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Strategies for deployment of reproductive material under supply limitations – a case study of Norway spruce seed sources in Sweden

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ABSTRACT
The aim of this study was to analyze and compare the performance of Norway spruce seed sources from Swedish stands of East European origin (SweEast) with material from Swedish (SweSO) and East European (EastSO) seed orchards, and with material from Swedish (SweS) and East European (EastS) unimproved stands. The seed sources were field tested at six locations in southern Sweden and assessed for growth and phenology. The assessment of growth traits indicated that trees from SweSO and EastSO had 9–15% greater growth with respect to tree height and diameter in comparison to trees from Swedish local unimproved stands (SweS). Trees from SweEast and EastS showed around 5–7% greater growth. With respect to phenological traits, the expected later bud burst for EastS and EastSO in comparison to SweS, SweSO and SweEast was verified. However, SweEast exhibited earlier bud burst compared to EastS than what could be explained by pollination by Swedish pollen. This was explained by early land race formation for that trait. A strong positive correlation was observed between bud burst and frost damage, which indicates that earlier bud burst does indeed increase the risk of damage from late spring frost at frost-prone sites.

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Picea abies; spring frost; seed shortage; bud flush

Introduction

In several Nordic countries seed deployment using improved Norway spruce material is often a challenge due to the fact that seed production in seed orchards are sparse or can vary between years (Crain and Cregg 2018). To be able to meet the demand for improved material nonnative seeds are usually imported from other countries (Myking et al. 2016). In case this is not possible trees with lower performance have to be used which in turn yields lower growth and quality (Liziniewicz and Berlin 2019; Haapanen, 2020). The nonnative seeds can also be a potential source of nonnative pests, which needs to be considered when importing material from other countries (Franić et al. 2019). Another aspect of this is how the climate will change in the future where local trees will not be able to disperse, establish or adapt as fast as needed. To be able to adapt to climate changes assisted migration is needed, where trees with desirable properties are transferred from one place to another (Williams and Dumroese 2013; Koralewski et al. 2015). For example, Norway spruce seeds from southern regions are moved northward for improved growth rhythm adaptation and performance (Kroon and Rosvall 2004).

In Sweden, 348 million seedlings are planted each year (average 2001–2017), and of these, 199 million are Norway spruce (Skogsstyrelsen 2019). Genetically improved Norway spruce trees can be deployed to achieve an expected higher performance (genetic gain) in growth and quality compared to unimproved trees. During recent decades seed orchards established before 1990 have been used and give around 10-15% higher genetic gain in growth, but now plant material with higher genetic gain (up to 25%) is starting to become available (Rosvall et al. 2001; Remröd et al. 2003). For several years there has been a shortage of improved Norway spruce seeds (Almqvist 2014) due to poor or no crop production because of irregular flowering by the species (Lindgren et al. 1977; Crain and Cregg 2018), as well as damage to the seed orchard crops by pests (Almqvist and Rosenberg 2016; Capador et al. 2018). Historically, in order to counteract the shortage and maintain a high and robust productivity, seeds from different European sources have been imported. Seed sources from eastern Europe have been considered a good alternative in southern Sweden due to their superior performance compared to seed of other provenances (Langlet 1960; Persson and Persson 1992; Danusevicius and Persson 1998). Since 2001, an average of 54% of the seedlings originate from Swedish seed orchards, 21% from foreign stands, 17% from Swedish stands, 6% from foreign seed orchards, whilst the origin of 2% is not specified (Skogsstyrelsen 2019). The imported Norway spruce seeds are mostly from Belarus, Poland, Lithuania, Finland, Latvia and Norway (more than 100kg seeds between 2004 and 2018) (Skogsstyrelsen 2020). Provenances

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from the Baltic regions and Belarus have later bud burst which in turn results in less damage due to spring frost events. This is important because climate change will result in warmer and longer growing seasons, but also more temperature variability in the spring causing more spring frost events. These will cause severe damage to trees, especially Norway spruce in Scandinavia (Jönsson and Bärring 2004, 2011; Langvall 2011). Provenances from eastern Europe also have later bud set, which results in a longer vegetation period and thus increased growth. This can increase the risk of autumn frost events affecting the trees, but in the southern part of Sweden the risk of frost in the autumn is low (Langlet 1960; Skrøppa and Magnussen 1993). The recommendation today for deployment of Norway spruce in the north of Sweden is that a latitudinal transfer often delivers a strong positive effect, with seeds moved to the north compared to their origin. This transfer yields a higher survival and growth (Rosvall 1982; Kroon and Rosvall 2004). In southern Sweden seeds from Eastern Europe are commonly used and perform better due to the late bud flush and higher growth (Werner and Karlsson 1982; Persson and Persson 1992). Importing seeds from countries within EU is allowed (EU 2000, 2008) but seed import from Belarus was only allowed up to 31 December 2019 (EU 2015). Before that more than 4000 kg seeds were imported to Sweden from 2004 until 2018 (Skogsstyrelsen 2020). Thus, material from other sources needs to be tested in order to find out how it compares with Swedish stand material in terms of growth and vitality, and to determine whether the phenology differs with respect to the risk of spring frost damage. Across Sweden there are several stands that have documented East European origin, giving rise to the idea that this material could be used for seed production if the superior performance from the original provenance is preserved.

Some research suggests that the conditions under which the seeds develop have epigenetic effects, regardless of where the seeds are planted (Kvaalen and Johnsen 2008; Skrøppa et al. 2009). This would mean that the place where the seeds mature will affect the characteristics of the trees later, especially with respect to growth rhythm characteristics such as bud burst and bud set, for instance that seeds that mature in warmer temperatures exhibit later bud burst. Even after a single generation some clear differences are visible, with the offspring behaving more like the local trees than the parent trees (Skrøppa and Steffenrem 2016).

The aim of this report was to generate new information on the selection and deployment of reproductive material for Norway spruce in situations where import is not possible, and if it is an option to use second generation material, offspring from seed sources of desired provenances that already exist in the country. To do so, we compared material from second generation material with various contemporary seed sources to determine whether the former represent an appropriate alternative as forest reproductive material in case of a shortage of improved seed orchard material or as a result of a ban on importing eastern seed from outside the EU. We intended to generate information on the selection and deployment of Norway spruce reproductive material in southern Sweden. The results could be applicable also for southern Norway and Finland as both the imported material and climatic properties are similar.

This study had the following specific objectives:

(i) To compare seeds from Swedish stands of documented East European origin (second generation material) with autochthonous stand seed and seed orchards from both Sweden and Eastern Europe, we investigated if they differed in (i) growth; (ii) survival; (iii) growth rhythm; (iv) frost damages, as these properties are important for the performance of Norway spruce.

We hypothesized that seeds from the second generation material would be a feasible choice with respect to growth and survival in case of seed shortage, but we expect differences with respect to phenological traits (Skrøppa and Steffenrem 2016).

(ii) To determine if the performance of seed sources from (i) are stable over the intended area of utilization we analyzed their performance between different locations in order to get an indication of genotype versus environment (G×E) interactions. Our expectation based on earlier studies was that GxE should be low but also that it is important to look at the phenological properties (Berlin et al. 2015; Chen et al. 2017).

Materials and methods

Seed sources

The plant material used in this study originated from 50 different seed sources, which were separated into five groups (Table 1) according to the origin of the seed. For a detailed description of the different seed sources see appendix 1 Table A1.

The seeds that comprised the 20 seed sources of SweEast were collected in the autumn of 1998 from mature fully stocked stands. Certain standards were followed while collecting the material - the stands from which the seeds were sourced were documented as having been planted with seedlings of Eastern European origin, and there was a sufficiently large number of trees bearing cones. In each stand, 7–10 representative trees with cones were cut down and the cones were collected as one seed source.

The other 30 commercial seed sources were obtained in the spring of the year 2000. The Eastern European seed orchards and local unimproved stand seeds were in Latvia, Lithuania, Belarus and Poland (only stand material).

Table 1. The groups of seed sources included in the study. A detailed description of the different seed sources is given in Appendix A.

Group		Number of seed sources
SweEast	Progeny from Swedish stands of documented Eastern European origin (one generation in Sweden)	20
SweS	Progeny from indigenous Swedish stands	6
EastS	Progeny from indigenous Eastern European stands	12
SweSO	Seeds from Swedish seed orchards	6
EastSO	Seeds from Eastern European seed orchards	6

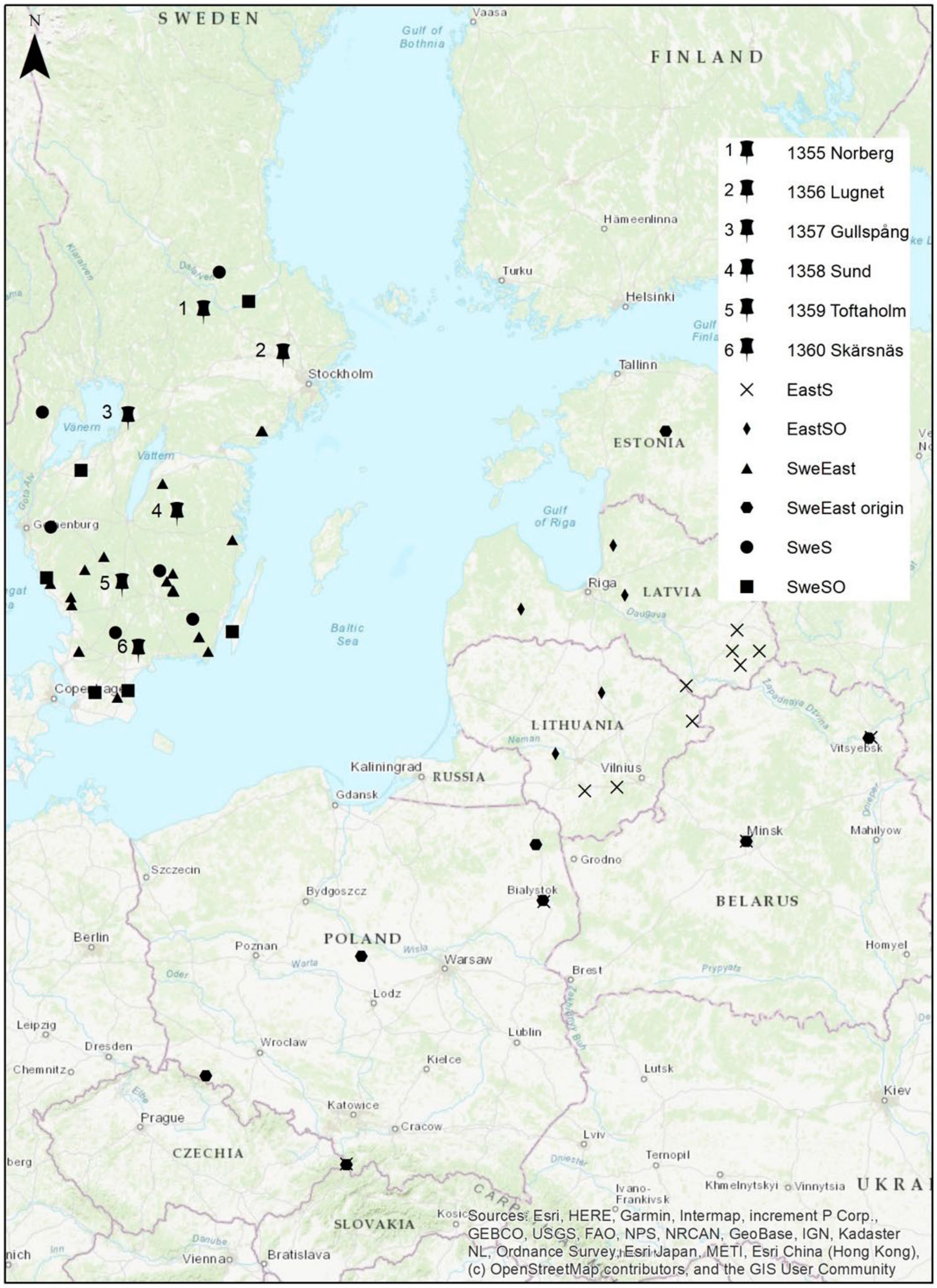

Figure 1. Trial locations used in this study (1–6), the five different groups (EastS, EastSO, SweEast, SweS and SweSO) and the origin of the SweEast stand seeds (SweEast origin).

Planting and trials

The seedlings were grown in the nursery at the Skogforsk research station Ekebo for two years (2000–2002). Field trials were established in the spring of the year 2002 at six different locations in both southern and central Sweden (Figure 1).

The trials were planted as single tree plots in a randomized block design with 25 replicates with the same set of seed sources in each. In trials 1355-57 (Norberg, Lugnet and Gullspång) the initial spacing was 2×2 m while it was 1.8×1.8 m in trials 1358-60 (Sund, Toftaholm and Skärsnäs).

Assessments

The trial series have been assessed four times: in the spring of 2004, late in the summer of 2005, autumn 2007 and autumn 2014. The growth traits measured were height at the plant age of seven (H7), and diameter at breast height at the plant age of 14 (DBH14). In order to examine growth rhythm, bud burst (BB) according to Krutzsch scale (Krutzsch 1973) and the top shoot was scored according to the proportion of lignification (L) (the percentage of top shot that was brown/lignified compared to the green active part) and in addition survival (alive/dead) at the plant age of four (S4), seven (S7) and 14 (S14) were assessed. Frost damage

Table 2. Description of measured and analyzed traits.

Trait	Abbreviation	Time of recording	Explanation
Bud burst	BB	Spring 2004	According to the Krutzsch scale (Krutzsch 1973) 0 = resting bud, 8 = new buds sprouting and needles spreading
Frost injuries	F	Spring 2004	Damage by spring frost[a] 0 = undamaged, 1 = damaged
Lignification	L	Late summer 2005	Percentage of lignification in the top shoot (%)
Tree height	H	Autumn 2007	Tree height (cm) H7
Survival	S	Spring 2004 and Autumn 2007 and 2014	Survival, 0 = dead, 1 = alive S4, S7 and S14
Diameter at breast height	DBH	Autumn 2014	Diameter at breast height (cm) DBH14

[a]The frost scores from 1 to 3 added together to obtain an indication of all the trees damaged by frost (1).

(F) observations were most commonly assessed at the plant age of four. Table 2 presents the traits recorded.

Statistical analysis

Prior to any other analysis all the class and binary variables (BB, F and L) were normal score transformed with mean zero and standard deviation one within each block to linearize the data (Gianola and Norton 1981).

Spatial analysis

To adjust the data for within-trial environmental effects a univariate single-site spatial analysis was performed using ASReml 4.1 (Gilmour et al. 2015), according to this model:

$$y = Xb + Zu + e \tag{1}$$

Where y is the vector of individual tree observations, b is a vector of fixed effects (intercept), X is its design matrix, u is a vector of random effects (trial design parameters and family effects), Z is its design matrix and e is the vector of random residuals.

First, a model with only the experimental design features and independent error was used, to check the spatial distribution of the residuals; if the residuals were non-randomly distributed a second spatial model was used in which the residual variances are separated into an independent component and a two dimensional spatially auto-correlated component as:

$$R = \sigma_\xi^2[AR1(\rho_{col}) \otimes AR1(\rho_{row})] + \sigma_\eta^2 I \tag{2}$$

Where σ_ξ^2 is the spatial-dependent residual variance, σ_η^2 is the spatial-independent residual variance, $\otimes$ is the matrix Kronecker product of two matrices, and $AR1(\rho_{col})$ and $AR1(\rho_{row})$ are the first-order autoregressive correlation matrices in the column and row directions, respectively.

To detect design, treatment, local and extraneous effects different diagnostic tools, variograms and plots of spatial residuals were used in ASReml 4.1 (Gilmour et al. 2015). All the environmental effects were removed from the raw data by extracting the predicted design effects and spatial residuals from the ASReml output files (Dutkowski et al. 2002, 2006; Chen et al. 2017) for all the traits in each of the trials, and the spatially adjusted data were used for all other analysis.

Statistics

The statistical model used for single site analysis for each trial was:

$$Y_{ij} = \mu + G_i + FG_{ij} + E_{ij} \tag{3}$$

Where Y_{ij} is the value of tree ij, μ is the average of the trial, G is the effect of the group (i=1,2, … 5), FG is the effect of every seed source (j) in the group (i) and E is a random residual. All effects except the residual were considered to be fixed.

The statistical model used for multi-site analysis of all the trials was:

$$Y_{ijk} = \mu + G_i + FG_{ij} + T_k + T_k{*}FG_{ij} + T_k{*}G_i + E_{ijk} \tag{4}$$

Where Y_{ijk} is the value of tree ijk, μ is the average of the trial, G is the effect of the group (i), FG is the effect of every seed source (j) in the group (i), T is the effect of the trial (k), $T*FG$ is the effect of every seed source (j) in the group (i) by environment (T), $T*G$ is the effect of the group (i) by environment (T) and E is a random residual. G and FG were considered to be fixed, while the other variables were considered to be random.

SAS Proc Mixed (SAS Institute Inc. 2011) was used for the analysis, in which the group averages were obtained through least square means in the LSMEANS statement of Proc Mixed. TUKEY/Kramer (Proc Mixed, SAS Institute Inc. 2011) was used as for pairwise comparisons between the groups.

Results

For the multi-site analysis, the fixed variables were significant for all the traits and the covariance parameters for the random variables are seen in Table 3. The trees from SweSO were on average taller and wider than the rest, but no significant difference to EastSO for DBH14 and, EastSO and SweEast for H7 (Table 4). The smallest and thinnest trees on average were found in the SweS group. The seed sources from

Table 3. Covariance parameter estimates for the random variables for the mixed model analysis.

Cov Parm/trait	DBH14	H7	L	BB	F	S4	S7	S14
T	133	2920	0.07	0.300	0.041	0.044	0.042	0.0412
T*G	2	14	0.03	0.001	0.005	0.001	0.001	0.0004
T*FG	8	58	0.01	0.002	0.003	0.002	0.003	0.0033
Residual	278	1913	0.63	0.472	0.263	0.353	0.370	0.3747

Table 4. Least square average of the traits DBH14 and H7 and their standard errors (SE) with pairwise comparisons between all the groups.

Group/trait	DBH14	SE	Sig.	H7	SE	Sig.
SweSO	73.02	4.79	A	203.52	22.19	A
EastSO	69.45	4.78	AB	200.20	22.19	AB
SweEast	68.34	4.75	B	192.52	22.14	AB
EastS	67.62	4.76	B	195.33	22.15	B
SweS	63.69	4.78	C	183.25	22.18	C

Different letters in the sig. columns indicate significant differences for the pairwise comparisons (DBH14 – Diameter at Breast Height at the age of 14, H7 – Height at the age of 7).

SweSO had 11-14.6% higher gain in growth for DBH14 and H7 respectively, compared to those from SweS. The gain for EastSO was 9%, EastS 6-7% and SweEast 5-7%. For spring frost damage, no significant differences were found between the groups but the SweS had most extensive frost damage on average (Table 5).

Bud flush scoring showed that the seed sources in the group SweS flushed significantly earlier than all other groups (Table 5) with an average of bud flush score 5, followed by SweEast (4.7), SweSO (4.6), EastSO (3.6) and EastS (3.3). The relationship between the different groups is similar in all the trials with the highest bud flush score for SweS and the lowest for EastS and EastSO. Timing of bud flush was significantly different between the Eastern material compared to the Swedish material (Table 5). The growth cessation measured as lignification followed a similar pattern (Table 5) with East European material significantly different from the Swedish material.

Correlating bud flush to frost damage (Figure 2) indicated that seed sources with earlier bud flush also suffer more from frost damage. Trial 1359 Toftaholm had the highest percentage of frost damage (23%); in addition, a high correlation between frost damage and bud flush could be seen (Figure 2), with the Eastern European groups less damaged than the Swedish groups. This trend could also be seen in trials 1357 Gullspång (6% frost) and 1360 Skärsnäs (4% frost) but was less pronounced (Figure 2).

In order to study the performance of the origins across sites, a ranking from the least square means was performed on the single site analysis (Appendix 1). For diameter at breast height at the age of 14 (Appendix 1, Table A2), SweSO was widest on average in all the trials, while SweS was thinnest. For the height at age 7 (Appendix 1, Table A3), SweSO was highest on average in all trials except for trial 1357 where EastSO was highest, and SweS was shortest on average. For frost damage (Appendix 1, Table A4), SweS had on average most damage in all the trials while EastS had least damage. EastS had latest bud burst and shortest lignification in almost all the trials (Appendix 1, Table A5 and A6), while SweS had earliest bud burst and longest lignification. For survival at age of 14 (Appendix 1, Table A7), SweS had significant highest survival while EastS had lowest survival (Table 5).

To visualize the variation of performance within the different groups, the seed sources were ranked to see how the seed sources in the groups behave in the different trials (Appendix 2). Overall the different seed sources show similar behaviour in the same group, but some seeds sources stand out with higher or lower rank compared to other seed sources in the same group.

The majority of the recorded mortality occurred soon after establishment, and after the year 2 field assessment, the survival rate was stable. The same trend could be seen in all the trials (1.7–5.6% loss) and all the groups (2.5–3.8% loss). The lowest survival percentage, based on growing site, was in trials 1358 Sund and 1359 Toftaholm, with around 65%, while trial 1357 Gullspång and 1360 Skärsnäs had the highest survival of 88%. For the different provenances, group SweS had the highest survival with 85.8% alive after 2 years and 81.8% alive after 12 years, while SweSO had the lowest survival with 72% of the trees alive after 12 years.

Discussion

According to the current study, the seed-producing Swedish stands of documented East European origin (SweEast) may constitute a feasible choice in case of a shortage of seeds. The observed higher growth of SweEast and EastS as compared to SweS could be explained by the fact that they are more adapted to the sites. The fact that we found the bud burst in SweEast to be so much earlier than EastS (Table 5) suggests that not only pollination from Swedish stands can explain the difference. If the SweS pollen had contributed 100% to the offspring, the SweEast group mean should have been closer to the EastS material. In addition, it is not likely that the pollen cloud came only from external sources. The fact that height in SweEast and EastS were approximately equal indicates that most of the pollination was from within the stand. Thus, even after one generation, the environment of the area where the seeds are planted has a great influence on the performance of the next generation. This was also reported by Skrøppa and Steffenrem (2016). Another explanation for the results could be that the individual trees that have not adapted to the new site will die. However, mortality was low in the SweEast stands, suggesting that this effect should have been low. Naturally regenerated seedlings from the surrounding indigenous stands could have been another explanation but they should have been

Table 5. Least square averages on normal score data of the traits L, BB, F and S14 and their standard errors (SE) with pairwise comparisons between all the groups.

Group/Trait	L ns lsmean	SE	Sig.	BB ns lsmean	SE	Sig.	F ns lsmean	SE	Sig.	S14 ns lsmeans	SE	Sig.
EastS	−0.42	0.14	B	−0.58	0.22	D	−0.08	0.13	A	−0.01	0.084	B
EastSO	−0.35	0.14	B	−0.39	0.22	C	−0.06	0.13	A	−0.02	0.085	B
SweSO	0.07	0.14	A	0.16	0.22	B	0.08	0.13	A	−0.07	0.085	B
SweEast	0.15	0.14	A	0.22	0.22	B	0.08	0.13	A	−0.02	0.084	B
SweS	0.39	0.14	A	0.41	0.22	A	0.13	0.13	A	0.09	0.085	A

Different letters in the sig. columns indicate significant differences for the pairwise comparisons (L – Lignification at the age of 5, BB – Bud burst at the age of 4, F – Frost at the age of 4, S14 – Survival at the age of 14).

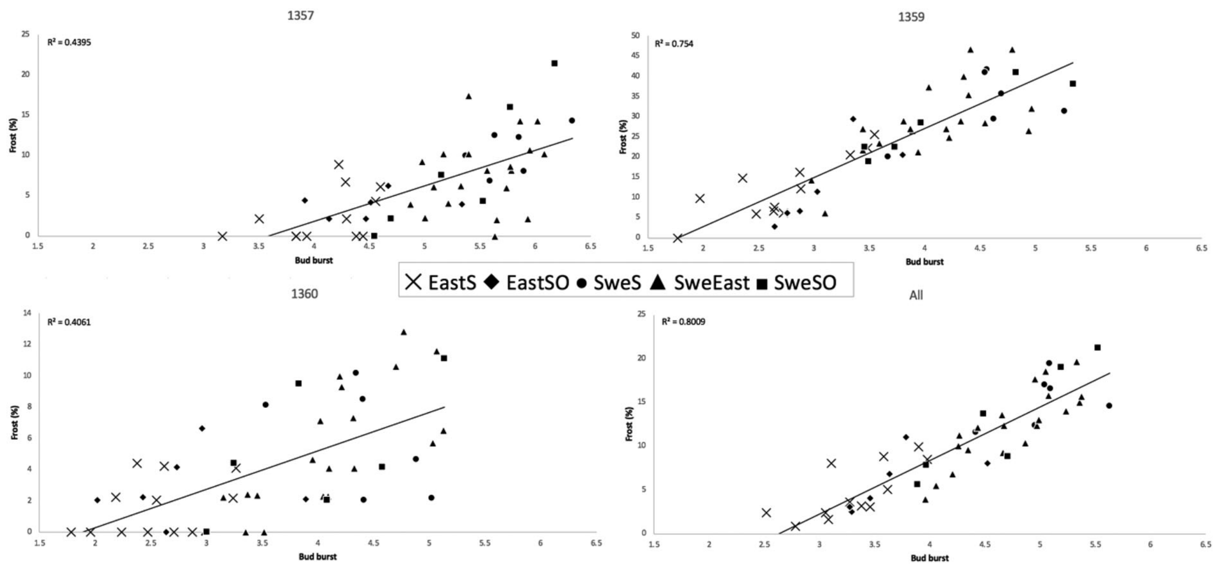

Figure 2. Bud burst versus frost damage for trials 1357 Gullspång, 1359 Toftaholm, 1360 Skärsnäs and these three together (all).

smaller and removed by thinning or died by competition. Influence of natural regeneration in the final stand increases if the mortality is high and, in our case the mortality for the deployed material was low. Even if the SweEast group is only partly the same as the East European material (Figure 1), both materials are expected to have similar bud burst. The result, therefore, indicates a formation of land race, where trees from SweEast have adapted to the Swedish climate.

It is important to note the SweEast material behaves more like Swedish origin than East European origin material when considering phenological traits, especially bud burst. Therefore, SweEast has a higher risk of damage from spring frosts compared to seed sources originating from Eastern Europe.

The best performance was found in trees grown from seed orchard sources, with the Swedish orchards slightly better than the Eastern European ones (Table 4). It is interesting to note that SweEast seed sources differ more from SweS with respect to growth traits than phenology, indicating that the possible landrace formation did not affect those traits as much. This is as expected since reports about epigenetic effects most often highlight adaptive traits such as bud burst and growth termination (Skrøppa et al. 2007). In our study, both the ranking of the best group as well as the level of gain in growth were as expected based on Liziniewicz and Berlin 2019; Liziniewicz et al. 2019 and Haapanen, 2020. In locations with a high risk of spring frost damage, trees with later bud flush are to be preferred, thus East European material is a good choice as well as the Swedish seed orchards that exhibit later bud flushing.

The overall performance of different groups in different trials is similar and only small variances within the groups could be seen. These variances suggesting that seed sources may behave differently in different locations (Appendix 2). For example, the seed sources 137 (Hallaryd) was ranked much higher for H7 in the southern sites and lower in the northern sites (Table B2), indicating that trees from 137 was taller in the southern sites. This is probably due to the fact that the northern sites and southern sites are in different seed zones and some sites are frost prone sites (Berlin et al. 2015). When selecting material for deployment, it is not only important to select from the right group, it is also important to select the right kind of seed source. Thus, it is important to consider seed sources x site interaction when selecting material for deployment and adapt it to the site you have, especially regarding growth rhythm.

The low GxE in this study indicate a high plasticity of Norway spruce but with climate change and higher temperature in the future it will be harder for the trees to adapt. For Norway spruce it is the growth rhythm that is important. Especially how the connection between bud burst and the risk of spring frost damage is affected by the climate change (Langvall 2011; Svystun et al. 2020). This in turn will create a need for transfers of trees with desirable properties, assisted migration (Williams and Dumroese 2013; Koralewski et al. 2015).

Bud burst was strongly correlated with frost damage (Figure 2), indicating that seed sources with earlier bud burst are more severely damaged. This has been shown in several other studies (Prescher 1982; Werner and Karlsson 1982; Hannerz 1994; Jönsson and Bärring 2004) and it supports the hypothesis that trees with later bud burst are more frost hardy in the spring.

When moving seeds from one country to another it is important to think about the aspect with introducing nonnative pests (Franić et al. 2019). However, the biggest risks are associated with transport of alive plants and moving plants from one continent to another (Santini et al. 2012). In our study Norway spruce seeds are only moved from Eastern Europe to Sweden, therefore the risk of nonnative pests should be low.

The majority of the recorded mortality occurred soon after establishment, and after 2 years in the field it levelled off and stabilized. We suspect that the early mortality is mainly due to fungal infection in the nursery. Many plants were affected, and plants that grew more rapidly were more affected due to higher plant density. During trial establishment plants with decreased vitality were observed by the planters. This may explain why seed sources with taller trees had the highest mortality at the beginning. To support this, it is clear that tree mortality was very low and similar for all the groups at all assessments after 2 years in the field. We therefore believe that this result should not be generalized to support the conclusion that the best growing trees will have lower survival in the forest.

Conclusions

In several Nordic countries there are seed shortage of improved Norway spruce seeds but in many of these countries there exist native seed sources of desired provenances like second generation material. In our study the second generation material have a growth rhythm similar to autochthonous Swedish material, indicating the development of a land race with respect to phenological traits. Seeds from Swedish seed orchards (SweSO) exhibited the highest growth, with seeds from Eastern European seed orchards (EastSO) close after, then seeds from Eastern European stands (EastS) and seeds from second generation material (SweEast), and finally, with the lowest growth, seeds from Swedish stands (SweS). There is variation within the different groups which indicate that it is important not only to select one group but also to select the right seed source within the selected group.

In locations where spring frost damage was recorded, a strong relationship between late bud flush and reduced damage could be seen which is in line with previous studies.

Although GxE was generally low in this study, indicating high plasticity of Norway spruce, global warming can result in very fast changes of climatic conditions, highlighting the need for assisted migration.

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Data availability statement

All raw data are archived in DATAPLAN®.

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Appendices

Appendix 1

Table A1. All the seed sources used in the study.

ID	Name	Group	Latitude	Longitude	Country
121	Ön 444	SweSO	60.23	16.78	Sweden
122	Saleby	SweSO	58.36	13.15	Sweden
123	Slogstorp	SweSO	55.75	13.45	Sweden
124	Runesten	SweSO	57.12	12.41	Sweden
125	Maglehem	SweSO	55.77	14.17	Sweden
126	Bredinge	SweSO	56.48	16.43	Sweden
127	Sakiai	EastSO	55.00	23.42	Lithuania
128	Panevezys	EastSO	55.75	24.42	Lithuania
129	Glopquel/Vitebsk	EastSO	55.19	30.19	Belarus
130	Remte	EastSO	56.75	22.67	Latvia
131	Suntazi	EastSO	56.92	24.92	Latvia
132	Katvari	EastSO	57.50	24.67	Latvia
133	Ängelsfors	SweS	60.54	16.14	Sweden
134	Laxarby	SweS	59.02	12.32	Sweden
135	Bollebygd	SweS	57.71	12.50	Sweden
136	Ramkvilla	SweS	57.20	14.85	Sweden
137	Hallaryd	SweS	56.47	13.90	Sweden
138	Emmaboda	SweS	56.63	15.57	Sweden
139	Rezekne1	EastS	56.50	27.35	Latvia
140	Punia	EastS	54.53	24.05	Lithuania
141	Ignalina	EastS	55.40	26.38	Lithuania
142	Trakai	EastS	54.58	24.75	Lithuania
143	Vitebsk	EastS	55.20	30.25	Belarus
144	Minsk	EastS	53.90	27.55	Belarus
145	Bialystok	EastS	53.12	23.17	Poland
146	Istebna	EastS	49.57	18.89	Poland
147	Svente	EastS	55.83	26.25	Latvia
148	Istra	EastS	56.25	27.83	Latvia
149	Malta	EastS	56.25	27.25	Latvia
150	Rezekne2	EastS	56.08	27.42	Latvia
165	Andrarums fälad	SweEast	55.69	13.94	Sweden
166	Grettlinge	SweEast	56.24	15.90	Sweden
167	Djuraskogsvägen, Össjö	SweEast	56.25	13.11	Sweden
168	Össjö 120	SweEast	56.25	13.10	Sweden
169	Flaken	SweEast	56.42	15.70	Sweden
170	Bonnarp	SweEast	56.42	15.71	Sweden
171	Oskarsström	SweEast	56.80	12.95	Sweden
172	Skårebo	SweEast	56.89	12.93	Sweden
173	Linnebjörke 217	SweEast	56.96	15.15	Sweden
174	Linnebjörke 178 – Sjöborgen	SweEast	56.97	15.15	Sweden
175	Linnebjörke 164-Kvarnavägen	SweEast	56.98	15.14	Sweden
176	Böksholm	SweEast	57.08	15.00	Sweden
177	Klev	SweEast	57.05	12.48	Sweden
178	Källehult	SweEast	57.17	15.14	Sweden
179	Påbo	SweEast	57.22	13.23	Sweden
180	Hagelstorp	SweEast	57.37	13.64	Sweden
181	Marsgölehult	SweEast	57.56	16.42	Sweden
182	Långsten	SweEast	58.21	14.92	Sweden
183	Bergstugan	SweEast	58.81	17.05	Sweden
184	Oxlöth	SweEast	58.81	17.08	Sweden

Group according to origin and type of seed source, SweSO – Swedish seed orchards, SweS – Swedish stands, EastSO – East European seed orchards, EastS – East European stands, and SweEast – Swedish stands with East European origin.

Table A2. Diameter at breast height at the age of 14 (DBH14) ranked from wide to thin according to the least square means from the single site analysis.

Group/trial	1355	1356	1357	1358	1359	1360
SweSO	1	1	1	1	1	1
EastSO	4	3	2	2	2	3
SweEast	2	2	3	4	4	2
EastS	3	5	4	3	3	4
SweS	5	4	5	5	5	5

Table A3. Height at the age of 7 (H7) ranked from tall to short according to the least square means from the single site analysis.

Group/trial	1355	1356	1357	1358	1359	1360
SweSO	1	1	2	1	1	1
EastSO	3	2	1	2	2	3
SweEast	2	5	4	4	4	2
EastS	4	3	3	3	3	4
SweS	5	4	5	5	5	5

Table A4. Frost (F)for the trees ranked from most to least damage according to the least square means from the single site analysis.

Group/trial	1357	1359	1360
SweSO	2	3	2
EastSO	4	4	4
SweEast	3	2	3
EastS	5	5	5
SweS	1	1	1

Table A5. Lignification (L) for the trees ranked from least to most lignification in the top shoot according to the least square means from the single site analysis.

Group/trial	1355	1356	1357	1359	1360
SweSO	4	4	3	5	3
EastSO	2	2	2	2	2
SweEast	3	4	4	4	4
EastS	1	1	1	1	1
SweS	5	5	5	3	5

Table A6. Bud burst (BB) for the trees ranked from latest to earliest bud burst according to the least square means from the single site analysis.

Group/trial	1355	1356	1357	1358	1359	1360
SweSO	3	3	3	4	4	3
EastSO	2	2	2	2	2	2
SweEast	4	4	4	3	3	4
EastS	1	1	1	1	1	1
SweS	5	5	5	5	5	5

Table A7. Survival for the trees at age 14 (S14) ranked from highest to lowest survival according to the least square means from the single site analysis.

Group/trial	1355	1356	1357	1358	1359	1360
SweSO	5	5	5	5	4	4
EastSO	3	4	4	4	2	2
SweEast	4	2	3	2	5	5
EastS	2	3	2	3	3	3
SweS	1	1	1	1	1	1

Appendix 2

Table B1. Ranking of seed sources according to least square means averages on diameter at breast height at age of 14 (DBH14) for all the trials.

Group	Seed source	1355	1356	1357	1358	1359	1360
SweSO	121	40	3	21	41	27	33
SweSO	122	38	2	20	29	26	16
SweSO	123	36	7	19	6	17	7
SweSO	124	16	4	16	8	1	3
SweSO	125	1	6	1	2	5	1
SweSO	126	2	16	7	12	18	10
EastSO	127	21	45	12	19	14	23
EastSO	128	48	34	11	36	24	35
EastSO	129	29	36	14	25	20	27
EastSO	130	23	22	13	13	15	17
EastSO	131	30	11	28	10	22	36
EastSO	132	10	13	6	28	13	24
SweS	133	50	37	49	44	44	43
SweS	134	43	41	44	50	47	32
SweS	135	27	38	46	45	41	46
SweS	136	41	8	47	38	46	48
SweS	137	24	19	27	7	11	6
SweS	138	37	40	45	32	49	44
EastS	139	11	20	37	22	35	28
EastS	140	19	32	25	21	16	26
EastS	141	35	43	8	14	10	18
EastS	142	9	33	26	37	34	31
EastS	143	47	50	50	49	36	49
EastS	144	42	48	39	30	28	20
EastS	145	22	46	22	27	9	42
EastS	146	15	9	5	5	2	4
EastS	147	45	39	35	17	31	19
EastS	148	32	29	24	35	33	50
EastS	149	13	23	33	9	23	39
EastS	150	25	14	36	23	21	29
SweEast	165	17	5	38	34	43	30
SweEast	166	5	44	29	43	38	40
SweEast	167	20	47	34	40	42	25
SweEast	168	8	15	3	3	3	5
SweEast	169	4	31	18	31	29	15
SweEast	170	6	12	15	4	12	2
SweEast	171	18	27	4	1	7	8
SweEast	172	12	42	9	20	4	14
SweEast	173	31	35	32	39	30	45
SweEast	174	44	18	41	48	48	41
SweEast	175	33	10	42	46	50	38
SweEast	176	14	30	10	11	19	13
SweEast	177	3	1	2	16	6	9
SweEast	178	49	21	48	33	45	47
SweEast	179	26	28	40	26	32	34
SweEast	180	28	17	31	42	40	21
SweEast	181	7	26	17	15	8	11
SweEast	182	46	49	43	47	39	37
SweEast	183	34	24	30	18	37	12
SweEast	184	39	25	23	24	25	22

Table B2. Ranking of seed sources according to least square means averages on height at age of 7 (H7) for all the trials.

Group	Seed source	1355	1356	1357	1358	1359	1360
SweSO	121	32	7	4	35	21	13
SweSO	122	46	3	23	7	27	12
SweSO	123	37	11	30	4	19	15
SweSO	124	11	33	21	2	1	1
SweSO	125	7	35	8	10	22	8
SweSO	126	2	22	5	15	13	14
EastSO	127	10	44	11	3	8	16
EastSO	128	39	14	1	41	18	25
EastSO	129	21	20	12	17	20	22
EastSO	130	35	9	3	14	16	28
EastSO	131	24	6	20	8	29	30
EastSO	132	17	12	2	33	17	33
SweS	133	50	29	46	43	37	38
SweS	134	48	17	36	48	43	36
SweS	135	22	47	47	44	40	46
SweS	136	49	5	49	40	46	50
SweS	137	45	37	41	9	6	6
SweS	138	33	34	39	29	50	45
EastS	139	4	18	31	16	33	26
EastS	140	13	40	24	22	12	19
EastS	141	20	26	6	6	4	5
EastS	142	18	4	15	32	35	31
EastS	143	40	38	50	50	36	48
EastS	144	38	36	28	24	24	18
EastS	145	28	30	19	28	3	35
EastS	146	42	39	17	26	2	2
EastS	147	36	19	25	21	25	29
EastS	148	19	28	16	39	28	49
EastS	149	16	1	22	12	26	32
EastS	150	14	15	43	19	31	27
SweEast	165	29	2	40	38	49	39
SweEast	166	5	46	38	49	42	41
SweEast	167	12	45	32	34	48	34
SweEast	168	31	49	10	13	5	11
SweEast	169	1	10	7	11	23	9
SweEast	170	26	32	35	20	11	4

(*Continued*)

Table B2. Continued.

Group	Seed source	1355	1356	1357	1358	1359	1360
SweEast	171	27	43	18	1	7	3
SweEast	172	6	42	27	31	9	23
SweEast	173	9	27	26	42	30	43
SweEast	174	43	31	34	46	41	42
SweEast	175	30	13	45	45	47	47
SweEast	176	15	48	33	30	32	24
SweEast	177	8	8	9	23	10	10
SweEast	178	47	21	44	27	39	37
SweEast	179	25	25	29	25	34	40
SweEast	180	3	16	13	36	38	7
SweEast	181	34	41	37	5	15	20
SweEast	182	44	50	48	47	44	44
SweEast	183	41	23	42	37	45	21
SweEast	184	23	24	14	18	14	17

Table B3. Ranking of seed sources according to least square means averages on frost (F) at age of 4 for trials 1357, 1359 and 1360.

Group	Seed source	1357	1359	1360
SweSO	121	31	26	38
SweSO	122	3	6	22
SweSO	123	47	29	40
SweSO	124	1	9	3
SweSO	125	21	15	8
SweSO	126	41	35	16
EastSO	127	39	42	44
EastSO	128	33	49	29
EastSO	129	36	13	12
EastSO	130	22	40	19
EastSO	131	30	47	39
EastSO	132	32	33	32
SweS	133	8	4	37
SweS	134	6	12	34
SweS	135	18	8	5
SweS	136	9	3	9
SweS	137	20	16	18
SweS	138	13	31	11
EastS	139	29	23	23
EastS	140	45	41	42
EastS	141	44	45	50
EastS	142	23	38	17
EastS	143	46	39	46
EastS	144	35	50	49
EastS	145	48	43	31
EastS	146	15	34	47
EastS	147	50	36	45
EastS	148	49	44	21
EastS	149	40	48	36
EastS	150	26	30	35
SweEast	165	14	5	27
SweEast	166	10	27	20
SweEast	167	37	10	13
SweEast	168	38	32	48
SweEast	169	24	22	41
SweEast	170	7	25	2
SweEast	171	11	17	28
SweEast	172	43	20	10
SweEast	173	28	37	43
SweEast	174	27	7	24
SweEast	175	19	21	6
SweEast	176	25	28	26
SweEast	177	4	11	14
SweEast	178	17	2	7
SweEast	179	42	19	30
SweEast	180	12	14	25
SweEast	181	2	24	1
SweEast	182	16	18	4
SweEast	183	5	1	15
SweEast	184	34	46	33

Table B4. Ranking of seed sources according to least square means averages on lignification (L) at age of 5 for trials 1355, 1356, 1357, 1359 and 1360.

Group	Seed source	1355	1356	1357	1359	1360
SweSO	121	43	35	36	42	32
SweSO	122	46	44	40	41	43
SweSO	123	28	25	15	11	19
SweSO	124	34	36	39	20	38
SweSO	125	20	30	23	33	27
SweSO	126	15	14	13	10	17
EastSO	127	9	1	3	8	6
EastSO	128	12	15	11	5	3
EastSO	129	13	20	12	22	10
EastSO	130	5	24	10	27	15
EastSO	131	1	5	7	21	8
EastSO	132	22	23	19	18	34
SweS	133	49	41	45	50	49
SweS	134	50	47	50	45	50
SweS	135	48	38	43	47	45
SweS	136	45	43	38	44	48
SweS	137	27	46	44	36	35
SweS	138	32	29	29	31	26
EastS	139	18	22	20	24	9
EastS	140	3	13	1	3	5
EastS	141	2	12	2	2	1
EastS	142	8	3	9	25	7
EastS	143	11	9	8	17	11
EastS	144	6	2	6	1	2
EastS	145	7	4	4	4	4
EastS	146	4	10	14	6	13
EastS	147	14	8	17	14	12
EastS	148	10	6	5	7	20
EastS	149	17	7	16	12	14
EastS	150	30	17	25	19	23
SweEast	165	40	33	49	46	46
SweEast	166	36	31	30	34	41
SweEast	167	44	45	41	39	30
SweEast	168	25	11	27	35	28
SweEast	169	24	19	21	23	22
SweEast	170	39	34	48	28	39
SweEast	171	19	16	22	26	16
SweEast	172	26	27	24	16	18
SweEast	173	33	28	26	38	24
SweEast	174	47	39	47	48	42
SweEast	175	41	26	32	40	44
SweEast	176	21	42	34	32	29
SweEast	177	35	49	37	15	33
SweEast	178	42	37	31	29	36
SweEast	179	23	21	35	37	31
SweEast	180	31	40	28	30	25
SweEast	181	29	50	33	13	37
SweEast	182	38	32	46	49	47
SweEast	183	37	48	42	43	40
SweEast	184	16	18	18	9	21

Table B5. Ranking of seed sources according to least square means averages on bud burst (BB) at age of 4 for all the trials.

Group	Seed source	1355	1356	1357	1358	1359	1360
SweSO	121	41	33	32	34	26	34
SweSO	122	46	39	41	41	46	42
SweSO	123	14	19	15	21	18	17
SweSO	124	48	42	49	47	50	50
SweSO	125	30	27	24	31	33	28
SweSO	126	16	16	19	24	20	19
EastSO	127	11	8	7	8	10	12
EastSO	128	9	7	13	5	5	3
EastSO	129	15	15	14	17	17	15
EastSO	130	12	14	18	11	14	13
EastSO	131	10	11	6	14	8	7
EastSO	132	23	29	28	30	30	27

(Continued)

Table B5. Continued.

Group	Seed source	1355	1356	1357	1358	1359	1360
SweS	133	34	49	42	39	42	41
SweS	134	50	50	50	49	49	47
SweS	135	44	30	44	40	44	39
SweS	136	40	45	36	45	40	40
SweS	137	29	36	34	32	43	45
SweS	138	21	28	30	28	25	25
EastS	139	17	22	16	16	24	21
EastS	140	4	1	1	1	2	1
EastS	141	3	3	3	3	7	5
EastS	142	1	5	11	10	3	6
EastS	143	6	10	10	7	12	8
EastS	144	2	2	2	2	1	2
EastS	145	5	6	4	4	9	4
EastS	146	7	12	8	13	23	11
EastS	147	18	13	12	6	11	14
EastS	148	8	4	5	9	6	10
EastS	149	13	9	9	12	4	9
EastS	150	19	17	17	20	16	20
SweEast	165	37	40	48	44	38	31
SweEast	166	24	21	25	23	19	29
SweEast	167	45	38	46	36	39	33
SweEast	168	32	18	22	18	31	26
SweEast	169	25	24	27	25	21	23
SweEast	170	38	43	45	50	47	48
SweEast	171	27	26	21	22	36	22
SweEast	172	42	34	35	35	34	37
SweEast	173	22	23	26	19	13	16
SweEast	174	36	46	38	37	32	38
SweEast	175	26	37	33	26	27	36
SweEast	176	31	25	23	29	22	24
SweEast	177	39	48	47	42	48	46
SweEast	178	35	41	40	43	37	35
SweEast	179	28	31	37	33	29	30
SweEast	180	33	32	29	27	28	32
SweEast	181	43	35	31	38	35	44
SweEast	182	47	44	39	48	41	43
SweEast	183	49	47	43	46	45	49
SweEast	184	20	20	20	15	15	18

Table B6. Ranking of seed sources according to least square means averages on survival at age of 14 (S14) for all the trials.

Group	Seed source	1355	1356	1357	1358	1359	1360
SweSO	121	25	21	36	33	6	11
SweSO	122	5	3	14	20	3	15
SweSO	123	31	41	16	48	34	8

(*Continued*)

Table B6. Continued.

Group	Seed source	1355	1356	1357	1358	1359	1360
SweSO	124	46	48	48	49	50	50
SweSO	125	50	45	50	41	49	43
SweSO	126	16	29	31	36	5	27
EastSO	127	41	50	40	26	47	28
EastSO	128	37	35	24	35	9	5
EastSO	129	27	28	30	31	23	18
EastSO	130	29	42	39	39	16	23
EastSO	131	24	6	47	32	24	35
EastSO	132	17	2	6	22	4	25
SweS	133	1	4	8	8	10	6
SweS	134	3	5	5	1	17	34
SweS	135	2	17	11	3	2	16
SweS	136	19	1	26	10	11	22
SweS	137	44	25	44	42	19	30
SweS	138	13	19	2	16	43	10
EastS	139	32	18	37	18	20	2
EastS	140	49	49	42	37	38	14
EastS	141	34	44	45	45	41	38
EastS	142	35	38	33	21	26	17
EastS	143	20	36	28	27	29	12
EastS	144	18	22	13	38	25	33
EastS	145	23	27	27	25	37	31
EastS	146	36	39	41	34	44	45
EastS	147	10	34	1	17	1	40
EastS	148	4	15	4	11	7	13
EastS	149	11	23	10	28	21	1
EastS	150	8	24	15	29	18	26
SweEast	165	21	12	19	14	27	42
SweEast	166	43	14	7	5	32	32
SweEast	167	38	32	35	40	42	36
SweEast	168	48	30	46	44	28	48
SweEast	169	15	31	12	7	12	21
SweEast	170	30	7	25	19	36	41
SweEast	171	39	40	49	50	40	44
SweEast	172	40	43	29	43	8	46
SweEast	173	26	20	17	6	14	20
SweEast	174	6	16	3	12	39	3
SweEast	175	9	26	18	9	31	7
SweEast	176	42	9	23	15	13	39
SweEast	177	47	46	43	46	48	49
SweEast	178	14	13	9	30	22	29
SweEast	179	22	10	20	2	15	37
SweEast	180	7	8	22	23	30	4
SweEast	181	45	47	34	47	45	47
SweEast	182	28	11	32	4	46	19
SweEast	183	33	33	38	13	33	9
SweEast	184	12	37	21	24	35	24