1 **Juvenile Root Vigour Improves Phosphorus Use Efficiency of Potato**

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Abstract

Aims Potato (*Solanum tuberosum* L.) has a large phosphorus (P)-fertiliser requirement. This is thought to be due to its inability to acquire P effectively from the soil. This work tested the hypothesis that early proliferation of its root system would enhance P acquisition, accelerate canopy development, and enable greater yields.

Methods Six years of field experiments characterised the relationships between (1) leaf P concentration ($[P]_{leaf}$), tuber yield, and tuber P concentration ($[P]_{tuber}$) among 27 Tuberosum, 35 Phureja and 4 Diploid Hybrid genotypes and (2) juvenile root vigour, P acquisition and tuber yield among eight Tuberosum genotypes selected for contrasting responses to P-fertiliser.

Results Substantial genetic variation was observed in tuber yield, $[P]_{leaf}$ and $[P]_{tuber}$. There was a strong positive relationship between tuber yields and P acquisition among genotypes, whether grown with or without P-fertiliser. Juvenile root vigour was correlated with accelerated canopy development and both greater P acquisition and tuber biomass accumulation early in the season. However, the latter relationships became weaker during the season.

Conclusions Increased juvenile root vigour accelerated P acquisition and initial canopy cover and, thereby, increased tuber yields. Juvenile root vigour is a heritable trait and can be selected to improve P-fertiliser use efficiency of potato.

Keywords Phosphorus - potato (*Solanum tuberosum* L.) - root morphology - tuber yield

58   **Introduction**

59

60   A disproportionately large amount of phosphorus (P)-fertiliser is applied to potatoes (*Solanum tuberosum*

61   L.) compared to other field crops (Fixen and Bruulsema 2014; Hopkins et al. 2014; Ruark et al. 2014;

62   White et al. 2005b, 2007). For example, in 2016 potatoes occupied 3.0% of the arable land in Great Britain

63   but consumed >12% of all the inorganic P-fertiliser applied to tillage crops (Defra 2017). As a

64   consequence, the potato crop is associated with high P-losses from fields and, consequently, environmental

65   pollution (Dampney et al. 2002; Davenport et al. 2005; Ruark et al. 2014).

66   The large P-fertiliser requirement of potatoes is thought to be due to their inability to acquire P

67   effectively from the soil (Dampney et al. 2002; Fageria et al. 2011; Fixen and Bruulsema 2014; Hopkins et

68   al. 2014; Syers et al. 2008; Thornton et al. 2014; White 2018; White et al. 2005b). The potato crop

69   generally recovers <10% of broadcast P fertiliser in the year it is applied (Dampney et al. 2002; Fernandes

70   and Soratto 2016a; Syers et al. 2008) and, although the application of research to optimise the timing,

71   quantities, and methods of P-fertiliser application can reduce inputs of P-fertiliser and P-losses to the

72   environment (e.g. Burns et al. 2010; Davenport et al. 2005; Hopkins et al. 2014; Syers et al. 2008; White

73   2018; White et al. 2007), the impact of agronomic methods alone to reduce the amount of P-fertiliser

74   applied to the potato crop has been limited (Defra 2017). To reduce P-fertiliser inputs and environmental

75   pollution further requires the development of potato varieties that use P-fertiliser inputs more effectively to

76   produce commercial yields. However, there has been little effort to develop new potato varieties that use P-

77   fertiliser inputs more efficiently (Thornton et al. 2014; Trehan and Sharma 2005; White et al. 2005b).

78   Agronomic phosphorus use efficiency (PUE) is commonly defined as crop dry matter (DW) yield

79   per unit of P available in the soil (g DW g^{-1} P_{soil}; Fernandes and Soratto 2016a; Sandaña 2016; White et al.

80   2005a). This is numerically equal to the product of P acquisition efficiency (PUpE), which is defined as the

81   P acquired by the crop per unit of available P (g P_{crop} g^{-1} P_{soil}), and crop physiological utilisation efficiency

82   (PUtE), which is defined as the yield per unit P acquired by a crop (g DW g^{-1} P_{crop}). Differences in yield

83   responses to P-fertiliser applications between crop genotypes, including potato, are often correlated with

84   PUpE, but rarely correlated with PUtE (Balemi and Schenk 2009; Fernandes and Soratto 2016a; Sandaña

85   2016; Soratto et al. 2015; Thornton et al. 2014; Trehan and Sharma 2005; White 2018; White and

86   Hammond 2008; White et al. 2005a, 2013). In potato, greater PUpE has been attributed to increased

87   biomass allocation to roots, greater exploitation of the soil volume through the production of more lateral

88   roots, longer root hairs and roots with a greater length/mass ratio, topsoil foraging, and the exudation of

89   organic acids and phosphatases into the rhizosphere (Balemi and Schenk 2009; Dechassa et al. 2003;

90   Fernandes et al. 2014; Opena and Porter 1999; Sattelmacher et al. 1990; Trehan and Sharma 2003, 2005;

91   White 2018; White et al. 2005ab). Simulations of P acquisition by potato plants suggest that PUpE is

92   determined to a large extent by the size and morphology of the root system and, to a lesser extent, by the

93   kinetics of P uptake by root cells (Balemi and Schenk 2009; Dechassa et al. 2003).

94   There is limited information on genetic variation in PUE, PUpE or PUtE among commercial
95 potato germplasm (Fernandes and Soratto 2016ab; Hailu et al. 2017; Nyiraneza et al. 2017; Sandaña 2016;
96 Trehan and Singh 2013). However, variation has been observed among genotypes of European potato (*S.*
97 *tuberosum* Group Tuberosum) in the following traits:

98 • Tuber yield (e.g. Allen and Scott 1992; Bradshaw et al. 2008; Daoui et al. 2014; Fernandes and Soratto
99   2013, 2016ab; Fixen and Bruulsema 2014; Hailu et al. 2017; Lahlou and Ledent 2005; Lee et al. 2013;
100   Manorama et al. 2017; McCord et al. 2011; Nyiraneza et al. 2017; Sandaña 2016; Sandaña and
101   Kalazich 2015; Soratto and Fernandes 2016; Soratto et al. 2015; Trehan and Singh 2013; White et al.
102   2009)

103 • Phosphorus acquisition (Balemi 2011; Carpenter 1963; Fernandes and Soratto 2013, 2016a; Fernandes
104   et al. 2014, 2015; Hailu et al. 2017; Nyiraneza et al. 2017; Sandaña 2016; Soratto et al. 2015; Trehan
105   and Sharma 2003, 2005; Trehan and Singh 2013)

106 • Leaf P concentration (Balemi 2011; Balemi and Schenk 2009; Carpenter 1963; Dampney et al. 2002;
107   Fernandes and Soratto 2016ab; Fernandes et al. 2014, 2015; Kärenlampi and White 2009; Lee et al.
108   2013; Sandaña 2016; Soratto and Fernandes 2016; Soratto et al. 2015; Trehan and Sharma 2003, 2005)

109 • Tuber P concentration (Bethke and Jansky 2008; Carpenter 1963; Dampney et al. 2002; Ereifej et al.
110   1998; Fernandes and Soratto 2016a; Fernandes et al. 2015; Lee et al. 2013; Leonel et al. 2017;
111   Lombardo et al. 2014; Randhawa et al. 1984; Sandaña 2016; Soratto and Fernandes 2016; Tekalign
112   and Hammes 2005; Thornton et al. 2014; Trehan and Sharma 2003; White et al. 2009)

113 • Tuber yield / crop P accumulation (Fernandes and Soratto 2013; Fernandes et al. 2014; Hailu et al.
114   2017; Nyiraneza et al. 2017; Sandaña 2016; Trehan and Sharma 2003)

115 • Tuber yield response to P availability (Daoui et al. 2014; Fernandes and Soratto 2016a; Freeman et al.
116   1998; Hailu et al. 2017; Jenkins and Ali 1999; Manorama et al. 2017; Nyiraneza et al. 2017; Sandaña
117   2016; Sandaña and Kalazich 2015; Soratto and Fernandes 2016; Soratto et al. 2015; Thornton et al.
118   2014; Trehan and Singh 2013)

119   The effects of P acquisition on tuber numbers and crop yields are believed to be mediated through
120 canopy development and radiation absorption at tuber initiation, which occurs two to three weeks after
121 shoot emergence in most varieties, and during tuber bulking, respectively (Allison et al. 2001; Dampney et
122 al. 2002; Fernandes et al. 2014; Harris 1992; Haverkort 2007; Jenkins and Ali 1999, 2000; Kolbe and
123 Stephan-Beckmann 1997b; O'Brien et al. 1998; Sandaña and Kalazich 2015; White 2018; White et al.
124 2005b). Thus, it has been speculated that rapid development of the root system will enhance the ability to
125 acquire P, accelerate canopy development, increase tuber numbers and enable greater yields (White 2018;
126 White et al. 2005b). This is consistent with observations that tuber yield is positively correlated with root
127 dry weight not only among genotypes of *S. tuberosum* Group Tuberosum but also among *S. tuberosum*
128 genotypes *sensu lato* and other tuber-bearing *Solanum* species (Iwama 2008; Iwama et al. 1981ab, 1999;
129 Lahlou and Ledent 2005; Sattelmacher et al. 1990; Wishart et al. 2013).

130   There is considerable genotypic variation in both root growth and root architecture in potato

131 (Ahmadi et al. 2017; Allen and Scott 1992; Fernandes et al. 2014; Harris 1992; Iwama 1998, 2008; Iwama

132 and Nishibe 1989; Iwama et al. 1981ab, 1999; Jefferies 1993; Kratzke and Palta 1992; Lahlou and Ledent

133 2005; MacKerron and Peng 1989; Puértolas et al. 2014; Sattelmacher et al. 1990; Stalham and Allen 2001;

134 Steckel and Gray 1979; Trehan and Sharma 2003, 2005; Trehan and Singh 2013; van Loon 1986; White et

135 al. 2005a; Wishart et al. 2013, 2014). Furthermore, genotypic variation in the number, diameter, length,

136 surface area and fresh weight (FW) of basal and stolon roots observed in field-grown plants 10 weeks after

137 planting can also be observed in glasshouse-grown plants two weeks after emergence (Wishart et al. 2013),

138 suggesting that relevant aspects of root architecture can be screened rapidly and cost effectively. Although

139 commercial potato varieties often show little variation in their maximal root growth rates, the eventual

140 depth of rooting differs between varieties because the duration of active root growth varies and is

141 particularly extended in indeterminate varieties (Ahmadi et al. 2017; Allen and Scott 1992; Iwama 1998,

142 2008; Lahlou and Ledent 2005; Stalham and Allen 2001). For example, Cara, an indeterminate variety with

143 exceedingly long haulm longevity, produces a larger and deeper root system than the indeterminate

144 varieties Maris Piper, Desiree and Hermes, which, in turn, have deeper root systems than the partially

145 determinate varieties Estima and Wilja (Allen and Scott 1992; Harris 1992; Jefferies 1993; Stalham and

146 Allen 2001, Wishart et al. 2009). Thus, there appears to be potential for the selection or breeding of potato

147 genotypes with root systems that exploit the soil volume and acquire P more efficiently.

148   In this paper, (1) genetic and environmental variation in PUE, PUpE and PUtE is quantified in a

149 collection of commercial germplasm containing *S. tuberosum* Group Tuberosum, Group Phureja and

150 Diploid Hybrid genotypes, and (2) the relationships between the biomass of the juvenile root system and P

151 acquisition, canopy development, and subsequent tuber yield are tested.

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153

154 **Materials and Methods**

155

156 Quantifying variation among potato genotypes in the field

157

158 Field trials incorporating tetraploid and diploid *Solanum tuberosum* genotypes were conducted at Gourdie

159 Farm, Dundee (56°28'N, 03°07'W), in 2006, 2007 and 2008 (Experiment 1; Table 1). The 23 tetraploid

160 (*Solanum tuberosum* Group Tuberosum) genotypes included in all three trials were the breeding clone

161 12601ab1, 'Ailsa', 'Anya', 'Brodick', 'Cara', 'Desiree', 'Estima', 'Golden Millennium', 'Hermes', 'Home

162 Guard', 'Harborough Harvest', 'Maris Piper', 'Montrose', 'Nadine', 'Pentland Dell', 'Pentland Squire',

163 'Record', 'Saxon', 'Scarborough', 'Stirling', 'Tay', 'Vales Everest', and 'Wilja'. The varieties 'Eve

164 Balfour', 'Lady Balfour' and 'Vales Sovereign' were included in trials in 2006, and four replicates of

165 'Edzell Blue' were included in trials in 2008. Diploid *S. tuberosum* Group Phureja genotypes present in all

166 three trials included the six commercial varieties 'Mayan Gold' [DB.337(37)], 'Inca Dawn' [DB.375(1)],

167 'Inca Sun' [DB.378(1)], 'Mayan Star' [DB.384(4)], 'Mayan Queen' [DB.520(11)] and 'Mayan Twilight'
168 [PHU.95(1901)] and 29 breeding lines. Group Phureja genotype TC.43(45) was included in trials in 2006
169 and 2007. Two diploid genotypes, HB.165(1) and HB.171(13), originating from crosses between Diploid
170 Tuberosum and Phureja genotypes were also present in all three trials, whereas the Diploid Tuberosum
171 genotype 2DH40(3) and genotype 99.FT1(5), which originated from a cross between 2DH40(3) and Mayan
172 Gold, were only included in 2007 (Table 1). All husbandry, including fertiliser additions, followed standard
173 UK agronomic practices. Plants were grown in randomized block designs, with eight plants per plot and
174 two replicate plots per genotype. Seed potatoes were planted in late April, diagnostic leaves, defined as
175 youngest fully expanded leaves (Fageria et al. 2011; White 2018; White et al. 2007) were sampled in the
176 second week of July, and tubers were harvested at commercial maturity in September. The fresh weights
177 (FWs) of tubers from each plot were determined at harvest.

178 Field trials incorporating 23 Tuberosum genotypes, seven Phureja genotypes and two diploid
179 hybrids were performed in Dron Field, Balruddery Farm, Dundee (56°28'N, 03°03'W), in 2009 and 2010
180 (Experiment 2; Table 2). The Tuberosum genotypes were the breeding clone 12601ab1, 'Ailsa', 'Anya',
181 'Brodick', 'Cara', 'Desiree', 'Estima', 'Golden Millennium', 'Hermes', 'Home Guard', 'Harborough
182 Harvest', 'Maris Piper', 'Montrose', 'Nadine', 'Pentland Dell', 'Pentland Squire', 'Record', 'Saxon',
183 'Scarborough', 'Stirling', 'Tay', 'Vales Everest', and 'Wilja'. The seven phureja genotypes were 'Mayan
184 Gold' [DB.337(37)], 'Inca Dawn' [DB.375(1)], 'Inca Sun' [DB.378(1)], 'Mayan Star' [DB.384(4)],
185 'Mayan Queen' [DB.520(11)], 'Mayan Twilight' [PHU.95(1901)] and DB.226(70). The two diploid
186 hybrids were 99.FT1(5) and HB.171(13). Two treatments were imposed by the addition, or not, of P-
187 fertiliser at a rate of 147 kg ha^{-1} P_2O_5 (Defra 2010). Prior to the addition of P-fertiliser, Olsen-P
188 concentrations (Olsen et al. 1954) in the soil were 43 mg kg^{-1} and 40 mg kg^{-1} in 2009 and 2010,
189 respectively. All other husbandry followed standard UK agronomic practices. For each P-fertiliser
190 treatment, plants were grown in randomized block designs, with five plants per plot and two replicate plots
191 per genotype. In both years, seed potatoes were planted in the first week of May, diagnostic leaves were
192 sampled in the second week of July, and tubers were harvested at commercial maturity in the first week of
193 September. The FWs of tubers from each plot were determined at harvest.

194

195 Relationships between the size of the juvenile root system and crop establishment, canopy development and
196 tuber yield

197

198 In 2011, field trials incorporating eight Tuberosum genotypes (Experiment 3) were performed in School
199 Field, Mylnefield Farm, Dundee (56°27'N, 03°03'W). The genotypes were the breeding clone 12601ab1,
200 'Ailsa', 'Cara', 'Home Guard', 'Maris Piper', 'Nadine', 'Pentland Dell' and 'Stirling'. Two treatments
201 were imposed by the addition, or not, of P-fertiliser at a rate of 147 kg ha^{-1} P_2O_5 (Defra 2010). Prior to the
202 addition of P-fertiliser, the Olsen-P concentration in the soil was 49 mg kg^{-1} P_2O_5. All other husbandry
203 followed standard UK agronomic practices.

204   In each P-fertiliser treatment, plants were grown in seven experimental sections with 16 plots per

205 section. Within each section, plants were grown in a randomized block design with two replicate plots per

206 genotype. Sections 1 and 2 contained single plant plots to allow the excavation of juvenile root systems,

207 whilst sections 3 to 7 contained five experimental plants per plot. Guard plots were planted with 'Edzell

208 Blue' on the sides of the experiment, and as single plants, on the edges of sections 3 to 7 to reduce edge

209 effects. The date of emergence was recorded for each plot in each section and photographs were taken

210 fortnightly to estimate percentage ground cover. Sections 1 and 2 were harvested between 29 and 30 June,

211 2011, approximately three weeks after emergence (Harvest 1). Section 3 was harvested on 14 July, when

212 the canopy had about 50% ground cover (Harvest 2). Section 4 was harvested on 27 July, close to canopy

213 closure (Harvest 3). Section 5 was harvested on 9 August (Harvest 4). Section 6 was harvested on 23

214 August, when the canopy had begun to sag (Harvest 5). Section 7 was harvested on 3 October (Harvest 6).

215   At planting, the seed tuber FW / dry weight (DW) quotient was determined for each variety

216 according to the following procedure. Five representative tubers were washed, dried, and their combined

217 FW determined. The tubers were then cut into eighths and freeze-dried (Millitorr S3921 Vacuum Freeze-

218 Drying Unit; Millitorr Engineering Ltd., Manchester, UK). Freeze-dried material was weighed to determine

219 the combined DW of the five representative tubers. Three replicate samples were processed for each

220 variety.

221   At Harvest 1, individual plants were lifted *in situ* using a JCB forklift and bucket (JCB, Rochester,

222 UK) and carefully excavated from the soil by a team of people. Plants were then separated into seed tuber,

223 new tuber, root and shoot material. Fresh weights of each plant part were determined immediately. At all

224 other harvests, the shoot of the middle plant of each plot was first removed by excision at the soil surface

225 using secateurs and processed separately. Shoot material from the remaining plants of each plot was then

226 removed, and, finally, tubers from each plot were harvested using a potato harvester (Grimmie,

227 Swineshead, Lincolnshire, UK). The FWs of shoot material from the middle plant and from the other plants

228 in the plot were determined separately. These data were combined to give values for the plot. The FWs of

229 tubers harvested from each plot were determined.

230   Root and shoot samples from Harvest 1 were oven-dried at 70 ℃ for 72 h and their DWs

231 determined. Whole shoots from the middle plant of each plot from Harvests 2 to 6 were oven-dried at 70 ℃

232 for 72 h and their DWs determined. These data were combined with data on the FWs of shoot material

233 collected from an entire row to calculate shoot DW for that plot. Tubers from Harvests 2 to 6 were first

234 washed. A minimum of six representative tubers from each plot from Harvest 2 were combined, weighed

235 fresh, chopped and freeze dried. The DW of these representative tubers was used to determine dry matter

236 content. Five representative tubers from each plot of Harvests 3 to 6 were combined, weighed fresh,

237 chopped and a sub-sample of the chopped material of known FW was freeze dried. The DW of these

238 subsamples of representative tubers was used to determine dry matter content.

239

240 Estimation of ground covered by the crop canopy

241

242   The ground covered by the crop canopy was estimated for each plot according to the following procedure.

243   First a white plastic quadrat (dimensions 40 x 90 cm) was placed over the middle plant of the plot. Then, an

244   image containing the entire quadrat was acquired from a position approximately 2 m above the ground.

245   Images were analysed semi-automatically using customised scripts executed in ImageJ (Rasband 2014). A

246   binary (black and white) image was obtained from a greyscale image by applying a fixed threshold. The

247   boundaries of white regions in the image were identified using an edge tracing algorithm. Gaussian noise

248   and smoothing was applied to these regions to create local maxima and a convex hull was created around

249   the local maxima to identify the frame of the quadrat. Leaves were then identified from the colour image,

250   which was converted to a grayscale image using the transformation $b^3/\max(r)\max(g)$, where r, g and b

251   represent the pixel intensities in the red, green and blue channels, respectively. A binary (black and white)

252   image was obtained by applying a fixed threshold and the boundaries of white regions in the image

253   (representing the leaves) were identified using an edge tracing algorithm. The area of leaves was expressed

254   as a percentage of the total area within the quadrat.

255

256   Analysis of tissue phosphorus concentrations

257

258   Phosphorus concentrations of root, tuber, leaf and shoot material were determined on acid-digested dried

259   plant material using either inductively-coupled plasma emission spectrometry (ICP-AES; JY Ultima 2;

260   Jobin Yvon Ltd., Stanmore, UK) or inductively-coupled plasma mass spectrometry (ICP-MS; ELAN

261   DRCe; PerkinElmer, Waltham, MA, USA) following published methods (Hammond et al. 2009;

262   Subramanian et al. 2011).

263   Diagnostic leaves from Experiments 1 and 2 were freeze-dried and their DW determined. Tubers

264   from Experiments 1 and 2 were processed as described by White et al. (2012). Three representative tubers

265   from each plot were washed and cut into eighths by first slicing horizontally from rose-to-heel, then

266   vertically from rose-to-heel, and finally vertically midway between rose and heel. Subsamples from each

267   plot, comprising four diagonally opposite eighths of all representative tubers sampled from that plot, were

268   weighed fresh and freeze-dried. Freeze-dried tuber material was weighed to determine dry matter content.

269   Freeze-dried leaf and tuber material was milled to a powder using a ball-mill. Accurately weighed sub-

270   samples (approx. 100 mg DW) of each milled sample were digested using the micro-Kjeldahl method and P

271   concentrations were determined using ICP-AES as described by Hammond et al. (2009).

272   Sub-samples of dried plant material from Experiment 3 were milled to a powder (C+N Laboratory

273   Mill; Christy and Norris Ltd., Chelmsford, UK). Phosphorus concentrations in the powdered samples were

274   determined as described by Subramanian et al. (2011). Accurately weighed sub-samples (approx. 50 mg

275   DW) of each milled material were digested with 3.0 ml concentrated nitric acid and 1.0 ml of 30% (v/v)

276   hydrogen peroxide in closed vessels using a microwave digester (MARS Xpress; CEM Microwave

277   Technology, Buckingham, UK) with the following programme: 2 min at 100°C, 1 min at 120°C, 2 min at

278 160°C, 20 min at 180°C, and 20 min cooling time. Each digested sample was diluted to 50 ml with sterile

279 MilliQ water (18.2 MΩ cm) prior to elemental analyses. Blank digestions were also performed and the

280 National Institute of Standards and Technology (NIST, Gaithersburg, MD, USA) tomato leaf standard

281 (Reference Number 1573a) was used as an internal control. Phosphorus concentrations in digested plant

282 samples were determined using ICP-MS.

283

284 Statistical analyses

285

286 Data are expressed as means ± standard errors from n determinations unless indicated otherwise. The

287 significance of the difference between two sets of data was attributed through the Student's *t*-test. Linear

288 regressions and analysis of variance (ANOVA) were performed using Microsoft Office Excel (Microsoft

289 Corporation, Redmond, WA, USA).

290

291

292 **Results**

293

294 Genetic and environmental effects on tuber yield, tuber P concentration and leaf P concentration

295

296 Genetic variation was observed in tuber yield, P-concentration in diagnostic leaves ($[P]_{leaf}$) and P

297 concentration in tubers ($[P]_{tuber}$) among potato genotypes grown in the field following standard UK

298 agronomic practices (Tables 1, 2). In Experiment 1, the yield of Tuberosum genotypes, averaged across

299 three years for genotypes present in all trials, was greater than that of Diploid Hybrid genotypes or Phureja

300 genotypes (Table 1). The $[P]_{leaf}$ of Tuberosum genotypes, averaged across two years for genotypes present

301 in all trials, was less than that of Diploid Hybrid genotypes or Phureja genotypes, but $[P]_{tuber}$ of Tuberosum

302 genotypes, averaged across three years for genotypes present in all trials, was similar to that of Diploid

303 Hybrid genotypes and Phureja genotypes (Table 1). The product of yield and $[P]_{leaf}$, which can be used as a

304 proxy for PUpE assuming similar partitioning of biomass and P among genotypes (White et al. 2005a),

305 averaged across two years for genotypes present in all trials, was significantly greater for Tuberosum

306 genotypes than Phureja genotypes, because of their higher yields and lower $[P]_{leaf}$ (Table 1).

307 The data obtained in Experiment 2 were consistent with those of Experiment 1. In Experiment 2,

308 the yield of Tuberosum genotypes, averaged across both years, was greater than that of Diploid Hybrid

309 genotypes or Phureja genotypes, whether grown with or without P-fertiliser application, and $[P]_{leaf}$ of

310 Tuberosum genotypes, averaged across both years, was similar to that of Diploid Hybrid genotypes and

311 Phureja genotypes, whether grown with or without P-fertiliser application, and $[P]_{tuber}$ of Tuberosum

312 genotypes, averaged across both years, was similar to those of Diploid Hybrid genotypes and Phureja

313 genotypes, whether grown with or without P-fertiliser application (Table 2). The product of yield and $[P]_{leaf}$

314   for genotypes averaged across both years was significantly greater for Tuberosum genotypes than Diploid

315   Hybrid genotypes or Phureja genotypes, whether grown with or without P-fertiliser application (Table 2).

316   According to ANOVA, there were significant effects of both genetic group (Tuberosum, Phureja,

317   Diploid Hybrid) and year on tuber yield in both Experiment 1 (P<0.001, n=3 groups; P<0.001, n = 3 years)

318   and Experiment 2 (P<0.001, n=3 groups; P<0.001, n = 2 years). However, there was no significant

319   interaction between genetic group and year on tuber yield in Experiment 1 (P=0.504) or Experiment 2

320   (0.790). A significant effect of P-fertiliser application on tuber yield was observed in Experiment 2

321   (P=0.003, n=2 treatments), but no significant interactions between P-fertiliser application and year

322   (P=0.077), genetic group and P-fertiliser application (P=0.712), or genetic group, year and P-fertiliser

323   application (P=0.575) on tuber yield were apparent. Similarly, there were significant effects of both genetic

324   group and year on $[P]_{leaf}$ in both Experiment 1 (P<0.001, n=3 groups; P<0.001, n = 2 years) and Experiment

325   2 (P=0.014, n=3 groups; P<0.001, n = 2 years). A significant interaction between genetic group and year on

326    $[P]_{leaf}$ was observed in Experiment 1 (P<0.001), but not in Experiment 2 (P=0.576). No effect of P-fertiliser

327   application on $[P]_{leaf}$ was observed in Experiment 2 (P=0.221) and no significant interactions between P-

328   fertiliser application and year (P=0.590), genetic group and P-fertiliser application (P=0.550) or genetic

329   group, year and P-fertiliser application (P=0.147) were apparent. For the product of yield and $[P]_{leaf}$ (as a

330   proxy for PUpE), there were significant effects of both genetic group and year in Experiment 1 (P<0.001,

331   n=3 groups; P<0.001, n = 2 years), but only effects of genetic group (P<0.001, n=3 groups) and not year

332   (P=0.670) in Experiment 2. There was a significant interaction between genetic group and year on PUpE in

333   Experiment 1 (P=0.002), but not in Experiment 2 (P=0.697). An effect of P-fertiliser application on PUtE

334   was observed in Experiment 2 (P=0.006), but no significant interactions between fertiliser application and

335   year (P=0.129), genetic group and P-fertiliser application (P=0.889) or genetic group, year and P-fertiliser

336   application (P=0.636) interactions were apparent.

337   There was a strong positive linear relationship between tuber yield when grown without P-

338   fertiliser application and tuber yield when grown with P-fertiliser application among genotypes (Fig. 1A) in

339   both 2009 (R^2=0.8836, P<0.0001, n=32) and 2010 (R^2=0.7002, P<0.0001, n=32). However, the effect of P-

340   fertiliser application on tuber yield was less in 2009 than in 2010 (Fig. 1A). Expressing the response of

341   tuber yield to P-fertiliser application as (1-(yield unfertilised / yield fertilised)) x 100, this value averaged

342   4.78% across all genotypes in 2009 and 13.13% across all genotypes in 2010. The response of tuber yield

343   to P-fertiliser application, averaged across both years, did not differ significantly between Tuberosum,

344   Phureja or Diploid Hybrid genotypes (Table 2).

345   There was also a strong positive relationship between $[P]_{leaf}$ when grown without P-fertiliser

346   application and $[P]_{leaf}$ when grown with P-fertiliser application among genotypes (Fig. 1B) in both 2009

347   (R^2=0.3515, P=0.0003, n=32) and 2010 (R^2=0.6139, P<0.0001, n=32). In 2009, $[P]_{leaf}$ averaged across all

348   genotypes was 2.8% greater in plants grown with P-fertiliser application than in plants grown without P-

349   fertiliser application. In 2010, $[P]_{leaf}$ averaged across all genotypes was 5.5% greater in plants grown with

350   P-fertiliser application than in plants grown without P-fertiliser application.

351   No significant relationships among genotypes between tuber yield and $[P]_{leaf}$ nor between $[P]_{tuber}$

352   and $[P]_{leaf}$ were observed in any year or for any P-fertiliser application rate, although the relationships

353   between $[P]_{tuber}$ and $[P]_{leaf}$ among genotypes generally showed a positive trend (Tables 1, 2) The $[P]_{tuber}$ /

354          $[P]_{leaf}$ quotients averaged across all genotypes receiving P-fertiliser applications were 0.49 ± 0.013 (n=64),

355   0.47 ± 0.012 (n=63), 0.44 ± 0.020 (n=32), and 0.53 ± 0.015 (n=32) in 2006, 2007, 2009 and 2010,

356   respectively. These data are consistent with $[P]_{tuber}$ / $[P]_{leaf}$ quotients obtained in previous studies of the

357   same genotypes and the observation that P is relatively mobile in the phloem of potato plants (e.g.

358   Kärenlampi and White 2009; White 2018).

359   Agronomic phosphorus use efficiency (PUE) is defined as tuber yield per unit of P available in the

360   soil (Fernandes and Soratto 2016a; Sandaña 2016; White et al. 2005a). Assuming similar biomass and P

361   partitioning among the potato genotypes studied here, the product of yield and $[P]_{leaf}$ can be used as a proxy

362   for PUpE and $[P]_{leaf}$ can be used as a reciprocal proxy for PUtE such that smaller $[P]_{leaf}$ indicates greater

363   PUtE (White et al. 2005a). In the experiments reported here, PUE appears to be strongly correlated with the

364   product of yield and $[P]_{leaf}$ (PUpE) among genotypes (Fig. 2B; R^2=0.7087, P<0.0001, n=128), with $[P]_{leaf}$

365   (PUtE) varying little between genotypes (Tables 1, 2), whether these values are obtained with or without

366   the addition of P-fertiliser.

367

368   Relationships between the size of the juvenile root system, P acquisition, canopy development and tuber

369   yield

370

371   The relationships between PUE and PUpE and PUtE were tested directly using eight Tuberosum

372   genotypes selected for contrasting yield (PUE), yield loss without P-fertiliser application, $[P]_{leaf}$ (1/PUtE)

373   and the product of yield and $[P]_{leaf}$ (PUpE). 'Nadine' is characterised by high yields, high yield loss without

374   P-fertiliser application, low $[P]_{leaf}$ and high PUtE (Tables 1,2). 'Maris Piper' is characterised by high yields,

375   high yield loss without P-fertiliser application and good PUtE. 'Stirling' is characterised by high yields,

376   low yield loss without P-fertiliser application and good PUtE. 'Cara' is characterised by medium yields,

377   low yield loss without P-fertiliser application, high $[P]_{leaf}$ and high PUtE. 'Ailsa' is characterised by low

378   yields, low yield loss without P-fertiliser application, high $[P]_{leaf}$ and average PUtE. 'Home Guard' is

379   characterised by low yield, low yield loss without P-fertiliser application, low $[P]_{leaf}$ and low PUtE.

380   'Pentland Dell' is characterised by low yields, low $[P]_{leaf}$ and low PUtE. Genotype 12601ab1, a processing

381   clone with high dry matter content, is characterised by low yields, high $[P]_{leaf}$ and low PUtE.

382   There was a strong linear relationship between root DW and shoot DW at crop establishment in

383   the field across both P-fertiliser treatments for the eight Tuberosum genotypes selected for study (Fig. 3;

384   R^2=0.7499, P<0.0001, n=16). The application of P-fertiliser increased both root and shoot DWs. The

385   genotype 'Ailsa' had the largest root DW and 'Pentland Dell' had the smallest root dry weight of the eight

386   genotypes studied in the absence of P-fertiliser application. There were also strong linear relationships

387   between root DW at crop establishment and (1) the time to reach canopy closure (Fig. 4; R^2=0.6128,

388   P=0.0003, n=16) and (2) the plant P accumulated at crop establishment (Fig. 5; R^2=0.8098, P<0.0001,

389   n=16) across both P-fertiliser treatments for the eight Tuberosum genotypes studied. Differences in shoot

390   and tuber DWs between plants grown with and without P-fertiliser application were maintained throughout

391   the season, as illustrated for 'Stirling' in Fig. 6. However, the initial strong positive linear relationship

392   between root DW at crop emergence and tuber DW among genotypes (Fig. 7 Harvest 2; R^2=0.4216,

393   P=0.0064, n=16) became weaker as the season progressed and was not observed in tuber yields at the final

394   harvest (Fig. 7 Harvest 6; R^2=0.0059, P=0.7766, n=16). Similarly, the strong linear relationship between

395   root DW and plant P accumulation observed at crop establishment in the field became weaker as the season

396   progressed and was not observed at the final harvest (Fig. 5; R^2=0.0393, P=0.4615, n=16). Nevertheless,

397   plants supplied P-fertiliser had greater shoot and tuber P content, and (generally) higher $[P]_{shoot}$ and $[P]_{tuber}$

398   than plants grown without P-fertiliser applications throughout the season, as illustrated for 'Stirling' in Fig.

399   8. It was observed that both $[P]_{shoot}$ and $[P]_{tuber}$, decreased during the season, especially in plants that had

400   received P-fertilisers, which is consistent with previous studies (e.g. Carpenter 1963; Harris 1992; Kolbe

401   and Stephan-Beckmann 1997ab; White 2018). Tuber yield (PUE) was strongly correlated with plant P

402   content (PUpE) but not with the yield / plant P content quotient (PUtE), whether these values were obtained

403   with or without the addition of P-fertiliser (Fig. 9), as was observed by proxies in Experiments 1 and 2

404   (Tables 1,2; Fig. 2).

405

406

407   **Discussion**

408

409   The large P-fertiliser requirement of a potato crop is thought to be a consequence of the inability of its root

410   system to acquire P effectively from the soil and it has been hypothesized that a vigorous juvenile root

411   system will enhance P acquisition, accelerate canopy development and enable greater tuber yields (White et

412   al. 2005b; White 2018).

413   Substantial genetic variation was observed in tuber yield, $[P]_{tuber}$, $[P]_{leaf}$ (a reciprocal proxy for

414   PUtE) and the product of yield and $[P]_{leaf}$ (a proxy for PUpE) among Tuberosum, Phureja and Diploid

415   Hybrid genotypes grown in the field (Tables 1, 2). This is consistent with previous observations that

416   Tuberosum genotypes generally yield more than Phureja genotypes when grown together in the same

417   environment (Cabello et al. 2012; Iwama and Nishibe 1989; Sattelmacher et al. 1990; Wishart et al. 2013,

418   2014) and reports that Tuberosum genotypes differ in their yield, $[P]_{tuber}$, $[P]_{leaf}$, and PUpE (see

419   Introduction). Thus, there appears to be significant genetic variation in PUtE and PUpE that might be

420   harnessed to improve PUE in the potato crop.

421   The application of P-fertiliser increased tuber yields, which is consistent with many previous

422   studies (Dampney et al. 2002; Harris 1992; Johnston et al. 1986; Rosen et al. 2014; White 2018), but did

423   not affect $[P]_{leaf}$ (Table 2). The lack of a significant effect of P-fertiliser application on $[P]_{leaf}$ was

424   unexpected, but might be explained because the $[P]_{leaf}$ of all genotypes studied were greater than the critical

425 $[P]_{leaf}$ for a potato crop (1.5 – 2.5 mg g^{-1} DW, White 2018) whether or not P-fertiliser had been applied

426 (Table 2). Strong positive relationships were observed for both tuber yields and $[P]_{leaf}$ among genotypes

427 grown with and without P-fertiliser application (Fig. 1). The strong positive relationship between tuber

428 yields when grown with and without P-fertiliser application among genotypes suggests that the genotypes

429 studied generally responded similarly to the application of P-fertiliser and is consistent with observations

430 that tuber yields of potato genotypes grown with low P inputs are correlated with their maximum yield

431 potential (e.g. Fernandes and Soratto 2016ab; Sattelmacher et al. 1990). However, genetic variation in yield

432 loss upon reduction of P-fertiliser input was observed (Table 2), which is consistent with studies suggesting

433 that potato genotypes can differ in their yield response to P availability (Daoui et al. 2014; Fernandes and

434 Soratto 2016a; Freeman et al. 1998; Hailu et al. 2017; Jenkins and Ali 1999; Manorama et al. 2017;

435 Nyiraneza et al. 2017; Sandaña 2016; Sandaña and Kalazich 2015; Soratto and Fernandes 2016; Soratto et

436 al. 2015; Thornton et al. 2014; Trehan and Singh 2013).

437   The relationship between $[P]_{leaf}$ (a proxy for 1/PUtE) and tuber yield among Tuberosum, Phureja

438 and Diplioid Hybrid genotypes was weak (Fig. 2A; R^2=0.0207, P=0.1056, n=128), but, there was a strong

439 positive relationship between tuber yield and the product of yield and $[P]_{leaf}$ (a proxy for PUpE) (Fig 2B;

440 R^2=0.7087, P<0.0001, n=128). These observations are consistent with previous studies suggesting that

441 differences in PUE are correlated with PUpE, rather than PUtE, among potato genotypes (Balemi and

442 Schenk 2009; Fernandes and Soratto 2016a; Sandaña 2016; Sattelmacher et al. 1990; Soratto et al. 2015;

443 Thornton et al. 2014; Trehan and Sharma 2005; White 2018; White et al. 2005a). It has been hypothesised

444 that PUpE influences PUE by accelerating canopy development and radiation absorption (White et al.

445 2005b).

446   The relationships between tuber yield (PUE), P acquisition (PUpE) and physiological P utilisation

447 (PUtE) were tested directly using eight Tuberosum genotypes with contrasting phenotypes grown with and

448 without P-fertiliser application in the field. Tuber yield (PUE) was strongly correlated with plant P content

449 (PUpE; R^2=0.6506, P=0.0002, n=16) but not with the yield / plant P content quotient (PUtE; R^2=0.0255,

450 P=0.5550, n=16), whether these values were obtained with or without the addition of P-fertiliser (Fig. 9),

451 suggesting that root traits contributed most to PUE in potato. It was observed that juvenile root vigour was

452 correlated with accelerated canopy development during crop establishment (Fig. 3), and greater P

453 acquisition (Fig. 5) and tuber biomass accumulation (Fig. 7) during the early season. These observations are

454 consistent with the hypothesis that rapid development of the root system enhances the ability of the potato

455 crop to acquire P to enable plant growth and canopy development (White 2018; White et al. 2005b).

456 Accelerated canopy development should enable greater accumulation of photosynthetically active radiation

457 and greater tuber yields (Balemi et al. 2009; Harris 1992; Jenkins and Ali 1999; Rosen et al. 2014; Sandaña

458 and Kalazich 2015). However, the relationships between root mass at establishment and P acquisition and

459 tuber yield became weaker during the season (Figs 5, 7). The latter might reflect the indirect effect of

460 juvenile roots on plant growth and biomass accumulation (White et al. 2005b). Other factors, such as

461 differences in photosynthetic efficiency, haulm longevity, root system senescence and biomass partitioning

462 (Harvest Index) between genotypes are likely to contribute to the weakening of the relationship between
463 root mass at establishment and tuber yield as the season progresses (Balemi 2009; Sandaña and Kalazich
464 2015; Soratto et al. 2015).

465   In conclusion, there is genetic variation within *Solanum tuberosum* in tuber yield, P acquisition
466 (PUpE) and physiological P utilisation (PUtE). Tuber yield (PUE) is strongly positively correlated with
467 PUpE, but not PUtE. One mechanism to achieve greater PUpE is to enhance juvenile root vigour, which is
468 correlated with greater P acquisition, accelerated canopy development, and tuber biomass accumulation
469 early in the season. Improving juvenile root vigour should, therefore, improve tuber yields of early varieties
470 and short season crops. It is likely that the effect of juvenile root vigour will depend upon soil P availability
471 and will be greater in soils with low P availability. Juvenile root vigour is a heritable trait and can be
472 selected to improve the PUE of potato. The next step in developing potato genotypes with greater juvenile
473 root vigour, PUpE and potential yield will be to identify the genetic basis of these traits by, for example, the
474 detection of Quantitative Trait Loci using genetic-mapping populations (Bradshaw 2017; Fernandez-Pozo
475 et al. 2015).

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497 **References**
498

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692　　　　378:351-363

693

694   **Figure Legends**
695

696   **Fig. 1** (a) Relationship between tuber FW yield per plot of five plants for 32 *Solanum tuberosum* genotypes
697   cultivated in the field with or without P-fertiliser application in 2009 (circles; y=0.9814x + 0.7368,
698   R^2=0.8836, P<0.0001, n=32) and 2010 (squares, y=1.1255x + 0.7198, R^2=0.7002, P<0.0001, n=32). (b)
699   Relationship between $[P]_{leaf}$ of plants grown without P-fertiliser application and $[P]_{leaf}$ of plants grown with
700   P-fertiliser application for 32 *Solanum tuberosum* genotypes grown in the field in 2009 (circles; y=4901x +
701   2.0065, R^2=0.3515, P=0.0003, n=32) and 2010 (squares; y=0.9501x + 0.3139, R^2=0.6139, P<0.0001,
702   n=32). All data are means of 2 plots. Group Tuberosum = black symbols; Group Phureja = purple symbols;
703   Diploid Hybrids = blue symbols. Lines indicate a quotient of unity.

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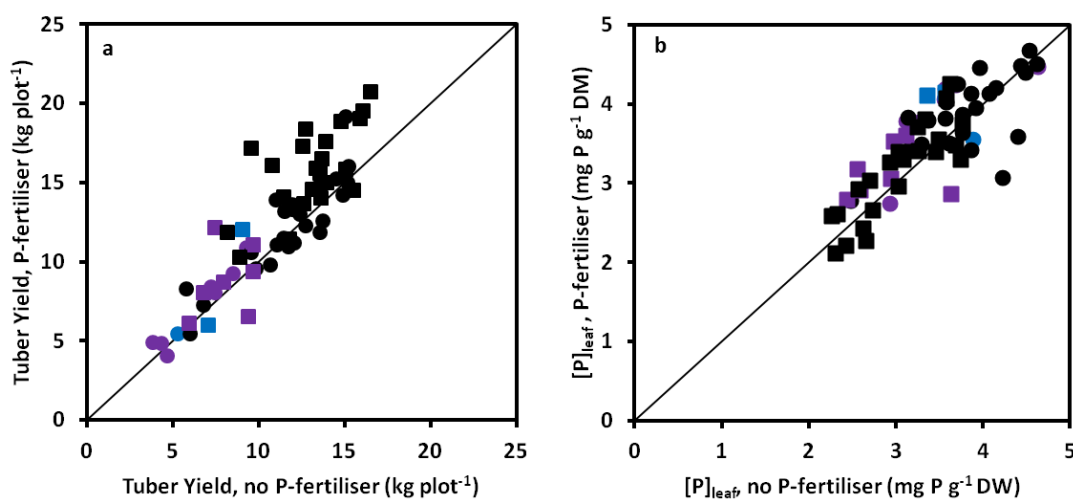
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707   **Fig. 2** The relationships between tuber FW yield (kg $plot^{-1}$) and (a) P concentration of diagnostic leaves
708   ($[P]_{leaf}$) or (b) the product of tuber yield and $[P]_{leaf}$ quotient for 32 *Solanum tuberosum* genotypes grown in
709   the field with (closed symbols) or without (open symbols) P-fertiliser application in 2009 (circles) or 2010
710   (squares). Data are means of 2 plots. Linear regression of all data presented in panel (a) yielded y = 14.56 –
711   0.8493x (R^2=0.0207, P=0.1056, n=128). Linear regression of all data presented in panel (b) yielded y =
712   2.494 + 2.274x (R^2=0.7087, P<0.0001, n=128).

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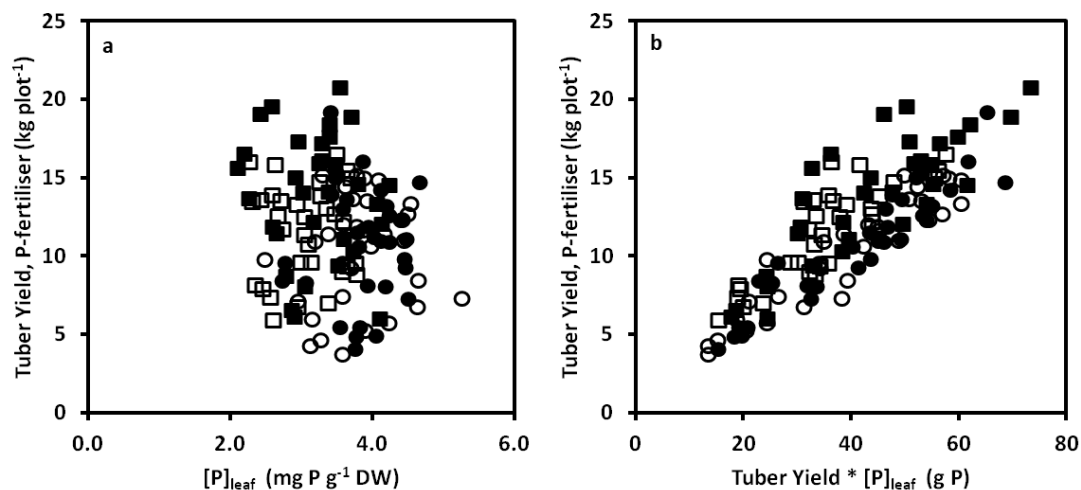
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716 **Fig. 3** The relationship between root mass and shoot mass of eight Tuberosum genotypes three weeks after
717 emergence (Harvest 1). Data show means of four individual plants grown with (closed circles) or without
718 (open circles) P-fertiliser application. Linear regression of all data yielded y = 8.871x - 14.01 (R^2=0.7499,
719 P<0.0001, n=16).
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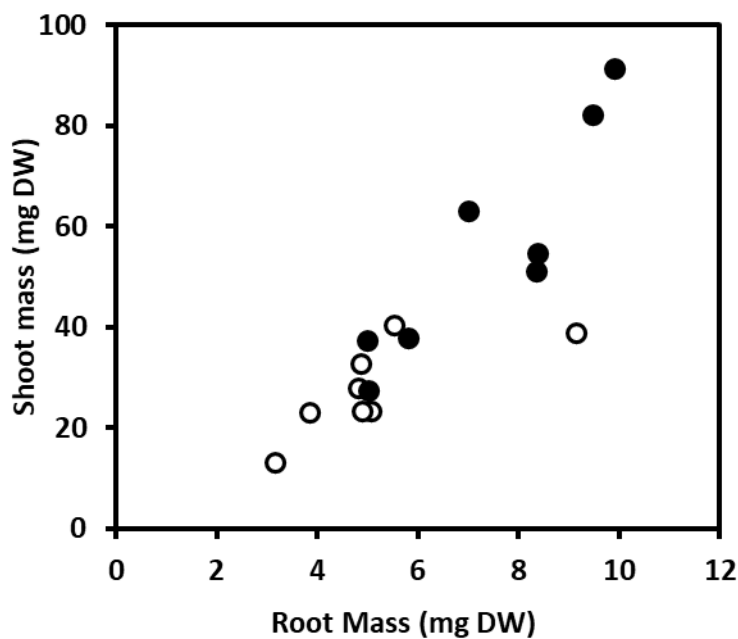
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723 **Fig. 4** The relationship between root mass of eight Tuberosum genotypes three weeks after emergence
724 (Harvest 1) and the days after crop emergence to reach 50% canopy closure. Data show means of four
725 individual plants grown with (closed circles) or without (open circles) P-fertiliser application. Linear
726 regression of all data yielded y = 44.09x - 1.806 (R^2=0.6128, P=0.0003, n=16).

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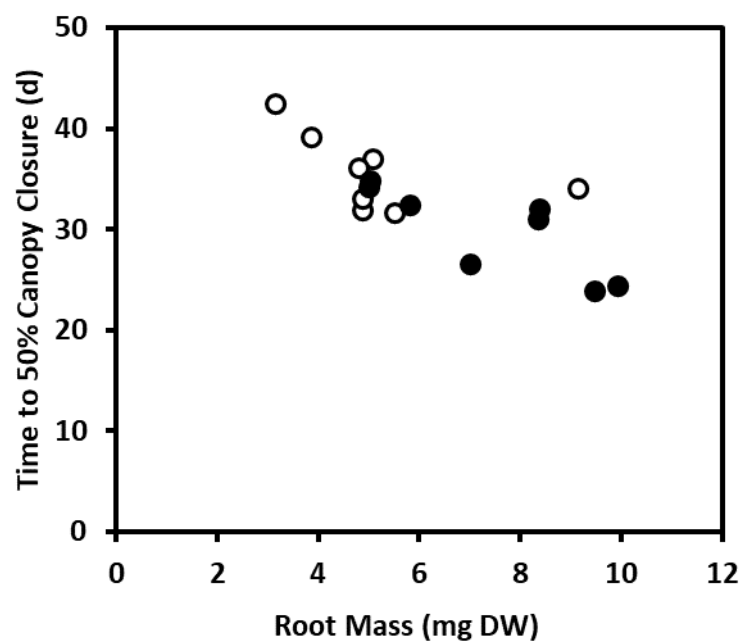
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730 **Fig. 5** Relationships between the root DWs at establishment (Harvest 1) of eight Tuberosum genotypes and
731 their P content at establishment (Harvest 1), close to canopy closure (Harvest 3) and at final harvest
732 (Harvest 6). Data for root DWs are means of four individual plants and data for plant P content are means
733 of two replicate plots of five plants cultivated with (closed symbols) or without (open symbols) P-fertiliser
734 application. Regression lines were $y = 0.1411x - 0.1230$ ($R^2=0.8098$, P<0.0001, n=16, Harvest 1), $y =$
735 $0.201x + 1.4243$ ($R^2=0.4419$, P=0.0050, n=16, Harvest 3), and $y = 0.0778x + 3.8214$ ($R^2=0.0393$,
736 P=0.4615, n=16, Harvest 6).
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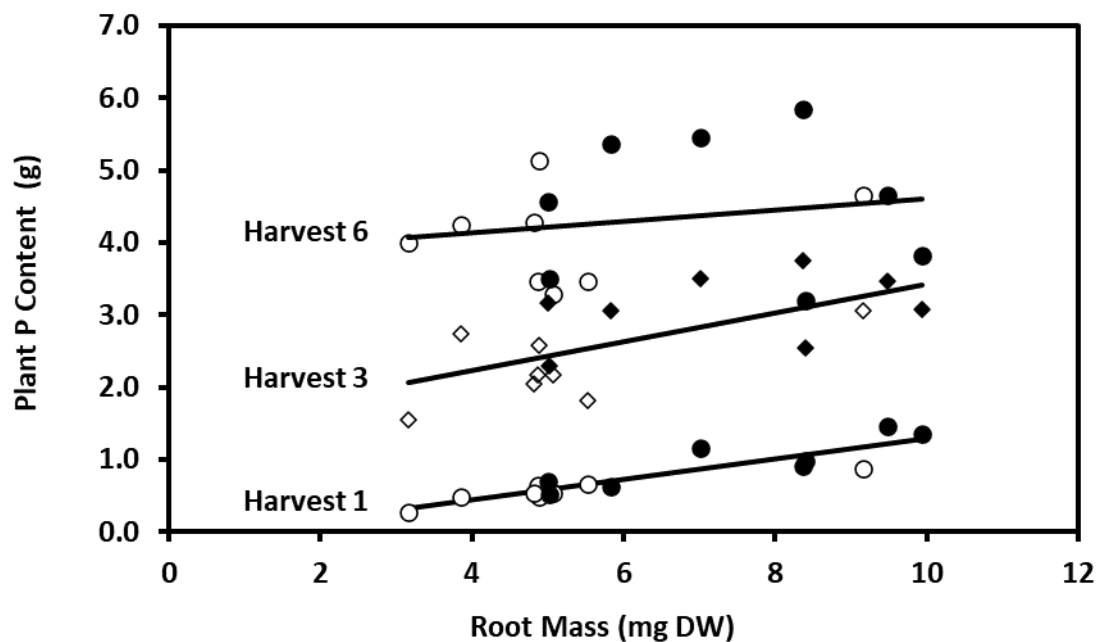
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740 **Fig. 6** The accumulation of (a) shoot mass, (b) tuber mass in the Tuberosum genotype 'Stirling'. Data are

741 shown as individual plots of five plants grown with (closed circles) or without (open circles) P-fertiliser

742 application. Plants were harvested at establishment (Harvest 1), when the canopy had approximately 50%

743 ground cover (Harvest 2), close to canopy closure (Harvest 3), mid-canopy duration (Harvest 4), when the

744 canopy had begun to sag (Harvest 5), and two weeks after canopy sagging at final harvest (Harvest 6).

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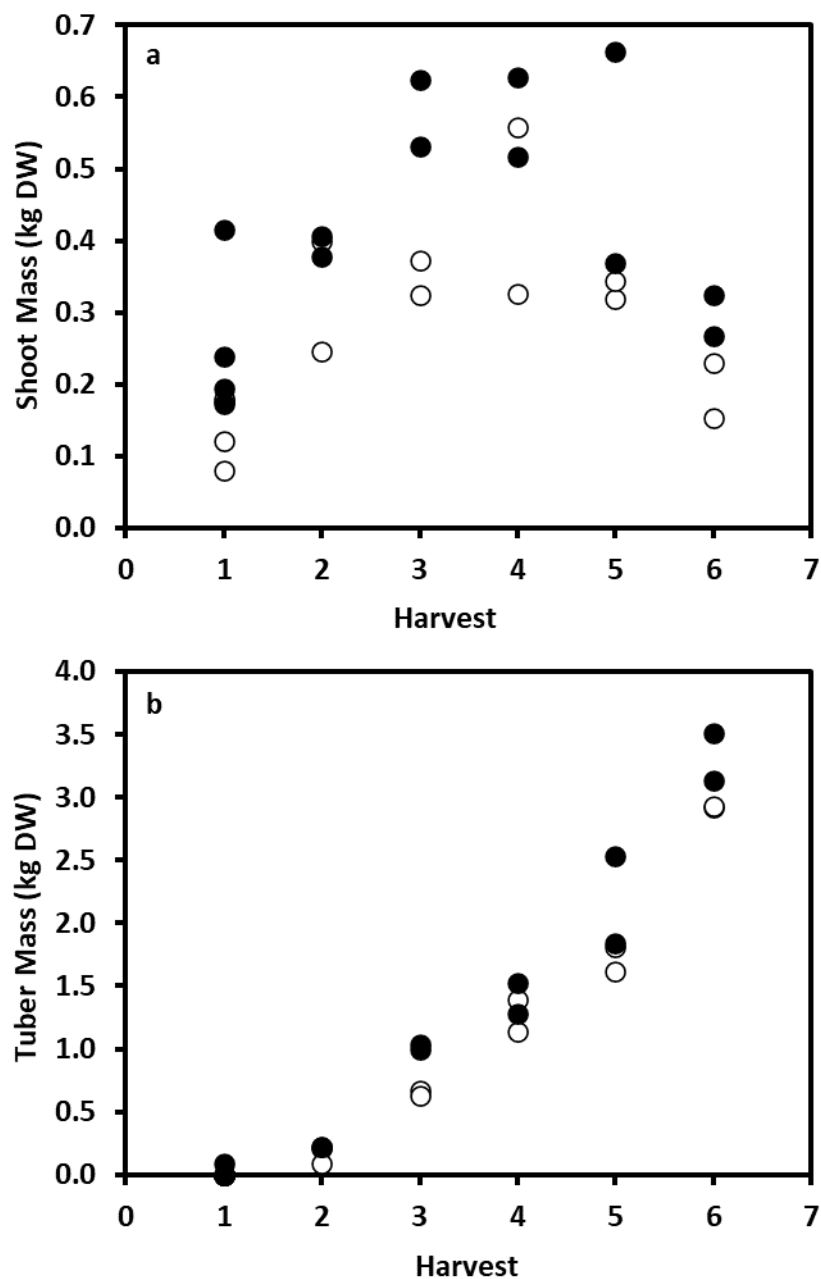
Fig. 7 Relationships between the root DWs at establishment (Harvest 1) of eight Tuberosum genotypes and their tuber DWs when the canopy had approximately 50% ground cover (Harvest 2), when the canopy had full ground cover (Harvest 4) and at final harvest (Harvest 6). Data for root DWs are means of four individual plants and data for tuber DWs are means of two replicate plots of five plants cultivated with (closed symbols) or without (open symbols) P-fertiliser application. Regression lines were y = 0.052x − 0.0495 (R^2=0.4216, P=0.0064, n=16, Harvest 2) y = 0.091x + 0.9392 (R^2=0.2179, P=0.0683, n=16, Harvest 4) and y = 0.0176x + 2.6293 (R^2=0.0059, P=0.7766, n=16, Harvest 6).

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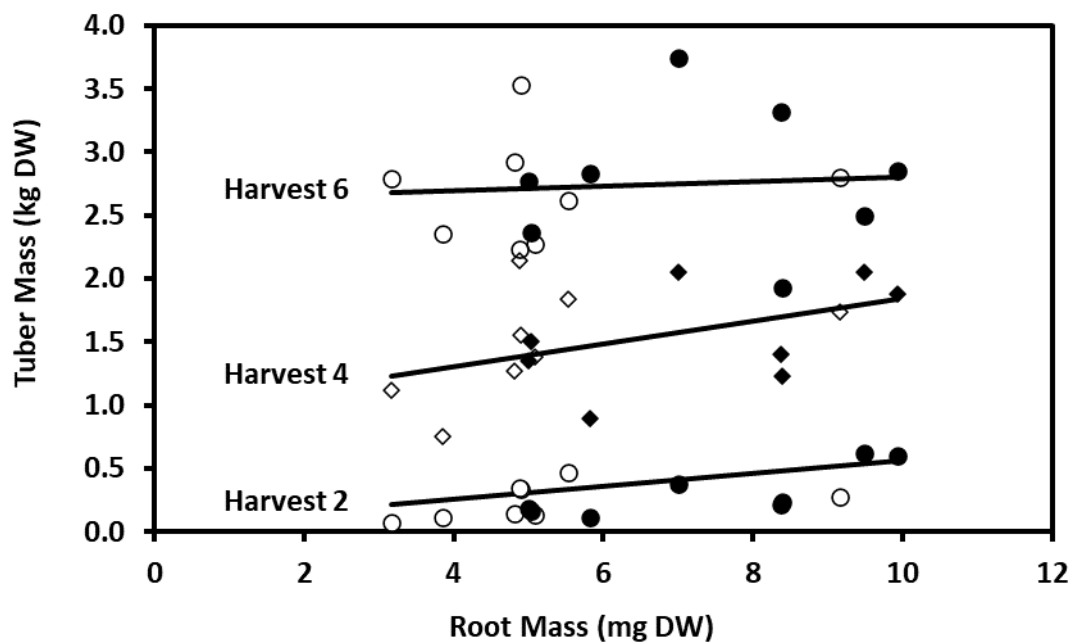
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758 **Fig. 8** The accumulation of phosphorus in (a) shoots and (b) tubers, and the P concentrations in shoots (c)

759 and tubers (d) of the Tuberosum genotype 'Stirling'. Data are shown from individual plots of five plants

760 cultivated with (closed circles) or without (open circles) P-fertiliser application. Plants were harvested at

761 establishment (Harvest 1), when the canopy had approximately 50% ground cover (Harvest 2), close to

762 canopy closure (Harvest 3), mid-canopy duration (Harvest 4), when the canopy had begun to sag (Harvest

763 5), and two weeks after canopy sagging at final harvest (Harvest 6).

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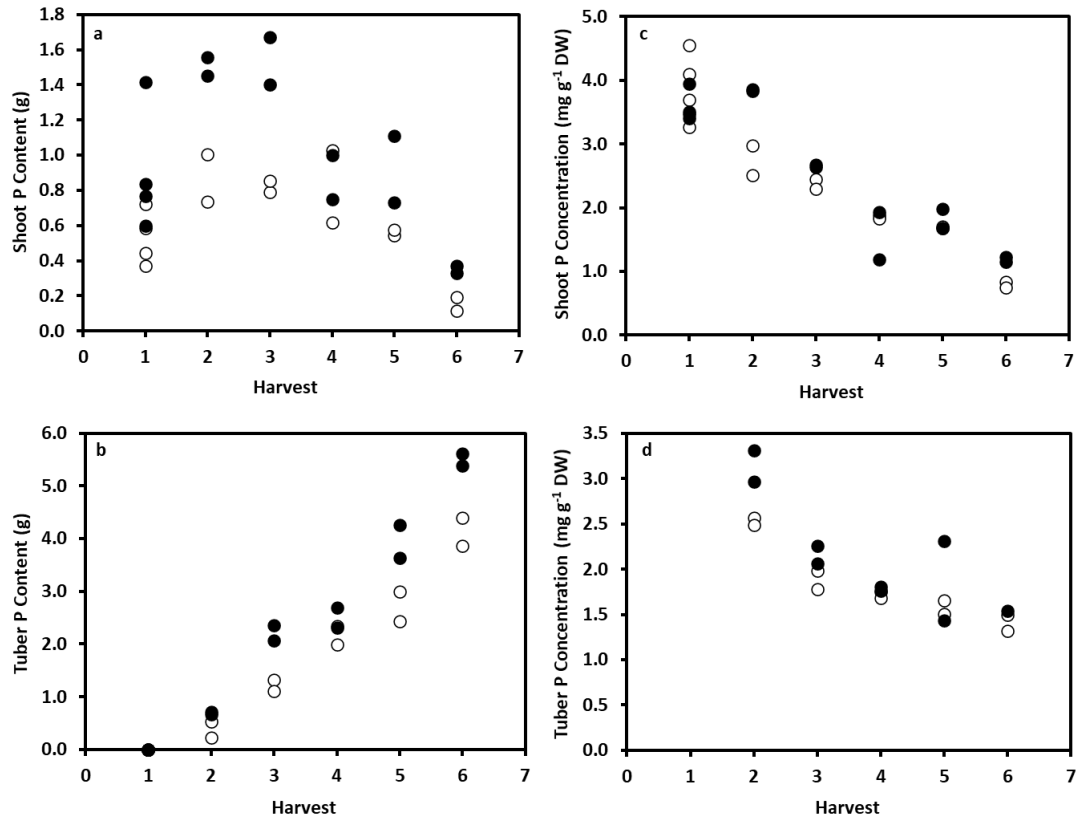
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767 **Fig. 9** The relationships between tuber DW yield (kg plot[-1]) and (a) yield divided by plant P content (PUtE)
768 or (b) plant P content (PUpE) for eight Tuberosum genotypes grown in the field with (closed symbols) or
769 without (open symbols) P-fertiliser application. Data are means of 2 plots, each containing 5 plants. Linear
770 regression of all data presented in panel (a) yielded y = 3.411 – 0.4254x (R^2=0.0255, P=0.5550, n=16).
771 Linear regression of all data presented in panel (b) yielded y = 0.7208 + 0.4684x (R^2=0.6506, P=0.0002,
772 n=16).
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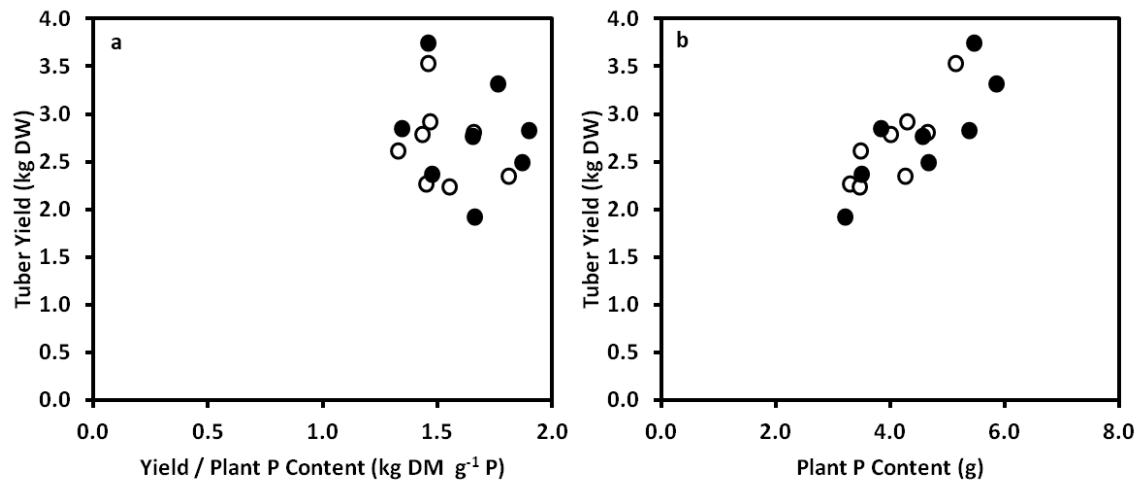
776 **Table 1.** Yields per plot of eight plants (kg FW plot^{-1}), P concentration of diagnostic leaves ([P]$_{leaf}$, mg g^{-1}
777 DW), P concentration of tubers ([P]$_{tuber}$, mg g^{-1} DW) and yield * [P]$_{leaf}$ for PUpE, for genotypes cultivated
778 in Experiment 1. Data are expressed as mean ± SE either for n years (for individual genotypes) or for n
779 genotypes present in all years of Experiment 1 (2006, 2007, 2008).

Genotype	Group	Tuber yield (kg FW plot^{-1}) mean	SE	n	[P]$_{leaf}$ (mg g^{-1} DM) mean	SE	n	[P]$_{tuber}$ (mg g^{-1} DM) mean	SE	n	Yield*[P]$_{leaf}$ mean	SE	n
99.FT 1 (5)	Diploid Hybrid	14.8		1	3.10		1	2.10		1	45.89		1
HB.165 (1)	Diploid Hybrid	11.4	1.87	3	3.98	0.27	2	1.74	0.07	3	45.93	7.38	2
HB.171 (13)	Diploid Hybrid	16.7	13.22	3	3.87	0.75	2	2.32	0.17	3	73.94	42.00	2
2DH40 (3)	Diploid Tuberosum	2.2		1	3.90		1	1.69		1	8.47		1
71.P.10	Phureja	12.4	2.78	3	3.42	0.09	2	1.49	0.07	3	45.41	3.61	2
71.T.46	Phureja	11.7	3.56	3	4.05	0.04	2	1.77	0.23	3	47.87	8.77	2
71.T.6	Phureja	11.5	5.06	3	3.78	0.31	2	1.54	0.26	3	41.76	13.55	2
80.CP.23	Phureja	10.9	3.14	3	4.26	0.80	2	1.36	0.12	3	41.89	4.26	2
81.S.66	Phureja	15.6	3.52	3	3.42	0.33	2	1.57	0.14	3	53.63	12.05	2
84.2.P75	Phureja	5.9	1.82	3	3.57	0.06	2	1.77	0.12	3	22.25	2.74	2
85.1.T8	Phureja	12.7	2.70	3	3.98	0.67	2	1.68	0.01	3	48.68	12.19	2
DB.161 (10)	Phureja	12.2	3.65	3	3.33	0.07	2	1.62	0.13	3	44.41	3.45	2
DB.168 (11)	Phureja	8.0	4.10	3	3.67	0.11	2	1.27	0.02	3	32.19	8.21	2
DB.170 (35)	Phureja	9.0	5.26	3	4.78	0.45	2	1.62	0.20	3	44.61	18.57	2
DB.175 (5)	Phureja	10.9	7.07	3	3.71	0.16	2	1.49	0.14	3	42.19	12.67	2
DB.199 (10)	Phureja	13.3	2.90	3	2.96	0.54	2	1.83	0.28	3	36.93	3.01	2
DB.207 (35)	Phureja	11.8	4.59	3	4.07	0.22	2	1.92	0.23	3	48.94	13.40	2
DB.226 (70)	Phureja	16.2	6.09	3	3.61	0.14	2	1.48	0.15	3	63.82	11.91	2
DB.244 (37)	Phureja	14.8	2.92	3	3.34	0.37	2	1.60	0.19	3	47.79	0.09	2
DB.257 (28)	Phureja	13.3	3.75	3	3.75	0.36	2	1.46	0.16	3	51.85	12.87	2
DB.270 (43)	Phureja	14.6	15.11	3	4.01	0.42	2	1.72	0.22	3	66.11	40.83	2
DB.271 (39)	Phureja	12.7	4.39	3	4.01	0.32	2	1.85	0.08	3	55.23	12.03	2
DB.299 (39)	Phureja	12.2	4.07	3	3.84	0.44	2	1.21	0.08	3	49.25	14.13	2
DB.323 (3)	Phureja	11.6	7.30	3	3.62	0.74	2	1.54	0.17	3	46.55	23.94	2
DB.333 (16)	Phureja	16.0	7.51	3	3.66	0.46	2	2.12	0.28	3	50.47	4.13	2
DB.337 (37)	Phureja	13.3	1.08	3	3.80	0.28	2	1.43	0.10	3	49.85	1.41	2
DB.354 (901)	Phureja	12.8	9.96	3	3.82	0.43	2	1.48	0.20	3	55.67	26.38	2
DB.358 (23)	Phureja	13.3	7.03	3	3.50	0.37	2	1.59	0.25	3	47.73	19.11	2
DB.358 (24)	Phureja	9.2	2.97	3	3.64	0.63	2	1.21	0.14	3	35.01	12.08	2
DB.358 (30)	Phureja	13.5	4.63	3	3.57	0.53	2	1.63	0.12	3	52.10	16.04	2
DB.375 (1)	Phureja	11.0	7.09	3	3.10	0.56	2	1.33	0.11	3	36.69	18.92	2
DB.375 (2)	Phureja	12.5	1.02	3	3.42	0.17	2	1.46	0.12	3	42.30	3.87	2
DB.377 (4)	Phureja	10.5	3.07	3	3.48	0.27	2	1.34	0.07	3	33.12	0.59	2
DB.378 (1)	Phureja	11.4	3.00	3	2.96	0.73	2	1.48	0.18	3	34.26	13.20	2
DB.384 (4)	Phureja	12.4	2.10	3	3.46	0.07	2	1.54	0.05	3	44.42	2.17	2
DB.441 (2)	Phureja	10.3	3.28	3	3.79	0.49	2	1.84	0.22	3	36.14	8.52	2
DB.520 (11)	Phureja	8.5	3.82	3	3.95	0.27	2	1.26	0.14	3	38.21	7.47	2
PHU.95 (0412)	Phureja	11.5	2.72	3	3.26	0.42	2	1.62	0.17	3	38.52	9.90	2
PHU.95 (1901)	Phureja	9.3	2.89	3	3.44	0.38	2	2.41	0.16	3	32.07	1.91	2
TC.43 (45)	Phureja	14.2	0.97	2	3.76	0.32	2	1.99	0.35	2	53.67	6.41	2
12601 ab 1	Tuberosum	11.5	1.04	3	3.60	0.87	2	1.38	0.16	3	41.35	11.91	2
Ailsa	Tuberosum	18.7	5.40	3	3.61	1.02	2	1.70	0.15	3	71.07	30.32	2
Anya	Tuberosum	11.9	6.23	3	2.74	0.45	2	1.38	0.09	3	34.23	15.22	2
Brodick	Tuberosum	18.1	2.72	3	3.17	0.53	2	1.69	0.18	3	54.99	11.24	2
Cara	Tuberosum	21.3	8.80	3	4.06	0.72	2	1.71	0.21	3	87.73	35.14	2
Desiree	Tuberosum	20.7	2.78	3	3.32	0.93	2	1.35	0.14	3	71.97	23.78	2
Edzell Blue	Tuberosum	13.7		1				1.71		1			
Estima	Tuberosum	17.7	7.73	3	2.66	0.89	2	1.20	0.07	3	50.13	27.19	2
Eve Balfour	Tuberosum	18.7		1	2.62		1	1.27		1	48.90		1
Golden Millenium	Tuberosum	16.8	2.21	3	2.88	0.44	2	1.52	0.13	3	49.41	11.13	2
Harborough Harvest	Tuberosum	15.5	6.21	3	4.17	0.95	2	1.72	0.18	3	60.95	0.33	2
Home Guard	Tuberosum	14.3	2.39	3	2.57	1.05	2	1.38	0.32	3	36.90	17.61	2
Hermes	Tuberosum	18.7	7.54	3	3.27	0.27	2	1.57	0.22	3	53.41	7.27	2
Lady Balfour	Tuberosum	20.0		1	2.76		1	1.24		1	55.36		1
Maris Piper	Tuberosum	23.5	3.70	3	3.22	0.52	2	1.60	0.09	3	76.04	18.77	2
Montrose	Tuberosum	20.5	1.48	3	3.08	0.65	2	1.68	0.15	3	64.76	15.21	2
Nadine	Tuberosum	22.3	7.81	3	3.10	1.34	2	1.81	0.25	3	59.29	17.16	2
Pentland Dell	Tuberosum	14.2	3.66	3	2.59	0.90	2	1.42	0.09	3	39.95	18.12	2
Pentland Squire	Tuberosum	20.7	6.08	3	3.76	0.98	2	1.69	0.15	3	78.70	32.14	2
Record	Tuberosum	17.0	2.75	3	3.79	0.79	2	1.48	0.16	3	61.67	15.48	2
Saxon	Tuberosum	18.7	5.18	3	2.53	0.61	2	1.55	0.16	3	49.61	19.16	2
Scarborough	Tuberosum	19.2	1.85	3	3.27	0.38	2	1.63	0.20	3	64.77	8.97	2
Stirling	Tuberosum	21.6	11.31	3	3.09	0.58	2	1.79	0.08	3	74.20	32.10	2
Tay	Tuberosum	17.4	3.84	3	3.21	0.83	2	1.68	0.21	3	57.15	21.35	2
Vales Everest	Tuberosum	20.0	4.31	3	3.61	1.03	2	1.70	0.17	3	78.09	26.51	2
Vales Sovereign	Tuberosum	10.6		1	3.48		1	1.40		1	36.77		1
Wilja	Tuberosum	22.8	4.56	3	3.33	0.85	2	1.58	0.14	3	75.62	26.67	2

*Mean, SE (3 years)	Diploid Hybrid	14.0	2.6	2	3.93	0.06	2	2.03	0.29	2	59.93	14.00	2
	Phureja	11.9	0.4	35	3.66	0.06	35	1.59	0.04	35	44.51	1.55	35
	Tuberosum	18.4	0.7	23	3.25	0.10	23	1.57	0.03	23	60.52	3.08	23

780

Table 2. Yields per plot of five plants (kg FW plot^{-1}), P concentration of diagnostic leaves ($[P]_{leaf}$, mg g^{-1} DW), P concentration of tubers ($[P]_{tuber}$, mg g^{-1} DW) and yield * $[P]_{leaf}$ for genotypes cultivated either with (high P) or without (low P) P-fertiliser additions in Experiment 2 (2009, 2010). Yield loss for each genotype grown without P-fertiliser applications is expressed in percentage terms as (1-(yield unfertilised / yield fertilised)) x 100. Data are expressed as mean ± SE either for n years (for individual genotypes) or for n genotypes.

Genotype	Group	n	Yield (high P) (kg FW plot^{-1}) mean	SE	Yield (low P) (kg FW plot^{-1}) mean	SE	Yield loss (%) mean	SE	$[P]_{leaf}$ (high P) (mg g^{-1} DM) mean	SE	$[P]_{leaf}$ (low P) (mg g^{-1} DM) mean	SE	$[P]_{tuber}$ (high P) (mg g^{-1} DM) mean	SE	$[P]_{tuber}$ (low P) (mg g^{-1} DM) mean	SE	Yield*$[P]_{leaf}$ (high P) mean	SE	Yield*$[P]_{leaf}$ (low P) mean	SE
99.FT 1 (5)	Diploid Hybrid	2	10.07	1.96	8.17	0.02	17.4	14.8	4.03	0.10	4.41	1.68	2.00	0.24	1.72	0.05	40.83	8.91	35.31	3.01
HB.171 (13)	Diploid Hybrid	2	5.72	0.27	6.15	0.02	-7.1	20.8	3.83	0.28	3.63	0.52	2.80	0.04	2.31	0.40	21.95	2.60	22.09	1.59
DB.226 (70)	Phureja	2	9.32	0.04	9.06	0.02	2.9	11.5	3.99	0.47	3.81	1.65	1.46	0.25	1.24	0.05	37.22	4.22	34.02	5.29
DB.337 (37)	Phureja	2	10.99	0.07	9.46	0.01	13.9	2.4	3.91	0.32	3.41	0.56	1.73	0.04	1.56	0.01	43.00	3.30	32.16	2.03
DB.375 (1)	Phureja	2	8.52	3.65	5.86	0.01	25.2	27.8	3.47	0.30	2.84	0.56	1.43	0.04	1.32	0.08	28.47	10.13	16.24	2.76
DB.378 (1)	Phureja	2	8.58	0.16	7.56	0.02	12.0	5.6	2.76	0.03	2.69	0.50	1.67	0.04	1.46	0.09	23.71	0.66	20.26	0.84
DB.384 (4)	Phureja	2	8.05	0.00	7.11	0.01	11.8	8.2	3.62	0.57	3.26	0.62	1.55	0.15	1.57	0.04	29.13	4.54	23.26	3.27
DB.520 (11)	Phureja	2	5.73	0.84	6.59	0.01	-10.2	65.6	3.46	0.59	3.60	0.08	1.24	0.04	1.31	0.15	19.32	0.52	23.86	10.34
PHU.95 (1901)	Phureja	2	5.11	1.02	5.30	0.03	-5.4	17.6	3.33	0.43	2.93	0.67	2.09	0.47	1.77	0.13	16.60	1.21	15.32	0.06
12601 ab 1	Tuberosum	2	8.78	1.51	7.81	0.01	10.4	6.9	4.12	0.38	4.20	0.86	1.38	0.02	1.42	0.05	35.56	2.87	32.34	1.07
Ailsa	Tuberosum	2	12.19	2.38	11.87	0.02	0.8	19.0	4.13	0.33	3.66	0.62	1.90	0.15	1.60	0.03	49.52	5.85	43.05	0.70
Anya	Tuberosum	2	9.86	1.55	8.76	0.01	13.8	33.6	2.86	0.20	3.48	1.49	1.56	0.07	1.35	0.01	27.85	2.43	28.25	3.89
Brodick	Tuberosum	2	13.87	1.99	14.29	0.02	-4.4	19.4	3.71	0.23	3.81	0.22	1.75	0.02	1.62	0.06	50.97	4.13	54.34	1.19
Cara	Tuberosum	2	13.42	1.12	14.09	0.03	-4.9	3.4	4.32	0.08	4.06	0.86	2.40	0.12	1.80	0.08	57.85	3.78	56.60	0.36
Desiree	Tuberosum	2	13.09	1.90	12.97	0.02	-0.2	14.6	3.47	0.55	3.08	1.01	1.63	0.08	1.44	0.00	44.34	0.65	39.52	3.64
Estima	Tuberosum	2	14.63	1.00	12.74	0.01	12.9	1.2	2.87	0.76	3.04	1.46	1.20	0.03	1.25	0.11	41.23	8.32	38.12	6.89
Golden Millenium	Tuberosum	2	13.99	0.07	12.27	0.01	12.3	17.7	3.23	0.20	2.94	0.47	1.51	0.03	1.62	0.13	45.13	2.64	35.80	0.90
Harborough Harvest	Tuberosum	2	13.34	2.77	10.16	0.02	21.4	23.5	3.55	0.26	3.33	0.48	1.47	0.00	1.54	0.16	46.69	6.33	33.66	0.44
Home Guard	Tuberosum	2	11.63	2.07	11.20	0.03	2.7	11.2	2.52	0.25	2.57	0.18	1.38	0.01	1.25	0.03	28.81	2.28	28.95	4.53
Hermes	Tuberosum	2	15.96	1.24	11.45	0.02	26.9	35.1	3.98	0.69	4.14	0.78	1.50	0.12	1.33	0.13	62.66	6.12	48.21	12.34
Maris Piper	Tuberosum	2	16.82	0.79	14.53	0.01	13.2	15.8	3.63	0.23	3.52	0.50	1.74	0.01	1.37	0.10	60.93	0.98	51.26	5.93
Montrose	Tuberosum	2	14.40	2.88	11.98	0.01	14.1	26.9	3.37	0.42	3.21	0.33	1.59	0.14	1.68	0.13	47.32	3.70	38.31	0.28
Nadine	Tuberosum	2	19.12	0.05	15.44	0.02	19.2	4.8	2.92	0.49	3.25	1.25	1.52	0.02	1.57	0.00	55.84	9.57	49.91	8.25
Pentland Dell	Tuberosum	2	8.65	3.20	7.07	0.01	10.7	41.1	3.21	0.61	2.74	0.81	1.43	0.16	1.28	0.02	25.85	4.97	18.93	0.11
Pentland Squire	Tuberosum	2	16.28	2.08	13.79	0.01	13.1	35.4	3.76	0.36	3.77	0.61	1.71	0.02	1.56	0.03	60.41	1.87	52.27	8.27
Record	Tuberosum	2	12.17	1.12	11.64	0.02	4.1	7.6	4.27	0.20	4.01	0.85	1.51	0.13	1.56	0.06	51.77	2.33	46.40	2.49
Saxon	Tuberosum	2	15.77	0.76	14.40	0.02	8.2	18.5	2.84	0.64	2.86	0.87	1.75	0.08	1.56	0.09	44.34	7.93	41.53	8.43
Scarborough	Tuberosum	2	14.55	1.39	12.40	0.02	14.6	3.3	3.73	0.47	3.54	1.21	1.78	0.04	1.77	0.02	53.60	1.67	43.37	4.19
Stirling	Tuberosum	2	16.67	4.09	15.10	0.01	5.9	29.2	3.89	0.35	3.60	0.22	1.95	0.19	1.73	0.13	63.46	10.09	54.22	3.42
Tay	Tuberosum	2	12.54	1.58	11.54	0.02	6.4	25.8	3.76	0.37	3.45	0.83	1.63	0.09	1.31	0.48	46.51	1.33	39.89	5.24
Vales Everest	Tuberosum	2	17.04	1.81	14.61	0.02	13.4	16.9	3.60	0.10	3.43	0.36	1.80	0.06	1.43	0.01	61.51	8.21	50.16	2.17
Wilja	Tuberosum	2	16.27	3.27	14.20	0.02	11.4	12.9	3.08	0.50	3.34	2.14	1.70	0.26	1.66	0.05	48.54	1.91	45.39	9.01
*Mean +/- SE	Diploid Hybrid	2	7.90	2.18	7.16	1.01	5.17	12.25	3.93	0.10	4.02	0.39	2.40	0.40	2.01	0.29	31.4	9.44	28.7	6.61
	Phureja	7	8.04	0.77	7.28	0.59	7.17	4.61	3.51	0.15	3.22	0.16	1.59	0.10	1.46	0.07	28.2	3.57	23.6	2.74
	Tuberosum	23	13.96	0.56	12.36	0.47	9.83	1.63	3.51	0.10	3.44	0.09	1.64	0.05	1.51	0.04	48.3	2.30	42.2	2.01