Institutionen för skoglig genetik och växtfysiologi

Altitudinal transfer of Norway spruce (*Picea abies* (L.) Karst.) provenances in northern Sweden

Höjdförflyttning av granprovenienser i norra Sverige

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Preface

This thesis is written as a 20-credit project within the Master Program in Forestry at SLU.

During the last five years I have tried to get a relatively broad education in the field of forestry and my interests range from ecology to wood science. For this thesis I wanted a topic that is closely related to practical forestry and to find a suitable project I contacted Ola Rosvall at SkogForsk, the Forestry Research Institute of Sweden. After visiting several field experiments that were waiting to be analyzed we decided on a recently rediscovered series of Norway spruce provenance trials where we could study the altitudinal aspect of transfers.

I would like to thank my supervisors, Johan Westin at SkogForsk for his help from the early planning phase to the very last day of writing, preparing me for the fieldwork, running the SAS program for the data analysis and providing me with useful literature, archive data and maps, and Jan-Erik Nilsson at SLU for valuable comments on the statistics and the writing. Thanks also to Henrik von Stedingk for an interesting discussion on the immigration history of Norway spruce.

The assessment of one of the trials was already finished, thanks to Mikael Westerlund and Tomas Sandström. The deal was that I would do another trial as a return favor for SkogForsk, which was good because it gave me the opportunity to get acquainted with the equipment and with those partly spoiled and therefore abandoned and forgotten field trials. The greatest challenge was to actually find the trials and then to find the corner posts and the trees that belong to each row. Special thanks to Alina Cushing who helped me with the fieldwork. After coming all the way from Alaska via Iceland, to do an internship at SkogForsk, the first thing they had planned for her was to take a trip to the Norwegian border to assess these trials with me. Here, the return favor was to show her some of our prettier, admittedly, lodgepole pine plantations to take increment cores for her project. It was great to have her along.

Thanks to Karlssons who let us borrow their worn down but still rain proof hunting cabin which had the advantage of being right next to one of the study sites, thus saving us the trouble of hiking up and down that mountain more than once to do the inventory. Thinking of the location of the field trials, maybe we should also give credit to the people who planned and established them in the 1940s. There was obviously nothing wrong with their enthusiasm and motivation and it was interesting to read about their observations and ideas in the trial journals.

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Abstract

Provenances of Norway spruce (*Picea abies* (L.) Karst.) are generally transferred from lower latitudes and elevations to areas where the local seed production is insufficient and with the goal to increase volume production because growth cessation in the fall is induced later in northward transferred material. The aim of this study was to analyze the effect of altitudinal transfer on volume production and survival in three mature field trials located at 420, 500, and 620-650 m a.s.l. in northern Sweden. A total of 13 provenances from latitudes between 61 and 64.5 ºN and altitudes between 50 and 500 m a.s.l. were included. The trials consisted of 2-4 blocks and 8-9 provenances planted in plots of 10x10 or, in one trial, 12x20 trees. In the field inventory diameter at breast height and stem damage were recorded for all trees and height measurements were taken on 4-5 trees per plot. The volume of the selected trees was used to obtain a secondary volume function for each trial. In the statistical analysis no significant differences between the provenances were found for volume per ha and damage frequency and severity in 2003. Survival data were analyzed from 1956, 1970, and 2003. The latitudinal origin of the provenance influenced survival in the trial at the lowest elevation in 1956 and 2003, but in the intermediate elevation trial no correlation was found between survival and latitudinal or altitudinal origin. In the trial at the high elevation site, close to the tree line, survival decreased with increasing altitudinal transfer in 1956 and 1970, but the trend was not significant in 2003. At such extreme sites seed sources from much lower elevations should be avoided, but on sites with more favorable conditions they can probably be used without risk for increased mortality.

Introduction

The Swedish Forestry Act of 1948 included for the first time the principle of sustainable management. The idea of sustainability, however, had already existed for about half a century and could now be applied throughout the country, primarily by educating landowners. The earlier acts of 1903 and 1923 already required regeneration after harvesting but the forests were not in a satisfactory condition at the time, especially in northern Sweden. There was need for more explicit laws, research and the production of high quality regeneration material. Numerous field experiments were established in the 1940s to study silvicultural treatments and regeneration methods in northern Sweden. Early results from series of provenance trials served as guidelines for the restoration of forests beginning in the 1950s. (Enander 2001)

Experiments with spruce provenances not only showed that transfers to higher latitudes and elevations could help provide seeds for the regeneration of areas with harsh climatic conditions where locally produced seeds were rare, but also that these transfers resulted in increased growth (Remröd 1975, Remröd *et al.* 1972). The gain in volume production, however, has this far been estimated with a theoretical model (Rosvall *et al.* 1998) and it is uncertain whether the early effects are persistent throughout the rotation period. Most studies concerning the effects of provenance transfers are conducted in nurseries and young field trials. It is therefore difficult to estimate the genetic gain from transfers of natural-stand material as well as improved seed-orchard material. Seed orchards are estimated to increase per hectare production by 10 % for untested plus-trees, 25 % after intense selection from field-tested plus-trees, and an additional 10 % for each generation thereafter (Rosvall *et al.* 2001).

The optimum transfer seems to be mainly dependent on site conditions (Rosvall & Ericsson 1982). The greatest effect can thus be obtained when seed sources are moved far to sites with a favorable local climate. Northward transfers of spruce are estimated to yield a 5-15 %

increase in volume depending on climatic conditions and distance (Rosvall & Ericsson 1982, Remröd 1975, Remröd *et al.* 1972). Latitudinal transfers are relatively well documented while little is known about the effect of altitude. It has been suggested that an altitudinal transfer of 400 m corresponds to one degree of latitudinal transfer (Rosvall & Ericsson 1982, Remröd 1975). The practical recommendation still used today is to reduce the northward movement by 0.5 degrees of latitude for every 200 m in elevation (upward transfer). Also, altitudinal transfer should not exceed 400 m, which was based on observations of mortality and damage on the most severe sites in a series of provenance trials in northern Sweden (Rosvall & Ericsson 1982). Earlier studies suggested that one degree of latitudinal transfer was comparable to 50 m of altitudinal transfer in southern Norway and 60 m in Sweden (Dietrichson 1964). However, the influence of photoperiod was not taken into consideration and the recommendation was based on climatic variables only. Bergman (1965), for example, used this rule of thumb when analyzing a series of Swedish provenance trials.

The aim of this study was to investigate the effect of altitudinal transfer on survival and volume production of Norway spruce in northern Sweden. The question was if a certain altitudinal transfer corresponds to a certain latitudinal transfer and thus has to be taken into account when seed is moved to higher elevations.

Material and methods

A series of provenance trials established in 1948/49 was used for this project. Short distance transfer of Norway spruce in northern Sweden could be studied with focus on the effect of altitude because these trials include provenances from a limited range of latitudes.

Field experiments

The field experiments in this study belong to a larger series of provenance trials. The objective with these trials was to test the possibility of transferring spruce seed to higher elevations above sea level in this part of northern Sweden. In the years 1943-44, twelve study sites were established by direct seeding, and in 1948-49 an additional four sites were planted (Bergman 1965, Remröd *et al.* 1972). One of the planted sites was abandoned early due to frost damage. It was located further north than the other trials to test the latitudinal transfer of the material. In the planted trials a randomized block design was used with one provenance per plot. The spacing was 1.5x1.5 m. The Sätertjärn trial was set up in the spring of 1948 with 2 blocks and 12x20 plants in each plot. Kvarntjärn and Bränndalsbodarna were established in the spring of 1949 with plots of 10x10 plants, and with 3 blocks in Kvarntjärn and 4 blocks in Bränndalsbodarna. Site conditions and previous treatments also vary between the trials (Table1). The temperature sum (Tsum) for the trial locations was calculated with an approximate formula based on a nomogram by Odin *et al.* (1983). Temperature sum is the accumulated daily mean temperatures exceeding the threshold value of +5 ºC during the growing season for a certain location.

Sätertjärn was planted under a shelter of mainly birch (*Betula pubescens* Ehrh. ssp. *tortuosa* (Ledeb.) Nyman) and sallow (*Salix caprea* L.). These shelter trees were already present on the site and are therefore not equally distributed over the area. The trial is located on a southwest-facing slope with high precipitation. The soil is calcareous and very fertile. The Kvarntjärn trial is found on a wind-exposed site that is slightly elevated above the adjacent mire. The ground cover consists mainly of ericaceous dwarf shrubs (*Vaccinium* spp.). Bränndalsbodarna was established on land that was previously used for agriculture and pasture. It is, like Sätertjärn, very fertile and covered with herbs. The trial is surrounded by spruce forest.

Table 1. Trial location and previous treatments.

Field trial	Location				Treatments	
	Latitude °N	Longitude °E	Altitude m a.s.l.	Tsum	Additional planting year	Thinning/clearing year
Bränndalsbodarna	63° 33'	15° 12'	420	820	Few plants added in 1950	Systematic thinning by removing diagonal rows (ca. 50 % of the trees) in 1970
Kvarntjärn	64° 36'	14° 09'	500	670	88 plants added in 1951	Birch cleared in 1970
Sätertjärn	64° 41'	13° 48'	620-650	490	Additional planting in 1948	Grass cleared in 1955 and 1956, wind felled trees cut in 1956

Provenances

Seed collection for these and other experiments started in 1942. The provenances abbreviated with Y5-Y10 come from natural populations in the area around Kramfors and between Junsele and Åsele, further upstream in the Ångerman River valley. The experiments further include the provenances named Billtjärn (Y1), Muruåsen (Z1), Långbäcksbrånan (AC3), Svanavattnet (AC4), Överrissjö (AC5), Högland (AC12) and Lima (Bg1), all collected in natural populations. A total of 13 provenances from elevations between 50 and 500 m a.s.l. were tested with 8 or 9 occurring in each trial (Table 2). Figure 1 shows the location of the field trials and seed collection areas.

Table 2. Origin of provenances used in the field experiments. "X" indicates that the provenance is present in the trial. More detailed information about the material can be found in the appendix (Appendix 1).

Provenance (abbr.)	Latitude °N	Altitude m a.s.l.	Field experiments: Bränndalsbodarna	Kvarntjärn	Sätertjärn
Y1	63° 15'	225			X
Y5	62° 55'	50-100	X	X	X
Y6	62° 55'	100-150	X	X	X
Y7	62° 55'	150-200	X	X	X
Y8	62° 55'	200-250	X	X	
Y9	63°30'-64°	200-250	X	X	
Y10	64°	300-350	X		X
Z1	64° 30'	375-400			X
AC3	64° 22'	450			X
AC4	64° 06'	400-450		X	X
AC5	64°	350-400	X		
AC12	64°	450-500	X	X	X
Bg1	61°	350-400	X	X	

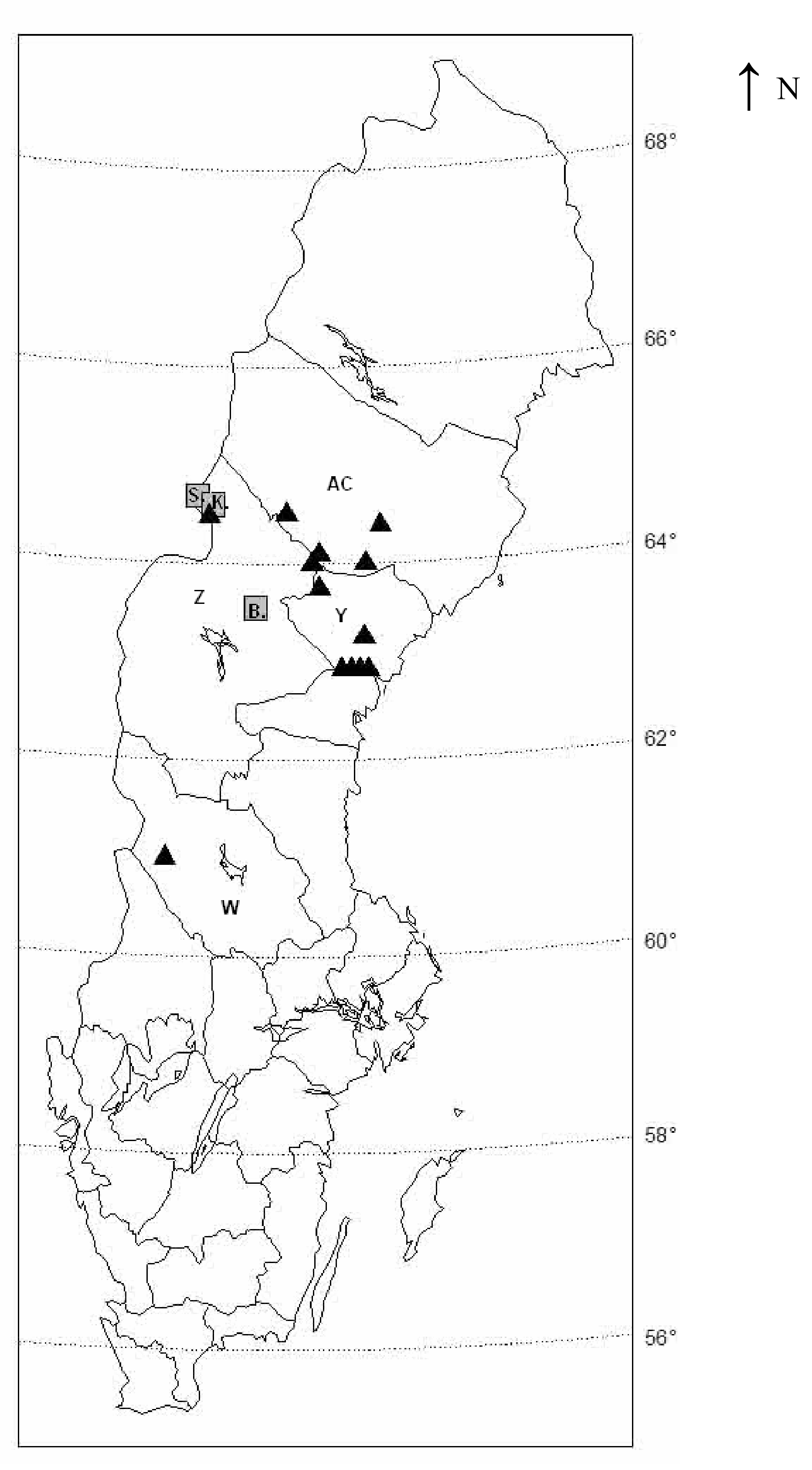

Figure 1. Map of Sweden showing the location of the field trials (S. = Sätertjärn, K. = Kvarntjärn, B. = Bränndalsbodarna) and the approximate origin of the provenances (▲). AC, Z, and Y stand for the provinces of Västerbotten, Jämtland, and Västernorrland. The provenance Bg1 originates from Lima in the province of Dalarna (W).

Inventory and variables

The three trials were assessed in 1956, 1960, 1970, and 2003, Kvarntjärn additionally in 1952. For this project the data collection was done in May 2003 in Bränndalsbodarna and in August the same year in the remaining trials Kvarntjärn and Sätertjärn. Archive data from earlier assessments were also included in the statistical analysis to compare mortality rates of the different provenances between the times of inventory. Information on survival in 1952 and 1960 was only available for Kvarntjärn.

The recorded variables in 2003 included diameter at breast height (DBH) for all trees and tree height for 3-4 randomly selected trees and the one with the largest diameter in each plot. If a tree had multiple stems at breast height an average diameter was calculated based on the measures of the two largest stems.

In the trials Kvarntjärn and Bränndalsbodarna damage codes were recorded with increasing severity in classes from 1 to 4 (Karlman *et al*. 1982). The classes are based on tree vigor, where 1 = healthy, 2 and 3 = reduced vigor, and 4 = dying. Undamaged trees received the value 0 and the average severity of the damage was then calculated for every plot. Stem breakage was the only type of damage included in the statistical analysis. ("Competing vegetation" and "leaning" was recorded for a few trees).

In the Sätertjärn trial we counted the number of breakages along the main stem or noted shrublike growth form and recorded the tree's condition using 4 classes, 1 = healthy, 2 = less vital, 3 = dying or suppressed, 4 = dead. Based on this information each tree was later assigned a severity value that is comparable to the damage codes in the other trials and the average severity for every plot could be calculated. Further, we recorded the location of living and dead deciduous trees that grew close enough to surviving spruce trees to have a sheltering effect. See an example in Figure 2.

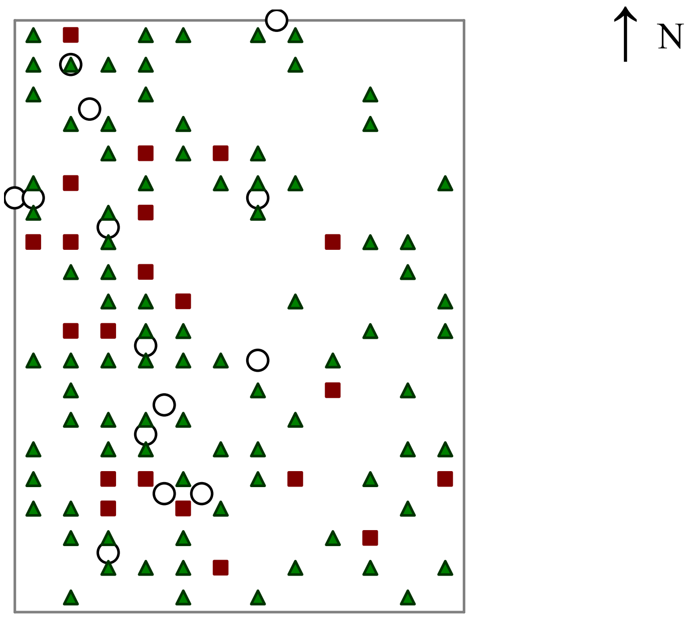

Figure 2. Map of plot 2 in block 1 of the Sätertjärn trial in 2003. (18x30m). Birches and other hardwoods growing close to remaining spruce trees are shown with circles. Squares indicate dead and triangles living spruce trees.

Brandel's volume function for individual trees (spruce in northern Sweden, DBH >5) was used to calculate the volume of the randomly selected trees (Brandel 1990):

$$V = 10^{-0.79783} \cdot d^{2.07157} \cdot d20^{-0.73882} \cdot h^{3.16332} \cdot h13^{-1.82622} \qquad (1)$$

where:

V	=	stem volume (dm^3)
d	=	DBH (cm)
d20	=	d+20cm
h	=	total tree height (m)
h13	=	h-1.3m

To assign a volume to the remaining trees without height measures, a secondary volume function was calculated for each trial as described by Hoffmann (1982). The GLM procedure in SAS was used for this calculation (model 2).

$$Ln(v) = b0 + b1 \cdot \ln(d) + b2 \cdot \ln^4(d) + 0.5 \cdot s^2(res) \qquad (2)$$

where:

Ln(v)	=	natural logarithm of stem volume (dm^3)
d	=	DBH (cm)
s^2(res)	=	residual variation

To eliminate edge effects the outermost trees in each plot were not included. The function is corrected for logarithmic bias by adding 0.5 * s^2(res). The term $\ln^4$(d) is included only if significant in the regression.

Bränndalsbodarna:	Volume	=	$e^{-52.66016524 + 19.63766300 * \ln(d) + -0.09044898 * \ln(d)^4 + 0.5 * 0.158320^2}$
Kvarntjärn:	Volume	=	$e^{-2.154978436 + 2.495041414 * \ln(d) + 0.5 * 0.124603^2}$
Sätertjärn:	Volume	=	$e^{-0.915079477+ 1.654873023* \ln(d) + 0.012042550* \ln(d)^4 + 0.5 * 0.175569^2}$

Statistical analysis

The trials were analyzed separately by stepwise regression of plot values (model 3) in the statistical program Minitab. Dependent variables in the model were volume (m^3/ha, natural log transformed values), percentage of trees with stem damage, severity (average class value), and the survival proportions (arcsin-transformed values) in 1956, 1970, and 2003.

$$y_{ij} = \mu + \alpha_i + \beta \cdot (dalt) + \gamma \cdot (dlat) + \delta \cdot (dalt^2) + \varepsilon \cdot (dlat^2) + \zeta \cdot (daltdlat) + e_{ij} \qquad (3)$$

where:

y_{ij}	=	volume, etc. for block i, provenance j
μ	=	intercept (overall mean of the trial)
α_i	=	fixed effect of block i; i = 1,2,(3),(4)
$\beta, \gamma, \ldots$	=	regression coefficients
dalt	=	difference in altitude between trial location and origin of the provenance
dlat	=	difference in latitude between trial location and origin of the provenance
$dalt^2$	=	dalt·dalt
$dlat^2$	=	dlat·dlat
daltdlat	=	dalt·dlat
e_{ij}	=	random residual effect for provenance j in block i , NID($0,\sigma^2$)

The shelter effect in the Sätertjärn trial was estimated by analysis of variance (general linear model). Only living trees above 1.3 m were included. The analysis was performed with data from single tree observations according to model 4.

$$y_{ijk} = \mu + \alpha_i + \beta_j + \gamma_k + e_{ijk} \qquad (4)$$

where:

y_{ijk} = stem volume (dm^3, natural log transformed values), number of stem breakages (values 1-9), tree condition (1-4), or diameter (DBH)
μ = intercept (overall mean of the trial)
α_i = fixed effect of block i; i = 1, 2
β_j = fixed effect of provenance j; j = 1,…,9
γ_k = fixed effect of shelter; k = 1 if shelter tree present and 0 if not
e_{ijk} = random residual effect for shelter k in provenance j in block i , NID(0,σ^2)

Results

Survival

Bränndalsbodarna showed the lowest mortality with 3 % dead trees in 1956, and 5 % in 1970. The trial was thinned after the inventory in 1970 when about 50 % of the trees were removed. The mortality continued to be low with 81 dead trees recorded in 2003. Then, about 44 % of the originally planted trees were remaining in the trial. At Kvarntjärn an initial loss of about 16 % of the trees was recorded in 1960. The number of remaining trees was thereafter stable until 1970 and decreased slightly between 1970 and 2003, when 22.5 % of the trees had died. In Sätertjärn the mortality was considerably higher than in the other trials. About 28 % of the planted trees survived until 2003. 263 dead trees were recorded in 2003, which is 6 % of the original number of trees. The other dead trees (66 %) had already decomposed. The mortality rate was highest in the beginning, then decreased between 1956 and 1970 and increased again after 1970. Figure 3 shows the percentage of surviving trees at times of inventory in the three field trials.

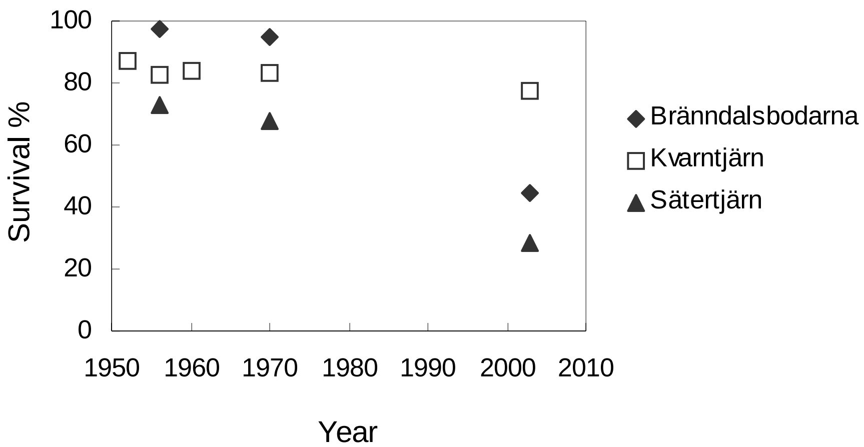

Figure 3. Percentage of surviving trees in the three field trials in 1956, 1970, and 2003. Survival data from 1952 and 1960 are shown for Kvarntjärn only. Thinning reduced the number of trees in Bränndalsbodarna by ca. 50 % in 1970.

In Bränndalsbodarna and Kvarntjärn the altitudinal origin of the provenance did not influence survival in 2003. Only in the Sätertjärn trial the survival decreased slightly with increasing altitudinal transfer (Figure 4), but this negative trend was not significant in the statistical analysis (Table 3).

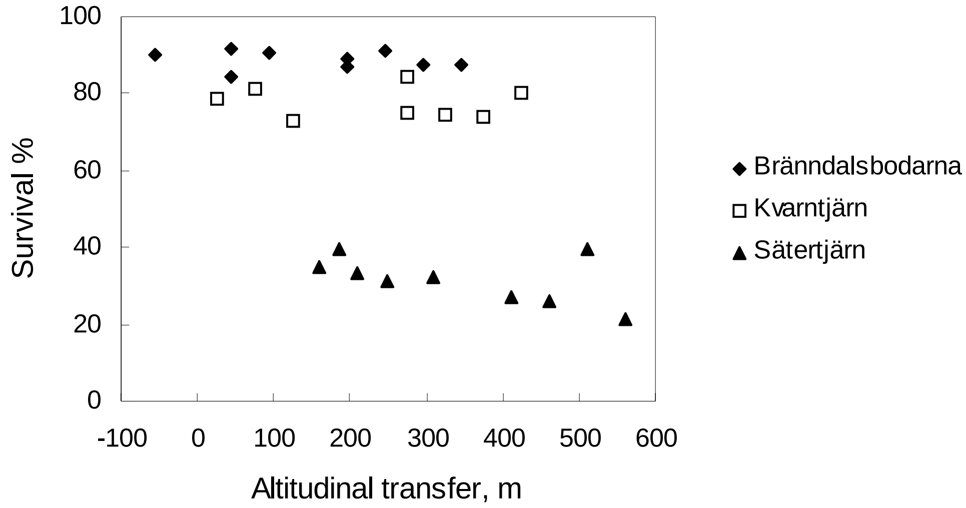

Figure 4. Percentage of surviving trees in 2003 plotted against altitudinal transfer in meters (upward movement) for each provenance in the three field trials. Survival in Bränndalsbodarna is shown as percentage after removal of 50 % of the trees.

The results of the regression analyses are summarized in Table 3. In Bränndalsbodarna the latitudinal origin of the provenance was correlated with survival in 1956 and 2003, but no such effect was found in 1970. In 2003, increasing northward transfer had a negative effect on survival. The trends are shown in Figure 5. In Sätertjärn the survival was influenced by the altitudinal origin in 1956 and 1970 (Figure 6). Survival decreased with increasing upward transfer. Kvarntjärn did not show effects of latitude or altitude on survival.

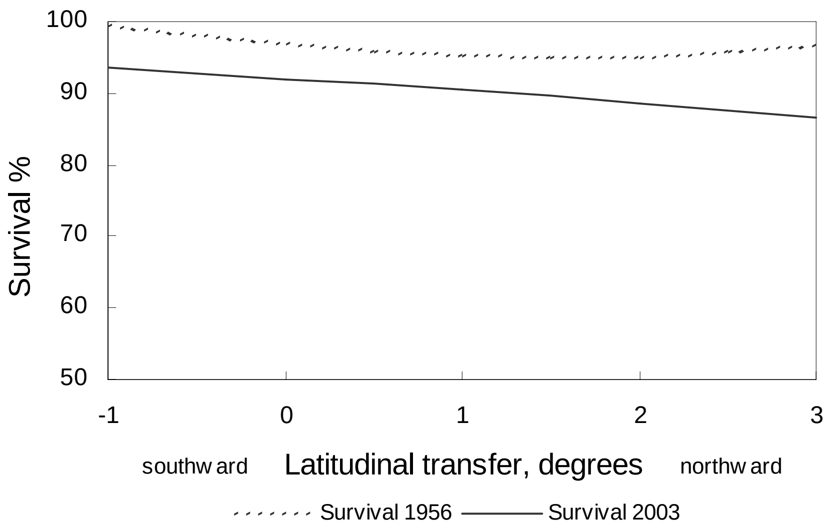

Figure 5. Bränndalsbodarna, survival 1956 and 2003 vs latitudinal transfer.

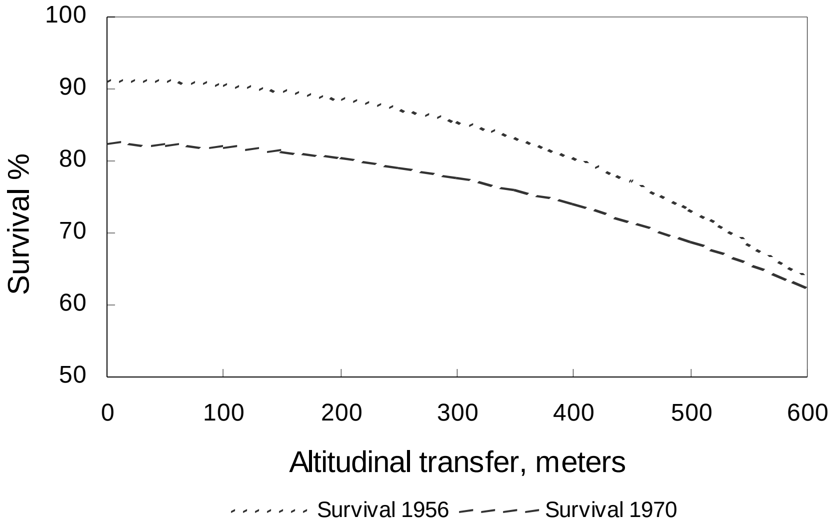

Figure 6. Sätertjärn, survival 1956 and 1970 vs altitudinal transfer in meters (upward movement).

Volume production and stem damage

The standing volume and the percentage of trees with stem damage varied greatly between the three trials but there was little difference between the provenances. The volume per ha in 2003 is shown as a function of altitudinal transfer in Figure 7. In Bränndalsbodarna the volume ranged from 345 to 548 m^3/ha in the 36 plots. The average volume was 469 m^3/ha. These figures do not include the volume removed at the thinning in 1970. Kvarntjärn produced an average volume of 119 m^3/ha, but the variation between the 24 plots was greater, from 51 to 205 m^3/ha. Sätertjärn had the lowest volume, 23 m^3/ha on average and ranging from 9 to 54 m^3/ha in the 18 plots. The statistical analysis showed significant differences between the blocks in Kvarntjärn and Sätertjärn, but there were no effects of latitudinal or altitudinal transfer on volume production in 2003 (Table 3).

In 2003, 17 % of the surviving trees were undamaged in the Sätertjärn trial, 55 % had no main stem (shrublike growth form, see Figure 8), and 28 % had at least one breakage along the main stem. The average severity of the stem damage measured in reduced tree vigor was 2.2 in Sätertjärn and 0.1 in Kvarntjärn and Bränndalsbodarna. 5 % of the surviving trees were damaged in Kvarntjärn and 4 % in Bränndalsbodarna. The altitudinal and latitudinal origin of the provenance did not influence the stem damage frequency and severity in the three trials.

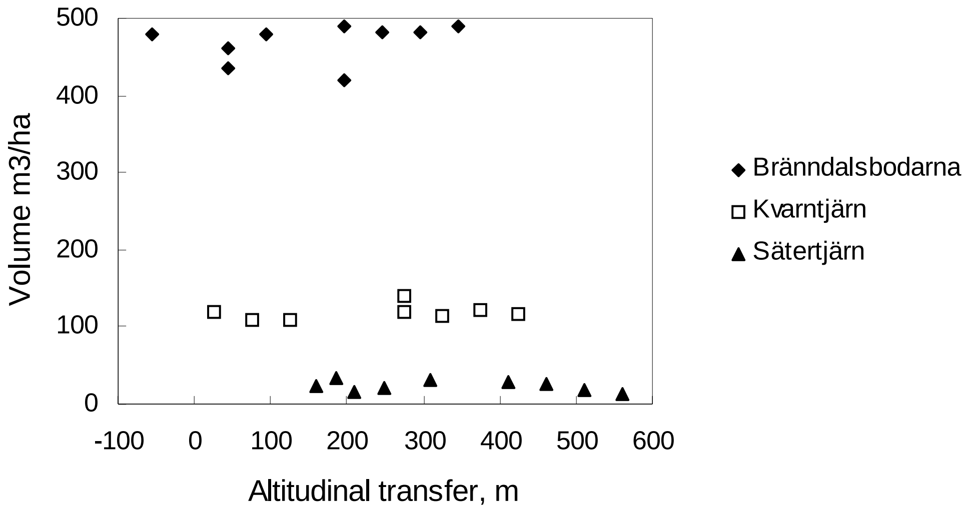

Figure 7. Volume per ha in 2003 plotted against altitudinal transfer in meters (upward movement) for each provenance in the three field trials.

Figure 8. Sätertjärn, tree with shrublike growth form.

Table 3. Results of stepwise regression with α = 0.15 to enter or remove variables. The estimated regression coefficients and significance levels (below) are shown for the included variables. (Log volume = natural log values of volume per ha; survival 1956, 1970, and 2003 = arcsin-transformed values of survival proportions in different years; R = multiple correlation coefficient; lower R^2-values from regression analyses with blocks only; N = number of observations)

Field trial	Dependent variable	Constant	Block1	Block2	Block3	Block4	Dlat	$Dlat^2$	Dalt/100	$(Dalt/100)^2$	Daltlat/100	R^2 (R^2_{block})	N
Bränndalsbodarna	Log volume	6.117	-	-	-	-	-	-	-	-	0.035 0.051	0.11 (0.04)	36
	Survival 1956	1.397	-	-	-0.039 0.109	0.041 0.091	-0.143 **0.011**	0.048 **0.021**	-	-	0.038 0.143	0.44 (0.16)	36
	Survival 1970	1.378	-	-	-	-0.092 **0.001**	-	-	-	-	-	0.28 (0.29)	36
	Survival 2003	1.284	-	-0.044 **0.041**	-	-0.108 **<0.001**	-0.0288 **0.004**	-	-	-	-	0.54 (0.40)	36
Kvarntjärn	Log volume	4.920	-0.62 **<0.001**	-	-	-	-	-	-	-	-	0.61 (0.63)	24
	Survival 1956	-	-	-	-	-	-	-	-	-	-	- (0.05)	24
	Survival 1970	-	-	-	-	-	-	-	-	-	-	- (0.04)	24
	Survival 2003	-	-	-	-	-	-	-	-	-	-	- (0.03)	24
Sätertjärn	Log volume	2.685	0.66 **0.002**	-	-	-	-	-	-	-	-	0.45 (0.45)	18
	Survival 1956	1.266	-	-	-	-	-	-	-	-0.0095 **0.002**		0.46 (0.02)	18
	Survival 1970	1.138	-	-	-	-	-	-	-	-0.0063 **0.013**	-	0.33 (0.00)	18
	Survival 2003	0.6781	-	-	-	-	-	-	-0.024 0.091	-	-	0.17 (0.00)	18

The shelter effect of birch in Sätertjärn

Figure 9 shows a picture of birches growing close to undamaged spruce trees. It is possible that these shelter trees have a positive effect. The results of the analysis of variance are presented in Table 4. The tested variables stem breakage, tree condition, diameter at breast height, and volume showed a significant effect of the shelter.

Figure 9. Is there a shelter effect from these birches in the Sätertjärn trial?

Table 4. Results of the analysis of variance.

Source	df	Stem breakage		Tree condition		Diameter (DBH)		Log volume	
		SS	p	SS	p	SS	p	SS	p
Block	1	559.67	<0.001	16.4332	<0.001	128215	<0.001	141.484	<0.001
Provenance	8	187.26	0.143	8.4228	0.055	84966	<0.001	128.783	<0.001
Shelter	1	190.54	**0.001**	4.6803	**0.003**	8827	**0.041**	30.998	**0.002**
Error	1123	17896.97		602.3368		2363615		3667.928	
R^2		0.050		0.047		0.086		0.076	

Discussion

The environmental conditions varied greatly between the three field trials and the results from these locations cannot be easily compared. The limited material does not allow drawing general conclusions with certainty. One problem with the experimental design was that most provenances were moved to the northwest, which involves both altitudinal and latitudinal transfer. It was therefore difficult to separate the effects of altitudinal and latitudinal origin on survival and volume production. Remröd *et al.* (1972) investigated these field experiments in the 1970s and found that the altitudinal origin influenced plant height of Norway spruce provenances. The effect was greatest if the provenance originated from nearly the same latitude as the field trial location. Their study implied that provenances from different altitudes along the same latitude were not equal in their growth rate. In the seeded trials that belong to the same series of experiments survival was difficult to estimate but no differences between the provenances were observed in 1970. A moderate upward transfer seemed to increase growth, but the latitudinal transfer was probably more important for the differences in tree heights (Remröd *et al.* 1972). The provenances from lower elevations grew well in these experiments from the beginning (Stefansson 1953) and, based on tree heights from the assessments in 1960, the optimum upward transfer was about 200-250 m (Bergman 1965).

Some problems encountered at the inventory in Sätertjärn were a few missing corner posts, landslide in the upper portion of the trial and generally high mortality. It was somewhat difficult to find the plot boundaries and tree rows. The secondary volume function was obtained from trees with straight stems only. All trees, including the ones with shrublike growth form, were assigned a volume based on the diameter at breast height and the secondary volume function. The volume estimate for the Sätertjärn trial is therefore not very accurate. Also, it was not possible to tell the difference between originally planted and naturally regenerated trees in the trial. Due to the dense ground cover and the limitations to seed maturation in this area, however, the possibility of natural regeneration can probably be neglected.

The survival percentage at Bränndalsbodarna was influenced by the latitudinal origin in 1956 and 2003. However, the negative trend with increasing latitudinal transfer was not yet obvious in 1956. A possible explanation for the mortality recorded in 1970 and 2003 is self-thinning if the southern provenances produced more volume and more trees died due to competition in these plots. Therefore, the northward transfer showed a negative trend in 2003. In the journal kept by the responsible research station thinning was recommended after inspection of the trial in 1970. This indicates high standing volume and possibly self-thinning observed in some plots. A second thinning was planned after the assessment in 2003. The early mortality in both Bränndalsbodarna and Kvarntjärn could be due to frost, drought, insects or other factors. After the initial loss of seedlings the Kvarntjärn trial experienced only a slight decrease in the number of trees between 1960 and 2003. No differences in survival between the provenances could be detected in Kvarntjärn whereas survival in Sätertjärn was affected by the altitudinal origin. It seems that far upward transfers result in slightly higher mortality but moderate transfers do not.

Volume production and damage frequency were dependent on environmental factors and were not influenced by the latitudinal or altitudinal origin of the provenance. In the statistical analysis, the most obvious difference in volume production was found between blocks in the trials Kvarntjärn and Sätertjärn. An important factor for the block differences in Kvarntjärn was probably soil moisture or ground water levels. Bränndalsbodarna produced considerably more volume than the other trials, which is to some extent due to more favorable climatic conditions but mostly the previous land use that improved soil fertility. In terms of productivity, the Bränndalsbodarna site did not reflect the conditions at this particular geographic location.

The Sätertjärn trial gave the impression that deciduous shelter trees could be important for reforestation with Norway spruce at tree-line sites because the spruce trees seemed to have developed better and be less damaged near the shelter trees. The statistical analysis provided some evidence for this. The model, however, was simplified and assumes that only the trees in the immediate vicinity were under the influence of the shelter trees. The shelter effect can be explained with the physical protection the deciduous trees provide against snow and wind. So, they probably affected not only the closest spruce trees but also a few further downhill. Another beneficial effect of the deciduous trees is keeping ground vegetation low in the trial, allowing the spruce seedlings to grow up above the shading and competing grasses and herbs (Stefansson unpublished). The Sätertjärn trial is located on a southwest-facing slope in an area with abundant precipitation, and deep snow cover is probably the most important damaging agent for spruce trees on the site. Stem breakage is also a major reason for the still relatively high mortality and some additional damage can be expected when more of the spruce trees grow into the crowns of the birches.

An important question is if the effect of altitudinal and latitudinal transfer can be compared. Some traits that are critical for survival and growth are under the control of temperature while others are more dependent on light conditions. Transfers to higher elevations do not involve a change in photoperiod. Thus, no increased volume production can be expected due to a longer growth period in the case of altitudinal transfer. While the release of dormancy in the spring is mostly temperature dependent, the onset of dormancy is strongly controlled by photoperiod. The critical night length that is required for growth termination in the fall is about 2 hours for provenances originating north of latitude 67 and increases towards the south. Between latitude 56 and 60 about 6 hours of darkness are needed to trigger growth cessation (Dormling 1971). Because of the photoperiodism growth terminates later when spruce seed is moved to higher latitudes (Rosvall *et al.* 1998). Therefore, southern provenances produce more volume when survival is not affected negatively. The increasing temperature in the spring triggers bud burst and northern provenances react to lower temperatures than southern provenances. Northward transfer results in later bud burst, which makes the trees less susceptible to spring frost. When transferred in latitude or altitude, the trees still react to the same night length to which they are adapted (Rosvall *et al.* 1998). The critical night length is the same for provenances from different elevations in Sweden (Dormling 1971). If there are differences in volume production and survival between provenances transferred in altitude they might be explained by the effect of temperature on, for example, frost tolerance. It would be interesting to study provenances from locations with the same temperature climate from different combinations of latitude and altitude.

For Scots pine (*Pinus sylvestris* L.) provenances a southward transfer is recommended in northern Sweden. Provenances that are moved southward utilize a shorter period of the growing season and thus, produce less volume per individual, but due to the increased survival they produce more volume per unit area than the local provenance. The effect of latitudinal transfer is greatest in areas with harsh climatic conditions (Rosvall *et al.* 1998). The altitudinal origin, however, does not influence hardiness and a transfer from higher elevations does therefore not result in higher survival rates or volume production compared to the local provenance (Andersson & Sundblad 1998, Rosvall *et al.* 1998).

Norway spruce can be transferred to higher latitudes and altitudes to some extent without increasing mortality. The so-called overhardiness of Norway spruce is often explained by the immigration direction after the last ice age (e.g. Remröd 1975). The generally accepted immigration model for spruce in Fennoscandia has, for example, been described by Moe (1970) and Tallantire (1972). The prevailing argument is that the main population of Norway spruce entered the country from the northeast and east where less frost tolerant genotypes could not survive. Before entering Sweden, however, there was a considerable northward movement from the ice age refuge areas to northern Finland and from there the spruce trees spread to the south and west during a much shorter time period. They obviously adapted to the changing conditions on the way but the direction of spread does not explain the hardiness of Norway spruce populations in northern Sweden. Also, new theories arise suggesting that spruce was present much earlier and came from other directions than generally believed (Segerström & von Stedingk 2003). There is even the possibility that spruce could have survived the ice age in a refuge somewhere at the Norwegian coast when the sea level was much lower (Kullmann 2001). Evidence supporting these ideas comes from recent macrofossil and pollen analyses.

Along a gradient from the coast to the mountains, the genetic variation within Norway spruce appears to be rather continuous. There are no barriers across the range of spruce in Sweden isolating populations and leading to the development of distinct ecotypes. Viable seeds can be dispersed far from the mother tree as they are released early in spring and transported by wind on the snow surface, and some far spread background pollen also contributes to the genetic exchange. In the boreal region fire is a major ecological factor that causes large-scale disturbances in the interior, whereas other factors like snow, ice, and wind are more important at tree-line and coastal sites. Some environmental factors lead to adaptations. For example, the narrow crown shape is prevailing where resistance to snow breakage is critical for the survival of Norway spruce. The arctic and alpine tree lines are mainly determined by the temperature that restricts seed maturation (Skre, 1993). Intervals between good seed crops can be very long at high elevations (Remröd *et al.* 1972). Vegetative reproduction can therefore be more important for the survival of the species at tree line, which means that the genotypes stay the same.

Differences between provenances are not always due to environmental adaptations but can also be the result of random processes (Smith *et al.* 1997). Even so, the evolutionary history of a species is important for the genetic variation today (Eriksson & Ekberg 2001). Trees that are naturally occurring on the site in question do not necessarily have the attributes desired by humans like stem straightness and other quality traits or high production rates. By transferring seeds to higher latitudes and elevations increased growth is gained but often at the expense of increased risk of damage. The safe distance for moving seed in elevation or latitude is different for each species and location (Smith *et al.* 1997).

Conclusions and recommendations

A moderate transfer in altitude did not affect survival of Norway spruce provenances in this study. Transfers to higher elevations did not increase per hectare production. The study did not support the idea that a certain altitudinal transfer corresponds to a certain latitudinal transfer. At extreme sites, close to the tree line, it is advisable to avoid seed sources from very low elevations. Low elevation provenances probably have a higher proportion of trees that do not tolerate the climatic conditions at the high elevation site. A transfer of more than 400 m in altitude is therefore not recommended.

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Appendix 1: Origin of provenances used in the field trials

Field Trial No.	Provenance Reg. No.	Seed source	Origin	Latitude ° N	Altitude m a.s.l.	Plant age
Sätertjärn						
S23F4820060	S23A2Y5	KRAMFORS seed lot 3	KRAMFORS	62.92	75	3/0
S23F4820060	S23A2Y6	KRAMFORS seed lot 4	KRAMFORS	62.92	125	3/0
S23F4820060	S23A2Y7	KRAMFORS seed lot 5	KRAMFORS	62.92	175	3/0
S23F4820060	S23A2Y1	BILLTJÄRN (18 trees)	BILLTJÄRN, Överlännäs county	63.25	225	2/3
S23F4820060	S23A2Y10	KRAMFORS seed lot 9	BACKE, ÅSELE, HOTING	64	325	3/0
S23F4820060	S23A2AC4	SVANAVATTNET	HEMBERGET, SVANABYN, Dorotea county	64.1	425	3/0
S23F4820060	S23A2AC3	LÅNGBÄCKSBRÅNAN	LÅNGBÄCKSBRÅNAN, LÅNGBÄCKEN, Fredrika county	64.38	450	2/3
S23F4820060	S23A2AC12	KRAMFORS seed lot 15	ÖVERRISSJÖ, Åsele county	64	475	3/0
S23F4820060	S23A2Z1	MURUÅSEN	MURUÅSEN, Frostviken county	64.5	387.5	2/3
Kvarntjärn						
S23F4920082	S23A2Y5	KRAMFORS seed lot 3	KRAMFORS	62.92	75	2/2
S23F4920082	S23A2Y6	KRAMFORS seed lot 4	KRAMFORS	62.92	125	2/2
S23F4920082	S23A2Y7	KRAMFORS seed lot 5	KRAMFORS	62.92	175	2/2
S23F4920082	S23A2Y9	KRAMFORS seed lot 7	KRAMFORS, JUNSELE, BACKE	63.75	225	2/2
S23F4920082	S23A2Y8	KRAMFORS seed lot 6	KRAMFORS	62.92	225	2/2
S23F4920082	S23A2BG1	Population BG 1, LIMA	LIMA county	61	375	2/2
S23F4920082	S23A2AC4	SVANAVATTNET	HEMBERGET, SVANABYN, Dorotea county	64.1	425	2/2
S23F4920082	S23A2AC12	KRAMFORS seed lot 15	ÖVERRISSJÖ, Åsele county	64	475	2/2
Bränndalsbodarna						
S23F4920083	S23A2Y5	KRAMFORS seed lot 3	KRAMFORS	62.92	75	2/2
S23F4920083	S23A2Y6	KRAMFORS seed lot 4	KRAMFORS	62.92	125	2/2
S23F4920083	S23A2Y7	KRAMFORS seed lot 5	KRAMFORS	62.92	175	2/2
S23F4920083	S23A2Y8	KRAMFORS seed lot 6	KRAMFORS	62.92	225	2/2
S23F4920083	S23A2Y9	KRAMFORS seed lot 7	KRAMFORS, JUNSELE, BACKE	63.75	225	2/2
S23F4920083	S23A2Y10	KRAMFORS seed lot 9	BACKE, HOTING, DOROTEA, ÅSELE	64	325	2/2
S23F4920083	S23A2BG1	Population BG 1, LIMA	LIMA county	61	375	2/2
S23F4920083	S23A2AC5	KRAMFORS seed lot 17	HÖGLAND, Dorotea county	64.5	375	2/2
S23F4920083	S23A2AC12	KRAMFORS seed lot 15	ÖVERRISSJÖ, Åsele county	64	475	2/2