

## 1 Title

2 Phenotypic trait variation in a long-term, multisite common garden of Scots pine in Scotland.

## 3 Authors

4 Joan Beaton<sup>1</sup>, Annika Perry<sup>2</sup>, Joan Cottrell<sup>3</sup>, Glenn Iason<sup>1</sup>, Jenni Stockan<sup>1</sup>, Stephen Cavers<sup>2</sup>

## 5 Affiliations

- 6 1. Ecological Sciences, James Hutton Institute, Craigiebuckler, Aberdeen, AB15 8QH
- 7 2. UK Centre for Ecology & Hydrology (UKCEH), Bush Estate, Penicuik, Midlothian, EH26
- 8 0QB
- 9 3. Forest Research, Northern Research Station, Roslin, Midlothian, Scotland, EH25 9SY

10 corresponding author: Annika Perry (annt@ceh.ac.uk)

## 11 Abstract

12 Multisite common garden experiments, exposing common pools of genetic diversity to a  
13 range of environments, allow quantification of plastic and genetic components of trait  
14 variation. For tree species, such studies must be long term as they typically only express  
15 mature traits after many years. As well as evaluating standing genetic diversity, these  
16 experiments provide an ongoing test of genetic variation against changing environmental  
17 conditions and form a vital resource for understanding how species respond to abiotic and  
18 biotic variation. Finally, quantitative assessments of phenotypic variation are essential to pair  
19 with rapidly accumulating genomic data to advance understanding of the genetic basis of  
20 trait variation, and its interaction with climatic change.

21 We describe a multisite, population-progeny, common garden experiment of the  
22 economically and ecologically important tree species, Scots pine, collected from across its  
23 native range in Scotland and grown in three contrasting environments. Phenotypic traits,  
24 including height, stem diameter and budburst were measured over 14 growing seasons from  
25 nursery to field site. The datasets presented have a wide range of applications.

## 26 Background & Summary

27 The need for comprehensive empirical assessments of genetic variation in tree species has  
28 never been greater. There is great interest around the world in growing more trees<sup>1</sup>, for their  
29 carbon sequestration abilities in the race for 'net zero' carbon emissions, to arrest  
30 biodiversity loss and forest decline<sup>2</sup>, and to manage watersheds<sup>3</sup>, as well as for the products  
31 they provide. However, there is considerable uncertainty in the accuracy of forecasts of  
32 future climate and the responses of tree species to those changes<sup>4</sup>. Intraspecific genetic  
33 variation and phenotypic plasticity will play key roles in determining how resilient existing  
34 and new tree populations are to the challenges ahead<sup>5</sup>. We are in urgent need of robust  
35 empirical data to calibrate the relationships between genetic variation within species and the  
36 environmental variables that will define future climates<sup>6</sup>. In parallel, the genomic revolution  
37 has provided a dramatic increase in the accessibility and scale of molecular data, and trees  
38 can now be genotyped faster, more cheaply and in greater number than ever before.  
39 However, there is a limit to what these new data can tell us without objective evaluation of  
40 the associated phenotypes, for which common garden and reciprocal transplant approaches  
41 remain key experimental tools<sup>7,8</sup>. We aimed to link these genomic and common garden  
42 approaches to better understand the genetic basis of phenotypic variation in trees, and to

43 improve forecasting of how tree species will respond to climate change. Here we describe  
44 the research platform that we established to conduct these urgently needed long-term  
45 studies.

46 Scots pine (*Pinus sylvestris* L.) is globally very widely distributed, occurring predominantly  
47 from eastern Europe and Scandinavia to eastern Siberia, but with substantial populations in  
48 Scotland, southern Europe, Turkey and the Caucasus<sup>9</sup>. In Scotland, the remnant native  
49 populations, known locally as the Caledonian pinewoods, are typically small and highly  
50 fragmented and are distributed across a highly heterogeneous landscape that varies from  
51 oceanic (mild, very wet) environments in the west to more continental (drier, colder) in the  
52 east (Fig.1). This steep gradient of variation on a short spatial scale bears comparison to  
53 environmental gradients over much wider spatial scales across Europe (see Fig. 4 in Metzger  
54 et al., 2005<sup>10</sup>. To further the conservation of the pinewoods, specific action plans have been  
55 developed, including management of seed movements through a series of seven seed zones  
56 (Fig. 2<sup>11</sup>), the context and motivation for which are covered by Salmela et al., 2010<sup>12</sup>.

57 A key knowledge gap remained in the early 21st century, namely the extent to which the  
58 current seed zone system for managing seed sourcing for the native populations of Scottish  
59 Scots pine reflects genuine genetic differences, and whether the zones conform to patterns  
60 of adaptation which are of relevance to ecological conservation and forestry when assessed  
61 using traits such as growth, mortality, phenology and resistance to pests and pathogens. To  
62 address this gap, as well as to evaluate the likely responses of indigenous Scots pine to  
63 ongoing climate change, an extensive, long-term assessment of genetic variation in Scots  
64 pine under contrasting environmental conditions, was founded by the Macaulay Institute  
65 (now the James Hutton Institute). A collaboration with the UK Centre for Ecology &  
66 Hydrology and Forest Research was subsequently created to develop the studies of  
67 adaptation to climate and disease resistance, to apply and advance emerging methods for  
68 assessing genetic variation, and to secure the continuation of the study. At the outset, an  
69 explicit objective was to sample genetic diversity widely without favouring any particular  
70 form or trait, and to undertake a wide ranging evaluation of traits covering different life  
71 history dimensions as far as practically possible. The common environment study was also  
72 intended to provide a long term experimental platform to facilitate future studies of the  
73 basis for variation in the extended phenotype of Scots pine including associated assemblages  
74 of organisms and community function.

75 The following describes the origins, design and initial measurements of a multi-site  
76 experiment in Scots pine, including protocols adopted during both the initial nursery phase  
77 and the final field experiment.

## 78 **Methods**

### 79 Seed sampling and germination

80 Seed from ten trees from each of 21 native Scottish Scots pine populations (Table 1) were  
81 collected in March 2007 and germinated at the James Hutton Institute, Aberdeen (latitude  
82 57.133214, longitude -2.158764) in June 2007. Populations were chosen to represent the  
83 species' native range in Scotland and to include three populations from each of the seven  
84 seed zones (Fig. 2). There was no selection of seed-trees on the basis of any traits except for  
85 the possession of cones on the date of sampling. Ten seed trees were sampled from each  
86 population according to a spatial protocol designed to cover a circle of approximately 1 km in  
87 diameter located around a central tree. The sampling strategy identified nine points each in  
88 a pre-determined random direction from the central point, whilst stratifying the number  
89 sampled with increasing distance from the central point in the ratio 1: 3: 5. This strategy

90 avoids over-sampling the areas close to the centre point. For smaller fragments of woodland,  
91 or where only a few trees with cones were present, then the directions of the sampled trees  
92 from the central tree were maintained to give a wide coverage of the woodland area, but the  
93 distances between trees varied but were never closer than 50 m. To break dormancy, seeds  
94 were soaked for 24 hours on the benchtop at room temperature, after which they were  
95 stored in wet paper towels and refrigerated in darkness at 3-5 °C for approximately 4 weeks.  
96 Seeds were kept moist and transferred to room temperature until germination began  
97 (approx. 5-7 days), then transplanted to 8 cm x 8 cm x 9 cm, 0.4 L pots filled with Levington's  
98 C2a compost and 1.5g of Osmocote Exact 16-18 months slow release fertiliser and kept in an  
99 unheated glasshouse. The compost was covered with a layer of grit to reduce moss and  
100 liverwort growth. Seedlings from the same mother tree are described as a family and are  
101 assumed to be half-siblings.

#### 102 Experimental design: nurseries

103 The full collection consisted of 210 families (10 families from each of 21 populations) each  
104 consisting of 24 half sibling progeny (total 5,040 individuals); needle tissue was sampled from  
105 each seedling and preserved for long term storage, one needle on silica gel, 2-5 needles at -  
106 20 °C. After transfer into pots, 8 seedlings per family were moved to one of three nurseries  
107 (total 1,680 seedlings per nursery): outdoors at Inverewe Gardens in western Scotland  
108 (nursery in the west of Scotland: coded NW, latitude 57.775714, longitude -5.597181, Fig. 2);  
109 outdoors in a fruit cage (to minimise browsing) at the James Hutton Institute in Aberdeen  
110 (nursery in the east of Scotland: NE); in an unheated glasshouse at the James Hutton  
111 Institute in Aberdeen (nursery in a glasshouse: NG). Trees were arranged in 40 randomised  
112 trays (blocks) in each nursery. Each block contained two trees per population (total 42 trees).  
113 Watering was automatic in NG, and manually as required for NE and NW. No artificial light  
114 was used in any of the nurseries. In May 2010 the seedlings from NG were moved outdoors  
115 to Glensaugh in Aberdeenshire (latitude 56.893567, longitude -2.535736). In 2010 all plants  
116 were repotted into 19 cm (3 L) pots containing Levingtons CNSE Ericaceous compost with  
117 added Osmocote STD 16-18 month slow release fertilizer.

#### 118 Experimental design: field sites

119 In 2012 the trees were transplanted to one of three field sites: Yair in the Scottish Borders  
120 (field site in the south of Scotland: FS, latitude 55.603625, longitude -2.893025); Glensaugh  
121 (field site in the east of Scotland: FE); and Inverewe (field site in the west of Scotland: FW).  
122 All trees transplanted to FS were raised in the NG and all but four of the trees transplanted  
123 to FE were raised locally in the NE (the remainder were grown in NG). In contrast, following  
124 mortality and 'beating up' (filling gaps where saplings had died), the FW experiment  
125 ultimately contained cohorts of trees raised in each of the three nurseries as follows: 290  
126 grown locally in the NW; 132 were grown in the NG; and 82 were grown in the NE.

127 *Site histories:* The Yair site (FS) had previously been used for growing Noble fir (*Abies*  
128 *procera*) for Christmas trees and Lodgepole pine (*Pinus contorta*), a section of the former  
129 were felled and chipped to create a clear area prior to planting. The planting site is also  
130 adjacent to a large block of commercial Sitka spruce (*Picea sitchensis*) forestry, and the  
131 Glenkinnon Burn Site of Special Scientific Interest (SSSI naturescot site code 736; EU site  
132 code 135445), an area of mixed broadleaf woodland. Prior to planting, major areas of tall  
133 weeds were trimmed. The site was protected by a deer fence. The experiment was planted  
134 8-11 October 2012. The Glensaugh site (FE) is in Forestry Compartment 3 of the Glensaugh  
135 Research Station, adjacent to Cleek Loch. It is thought to have been cleared of Scots pine and  
136 Larch (*Larix decidua*) around 1917, after which it reverted to rough grazing. An attempt to  
137 reseed part of the site in the 1980s was unsuccessful and it quickly reverted to rough grazing

138 for a second time. The whole site (within which the experimental area is embedded) was  
139 deer fenced and re-planted under the Scottish Rural Development Programme (SRDP) in  
140 2012. The experimental plot was planted up 7-9 March 2012. The Inverewe site (FW) had  
141 previously been a Sitka spruce and Lodgepole pine plantation (50:50 mix) that had been  
142 clear-felled in 2010 following substantial windthrow. The experimental site was deer fenced  
143 in early 2012, and the experiment was planted 12-16 March 2012, followed by beating up on  
144 27-28 March 2013 and 22-24 October 2013. There had been minimal preparation of the site  
145 in line with current practice for restocking sites. The experimental site is included in the  
146 Inverewe Forest Plan, which included deer fencing of a larger area (2014) around the  
147 experimental site. Planting of this area was completed in early 2015, funded by NTS  
148 (National Trust for Scotland), although natural regeneration is also taking place.

149 At each site, trees were planted in randomised blocks at 3 m x 3 m spacing. There are four  
150 randomised blocks in both FS and FE and three in FW. A guard row of Scots pine trees was  
151 planted around the periphery of the blocks. Each block comprised one individual from each  
152 of eight (of the 10 sampled) families per 21 populations (168 trees). Although most families  
153 (N = 159) were represented at each of the three sites, families with insufficient trees (N = 9)  
154 were replaced in one site (FS) with a different family from the same population. Each  
155 experimental site was designed with redundancy such that, if thinning becomes necessary as  
156 the trees mature, then the systematic removal of trees (i.e. trees 1,3,5,7, etc of row 1, and  
157 2,4,6,8, etc of row 2, 1,3,5,7,etc of row 3) will maintain a balanced design of the experiment,  
158 with sufficient family and population representation to provide an ongoing experiment with  
159 full geographic coverage.

160 The field sites generally experience different climates, with FW typically warmer and wetter  
161 and with more growing degree days per year and a much longer growing season than both  
162 FE and FS (Table 2). The coldest site with the shortest growing season is generally FE.

### 163 Phenotype assessments

164 *Maternal traits:* Following seed collection, a range of traits were measured in the mother  
165 trees in order to control for maternal effects in subsequent measurements of their progeny  
166 (Table 3). For each mother tree, measurements of height and diameter at breast height  
167 (DBH) were taken, and ten cones were collected and assessed in detail. Cone width and  
168 length were measured prior to drying the cones (when they were still closed). Cone weight  
169 was measured post-drying. Seed removed from each cone was assessed for total weight and  
170 for the count and percentage of seeds which were classed as viable (viable seed were those  
171 which had both a wing and an obvious seed).

172 *Nursery traits:* Seedling phenotype assessments were performed annually from 2007-2010  
173 for three different trait types: phenology (budburst and growth cessation); form (total  
174 number of buds, needle length); cumulative growth (stem diameter and height, canopy  
175 width). Measurements of tree form and cumulative growth traits were taken after the end of  
176 each growing season. Phenology was assessed weekly during the spring and autumn of 2008  
177 for budburst and growth cessation, respectively. Budburst was defined as the number of  
178 days from 31 March 2008 to the time when newly emerged green needles were observed.  
179 Growth cessation was defined as the number of days from 1 September 2008 to the time  
180 when no further growth was observed. Canopy width (widest point) was measured at two  
181 perpendicular points in the horizontal plane. Needle length was measured for three needles  
182 per tree. Mortality was recorded each year from 2007 to 2010.

183 *Field traits:* Tree height was measured in the field in the winter after each growing season  
184 from 2013 at FE and FW, and from 2014 to 2020 at all sites. Height was taken as the vertical

185 measurement in cm from top bud straight to the ground. Basal stem diameter was measured  
186 at the end of the growing season for trees growing at FE and FW from 2014 to 2020 and for  
187 FS in 2020.

188 Phenology assessments were performed in spring at each site from 2015 to 2019. Seven  
189 distinct stages of budburst were defined (Supplementary Table 1) although only stages 4 to 6  
190 are considered for analysis due to high proportions of missing data for the early and late  
191 stages. Each tree was assessed for budburst stage at weekly intervals from early spring until  
192 budburst was complete, annually from 2015 until 2019. In order to allow comparisons within  
193 and among sites and years, the date at which each stage of budburst occurred was  
194 considered relative to 31 March of that year. For example, 25 May 2019 is recorded as 55  
195 days since 31 March 2019. The duration of budburst (time taken to reach stage 6 from stage  
196 4) was also estimated.

197 When trees progressed through budburst stages rapidly, skipping a stage between  
198 assessments, a mean value was taken from the two assessment dates. For example, if a tree  
199 was at stage 4 on day 55 and was recorded as stage 6 at the next assessment on day 62, it is  
200 assumed to have reached stage 5 at day 58.5.

## 201 **Data Records**

202 Data are deposited with the Environmental Information Data Centre (<http://eidc.ac.uk>)

203 DOI for maternal traits datasets: [doi.org/10.5285/ac687a66-135e-4c65-8bf6-c5a3be9fd9aa](https://doi.org/10.5285/ac687a66-135e-4c65-8bf6-c5a3be9fd9aa)

204 DOI for nursery traits dataset: [doi.org/10.5285/29ced467-8e03-4132-83b9-dc2aa50537cd](https://doi.org/10.5285/29ced467-8e03-4132-83b9-dc2aa50537cd)

205 DOI for field traits dataset: [doi.org/10.5285/f463bc5c-bb79-4967-a8dc-f662f57f7020](https://doi.org/10.5285/f463bc5c-bb79-4967-a8dc-f662f57f7020)

206 In *all* datasets, the first two columns are:

207 1: Population code (code for forest of origin, 21 total)

208 2: Family (unique mother tree code: progeny described in nursery traits dataset and field  
209 trait dataset from the same family are putative half-siblings)

210 There are two maternal traits datasets: one for traits relating directly to the mother tree  
211 (MotherTraits.txt) in which each row represents one tree, and a second for traits relating to  
212 cones and seed collected from each mother tree in which each row represents one cone  
213 collected from each tree. Columns are defined as follows:

214 *Maternal dataset:* MotherTraits.txt

215 3: Population (name of forest of origin, 21 total)

216 4: Seed zone

217 5-13. Location reference and immediate environment for each tree: Latitude [decimal];  
218 Longitude [decimal]; Aspect; Slope; Altitude [m]; Regeneration [1-4]; Peat depth [cm]; soil  
219 moisture [1-5]; mean distance to nearest three trees [M]

220 14-15. Mother tree traits (absolute height [M]; diameter at breast height [M])

221 *Maternal dataset:* ConeSeedTraits.txt

- 222 3. Cone number (1-10)  
223 4-6. Cone traits (Width [mm], Length [mm], Weight [g])  
224 7-9. Seed traits (Viable seeds [count], Percentage viable seeds (%), Viable seeds weight [g])  
225 *Nursery traits dataset:*  
226 3. Seedling id  
227 4. Nursery site [NE; NW; NG]  
228 5-6. Nursery block number: from 2007 to 2010 [1-40]; from 2010 to 2012 [1-98]  
229 7. Field code if transplanted [4 digit code; not transplanted = NA]  
230 8-40. Nursery traits (see Table 3 for list of traits and format of column header)  
231 41-44. Status [Alive; Dead] for each year 2007-2010 (inclusive)

232 *Field traits dataset:*

- 233 3. Field site [FE; FS; FW]  
234 4. Field code [4 digit code]  
235 5. Block number [A; B; C; D]  
236 6-56. Field traits (see Table 3 for list of traits and format of column header)

237

238 **Technical Validation**

239 Measurements repeated annually are performed at the same time of year to ensure  
240 consistency of the method, e.g. height is measured during winter to avoid the possibility of  
241 active growth occurring after the trees are measured. Data were checked after each survey  
242 and inconsistent values (i.e. where height was less than the previous year) were re-  
243 measured. Where height increment was found to be less than 0 mm (due to an error in  
244 measurement or an effective loss in height due to damage) values were removed and classed  
245 as missing (NA). Annual stem diameter increment was estimated as the increase in stem  
246 diameter from the end of one growing season to the end of the next. Where stem diameter  
247 increment was estimated between 0 and -2 mm, the error was assumed to be caused by  
248 differences in orientation of measurement between years and increment values were  
249 adjusted to 0. Where stem diameter increment was found to be less than -2 mm, the  
250 increment and most recent stem diameter measurements were both classed as missing (NA).

251 We used boxplots to visualize data range and data distribution for each trait in each year  
252 over all nursery and field sites and all populations (Fig. 3). The use of outliers in subsequent  
253 analyses should be treated with caution.

254

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## 268 Author contributions

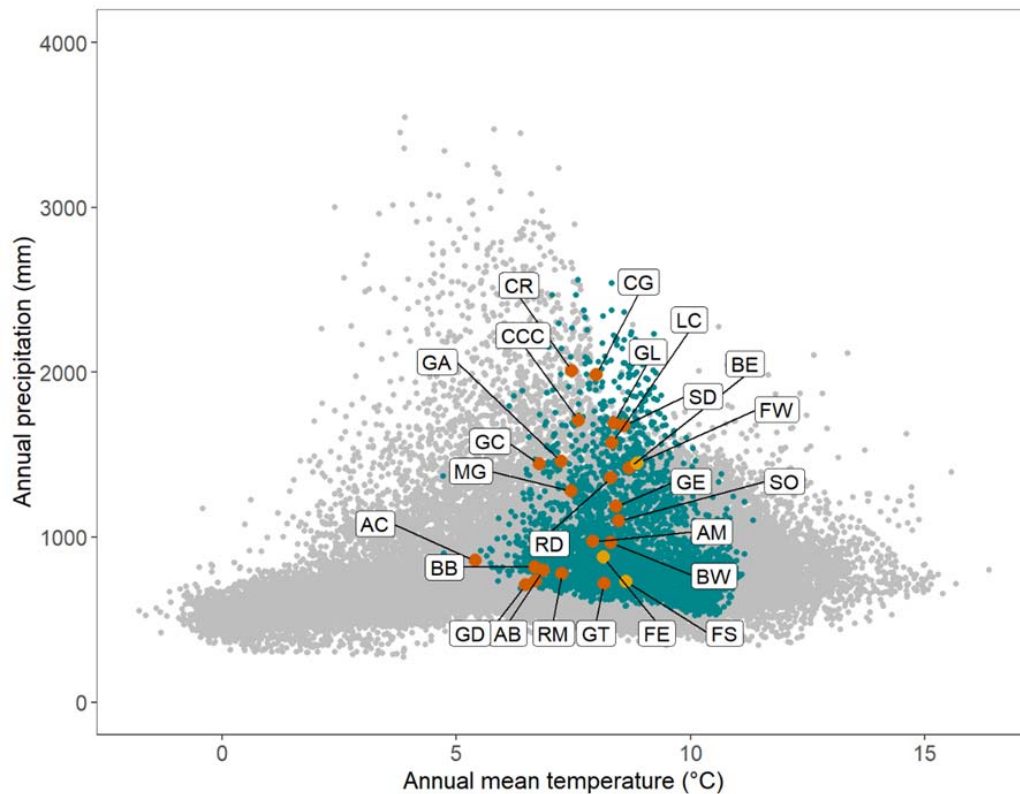
269 GI originated and initiated the project, including design of the seed collection and nursery  
270 experiment, and design of the field experiment, along with SC (and assistance of Betty Duff,  
271 BioSS). JB performed seed collections, nursery and transplanting work, and collated data and  
272 managed the nursery experiment and the FE and FW field sites. SC, AP, JC planted and  
273 managed the FS site. All authors contributed to data collection and maintenance of the field  
274 experiments.

## 275 Competing interests

276 The authors declare no conflict of interest

## 277 Figures

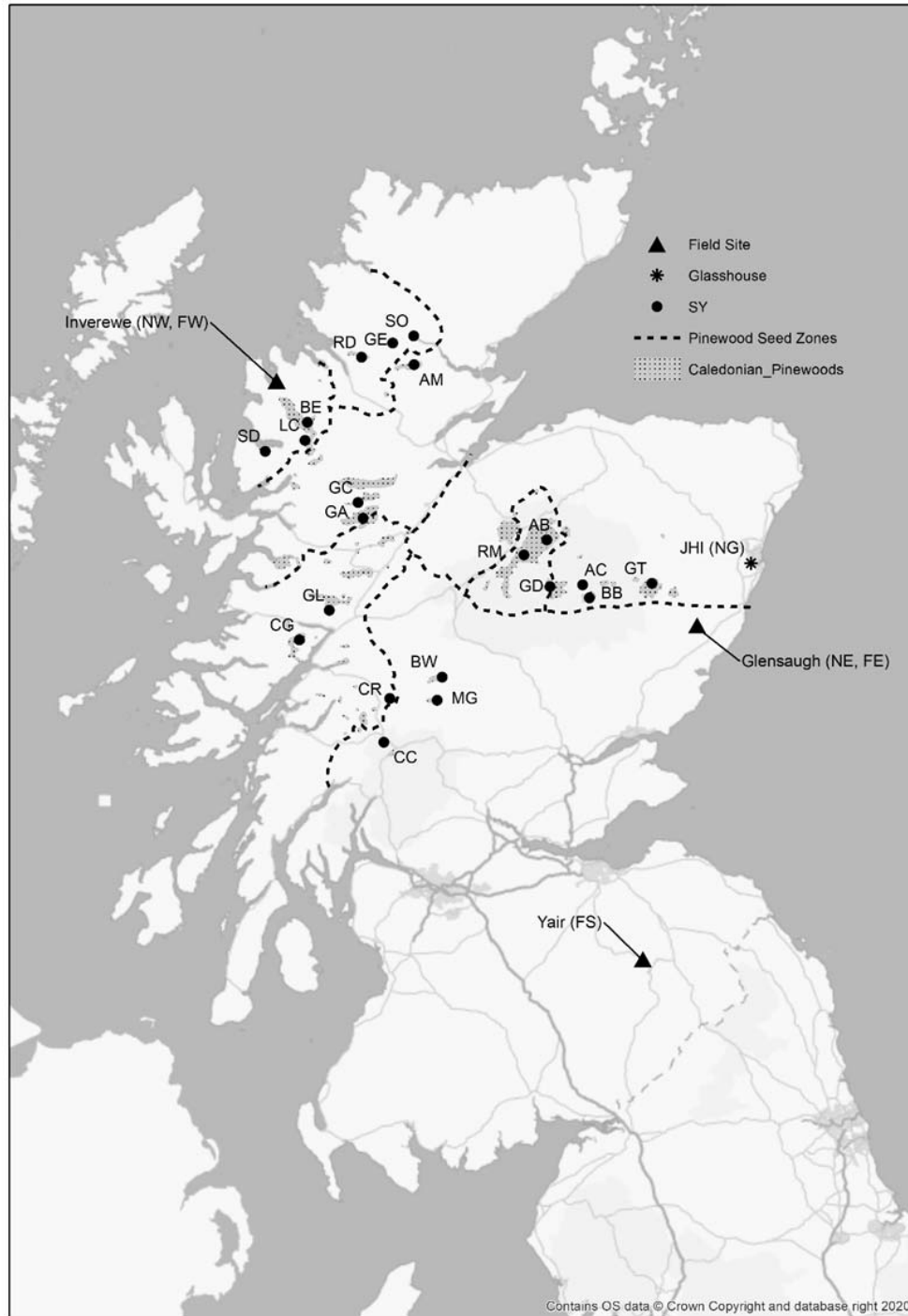
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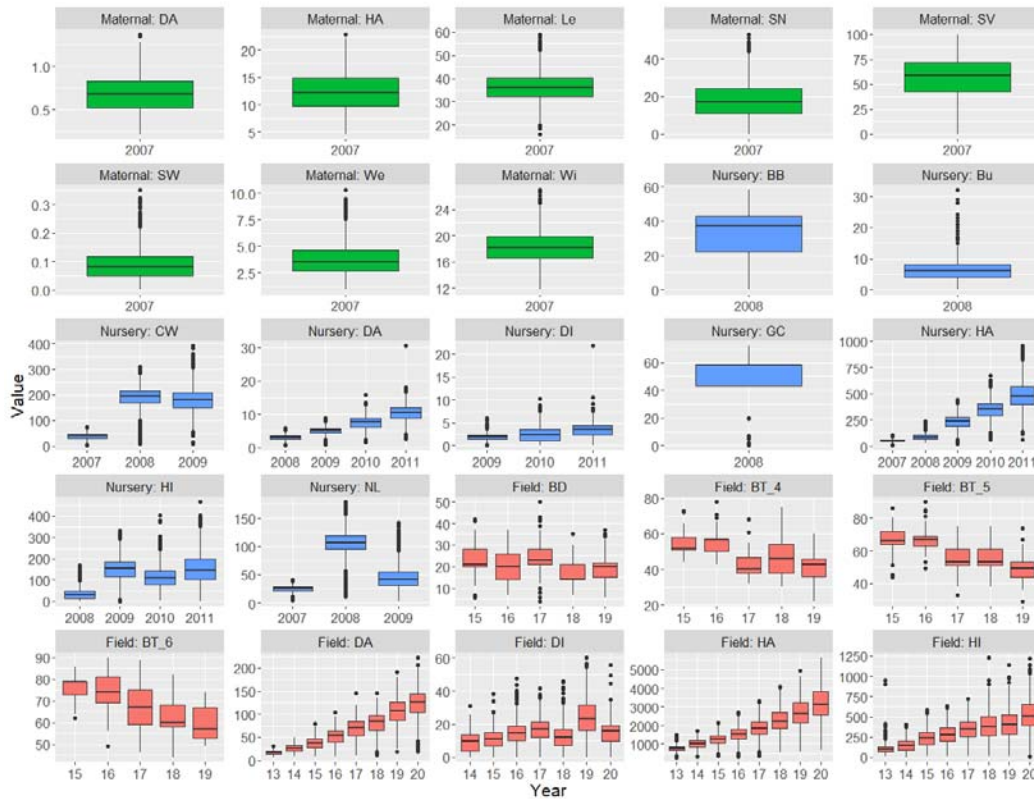
280 Figure 1

281



282  
283 Figure 2  
284





285  
286 Figure 3

287  
288 **Figure Legends**

289 Figure 1. Ordination of 21 source populations in environmental space. Gray dots: global Scots  
290 pine distribution (distribution - EU-Forest database<sup>15</sup> and associated climate data (CHELSA  
291 database<sup>16</sup>, <https://chelsa-climate.org/>). Blue dots: Scots pine distribution in the United  
292 Kingdom. Orange dots: populations sampled for the experiment; letter codes match those in  
293 Table 1. Yellow dots: trial sites.

294  
295 **Figure 2:** Location of the 21 source populations sampled for the experiment; letter codes  
296 match those in Table 1. Also shown are James Hutton Institute (JHI), location of eastern  
297 nursery (NE) and glasshouse (NG); three field sites - Inverewe (FW, also location of western  
298 nursery: NW), Glensaugh (FE) and Yair (FS).

299  
300 **Figure 3.** Box and whisker plots of trait values for each trait in each year over all nursery/field  
301 sites and all populations. Trait value units are listed in Table 3. Year for field dataset traits are  
302 abbreviated (e.g. 2015 = '15'). Solid black lines indicate the median trait value. The bottom  
303 and top of boxes indicate the first and third quartile. The upper and lower whiskers extend to  
304 the highest and lowest values within 1.5 times the interquartile range. Individual points  
305 indicate outliers. Traits derived from the maternal datasets are green, those from the  
306 nursery dataset are blue and those from the field dataset are red.

307  
308 **Tables**

309 **Table 1:** Locations and basic environmental data for the populations sampled for seed to  
310 establish the trial. See the maternal traits dataset ([doi.org/10.5285/ac687a66-135e-4c65-8bf6-c5a3be9fd9aa](https://doi.org/10.5285/ac687a66-135e-4c65-8bf6-c5a3be9fd9aa)) for precise data for each mother tree sampled.  
311

Population	Lat. (N)	Long. (W)	Alt. (m)	Area (ha)	GSL	GDD	FMT (°C)	JMT (°C)
Abernethy (AB)	57.21	3.61	311-370	2452	211	990	1.1	12.7
Allt Cul (AC)	57.04	3.35	435-512	13	145	513	-1.0	10.4
Amat (AM)	57.87	4.60	39-201	181	214	892	1.2	12.3
Ballochbuie (BB)	56.98	3.30	421-531	775	116	446	-1.7	9.5
Beinn Eighe BE)	57.63	5.40	17-91	182	283	1329	3.7	14.2
Black Wood of Rannoch (BW)	56.68	4.37	250-321	1011	254	1138	2.1	13.5
Coille Coire Chuilc (CCC)	56.42	4.71	222-311	67	226	928	1.6	12.3
Conaglen (CG)	56.79	5.33	89-193	189	246	887	2.2	11.7
Crannach (CR)	56.58	4.68	258-338	70	231	1019	1.8	12.6
Glen Affric (GA)	57.26	4.92	205-293	1532	210	769	0.9	11.6
Glen Cannich (GC)	57.35	4.95	182-381	301	212	778	1.0	11.7
Glen Derry (GD)	57.03	3.58	426-493	235	168	593	-0.5	11.3
Glen Einig (GE)	57.96	4.76	45-92	27	242	1089	2.2	13.2
Glen Loy (GL)	56.91	5.13	136-219	74	191	541	0.5	9.8
Glen Tanar (GT)	57.02	2.86	289-422	1564	235	1105	2.2	13.6
Loch Clair (LC)	57.56	5.36	98-166	126	277	1253	3.4	13.7
Meggernie (MG)	56.58	4.35	254-385	277	223	916	1.1	12.0
Rhidorroch (RD)	57.89	4.98	138-220	103	221	840	1.5	11.6
Rothiemurchus (RM)	57.15	3.77	295-329	1744	224	1087	1.4	13.1
Shieldaig (SD)	57.50	5.63	44-132	103	273	1093	3.2	12.8
Strath Oykel (SO)	57.98	4.61	35-160	14	257	1276	2.7	14.0

312 Alt. - altitudinal range sampled within each population, Area - core pinewood area<sup>13</sup>. Average (1961-  
 313 2000) climate variables from UK Met Office<sup>14</sup>; GSL - growing season length (days), GDD - growing  
 314 degree days (day degrees), FMT - February and JMT - July mean temperatures (°C).

315 **Table 2.** Average climatic variables at Glensaugh (FE), Inverewe (FW) and Yair (FS) from  
 316 planting in 2012 until 2020. Climatic variables are derived from data provided by the Met  
 317 Office (daily mean, minimum and maximum temperatures and monthly rainfall).

Measure	FE	FW	FS
Average Maximum Daily Temperature (deg C)	11.43	12.73	12.33
Average Minimum Daily Temperature (deg C)	4.85	6.50	5.03
Average Mean Daily Temperature (deg C)	8.14	9.62	8.68

Growing Degree Days (deg C) <sup>1</sup>	1466	1830	1664
Growing Season Length (days) <sup>2</sup>	258	332	280
Average Total Rainfall (mm)	91.42	138.23	82.48

318 <sup>1</sup> Growing degree days: the mean number of degrees by which the air temperature has gone above 5 °C  
 319 calculated day by day and summed over the year

320 <sup>2</sup> Growing season length: period bounded by daily mean temperature > 5 °C for > 5 consecutive days and daily  
 321 mean temperature < 5 °C for > 5 consecutive days (after 1 July)

322 **Table 3:** Traits assessed in mother trees, cones, seeds, nursery seedlings and field trials.  
 323 Within the datasets, traits are recorded in a single column for each year using the format  
 324 Code-Year (e.g. absolute height in 2008 = HA08) except for the maternal traits datasets  
 325 which were all measured in 2007. Where multiple measurements are made in a single year  
 326 (i.e. for canopy width and needle length) the suffix “\_X” is added to the column header,  
 327 where X is the measurement number (e.g. canopy width measured in 2007, second  
 328 measurement = CW07\_2). Where multiple stages are recorded in a single year (i.e. for  
 329 budburst timing) the suffix “\_Y” is added to the column header, where Y is the budburst  
 330 stage.

Trait	Code	Unit	Dataset	Year(s)
Cone length	Le	mm	Maternal	2007
Cone weight	We	G	Maternal	2007
Cone width	Wi	mm	Maternal	2007
Height: absolute	HA	M mm mm	Maternal Nursery Field	2007 2007-2011 <sup>A</sup> 2013-2020 <sup>B</sup>
Height: increment	HI	mm mm	Nursery Field	2008-2011 <sup>A</sup>
Viable seed number	SN	Count	Maternal	2007
Viable seed weight	SW	G	Maternal	2007
Seed viability	SP	%	Maternal	2007
Stem diameter: absolute <sup>C</sup>	DA	M mm mm	Maternal Nursery Field	2007 2008-2011 <sup>A</sup> 2013-2020 <sup>D</sup>
Stem diameter: increment	DI	mm mm	Nursery Field	2009-2011 <sup>A</sup>
Canopy width	CW	mm	Nursery	2008
Growth cessation	GC	Days since 1 Sep 2008	Nursery	2008
Needle length	NL	mm	Nursery	2007-2009
Number of buds	Bu	Count	Nursery	2008

Budburst duration	BD	Days	Field	2015-2019
Budburst timing	BB BT	Days since 31 March	Nursery Field	2008 2015-2019



331 <sup>A</sup> 2011 measurement only in FE and FW



332 <sup>B</sup> 2013 measurement only in FE and FW


333 <sup>C</sup> Stem diameter measured at breast height for maternal traits dataset and at base for nursery and  
334 field traits datasets

335 <sup>D</sup> Stem diameter only measured at FS in 2020

336 **Supplementary Table 1:** Phenological stages of bud burst assessed in field trials.

Stage	Description	Image
1	Dormant	
2	Bud swelling. Bud shows signs of expansion, usually linear expansion in length. Bud lengthens to finger-shape	
3	Scales open at base. Bud swells to a club shape – no green tissue can be seen at the tip. Scales are typically open at the base where the bud is elongating - showing green tissue underneath. Otherwise, all growth is encased by bud scales. White developing needles might be seen through the bud scales at the tip, as the scales become thinner overlying the expanding bud-tip. But no scales have emerged, the surface of the bud is still smooth with scales.	

4	<p>Scales open along length of shoot, no needles. The tip of the bud swells further in diameter and the scales are forced open revealing some green underlying tissue or white tips of new needles visible (like teeth). The casing of brown bud scales is definitely partially disrupted, usually at the tip first although occasionally closer to the base of the bud first.</p>	
5	<p>White tipped needles visible. White tipped or green needles can be clearly seen through the remnants of the scales. In order to score '5' then at least one of the white-tipped very young needles should be elongating and growing away from the stem so daylight is visible between the elongating needle and the stem. (Distinct from 4 where white tips are present but flat against the stem). Elongation and separation can happen at the tip first but is often seen closer to the base first. The scales are open or away from bud for at least part of its length.</p>	

6	Green needles. Identifiable needles that have elongated somewhat and have emerged along the entire length of the bud and entirely around the bud from top to bottom. They are not covered by any scales and are all growing out from the long axis of the bud. i.e. daylight visible between them and the stem. Shoot has a bottle brush appearance at this stage.	
7	Needle separation and terminal bud. Next year's terminal bud is usually formed and clearly visible. Needles have separated.	

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