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Changes in defense traits of young leaves in subtropical forests succession

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Abstract Plants develop diverse adaptive traits in changeable environments, yet whether plant defense traits change during succession remains unclear. In this study, we investigated the young leaf physical traits (i.e., upright orientation of leaves, trichomes, an enhanced cuticle, and a multilayered epidermis) and leaf color trait (i.e., red pigmentation) of dominant plants in three subtropical forests. These forests included a pioneer forest, a mixed coniferous-broad-leaved forest, and a monsoon-evergreen broadleaved forest representing early, middle, and later successional stages, respectively. Our results show that the red color trait in young leaves is related to anti-herbivory defense, and the percentage of species with red young leaves is higher in later than in early succession. Physical defense tends to be weaker for red young leaves than for green young leaves in early and middle successions. In addition, the number of defense traits of young leaves increases with succession. We speculate that young leaves in subtropical forests depend increasingly on multiple defense traits during succession because of the increased biotic stresses and environmental complexity in later succession.

Keywords Adaptation · Environmental stress · Multiple defense · Red leaves · Successional stage

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Introduction

Across a growing season, the leaf color of many woody plants changes from green to pink or red (Archetti et al. 2009; Chen and Huang 2013). The red color in leaves results from the accumulation of anthocyanin, one of the most conspicuous classes of flavonoids together with proanthocyanidins and flavonols (Grotewold 2006). There are presently two major hypotheses regarding the development of red leaves (Schaefer and Wilkinson 2004; Tattini et al. 2014; Landi et al. 2015). First, the photo-protection hypothesis predicts that anthocyanin may directly shield leaf tissues from the harmful effects of light, thereby reducing photo-oxidative stress (Lee and Gould 2002), and may also indirectly protect leaf tissues by blocking reactive oxygen stress and possibly other photo-reactive molecules (Manetas et al. 2002; Mittler 2002). Second, the coevolution hypothesis states that anthocyanin and the red color in leaves reflect increased chemical defense against herbivory by insects (Archetti et al. 2009). In both the hypotheses, the accumulation of anthocyanin appears to be an adaptive response to stress for plants. The metabolic pathways of many secondary metabolites that function as plant defense compounds normally share the same pathways responsible for anthocyanin synthesis and accumulation. Thus, the changes in leaf color from green to red may be a general indicator of defense mechanisms that enable plant to respond to the complex environmental stresses (especially from the herbivory) (Kursar and Coley 1992).

Plant structural (physical) defense is an important herbivory-resistance mechanism. Hanley et al. (2007) defined physical defense as any morphological or anatomic trait that confers a fitness advantage to the plant by directly deterring herbivores' feeding. Many physical defense traits have been investigated, including various types of spines and thorns, trichomes, and toughened or hardened leaves (Wagner 1991; Pritsch et al. 2000). Trichomes are hair-like appendages that extend from the epidermis of aerial tissues (Levin 1973). For example, in North America, the trichomes of *Verbascum thapsus* may act as a structural defense against grasshoppers and may also protect young leaves from water loss (Woodman and Fernandes 1991). Although trichomes may have evolved as physical barriers against water loss and excessive heat gain (Gutschick 1999), they also have the function of protecting plant tissues from UV radiation and herbivory (Hanley et al. 2007). Toughened or hardened leaves reduce wilting and increase water or nutrient conservation (Iii and Pugnaire 1993; Lamont et al. 2002; Chabot and Hicks 1982). Other studies have also demonstrated that leaf toughness may affect invertebrate herbivory (Erickson et al. 2004). In addition, an enhanced cuticle may reduce water loss from leaves as well (Kirkwood 1999).

Plant succession usually involves changes in plant traits that reflect the relationship between plants and their environments. In other words, plants may develop different functional traits to adapt to changing biotic and abiotic conditions (Raevel et al. 2012). However, most studies on plant defense have so far focused on secondary metabolites or hormones produced by plants (Bennett and Wallsgrove 1994; Bari and Jones 2009). The relative role of defense traits during succession has rarely been examined (Moles et al. 2011; Eichenberg et al. 2015). Furthermore, as the emerging leaves on mature plants may be more vulnerable to herbivory than mature leaves (Hanley et al. 2007), the defense of young leaves may be especially important for plants (Barton and Koricheva 2010). Information on how defense traits of young leaves change with succession is critically needed for better understanding of the interactions between plant defenses and environmental changes.

To explore the changes in plant defense during succession, we assess the defense traits (i.e., upright orientation of leaves, trichomes, an enhanced cuticle, a multilayered epidermis, and a red color in leaves) in young leaves of the dominant species in three successional forests in South China. The forests represent early, middle, and later successional stages: a pioneer forest, a mixed coniferous-broadleaved forest, and a monsoon-evergreen broadleaved forest. Extensive studies have demonstrated that the available resources gradually decrease during forest succession, while competition and biodiversity (including the number of herbivore species) increase with succession (Davidson 1993; Peng and Ren 1998; Guo 2003). In addition, Kursar and Coley (1992) reported that delayed greening (red leaves) had evolved as a mechanism for minimizing losses to herbivores and such plants could benefit more from the low light intensity over the high light intensity. We here aim to answer the following questions: (1) Is the percentage of species with red young leaves higher in later than in early succession owing to the lower light intensity in later succession? (2) Do green young leaves have higher number of physical defense traits than red young leaves, and what may such possible changes be related to? (3) Does the number of defense traits change in young leaves during subtropical forest succession?

Materials and methods

Study area

This study was conducted at the Dinghushan Forest Ecosystem Research Station, which is one of the five regional background research stations of Chinese Ecosystem Research Network (CERN) (Wu et al.

2016). Located in the northeastern suburb of Zhaoqing, about 80 km from Guangzhou (E112°32′57″, N23°9′51″), the site is on a hill top and has an area of 1155 km^2 and a subtropical humid monsoon climate. The mean annual temperature is about 21.0 °C, with an average monthly high of 28 °C in July and an average monthly low of 12.6 °C in January. The annual rainfall is about 1927 mm (Liu et al. 2015), and more than 80% of the rainfall occurs from summer to early fall (Zhou et al. 2007). The key vegetation types include pioneer forest (PF), mixed coniferous-broad-leaved forest (MF) and monsoon evergreen broad-leaved forest (BF), and these represent three successional stages (Zhou et al. 2007). Additional details regarding the species composition of the three forests are provided in "Appendix 1".

Field sampling and laboratory analysis

In a survey of the three forests (PF, MF, and BF) in 2010, we counted the number of plant species and the number of individuals for each species. We then used these data to determine importance values (IV) for these species in each forest. IV was calculated as follows:

$$\mathrm{IV} = (\text{relative density} + \text{relative dominance} + \text{relative frequency})/3 \quad (1)$$

IV = (relative density + relative dominance + relative frequency)/3.

Based on IV values (see "Appendix 1"), we identified the dominant species in each forest as the ones with the highest IV values. The sum of IV values of these species represented > 80% of the sum of all IV values in each forest (Peng 1996).

To examine the relationship between red leaves and the function of anti-herbivory, we randomly selected eight dominant species in the three forests (PF, MF and BF) in 2015 (all mature leaves of the eight species were green). We examined 3–5 trees of each species, and sampled 5–10 young and mature leaves from each tree and then counted the punctured (with herbivory) and unbroken leaves (without herbivory). The young leaves were about 30–50% smaller than mature leaves (Chen and Huang 2013). Based on previous research concerning the defense traits of young leaves (Chen and Huang 2013), we characterized the physical defense in terms of leaf orientation (an upright orientation was considered defensive) and the presence of trichomes, an enhanced cuticle, and a multilayered epidermis.

From May to August in 2015, during which time the young leaves of most plant species emerged, young and mature leaves of the selected dominant species were randomly sampled in each forest in the morning. We randomly selected three mature trees of each dominant species in each forest. Five young leaves and five mature leaves were then collected from a twig on each individual tree (Heil and Ton 2008; Eichenberg et al. 2015). We recorded whether the leaves were horizontal or upright based on assessment of at least 15 leaves from three trees per species. The fresh leaves were then placed in coolers with ice packs and were transported to the laboratory for further examination.

Because many species with red pigments in their leaves lack visible red pigments on the leaf surface (Chen and Huang 2013), we determined leaf coloration, i.e., the presence of visible red pigments in leaf cells by dissecting and examining both the adaxial and abaxial surface of each leaf with a microscope (LIOO JS-500). Following Chen and Huang (2013), we also assessed each leaf for trichomes, enhanced cuticles, and multilayered epidermis with a stereomicroscope (INSTRUMENT JSM-6360). We determined whether cuticles were enhanced based on the cuticle thickness in young and mature leaves. Because the trait of upright leaves might be correlated with plant defense mechanisms and solar radiation interception (Gutterman and Chauser-Volfson 2000; Sangoi et al. 2002), we also considered the presence of upright leaves as one physical defense trait. Due to plant physical defense being a combination of multiple traits, we considered the species characterized by physical defense if they had one or more physical defense traits. The detailed defense traits were given in "Appendix 2".

Statistical analysis

To minimize possible ontogenetic influence on the relationship between leaf red color and the function of anti-herbivory, we calculated the leaf predation probability (LPP) by the punctured/unbroken leaf ratio in young and mature leaves respectively. We then calculated the LPP_{young}/LPP_{mature} (Y/M) ratio to determine if the young leaves were more inclined to be eaten (Table 1). The nonparametric Mann–Whitney

Table 1 The comparison of leaf predation probability (LPP) values in relation to leaf color and age (young vs. mature) across different successional stages of subtropical forests in South China

Succession stage	Species	Young leaf		Mature leaf		Y/M
		Leaf color	LPP	Leaf color	LPP	
PF	*Pinus massoniana*	G	0.21	G	0.28	0.74
PF	*Toxicodendron succedaneum*	R	0.14	G	0.24	0.59
MF	*Castanea henryi*	R	0.26	G	0.53	0.50
MF	*Schima superba*	R	0.20	G	0.52	0.38
MF	*Psychotria rubra*	G	1.00	G	0.82	1.22
BF	*Aporosa yunnanensis*	G	0.43	G	0.56	0.77
BF	*Blastus cochinchinensis*	R	0.35	G	0.67	0.52
BF	*Cryptocarya concinna*	R	0.30	G	0.45	0.67

Notes PF, MF, and BF represent coniferous forest (early succession), mixed coniferous-broadleaved forest (middle succession), and monsoon-evergreen broadleaved forest (later succession), respectively. *G* green, *R* red, and Y/M = LPP_{young}/LPP_{mature}

U-tests were used to determine if there were differences in Y/M between species with red young leaves and those with green young leaves (with one-tailed *p*-values). We characterized the function of anti-herbivory of young leaves in terms of leaf color. For example, red leaves may indicate the presence of anti-herbivory only if the Y/M is significantly higher in species with green young leaves than that with red young leaves. In addition, we also used the nonparametric Wilcoxon Signed Ranks Test to affirm if the LPP was different between young leaves and mature leaves in all dominant species (with two-tailed *p*-values) and if the LPP of young leaves was lower than mature leaves in all species with red young leaves (with one-tailed p-values).

To determine if the leaves had enhanced cuticles, we used independent-sample *t*-tests (if homogeneity of variance and normal distribution could be demonstrated) or Mann–Whitney *U*-tests to compare the cuticle thickness between young and mature leaves for each species. If the thickness was greater for young leaves than for mature leaves, we recorded the cuticle of young leaves as enhanced; if the thickness was greater for mature leaves than for young leaves, we recorded the cuticle of mature leaves as enhanced (Kursar and Coley 1992; Chen and Huang 2013). Because the number of dominant species differed among the three forests, we calculated the percentage of dominant species young leaves (red or green) of which exhibited the indicated defense traits (Table 2). We then used G-tests to determine whether defense traits differed among the three forests. We used Benjamini–Hochberg procedure to correct the significance results of G-tests when comparing defense traits across all successional stages and the given p-values of such analysis in the Result were all corrected.

Results

Comparisons of LPPs between leaf color and age (young vs. mature)

Mann–Whitney *U*-tests and Wilcoxon Signed Ranks Tests showed that the LPP of young leaves of all selected species was not different from that of mature leaves ($Z = -1.82$, $p = 0.07$). For the species with red young leaves, however, LPP was significantly lower than in that mature leaves ($Z = -2.02$, $p = 0.04$). In addition, the Y/M of species with green young leaves was significantly higher than that of the species with red young leaves ($Z = -2.24$, $p = 0.01$).

Changes in leaf color with succession and age (young vs. mature)

The percentage of dominant species with red young leaves increased from 14% in the PF (early succession), to 50% in the MF (middle succession), and to 62% in the BF (later succession) (Fig. 1). However, *G*-tests showed that the percentage of species with red

Table 2 The leaf colors of young and mature leaves in different successional stages of subtropical forests in South China

Succession stage	Species	Young leaf color	Mature leaf color	Succession stage	Species	Young leaf color	Mature leaf color
PF	*Pinus massoniana*	G	G	BF	*Schima superba*	R	G
PF	*Evodia lepta*	G	G	BF	*Tsoongiodendron odoru*	G	G
PF	*Mallotus paniculatus*	G	G	BF	*Blastus cochinchinensis*	R	R
PF	*Ficus variolosa*	G	G	BF	*Gironniera subaequalis*	G	G
PF	*Toxicodendron succedaneum*	R	G	BF	*Acmena acuminatissima*	R	G
PF	*Schefflera octophylla*	G	G	BF	*Mischocarpus pentapetalus*	G	G
PF	*Mallotus apelta*	G	G	BF	*Syzygium rehderianum*	R	G
MF	*Castanea henryi*	R	G	BF	*Cryptocarya chinensis*	R	G
MF	*Schima superba*	R	G	BF	*Ormosia glaberrima*	R	G
MF	*Pinus massoniana*	G	G	BF	*Craibiodendron scleranthum*	R	G
MF	*Ardisia quinquegona*	R	G	BF	*Lindera chunii*	R	G
MF	*Ficus variolosa*	G	G	BF	*Sarcosperma laurinum*	G	G
MF	*Psychotria rubra*	G	G	BF	*Ardisia quinquegona*	R	G
MF	*Schefflera octophylla*	G	G	BF	*Xanthophyllum hainanense*	R	G
MF	*Diospyros morrisiana*	R	G	BF	*Schefflera octophylla*	G	G
BF	*Aidia canthioides*	R	G	BF	*Pterospermum lanceifolium*	G	G
BF	*Aporosa yunnanensis*	G	G	BF	*Mallotus paniculatus*	G	G
BF	*Macaranga sampsonii*	R	G	BF	*Cryptocarya concinna*	R	G

Notes PF, MF, and BF represent coniferous forest (early succession), mixed coniferous-broadleaved forest (middle succession), and monsoon-evergreen broadleaved forest (later succession), respectively. *G* green, and *R* red

young leaves did not increase significantly with succession ($G = 5.16$, $p = 0.08$), but there was a significant difference between PF and BF ($G = 5.16$, $p = 0.04$). Among the six dominant plant species in the PF, only one species (*Toxicodendron succedaneum*) had young leaves with red pigments (Table 2), and all mature leaves in the PF, including those of *T. succedaneum*, were green (Table 2). Among the eight dominant species in MF, four had young leaves with red pigments, and all mature leaves were green (Table 2). In BF, 13 of 21 dominant species had red young leaves; among them, only the leaves of *Blastus cochinchinensis* were still red when mature (Table 2). Overall, 17 out of the 29 dominant species in the three forests had red young leaves (Table 2), and 16 of the 17 species with red young leaves had green mature leaves.

Physical defense traits of young leaves in different forests

Results of G-tests also showed that the percentage of all physical defense traits including leaves with upright orientation ($G = 0.87$, $p = 0.65$), enhanced cuticles ($G = 0.53$, $p = 0.77$), trichomes ($G = 0.25$, $p = 0.88$), and multilayered epidermis ($G = 1.04$, $p = 0.60$) did not differ significantly among different successional forests, although some of them tended to increase with succession (Fig. 2).

In the PF, the only species with red young leaves, *Toxicodendron succedaneum,* did not have any physical defense traits. In contrast, five of the six species with green young leaves had one or more physical defense traits, and 28.6% of these species had leaves with upright orientation. A similar proportion was also detected in the species with enhanced cuticles and multilayered epidermis. Additionally, 43% species had trichomes (Fig. 3). The physical defense traits

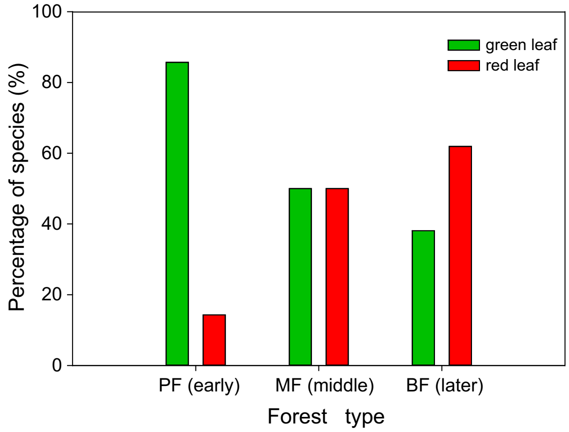

Fig. 1 Percentages of dominant species young leaves of which were green vs. red in the three successional forests in South China. PF, MF, and BF represent coniferous forest (early succession), mixed coniferous-broadleaved forest (middle succession), and monsoon-evergreen broadleaved forest (later succession), respectively

were significantly more frequent in species with green than those with red young leaves in PF ($G = 2.97$, $p = 0.04$). In the MF, among the species with green young leaves, 25% species had leaves with upright orientation, 37.5% had enhanced cuticles, 12.5% had trichomes, and 25% had multilayered epidermis.

However, the species with red young leaves merely had two kinds of physical defense: upright orientation of leaves (12.5%) and trichomes (25%) (Fig. 3).

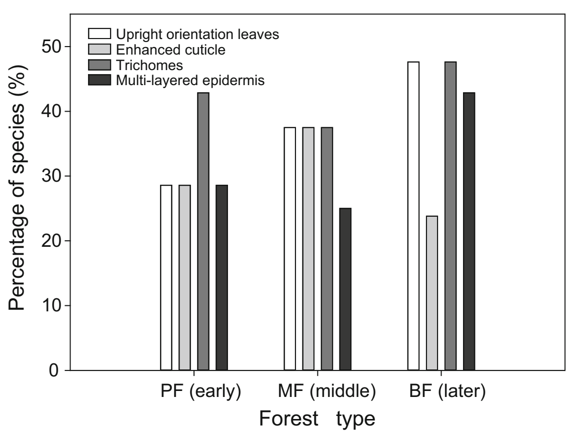

Fig. 2 Percentages of dominant species young leaves of which had the indicated physical defense traits in the three successional forests in South China. PF, MF, and BF represent a coniferous forest (early succession), a mixed coniferous-broadleaved forest (middle succession), and a monsoon-evergreen broadleaved forest (later succession), respectively

Moreover, species with green young leaves developed more than one physical defense traits than those with red young leaves ($G = 8.32$, $p < 0.01$) in MF. In addition, the young leaves of the *Psychotria rubra* had no physical defense traits in MF. In the BF, 19.04%, 14.28%, 23.81%, 14.26% species with green young leaves had leaves with upright orientation, enhanced cuticles, trichomes, and multilayered epidermis respectively. The corresponding values were 28.58%, 9.52%, 23.81%, and 28.57% for species with red young leaves (Fig. 3). There was no difference in the number of physical defense traits between species with green young leaves and those with red young leaves ($G = 3.07$, $p = 0.38$). For every physical defense trait, it seemed that there was no difference between species with green and red young leaves (upright orientation of leaves ($G = 0.03$, $p = 0.86$), enhanced cuticles ($G = 1.31$, $p = 0.25$), trichomes ($G = 1.16$, $p = 0.28$), multilayered epidermis ($G = 0.15$, $p = 0.70$)).

The numbers of total defense traits in young leaves among different forests

In the PF, the species with only one defense trait accounted for 42.9% (Fig. 4), followed by species with two defense traits (28.6%). In the MF, 50% of the dominant species had two defense traits, followed by species with three defense traits, which accounted for 25%. In the BF, 38.1% of the species had three defense traits, 33% of the species had two defense traits, and another 4.7% of species had four defense traits. Overall, the proportion of species with multiple defense traits increased with succession. Meanwhile, more than one defense trait tended to be more frequent in the species of BF than in PF ($G = 2.55$, $p = 0.06$).

Discussion

Changes in the color and physical defense traits of young leaves in succession

In general, the emerging leaves on mature plants may be more vulnerable to herbivory than mature leaves which have much more physical and chemical defense traits (Coley and Barone 1996; Hanley et al. 2007). Therefore, the punctured ratio (feeding by herbivory) of young leaves may be higher than that of the mature

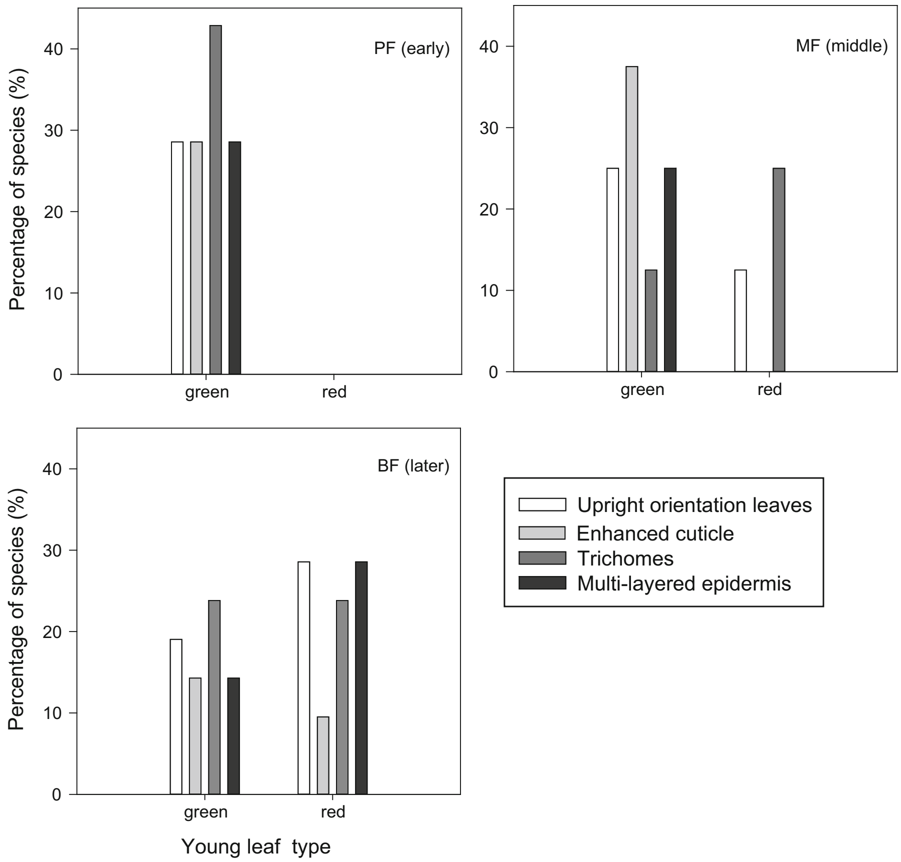

Fig. 3 Percentage of dominant species green and red young leaves of which had the indicated physical defense traits in the three successional forests in South China. PF, MF, and BF represent a coniferous forest (early succession), a mixed coniferous-broadleaved forest (middle succession), and a monsoon-evergreen broadleaved forest (later succession), respectively

leaves owing to the feeding preferences by herbivores. In our study, however, we found that the LPP of red young leaves was significantly lower than that of mature leaves, and the punctured ratio seemed to be higher in green young leaves than that in red young leaves. We also found that the physical defense of red young leaves was weaker than that of green leaves in PF and MF. This implies that the red color trait in young leaves may be an anti-herbivory defense trait that protects young leaves from herbivory in the leaf developing stage. Such results may be indirect evidence in support of the coevolution hypothesis. Kursar and Coley (1992) also suggested that the delayed greening (red leaves) may be evolved as an anti-herbivory defense.

In our study, the percentage of dominant species with red young leaves tended to increase with succession, although the difference was not significant. However, we found such significant difference between the early successional forest (PF) and later successional forest (BF). We found that the percentage of species with red young leaves was higher in later than in early succession in our study site. Kursar and Coley (1992) also found a similar result that delayed greening is more common in shaded understory other than in open environments. Since young leaves with delayed greening (red leaves) have approximately 10–20% lower level of light harvesting proteins, photosynthetic enzymes, chlorophyll, and lipid-rich membranes than normally greening leaves (Coley and Barone 1996), green young leaves must lose much more energy in a given amount of herbivory in shaded environment compared with red young leaves. This is because such leaves have to allocate more energy to defense and have already put

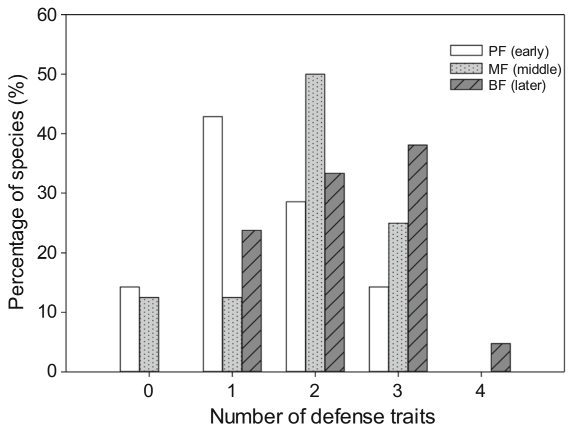

Fig. 4 Percentage of dominant species young leaves of which had 0–4 defense traits in different successional forests. PF, MF, and BF represent a coniferous forest (early succession), a mixed coniferous-broadleaved forest (middle succession), and a monsoon-evergreen broadleaved forest (later succession), respectively. Possible defense traits include four physical traits (leaves that are upright or have enhanced cuticles, trichomes, or a multilayered epidermis) and young leaf color traits (indicating anti-herbivory)

more energy in chlorophyll than red leaves in shaded environment.

In early succession, the percentage of species with green young leaves is higher than that with red young leaves ($G = 7.93, p < 0.01$), but there is no difference in later succession (BF: $G = 2.40, p = 0.12$). Peng and Ren (1998) have shown that herbivory is more likely to appear in later than in early succession at our study site. In our study, we have shown higher percentage of species with red young leaves in later than early succession, and red young leaves are related to anti-herbivory. Therefore, we believe that the red color trait in young leaves may be evolved as an anti-herbivory defense trait and may mainly adapt to the more complex environment in later succession with lower light intensity ("Appendix 3") but more herbivory.

Among the physical defense traits in young leaves, the percentage of species young leaves of which had trichomes, multilayered epidermis, and upright orientation of leaves tended to increase with succession, although such increase was not significant. These results indicate that in early succession, the young leaves of the most dominant species depend on only one or two of the four physical traits (upright leaves, trichomes, a multilayered epidermis, or enhanced cuticles) in response to the high light intensity and low water availability environment ("Appendix 3"). With forest succession, however, the dominant species are those that utilize more than one physical trait to respond to the more stressful environment, i.e., lower light intensity ("Appendix 3") and more competition and herbivory.

Differences in physical defense traits between red and green young leaves

In our study, the dominant species with red young leaves lacks physical defense traits in early succession (PF). As succession proceeded, however, such species tended to gradually develop more physical defense traits, and the green young leaves still developed more physical defense traits in MF. Such difference, however, was not significant in the later succession (BF). Chen and Huang (2013) previously reported that red young leaves had fewer physical defense traits than green young leaves. The current results are consistent with those of Chen and Huang in that physical defense traits were more common in green young leaves than in red young leaves in early and middle succession.

In both green and red young leaves, the percentages of dominant species with leaf trichomes varied across successional stages but tended to be the highest in later succession, perhaps because of the increased pressure from herbivores (Peng and Ren, 1998). The trichomes function to resist herbivores has been accepted in some previous studies (Dalin and Björkman 2003; Hanley et al. 2007), although some researchers suggest that trichomes primarily reduce water loss and excessive heat gain (Gutschick 1999) and exposure to UV radiation (Manetas 2003). In this study, we also found that enhanced cuticles tend to be more frequent in green young leaves than in red young leaves in the middle succession (Fig. 3). In addition, owing to the high light intensity, low water availability ("Appendix 3"), and low herbivory (Peng and Ren 1998) in early succession, we infer that the enhanced cuticles may be related to abiotic stresses (e.g., high light intensity, drought) in early succession, which is consistent with many studies (Martin 2003; Chassot et al. 2008; Kachroo and Kachroo 2009). For example, Serrano et al. (2014) concluded that the cuticle was a physical barrier that prevented water loss.

Changes in the number of defense traits in young leaves

Our results show that, during forest succession, the percentage of the dominant species young leaves of which have multiple defense traits gradually increases, while the percentage of the young leaves which have only one defense trait gradually decreases. Consistent with Agrawal et al. (2006), our results also indicate that plants require more defense traits to response to increasing herbivory and competition and decreasing light intensity during forest succession.

Conclusion

Our study indicates that the percentage of species with red young leaves is higher in later than in early or middle succession in the subtropical forests in China. We believe that the red color trait in young leaves may be related to anti-herbivory defense. Physical defense tend to be weaker for red young leaves than that for green young leaves in early and middle succession. In addition, the defense of young leaves also increases during succession in that young leaves tend to rely on fewer defense traits in early or middle succession and multiple defense traits in later succession. We speculate that young leaves in subtropical forests of China depend increasingly on multiple defense traits as succession proceeds owing to the increasing biotic stresses and environmental complexity during succession.

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Appendix 1

See Table 3.

Table 3 The species compositions and species important values in the three successional forests

Species	Frequentness	Number of trees	Basal area	Relative frequency	Relative density	Relative dominance	Important value(IV)	Sum of IV
Sum of BF	13.65	1100	47,796.69	1	1	1	1	0
Aidia canthioides	0.9	236	982.96	0.07	0.21	0.02	0.1	0.1
Aporosa yunnanensis	0.95	140	3791.79	0.07	0.13	0.08	0.09	0.19
Macaranga sampsonii	0.4	167	1463.89	0.03	0.15	0.03	0.07	0.26
Schima superba	0.25	8	8053.59	0.02	0.01	0.17	0.06	0.33
Tsoongiodendron odoru	0.05	1	8654.63	0	0	0.18	0.06	0.39
Blastus cochinchinensis	0.85	116	192.87	0.06	0.11	0	0.06	0.45
Gironniera subaequalis	0.55	21	3734.65	0.04	0.02	0.08	0.05	0.49
Acmena acuminatissima	0.55	24	2992.94	0.04	0.02	0.06	0.04	0.53
Mischocarpus pentapetalus	0.85	40	386.31	0.06	0.04	0.01	0.04	0.57
Syzygium rehderianum	0.6	24	1066.37	0.04	0.02	0.02	0.03	0.6
Cryptocarya chinensis	0.25	28	1912.31	0.02	0.03	0.04	0.03	0.63
Ormosia glaberrima	0.45	30	364.23	0.03	0.03	0.01	0.02	0.65
Craibiodendron scleranthum	0.15	4	2374.57	0.01	0	0.05	0.02	0.67
Lindera chunii	0.25	33	572.21	0.02	0.03	0.01	0.02	0.69
Sarcosperma laurinum	0.35	15	997.67	0.03	0.01	0.02	0.02	0.71
Ardisia quinquegona	0.55	19	65.91	0.04	0.02	0	0.02	0.73
Xanthophyllum hainanense	0.4	16	547.84	0.03	0.01	0.01	0.02	0.75
Schefflera octophylla	0.35	15	530.73	0.03	0.01	0.01	0.02	0.77

Table 3 continued

Species	Frequentness	Number of trees	Basal area	Relative frequency	Relative density	Relative dominance	Important value(IV)	Sum of IV
Pterospermum lanceifolium	0.2	13	1094.57	0.01	0.01	0.02	0.02	0.78
Mallotus paniculatus	0.25	20	606.04	0.02	0.02	0.01	0.02	0.8
Cryptocarya concinna	0.45	16	50.25	0.03	0.01	0	0.02	0.82
Psychotria rubra	0.4	11	82.3	0.03	0.01	0	0.01	0.83
Machilus chinensis	0.1	2	1495.17	0.01	0	0.03	0.01	0.84
Pygeum topengii	0.15	4	1202.82	0.01	0	0.03	0.01	0.86
Canarium album	0.3	7	129.16	0.02	0.01	0	0.01	0.87
Microdesmis caseariifolia	0.2	10	195.94	0.01	0.01	0	0.01	0.88
Castanea henryi	0.05	1	1006.09	0	0	0.02	0.01	0.88
Nephelium chryseum	0.1	2	682.07	0.01	0	0.01	0.01	0.89
Engelhardtia Roxb	0.1	2	660.97	0.01	0	0.01	0.01	0.9
Ficus esquiroliana	0.2	5	89.47	0.01	0	0	0.01	0.91
Canthium dicoccum	0.2	5	76.51	0.01	0	0	0.01	0.91
Syzygium levinei	0.2	5	75.71	0.01	0	0	0.01	0.92
Memecylon ligustrifolium	0.15	6	152.58	0.01	0.01	0	0.01	0.93
Acronychia pedunculata	0.1	3	413.5	0.01	0	0.01	0.01	0.93
Ilex chapaensis	0.1	2	357.99	0.01	0	0.01	0.01	0.94
Bridelia insulana	0.1	7	33.93	0.01	0.01	0	0	0.94
Carallia brachiata	0.15	3	29.46	0.01	0	0	0	0.95
Lasianthus chinensis	0.1	4	9.54	0.01	0	0	0	0.95
Caryota ochlandra	0.05	1	298.5	0	0	0.01	0	0.96
Sterculia lanceolata	0.1	3	23.75	0.01	0	0	0	0.96
Elaeocarpus sylvestris	0.1	2	21.89	0.01	0	0	0	0.96
Chrysophyllum lanceolatum	0.1	2	11.18	0.01	0	0	0	0.97
Diospyros eriantha	0.1	2	3.09	0.01	0	0	0	0.97
Saurauia tristyla	0.05	4	86.17	0	0	0	0	0.97
Macaranga andamanica	0.05	3	54.33	0	0	0	0	0.97
Aquilaria sinensis	0.05	3	10.25	0	0	0	0	0.98
Ficus fistulosa	0.05	1	55.39	0	0	0	0	0.98
Garcinia oblongifolia	0.05	1	29.21	0	0	0	0	0.98
Meliosma rigida	0.05	1	25.5	0	0	0	0	0.98
Ilex cochinchinensis	0.05	1	12.56	0	0	0	0	0.98
Syzygium championii	0.05	1	8.55	0	0	0	0	0.98
Canthium horridum	0.05	1	8.04	0	0	0	0	0.99
Homalium cochinchinense	0.05	1	4.91	0	0	0	0	0.99
Elaeocarpus dubius	0.05	1	4.15	0	0	0	0	0.99
Artocarpus styracifolius	0.05	1	2.83	0	0	0	0	0.99
Euonymus laxiflorus	0.05	1	1.54	0	0	0	0	0.99
Neolitsea cambodiana	0.05	1	1.33	0	0	0	0	0.99
Evodia lepta	0.05	1	1.13	0	0	0	0	1

Table 3 continued

Species	Frequentness	Number of trees	Basal area	Relative frequency	Relative density	Relative dominance	Important value(IV)	Sum of IV
Wikstroemia nutans	0.05	1	1.13	0	0	0	0	1
Ficus variolosa	0.05	1	0.95	0	0	0	0	1
Clerodendrum canescens	0.05	1	0.79	0	0	0	0	1
Sum of MF	8.65	631	60,401.88	1	1	1	1	0
Castanea henryi	0.95	118	33,318.48	0.11	0.19	0.55	0.28	0.28
Schima superba	0.85	102	12,276.79	0.1	0.16	0.2	0.15	0.44
Pinus massoniana	0.6	23	11,319.94	0.07	0.04	0.19	0.1	0.53
Ardisia quinquegona	0.6	99	279.6	0.07	0.16	0	0.08	0.61
Ficus variolosa	0.8	68	244.02	0.09	0.11	0	0.07	0.68
Psychotria rubra	0.7	71	213.99	0.08	0.11	0	0.07	0.75
Schefflera octophylla	0.7	27	327.37	0.08	0.04	0.01	0.04	0.79
Diospyros morrisiana	0.6	20	746.34	0.07	0.03	0.01	0.04	0.83
Cratoxylum cochinchinense	0.5	16	307.58	0.06	0.03	0.01	0.03	0.86
Litsea coreana	0.2	25	78.21	0.02	0.04	0	0.02	0.88
Toxicodendron succedaneum	0.25	6	30.84	0.03	0.01	0	0.01	0.89
Aporosa dioica	0.2	5	128.95	0.02	0.01	0	0.01	0.9
Cryptocarya concinna	0.2	6	20.76	0.02	0.01	0	0.01	0.91
Canthium dicoccum	0.15	5	51.27	0.02	0.01	0	0.01	0.92
Gardenia jasminoides	0.15	4	4.95	0.02	0.01	0	0.01	0.93
Aidia canthioides	0.15	3	12.32	0.02	0	0	0.01	0.94
Ilex pubescens	0.15	3	8.2	0.02	0	0	0.01	0.94
Craibiodendron scleranthum	0.1	6	29.63	0.01	0.01	0	0.01	0.95
Machilus chinensis	0.05	2	724.66	0.01	0	0.01	0.01	0.96
Canarium album	0.1	3	84.47	0.01	0	0	0.01	0.96
Aporosa yunnanensis	0.1	3	23.07	0.01	0	0	0.01	0.97
Evodia lepta	0.1	2	3.6	0.01	0	0	0	0.97
Itea chinensis	0.05	5	35.61	0.01	0.01	0	0	0.98
Sterculia lanceolata	0.05	2	33.57	0.01	0	0	0	0.98
Rapanea neriifolia	0.05	1	35.24	0.01	0	0	0	0.98
Syzygium levinei	0.05	1	25.5	0.01	0	0	0	0.99
Acronychia pedunculata	0.05	1	17.34	0.01	0	0	0	0.99
Litsea cubeba	0.05	1	11.34	0.01	0	0	0	0.99
Melastoma sanguineum	0.05	1	3.8	0.01	0	0	0	1
Aquilaria sinensis	0.05	1	3.14	0.01	0	0	0	1
Memecylon ligustrifolium	0.05	1	1.33	0.01	0	0	0	1
Sum of PF	8.35	698	37,203.69	1	1	1	1	0
Pinus massoniana	0.95	70	30,537.79	0.11	0.1	0.82	0.34	0.34
Evodia lepta	1	241	2603.84	0.12	0.35	0.07	0.18	0.52
Mallotus paniculatus	1	136	2106.07	0.12	0.21	0.06	0.13	0.65
Ficus variolosa	0.8	54	173.88	0.1	0.08	0	0.06	0.71

Table 3 continued

Species	Frequentness	Number of trees	Basal area	Relative frequency	Relative density	Relative dominance	Important value(IV)	Sum of IV
Toxicodendron succedaneum	0.7	34	481.19	0.08	0.05	0.01	0.05	0.76
Schefflera octophylla	0.45	40	395.8	0.05	0.06	0.01	0.04	0.8
Litsea cubeba	0.55	16	151.55	0.07	0.02	0	0.03	0.83
Cratoxylum cochinchinense	0.35	28	369.65	0.04	0.04	0.01	0.03	0.86
Psychotria rubra	0.4	21	70.77	0.05	0.03	0	0.03	0.89
Litsea coreana	0.4	19	67.67	0.05	0.03	0	0.03	0.91
Rhaphiolepis indica	0.3	7	25.39	0.04	0.01	0	0.02	0.93
Melastoma sanguineum	0.2	4	14.22	0.02	0.01	0	0.01	0.94
Clerodendrum fortunatum	0.15	3	4.73	0.02	0	0	0.01	0.94
Eurya chinensis	0.1	5	8.99	0.01	0.01	0	0.01	0.95
Cinnamomum bodinieri	0.1	2	7.05	0.01	0	0	0.01	0.96
Aporosa dioica	0.1	2	6.92	0.01	0	0	0.01	0.96
Gardenia jasminoides	0.1	2	5.41	0.01	0	0	0	0.97
Ilex asprella	0.05	5	8.4	0.01	0.01	0	0	0.97
Eucalyptus robusta	0.05	1	118.76	0.01	0	0	0	0.97
Rhodomyrtus tomentosa	0.05	3	3.41	0.01	0	0	0	0.98
Ilex pubescens	0.05	2	25.37	0.01	0	0	0	0.98
Sapium discolor	0.05	1	11.94	0.01	0	0	0	0.99
Alchornea trewioides	0.05	1	3.14	0.01	0	0	0	0.99
Glochidion eriocarpum	0.05	1	1.77	0.01	0	0	0	1

Notes PF, MF, and BF represent a coniferous forest (early succession), a mixed coniferous-broadleaved forest (middle succession), and a monsoon-evergreen broadleaved forest (later succession), respectively

Appendix 2

See Table 4.

Table 4 The defense traits of dominant species in different successional stages of subtropical forests in South China

Succession stage	Species	Young leaf					Mature leaf				
		Leaf color	Upright orientation leaf	Enhanced cuticle	Trichomes	Multilayered epidemis	Leaf color	Upright orientation leaf	Enhanced cuticle	Trichomes	Multilayered epidemis
PF	*Pinus massoniana*	G	Y	Y	N	2	G	Y	Y	N	2
PF	*Evodia lepta*	G	N	N	N	1	G	N	Y	N	1
PF	*Mallotus paniculatus*	G	N	N	Y	1	G	N	N	Y	1
PF	*Ficus variolosa*	G	Y	Y	N	1	G	Y	Y	N	1
PF	*Toxicodendron succedaneum*	R	N	N	N	1	G	N	N	N	1
PF	*Schefflera octophylla*	G	N	N	Y	2	G	N	Y	N	2
PF	*Mallotus apelta*	G	N	N	Y	1	G	N	N	Y	1
MF	*Castanea henryi*	R	Y	N	N	1	G	N	Y	N	1
MF	*Schima superba*	R	N	N	Y	1	G	N	Y	N	1
MF	*Pinus massoniana*	G	Y	Y	N	2	G	Y	Y	N	2
MF	*Ardisia quinquegona*	R	N	N	N	1	G	N	N	N	1
MF	*Ficus variolosa*	G	Y	Y	N	1	G	Y	Y	N	1
MF	*Psychotria rubra*	G	N	N	N	1	G	N	N	N	1
MF	*Schefflera octophylla*	G	N	Y	Y	2	G	N	Y	N	2
MF	*Diospyros morrisiana*	R	N	N	Y	1	G	N	Y	N	1
BF	*Aidia canthioides*	R	Y	N	N	1	G	Y	Y	N	1
BF	*Aporosa yunnanensis*	G	Y	N	N	2	G	N	Y	N	1
BF	*Macaranga sampsonii*	R	N	Y	Y	1	G	N	Y	Y	1
BF	*Schima superba*	R	N	N	Y	1	G	N	Y	N	1
BF	*Tsoongiodendron odoru*	G	Y	Y	Y	1	G	N	Y	Y	1
BF	*Blastus cochinchinensis*	R	Y	Y	N	1	R	N	Y	N	1
BF	*Gironniera subaequalis*	G	N	N	Y	1	G	N	N	Y	1
BF	*Acmena acuminatissima*	R	Y	N	N	2	G	N	N	N	1
BF	*Mischocarpus pentapetalus*	G	Y	N	N	1	G	N	N	N	1
BF	*Syzygium rehderianum*	R	Y	N	N	3	G	Y	N	N	1
BF	*Cryptocarya chinensis*	R	N	N	Y	3	G	N	Y	N	1
BF	*Ormosia glaberrima*	R	N	N	N	2	G	N	Y	N	1
BF	*Craibiodendron scleranthum*	R	Y	N	Y	2	G	Y	Y	N	1
BF	*Lindera chunii*	R	Y	N	Y	1	G	Y	Y	Y	1

Table 4 continued

Succession stage	Species	Young leaf					Mature leaf				
		Leaf color	Upright orientation leaf	Enhanced cuticle	Trichomes	Multilayered epidemis	Leaf color	Upright orientation leaf	Enhanced cuticle	Trichomes	Multilayered epidemis
BF	*Sarcosperma laurinum*	G	Y	N	N	2	G	N	N	N	2
BF	*Ardisia quinquegona*	R	N	N	N	1	G	N	Y	N	1
BF	*Xanthophyllum hainanense*	R	N	N	N	2	G	N	Y	N	1
BF	*Schefflera octophylla*	G	N	Y	Y	2	G	N	Y	N	2
BF	*Pterospermum lanceifolium*	G	N	Y	Y	1	G	N	Y	Y	1
BF	*Mallotus paniculatus*	G	N	N	Y	1	G	N	N	Y	1
BF	*Cryptocarya concinna*	R	N	N	N	1	G	N	Y	N	1

Notes PF, MF, and BF represent a coniferous forest (early succession), a mixed coniferous-broadleaved forest (middle succession), and a monsoon-evergreen broadleaved forest (later succession), respectively. *G* green, *R* red, *N* not, *Y* yes, 1, 2, 3 represent 1-, 2-, and 3-layered epidermis respectively

Appendix 3

See Table 5.

Table 5 The environment factors in the three successional forests in South China (unpublished)

Succession stage	LAI ($n = 5$)	EK (cmol/kg) ($n = 6$)	ENa (cmol/kg) ($n = 6$)	TN (g/kg) ($n = 6$)	TP (g/kg) ($n = 6$)	SMC (g/cm^3) ($n = 6$)
PF	3.55 ± 0.24	0.02 ± 0.01	0.02 ± 0.01	1.35 ± 0.23	0.20 ± 0.03	0.11 ± 0.01
MF	5.33 ± 0.19	0.02 ± 0.01	0.02 ± 0.01	2.23 ± 0.61	0.32 ± 0.04	0.15 ± 0.01
BF	6.41 ± 0.20	0.13 ± 0.03	0.05 ± 0.02	1.91 ± 0.17	0.26 ± 0.02	0.16 ± 0.02

Notes LAI (leaf area index), which could be used as a sign of light intensity under forests, the smaller of this value, the stronger of the light intensity; EK, exchangeable K cation content in the 0–20cm topsoil; ENa, exchangeable Na cation content in the 0–20cm topsoil; TN, total N content in the 0–20cm topsoil; TP, total P content in the 0–20cm topsoil; SMC, Soil moisture-holding capacity the 0–20cm topsoil. PF, MF, and BF represent a coniferous forest (early succession), a mixed coniferous-broadleaved forest (middle succession), and a monsoon-evergreen broadleaved forest (later succession), respectively. All the data was collected in 2016

Krukal–Wallis Tests showed significant differences in all the environment factors during succession (LAI, $p = 0.003$; EK, $p = 0.002$; ENa, $p = 0.008$; TN, $p = 0.011$; TP, $p = 0.003$; SMC, $p = 0.003$)

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