Trade-off between leaf traits in a burned area of Picea asperata-Abies fabri forest of the Qinghai-Tibetan Plateau

[redacted]
Gansu Agricultural University
Tian Qing (tqing@gsau.edu.cn)
Gansu Agricultural University
Zhou Xiaolei
Gansu Agricultural University

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Xue-ping Cao [1], Qing Tian [1,2*], Xiao-lei Zhou [1*], An Zhao [3], Hai-xia Huang [1], Gang Lu [1], Wang-peng He [1]

[1]College of Forestry, Gansu Agricultural University, Lanzhou 730070, Gansu, China;
[2]Jinchang Municipal Government, Jinchang,737100,China;
[3]Qiandongnan Institute of Forestry, Kaili 556000,China

*** Correspondence:**
Corresponding Authors：
Name: Tian Qing
E-mail: tqing@gsau.edu.cn
Name: Zhou Xiao-lei
E-mail: zhouxl@gsau.edu.cn

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Xue-ping Cao [1], Qing Tian [1,2*], Xiao-lei Zhou [1*], An Zhao [3], Hai-xia Huang [1], Gang Lu [1], Wang-peng He[1]

Abstract

Climate change and disturbed are testing the resilience of forests worldwide, Exploring the adaptation strategies of plants in alpine regions could provide reliable suggestions for plant conservation. As an indispensable organ, the functional traits and correlations of leaves are most closely related to the environment, and are the main indicators to measure the suitability of plant survival. The scaling relationship of leaf mass, leaf area and leaf thickness in the area of fire site is still lacking. On the basis of survey data, we measured leaf traits and correlation of shrub in the burned area of *Piceaasperata-Abies fabri* forest of the Qinghai-Tibetan Plateau. Our results showed that: the families *Salicaceae* belong to quick investment-return, the *Caprifoliaceae* belong to slow investment-return. The scaling relationship of leaf fresh mass and leaf dry mass showed that the families *Salicaceae* and *Saxifragaceae* the scaling exponent (α) overlapped with one, means the change in leaf dry mass were proportional to the change in leaf fresh mass. For *Gramineae* was significantly greater than 1.0, while the *Rosaceae* and *Caprifoliaceae* was less than 1.0, which meant that the increase of leaf dry mass did not keep pace with the increase of leaf fresh mass in some species. The scaling relationship between leaf mass and leaf area was relatively complex, and α for all families did not include unity. The coefficients of determination (i.e. R^2) for leaf fresh mass vs. leaf area were always greater than that of leaf dry mass vs. leaf area. The family *Rosaceae*, the 95% *CI* of the scaling exponent of the leaf area vs. leaf thickness relationship overlapped with one; the leaf area increased with increasing leaf thickness, the relationship did not show similar results in the other families. In future studies, we need more comprehensive data sets containing more species living under the fire site to assess the generality of the diminishing returns hypothesis. This will provide a new perspective to understand the adaptation of plants regenerated after the fire to harsh habitats.

Key words: spruce-fir forest burned areas, allometry, dimingishing returns, leaf traits, shrub.

1 Introduction

For a plant, the leaves are highly sensitive to climate change(Tozer et al., 2015).Plant leaf traits are measurable features of an individual. Moreover, plant leaf traits are critical in determining and predicting an individual's competitive ability and plant species' responses to the biophysical environment, thus, influencing the entire ecosystem function (Huang, Su, et al., 2019). Most of important leaf functional traits (e.g., leaf surface area, LA; leaf mass, LM; specific leaf area, SLA; leaf dry matter content, LDMC; and leaf thickness, LT.) are known to affect variation in physiological and life processes, including plant growth, survival, carbon assimilation, and reproduction (Chen et al., 2021). Leaf traits can also be used to predict their growth strategies and responses to environmental variations (Milla & Reich, 2007). It has been verified that LA and SLA are closely related to the material and energy cycle in plants; it is the most important traits in the economic spectrum of leaves (WANG et al., 2020). In addition, LM is closely linked to plant carbon capture，plant growth rates, resource acquisition, and leaf turnover(Polley et al., 2020). Because LM is a composite index that includes leaf water and tissue mass, the relationship between LM and LA reflects the optimal allocation and trade-off of individual resource utilization and the adaptive strategies of plants to their surrounding environment (Yang et al., 2021).LWC is associated with stomatal conductance, turgor pressure and leaf growth rate (Lin Zhang et al., 2020). Although variations in leaf and scaling relationships between different climatic regions and plant community have been extensively researched in recent years (Niklas et al., 2007; Li et al., 2008), how their relationship to change in the burn site remains unclear. Another very important aspect is that multipe studies only focus on the changes of leaf traits along the dynamic changes among traits, and such static changes only represent the leaves' current situation, while the dynamic changes among traits, such as scaling relationship or allometric relationship, are neglected.

Fire is one of the significant and common form of natural disturbances in terrestrial ecosystems, driving forest community structure, diversity, and succession at local,regional, and global scales(He et al., 2016). With the global climate change and increased human activities disturbances (Keeley et al., 2011; N et al., 2017), there has been a significant increase in the frequency, severity, and sizes of fires(Miller et al., 2009). Fires have many complex effects on vegetation and ecosystem function. These range from relatively minor injuries to tissues and organs (e.g., fire scars and crown scorch) to whole plant mortality and forest stand replacement. Therefore, understanding how vegetation regenerates post-fire is essential in mitigating the ecological effects of fire and implementing accelerated ecosystem recovery after fire damage (Dove et al., 2021). Particularly, understanding plant functional traits in post-fire conditions is important to predict the changes in fire-prone vegetation. Despite the increased number of studies on plant functional traits within artificial landscapes (Cheng et al., 2015), hzowever, limited information on plant functional traits from fire-prone regions greatly limits our understanding of the post-fire adaptive strategies of plants. A deep understanding of the variation in post-fire plant functional traits may help to understand the plant responses to fire disturbance under climate change.

Located on the northeastern edge of the Qinghai-Tibetan Plateau, the Diebu forest region is among the 36 global biodiversity hotspots identified by Conservation International (An et al., 2021). The forest region is located on the periphery of the Diebu, Axia Giant Panda Nature Reserve and is considered one of the major water-conserving forest bases in the upper reaches of the Yangtze River. However, increased human activities due to the settlement of local farmers and

herders in the forest mosaic put pressure on the nature reserve. In addition, some of the forest areas within the nature reserve have been exposed to frequent fires caused by anthropogenic activities. Due to the lack of science-based restoration efforts, some fire-affected forest sites become fragmented and experience further degradation, including soil erosion, thus affecting the integrity of the giant panda habitat.

Table 1. Abbreviations used in this article.

Abbreviation	Full name	Units
LA	Leaf area	cm^2
LM	Leaf mass	g
SLA	Specific leaf area	$cm^2\ g^{-1}$
LDMC	Leaf day matter content	%
LWC	Leaf water content	%
LFM	Leaf fresh mass	g
LDM	Leaf dry mass	g
LT	Leaf thickness	mm

2 Materials and methods

2.1 Study site

The study was conducted on the Northern slopes of the Die Mountains on the north-eastern edge of the Qinghai-Tibetan Plateau in Gansu Province, China (34° 10' 40.66″~34° 10' 47. 30″ N and 103° 12' 51.35″~103° 12' 57.43″ E). The study area lies between 2981 m above sea level (asl) and 3408 masl and at the confluence of transitional climate between the northern subtropics and the alpine climate on the eastern edge of the Qinghai-Tibetan Plateau. The area receives a mean annual rainfall of 568 mm with 1444.2 mm of mean annual evaporation and 7.5℃ of mean annual temperature. Due to regional micro-topography, the study area experiences significant vertical climate differences (Xiao-lei et al., 2022). The burn site within the spruce-fir forest has a "Saddle-shaped" topography, while the sampling slopes are oriented to the east, north-east, north, and north-west. In the study site, the forest fire occurred on April 19, 2005, and burned about 5.72 hm^2 area. The forest fire spread from the lower slope to the upper with high intensity causing significant damage to the forest ecosystem, including a complete loss of forest biodiversity. Shrub species now represent the established plant species in the study area, the forest coverage rate is 55%, and the survey found that there are 17 kinds of shrub plants in the burnt land.

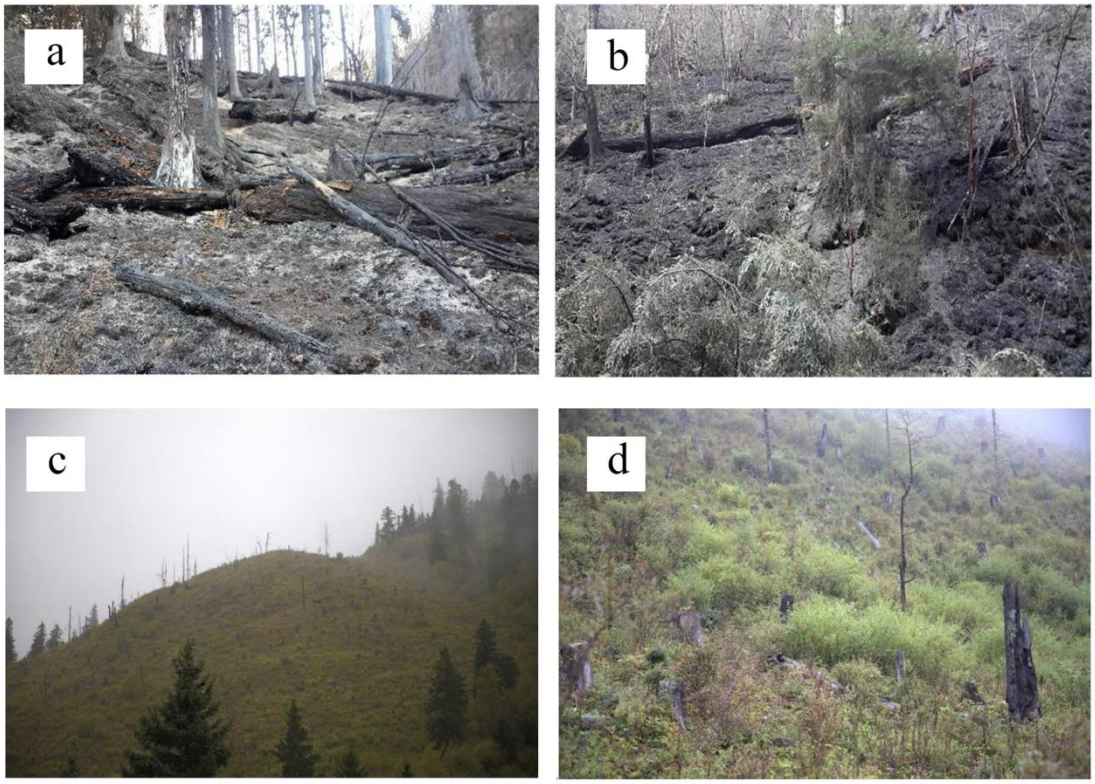


Figure 1. The photograph of the study sites. Panel **(a-b)** burn site in the Diebu forest area. Panel **(c-d)** status of plant diversity in after fire burnt sites in the Diebu forest area.

2.2 Experimental design

Field sampling was conducted in the summer of 2020-2021 from mid-July to late August. In the *Picea asperata-Abies fabri* forest burn site, choosing representative portions forest without visible signs of human disturbance. We established a total of 15 sample plots (20×20 m^2) (Table 2). Each sample plot comprised five 5 m × 5 m subplots to measure shrub vegetation (shrub samples), and each shrub plot comprised one 1 m × 1 m subplot to measure herbaceous vegetation. In each 20×20 m^2 sample plot, we recorded slope direction, slope, slope position, elevation, soil depth, and thickness of deadfall.

Table 2. General characteristics of 15 sampling plots.

Plot	Latitude (M)	Slope (°)	Aspect (°)	Coverage (%)	Disturbance regimes
1	2975	22	294	75	Moderate
2	3045	38	308	70	Moderate
3	3187	52	332	73	Slight
4	3285	43	326	68	Slight
5	3390	27	314	60	Slight
6	2981	41	351	76	Moderate
7	3075	47	339	75	Moderate
8	3147	32	12	75	Slight
9	3286	20	8	72	Slight
10	3045	30	62	70	Moderate
11	3125	24	48	72	Slight
12	3381	35	65	55	Slight
13	2895	60	81	71	Moderate
14	3145	43	68	64	Slight
15	3298	28	107	60	Slight

Note: The disturbance regimes were determined according to the degree of loss of plants and ground cover: Slight (<20%); Moderate (20~40%); Gravity (>40%).

Within a relatively open habitat, we did a basic phytocoenology survey and measured some variables. For every sample plot, three individuals of average height were selected within a relatively open habitat, and 10–15 undamaged one-year leaves from annual shoots in the upper crown of each individual were collected at 9:00–12:00 a.m. Collecting leaves at a fixed time of day helps to avoid temporal variation in leaf functional traits. All the samples were put into sealing bags (30 cm × 20 cm), storing with an incubator (50 cm × 30 cm × 30 cm) with ice bags, and then brought to the Forest Research Station. Indoor plant leaf functional traits were measured within 8 hours of sample collection. These samples were used to measure a suite of leaf functional traits. Subsamples of collected leaves from each plot were randomly selected to measure LM (include LFM and LDM) , LT and LA (Cornelissen et al., 2003).

Each leaf was taken using a 45-megapixel Nikon Coolpix 4500 digital camera. The leaf length, leaf width, and leaf area were measured using Image J (version 1.48, NIH, Maryland, America). Fresh leaves were weighed and dried to a constant dry weight in a ventilated oven (Taisite, WHL45B, Tianjin, China) at 105 °C. The oven was then turned to 70 °C , and the samples were dried until a constant dry weight was achieved. The fresh leaf mass and leaf constant dry mass were measured using an electronic balance with 0.0001 g accuracy (140 BMS, Zhuojing Experimental Equipment Co. Ltd., Shanghai, China).

2.3 Statistical analyses

The degree of species dominance in the forest community was determined by calculating the Important Value Index (IVI). The IVI was calculated as:

1) $\text{IVI} = (\text{Relative frequency} + \text{Relative dominance} + \text{Relative density})/3$

Where:

2) $\text{Relative frequency} = \frac{Frequency\ of\ a\ species}{Sum\ of\ frequency\ of\ all\ the\ species} * 100$

3) $\text{Relative dominance} = \frac{Total\ stand\ basal\ cover\ of\ the\ species}{Total\ stand\ basal\ cover\ of\ all\ the\ species} * 100$

4) $\text{Relative density} = \frac{Density\ of\ a\ species}{Sum\ of\ density\ of\ all\ the\ species} * 100$

The scaling relationships between leaf functional traits were measured as the anisotropic growth relationships between LA, LFM, LDM and LT (i.e., LFM vs. LDM, LFM vs. LA, LDM vs. LA, and LT vs. LA) using a mathematical equation $y = \beta x^{\alpha}$. The leaf trait data were log-transformed to meet the assumptions of normality and homogeneity ($log\ (y) = log\ (\beta) + \alpha\ log\ (x)$), where x and y determine whether the relationship is isometric ($\alpha = 1.0$) or allometric ($\alpha > 1.0$ or $\alpha < 1.0$), β is the y-intercept of the relation, and α is the scaling exponent (Xiang et al., 2009). The 95% confidence intervals for α and β were also calculated using the SMATR software (Yang et al., 2021). We also assessed whether the estimated slope parameters differed from 1.0. All the statistical analyses were performed using SMATR Version 2.0 (Falster, 2006) and R 4.1.2 (http：//www.r-project.org/).

Table 3. Basic information about shrub species on burned sites.

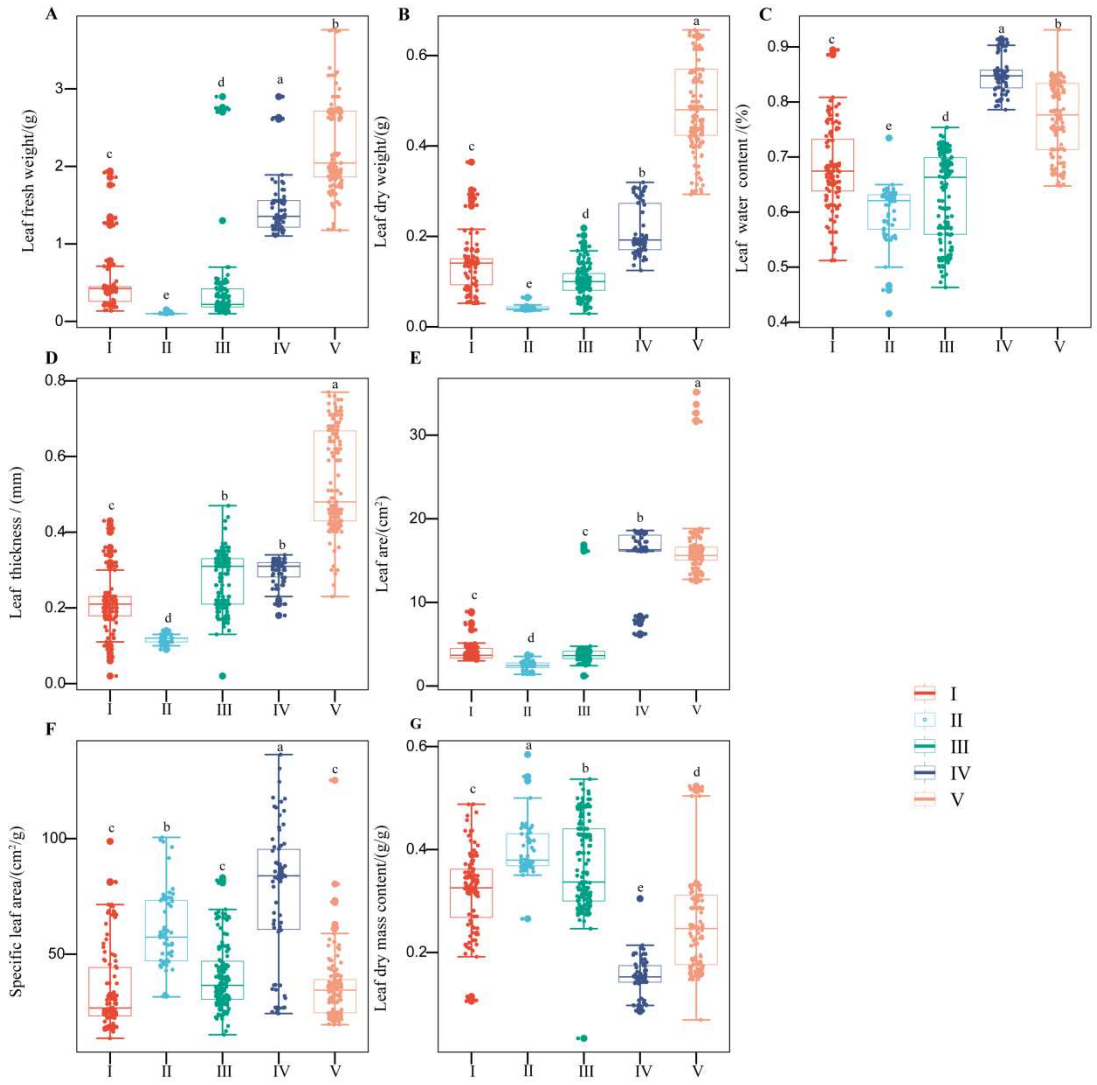
Family	Tree species	Mean *H*	Mean *BD*	Important value
Salicaceae	*Salix heishuiensis*	89.7619	11.3484	0.1634
Gramineae	*Fargesia spathacea*	72.7281	4.2129	0.1443
Saxifragaceae	*Ribes alpestre*	48.3913	5.6123	0.1129
Rosaceae	*Rosa omeiensis*	86.4382	8.8822	0.1073
Caprifoliaceae	*Lonicera tangutica*	64.6739	6.0350	0.1068
Saxifragaceae	*Philadelphus incanus*	38.0990	4.3637	0.1019
Rosaceae	*Rosa sweginzowii*	86.3529	11.1106	0.0871
Caprifoliaceae	*Lonicera trichosantha*	68.6563	8.6713	0.0555
Rosaceae	*Rosa willmottiae*	123.8824	14.0788	0.0328
Rosaceae	*Rosa tsinglingensis*	108.3652	12.3632	0.0228
Salicaceae	*Clematoclethra scandens*	99..7254	13.5846	0.0208
Caprifoliaceae	*Lonicera caerulea*	63.5556	9.0511	0.0158
Caprifoliaceae	*Lonicera nervosa*	52.4	8.05	0.0118

Note: *H*, plant height; *BD*, basal diameter.

3. Results

3.1. Variation in leaf traits across families

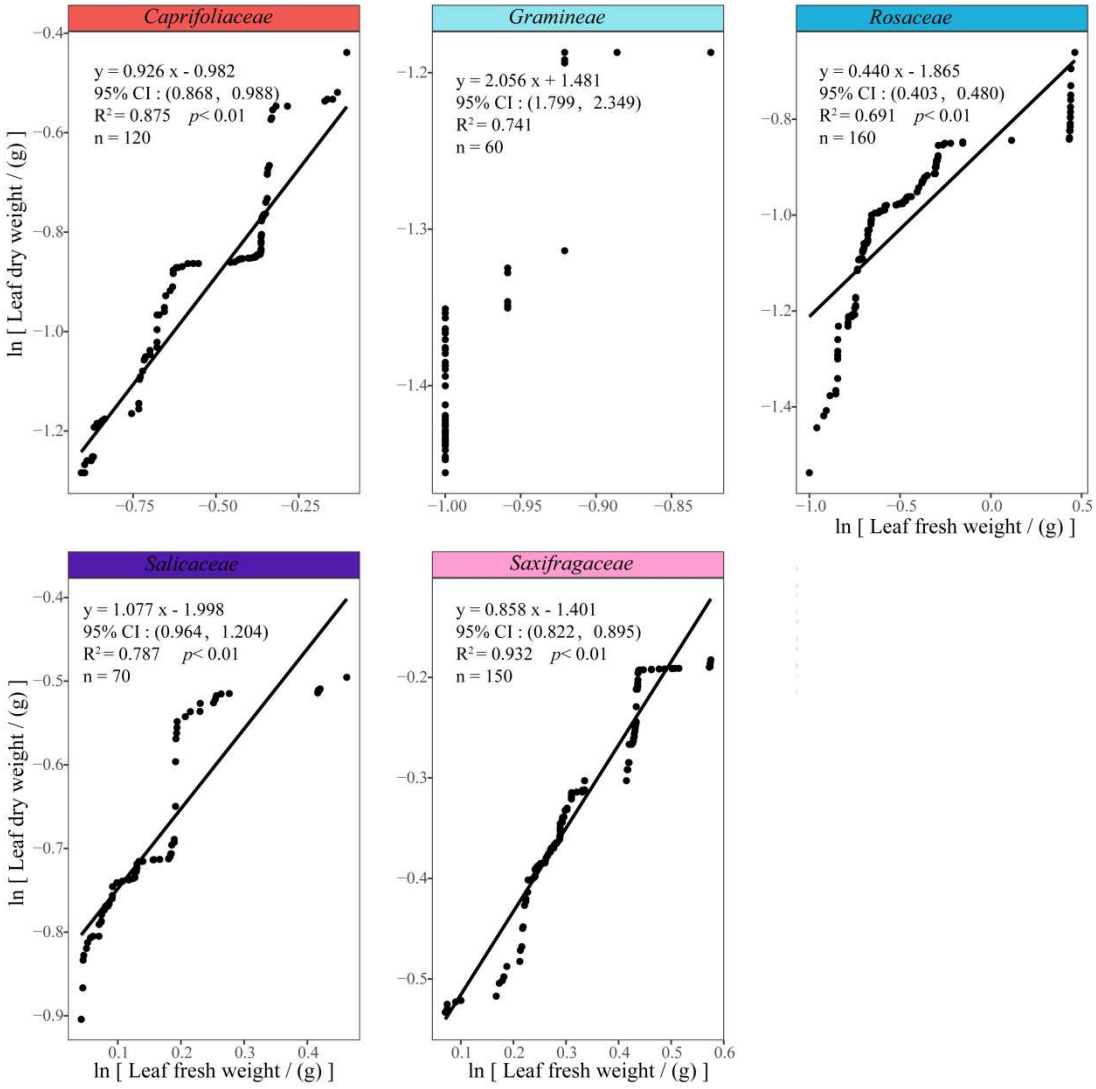
The average LFM, LDM, LT, and LA (mean±SD) recorded for the family *Saxifragaceae* were 2.25±0.56 g, 0.49±0.10 g, 0.54±0.13 mm, and 16.17±3.48 cm^2, respectively (**Fig. 2**). For the family *Caprifoliaceae*, the average LFM, LDM, LT, and LA were 0.34±0.14 g, 0.14±0.06 g,0.02±0.08 mm, and 3.01±1.00 cm^2, respectively. Similarly, for the family *Gramineae*, we recorded 0.10±0.01 g, 0.04± 0.01 g, 0.12±0.01 mm, and 2.45±0.57 cm^2, the average LFM, LDM, LT, and LA, respectively. We recorded 0.53±0.75 g, 0.10±0.03 g, 0.28±0.07 mm, and 4.04± 2.31 cm^2 of average LFM, LDM, LT, and LA, respectively, for the family *Salicaceae*.



Fight. 2. Comparison of leaf functional traits among five advantage families, including **(A)** leaf fresh weight, **(B)** leaf dry weight, **(C)** leaf water content, **(D)** leaf thickness, **(E)** leaf area, **(F)** specific leaf area, and **(G)** leaf day mass content. In each panel, different lowercase letters indicate significant differences ($p<0.05$). **(I)** *Caprifoliaceae*, **(II)** *Gramineae*, **(III)** *Rosaceae*, **(IV)** *Salicaceae*, and **(V)** *Saxifragaceae*.

3.2. **Scaling relationship between leaf fresh weight and leaf dry weight**

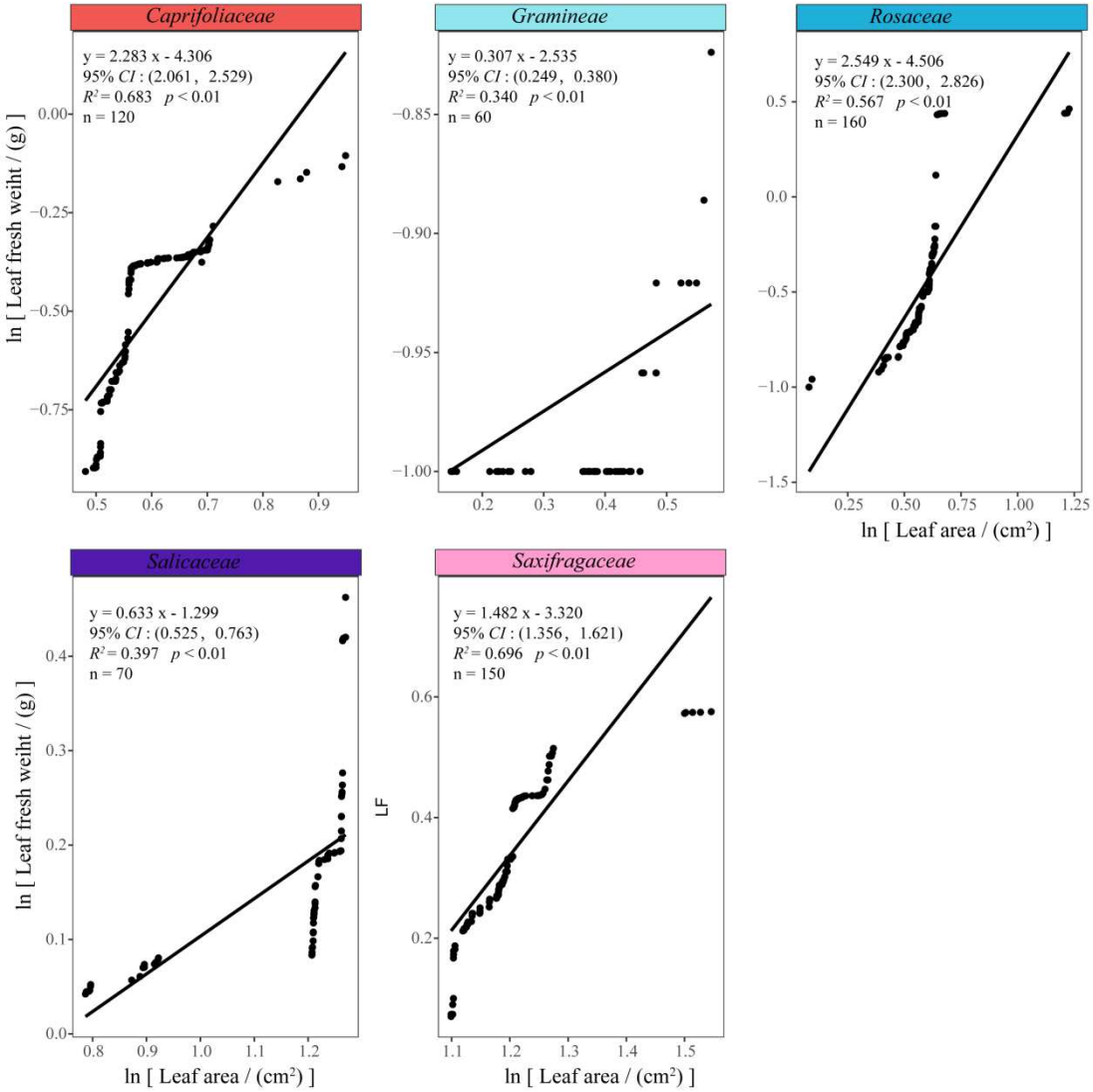
The scaling relationship between leaf fresh weight and leaf dry weight was statistically robust for all five advantage families (**Fight. 3**). The 95% confidence interval (*CI*) for families *Salicaceae* and *Saxifragaceae* was equal to 1.0 (unity). In contrast, the 95% *CI* for *Rosaceae* and *Caprifoliaceae* was significantly lower than 1.0 ($p<0.01$). For *Gramineae*, the 95% *CI* was significantly higher than 1.0 ($p<0.01$).



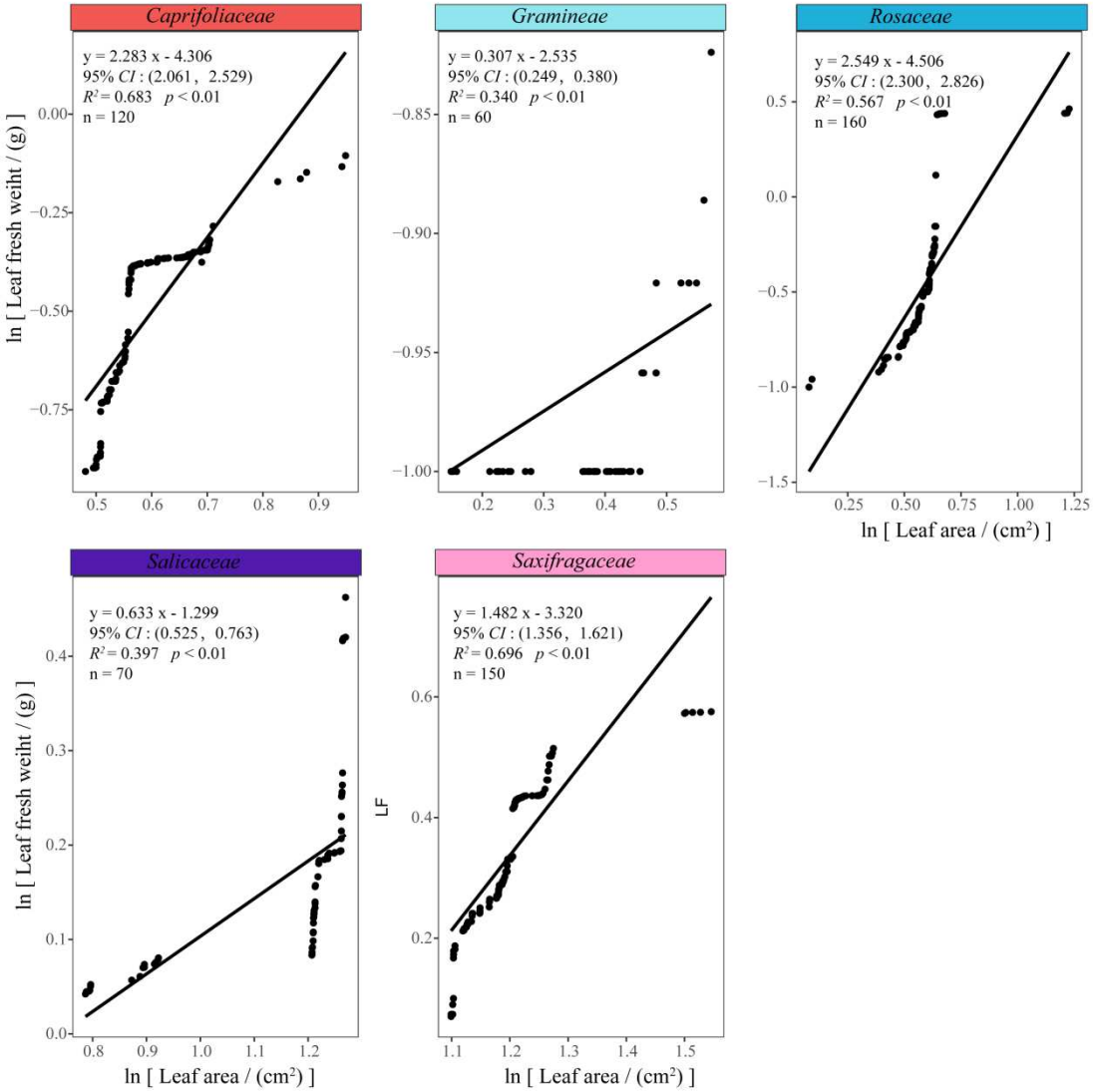
Fight. 3. The fitted linear regression lines showing the scaling relationships between leaf fresh weight and leaf dry weight for five advantage families. In each panel, n represents the number of leaves sampled.

3.4. Scaling relationship between leaf area and leaf weight

The scaling relationship between leaf area and leaf fresh (**Fight. 4**) weight relatively complex, and α for all five advantage families did not include unity. For *Gramineae* and *Salicaceae*, the α was significantly lower than 1.0; however, for the other three families, α was significantly greater than 1.0. The scaling relationship between leaf area and leaf dry weight was similar to this (**Fight. 5**). These results suggest an allometric relationship between leaf area vs. leaf dry weight. However, the R^2 for the leaf area vs. leaf dry weight scaling relationships was lower than for the leaf area vs. leaf fresh weight.



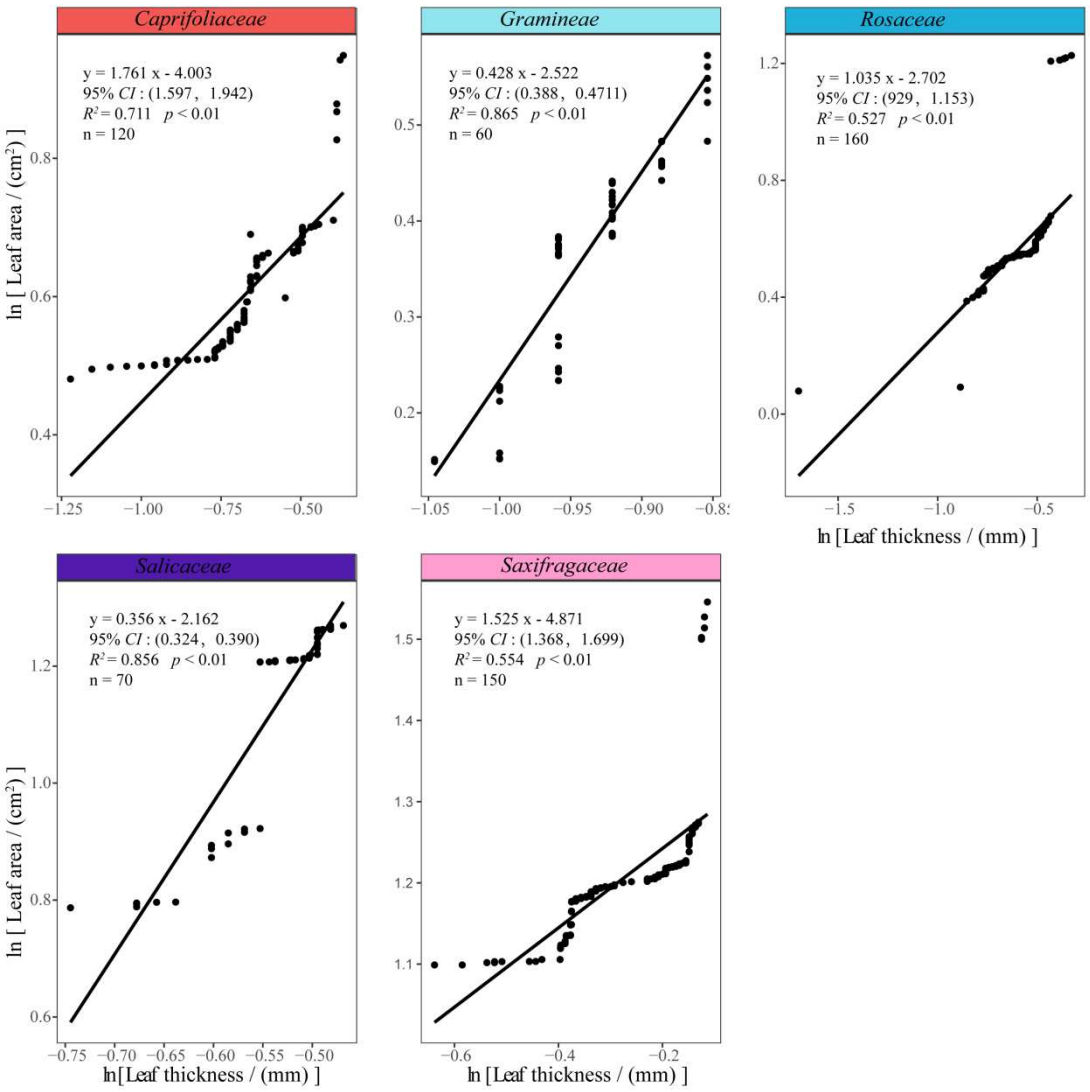
Fight. 4. The fitted linear regression lines showing the scaling relationships between leaf area vs. leaf fresh weight for five advantage families. In each panel, n represents the number of leaves sampled.



Fight. 5. The fitted linear regression lines showing the scaling relationships between leaf area vs. leaf fresh weight for five advantage families. In each panel, n represents the number of leaves sampled.

3.5. Scaling relationship between leaf thickness and leaf area

For the family *Rosaceae*, the R^2 was smaller than other families, and 95% *CI* of α included 1.0. The leaf thickness and leaf area showed an isometric relationship and did not support diminishing returns (**Fight. 6**). The *α* value for leaf thickness and leaf area in *Caprifoliaceae* and *Saxifragaceae* families, however, exceeded 1.0, supporting diminishing returns. For the other two families, the 95% *CI* of α was significantly lower than 1.0.



Fight. 6. The fitted linear regression lines showing the scaling relationships between leaf thickness vs. leaf area for five advantage families. In each panel, n represents the number of leaves sampled.

4. Discussion

Studying post-fire plant leaf functional traits and their relationships helps to understand their adaptation to fire regimes and the trade-off strategies of resource utilization after the fire. In this study, after 15 years of post-fire vegetation recovery, we reported complex responses of leaf functional traits to fire across five families within a burned *Picea asperata-Abies fabri* forest in the northeastern margin of the Qinghai-Tibetan Plateau，Gansu. What is move, the present study with the objective of assess whether the diminishing return hypothesis applies to species leaf traits restored in fire burn sites.

The leaf economic spectrum(LES) provides convincing evidence of a consistent and continuous relationship among the leaf traits, reflecting a gradient of slow (conservative) to fast (acquisitive) strategies in terms of investment and use of nutrients and other non-biological resources(Reich et al., 1997) (Shipley, 2016). The leaves of post-fire renewal communities were situated in different positions of the LES, which probably avoided the competition for moisture or sunlight resources among species of the same family or/and genus, thereby improved their survival status(Simon et al., 2016; Yanjie et al., 2016). It is worth to raise that the bushes in this study were generally low, among them, the mean of *H* the *Philadelphus incanus* in the families *Saxifragaceae* was the lowest, which is 38.0990 cm, in contrast, the highest is the *Rosa willmottiae* in the families *Rosaceae*, which is 128.8824 cm. For the mean *BD*, the families *Gramineae* was the smallest (4.2129 mm) and the largest is *Rosa willmottiae* the families *Rosaceae*, also. We speculated that after 15 a severe fire in the forest, the vegetation was in the early stage of succession and recovery, and in this process, the composition and structure of the community are changing rapidly, in summary, light-loving shrub species grow quickly in order to obtain more sunlight and nutrients. Besides, the SLA of the families *Salicaceae* was larger, but the LDMC was smaller. On the contrary, the SLA of the families *Caprifoliaceae* was smaller, the LDMC was the opposite. One plausible explanation is that the families *Salicaceae* located in the quick-return end, which species with high leaf nutrient concentrations and high rates of photosynthesis and respiration, short leaf lifetimes and low LDMC. Obviously, the families *Caprifoliaceae* belong to the slow-return end, with long leaf lifetimes, expensive high-LMA leaf construction, low nutrient concentrations and rates of photosynthesis and respiration(Wright et al., 2004). After years of research showed that plant traits were multifunctional, and linked to multiple traits through complex direct and indirect interactions(Homeier et al., 2021). Our results showed that for the families *Salicaceae* and *Saxifragaceae* the change in LDM was proportional to the change in LFM. These relationships imply that the absolute LWC generally kept pace with LDM in these two advantage families. In addition, our study results supported the law of isometric (i.e., scaling exponent (α) =1.0) for LFM and LDM in *Salicaceae* and *Saxifragaceae*. Notably, the scaling exponent for LDM vs. LFM in *Gramineae* was significantly greater than 1.0, while it was significantly lower than 1.0 in the *Rosaceae* and *Caprifoliaceae*. Our results showed significant differences in leaf functional traits concerning fire adaptation and post-fire resource allocation strategies across five families. In this study, leaves representing the family *Gramineae* were sampled from the species *Fargesia spathacea* Franch， their vegetative leaves were typically simple, their phyllotaxy was relatively singlenss and simple(Lin et al., 2020), with greater densely packed leaf cells (Pyankov et al., 2010; Vasfilov, 2012), allowing the thinner leaves to catch more light(Huang, Olson, et al., 2020; L. Zhang et al., 2020). On the contrary, plant leaves from the

family *Rosaceae* and *Caprifoliaceae* have villi and small thorns that help to conserve water through absorption and accumulation. Differences in the shape of the leaves and epidermal layer may explain the allometric relationships between LFM and LDM. Due to the intense fire, the tall canopy of *Picea asperata-Abies fabri* forest was removed, altering plant community structure and competition dynamics among plant species. In addition, intense forest fire results in high water repellent soils, reducing soil moisture availability to regenerating plants. Therefore, the variation in the scaling relationship between LFM and LDM reported here may be an vital survival strategy for plants adaption to low soil moisture conditions (Huang, Reddy, et al., 2020).

Previous studies have shown that leaf area is an important functional trait closely associated with the plant's ability to intercept light and biomass production(Gifford et al., 1984; Dwelle, 1985). The SLA of a plant species is often positively correlated with the relative growth rate or mass-based maximum photosynthetic rate. Lower SLA values tend to correspond with relatively high investments in leaf "efences"(particularly the structure) and leaf lifespan (Osone et al., 2008; Yu et al., 2019). The SLA and leaf area are functionally linked. In this study, we examined the scaling relationship between leaf mass and leaf area to quantify how a change in leaf size affects SLA. The results showed that the scaling exponents between LFM and LA varied across the five advantage families. Indeed, the scaling exponents between LFM and LA for *Gramineae* and *Salicaceae* were significantly lower than 1.0. In contrast, scaling exponents between LFM and LA in the other three families were significantly greater than 1.0, indicating that these families follow the law of diminishing returns.

The relationship between LDM and LA was comparable to that between LFM and LA, suggesting that LWC in different species representing different families may not be the same. Notably, results showed a stronger scaling relationship between LDM and LA than between LFM and LA. These results are different from Huang et al. (Huang, Ratkowsky, et al., 2019) findings. It was found that the goodness of fit between LDW and LA was better than that between LFM and LA, on the other hand Chen found that. After a major fire, the local government sealed off the fire site and prevented it from further anthropogenic disturbances, providing opportunities for vegetation to recover naturally. In addition, complex topography and high altitude limit public access to the site, providing conditions for natural recovery (Whipple et al., 1999; Y. Liu et al., 2016). Therefore, the relationships between leaf mass and leaf area of plants regenerated after the fire are highly variable, reflecting the species-specific strategies to adapt to harsh environmental conditions.

Leaf thickness(LT) is considered a valuable property because of its direct link to resource acquisition, carbon assimilation, plant cell volume, and water reserves in plants(J. Liu et al., 2006; Gonzalez-Paleo & Ravetta, 2018). In this study, in the family *Rosaceae*, the 95% CI of the scaling exponent of the LA vs. LT relationship overlapped with one; the LA increased with increasing LT. However, the relationship did not show similar results in the other families. Previous studies have shown that the variations in leaf thickness and leaf area are closely related to light distribution and water allocation. In this study, the mean leaf area for the family *Rosaceae* was 4.04 cm^2 and the leaf thickness was 0.28 mm. To harsh environmental conditions (e.g., drought and intense light), a plant species must produce small thick leaves that help avoid excess water loss. In the Qinghai-Tibetan Plateau, the sunlight is intense. After the fire, the soil water repellency was likely higher, reducing soil moisture content for a long duration. Under moisture-limited conditions, increasing leaf thickness may help plants retain water in leaf tissues and enhance photosynthesis.

Indeed, the thickness of guard tissue and sponge tissue has been suggested to have a close link to the photosynthetic and transpiration rates of the leaves.

Generally speaking, our study presented the evidence to support the law of diminishing returns in plants regenerated after the fire that has rarely been studied in previous cases. On the whole, our finding was generally consistent with most previous studies on the artificial landscapes, there were trade-offs between different traits. It was reasonable to speculate that the allometric relationship between leaf traits likely held true for all sorts of plant species in different environments.

5. Conclusion

In summary, by measuring the leaf functional traits(including LFM, LDM, LA and LT) of fire across within a burned *Picea asperata-Abies fabri* forest in the northeastern margin of the Qinghai-Tibetan Plateau, we found suggest that the relationship between LFM and LDM were not only isometric but also allometric. The goodness of fit between LDW and LA was better than that between LFM and LA. Future investigations using strategies reported functional traits of plant leaves after a fire will likely illuminate novel function of adaptability of plants to the fire environment. In conclusion, we need more comprehensive data sets containing more species living under after fire environmental conditions and different years to assess the generality of the diminishing returns hypothesis, for another, identify the main factors that influence the trade-off between traits. This will provide a theoretical basis for the protection of plants regenerated after the fire.

Author Contributions: Cao Xueping, Tian Qing, Zhou Xiaolei, Huang Haixia contributed to the conception of the study; Cao Xueping, Zhou Xiaolei, Huang Haixia, Zhao An, Lu Gang, He Wang-peng performed the experiment; Cao Xueping, Zhou Xiaolei contributed significantly to analysis and manuscript preparation; Cao Xueping, Zhou Xiaolei performed the data analyses and wrote the manuscript; Cao Xueping, Zhou Xiaolei helped perform the analysis with constructive discussions.

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