INTRODUCTION

Plants have evolved to exist in conditions that are rarely ideal for normal maintenance and may be at the survival limit. In response, plants can adapt to avoid and overcome stress by using various rapid or slow responding mechanisms, such as leaf movement and phenotypic plasticity (Kato et al., 2003; Shepherd & Griffiths, 2006; Xu et al., 2009a). As the fundamental energy unit of plants, leaves are considered as a nexus between plants and environments, which can have important ecological implications for species survival, growth, and distribution. Recently, general scaling relationships between leaf traits and climate have been the subject of interest. A worldwide “economic” spectrum of correlated leaf traits (that can provide a link between the various environmental factors and leaf...
functions) has been identified (Niinemets, 2001; Westoby et al., 2002; Westoby & Wright, 2003; Wright et al., 2004, 2007; Shipley et al., 2006a) and widely used from functional individuals to communities and ecosystems (Garnier et al., 2004; Shipley et al., 2006b; Westoby & Wright, 2006). In addition, this spectrum of traits has become the proxy for reconstructing paleoclimates or predicting future climates (Royer et al., 2005; Whitfield, 2006).

Leaf morphological characteristics are a useful visual guide for constructing relationships between different plants as well as between plants and their environments (Navas & Garnier, 2002; Roche et al., 2004). Leaf physiognomy can serve as an excellent tool for botanical and ecological studies (Traiser et al., 2005). Plant species with widely varying leaf shapes, sizes and venation co-occur in vegetation. The significance of leaf variations for species niche differentiation is still not entirely understood, whereas the differences in leaf physiognomy have been the subject of extensive research (Niinemets et al., 2007b). The morphological traits of leaves are often used in taxonomy. However, attention needs to be given to the problem of the reliability of leaf morphological characteristics, which are dependent on environmental conditions (Viscosi et al., 2009). The development of digital image processing and analysis technology has improved the ability to recognize and conduct geometric measurements of leaf morphology in the field (Du et al., 2007), which has led to the increased number of studies on the sensitivity of leaf physiognomy to climate.

Environmental sensitivity of leaf physiognomy has led to an upsurge in developing the technique for climate proxies. The most common leaf physiognomic methods are leaf-margin analysis and leaf-area analysis, both of which are based on a single variable, namely, the percentage of untoothed species at a site and site-mean leaf size, respectively (Peppe et al., 2011). The Climate-Leaf Analysis Multivariate Program, which uses additional categorical leaf states, was developed to obtain more accurate climate estimates compared to the results of univariate approaches (Wolfe, 1995). However, errors and biases were also found in problems related to character definitions, states, and analysis methods in the predictive framework. An ameliorative digital leaf physiognomy, which uses continuous variables to replace the discrete ones, is considerably more accurate because it uses stricter character definitions (Huff et al., 2003). Multiple linear regression models are the preferred multivariate analysis methods for simple application (Royer et al., 2005; Peppe et al., 2011). Other complex analyses based on computer algorithms have also been applied (Meziane & Shipley, 2001; Blonder et al., 2011). These previous studies were usually based on the averages of several species, i.e. site-based analysis (Greenwood, 2005; Royer et al., 2009). In such case, the climate was predicted at large scales, while predictions at local scale have not been conducted yet. Therefore, species-based analysis of leaf physiognomy may reveal new insights concerning its relation with microclimate. A contour method, which is usually used in geography, can display the continuous variations of multi-parameters and account for small changes of leaf characteristics according to microclimate. In the present study, we originally developed a contour extraction method to construct the visual relationships between leaf physiognomy and microclimate.

The oak species of genus Quercus L. generally exhibit large plasticity in leaf morphology and have been commonly used for the analysis of leaf-climate relationships (Sisó et al., 2001; Quero et al., 2006; Royer et al., 2008; Viscosi et al., 2009; Zhu et al., 2012). Quercus acutissima Carr. is one of the most widespread oak species in north China and is the dominant deciduous broadleafed species in the study area. The growth of Q. acutissima can be mainly affected by restrictions caused by habitat conditions. Increasingly different environmental conditions result in an increasingly different phenotypic plasticity of the whole plant and leaf traits (Xu et al., 2008). In addition, many Q. acutissima forests exhibit patch distribution because of anthropogenic disturbance. Other strong competitors, such as Robinia pseudoacacia L., are gradually invading and changing native habitats, which lead to the decline in seedling recruitment and decrease in growth rates through aggressive capture of light and water resources (Xu et al., 2010). The adaptive mechanisms may be investigated by analyzing the leaf morphology of Q. acutissima and the function of environmental indication in response to diverse water and light conditions, which are conducive for guiding vegetation maintenance and restoration.

We designed an experiment with controlled water and light conditions to investigate responses of leaf size, shape, and venation pattern in the seedlings of Q. acutissima to different gradients of water and light availability. In previous studies, we have found that variations of leaf physiognomy in the nature can be simulated artificially and there are interspecific differences between coexisted species (Xu et al., 2008, 2009b).
On this basis, the objectives of this study were to (1) investigate the role of intraspecific variation in leaf-climate relationships, (2) develop microclimate prediction models by using variables derived from leaf physiognomy, and (3) assess the potential application of models as microclimate proxies.

**MATERIALS AND METHODS**

**Study site**

The study was conducted at the Fanggan Research Station of Shandong University, Shandong Province, China (36°26′N, 117°27′E). The site is characterized by a warm temperate monsoon climate, with a mean annual temperature of 13 ± 1°C and a mean annual precipitation of 700 ± 25 mm, which occurs mostly during the summer. The soil of the area is a cinnamon-type, and the parent material is limestone (Xu et al., 2008). Sawtooth oak (*Q. acutissima*) and black locust (*R. pseudoacacia*) coexist and form mixed forests in this area. The canopy has a dominant layer which reaches 14 m, and the lower limits of the crown are at about 9 m. The leaf area index can reach ~5.12 when the trees are flourishing in August (Xu et al., 2009b).

**Plant materials**

One-year-old seedlings of *Q. acutissima* were used as experimental materials in this study. Acorns of *Q. acutissima* were collected from a hill near the research station in early spring and planted in plastic pots (32 × 29 cm in height × diameter, one acorn in each pot). The soil was a 64:22:14 (v/v/v) mixture of humic soil, sand, and loam, with a saturated water content of 36% by mass, the largest volumetric water content of 28%, and 68% porosity. The pH was 4.4, and the major chemical components included 88.4 g organic matter, 3.7 g total nitrogen and 42.3 mg available phosphorus per kilogram. All the pots were regularly irrigated and subjected to weed control before the beginning of the experiment.

**Experimental design**

The seedlings were submitted to controlled experiments from July to September. A factorial experiment of two factors (water and light) of four and three levels, respectively, was designed. Water was withheld from the drought groups until the soil moisture reached ~50% (W2), 30% (W3), and 10% (W4) of field capacity, whereas the well-watered groups received daily irrigation to maintain soil water content between 70% and 80% (W1) of field capacity. All the pots were moved into a rain-out shelter to avoid precipitation disturbance. The soil water content was controlled by gravimetric probe and the pots were weighed daily to maintain the four different water contents. Top irrigation evenly supplemented the water lost via transpiration and evaporation.

The light-control treatment was conducted in shade shelters covered by plastic films or woven black nylon nets. The frame of the shelter was 5.0 × 2.5 × 3.0 m (length × width × height). The microclimate was monitored daily by using a micro-quantum sensor and a temperature sensor of Mini-PAM (Walz GmbH, Effeltrich, Germany). The average Photosynthetic Active Radiation (PAR) measured from 07:00 to 16:00 was 544 ± 71, 361 ± 17, and 56 ± 6.7 μmol m⁻² s⁻¹ in the open field (L1), under plastic films (L2), and nylon nets (L3), respectively. The light transmission ratio was ~66% and 10% under the stress condition compared with the control. Analysis of variance (ANOVA) found no significant difference (p = 0.534) in air temperature between the three light gradients (32.8 ± 0.46, 32.4 ± 0.40 and 32.1 ± 0.39°C).

The Relative Water Content (RWC) and Relative Light Intensity (RLI) were used as the standards to quantify the gradients of water and light availability. RWC was calculated by averaging the diurnal soil water content of the sampled seedlings. The average light intensity of the sampled seedlings was obtained by measuring PAR in four directions where the seedlings were located. RLI was then calculated by dividing the average light intensity with the maximal value. Ten pots were randomly assigned to each water and light availability treatment. The gradients of W2 and W4 were eliminated from the high (L1) and low (L3) gradients of light availability considering the heavy management and measurement workload. After a two-month treatment period, 15 mature leaves from three seedlings per treatment were taken for morphological measurements.

**Morphological measurements**

The leaf area was measured by using a CI-203 laser area meter (CID Inc., Washington, USA). The linear measurement was taken using a digital caliper. Leaf dry mass was measured after oven drying at 80°C for 48 hrs. The detailed information of the morphological parameter measurements and definitions are shown in Figure 1 and Table 1.
Statistical analysis

Two-way ANOVA with type III sums of squares was used to test the interactive effects of environmental factors on leaf physiognomy. Pearson’s correlations between leaf morphological traits and climate parameters were calculated, and Ordinary Least Square (OLS) regression lines were fitted to predict the habitat information by using variables that were considered to represent the primary responses. The multicollinearity influence could be ignored without using elimination methods (e.g., stepwise or ridge regression) because focus was given only to the predictive power of the functions (Mela & Kopalle, 2002; Dormann et al., 2013). The jackknife-type approach was used to evaluate the accuracy of the regression functions to build a group of virtual data as the test set, and the absolute residuals were used as the predictive criterion. The level of response to the variation of each factor (water and light) was estimated by using the PI_{RWC} and PI_{RLI} indices, respectively, which ranged from 0 to 1. The index of plasticity (PI) was calculated as the difference between the maximum and the minimum mean values divided by the maximum mean value (Valladares et al., 2000b). The changes of leaf morphological variables in the different gradients of water and light availability were illustrated in three-dimensional surface and contour plots. The smoothing cubic spline was employed to trace the variability of the leaf variables (Schimek, 2000), and contour extraction was carried out by adjusting the step and minor number for values of the Z-axis (data of leaf morphology). The intersections of contours from different leaf variables, which are considered to provide information about the habitat, were easily fixed by graph-merged and data-drawn application. All statistical analyses were performed by using the SPSS 13.0 software package (SPSS Inc., Chicago, USA). Plots were drawn by using the Statistica 6.0 software (StatSoft Inc., Oklahoma, USA).

RESULTS

LA significantly increased at increasing water and light availability (Fig. 2A, Table 2). The range of the changes was broader with sufficient resources than with seedlings under serious stress. Similar to LA, variables LDM, LL, and LW were positively correlated with water and light availability, respectively (Fig. 2B, D, E). SLA showed a positive correlation with water availability, but was negatively correlated with light availability. The variations were nearly linear in the surface plot (Fig. 2C). Although LPL was significantly correlated with water and light availability, the trend was not consistent with environmental gradients be-
FIG. 2. Three-dimensional surface plots for LA (A), LDM (B), SLA (C), LL (D), LW (E), LPL (F), LE (G), LL/LPL (H), LWD (I), LBD (J), NLT (K) and MDV (L) of *Q. acutissima* in the different gradients of water and light availability. The grayscale maps indicate that the darker chroma corresponds to the higher value of leaf morphological variable. The spline function is employed in the curved surface fitting and $n = 120$ for each variable contained climate information.
TABLE 2. Pearson's correlation coefficients between *Q. acutissima* leaf morphological traits and climate parameters (N = 120 for each leaf trait, and n = 24 for each factor of environments with five replications). Significance level: \( p > 0.05 \), \( p \leq 0.05 \), \( p \leq 0.01 \), *** \( p \leq 0.001 \)

<table>
<thead>
<tr>
<th>Variable</th>
<th>LA</th>
<th>LDM</th>
<th>SLA</th>
<th>LL</th>
<th>LW</th>
<th>LPL</th>
<th>LE</th>
<th>LL/LPL</th>
<th>LWD</th>
<th>LBD</th>
<th>NLT</th>
<th>MDV</th>
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<tr>
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<td>-0.43***</td>
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<tr>
<td>LL</td>
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<td>0.73***</td>
<td>-0.21*</td>
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<td>LW</td>
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<td>0.73***</td>
<td>-0.38***</td>
<td>0.75***</td>
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<td>-0.13ns</td>
<td>0.44***</td>
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<td>LE</td>
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<td>0.33***</td>
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<td>0.07ns</td>
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<td>0.09ns</td>
<td>0.03ns</td>
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<td>0.05ns</td>
<td>-0.08ns</td>
<td>-0.29**</td>
<td>-0.03ns</td>
<td>0.66***</td>
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<td>0.06ns</td>
<td>0.02ns</td>
<td>0.25**</td>
<td>0.18*</td>
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<td>0.31***</td>
<td>-0.19*</td>
<td>0.46***</td>
<td>0.48***</td>
<td>0.32***</td>
<td>-0.17ns</td>
<td>-0.06ns</td>
<td>-0.22*</td>
<td>-0.13ns</td>
<td>-0.69***</td>
<td></td>
</tr>
<tr>
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<td>0.28**</td>
<td>0.40****</td>
<td>0.24**</td>
<td>0.22*</td>
<td>0.27**</td>
<td>-0.04ns</td>
<td>-0.15ns</td>
<td>-0.01ns</td>
<td>-0.14ns</td>
<td>0.20*</td>
<td>-0.02ns</td>
</tr>
<tr>
<td>RLI</td>
<td>0.42***</td>
<td>0.71***</td>
<td>-0.72***</td>
<td>0.38***</td>
<td>0.43***</td>
<td>0.23*</td>
<td>-0.20*</td>
<td>-0.03ns</td>
<td>-0.16ns</td>
<td>-0.26**</td>
<td>0.08ns</td>
<td>0.21*</td>
</tr>
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</table>
cause of a high value under combined drought and shade conditions (Fig. 2F).

LE and LL/LPL were found to increase in shade and decrease in sunlight with increasing water availability, whereas LWD and LBD showed inverse trends (Fig. 2G-J). Conflicting variations also occurred in the gradients of light availability. LE and LL/LPL increased in drought and decreased under well-watered conditions, whereas LWD and LBD decreased in drought and increased in well-watered conditions with increasing light availability. These results caused either weak or zero correlations for these four variables with water and light availability (Table 2).

NLT only showed significant correlation with water availability (Table 2). Water scarcity resulted in fewer leaf teeth. NLT increased along the gradient of light availability with abundant irrigation. On the contrary, NLT decreased in high irradiance when the drought stress was a burden (Fig. 2K). MDV only showed significant correlation with light availability and mainly increased with increasing light availability except when the water resources were sufficient. The maximum values of MDV appeared when high irradiance and serious drought were simultaneously imposed (Fig. 2L).

The correlation coefficients of leaf traits to RWC were smaller than those of RLI, except for LPL, LL/LPL, and NLT, whose water-induced responses were higher and under the diagonal of the bivariate diagram (Fig. 3). A high variation existed in the degree of response to light versus water. The response to light had a mean value of 0.17 (range 0.03-0.54), while the response to water had a mean value of 0.12 (range 0.02-0.30).

The overall determination coefficient of multiple linear regression was larger for RLI than that for RWC (Table 3). The mean values of absolute residuals were 9.20 for RWC and 6.43 for RLI, which indicated a 95% confidence interval on the RWC prediction wider than that of RLI (Fig. 4). The predicted values were significantly overestimated and significantly underestimated in the lower left and upper right of the scatter plots, respectively, for both RWC and RLI predictions by t-tests ($p < 0.05$).

Actually, the leaf traits did not show absolutely linear correlations with RWC and RLI, especially in the prediction of the bivariate of dependence. The effects of linear and spline functions fitted on the leaf traits to the environmental gradients in contour plots for the case of LDM are shown in Figure 5. LDM was used as an example because it was significantly corre-

\begin{table}[h]
\centering
\begin{tabular}{|c|c|c|}
\hline
Variables & Coefficient for RWC & Coefficient for RLI \\
\hline
Intercept & $-154.91^*$ & $-150.99^*$ \\
LA (cm²) & $-2.56^{ns}$ & $-1.75^{ns}$ \\
LDM (g) & 115.50 *** & 239.98 *** \\
SLA (cm² g⁻¹) & 0.33 *** & $-0.36^{***}$ \\
LL (cm) & 2.67^{ns} & $-20.15^*$ \\
LW (cm) & 29.23^{ns} & 65.04* \\
LPL (cm) & 76.12 ** & 25.75* \\
LE & & 90.42* \\
LBD & & $-23.45^{***}$ \\
NLT (ea) & 0.55* & -- \\
MDV (cm) & & 0.57^{ns} \\
$r^2$ & 0.49 *** & 0.81 *** \\
\hline
\end{tabular}
\caption{Multiple linear regression functions for predicting RWC and RLI of Q. acutissima from leaf physiognomy. Ordinary least squares (OLS) regressions were used by setting climate as the dependent variable and leaf traits as the independent variables. The leaf parameters chosen in the functions show significant correlations with RWC and RLI according to the analysis in Table 2. The significance level of each variable: $^*p > 0.05$, $^p \leq 0.05$, $^{**}p \leq 0.01$, $^{***}p \leq 0.001$}
\end{table}
when both were at the lower gradients because the linear contour was above the spline contour with the same values in the shadowed area (Fig. 5C). The area outside the shadowed area indicated an underestimation that frequently occurs at the higher gradients.

We applied the contours of SLA and NLT, which are widely used as important leaf traits functionally linked to climate, in the contour extraction method to gauge the accuracy of predictions (Fig. 6 and online supplementary material Fig. S1). The intersections directly showed the environmental information in the plots. The mean values of absolute residuals were 3.45 for RWC and 2.50 for RLI. Furthermore, a paired t-test indicated that the values of the residuals were significantly smaller in the contour extraction method than in the multiple linear regressions for RWC ($p = 0.014$) and RLI ($p = 0.038$), respectively.

**DISCUSSION**

*Sensitivity of leaf size and shape to climate*

In the current research, leaf size was obviously restricted by the shortage of water and light as shown by LA and LDM. Although leaf size variation in *Q. acutissima* can be partly linked to allometric factors, the ecological strategy with respect to environmental stress has an important role (Xu et al., 2008, 2009b). Variations in leaf size along the climatic gradients may result from higher water demand and overheating of larger leaves because of photosynthesis-transpiration compromise and heat dissipation. The trend of selecting relatively small leaves may be caused by o-
FIG. 6. Validation experiment for the RWC and RLI of *Q. acutissima* in the treatment of W1L1 (A), W3L1 (B), W1L2 (C), W2L2 (D), W3L2 (E), W4L2 (F), W1L3 (G) and W3L3 (H) by using the contour extraction method. Solid and dashed lines refer to the contours of SLA and NLT, respectively. The intersections are established by the tool of drawing data. When two intersections appear in a plot, the mean value is used as a substitute.
verall resource limitation in stressful environments, which makes the construction of large leaves with extensive vascular and cell-wall fractions overly expensive and will reduce the investment in LDM (Niinemets et al., 2007a). Furthermore, smaller leaves have an advantage in minimizing self-shading (Falster & Westoby, 2003).

An integrated variation of LA and LDM can be expressed by SLA. This functional trait of leaves is important in connection with other traits and the climate (Wright et al., 2004). To achieve different ameliorative aims under resource stress, the variations along the gradients of water and light availability exhibited divergence. Lower values in water-limited environments tend to correspond to relatively high investments in leaf defenses and long leaf lifespan. Shade-tolerant leaves have remarkably larger SLA, which is an accommodation to decrease self-shading of chloroplasts in the abaxial surface of leaves (Quero et al., 2006). Another advantage is that the construction and maintenance costs of the production of leaves with more symplastic component in shade are reduced (Lusk et al., 2008).

LE, calculated as LL divided by LW, characterizes the overall slenderness of the leaves (Niinemets et al., 2007b), and often changes with leaf size because of the effect of allometry. However, plasticity to environmental conditions also occurs (Tsialtas & Maslaris, 2007; Xu et al., 2009b). Leaves became longer instead of wider in the open field with the decrease of water availability. This correlation most likely allows the leaves to reduce transpiration by reducing the size of the boundary layer and to shed heat better in warm habitats. Leaves were also narrower in the shade and moist conditions, which is thought to be an adaptation to decrease self-shading and curliness of leaves with high SLA.

Leaf shape was not only represented by the integrated changes of leaf major and minor axes, but the distribution of leaf area fractions (partitioned by LWD and LBD) in the present research also includes additional information. When LE increased, lamina areas located close to the leaf apex decreased, which represents the narrow part of the leaf increasing in proportion to the whole leaf lamina. The cooperation between LE and leaf area fractions was also displayed in the case of the formation of wider leaves, which are capable to maximize their areas for light capture.

Synergy between leaf venation pattern and leaf dimension

In the present study, the changes of LPL were consistent with leaf size, which provides an available proxy for leaf size from petiole dimensions when the leaf blade was disfeatured (Jordan, 2011). The elongation of petioles will achieve optimal leaf display to deal with the shade stress. The increases in the relative distance of LA from the stem by longer petioles can reduce the between-row shading. Furthermore, a leaf with a narrow blade can reduce both between-row and within-row shadings (Takenaka, 1994). Leaf petiole and shape alternatively contributed to larger light capture in this research, shown by the similar changes in LE and LL/LPL, as plants had a tradeoff between the need for increasing interception areas and support structures. Increasing the investment in petioles requires the synthesis of more xylogens and limits the biomass invested into functional leaf activity. Longer petioles also have a disadvantage which leads to the bending of the shaded leaf in a moist habitat (Pickup et al., 2005).

Large leaves require disproportionately more mass allocated to petioles and veins for mechanical support (Niklas et al., 2007), especially for thin leaves. A shade-tolerant leaf shape, whose centroid is far from the leaf base, requires higher vein density to withstand the increased bending moment. Also, closer spacing of veins (decreased MDV) results in both higher water fluxes and carbon assimilation rates because of shorter path lengths between veins and stomata (Brodribb et al., 2007; Brodribb & Field, 2010). However, investments in support will transform the invested biomass into functional leaf activity. This inverse relationship is likely because of the displacement of the lamina tissue by non-photosynthetic venation tissue (Poorter et al., 2006). Xeromorphic leaves eliminated the dependence of veins because of the self-support of lamina, which can rely on lamina cells (non-specific support) in addition to vasculature (Niinemets, 2001).

Characteristics of leaf teeth are functional traits to reflect a tradeoff between carbon uptake and water loss. The relationship between leaf teeth and enhanced sap flow may help explain why leaf teeth are more absent in drought environments where the water cost associated with teeth may be more important (Peppe et al., 2011). This pulse in gas-exchange activity may be also adaptive in a shade condition because it may extend the season of potential growth (Royer & Wilf, 2006). In contrast, tooth-driven pulse in sap flow is
The contour extraction method in the present research had some advantages in climate prediction over multiple linear regressions. First, the characteristics of our prediction system are flexible for using spline curves. Therefore, a good foundation for predictive accuracy is established. Second, more alternatives are available in choosing leaf traits for prediction. Any two or more leaf traits that are not perfectly collinear can locate the climate information. The contour extraction method is suitable for application to dead or fossil leaves, because some leaf traits (e.g. SLA) cannot be reliably reconstructed (Royer et al., 2007). Third, the bi-variables of environmental gradients can be synchronously estimated, which means that the variability of leaf traits should consider the effects of double environmental factors at the same time. However, the effects are discrete in multiple linear regressions because of one function for each environmental factor prediction. The ignored factor will introduce an error in estimation of another factor, because at a given value of one factor, the leaf traits will also vary significantly as a result of the effect of the other factors (Peppe et al., 2011). This may be another reason why the accuracy of multiple linear regressions is lower than that of contour extraction method. However, the contour extraction method has been recognized to have its own shortcomings in prediction. The value intervals for the test set are limited because the contours are drawn based on the sample set. Any leaf whose values of traits are beyond the range of the models will have no contour to extract. Therefore, this method does not fit for leaves derived from different regions or growth phases as well as those abnormally derived. Furthermore, the method cannot perform batch processing as one value of leaf trait corresponds to one contour to extract.

Implications and future research
Sensitivity of leaf physiognomy to climate established a foundation for constructing and improving leaf-climate analysis methods for microclimate prediction. The oak species investigated in the present study share a general trend of leaf traits that can be suited to a tradeoff demand for resources as well as part of a conservative resource-use strategy (Valladares et al., 2000a; Xu et al., 2010). The response of the leaves can even occur due to the effect of climate in the current-year growing season, which serves as a significant extension for dynamic prediction by investigating the leaves in different temporal and spatial scales.
The contour extraction method in the present study is more precise compared with the multiple linear regressions, especially for the combined predictions of extreme environments. However, the diversity of the sampled leaves may result in the invalidity of this method. Therefore, the allometric relationships of leaf traits must be established to improve the applicability of the contour extraction method (Niklas et al., 2009). In addition, other environmental factors (e.g. air temperature, soil fertility, wind) may affect the leaf morphological plasticity in the field (Royer et al., 2008). Regional differences and genetic variability will also introduce errors to leaf-climate relationships (Hameed et al., 2012). Further extensions, coupled with more detailed experimental measurements of the traits and modified relationships between leaf and climate, will enable leaf physiognomy to become a robust proxy to macro- and microclimate.

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