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

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30

31

32 **Abstract**

33

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

38

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

43

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

49

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

53

54

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

56

57

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 ($\text{g DW g}^{-1} \text{P}_{\text{soil}}$; 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 ($\text{g P}_{\text{crop}} \text{g}^{-1} \text{P}_{\text{soil}}$), and crop physiological utilisation efficiency
82 (PUtE), which is defined as the yield per unit P acquired by a crop ($\text{g DW g}^{-1} \text{P}_{\text{crop}}$). 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 PUE 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 PUE 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.

152

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', 'Brodict', '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 ‘Brodict’, ‘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 P₂O₅ (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 P₂O₅ (Defra 2010). Prior to the
202 addition of P-fertiliser, the Olsen-P concentration in the soil was 49 mg kg⁻¹ P₂O₅. 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 °C 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 °C
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 ($[P]_{\text{leaf}}$) and P
297 concentration in tubers ($[P]_{\text{tuber}}$) 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 $[P]_{\text{leaf}}$ 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 $[P]_{\text{tuber}}$ 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 $[P]_{\text{leaf}}$, 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 $[P]_{\text{leaf}}$ (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 $[P]_{\text{leaf}}$ 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 $[P]_{\text{tuber}}$ 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 $[P]_{\text{leaf}}$

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 ($P = 0.790$). 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 $[P]_{\text{leaf}}$ 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 $[P]_{\text{leaf}}$ was observed in Experiment 1 ($P < 0.001$), but not in Experiment 2 ($P = 0.576$). No effect of P-fertiliser
 327 application on $[P]_{\text{leaf}}$ 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 $[P]_{\text{leaf}}$ (as a
 330 proxy for PUE), 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 PUE in
 333 Experiment 1 ($P = 0.002$), but not in Experiment 2 ($P = 0.697$). An effect of P-fertiliser application on PUE
 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 $(1 - (\text{yield unfertilised} / \text{yield fertilised})) \times 100$, 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 $[P]_{\text{leaf}}$ when grown without P-fertiliser
 346 application and $[P]_{\text{leaf}}$ 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, $[P]_{\text{leaf}}$ 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, $[P]_{\text{leaf}}$ 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 $[P]_{\text{leaf}}$ nor between $[P]_{\text{tuber}}$
 352 and $[P]_{\text{leaf}}$ were observed in any year or for any P-fertiliser application rate, although the relationships
 353 between $[P]_{\text{tuber}}$ and $[P]_{\text{leaf}}$ among genotypes generally showed a positive trend (Tables 1, 2) The $[P]_{\text{tuber}} /$
 354 $[P]_{\text{leaf}}$ 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 $[P]_{\text{tuber}} / [P]_{\text{leaf}}$ 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 $[P]_{\text{leaf}}$ can be used as a proxy
 362 for PUpE and $[P]_{\text{leaf}}$ can be used as a reciprocal proxy for PUE such that smaller $[P]_{\text{leaf}}$ indicates greater
 363 PUE (White et al. 2005a). In the experiments reported here, PUE appears to be strongly correlated with the
 364 product of yield and $[P]_{\text{leaf}}$ (PUpE) among genotypes (Fig. 2B; $R^2=0.7087$, $P<0.0001$, n=128), with $[P]_{\text{leaf}}$
 365 (PUE) 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 PUE were tested directly using eight Tuberosum
 372 genotypes selected for contrasting yield (PUE), yield loss without P-fertiliser application, $[P]_{\text{leaf}}$ ($1/\text{PUE}$)
 373 and the product of yield and $[P]_{\text{leaf}}$ (PUpE). ‘Nadine’ is characterised by high yields, high yield loss without
 374 P-fertiliser application, low $[P]_{\text{leaf}}$ and high PUE (Tables 1,2). ‘Maris Piper’ is characterised by high yields,
 375 high yield loss without P-fertiliser application and good PUE. ‘Stirling’ is characterised by high yields,
 376 low yield loss without P-fertiliser application and good PUE. ‘Cara’ is characterised by medium yields,
 377 low yield loss without P-fertiliser application, high $[P]_{\text{leaf}}$ and high PUE. ‘Ailsa’ is characterised by low
 378 yields, low yield loss without P-fertiliser application, high $[P]_{\text{leaf}}$ and average PUE. ‘Home Guard’ is
 379 characterised by low yield, low yield loss without P-fertiliser application, low $[P]_{\text{leaf}}$ and low PUE.
 380 ‘Pentland Dell’ is characterised by low yields, low $[P]_{\text{leaf}}$ and low PUE. Genotype 12601ab1, a processing
 381 clone with high dry matter content, is characterised by low yields, high $[P]_{\text{leaf}}$ and low PUE.

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 $[P]_{\text{shoot}}$ and $[P]_{\text{tuber}}$
398 than plants grown without P-fertiliser applications throughout the season, as illustrated for ‘Stirling’ in Fig.
399 8. It was observed that both $[P]_{\text{shoot}}$ and $[P]_{\text{tuber}}$, 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, $[P]_{\text{tuber}}$, $[P]_{\text{leaf}}$ (a reciprocal proxy for
414 PUtE) and the product of yield and $[P]_{\text{leaf}}$ (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, $[P]_{\text{tuber}}$, $[P]_{\text{leaf}}$, 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 $[P]_{\text{leaf}}$ (Table 2). The lack of a significant effect of P-fertiliser application on $[P]_{\text{leaf}}$ was
424 unexpected, but might be explained because the $[P]_{\text{leaf}}$ 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 Diploid Hybrid genotypes was weak (Fig. 2A; R²=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 R²=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; R²=0.6506, P=0.0002, n=16) but not with the yield / plant P content quotient (PUtE; R²=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).

476

477

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479

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497 **References**

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- 499 Ahmadi SH, Agharezaee M, Kamgar-Haghighi AA, Sepaskhah AR (2017) Compatibility of root growth
500 and tuber production of potato cultivars with dynamic and static water-saving irrigation
501 managements. *Soil Use Manage* 33:106-119
- 502 Allen EJ, Scott RK (1992) Principles of agronomy and their application in the potato industry. In: Harris
503 JM (ed) *The potato crop: the scientific basis for improvement*. London, Chapman and Hall, pp
504 816-881
- 505 Allison MF, Fowler JH, Allen EJ (2001) Effects of soil- and foliar-applied phosphorus fertilizers on the
506 potato (*Solanum tuberosum*) crop. *J Agric Sci* 137: 379-395
- 507 Balemi T (2009) Effect of phosphorus nutrition on growth of potato genotypes with contrasting phosphorus
508 efficiency. *Afr Crop Sci J* 17:199-212
- 509 Balemi T (2011) Screening for genotypic variation in potato for phosphorus efficiency. *Int Res J Plant Sci*
510 2:233-243
- 511 Balemi T, Schenk MK (2009) Genotypic variation of potato for phosphorus efficiency and quantification of
512 phosphorus uptake with respect to root characteristics. *J Plant Nutr Soil Sci* 172:669-677
- 513 Bethke PC, Jansky SH (2008) The effects of boiling and leaching on the content of potassium and other
514 minerals in potatoes. *J Food Sci* 73:H80-H85
- 515 Bradshaw JE (2017) Review and analysis of limitations in ways to improve conventional potato breeding.
516 *Potato Res* 60:171-193
- 517 Bradshaw JE, Hackett CA, Pande B, Waugh R, Bryan GJ (2008) QTL mapping of yield, agronomic and
518 quality traits in tetraploid potato (*Solanum tuberosum* subsp. *tuberosum*). *Theor Appl Genet*
519 116:193-211
- 520 Burns IG, Hammond JP, White PJ (2010) Precision placement of fertiliser for optimising the early nutrition
521 of vegetable crops – a review of the implications for the yield and quality of crops, and their
522 nutrient use efficiency. *Acta Hort* 852:177-187
- 523 Cabello R, De Mendiburu F, Bonierbale M, Monneveux P, Roca W, Chujoy E (2012) Large-scale
524 evaluation of potato improved varieties, genetic stocks and landraces for drought tolerance. *Am J*
525 *Potato Res* 89:400-410
- 526 Carpenter PN (1963) Bulletin 610. Mineral accumulation in potato plants as affected by fertilizer
527 application and potato variety. University of Maine, Orono
- 528 Dampney P, Johnson P, Goodlass G, Dyer C, Sinclair A, Edwards T (2002) Review of the response of
529 potatoes to phosphate. Final Report on Defra Project PE0108. Department for Environment, Food
530 and Rural Affairs, London
- 531 Daoui K, Mrabet R, Benbouaza A, Achbani EH (2014) Responsiveness of different potato (*Solanum*
532 *tuberosum*) varieties to phosphorus fertilizer. *Procedia Eng* 83:344-347
- 533 Davenport JR, Milburn PH, Rosen CJ, Thornton RE (2005) Environmental impacts of potato nutrient
534 management. *Am J Potato Res* 82:321-328

- 535 Dechassa N, Schenk MK, Claasen N, Steingrobe B (2003) Phosphorus efficiency of cabbage (*Brassica*
536 *oleracea* L. var. *capitata*), carrot (*Daucus carota* L.), and potato (*Solanum tuberosum* L.). *Plant*
537 *Soil* 250:215-224
- 538 Department for Environment, Food and Rural Affairs [Defra] (2010) Fertiliser manual (RB209), 8th edn.
539 The Stationery Office, London
- 540 Department for Environment, Food and Rural Affairs [Defra] (2017) The British survey of fertiliser
541 practice. Fertiliser use on farm crops for crop year 2016. Department for Environment, Food and
542 Rural Affairs and The Scottish Government, London
- 543 Ereifej KI, Shibli RA, Ajlouni MM, Hussein A (1998) Mineral contents of whole tubers and selected
544 tissues of ten potato cultivars grown in Jordan. *J Food Sci Technol* 35:55-58
- 545 Fageria NK, Baligar VC, Jones CA (2011) Growth and mineral nutrition of field crops, 3rd edn. CRC
546 Press, Boca Raton
- 547 Fernandes AM, Soratto RP (2013) Absorption and nutrients use efficiency by potato cultivars. *Biosci J*
548 29:91-100
- 549 Fernandes AM, Soratto RP (2016a) Response of potato cultivars to phosphate fertilization in tropical soils
550 with different phosphorus availabilities. *Potato Res* 59:259-278
- 551 Fernandes AM, Soratto RP (2016b) Phosphorus fertilizer rate for fresh market potato cultivars grown in
552 tropical soil with low phosphorus availability. *Am J Potato Res* 93:404-414
- 553 Fernandes AM, Soratto RP, Gonsales JR (2014) Root morphology and phosphorus uptake by potato
554 cultivars grown under deficient and sufficient phosphorus supply. *Sci Hortic* 180:190-198
- 555 Fernandes AM, Soratto RP, Pilon C (2015) Soil phosphorus increases dry matter and nutrient accumulation
556 and allocation in potato cultivars. *Am J Potato Res* 92: 117-127
- 557 Fernandez-Pozo N, Menda N, Edwards JD, Saha S, Teclé IY, Strickler SR, Bombarely A, Fisher-York T,
558 Pujar A, Foerster H, Yan AM, Mueller LA (2015) The Sol Genomics Network (SGN) - from
559 genotype to phenotype to breeding. *Nucleic Acids Res* 43:D1036-D1041.
- 560 Fixen PE, Bruulsema TW (2014) Potato management challenges created by phosphorus chemistry and
561 plant roots. *Am J Potato Res* 91:121-131
- 562 Freeman KL, Franz PR, de Jong RW (1998) Effect of phosphorus on the yield, quality and petiolar
563 phosphorus concentrations of potatoes (cvv. Russet Burbank and Kennebec) grown in the
564 krasnozem and duplex soils of Victoria. *Aust J Exp Agric* 38:83-93
- 565 Hailu G, Nigussie D, Ali M, Derbew B (2017) Nitrogen and phosphorus use efficiency in improved potato
566 (*Solanum tuberosum* L.) cultivars in southern Ethiopia. *Am J Potato Res* 94:617-631
- 567 Hammond JP, Broadley MR, White PJ, King GJ, Bowen HC, Hayden R, Meacham MC, Mead A, Overs T,
568 Spracklen WP, Greenwood DJ (2009) Shoot yield drives phosphorus use efficiency in *Brassica*
569 *oleracea* and correlates with root architecture traits. *J Exp Bot* 60:1953-1968
- 570 Harris PM (1992) Mineral nutrition. In: Harris JM (ed) *The potato crop: the scientific basis for*
571 *improvement*. Chapman and Hall, London, pp 162-213

- 572 Haverkort AJ (2007) Potato crop response to radiation and daylength. In: Vreugdenhil D (ed) Potato
573 biology and biotechnology: advances and perspectives. Elsevier, Amsterdam, pp 353-365
- 574 Hopkins BG, Horneck DA, MacGuidwin AE (2014) Improving phosphorus use efficiency through potato
575 rhizosphere modification and extension. *Am J Potato Res* 91:161-174
- 576 Iwama K (1998). Development of nodal and lateral roots in potato under field conditions. *J Fac Agric*
577 *Hokkaido Univ* 68:33-44
- 578 Iwama K (2008) Physiology of the potato: New insights into root system and repercussions for crop
579 management. *Potato Res* 51:333-353
- 580 Iwama K, Nishibe S (1989) Comparison of root characters among cultivated potatoes (*Solanum tuberosum*)
581 and their wild relatives. *Jpn J Crop Sci* 58:126-132
- 582 Iwama K, Nakaseko K, Isoda A, Gotoh K, Nishibe Y (1981a) Relations between root system and tuber
583 yield in the hybrid population of the potato plants. *Jpn J Crop Sci* 50:233-238
- 584 Iwama K, Nakaseko K, Isoda A, Gotoh K, Nishibe Y (1981b) Comparison of root systems among hybrid
585 populations derived from different crosses in potato (*Solanum tuberosum*). *Jpn J Crop Sci* 50:365-
586 372
- 587 Iwama K, Hasegawa T, Nakaseko K (1999) New potato lines with high productivity and drought tolerance.
588 In: Proceedings of the international symposium on world food security, Kyoto, Japan, pp 189-193
- 589 Jefferies RA (1993) Cultivar responses to water stress in potato: effects of shoot and roots. *New Phytol*
590 123:491-498
- 591 Jenkins PD, Ali H (1999) Growth of potato cultivars in response to phosphate fertiliser. *Ann Appl Biol*
592 135:431-438
- 593 Johnston AE, Lane PW, Mattingley GEG, Poulton PR, Hewitt MV (1986) Effects of soil and fertilizer P on
594 yields of potatoes, sugar beet, barley and winter wheat on a sandy clay loam soil at Saxmundham,
595 Suffolk. *J Agric Sci* 106:155-167
- 596 Kärenlampi SO, White PJ. 2009. Potato proteins, lipids and minerals. In: Singh J, Kaur L (eds) Advances in
597 potato chemistry and technology. Academic Press, London pp 99-126
- 598 Kolbe H, Stephan-Beckmann S (1997a) Development, growth and chemical composition of the potato crop
599 (*Solanum tuberosum* L.). I. Leaf and stem. *Potato Res* 40:111-129
- 600 Kolbe H, Stephan-Beckmann S (1997b) Development, growth and chemical composition of the potato crop
601 (*Solanum tuberosum* L.). II. Tuber and whole plant. *Potato Res* 40:135-153
- 602 Kratzke MG, Palta JP (1992) Variations in stolon length and in incidence of tuber roots among eight potato
603 cultivars. *Am Potato J* 69:561-570
- 604 Lahlou O, Ledent J-F (2005) Root mass and depth, stolons and roots formed on stolons in four cultivars of
605 potato under water stress. *Eur J Agron* 22:159-173
- 606 Lee WC, Liu G, Alva AK (2013) Potato cultivar evaluation for phosphorus-use efficiency. *J Crop Improv*
607 27:617-626

- 608 Leonel M, do Carmo EL, Fernandes AM, Soratto RP, Eburneo JAM, Garcia EL, dos Santos TPR (2017)
609 Chemical composition of potato tubers: the effect of cultivars and growth conditions. J Food Sci
610 Technol 54:2372-2378
- 611 Lombardo S, Pandino G, Mauromicale G. 2014. The mineral profile in organically and conventionally
612 grown “early” crop potato tubers. Sci Hortic 167:169-173
- 613 MacKerron DKL, Peng ZY. 1989. Genotypic comparisons of potato root growth and yield response to
614 drought. Asp of Appl Biol 22:199-206
- 615 Manorama K, Govindakrishnan P, Lal SS (2017) Phosphorus efficient potato cultivars for Nilgiris. Indian J
616 Hortic 74:618-622
- 617 McCord PH, Sosinski BR, Haynes KG, Clough ME, Yencho GC (2011) Linkage mapping and QTL
618 analysis of agronomic traits in tetraploid potato (*Solanum tuberosum* subsp. *tuberosum*). Crop Sci
619 51:771-785
- 620 Nyiraneza J, Bizimungu B, Messiga AJ, Fuller KD, Fillmore SAE, Jiang Y (2017) Potato yield and
621 phosphorus use efficiency of two new potato cultivars in New Brunswick, Canada. Can J Plant Sci
622 97:784-795
- 623 O’Brien PJ, Allen EJ, Firman DM (1998) A review of some studies into tuber initiation in potato (*Solanum*
624 *tuberosum*) crops. J Agric Sci 130:251-270
- 625 Olsen SR, Cole CV, Watanabe FS, Dean LA (1954) USDA Circular 939. Estimation of available
626 phosphorus in soil by extraction with sodium bicarbonate. US Government Printing Office,
627 Washington
- 628 Opena GB, Porter GA (1999) Soil management and supplemental irrigation effects on potato: II. Root
629 growth. Agron J 91:426-431
- 630 Puértolas J, Ballester C, Elphinstone ED, Dodd IC (2014) Two potato (*Solanum tuberosum*) varieties differ
631 in drought tolerance due to differences in root growth at depth. Funct Plant Biol 41:1107-1118
- 632 Randhawa KS, Sandhu KS, Kaur G, Singh D (1984) Studies of the evaluation of different genotypes of
633 potato (*Solanum tuberosum* L.) for yield and mineral contents. Qual Plant 34:239-242
- 634 Rasband WS (2014) ImageJ. US National Institutes of Health, Bethesda. <http://imagej.nih.gov/ij/>
- 635 Ruark MD, Kelling KA, Good LW (2014) Environmental concerns of phosphorus management in potato
636 production. Am J Potato Res 91:132-144
- 637 Sandaña P (2016) Phosphorus uptake and utilization efficiency in response to potato genotype and
638 phosphorus availability. Eur J Agron 76:95-106
- 639 Sandaña P, Kalazich J (2015) Ecophysiological determinants of tuber yield as affected by potato genotype
640 and phosphorus availability. Field Crops Res 180:21-28
- 641 Sattelmacher B, Kuene R, Malagamba P, Moreno U (1990) Evaluation of tuber bearing *Solanum* species
642 belonging to different ploidy levels for its yielding potential at low soil fertility. Plant Soil
643 129:227-233

- 644 Soratto RP, Fernandes AM (2016) Phosphorus effects on biomass accumulation and nutrient uptake and
645 removal in two potato cultivars. *Agron J* 108:1225-1236
- 646 Soratto RP, Pilon C, Fernandes AM, Moreno LA (2015) Phosphorus uptake, use efficiency, and response of
647 potato cultivars to phosphorus levels. *Potato Res* 58:121-134
- 648 Stalham MA, Allen EJ (2001) Effect of variety, irrigation regime and planting date on depth, rate, duration
649 and density of root growth in the potato (*Solanum tuberosum*) crop. *J Agric Sci* 137:251-270
- 650 Steckel JRA, Gray D (1979) Drought tolerance in potatoes. *J Agric Sci* 92:375-381
- 651 Subramanian NK, White PJ, Broadley MR, Ramsay G (2011) The three-dimensional distribution of
652 minerals in potato tubers. *Ann Bot* 107: 681-691
- 653 Syers JK, Johnston AE, Curtin D (2008) FAO fertilizer and plant nutrition bulletin 18. Efficiency of soil
654 and fertilizer phosphorus use. Food and Agriculture Organization of the United Nations, Rome
- 655 Tekalign T, Hammes PS (2005) Growth and productivity of potato as influenced by cultivar and
656 reproductive growth. II. Growth analysis, tuber yield and quality. *Sci Hortic* 105:29-44
- 657 Thornton MK, Novy RG, Stark JC (2014) Improving phosphorus use efficiency in the future. *Am J Potato*
658 *Res* 91:175-179
- 659 Trehan SP, Sharma RC (2003) External phosphorus requirement of different potato (*Solanum tuberosum*)
660 cultivars resulting from different internal requirements and uptake efficiencies. *Indian J Agric Sci*
661 73:54-56
- 662 Trehan SP, Sharma RC. 2005. Differences in phosphorus use efficiency in potato genotypes. *Adv Hortic*
663 *Sci* 19:13-20
- 664 Trehan SP, Singh BP (2013) Nutrient efficiency of different crop species and potato varieties - in retrospect
665 and prospect. *Potato J* 40:1-21
- 666 Van Loon CD (1986) Drought, a major constraint in potato production and possibilities for screening for
667 drought resistance. In: Beekman AGB et al. (Eds) *Potato research of tomorrow*. Pudoc,
668 Wageningen, pp 5-16
- 669 White PJ (2018) Improving nutrient management in potato cultivation. In: Wale S (ed) *Achieving*
670 *sustainable cultivation of potatoes*. Vol. 2: Production and storage, crop protection and
671 sustainability. Burleigh Dodds, Cambridge, in press.
- 672 White PJ, Hammond JP (2008) Phosphorus nutrition of terrestrial plants. In: White PJ, Hammond JP (eds)
673 *The ecophysiology of plant-phosphorus interactions*. Springer, Dordrecht, pp 51-81
- 674 White PJ, Broadley MR, Greenwood DJ, Hammond JP (2005a) Proceedings of The International Fertiliser
675 Society 568. Genetic modifications to improve phosphorus acquisition by roots. International
676 Fertiliser Society, York
- 677 White PJ, Broadley MR, Hammond JP, Thompson AJ (2005b) Optimising the potato root system for
678 phosphorus and water acquisition in low-input growing systems. *Asp Appl Biol* 73:111-118
- 679 White PJ, Wheatley RE, Hammond JP, Zhang K (2007) Minerals, soils and roots. In: Vreugdenhil D (ed)
680 *Potato biology and biotechnology: advances and perspectives*. Elsevier, Amsterdam, pp 739-752

- 681 White PJ, Bradshaw JE, Dale MFB, Ramsay G, Hammond JP, Broadley MR (2009) Relationships between
682 yield and mineral concentrations in potato tubers. *HortScience* 44:6-11
- 683 White PJ, Broadley MR, Hammond JP, Ramsay G, Subramanian NK, Thompson J, Wright G (2012)
684 Biofortification of potato tubers using foliar zinc-fertilisers. *J Hortic Sci Biotechnol* 87:123-129
- 685 White PJ, George TS, Gregory PJ, Bengough AG, Hallett PD, McKenzie BM (2013) Matching roots to
686 their environment. *Ann Bot* 112:207-222
- 687 Wishart J, George TS, Brown LK, Ramsay G, Bradshaw JE, White PJ, Gregory PJ (2013) Measuring
688 variation in potato roots in both field and glasshouse: the search for useful yield predictors and a
689 simple screen for root traits. *Plant Soil* 368:231-249
- 690 Wishart J, George TS, Brown LK, White PJ, Ramsay G, Jones HG, Gregory PJ (2014) Field phenotyping
691 of potato to assess root and shoot characteristics associated with drought tolerance. *Plant Soil*
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 $[P]_{\text{leaf}}$ of plants grown without P-fertiliser application and $[P]_{\text{leaf}}$ 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.
704

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

712 **Fig. 3** The relationship between root mass and shoot mass of eight Tuberosum genotypes three weeks after
713 emergence (Harvest 1). Data show means of four individual plants grown with (closed circles) or without
714 (open circles) P-fertiliser application. Linear regression of all data yielded $y = 8.871x - 14.01$ ($R^2=0.7499$,
715 $P<0.0001$, $n=16$).
716

717 **Fig. 4** The relationship between root mass of eight Tuberosum genotypes three weeks after emergence
718 (Harvest 1) and the days after crop emergence to reach 50% canopy closure. Data show means of four
719 individual plants grown with (closed circles) or without (open circles) P-fertiliser application. Linear
720 regression of all data yielded $y = 44.09x - 1.806$ ($R^2=0.6128$, $P=0.0003$, $n=16$).
721

722 **Fig. 5** Relationships between the root DWs at establishment (Harvest 1) of eight Tuberosum genotypes and
723 their P content at establishment (Harvest 1), close to canopy closure (Harvest 3) and at final harvest
724 (Harvest 6). Data for root DWs are means of four individual plants and data for plant P content are means
725 of two replicate plots of five plants cultivated with (closed symbols) or without (open symbols) P-fertiliser
726 application. Regression lines were $y = 0.1411x - 0.1230$ ($R^2=0.8098$, $P<0.0001$, $n=16$, Harvest 1), $y =$
727 $0.201x + 1.4243$ ($R^2=0.4419$, $P=0.0050$, $n=16$, Harvest 3), and $y = 0.0778x + 3.8214$ ($R^2=0.0393$,
728 $P=0.4615$, $n=16$, Harvest 6).
729

730 **Fig. 6** The accumulation of (a) shoot mass, (b) tuber mass in the Tuberosum genotype 'Stirling'. Data are
731 shown as individual plots of five plants grown with (closed circles) or without (open circles) P-fertiliser

732 application. Plants were harvested at establishment (Harvest 1), when the canopy had approximately 50%
733 ground cover (Harvest 2), close to canopy closure (Harvest 3), mid-canopy duration (Harvest 4), when the
734 canopy had begun to sag (Harvest 5), and two weeks after canopy sagging at final harvest (Harvest 6).

735

736 **Fig. 7** Relationships between the root DWs at establishment (Harvest 1) of eight *Tuberosum* genotypes and
737 their tuber DWs when the canopy had approximately 50% ground cover (Harvest 2), when the canopy had
738 full ground cover (Harvest 4) and at final harvest (Harvest 6). Data for root DWs are means of four
739 individual plants and data for tuber DWs are means of two replicate plots of five plants cultivated with
740 (closed symbols) or without (open symbols) P-fertiliser application. Regression lines were $y = 0.052x -$
741 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
742 4) and $y = 0.0176x + 2.6293$ ($R^2=0.0059$, $P=0.7766$, $n=16$, Harvest 6).

743

744 **Fig. 8** The accumulation of phosphorus in (a) shoots and (b) tubers, and the P concentrations in shoots (c)
745 and tubers (d) of the *Tuberosum* genotype 'Stirling'. Data are shown from individual plots of five plants
746 cultivated with (closed circles) or without (open circles) P-fertiliser application. Plants were harvested at
747 establishment (Harvest 1), when the canopy had approximately 50% ground cover (Harvest 2), close to
748 canopy closure (Harvest 3), mid-canopy duration (Harvest 4), when the canopy had begun to sag (Harvest
749 5), and two weeks after canopy sagging at final harvest (Harvest 6).

750

751 **Fig. 9** The relationships between tuber DW yield (kg plot^{-1}) and (a) yield divided by plant P content (PUtE)
752 or (b) plant P content (PUpE) for eight *Tuberosum* genotypes grown in the field with (closed symbols) or
753 without (open symbols) P-fertiliser application. Data are means of 2 plots, each containing 5 plants. Linear
754 regression of all data presented in panel (a) yielded $y = 3.411 - 0.4254x$ ($R^2=0.0255$, $P=0.5550$, $n=16$).
755 Linear regression of all data presented in panel (b) yielded $y = 0.7208 + 0.4684x$ ($R^2=0.6506$, $P=0.0002$,
756 $n=16$).

757

Table 1. Yields per plot of eight 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 PUpE, for genotypes cultivated in Experiment 1. Data are expressed as mean ± SE either for n years (for individual genotypes) or for n genotypes present in all years of Experiment 1 (2006, 2007, 2008).

Genotype	Group	Tuber yield (kg FW plot ⁻¹)			[P] _{leaf} (mg g ⁻¹ DM)			[P] _{tuber} (mg g ⁻¹ DM)			Yield*[P] _{leaf}		
		mean	SE	n	mean	SE	n	mean	SE	n	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	1.71		1			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

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)		Yield (low P) (kg FW plot ⁻¹)		Yield loss (%)		[P] _{leaf} (high P) (mg g ⁻¹ DM)		[P] _{leaf} (low P) (mg g ⁻¹ DM)		[P] _{tuber} (high P) (mg g ⁻¹ DM)		[P] _{tuber} (low P) (mg g ⁻¹ DM)		Yield*[P] _{leaf} (high P)		Yield*[P] _{leaf} (low P)	
			mean	SE	mean	SE	mean	SE	mean	SE	mean	SE	mean	SE	mean	SE	mean	SE	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

Figure 1

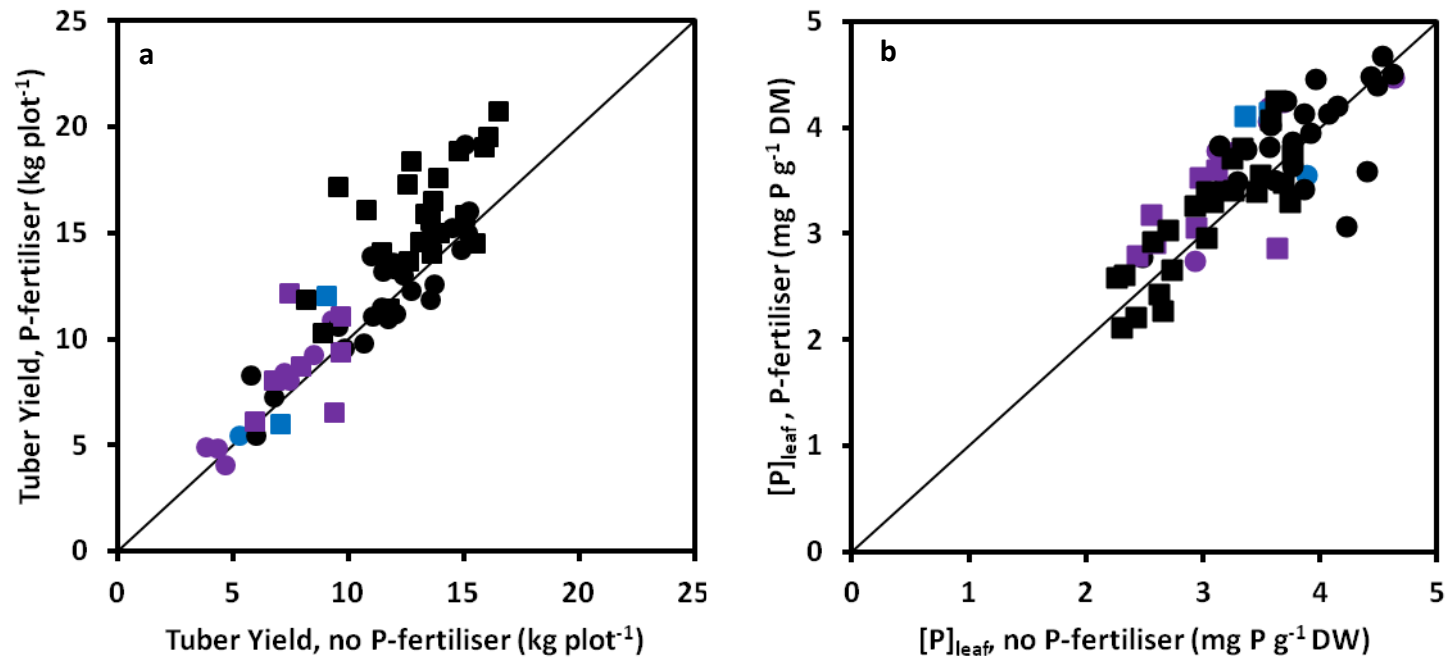


Figure 2

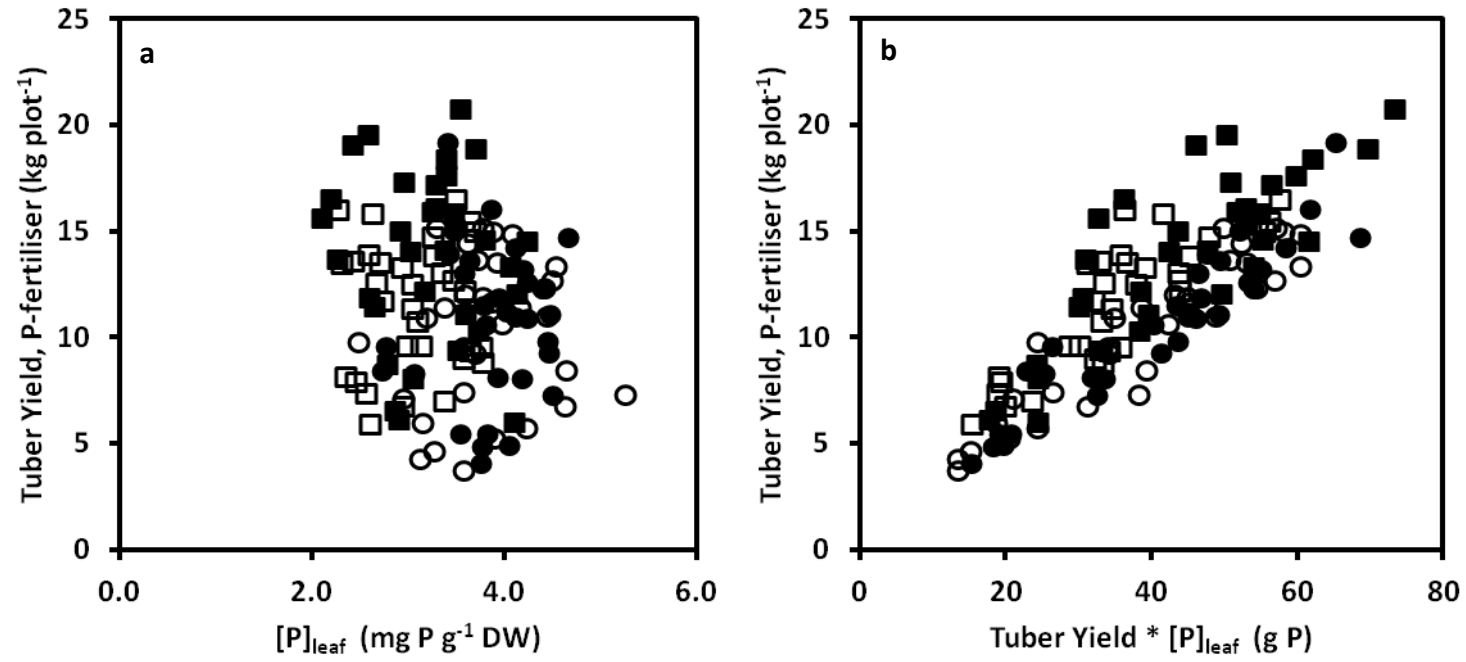


Figure 3

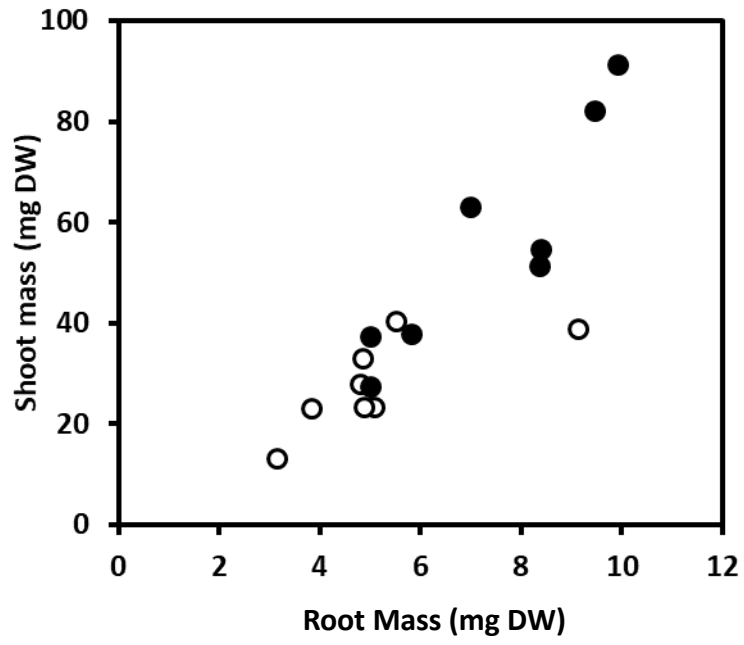


Figure 4

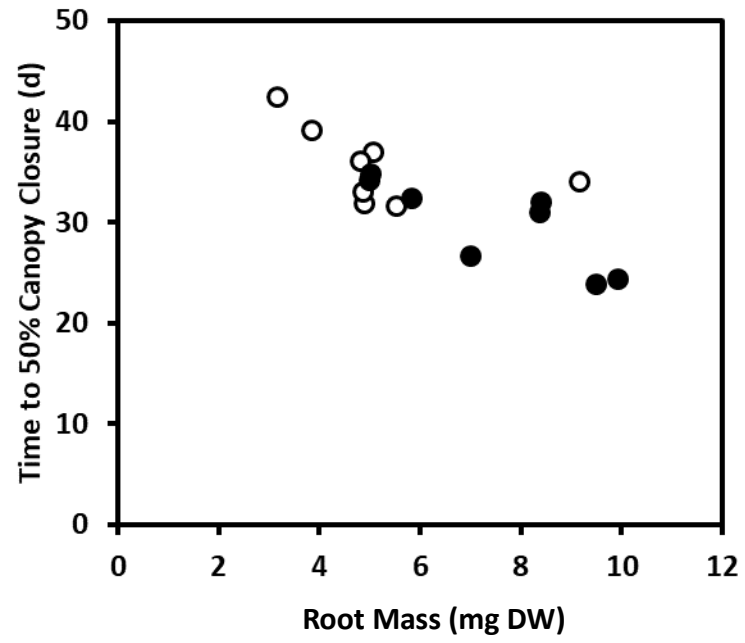


Figure 5

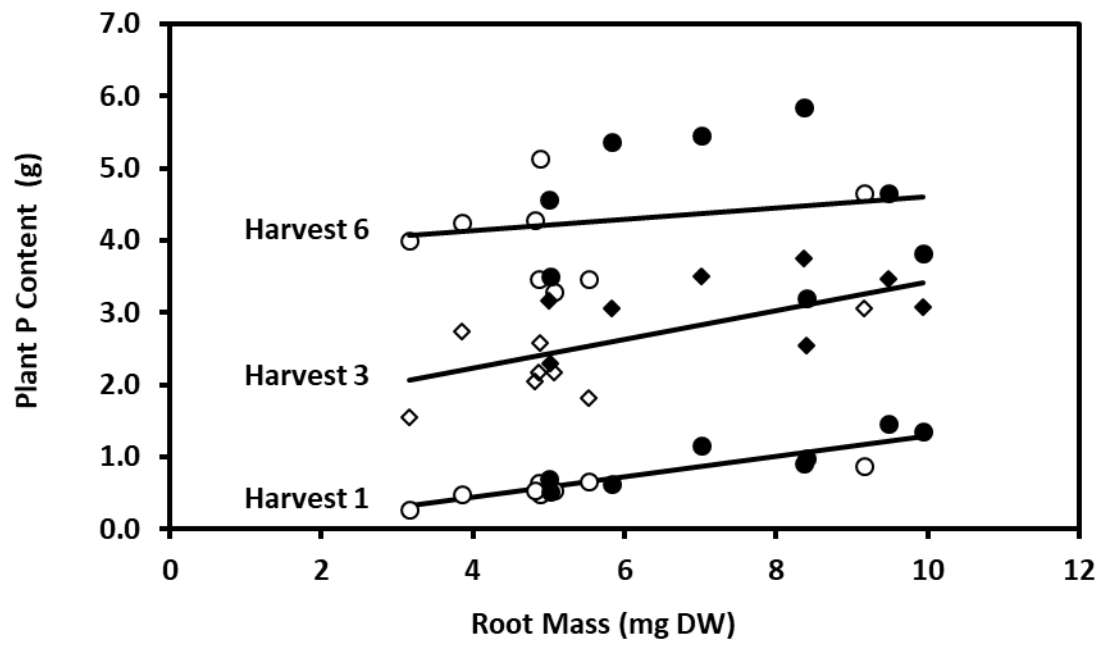


Figure 6

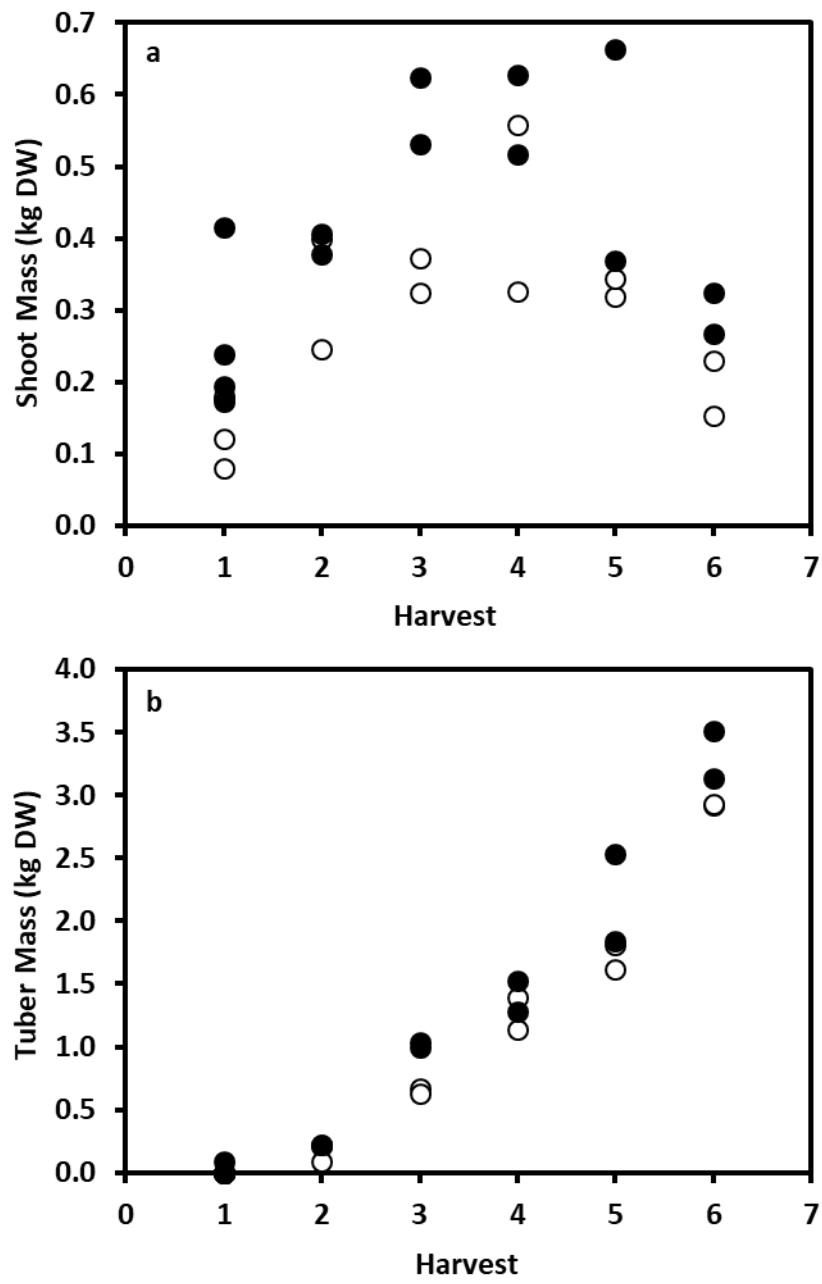


Figure 7

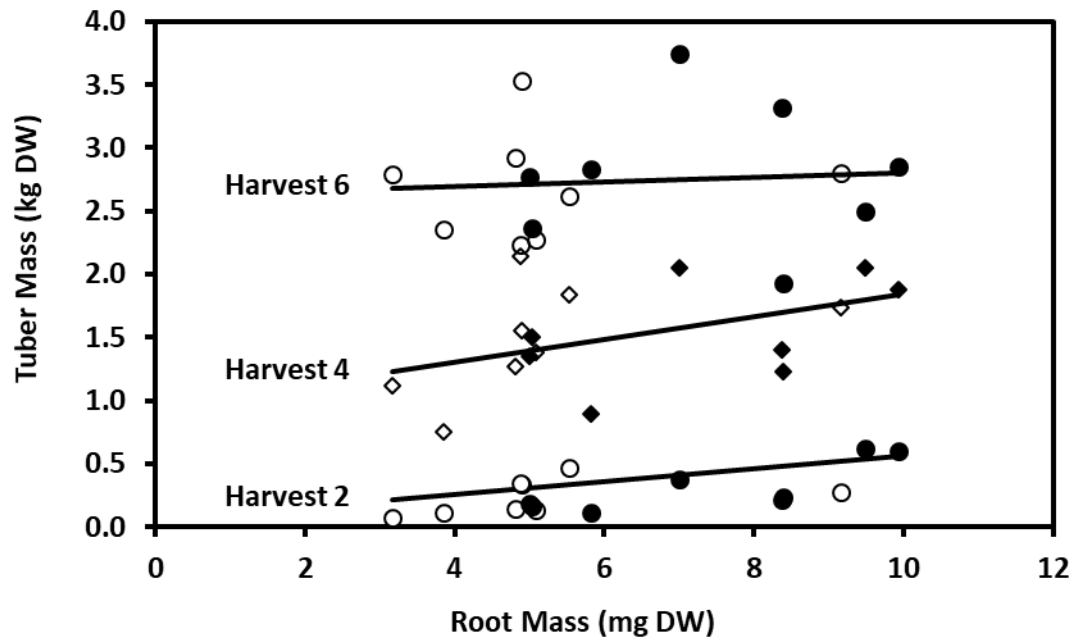


Figure 8

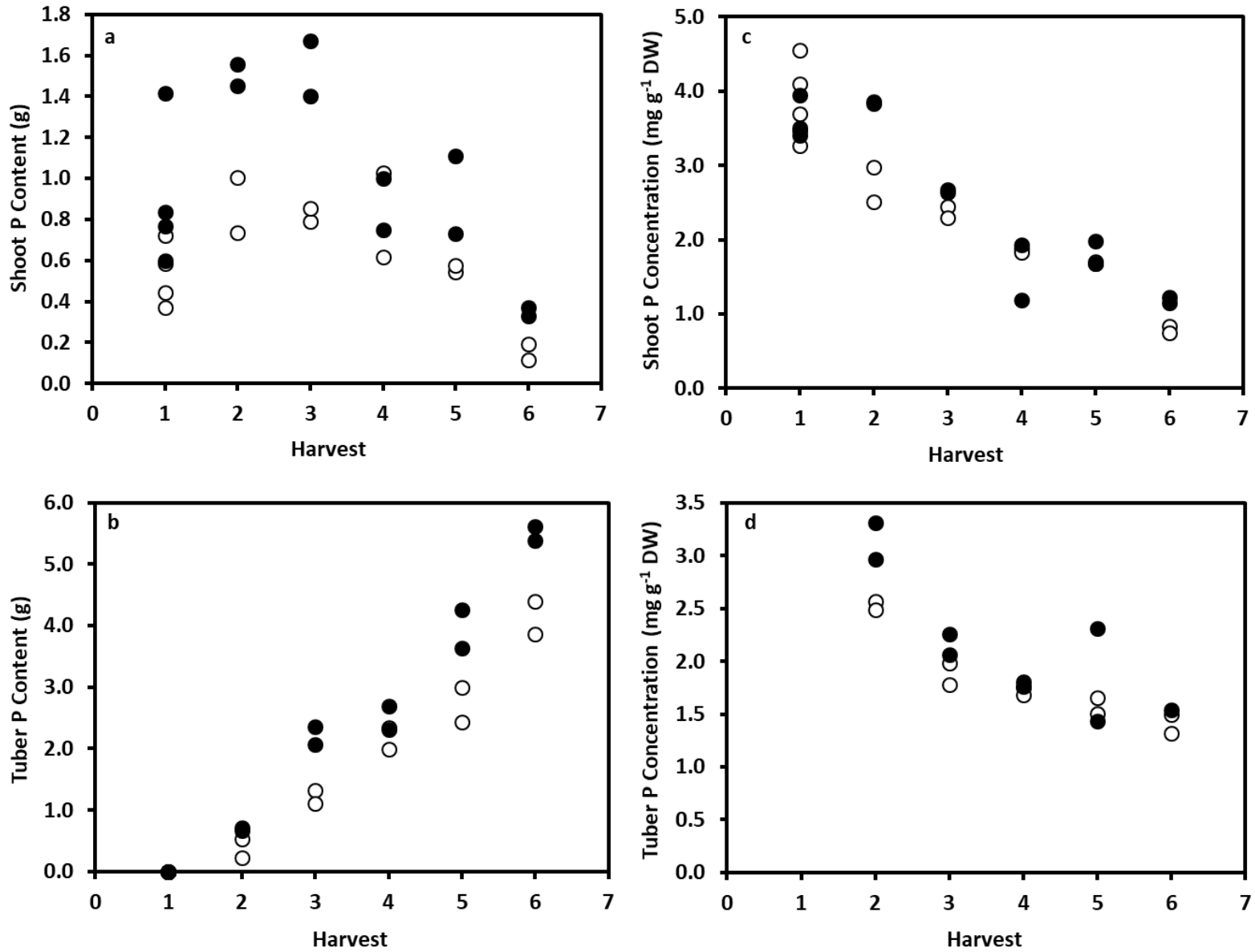


Figure 9

