Height Growth and its Relation to the Branching Habits of Wych Elm (*Ulmus glabra* Hudson) in Lithuania

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Abstract

It is well known that since trees grow additively, existing morphological traits may constrain future morphology and growth. Therefore, the branching habits of Wych elm (*Ulmus glabra* Hudson) have been investigated to establish a predictive model for height growth of trees. Open pollinated progeny from 6 Lithuanian populations were evaluated at seven years of age in a field trial in central Lithuania. To predict the presence of growth intensity based on values of a set of branching parameters (including basal bud number, branching trend, stem form, and natural pruning) the predictions were accomplished at the species level by applying the binary logistic regression procedure. In conclusion, selection for the greater height of Wych elm trees also means selection for the basal bud presence, amphitony, stem dominance, and perfect stem pruning.

Key words: Ulmus glabra, Wych elm, branching habits, height growth, growth intensity

Introduction

Mature ash stands are remarkable for the largest growing stock volume of Wych elm (*Ulmus glabra* Hudson = *U. montana* With.) in Lithuania (Kuliešis and Kulbokas 2009). In general, the Wych elm is a minor tree species in Lithuania, but against a background of ash decline it is important to provide some guidance for the improved initial selection of trees.

This paper reports the effect of the branching structure on height growth of Wych elm. Height growth has commonly been used as the primary trait for the selection in forest tree breeding. Less attention has been given to the relationships between the height growth and branching pattern. This study is an attempt to quantify various branching patterns. The term "branching pattern" will refer here to the branching and natural pruning occurring as the result of ontogenetic (size-related) variations in the structural traits of tree axes.

Farnsworth and Niklas (1995) point out that since plants grow additively existing morphological traits tend to constrain future morphology and growth. The hypothesis of this paper is that growth intensity is related to particular architectural phenomena (see Barthélémy and Caraglio 2007), as adaptation to the environment seems to hinge on interactions between individual modules or iterated units, such internodes,

or groupings of these components, such as shoots and branches (Hallé 1986, Oborny 2004). In analyzes of phenotypic variation in plants genetically programmed ontogenetic changes in form and function (e.g. metamorphosis) can be similar in pattern to environmentally induced changes (plasticity), yet the metamorphosis is subject to plasticity (Diggle 2002).

Importantly, variation in phenetic parameters of different taxa is not continuous and character states (variants of characters) are not combined randomly. Wych elm is sometimes divided into subspecies (Uotila 1997, Myking and Yakovlev 2006). Ssp. glabra (in the south of the species' range) has leaves that are relatively broad, short tapering, with acute lobes present, trees often have a short, forked trunk and a low, broad crown. Ssp. montana (Stokes) Lindqvist. (in the north of the species' range – northern Britain, Scandinavia) has leaves that are relatively long, long tapering, without acute lobes, the upper surface of which are strigose (Sherman-Broyles 2007), trees commonly have a long single trunk and a tall, narrow crown. The subspecies are not accepted by Flora Europaea (Tutin et al. 1968), as there is much overlap between populations in these characters and the distinction may be owing to environmental influence, rather than genetic variation. However, the origin of species differences, and of novel phenotypes in general, involves the developmental recombination followed by the genetic

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accommodation of change (West-Eberhard 2005), therefore character states of the Wych elm are to be investigated and described to advance current understanding of speciation processes.

In the above context, it was important to identify whether growth intensity was associated with branching habits in Wych elm. So, branching architecture traits (e.g. branching trend, stem form, natural pruning, and basal buds) of trees were examined in accordance with the ontogenetic, size-related effects (Chambel et al. 2005) of height and diameter growth, to develop a predictive tool for the growth and form of Wych elm trees.

Materials and methods

Study site and plant material

The Wych elm half-sibs from the 6 natural regions of Lithuanian forests grown in central Lithuania were evaluated at seven years of age in the field trial of *Ulmus* spp., latitude 54°51'N, longitude 24°03'E. In general, the location of field trial, formerly a mixed forest site on normally moist fertile soil, is flat, with some northerly aspect. Mother-tree-sites of half-sibs – originally forest land – represent the major soil types in which Wych elm is typically planted in Lithuanian forests (Table 1). The selection of seed trees for this trial was based on provenance concept of geographic representation of tree populations, the available information on autochthonous origin, and some adaptive traits including disease resistance.

Table 1. Composition of Wych elm progeny and soil fertility categories of mother-tree-sites of Dubrava field trial $(n - \text{number of measured individuals, } n_e - \text{number of families})$

Population	Latitude	Longitude	n	n_f	Soil typological group
Kaišiadorys	54°50'	24°12'	17	8	Normally moist fertile
Utena	55°09'	25°28'	32	11	Normally moist or temporarily wet very fertile
Trakai	54°41'	24°48'	31	13	Temporarily wet very fertile
Kėdainiai	55°14'	23°43'	16	6	Permanently wet particularly fertile
Jonava	55°13'	24°23'	40	14	Normally moist particularly fertile
Telšiai	56°02'	22°25'	41	14	Temporarily wet particularly fertile

The trial was established in 2002 by the Lithuanian Forest Research Institute at the nursery of Dubrava experimental and training forest enterprise in randomized design with two to four single-tree plots of each family. In total about 224 trees were planted. The spacing between trees was 2.1 by 2.1 m. Each row was surrounded by a single buffer row with the same spacing. Information on identity and origin of families is presented in Table 1 (from Abraitis 2000).

Trait evaluation and variables

Wych elm traits were evaluated at seven years; the number of individuals was 171. All the evaluated

tree characteristics were transformed to dichotomous variables. As no information were available *a priori* on the biophysical attributes of the parents, the total sample of the half-sib progenies from 6 Lithuanian populations in terms of those attributes can be considered as random.

Height and diameter increment of the tree stems were measured on standing trees at the height of the stem (= tree axis of order 1) and the diameter of the stem (over bark; crosswise calliper measurement at root neck at the end of vegetation period); stem size, i.e. height size and diameter size: 0- less than mean – 53.2% and 51.5% of the individuals, respectively, 1-greater than mean – 46.8% and 48.5% of individuals, respectively.

Stem form and forking was evaluated as the dominance of stem axis whereby the main central stem of the plant is dominant over (i.e. grows more strongly than) other side stems (Figure 1). Ultimate shapes of the strongest parent axes from order one to the ultimate orders for Wych elm were as follows (Petrokas 2008a): 1- multi-dominant axes: the union of several stems/branches at the root neck/branch base – 4.1%, 2- co-dominant axes: at the basal zone of stem/branch - the diameter of any side axis is about half the diam-



Figure 1. Multi-dominant (1), co-dominant (2), decurrent (3), apparent (4), and excurrent (5) stem axes of Wych elm at age seven

eter of the base of union – 11.7%, 3- decurrent axis: the axis is bifurcated or trifurcated; lower offshoot of supposed axis is prevailing – 45%, 4- apparent axis: some offshoot of supposed axis is prevailing at the furcations – 32.7%, 5- excurrent axis: there are no furcations of axis – rectilinear axis is prevailing at full height/length – 6.4% of valid cases; stem form: 0- no stem dominance $(1^{st}+2^{nd}+3^{rd})$, 1- dominant stem $(4^{th}+5^{th})$; stem character: 0- minor categories of stem form $(1^{st}+2^{nd}+4^{th}+5^{th})$, 1- prevailing category of stem form, i.e. 3^{rd} .

The privileged repartition of sibling shoots (Troll 1937) on the upper, lateral or basal position of a slanted or horizontal parent shoot is referred to, respectively,

as epitony, amphitony or hypotony. The privileged repartition of sibling axes from order 2 to the ultimate orders or branching trend was defined as the (1) amphitony (Figure 2) – 29.8% or (0) amphitony-epitony – 70.2% of individuals. Amphitony-hypotony is not found yet.

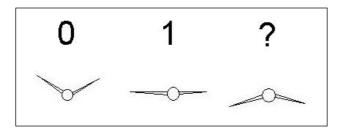


Figure 2. Amphitony-epitony (0), amphitony (1), and amphitony-hypotony (not found yet) seen in the cross-sections of Wych elm branchlets

Natural pruning of stem axis was evaluated as the timing and intensity of knot occlusion (Petrokas 2008a) at the crown base of stem (= order 1 parent axis): 1-limb failure (stubs) – 66.7%, 2- decomposed limb knotholes – 18.1%, 3- branch occlusion (knots) – 15.2%, 4- branch shedding (scars) – 0% of the individuals; stem pruning: 0- prevailing category, i.e. 1^{st} , 1- minor categories ($2^{nd}+3^{rd}$).

Bud burst progress was defined between annual shoots of strongest axes of sequencing orders (Petrokas 2008b): 1- leaf buds are swollen, the apex of the buds is brownish – 0%, 2- buds are still closed, the apex of the buds is pea-green – 15.2%, 3- buds start opening and extremities of the first leaves are visible at the apex of the buds – 28.7%, 4- extremities of some leaves are out but laminas are cuddled together – 31%, 5- laminas are separate, but not yet spread – 18.7%, 6- laminas are spreading – 5.8%, 7- first leaves are fully extended – 0.6% of the individuals; bud burst character: 0- minor stages (2nd+3rd+5th+6th+7th), 1- prevailing stage, i.e. 4th.

Basal bud presence (Petrokas 2008a) was evaluated as the number of small dormant buds (at the end of vegetation period) without a subtending leaf at the base of sterile annual shoots of order 1 or 2 strongest axes: 0- no basal bud – 52.6%, 1- basal bud present – 47.4% of the individuals.

Data analyses

The prediction of the presence or absence of growth intensity characteristics based on values of a set of branching variables were accomplished by applying binary logistic regression procedure of SPSS (Statistical Package for the Social Sciences) 16.0 for Windows®. The goal of logistic regression (Garson 2008) is to find the best fitting (yet biologically rea-

sonable) model to describe the relationship between the binary or dichotomous characteristic of interest (dependent variable = outcome variable containing data coded as 1 or 0) and a set of independent (predictor or explanatory) variables. Logistic regression predicts the logit of the dependent event. The "event" is a particular value of y, the dependent variable. By default the event is y = 1 for binary dependents coded 0,1, and the reference category is 0. Logistic regression generates the coefficients and its standard errors and significance levels of a formula to predict a logit transformation of the probability of presence of the dependent variable:

logit(p) = ln(odds(event)) = $b_0 + b_1 X_1 + b_2 X_2 + b_3 X_3 + ... + b_k X_k$

where p is the probability of the event occurring, b₀ is a constant, k is the number of predictors X, i=1,2,...,k. The regression coefficients are the coefficients b_0 , b_1 , b_2 , ... b_k of the regression equation. An independent variable with a regression coefficient not significantly different from 0 (p>0.05) can be removed from the regression model; if p<0.05 then the variable contributes significantly to the prediction of the outcome. The logistic regression coefficients showed the change (increase when b_i>0, decrease when b_i<0) in the predicted logged odds of having the characteristic of interest for a one-unit change in the independent variables. Each regression coefficient was evaluated using a Wald test. The ratio of the coefficient to its standard error squared, equals the Wald statistic. The Wald chi-square statistic tests the unique contribution of each predictor in the context of the other predictors – that is, holding constant the other predictors - that is, eliminating any overlap between predictors. If the significance level of the Wald statistic is small (less than significance level $\alpha = 0.05$) then the parameter is useful to the model.

The logit transformation was defined as the natural log of the probability of the event occurring divided by the probability of the event not occurring. By taking the exponential of both sides of the regression equation as given above, the equation is as follows:

odds(event) =
$$e^{b_0} \times e^{b_1X_1} \times e^{b_2X_2} \times e^{b_3X_3} \times ... \times e^{b_kX_k}$$

It is clear that when variable X_i increases by 1 unit, with all other factors remaining unchanged, then

the odds will increase by factor e^{b_i} . This factor e^{b_i} is the odds ratio of the row independent X_i (the predictor) with the dependent and it is the predicted change in odds for a unit increase in the corresponding independent variable. The odds ratio (Exp(b)) is the fac-

tor by which the independent increases or (if negative) decreases the log odds of the dependent. When b=0, Exp(b)=1, so therefore an odds ratio of 1 corresponds to an explanatory variable which does not affect the dependent variable.

Estimation in logistic regression chooses parameters that maximize the likelihood of observing the sample values. The *null model* -2 log-likelihood is given by $-2 * ln(L_0)$ where L_0 is the likelihood of obtaining the observations if the independent variables had no effect on the outcome. The full model -2 loglikelihood is given by -2 * ln(L) where L is the likelihood of obtaining the observations with all independent variables incorporated in the model. The difference of these two yields a chi-square statistic (χ^2) which is a measure of how well the independent variables affect the outcome or dependent variable. If the p-value for the overall model fit statistic was less than the conventional 0.05 then there was evidence that at least one of the independent variables contributed to the prediction of the outcome. Cox and Snell's R-square (Cox and Snell 1989) is based on the log-likelihood for the model compared to the log-likelihood for a baseline model and it takes the sample size into account. With categorical outcomes, it has a theoretical maximum value of less than 1, even for a "perfect" model, however the greater the value, the greater the improvement of the full model over the intercept model. Nagelkerke's R-square (Nagelkerke 1991) is an adjusted version of the Cox and Snell R-square that adjusts the scale of the statistic to cover the full range from 0 to 1. The Hosmer and Lemeshow goodness-of-fit test (Hosmer and Lemeshow 2000) tests the null hypothesis that there is a linear relationship between the predictor variables and the log odds of the criterion variable. The Hosmer-Lemeshow goodness-of-fit statistic (χ^2_{HI}) helps to determine whether the final model adequately describes the data.

The classification table was used to evaluate the predictive accuracy of the logistic regression model. To use the results of logistic regression to classify subjects, my decision rule took the following form: if the probability of the event is greater than or equal to some threshold (by default, it is set at 0.5), I shall predict that the event will take place. In the classification table the observed values for the dependent outcome and the predicted values were cross-classified. In a perfect model, all cases are on the diagonal and the overall percent correct is 100%.

Tests of independence and measures of association and agreement for the data were accomplished by applying crosstab procedure (SPSS 16.0 for Windows®). Gamma, a symmetric measure of association, was used to summarize the strength of the relationship between

two variables. As gamma approaches either -1 or +1, the relationship becomes increasingly stronger and more significant. Gamma does not make an adjustment for either ties or table size so it was related to other correlation coefficients, e.g. Kendall's tau-b and Somers' d. All of these correlations are based on identifying concordant, discordant, and tied pairs of observations. Gamma (γ) is the surplus of concordant pairs (P) over discordant pairs (Q), as a percentage of all pairs ignoring ties. It is computed as (P - Q)/(P + Q). Kendall's tau-b takes ties into account. It is computed as the excess of concordant over discordant pairs (P - Q), divided by a term representing the geometric mean between the number of pairs not tied on $x(X_0)$ and the number not tied on y (Y_0) : tau-b = $(P - Q)/\sqrt{[((P - Q)/\sqrt{(P - Q)/(P - Q)})]}$ $+ Q + Y_0(P + Q + X_0)$]. Tau b is the most appropriate with square tables in which the number of rows and the number of columns are equal. Somers' d is gamma modified to penalize for pairs tied only on x and only on y. Somers' d, $d_{yy} = (P - Q)/(P + Q + Y_0)$ for the hypotheses in which x causes or predicts y. For the directional (asymmetric) hypotheses in which y causes or predicts x, the formula is: $d_{xy} = (P - Q)/(P + Q + Q)$ X_0). Y_0 is pairs tied on Y, and X_0 is pairs tied on X. Kendall's tau-b and Somers' d ranges from -1 to +1. Rules of thumb for determining the strength of association between variables (Table 2): (1) a correlation coefficient's size indicates the strength of association between two variables, (2) the sign (+ or -) indicates the direction of the association.

Table 2. Coefficient range of Kendall's tau b, gamma, and Somers'd for determining the strength of association between variables

Coefficient range	Strength of association*
±0.81 to ±1.00	Strong
±0.61 to ±0.80	Moderate
±0.41 to ±0.60	Weak
±0.21 to ±0.40	Very weak
±0.00 to ±0.20	None

^{*}Assuming the correlation coefficient is statistically significant

Results

The combined tests for the prediction model of stem height size by basal buds, branching trend, stem form, and stem pruning showed that the effect of each predictor in Wych elm progeny at age seven contributes to the binary logistic regression model, as the significance of model coefficients (final step, block, or model chi-square of 34.453 on 4 df) is very small – p = 0.000 (less than i = 0.05). Binary logistic regression model summary: -2 Log likelihood = 201.895, Cox and Snell's R-square = 0.182, Nagelkerke's R-square =

0.244. The nonsignificant chi-square of Hosmer-Lemeshow goodness-of-fit test (= 4.298, p = 0.745) was computed from the chi-square distribution with 7 degrees of freedom and indicated that the data fit the model well.

The classification table (Table 3) shows the practical results of using the logistic regression model, which assumes that height size (less than the mean or greater than the mean – see descriptive statistics of stem height in Table 4) is linearly related to the structural predictors: basal buds, branching trend, stem form, and stem pruning. By default, the classification table shows that decision rule allows us to correctly classify 44 / 80 = 55% of the subjects where the predicted event – height size, greater than the mean, - was observed. This is known as the sensitivity of prediction, that is, the percentage of occurrences correctly predicted. We also see that decision rule allows us to correctly classify 70 / 91 = 77% of the subjects where the predicted event was not observed. This is known as the specificity of prediction, that is, the percentage of nonoccurrences correctly predicted. Overall our predictions were correct 114 out of 171 times, for an overall success rate of 67%. This suggests that overall, the model is in fact correct about two out of three times.

Table 3. Relating height size to the predictors – basal buds, branching trend, stem form, and stem pruning – in Wych elm at age seven: the classification

Observed		Predicted					
		Heiç	Percentage				
		less than	greater than	correct			
		mean	mean				
Height size	less than mean	70	21	76.9			
Height Size	greater than mean	36	44	55.0			
Overall percentage				66.7			

Table 4. Descriptive statistics of stem diameter and height in Wych elm at age seven. S.E.=standard error

Variable	Min.	Max.	Mean± S.E.	Std. Deviation	Variance
Stem diameter (cm)	2.0	15.0	7.5±0.2	2.3	5.3
Stem height (cm)	140.0	740.0	387.0±8.4	110.1	1.2

The parameter estimates table summarizes the effect of each predictor (Table 5). Significance levels (p) of the Wald statistic were small (less than 0.05) then all the parameters were useful to the final model. All the predictors with positive regression coefficients – basal buds, branching trend, stem form, and stem pruning – show the increase in the likelihood of event category of height size (greater than the mean) with respect to the reference category (less than the mean).

Table 5. The effect of each predictor of height size in Wych elm at age seven shown in the final step of binary logistic regression procedure: variables in the equation. B=regression coefficient, S.E.=standard error of regression coefficient, p=significance level of Wald chi-square, Exp(B)=odds ratio for the predictor, CI=confidence interval

Predictor (cause category)	В	S.E.	Wald chi-square	р	Exp(B)	95.0% CI for Exp(B)
Basal buds (1= present)	1.03	0.35	8.79	0.003	2.81	[1.42-5.56]
Branching trend (1= amphitony)	1.13	0.41	7.66	0.006	3.08	[1.39-6.84]
Stem form (1= dominant stem)	0.84	0.35	5.69	0.017	2.33	[1.16-4.65]
Stem pruning (1= knotholes or knots)	1.47	0.38	15.05	0.000	4.36	[2.07-9.18]
Constant	-2.25	0.49	20.77	0.000	0.11	

For every unit increase in basal buds, a 1.03 unit increase in height size score is predicted, holding all other variables constant. Since basal buds are coded 0/1 (the reference category is 0 = absent, the cause category is 1 = present) the interpretation is simple: for present basal buds, the predicted height size score would be 1.03 points higher than for absent. Wych elm trees with basal buds are about 3 times more likely to have greater height size than are trees with no basal buds as the odds ratio (Exp(B)) of this variable with the height size is 2.81; the 95% confidence interval for the odds ratio varies from 1.42 to 5.56. For every unit increase in branching trend, a 1.13 unit increase in height size score is predicted, holding all other variables constant. Since branching trend is coded 0/1 (the reference category is 0 = amphitony-epitony), for amphitony, the predicted height size score would be 1.13 points higher than for amphitony-epitony. The odds ratio of branching trend with the height size is 3.08. This means that in the model the odds for a positive relationship in case of amphitony are 3 times higher than in case of amphitony-epitony; the 95% confidence interval for the odds ratio varies from 1.39 to 6.84. The same reasoning applies to the rest of predictors, i.e. stem form and stem pruning (see Table 5). The effect of stem pruning is most remarkable in comparison to the rest of the effects. Since stem pruning is coded 0/1 (0 = stubs) the interpretation is the following: for knotholes or knots, the predicted height size score would be 1.47 points higher than for stubs. Trees with knotholes or knots are over 4 times more likely to have greater height size than are trees with stubs as in the model the odds for a positive relationship in case of minor categories, i.e. knotholes or knots, are over 4 times higher than in case of prevailing category, i.e. stubs.

For the rest of data tests of independence and measures of association and agreement were accomplished by applying the crosstab procedure. The statistically significant relationship between stem diameter size and stem pruning was assessed ($\chi^2 = 5.666$, df = 1, p = 0.017). In the crosstabulation output you will see that 38.6% of the "less than mean" category

and 28.1% of the "greater than mean" category of stem diameter size were prevailing category of stem pruning, i.e. stubs, "66.7% of total. The exact significance value of each measure of association is less than 0.03 (Table 6), therefore it can be concluded there is a statistically significant relationship between the ordinal variables of stem diameter size and stem pruning. The relationship is very weak. Gamma is 0.37, hence we may say that knowing the independent variable reduces our errors in predicting the rank (not value) of the dependent variable by 37%. The statistically significant relationship between bud burst character and stem character was assessed as well ($\chi^2 = 9.217$, df = 1, p = 0.002). 43.3% of the "minor stages" category and 19.3% of the "prevailing stage" category (4th - medium flushing) of bud burst character were different categories of stem character in total. The exact significance value of each measure of association is less than 0.004 (Table 7), therefore it can be concluded there is a statistically significant weak relationship between bud burst character and stem character. Gamma is 0.47, hence we may say that knowing the independent variable reduces our errors in predicting the rank of the dependent variable by 47%.

Table 6. The strength of the relationship between stem diameter size and stem pruning in Wych elm at age seven. S.E.=standard error, Sig.=significance

Measures of association	Value	Asymp. S.E. ^a	Approx. T ^b	Approx. Sig.	Exact Sig.
Symmetric					
Kendall's tau-b	0.18	0.08	2.41	0.016	0.023
Gamma	0.37	0.14	2.41	0.016	0.023
Directional - Somers' d					
Symmetric	0.18	0.08	2.41	0.016	0.023
Stem diameter size Dependent	0.19	0.08	2.41	0.016	0.023
Stem pruning Dependent	0.17	0.07	2.41	0.016	0.023

^a Not assuming the null hypothesis

Table 7. The strength of the relationship between bud burst character and stem character in Wych elm at age seven. S.E.=standard error, Sig.=significance

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Measures of association	Value	Asymp. S.E. ^a	Approx. T ^b	Approx. Sig.	Exact Sig.
Symmetric					
Kendall's tau-b	0.23	0.08	3.06	0.002	0.003
Gamma	0.47	0.13	3.06	0.002	0.005
Directional - Somers' d					
Symmetric	0.23	0.08	3.06	0.002	0.003
Bud burst character Dependent	0.22	0.07	3.06	0.002	0.003
Stem character Dependent	0.25	0.08	3.06	0.002	0.003

^a Not assuming the null hypothesis

Discussion and conclusions

The rules of forest tree breeding and tree selection during growth are based on phenotype and growth characteristics of every particular tree. The presented work justifies some characteristics as predictors of growth rate and valuable stem form of the young (seven year old) elm trees, using logistic regression as statistical verification of dependences. The study presents a new approach of this topic.

The practical results of using the binary logistic regression model, which assumes that height of Wych elm trees, greater than the mean, is related to the structural predictors (phenotypic markers for early determination of height?) are the following: (1) the odds for a positive relationship in case of basal bud presence are about 3 times higher than in case of no basal buds, (2) the odds for a positive relationship in case of amphitony are 3 times higher than in case of amphitony-epitony, (3) the odds for a positive relationship in case of dominant stem are over 2 times higher than in case of no stem dominance, (4) the odds for a positive relationship in case of minor categories of stem pruning, i.e. knotholes or knots, are over 4 times higher than in case of prevailing category, i.e. stubs. In conclusion, selection for the greater height of Wych elm trees also means selection for the basal bud presence, amphitony, stem dominance, and perfect stem pruning.

In Wych elm terminal growth succeeds topologically from a lateral branching as a result of apical mortality (Troll 1937, Hallé et al. 1978, Barthélémy et al. 1989, 1991, Barthélémy and Caraglio 2007), therefore scaffold (primary) branches may become the main structural system of a tree - growing away from the stem, they receive more light than would a bundle of branches lying close to the stem and pointing upwards (Mattheck 1998). This is why Wych elm trees with present basal buds are about 3 times more likely to have greater height than are trees with no basal buds in contrast to Harmer (1989), Buck-Sorlin and Bell (2000), who regarded lower number of basal buds as fairly good measure for shoot vigor in Quercus petraea and Quercus robur. The effect of stem form on height of Wych elm trees is originating from the same axis orders in different tree parts and thus may be considered as an effect of meristem differentiation, while the effect of stem pruning may be considered as a local position (architectural, sensu Diggle 1995) effect originating from different branching orders in the same section of a crown (see Klaehn 1963, Barthélémy and Caraglio 2007). Branching order is composed of all categories of successive units (Figure 3) presenting the same differentiation of a meristem (Klaehn 1963, Barthélémy et al. 1997). When succes-

^b Using the asymptotic standard error assuming the null hypothesis

^b Using the asymptotic standard error assuming the null hypothesis

sive units, even though not strictly edified by a single meristem, are more or less in a rectilinear disposition, it can be considered that the general spatial direction of such a succession constitutes an axis. Amphitony is a frequent feature in rectilinear branches whereas epitony and hypotony are characterized by the predominant development of lateral axes on the convex side of the curved, downwardly or upwardly orientated branches (Caraglio and Barthélémy 1997). The term "amphitony-hypotony" (see Figure 2) is here a reference to the probability that some types of Wych elm may have very pendulous twigs, a factor which could make them unattractive to foraging beetles – vectors of the Dutch elm disease (see Webber 2008).

Finally, using crosstabs' ordinal-by-ordinal measures, it was found a statistically significant weak and positive association between the stem diameter and stem pruning, and similarly between bud burst and stem form. The positive association between bud burst and stem form may indicate that spring phenology is related to life history in Wych elm.

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References

- Abraitis, R. 2000. Growth behaviour of elm (*Ulmaceae*) tree species in Lithuania. In: S. Mizaras and O. Belova (Compilers), Science and forestry on the eve of XXI century. Lithuanian Forest Research Institute. Kaunas, "Lututė", p. 23–26 (In Lithuanian with English abstract).
- Barthélémy, D. and Caraglio, Y. 2007. Plant Architecture: A Dynamic, Multilevel and Comprehensive Approach to Plant Form, Structure and Ontogeny. *Annals of Botany* 99: 375-407.
- Barthélémy, D., Edelin, C., and Hallé, F. 1989. Architectural concepts for tropical trees. In: L.B. Holm-Nielsen and H. Balslev (Editors), Tropical forests: botanical dynamics, speciation and diversity. London, Academic Press, p. 89-100.
- Barthélémy, D., Edelin, C., and Hallé, F. 1991. Canopy architecture. In: A.S. Raghavendra (Editor), Physiology of trees. London, J. Wiley & Sons, p. 1–20.

- **Buck-Sorlin, G.H. and Bell, A.D.** 2000. Models of crown architecture in *Quercus petraea* and *Q. robur*: shoot lengths and bud numbers. *Forestry* 73(1): 1-19.
- Caraglio, Y. and Barthélémy, D. 1997. Revue critique des termes relatifs a la croissance et a la ramification des tiges des végétaux vascularies. In: J. Bouchon, P. de Reffye, and D. Barthélémy (Editors), Modélisation et simulation de l'architecture des végétaux. INRA Editions, Paris, p. 11-87 (In French).
- Chambel, M.R., Climent, J., Alka, R., and Valladares, F. 2005. Phenotypic plasticity: a useful framework for understanding adaptation in forest species. Forest Systems 14(3): 334-344.
- Cox, D.R. and Snell, E.J. 1989. The Analysis of Binary Data, 2nd ed. London: Chapman and Hall.
- Diggle, P.K. 1995. Architectural effects and the interpretation of patterns of fruit and seed development. Annual Review of Ecology, Evolution, and Systematics 26: 531– 552.
- Diggle, P.K. 2002. A developmental morphologist's perspective on plasticity. Evolutionary Ecology 16: 267-283.
- Farnsworth, K.D. and Niklas, K.J. 1995. Theories of optimization, form and function in branching architecture in plants. Functional Ecology 9: 355"363.
- Garson, G.D. 2008. Logistic regression. Internet site: http://www2.chass.ncsu.edu/garson/PA765/logistic.htm [Cited 12 Nov. 2010].
- Hallé, F. 1986. Modular growth in seed plants. *Philosophical Transaction of the Royal Society B* 313: 77-88.
- Hallé, F., Oldeman, R.A.A., and Tomlinson, P.B. 1978.
 Tropical Trees and Forests: An Architectural Analysis. New York: Springer-Verlag, 441 pp.
- **Harmer, R.** 1989. Some aspects of bud activity and branch formation in young oak. *Annales des sciences forestičres* 46: 217-219.
- Hosmer, D.W. and Lemeshow, S. 2000. Applied Logistic Regression, 2nd ed. New York: John Wiley and Sons.
- Klaehn, F.U. 1963. The relationship of vegetative propagation to topophysis, cyclophysis and periphysis in forest trees. Proceedings of the 10th Northeastern Forest Tree Improvement Conference Durham, New Hampshire August 8-9, 1962. Durham, NH, USA, p. 42–50. Available at: http://www.rngr.net/publications/tree-improvement-proceedings/neftic/1962/the-relation-of-vegetative-porpagation-to-topophysis-cyclophysis-and-periphysis-in-forest-trees [Cited 1 Mar. 2011].
- Kuliešis, A. and Kulbokas, G. 2009. Lietuvos nacionalinė miškų inventorizacija 2004-2008. Miškų ištekliai ir jų kaita [Lithuanian national forest inventory 2004-2008. Forest resources and their dynamics]. Lietuvos miškų ūkio statistika 2009, II dalis. Aplinkos ministerija, Valstybinė miškotvarkos tarnyba. Kaunas: Lututė, 88 p. (In Lithuanian). Available at: http://www.lvmi.lt/vmt [Cited 28 Dec. 2010].
- Mattheck, C. 1998. Design in nature: learning from trees. Berlin, Heidelberg, New York, Springer-Verlag, 276 pp.
- Myking, T. and Yakovlev, I. 2006. Variation in leaf morphology and chloroplast DNA in *Ulmus glabra* in the northern suture zone: Effects of distinct glacial refugia. *Scandinavian Journal of Forest Research* 21(2): 99–107.
- Nagelkerke, N.J.D. 1991. A note on the general definition of the coefficient of determination. *Biometrika* 78(3): 691-692.
- **Oborny, B.** 2004. External and internal control in plant development. *Complexity* 9(3): 22–28. Available at: http://www.santafe.edu/research/publications/workingpapers/03-05-034.pdf [Cited 12 Nov. 2009].

- Petrokas, R. 2008a. Growth trait correlation of Wych elm (Ulmus glabra Huds.) half-sibs in field trial. Miškininkystė 2(64): 38–48 (In Lithuanian with English abstract).
- Petrokas, R. 2008b. Growth vigor in Wych elm (Ulmus glabra Huds.). Baltic Forestry 14(2): 204-215.
- Sherman-Broyles, S.L. 2007. Ulmus glabra. Internet site: Flora of North America @ efloras.org. http://www.efloras. org/florataxon.aspx?flora_id=1&taxon_id=233501327 [Cited 20 Apr 2007].
- Troll, W. 1937. Vergleichende Morphologie der höheren Pflanzen 1(1:3). Berlin, Borntraeger (In German).
- Tutin, T.G., Heywood, V.H., Burges, N.A., Moore, D.M., Valentine, D.H., Walters, S.M., and Webb, D.A. 1968. Flora Europaea. Volume 2. London, UK: Cambridge University Press.
- Uotila, P. 1997. Jalavan suku sekä lehto- ja vuorijalavan taksonomia [The genus Ulmus, and the taxonomy of U. minor and U. glabra]. Sorbifolia 28: 5-16 (In Finnish).
- Webber, J. 2008. Dutch elm disease in Britain. Forest Research, Forestry Commission, Alice Holt, Farnham, Surrev.
- West-Eberhard, M.J. 2005. Developmental plasticity and the origin of species differences. PNAS 102(1): 6543-6549.

ВЫСОТА РОСТА И ЕГО СВЯЗЬ С ХАРАКТЕРОМ ВЕТВЛЕНИЯ У ИЛЬМА (ULMUS GLABRA HUDSON) В ЛИТВЕ

Р. Петрокас

Резюме

Известно, что из-за аддитивного роста будущая морфология дерева предопределена его настоящими морфологическими чертами. Таким образом, при исследовании признаков ветвления ильма (Ulmus glabra Hudson) была установлена модель прогнозирования роста деревьев в высоту. Оценка признаков семилетних полусибсов, являющихся потомками открытого опыления из шести литовских популяций, произведена на испытательном участке в центральной Литве. Прогноз по интенсивности роста выполнен на основе параметров характера ветвления (в т.ч. числа базальных почек, направления бокового ветвления, формы стебля и самоочищения от сучьев). Это сделано при помощи процедуры бинарной логистической регрессии. По данным исследования, в селекции ильма превосходство по высоте роста означает присутствие базальных почек, амфитонию, доминирующую ось стебля и хорошее самоочищение от сучьев.

Ключевые слова: Ulmus glabra, ильм, характер ветвления, высота роста, интенсивность роста.

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