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Results of Sequoiadendron giganteum ([Lindl.] Buch.) Provenance Experiment in Germany

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Abstract

30 provenances of *Sequoiadendron giganteum* from the natural range and 2 single trees from Germany were tested with seedlings and cuttings on 3 different sites in the mountain region of southern Lower Saxony in elevation between 300m and 400m.

Mortality and height growth up to age 12 were evaluated. Average mortality ranged from 16% in Bad Grund to 60% in Uslar with considerable differences between provenances. There was no significant correlation between latitude, longitude, and elevation of origin and mortality.

Mean height growth ranged between 2.94 m and 3.38 m. Site and provenance effects are significant. There was no significant difference between seedlings and cuttings. The fastest growing provenances were Whitaker's Forest, Standard USA and Mountain Home. Slow growing provenances were Merced Grove, Grant Grove and Windy Gulch.

The best growth was found in provenances from the central and southern central portion of the natural range. Certain provenances were poor survivors and performers on most sites.

The results are discussed especially with regard to the results of FINS and possible inbreeding.

The experiments must be followed further before recommendations for seed import can be derived.

Key words: Sequoiadendron giganteum, provenance experiment, mortality, growth, geographic variation.

Zusammenfassung

30 Herkünfte von *Sequoiadendron giganteum* aus dem natürlichen Verbreitungsgebiet und 2 Einzelbaumbeerntungen aus Deutschland wurden als Sämlinge und Stecklinge auf 3 verschiedenen Standorten im südniedersächsischen Bergland in Höhenlagen zwischen 300 m und 400 m über NN. geprüft.

Ausfälle und Höhenwachstum bis zum Alter 12 wurden ausgewertet. Die durchschnittlichen Ausfälle je Herkunft reichten von 16% in Bad Grund bis zu 60% in Uslar. Es gab keine signifikanten Zusammenhänge zwischen geographischer Länge und Höhenlage des Herkunftsortes mit der Mortalität.

Die Mittelhöhen reichen von 2,94 m bis 3,38 m. Standort- und Herkunftseinflüsse sind signifikant. Es gibt keine signifikanten Unterschiede zwischen Sämlingen und Stecklingen. Die raschwüchsigsten Herkünfte sind Whitacker's Forest, Standard USA und Mountain Home. Langsamwüchsige Herkünfte sind Merced Grove, Grant Grove und Windy Gulch.

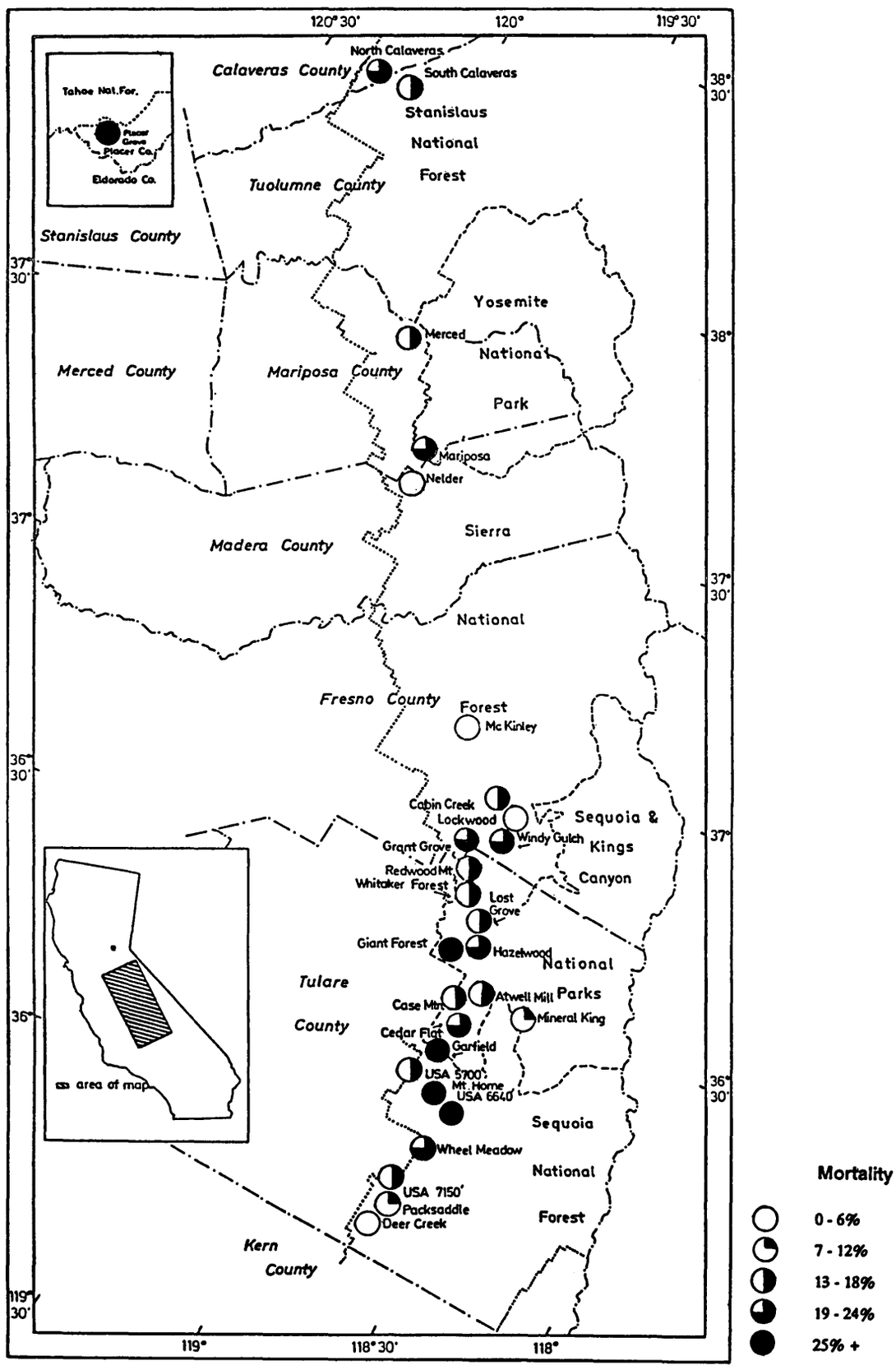
Die bestwüchsigen Herkünfte stammen aus dem zentralen und südlich-zentralen Teil des natürlichen Verbreitungsgebietes. Einige Herkünfte zeigen geringes Überleben und schlechtes Wachstum auf den meisten Standorten.

Die Ergebnisse werden besonders im Hinblick auf die Ergebnisse von FINS und mögliche Inzucht diskutiert.

Die Versuchsflächen müssen weiter verfolgt werden, ehe Empfehlungen für Saatgutimport gegeben werden können.

Introduction

Giant sequoia (*Sequoiadendron giganteum* (LINDL.) BUCH.) is the most massive living organism known and is second only to bristlecone pine (*Pinus aristata* ENGELM.) in verified



From MEYER, 1952

Figure 1. — Map of Sierra sequoia groves, showing mortality by grove from pooled data of Bad Grund and Escherode.

longevity (HARTESVELDT et al., 1975). However, it is not these features, but the fact that it is one of the world's fastest growing conifers (LIBBY, 1981) that makes it interesting to tree breeders and foresters. Although research in the species is presently still in the exploratory stage, early results show that there is good potential for its use in practical forestry.

Basic research by FINS (1979) greatly aided the understanding of the species and its variability. Population architecture studies showed a fair amount of inter-provenance variation, not surprising as sequoia tends to grow in disjoint stands rather than in a continuous distribution. This is especially pronounced at the northern edge of its range, where 8 groves are located well apart from each other and beyond the logical limit for gene flow through pollen distribution. FINS established that, in terms of isozyme studies, the northern groves are less variable than the southern ones, as measured by the observed level of heterozygosity, and concluded that this may be the result of inbreeding and/or bottlenecking of the populations.

Sequoia has shown itself to be adaptable to a wide range of climates, which makes its natural distribution a mystery. It occurs naturally only in a 420 km-long band that is never wider than 24 kms on the western slope of California's Sierra Nevada mountains, between latitudes 35°5' and 39°3' (*Figure 1*). Yearly precipitation generally averages more than 1000 mm, and falls in the form of snow or rain almost entirely in the winter, as this area is characterized by a Mediterranean-like summer drought.

In contrast, it has been successfully planted in New Zealand, Australia, and in Europe in Great Britain, France, the Benelux countries, Germany, Switzerland, Czechoslovakia, Hungary, Romania, Bulgaria, and along the Black Sea coast in the USSR (FINS, 1979; HARTESVELDT, 1969). Most of the European countries are located considerably further to the north than sequoia in its natural range, and have a colder, wetter climate. However, performance in Europe has been generally good to excellent (LIBBY, 1981), although troubles with frost hardiness and honey mushroom (*Armellaria mellea* (VAHL.) QUÉL) occur on some sites, and recently a new problem with a strain of Phomopsis has been developing in the warmer lowlands of France (LIBBY, personal communication).

European interest in sequoia as an exotic began shortly after the species was discovered by white settlers in California in 1852. Seeds were introduced to Europe from 1853 onwards and planted in several countries in arboreta, parks and botanical gardens, but no attempt to record the Californian provenance was made. Consequently, though there are many individuals in Europe, nothing is known about the origin of most of them.

After the second World War, selection and propagation of *Sequoiadendron* was started as a hobby by a dentist couple in Germany (MARTIN, 1957/1958). Through their activities a number of young stands were established in different parts of southern and western Germany. In 1955 R. KLEINSCHMIT began a conservation program for *Sequoiadendron* specimens older than 60 years north of the Main river. The basis for the selection of these trees was that they had already shown to be frost hardy enough to survive under comparably harsh conditions. These trees were grafted and planted in a seed orchard in Escherode, on the border between Lower Saxony and Hessia. Increment data from the few older stands show that *Sequoiadendron* is one of the most productive tree species and by far the most productive conifer which can be grown in Europe (KLEINSCHMIT, 1984). Frost sensitivity in the nursery stage is a major obstacle for this species in Germany. Variability was observed in many other characteristics as well, which motivated the establishment of provenance trials in Europe. Collections and outplantings for the Lower Saxony experiments were made in the 1970's and 1980's.

An intensive study of the wood characteristics of *Sequoiadendroi* in Europe, startet by KNIGGE and coworkers (KNIGGE and WENSEL, 1982; KNIGGE, PELLINEN and SCHILLING, 1983; KNIGGE and LEWARK, 1984; GUINON et al., 1983), showed that the trees grown in Europe were comparable to second-growth trees in the United Staates. The wood characteristics of these trees are not very different from the Coast Redwood (*Sequoia sempervirens* [D. DON] ENDL.) which is one of the most important commercial species in California.

Materials

Details of seed collection

LAUREN FINS made an extensive seed collection of natural populations of *Sequoiadendron* in 1974 to 1976. Seeds from 23 of these provenances were furnished by FINS and sown in 1976 to constitute the basic material for provenance research in Lower Saxony (*Table 1*). Material from these provenances was also used for climate chamber studies to evaluate frost hardiness (GUINON et al., 1982). In addition, seeds from a number of other sources in the U.S. and Germany were also sown in 1976 to supplement the provenance study and to evaluate the performance of seeds from trees raised in Germany that had survived the harsher climatic regime. In 1978 stecklings (rooted cuttings) were rooted from this material, and more seedlings were planted. Initially, 2 field tests were established in 1982 as experimental trials, at Bad Grund and Escherode (*Table 2*). An additional plantation, designed for use as a seed orchard, was established with the same material in Uslar (*Tab. 2*).

Site characteristics of provenance tests

All of the provenance tests are located in the state of Lower Saxony. In general, Lower Saxony has cool summers and cold winters, with regular precipitation throughout the year. Winter snowfall is common in the mountain areas and occasional in the valleys and plains.

Bad Grund: This field is located in the Harz Mountains of southern Lower Saxony, and was previously forested with norway spruce. It is 0.57 ha in size. The field was cleared but not cultivated before being planted with single tree plots in the spring of 1982 with 4-year-old stecklings and 3-year-old seedlings. The soil is a medium-weight, medium-moist loamy earth on a Greywacke parent material with a clay schist horizon. The average temperature for the year is 7.4°C, with a low of —1.5°C in January and a high of 16.4°C in July. The yearly variation is therefore 17.9°C, and on average there are 163 frost-free days in the year. The last spring frost occurs in early May, and the first winter frost occurs in the middle of October. Precipitation averages 1174 mm in a year, with July the rainiest period and March the driest. Height measurements were taken on this field in 1981, 1983, 1987 and 1990.

Escherode: This 0.55 ha field is located at the southernmost tip of Lower Saxony, on a site that was previously wooded with beech and spruce. It is surrounded on 3 sides by an old spruce/beech stand. The site was cleared, with

Table 1. — Provenances of *Sequoiadendron giganteum* tested.

SEQUOIADENDRON GIGANTEUM - PROVENANCES TESTED

N/S	#NFV	PROVENANCE	LONG.	LAT.	ELEV.
1	34	PLACER GROVE	120 34	39 04	1650
2	17	NORTH CALAVERAS	120 18	38 16	1463
3	7	SOUTH CALAVERAS	120 14	38 14	1494
4	20	MERCED GROVE	119 50	37 45	1753
5	24	YOSEMITE(BINNEWIES)			
6	4	MARIPOSA GROVE	119 37	37 31	1768
7	22	NELDER	119 36	37 26	1615
8	21	MCKINLEY GROVE	119 07	37 02	1920
9	10	CABIN CREEK	118 57	36 50	1798
10	5	LOCKWOOD	118 52	36 49	1920
11	12	WINDY GULCH	118 49	36 46	2073
12	11	GRANT GROVE	118 57	36 44	1920
13	13	REDWOOD MOUNTAIN	118 55	36 41	1768
14	35	WHITAKER'S FOREST	118 55	36 41	1500
15	3	LOST GROVE	118 49	36 39	1524
16	1	GIANT FOREST	118 44	36 34	1951
17	37	HAZELWOOD	118 44	36 34	1900
18	23	ATWELL MILL	118 40	36 28	1966
19	8	CASE MOUNTAIN	118 47	36 23	1858
20	19	CEDAR FLAT	118 44	36 22	1554
21	31	SEQUOIA NAT. FOREST	118 36	36 36	1750
22	36	GARFIELD GROVE	118 43	36 20	1980
23	28	USA 5700'	118 45	36 15	1730
24	14	MOUNTAIN HOME	118 41	36 13	1981
25	30	USA 6640'	118 40	36 15	2020
26	2	WHEEL MEADOW	118 34	36 07	1676
27	29	USA 7150'	118 35	36 00	2170
28	16	PACKSADDLE GROVE	118 34	35 56	1067
29	15	DEER CREEK	118 35	35 53	1798
30	33	STANDARD USA			
31	26	HERMESKEIL W. 1, GERMANY	6 57	49 39	750
32	27	HERMESKEIL W. 2, GERMANY	6 57	49 39	750

#N/S indicates north to south progression.
#NFV indicates number assigned to provenance at the research institute.

Table 2. — Site and layout information for provenance trials. Precipitation in mm per year, temperature in degrees Celsius.

(Forest district, establishment date, spacing, layout, longitude, latitude, elevation, precipitation, mean annual temperature and average number of frost-free days of provenance trials).

Forest	Established	Spacing	Layout	Long	Lat	Elev	Ppt	Temp	Warm days*
Bad Grund	spring 1982	4 x 4 m	STP	10 14	51 49	375	1108	7.4	163
Escherode	spring 1983	3 x 3 m	STP	9 45	51 20	350	800	8.0	160
Uslar	spring 1982	5 x 5 m	STP	9 44	51 41	330	950	6.7	164

*) frost-free
STP = Single Tree Plots

debris piled in windrows by a bulldozer. It was not cultivated before planting 5-year-old stecklings and 4-year-old seedlings in single tree plots in the spring of 1983. The soil is a medium-weight, medium moist loamy brown soil on a parent material of new red sandstone. On average, the yearly temperature is 7.6°C, ranging from a low of —1.3°C in January to a high of 16.3°C in July. There are about 160 frost-free days in the year, with the latest spring frost around the first of May and the earliest winter frost around the middle of October. Precipitation averages 765 mm per year, with the month of July the rainiest period and the months of February-March the driest. Height measurements were made on trees in this field in 1982, 1986 and 1990.

Uslar: This field is located in south Lower Saxony, on a site that had previously been used for pasturage. It is 2.38 ha in size and was planted as a seed orchard in single-tree plots with a mixture of 4-year-old stecklings and 3-year-old seedlings in 1982. The site had a cover of alder and a considerable number of other tree species were present. The site was not prepared before planting, and was overgrown with weeds. The soil is a medium weight, medium moist podzolic brown soil on a red sandstone parent material. The average yearly temperature is 6.7°C, with a low of 0°C in January and a high of 17°C in July, and an average yearly variation of 16.7°C. There are between 155 to 173 frost-free days in a year, with the last spring frost usually occurring in early June and the first

Table 3. — Mortality percentages for the provenance trials. #N/S indicates north to south progression, and #NFV indicates number assigned to provenance at the research institute. N refers to the number of individuals originally planted. The formula for calculating adjusted mortality permits calculation of negative mortality percentages. These values have been rounded to 0.0. The mortality percentages for the pooled data and the Uslar seed orchard were not adjusted.

MORTALITY

			BAD GRUND			ESCHERODE			POOLED			USLAR		
#N/S	#NFV	Provenance	N	Adj(%)	Rank	N	Adj(%)	Rank	N	Raw(%)	Rank	N	Raw(%)	Rank
1	34	PLACER GROVE	8	65.44	32	13	12.56	5	21	33.30	32	26	62	15
2	17	NORTH CALAVERAS	9	31.44	28	6	14.56	8	15	20.00	23	10	70	18
3	7	SOUTH CALAVERAS	8	2.44	1	31	20.56	14	39	17.95	17	25	40	2
4	20	MERCED GROVE	9	13.44	14	9	19.56	13	18	16.67	14	15	67	16
5	24	YOSEMITE BINNEWIES	18	8.44	13	-	--	-	18	6.00	6	10	40	2
6	4	MARIPOSA GROVE	8	2.44	1	34	21.56	16	42	19.05	20	20	45	6
7	22	NELDER	7	2.44	1	-	--	-	7	0.00	1	4	75	25
8	21	McKINLEY GROVE	1	2.44	1	-	--	-	1	0.00	1	2	100	31
9	10	CABIN CREEK	9	2.44	1	13	28.56	20	22	18.18	18	23	57	13
10	5	LOCKWOOD	5	2.44	1	-	--	-	5	0.00	1	4	50	9
11	12	WINDY GULCH	10	22.44	22	-	--	-	10	20.00	23	6	83	29
12	11	GRANT GROVE	9	2.44	1	12	30.56	21	21	19.05	20	12	50	9
13	13	REDWOOD MOUNTAIN	23	15.44	17	24	18.56	11	47	17.02	15	26	73	23
14	35	WHITAKER'S FOREST	9	2.44	1	46	17.56	9	55	16.36	13	25	68	17
15	3	LOST GROVE	10	13.44	14	1	0.00	1	11	9.09	7	10	80	28
16	1	GIANT FOREST	8	40.44	31	28	22.56	17	36	27.78	30	25	44	5
17	37	HAZELWOOD	9	13.44	14	22	20.56	14	31	19.35	22	10	60	14
18	23	ATWELL MILL	8	2.44	1	15	17.56	9	23	13.04	9	20	70	18
19	8	CASE MOUNTAIN	9	16.44	19	-	--	-	9	14.29	10	-	-	-
20	19	CEDAR FLAT	7	22.44	22	19	18.56	11	26	20.59	25	14	71	22
21	31	SEQUOIA N.F.	19	7.44	12	-	--	-	19	5.26	5	27	70	18
22	36	GARFIELD GROVE	10	22.44	22	6	30.56	21	16	25.00	27	20	70	18
23	28	USA 5700'	22	16.44	19	27	12.56	5	49	14.29	10	47	45	6
24	14	MOUNTAIN HOME	30	22.44	22	58	26.56	19	88	26.14	28	64	50	9
25	30	USA 6640'	23	37.44	30	75	31.56	23	98	27.55	29	57	73	23
26	2	WHEEL MEADOW	9	2.44	1	17	32.56	24	26	23.08	26	24	42	4
27	29	USA 7150'	22	29.44	27	40	10.56	4	62	17.74	16	46	48	8
28	16	PACKSADDLE GROVE	8	15.44	17	9	8.56	3	17	11.76	8	8	75	25
29	15	DEER CREEK	4	2.44	1	-	--	-	4	0.00	1	4	75	25
30	33	STANDARD USA	21	16.44	19	75	13.56	7	96	15.63	12	52	37	1
31	26	HERMESKEIL W. 1	10	22.44	22	1	0.00	1	11	18.18	18	8	88	30
32	27	HERMESKEIL W. 2	32	34.44	29	30	24.56	18	62	29.03	31	58	53	12

winter frost generally occurring at the end of October. Precipitation averages between 800 mm and 1100 mm per year, with June-July-August the rainiest period and February-March-April the driest. Only a portion of the total hectarage is analyzed here, as mortality was high in one experiment and another is confounded by the presence of a number of older sequoias planted in the mid-1970's that may be retarding growth. Height measurements were made in 1981, 1983, 1987 and 1990.

Methods

Measurements of the trials were made about once every 2 years, though longer periods occured. Tree height was measured and stem form damage noted when present. Results were analyzed both separately by field and combined with the other fields. Hierarchical analyses were made in each case as the 3 fields in the experiment differed from the others with regards to composition of provenances and number of individuals representing each provenance. Provenances represented by only 1 or 2 individuals were dropped from the regression analysis. For the pooled analysis, provenances that were represented by fewer than three individuals on 1 of the 2 sites were also dropped from the regression analysis.

Mortality calculations were adjusted to remove the effect of site by using the equation:

$$Xij^* = Xij—(x.j—\bar{x}..)$$

where Xij* is the adjusted mortality of a given provenance on a given site, Xij is the raw mortality, x.j is the average mortality on a given site over all provenances that are represented on both the Bad Grund and Escherode sites, and $\bar{x}..$ is the mean mortality of all provenances represented on both sites. This formula permits the creation of negative mortality percentages, which were rounded to 0%. All mortality percentages given for Bad Grund or Escherode are adjusted, except for the pooled data where this equation is illogical. For the pooled data, number of surviving individuals in both fields was divided by number originally planted (raw mortality percentage). As the Uslar field was planted as a seed orchard rather than as a field trial, its layout was not statistically designed and hence its mortality was not adjusted nor pooled with Bad Grund and Escherode.

Results

Mortality

Mortality was comparatively low in Bad Grund, varying from 2.44% to 65.44% (*Table 3*). Over all provenances,

mortality was 16.3% (unadjusted). Provenances with 2.44% mortality of at least 5 individuals included Wheel Meadow (9), Mariposa (8), Lockwood (5), South Calaveras (8), Cabin Creek (9), Grant Grove (9), Nelder (7), Atwell Mill (8), and Whitaker's Forest (9). High mortality was seen in Placer Grove (3 of 8 trees surviving), Giant Forest (5 of 8 surviving), USA 6640' (15 of 23 surviving) and Hermeskeil West 2 (22 of 32 surviving).

The field test in Escherode had somewhat higher mortality, varying between 0% and 32.56% (*Table 3*). Average mortality was 21.2% (unadjusted). Provenances with low mortality include Packsaddle Grove (8 of 9 trees surviving), USA 7150' (35 of 40 surviving), USA 5700' (23 of 27 trees surviving) and Placer Grove (11 of 13 trees surviving). High-mortality provenances are Wheel Meadow (11 of 17 trees surviving), USA 6640' (56 of 75 trees surviving), Grant Grove (8 of 12 trees surviving) and Garfield Grove (4 of 6 trees surviving).

Over these 2 fields, mortality averaged 19.7% (unadjusted) (*Figure 1*) (*Table 3*). Of the provenances represented in both fields, Lost Grove has the lowest mortality (9.09%, 10 of 11 surviving). Other provenances with low mortality are Packsaddle Grove (15 of 17 trees surviving), Atwell Mill (20 of 23 trees surviving) and USA 5700' (42 of 49 trees surviving). Provenances with high mortality include Placer Grove (14 of 21 trees surviving), Hermeskeil West 2 (44 of 62 trees surviving), Giant Forest (26 of 36 trees surviving) and USA 6640' (71 of 98 trees surviving).

The seed orchard in Uslar suffered from an unusually high degree of competition from weed species, giving it an overall mortality of 59.9% (*Table 3*). All provenances had severe losses, varying from 37% killed to 88%. Lowest mortality was shown by Standard USA (33 of 52 trees surviving), South Calaveras (15 of 25 trees surviving) Yosemite (Binnewies) (grove unknown) (6 of 10 trees surviving) and Wheel Meadow (14 of 24 trees surviving). Hardest hit were McKinley Grove (100%), Hermeskeil West 1 (1 of 8 trees surviving), Windy Gulch (1, of 6 trees surviving), Lost Grove (2 of 10 trees surviving) and Packsaddle Grove (2 of 8 trees surviving).

Regression analysis was performed to discover if a relationship existed between a provenance's mortality and the latitude, longitude and elevation of origin. This relationship was found to be nonsignificant. It was hypothesized that mortality in the eight disjunct northern populations, of which seven are represented in the Lower Saxony tests, may be higher as a result of inbreeding. It was thought that this may support Fins' assertion that the northern populations may be more inbred and also be subject to a strict regime of selection against inbred individuals. However, mortality in Escherode and Bad Grund for these northern populations was slightly less than overall, at 19.6%. Therefore, evidence of inbreeding is not apparent when considering mortality figures alone. However, mortality figures here only consider those that died after outplanting; the percentage that died in the nursery is not considered.

Height Growth

These trees were either 11 years from seed or 12 years from rooting in 1990.

Bad Grund: In 1990, the average height across the field was 2.94 m. Significant between-provenance differences existed ($p<0.003$), though differences between seedlings and stecklings were not significant. A DUNCAN's test for between-provenance differences made 5 groups (*Table* 4). The Lost Grove provenance was tallest in this field at 3.83 m, significantly taller than the Case Mountain, Garfield Grove, USA 7150', USA 6640', Deer Creek, Cedar Flat, Hermeskeil W. 2, South Calaveras, Grant Grove, Lockwood, Windy Gulch, Merced Grove, Placer Grove, and Hermeskeil West 1 provenances. Second tallest at 3.38 m was a source collected at an unnamed site in Sequoia National Forest. It too was significantly better than the Merced Grove, Placer Grove and Hermeskeil West 1 provenances. Third tallest at 3.33 m was Wheel Meadow provenance, significantly taller than Merced Grove, Placer Grove and Hermeskeil West 1.

Escherode: The average height in this field, 3.38 m, was the greatest of the three fields in this experiment, though they were outplanted a year later. Highly significant differences existed between provenances ($p<0.0001$), although differences between seedlings and stecklings were not significant. A DUNCAN's test between provenances made seven groups (*Table 5*). Tallest at 3.84 m was Whitaker's Forest provenance, significantly better than Grant Grove, South Calaveras, Mariposa Grove, Placer Grove, Wheel Meadow, Garfield Grove, Cabin Creek, USA 5700', North Calaveras and Merced Grove. Second tallest at 3.79 m was "Standard USA", a source received from a seed company with unknown geographic coordinates. This provenance was significantly taller than South Calaveras, Mariposa Grove, Placer Grove, Wheel Meadow, Garfield Grove, Cabin Creek, USA 5700', North Calaveras and Merced Grove. Third tallest at 3.69 m was USA 7150', significantly taller than Wheel Meadow, Garfield Grove, Cabin Creek, USA 5700', North Calaveras and Merced Grove.

Pooled estimates: Overall the average height was 3.20 metres. Analysis of variance showed that experimental field and provenance were both highly significant ($p<0.0002$). The difference between stecklings and seedlings for the pooled group was not significant. DUNCAN's multiple

Table 4. — DUNCAN's multiple range test showing average height by provenance at Bad Grund. N indicates number of individuals Heights and standard deviations in metres.

Provenance	N	Mean(±SD)	Group
Lost Grove	9	3.83(±.56)	a
Sequoia N.F.	18	3.38(±.73)	ab
WheelWheel Meadow	9	3.33(±.86)	ab
Mountain Home	24	3.25(±.89)	ab
Atwell Mill	8	3.22(±1.12)	ab
Nelder	7	3.19(±.60)	ab
Redwood Mountain	20	3.19(±.70)	ab
Standard USA	18	3.17(±.88)	ab
North Calaveras	7	3.16(±.70)	ab
Whitaker's Forest	9	3.13(±.73)	abc
Hazelwood	8	3.08(±.89)	abcd
USA 5700'	19	3.05(±1.09)	abcd
Packsaddle Grove	7	2.99(±.96)	abcde
Mariposa Grove	8	2.98(±1.12)	abcde
Yosemite Binnewies	17	2.97(±.96)	abcde
Cabin Creek	9	2.88(±.96)	abcde
Giant Forest	5	2.87(±.63)	abcde
Case Mountain	6	2.83(±.86)	bcde
Garfield Grove	8	2.82(±.70)	bcde
USA 7150'	16	2.82(±.73)	bcde
USA 6640'	15	2.78(±.63)	bcde
Deer Creek	4	2.70(±.66)	bcde
Cedar Flat	12	2.66(±.60)	bcde
Hermeskeil West 2	22	2.63(±1.06)	bcde
South Calaveras	8	2.62(±.50)	bcde
Grant Grove	9	2.52(±.89)	bcde
Lockwood	5	2.49(±.56)	bcde
Windy Gulch	8	2.48(±.76)	bcde
Merced Grove	8	2.17(±.63)	cde
Placer Grove	3	2.13(±.43)	de
Hermeskeil West 1	8	2.03(±.83)	e

Table 5. — DUNCAN'S multiple range test showing average height by provenance at Escherode. N indicates number of individuals. Heights and standard deviations in metres.

Provenance	N	Mean(±SD)	Group
Whitaker's Forest	37	3.84(±.83)	a
Standard USA	63	3.79(±.95)	ab
USA 7150'	35	3.69(±.76)	abc
Mountain Home	41	3.63(±.86)	abcd
Giant Forest	21	3.62(±.60)	abcd
Atwell Mill	12	3.48(±.89)	abcde
Hazelwood	17	3.42(±.63)	abcde
Redwood Mountain	19	3.42(±.99)	abcde
USA 6640'	56	3.39(±.92)	abcde
Hermeskeil West 2	22	3.23(±.92)	abcde
Cedar Flat	15	3.10(±.69)	abcdef
Packsaddle Grove	8	3.09(±.89)	abcdef
Grant Grove	8	3.04(±.73)	bcdefg
South Calaveras	24	3.01(±.73)	cdefg
Mariposa Grove	26	2.99(±.56)	cdefg
Placer Grove	11	2.97(±.66)	cdefg
Wheel Meadow	11	2.88(±.86)	defg
Garfield Grove	4	2.88(±.56)	defg
Cabin Creek	9	2.86(±.66)	defg
USA 5700'	23	2.80(±.86)	efg
North Calaveras	5	2.41(±.53)	fg
Merced Grove	7	2.29(±.60)	g

range test placed the provenances into 6 different but highly overlapping groups (*Table 6*). The tallest provenance overall was Whitaker's Forest, at 3.70 m. It was significantly taller than Mariposa Grove, Yosemite (Binnewies), Hermeskeil West 2, South Calaveras, USA 5700', Cedar Flat, Cabin Creek, North Calaveras, Garfield Grove, Case Mountain, Placer Grove, Grant Grove, Deer Creek, Lockwood, Windy Gulch and Merced Grove. Second tallest overall at 3.65 m was Standard USA, significantly taller than Hermeskeil West 2, South Calaveras, USA 5700', Cedar Flat, Cabin Creek, North Calaveras, Garfield Grove, Case Mountain, Placer Grove, Grant Grove, Deer Creek, Lockwood, Windy Gulch and Merced Grove. Third tallest at 3.49 m was Mountain Home, significantly taller than Deer Creek, Lockwood, Windy Gulch and Merced Grove.

To supplement the results from the experimental trials,

Table 6. — DUNCAN'S multiple range test showing average height by provenance in the pooled Bad Grund/Escherode set. N indicates number of individuals. Heights and standard deviations in metres.

Provenance	N	Mean(±SD)	Group
Whitaker's Forest	46	3.70(±.84)	a
Standard USA	81	3.65(± 1.01)	ab
Mountain Home	65	3.49(±.89)	abc
Giant Forest	26	3.47(±.66)	abc
USA 7150'	51	3.41(±.86)	abcd
Sequoia N.F.	18	3.38(±.73)	abcd
Atwell Mill	20	3.38(±.96)	abcd
Hazelwood	25	3.31(±.73)	abcd
Redwood Mountain	39	3.30(±.84)	abcd
USA 6640'	71	3.26(±.89)	abcd
Nelder	7	3.19(±.59)	abcde
Wheel Meadow	20	3.08(±.87)	abcde
Packsaddle Grove	15	3.04(±.89)	abcde
Mariposa Grove	34	2.99(±.73)	bcde
Yosemite Binnewies	17	2.97(±.96)	bcde
Hermeskeil West 2	44	2.93(±1.02)	cdef
South Calaveras	32	2.92(±.69)	cdef
USA 5700'	42	2.91(±.96)	cdef
Cedar Flat	27	2.91(±.68)	cdef
Cabin Creek	18	2.87(±.79)	cdef
North Calaveras	12	2.85(±.73)	cdef
Garfield Grove	12	2.84(±.63)	cdef
Case Mountain	6	2.83(±.86)	cdef
Placer Grove	14	2.79(±.69)	cdef
Grant Grove	17	2.76(±.83)	cdef
Deer Creek	4	2.70(±.66)	def
Lockwood	5	2.49(±.56)	ef
Windy Gulch	8	2.48(±.76)	ef
Merced Grove	15	2.23(±.59)	f

Table 7. — DUNCAN'S multiple range test showing average height by provenance in the Uslar seed orchard. N indicates number of individuals. Heights and standard deviations in metres.

Provenance	N	Mean(±SD)	Group
Redwood Mountain	7	2.89(±.21)	a
USA 7150'	24	2.87(±.59)	a
Yosemite Binnewies	6	2.78(±.74)	a
South Calaveras	15	2.76(±.51)	a
Cedar Flat	4	2.70(±1.05)	ab
Mountain Home	32	2.69(±.91)	ab
Standard USA	33	2.67(±.77)	ab
Sequoia N.F.	8	2.66(±.74)	ab
Wheel Meadow	14	2.61(±.54)	ab
North Calaveras	3	2.60(±.59)	ab
Atwell Mill	6	2.60(±.94)	ab
Mariposa Grove	11	2.51(±.94)	ab
Giant Forest	14	2.50(±.50)	ab
Grant Grove	7	2.46(±.95)	ab
Whitaker's Forest	8	2.46(±.85)	ab
Hazelwood	4	2.35(±.38)	ab
Garfield Grove	6	2.30(±.28)	ab
Hermeskeil 2	27	2.22(±.62)	ab
Placer Grove	10	2.22(±.55)	ab
USA 5700'	26	2.20(±.68)	ab
USA 6640'	34	2.15(±.56)	ab
Cabin Creek	10	2.04(±.42)	ab
Merced Grove	5	1.77(±.28)	b

the Uslar seed orchard results: Average height across the field in 1990 was 2.48 metres. Significant differences between provenances existed ($p<0.01$), although not between stecklings and seedlings. A DUNCAN's test of provenances made three highly overlapping groups (*Table 7*). Tallest at 2.89 m was Redwood Mountain provenance, significantly taller than Merced Grove. Second and third tallest at 2.87 m and 2.78 m respectively were USA 7150' and Yosemite Binnewies provenance. They were also significantly taller than Merced Grove.

Discussion

It is somewhat inappropriate to call certain of the provenances tested true provenances, as they originate from a single tree. These include Hermeskeil West 1, Hermeskeil West 2, Escherode 1977 Young and Escherode 1977 Old (the Young and Old designation refer to the age of cones that yielded seed). Furthermore, some of the provenance differentiations are somewhat artificial, such as Hazelwood, which is an extension of the Giant Forest stand, and Whitaker's Forest, the southern tip of the Redwood Mountain stand. A future project giving a standardized set of provenances with geographical boundaries in the native range might be helpful.

Mortality did not follow a generally geographic pattern, nor was it influenced by the elevation of the seed source. Provenances with higher mortality were found close to provenances with low mortality (Giant Forest between Lost Grove and Atwell Mill, USA 7150' near Packsaddle Grove). In addition, high-mortality provenances on one site were often low-mortality provenances on another.

Best performance was found in provenances from the central and southern central portion of the range. Notable provenances are Whitaker's Forest, Mountain Home, Redwood Mountain, Atwell Mill, Hazelwood, and Nelder. Possibly interesting provenances include Lost Grove, which was the tallest at Bad Grund but was represented at Escherode by only one individual, and Sequoia National Forest, doing well at Bad Grund but unrepresented at Escherode. It seems that provenances from the edges of the range, as Placer Grove, Merced, Deer Creek, and Packsaddle Grove, were generally poorer performers.

Certain provenances seemed to be poor survivors and performers on most sites, such as Placer Grove and Hermeskeil West 1. The problem in both cases may be related to inbreeding. Placer Grove is the furthest north of the natural stands, and consists of only seven individuals which are almost certainly related. As it is beyond the range for pollen dispersion from other groves, seeds must have been fertilized within the grove. The Hermeskeil West trees, 1 and 2, are two individuals standing next to each other with no other trees in the area. While the origin of these two trees is unknown, one might hypothesize that they were brought by an individual from the same grove in California, perhaps from the same tree. If so, seeds from either of these trees would be either selfs or full-sib offspring of halb-sib parents.

It may be that inbreeding is a more widespread problem, masked in our provenance trials as most of the material we have tested has had no opportunity to be outcrossed and replanted. Some seeds collected from European stands may be outcrossed progenies, depending on the composition of the stands. The performance of the 2 Escherode sources tested is not particularly outstanding, though they come from a mixed-provenance stand. Both seeds collected directly from natural stands and stecklings made from these seedlings is suspect with regards to possible inbreeding, the more so with FINS' assertion that there is little gene flow between groves. FINS comments as well that there may be rigorous selection against selfed and otherwise inbred trees as evidenced by the differing levels of heterozygosity between mature trees and seeds. FINS suggests that many trees raised in the nursery and outplanted may not be subject to this rigorous selection and so survive, thus degrading the population. Clearly the next step in Lower Saxony is to begin outplanting open-pollinated seeds gathered from the seed orchards in Escherode and Uslar and from the experimental trials. This should relieve any possible inbreeding depression, as each seed orchard and experimental trial comprises trees from most provenances.

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Modélisation du Profil Vertical des Diamètres, Angles et Nombres de Branches pour Trois Provenances d'Epicea Commun

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Résumé

Les profils verticaux des diamètres, des angles et des nombres de branches de 3 provenances françaises de *Picea abies* ont été modélisés et comparés sur des arbres âgés de 27 ans, de mêmes dimensions et statut social. Bien que significatives, les différences de diamètres de branches entre provenances sont très faibles lorsque l'effet de la vigueur individuelle est éliminé. Ce n'est pas le cas pour les angles où les provenances s'individualisent bien. Les nombres de branches verticillaires et de diamètre supérieur à 1cm ne diffèrent pas quant à eux d'une provenance à l'autre, au contraire du nombre de branches total et du nombre de branches de diamètre > 0,5cm. L'originalité de la méthode utilisée — modélisation des profils verticaux complets pour les angles et les diamètres, prise en compte de l'effet longueur des unités de croissance et d'une distribution log-normale des résidus pour les nombres de branches — est discutée dans divers contextes: amélioration génétique, évaluation de la qualité des bois et étude de l'architecture des arbres.

Mots-clés: *Branchaison*, provenance, *Picea abies*, ressource forestière, qualité des bois, diamètre de branche, nombre de branches, angle de branche.

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Abstract

The vertical distributions of branch diameters, angles and numbers are modelled and compared for 3 *Picea abies* provenances on 27-years old trees that have about the