

## Original Articles

# Are reproductive traits of dominant species associated with specific resource allocation strategies during forest succession in southern China?

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## ABSTRACT

Plant reproductive traits have often evolved to optimize plant fitness under different environmental conditions, and their relationships with vegetative functional traits reflect more general plant reproduction and resource allocation strategies. How those relationships change during succession remains unclear. Here, we investigated the relationships between 8 reproductive traits and 18 functional traits of leaves, stems and whole plants during succession of a subtropical forest. We found that most leaf traits of dominant species were associated with seed/fruit dispersal mode and pollination pattern in the early successional forest, while with flower and fruit phenology in the middle and late successional forests. Plant reproduction traits were associated with specific resource utilization strategies during succession, i.e., plants with acquisitive resource utilization strategies tended to have long-distance fruit dispersal in the early succession, while with conservative resource utilization strategies tended to have early flowering (fruiting) or a long flowering (fruiting) period in the late succession. Our results indicate that acquisitive species may invest less energy and resources on reproduction in early succession, and that the conservative species may invest more energy and resources on reproduction in late succession.

## 1. Introduction

Plant fitness under different environmental conditions has long been recognized to depend on reproductive functional traits (e.g., seeds) and reproductive phenology (Fitter and Fitter, 2002; Körner and Basler, 2010; Wolkovich and Cleland, 2014). Advances in studying reproductive phenology are needed to make better predictions under future environmental change (Volis and Bohrer, 2013; Wolkovich and Ettinger, 2014). However, progress towards such goals have been stymied by the high variation in reproductive traits across species. One urgent question is which reproductive traits (e.g., seed and flower phenology) are associated with species that have specific resource utilization strategies. Building upon research over the past decades, Wolkovich and Cleland (2014) pointed out that the covariance between variation in plant reproductive traits and other vegetative functional traits should be investigated under different environments. Many

studies, however, have largely ignored the role of reproductive phenology (Wright et al., 2005b; Lebrija-Trejos et al., 2010; Lohbeck et al., 2013; Salguero-Gómez et al., 2016). It is suggested that a combined investigation of reproductive traits and other plant functional traits during succession would increase our understanding of the reproductive strategies of species that differ in allocation during succession (Karlsson, 1994; Obeso, 2002; Salguero-Gómez et al., 2016; Santangelo et al., 2019).

Succession is a community assembly process, in which species replacement occurs due to the adaptation of species to changing light and water conditions (Lebrija-Trejos et al., 2010; Lohbeck et al., 2013). Because of the ecological importance and ease of measurement, leaf economic traits have often been used to represent plant adaptation and resource utilization strategies during succession (Wright et al., 2005b; Lebrija-Trejos et al., 2010; Lasky et al., 2014; Wigley et al., 2016). For example, specific leaf area (SLA) and leaf photosynthesis are usually

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considered as proxies of plant light capture and use efficiency, respectively (Wright et al., 2001; Poorter and Bongers, 2006; Wright et al., 2005b). Plant functional traits have been recognized as measurable indicators of acquisitive and conservative strategies of plants, reflecting how plants adopt and influence their habitats (Balachowski and Volaire, 2018). In general, acquisitive species have higher resource capture and growth rates than conservative species. Previous studies have found that acquisitive species in early succession generally have a high leaf maximum net photosynthetic rate per unit leaf mass ( $A_{\text{mass}}$ ), a high leaf maximum stomatal conductance rate per unit leaf mass ( $g_s$ ), a high SLA, and a high leaf stomatal density (SD), while conservative species in late succession have a high leaf dry matter content (LDMC), a high leaf thickness (LT), and a high woody density (WD) (Wright et al., 2005a; Wright et al., 2005b; Marino et al., 2010; Ali and Yan, 2017).

Theoretical arguments about plant reproductive traits suggest that reproductive phenology and seed traits have particular biological attributes, and often lead to different ecological responses to environmental gradients (Kunin and Shmida, 1997; Fitter and Fitter, 2002; Körner and Basler, 2010; Thomann et al., 2015). For example, the numbers of staminate and pistillate inflorescences of *Xanthium strumarium* are significantly greater in a resource-rich garden than in a resource-poor garden (Lechowicz and Blais, 1988). Early flowering species might be particularly sensitive to drought during seed maturation (Segrestin et al., 2018). Water availability influences the fruiting patterns of tropical plants (Primack, 1987). In addition, Lechowicz and Blais (1988) reported that sustained growth and reproduction depend not only on resource availability in the local environment but also on their allocation to structures and metabolic activities. As an example, cocklebur plants with higher rates of photosynthesis and transpiration tend to produce more fruits than those with lower rates (Lechowicz and Blais, 1988). Adler et al., (2014) found that species that invest in a few large seeds tend to have a greater influence of survival and a weaker influence of individual growth and fecundity on population growth rates. Therefore, the relationships between reproductive traits and other plant or leaf traits may be affected not only by different environmental conditions (e.g., constraints of light, water, or nutrients), but also by different resource utilization strategies of species (Ashman, 1994; Obeso, 2002; Santangelo et al., 2019). That is, the relationships between specific reproductive traits and other vegetative plant functional traits could increase our understanding of the responses of plant reproductive strategies to different environmental conditions.

In general, acquisitive species produce many small seeds, while conservative species produce a small number of large seeds (Foster and Janson, 1985). The small seeds of acquisitive species in the early succession have a higher probability of wind dispersal (a common seed/fruit dispersal mode) than the large seeds of conservative species in the late succession (Hammond and Brown, 1995). Santangelo et al., (2019) have also found certain associations between plant defenses and flower size. However, owing to the logistical challenges associated with the field measurement of reproductive phenological traits, which requires intensive and repeated sampling over time, research aimed at understanding how phenology is related to other traits has been quite limited over the past 30 years (Wolkovich and Ettinger, 2014; Lozanovska et al., 2018). Although Wolkovich and Cleland (2014) reported important associations between flowering phenology and vegetative functional traits related to return in investment for temperate herbaceous species, whether reproductive traits such as flower or fruit phenology and pollination pattern are also related to plant resource utilization strategies still requires investigation in subtropical successional forests (Lechowicz and Blais, 1988; Körner and Basler, 2010).

As a zonal vegetation type of the subtropical region in southern China, the monsoon evergreen broadleaved forest has long been disturbed by human activities (Yan et al., 2006a; Yan et al., 2006b). Our study site in this region, the Dinghushan National Nature Reserve, is now composed of several different communities, including a three-stage succession series of subtropical forest, i.e. coniferous forest (Suc-1),

mixed coniferous and broadleaved forest (Suc-2), and monsoon evergreen broadleaved forests (Suc-3). Extensive long-term studies of community structures, functions, and dynamics have been conducted in these subtropical forests, and the plant functional traits have been found to be good predictors of community dynamics (Yan et al., 2006b; Li et al., 2015; Zhang et al., 2018). Systematic researches on reproductive traits of these forests, however, are needed to understand species fitness and replacement during succession. As part of a research program on field reproductive traits in this region, we studied 8 reproductive traits, and 18 plant leaf, stem, and whole-plant traits for the dominant species in each stage of the three-stage forest succession series. By analyzing how the reproductive traits covary with other vegetative functional traits during succession, we attempted to answer the following two questions:

- 1) How do the relationships among reproductive traits vary during succession?
- 2) Are reproductive traits of specific dominant species associated with specific resource-use strategies during succession?

## 2. Materials and methods

### 2.1 Research site

This study was conducted at the Dinghushan National Nature Reserve, southern China (E 112°32'57", N 23°9'51"), which has a mean annual precipitation of 1788 mm and a mean annual temperature of 21.9 °C. Most precipitation falls from April to September, and the coldest mean monthly temperature (12.6 °C) occurs in January (Lu et al., 2018). Previous studies have determined that the forests in this nature reserve represent a three-stage forest succession series, including a coniferous forest (Suc-1, about 60 years old), a mixed coniferous broadleaved forest (Suc-2, about 100 years old), and an old-growth monsoon evergreen broadleaved forest (Suc-3, about 400 years old) (Brown et al., 1995; Ouyang et al., 2003; Mo et al., 2003; Yan et al., 2006b; Zhao et al., 2011; Liu et al., 2012; Sun et al., 2013). Among them, Suc-1 is dominated by *Pinus massoniana*, one of the coniferous species that are usually considered as acquisitive species; the Suc-2 is dominated by both coniferous and broadleaved species: *Castanea henryi*, *Schima superba* and *Pinus massoniana*; and the Suc-3 is only dominated by broadleaved species: *Macaranga sampsonii*, *Schima superba* and *Blastus cochinchinensis* (see Supplementary Table S1 for details). In addition, all the three types of forests are characterized by small hills and a low soil pH (< 4.0). The dominant species in each forest were determined as those having the sum of their "importance values" (IV) (Peng, 1996) exceeding 75% of the total IV based on the community survey in 2015 at Dinghushan (the dominant species were shown in Supplementary Table S1).

### 2.2 Plots

We established five 30 m × 30 m plots in each of the three forests in 2016; all plots had similar altitudes, slopes, and aspects. In each plot, we assessed 8 reproductive traits including seed/fruit dispersal mode (DM), pollination pattern (PP), fruit type (FT), flower and fruit phenology; and 18 vegetative traits including 16 leaf traits, 1 stem trait, and 1 whole-plant trait (Table 1). All the 24 traits were selected because they are important for competition, defense, and reproduction. The reproductive traits were assessed throughout 2016 and 2017, and vegetative plant traits were measured from June to August in 2016 and 2017. Most traits in this study were measured following the standard protocols of Cornelissen et al., (2003).

#### 2.2.1. Reproductive traits

In 2016, we randomly selected three mature individuals (females were selected for dioecious species) for each dominant species from the

**Table 1**  
Background information on the traits assessed in this study.

Trait	Kind of trait	Strategy	Specific Function	References
Dispersal mode (DM 0 = close, 1 = medium, 2 = long)	Reproductive	Reproduction	Dispersal distance, colonization chance	Hammond and Brown, 1995; Lohbeck et al., 2013
Fruit type (FT 0 = fleshy, 1 = dried)	Reproductive	Reproduction	Food for animals, dispersal structure or propagule	Cornelissen et al., 2003
Pollination pattern (PP 0 = insect, 1 = wind)	Reproductive	Reproduction	Food for insects, pollination chance,	Faegri and Van, 1979; Fenster et al., 2004
First flowering time (FFL month)	Reproductive	Reproduction	Reproduction chance, flowering phenology, response to climatic changes	Fitter and Fitter, 2002; Lohbeck et al., 2013
Length of flowering cycle (LFL month)	Reproductive	Reproduction	Reproduction chance, flowering phenology, response to climatic changes	Fitter and Fitter, 2002; Lohbeck et al., 2013
First fruiting time (FFR month)	Reproductive	Reproduction	Reproduction chance, fruiting phenology, food for animals, optimal dispersal date	Galetti et al., 1999; Chapman et al., 2005; Lohbeck et al., 2013
Length of fruiting cycle (LFR month)	Reproductive	Reproduction	Reproduction chance, fruiting phenology, food for animals, optimal dispersal date	Galetti et al., 1999; Chapman et al., 2005; Lohbeck et al., 2013
Seed mass (SM g)	Reproductive	Reproduction	Investment in reproduction, longevity in seedbanks, number of seeds	Hammond & Brown 1995, Cornelissen et al. 2003; Lohbeck et al., 2013
Leaf thickness (LT mm)	Leaf	Conservation	Construction costs, against mechanical and herbivore damage	Loranger and Shipley, 2010; Lohbeck et al., 2013
Specific leaf area (SLA cm <sup>2</sup> g <sup>-1</sup> )	Leaf	Acquisition	Light capture economics, net assimilation rate, photosynthetic capacity	Poorter and Bongers, 2006; Sterck et al., 2006; Lohbeck et al., 2013
Leaf dry matter content (LDMC g g <sup>-1</sup> )	Leaf	Conservation	Leaf longevity, against mechanical and herbivore damage, construction costs	Garnier et al., 2004; Lohbeck et al., 2013
Stoma density (SD, stoma cm <sup>-2</sup> )	Leaf	Acquisition	Leaf respiration rate, leaf gas exchange, stomatal conductance, photosynthesis rate	Wright et al., 2005a; Loranger and Shipley, 2010; Marino et al., 2010
Leaf N content (LN g Kg <sup>-1</sup> )	Leaf	Acquisition	Mass-based maximum photosynthetic rate, N availability	Cornelissen et al., 2003; Lu et al., 2018
Leaf P content (LP g Kg <sup>-1</sup> )	Leaf	Acquisition	Mass-based maximum photosynthetic rate, P availability	Cornelissen et al., 2003; Lu et al., 2018
Leaf chlorophyll content per square centimeter leaf area (GHI)	Leaf	Acquisition	Maximum photosynthetic rate, photosynthetic electron transfer efficiency	Gitelson et al., 2003
Leaf enhanced cuticle (EC 1 = yes, 0 = no)	Leaf	Conservation	Construction costs, structural defense, against herbivore damage	Pritsch et al., 2000; Chabot and Hicks, 1982
Leaf trichome (Tr 1 = yes, 0 = no)	Leaf	Conservation	Construction costs, structural defense, against herbivore damage	Levin, 1973; Pritsch et al., 2000
Leaf multi-layer epidermis (LME 1 = yes 0 = no)	Leaf	Conservation	Construction costs, structural defense, against herbivore damage	Pritsch et al., 2000; Chabot and Hicks, 1982
Leaf maximum net photosynthetic rate per leaf mass (A <sub>mass</sub> μmol CO <sub>2</sub> kg <sup>-1</sup> s <sup>-1</sup> )	Leaf	Acquisition	Plant light use efficiency, competitive capacity, leaf economic spectrum	Wright et al., 2001; Wright et al., 2005a; Wright et al., 2005b
Leaf maximum stomatal conductance per leaf mass (g, mmol H <sub>2</sub> O kg <sup>-1</sup> s <sup>-1</sup> )	Leaf	Acquisition	Plant water use efficiency, competitive capacity	Wright et al., 2001; Wright et al., 2005a; Wright et al., 2005b
Leaf dark respiration rate per leaf mass (R <sub>mass</sub> μmol CO <sub>2</sub> kg <sup>-1</sup> s <sup>-1</sup> )	Leaf	Conservation	Construction costs	Wright et al., 2005a; Wright et al., 2005b
Leaf transpiration rate per leaf mass (T <sub>mass</sub> mmol H <sub>2</sub> O kg <sup>-1</sup> s <sup>-1</sup> )	Leaf	Acquisition	Plant water use efficiency, competitive capacity, leaf economic spectrum	Wright et al., 2001; Wright et al., 2005a; Wright et al., 2005b
Leaf photosynthetic nitrogen use efficiency (PNUUE μmol C mol <sup>-1</sup> N s <sup>-1</sup> )	Leaf	Acquisition	Plant nutrient use efficiency, competitive capacity, leaf economic spectrum	Wright et al., 2001; Wright et al., 2005a; Wright et al., 2005b
Leaf photosynthetic phosphorus use efficiency (PPUE μmol C mol <sup>-1</sup> P s <sup>-1</sup> )	Leaf	Acquisition	Plant nutrient use efficiency, competitive capacity, leaf economic spectrum	Wright et al., 2001; Wright et al., 2005a; Wright et al., 2005b
Wood density (WD g cm <sup>-3</sup> )	Stem	Conservation	Construction costs, against mechanical and herbivore damage	Baker et al., 2010; Zhu et al., 2015
Maximum height (H m)	Whole-plant	Acquisition	Plant competitive capacity, light use strategies	Baker et al., 2010; Zhu et al., 2015

**Notes:** The strategy with high values of these traits refer to: Acquisition = acquisitive effort, Conservation = conservative effort, Reproduction = reproductive effort (Marino et al., 2010).

**Table 2**  
Methods for the measurements of plant flower and fruit phenology in 2016 and 2017.

Plant phenology traits	Abbreviations	Descriptions
First flowering (fruiting) time	FFL or FFR (month)	Total days from 1 January to first flowering (fruiting) divided by 30
Maximum flowering (fruiting) time	MFL or MFR (month)	Total days from 1 January to maximum flower (fruit) count on each tree divided by 30
Length of flowering (fruiting) period	LFL or LFR (month)	Total days that plant remained in bloom or fruit divided by 30

five 30 m × 30 m plots in each forest. Flowering and fruiting phenology were monitored at a 15-d intervals for a total of 24–25 census days in 2016 and again in 2017 (Giménez-Benavides et al., 2006). At each census, we recorded whether there were any flowers or fruits on each tree. We also collected mature fruits from each individual tree and removed their appendage (e.g., pulp) to obtain the seeds. The seed mass was measured as the dry weight of 1000 seeds because many of them were too small to be weighed individually. PP, DM, and FT were determined based on field observations, local informants, and literatures (Pei, 2011; Lin, 2012).

Flowering and fruiting phenology were characterized for each dominant species by measuring three variables (Table 2): (1) first flowering or fruiting time (FFL or FFR), i.e., the total days from 1 January to first flowering or fruiting divided by 30; (2) maximum flowering or fruiting time (MFL or MFR), i.e., the total days from 1 January to the day of maximum flower or fruit count on each tree divided by 30; (3) the length of flowering or fruiting period (LFL or LFR), i.e., total days that the individuals remained in bloom or fruit divided by 30 (Giménez-Benavides et al., 2006). Because strong positive correlations between FFL and MFL, and between EFR and MFR were found in our pilot study, we selected FFL, FFR, LFL, and LFR as the flowering and fruiting phenology traits.

### 2.2.2. Leaf functional traits

We sampled 50–100 fully expanded outer canopy leaves for each dominant species in each plot in 2016 and again in 2017. To maintain moisture, the leaves were sealed in polyethylene bags and transported to the laboratory within 3 h. LT was measured by a thousandths digital thickness gauge (EXPLOIT, China) for 15–20 leaves, which were also used to measure chlorophyll content per unit area (CHI) with a SPAD-502Plus chlorophyll meter (Konica Minolta, China) (Rozenaal et al., 2006). SLA was defined as leaf area (LA) divided by leaf dry weight (DW). Leaf mass per area (LMA) was defined as the DW divided by LA. LA was measured with a LI-3000C portable area meter (LI-COR, USA). The fresh weight (FW) was defined as the leaf weight minus the leaf petiole. DW was determined after leaves were oven-dried at 60 °C for 72 h. Leaf dry matter content (LDMC) was defined as DW divided by FW. Leaf N and P content were measured by the modified Kjeldahl method, and molybdenum anti-colorimetric method, respectively (Dong, 1997). We also used a stereo-microscope (JSM-6360LV, Japan) to determine the stomatal density (SD).

During June to August in 2016 and 2017, a LI-COR 6400 photosynthesis system (LI-COR, USA) was used to measure the leaf physiological traits per leaf area (this was done with fully developed mature leaves in the morning of each day between 8:30–12:00am). We measured 3–6 light response curves for each dominant species. The light intensity gradient was set as 1600, 1200, 1000, 800, 600, 400, 200, 100, 50, 20, or 0  $\mu\text{mol m}^{-2} \text{s}^{-1}$  with a red-blue LED light source; the chamber temperature was set at 25 °C, and the CO<sub>2</sub> concentration was set at 400  $\mu\text{mol mol}^{-1}$  (Lu et al., 2018). By using a light curve-fitting SAS program (Dubois et al., 2010), we calculated the maximum net photosynthetic rate per unit of leaf area ( $A_{\text{area}}$ ), maximum transpiration rate per unit of leaf area ( $T_{\text{area}}$ ), maximum stomatal conductance per unit of leaf area ( $g_a$ ), and leaf dark respiration rate per unit of leaf area ( $R_{\text{area}}$ ). The physiological traits per leaf mass were calculated by dividing by LMA (i.e.,  $A_{\text{mass}} = A_{\text{area}}/\text{LMA}$ ;  $T_{\text{mass}} = T_{\text{area}}/\text{LMA}$ ;  $R_{\text{mass}} = R_{\text{area}}/\text{LMA}$ ;  $g_s = g_a/\text{LMA}$ ) (Osnas et al., 2013). Photosynthetic

N-use efficiency (PNUE) and photosynthetic P-use efficiency (PPUE) were determined as the ratio of  $A_{\text{mass}}$  to leaf N, P content, respectively (Wright et al., 2005b).

Using a stereo-microscope (JSM-6360LV, Japan), we determined whether a multi-layered epidermis (MLE), trichomes (Tr), or enhanced cuticles (EC) were evident on five leaves for each species (Chen and Huang, 2013). EC was defined based on the cuticle thickness in young and mature leaves. If the mature leaves were thicker than young leaves, we recorded the cuticle of mature leaves as “enhanced” (Kursar and Coley, 1992; Chen and Huang, 2013).

### 2.2.3. Other traits

Wood density (WD) (stem-specific density) was defined as the oven-dry weight of the main stem divided by its volume. According to Cornelissen et al. (2003), the volume was measured by volume replacement method. We determined WD for five individuals of each species in each forest. In addition, the tree height (H) was determined for 20–30 mature tree in each forest.

### 2.3. Statistical analysis

Because of the wide range of values for most traits among different species and the high species turnover during succession, we used the average trait values for each species to answer our questions, although we recognize that intraspecific trait variation might be important in species adaptation during succession (Lohbeck et al., 2013; Plourde et al., 2015). All functional traits except the categorical traits were log<sub>10</sub>-transformed before regression analysis. We also averaged the data of two years for each trait of each species in each forest to reduce the influence of year and to obtain more accurate estimations. Linear regression was used to assess the relationships among traits because it can deal with the naturally occurring variations in reproductive costs (Reznick, 1985). Standardized major axis (SMA) regression was used to assess the relationships between two traits because it can describe the best-fit scaling relationship between traits (Leishman et al., 2007; Crous et al., 2017). Statistical significance was set at  $P < 0.05$ . Data analysis was conducted using packages “psych”, “smatr”, and “ade4” in R 3.4.4 (Warton et al., 2012; Bougeard and Dray, 2018; Revell, 2018).

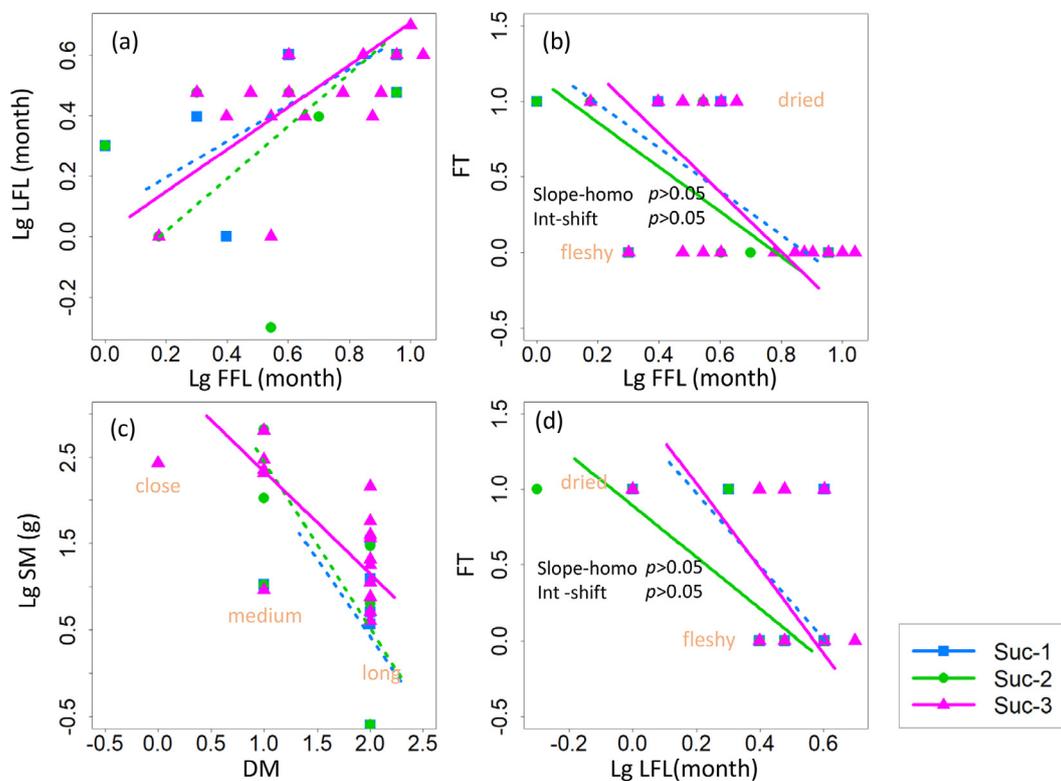
## 3. Results

### 3.1. Relationships among reproductive traits during succession

The relationship between FFL and LFL was significantly positive in Suc-3, but not in Suc-1 or Suc-2 (Fig. 1a; Table S2). FFL was negatively related to FT in Suc-2 and Suc-3, and the slopes and intercepts of their fitted lines were not different (Fig. 1b; Table S2). A negative relationship between DM and SM was evident only in Suc-3 (Fig. 1c; Table S2). LFL was negatively related to FT in Suc-2 and Suc-3, and neither the slopes nor intercepts of the fitted lines differed between the two successional stages (Fig. 1d; Table S2).

### 3.2. Relationships between reproductive traits and vegetative traits during succession

We detected many significant relationships between reproductive traits and other vegetative traits. DM was positively related to  $A_{\text{mass}}$ ,  $g_s$ ,



**Fig. 1.** Relationships among reproductive traits in three successional stages (Suc-1, Suc-2, and Suc-3) in Dinghushan. Suc-1, Suc-2, and Suc-3 represent the coniferous forest, mixed coniferous broadleaved forest, and monsoon evergreen broadleaved forest, respectively. (a) first flowering time (FFL) vs. length of flowering cycle (LFL); (b) FFL vs. fruit type (FT); (c) seed/fruit dispersal mode (DM) vs. seed mass (SM); and (d) LFL vs. FT. All values are shown on a log<sub>10</sub> scale except those for FT and DM. Standardized major axis (SMA) analyses were performed at the species level (average value for observations of three individual trees for reproductive traits) among three successional stages in Dinghushan. Solid lines and dotted lines indicate that the fitted lines are significant, and non-significant, respectively. “Slope-homo” and “Int-shift” indicate the significance of the SMA tests for slope heterogeneity and intercept shift; “dried” and “fleshy” indicate dried fruit and fleshy fruit; “close”, “medium”, and “long” indicate close-, medium-, and long-distance fruit dispersal, respectively.

$R_{mass}$ , SLA, and SD in Suc-1 (Fig. 2a, b, c, d, e; Table S2), and was negatively related to LT in Suc-1 (Fig. 2f; Table S2). We found the PP had negative relationships with  $A_{mass}$ ,  $g_s$ ,  $R_{mass}$ , SLA, and SD in Suc-1 or Suc-2 (Fig. S1a, b, c, d, e; Table S2) and had a positive relationship with LT in Suc-1 (Fig. S1f; Table S2).

The relationship between FFL and  $R_{mass}$  was positive in Suc-3 (Fig. 3a; Table S2). LFL was positively related to LDMC in Suc-2 and Suc-3 (Fig. 3b; Table S2), and negatively related to H in Suc-3 (Fig. 3c; Table S2). For the relationship between LFL and LDMC, the slopes and intercepts of the fitted lines did not significantly differ between Suc-2 and Suc-3.

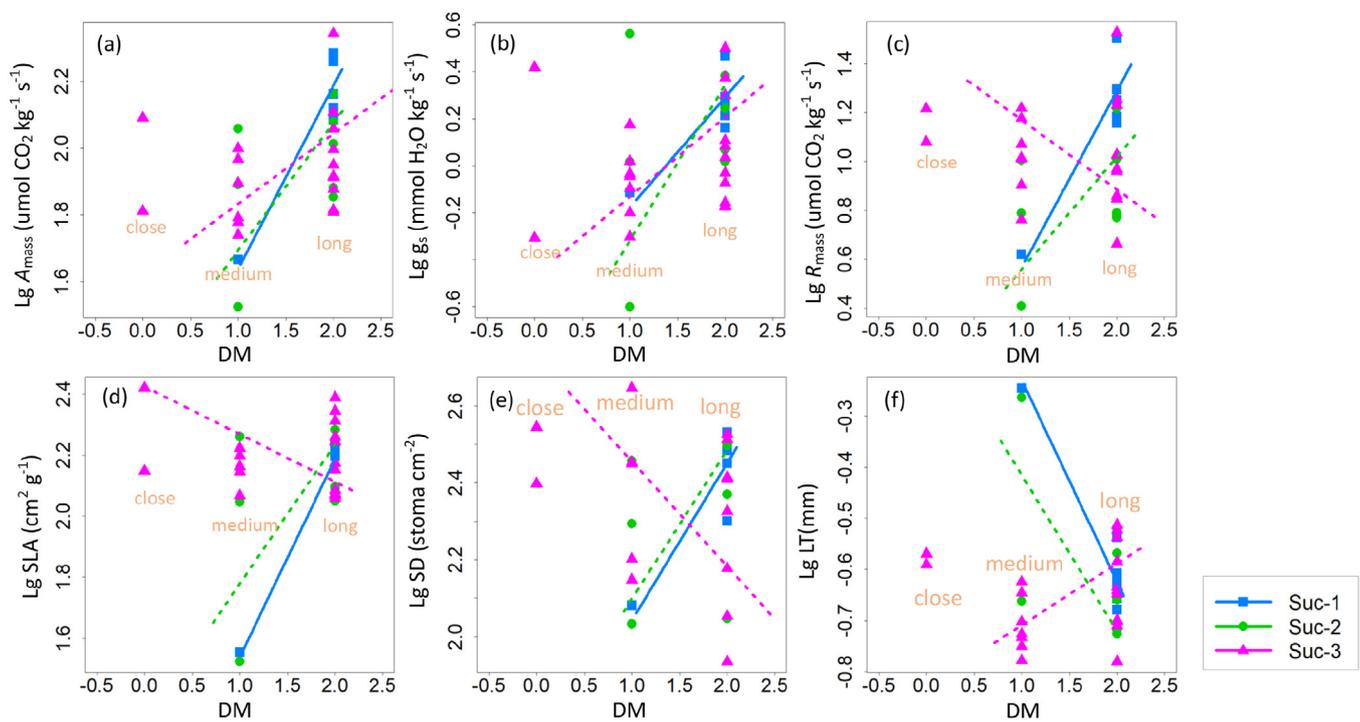
FFR was negatively related to MLE and LDMC in Suc-3 (Fig. 3d, e; Table S2). The relationship between LFR and WD was significantly positive in Suc-3 (Fig. 3f; Table S2).

## 4. Discussion

### 4.1. Changes in relationships among reproductive traits during succession

Our results showed that almost all the significant relationships among reproductive traits were observed in the middle or late succession (Suc-2 and 3), rather than in the early succession (Suc-1). The different relationships among FFL, LFL, and FT suggested that, in the middle or late succession, early flowering plants tended to have shorter flowering periods and higher probabilities of dried fruits than later flowering plants. In general, the timing of flowering is usually linked to the abundance of pollinators (Primack, 1987; Sandring and Ågren, 2009; Segrestin et al., 2018). We therefore infer that the early flowering species in our study may be associated with the strength of wind, because these species tend to bloom between January to February when

the wind is stronger than other times; and also because the taller height of them (Fig. 1a, 3c) than other species in the communities, which may contribute to wind pollination. The observation that these early flowering species have a shorter flowering period than late flowering species may be because a long flowering period would require a substantial investment of energy and resources when the climate is cold, which is not an optimal resource allocation strategy (Williams, 1966; Levis, 1968). In addition, the time-size trade-off hypothesis predicts that early flowering species would have a longer time to mature seeds than later flowering species (Bolmgren and Cowan, 2008; Segrestin et al., 2018), that may also be a reason for our finding that early flowering species have short flowering period since they may need more time to mature seeds. The high probability of dried fruits associated with early flowering species could also be explained by the greater height of the early flowering species, because seed/fruit dispersal by wind would be more efficient than other dispersal modes (e.g., by animals) in the relatively open environment of the upper canopy. In contrast, the later flowering species tend to have long flowering periods and high probabilities of fleshy fruits in the late succession. This could be caused by the relatively low height as well as the coincidence between the flowering/fruitletting time and a period when most insects and animals are active (which promote pollination and dispersal) (Thompson and Willson, 1979; Primack, 1987). Meanwhile, the time-size trade-off hypothesis suggests that species flower later may have a short seed maturation period to decrease the potential seed exposure in stressful conditions, may indirectly explain the association between later flowering and long flowering period (Bolmgren and Cowan, 2008; Segrestin et al., 2018). We therefore speculate that in the late succession, early flowering species mainly depend on wind pollination, while later flowering species mainly depend on biotic pollination. This would be consistent with



**Fig. 2.** Relationships between seed/fruit dispersal mode (DM) and other plant traits in three successional stages (Suc-1, Suc-2, and Suc-3) in Dinghushan. Suc-1, Suc-2, and Suc-3 represent the coniferous forest, mixed coniferous broadleaved forest, and monsoon evergreen broadleaved forest, respectively. (a) DM vs. mass-based leaf light-saturated photosynthesis ( $A_{\text{mass}}$ ); (b) DM vs. mass-based leaf stomatal conductance ( $g_s$ ); (c) DM vs. mass-based leaf respiration rate ( $R_{\text{mass}}$ ); (d) DM vs. specific leaf area (SLA); (e) DM vs. stomatal density (SD); and (f) DM vs. leaf thickness (LT). All values were shown on a log<sub>10</sub> scale except those for DM. Standardized major axis (SMA) analyses were performed at the species level (average value of observations for three reproductive traits and five individual trees for other plant traits) among three successional stages in Dinghushan. Solid lines and dotted lines indicate that the fitted lines are significant, and non-significant, respectively. “close”, “medium”, and “long” indicate close-, medium-, and long-distance fruit dispersal, respectively.

the finding that herbivory is more likely in the late than in the early succession at our study site (Peng and Ren, 1998).

#### 4.2. Changes in relationships between reproductive traits and other plant traits

One important finding in our study was that most leaf traits were associated with DM, and PP in the early succession, while with flower and fruit phenology in the late succession (some leaf traits were also associated with flower and fruit phenology in the middle succession). According to Bawa (2016), our finding may be because that most dominant species mainly depend on long-distance dispersal in the relatively open environments in the early successional forests (Fig. 2). In the late successional forests, in contrast, plants must diversify their reproductive phenology to sustain their suitable niche owing to the closed, competitive environment (Figs. 1, 3). This observation is consistent with the theoretical arguments that different plant reproductive traits may respond differently to environmental conditions (Jacquelyn et al., 2012).

##### 4.2.1. Early successional stage

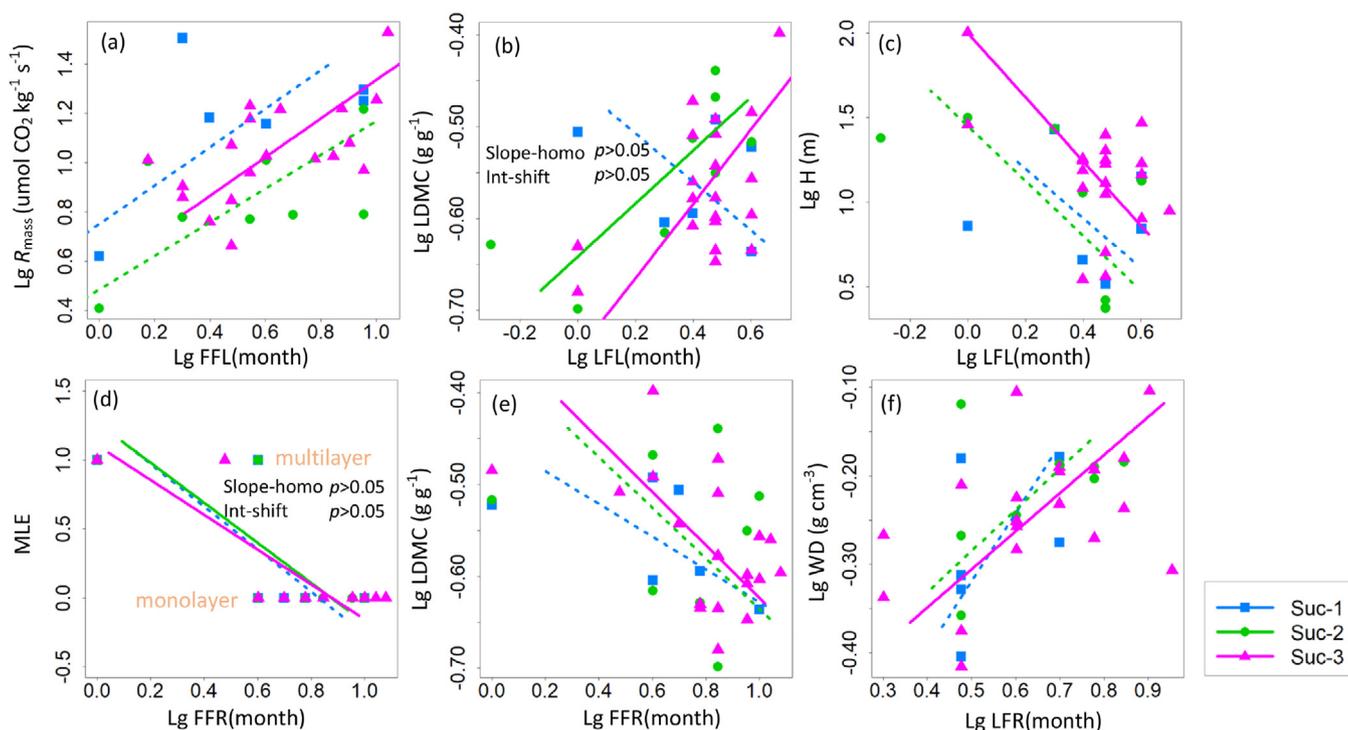
Reproductive traits in the early succession should be related to functional traits that represent the attributes of acquisitive species (e.g., high  $A_{\text{mass}}$ , high SLA, and high SD) based on the trade-offs between growth and reproduction and the relative dominance of acquisitive species in the early successional forest (Reekie and Bazzaz, 1987; Lohbeck et al., 2013). In current study, the dominant species in the early succession were found to have high values for leaf photosynthesis rate, respiration rate, stomatal conductance, stomatal density, and SLA, but low values of LT. That is, the characters of acquisitive species in this study were usually associated with the attributes of long-distance fruit dispersal. In general, wind-pollinated species typically have small

flowers in which elements of the perianth have been reduced or even lost (Primack, 1987; Warring et al., 2016). Fruits that are wind-dispersed tend to be small and light in weight, and their dispersal distances are greater than those of large fruits (Augsburger, 1986; Segrestin et al., 2018). In our study, although we did not measure the sizes of flowers and fruits of the dominant species, we observed that the flowers and fruits of the dominant species tended to be smaller in the early than late succession (personal observations), which was proved by many previous studies (e.g., Jansen et al., 2008; Lohbeck et al., 2013; Warring et al., 2016).

In a review, Primack (1987) showed that species with small seeds tend to occupy habitats that are relatively sunnier, drier and more disturbed. We also found that the acquisitive species in our study tended to have small seeds and fruits, and were mostly distributed in the relatively open and dry early successional forest. Segrestin et al. (2018) reported that seed mass is significantly lower in wind-dispersed than in animal- and gravity-dispersed species. Obeso (2002) showed that plants with larger flowers generally invest more resources in reproduction than those with smaller flowers, and there must be a trade-off in resource allocation between vegetative growth and reproduction. We therefore speculate that, in terms of resource allocation, acquisitive species in the early succession may invest less energy and resources in reproduction than conservative species.

##### 4.2.2. Middle or late successional stage

Reproductive traits in the late succession should be related to traits that represent the attributes of conservative species (i.e., high LDMC, WD, LT, multilayer epidermis, low  $R_{\text{mass}}$ , and low H). In this study, flower and fruit phenology had significant relationships with these conservative attributes of plants in the late succession (some of these relationships were also significant in middle succession). In terms of flower phenology, we found that early flowering species tended to have



**Fig. 3.** Relationships between flower and fruit phenology traits and other plant traits in three successional stages (Suc-1, Suc-2, and Suc-3) in Dinghushan. Suc-1, Suc-2, and Suc-3 represent the coniferous forest, mixed coniferous broadleaved forest, and monsoon evergreen broadleaved forest, respectively. (a) first flowering time (FFL) vs. mass-based leaf respiration rate ( $R_{mass}$ ); (b) length of flowering cycle (LFL) vs. leaf dry matter content (LDMC); (c) LFL vs. tree height (H); (d) first fruiting time (FFR) vs. the number layer of epidermal cell of leaf (MLE); (e) FFR vs. LDMC; and (f) length of fruiting cycle (LFR) vs. wood density (WD). All values were shown on a  $\log_{10}$  scale except those for MLE. Standardized major axis (SMA) analyses were performed at the species level (average value for observations of three individual trees for reproductive traits) among three successional stages in Dinghushan. Solid lines and dotted lines indicate that the fitted lines are significant, and non-significant, respectively. “Slope-homo” and “Int-shift” indicate the significance of the SMA tests for slope heterogeneity and intercept shift; “multilayer” and “monolayer” indicate that the leaf epidemic cell was multilayer or monolayer.

lower respiration rates than the later blooming species; and the species with a longer flowering period tended to have a lower tree height and a higher LDMC value than species with a shorter flowering period. Given that a high value of LDMC, a low rate of leaf respiration, and a low tree height are typical traits of conservative species (Lohbeck et al., 2013), our results indicate that the dominant conservative species in the late (or middle) successional stage are associated with either an early flowering (fruiting) or a long flowering (fruiting) period. Plants are expected to invest more energy and resources into reproduction if they have a longer flowering period that would enable the success of pollination by specific pollinators. They would need this increased investment to maintain and also to deal with the flowers that are easily damaged by other biotic or abiotic factors during a long period of exposure (Santangelo et al., 2019). This explanation is consistent with the finding that fruit development will normally occur as rapidly as possible to minimize exposure to seed predators and to minimize metabolic costs (Augspurger, 1981; Primack, 1987; Bolmgren and Cowan, 2008; Segrestin et al., 2018). Because of a lack of relevant data, however, additional studies are needed to clarify the trade-offs between reproduction investments and growth investments during succession in subtropical forests in the future.

In the late succession, we also found that the earlier fruiting species tended to have leaves with a multilayer epidermis and high LDMC values, while species with later and longer fruiting periods tended to have high WD values. Conservative species of late successional stages generally have a multilayer leaf epidermis and high values for LDMC and WD (Lohbeck et al. 2013), and are associated with either an early fruiting or a long fruiting period. Plants are expected to invest more energy and resources in fruits if they have a long fruiting period.

## 5. Conclusions

Our study of subtropical dominant trees shows that reproductive strategies are usually associated with different resource utilization strategies in different successional stages. In the lower subtropical region of China, acquisitive species appear to invest less energy and resources on reproduction in the early succession, while the conservative species appear to invest more energy and resources on reproduction in the late succession. Plants with acquisitive strategies tend to have long-distance fruit dispersal in the early succession. Plants with conservative strategies tend to have early flowering (fruiting) or a long flowering (fruiting) period in the late succession. Our results also indicate that early flowering species mainly depend on wind pollination, while later flowering species mainly depend on biotic pollination in late succession. Our analyses on the relationships between vegetative functional traits and reproductive traits can help us better understanding plant adaptation to successional environmental changes. Owing to the lower variations of reproductive phenology compared with conservative species, we suggest that the acquisitive species might be ideal candidates for predicting the global climate change using plant phenology.

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## Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ecolind.2019.03.007>.

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