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Do leaf traits affect insect herbivory in a Chinese cork oak forest?

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Abstract

Background: It is widely accepted that certain leaf traits indicating leaf quality play an important role in regulating insect herbivory. Numerous studies have attempted to find a clear relationship between insect herbivory and leaf traits. However, the results are inconsistent. In particular, it is still unclear whether leaf traits of a tree species affect insect herbivory in the field.

Methods: We examined the effects of leaf traits including structural defensive traits (specific leaf area), nutritional traits (nitrogen content, water content, and soluble sugar content), and chemical defensive traits (tannin content and carbon content) on variation of insect herbivory among three forest strata (vertical variability) and 18 locations (horizontal variability) in a Chinese cork oak (*Quercus variabilis*) forest landscape.

Results: Vertically, insect herbivory in the low-canopy stratum was significantly higher than in the other strata, but variation of leaf traits among strata had little explanatory power for the vertical pattern of insect herbivory. Horizontally, leaf carbon content had weak negative effects on insect herbivory while leaf tannin content had weak and divergent effects on insect herbivory in different strata.

Conclusions: Leaf traits selected in this study have weak effects on insect herbivory in the Chinese cork oak forests we studied. These effects may be masked by other abiotic and biotic factors, but further examination is needed.

Keywords: Forest strata; Insect herbivory; Insect-herbivore interactions; Leaf chemistry; Leaf quality; Leaf traits

Introduction

Insect herbivory plays a crucial role in forest regeneration and dynamics (Martini et al. 2021), exerting profound influences on ecosystem functions and services (Shao et al. 2021; Wang et al. 2022). Recognising the key drivers of insect herbivory has received great interest (Castagneyrol et al. 2019; Shao et al. 2021; Valdés-Correcher et al. 2019).

It is generally accepted that unfavourable leaf traits such as higher specific leaf area (SLA) (a structural defensive trait), lower leaf nitrogen, water, and sugar content (nutritional traits), and higher leaf phenolics (a chemical defensive trait) indicate lower leaf quality and have negative effects on insect herbivory (Castagneyrol et al. 2019; Castagneyrol et al. 2018a; Kause et al. 1999; Stiegel et al. 2017; Ximénez-Embún et al. 2016). Many studies have reported the linkage between insect herbivory and certain leaf traits (Martini et al. 2022; Schmitt & Burghardt 2021; Wang et al. 2022). For example, herbivory by leaf-chewing insects in European beech (*Fagus sylvatica* L.) decreased from the understorey to the high-canopy stratum and positively correlated with SLA (Stiegel et al. 2017). Insect herbivory was positively correlated with SLA along the vertical gradient of pedunculate oak (*Quercus robur*) forest (Castagneyrol et al. 2019). Higher leaf nitrogen content promoted leaf consumption in sugar maple (*Acer saccharum*) (Fortin & Mauffette 2002) and *Handroanthus ochraceus* (Bignoniaceae) (Silva et al. 2012). de Sena et al. (2021) found that the high content of leaf phenolic compounds of *Aspidosperma pyrifolium* and *Cenostigma pyramidale* can negatively influence insect herbivory.

However, other studies reported no effects of these variables on herbivory, and there is no consensus in the literature. For example, Martini et al. (2022) showed that SLA had no effects on insect herbivory of tree and shrub seedlings in both plantation and natural subtropical forests. English oak (*Quercus robur*) in rural areas had lower leaf nitrogen content but higher leaf chewer damage than in urban areas (Moreira et al. 2019). Leaf phenolics were not always found affect insect herbivory (Dudt & Shure 1994; Roslin & Salminen 2008). In other studies, the concentration of leaf phenolic compounds even had a positive effect on insect herbivory of *Handroanthus ochraceus* and six other deciduous and evergreen tree species in a tropical dry forest (Silva et al. 2012; Silva et al. 2015; Silva et al. 2020).

Multiple hypotheses that could explain the mechanisms behind such patterns have been proposed. From the point of view of leaf quality, insect herbivores may prefer leaves with higher nutritional quality (Boege & Marquis 2005; Carmona et al. 2011; Clissold et al. 2009; Muiruri et al. 2019). However, confounding factors such as drought and plant neighbourhood can also lead insect herbivores to increase their consumption on low-quality plants to meet their nutritional requirements (Castagneyrol et al. 2018b; Fernandez et al. 2021; Lincoln et al. 1993). On the other hand, high leaf chemical defences such as light-induced phenolics are often considered to influence insect herbivory negatively by reducing protein availability to herbivores (Dudt & Shure 1994; Mole et al. 1988; Salminen & Karonen 2011). However, this hypothesis is doubtful since in many arthropod herbivores (especially in lepidopteran larvae), the effects of tannins can be fully inhibited by alkaline gut conditions and gut surfactants (Martin et al. 1987; Salminen & Karonen 2011). This may be why leaves from the whole light gradient may be acceptable, although tannin in the most shaded leaves can lead to precipitation of all the foliar protein (Mole et al. 1988). Mason et al. (2011) suggested that host preferences of insect herbivores do not necessarily relate to leaf quality. Low leaf quality, which is often expressed as leaf traits, may have positive, negative, or neutral effects on insect herbivory (Kause et al. 1999).

Consequently, the effects of leaf traits on insect herbivory in forests are still unclear. In fact, for certain moth species, leaf quality of different host plant species can have significant effects on insect herbivory (Schädler et al. 2005; White & Whitham 2000), whereas variation in leaf quality of a host species may have no significant effects on insect herbivory (Cipollini et al. 2002; Ruhnke et al. 2009) (but see Murakami & Wada (1997) as an example of old leaves being no longer edible for larvae that hatch later, in relation to leaf phenology). Furthermore, significant effects of leaf traits on leaf palatability and insect performance assessed in the laboratory may disappear when tested under field conditions (Alalouni et al. 2014; Ruhnke et al. 2009). Therefore, variation in leaf traits may have effects on insect herbivory but these effects may be masked by other abiotic and biotic factors operating in the field.

Studies that estimate variation in a host's leaf traits and correlate it with insect herbivory often involve different environments with varying in altitude (Abdala-Roberts et al. 2016), latitude (Loughnan et al. 2019), successional stage (Silva et al. 2012), forest type (Castagneyrol et al. 2019) or landscape (Moreira et al. 2019). Therefore, it is difficult to determine the relationship between leaf traits and insect herbivory when there are significant differences in such environmental factors that may lead to biases in the results of studies. Thus, we were interested in examining the effects of leaf traits of one tree species on insect herbivory within a relatively small, homogeneous forest landscape to reduce the potential influence of other environmental factors.

In this study, we tested the effects of reputedly important leaf traits on insect herbivory within a Chinese cork oak (*Quercus variabilis* Blume) forest landscape. Since the forest stratum may have significant effects on leaf traits and insect herbivory (Castagneyrol et al. 2019; Shao et al. 2021), we examined insect herbivory and the leaf structural defensive trait SLA, leaf nutritional traits (nitrogen content, water content, and soluble sugar content), and leaf chemical defensive traits (tannin content and carbon content) in different vertical strata and different horizontal locations within the landscape. We analysed the correlation between insect herbivory and leaf traits, and we discuss the potentially underlying mechanism of insect herbivory in field conditions, which may advance the understanding of insect-herbivore interactions and offer some insights for future studies.

Methods

Study area

Our study was carried out in a ca. 200 ha area located on the south side of Songshan Mountain, west of Dengfeng City, Henan, China (34°26′-34°33′ N, 112°44′-113°5′ E). This region harbours extensive plantations of Chinese cork oak (*Quercus variabilis*) and some of them contain a minor amount of other tree species such as Oriental arbor-vitae (*Platycladus orientalis* (L.) Franco) and Oriental white oak (*Quercus aliena* Blume) (Shao et al. 2021). The study area is covered by pure Chinese cork oak forest, the stand age was 30 years, the stand density was 1437 stems/ha, and the average tree height and DBH were 7.8 m and 11.8 cm, respectively. *Culcula panterinaria* (Bremer et Grey) and *Phalera assimilis* (Bremer et Grey) are the main insect herbivores on Chinese cork oak trees (Shao et al. 2021).

Sampling and measurement

Sampling and leaf measurements were carried out in late September 2019. We laid out 18 10×10 m plots, and the distance between every two plots was at least 200 m. In each plot, oak tree canopies were divided, in relative terms, into the high-canopy stratum, the low-canopy stratum, and the sapling stratum. In each stratum, we randomly selected individual oak trees and collected 30 mature leaves haphazardly. Leaf samples were placed into plastic bags and stored in a cooling box for later examination. In high-canopy and low-canopy strata, we used a telescopic pole pruner to collect leaves from at least three trees. In the sapling stratum, we collected leaves from at least six saplings by hand. Insect herbivory and leaf traits were measured in the laboratory. We examined only the damage caused by chewers since other feeding guilds (skeletonisers, leaf-rollers, leaf-miners) caused too little damage to consider for separate analyses. We used a grid of 0.25 cm^2 (0.5×0.5 cm) printed on a sheet of blank paper and overlaid the leaves on it to estimate the leaf missing area (Shao et al. 2021). We calculated the mean area removed per leaf using total leaf area removed divided by the number of leaves examined (Castagneyrol et al. 2019; Shao et al. 2021).

For leaf traits, we examined specific leaf area (SLA), leaf nitrogen content, leaf water content, leaf soluble sugar content, leaf tannin content, and leaf carbon content in each stratum per plot. SLA and water content were measured on six mature, fully expanded, and undamaged leaves. Leaf surface was measured with a planimeter (CL-203 Laser Area Meter, Bio-Science Inc., USA). The leaves were weighed and oven-dried for 48 h at 60 °C. Leaf fresh weight and dry weight were measured with a balance (JEA3002 Electronic Balance, Shanghai Puchun Metrical Instrument Co., Ltd., China). Leaf water content was calculated using the difference between leaf fresh weight and dry weight, divided by leaf fresh weight. SLA was measured as leaf surface area divided by leaf dry weight. The leaf soluble sugar content was determined by KT-1-Y kit (Suzhou Keming Biotechnology Co. Ltd.). The leaf tannin content was determined by ND-1-Y kit (Suzhou Keming Biotechnology Co. Ltd.). Operating procedures were according to the instructions provided by the manufacturers. Leaf carbon content and leaf nitrogen content were examined using a Euro EA 3000 elemental analyser (HEKAtech GmbH, Wegberg, Germany).

Data analyses

We estimated the contrasts of insect herbivory and leaf traits among forest strata using ANOVA and post-hoc tests. Linear mixed-effect models (LMM) were used to analyse the effects of forest stratum (high-canopy, low-canopy and sapling) and leaf traits (SLA, nitrogen content, water content, soluble sugar content, tannin content, and carbon content) on insect herbivory with plot identity as a random factor. Forest stratum, leaf traits (covariates) and forest stratum × leaf traits were included as fixed effects. The relationship between insect herbivory and leaf traits was determined by regression analysis. We analysed the correlation between insect herbivory and leaf traits in each forest stratum separately when significant interactions between forest stratum and leaf traits were found. Analyses were conducted using IBM SPSS Statistics 20 (SPSS Inc, Chicago, IL, USA). Graphs were plotted using Origin 2018 (OriginLab, Northampton, MA, USA).

Results

Vertical patterns of insect herbivory and leaf traits

Insect herbivory was significantly higher in the low-canopy stratum than that in the high-canopy and sapling strata, but there was no difference between the high-canopy and the sapling stratum (Figure 1). specific leaf area differed significantly among forest strata and increased from the high-canopy stratum to the sapling stratum (Figure 1). Leaf soluble sugar content was significantly higher in the high-canopy stratum than that in the low-canopy and sapling strata whereas there was no difference between the latter two (Figure 1). Compared to other strata, leaf water content appeared to be lowest in the high-canopy stratum, whereas leaf tannin content, leaf nitrogen content and leaf carbon content appeared to be lowest in the low-canopy stratum, but these differences among strata were not significant (Figure 1).

Effects of forest stratum and leaf traits on insect herbivory

In the model testing effects of forest stratum and water content on insect herbivory, forest stratum had significant effects on insect herbivory, and forest stratum and leaf water content had significant interactive effects on insect herbivory (Table 1). For effects of forest stratum and leaf tannin content, forest stratum had significant effects on insect herbivory, and forest stratum and leaf tannin content had significant interactive effects on insect herbivory (Table 1). None of the other predictors tested had significant effects on herbivory.

Correlations between insect herbivory and leaf traits

Insect herbivory appeared to decrease with leaf carbon content across the strata (Figure 2) and with leaf tannin content in the low-canopy stratum (Figure 3), while it appeared to increase with leaf tannin content in the sapling stratum (Figure 3). However, none of these effects were statistically significant.

Discussion

Effects of leaf traits on insect herbivory may be weak or masked by other complex factors in the Chinese cork oak forests we studied. In our studies, variation of leaf traits among strata had little explanatory power for the vertical pattern of insect herbivory (Figure 1). Leaf traits assumed to be favourable for herbivory (i.e., higher SLA, leaf nitrogen content, leaf soluble sugar content, and leaf water content) (Castagneyrol et al. 2019; Fortin &

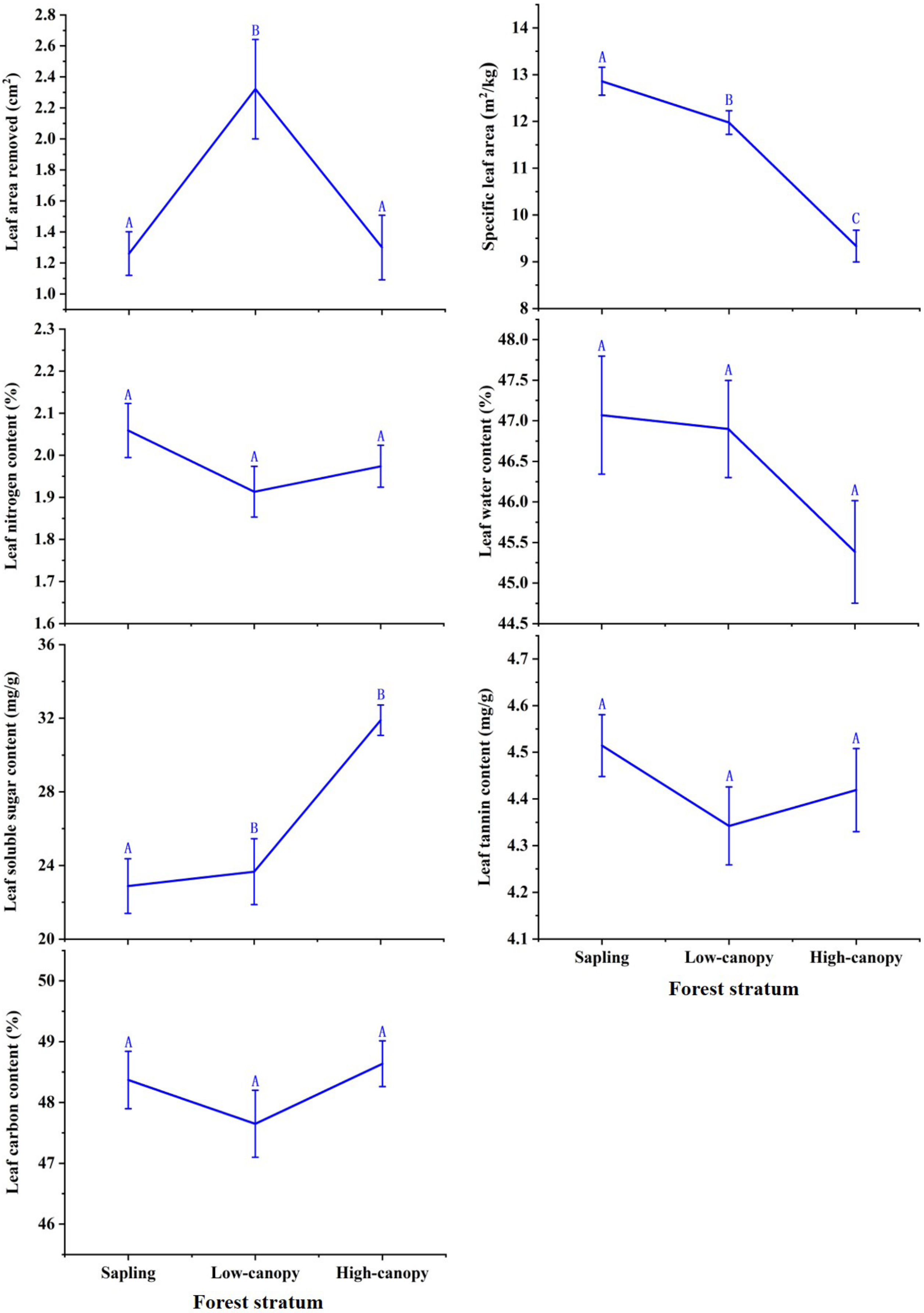

FIGURE 1: Variation of insect herbivory (i.e., leaf area removed) and leaf traits among forest strata (means ± SE, n = 18). Letters above bars indicate significant differences between strata.

TABLE 1: Summary of linear mixed models testing for effects of forest stratum and leaf traits on insect herbivory. Significant effects are indicated in bold.

Predictors	**Insect herbivory**	
Forest stratum	$F_{(2,\ 40.58)} = 0.15$	P = 0.860
Specific leaf area (SLA)	$F_{(1,\ 45.48)} = 0.06$	P = 0.803
Forest stratum × SLA	$F_{(2,\ 40.32)} = 0.24$	P = 0.787
Forest stratum	$F_{(2,\ 36.85)} = 1.77$	P = 0.184
Nitrogen content	$F_{(1,\ 36.8)} = 0.01$	P = 0.946
Forest stratum × Nitrogen content	$F_{(2,\ 37)} = 2.88$	P = 0.069
Forest stratum	$F_{(2,\ 46.84)} = \mathbf{4.94}$	P = **0.011**
Water content	$F_{(1,\ 45.08)} = 1.58$	P = 0.216
Forest stratum × Water content	$F_{(2,\ 46.99)} = \mathbf{4.49}$	P = **0.016**
Forest stratum	$F_{(2,\ 41.57)} = 0.63$	P = 0.538
Sugar content	$F_{(1,\ 47)} = 0.05$	P = 0.833
Forest stratum × Sugar content	$F_{(2,\ 42)} = 1.66$	P = 0.202
Forest stratum	$F_{(2,\ 46.72)} = \mathbf{1.14}$	P = **0.007**
Tannin content	$F_{(1,\ 46.53)} = 0.04$	P = 0.850
Forest stratum × Tannin content	$F_{(2,\ 42.32)} = \mathbf{4.62}$	P = **0.015**
Forest stratum	$F_{(2,\ 44.06)} = 0.43$	P = 0.655
Carbon content	$F_{(1,\ 45.46)} = 2.34$	P = 0.133
Forest stratum × Carbon content	$F_{(2,\ 44.09)} = 0.46$	P = 0.634

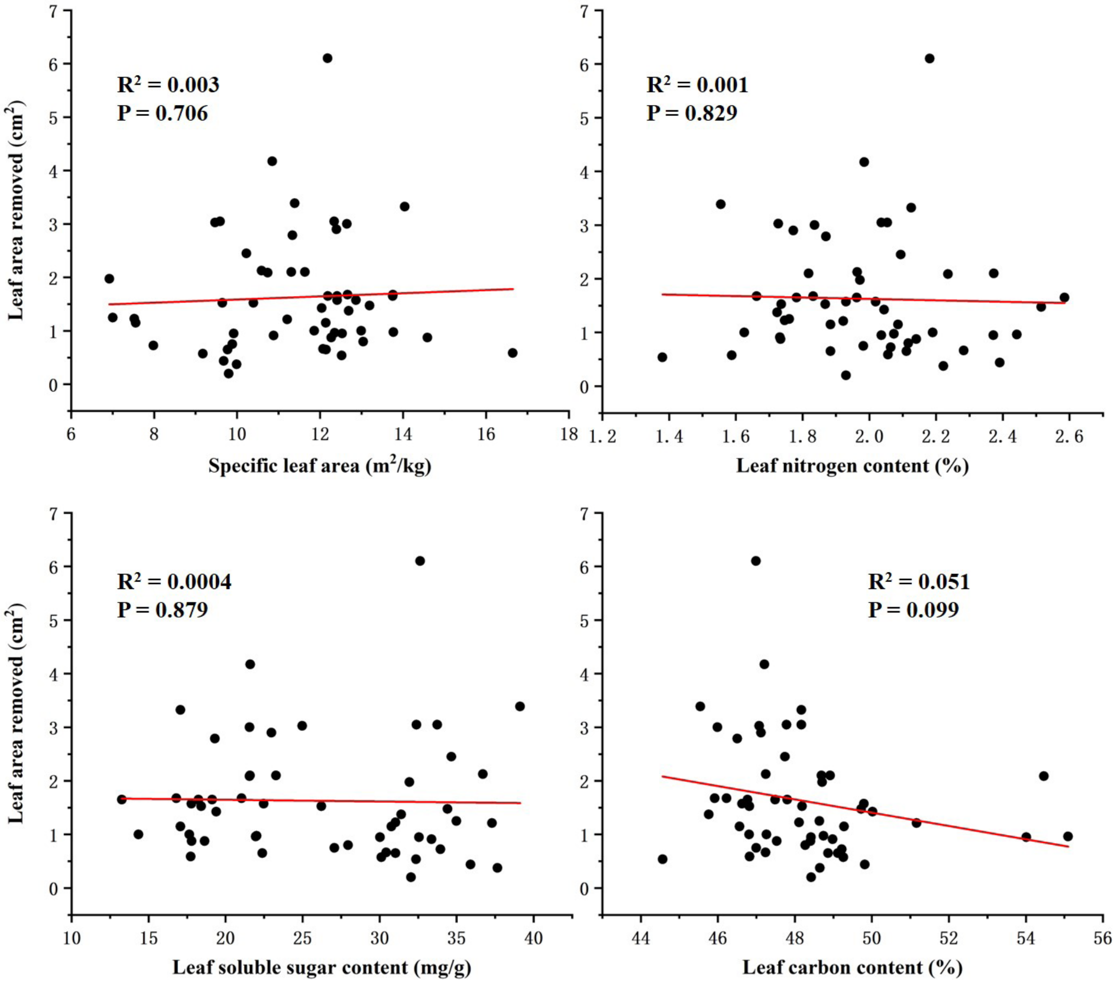

FIGURE 2: Effects of specific leaf area, leaf nitrogen content, leaf soluble sugar content and leaf carbon content on insect herbivory. Dots show the original data.

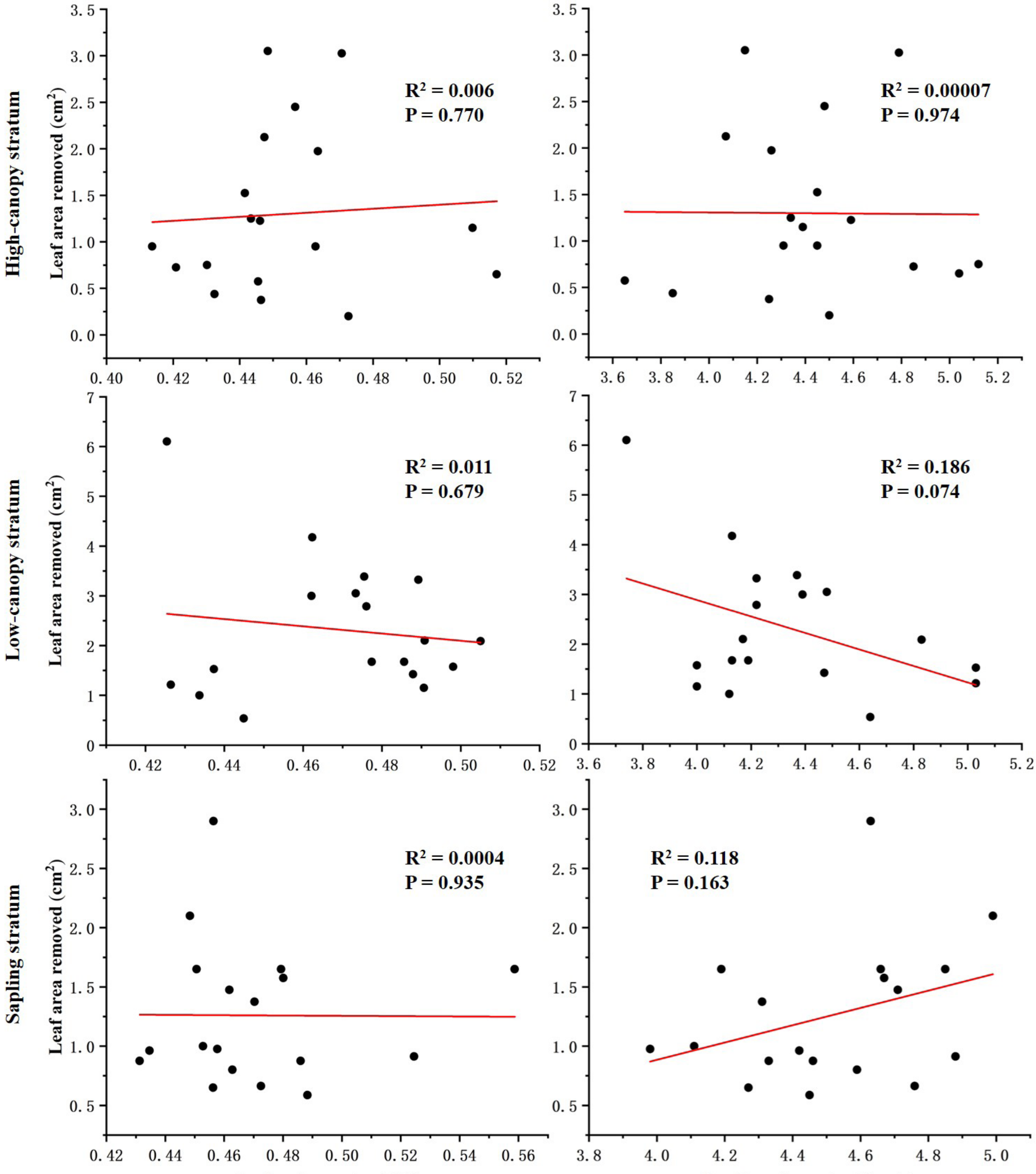

FIGURE 3: Effects of leaf water content and leaf tannin content on insect herbivory in each forest stratum. Dots show the original data.

Mauffette 2002; Kause et al. 1999) did not promote insect herbivory, while leaf traits thought to be unfavourable (i.e., higher leaf carbon content and leaf tannin content) (de Sena et al. 2021; Stiegel et al. 2017) did not inhibit insect herbivory. Horizontally, no significant correlation was found between insect herbivory and leaf traits (Figures 2 & 3). These results are consistent with our hypothesis that leaf traits of a specific host tree species may not exert significant effects on insect herbivory under similar field conditions.

In fact, a growing number of studies have shown that there is no clear relationship between insect herbivory and leaf traits (Alves et al. 2021; Moreira et al. 2019; Salminen & Karonen 2011), implying that leaf traits should be used with caution when predicting insect herbivory under field conditions. Thus, why do leaf traits that indicate leaf quality often have ambiguous effects on insect herbivory? There are three possible explanations. First, many leaf traits (examined and unexamined) may affect insect herbivory, and different leaf traits may have divergent effects on insect herbivory. When we report the effects of selected leaf traits on insect herbivory, it is difficult to completely exclude the influence of other leaf traits. Leaf quality, which is often indicated by few and simple leaf traits (Castagneyrol et al. 2018a; Valdés-Correcher et al. 2021), may also face the same problem because it is difficult to use single or few leaf traits to explain leaf quality (Kause et al. 1999). Second, different insect herbivores may have differential nutritional requirements (Kause et al. 1999) and may show differential or even contrasting responses to the same leaf trait (e.g., leaf phenolics) (Ali & Agrawal 2012; Damestoy et al. 2019; Hernández-Cumplido et al. 2021; Slinn et al. 2018). Therefore, “leaf quality” is relative and probably depends of the species-specific interactions between a plant and an insect herbivore. The reputedly favourable/unfavourable leaf traits do not necessarily have positive or negative effects on all insect herbivores. Insect performance or leaf palatability must be examined through feeding experiments before judging leaf quality (high or low) of a plant for an insect herbivore. Third, even so, however, insect performance or leaf palatability is not consistently correlated with insect herbivory in the field (Alalouni et al. 2014; Fortin & Mauffette 2002; Niesenbaum & Kluger 2006; Ruhnke et al. 2009), indicating other biotic and abiotic factors under filed conditions may play an important role in affecting insect herbivory. That is, effects of leaf traits on insect herbivory may also be hidden by other local environmental factors.

Understorey vegetation in the sapling stratum and unfavourable microclimatic conditions in the high-canopy stratum may negatively affect insect herbivory. Since most insect herbivores complete the feeding stage on a single plant (Barbosa et al. 2009; Fox & Morrow 1981), the general patterns of insect herbivory are determined by a variety of factors that influence host-finding of the female adult (Beyaert & Hilker 2014; Castagneyrol et al. 2019; Shao et al. 2021; Webster & Cardé 2017). In our study, insect herbivory in the sapling stratum was significantly lower than that in the low-canopy stratum, which may be due to the fact that most oak saplings in our study area are surrounded by various non-host grasses and shrubs which probably increased the physical and chemical interruption of host-finding by insect herbivores (Castagneyrol et al. 2013; Finch & Collier 2000; Moreira et al. 2016). In addition, a large number of studies have demonstrated that the high-canopy stratum of the forest has the lowest insect herbivory (Castagneyrol et al. 2019; Niesenbaum & Kluger 2006; Stiegel et al. 2017; Yamasaki & Kikuzawa 2003). Our study also revealed this pattern. However, feeding experiments have demonstrated that sun leaves often have higher palatability, and insect larvae perform better when feeding on sun leaves compared to shade leaves in lower forest strata (Fortin & Mauffette 2002; Niesenbaum & Kluger 2006). A previous study has revealed that the predation pressure of both birds and invertebrate predators in temperate forest decreases with height and is the lowest in the high-canopy stratum (Aikens et al. 2013). Therefore, we speculate that abiotic factors rather than leaf traits or predation pressure may exert important effects on insect herbivory in the high-canopy stratum, at least in our study system. In forests, there are microclimate gradients across different strata (Ellsworth & Reich 1993; Stiegel et al. 2017). Microclimate in different parts of the host plant has strong direct effects on insect herbivores (Stiegel et al. 2017; Uemura et al. 2020). In contrast to lower canopy strata, the high-canopy stratum experiences high irradiance, vapor pressure deficit, wind speed, and temperature fluctuations, as well as low air humidity (Eisenring et al. 2021; Randlkofer et al. 2010; Stiegel et al. 2017). These microclimate conditions in the high-canopy stratum may not be conducive to feeding and growth of insect larvae and thus negatively influence the herbivory. However, the validity of this explanation needs further examination.

Conclusions

The selected leaf traits, which are often used to indicate leaf quality for herbivores, did not exert significant effects on insect herbivory in a Chinese cork oak (*Quercus variabilis*) forest landscape. Insect herbivory is determined by various biotic and abiotic factors, and it is difficult to predict with a single or few leaf parameters under field conditions. Since microclimate conditions may have a direct and significant effect on insect herbivores, the effects of forest microclimate should be further investigated.

Competing interests

The authors declare that they have no competing interests.

Authors’ contributions

XS initiated this study, XS, KC and QZ conducted the experiments, XS, QZ, FX and LL conducted analyses, review and discussion. All authors contributed to writing the manuscript.

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