN): 0.34 g/kg, total phosphorus (TP): 0.16 g/kg, total potassium (TK): 8.82 g/kg, alkaline hydrolysis nitrogen (AHN): 30.74 mg/kg, available phosphorus (AP): 0.30 mg/kg, and rapidly available potassium (AK): 10.42 mg/kg.

Growth Traits

The diameter at breast height (DBH) and height of all *E. urophylla* × *E. grandis* were measured in July 2019 and July 2020. The number of measurements for each treatment were 150 (CK), 189 (W), 146 (F), and 168 (WF). In July 2020, 5 standard trees of each treatment fell to estimate the aboveground biomass. The aboveground part was broken down into stem, twig, leaf, and fruit. All the materials were dried and weighed to calculate the biomass of each organ under various treatments.

Litterfall Deposition and Decomposition

In July 2019, 5 collectors were set in each block using five-point sampling method to measure litterfall deposition, 1 m × 1 m (1 m^2) in size, made from mesh gauze (2 mm diameter), with collectors installed at a height of 1 m above the ground to ensure the separation of the mesh gauze from the surface. The litterfall was collected monthly (the end of each month) and classified into organs: leaf, twig, fruit, and bark. The litterfall deposition was monitored from August 2019 to July 2020. All samples were dried in an oven at 65°C to constant weight and then weighed.

In July 2019, fresh litterfall was collected from the plantation's floor and air-dried to constant weight in a laboratory. Portions of 10 g of leaves and twig samples (cut into 10 cm length) were separately packed in corrosion-resistant plastic bags with 2 mm^2 mesh and measuring 25 cm × 25 cm. A 20 leaf bags and 20 twig bags were placed under the litter layer in each plot using five-point methods at the end of July. We planned for 4 successive harvests in each plot during the experiment: 5 leaf bags and 5 twig bags in each plot were collected at 3, 6, 9, 12 months after placing litter bag to measure litter decomposition. After collection, the materials contained in the plastic bags were cleaned with a brush to remove the attachments like weed and soil particles. Afterward, the materials were dried in an oven at 65°C to constant weight (M_t). Leaves and twig litter for each treatment were oven-dried to constant weight at 65°C to determine the ratio between air-dried mass and oven-dried. Then, the ratio was used to convert the weight of initial air-dried litter to the weight of oven-dried litter (M_0). The nutrient content of the original samples (C_0) and 12 months decomposed samples (Ct) for each treatment were analyzed. Samples for chemical analysis were ground and passed through a 0.5 mm sieve for testing the concentrations of C, nitrogen (N), phosphorus (P), and potassium (K) (refer to soil chemical analysis methods). The mass loss rate (L), proportion

of nutrient released (F′), and Olson model were calculated as follows:

$$L = [(M_0 - M_t)/M_0] \times 100\%$$

$$F' = 100\% - (C_t \times M_t)/(C_0 \times M_0) \times 100\%$$

Olson negative exponential decay model: $y = a \times e^{-kt}$

In the Olson model: y means the remaining mass rate of litter; a means the fitting parameter; k means the annual decomposition coefficient; t means the decomposition time.

Environmental Factors

The soil water content (SWC) was measured at the end of each month with 15 repeats for each treatment. Soil samples 40 cm deep (40 cm away from the trees) were obtained with a soil drill in three random places of each block. The soil samples were collected in an aluminum box to be weighed and dried at 105°C to constant weight in an oven. Then record the dry weight to compute the SWC. SWC (%) = (fresh weight – dry weight)/(dry weight – box weight) × 100%. The relative soil water content (SWC_r) = SWC/field moisture capacity. The field moisture capacity was measured with cutting ring methods (Ministry of Agriculture of the People's Republic of China, 2010). In July 2019, soil field water-holding capacity of 0 – 20 cm and 20 – 40 cm was measured for each plot. One profile was sampled for each plot, with disturbed and undisturbed soil samples collected from the top soil to 10 and 30 cm. Three undisturbed soil samples were collected from each soil layer with a cutting ring (70 mm diameter and 52 mm height). The disturbed soil samples were collected from the soil around the cutting ring and air dried for 3 days in a laboratory. The undisturbed soil samples were placed in a tray filled with water to a level of 2 – 5 mm below the upper rim of the cutting ring. After air dried for 3 days, the disturbed soil samples sifted by 2 mm sieve and filled with a cutting ring. Next, the undisturbed soil samples were soaked for 24 h, and then put on sand. After the undisturbed soil samples were saturated, the samples were placed on the cutting ring of disturbed soil samples. In order to ensure that the two cutting rings were contacted tightly, a 2 kg brick was placed on the top of the undisturbed soil samples. After the samples were stand for 8 h, 20 – 30 g soil samples from the cutting ring of the wet undisturbed soil samples were collected into an aluminum box of known weight (m_0), and then weighed immediately (m_1). Finally, the samples in the aluminum box were dried to constant weight (m_2) in an oven of 105°C. The formula for field water-holding capacity (FC) is: FC = (m_1 – m_2) × 1,000/(m_2 – m_0).

The soil nutrient content was measured once in the dry season (January 2020) and the rainy season (July 2020) with five repeats for each treatment. In each block, a bag of soil samples (0 – 10 cm depth) was taken from 5 places under the litter bags. The soil samples were air-dried for 3 days in the laboratory and then sifted in a mill with 2 mm sieve for testing the concentrations of C, TN, TP, TK, AHN, AP, and AK. Chemical analysis was referenced standard analysis methods (Lu, 2000; Carter and Gregorich, 2007). Organic carbon concentration was determined with the traditional potassium dichromate heating oxidation –

volumetric method (Carter and Gregorich, 2007). After sulfuric acid and hydrogen peroxide digestion, the TN concentration was determined by the distillation titration method (Lu, 2000). TP concentration was determined by the vanadium molybdate yellow colorimetric method after digesting with sulfuric acid and hydrogen peroxide (Lu, 2000). TK concentration was determined by flame photometer method after digesting with sulfuric acid and hydrogen peroxide (Lu, 2000). Hydrolytic reduction was carried out in sodium hydroxide and ferrous sulfate solutions, and then the AHN concentration was determined by sulfuric acid titration with boric acid as an indicator (Lu, 2000). After soaking with HCl-HF reagent, AP was determined by the molybdenum antimony colorimetric method. The sample was extracted with ammonium acetate and the AK was determined by flame photometer method (Lu, 2000).

Soil Enzyme Activity

The samples of soil enzyme were collected in January 2020 with 5 repeats for each treatment. In each block, a bag of soil samples (0 – 10 cm depth) was taken from 5 places under the litter bags and stored in an cryogenic container. The soil samples were sifted in a mill with 1 mm sieve in a laboratory. The samples were stored at 4°C and measured within 1 week.

Soil enzyme activity analysis was referenced standard analysis methods. Enzyme activity is expressed as the mass of specific product generated per unit of dry soil weight per unit time. Acid phosphatase activity was analyzed using *p*-nitrophenyl-phosphate as substrate, and then using a spectrophotometer to measure absorbance at 410 nm to calculate activity (Santos et al., 2018). β -glucosidase activity was analyzed using sodium acetate (pH 5.5) as buffer and using 4-nitrophenyl β-D-glucopyranoside as substrate, and then using a spectrophotometer to measure absorbance at 410 nm to calculate activity (Santos et al., 2018). Urease activity was measured by phenol-sodium hypochlorite colorimetric and assayed at 540 nm, using urea as substrate (Zhen et al., 2019). Using the phenolic amino acid L-3,4-dihydroxy phenylalanine (L-DOPA) as the substrate, polyphenol oxidase activity was analyzed by spectrophotometer at 475 nm (Prosser et al., 2011). Cellulase activity was determined by 3,5-Dinitrosalicylic acid colorimetry Method. The amount of glucose released over 72 h was assayed colorimetrically at 540 nm (Guan, 1986).

Data and Statistical Analysis

Excel 2021 was used for data sorting, SPSS 22.0 was used for ANOVA analysis, Duncan's multiple comparison analysis, Pearson correlation analysis, and Olson negative exponential decay model. Origin 2021 software was used for principal component analysis (PCA) and making figures.

The annual litterfall production (total or each type) was calculated by adding up the amount of monthly litterfall production in each block. After using Grubbs method to delete outliers, one-way ANOVA following Duncan's multiple comparison analysis (normal distribution and variance homogeneity of the data have tested) was used to test the effects of treatment on litterfall production, aboveground biomass, percentages of litter remaining mass, C and nutrient

concentrations, proportion of C and nutrient released, and soil enzyme activity. Pearson correlation coefficients were estimated between environmental factors and monthly litterfall productions, litter remaining mass, and soil/litter chemical traits, litter nutrient released proportion and soil/litter chemical traits. The Pearson correlation analysis, Olson negative exponential decay model, and PCA were made using the average per plot ($n = 5$).

RESULTS

Biomass

Fertilization increased the biomass of leaf, twig, and stem 3 years after plantation (**Table 1**), while dry-season irrigation increased the biomass of stem ($P < 0.05$). The biomass of stem under dry-season irrigation showed further increase by 14.7% on the basis of fertilization treatment ($P < 0.05$).
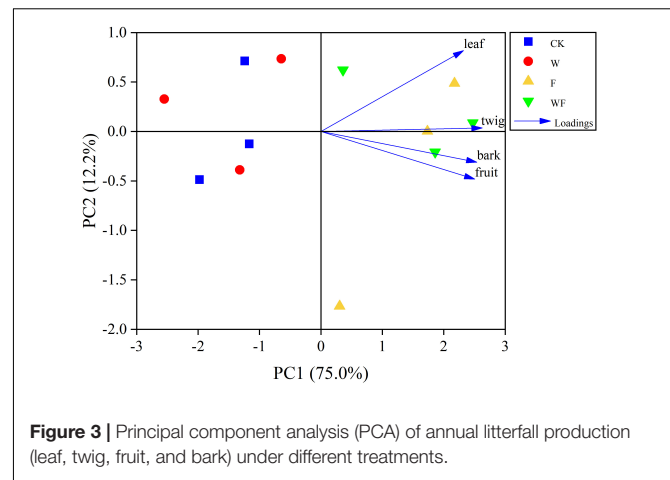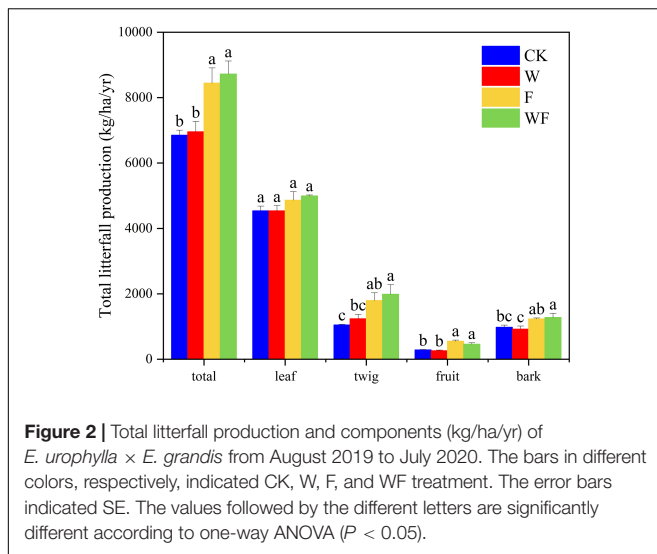
Litterfall Deposition

In *E. urophylla* × *E. grandis* plantations under different treatments, the average litterfall productions ranged from 6852.8 kg/ha/yr under CK treatment to 8720.3 kg/ha/yr under WF treatment (**Figure 2**). The total litterfall productions with fertilizer addition (F and WF) were higher than that with no fertilizer ($P < 0.05$). Dry-season irrigation had no effect on litterfall production ($P > 0.05$). Dry-season irrigation increased litterfall production but without forming significant differences. The leaf fraction showed the highest contribution in total litterfall production (average 4733.9 kg/ha/yr), without statistical differences between various treatments. The second largest contribution to total litterfall production was twig (average 1517.5 kg/ha/yr). Fertilization increased the twig (61–71%) and fruit (77–93%) production, while the twig and fruit production did not differ under dry-season irrigation. Barks were significantly different between fertilization and non-fertilization. The PCA depicted similarities/differences between treatments: there were obvious differences between fertilizer (F and WF) and no fertilizer (CK and W), and a small difference between dry-season irrigation and no dry-season irrigation (**Figure 3**).

The litterfall production of all treatments followed a seasonal pattern throughout the experimental period (**Figure 4**). The deposition over 72% occurred in the rainy season (from April to September), strongly affected by the leaf and twig productions

TABLE 1 | Aboveground biomass of *E. urophylla* × *E. grandis* 3 years after plantation.

Treatment	Leaf (kg/tree)	Twig (kg/tree)	Stem (kg/tree)
CK	1.108 ± 0.064b	1.481 ± 0.053b	11.310 ± 0.609c
W	1.221 ± 0.122b	1.664 ± 0.152b	13.973 ± 0.515c
F	2.165 ± 0.163a	4.187 ± 0.355a	37.602 ± 1.313b
WF	2.362 ± 0.209a	3.767 ± 0.444a	43.127 ± 1.205a

Means ± standard error (SE) were shown (n = 5). The letter after the numbers represented the Duncan's multiple comparison results. Different lower-case letters indicate differences between various treatments.

Figure 2 | Total litterfall production and components (kg/ha/yr) of *E. urophylla* × *E. grandis* from August 2019 to July 2020. The bars in different colors, respectively, indicated CK, W, F, and WF treatment. The error bars indicated SE. The values followed by the different letters are significantly different according to one-way ANOVA ($P < 0.05$).

Figure 3 | Principal component analysis (PCA) of annual litterfall production (leaf, twig, fruit, and bark) under different treatments.

(**Supplementary Figure 1**). The productions of leaf, twig, and bark peaked in May and fruit in July. In particular, fruit and bark fall rarely occur during the dry season, while leaf and twig are maintained at a low level (**Figure 4** and **Supplementary Figure 1**). In Pearson correlation analysis, litterfall deposition showed positive correlations with temperature and precipitation (**Table 2**). Temperature had positively correlated with twig and fruit production ($P < 0.05$), which was not affected by dry-season irrigation and fertilization. Precipitation had positively correlations with total, leaf, twig, and bark production, but the correlation with leaf production disappeared under dry-season irrigation and fertilization.

Litter Decomposition

The Olson negative exponential decay model adequately described the decomposition rates of leaf and twig under different treatments, with R^2 values ranging from 0.70 to 0.98 (**Table 3**). The decomposition rates of the twig were lower than that of the leaf. In the first 90 days, the rates of decomposition under all treatments were more intense than in other periods (**Figure 5**). After 360 days of decomposition, the average litter decomposition rates of leaf and twig for all treatments were 30 and 12%. Different treatments had significant influences on litter decomposition. Fertilization and dry-season irrigation were beneficial to leaf and twig decomposition (**Figure 5**), of which under WF treatment attained the highest rates of decomposition with 34% (leaf) and 15% (twig), respectively, after 360 days ($P < 0.05$). According to the Olson model, the time required to decompose 95% of leaf and twig had been, respectively, reduced by 16.8 to 34% and 20.8 to 43.8% under fertilization and dry-season irrigation. In the experimental period, the remaining mass negatively correlated with initial C, N, P, and K concentration, and positively correlated with C/N, C/P, and C/K (**Table 4**). In addition, leaf decomposition was related to the activity of β - glucosidase, Urease, and Polyphenol oxidase in the dry season ($P < 0.05$), while twig decomposition was related to the activity of Urease and Polyphenol oxidase (**Table 5**).
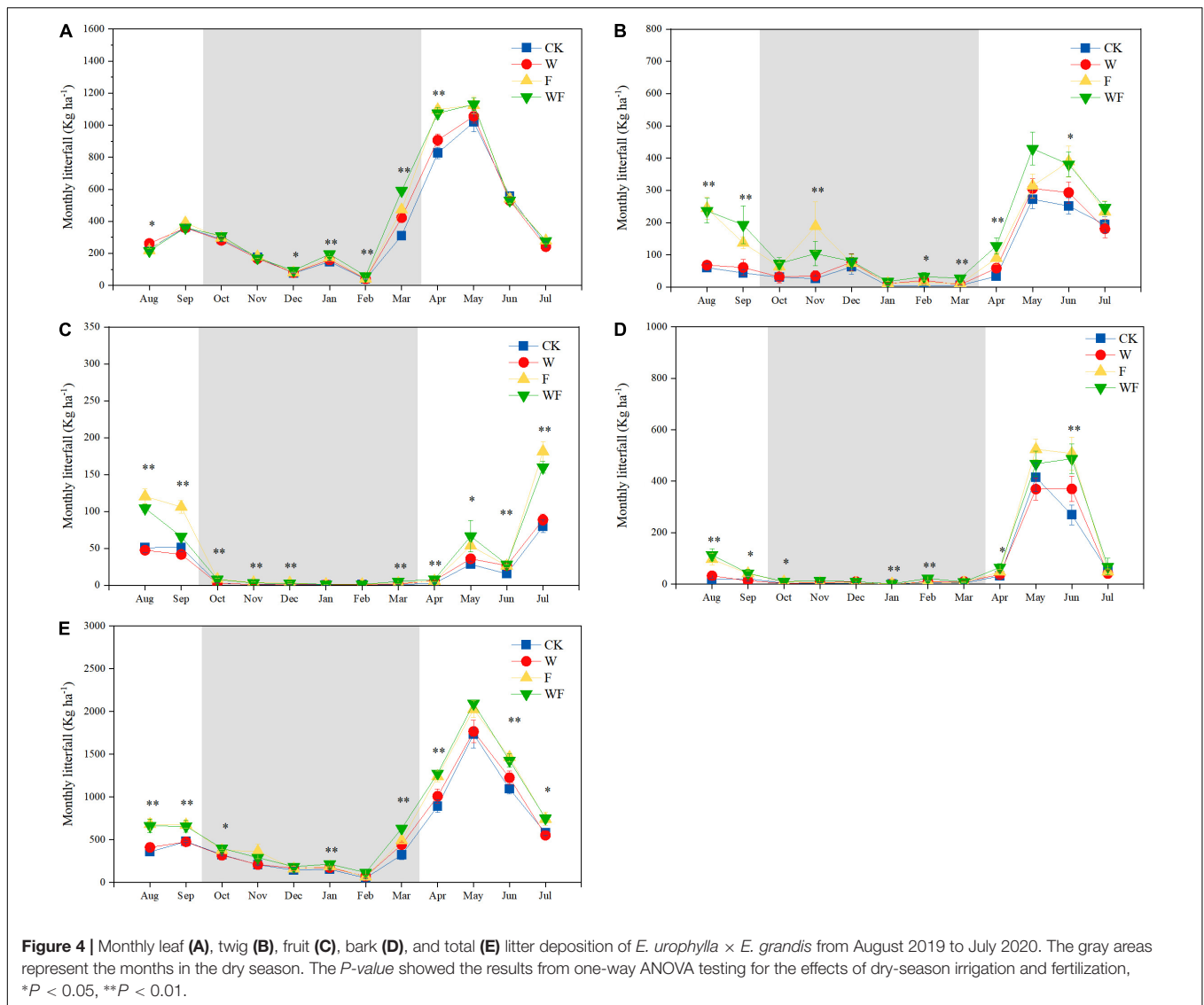
Nutrients Released

Most of initial litter C and nutrient concentrations were influenced by fertilization, but not by dry-season irrigation (**Table 6**). Initial foliar C concentrations increased by 2.6 – 2.7% under fertilization ($P < 0.05$). Affected by the increase of P concentrations in leaf (26.1 – 27.8%) and twig (48.6 – 65.6%), C/P under fertilization were decreased (leaf, 18.8 – 20.1%; twig, 30.4 – 37.3%). Compared to CK, dry-season irrigation increased foliar K concentration by 55.9 – 58.5%, while fertilization increased the K concentrations of twig by 27.0 – 39.7% ($P < 0.05$). After decomposing 360 days, C, N, and P concentrations greatly decreased, and their difference narrowed between treatments. Meanwhile, the K concentration of twigs decreased immensely, but foliar K concentrations change little.

After 360 days of decomposition, the quantities of C, N, P, and K in leaf and twig decreased for both treatments (**Figure 6**). In leaf litter, the released proportions of N (16.2 – 18.2%) and P (22.7 – 31.5%) under fertilization were higher than that under non-fertilization ($P < 0.05$). Compared to non-fertilization, fertilization increased the C release proportion by 111.2 – 145.4%, N release proportion by 46.6 – 72.9%, and P release proportion by 121.5 – 136.4% of twig ($P < 0.05$), respectively. In particular, the C/N of WF in leaf litter was higher than that of CK (22.4%) and the C/P of WF in twig litter was higher than that of CK (49.7%) and W (34.3%). The released proportions of K were different from that of C, N, and P. Fertilization and dry-season irrigation promoted the release of foliar K, and the effect of dry-season irrigation was greater than fertilization. The release of twig K was inhibited by dry-season irrigation, but the combination of dry-season irrigation and fertilization promoted the release of twig K ($P < 0.05$).

DISCUSSION

Litterfall Production Under Different Treatments

Litterfall production generally exhibits seasonal patterns, which varies with forest types and environmental factors

FIGURE 4 | Monthly leaf **(A)**, twig **(B)**, fruit **(C)**, bark **(D)**, and total **(E)** litter deposition of *E. urophylla × E. grandis* from August 2019 to July 2020. The gray areas represent the months in the dry season. The *P-value* showed the results from one-way ANOVA testing for the effects of dry-season irrigation and fertilization, *P < 0.05, **P < 0.01.

TABLE 2 | Analysis of the correlation between environmental factors and monthly litterfall productions from August 2019 to July 2020.

Treatment	Variables	Total	Leaf	Twig	Fruit	Bark
CK	Temperature	–	–	0.627*	0.802**	–
	Precipitation	0.734**	0.589*	0.728*	–	0.799**
W	Temperature	–	–	0.632*	0.830**	–
	Precipitation	0.759**	–	0.772**	–	0.863**
F	Temperature	0.604*	–	0.773**	0.779**	–
	Precipitation	0.776**	–	0.784**	–	0.893**
WF	Temperature	–	–	0.792**	0.800**	–
	Precipitation	0.765**	–	0.830**	–	0.909**

*Correlations coefficients by Pearson correlation are shown, – P > 0.05, *P < 0.05, **P < 0.01.*

TABLE 3 | Decomposition equations of Olson negative exponential decay model of leaf and twig for all treatments.

Fraction	Treatment	Equation	R^2	k	$t_{0.5}(a)$
Leaf	CK	$Y = 92.666e^{-0.238t}$	0.7086	0.238	2.91
	W	$Y = 91.968e^{-0.286t}$	0.7405	0.286	2.42
	F	$Y = 92.462e^{-0.314t}$	0.7936	0.314	2.21
	WF	$Y = 92.632e^{-0.362t}$	0.8404	0.326	1.91
Twig	CK	$Y = 98.96e^{-0.114t}$	0.961	0.114	6.08
	W	$Y = 99.467e^{-0.144t}$	0.9753	0.144	4.81
	F	$Y = 99.78e^{-0.19t}$	0.9741	0.190	3.65
	WF	$Y = 99.84e^{-0.203t}$	0.9857	0.203	3.41

k, the annual decomposition coefficient in Olson model; $t_{0.5}$, time to decompose 50% of the litter; $t_{0.95}$, time to decompose 95% of the litter.

(Staelens et al., 2011; Zhang et al., 2014). The litterfall in the present study was collected from the *E. urophylla × E. grandis* plantation after 3 years of fertilization and dry-season irrigation.

On average, the litterfall productions observed in the present study (6.85 to 8.72 Mg/ha/yr) are close to values of mature *Eucalyptus* plantations (3.57–6.04 Mg/ha/yr) in Brazil
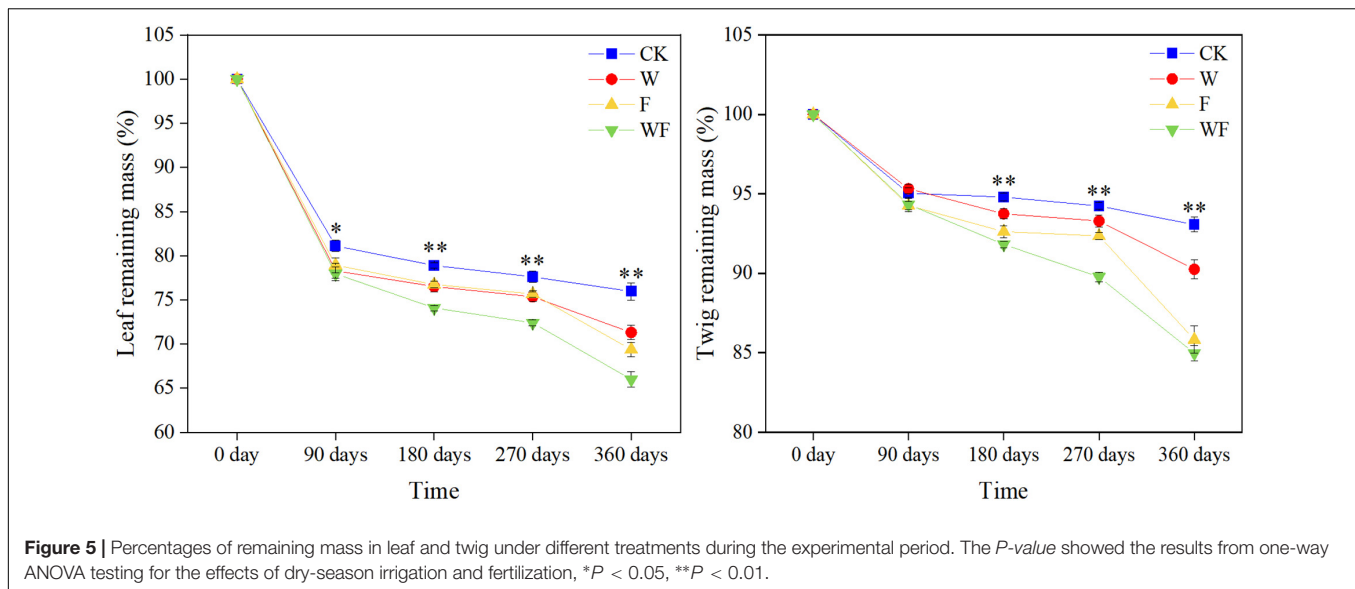
FIGURE 5 | Percentages of remaining mass in leaf and twig under different treatments during the experimental period. The *P-value* showed the results from one-way ANOVA testing for the effects of dry-season irrigation and fertilization, *$P < 0.05$, **$P < 0.01$.

TABLE 4 | Pearson correlation analysis between litter remaining mass (leaf and twig) and initial chemical traits.

Time	Initial C	Initial N	Initial P	Initial K	Initial C/N	Initial C/P	Initial C/K
90 days	−0.890**	−0.941**	−0.860**	−0.796**	0.905**	0.873**	0.875**
180 days	−0.914**	−0.964**	−0.902**	−0.818**	0.919**	0.890**	0.911**
270 days	−0.910**	−0.960**	−0.900**	−0.817**	0.921**	0.895**	0.907**
360 days	−0.874**	−0.931**	−0.886**	−0.821**	0.889**	0.898**	0.895**

*Correlation coefficients of Pearson correlation are shown (n = 20), **P < 0.01.*

TABLE 5 | Pearson correlation analysis between the percentage of remaining mass and enzyme activity of surface soil (10 cm) in the dry season.

Litter	Acid phosphatase	β -glucosidase	Urease	Polyphenol oxidase	Cellulase
Leaf	–	−0.568**	−0.611**	−0.544*	–
Twig	–	–	−0.473**	−0.608**	–

*Correlation coefficients of Pearson correlation are shown (n = 20), *P < 0.05, **P < 0.01.*

(Barlow et al., 2007; Ribeiro et al., 2018), but higher than that of a *E. urophylla × E. grandis* plantation (3.09 Mg/ha/yr) in southern China (Liu et al., 2009). In comparison with other studies demonstrating that litterfall production did not change with biomass (Demessie et al., 2012; Xu et al., 2019), the increases of litterfall production in our research are caused by increased biomass (**Table 1** and **Supplementary Table 1**). Our results indicate a higher leaf production, followed by twig, bark, and fruit, which was consistent with the pattern observed in other studies (Da Silva et al., 2018; De Queiroz et al., 2019). Fertilization increases all types of litterfall production except for leaf, but dry-season irrigation had little effect on these (**Figure 2**). This difference may be related to the fact that fertilization greatly increased aboveground biomass, while dry-season irrigation did not.

The value of litterfall production in tropical/subtropical forests is known to follow a seasonal pattern. Affected by environmental factors and forest types, the monthly dynamics of litterfall showed unimodal, bimodal, and irregular models

(Zhang et al., 2014). The variations of total litterfall, leaf, and twig under different treatments show bimodal models, which was consistent with the studies in tropical forests (De Queiroz et al., 2019; Zhu et al., 2021). Our results show leaf litter dominated the temporal dynamics of litterfall. Previous studies have indicated that the peak of leaf abscissions of seasonally dry forests occurred in the dry season, which is the physiological mechanism of drought adaptation (Chave et al., 2010; Zhu et al., 2019, 2021). However, our results indicating that the peak of litterfall production occurred in the mid-rainy season were contrary to our hypothesis, but consistent with other studies of *Eucalyptus* (Barlow et al., 2007; Cizungu et al., 2014). Although drought stress was observed during dry season in our plantation (Hua et al., 2021), litterfall productions remained at a low level during the dry season. Moreover, dry-season irrigation and fertilization only weaken the correlation between leaf production and precipitation. Litterfall production mainly affected by precipitation (**Table 2**) may be caused by the heavy rainfall and powerful wind events

TABLE 6 | C and nutrient concentrations, C/N and C/P ratio of leaf and twig litter under various treatments after 0 and 360 days decomposition.

Time	Litter	Treatment	C(g/kg)	N(g/kg)	P(g/kg)	K(g/kg)	C/N	C/P	C/K
0 day	Leaf	CK	528.100 ± 3.799bc	8.394 ± 0.443a	0.314 ± 0.014b	2.044 ± 0.246a	63.647 ± 3.528a	1695.761 ± 74.512a	274.92 ± 34.63a
		W	520.700 ± 5.201c	8.418 ± 0.535a	0.299 ± 0.013b	3.187 ± 0.334a	62.846 ± 3.939a	1757.545 ± 81.169a	169.86 ± 15.62b
		F	542.320 ± 5.106a	9.308 ± 0.469a	0.396 ± 0.014a	2.451 ± 0.344ab	58.779 ± 2.535a	1377.602 ± 54.641b	241.21 ± 36.75ab
		WF	534.820 ± 2.270ab	9.312 ± 0.479a	0.382 ± 0.011a	3.239 ± 0.380a	57.990 ± 2.750a	1404.272 ± 44.885b	178.14 ± 28.36b
	twig	CK	478.520 ± 3.969a	2.158 ± 0.233a	0.070 ± 0.006b	0.277 ± 0.039b	232.219 ± 24.836a	7102.376 ± 685.106a	1854.55 ± 236.70ab
		W	473.200 ± 6.498a	1.940 ± 0.172a	0.061 ± 0.003b	0.253 ± 0.038b	250.992 ± 20.163a	7806.175 ± 415.882a	2018.45 ± 247.97a
		F	480.080 ± 4.888a	2.426 ± 0.237a	0.104 ± 0.014a	0.387 ± 0.033a	206.438 ± 21.850a	4945.722 ± 678.118b	1274.75 ± 110.48b
		WF	481.520 ± 4.256a	2.380 ± 0.131a	0.101 ± 0.009a	0.352 ± 0.023ab	204.784 ± 11.576a	4892.228 ± 875.848b	1394.02 ± 109.10b
360 days	Leaf	CK	406.960 ± 21.664a	5.590 ± 0.205a	0.195 ± 0.011a	2.410 ± 0.254a	72.617 ± 1.540b	2100.258 ± 103.828a	181.30 ± 29.90a
		W	421.340 ± 18.117a	5.342 ± 0.180a	0.214 ± 0.021a	2.173 ± 0.182a	79.622 ± 5.986ab	2035.755 ± 198.742a	198.89 ± 17.41a
		F	427.860 ± 17.728a	5.586 ± 0.187a	0.202 ± 0.009a	2.330 ± 0.183a	76.790 ± 3.415ab	2120.778 ± 90.760a	190.12 ± 20.97a
		WF	458.580 ± 8.571a	5.192 ± 0.251a	0.203 ± 0.005a	2.303 ± 0.090a	88.910 ± 3.457a	2270.009 ± 62.744a	201.46 ± 10.26a
	twig	CK	492.720 ± 2.716a	1.480 ± 0.073a	0.053 ± 0.002ab	0.155 ± 0.024bc	336.759 ± 17.874a	9363.232 ± 376.895a	3408.70 ± 399.50ab
		W	492.820 ± 4.537a	1.800 ± 0.280a	0.059 ± 0.010a	0.203 ± 0.028ab	292.556 ± 30.529a	9425.894 ± 1540.137a	2588.11 ± 311.20bc
		F	501.900 ± 2.598a	1.410 ± 0.151a	0.045 ± 0.005ab	0.252 ± 0.028a	374.234 ± 44.413a	11726.384 ± 1290.593a	2102.97 ± 248.75c
		WF	494.380 ± 2.876a	1.266 ± 0.129a	0.037 ± 0.012c	0.119 ± 0.012a	408.203 ± 43.970a	14033.825 ± 1632.545a	4289.03 ± 376.50a

Means ± SE were shown (n = 5). The letter after the numbers represented the Duncan's multiple comparison results. Different letters indicated significant differences between various treatments.
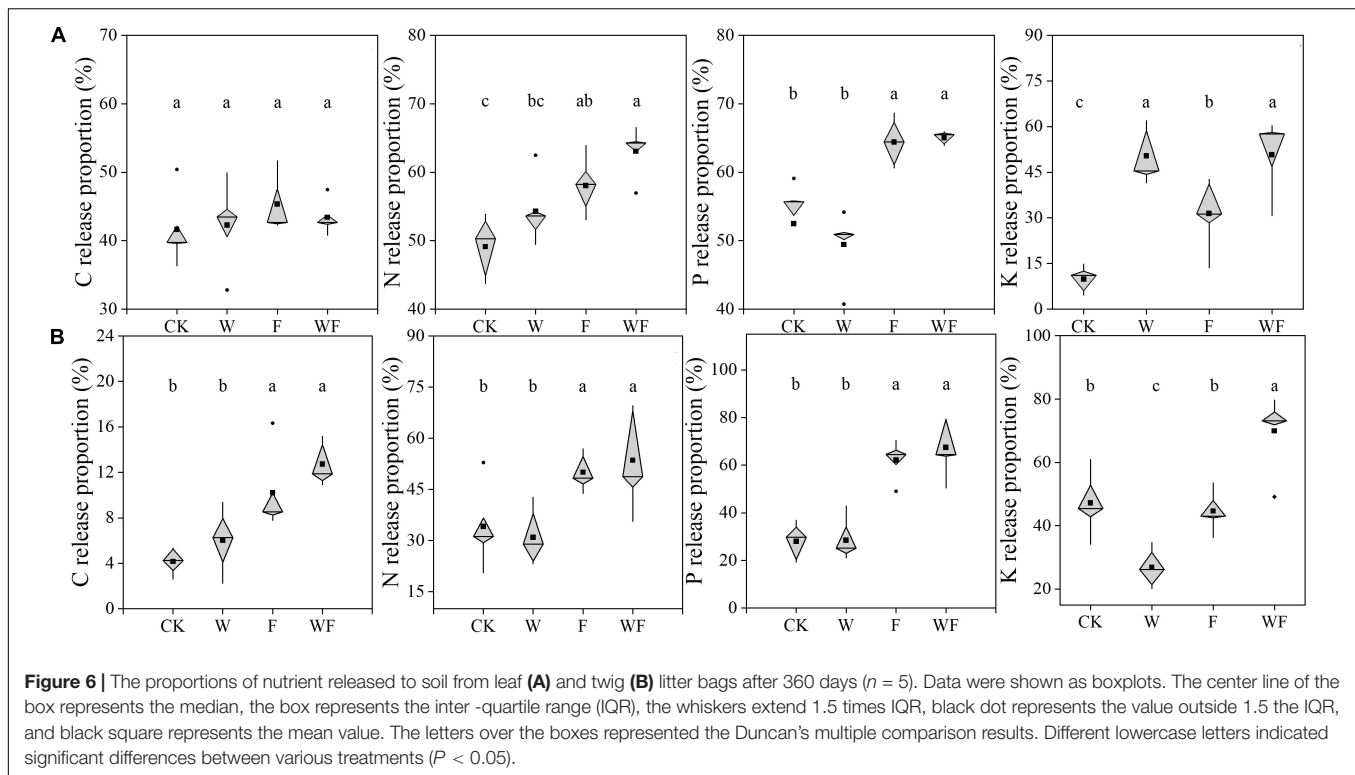
in the rainy season shaking off the dead hanging tissues (Dawoe et al., 2010).

Litter Decomposition Under Various Treatments

Litter decomposition is an important process of nutrient cycling in ecosystems (Yin et al., 2019). The decomposition of litter is mainly related to the initial nutrient concentrations (**Table 4**), which is consistent with previous studies that show decomposition rate is primarily determined by its traits. High nutrient concentration and corresponding low carbon: nutrient ratio increases litter attractiveness to microorganisms, which enhances the biodiversity and the activity of soil decomposers, resulting in higher decomposition rates (Zhang et al., 2019; Rawat et al., 2020). Since soil is the main source of plant nutrients, element concentrations in plants are affected by soil chemical properties (Bai et al., 2019). Fertilization increases the initial litter N, P, and K concentrations and decreases the C/N and C/P, while dry-season irrigation has little effect (**Table 6**). Low C/N and C/P indicates low recalcitrant substrate content and high nutrient content, facilitates microbial activity (Yin et al., 2019; Hou et al., 2021), and degrades organic matter (Zhang et al., 2019; Mora-Gómez et al., 2020). Meanwhile, the organic compounds from litter can influence the diversity and composition of microbial communities, further affecting the decomposition rates (McBride et al., 2020). In the present study, the average decomposition rate of leaf (30%) is much higher than that of twig (14%; **Table 3**). Compared to twig, the C/N and C/P of leaf are lower (**Table 6**), which is beneficial to decomposition (Zhang et al., 2019).

Generally, soil microbes secrete enzymes related to their nutrient demands, and enzyme activity is highly correlated with microbial activity (Frey et al., 2004; Li, 2006; Santos et al., 2018). Fertilization increased the activities of β -glucosidase, urease, and polyphenol oxidase, but not acid phosphatase and urease (**Supplementary Table 2**), indicating that N concentration limits microbial metabolism (Antonious, 2009; Wang et al., 2011). After fertilization, increased polyphenol oxidase activity was conductive to decompose recalcitrant polymers (such as lignin) of litterfall (Allison et al., 2008). Instead of cellulase, microbes in the soil of E. urophylla × E. grandis tend to secrete β - glucosidase to break down cellulose. Dry-season irrigation has little effect on soil enzyme activities during the dry season, which might be related to no differences in surface SWC$_r$ caused by high evaporation (**Supplementary Tables 2, 3**). Contrary to most previous studies (Salazar et al., 2011; Wang et al., 2012), the variation of soil enzyme activities is driven by foliar litter quality rather than soil nutrient (**Supplementary Tables 4, 5**). The increased soil enzyme activities under fertilization may be caused by diverse substrate availability (Christina and John, 2000; Hu et al., 2006).

Our results indicate that decomposing 50% of leaf litter takes 2.9 years (**Table 3**), longer than that (2.1 years) in tropical forests (De Queiroz et al., 2019). Compared to other Eucalyptus species, the higher C/N may be the main reason for the slow decomposition rate of E. urophylla × E. grandis litter (Demessie et al., 2012; Cizungu et al., 2014). Fertilization

Figure 6 | The proportions of nutrient released to soil from leaf **(A)** and twig **(B)** litter bags after 360 days (*n* = 5). Data were shown as boxplots. The center line of the box represents the median, the box represents the inter-quartile range (IQR), the whiskers extend 1.5 times IQR, black dot represents the value outside 1.5 the IQR, and black square represents the mean value. The letters over the boxes represented the Duncan's multiple comparison results. Different lowercase letters indicated significant differences between various treatments (*P* < 0.05).

and dry-season irrigation accelerate litter decomposition rates, which is consistent with other studies (Sanaullah et al., 2012; Petraglia et al., 2019; Liu et al., 2021). By contrast with dry-season irrigation, fertilization had greater influences on the decomposition of low quality litter (Liu et al., 2006). After litter quality was increased by fertilization, dry-season irrigation further increased the decomposition rate. In the present study, fertilization stimulates litter decomposition by increasing litter quality and soil enzyme activities (Zhong et al., 2017; Hou et al., 2021; Liu et al., 2021). However, dry-season irrigation promoted litter decomposition with relatively little effect on litter quality or soil enzymes, contrary to previous studies (Prieto et al., 2019; Malik et al., 2020). The promotion of litter decomposition by dry season irrigation may be due to an increase in soil water content, which promotes soluble fraction leaching (Schreeg et al., 2013). These findings may only indicate the short-term effects of dry-season irrigation on litterfall decomposition, and further investigation should be conducted to uncover the underlying mechanisms.

Nutrient Release

In the present study, most leaf nutrients are released under different treatments after decomposing for 360 days, which was similar to Chen's study Chen et al. (2019). The released proportion of nutrients of twig are much lower than that of leaf, especially the C (**Figure 6**). The C, N, P, and K are not released at similar proportional rates in twig, leading to the inhibition of C release at the later stage of decomposition (Yin et al., 2019; Hou et al., 2021). High nitrogen concentration (Liu et al., 2021),

high labile compounds content (Pei et al., 2019, 2020), and high surface area: volume ratio (Angst et al., 2018) of litter were all beneficial for releasing C and nutrients by improving microbial activity and contact area.

The effect of dry-season irrigation and fertilization on the proportions of released nutrients was mainly driven by the variation of initial stoichiometric characteristics (**Supplementary Table 6**). We find that fertilization increases the proportions of released N and P by increasing litter C/N and C/P, while dry-season irrigation affects the proportion of released K by increasing foliar C/K and decreasing C/K. This result is consistent with previous studies suggesting that initial stoichiometric characteristics (C/N, C/P, and C/K) were key determinants of nutrient release (Lanuza et al., 2018; Wang et al., 2021). Due to high N concentration suppressing the activity of ligninolytic enzymes, fertilization had little effect on C release of leaf (Frey et al., 2004). In previous studies, irrigation was shown to increase (Sanaullah et al., 2012; Santonja et al., 2017; Zhong et al., 2017), decrease (Walter et al., 2013), or have no effect on decomposition rate (Zhao et al., 2012), which would affect the proportions of released nutrients. However, our results show that dry-season irrigation influences the proportion of released K through C/K, but not the decomposition rate. The variation of initial C/K might be related to the change of K retranslocation under dry-season irrigation (Wan et al., 2021). Over the experimental period, fertilization and dry-season irrigation change the litter decomposition rate by affecting the stoichiometric characteristics of litter. But it is unclear how dry-season irrigation increases decomposition rate without affecting nutrient release. It is

necessary to further explore the effects of irrigation on nutrient cycling in *Eucalyptus* plantations under drier conditions.

Effect of Litterfall on Compensatory Growth

Previous studies on the effects of fertilization and irrigation on *Eucalyptus* growth have shown increased DBH, height, and biomass (Wright et al., 2011; Hua et al., 2021). In this study, fertilization and dry-season irrigation promoted the growth of DBH, height, and biomass, even though the effects of dry-season irrigation were not significant (**Supplementary Table 1**). This suggested that some compensatory responses occurred after nutrient and water restrictions were lifted. A high compensatory growth under fertilization may result from the up-regulation of photosynthesis capabilities and leaf biomass. Previous studies at this site have demonstrated that fertilization can increase photosynthesis (Hua et al., 2021) and promotes leaf growth (Yu et al., 2019a). By comparing the variations of biomass and litterfall production, it was found that the rise in biomass was much greater than that in litterfall production, promoting the growth of leaf biomass. Increased leaf biomass is especially beneficial for increasing photosynthetic products, which further enhances compensatory growth (Ma et al., 2020). Although the surface soil relative water content remained at a low level (**Supplementary Table 3**), dry-season irrigation had little effect on compensatory growth, which may be due to the utilization of deep soil water to alleviate water stress (Asensio et al., 2020). Another strategy that can be used to influence compensatory growth is altering the decomposition rate and release of nutrients in order to accelerate the nutrient cycle. The increase of decomposition rate and nutrient release under fertilization and dry-season irrigation can accelerate the nutrient cycle, and provide sufficient resources for compensatory growth (Van Staalduinen et al., 2010; Fischer et al., 2019).

CONCLUSION

Our results indicate that litterfall production of *E. urophylla* × *E. grandis* follows a seasonal pattern and its peak occurs in the rainy season. Fertilization significantly increases litterfall production (except leaf) while dry-season irrigation does not. Although temperature and rainfall are related to litterfall production, it is unclear whether this is caused by physical impacts (powerful wind or rain) or physiological characteristics. When litter enters topsoil, its decomposition is mainly affected by its traits (C/N, C/P, and C/K), followed by soil enzyme activity. Nutrients, rather than water, are the main factor limiting the litter decomposition in *E. urophylla* × *E. grandis* plantation. The positive effects of dry-season irrigation can be reflected

only when nutrient limitation is alleviated. However, irrigation has little effect on litter nutrient release, which is contrary to previous studies. Therefore, more water supplement experiments in tropical/subtropical *Eucalyptus* plantations should be done to realize the effects of dry-season irrigation on the nutrient cycle under seasonal drought. Our finding shows that plantation management not only increased stand productivity, but also played an important role in the nutrient cycle.

DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/**Supplementary Material**, further inquiries can be directed to the corresponding author.

AUTHOR CONTRIBUTIONS

JL and QQ: mainly contribute to the conceptualization of the work, funding acquisition, and investigation. JK, YL, and FH: methodology and analysis. YS, QH, and JK: project administration. WL, YS, JL, and QQ: resources. JK and WL: software. JK: visualization. QQ and QH: writing—original draft preparation. JK, QQ, and GW: writing—review, and editing. All authors have read and agreed to the version of manuscript to be published.

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SUPPLEMENTARY MATERIAL

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