

Growth and Leaf Morphology Response to Drought Stress in the Riparian Broadleaved Tree, *Ulmus laevis* (Pall.)

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Abstract

Open pollinated progeny from eight maternal trees from three European populations of *Ulmus laevis* Pall. (European white elm) were cultivated in a growth chamber for one growth period in either a well watered or a drought stress treatment. Traits important for adaptation such as growth rate, time of budset and final dry weight were measured. Two leaves were removed from each plant for analysis of leaf morphology, as described by moment invariants and elliptic Fourier coefficients. We used univariate and multivariate analyses of variance to calculate genetic parameters in order to answer the questions: i) How much genetic variation is present in populations and families of *U. laevis*? ii) What is the effect of the water regime on the expression of genetic variation? Treatment effects and genotype rank changes were relatively small, but the strongly significant population and family differentiation across and within treatments for most adaptive traits and for some of the leaf shape components suggest that there is substantial additive genetic variation within these populations of *U. laevis* which could serve as a genetic basis for adaptation to future changes in water availability. Furthermore, the amounts of genetic variation for adaptive traits and leaf morphology were of similar magnitude within both watering regimes, i.e. there was no straightforward relationship between the water treatments and the expression of genetic variation.

Key words: Drought, *Ulmus laevis*, European white elm, genetic variation, growth chamber, leaf shape.

Introduction

An accelerated rate of climatic change is predicted owing to an increase of greenhouse gases in the atmosphere (HOUGHTON et al., 1996). It is anticipated that extreme weather conditions, particularly in terms of temperature and precipitation, will be more frequent in the future (BOYLE, 1994). Fluctuations in water availability, including periods of drought, may become more common. For populations to respond to selection and adapt to environmental change, additive genetic variance in quantitative traits is required (LYNCH and LANDE, 1993). An alternative and more rapid means of individual adaptation is phenotypic plasticity, i.e. the modification of a certain genotype in response to environmental variation. Species with long generation times, such as trees, might experience large environmental heterogeneity during their lifetime. Thus, high additive genetic variation and phenotypic plasticity are especially important for their long-term survival (ERIKSSON, 1999).

It has been hypothesized that environmental stress influences quantitative genetic parameters such as additive genetic variance and narrow-sense heritability (the genetic variance expressed as a fraction of the total phenotypic variance) (HOFF-

MANN and PARSONS, 1991; HOFFMANN and MERILÄ, 1999). Some authors have proposed that mutation and recombination rates increase with the amount of stress experienced by each individual or that the phenotypic expression of particular genes is enhanced under harsh conditions (HOLLOWAY et al., 1990; HOFFMANN and PARSONS, 1991; SKRØPPA and JOHNSEN, 1999). BLUM (1988) suggested that organisms do not reach their genetic potential for growth under stress and that the heritability of a trait decreases under stress as a consequence of an increase in the environmental variance.

Quantitative genetic analysis may also include the study of traits with less obvious adaptive value, such as leaf shape. Moment invariants (DUDANI et al., 1977) and elliptic Fourier coefficients (KUHLE and GIARDINA, 1982) are two image descriptor systems that allow rapid and cost-effective automated scoring of e.g. leaf shapes for a large number of plants. They have previously been used in various taxonomic, ecological and developmental contexts to describe variation in leaf shape between and within taxa e.g. *Betula* (WHITE et al., 1988), *Acer* (KINCAID and SCHNEIDER, 1982; McLELLAN and ENDLER, 1998) and *Nothofagus* (PREMOLI, 1996).

Ulmus laevis Pall., the European white elm, has a central and eastern European distribution. It is usually confined to riparian forests along large rivers or to other wet soils. It is one of the rare European tree species that thrive in soils that are periodically flooded. In Sweden the species is present only on the Baltic island of Öland where it occurs locally in damp deciduous forests. The species is classified in Sweden as 'Vulnerable' (VU) according to the World Conservation Union (IUCN) criteria used to draw up the the Swedish Red List of endangered species (GÄRDENFORS, 2000). *Ulmus laevis* is wind-pollinated, hermaphroditic and seed production is generally prolific, the seeds being dispersed by wind. Owing to its lowland riparian habit, *U. laevis* has lost a great deal of habitat to deforestation and drainage of lowland areas of Western Europe for agriculture and industry (GÄRDENFORS, 2000; COLLIN et al., 2001). Today, many populations in the western part of the species' range are small and relatively isolated. Although *U. laevis* is susceptible to Dutch elm disease (DED) (*Ophiostoma novo-ulmi*), the disease is not thought to pose an immediate threat to the species, at least in the western part of the distribution area. Studies have shown that the *Scolytus* beetle species acting as vectors for the fungal pathogen appear to find *U. laevis* unattractive as a food plant, strongly preferring *Ulmus minor* (WEBBER, 2000).

In the present study, we cultivated first year seedlings of *U. laevis* in two controlled watering environments: one well watered (free water access) and one with a severely limited water supply (drought stress). We measured plant height growth, final biomass and time of budset and we investigated leaf morphology as described by moment invariants and Fourier coefficients, using two leaves per plant. Using multivariate and univariate analysis of variance, and assessing genetic parameters (additive genetic variance and coefficients of additive variation, CV_A), we addressed the following questions: i)

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How much additive genetic variation is present for growth traits (height growth, biomass etc.), timing of budset, and leaf morphology in populations and families of *U. laevis*? ii) What is the effect of watering regime on the expression of genetic variation?

Material and Methods

Study populations

Three study populations, one each from France, Sweden and Germany, were examined in this study. The French *U. laevis* population (latitude 43°52'N, longitude 1°20'E) is situated in a steep-sided valley in southern France and consists of approximately 200 individuals along a 4.5 km stretch of the river Garonne. The Swedish population (latitude 56°44'N, longitude 16°30'E) is composed of several hundred individuals scattered over the whole of "Mittlandsskogen", an area of approximately 10 km by 25 km in the central region of the Baltic island of Öland. The German population (latitude 51°31'N, longitude 13°03'E) lies on the Elbe floodplain and consists of several hundred trees, many growing along the banks of the river itself. During May and June 2000, seeds were sampled at random from adult trees within all populations.

Plant cultivation and trait registration in growth chambers

Plants used in the present study were open-pollinated progeny from eight maternal trees per population. Each family was represented by 20 seedlings in each of two watering regimes, resulting in a total of 960 plants (3 populations x 8 families x 2 treatments x 20 seedlings). The seeds were stored at +4°C until sowing in February 2002 in seed trays with a mixture of perlite, vermiculite, sand and gravel, in growth chambers (20 h light and 4 h darkness, 20°C). Seeds started to germinate after a few days. Pots without plant material were weighed twice: first with dry mineral wool ("Grodan"), and again after being watered until field capacity. After approximately ten days, seedlings were transplanted into these separate pots and were placed in trucks with 15 plants per truck in a total of 64 trucks. Seedlings were pre-cultivated at 20°C (photoperiod 21 h light / 3 h darkness) for three weeks in growth chambers. During the whole pre-treatment period, the light from 250 W daylight Osram HQi-E lamps provided an irradiance of 300 μmol m⁻²s⁻¹ in the 400–650 nm spectrum, the relative air humidity was 75%, and the plants were watered with a 50% nutrient solution, 2L-6513, as described by INGESTAD (1967).

Three trucks per treatment were randomly chosen and weighed before and after watering until saturated. At a height of about 11 cm, 40 seedlings per family were arranged in randomized single-tree plots divided into 40 blocks with 24 plants per block before transferring to one of the two watering regimes. Plants were cultivated for 11 weeks in the watering treatments, and during the course of the experiment, the three selected trucks per treatment were weighed every day or every second day to estimate their water content and to determine when watering was required. Experimental plants were watered when the truck weight was no less than 80% of the saturated weight in the well watered treatment and approximately 40% in the drought stress treatment. A pilot study indicated that drought stress below 40% resulted in severe leaf wilting and mortality of the seedlings (data not shown). The drought stress treatment was not intended to kill the seedlings but to reduce their growth compared with those in the well watered treatment.

Cultivation of plants in growth chambers provided an opportunity to minimize both spatial variation in growth conditions and confounding effects of factors other than water availability.

The light levels, air humidity and nutrient solution used were the same as in the pre-treatment. Photoperiod and temperature regimes were chosen to simulate natural spring to autumn conditions in southern Sweden: the night length increased from 6 h (1st week in water treatment) to 16 h (11th week in water treatment), whereas the night temperature decreased from 15°C to 2°C over the same period. The day temperature was 3–7°C higher than the night temperature.

Total seedling height was measured on eight occasions in both treatments. Budset was scored twice using a four-point scale (0 = no visible bud, 1 = beginning of bud development, 2 = green bud, 3 = clear brown bud). Leaf number per plant was registered at harvest and dry weight of roots and shoots was recorded after drying for 40 h at 70°C. Total height increment, dry weight, and shoot:root dry weight ratio were also measured (Table 1).

Table 1. – Trait abbreviation and description of growth traits and timing of budset measured in a growth chamber experiment in *Ulmus laevis*.

Trait	Description, unit, transformation type
Height 1 (covariate)	Plant height when transferred to water treatments, day 0 (cm)
Height 5w	Plant height after five weeks in water treatments (cm)
Total increment	Final height (at harvest) – Height 1 (cm)
Total biomass	Dry weight of shoot and root (g)
Shoot:root biomass	Dry weight ratio shoot:root
Leaf number	Leaf number at harvest
Budset 9w	Budset stage after nine weeks in water treatments
Budset 10w	Budset stage after 10 weeks in water treatments
Leaf size	Moment invariant 1: overall leaf size, the higher value, the larger leaf
Leaf roundness	Moment invariant 2: discriminates between round and narrow leaves, the higher value, the more narrow leaf
Leaf lanceolateness	Moment invariant 3: contrasts lanceolate leaves with leaves that are widest at the apical or basal part of the lamina. The higher value, the more lanceolate leaf

Statistical analyses of growth traits and time of budset

Character mean values across treatments were calculated for each population. Nested factorial analysis of variance was conducted for each trait using type III sum of squares (PROC GLM, SAS Institute, Release 6.12, 1989). Preliminary analyses revealed significant effects of covariate (Height 1 = initial plant length when transferred to each treatment) and block, so these effects were included in the final analyses. Appropriate denominators for each F-test were synthesized with the Satterthwaite approximation using the TEST option in the RANDOM statement of PROC GLM (SAS 1989). Phenotypic plasticity was estimated as the treatment effect, and the amount of genetic variation for phenotypic plasticity was estimated as the genotype x environment (g x e) term in the general linear model ANOVAs. In order to estimate genetic variation within and between treatments and populations (model 1), and within separate treatments across and within populations (model 2), the following GLM ANOVA models were used:

$$y_{hijkl} = \mu + cx_{hijkl} + t_i + b_{j(i)} + p_k + f_{l(k)} + (tp)_{ik} + tf_{il(k)} + e_{hijkl} \quad [1]$$

$$y_{hijkl} = \mu + cx_{hijkl} + b_j + p_k + f_{l(k)} + e_{hijkl} \quad [2]$$

where y_{hijkl} and y_{hijkl} are values of single observations, μ = grand mean, c = coefficient, x_{hijkl} = covariate (initial plant height), t_i = fixed effect of water treatment i , $b_{j(i)}$ = random effect of block j within treatment i , b_j = random effect of block j , p_k = fixed effect of population k , $f_{l(k)}$ = random effect of family l within population k , $(tp)_{ik}$ = fixed interaction effect of treatment i and population k , $tf_{il(k)}$ = random interaction effect of treatment i and family l within population k , e_{hijkl} = residual error.

The variance components for each of the random factors were calculated as the ratio of the variance component to the

sum of all random components. Estimates of the variance components were obtained using the REML option in PROC VARCOMP (SAS, 1989) and the standard errors of the relative components were found using the Delta technique (BULMER, 1980). At the family level, we calculated the additive coefficients of variation,

$$CV_A = (\sqrt{4\sigma_f^2})100/\bar{x} \quad [3]$$

where σ_f^2 = family variance component and \bar{x} = phenotypic mean of the trait.

Leaf sampling and statistical analysis

Sampling for leaf shape analysis was done when all plants had spent eight weeks in the water treatments (i.e. three weeks before harvest) and had ceased growing due to the progressively decreasing day length and temperatures in the growth chambers. To standardize the sampling procedure, we used two adjacent leaves at the midpoint of each plant. 453 and 392 plants were included from the drought stress and well watered treatments respectively. All sampled leaves were pressed and photocopied before the measurements.

Moment invariants describe the distribution of the Cartesian co-ordinates (x and y) of image points along the outline of the leaf (DUDANI et al., 1977; WHITE et al., 1988). The first parameter (Moment 1) is a size component, Moment 2 distinguishes between round and narrow leaves, while Moment 3 contrasts lanceolate leaves with leaves that are widest at the apical or basal part of the lamina (R. I. WHITE, personal communication, School of Biological Sciences, University of Southampton, Southampton SO167PX, Great Britain). Elliptic Fourier analysis is an accurate method for quantifying the shape of two-dimensional objects, such as leaves, using a number of two-dimensional wave functions (harmonics), each being comprised of four Fourier coefficients (KUHLE and GIARDINA, 1982). The precision of the description is dependent on how many harmonics are specified: low-numbered harmonics describe the overall shape of the outline, whereas higher harmonics describe increasingly fine detail (KINCAID and SCHNEIDER, 1982; WHITE et al., 1988).

Automated image analysis (WHITE et al., 1988) was used to provide data for quantitative genetic analyses of leaf morphology. Leaf outlines, digitised by a video camera connected to a personal computer, were analysed using the program ARBO (by R. I. WHITE, personal communication). Descriptors chosen were moment invariants (three parameters) and elliptic Fourier harmonics (nine harmonics, corresponding to 34 coefficients, including two coefficients in the first harmonic which become constant after normalisation). A nested, factorial multivariate analysis of variance (MANOVA), using Wilk's lambda test,

Table 2. – Mean values across two water regimes for growth traits, timing of budset and the first three moment invariant leaf shape descriptors (Moments 1–3) in three populations of *Ulmus laevis*. Standard deviations are given within parentheses.

Trait	Sweden	France	Germany
Height 1 (covariate) (cm)	10.2 (0.81)	11.4 (1.2)	12.8 (1.1)
Height 5w (cm)	73.9 (2.7)	82.4 (2.2)	85.2 (4.6)
Total increment (cm)	70.6 (3.8)	81.3 (2.6)	82.9 (2.6)
Total biomass (g)	8.0 (0.71)	8.9 (0.80)	9.6 (0.80)
Shoot:root biomass	2.3 (0.14)	2.6 (0.17)	2.8 (0.17)
Leaf number	20.4 (0.67)	24.4 (1.3)	24.3 (1.3)
Budset 9w	0.80 (0.09)	0.24 (0.12)	0.32 (0.12)
Budset 10w	1.3 (0.20)	0.56 (0.13)	0.75 (0.13)
Leaf size	5.2 (0.61)	4.7 (0.45)	5.1 (0.61)
Leaf roundness	0.42 (0.07)	0.43 (0.06)	0.45 (0.06)
Leaf lanceolateness	0.15 (0.04)	0.14 (0.05)	0.14 (0.04)

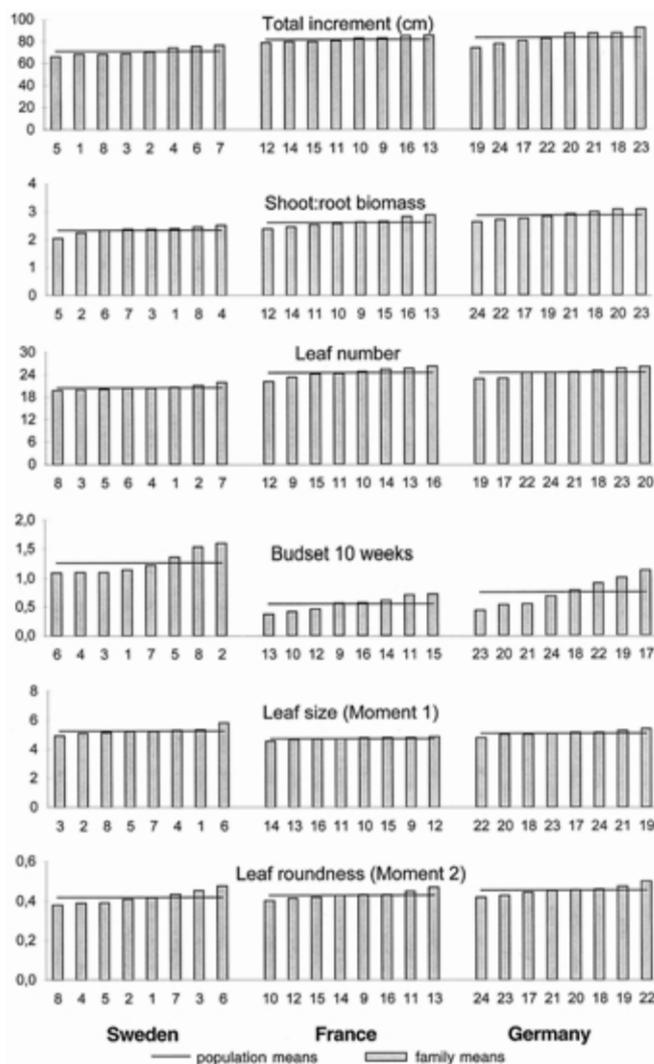


Figure 1. – Mean values of growth traits, time to budset and moment invariants leaf shape components in open pollinated families from three populations of *Ulmus laevis* cultivated across two water regimes in growth chambers. The x-axis represents the families and population mean values are indicated. For a character description, see Table 1.

were performed on the moment invariants and Fourier coefficients to check for significant effects of treatments (tested against block), populations (tested against family across and within treatments), and families (tested against error across and within treatments) (option MANOVA in PROC GLM, SAS 1989). The Fourier MANOVA's were done for Fourier coefficients 1 and 4 (corresponding to harmonic 1), coefficients 5–20 (harmonics 2–5), and coefficients 21–36 (harmonics 6–9). The same univariate ANOVA models as applied for growth traits and time at budset were then used to assess genetic variation across and within treatments for the moment invariants.

Results

Genetic variation and phenotypic plasticity in *Ulmus laevis*

According to mean values (Table 2), the Swedish population showed the smallest height increment, the fewest leaves and the earliest budset. Mean values of the moment invariants showed that leaves from the Swedish plants were larger (Moment 1) and rounder (Moment 2) than those representing the French or German individuals (Table 2). Families (Figure 1) and populations possessed large genetic variation for a number

Table 3. – F-ratios from analysis of variance of growth traits, time to budset and leaf morphology (Moment invariants 1–3) in three populations of *Ulmus laevis* cultivated in growth chambers across two water regimes.

Trait	Covariate (1)	Treatment (1)	Block (38)	Population (2)	Family (21)	Treatment x Population (2)	Treatment x Family (21)
Height 5w	508***	0.07	2.96***	3.30	2.52*	4.05*	2.10**
Total increment	230***	0.23	2.22***	5.20*	2.83*	3.56*	1.97**
Total biomass	390***	0.46	2.34***	0.53	1.16	1.67	1.65*
Shoot:root biomass	27.4***	0.12	3.54***	11.5***	2.45*	3.83*	1.97**
Leaf number	339***	0.69	4.84***	17.7***	4.55***	1.73	1.01
Budset 9w	37.0***	3.69	2.28***	32.3***	2.88**	1.70	0.91
Budset 10w	33.2***	10.7**	2.81***	21.7***	3.58**	2.20	1.12
Leaf size	0.96	26.09***	2.25***	16.70***	2.68*	4.92*	2.07**
Leaf roundness	22.02***	6.10*	1.96**	6.80**	11.11***	0.90	0.54
Leaf lanceolateness	7.18**	0.90	0.98	0.27	1.71	1.66	0.96

Degrees of freedom are given within parentheses.

Block was nested within treatment and family was nested within population.

* $p \leq 0.05$, ** $p \leq 0.01$, *** $p \leq 0.001$

Table 4. – Relative variance components (%) and additive coefficients of variation, CV_A , for growth traits, time to budset and leaf shape descriptors (Moments 1–3) in 24 half-sib families representing three populations of *Ulmus laevis* cultivated across (A) and within drought stress (D) and well watered (W) treatments in growth chambers.

Trait	A			D		W	
	Variance Family	Variance Treatment x Family	CV_A Family	Variance Family	CV_A Family	Variance Family	CV_A Family
Height 5w	4.2 (2.4)	1.8 (1.9)	6.3	2.2 (2.1)	3.9	8.2 (3.6)	9.9
Total increment	5.0 (2.8)	2.7 (2.2)	8.4	6.9 (3.4)	27.1	8.1 (3.7)	12.0
Total biomass	5.9 (3.1)	2.9 (2.2)	14.8	2.4 (2.2)	7.6	12.2 (4.6)	24.9
Shoot:root biomass	6.1 (3.1)	3.2 (2.2)	9.8	10.4 (4.2)	12.2	8.2 (3.6)	12.0
Leaf number	6.0 (2.4)	0	8.1	2.0 (1.9)	4.6	8.4 (3.7)	9.8
Budset 9w	2.9 (1.4)	0	-	1.9 (2.1)	-	5.3 (3.0)	-
Budset 10w	5.8 (2.4)	0	-	7.9 (3.6)	-	3.6 (2.5)	-
Leaf size	8.6 (4.0)	4.3 (2.9)	6.3	15.2 (5.2)	7.8	11.2 (4.7)	7.7
Leaf roundness	15.3 (4.7)	0	-	15.8 (5.4)	-	11.8 (4.9)	-
Leaf lanceolateness	3.8 (2.3)	0.2 (1.8)	-	5.9 (3.3)	-	1.9 (2.4)	-

CV_A was not calculated for time to budset or Moments 2–3 due to low mean values for these characters. The family effect was nested within populations. Standard errors are given within parentheses.

of the height growth, timing of budset and leaf shape characters. The effect of the water regimes was significant only for few traits: in the well-watered treatment, budset at 10 weeks was earlier than in drought, and leaves were also larger and narrower (ANOVA model 1, Table 3). The population and family x treatment interactions were moderate for height growth and time of budset, and low for the leaf shape components (Table 3). The family variances were higher than the family x treatment variances (Table 4). Family CV_A ranged from 6.3 to 14.8 for the growth traits and for overall leaf size (Table 4). CV_A values were not calculated for budset and Moments 2–3, as the low mean values (<1) for these traits would lead to an overestimation of CV_A . The MANOVA of the moment invariants and five first harmonics demonstrated significant effects of treatment, i.e. leaves were larger, narrower and more lanceolate in the well-watered treatment (Table 5). Strong population and family differentiation was found for the moment invariants and Fourier coefficients (Table 5). A reconstruction of the leaf outline illustrated that the major pattern of the leaf shape can be re-created using nine harmonics (Figure 2).

The effect of the water regimes on the expression of genetic variation

Similar amounts of genetic variation for growth traits, timing of budset and leaf morphology were expressed within both

Table 5. – F-ratios from Wilk's lambda test in a multivariate analysis of variance of leaf shape as described by elliptic Fourier coefficients (FC) and three moment invariants in three populations of *Ulmus laevis* cultivated across and within two water regimes in growth chambers.

Treatment /Leaf statistics	Treatment (1)	Population (2)	Family(Population) (21)
<i>Both water regimes</i>			
FC 1,4 (harmonic 1)	21.30***	15.29***	5.08***
FC 5-20 (harmonics 2-5)	5.13***	4.28**	2.64***
FC 21-36 (harmonics 6-9)	1.88	7.63***	1.77***
Moment invariants	10.00***	7.52**	4.24***
<i>Drought stress regime</i>			
FC 1,4 (harmonic 1)	-	9.47***	3.65***
FC 5-20 (harmonics 2-5)	-	2.08	1.96***
FC 21-36 (harmonics 6-9)	-	2.51*	1.42***
Moment invariants	-	4.39**	3.12***
<i>Well watered regime</i>			
FC 1,4 (harmonic 1)	-	14.94***	2.45***
FC 5-20 (harmonics 2-5)	-	1.25	1.72***
FC 21-36 (harmonics 6-9)	-	1.74	1.34***
Moment invariants	-	7.56***	2.31***

Degrees of freedom are given within parentheses.

* $p \leq 0.05$, ** $p \leq 0.01$, *** $p \leq 0.001$

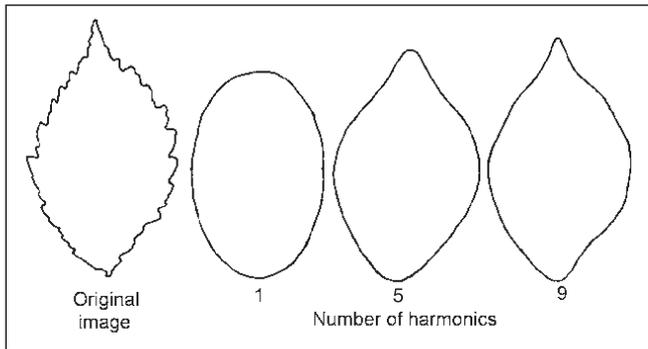


Figure 2. – Computer reconstructions of the leaf shape of one *Ulmus laevis* leaf using elliptic Fourier analysis. Two-dimensional wave functions (harmonics), each being comprised of four Fourier coefficients, are used. The low-numbered harmonics describe the overall shape of the outline, whereas higher harmonics describe increasingly fine detail. The *U. laevis* leaf is gradually built-up as the number of elliptic Fourier harmonics increases from 1, 5 to 9.

water regimes (ANOVA model 2). Families varied for the majority of traits irrespective of treatment, whereas population differences in growth traits were slightly more common in the drought stress than in the well watered treatment (Table 6). The family variances were in general lower for growth traits and timing of budset in the drought stress (averaged across traits = 4.8%) than in the well-watered treatment (average: 7.7%), while the opposite pattern was observed for the leaf morphology traits (average: drought 12.3%, well watered 8.3%) (Table 4). Family CV_A s for growth and overall leaf size were of similar magnitude within both treatments (drought stress: 3.9–27.1; well watered: 7.7–24.9) (Table 4). Within both water regimes, the multivariate analysis revealed population variation mainly for the first Fourier harmonic and the moment invariants, whereas family differences were strongly significant for all leaf shape traits (Table 5).

Discussion

Growth traits and fecundity variation across water environments

Additive genetic variation was strong both between and within the three populations of *U. laevis*. According to the population mean values, Swedish plants were the first to respond to increased night length and lower temperatures by growth cessation and budset, supporting the general theory that the most rapid response to photoperiodic change occurs in populations originating at the highest latitudes (ERIKSSON and EKBERG, 2001). There were some population and family rank differences between the two water regimes, indicating differences in adaptedness among populations and families to changes in water availability. Significant interaction effects were found mainly for growth characters and overall leaf size, both sets of traits being cumulative. Thus it is likely that existing early genotype differences may increase during the experimental period. The lack of genotype x environment interaction for budset supports evidence from quantitative trait locus and candidate gene mapping studies that this trait is under strong genetic control (FREWEN et al., 2000), the timing of budset being critical for individual survival and growth.

The variance components, especially for the family x treatment interaction, were relatively low, as was the precision of these estimates for some traits. Family CV_A values were also rather low. HOULE (1992) suggested that CV_A is usually more useful than family variance components as an indicator of potential for long-term survival. However, the denominator in the ratio for the derivation of CV_A s is the trait mean value, and in non-continuous traits, and traits with low mean values, CV_A s may be over-estimated and difficult to interpret. Consequently, we calculated CV_A s only for growth traits and for overall leaf size. In other broad-leaved species, CV_A s for height growth in nursery and progeny trials have been estimated at 0–42 in *Quercus robur* (BALIUCKAS and PLIURA, 2003), 11–19 in *Fraxinus excelsior* and *Prunus avium* (BALIUCKAS et al., 2000), and 16–57 in growth traits in *Castanea sativa* seedlings culti-

Table 6. – F-ratios from analysis of variance of growth traits, timing of budset and leaf morphology (Moment invariants 1–3) in three populations of *Ulmus laevis* cultivated in growth chambers within a drought stress and a well watered treatment.

Treatment / Trait	Covariate (1)	Block (19)	Population (2)	Family (21)
<i>Drought stress</i>				
Height 5w	210.88***	2.52***	6.60**	3.91***
Total increment	76.12***	2.68***	7.97**	4.35***
Total biomass	137.78***	1.39	1.80	1.02
Shoot:Root biomass	0.24	3.51***	11.12***	3.44***
Leaf number	163.70***	7.44***	17.72***	3.18***
Budset 9w	12.99***	2.48***	28.97***	1.52
Budset 10w	6.10*	3.34***	16.53***	2.91***
Leaf size	14.02***	2.53***	7.90**	4.18***
Leaf roundness	6.07*	1.57	4.03*	4.09***
Leaf lanceolateness	1.21	0.77	0.63	1.77*
<i>Well watered</i>				
Height 5w	317.64***	3.59***	0.91	2.75***
Total increment	166.52***	2.09***	2.32	2.54***
Total biomass	275.88***	3.24***	0.44	1.54
Shoot:Root biomass	49.15***	3.85***	9.12**	2.63***
Leaf number	177.03***	2.52***	13.42***	2.05**
Budset 9w	25.39***	2.11**	20.65***	1.94**
Budset 10w	34.62***	2.28**	19.96***	1.96**
Leaf size	23.57***	2.15**	16.95***	3.38***
Leaf roundness	18.27***	1.75*	9.21**	2.62***
Leaf lanceolateness	7.47**	1.09	0.05	1.03

Degrees of freedom are given within parentheses. Families are nested within populations.

* $p \leq 0.05$, ** $p \leq 0.01$, *** $p \leq 0.001$

vated in growth chambers in a temperature x watering experiment (PLIURA and ERIKSSON, 2002). Our CV_A estimates in *U. laevis* (rarely exceeding 15) were thus relatively low, but were comparable to CV_A values we have estimated in the same populations of *U. laevis* grown in a field trial, which ranged from 0–14.5 for plant height (WHITELEY et al., 2003a). Given the variation in CV_A values obtained in the studies cited above, and the range of different conditions used in these studies, we think it would be premature to draw firm conclusions about the long-term evolutionary potential of *U. laevis* from the relatively low CV_A values we obtained.

Leaf shape variation across and within water environments

The multivariate analyses of leaf shape characters yielded a significant separation at the population and family levels, which was also supported by the ANOVAs for the moment invariants. Due to the large size of the Fourier data set and lack of degrees of freedom, the MANOVAs were partitioned into three analyses: one for the first harmonic alone (two coefficients) and two analyses with four harmonics (16 coefficients) each. The first harmonic was treated separately as it describes the overall leaf shape, and it clearly showed strong treatment and genetic effects, as did harmonics 2–5 across water regimes. Population effects within treatments were not, or only very weakly, significant for harmonics 2–9, while family differentiation was strong for all harmonics irrespective of treatment. As shown in *Figure 2*, the major features of the leaf shape can be reconstructed using the first nine harmonics, although the finer details at the leaf margin are not described. To describe such details, several additional harmonics are required (MCEL-LAN and ENDLER, 1998), but these higher order harmonics are more susceptible to random environmental noise, e.g. insect nibbling or damage due to handling during leaf collection and scoring. We performed additional MANOVAs for each of the remaining harmonics (10–20) but observed no treatment effects and only, for a few of the harmonics, a random pattern of weakly significant population or family effects (data not shown).

The overall size (Moment 1) of the *U. laevis* leaves was larger in the well-watered than in the drought stress treatment. BRADFORD and HSIAO (1982) suggest that “Expansive growth can be viewed as an integrator of the environmental and metabolic events that influence overall plant productivity”. Low leaf area can contribute to reduction of leaf water vapour conductance and is therefore likely to be an adaptive advantage under drought stress conditions (LEIVA and FERNÁNDEZ-ALÉS, 1998). The size of a leaf also determines the active photosynthetic surface area and thus contributes to individual fitness. For leaf roundness, leaf lanceolateness and the Fourier coefficients, the adaptive significance is less clear. We included these statistics to provide more detailed information on the two-dimensional leaf shape, and how it was affected by differences in water availability, than we could obtain if we had used ordinary measures of the leaf surface area. Moreover, complementing our data on adaptive traits by using moment invariants and Fourier coefficients allowed us to discriminate between populations and families of *U. laevis* and to partition the variance in leaf morphology into environmental and genetic components.

The expression of genetic variation within the water regimes

Populations, and particularly families, revealed high variation in growth traits and in leaf shape components within both of the treatments. There were no clear effects of the water environments on the expression of genetic variation, which may be partly explained by the lack of a treatment effect on the trait mean values. In a growth chamber study of seedlings of *Betula pendula* and *Acer platanoides*, BLACK-SAMUELSSON and ERIKSSON

(2002) reported significant effects of a limited compared to a free access nutrient regime, while amounts of growth and fecundity variation were similar within treatments, except for one of the birch populations which was more genetically variable in the free access nutrient treatment. PLIURA and ERIKSSON (2002) cultivated *Castanea sativa* seedlings in a factorial temperature x watering experiment in growth chambers and found that CV_A s for growth in general were large across treatments, while CV_A values within the water treatments did not differ. Comparing additive variances for growth traits at the same temperature but in different water environments (drought versus well-watered), family heritabilities (h^2) were higher for drought stressed seedlings at 25°C, but generally lower in the drought regime at 32°C (PLIURA and ERIKSSON, 2002). In another factorial temperature x water study, growth trait h^2 s in *Pinus sylvestris* seedlings were slightly higher in the drought stress treatment at 18°C, while h^2 s were higher at 25°C within the well watered treatment (SONESSON and ERIKSSON, 2000). In a similar experiment with *Picea abies* seedlings, h^2 s for biomass traits were generally higher within the well watered treatment irrespective of temperature (18°C/25°C) (SONESSON et al., 2002). These studies and others (reviewed in HOFFMANN and MERILÄ, 1999) suggest that there is no straightforward relationship between levels of genetic variation and abiotic stress for the traits in question, and that different combinations of environmental parameters may affect the magnitude of genetic variation expressed.

The response to drought stress in growth and leaf shape

The watering regimes had little effect on growth and leaf morphology in *U. laevis*, perhaps as a result of the experimental design and/or genetic factors. From a technical standpoint the 40% water availability, combined with the other cultivation conditions used, may have imposed too weak a level of stress to bring about observable growth differences. However, in our pilot study, water levels below 40% of the original watered weight caused the *U. laevis* seedlings to wither rapidly, and once a plant had started withering, it ceased growing or died (data not shown). BRADFORD and HSIAO (1982) recognized that a general drought stress response among plants involves a physiological adaptation in growth and productivity until a certain “breaking point” where the stress becomes so severe that the plants die. In order to not impose mortality on our *U. laevis* seedlings, we chose a drought stress level just above the 40% threshold. We also carefully weighed the mineral wool in each pot to ensure identical amounts of substrate were available to absorb and retain the water. Then, when the first signs of withering within the drought stress environment became evident, we watered all plants.

From a genetic point of view, the similar treatment mean values for most traits imply homeostatic (stable) phenotypes, which in turn suggest that these *U. laevis* seedlings have a very good buffering capacity against varying water levels, provided that water availability is above the “wilting threshold”. PIGLIUCCI (2001) classified species as generalist or specialist according to their ecotype and the amount of phenotypic plasticity they displayed. According to this classification, the un-plastic reaction norms we obtained for *U. laevis* are characteristic of a generalist species, displaying a sub-optimal phenotype across a large range of environments. For such a generalist, survival depends not only on selection, but also on random drift and migration, especially in fragmented populations (DEN BOER, 1999).

Lack of phenotypic plasticity need not always be maladaptive. SULTAN (1987) described plasticity to be adaptive when it enhances relative fitness and plant vigour across environ-

ments, whereas a plastic response involving a deterioration with respect to individual fitness, would be considered as non-adaptive. Thus, the apparent growth and vitality in the *U. laevis* populations and families within two such different water regimes as were used in the present study, are evidence of a degree of genetic adaptation through phenotypic stability. A possible explanation in the case of the French and German trees is that the source populations are located on soils which are often waterlogged but which are also characterized by dramatic seasonal and year-to-year fluctuations in water level (personal observation).

As drought stress response is likely to vary between traits, it is probable that the phenotypic plasticity of other physiological traits, e.g. absolute water tissue content, leaf turgor pressure or osmotic potential, may have differed from the responses in growth traits, budset and leaf shape components we observed. Effects of low water availability in plants include limited cellular expansion and growth and also restricted xylem vessel expansion (see references in SOLLA and GIL, 2002). These authors observed increased wilting and the development of larger xylem vessel diameters in *Ulmus minor* clones subjected to heavy initial watering followed by light watering, than in those plants that were initially cultivated in light watering followed by heavy watering. They also found that larger vessel formation prior to inoculation with spores of *Ophiostoma novo-ulmi*, increased observed symptoms of Dutch elm disease (SOLLA and GIL, 2002).

Concluding remarks

We have used two sets of quantitative characters: adaptive traits related to growth and phenology, and leaf morphology as described by moment invariants and elliptic Fourier coefficients, to discriminate between populations and families of *U. laevis*. We cultivated the seedlings in a growth chamber under a well watered and a drought stress treatment in order to reduce environmental noise and to enable us to study the variation in genetic response to a specific and important environmental parameter. Using this experimental design, the validity of our results for the species growing in natural conditions should be interpreted with caution. However, the strongly significant population and family differentiation across and within treatments for a majority of the traits suggests that there is substantial additive genetic variation within these populations of *U. laevis*. This could serve as the genetic basis for adaptation to pronounced future changes in water availability for conservation and breeding purposes. The low phenotypic plasticity further suggests that the populations and families possess a remarkable degree of stability with respect to water availability. We found no consistent relationship between the expression of genetic variation and water availability, which reflects previous ambiguous results from similar growth chamber studies on temperate tree seedlings cultivated under stressful and favourable conditions. Our study is part of a larger investigation of genetic variation as assessed by microsatellite markers (WHITELEY et al., 2003b) and in a field trial in *U. laevis* (WHITELEY et al., 2003a). We believe that the combined results will be useful both in understanding various aspects of genetic variation in *U. laevis* and in planning appropriate conservation genetic strategies for the Swedish marginal population of this vulnerable species.

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Buchbesprechungen

Waldgesellschaften in Bayern. Vegetationskundliche und forstgeschichtliche Darstellung der natürlichen und naturnahen Waldgesellschaften. Von R. SAUTTER. 2003. Ecomed Verlagsgesellschaft, Landsberg. ISBN 3-609-55008-2. 224 Seiten mit 128 Abbildungen. 34,00 EUR (D).

Die Vielzahl der bayerischen Naturräume findet ihr Spiegelbild in der Vielzahl der Waldtypen, die von den Schnee-Heide-Wäldern der Alpen über Silber-Weiden-Auwälder bis hin zu den wärmeliebenden Fingerkraut-Eichenwäldern Unterfrankens nahezu das gesamte Spektrum der in Süddeutschland vorkommenden Waldgesellschaften abdeckt. Nach RUBNERS Übersicht „Die Waldgesellschaften in Bayern“ (1949) und SEIBERTS Erläuterungen zur „Übersichtskarte der natürlichen Vegetationsgebiete von Bayern“ (1968) ist mit dem vorliegenden Band eine aktuelle zusammenfassende Darstellung der in Bayern nachgewiesenen Waldgesellschaften erschienen.

Der Verfasser führt den Leser in die Fachbegriffe der pflanzensoziologischen Gesellschaftsdynamik und in die systematische Übersicht der Vegetationseinheiten ein, bevor ausführliche Beschreibungen die Waldgesellschaften charakterisieren. Nach der deutschen Bezeichnung der Waldgesellschaft werden die zur Zeit allgemein akzeptierten wissenschaftlichen Assoziations-Benennungen und gebräuchliche Gesellschaftssynonyme aufgelistet. Die umfassenden Beschreibungen der Waldtypen behandeln jeweils Aspekte der Verbreitung, Synsystematik, Standortsökologie, Nutzungsgeschichte und Gefährdung. Dabei wird der vegetationskundliche Teil wiederholt durch lebendige Schilderungen zur wechselnden Forstgeschichte ergänzt. Gute Farbfotos geben typische Aspekte der Waldtypen und ausgewählte charakteristische Arten wieder. Die Beschreibung einer Waldgesellschaft schließt mit einer Literaturliste, in ihr sind auch Quellen aufgeführt, die im Text nicht zitiert wurden, aber weiterführende Informationen zu der jeweiligen Waldgesellschaft enthalten. Vermissen tut der in Bayern nicht heimischen Leser lediglich die ein oder andere Karte, in der die Hauptverbreitung einzelner Waldgesellschaften dargestellt sind. Ein umfangreiches Literaturverzeichnis, das zahlreiche neu erschienene Arbeiten der letzten Jahre beinhaltet und das die verstreute geobotanisch-forstliche Literatur erschließt, und ein Stichwortverzeichnis runden das Buch ab.

Für Fachleute und naturkundlich Interessierte auch außerhalb Bayerns werden umfassende Informationen zu den Waldgesellschaften und Waldlandschaften von der Rhön bis zu den Alpen geliefert. Damit ergänzt der vorliegende Band das vom Bayerischen Forstverein herausgegebene Buch „Bäume und Wälder in Bayern“ (2. Aufl. 1997 ebenfalls bei der Ecomed Verlagsgesellschaft erschienen), welches in erster Linie Wissens-

wertes zu Nutzung, Vermehrung und waldbauliche Verwendung der heimischen Baumarten mit einem geschichtlichen und regionalen Überblick vermittelt.

Title: „Forest communities in Bavaria. A description of phytosociology and forest history of the natural and semi-natural forest communities“.

M. LIESEBACH (Waldsiefersdorf)

Die Freiland-Schmuckstauden: Handbuch und Lexikon der Gartenstauden (in 2 Bänden). Begr. von L. JELITTO und W. SCHACHT. Neu hrsg. von H. SIMON. 2002. Verlag E. Ulmer, Stuttgart. ISBN 3-8001-3265-6. 976 Seiten mit 1023 Farabbildungen. Gebunden im Schuber. 199,00 EUR (D).

Das Handbuch und Lexikon der Gartenstauden liegt mittlerweile in fünfter und völlig neu bearbeiteter Auflage vor. Der Herausgeber der Neuauflage ist kein geringerer als Dr. HANS SIMON, Träger der höchsten Auszeichnung für Staudenexperten – des „Karl-Foerster-Ringes“ – und Seniorchef einer Sortiments- und Versuchsgärtnerei. Neben ihm waren an der Neuauflage weitere 32 Experten aus Deutschland, Österreich und der Schweiz beteiligt.

Das zweibändige Werk beschreibt etwa 1100 Staudengattungen mit ihren kultivierten Arten und Sorten. Der 1. Band enthält die Beschreibung der Stauden von A bis H, der 2. Band die von I bis Z sowie verschiedenen Verzeichnisse. Die Beschreibungen enthalten Angaben über Herkunft und Vorkommen der Pflanzen, die wichtigsten morphologischen Merkmale, Hinweise zu Verwendung und geeigneten Nachbarpflanzen sowie gesicherte Informationen über Vermehrung und Kultur. Im Anschluss an die Beschreibung einer Familie ist häufig ein Hinweis auf weiterführende Literatur aufgenommen. Neben Prachtstauden, altbewährten Sorten, Neuzüchtungen und neu eingebürgerten Arten werden auch Wildstauden für den naturnahen Garten sowie ingenieurbologisch relevante Arten und Raritäten vorgestellt. Außerdem sind zahlreiche Zwiebelpflanzen, Knollengewächse und Nutzpflanzen enthalten. Das Werk dokumentiert die seit Jahren innerhalb bestimmter Gattungen bzw. Gruppierungen von Arten geleistete Züchtungsarbeit. Diese stellt eine wichtige Grundlage für den sicheren Erhalt wertvoller, alter Sorten dar. Zu ergänzen wäre lediglich das Jahr der Einführung bzw. Züchtung bei den Kultivaren, welches Rückschlüsse auf bewährte alte bzw. neueingebürgerte Taxa gäbe. Diese Angabe findet der Leser leider nur selten. Bei der Benennung der Stauden wurden neue Erkenntnisse inner-