

Plant functional traits of *Dasiphora fruticosa* shrub have a stronger response to soil properties in Qinghai-Tibet Plateau, China

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Research Article

Keywords: Morphological traits, Stoichiometric traits, Soil properties, *Dasiphora fruticosa*, Qinghai-Tibet Plateau, Altitude

Posted Date: September 12th, 2024

DOI: <https://doi.org/10.21203/rs.3.rs-4873146/v1>

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Abstract

Dasiphora fruticosa widely distributes in subalpine and alpine regions in the world, and is originated from Qinghai-Tibet Plateau. Further exploration of influence of environmental factors on plant functional traits of *Dasiphora fruticosa* in Qinghai-Tibet Plateau is essential to predict the growth and distribution under climate change more accurately. The *Dasiphora fruticosa* shrub on 24 plots were sampled at the altitude gradient of 2550-5200 meters above sea level on Qinghai-Tibet Plateau. Totally 13 plant functional traits of *Dasiphora fruticosa* were measured, including morphological traits (plant height, crown width, specific leaf area and leaf dry matter content) and stoichiometric traits (carbon, nitrogen and phosphorus content in leaves, flowers and stems). The results showed that morphological traits of *Dasiphora fruticosa* changed significantly along altitude. With the increase of altitude, plant height and crown width tended to be shorter. Leaf dry matter content also decreased along altitude. The stoichiometric traits varied along altitude, and were different in organs. Specifically, the phosphorus content in organs increased significantly along altitude. The morphological traits had large coefficient of variation. Soil properties were the main drivers of most of plant functional traits. Soil properties significantly directly affected the morphological traits and carbon and phosphorus contents while mean annual precipitation significantly indirectly affected them by affecting soil nutrients. *Dasiphora fruticosa* adapts to diverse habitats by adjusting its morphological traits and phosphorus content in organs. Soil properties have a stronger influence and act as a direct filter on plant functional traits of *Dasiphora fruticosa* in alpine regions.

Introduction

Shrubs are woody plants with the highest and the northernmost known distribution (Liang et al. 2012; Lu et al. 2022; Walker et al. 2005). Compared with grasslands and forests, shrubs have lower productivity and biodiversity, so they have not been widely concerned in ecological research (Guo et al. 2021; Lieth and Whittaker 1975; Zhang et al. 2017). However, in the context of global warming, shrubs tend to expand globally, such as intrusion of drought-tolerant shrubs and emergence of desert shrubs in semi-arid areas, and warming may promote upward treeline and shrub line shift in alpine regions (Archer et al. 2001; Li et al. 2023). Response mechanism of plant functional traits to the environment are important methods for understanding the mechanism of shrub expansion (Harte and Shaw 1995; Li et al. 2020; Montane et al. 2007). In recent years, more and more studies have explored the adaptation strategies of plant populations and communities through quantitative plant functional traits and their responses to the environment (He et al. 2018; He and Ye 2019; Storkey and Macdonald 2022).

In the long process of evolution and development, plants interact with the environment and gradually form many internal physiological and external morphological adaptation strategies to minimize the adverse effects of the environment, the performance of these adaptation strategies is plant traits (McIntyre et al. 1999; Meng et al. 2007; Weiher et al. 1999). Plant functional traits refer to a series of plant traits that have potential significant effects on plant colonization, survival, growth and death, and different traits have different response characteristics to different environmental gradients (Cornelissen et al. 2003; Liu and Ma 2015; Reich et al. 2003). Studying plant functional traits of individual species

along environment gradients can reveal the adaptability of species to environment and the width of ecological amplitude (Violle and Jiang 2009; Westerland et al. 2021). Researches on the variation of plant functional traits along environmental gradients have found that some traits are more sensitive to environmental changes, such as plant height (Barker et al. 2019), stomatal behavior (Oren et al. 1999), rooting depth (Schenk and Jackson 2002), photosynthetic capacity (Vogan and Maherali 2014), leaf morphology (Steinger et al. 2003), phenology (Franks 2011), and physiology (Sherrard and Maherali 2006), compared to other traits such as floral traits (Caruso 2006; Caruso et al. 2020) and chemical defense traits (Barker et al. 2019). In mountainous ecosystems, environmental factors have formed distinct gradients with increasing altitude, such as decreasing temperature, lowering atmospheric pressure, increasing light intensity, and fluctuating precipitation (Körner 2007; Wakui et al. 2017). Plants also develop corresponding functional trait characteristics to adapt to these changes but there is no unified understanding of its adaptation mechanism (Ackerly and Reich 1999; Nicotra et al. 2010; Swenson and Enquist 2007). For example, with increasing altitude, specific leaf area increases (Körner et al. 1989; Körner and Paulsen 2004) or decreases (Midolo et al. 2019), leaf nitrogen content decreases (Midolo et al. 2019; Read et al. 2014), photosynthetic rate declines (Wright et al. 2004), xylem conduits become narrower (Yang et al. 2020), leaf dry matter content decreases and leaf water content increase (Feng et al. 2022), while leaf mass per area and carbon isotope composition increase (Midolo et al. 2019). Among many environmental factors that affect plant functional traits, climatic factors have been widely concerned (Bond and Midgley 2003; Chaturvedi et al. 2021; Hoffmann et al. 2011; Johnson et al. 2016; Poorter and Markesteijn 2008; Reich and Oleksyn 2004; Sardans et al. 2012; Wright et al. 2004). As the mean annual temperature (MAT) becomes colder, plant growing season is shorter, the plant height becomes smaller, and leaf dry matter content decreases more (Wright et al. 2005). With the increase of precipitation, leaf nitrogen and phosphorus content, specific leaf area, and maximum photosynthetic rate have been observed to increase, while leaf dry matter content tends to decrease (Díaz et al. 2004; Reich et al. 1999; Vitousek et al. 2010; Wright et al. 2004). Soil is an important factor for plant growth (Caminha-Paiva et al. 2021; Díaz et al. 1998; Violle et al. 2014). Soil physical and chemical properties such as soil texture, bulk density, organic carbon and pH determine soil water retention capacity and soil nutrient status (Liu et al. 2006). Soil nutrient such as nitrogen, phosphorus and potassium can affect plant stoichiometric traits, biomass allocation and even ecological strategies (Güsewell 2004; Hogan et al. 2010; Liu et al. 2024; Tessier and Raynal 2003; Wang et al. 2019). Plants grown on fertile soil invest more resources in growth and reproduction and have larger leaf surface area volume ratio, specific leaf area and higher relative growth rate (Jager et al. 2015; Roderick et al. 2000). Barren soils serve as a crucial environmental catalyst for nutrient conservation and slow-growth strategies (Hopper 2009; Hopper et al. 2016). Many studies have shown that leaf nitrogen content and phosphorus content are significantly correlated with soil nitrogen and phosphorus content, especially, leaf phosphorus content is significantly affected by soil phosphorus (Maire et al. 2015; Ordoñez et al. 2009; Reich and Oleksyn 2004). Soil is complex, embodying both large-scale zonal characteristics and local microhabitat variations (Aguar and Sala 1999; Charley and West 1975; Li et al. 2014; Lin et al. 2010; Schlesinger et al. 1996; Stock et al. 1999; Wang et al. 2009). Research on the effects of environment factors on plant functional traits is still vastly underexplored and necessitates further investigation.

Dasiphora fruticosa, a deciduous shrub about 50–100 cm high, originated from the Qinghai-Tibet Plateau, and is considered as a typical alpine deciduous shrub in Qinghai-Tibet Plateau (Elkington and Woodell 1963; Ma et al. 2014; Nie et al. 2023; Yashiro et al. 2010). It could be found from 2300 to 5200 meters above sea level in Qinghai-Tibet Plateau (Dorji et al. 2014; Feng et al. 2022; Qin et al. 2022). Today, *Dasiphora fruticosa* is distributed extensively, from Qinghai-Tibet Plateau to Eastern Asia, Northern Europe, the Mediterranean and the United States (Dai et al. 2021; He 2017). In addition, studies on the cytotaxonomy of *Dasiphora fruticosa* showed that the diploid was hermaphroditic and the tetraploid was dioecious (Elkington 1969; Grewal and Ellis 1972). *Dasiphora fruticosa* has a relatively wide ecological amplitude. It has the characteristics of cold tolerance and drought tolerance, the optimum temperature for its growth is about 7°C, and can withstand the severe cold of -50°C (He 2017; Su et al. 2020; Zhang 2015). It is mainly grown in mountainous shady slopes, flat beaches and wet ditch between the shoal as constructive or sub-constructive species (Ding 2023; He 2023; Su et al. 2020). There have been many studies focusing on the adaptive characteristics of *Dasiphora fruticosa* to the environment (Feng et al. 2022; Qin et al. 2022; Wei 2021). For instance, Meshinev (1973) studied the effect of light on the germination of *Dasiphora fruticosa* seeds. Guo et al. (2017) revealed the physiological and biochemical mechanism of *Dasiphora fruticosa* in response to high temperature stress from the aspects of leaf structure and physiological metabolism. Bai (2007) analyzed the leaf main chemical components such as tannin and flavonoid content in wild *Dasiphora fruticosa* at different altitudes in Qinghai-Tibet Plateau. Robertson and Lenz (1984) studied the environmental factors affecting the flower color and receptacle of *Dasiphora fruticosa*. In addition, researchers pay more attention to the changes of functional traits of *Dasiphora fruticosa* along altitude gradients (Feng et al. 2022; Qin et al. 2022; Wei 2021). For instance, on the northern slopes of the Qilian Mountains at 2000–5000 m.a.s.l., wood density and leaf dry matter content in *Dasiphora fruticosa* decreased significantly along altitude, while leaf area, leaf water content and specific leaf area did not change significantly (Feng et al. 2022). In the northeastern part of the Qinghai-Tibet Plateau at 2400–3800 m.a.s.l., leaf nitrogen concentration of *Dasiphora fruticosa* generally increased along altitude (Qin et al. 2022). At present, there are few studies on the functional traits of *Dasiphora fruticosa*, and the response characteristics of functional traits of *Dasiphora fruticosa* to the environment and the adaptation mechanisms need to be studied more comprehensively. On the one hand, the research ranges are more on small areas, such as watershed scale or a few mountain peaks. On the other hand, the research objects are often only one aspect of morphological or stoichiometric traits, and there is a lack of research on the more comprehensive characteristics of plant functional trait of *Dasiphora fruticosa* and overall response of traits to environmental changes.

This study took *Dasiphora fruticosa* shrub in Qinghai-Tibet Plateau as the research object, sampled on the whole Qinghai-Tibet Plateau (85.1996–100.9362°E, 29.2009–38.5728°N) along an altitude of 2550–5200 m.a.s.l., and obtained the morphological and stoichiometric traits of the whole plant, i.e., stems, leaves and reproductive organs to explore the influence of environmental factors on its functional traits, and its adaptability to environment factors.

Materials and Methods

Sampling and measurement

The *Dasiphora fruticosa* shrub on 24 plots were sampled on Qinghai-Tibet Plateau (85.1996-100.9362°E, 29.2009–38.5728°N), and at the altitude gradient of 2550–5200 m.a.s.l. (Fig. 1 and Table S1) in July and August of 2018–2021. All plots were on the sunny aspects with slope less than 10°.

At each site, we randomly selected 9 healthy and mature individuals to measure crown width and plant height in the field. The height of each selected shrub was measured from the base of the stem at ground level to the highest point of the plant. Crown width was determined by measuring the maximum horizontal spread of the canopy in two perpendicular axes, subsequent to which, the area of the ellipse, delineated by these axes serving as its major and minor axes respectively, was calculated to represent the crown width. Approximately 1,000 fully expanded, healthy and intact leaves were collected at each site to analyze morphological and stoichiometric traits. These leaves were immediately placed in labeled plastic bags and stored in an insulated container to avoid changes before laboratory analysis. Flower and stem samples were also collected to analyze stoichiometric traits. We randomly selected hundreds of open or unopened flowers and cut dozens of branches that are fully exposed to sunlight at each site. Flower and stem samples were placed in paper bags and dried for further analysis. We collected and measured seven plant functional traits of *Dasiphora fruticosa*, including morphological traits (plant height, crown width, specific leaf area and leaf dry matter content) and stoichiometric traits (carbon, nitrogen and phosphorus content in leaves, flowers and stems), referring to handbooks for standardized measurements of plant functional traits (Cornelissen et al. 2003; Pérez-Harguindeguy et al. 2013).

Climatic and soil variables

Yearly climatic conditions (mean air temperature and total precipitation) from 1998 to 2017 from the 1 km yearly temperature and precipitation grid data of the Qinghai Tibet Plateau and its surrounding areas were gathered (Ding 2019). Two climatic variables were calculated: mean annual temperature (MAT) and mean annual precipitation (MAP). Soil variables were the properties of 0–30 cm depth calculated from the basic soil property dataset of high-resolution China soil information grids (250 m resolution) (Liu et al. 2020; Liu et al. 2022; Zhang and Liu 2021), including soil bulk density (BD), sand content (Sand), silt content (Silt), clay content (Clay), soil organic carbon content (SOC), soil total nitrogen content (TN), soil total phosphorus content (TP), soil total potassium content (TK), soil cation exchange capacity (CEC), soil pH (pH), content in rock fragments (CF, >2mm), and soil thickness (Thick). As there is no direct 0–30 cm data in the dataset, the average value of three layers (0–5 cm, 5–15 cm, and 15–30 cm) weighted by soil layer depth was calculated:

$$X_{0-30} = \frac{X_1 * 5 + X_2 * (15 - 5) + X_3 * (30 - 15)}{30}$$

Where X_{0-30} is the converted value represents for the property value of 0–30 cm depth, X_1 to X_3 were the original value of the first to the third horizon.

Plots from the field surveys were matched one-by-one to individual pixels in the above two data by recorded latitude and longitude positions (Ren et al. 2023).

Statistical analysis

To explore whether and to what extent the plant functional traits varied along the altitude gradient, we used simple linear analysis and binomial regression analysis to evaluate the variation in trait values using altitude as a predictor variable. In order to obtain the variations of traits, we divided the standard deviation of trait by the average value of trait to calculate the coefficient of variation (CV) (Wang and Zhou 2017). Spearman's correlation analysis was used to explore the strength of association between plant functional traits and environmental factors. To assess the relative impact of environmental factors on plant functional traits, variance decomposition was performed using the R packages "hier.part". Considering the goodness of fit of the model, soil properties and plant functional traits were respectively reduced the dimension by principal component analysis (PCA). To clarify the direct and indirect drivers of plant functional traits, the piecewise structural equation modeling (piecewise SEM) was performed using the R package "piecewiseSEM".

Data calculations and analyses were performed in SPSS 24.0 and R v.4.2.2, plotting was performed in R.

Results

Variations in plant functional traits of *Dasiphora fruticosa* along altitude

Among the four morphological traits of *Dasiphora fruticosa*, plant height, crown width and leaf dry matter content were significantly decreased with the increase of altitude ($R^2 = 0.60$, $P < 0.01$; $R^2 = 0.29$, $P < 0.05$; $R^2 = 0.51$, $P < 0.01$, respectively, Fig. 2a, b and d), while specific leaf area had no significant correlation with altitude ($R^2 = 0.07$, $P > 0.05$, Fig. 2c).

As for stoichiometric traits of *Dasiphora fruticosa*, the content of carbon in leaves decreased significantly along altitude ($R^2 = 0.25$, $P < 0.05$, Fig. 2e), while phosphorus content in leaves increased significantly ($R^2 = 0.24$, $P < 0.05$, Fig. 2k). The nitrogen content in leaves fluctuated irregularly between 1.3% and 3.0% along altitude (Fig. 2h).

The contents of C, N and P in flowers changed significantly along altitude. Flower C content decreased significantly along altitude ($R^2 = 0.52$, $P < 0.01$, Fig. 2f), while P content in flowers increased significantly ($R^2 = 0.37$, $P < 0.05$, Fig. 2l). The variation of N content in flowers along altitude showed a secondary trend of increasing first and then decreasing with an inflection point at 3950 m ($R^2 = 0.34$, $P < 0.05$, Fig. 2i).

The content of P in stems of *Dasiphora fruticosa* had a relatively significant upward trend along altitude ($R^2 = 0.23$, $P < 0.05$, Fig. 2m), while the content of C and N in stems did not change significantly (R^2 was 0.11 and 0.02, respectively; $P > 0.05$, Fig. 2g and j).

Coefficient of variation of plant functional traits of *Dasiphora fruticosa* ranged from 0.03 to 1.48 (Fig. 3). Crown width and plant height exhibited the greatest variability, with coefficients of variation exceeding 0.85. Conversely, the variability of carbon content in stems, flowers, and leaves were minimal, with coefficients of variation less than 0.06. The coefficients of variation for the remaining traits ranged from 0.15 to 0.33 (Fig. 3).

Relationship of plant functional traits and environmental factors

In addition to N content in leaves and stems, soil silt content was significantly correlated with all plant functional traits of *Dasiphora fruticosa*. Soil total potassium was significantly correlated with C content in flowers. Soil organic carbon and total nitrogen, as well as total phosphorus and cation exchange capacity, had similar correlation with plant functional traits respectively, and all significantly correlated with leaf N content and flower C content. Mean annual precipitation was positively correlated with C content in leaves and N content in leaves and stems. Mean annual temperature was significantly positively correlated with leaf P content and flower C content (Fig. 4).

The morphological traits were significantly correlated with soil texture (sand and silt) and cation exchange capacity. The C content in leaves and flowers were significantly correlated with most of soil properties (Fig. 4).

The reduced-dimensional soil properties and plant functional traits were obtained from principal component analysis, respectively. The total explanation of the first three axes of soil properties was 87.51%. PC1 of soil properties was soil nutrient (SOC, TN, TP, negative pH, CEC, negative BD and soil texture, i.e. negative sand, silt, and clay) with an explanation of 60.35%, PC2 was soil physical properties (CF and negative thickness) with an explanation of 16.96%, and PC3 was soil potassium with an explanation of 10.20% (Fig. S3 and Table S3). The total explanation of the first three axes of plant functional traits was 63.36%. PC1 of plant functional traits with an explanation of 38.43% could be named “Morpho + C-P” because it included morphological traits (except for specific leaf area), C content and negative P content. PC2 was “LNC + FNC” (leaf and flower N content) with an explanation of 13.71%, and PC3 was “-SLA-SNC” (negative specific leaf area and negative stem N content) with an explanation of 11.22% (Fig. S4 and Table S4).

The relative effects of MAP, MAT, soil nutrient, soil physical properties and soil potassium on the three principal components of plant functional traits were analyzed by variance decomposition, respectively. Soil nutrient and soil potassium, i.e. PC1 and PC3 of soil properties, were the main drivers of “Morpho + C-P” (43.76% and 29.32%, respectively, Fig. 5a). The effects of three principal components of soil on “Morpho + C-P” were significant, and climatic factors were not significant (Fig. 5a). Soil nutrient and MAP were the main drivers of “LNC + FNC” (31.59% and 25.15%, respectively, Fig. 5b). Soil physical properties

and MAP were the main drivers of “-SLA-SNC” (51.46% and 18.57%, respectively, Fig. 5c). The effects of the five factors on “LNC + FNC” and “-SLA-SNC” were all not significant (Fig. 5b and c).

Direct and indirect effects of environmental factors to plant functional traits

The direct and indirect effects of climatic factors and soil properties on plant functional traits were determined by assuming a piecewise structural equation model of climatic factors, reduced-dimensional soil properties and reduced-dimensional plant traits (Fig. 6). The results showed that mean annual precipitation significantly indirectly affected the morphological traits and C and P contents of *Dasiphora fruticosa* by affecting soil nutrients and soil potassium, while mean annual temperature significantly indirectly affected them by affecting soil physical properties (Fig. 6a). SLA and N content in *Dasiphora fruticosa* had no significant response to the environmental factors selected in this study (Fig. 6b and c).

Discussion

Soil properties have a strong directly effect on plant functional traits of *Dasiphora fruticosa* on alpine region

Soil properties directly and significantly affected the morphological traits, carbon and phosphorus content in organs of above-ground parts of *Dasiphora fruticosa* (Figs. 5 and 6a), which is consistent with other research of *Dasiphora fruticosa* (Qin et al. 2022). Soil properties filter out the plant functional traits of *Dasiphora fruticosa* directly on alpine region.

As altitude increases, TN, TP, TK, CEC, Silt and Thick of soils significantly decreased, while Sand and BD significantly increased (Table S2), and *Dasiphora fruticosa* tended to be shorter and smaller (Fig. 2a and b). Crown width and plant height decreased significantly along altitude and had the largest coefficient of variation (Figs. 2 and 3), indicating significant variations with environment and adaptation to changes in soil properties especially soil texture (Figs. 4, 5a and 6a). Soil texture determines soil aeration, water permeability, water retention, and fertilizer retention, all of which can impact the plant's access to water, nutrients, and oxygen (Wu and Zhao 2019). This, in turn, affects the plant's ability to develop a strong root system, ultimately influencing the overall shape and growth of the plant.

The influence of soil thickness on plant growth was mainly reflected in the supply of water and nutrients. The thicker the soil is, the larger the space is, and the plant roots could penetrate deeper into the soil to obtain more water and nutrients (Mcconnaughay and Bazzaz 1991). Research on *Jatropha curcas* found that when the soil thickness was larger, the individual height was taller, and the vertical space resources were relatively fully utilized (He et al. 2010b).

Leaf dry matter content was mainly influenced by soil texture (mainly sand, silt content, and soil bulk density) in this study (Fig. 4). In a study on the effect of soil texture on dry matter accumulation of *Medicago sativa*, it was found that the total dry matter accumulation of *Medicago sativa* was greater in loam clay soils than in slit loam and clay soils, suggesting that soil texture affects leaf dry matter

content by affecting water and nutrient uptake by the plant (Zhao et al. 2007). LDMC is an important indicator of plant photosynthesis and biomass production (Cornelissen et al. 2003). Soil texture indirectly affects plant photosynthetic efficiency and biomass accumulation by influencing water and nutrient availability (Wu and Zhao 2019). For example, water stress reduces the rate of photosynthesis in plants and decreases the accumulation of leaf dry matter. The efficient supply of nutrients is the basis for photosynthesis and plant growth.

P content in organs of *Dasiphora fruticosa* was significantly affected by soil properties, especially related to soil texture (Figs. 4, 5a and 6a). In addition, P uptake by plant is indeed strongly influenced by soil texture. Soil texture determines the size, shape, and distribution of soil particles, and these factors directly affect soil porosity, infiltration rate, and water stability, which in turn affect phosphorus effectiveness and plant availability. The adsorption and desorption characteristics of phosphorus differ in soils with different textures (Chen et al. 2010; Gu et al. 2019). Under the same vegetation, loamy soils have higher C, N, and P than sandy soils (Huang et al. 2023). Soils with a high content of clay particles have a larger specific surface area and a higher cation exchange capacity, which enables them to adsorb more phosphorus. However, this adsorption may also result in the immobilization of phosphorus in the soil, with less phosphorus available to plants. In contrast, phosphorus immobilization is weaker in sandy soils, but plant uptake of phosphorus may be limited due to their lower water and fertilizer holding capacity.

As for the effect of soil nutrients, N is considered to be the main limiting factor for plant growth in many terrestrial ecosystems and one of the most important factors affecting the primary productivity (Jones et al. 2005; Luo et al. 2007; Vitousek 1982; Xing et al. 2000). The organic matter content, pH, structure and microbial activity of different soil will affect the effectiveness of nitrogen and the ability of plants to absorb nitrogen (Birch 1958; Henry and Raper 1989; Luo et al. 2007). With weak correlation to soil nutrients, nitrogen content can be stable, thereby plants exhibit stronger nitrogen retention capacity, particularly under stressful environmental conditions such as low temperature, drought and poor nutrient (He et al. 2010a; Hong et al. 2015; Zhao et al. 2017). The nutrients required for plant growth are not only dependent on the absorption of roots and leaves from soil and atmosphere, but also through the internal redistribution of nutrients in plants (Aerts 1996; Aerts and Chapin 2000; Killingbeck 1986; Xing et al. 2000). Leaf N and C contents correlated well with soil properties (Fig. 4). The poorer the soil (i.e., low in SOC, TN, TP, etc.), the lower the C and N contents in leaves and reproductive organs (Fig. 4). Overall the C and N contents in organs of *Dasiphora fruticosa* were less variable and maintained relatively stable contents (Figs. 2 and 3). Whereas, the relationship between P content in organs of *Dasiphora fruticosa* and some soil nutrients (such as SOC, TN, and TK) was not significant (Fig. 4). Qin et al. (2022) found that for leaf stoichiometric traits of *Dasiphora fruticosa*, P content in leaves had no significant relationship with altitude and soil properties, including SOC, TP and pH. However, leaf P content of 753 terrestrial plant species in China increased significantly with increasing soil P content (Han et al. 2005). In alpine, the stress of hydrothermal factors is greater than that of nutrients (Körner 2003; Körner et al. 1989), so that the P content in plant organs is more correlated with the soil physical properties and less correlated with the chemical properties. In addition, we only had total amounts of N, P, and K in soil, and

did not measure available N, P, and K. Whether plant functional traits have a more direct response to available N, P, and K needs further study.

The change of morphological traits of *Dasiphora fruticosa* with environmental factors is its overall adaptation to climate, soil, altitude and other natural conditions (He 2017). It is not only affected by soil properties, but also may be an adaptive response to other environmental factors such as air temperature, precipitation, high ultraviolet radiation, low air pressure, and strong winds (Chen et al. 2015; Gao and Liu 2018; Gong et al. 2019; Körner 2003; Pan et al. 2009). The influence of mean annual temperature on the functional traits of *Dasiphora fruticosa* was not significant, while the mean annual precipitation had a significant effect, primarily through its indirect impact on soil chemical properties, affecting the functional traits of *Dasiphora fruticosa* (Figs. 5 and 6). It verified the importance of water availability in regulating the variation of plant functional traits of *Dasiphora fruticosa* in Qinghai-Tibet Plateau, as precipitation regulates the mobilization of soil nutrients (Müller et al. 2017; Zhao et al. 2017). Some traits that are more sensitive to temperature, such as photosynthetic resource utilization efficiency and root nutrient content (Wei et al. 2023), were not measured in this study and need further research in the future.

Dasiphora fruticosa adapts to diverse habitats by adjusting its morphological traits and phosphorus content in organs

In alpine regions, plants will undergo a series of changes to adapt to harsh environment. Among plant functional traits, morphological traits change more significantly with environment factors (Reich et al. 1999; Wright et al. 2001), which is also consistent with our findings. In this study, with the increase of altitude, plant height and crown width of *Dasiphora fruticosa* decreased significantly. There are similar response for other species, such as *Picea abies* and *Larix decidua* in subalpine areas (Li et al. 2003; Oleksyn et al. 1998). Mao et al. (2018) found that plant height of 4295 species of angiosperms including herbaceous plants, shrubs, and trees in Qinghai-Tibet Plateau decreased significantly along altitude. The height increment of *Fagus sylvatica*, *Acer pseudoplatanus*, *Tilia platyphyllos*, and *Fraxinus excelsior* in North-Hesse in Germany all decreased significantly along altitude (Hölscher et al. 2002). Plants grow small to adapt poor hydrothermal conditions in alpine area, which has been widely recognized in the ecological adaptation mechanism of alpine plants (Körner 2003; Körner et al. 1989; Loehle 1998).

Over a broad climatic gradient, specific leaf area and leaf dry matter content, representing leaf photosynthetic capacity, showed a trade-off relationship (Wright et al. 2004). With the increase of LDMC, leaf water content decreased, tissue density increased, so SLA decreased (Wilson et al. 1999). With the increase of altitude, temperature decreases, SLA decreases and LDMC increases (Dunbar-Co et al. 2009; Scheepens et al. 2010). This is because the colder and drier the environment, the thicker the leaves become, which increases mesophyll cell density (Zhang and Luo 2004). This allows plants to make full use of light energy, thereby to increase photosynthetic carbon fixation, and to strengthen the protective effect of leaves on high light and low temperature (Song et al. 2011). However, this study found that LDMC was significantly decreased along altitude while SLA had no significant correlation with altitude

(Fig. 2), indicating that they were decoupled, which is consistent with some small-scale studies (Dolezal et al. 2019; Pan et al. 2023). Li (1996) anatomized *Dasiphora fruticosa* at different altitudes on the Qinghai-Tibet Plateau and found that the epidermal cells on the leaves increased along altitude, and the cells were bulliform or chimeric. The presence of bulliform cells increased the saturated fresh weight of leaves and decreased LDMC. Bulliform cells are a beneficial variant of plants in the process of natural selection, which can enhance the drought and cold resistance of plants. Additionally, SLA and LDMC were changed relatively less compared to plant height and crown width (Fig. 3), indicating the capacity of *Dasiphora fruticosa* to keep stable leaf photosynthesis to a wide altitude range (Odum and Barrett 2004; Tang et al. 2016; Wilson et al. 1999), which may be one of the reasons for the broad ecological amplitude of *Dasiphora fruticosa*.

As for stoichiometric traits, the increase of P content along altitude could be due to the fact that enzymes involved in physiological processes, such as RuBPCase (Ribulose-1,5-bisphosphate carboxylase/oxygenase) in photosynthesis, require the involvement of phosphorus, and P is a critical component of ATP (adenosine triphosphate), which is the primary energy carrier in plants (Buchanan et al. 2000; Wu et al. 2004; Ye 2010). To cope with the chill stresses in alpine, plants may need to increase their enzymatic activity to maintain their physiological functions, including photosynthesis and respiration (Liu et al. 2000; Pan et al. 2009). In addition, as altitude increases, higher leaf P content is required to maintain leaf activity and the majority of absorbed phosphorus by woody plants is used for constructing defense structures and structural materials (Onoda et al. 2004; Xie et al. 2016).

Interestingly, nitrogen content in leaves and stems of *Dasiphora fruticosa* was not significantly correlated with altitude (Fig. 2h and j), and coefficient of variation of nitrogen content in organs was small (Fig. 3), indicating that N content in *Dasiphora fruticosa* was stable. The reasons why nitrogen content in *Dasiphora fruticosa* remained stable are complex. Leaf N content is crucial for maintaining the stability of ecophysiological traits of plant and may involve the homeostasis mechanism in plant (Güsewell and Koerselman 2002; Sterner and Elser 2002). Organisms have the ability to maintain the relative stability of their own chemical elements in a changing environment, that is, the homeostasis mechanism (Hong et al. 2013; Kooijman 1995).

In general, changing traits were more affected by environmental factors (Li et al. 2013; Li et al. 2021; Wang and Zhou 2017). The inert response of stoichiometric traits in *Dasiphora fruticosa* played an important role in fully utilizing resources in extreme habitats. At different altitudes, the main regulation strategy of *Dasiphora fruticosa* was to adjust morphological traits and phosphorus content in organs, and maintain the stability of specific leaf area and nitrogen content to maintain the stability of photosynthesis and respiration to adapt the changing environment.

Conclusion

Most functional traits of *Dasiphora fruticosa* changed significantly along altitude, and morphological traits had large coefficient of variation. Soil physical properties was the main driver of the most plant

functional traits of *Dasiphora fruticosa*. Soil properties significantly directly affected the morphological traits including plant height, crown width, leaf dry matter content) and C and P contents in organs, while mean annual precipitation significantly indirectly affected them by affecting soil properties. Our results confirmed that soil properties have a stronger influence and act as a direct filter on plant functional traits of *Dasiphora fruticosa* in alpine regions. However, the selection of environmental factors and functional traits will somehow affect the results, more variables can be considered in the future research.

Declarations

Acknowledgments

This work was supported by the second Tibetan Plateau Scientific Expedition and Research Program (STEP), China (Grant No. 2019QZKK0306), and the project of Beijing Key Laboratory of Traditional Chinese Medicine Protection and Utilization (BJLKF2023-3).

Funding

This work was supported by the second Tibetan Plateau Scientific Expedition and Research Program (STEP), China (Grant No. 2019QZKK0306).

Competing Interests

The authors have no relevant financial or non-financial interests to disclose.

Author Contributions

Y.L. conceived and designed the main conceptual ideas of this work, participated in field work, processed the laboratory experiments, performed data analysis, and wrote the manuscript. J.S., X.X., and Y.H. contributed to field work and laboratory analysis. Y.H. supervised the study, contributed to the revising of the manuscript, and contributed to the funding resources. All authors contributed to the interpretation of the results and approved the manuscript.

Data Availability

The original data presented in the study are included in this article and Supplementary Information, further inquiries can be directed to the corresponding author.

Compliance with Ethical Standards

Disclosure of potential conflicts of interest

The authors have no potential conflicts of interest to disclose.

Research involving Human Participants and/or Animals

Not applicable.

Informed consent

Not applicable.

Additional supporting information in the online version of this article can be seen on “Supplementary Material”.

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Figures

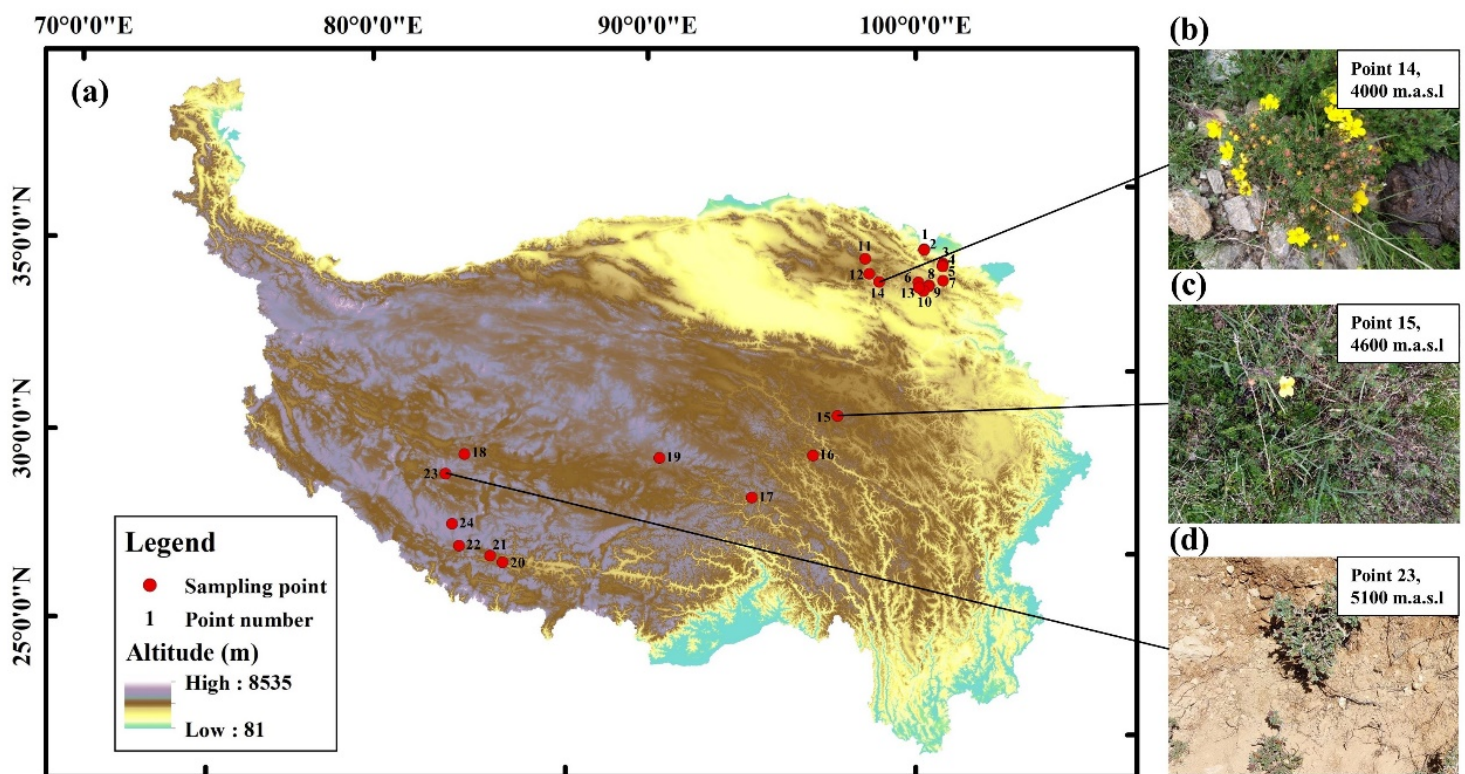


Figure 1

The sampling points of *Dasiphora fruticosa* (a) and *Dasiphora fruticosa* growing at 4000 m.a.s.l. (b), 4600 m.a.s.l. (c), and 5100 m.a.s.l. (d)

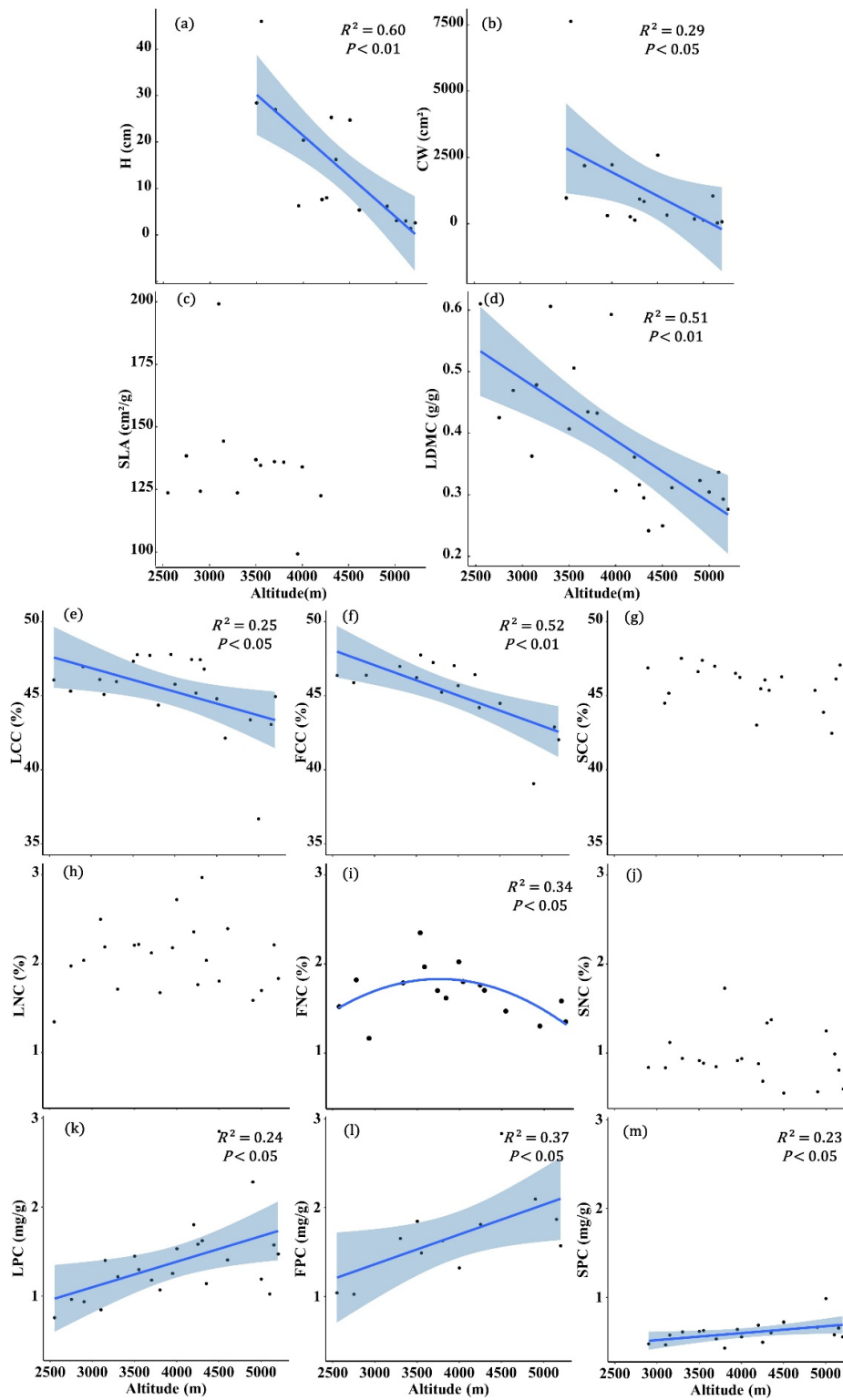


Figure 2

Variations in plant functional traits of *Dasiphora fruticosa* along altitude. H plant height, CW crown width, SLA specific leaf area, LDMC leaf dry matter content, LCC carbon content in leaves, FCC carbon content in flowers, SCC carbon content in stems, LNC nitrogen content in leaves, FNC nitrogen content in flowers, SNC nitrogen content in stems, LPC phosphorus content in leaves, FPC phosphorus content in flowers, SPC phosphorus content in stems

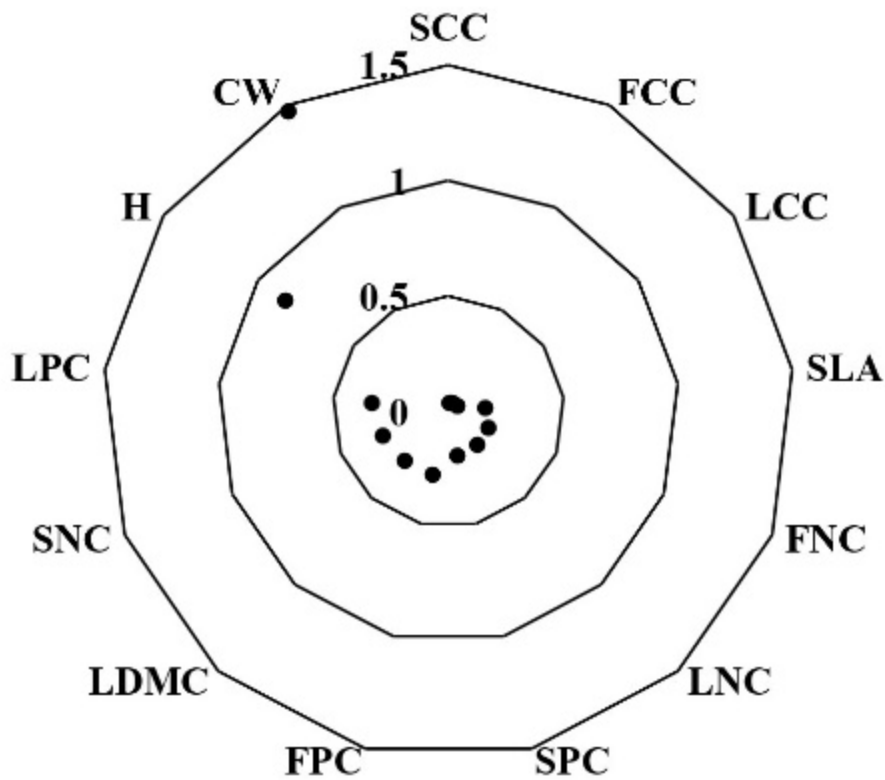


Figure 3

Coefficient of variation of plant functional traits of *Dasiphora fruticosa*. CW crown width, H plant height, LPC phosphorus content in leaves, SNC nitrogen content in stems, LDMC leaf dry matter content, FPC phosphorus content in flowers, SPC phosphorus content in stems, LNC nitrogen content in leaves, FNC nitrogen content in flowers, SLA specific leaf area, LCC carbon content in leaves, FCC carbon content in flowers, SCC carbon content in stems

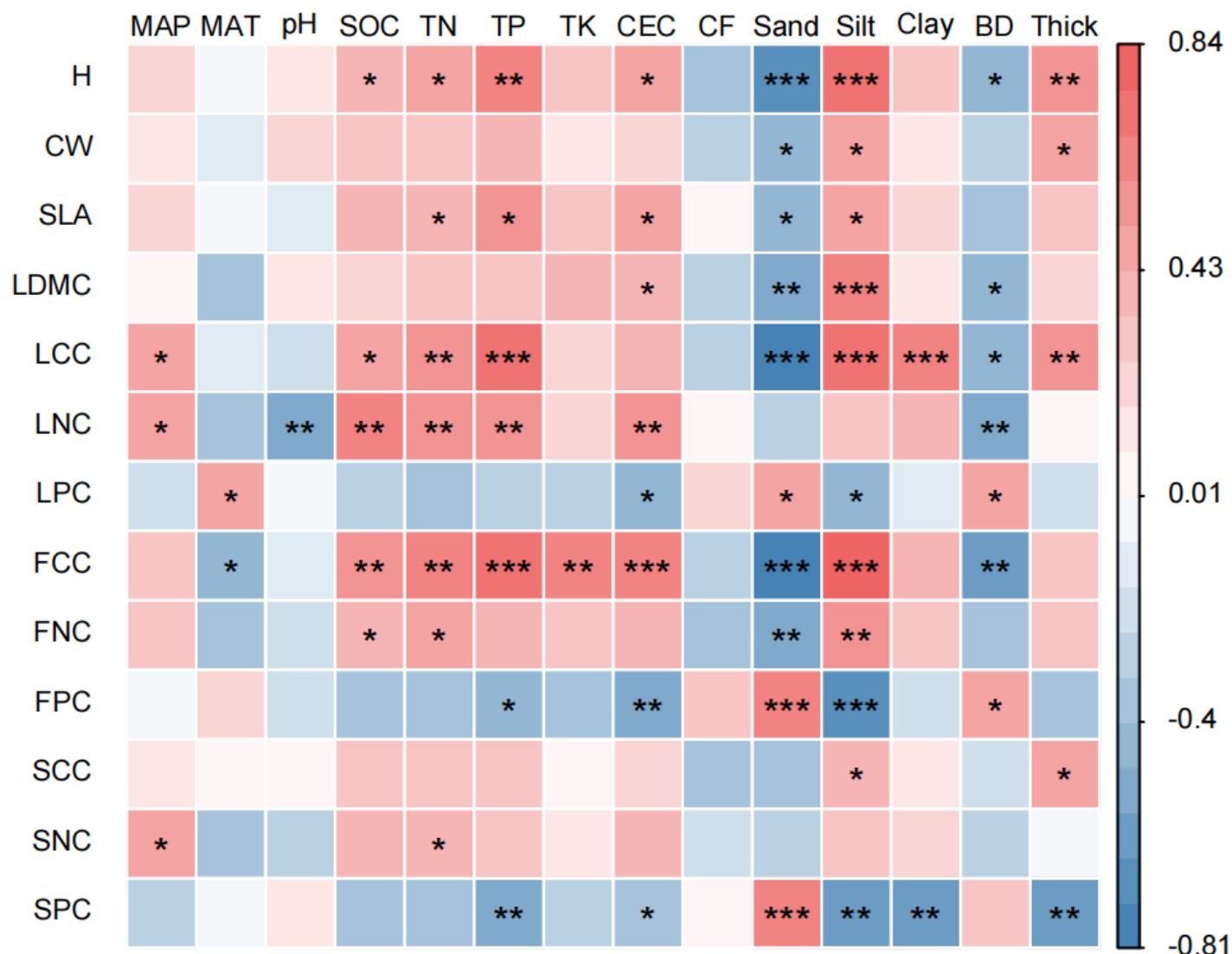


Figure 4

Spearman's correlations between environmental factors and plant functional traits of *Dasiphora fruticosa*. Environmental factors include: MAP (mean annual precipitation), MAT (mean annual temperature), pH (soil pH), SOC (soil organic carbon content), TN (soil total nitrogen content), TP (soil total phosphorus content), TK (soil total potassium content), CEC (soil cation exchange capacity), CF (content in rock fragments, >2mm), Sand (sand content), Silt (silt content), Clay (clay content), BD (soil bulk density) and Thick (soil thickness). Plant functional traits include: H (plant height), CW (crown width), SLA (specific leaf area), LDMC (leaf dry matter content), LCC (carbon content in leaves), LNC (nitrogen content in leaves), LPC (phosphorus content in leaves), FCC (carbon content in flowers), FNC (nitrogen content in flowers,) FPC (phosphorus content in flowers), SCC (carbon content in stems), SNC (nitrogen content in stems), SPC (phosphorus content in stems). * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

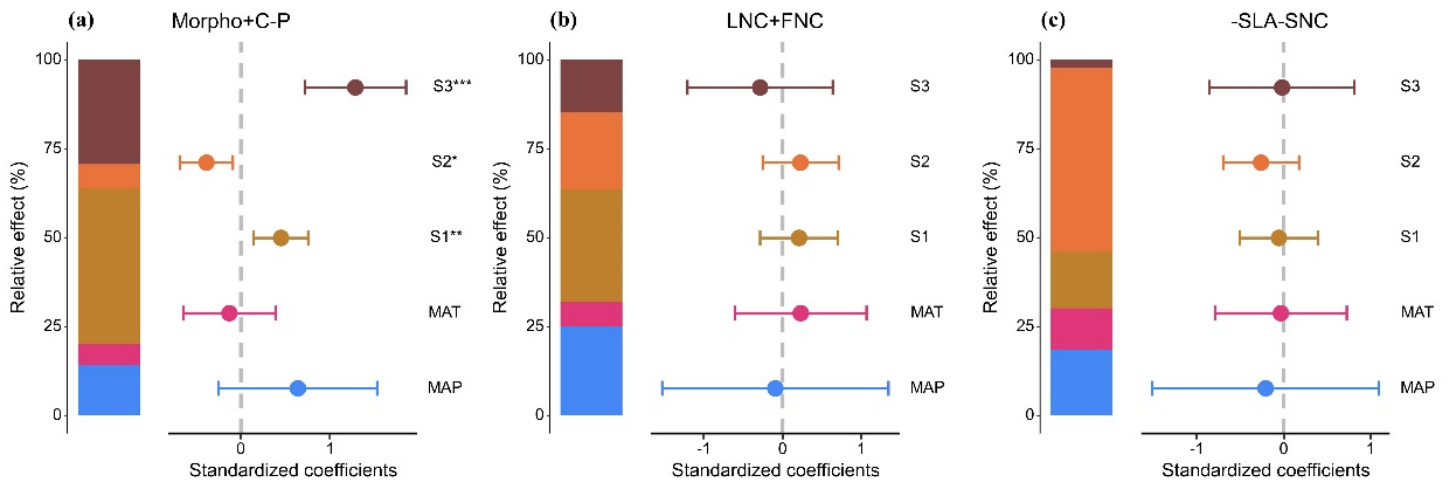


Figure 5

Relative effects of multiple predictors on PC1 (a), PC2 (b) and PC3 (c) of plant functional traits of *Dasiphora fruticosa*. The standardized coefficients (model-averaged estimates) of the model predictors are shown with their associated 95% confidence intervals. The stacked bars show the relative importance (percentage of variance explained) of each type of predictors. The graphs show the best model selected based on the AICc. **MAP** mean annual precipitation, **MAT** mean annual temperature, **S1** PC1 of soil properties, including pH (soil pH), SOC (soil organic carbon content), TN (soil total nitrogen content), TP (soil total phosphorus content), CEC (soil cation exchange capacity), Sand (sand content), Silt (silt content), Clay (clay content), and BD (soil bulk density), **S2** PC2 of soil properties, including CF (content in rock fragments, >2mm) and Thick (soil thickness), **S3** PC3 of soil properties, including TK (soil total potassium content). * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

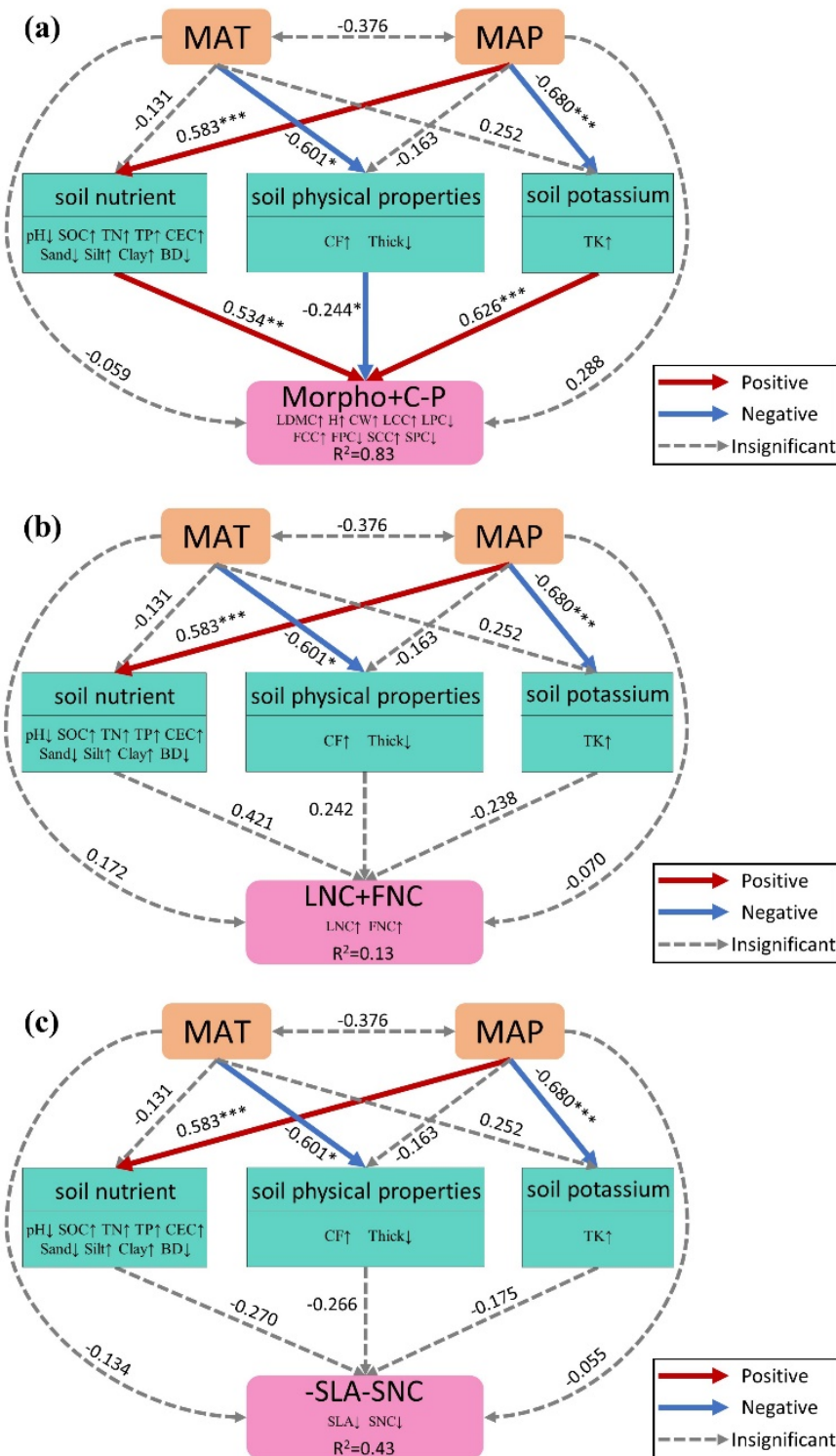


Figure 6

Piecewise structural equation modeling (piecewise SEM) examining the effects of climatic factors and soil properties on PC1 (a), PC2 (b) and PC3 (c) of plant functional traits of *Dasiphora fruticosa*. Red and blue solid arrows indicate positive and negative associations, respectively. Dotted lines represent pathways that are not significant. Numbers adjoining the arrows indicate standardized path coefficients. The up and down vertical arrows within rectangles respectively represent the positive and negative

relationships between PC and properties or traits. Climatic factors include MAT (mean annual temperature) and MAP (mean annual precipitation). Soil properties were reduced to three principal components, i.e. soil nutrient, soil physical properties and soil potassium. Soil nutrient include pH (soil pH), SOC (soil organic carbon content), TN (soil total nitrogen content), TP (soil total phosphorus content), CEC (soil cation exchange capacity), Sand (sand content), Silt (silt content), Clay (clay content) and BD (soil bulk density). Soil physical properties include CF (content in rock fragments, >2mm) and Thick (soil thickness). Soil potassium include TK (soil total potassium content). Plant functional traits were reduced to three principal components. "Morpho+C-P" include H (plant height), CW (crown width), LDMC (leaf dry matter content), LCC (carbon content in leaves), LPC (phosphorus content in leaves), FCC (carbon content in flowers), FPC (phosphorus content in flowers), SCC (carbon content in stems), and SPC (phosphorus content in stems). "LNC+FNC" include LNC (nitrogen content in leaves) and FNC (nitrogen content in flowers). "-SLA-SNC" include SLA (specific leaf area) and SNC (nitrogen content in stems). * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

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