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ANALYSIS OF A 17-YEAR OLD DUTCH OPEN-POLLINATED PROGENY TRIAL WITH *QUERCUS ROBUR* (L.)

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ABSTRACT

Height, DBH, epicormics, stem straightness and forking have been recorded in an open-pollinated progeny trial at the age of 17 years from sowing. The material is of local Dutch origin and comprises 37 open-pollinated progenies of 6 plus-trees selected in each of 6 stands supplemented with 3 arboretum-progenies of *Quercus petraea* (Matt.) Lieb. Population-samples from each of the 6 base provenances as well as 17 additional Dutch provenances are included in the fully randomised block experiment with 24-plants plots. Significant provenance as well as family within provenance variation was detected in most situations. Especially high heritabilities were detected for stem straightness and epicormic formation. Low level of epicormic formation and high level of stem straightness is positively correlated with height, indicating favourable conditions for obtaining useful genetic gains for a combination of these traits.

Keywords: *Quercus robur*, progeny trials, quantitative genetic parameters, genetic gains, stem form, epicormics.

INTRODUCTION

Quercus robur and *Quercus petraea* are both of major importance in larger parts of Europe. The oaks are relative slow growing with extended rotations, are highly estimated for recreational value and the end timber-products are of high value. In Denmark oak is reforestated at moderate levels, but planned extensions of the Danish forest area will increase the need for afforestation with this species in the future.

In Europe a recent trend in shift of interest from conifers to broadleaves has promoted the interest in oak, including choice of plant material (FLIES 1993). Serious considerations have been given to genetic origin and structure as well as identification of seed transfer zones etc. In such investigations, genetic information on adaptive traits are of great concern.

In historical time natural forests have often been heavily exploited. Concerning Danish native oak forests, especially straight growing trees have been extracted for construction purposes as well as for poles for fences etc. It is suspected, that the predominant crooked remnants of these natural resources partly are a result of this exploitation.

In oak-reforestation in the last 100 years, a large proportion of exotic origins from neighbouring Germany, The Netherlands, Sweden and Norway has been introduced, resulting in a mixed gene pool of large diversity.

On harsh locations in Denmark, local seed sources of Danish origin are preferred due to insufficient climatic adaptation of some exotic origins, as those from the Netherlands.

Because of this coincident of conditions, it was decided to evaluate older provenance trials in Denmark, tighten-up the seed supply by identification of more selected seed stands of Danish origin and to launch an improvement program.

According to the performed evaluation (JENSEN 1993) genetic variation is documented for important traits at the provenance level. An early pioneer in forest genetics detected already in 1930's pronounced within-stand genetic variation in stem straightness (OPPERMAN 1932). However, to approach an optimal breeding strategy for oak, more reliable estimates of quantitative genetic parameters between and especially within provenances are in high demand for a number of potential breeding objectives.

In The Netherlands extensive provenance and open-pollinated progeny tests were established in the 1970's, mainly to test a large number of commercial seed sources (OOSTERBAAN 1988). Seed and plants from these sources have been widely exported to Germany, Britain, Sweden and Denmark (GORDON & FRASER 1982). Most of these sources are roadside trees in avenues and Dutch oak has in Denmark a reputation for being extraordinary straight, a character selected for in Dutch nurseries aiming at this particular end-product, straight growing avenue trees.

The present investigation of one of the largest open-pollinated progeny tests in the Netherlands was initiated to obtain a better platform for formulation of a breeding strategy for oak in Denmark. The investigation was carried out as a joint project between the Institute for Forestry and Nature Research (IBN-DLO) in the Netherlands and the Hørsholm Arboretum in Denmark.

MATERIAL AND METHODS

Plant material

Genetic entries are of two sorts, 37 open-pollinated offspring families from individual trees within 6 provenances and 23 bulked provenance samples. The open pollinated families are offspring from 6–7 trees in each of 6 provenances supplemented with 3 *Quercus petraea* families from the Arboretum in Wageningen. The provenances from which the individual-tree offspring originate, are represented among the 23 bulked provenance samples. The total number of genetic entries sums up to 64.

The provenances represent current seed sources in The Netherlands, all of which are roadside trees in avenues. Their exact origin is unknown.

Field trial

The field trial is located on the polder in Flevoland at Larserbos on very fertile and loamy soils. The trial was planted in 1980 with 2-year old plants on a spacing of 2.5 x 1.5 m with 24 plants per plot. Experimental design is randomised blocks with 5 replications. Plots are completely randomized within blocks without regard if the content was provenance-samples or open-pollinated families.

At the 17-year old stage of the reported observations, the environment appeared quite uniform with no visible variation in the terrain. Competition was evident, as the trial has never been thinned. The mean annual increment is estimated to more than 13 m^3·ha. The environment may be too fertile to be optimal for growing high-quality oak. Such a trend has been experienced in Denmark (JENSEN 1993).

Recorded traits

The following traits were recorded and analysed: Height, DBH, stem straightness, epicormics, branch angle, forking and axis deformation.

Stem straightness and epicormics were scored as separate traits on 1–9 scales, where 9 represents the desired stage, perfect straightness and absence of epicormics and 1 represents the worst stage, crooked trees and abundant occurrence of epicormics. The justification of such a fine-graded system is to create a variable approaching a true metric stage.

Branch angle too was scored on a 1–9 scale, where 9 represent steep branch angles at about 30° (not desired) and 1 represent horizontal branches close to 90° (desired).

Forking and axis deformation were recorded as labels. Axis deformation was a special phenomenon in this particular trial, where nearly all trees in a certain height showed leader breaks.

Height was recorded at age 14 and the remaining traits were recorded at age 17 from sowing. Epicormics were recorded in replication 1 and 2, axis deformation and forking in replication 3–5, whereas the remaining traits were recorded in all replications.

Statistical analyses

All subsequent analyses are based on simple plot averages. Two analyses have been performed, one based on the 37 open-pollinated (OP) families of *Quercus robur*, excluding the bulked provenance samples and another on the provenance samples excluding the family plots.

On the OP-families the following model has been applied:

$$Y_{ijk} = \mu + prov_i + fam_j(prov_i) + rep_k + e_{ijk}$$

where: Y_{ijk} – plot average, μ – general mean, $prov_i$ – random effect of provenance i, $fam_j(prov_i)$ – random effect of family j within provenance i, rep_k – fixed effect of replication k, e_{ijk} – random error of plot averages.

On the provenance samples, the following simple model has been applied:

$$Y_{ik} = \mu + prov_i + rep_k + e_{ik}$$

The analyses were executed by the statistical software package SAS applying the procedure GLM (ANONYMOUS 1989). Variance components of the random effects are estimated by equating mean squares to expected values.

Quantitative genetic analyses

Heritabilities are estimated at two levels, family heritabilities and individual heritabilities.

Family-heritability is a very robust variable, which can be estimated in any field trial regardless of which genetic entries are involved. It is calculated according to the following formula, originally suggested by BURLEY and WOOD (1976) for provenances:

$$h^2_{fam} = \frac{\sigma^2_{fam}}{\sigma^2_{fam} + \frac{\sigma^2_e}{r}}$$

where σ^2_{fam} is the variance component for families, σ^2_e is the error variance of plot means, both obtained from the ANOVA of plot means, and r is the number of replications. σ^2_e/r is the error variance of family means over r replications.

A general problem of interpretation of open-pollinated (OP) families exists. The problem is associated with the paternity of the analysed families. Three questions are relevant, (i) is selfing occurring ?, (ii) how many fathers are involved ?, and iii) are the effective fathers a representative sample of the surrounding population, preferable the base population of which the selected mother tree is a member? These questions have for forest trees earlier been addressed by NAMKOONG (1965), SQUILLACE (1974), BORRALHO (1994) and (ASKEW & EL KASSABY 1994).

For oak only scarce information exists about seed and pollen dispersal (DUCOUSSO et al 1993), however (DOW & ASHLEY 1996) in their DNA marker study (SSR) provided evidence for long distance pollen transportation.

In standard interpretation of open-pollinated families, it is assumed that no selfing occurs, and the effective 'pollen cloud' is a sufficiently large sample of the surrounding stand to be representative of this 'base population.' If the state of nature is reasonable close to this idealized situation, the current interpretation of OP-families are straightforward, and in our material the OP-families are interpreted as being unrelated half-sibs and we can use the current quantitative genetic models for half-sibs as presented by *e.g.* FALCONER (1989) and BECKER (1984).

Individual heritabilities are estimated within a sample plot corresponding to replications in the analysed field trial and representing the population of OP-families within provenances. Heritabilities are estimated under the assumption of three alternative paternities: (i) the effective pollen cloud represent the above-mentioned idealized situation, i.e. the family members are half-sibs, (ii) one neighbouring oak is the only partner, i.e. family-members are full sibs, and iii) an intermediate situation. Formulas for heritabilities corresponding to these three paternities are the following when we ignore variance components for non-additive gene-effects:

$$h^2 = \frac{4\sigma^2_{fam}}{\sigma^2_P} \quad [1]$$

$$h^2 = \frac{2\sigma^2_{fam}}{\sigma^2_P} \quad [2]$$

$$h^2 = \frac{3\sigma^2_{fam}}{\sigma^2_P} \quad [3]$$

where σ^2_P represents the within-replication phenotypic variance in the offspring population. As this offspring population is split-up into 6–7 families within each of the 6 provenances, a representative within-provenance phenotypic variance which is not confounded with between-provenance variation is obtained by merging the 6 families from each provenance into a non-contiguous main plot and calculate the individual variance within each of these main plots. The overall σ^2_P is then obtained by pooling these variances over provenances and replications.

Any significant proportion of selfing has been ignored as it has been demonstrated, that the oaks apparently have an effective mechanism against selfing (AAS 1988, STEINHOFF 1993, SCHÜTE 1995).

Phenotypic correlations between traits are estimated by pooling between family-mean variances and covariances within provenances. The phenotypic correlations are thus refering to family within provenance means, and therefore close to genetic correlations due to the general high level of family heritabilities.

Estimates of genetic correlations were not performed due to complications originating from the applied sampling of observations for epicormics and axis deformations in different replications.

Response to selection

For three steps of selection, genetic responses for single traits have been predicted for a standardised selection intensity of one. The three steps are

(i) Individual within-provenance mass selection of first generation plus trees (at the age of 17 years, age as those represented in the trial),

(ii) Backward selection amongst first generation plus-trees after open-pollinated progeny tests,

(iii) Between provenance selection.

Predictions are based on the obtained estimates of genetic parameters in the present field experiment analysed at age 17. Reduction of genetic gains due to imperfect juvenile-mature correlations and genotype x environment interactions are not taking into account.

ad i)

The applied response formula is

$$R = i\ \sigma_P\, h^2$$

where σ_P and h^2 refers to individuals in sample plots of size and environment comparable to replications in the analysed field trial, *i.e.* a size of 0.58 ha on comparable locations in the Netherlands. *i* refers to the applied selection intensity for the specified trait.

ad ii)

It is assumed, that a sufficient large number of first generation plus-tree clones are put into an isolated clonal seed orchard and this orchard is designed so it is possible to perform a genetic thinning corresponding to reasonable selection intensities. It is further assumed, that the orchard clones are tested by open-pollinated progeny test of the ortets at a comparable environment. In this case, the applied response formula is

$$R = 2(i\ \sigma_P\ h^2)$$

where σ_P and h^2 in this case refer to open-pollinated family means in progeny trials corresponding to the analysed field trial. i refer to the applied selection intensity amongst the parent clones represented in the orchard, i.e. it is based on the proportion of clones which are roqued from the orchard (~ genetic thinning). The response ($i\ \sigma_P\ h^2$) is multiplied by two because we are judging the breeding value of the open-pollinated female parent after mating with not-selected fathers supposed to be random members of the base population. Even if only a restricted number of father are actually fertilising the individual plus-tree, these fathers are – for all populations of open-pollinated families – still to be considered as a random sample of the base population.

Ad iii)

The applied response formula for selecting provenances among a set tested in a provenance tests is the standard response expression

$$\mathrm{R} = i\ \sigma_P\ h^2$$

where all components refer to provenance means. It is assumed, that provenance means are normally distributed; this may in general be fulfilled for provenances sampled within provenance regions (NIELSEN 1994). If this conditions is not fulfilled, an alternative option is to consider provenances as fixed effects and apply the more general response formula

$$\mathrm{R} = h^2 D$$

where *D* now is the selection differential of the selected provenances, i.e. the deviation of the selected provenances from the mean of the tested sample.

RESULTS

Table 1 and 2 show – for the five traits height, DBH, stem straightness, epicormics and axis defects – basic statistics from the ANOVAs of the families within provenances and the bulked provenance samples. Concerning the remaining traits, forking and branch angles, no significant genetic variation are recorded (not shown). Highly significant variation is detected

Table 1. Basic statistics from the ANOVA of the 37 progenies within 6 provenances. Experiment mean, R^2, F-value for provenance, family within provenance, and variance components for family within provenance

Trait	Experiment mean	ANOVA statistics			
		R^2	F_{prov}	$F_{fam(prov)}$	$\sigma^2_{fam(prov)}$
Height (m)	6.7	0.53	1.12	4.24***	0.136
DBH (cm)	10.7	0.46	2.54*	2.33***	0.228
Stem str. (1–9)	5.6	0.77	2.23*	9.44***	0.305
Epicorm (1–9)	5.2	0.77	0.34NS	4.01***	0.308
Axis def. (%)	24.4	0.47	0.62NS	1.43NS	(22.7)

Significance levels: $0.05 < p$; *: $0.01 < p < 0.05$; **: $0.001 < p < 0.01$; ***: $p < 0.001$

Table 2. Basic statistics from the ANOVA of the 23 bulked provenance samples. Experiment mean, R^2, F-value and variance component (provenance).

Trait	Experiment mean	ANOVA statistics		
		R^2	F_{prov}	σ^2_{prov}
Height (m)	6.6	0.43	2.89***	0.0721
DBH (cm)	10.7	0.36	1.78*	0.166
Stem str. (1–9)	5.4	0.62	3.67***	0.081
Epicorm (1–9)	4.9	0.59	1.25NS	(0.026)
Axis def. (%)	24.3	0.66	2.05*	65.9

Table 3. Key within provenance quantitative genetic parameters for the 4 candidate traits for selection: σ^2_P – within replication, within provenance phenotypic variance; h^2 – within-replication, within provenance heritability; OP:HS – open-pollinated families assumed half-sibs; OP:FS – open-pollinated families assumed full-sibs: OP:mix – open-pollinated families assumed an intermediate situation between HS and FS.

Trait	$\sigma^2_{fam(prov)}$	$h^2_{fam(prov)}$	σ^2_p	h^2		
				OP:HS	OP:FS'	OP:mix
Height (m)	0.136	0.76	1.19	0.46	0.23	0.34
DBH (cm)	0.158	0.57	9.38	0.10	0.05	0.07
Stem str (1–9)	0.305	0.89	1.55	0.79	0.39	0.59
Epicorm (1–9)	0.308	0.75	2.41	0.51	0.26	0.38

Table 4. Within-provenance phenotypic correlations. Calculations based on between-family within provenance variances and covariances.

Trait	Height (m)	DBH (cm)	Stem straight 1–9	Epicorm 1–9	Axis deform. %
Height (m)	1.00	0.56**	0.46*	0.49**	–0.25
DBH (cm)		1.00	0.06	0.41	0.07
Stem straight 1–9			1.00	0.14	– 0.41
Epicorm 1–9				1.00	0.06
Axis deform. %					1.00

Table 5. Key between-provenance quantitative genetic parameters for the 4 candidate traits for selection. Between provenance variance component – σ^2_{prov}; povenance heritability– h^2_{prov}; and phenotypic variance between provenances – σ^2_P.

Trait	σ^2_{prov}	h^2_{prov}	σ^2_p
Height (m)	0.072	0.65	0.11
DBH (cm)	0.162	0.44	0.37
Stem straight (1–9)	0.0811	0.73	0.11
Epicorm (1–9)	(0.026)	0.20	0.14

Table 6. Components of possible genetic responses to within- and between provenance selection. Responses for height and DBH are presented in percentages. σ_p – within provenance phenotypic standard deviation; h^2 – within provenance heritability, paternity option [3]; $\sigma_{p(fam)}$ – within-provenance phenotypic standard deviation between family means; h^2_{fam} – heritability of family means; $\sigma_{p(prov)}$ – phenotypic standard deviation between provenance means; h^2_{prov} – heritability of provenance means

Trait	Within-provenance selection						Between-provenance selection		
	Individual mass selection			Backward selection after progeny tests					
	σ^2_p	h^2	Response $i = 1$	$\sigma_{p(fam)}$	h^2_{fam}	Response $i = 1$	$\sigma_{p(prov)}$	h^2_{prov}	Response $i = 1$
Height (m)	1.09	0.34	5.5%	0.42	0.76	9.5%	0.33	0.65	3.27%
DBH (cm)	3.06	0.07	2.0%	0.64	0.57	6.8%	0.61	0.44	2.49%
Stem straight 1–9	1.24	0.59	0.7	0.58	0.89	1.0	0.33	0.73	0.2
Epicorm 1–9	1.55	0.38	0.6	0.65	0.75	1.0	0.38	0.20	0.1

Table 7. Phenotypic means – P – and predicted genetic gains – Δ_G – for *Quercus petraea* samples (one provenance and 3 open pollinatred progenies) and 23 bulked *Q. robur* provenances. Most *Q. robur* provenances are seed production stands.

Nr	Provenance	Height (m) $h^2 = 0.65$		DBH (cm) $h^2 = 0.44$		Stem str. (1–9) $h^2 = 0.73$		Epicorm (1–9) $h^2 = 0.2$ NS		Axis def (%) $h^2 = 0.51$	
		P	$\Delta_{G\%}$	P	$\Delta_{G\%}$	P	Δ_G	P	Δ_G	P	Δ_G
1	*Q. petraea* – Elspeet	5.69	–2.0	9.8	1.5	4.50	0.03	3.63	–0.16	10	0.00
2	*Q. petraea* – halfsib	5.96	1.0	9.1	–1.6	4.11	–0.26	5.05	0.13	3	–0.04
3	*Q. petraea* – halfsib	5.26	–6.8	9.1	–1.5	4.70	0.18	4.00	–0.08	16	0.03
4	*Q. petraea* – halfsib	6.58	7.9	9.8	1.7	4.53	0.05	5.00	0.12	13	0.01
	Mean *Quercus petraea*	**5.87**		**9.5**		**4.46**		**4.42**		**11**	
3	Epe – Vassen	6.66	0.2	11.7	4.1	5.22	–0.13	4.84	–0.01	47	0.11
6	Renswoude	6.98	3.3	11.7	4.1	5.17	–0.17	5.15	0.05	33	0.04
7	Ede-de Klomp	6.77	1.3	10.5	–1.1	5.86	0.34	5.09	0.04	4	–0.10
18	Teuge	6.40	–2.3	10.8	0.3	5.39	0.00	4.95	0.01	42	0.09
19	Lochem – Goor	6.79	1.4	11.1	1.6	5.22	–0.13	5.14	0.05	30	0.03
29	Bennekom	7.19	5.4	11.8	4.4	5.46	0.04	4.81	–0.01	17	–0.04
30	Wageningen	6.84	2.0	11.0	0.9	5.38	–0.01	5.73	0.17	28	0.02
32	Hoffsttäterlaan	6.97	3.2	10.9	0.8	5.42	0.02	4.83	–0.01	14	–0.05
33	Smidsallée	6.97	3.3	11.6	3.7	5.21	–0.13	4.66	–0.04	13	–0.06
35	Zevenaar – Babberich	6.70	0.6	10.2	–2.2	5.22	–0.13	5.33	0.09	27	0.02
36	Zevenaar – Duiven	6.63	–0.1	11.1	1.6	4.65	–0.54	4.30	–0.12	32	0.04
44	Hof te Dieren	5.76	–8.7	9.9	–3.4	5.15	–0.18	5.00	0.02	42	0.09
47	Heesch (ost)	6.20	–4.3	10.1	–2.5	5.18	–0.15	4.43	–0.09	30	0.03
47*	Heesch (west)	6.61	–0.3	10.3	–1.6	6.01	0.45	4.14	–0.15	12	–0.06
50	St. Anthonis – Boxmeer	6.52	–1.2	10.5	–0.9	5.37	–0.02	4.88	0.00	13	–0.06
51	Haps	6.66	0.2	10.7	–0.2	5.91	0.37	5.16	0.06	14	–0.05
58	St. Anthonis	6.82	1.8	10.6	–0.3	5.61	0.15	4.81	–0.01	20	–0.02
72	Nuennen	6.62	–0.2	10.3	–1.8	5.65	0.18	5.52	0.13	30	0.03
75	Heeze – Leende	6.11	–5.2	10.7	–0.2	5.50	0.07	4.93	0.01	17	–0.03
76	Wilheminalaan	6.33	–3.1	10.1	–2.5	5.67	0.20	4.88	0.00	28	0.02
79	Elsendorp-de Rips	6.91	2.7	11.1	1.6	5.87	0.35	4.52	–0.07	36	0.06
81	Weert – Nederweert	6.94	3.0	9.7	–4.2	5.09	–0.22	4.65	–0.05	18	–0.03
88	Kasteellaan	6.33	–3.0	10.2	–2.3	4.90	–0.35	4.50	–0.05	11	–0.07
	Mean *Quercus robur*	**6.64**		**10.7**		**5.40**		**4.88**		**24**	

for most of the five traits, more pronounced within than between provenances.

In table 3 key within-provenance quantitative genetic parameters are presented for individual traits and in table 4 mutual phenotypic correlations between traits are presented based on the between family within provenance phenotypic variances and covariances. In table 5 the corresponding information on between provenance parameters are presented.

In table 6 components of possible genetic responses to within- and between provenance selection for individual traits are presented.

For general information in table 7, phenotypic for the *Q. petraea* samples and the bulked 23 *Q. robur* provenances are presented for height, diameter, stem straightness, epicormics and the frequence for axis deformation.

DISCUSSION

When interpreting the results from the present progeny trial F.50, it is necessary to compare the results with other investigations.

General variation of growth between provenances have been shown by several authors (JENSEN 1993). Evidence of substantial within provenance region variation have been reported by KLEINSCHMIT and SVOLBA (1995) and JENSEN (op.cit.). Among Dutch provenances relative difference in growth characters is not exceeding 5 %. In a Danish provenance trial (with comparable age and growth), even lower provenance variation between provenances have been found (JENSEN op.cit.). Doubt of the origin of the Dutch avenue provenances have been risen (DE VRIES, unpublished). The Dutch provenances do not appear so variable in growth, as they may have been if they were brought together from different locations in Europe.

Dutch provenances have been cultivated in Denmark for decades, and they are quite homogeneuos and distinct to other provenance groups in regard to important adaptive characters as late flushing and budset.

Provenance variation has been presented for many oak species, see KLEINSCHMIT (1993) for a review, and choice of provenance may have substantial importance for growth, stem straightness and even epicormic formation.

Knowledge is scarce concerning genetic parameters from open-pollinated or clonal trials of oak (SAVILL & KANOWSKI 1993). Most information is gathered around wood quality parameters, see NEPVEU (1993) for a review. According to SAVILL & KANOWSKI (1993), P. Mather found a family heritability for epicormic production of 0.38 in a young German trial with open-pollinated progenies of *Q. robur* and *Q petraea* (MATHER, personal communication). In a 14 year old trial with open-pollinated families of greyish oak (*Q. pedunculiflora*), ENESCU (1993) reported a high family heritability of 0.7 on stem form, and a more moderate 0.4–0.5 for height and diameter growth.

Our results further agree with the observations of OPPERMANN (1932), who investigated the relation between progenies of 41 trees and 21 provenances and their offspring and found a high heredity for stem form. Parallel with the present investigation, another Dutch combined provenance and open-pollinated family test (Z–72) with 5 bulked provenances and 8 families was analysed. In spite of the much smaller sample size, the result was consistent with the present investigation. Higher heritabilities were revealed for epicormic production ($h_{\mathrm{fam}}^2 = 0.90$, $h^2 = 0.57$), which is probable due to older and larger trees (19 years) (JENSEN, *et al.* unpublished data).

The heritabilities for stem form is in present investigation quite high. As mentioned in the Introduction, two examples of realised responses to past selection are suspected today:

The overall crooked phenotypes of remnants of the original Danish origins.

The overall straight phenotypes of the current domesticated land race of Dutch origin growing in Denmark.

These examples of response to past two-way selection after exploiting the natural Danish oak forest for straight phenotypes and the systematic selection favouring straight growing avenue trees in commercial Dutch nurseries are more plausible on the background of the obtained information of the present investigation. According to the data presented in table 6, responses to simple phenotypic mass selection for stem straightness with the modest selection intensity of 2 result after two generations in a difference between upward and downward selection of:

$$2 \times 2 \times (i \cdot \sigma_P \cdot h^2) \approx 2 \times 2 \times (2 \times 1.24 \times 0.59) \approx 6$$

i.e. 6 classes on the 1 to 9 scoring scale for stem straightness. Even if the assumptions are only approximately fulfilled, it demonstrates that past divergent selection may explain a substantial part of the present differences in straightness between remnants of natural Danish oak resources and the current land race of Dutch avenue oaks.

Implementing breeding program on oaks needs several considerations. We have analysed three types of trait:

1. Productivity associated traits as Height, and DBH after 14 and 17 years respectively.
2. Response to environmental stress: Epicormics.

3. Morphological: Stem straightness and Height/DBH proportion.

If an important part of the breeding objectives is productivity, delineation of breeding zones based on recording of genotype by environment interaction in already established series of parallel trials must be carried out. At the provenance level, pronounced G×E interaction across western and eastern Denmark has been observed (JENSEN 1993). As oak are grown for relatively long rotations , the problem for early selection for late response is serious. According to a general function of genetic correlations between early and late stages LAMBETH (1980), response to early selection based on height at age 15 will correlate with height at age 120 by a factor 0.38. As the heritability furthermore is only moderate, breeding for production traits alone is questionable.

Formation of epicormics is for the moment important for the specialized end product high quality veneer. An intermediate level heritability trait (h^2 ~ 0.38) it is according to silvicultural experience environmental sensitive for heavy thinning and other induced stress factors, as f.inst. frost damages and defoliation of insects. For this reason, precaution should be put forward to select strongly for lack of stress response, as this might deteriorate fitness. However, it might be pursued in sub-populations specifically aiming at production of high-value veneer at sheltered environments.

The morphological traits, stem straightness and Height/DBH proportion seem in the present investigation to be the most straight forward traits to improve in a breeding program. As the lower bole is formed within the first 20–30 years, perspectives for early selection is thus much more promising compared to growth.

The height/DBH proportion is judged to be a realistic breeding objective because both height and DBH at the family level showed reasonable high heritabilities and the estimated phenotypic correlations came out at the very modest level of 0.57. This implies, that it should be possible to identify diverse combinations of these two traits, f.inst. high narrow and short sturdy genotypes which may be relevant for divers users (*i.e.* forestry versus open land).

The correlations between growth and stem straightness and growth and epicormics are both positive. This is valuable considering the possible accumulated gains won by combined trait selection.

High and moderate single tree heritabilities for stem straightness and epicormics raises discussion on breeding strategy. Several options are possible *i.e.* choices between clonal seed orchard, seedling seed orchards and seed production areas. Gains through forward selection could be quite efficient, and simple mass selection at the nursery state might be economically more efficient than backward selection. Another paper will be subject to discussion of possible breeding strategies in oak.

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