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Variation Between Single Tree Progenies of *Fagus sylvatica* in Seed Traits, and its Implications for Effective Population Numbers

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Abstract

Variation between families in seed production, germination, dormancy and weights were studied in beechnuts collected from 20 individual beech (*Fagus sylvatica* L.) trees from a Danish stand, two different years (1993 & 1995). Combined cold treatment and germination at 5 °C was compared with cold treatment for 5, 7 and 9 weeks and germination at 15 °C. Finally, the effect of the pericarp on variation and level of dormancy was studied.

Significant family differences in seed weight, germination percentages, mean germination time (dormancy) and seed production were found. No simple correlation between germination and dormancy was observed: the correlation between germination and germination time was zero in 1993-seed lots, whereas there was observed a significant correlation between

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low germination and slow germination in 1995-seed lots. Seed weights correlated significant between the two years, indicating a genetic component in this trait, and the seed weight also correlated significantly with germination in 1995-seed lots, but not in the 1993-seed lots. Germination percent and germination time did in general not correlate with seed yield.

The effects of variation in germination percentages and dormancy on the effective population number (N_s) were moderate: decreases in N_s on 8–10 % for germination percentages and 10–12 % for dormancy, whereas variation in tree to tree seed production alone resulted in a decrease in N_s on 27 %. Combined cold treatment and germination at 5 °C resulted in higher germination percentages than cold treatment for 5, 7 and 9 weeks and subsequent transfer to 15 °C.

Removal of the pericarp resulted in 3 to 25 days reduction in mean germination time (mgt) for the different single tree seed lots. The mean reduction in mgt was 9–10 days. Germination in "pericarp extract" indicated that inhibiting substances in the pericarp play a major role in delaying germination, whereas delay in imbibition of water was found to be of minor significance.

Key words: Beech, *Fagus sylvatica*, seed dormancy, embryo dormancy, seed coat dormancy, pericarp, cold treatment, seed weight, seed production, variation and effective population number.

Introduction

Seed characteristics e.g. seed size and germinability are often observed to vary between individual trees. This can in principle result in an unintended selection during seed processing and germination, over representing some single tree seed lots and under representing others. The idea behind the present study was to quantify variation between single tree seed lots in a Danish seed source of Beech (*Fagus sylvatica*) and discuss the potential genetic impact on commercial planting stock.

Beechnuts are deeply dormant and need approximately 12 weeks cold treatment before they will germinate. Variation in cold requirement, both within and between seed lots, has been observed (HENRIK KNUDSEN, The Danish Tree Improvement Station, personal communication) and it has been discussed if non optimal pre-treatment could cause un-intended selective effects: during traditional stratification, beechnuts with a relatively low cold treatment demand can be lost due to pre-sprouting if the treatment is too long, and likewise can beechnuts with a relatively high cold treatment demand be lost due to insufficient treatment. In a relatively newly introduced method, pre-sprouting is prevented through controlling the seed moisture content during stratification. In this study, the variation in dormancy between trees and the effect of different cold treatment periods on the genetic composition was studied to shed light on the possible effect of pre-treatment length on the genetic basis on a seed lot by comparing the individual single tree seeds lot reaction norm in germination and dormancy.

Seed yield and weights were determined to quantify variation and to see if there was correlation with germinability. Furthermore, the effect of the pericarp on germination was investigated.

Variation in dormancy

EDWADS and EL-KASSABY (1995) demonstrated that the prescribed three weeks stratification period for Douglas-fir seed was insufficient to release dormancy for all of the 15 clones included in their study and thereby influencing the genetic composition of the combined seed lot. Similarly, variation in dormancy has been found for a number of other tree species (mostly conifers) as well as non-woody species (see *table 1*). In most cases variation is found between populations and between families. However, in some of these studies the germination percentages are low, and no viability tests have been performed after germination, to distinguish between dormancy and low viability.

Table 1. – Variation in seed dormancy.

Genetic unit	Species	Reference
Family	**Broadleaved**	
	Acer rubrum	PERONI, 1995
	Prunus virginiana	LOCKLEY, 1980
	Quercus rubra	MERCIER and RAINVILLE, 1996
	Prunus serotina	FARMER and BARNETT, 1972
	Conifers	
	Cupressus arizonia	CECCHERINI et al. 1998
	C. lusitanica	"
	C. numidica	"
	C. torulosa	"
	Picea glauca	CARON et al. 1988
	Pinus monticola	HOFF, 1986 and 1987
	Pinus palustris	MCLEMORE and HANSBROUGH, 1970
	Pinus taeda	MCLEMORE and BARNETT, 1966
	Pseudotsuga menziesii)	CHING and CHING, 1962
	"	EDWARDS and EL-KASSABY, 1995
	Non-woody	
	Avena barbata	JAIN, 1982
	Trifolium hirtum	"
Population*	**Broadleaved**	
	Betula papyrifera	BEVINGTON, 1986
	Prunus serotina	FARMER and BARNETT, 1972
	Quercus rubra	MERCIER and RAINVILLE, 1996
	Conifers	
	Abies amabilis	LEADEM, 1986
	Abies lasiocarpa	HANSEN and LEIVSON, 1990
	Cedrus deodora	THAPLIYAL and GUPTA, 1980
	Juniperus scopulorum	RIETVELD, 1989
	Juniperus virginiana	VAN HAVERBEKE and COMER, 1985
	Pinus brutia	SKORDILIS and THANOS, 1995
	Pinus edulis	GOTTFRIED and HEIDMANN, 1985
	Tsuga heterophylla	CAMPBELL and RITLAND, 1982
	Non-woody	
	Avena fatua	JAIN, 1982
	A. barbata	"
	Bromus mollis	"
	B. rigidus	"
	B. rubens	"
	Hordeum spontaneum	"
	Medicago polymorpha	"
	Phalaris paradoxa	GUTTERMAN and NEVO, 1994
	Trifolium hirtum	JAIN, 1982
		DRENNAN and BAIN, 1987
		JAIN, 1982
Clone	**Conifers**	
	Picea sitchensis	CHAISURISRI et al. 1992
	Pseudotsuga menziesii)	CHING and CHING, 1962
	"	EDWARDS and EL-KASSABY, 1995
Variety	**Non-woody**	
	Helianthus annuus	MWALE et al. 1994

* Including studies referring to seed sources and provenances

Seed size

Differences in seed size (including weight) have also mainly been found between poplations and between families (see *table 2*).

The effect of seed size on germination and seedling performance is generally positive, at least for initial seedling performance. Large seeds of loblolly pine (*Pinus taeda*) germinated faster and produced larger seedlings than smaller seeds (DUNLAP and BARNETT, 1983), even after 5, 10 and 15 years there was still a correlation between seed weight and volumes (ROBINSON and BULJTENEN, 1979). MIKOLA (1980) studied the effect of seed size on plant growth on scots pine (*Pinus sylvestris*) and norway spruce (*Picea abies*) and found a strong positive effect of seed weight in the first growing season, but with a subsequent decreasing effect thereafter, and SURESH et al. (1998) found a positive correlation between teak (*Tectona grandis*) fruit size and survival of stumps. Seed size did not affect 8-month-old seedlings of Sitka spruce (*Picea sitchensis*) (CHAISURISRI et al., 1994).

Table 2. – Variation in seed size (including weight).

Genetic unit	Species	Reference
Family	**Broadleaved**	
	Acacia holosericea	HELLUM, 1990
	Plantanus occidentalis	JOHNSON and KELLISON, 1984
	Prunus serotina	CECH and KITZMILLER, 1968
	"	FARMER and BARNETT, 1972
	Conifers	
	Picea abies	KJÆR & WELLENDORF, 1997
	Pinus sylvestris	LINDGREN, 1982
	Pseudotsuga menziesii	SILEN and OSTERHAUS, 1979
	Non-woody	
	Ludwigia leptocarpa	DOLAN, 1984
Population*	**Broadleaved**	
	Acacia mangium	SALAZAR, 1989
	Dalbergia sissoo	VAKSHASYA et al. 1992
	Fraxinus americana	DANIELS, 1979
	Prunus serotina	CECH and KITZMILLER, 1968
	"	FARMER and BARNETT, 1972
	Conifers	
	Pinus nigra	WRIGHT and BULL, 1962
Clone	**Conifers**	
	Picea sitchensis	CHAISURISRI et al. 1992
	Pinus sylvestris	LINDGREN, 1982
Variety	**Non-woody**	
	Avena sativa	PIETRZAK and FULCHER, 1995
	Glycine max	ARMSTRONG et al. 1988

* Including studies referring to seed sources and provenances

Dormancy and pericarp

Beechnuts consist of an embryo with large cotyledons, a thin seed coat and a thicker, hard pericarp. The seeds have been categorised as having embryo dormancy, but studies have shown that the covering structures also play a role in germination. Removal of the pericarp generally results in two weeks faster germination at 5 °C (POULSEN, 1992; NICOLÁS et al., 1996 and THOMSEN et al., 1997). Therefore, the variation in the effect of the pericarp on the length of cold treatment as well as the effect of the pericarp on germination through inhibition of water uptake and inhibitors were studied.

Material and Methods

This study is based on progenies from 20 trees and repeated in two years. Beechnuts were collected from nets on the ground under 20 trees, in a seed stand in Graasten in the two masting years: 1993 and 1995, where after the seeds were dried to approximately 9 % moisture content (fresh weight basis).

1993 trials: For each tree, four replicates of 25 beechnuts (with and without the pericarps) were germinated on paper in closed plastic boxes, with wicks into the water in the bottom of the boxes to ensure constant water supply. The boxes were kept at 5 °C (in the dark) until all seeds were either germinated or dead (combined cold treatment and germination). The germination criterion was emergence of minimum 2 mm of the embryo axis, and germination was recorded weekly. Non-germinated seeds were cut to determine if they were empty, dead or fresh, and the germination percentage was calculated on basis of full seeds. Mean germination time was calculated according to CZABATOR (1962) as a measure of dormancy.

To investigate the effect of the pericarp on germination, imbibition of whole seeds (including the pericarp) and seeds without the pericarp (embryo + seed coat) were compared using seeds from tree number 17. Eight times four replicates of 25 seeds were imbibed at 5 °C (in germination boxes), where after moisture contents were determined on the different seed parts after 4 hours, 6.5 hours, 1, 2, 3, 7, 10 and 14 days. Furthermore, the pericarps were removed from four replicates of 25 seeds from trees number 4, 5, 14, 16, 17 and 18, where after the pericarps were soaked in 25 ml of water at 15 °C for 24 hours. The water containing extracts from the pericarps were used to moisten the filter paper for the seeds in a subsequent germination test at 5 °C.

Seed moisture contents (expressed on fresh weight basis) were determined on 2–4 replicates of 15 seeds each after weighing and oven drying at 103 °C for 17 hours.

Fresh seed weights were determined individually for 30 seeds from each tree. Furthermore, the quantities of seeds collected per tree were determined.

1995 trials: Combined cold treatment and germination, with and without the pericarps, at 5 °C was repeated, together with moisture content and weight determinations. To investigate variation in dormancy between trees during cold treatment, samples were moved from 5 °C to 15°C after respectively 5, 7 and 9 weeks. The test was terminated after four weeks at 15 °C. The number of replicates, the number of seeds per replicate and other conditions were the same as when germinated at 5 °C but the experiment was only made on whole beechnuts. This experiment was started after 6 months, meanwhile the seeds were stored at 5°C.

Statistical analysis:

Variation between single tree seedlots in germination percent was analysed in two steps. First, a simple one way analysis was performed separately for the two years following model (1):

(1) $P_{ij} = \mu_s + F_i + \varepsilon_{ij}$

i= 1...19 (single-tree seedlot), j=1..4 (replication)

where F_i is the effect of family (single tree seedlot) assumed to be random.

Secondly, interaction between single tree and year was analysed by the mixed model (2):

(2) $P_{ijk} = \mu_s + F_i + Y_k + F_i{*}Y_k + \varepsilon_{ijk}$

i = 1...19 (single-tree seedlot), k=1,2.(year),
j(k) = 1..4 (replication)

F_i still being the random effect of family, Y_k is the fixed effect of year, and $F_i{*}Y_k$ is the random interaction term.

The average germination of each single tree seedlot in each of the two years was estimated based on the analysis. Correlation r_{jk} between these average seedlot performance P_{ik} in the two years was calculated. This was done in order to quantify potential change in ranking of the progenies between 1993 and 1995. Change in rank between the two years is interesting because it indicates that the impact from different germination varies from year to year (alternating selection favouring different trees), but also the degree of changes infer on likely degree of simple genetic control (cf. discussion below).

Variation in mean germination time was analysed similar to germination percent (cf. model (1) and (2)). The standard error for mean germination time (according to model 1) varied substantial between the two years, and the analysis across years according to model (2) was therefore modified by weighting with the inverse of the error variance in the respective years.

The effect of cold treatment period, and its interaction with family, were analysed by the mixed model (3):

(3) $P_{ijk} = \mu_s + F_i + T_k + F_i{*}T_k + \varepsilon_{ijk}$

i = 1..19(single-tree seedlot), k = 5,7,9 weeks,
j(k) = 1..4 (replication)

F_i still being the random effect of single tree seedlot, T_k is the fixed effect of treatment, and $F_i{*}T_k$ is the random interaction term.

Effective population number

The effect of unequal germination was quantified by using the theoretical framework of effective population number. The

concept of effective population number was introduced by WRIGHT (1931) in order to quantify the effects of deviation of natural populations from idealised panmictic breeding situations. Effective population number can be used to focus on either increased autozygosity (F) or genetic drift, and the result will in general not be the same (POLLAK, 1977; KJÆR, 1996). In the present investigation we decided to focus on the general increase in coancestry caused by uneven germination compared to a situation where all progenies germinated equally. For this purpose, the so-called status number (N_s) was calculated following the ideas of LINDGREN and MULLIN, (1997). First the relative contribution of each single-tree seed lot (r_i) to an (imaginary) bulked population of germinating embryos, was calculated as

(4) $r_i = p_i \,/\, \Sigma\, p_i$
$i = 1..19$ *(single trees)*

The corresponding effective population number (N_s) was then estimated for the two years

(5) $N_s\,(j) = 1 \,/\, \Sigma\, r_{ij}^2$
$j = 1993, 1995$

The study was based on 19 progenies, and the relative decrease in effective population number was therefore estimated as

(6) $N_r = N_s \,/\, 19$

It can easily be seen that $N_r = (1/\,\Sigma\, 1/19)^2)/19 = 1$, if all single-tree seed lots contribute equally to a bulked seed lot (i.e germinate equally).

This nice feature may at first sight be a bit surprising as fully equal contribution from all parents to the next generation (Vk = 0) nomally is associated with an affective population size of approximately twice the number of parents (see e.g. CROW and KIMURA, 1970). However, one should note that (5) only evaluates the effect of unequal contribution from each parent to the gamete pool. A second stage sampling error will be involved from the pool of many germinating seeds to the final population of mature trees. Only if this process is completely random (follow a binomial distribution), will the effective population number equal the number of parents (see KJÆR, 1996).

The effective population number estimated according to (5) is related to the build up of coancestry in the progeny (KJÆR and WELLENDORF, 1997), and is therefore an 'inbreeding type' of effective population number, (see e.g. CROW and KIMULA, 1970 for a discussion of the difference between inbreeding and variance effective population numbers), but is basically a feature of the collected seed crop rather than a population number (LINDGREN and MULLIN, 1997). Effect of pollen is not included in the analysis, and the effective population number should thus be seen as a female estimate (cf. e.g. BILA et al., 2000).

Results

The quantities of beechnuts that could be collected from each tree in 1993 varied from 65 g to 1665 g (mean = 922), indicating large variation in the fertility between the trees. When evaluated according to formula 5 & 6, this corresponds to N_s = 13.9 (N_r = 73 %), that is a decrease in N_s on 27 % compared to a situation where all trees had contributed equal amount of seed (*table 7*).

Germination

Germination percentages for the trees in 1993 were in the range of 54–90 % (SE = 3.7 %), mean = 69 %, and in 1995 in the range of 32–95 % (SE = 3.8 %), mean = 74 % (*figure 1A*). The differences between trees were significant in both 1993 and 1995 (*table 3*), but so was also the interaction between years and trees (*table 4*). This corresponds to a low, non-significant correlation (r = –0.27) between average progeny germination in the two years (*table 5*).

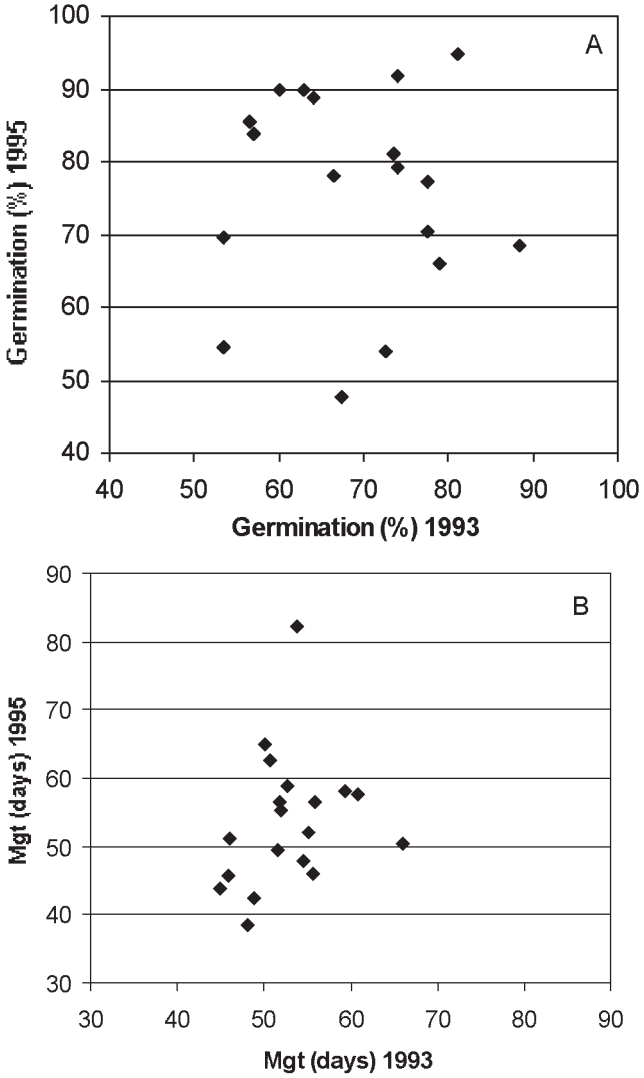


Figure 1. – Correlation between germination percentages (A) and mean germination time (B) at 5 °C for beechnuts from 20 individual trees in seed stand in Graasten, 1993 and 1995.

Although the progenies germinated significantly different in both years, the impact in terms of drop in effective population number was small compared to the effect of variation in seed production. The variation between the trees in germination resulted in respectively 2 % (1993) and 5 % (1995) decrease in the effective population number (*table 7*).

Dormancy

The results in terms of mean germination time follow germination percent (*figure 1B*). The mean germination time for all trees was almost the same in 1993 and 1995: 53 and 54 days, in 1993 ranging from 45–66 days (SE = 1.2 days) and in 1995 ranging from 38–83 (SE = 2.1 days). Although the differences between the trees were significant both years, the interaction was much larger than the main effects, and no significant correlation between the two years was found (*tables 3*–5).

Removal of pericarp

Removal of the pericarp resulted in 10 and 9 days reduction in the mean germination time for all the trees, with a range

Table 3. – Analysis of variance for 1993 and 1995. *F*-test for differences between families and level of significance (Pr>*F*) for germination percent and mean germination time.

Effects	MSf	MSe	Df	*F*	Pr>*F*
1993:					
Germination %	460.34	54.01	19;60	8.52	*<0.001*
Mean germination time	109.40	6.14	19; 60	17.82	*<0.001*
1995					
Germination %	1153.66	58.03	18; 57	19.88	*<0.001*
Mean germination time	390.06	17.85	18; 57	21.84	*<0.001*

Table 4. – Analysis of variance across the two years. *F*-test, degrees of freedom (Df) for *F*-test and level of significance (Pr>*F*).

Effects	MSf	Df	*F*	Pr>*F*
Germination percent				
Family	587.32	19; 18	0.58	*0.879*
Year	580.40	1; 18	0.57	*0.460*
Family*Year	1919.62	18; 117	18.21	*<0.001*
Error	55.97			
Mean germination time				
Family	25.53	18; 18	1.54	*0.185*
Year	2.39	1; 18	0.14	*0.709*
Family*Year	16.60	18; 114	16.23	*<0.001*
Error	1.03			

Note: Analysis of variance of mean germination time is weighted by inverse of year-wise standard error (see test).

between trees of 3 to 15 and 3 to 25 days reduction in mean germination time in 1993 and 1995 respectively (*figure 2B*). Furthermore, "naked seeds" obtained higher germination percentages than whole seeds (*figure 2A*). The pericarp delayed imbibition to 30 % moisture content with two days, and the embryo + seed coat had a 4 % lower moisture content after 14 days when imbibed with the pericarp compared to imbibition without (*figure 3*). Germination in "pericarp extract" had no effect on the final germination percentage, but delayed germination, resulting in 5.2 days longer mean germination time for the six trees tested (*figure 2*). The correlation between 1993-harvest and 1995-harvest in mean germination time was not improved by removal of the pericarp (r = –0.11), compared to germination with the pericarp (r = 0.25).

Cold treatment

Cold treatment for 5, 7 and 9 weeks, followed by germination at 15 °C, resulted in increasing germination at 5 °C before transfer to 15 °C (presprouting), increasing final germination percentages, a decreasing number of fresh non-germinated seeds and an increasing number of dead seeds (*figure 4*). The percentage germinated seeds after 5, 7 and 9 weeks (pre-sprouted seeds) were almost exactly the same as in the first germination test at 5 °C six months earlier. However, the mean germination percentage after 9 weeks cold treatment + germination at 15 °C was 64 %, which is 10 % below the mean germination percentage obtained for the seeds germinated at 5 °C. The mean percentage dead seeds after 9 weeks cold treatment and germination was 18.4 %, compared to 23.5 % dead seeds found in the first germination test at 5 °C.

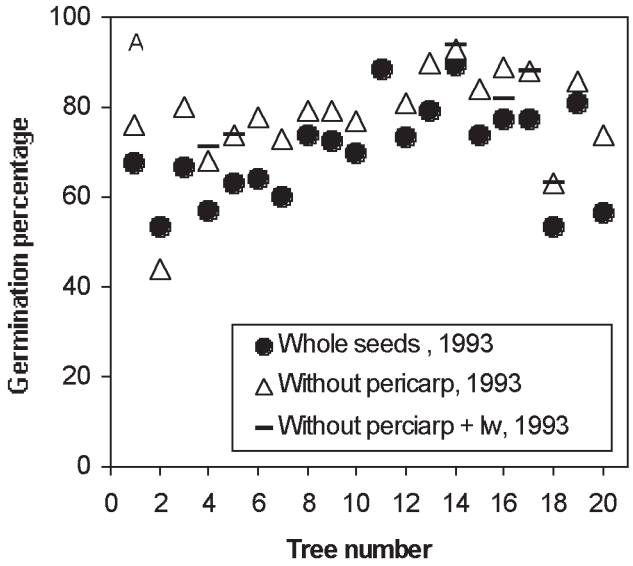
Final germination percentages increased with the length of the cold treatment: 48 % (5 weeks cold treatment), 54 % (7 week cold treatment) and 64 % (9 week cold treatment). These differences were highly significant. The families did react significantly differently on the cold treatment, but the interaction was relatively small compared to the main effects of families and treatments (*table 6*). Average family germination after 5 weeks cold treatment correlated well with germination after 7 weeks cold treatment (r(5w;7w) = 0.93); and fairly well with germination after 9 weeks cold treatment (r(5w;9w) = 0.78). Correlation germination after between 7 and 9 weeks treatment was 0.84.

The decrease in the effective population number (N_e) following the different cold treatments were 12 %, 12 % and 10 % for respectively 5, 7 and 9 weeks (*table 7*). The short cold treatment period (5 weeks) which resulted in substantially lower final germination (48 % compared to 64 %) thus only decreased the relative effective population number from 90 % (9 weeks) to 88 % (5 weeks). This corresponds with the relative high correlation between average single tree seedlot germination following the three treatment regimes.

Table 5. – Correlation coefficients between germination percentage, mean germination time (MGT), seed yield and seed weight in 1993 and 1995.

	Germination 1993	Germination 1995	MGT 1993	MGT 1995	Seed yield 1993	Seed weight 1993	Seed weight 1995
Germination 1993	1.00	-0.27	0.05	0.29	-0.32	-0.10	-0.29
	0.00	*0.27*	*0.85*	*0.23*	*0.19*	*0.68*	*0.23*
Germination 1995		1.00	0.04	-0.71	-0.43	0.10	0.52
		0.00	*0.87*	*0.00*	*0.07*	*0.68*	*0.02*
MGT 1993			1.00	0.25	-0.28	-0.14	-0.24
			0.00	*0.29*	*0.24*	*0.58*	*0.31*
MGT 1995				1.00	0.50	0.04	0.40
				0.00	*0.03*	*0.87*	*0.09*
Seed yield 1993					1.00	0.25	0.06
					0.00	*0.31*	*0.80*
Seed weight 1993						1.00	0.47
						0.00	*0.04*
Seed weight 1995							1.00
							0.00

Pearson Correlation Coefficients / Prob > |R| under Ho: Rho 0 = / N = 19
Note: Figure in italics is level of significance (H: r = 0).



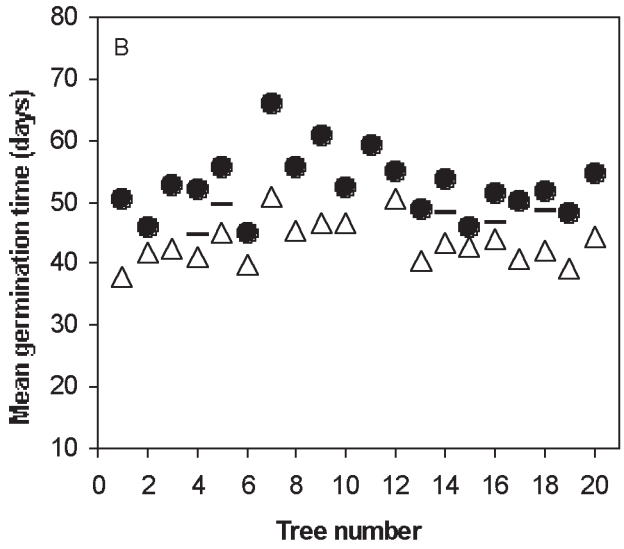


Figure 2. – Germination percentages (A) and mean germination time (B) at 5 °C for whole beechnuts, nuts without the pericarp and nuts without the pericarp germinated in an extract (lw) made on pericarps, from 20 individual trees in a seed stand in Graasten, 1993.

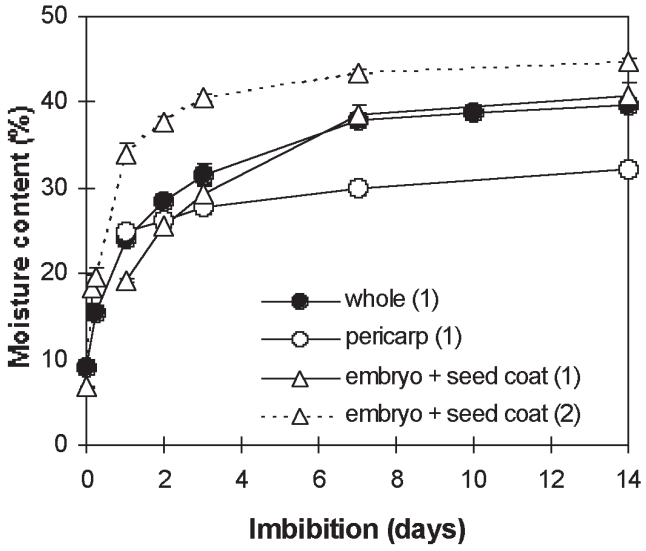


Figure 3. – Imbibition of whole beechnuts (1) and subsequent moisture content (m.c.) determination of whole beechnuts, pericarps and embryos + seed coats, and (2) imbibition and subsequent moisture content determination of embryos + seed coat. Beechnuts used were from tree number 17, 1993.

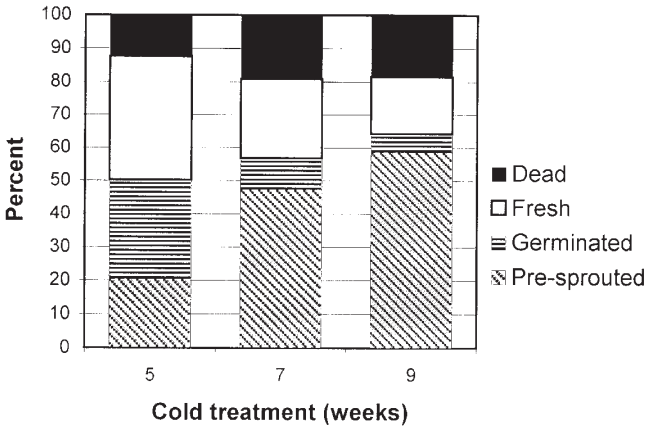


Figure 4. – Beechnuts cold treated for 5, 7 and 9 weeks at 5 °C before germination at 15 °C for four weeks. Presprouted seeds = % germinated seeds after cold treatment. Germinated seeds = % seeds germinated at 15 °C. Fresh seeds = % non-germinated, but seemingly viable, seeds after termination of the test. Dead seeds = % obviously dead seeds after termination of the test. Mean of 20 trees.

Seed weight

Mean fresh seed weights for the two years were identical: 0.20g ± 0.04g, and this trait correlated positive (r = 0.47) between the two years (*table 5*). In 1995 a positive correlation was also found between seed weights and germination percentages (r = 0.52) as well as mean germination time (r = 0.40), but this picture was not repeated in the 1993 progenies (*table 5*).

Discussion

The present study has revealed significant differences between progenies in germination capacity and dormancy, but it was not a simple pattern because the interaction between years was the most important source of variation. This means that it was different trees that were most successful in e.g. producing seed with high germination capacity and low dormancy in the two years. This can be a result of strong effects from the microenvironment of the single trees, which can vary from year to year and override additive genetic differences, i.e. effect of environment rather that genetics. It can be also be an effect of more genetic nature, if caused by interaction between microenvironment and the genotypes of the trees. These two possible effects can not be separated in the present study, but it can in any case be concluded that environmental variation has played an important role.

Although there were significant differences between the single tree seedlots with regard to germination percentages and dormancy, the effect of the variation in final germination percentages – as well as in germination percentages after different lengths of cold treatment – on the effective population number were in both cases moderate. Despite that 37 % of the seeds were dormant after 5 weeks cold treatment, the decrease in N_s was 'only' 12 %. The reduction in dormant seeds to 24 % and 17 %, after 7 and 9 weeks respectively, showed that the treatment was efficient in reducing the dormancy. However, the

Table 6. – Analysis of variance in germination for following the three cold treatments, *F*-test, degrees of freedom (Df) for *F*-test and level of significance (Pr>*F*).

Effects	MS	Df	*F*	Pr>*F*
Family	4486.80	17; 34	17.17	*<0.001*
Cold treatment	4965.12	2; 34	19.00	*<0.001*
Family*cold treatment	261.32	34; 162	2.40	*<0.001*
Error	55.97			

Table 7. – Relative effective population number (Nr) based on differences in seed yield (SY) and germination percent (*G%*).

	1993		*1995*			
	SY	*G%*	*G%*	*G%*(5w)	*G%*(7w)	*G%*(9w)
Ns	13.9	18.6	18.1	15.9	15.8	16.2
Nr	*73%*	*98%*	*95%*	*88%*	*88%*	*90%*

Note: G%(5w), G%(7w),G%(9w) refers to germinationf after cold treatment in 5, 7, and 9 weeks respectively (see text).

corresponding decrease in N_s was only reduced to 10 % (9 weeks of treatment), reflecting that the overall increase in germination was due to a general increase of all progenies, rather than a dramatic increase in a few progenies. The 10–12 % drop in N_s should be compared to the effects normally observed due to unequal flowering and fruiting. The variation in seed yield per tree in 1993 thus alone resulted in a 27 % decrease in N_s. This is in line with experiences from a large number of studies in natural stands and plantation of other broad leaves species, where unequal flowering often results in a decrease in effective population number on 50 %, sometimes more (cf. BILA et al., 2000, appendix 1 and references therein). The basic finding is thus that substantial variation between single tree seedlot was observed, but the impact of the effective population number was small compared to the normal fertility variation due to differences in seed production.

Genetic and environmental effects can not be separated based on the present analysis as mentioned. However, the low correlation at family level between germination and dormancy between the two years indicates low additive genetic control of the characteristics, or at least strong genotype x year interactions. Several factors have been reported to influence seed dormancy. Genetic components (e.g. CHAISURISRI et al., 1992), maturity (e.g. THOMSEN et al., 1997), as well as moisture content (THOMSEN, 1997), position on the plant (GUTTERMAN, 1980/81) and environmental factors during seed development such as temperature, light, water and nutrition (FENNER, 1991). Although the present experiment could not separate the effects into causal components, it clearly demonstrated the variation in seed characteristics experienced between single tree seedlots normally bulked in a seed lot. However, it also showed the variation in fertility due to variation in germination percent in this case was substantial lower than the fertility variation generated by difference in seed production.

The six months storage of the 1995-seed lots did not seem to have affected the level of dormancy, since similar germination percentages were obtained after 5, 7 and 9 weeks at 5°C in the two trials. Neither was there apparently any loss of viability, therefore comparison of the two methods should be possible. Complete release from dormancy was not obtained when cold treatment was followed by germination at 15 °C, even when almost 60 % of the seeds had germinated before transfer to 15 °C (after 9 weeks cold treatment) 17 % of the seeds were still dormant after the test was terminated. That is, combined cold treatment and germination at 5 °C gave the best germination in the present study. However, MULLER and BONNET-MASIMBERT (1989) obtained higher germination percentages as well as faster germination (after cold treatment with controlled moisture contents) at 5/15 °C compared to 4 °C. The effect of the temperature is not clear, because the seeds germinated at alternating temperatures received light during the day, whereas the other seeds were germinated at 4 °C in the dark. Still, both the present and the MULLER and BONNET-MASIMBERT (1989) study indicate that germination at 15 °C speed up germination of non-dormant seeds. Furthermore, it seems that a lower temperature is required to release the dormancy before this is possible, and that the two events: release of dormancy and germination are very close in time.

The effect of the pericarp on dormancy is probably a combination of several factors that delay or hinder germination. Mechanical resistance to germination is probably of small significance since the fruits tend to open in the end where the radicle protrudes. Hindrance of water uptake may contribute with a few days delay, i.e. the time it took to imbibe up to the 30 % moisture content where dormancy can be broken (MULLER and BONNET-MASIMBERT, 1989). Leaching substances from the pericarp seem to have a more pronounced effect. Five days delay in germination was obtained just by adding pericarp leachate water to the germination paper where the concentration of inhibiting substances must have been diluted over time, from the supply of clean water from the bottom of the germination box. It is likely that the dilution of inhibitors from the pericarp is much slower when the pericarp is still attached to the seed and therefore having a larger effect than in this experiment. Similar results have been obtained for *Fraxinus micrantha* (THAPLIYAL and NAUTIYAL, 1989). The inhibiting substances are probably phenolic compounds. Besides contributing to seed coat hardness and inhibiting growth of microorganisms (MOHAMED-YASSEEN et al., 1994 and WERKER, 1997), phenolic compounds in seed coats have been found to inhibit germination in *Chenopodium bonus-henricus* (DORNE, 1981), common buckwheat (*Fagopyrum esculemtum*) (SAMIMY, 1994), *Nyctanthes arbor-tristis* (BHATTACHARYYA et al., 1999), rye (*Secale cereale* L.), triticale (*Triticosecale*, cv Dagro), barley (*Hordeum vulgare* L. cv. Ars) and oat (*Avena sativa* L. cv.).

Significant differences between families with regard to germination percentages, mean germination time, seed weight and seed production were found. For seed weight, correlation between the two years were found, indicating a genetic component, contrary to germination and dormancy where no correlation was found. The variation between families interacted with the years, meaning that the ranking of families in terms of fertility varied between the investigated years. The pronounced variation between mature trees in their progenies (families) germination percentages and dormancy will have impact on the genetic composition of the seed lot. However, the impact was estimated to be moderate compared to the effect of variation in seed yield itself.

Apparently, the delay in germination which can be ascribed the pericarp is due to presence of inhibitors. Storage of dry beechnuts did not change the level of dormancy.

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