

# HABITAT EFFECTS ON LEAF MORPHOLOGICAL PLASTICITY IN *QUERCUS ACUTISSIMA*

FEI XU, WEIHUA GUO, WEIHONG XU AND RENQING WANG\*

*Institute of Ecology and Biodiversity, College of Life Sciences, Shandong University,  
Jinan, 250100, P. R. China*

Received May 29, 2008; revision accepted August 7, 2008

Phenotypic plasticity acts to increase the performance of plants under stress. Leaf morphological plasticity and its causes in different environments are incompletely understood. We measured the leaf morphological parameters of *Quercus acutissima* Carr. seedlings, including leaf size, leaf shape and venation pattern, assessing the effects of different habitat conditions on leaf morphological plasticity. A field study in forest edge and understory was combined with experiments simulating different light and water conditions. Leaf morphology variations occurred over most of the parameters, and the causes were consistent between the field study and lab experiment. Leaf size decreased with low supply of light and water. Leaf length and width were only affected by leaf area. The leaf petiole did not lengthen under shade stress, suggesting a trade-off relationship between functional tissues and support structures. Leaf shape became narrower in drought and broader in the shade, as reflected in changes in three leaf fractions. Higher vein density played a part in enhancement of mechanical support and water supply. Leaves with more teeth show more active photosynthesis, but are disadvantageous in xeric environments because of higher transpiration. Light was the main factor inducing leaf morphological plasticity. The variations caused by drought were due mainly to the allometry. Our results showed that the leaves of *Q. acutissima* seedlings respond to different habitats with phenotypic plasticity of morphology, suggesting that this is an important mechanism for seedlings to adapt to broader ecological amplitudes.

**Key words:** *Quercus acutissima* Carr., leaf morphological plasticity, allometric analysis, forest edge, understory, drought, shade, leaf shape, venation pattern.

## INTRODUCTION

Plasticity is one solution to the problem of adaptation to heterogeneous environments. Plant morphological plasticity enables a plant to change its growth pattern as it encounters different stresses (Guo et al., 2007). Morphological plasticity plays an important role in resource acquisition by plants; variation of the size and placement of resource-acquiring organs such as leaves are critical to a plant's adjustment to resource availability (Navas and Garnier, 2002). As the primary photosynthetic organs, leaves have an important role in the survival and growth of a plant. They also provide evidence for plant taxonomy. Leaf physiognomy can serve as an excellent tool for ecological studies (Wright et al., 2004; Traiser et al., 2005). With the development of digital scanning technology, it becomes easier to identify leaf traits (Lu et al., 2004; Du et al., 2007). Some leaf traits, such as the leaf area index, can reflect the status of the whole plant (Tsialtas and Maslaris, 2007). Leaves have to be opti-

mally adapted to environmental conditions, and react most sensitively to the environment. Thus, the causal relationships between various environmental factors and leaf traits can be recognized (Roche et al., 2004), such as the effects of soil moisture and irradiance (Cescatti and Zorer, 2003; Liao et al., 2007). The development of plant morphology is gene-regulated and environmentally affected (Kessler and Sinha, 2004; Barkoulas et al., 2007). Many previous studies have shown variations in leaf traits to be the result of adapting to growth habitats (Sisó et al., 2001; Pandey and Nagar, 2002), and there are consistent relationships across species (Karst and Lechowicz, 2007). The forest edge and understory are commonly considered as typically contrastive habitats. Microclimatic gradients occur in forests towards their edges (Young and Mitchell, 1994). It is known that irradiance increases with decreased canopy cover. Edge effects enhance transpiration and present a drought challenge for seedling recruitment and forest regeneration (López-Barrera et al., 2006;

\*e-mail: wrq@sdu.edu.cn

Herbst et al., 2007). Although there are numerous studies of edge effects in forest fragments (reviewed in: Murcia, 1995), our understanding of leaf morphological variations in the forest edge and the understory is still limited.

*Quercus acutissima* Carr. is the main deciduous broadleaved species in northern China, widely distributed on mountains and hills in Shandong Province (Wang and Zhou, 2000). Many forests of *Q. acutissima* show patch distributions due to anthropogenic disturbance. Seedlings should engage certain mechanisms to adapt to different habitats, including variation of leaf morphology. There have been studies employing geometric measurements of leaf morphology in other oak species (Blue and Jensen, 1988; Li et al., 2005), but the results indicated instability of some parameters, and with size correction the differences were not significant. Here we focused on the leaf morphological plasticity of *Q. acutissima* seedlings in the differing habitats of forest edge and understory, and sought the causes of morphological variation in the field and under experimental treatments.

The objectives of this study were (1) to investigate whether leaf morphological differences occur; (2) to clarify the causes underlying variations of leaf shape and venation pattern; and (3) to distinguish environmentally induced or size-dependent morphological differences as responses to the effects of different habitats, especially under different light and water conditions.

## MATERIALS AND METHODS

### STUDY SITE AND APPROACH TO FIELD STUDY

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 warm temperate monsoon climate, with mean annual temperature of 13±1°C and average annual precipitation of 600–850 mm, falling mostly during the summer. The soil type of this area is yellow cinnamon soil, and the parent material is limestone (Zhang et al., 2006). Field measurements were taken in a stand of *Q. acutissima* on a hill 2 km from the research station in July 2007. The dominant layer of canopy was 14 m high. The leaf area index (LAI) was 5.12. Five 1-year-old seedlings were sampled from the forest edge and from the understory; 3–5 leaves were taken from each seedling for morphological measurements. They were taken from the top of the plant to avoid self-shading.

### SEEDLING EXPERIMENTS

Acorns of *Q. acutissima* were collected from the same field in early spring and planted in plastic

pots (9 l volume, 32 cm high, 29 cm diam.). The soil contained a 64:22:14 (v/v/v) mixture of humic soil, sand and loam. Its saturated water content was 36% by mass, the largest volumetric water content was 28%, and porosity was 68%; 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. The experiment was carried out during July and August 2007. The seedlings were subjected to water and light stress (ten plants per stress type). Drought stress was achieved by maintaining soil moisture at 30–40% of water holding capacity (WHC), while the controls received daily irrigation to maintain the soil water content between 70% and 80% of WHC. The light-stress treatment was conducted in shaded shelters covered by woven black nylon nets. Light transmission under the stress conditions was 10% of the controls. The seedlings were divided into four groups: (Group 1) well-watered and sunlight; (Group 2) drought and sunlight; (Group 3) well-watered and shade; and (Group 4) drought and shade. After a one-month treatment period, fifteen leaves from three seedlings per treatment were taken for morphological measurements.

### MORPHOLOGICAL MEASUREMENTS

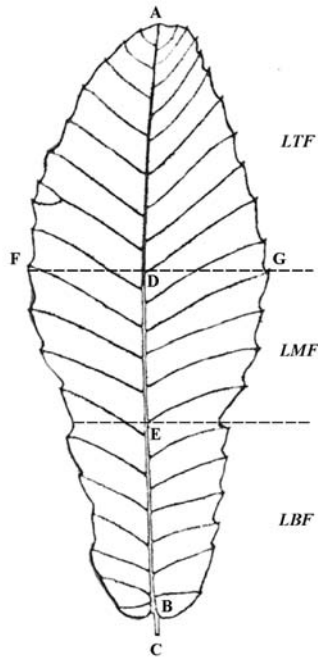
Leaf area was measured with a CI-203 laser area meter (CID Inc., Washington, U.S.A.). Linear measurements were taken with a digital caliper. Leaf dry mass was measured after oven-drying at 80°C for 48 h. Detailed information on the morphological parameters is given in Figure 1 and Table 1.

### STATISTICAL ANALYSIS

Analysis of variance (ANOVA) was used in the field study to test for differences between the two sites. To distinguish the effect of allometry under different treatments in the seedling experiments (Vretare et al., 2001; Kolb et al., 2002), analysis of covariance (ANCOVA) was used to test for differences between treatments in morphological parameters in relation to leaf area, and the means were compared by Duncan's multiple range test. All statistical analyses were done with SPSS 13.0 (SPSS Inc., Chicago, U.S.A.). Plots were drawn using Origin 7.5 (OriginLab Co., Massachusetts, U.S.A.).

## RESULTS

To eliminate morphological variations resulting from development stage or plant size, seedlings for the field study were selected for uniform size. There was no significant difference in height or in diameter at ground height (DGH) between the



**Fig. 1.** Diagram of leaf measurements. Dashed lines perpendicular to the midrib indicate the widest (above) and bulgy (below) parts of the leaf lamina. The two lines are determined by the angles between the midrib and the edge of the lamina. The positions where the angle is the smallest and largest represent the widest and the bulgy parts of the leaf lamina, respectively. The leaf is divided into three fractions by these two lines. The capital letters along the lines represent the positions located at the midrib or the edge of the lamina. See Table 1 for more details.

plants from the forest edge and understory (Tab. 2). Leaf area (LA), leaf length (LL), leaf width (LW), leaf bulgy division (LBD) and leaf middle fraction (LMF) did not significantly differ between the two sites. The values of leaf dry mass (LDM), leaf petiole length (LPL), leaf elongation (LE), leaf bottom fraction (LBF) and mean distance between veins (MDV) were significantly lower in the understory, while the values of specific leaf area (SLA), LL/LPL, leaf widest division (LWD), leaf top fraction (LTF) and number of leaf teeth (NLT) were significantly higher in the understory than in the forest edge (Tab. 3).

In the seedling experiments, water stress decreased nearly all the morphological parameters in both sunlight and shade. The shade treatments significantly increased SLA, LWD, LBD and NLT, and significantly lowered the values of LA, LDM, LL, LW, LL/LPL and MDV. There was no significant difference in LPL or LE in any treatments (Fig. 2). Treatment differences also altered the ratio of leaf fractions. The leaf top and middle fractions were significantly increased in the shade treatments. Accordingly, the leaf bottom fraction contributed

**TABLE 1.** Leaf morphological parameters and their definitions. The two capital letters in the definition demonstrate the linear distance between the corresponding two points indicated in Figure 1

Variable	Definition
LA (cm <sup>2</sup> )	Leaf area
LDM (g)	Leaf dry mass
SLA (cm <sup>2</sup> g <sup>-1</sup> )	Specific leaf area (ratio of leaf area to leaf mass)
LL (cm)	Leaf length= $AB$
LW (cm)	Leaf width= $FG$
LPL (cm)	Leaf petiole length= $BC$
LE	Leaf elongation (ratio of leaf length to leaf width)
LL/LPL	Leaf length to petiole length ratio
LWD	Leaf widest division= $AD/BD$
LBD	Leaf bulgy division= $AE/BE$
LTF (%)	Leaf top fraction= $AD/AB$
LMF (%)	Leaf middle fraction= $DE/AB$
LBF (%)	Leaf bottom fraction= $BE/AB$
NLT	Number of leaf teeth
MDV (cm)	Mean distance between veins= $2AB/(NLT+1)$

**TABLE 2.** Height and diameter at ground height (DGH) of *Q. acutissima* seedlings in the forest edge and understory. Data represent means  $\pm$  SE. df=1,9. ns – not significant at  $p>0.05$

	Forest edge	Understory	F	p
Height (cm)	50.60 $\pm$ 2.20	44.80 $\pm$ 2.29	3.33	0.105 <sup>ns</sup>
DGH (mm)	5.40 $\pm$ 0.37	6.00 $\pm$ 0.45	1.08	0.330 <sup>ns</sup>

significantly less to the leaf architecture. The effects of drought were the reverse of those caused by the shade treatments. They were also more significant in sunlight than in shade (Fig. 3). If the conditions for Group 2 (drought and sunlight) and Group 3 (well-watered and shade) are considered to be simulating factors in the forest edge and the understory, the trends of leaf morphological variation in the seedling experiments were consistent with those in the field study (Tab. 3, Figs. 2, 3).

The results of two-way ANCOVA are given in Table 4 for the effects of light and water treatments on leaf morphological parameters, using allometric relationships of seedlings. The differences in LL and LW between treatments were derived from the difference in LA between treatments. This is consistent with the field study results (Tabs. 3, 4).

TABLE 3. Effect of forest site on leaf morphological parameters of *Q. acutissima* seedlings, by one-way ANOVA. Data are means  $\pm$  SE. df=1,46. Significance levels: <sup>ns</sup>p>0.05, \*p<0.05, \*\*p<0.01, \*\*\*p<0.001

	Forest edge	Understory	ANOVA	
			F	p
LA (cm <sup>2</sup> )	31.97 $\pm$ 2.39	29.37 $\pm$ 1.36	0.91	0.345 <sup>ns</sup>
LDM (g)	0.27 $\pm$ 0.02	0.18 $\pm$ 0.01	17.27	0.000***
SLA (cm <sup>2</sup> g <sup>-1</sup> )	118.50 $\pm$ 1.94	168.67 $\pm$ 3.74	138.24	0.000***
LL (cm)	10.68 $\pm$ 0.37	10.39 $\pm$ 0.28	0.39	0.535 <sup>ns</sup>
LW (cm)	4.20 $\pm$ 0.11	4.41 $\pm$ 0.09	2.08	0.156 <sup>ns</sup>
LPL (cm)	0.58 $\pm$ 0.02	0.48 $\pm$ 0.03	9.93	0.003**
LE	2.55 $\pm$ 0.08	2.36 $\pm$ 0.04	5.00	0.030*
LL/LPL	18.51 $\pm$ 0.59	22.77 $\pm$ 0.83	17.42	0.000***
LWD	0.50 $\pm$ 0.02	0.57 $\pm$ 0.02	6.05	0.018*
LBD	2.54 $\pm$ 0.20	3.13 $\pm$ 0.22	3.91	0.054 <sup>ns</sup>
LTF (%)	33.19 $\pm$ 0.71	35.93 $\pm$ 0.84	6.14	0.017*
LMF (%)	37.08 $\pm$ 1.27	39.31 $\pm$ 1.60	1.17	0.286 <sup>ns</sup>
LBF (%)	29.73 $\pm$ 1.29	24.76 $\pm$ 1.40	6.74	0.013*
NLT	26.26 $\pm$ 0.62	28.17 $\pm$ 0.67	4.35	0.043*
MDV (cm)	0.76 $\pm$ 0.03	0.69 $\pm$ 0.02	4.42	0.041*

There was no difference in LPL, so the differences for LE and LL/LPL, which were calculated by LL, LW and LPL, were also derived from the difference of LA. Water had no effects on leaf morphological parameters except for LBF. Light had significant effects on LDM, SLA, LWD, LBD, LTF, LMF, LBF, NLT and MDV. The effects of LA on LDM, SLA and MDV were responsible for some of the differences between the effects of light treatments.

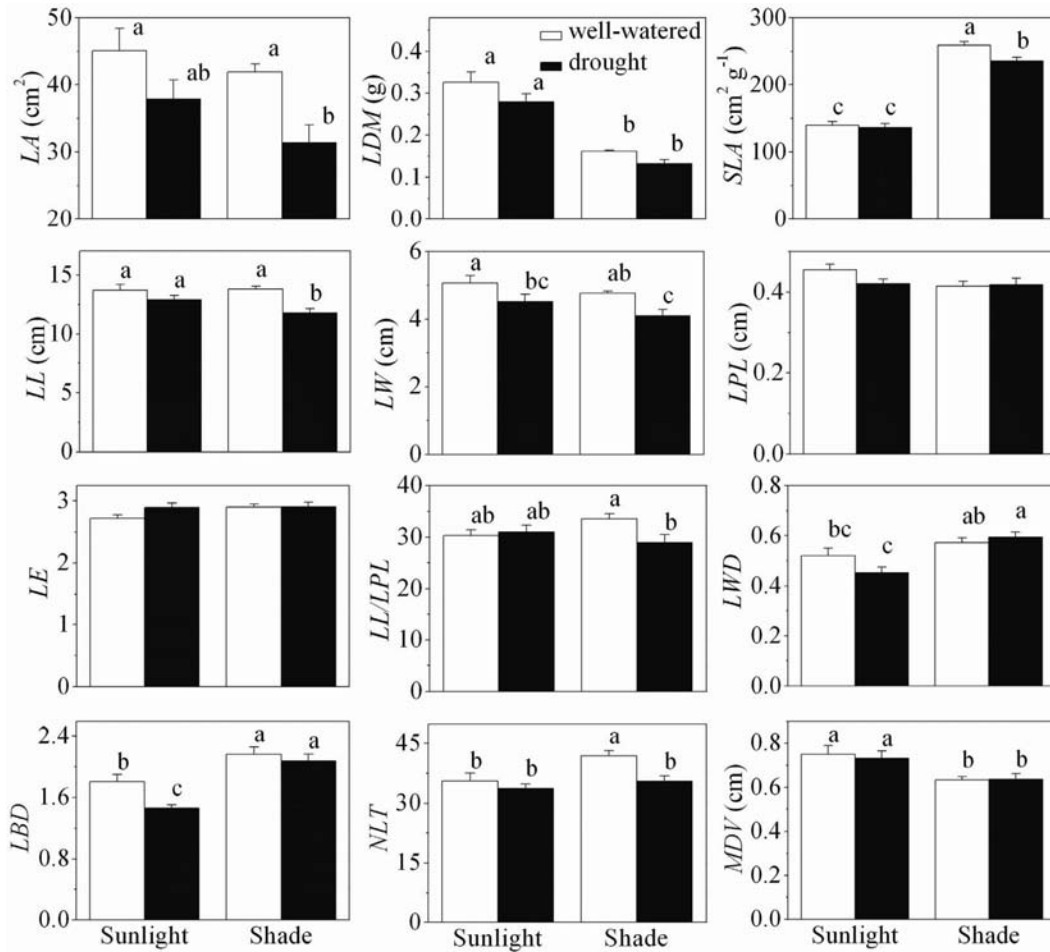
## DISCUSSION

The final size of a leaf depends on cell division and expansion. Any factor that can influence the number and size of leaf cells may affect the dimensions and size of the leaf (Tsukaya, 2003). Under short supply of light and water, leaf area and dry mass were obviously restricted in our experiments. Corresponding changes in leaf thickness also occurred, especially under shade conditions. Higher SLA is an accommodation to decrease self-shading of chloroplasts in the lower part of leaves (Parker and Mohammed, 2000; Quero et al., 2006; Feng et al., 2007). Increased efficiency of internal diffusion and investment of nitrogen in photosynthetic enzymes is reflected in a negative relationship between leaf photosynthetic capacity per dry mass and leaf dry mass per unit area (Niinemets et al., 2006a). Leaf shape is determined mainly in the brief period of primary morphogenesis, based on the possible participation of reaction-diffusion sys-

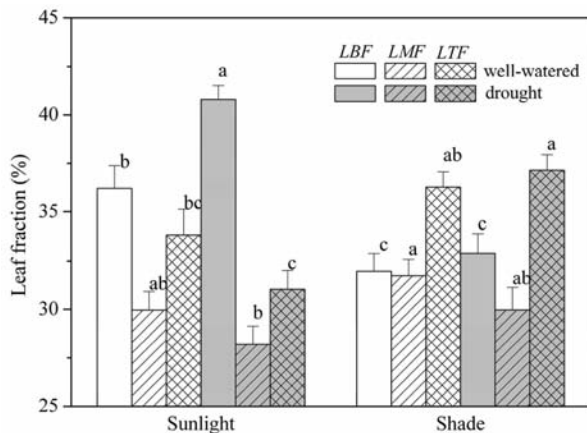
tems, and can be altered by allometric expansion (Franks and Britton, 2000; Dengler and Kang, 2001). In this present study, the lower values of leaf length, width and elongation under stress arose by allometry. However, it cannot be concluded that the effects of abiotic stress on leaf shape are negligible, because the changes in the three leaf fractions significantly differed. Drought caused the leaf bottom fraction, which represents the narrow part of the leaf, to increase in proportion to the whole leaf lamina. Overall the leaves narrowed, presumably as an adaptation to a xeric environment; narrow leaves can reduce transpiration by reducing the size of the boundary layer (Farris, 1984). The effects of shade on the leaf fractions were just the opposite, maximizing the light capture area (Takenaka, 1994). Changes of the three leaf fractions will also affect the location of the lamina centroid.

Leaf size and shape can modify the distribution of leaf biomass between support and functional tissues, and thus can alter the leaf venation pattern and leaf functioning in environments with different levels of resource availability (Niinemets et al., 2006b). As the plant develops, leaf display should be optimized to deal with canopy density. Possible strategies to minimize the amount of self-shading are to make fewer but larger leaves or to distribute leaves in a larger volume of canopy space (Niinemets and Fleck, 2002). This requires changes in petiole and vein architecture. In our study the changes of petiole length were correlated





**Fig. 2.** Changes of leaf morphological parameters of *Q. acutissima* seedlings under different light and water treatments. Boxes represent means and error bars represent the SE of the means ( $n=15$ ). Values with different letters differ significantly at  $p<0.05$  by Duncan's multiple range test.



**Fig. 3.** Changes of the three leaf fractions of *Q. acutissima* seedlings under different light and water treatments. Boxes represent means and error bars represent the SE of the means ( $n=15$ ). Values with different letters differ significantly at  $p<0.05$  by Duncan's multiple range test.

with the changes of leaf area and dry mass, indicating a positive relationship between leaf petiole length and leaf size. Considering the larger values of LL/LPL under the shade treatments, however, petiole elongation was not the main way of reducing self-shading, as the plants faced a trade-off between the needs to increase the interception area and the support structures. Increasing the investment in petioles demands synthesis of more xylogens, and longer petioles will cause the leaf to bend (Pickup et al., 2005). Year-old seedlings of *Q. acutissima* are nonbranching single-stem trees. Few leaves are produced, and only the upper leaves were selected for measurement. The measurements confirmed that to reduce self-shading there was no need to elongate the leaf petiole, as pointed out by Takenaka et al. (2001). Niinemets et al. (2007) also suggested trade-offs between the investments in central support and veins, which compensated for differences in leaf shape. The rel-

TABLE 4. Two-way ANCOVA for the effects of light and water treatment on leaf morphological parameters of *Q. acutissima* seedlings, with leaf area as covariate. Data are means  $\pm$  SE, n=60. Significance levels: <sup>ns</sup>p>0.05, \*p<0.05, \*\*p<0.01, \*\*\*p<0.001

	Light		Water		Covariate	
	F	p	F	p	F	p
LDM (g)	165.08	0.000***	0.67	0.418 <sup>ns</sup>	111.81	0.000***
SLA (cm <sup>2</sup> g <sup>-1</sup> )	443.65	0.000***	1.18	0.283 <sup>ns</sup>	8.99	0.004**
LL (cm)	1.42	0.238 <sup>ns</sup>	1.04	0.312 <sup>ns</sup>	401.83	0.000***
LW (cm)	0.78	0.381 <sup>ns</sup>	0.06	0.811 <sup>ns</sup>	729.37	0.000***
LPL (cm)	1.61	0.209 <sup>ns</sup>	0.36	0.552 <sup>ns</sup>	1.18	0.281 <sup>ns</sup>
LE	0.64	0.426 <sup>ns</sup>	0.01	0.962 <sup>ns</sup>	10.78	0.002**
LL/LPL	2.56	0.115 <sup>ns</sup>	0.12	0.731 <sup>ns</sup>	22.12	0.000***
LWD	13.51	0.001**	1.12	0.296 <sup>ns</sup>	0.34	0.561 <sup>ns</sup>
LBD	33.47	0.000***	3.87	0.054 <sup>ns</sup>	0.66	0.419 <sup>ns</sup>
LTF (%)	15.31	0.000***	1.27	0.265 <sup>ns</sup>	0.41	0.524 <sup>ns</sup>
LMF (%)	4.36	0.041*	1.32	0.256 <sup>ns</sup>	1.64	0.206 <sup>ns</sup>
LBF (%)	37.12	0.000***	5.23	0.026*	0.34	0.560 <sup>ns</sup>
NLT	9.21	0.004**	3.32	0.074 <sup>ns</sup>	3.10	0.084 <sup>ns</sup>
MDV (cm)	9.09	0.004**	1.63	0.207 <sup>ns</sup>	14.26	0.000***

actively broader and thinner leaf shape under the shade treatments showed higher vein density (lower MDV), preventing leaf margin drooping, because the centroid was far from the leaf base, increasing the overall bending moment. Apart from the role of mechanical support, veins also function in water import and photosynthate export (Park et al., 2008). There was a weak trend of increased vein density under drought stress, to obviate leaf dehydration.

Leaf lobation, like leaf teeth, is a functional trait, as shown by Sisó et al. (2001). Huff et al. (2003) found significant differences between tropical and temperate sites for several teeth characters. The relationship between leaf teeth and climate has been shown in woody and herbaceous species (Royer and Wilf, 2006; Semchenko and Zobel, 2007). Plants with toothed leaves have growth advantages, especially in non-optimal environments. Toothed leaves have smaller effective dimensions, reduced boundary layer thickness and higher heat transfer than leaves without teeth (Stokes et al., 2006). This makes toothed leaves more active with respect to photosynthesis and transpiration than non-toothed leaves (Royer and Wilf, 2006). Number of teeth, teeth area and degree of blade dissection are correlated with climate (Royer et al., 2005). This can explain why the leaves in the present experiments had more teeth in the understory and the shade treatments. As they can enhance sap flow and water loss rates, however, leaf teeth are disadvantageous for plants in water-stressed environments. We found

fewer leaf teeth in the drought treatments. It has been suggested that tooth area correlates negatively with leaf mass per area (Royer et al., 2005). The changes of the number of teeth and SLA (the reciprocal of leaf mass per area) in the present study showed a consistent trend under different treatments. There may be a nexus between leaf shape and leaf teeth in response to the environment.

Allometric relationships can result in apparent shape differences which are actually byproducts of size differences. This has been termed apparent plasticity, which is not real phenotypic plasticity (Weiner, 2004). Real plasticity is a change of the allometric trajectory. Plastic (treatment-induced) variations should be distinguished from nonplastic (developmental or size-induced) variations in order to reflect the degree of plant plasticity in response to environmental factors. López-Serrano et al. (2005) showed that allometric relationships may vary depending on the site. In the present study, leaves of *Q. acutissima* seedlings did show strong responses of several morphological characters to different habitats, and as allometric methods were used, these responses must be considered to be evidence of leaf morphological plasticity, due mainly to the effect of light.

This study of leaf trait differences may contribute to our understanding of optimum habitat conditions and the ecophysiological adaptations of plants. It argues for the need to consider intraspecific heterogeneity based on leaf allometry and phenotypic plasticity in resolving taxonomic prob-

lems (McLellan, 2000). Besides the effects of light and water, air temperature and humidity in the different forest habitats can also be expected to affect leaf morphological plasticity (Codarin et al., 2006; Koch et al., 2006). Further work on the morphological plasticity of *Q. acutissima* should include leaf positional and directional variation.

## ACKNOWLEDGEMENTS

We are grateful to Yinghua Wei and Yuanzu Xu for building the experimental equipment, to Yue Yu and Xiru Ye for assistance in the measurements, to Dr. Jian Liu for his valuable comments and suggestions on the manuscript, and to Dr. Edward C. Mignot of Shandong University for linguistic advice. This research was supported financially by the Key Project of the Natural Science Foundation of Shandong Province (Nos. Z2006D04; Z2007D02), the Program for New-Century Excellent Talents at the University of China (No. NCET-07-0511), and the Shandong Distinguished Middle-aged and Young Scientist Encouragement and Reward Foundation (No. 2006BS08004).

## REFERENCES

- BARKOULAS M, GALINHA C, GRIGG SP, and TSIANTIS M. 2007. From genes to shape: regulatory interactions in leaf development. *Current Opinion in Plant Biology* 10: 660–666.
- BLUE MP, and JENSEN RJ. 1988. Positional and seasonal variation in oak (*Quercus*; Fagaceae) leaf morphology. *American Journal of Botany* 75: 939–947.
- CESCATTI A, and ZORER R. 2003. Structural acclimation and radiation regime of silver fir (*Abies alba* Mill.) shoots along a light gradient. *Plant, Cell and Environment* 26: 429–442.
- CODARIN S, GALOPIN G, and CHASSERIAUX G. 2006. Effect of air humidity on the growth and morphology of *Hydrangea macrophylla* L. *Scientia Horticulturae* 108: 303–309.
- DENGLER N, and KANG J. 2001. Vascular patterning and leaf shape. *Current Opinion in Plant Biology* 4: 50–56.
- DU JX, WANG XF, and ZHANG GJ. 2007. Leaf shape based plant species recognition. *Applied Mathematics and Computation* 185: 883–893.
- FARRIS MA. 1984. Leaf size and shape variation associated with drought stress in *Rumex acetosella* L. (Polygonaceae). *American Midland Naturalist* 111: 358–363.
- FENG YL, WANG JF, and SANG WG. 2007. Biomass allocation, morphology and photosynthesis of invasive and noninvasive exotic species grown at four irradiance levels. *Acta Oecologica* 31: 40–47.
- FRANKS NR, and BRITTON NF. 2000. The possible role of reaction-diffusion in leaf shape. *Proceedings of the Royal Society B* 267: 1295–1300.
- GUO WH, LI B, ZHANG XS, and WANG RQ. 2007. Architectural plasticity and growth responses of *Hippophae rhamnoides* and *Caragana intermedia* seedlings to simulated water stress. *Journal of Arid Environments* 69: 385–399.
- HERBST M, ROBERTS JM, ROSIER PTW, TAYLOR ME, and GOWING DJ. 2007. Edge effects and forest water use: a field study in a mixed deciduous woodland. *Forest Ecology and Management* 250: 176–186.
- HUFF PM, WILF P, and AZUMAH EJ. 2003. Digital future for paleoclimate estimation from fossil leaves? Preliminary results. *Palaios* 18: 266–274.
- KARST AL, and LECHOWICZ MJ. 2007. Are correlations among foliar traits in ferns consistent with those in the seed plants? *New Phytologist* 173: 306–312.
- KESSLER S, and SINHA N. 2004. Shaping up: the genetic control of leaf shape. *Current Opinion in Plant Biology* 7: 65–72.
- KOCH K, HARTMANN KD, SCHREIBER L, BARTHLOTT W, and NEINHUIS C. 2006. Influences of air humidity during the cultivation of plants on wax chemical composition, morphology and leaf surface wettability. *Environmental and Experimental Botany* 56: 1–9.
- KOLB A, ALPERT P, ENTERS D, and HOLZAPFEL C. 2002. Patterns of invasion within a grassland community. *Journal of Ecology* 90: 871–881.
- LI M, HAN HR, KANG FF, and MA QY. 2005. Morphologic variation of leaves of *Quercus liaotungensis* Koidz. in Lingkong Mountain, Shanxi Province. *Journal of Beijing Forestry University* 27: 10–16.
- LIAO JX, SHI HW, JIANG MX, and HUANG HD. 2007. Leaf traits of natural populations of *Adiantum reniforme* var. *sinensis*, endemic to the Three Gorges region in China. *Photosynthetica* 45: 541–546.
- LÓPEZ-BARRERA F, MANSON RH, GONZÁLEA-ESPINOSA M, and NEWTON AC. 2006. Effects of the type of montane forest edge on oak seedling establishment along forest-edge-exterior gradients. *Forest Ecology and Management* 225: 234–244.
- LÓPEZ-SERRANO FR, GARCÍA-MOROTE A, ANDRÉS-ABELLÁN M, TENDERO A, and DEL CERRO A. 2005. Site and weather effects in allometries: a simple approach to climate change effect on pines. *Forest Ecology and Management* 215: 251–270.
- LU HY, LU CT, WEI ML, and CHAN LF. 2004. Comparison of different models for nondestructive leaf area estimation in taro. *Agronomy Journal* 96: 448–453.
- MCCLELLAN T. 2000. Geographic variation and plasticity of leaf shape and size in *Begonia dregei* and *B. homonyma* (Begoniaceae). *Botanical Journal of the Linnean Society* 132: 79–95.
- MURCIA C. 1995. Edge effects in fragmented forests: implications for conservation. *Trends in Ecology and Evolution* 10: 58–62.
- NAVAS ML, and GARNIER E. 2002. Plasticity of whole plant and leaf traits in *Rubia peregrina* in response to light, nutrient and water availability. *Acta Oecologica* 23: 375–383.
- NIINEMETS Ü, and FLECK S. 2002. Petiole mechanics, leaf inclination, morphology, and investment in support in relation to light availability in the canopy of *Liriodendron tulipifera*. *Oecologia* 132: 21–33.
- NIINEMETS Ü, CESCATTI A, RODEGHIERO M, and TOSENS T. 2006a. Complex adjustments of photosynthetic capacity and

- internal mesophyll conductance to current and previous light availabilities and leaf age in Mediterranean evergreen species *Quercus ilex*. *Plant, Cell and Environment* 29: 1159–1178.
- NIINEMETS Ü, PORTSMUTH A, and TOBIAS M. 2006b. Leaf size modifies support biomass distribution between stems, petioles and mid-ribs in temperate plants. *New Phytologist* 171: 91–104.
- NIINEMETS Ü, PORTSMUTH A, TOBIAS M. 2007. Leaf shape and venation pattern alter the support investments within leaf lamina in temperate species: a neglected source of leaf physiological differentiation? *Functional Ecology* 21: 28–40.
- PANDEY S, and NAGAR PK. 2002. Leaf surface wetness and morphological characteristics of *Valeriana jatamansi* grown under open and shade habitats. *Biologia Plantarum* 45: 291–294.
- PARK J, HWANG E, and NAM Y. 2008. Utilizing venation features for efficient leaf image retrieval. *The Journal of Systems and Software* 81: 71–82.
- PARKER WC, and MOHAMMED GH. 2000. Photosynthetic acclimation of shade-grown red pine (*Pinus resinosa* Ait.) seedlings to high light environment. *New Forests* 19: 1–11.
- PICKUP M, WESTOBY M, and BASDEN A. 2005. Dry mass costs of deploying leaf area in relation to leaf size. *Functional Ecology* 19: 88–97.
- QUERO JL, VILLAR R, MARAÑÓN T, and ZAMORA R. 2006. Interactions of drought and shade effects on seedlings of four *Quercus* species: physiological and structural leaf responses. *New Phytologist* 170: 819–834.
- ROCHE P, DÍAZ-BURLINSON N, and GACHET S. 2004. Congruency analysis of species ranking based on leaf traits: which traits are the more reliable? *Plant Ecology* 174: 37–48.
- ROYER DL, and WILF P. 2006. Why do toothed leaves correlate with cold climates? gas exchange at leaf margins provides new insights into a classic paleotemperature proxy. *International Journal of Plant Sciences* 167: 11–18.
- ROYER DL, WILF P, JANESKO DA, KOWALSKI EA, and DILCHER DL. 2005. Correlations of climate and plant ecology to leaf size and shape: potential proxies for the fossil record. *American Journal of Botany* 92: 1141–1151.
- SEMCHENKO M, and ZOBEL K. 2007. The role of leaf lobation in elongation responses to shade in the rosette-forming forb *Serratula tinctoria* (Asteraceae). *Annals of Botany* 100: 83–90.
- SISÓ S, CAMARERO JJ, and GIL-PELEGRÍN E. 2001. Relationship between hydraulic resistance and leaf morphology in broadleaf *Quercus* species: a new interpretation of leaf lobation. *Trees* 15: 341–345.
- STOKES VJ, MORECROFT MD, and MORISON JIL. 2006. Boundary layer conductance for contrasting leaf shapes in a deciduous broadleaved forest canopy. *Agricultural and Forest Meteorology* 139: 40–54.
- TAKENAKA A. 1994. Effects of leaf blade narrowness and petiole length on the light capture efficiency of a shoot. *Ecological Research* 9: 109–114.
- TAKENAKA A, TAKAHASHI K, and KOHYAMA T. 2001. Optimal leaf display and biomass partitioning for efficient light capture in an understorey palm, *Licuala arbuscula*. *Functional Ecology* 15: 660–668.
- TRAISSER C, KLOTZ S, UHL D, and MOSBRUGGER V. 2005. Environmental signals from leaves: a physiognomic analysis of European vegetation. *New Phytologist* 166: 465–484.
- TSIALTAS JT, and MASLARIS N. 2007. Leaf shape and its relationship with leaf area index in a sugar beet (*Beta vulgaris* L.) cultivar. *Photosynthetica* 45: 527–532.
- TSUKAYA H. 2003. Organ shape and size: a lesson from studies of leaf morphogenesis. *Current Opinion in Plant Biology* 6: 57–62.
- VRETARE V, WEISNER SEB, STRAND J, and GRANÉLI W. 2001. Phenotypic plasticity in *Phragmites australis* as a functional response to water depth. *Aquatic Botany* 69: 127–145.
- WANG RQ, and ZHOU GY. 2000. *The vegetation of Shandong Province*. Shandong Science and Technology Press, Jinan. 130–141.
- WEINER J. 2004. Allocation, plasticity and allometry in plants. *Perspectives in Plant Ecology, Evolution and Systematics* 6: 207–215.
- WRIGHT IJ, REICH PB, WESTOBY M, ACKERLY DD, BARUCH Z, BONGERS F, CAVENDER-BARES J, CHAPIN T, CORNELISSEN JHC, DIEMER M, FLEXAS J, GARNIER E, GROOM PK, GULIAS J, HIKOSAKA K, LAMONT BB, LEE T, LEE W, LUSK C, MIDGLEY JJ, NAVAS ML, NIINEMETS Ü, OLEKSYN J, OSADA N, POORTER H, POOT P, PRIOR L, PYANKOV VI, ROUMET C, THOMAS SC, TJOELKER MG, VENEKLAAS EJ, and VILLAR R. 2004. The worldwide leaf economics spectrum. *Nature* 428: 821–827.
- YOUNG A, and MITCHELL N. 1994. Microclimate and vegetation edge effects in a fragmented Podocarp-broadleaf forest in New Zealand. *Biological Conservation* 67: 63–72.
- ZHANG XQ, LIU J, WELHAM CVJ, LIU CC, LI DN, CHEN L, and WANG RQ. 2006. The effects of clonal integration on morphological plasticity and placement of daughter ramets in black locust (*Robinia pseudoacacia*). *Flora* 201: 547–554.