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Survival, Growth Trends and Genetic Gains in 17-year Old *Picea abies* Clones at Seven Test Sites

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(Received 23rd December 1994)

Abstract

Rooted cuttings (stecklings) from 40 different clones, and seedlings from one seed source of Norway spruce (*Picea abies* L. KARST.) were planted on 7 contrasting test sites in northern Germany. Survival rates and total heights (Ht) were observed at ages 3, 5, 8, 10, 13 and 17 years. Diameters at breast height (dbh) were also measured at age 17. Test site means for survival rate ranged from 81% to 95%, except site Kattenbühl (73%). About 70% of all deaths on the test sites occured within the first four growing seasons after outplanting. Clones taller in nursery tended to show higher death rates in the early years in the field than shorter clones. There were significant differences among the test sites in survival rates, but no rank interactions over the years. Seedlings and stecklings from the same origin (i.e. Westerhof) showed similar survival rates at all the test sites.

Stecklings planted on low elevation test sites showed better Ht performance than those at high elevation test sites (at age 17 years avg Ht at Syke 826 cm, at Lautenthal 492 cm). Overall means for Ht, dbh and volume index (VI) were 648 cm, 88 mm and 48.9 dm^3, respectively. Both the test sites and clones showed statistically significant differences in Ht, dbh and VI values. There were also significant clone x site interactions. Overall steckling Ht and VI values were larger than those of seedlings, relative difference being 11% and 37%, respectively, at age 17 years. Steckling heights at nursery were not reliable enough to predict future field performances. Broad sense heritabilities for Ht was 0.14, and for dbh was 0.13 at age 17 years. When 20% of the clones (8 clones out of 40) were selected, expected genetic gain in Ht is about 10.0%, in VI it is 33.0%.

Key words: Norway spruce, survival, height growth, clonal forestry, genetic gain, heritability.

FDC: 165.441; 232.11; 174.7 *Picea abies*.

Introduction

"Clonal Forestry" came into the scientific scene more intensively in the late 1960s. Its theoretical grounds and promising potentials in practical forestry have been discussed by several authors (e.g. KLEINSCHMIT et al., 1973; LEPISTO, 1974; TODA, 1974; SHELBOURNE and THULIN, 1974; KLEINSCHMIT and SCHMIDT, 1977; ROULUND, 1981; LIBBY, 1983). Along with these developments, many clonal experiments have been established at that period to realize the results of these potentials. The recent 2 books edited by AHUJA and LIBBY (1993) give an excellent overall review of the topic.

This study presents the results of 1 of those early clonal experiments which started in the late 1960s at the Lower Saxony Forest Research Institute (LSFRI), Dept. of Forest Tree Breeding. The objectives of this study are to examine the survival and growth trends over years in 17-year old trees, and estimate heritabilities for height and diameter growths.

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Materials and Methods

Clonal material

A program of large scale clonal propagation of *Picea abies* L. KARST. (Norway Spruce) has been described in earlier publications (KLEINSCHMIT et al., 1973; KLEINSCHMIT, 1974; KLEINSCHMIT and SCHMIDT, 1977). As part of this program, stecklings (rooted cuttings) are serially propagated on a 3-year cycle. Cuttings of the 40 clones used in this study were tertiary cuttings (third cycle of vegetative propagation started in 1968), which were rooted in spring 1977 and grown for 3 years in the nursery (*Table 5*, first column).

As a result of 3-year-cycle vegetative propagation program at the LSFRI, selection of best clones has been carried out at each propagation cycle based on nursery and field performance of clones. Therefore, the clones in this study are the outcome of such truncation selection. Prior to such selection, each clone was chosen from 13 different provenances of outstanding performance. One of these provenances was Westerhof where clone numbered 50 belongs to. Seedlings from a tested stand of Westerhof were also included in the study as a control for clone-seedling comparisons.

Test sites

During spring 1977, stecklings and control seedlings were planted at 7 contrasting test sites in northern Germany (*Table 1*). These sites represent an array of lands where Norway spruce clones from this program can be planted in the future. There were 20 experimental blocks within each test site. Each block contained 1 steckling from each clone, and 9 seedlings from Westerhof origin. Thus, initially 20 ramets per clone and 180 seedlings from Westerhof were represented at each test site.

Measurements

Number of alive trees were observed for each clone at ages 5, 8, 10, 13 and 17 years. Survival rate of clones was calculated by dividing the living number of trees in any observation year to the initial number of trees planted.

Height (Ht, cm) of each tree was measured at nursery before lifting at age 3, and again just after planting at each test site. Heights were also measured at the same observation years as survival. Diameter at breast height (dbh, mm) of each tree was measured at age 17 years. Volume Index (VI) at the same age was calculated by the following equation:

$$VI = (dbh/2)^2 \bullet Ht. 3.1416 \qquad \text{(Eqn. 1)}$$

and the results were expressed in dm^3.

Biostatistical analyses

a) Analysis of variance (ANOVA)

The ANOVA model in *table 2A* was applied for overall comparisons. The model was:

$Y_{ijk} = \mu + C_i + S_j + CS_{ij} + e_{ijk}$ where

Y_{ijk} = Observed value of the k_{th} ramet of the i_{th} clone at the j_{th} site;

μ = Overall mean (of N = s.c.t individuals);

C_i = Effect of the i_{th} clone (i=1, 2 ... c, c = 40);

S_j = Effect of the j_{th} site (j=1, 2 ... s, s = 7);

CS_{ij} = Interaction between i_{th} clone and j_{th} site;

e_{ijk} = Error term (within clone) (k=1, 2 ... t, t = number of trees (ramets) per clone. Initial number of t = 20).

Table 2. – ANOVA models used for comparisons of plant characteristics at different ages.

Source of Variation*	Degrees of Freedom*	Expected Mean Square*
A: FOR OVERALL COMPARISONS (Assuming completely random model)		
Sites	s-1	$V_e + t.\ V_{cs} + c.t.\ V_s$
Clones	c-1	$V_e + t.\ V_{cs} + s.t.\ V_c$
Clone x Site	(c-1)(s-1)	$V_e + t.\ V_{cs}$
Error	c.s.(t-1)	V_e
TOTAL	c.s.t-1	
B: FOR WITHIN-SITE COMPARISONS		
Clones	c-1	$V_e + n.\ V_c$
Error	c.(n-1)	V_e
TOTAL	c.n-1	

*) Number of sites, s = 7; Number of clones, c = 40; t = Effective number of ramets per clone per site (cst = N = 5591, 5179, 4953, 4806, 4738 and 4720 for the characters at ages 3, 5, 8, 10, 13 and 17 years, respectively). Ve = Within clone (error) variance; Vc = Variance due to clonal differences; Vs = Variance due to site differences; Vcs = Variance due to clone x site interactions. n = Effective number of ramets per clone within a site (cn = 584 in site K, 797 in site S, 798 in sites P, B, K, and 800 in H, L, M at age 17 years).

Table 1. – Some geographic, climatic and edaphic information on the test sites*).

Test Site (and its abbreviation)	Lat. N	Lon. E	Elev. m.	Mean Temp. °C Annual	Mean Temp. °C Growing Season	Mean Rainfall mm Annual	Mean Rainfall mm Growing Season	Soil Nutrient Status	Physical Soil Structure	Comments
Syke (Syk, S)	52° 50'	8° 49'	39	8.4	14.5	741	346	Good	Very good	Deep loam soil
Medingen (Med, M)	53° 06'	10° 32'	50	8.5	15.6	606	296	Medium	Good	Sandy soil with some finer components
Binnen (Bin, B)	52° 34'	8° 54'	40	8.5	14.9	670	320	Poor	Poor	Sandy soil, poor drainage below 60 cm
Paderborn (Pad, P)	51° 43'	8° 42'	340	7.8	13.8	1134	514	Medium	Very good	Loam soil with some sand components
Kattenbühl (Kat, K)	51° 20'	9° 40'	350	7.5	13.3	800	380	Medium	Good	Sandy soil with loam upper horizon
Holzminden (Hol, H)	51° 46'	9° 30'	445	7.5	13.4	900	420	Medium	Good	Sandy soil with some finer components
Lautenthal (Lau, L)	51° 52'	10° 17'	575	5.9	12.0	1344	550	Medium	Medium	Loam soil with some sand components

*) Data from ST. CLAIR and KLEINSCHMIT, 1986

The model in *table 2B* was used for clonal height comparisons within each test site. The models in *table 3A, 3B* and *3C* were used for comparisons of survival among the test sites, for comparisons of (pooled) clonal survival, and for comparisons of seedling-steckling survival, respectively. Variance components were calculated through "Expected Mean Square" components given on the right side on each ANOVA table. DUNCAN's Multiple Range Tests were applied to find out which entry is different from which ones.

Table 3. – ANOVA models used for survival.

Source of Variation*	Degrees of Freedom*	Expected Mean Square*
A: TEST SITES COMPARISONS		
Among sites	s-1	$V_e + c.V_s$
Error (within)	s(c-1)	V_e
Total	sc-1	
B: POOLED CLONAL COMPARISONS		
Among Clones	c-1	$V_e + s.V_c$
Error (within)	c(s-1)	V_e
Total	sc-1	
C: SEEDLING - STECKLING COMPARISONS		
Among Treatments	t-1	$V_e + s.V_t$
Error (within)	t(s-1)	V_e
Total	st-1	

*) Number of test sites, s = 7; Number of clones, c = 40; Treatment, t = 2 (Seedling vs steckling); Vs, Vc, Vt and Ve = Variances due to sites, clones, treatments and error.

b) Correlation coefficients

To determine the degree of associations between given character pairs, PEARSON correlation coefficients r_{xy} were calculated by the following equation:

$$r_{xy} = (Cov_{xy}) / \sqrt{(V_x \bullet V_y)} \qquad \text{(Eqn. 2)}$$

where:

r_{xy} = Phenotypic correlation coefficient;

Cov_{xy} = Covariance of variable X and variable Y;

V_x = Variance of variable X;

V_y = Variance of variable Y.

c) Heritability and gain estimates

Broad sense heritabilities (h^2B) and repeatabilities of clonal means (R_{cmn}) were calculated for total heights from age 3 to age 17, and for dbh at age 17 years, using the following equation:

$$h^2B = V_c/V_p \qquad \text{(Eqn. 3)}$$

where:

V_c = Variance due to clonal differences;

$V_p = V_c+V_{cs}+V_e$ = Phenotypic variance;

V_e = Within clone (error) variance.

Similarly,

$$R_{cmn} = V_c/V_{pcmn} \qquad \text{(Eqn. 4)}$$

where:

$V_{pcmn} = V_c + (V_{cs}/s) + (V_e/s.t)$

= Phenotypic variance of clonal means;

V_{cs} = Variance due to clone x site interactions.

Values in Eqn. 3 and Eqn. 4 were estimated employing overall ANOVA results as modeled in *table 2A*.

Genetic gain (GG_s) was calculated by:

$$GG_s = S.\ R_{cmn} \qquad \text{(Eqn. 5)}$$

where:

S = Selection differential;

= (Mean of the Selected Top Clones) - (Overall Mean).

In formulating the above equations, genetic principles as discussed in FALCONER (1981) and BECKER (1984) were followed. Several applications of these principles on forest trees were also referred (e.g. SHELBOURNE and THULIN, 1974; BURDON, 1977; ST. CLAIR and KLEINSCHMIT, 1986).

d) Non-parametric tests

KRUSKAL-WALLIS non-parametric tests (Chi Square approximation) were applied: i) To compare whether a given group has similar ranks across the observation years, and ii) To compare whether a given group has similar ranks across the test sites. All the above biostatistical procedures were performed using SAS programs (SAS, 1987).

Results and Discussion

A. Survival

Test site performances

Most of the deaths at the test sites occured within the first 2 years after outplanting (*Fig. 1, Table 4*). Average death rate was 7% from outplanting in spring 1977 to fall 1978, which is the first observation period. Average death rates during each of the subsequent observation periods were even smaller, being, 4%, 3%, 1% and 1%; at ages 8, 10, 13 and 17 years, respectively. Relatively high early losses were probably related mainly to transplanting shock experienced by plants in early years at the test sites. This hypothesis is supported by the trends that survival rates are more or less stabilized at all the test sites after the fifth year (age 8) in the field. Test sites showed statistically significant differences in their survival rates in all

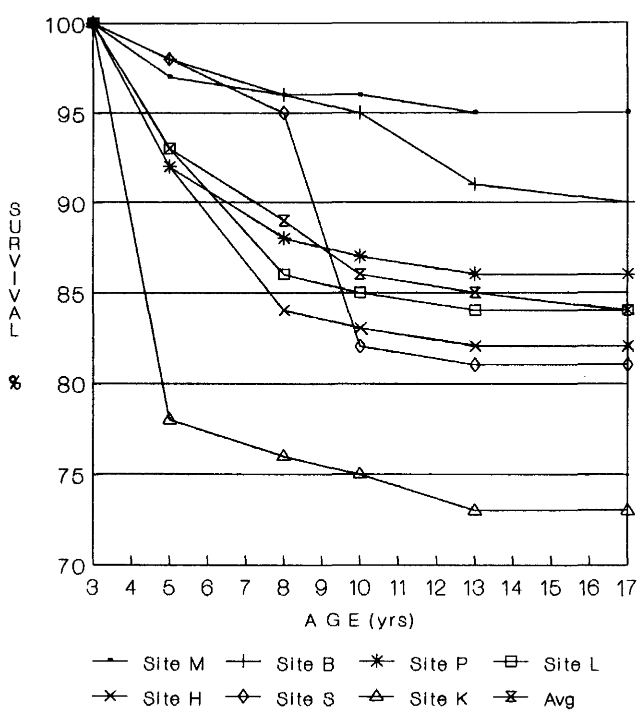

Figure 1. – Mean site-survival-rates of stecklings at 7 test sites from outplanting year to age 17 years. Overall average value is also indicated (Site abbreviations are the same as in *Table 1*).

Table 4. – Survival rates (S) of trees at test sites and their ranks (R) at different observation years following outplanting.

Age (year) :		5		8		10		13		17	
Observ. year :		1978		1981		1983		1986		1990	
Test Site	Ht (cm)†	S	R*	S	R*	S	R*	S	R*	S	R*
Syk	34.5	.98	1 a	.95	3 a	.82	6 d	.81	6 d	.81	6 d
Med	34.4	.97	3 a	.96	2 a	.96	1 a	.95	1 a	.95	1 a
Bin	36.4	.98	2 a	.96	1 a	.95	2 a	.91	2 b	.90	2 b
Pad	38.2	.92	6 b	.88	4 b	.87	3 b	.86	3 c	.86	3 c
Kat	36.7	.78	7 c	.76	7 c	.75	7 e	.73	7 e	.73	7 e
Hol	38.2	.92	5 b	.84	6 b	.83	5 cd	.82	5 cd	.82	5 cd
Lau	37.9	.93	4 b	.86	5 b	.85	4 bc	.84	4 c	.84	4 cd
Mean	36.6	.93		.89		.86		.85		.84	
Kat Seedl. ‡	-	.98		.98		.97		.97		.97	

†) Heights just after outplanting in spring 1977.

*) Test site means with a same letter in a given year are not significantly different from each other at the 5% level.

‡) Seedlings only from site Kattenbühl (for overall seedling means see *Table 5*).

observation years. Except site Syke, where 95% survival rate at age 8 suddenly dropped to 82% at age 10, each site more or less maintained the same rank orders over the years (*Table 4*).

Clonal comparisons

Clones 94, 50, 123 and 125 had the highest, and clones 173, 101 and 116 had the lowest overall survival rates (*Fig. 2, Table 5*). According to range tests, only these 2 groups of clones (but not the others) were significantly different from each other at the 5% level. KRUSKAL-WALLIS test showed that clones were inconsistent in their relative positions over the years (Significant at 0.001 level). However, after age 8 and 10 years, these rank changes were negligible (*Table 5*).

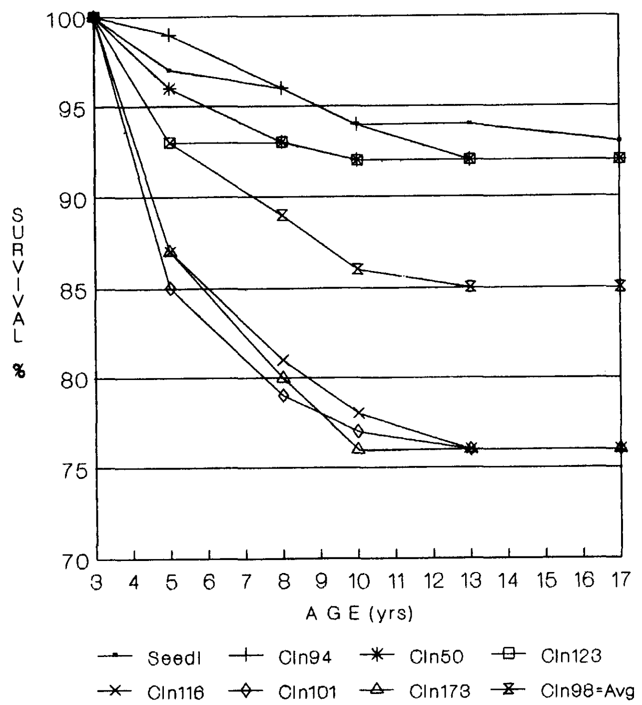

Figure 2. – Combined (of 7 test sites) mean survival rates of certain clones from outplanting year to age 17 years. Only the highest, average and the lowest surviving clones, and seedlings are shown in the figure (Clone numbers are the same as in *Table 5*, first column).

Table 5. – Overall clonal survival rates (S)†) and their ranks (R)‡) at different observation years following outplanting in spring 1977.

Age (years) :		5		8		10		13		17	
Observ. year :		1978		1981		1983		1986		1990	
Clone No.	Ht* (cm)	S	R	S	R	S	R	S	R	S	R
4	29.5	.91	30	.91	12	.86	24	.84	26	.84	26
9	33.5	.93	21	.90	16	.87	16	.86	17	.86	16
11	34.2	.89	33	.82	37	.79	37	.78	36	.77	36
15	40.2	.96	7	.90	18	.86	22	.86	21	.86	19
18	38.9	.91	31	.87	28	.83	30	.81	30	.81	30
26	41.4	.93	20	.92	10	.88	14	.87	10	.86	11
37	42.0	.94	17	.88	24	.87	17	.86	15	.86	12
41	36.0	.93	23	.89	23	.84	28	.84	28	.83	28
42	32.7	.96	4	.94	4	.91	5	.89	8	.89	8
45	28.6	.96	8	.94	3	.90	6	.89	6	.89	6
46	37.2	.94	11	.89	22	.89	12	.86	19	.86	18
50	34.9	.96	5	.93	5	.92	2	.92	2	.92	2
66	29.1	.94	13	.91	13	.88	15	.85	23	.85	22
87	37.4	.94	14	.90	19	.86	21	.86	20	.85	23
88	36.4	.92	26	.88	25	.86	20	.86	16	.86	14
90	33.0	.92	28	.87	26	.86	23	.86	18	.86	17
94	36.7	.99	1	.96	1	.94	1	.92	1	.92	1
95	38.1	.97	3	.93	8	.89	10	.89	7	.89	7
98	32.8	.93	22	.89	20	.86	25	.85	22	.85	21
101	39.0	.85	40	.79	40	.77	39	.76	39	.76	39
103	30.3	.96	6	.92	9	.89	11	.87	9	.86	10
104	31.2	.93	18	.91	15	.88	13	.87	13	.86	15
107	31.5	.87	39	.83	36	.80	36	.80	35	.79	35
112	39.0	.95	10	.86	32	.85	27	.84	27	.83	27
113	34.4	.88	36	.84	34	.83	31	.80	34	.79	34
115	34.5	.93	25	.86	30	.86	26	.85	25	.85	24
116	37.4	.87	37	.81	38	.78	38	.76	38	.76	38
118	36.2	.92	27	.89	21	.87	18	.87	12	.87	9
123	41.5	.93	19	.93	6	.92	3	.92	3	.92	3
125	35.1	.94	16	.90	17	.90	8	.90	4	.90	4
142	33.4	.95	9	.91	14	.90	9	.87	14	.86	20
143	38.1	.94	15	.91	11	.87	19	.85	24	.84	25
145	36.0	.94	12	.93	7	.90	7	.87	11	.86	13
152	30.3	.89	34	.86	31	.83	32	.81	32	.80	33
173	39.7	.87	38	.80	39	.76	40	.76	40	.76	40
181	40.5	.93	24	.87	27	.84	29	.82	29	.82	29
188	29.9	.98	2	.95	2	.91	4	.89	5	.89	5
189	26.8	.92	29	.86	29	.81	33	.81	33	.81	32
196	35.7	.88	35	.83	35	.81	35	.78	37	.77	37
197	33.7	.89	32	.84	33	.81	34	.81	31	.81	31
Mean	35.5	.93		.89		.86		.85		.84	
Seedlings ;		.97		.96		.94		.94		.93	

†) All 7 test sites are combined.

‡) Ranks are based on 4 digit pre-rounded up S values. "Tied" values, if any, received the smallest of the corresponding ranks.

*) Nursery heights of plants just before outplanting.

Clone x site interaction

Kruskal-Wallis test (df = 39, $Chi^2 = 37.27$) showed that rank order of clones across the test sites were not significantly different (i.e. a given clone did maintain its rank at the same level across the test sites). There are exceptions like clone 87 which had rank order 1 at Lau, but 35 at Kat (*Table 6*). A few extremely low surviving clones at certain test sites should be mentioned: Clone 101 had only 20% survival at site Kat, while average survival rate of the same clone at the remaining test sites was 85%. Similar, clone 11 at Kat, clones 173 and 196 at Lau had survival rates between 45% and 55%. The average survival rates of these clones at the remaining 6 sites were more than 80% (*Table 6*).

Seedling-steckling comparisons

Seedlings from Westerhof origin were compared with stecklings (clone 50) from the same origin. No significant differences were observed between these 2 groups of plants at all observation years (*Table 5* and *6*, bottom lines).

Seedlings and overall stecklings were also compared within each test site. No significant differences were found between them, except at site Kat. At site Kat, within the first 2 growing seasons, death rate of seedlings was only 2%, while death rate of stecklings was 22% (98% vs 78% survivals, respectively) (*Fig. 2, Table 4*). Why the losses of stecklings within the first 2 growing seasons at Kat are so high is not clear. However, there is evidence that higher death rates of stecklings at site Kat can partly be ascribed to relatively taller heights of stecklings planted on this site at plantation time (see survival-height relationships below). It should also be noted, that excluding the deaths during the first 2 years (which is the initial critical period for plantation establishment), survival rates of seedlings and stecklings remained stabilized in later years.

Survival-height-relationships

Using pooled data, correlation coefficients among clonal survival and clonal heights at different years were calculated. It appears that there is a negative association between clonal survival and average clonal height in the very early years. In other words, taller clones in the nursery seem to be suffered more by transplanting shock in the field than the shorter clones. After the second growing season in the field (age 5 from

Table 6. – Clonal survival rates and their ranks at age 17 years at 7 test sites.

Clone	Test Sites and Within-site Ranks (R)* of clones													
No:	Pad	R	Hol	R	Lau	R	Syk	R	Bin	R	Med	R	Kat	R
4	.80	28	.85	12	.90	13	.80	17	.95	7	.95	19	.65	30
9	.85	20	.85	12	.95	5	.80	17	.90	22	1.00	1	.65	30
11	.70	38	.85	12	.80	26	.85	7	.85	29	.80	38	.55	39
15	.90	10	.65	39	.90	13	.84	15	.90	22	1.00	1	.80	12
18	.85	20	.80	23	.65	37	.85	7	.85	29	1.00	1	.70	21
26	.85	20	.85	12	1.00	1	.80	17	.90	22	.95	19	.70	21
37	.90	10	.70	34	.85	19	.85	7	1.00	1	1.00	1	.75	16
41	.90	10	.75	28	.80	26	.70	36	1.00	1	1.00	1	.65	30
42	.95	4	.90	5	.90	13	.75	29	.90	22	.95	19	.85	6
45	.95	4	.80	23	1.00	1	.70	36	.95	7	1.00	1	.85	6
46	.80	28	.75	28	.85	19	.80	17	.95	7	1.00	1	.85	6
50	1.00	1	.85	12	.85	19	.95	1	1.00	1	1.00	1	.80	12
66	.90	10	.85	12	.90	13	.85	7	.65	39	.95	19	.85	6
87	.95	4	.85	12	1.00	1	.75	29	.89	28	.90	32	.60	35
88	.90	10	.85	12	.65	37	.80	17	1.00	1	1.00	1	.85	6
90	.80	28	.70	34	.95	5	.95	1	.95	7	.95	19	.70	21
94	.95	4	1.00	1	.95	5	.80	17	.95	7	.90	32	.90	2
95	.85	20	.85	12	.90	13	.75	29	.95	7	1.00	1	.90	2
98	.95	4	.85	12	.80	26	.85	7	.85	29	.95	19	.70	21
101	.90	10	.90	5	.75	30	.75	29	.85	29	.95	19	.20	40
103	.75	35	.90	5	.85	19	.70	36	.95	7	.95	19	.95	1
104	.84	26	.80	23	.95	5	.95	1	.95	7	.75	40	.80	12
107	.85	20	.80	23	.70	34	.65	40	.90	22	.95	19	.68	29
112	.90	10	.70	34	.75	30	.80	17	1.00	1	.80	38	.89	5
113	.90	10	.60	40	.90	13	.90	6	.65	40	.90	32	.70	21
115	.75	35	.90	5	.85	19	.80	17	.84	36	1.00	1	.80	12
116	.65	40	.70	34	.85	19	.75	29	.85	29	.95	19	.60	35
118	.75	34	.90	5	.95	5	.85	7	.95	7	1.00	1	.70	21
123	.95	4	.95	2	.95	5	.95	1	.95	7	.95	19	.75	16
125	1.00	1	.90	5	.75	30	.95	1	.95	7	.90	32	.85	6
142	.65	39	.95	2	.95	5	.79	28	.95	7	1.00	1	.70	21
143	1.00	1	.75	28	.75	30	.75	29	.90	22	1.00	1	.75	16
145	.80	27	.95	2	1.00	1	.85	7	.70	38	1.00	1	.75	16
152	.80	28	.75	28	.70	34	.70	36	.95	7	1.00	1	.70	21
173	.75	35	.75	28	.45	40	.84	15	.85	29	1.00	1	.65	30
181	.90	10	.80	23	.70	34	.75	29	1.00	1	.95	19	.65	30
188	.85	20	.90	5	.95	5	.80	17	.85	29	1.00	1	.90	2
189	.80	28	.70	34	.85	19	.80	17	.95	7	.95	19	.60	35
196	.79	33	.85	12	.55	39	.85	7	.75	37	.85	37	.75	16
197	.90	10	.75	28	.80	26	.80	17	.95	7	.90	32	.60	35
Mean	.86		.82		.84		.81		.90		.95		.73	
Seedl.	.92		.91		.95		.86		.94		.98		.97	

*) Ranks are based on 4 digit pre-rounded up S values. "Tied" values received the smallest of the corresponding ranks.

rooting), steckling height and survival rate showed statistically significant positive relationships (i.e., r = 0.33** between Ht and survival at age 5, N = 280). Similar trends were observed in later years. Starting at age 5, healtier and taller clones had higher survival rates in all subsequent years.

B. Heights

Test site performance

Test site means for height at different years are given in *table 7* and *figure 3*. There were significant differences among test sites for heights at all ages, and for dbh and VI at age 17 years (*Table 8*). At age 3 years, the relative difference between the tallest (Pad) and the shortest (Med) site was only 10.4%. This difference steadily increased and reached a peak at age 8 (84.9% between Syk and Lau), after which it smoothly declined, and came down to 51.6% at age 17. Starting at age 5 years, each site maintained more or less the same rank order over the years (*Fig. 3*).

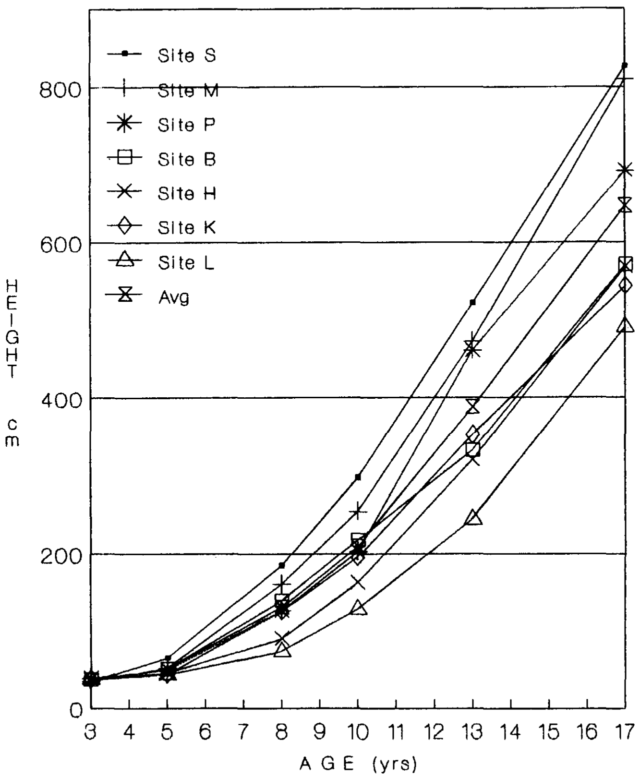

Figure 3. – Mean site values of total height of stecklings at 7 test sites from outplanting year to age 17 years. Overall average value is also indicated (Site abbreviations are the same as in *Table 1*).

Diameter (dbh) and Volume Index (VI) characters followed more or less the same ranking pattern as height at age 17 years (*Table 7*). Tallest test site (Syk) was not necessarily the thickest in dbh. Site Pad, although ranked third in height, was the thickest in dbh. VI of trees were 50.3%, 46.0% and 43.3% greater than the overall mean at site Med, site Syk and site Pad, respectively.

Clonal comparisons

Overall mean values of clonal heights, dbh and VI are presented in *table 9*. Relative difference between the tallest (clone 37) and the shortest (clone 189) clones was 42.8% at nursery. At age 17 years, relative difference became 33.8% (tallest: clone 123; shortest: clone 189). There were significant

Table 8. – Results of ANOVA tests based on individual observations (See *Table 2A* for the model applied).

Character	Source of Variation	d.f.	Sum of squares	F value
Height Age 3	Sites	6	12569	18.64 ***
	Clones	39	72260	16.48 ***
	C x S	234	26301	2.61 ***
	Error	5311	228975	
Height Age 5	Sites	6	247538	159.39 ***
	Clones	39	110791	10.98 ***
	C x S	234	60567	1.97 ***
	Error	4899	642819	
Height Age 8	Sites	6	6320243	436.93 ***
	Clones	39	1009657	10.74 ***
	C x S	234	564139	1.52 ***
	Error	4673	7395109	
Height Age 10	Sites	6	12585453	291.81 ***
	Clones	39	2546003	9.08 ***
	C x S	234	1682040	1.80 ***
	Error	4526	18068833	
Height Age 13	Sites	6	40701584	462.65 ***
	Clones	39	5908628	10.33 ***
	C x S	234	3430984	1.59***
	Error	4458	41204647	
Height Age 17	Sites	6	72750670	439.83 ***
	Clones	39	12285463	11.43 ***
	C x S	234	6450806	1.88 ***
	Error	4440	65254455	
dbh† Age 17	Sites	6	841997	165.19 ***
	Clones	39	397835	12.01 ***
	C x S	234	198787	1.71 ***
	Error	4440	2205995	
VI† Age 17	Sites	6	1998090	213.78 ***
	Clones	39	744822	12.26 ***
	C x S	234	364512	1.89 ***
	Error	4440	3662557	

†) dbh = Diameter at breast height, VI = Volume index.
***) Significant at the 0.01% level.

Table 7. – Height (Ht, cm), diameter (dbh, mm) and volume index (VI, Cubic dm) means through different ages (in years) at 7 test sites, and site comparisons by Multiple Range Test*).

Age :	3	5	8	10	13	17	17	17
Test Site	Ht	Ht	Ht	Ht	HT	Ht	dbh	VI
Pad	38.2 a	49.5 c	126.5 d	202.3 d	462.2 c	692.9 c	105.3 a	70.1 b
Hol	38.1 a	45.5 d	89.9 e	162.7 f	320.3 f	569.4 d	84.5 c	36.1 c
Lau	37.8 a	43.8 e	74.1 f	128.5 g	244.5 g	492.1 f	76.1 d	26.5 e
Syk	34.5 c	64.9 a	184.8 a	296.9 a	521.8 a	826.4 a	100.3 b	71.5 ab
Bin	36.4 b	50.6 c	139.5 c	217.9 c	333.1 e	571.5 d	71.4 e	31.4 d
Med	34.4 c	51.9 b	160.9 b	254.0 b	473.2 b	810.2 b	101.6 b	73.6 a
Kat	36.6 b	43.4 e	125.4 d	195.3 e	352.8 d	544.7 e	75.0 d	29.0 de
Mean	36.6	50.3	130.4	209.1	388.3	647.6	88.1	48.9

*) Test sites with the same letter in a given age are not significantly different from each other at the 5% level.

Table 9. – Overall clonal means of height (Ht, cm) at different ages, and of diameter (dbh, mm) and volume index (VI, cubic dm) at age 17 years.

Clone No	Ht Age3*	Ht Age3†	Ht Age5	Ht Age8	Ht Age10	Ht Age13	Ht Age17	R‡	dbh Age17	R‡	VI Age17	R‡
4	29.5	30.1	46.0	124.5	200.9	366.2	623.1	28	85.2	26	42.4	29
9	33.5	33.8	48.1	126.2	202.4	365.7	614.1	32	83.0	31	39.7	32
11	34.2	35.7	45.4	105.2	169.5	315.0	554.5	39	73.4	37	30.2	37
15	40.2	41.2	52.6	125.5	202.4	378.5	614.9	31	84.4	29	42.7	28
18	38.9	36.4	50.8	134.3	211.1	387.5	659.8	15	84.8	27	43.9	26
26	41.4	45.7	59.8	147.4	216.4	410.8	699.0	8	89.8	15	55.2	11
37	42.0	37.8	59.8	181.5	271.5	453.9	726.4	2	110.8	1	81.9	1
41	36.0	36.7	52.7	139.6	242.1	437.2	722.1	3	103.1	2	71.6	3
42	32.7	34.1	45.7	115.3	203.2	394.4	649.0	19	87.7	21	48.4	19
45	28.6	33.5	51.6	131.8	215.4	393.2	648.3	20	86.7	23	43.5	27
46	37.2	37.8	53.4	131.1	212.6	393.7	659.5	16	85.6	25	45.6	23
50	34.9	37.9	54.1	126.9	209.8	388.9	650.0	18	94.2	10	55.4	10
66	29.1	30.5	41.8	126.7	178.9	362.1	627.7	27	84.8	28	41.7	30
87	37.4	37.0	51.6	127.3	205.6	392.1	681.6	12	90.2	13	54.1	13
88	36.4	39.1	54.4	128.2	202.6	379.1	632.5	25	88.6	20	46.8	20
90	33.0	33.3	46.4	138.0	210.2	381.2	640.2	23	86.3	24	44.1	25
94	36.7	36.3	47.0	116.4	191.3	362.9	586.5	34	81.2	33	38.2	33
95	38.1	37.4	53.2	149.5	242.6	436.6	717.4	5	93.7	11	57.2	9
98	32.8	36.0	45.0	117.5	192.3	381.5	640.5	22	86.9	22	45.2	24
101	39.0	46.0	57.8	138.1	217.8	409.2	683.1	10	97.3	7	64.0	6
103	30.3	34.5	47.2	125.6	228.1	435.8	702.3	7	88.7	19	52.3	15
104	31.2	32.8	44.7	115.2	186.0	346.9	584.5	36	79.7	34	34.9	35
107	31.5	36.3	52.1	141.8	237.6	428.5	717.7	4	96.5	8	66.3	5
112	39.0	38.1	48.9	126.2	173.7	326.9	565.5	38	66.1	40	25.1	40
113	34.4	33.8	48.3	128.7	198.9	390.2	651.4	17	94.9	9	54.8	12
115	34.5	32.4	45.1	121.4	195.8	376.3	628.2	26	90.8	12	49.7	17
116	37.4	34.7	45.1	113.5	192.3	362.8	621.7	29	83.2	30	45.9	22
118	36.2	35.7	50.2	134.0	198.4	352.0	592.4	33	89.8	14	46.5	21
123	41.5	43.1	60.7	159.1	263.4	466.5	749.1	1	102.1	3	72.2	2
125	35.1	36.6	54.7	144.7	220.8	396.7	642.6	21	101.8	4	59.1	8
142	33.4	37.9	51.6	121.1	201.4	378.7	616.8	30	77.3	36	34.3	36
143	38.1	37.8	52.7	145.1	234.3	423.5	691.4	9	100.1	5	66.8	4
145	36.0	36.1	48.1	125.8	199.9	391.3	678.5	14	89.3	16	49.5	18
152	30.3	31.5	47.4	138.9	230.3	420.0	682.6	11	89.2	17	52.1	16
173	39.7	40.6	51.2	123.4	192.5	340.5	573.1	37	71.7	38	30.0	38
181	40.5	39.0	50.7	117.7	184.9	351.6	585.8	35	77.9	35	36.6	34
188	29.9	38.4	48.8	137.0	226.2	428.2	712.1	6	98.1	6	61.3	7
189	26.8	30.6	40.3	104.1	167.9	310.2	529.7	40	70.8	39	26.9	39
196	35.7	40.4	52.1	118.6	190.7	377.0	639.0	24	81.8	32	40.8	31
197	33.7	36.6	52.2	137.5	229.9	413.5	681.4	13	89.2	18	53.8	14
Mean	35.5	36.6	50.3	130.4	209.1	388.3	647.6		88.1		48.9	
Seedl. Mean	–	30.8	41.9	108.4	179.0	345.8	585.4		78.9		35.8	

*) Height at nursery just before outplanting.
†) Height just after outplanting.
‡) Rank order at age 17 years.

differences among the clones for heights at all ages, and for dbh and VI at age 17 years (*Table 8*).

Starting at age 5, clones 37 and 123 interchangeably ranked either the 1st or the 2nd. They may be called "consistently top performers" (*Fig. 4*). Clones 41, 87, 107 and 188 steadily improved their relative ranks, and thus they were "consistently upgrading performers". Clones 15, 88, 112, 118, 125, 173 and 181 did not maintain their relatively better earlier positions, and fall below the overall average at age 17 years. They were "consistently degrading performers". Clones 4, 9, 11, 66, 104, 115 , 116 and 189 were consistently low performers (*Table 9*). Apart from "upgrading" and "degrading" performers, most clones kept their relative ranks statistically at the same level across the observation years (KRUSKAL-WALLIS Tests: df. = 39, $Chi^2 = 162.55$, significant at the 0.01% level).

Clonal diameter (dbh) and Volume Index (VI) characters followed more or less the same ranking pattern as height at age 17 years. On the overall average, clones 37, 41 and 123 were among the top 3 in either Ht, dbh or VI (*Table 9*). Clones 107, 95, 103, 26, 152, 197, 18 and 46 were relatively tall, but not equally thick. Thus, these clones were relatively "slim clones". On the contrary, clones 125, 143, 101, 113, 50, 115 and 118 were relatively short but thick; thus, they were relatively "stout clones".

Clone x site interaction

Significant clone x site interaction were observed for total height (at all observed ages), and dbh and VI at age 17 years (*Table 8*). Plantation means of clonal heights, dbh and VI, and their rank orders at age 17 years are presented in *tables 10a*, *10b* and *10c*. Close examination of rank orders of the top 10 clones shows that clones 37, 95, 103, 173 and 188 were among the "most stable" (least interacting), and clones 87 and 101 were among the least stable (most interacting) clones in their

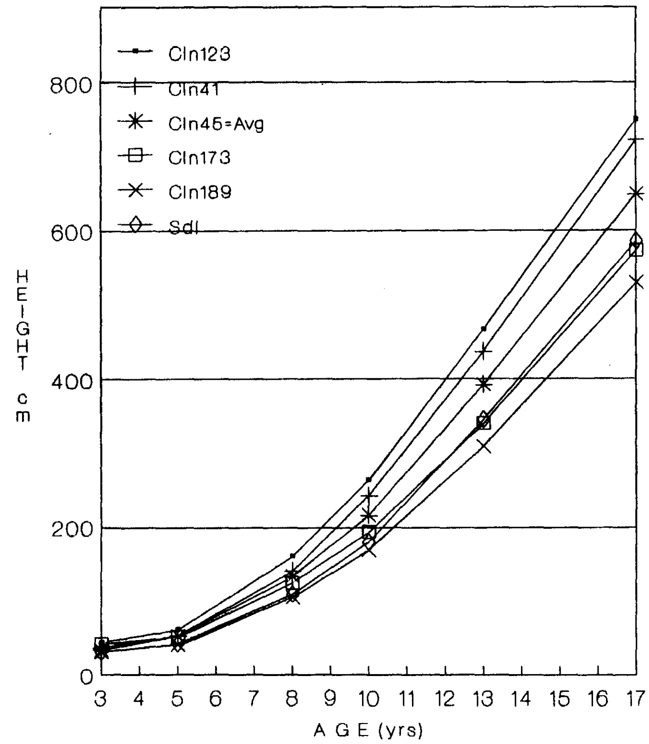

Figure 4. – Combined (of 7 test sites) mean total heights of certain clones from outplanting year to age 17 years. Only the highest, average and the lowest performing clones, and seedlings (Sdl) are shown in the figure (Clone numbers are as in *Table 5*, first column).

performance across the test sites. Most clones maintained their relative rank orders more or less at the same level across the sites (df. = 39, $Chi^2 = 185.19$, significant at the 0.01% level).

VI and dbh showed similar clone x site interaction trends as Ht at age 17 (*Table 10b, 10c*). As expected, these 3 characters were highly correlated (*Table 11*).

Further aspects of our findings on clone x site interactions in this experiment will be discussed in a separate article. It now suffices to indicate that, from the tree breeders' point of view the encouraging point is that many of the top clones were also relatively stable clones.

Seedling-steckling comparisons

The overall mean Ht of stecklings were always larger than that of seedlings at all observation years (*Fig. 4, Table 9*). At age 17 years, relative Ht and VI differences between seedlings and stecklings were 10.6% and 36.6%, respectively. All differences were highly significant at the 0.1% levels.

Separate evaluations of each test site showed that clones grew larger than seedlings at all sites except site Kat (*Table 10a*, bottom line). Relatively higher performance of seedlings at Kat probably arises from differential treatment of seedlings planted at this site (St. Clair and Kleinschmit, 1986), and also from relatively low survival rates of many top performing clones at Kattenbühl. The following additional information will clarify this point further. To start with, seedlings were 23% taller than stecklings in the outplanting year (Mean seedling Ht = 45 cm, steckling Ht = 36.0 cm). Furthermore, at the end of second growing season in the field at Kat, seedlings survival was 98% whereas that of clones was 78%. Survival rates of some faster growing clones (i.e., clones 4, 26, 37, 123, 143, 145) were below the site average. Combination of all of these factors might have contributed to the lower overall height performance of stecklings at Kattenbühl. It should, however, be noted that the initial 23% height difference between seedlings and stecklings at age 5 steadily declined and came down to 9% at age 17 years.

Age to age correlations

Steckling heights at nursery stage were significantly correlated with heights at the field only up to age 8 years (*Table 11*, second column). Therefore, mean nursery heights of clones were not necessarily a good indicator of heights at later years. Only after age 5 (i.e., second growing season in the field), tree heights at early years started to show statistically significant correlations with the heights at later years. It is also noted that there were very high and stable correlations among the plant heights at ages 10-, 13-, 17- and dbh and VI characters (*Table 11*). It means that Ht as early as at age 10 years is a very good indicator of both dbh and volume at later years.

Age dependency of variance components

Relative contribution of site variance (Vs) to total variance for height steadily increased up to age 8 years, after which it reached a relatively stable plateau around 45.0% (*Fig. 5*). This is expected because the test sites represent wide array of sites in northern Germany. On the contrary, error variance (Ve) decreased steadily and came down to about 40% level. These trends in age dependency of Vs and Ve were similar to those reported by Hühn et al. (1987) on a different set of clones on the same species. Relative contribution of clonal variance (Vc) to total variance for height was 20.0% at age 3 years (*Fig. 5*). Vc steadily decreased up to age 8 years, after which it came down to a stable level around 6.5%. This is not surprising, since the clones included in this study represent the best clones from earlier selections; thus they are genetically relatively homogeneous group.

Relative contributions of interaction variance (Vsc) to total variance over the years were also relatively small (*Table 12, Fig. 5*). Relative Vsc for Ht was about 6.0% at age 3 years. It decreased steadily up to age 8 years, after which it remained at a stable level around 2.0%.

Estimated heritabilities, repeatabilities and gains

Estimated variance components, and genetic parameters derived therefrom are presented in *table 12*. Broad sense heritability (h2B) based on overall evaluation for 3-year Ht was 0.21. The same estimates for Ht up to age 17 years remained between 0.10 and 0.14, and for dbh it was 0.13. These clonal heritability estimates are considered relatively low, which arise mainly due to relatively high contribution of Ve to the phenotypic variance (as in Eqn. 3). On the other hand, repeatability of clonal means (R_{cmn}) based on overall evaluation was quite high for Ht at all observation years (*Table 12*, last column). It remained within a relatively narrow range, being between 0.90 and 0.94 for the characters studied. These estimates are in accordance with the estimates made by St. Clair and Kleinschmit (1986) on the same experimental material at age 10 years.

Genetic gains (GG_s) in Ht and VI at different levels of selection intensity were also estimated (*Table 13, Fig. 6A, 6B*). When only the tallest clone (i.e., only one clone out of 40 clones) was selected, selection intensity being 2.161, the gain in Ht at age 17 years was 93.2 cm, which is 14.4% taller relative to overall clonal Ht means. When only the biggest clone (in VI, clone 37) was selected, the gain in VI at age 17 was 30.16 dm^3, which is 61.6% higher than overall clonal VI means. As intensity of selection is released, genetic gains decreased accordingly. For example, when 20 out of 40 clones (i.e., 50% selection level)

Table 10 A. – Clonal means of height (Ht, cm) and their rank orders (R) at each of the 7 test sites at age 17 years.

Site :	Paderborn		Holzminden		Lautenthal		Syke		Binnen		Medingen		Kattenbühl	
Clone No.	Ht	R*	Ht	R*	Ht	R*	Ht	R*	Ht	R*	Ht	R*	Ht	R*
4	647	33	548	27	487	21	825	20	532	27	723	37	615	5
9	695	18	537	31	475	26	788	29	497	32	745	33	557	15
11	594	40	467	38	391	38	700	40	530	28	716	39	453	37
15	668	28	498	35	494	19	795	25	544	24	769	29	490	33
18	660	30	580	17	504	16	818	21	574	19	849	11	535	22
26	757	3	571	20	544	7	906	7	590	17	940	2	578	10
37	749	6	621	7	574	2	915	6	679	6	840	14	666	3
41	732	8	654	2	556	4	940	3	664	7	923	3	533	24
42	692	19	612	8	515	13	843	18	493	35	830	16	571	11
45	664	29	582	16	516	12	853	16	614	12	792	22	547	18
46	674	25	549	26	479	24	873	10	564	22	843	13	611	6
50	682	23	565	22	455	31	864	13	612	13	794	21	519	27
66	634	35	517	33	543	8	772	34	570	21	790	23	538	20
87	725	12	652	3	468	29	917	5	571	20	901	6	541	19
88	719	14	595	13	473	27	790	28	541	25	776	27	489	35
90	672	26	600	11	506	14	811	22	516	30	783	25	566	13
94	683	22	546	30	431	35	775	33	450	38	760	31	495	30
95	736	7	625	5	554	5	889	9	684	3	874	9	666	2
98	691	20	571	21	446	33	797	24	610	14	760	30	560	14
101	712	15	552	24	504	15	901	8	620	10	844	12	492	32
103	708	16	622	6	535	10	956	2	683	4	875	8	580	9
104	643	34	561	23	415	37	729	38	528	29	726	35	510	29
107	819	1	599	12	444	34	960	1	682	5	910	5	549	17
112	619	37	525	32	463	30	743	36	391	40	718	38	525	26
113	728	9	460	40	542	9	808	23	546	23	806	18	552	16
115	728	10	547	29	480	23	793	26	500	31	797	19	534	23
116	659	31	547	28	454	32	864	14	485	36	794	20	519	28
118	634	36	479	37	470	28	785	31	496	34	790	24	471	36
123	726	11	716	1	557	3	857	15	748	1	944	1	676	1
125	679	24	591	14	533	11	737	37	598	15	757	32	570	12
142	684	21	576	18	478	25	777	32	596	16	727	34	494	31
143	698	17	574	19	487	20	866	12	690	2	819	17	658	4
145	783	2	607	10	545	6	831	19	534	26	831	15	590	8
152	720	13	608	9	497	18	920	4	586	18	869	10	528	24
173	605	38	462	39	365	40	791	27	482	37	724	36	423	39
181	670	27	505	34	365	39	772	35	497	33	776	26	448	38
188	755	4	640	4	588	1	850	17	643	8	911	4	593	7
189	597	39	482	36	431	36	702	39	436	39	662	40	342	40
196	652	32	583	15	482	22	785	30	632	9	774	28	490	34
197	752	5	550	25	498	17	867	11	619	11	878	7	535	21
Mean	693		569		492		826		572		810		545	
Seedl. Mean	642		518		447		663		514		717		595	

*) Ranks are based on 4 digit pre-rounded up Ht values.

were selected, the GG_s in Ht and VI were 5.8% and 18.1%, respectively. These gains seem to be small at first sight. However, it should be kept in mind that these values represent gains only from additional clonal selection from previously selected clones; and they do not include gains already achieved from earlier truncation selections.

Genetic Gains Relative to Seedlings

Gains mentioned above were relative only to overall clonal means. In order to compare gains from clonal selection to average seedling performance, a separate ANOVA (to fit model in *Table 2A*) was carried out with the inclusion of seedlings as another "entry" in the model (i.e., $c = 41$). Then, new variance components, clonal repeatabilities and gains were estimated. When only the best growing clone (in Ht, clone 123) was selected, the gain in Ht at age 17 years was 188.9 cm, which is 25.23% taller relative to seedling-Ht means. When only the biggest clone (in VI, clone 37) was selected, the gain in VI at age 17 was 95.4 dm^3, which is 116.49% higher than seedling-VI means. At 50% level of clonal selection the corresponding values were 15.84% and 57.66% for Ht and VI, respectively. As seen, estimated genetic gains are much higher when selected clones are compared to seedlings than they are compared to the other clones.

Conclusions

Survival

At age 17 years, test site means for survival rate ranged from 81% to 95%, except site Kat where the site mean was 73%. There were significant differences among the sites in their survival rates. However, differences among the clones in their overall survival rates at all observation years were not significant. Overall mean survival at age 17 was relatively high (i.e. 84%) to ensure operational plantations with clonal material of Norway spruce. The first four growing seasons after outplaning were the most critical period for clonal plantation establishment. About 70% of all deaths on the test sites took

Table 10 B. – Clonal means of diameter (dbh, mm) and their rank orders (R) at each of the 7 test sites at age 17 years.

Site :	Paderborn		Holzminden		Lautenthal		Syke		Binnen		Medingen		Kattenbühl	
Clone No.	dbh	R	dbh	R	dbh	R	dbh	R	dbh	R	dbh	R	dbh	R
4	99.1	27	81.4	25	72.5	25	110.9	5	63.6	30	93.1	31	79.0	11
9	108.8	18	75.8	30	74.3	23	99.3	22	56.4	38	94.2	29	71.0	27
11	87.7	37	69.1	39	54.0	38	86.7	37	66.7	27	87.0	37	60.6	37
15	102.6	22	71.5	36	75.7	20	94.3	30	69.9	22	97.7	25	73.9	19
18	96.8	31	79.5	29	74.3	22	94.7	27	69.0	23	101.2	20	70.3	30
26	104.2	21	91.9	9	77.6	16	105.9	13	66.3	28	109.6	11	71.7	24
37	131.6	1	101.0	3	101.3	1	131.7	1	90.8	2	119.9	3	97.8	2
41	115.6	8	99.8	4	91.9	4	117.8	2	85.6	5	129.3	1	74.0	18
42	98.6	28	93.2	8	80.7	12	104.3	16	59.6	32	104.4	17	73.7	21
45	97.7	30	87.7	14	78.3	15	99.2	23	77.0	14	95.1	27	73.8	20
46	99.5	26	80.0	28	67.6	30	100.9	21	67.1	25	101.3	19	83.5	6
50	109.4	16	82.9	22	70.8	26	107.1	9	84.7	6	118.1	4	78.5	12
66	91.9	36	73.1	34	89.3	7	94.4	29	66.8	26	94.8	28	77.4	13
87	100.4	24	95.9	5	66.5	32	106.0	12	71.8	19	114.7	5	75.0	16
88	116.1	7	89.2	12	75.4	21	94.6	28	76.3	15	93.1	30	72.7	23
90	102.0	23	93.8	6	81.9	10	97.6	25	58.6	36	95.6	26	76.0	14
94	108.5	20	82.4	24	62.1	36	92.8	32	56.1	39	98.6	24	70.3	29
95	114.0	9	83.3	21	81.9	11	102.6	19	82.1	9	110.8	9	81.8	10
98	111.2	14	87.5	15	67.1	31	97.6	24	71.0	20	92.4	33	74.7	17
101	116.3	6	85.7	18	77.4	17	114.0	4	79.1	12	114.5	6	71.0	28
103	93.8	35	82.5	23	76.8	18	104.2	17	82.9	8	100.7	21	83.3	7
104	94.8	34	83.6	20	63.3	34	88.6	35	70.5	21	84.4	38	75.8	15
107	130.1	2	86.5	16	61.6	37	115.0	3	89.7	3	111.9	8	71.3	25
112	78.5	39	70.0	38	67.8	29	75.0	40	38.8	40	72.1	40	66.5	32
113	113.2	11	72.5	35	89.7	6	105.5	14	77.0	13	108.4	12	83.2	8
115	120.8	3	86.3	17	79.7	14	92.8	31	68.0	24	104.7	16	82.9	9
116	98.0	29	80.4	26	70.4	27	106.6	11	57.2	37	99.3	23	71.0	26
118	108.6	19	89.2	13	88.0	8	103.5	18	64.2	29	105.3	15	68.7	31
123	113.9	10	104.4	2	86.5	9	107.6	8	88.7	4	122.9	2	87.7	5
125	110.8	15	110.2	1	99.2	2	105.5	15	84.6	7	112.2	7	88.5	3
142	100.3	25	74.2	32	62.9	35	85.3	38	73.6	16	88.7	35	60.2	38
143	118.6	4	93.4	7	80.1	13	106.6	10	94.5	1	102.4	18	99.2	1
145	113.1	12	90.0	10	90.8	5	95.2	26	63.0	31	93.1	32	73.5	22
152	108.9	17	85.6	19	74.2	24	110.3	6	72.1	18	106.0	14	64.0	35
173	82.7	38	66.7	40	43.4	40	88.1	36	58.8	34	87.2	36	57.3	39
181	95.7	33	74.7	31	52.1	39	92.0	34	58.7	35	100.4	22	65.4	33
188	117.0	5	89.7	11	96.3	3	102.5	20	81.9	10	110.7	10	88.1	4
189	77.5	40	73.8	33	70.3	28	83.1	39	59.4	33	77.4	39	50.0	40
196	96.6	32	80.2	27	64.4	33	92.0	33	80.7	11	90.0	34	62.1	36
197	112.9	13	70.2	37	76.6	19	107.8	7	73.4	17	108.4	13	65.1	34
Mean	105.3		84.5		76.1		100.3		71.5		101.6		75.0	
Seedl. Mean	94.6		74.6		69.1		78.3		64.7		89.8		81.0	

place within this period, which is most likely related to differential handling and transplanting shocks of the plantation material (BEINEKE and PERRY, 1965). Taller clones in the nursery tended to show higher death rates in the early years in the field than the shorter clones. Starting with the second growing season in the field, mean clonal heights in year n and clonal survival rates in the succeeding years showed significant positive relationships.

The relative rank order for survival of a given clone at a test site remained more or less at the same level on the other test sites, which implies no rank interaction across the test sites. Stecklings and seedlings from the same origin (i.e. Westerhof) showed similar survival rates at all test sites.

Heights, Diameter, Volume Index

On their average height, 17-years old clones grew largest at Syke (826 cm), and smallest at Lautenthal (492 cm). Generally, low elevation test sites performed better than high elevation test sites. Although trees at Syke were the tallest, they were not necessarily the thickest. Trees at site Paderborn had the largest average dbh (105.3 mm). In VI values, site Medingen was 50%, site Syke was 46% and site Paderborn was 43% greater than the overall mean (48.9 dm^3). Starting from the early years, each site maintained their relative height positions more or less at the same level over the years.

There were significant statistical differences among clones for heights at all observation years, and for dbh and VI at age 17. The relative difference between the tallest and the shortest clonal means was 34%, between the tallest and the overall clonal means was 15.7%. The corresponding proportions for VI were 226.0 and 67.0%, respectively.

Clones such as 41, 87, 107 and 188 were "consistently upgrading performers", i.e., they steadily improved their relative rank orders over the years. On the other hand, clones 15, 88, 112, 118 and 125 were "consistently degrading performers" since they did not maintain their relatively better earlier posi-

Table 10 C. – Clonal means of volume index (VI, cubic dm) and their rank orders (R) at each of the 7 test sites at age 17 years.

Site :	Paderborn		Holzminden		Lautenthal		Syke		Binnen		Medingen		Kattenbühl	
Clone No.	VI	R	VI	R	VI	R	VI	R	VI	R	VI	R	VI	R
4	59.1	29	30.3	27	22.0	26	81.2	13	21.9	29	53.3	33	32.5	10
9	66.6	21	25.5	33	23.3	24	62.5	26	16.2	37	55.6	32	26.8	22
11	44.4	37	19.9	40	11.0	39	47.1	37	24.2	27	47.2	37	14.8	38
15	61.9	25	27.6	31	26.2	17	60.4	28	28.3	22	63.1	25	25.2	26
18	54.3	34	30.3	26	24.1	22	60.5	27	28.7	21	73.0	21	22.0	32
26	73.9	16	38.8	13	27.3	14	89.8	7	27.4	23	100.1	4	27.5	21
37	110.2	2	52.9	4	48.1	1	131.7	1	53.2	3	111.9	3	55.5	2
41	87.9	8	53.7	3	40.5	4	107.6	2	46.8	5	124.6	1	25.8	25
42	63.5	24	45.0	7	30.7	11	75.5	17	20.5	31	76.4	18	28.1	18
45	58.2	32	38.1	14	25.8	20	67.3	21	32.7	17	59.3	29	26.7	23
46	59.6	28	29.6	29	19.6	29	71.9	19	25.1	26	75.8	19	35.3	8
50	70.2	18	35.1	19	19.4	30	81.5	12	45.2	7	94.1	8	30.4	13
66	48.9	36	27.6	30	35.9	8	58.2	29	23.5	28	62.1	27	28.9	14
87	64.5	23	48.4	5	19.4	31	83.7	11	32.7	18	99.7	5	28.1	19
88	79.2	11	42.1	10	26.1	18	57.6	31	33.2	16	59.0	30	24.6	28
90	58.8	30	42.4	9	29.3	12	66.0	23	18.2	34	63.3	24	28.7	17
94	67.3	20	30.2	28	15.2	37	56.8	32	15.0	39	62.4	26	24.5	29
95	82.9	9	37.4	16	31.1	10	80.4	15	41.9	10	87.4	10	40.7	4
98	74.2	15	36.4	17	19.3	32	64.9	24	26.6	25	57.0	31	28.9	15
101	91.8	4	37.9	15	25.9	19	98.2	4	38.8	12	96.3	6	26.0	24
103	61.0	26	34.8	20	26.9	15	86.9	8	45.7	6	80.8	13	37.5	7
104	49.6	35	32.5	24	17.6	34	48.6	36	26.7	24	47.7	36	24.8	27
107	117.7	1	39.5	12	15.7	36	103.4	3	52.6	4	94.1	9	27.9	20
112	36.3	39	22.9	37	21.1	27	35.4	40	8.3	40	32.4	40	21.5	33
113	77.1	14	25.3	34	37.3	6	78.1	16	34.4	15	77.7	16	33.7	9
115	88.5	7	34.7	21	28.3	13	56.2	33	28.9	20	78.2	15	31.8	12
116	65.5	22	33.9	22	22.5	25	81.0	14	16.5	36	72.0	22	28.8	16
118	72.2	17	32.2	25	31.5	9	71.4	20	20.5	32	74.3	20	22.9	30
123	91.6	5	65.3	1	36.9	7	85.1	10	56.8	1	117.7	2	46.5	3
125	78.9	12	58.0	2	43.9	2	66.4	22	43.4	8	79.2	14	38.6	6
142	58.7	31	27.0	32	17.2	35	46.8	38	30.9	19	48.4	35	15.7	37
143	95.6	3	47.8	6	26.5	16	96.6	5	56.6	2	76.5	17	57.1	1
145	82.4	10	41.7	11	39.3	5	63.5	25	21.8	30	61.3	28	31.9	11
152	69.0	19	36.3	18	23.4	23	90.0	6	35.8	14	81.1	12	21.3	34
173	41.3	38	21.3	39	6.6	40	49.9	35	15.1	38	46.9	38	12.1	39
181	54.5	33	24.4	36	13.2	38	54.4	34	17.2	35	65.9	23	18.3	35
188	89.8	6	44.9	8	43.8	3	74.5	18	42.4	9	94.3	7	39.1	5
189	35.0	40	22.4	38	20.6	28	41.8	39	19.1	33	36.2	39	7.9	40
196	60.4	27	32.6	23	18.7	33	57.7	30	39.0	11	51.5	34	17.6	36
197	78.8	13	25.0	35	25.3	21	86.5	9	37.6	13	87.1	11	22.2	31
Mean	70.1		36.1		26.5		71.5		31.4		73.6		29.0	
Seedl. Mean	53.3		27.2		19.7		36.7		24.5		52.9		35.7	

tions. Apart from these, most clones kept their rank orders roughly at the same level over the years.

Clones 107, 95, 103, 26 and 152 were relatively "slim clones", while clones 125, 143, 101, 113 and 50 were relatively "stout clones". Yet, there was a high positive correlation between the Ht and dbh of the trees ($r = 0.83^{***}$).

There were significant clone x site interactions in all the characters studied. Relative contribution of interaction variance to total variance was relatively low (around 2%) for Ht at age 17 years, which is a desirable outcome in tree breeding activities to plant certain superior genotypes to wide range of operational sites.

The overall mean Ht and VI of stecklings at age 17 years were always larger than those of seedlings, relative difference being 11% and 37%, respectively. Only at one site (Kattenbühl) where many of the fastest growing clones were represented by low number of trees due to relatively high death rates, seedlings mean was 9% taller than the overall steckling means.

Only after the second growing season in the field (i. e., age 5), steckling heights started to show significant positive correlations with heights at later years. Steckling heights at nursery were not reliable to predict future field performances.

Broad sense heritabilities for Ht was 0.14, and for dbh was 0.13 at age 17. These values seem to be relatively low, mainly due to high contribution of error variance (Ve) to the phenotypic variance. On the other hand, repeatability of clonal means was quite high, being between 0.90 and 0.94, for all characters at all years. When 20% of the clones (8 clones out of 40) were selected, expected genetic gain in Ht is about 10.0%, in VI about 33.0%. These gains represent gains from additional selection from the already selected clones; and they do not include gains already achieved from earlier truncation selection. The same expected gain values were much higher when selected clones were compared to seedlings.

Table 11. – Correlation matrix of plant characters at different ages.

Character†	HtNurs.	HtAge3	HtAge5	HtAge8	HtAge10	HtAge13	HtAge17	dbhAge17
HtAge3	.76 ***							
HtAge5	.69 ***	.80 ***						
HtAge8	.39 *	.34 *	.73 ***					
HtAge10	.22 ns	.26 ns	.65 ***	.88 ***				
HtAge13	.15 ns	.27 ns	.58 ***	.78 ***	.95 ***			
HtAge17	.15 ns	.27 ns	.55 ***	.76 ***	.90 ***	.98 ***		
dbhAge17	.16 ns	.17 ns	.54 ***	.80 ***	.85 ***	.85 ***	.83 ***	
VIAge17	.24 ns	.27 ns	.60 ***	.82 ***	.90 ***	.90 ***	.89 ***	.97 ***

†) HtNurs., HtAge3… = Plant height at nursery, at age 3 etc.. dbhAge 17, VIAge 17 = Diameter and Volume Index values at age 17 years.
ns), *), ***) Non significant and significant at the 5% and 0.1% levels respectively (df. = 38)

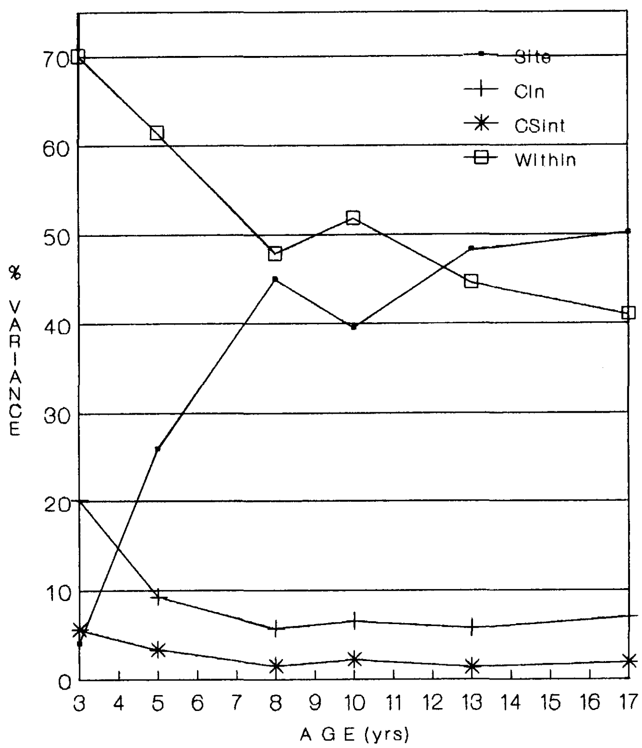

Figure 5. – Age dependency of different variance components for total height from outplanting to age 17 years.

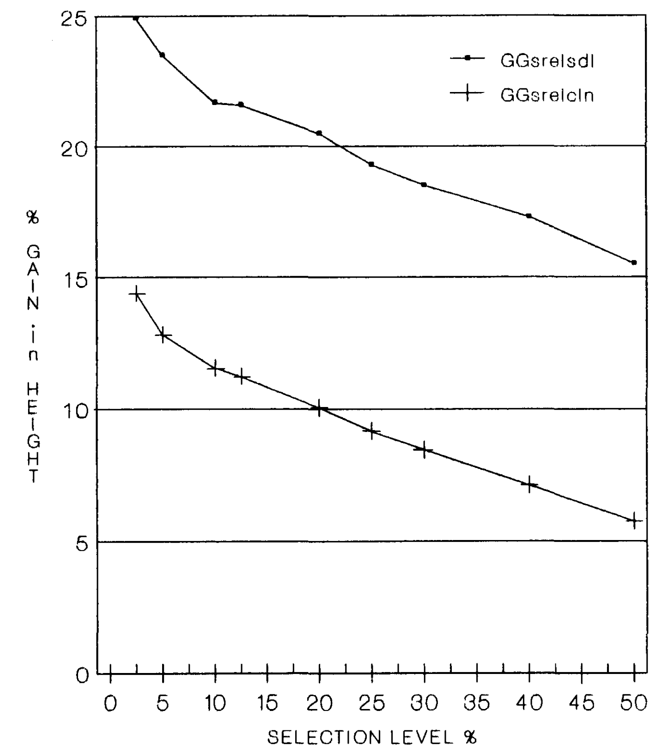

Figure 6a. – Genetic gains in height at different levels of selection of the top best clones at age 17 years. GGsrelsdl. = Genetic gain relative to seedlings. GGsrelcln = Genetic gain relative to clones.

Table 12. – Estimated variance components (EVC), heritabilities (h^2_B) and repeatibilities (Rcmn) for different clonal characteristics (Based on ANOVA model in *Table 2.* c = 40 clones).

EVC † :	V_s		V_c		V_{cs}		V_e			
Character‡	Abs.	%	Abs.	%	Abs.	%	Abs.	%	h^2_B	R_{cmn}
HtAge3	2.48	4.04	12.44	20.23	3.48	5.65	43.11	70.08	.211	.939
HtAge5	55.45	25.97	19.77	9.26	7.07	3.31	131.21	61.46	.125	.907
HtAge8	1486.78	44.98	187.43	5.67	49.07	1.48	1582.52	47.87	.103	.904
HtAge10	3048.24	39.53	501.28	6.50	168.64	2.19	3992.23	51.78	.107	.897
HtAge13	10011.27	48.29	1194.54	5.76	281.50	1.36	9242.85	44.59	.111	.909
HtAge17	17959.97	50.09	2510.14	7.00	690.47	1.92	14696.95	40.99	.140	.918
dbhAge17	206.98	25.74	77.10	9.59	23.11	2.87	496.85	61.80	.129	.911
VIAge17	491.91	32.60	145.11	9.61	47.08	3.12	824.90	54.67	-	-

†) Variance abbreviations are the same as in *table 2.*
‡) Abbreviations are the same as in *table 11.*

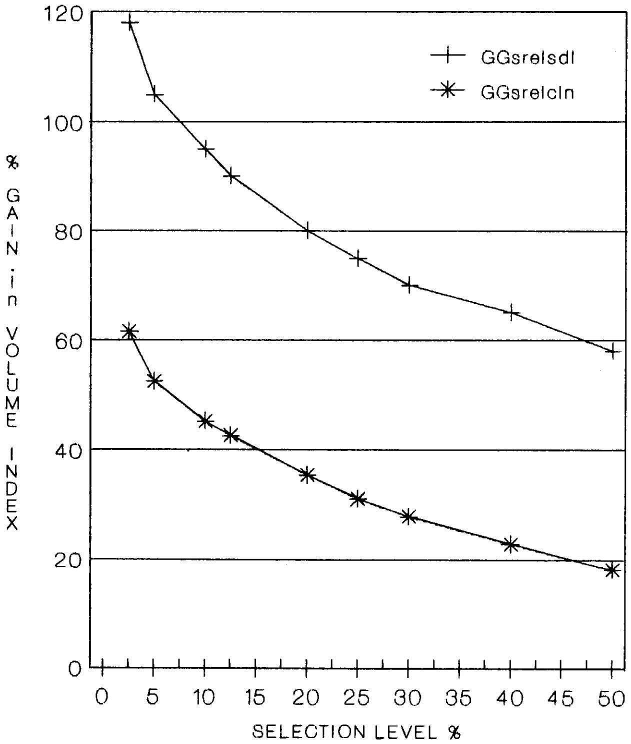

Figure 6b. – Genetic gains in volume index at different levels of selection of the top best clones at age 17 years. GGsrelsdl. = Genetic gain relative to seedlings. GGsrelcln = Genetic gain relative to clones.

Table 13. – Genetic gains (GGs) at different levels of selection of the top best clones (out of N = 40) at age 17 years.

Selection level†			GGs‡ Height (cm)		GGs‡ VI (cubic dm)	
n	%	i	Absolute	%	Absolute	%
1	2.5	2.161	93.21	14.39	30.16	61.59
2	5.0	1.957	82.80	12.79	25.70	52.48
4	10.0	1.694	74.61	11.52	22.11	45.14
5	12.5	1.596	72.52	11.20	20.86	42.60
8	20.0	1.365	64.93	10.03	17.34	35.41
10	25.0	1.242	59.24	9.15	15.22	31.08
12	30.0	1.134	54.65	8.44	13.61	27.79
16	40.0	0.947	46.09	7.02	11.15	22.77
20	50.0	0.782	37.26	5.75	8.87	18.10

†) n = Number of clones selected; % selected clones out of 40;
i = Selection intensity (after Becker, 1984).
‡) Genetic gain as calculated after Eqn. 5.

Acknowledgement

The authors gratefully acknowledge the assistance by BERND SEELMANN on the computer work. MANFRED HÜHN provided constructive criticisms of the manuscript. Most of the study was evaluated during KANI ISIK's visit in 1992 to 1993 as Alexander von Humboldt Research Scholar at LSFRI, Dept. of Forest Tree Breeding, Escherode, Germany.

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