

Scotland's Rural College

Variation in light interception traits in European spring barley landraces

Florence, A; Ennos, RA; Hoad, SP; Hoebe, PN

Published in:
Field Crops Research

DOI:
[10.1016/j.fcr.2019.06.006](https://doi.org/10.1016/j.fcr.2019.06.006)

Print publication: 01/09/2019

Document Version
Peer reviewed version

[Link to publication](#)

Citation for published version (APA):
Florence, A., Ennos, RA., Hoad, SP., & Hoebe, PN. (2019). Variation in light interception traits in European spring barley landraces. *Field Crops Research*, 241, [107549]. <https://doi.org/10.1016/j.fcr.2019.06.006>

General rights

Copyright and moral rights for the publications made accessible in the public portal are retained by the authors and/or other copyright owners and it is a condition of accessing publications that users recognise and abide by the legal requirements associated with these rights.

- Users may download and print one copy of any publication from the public portal for the purpose of private study or research.
- You may not further distribute the material or use it for any profit-making activity or commercial gain
- You may freely distribute the URL identifying the publication in the public portal ?

Take down policy

If you believe that this document breaches copyright please contact us providing details, and we will remove access to the work immediately and investigate your claim.

1 **Title:**

2 **Variation in light interception traits in European spring barley landraces**

3 **Authors:**

4 **Anna Florence^{*a}, Richard A. Ennos^b, Steve P. Hoad^a, Peter N. Høebe^a**

5 a Crop and Soil Systems Group, SRUC, West Mains Road, Edinburgh, EH9 3JG, UK

6 b Institute of Evolutionary Biology, School of Biological Sciences, Ashworth Laboratories, University of
7 Edinburgh, Edinburgh EH9 3JT, UK

8 *- corresponding author

9 **Corresponding author:**

10 Anna Florence (Anna.Florence@sruc.ac.uk)

11 **Funding Information:**

12 This work was supported by funding from the Scottish Government's Rural and Environmental Science
13 and Analytical Services (RESAS) division, with support to Anna Florence through a PhD studentship.

14 **Declaration:**

15 Authors have no competing interests to declare

16

17 **Abstract**

18 Improving the efficiency of photosynthesis is a potential strategy for increasing crop yields in the
19 future, but this is only possible if genetic variation exists for this attribute within crop germplasm
20 resources. A key component of photosynthetic efficiency is the plant's ability to intercept light. This
21 study examined the extent of genetic variation, available within barley landraces from Europe, for
22 parameters affecting light interception. Landraces varied in time spent between emergence and full
23 canopy establishment, with those from Northern latitudes reaching canopy closure between 2 and 8
24 days faster than those from Southern latitudes. There was significant variation in leaf chlorophyll
25 content between the landraces, but this was unrelated to site of origin. Landraces originating from
26 locations with cooler temperature over the growing season held their leaves in a more planophile
27 manner than those from warmer climates, resulting in a negative relationship between leaf angle and
28 mean temperature at site of origin. We conclude that substantial genetic variation in key parameters
29 affecting light interception have evolved among barley landraces in Europe that could be utilised in
30 future breeding programmes to improve the efficiency of photosynthesis and increase crop yields.

31 **Keywords:**

32 Photosynthesis; Landraces; Light Interception, Canopy Structure, Local Adaptation

33

34 1. Introduction

35 Cereal yield increases over the past century have mainly come about from improved harvest index
36 (HI), fertiliser responsiveness and increased arable land area (Evans, 1997; Fischer and Edmeades,
37 2010; Reynolds et al., 2011, 2009). Yields are now stagnating in many areas of the world in staple crops
38 such as wheat, maize and rice (Mackay et al., 2011; Ray et al., 2012). With potential arable area
39 reaching a limit due to increasing pressure for land use, new avenues for increasing yield must come
40 from increasing production per unit area of ground (Long et al., 2015; Zhu et al., 2010). Most modern
41 cereal breeding programs are derived from a small number of parent plants. Within these breeding
42 programmes there may not be sufficient genetic variation present to exploit novel traits for increasing
43 yield. Breeders may therefore need to look more widely to identify sources of suitable variation.

44 This situation is well illustrated by barley (*Hordeum vulgare* L.), one of the founding crops of modern
45 agriculture, with major uses in Europe including malt and animal feed. It is widely grown in Scotland
46 with 1.39million tonnes of spring barley and 268,124 tonnes of winter barley produced in 2018 (The
47 Scottish Government, 2018). Barley landraces represent a possible source of genetic variation that
48 could be used for improving traits related to yield (Rodriguez et al., 2008; Villa et al., 2005). A landrace
49 is defined as a 'heterogeneous (genetically and phenotypically variable) variety that is reproduced by
50 farmers as populations that are subject to both artificial and natural selection' (Bellucci et al., 2013).
51 In some marginal areas landraces have been seen to outperform conventional cultivars (Dwivedi et
52 al., 2016; Yahiaoui et al., 2014) as they can be locally adapted to climatic conditions (Bellucci et al.,
53 2013). Landraces have already been used successfully to introduce traits into maize and rice that have
54 increased yield under drought and submergence conditions respectively (Bailey-Serres et al., 2010;
55 Meseka et al., 2015, 2013; Xu and Mackill, 1996).

56 Yield formation can be summarised in an equation first proposed by Monteith (Monteith and Moss,
57 1977):

58
$$Y = 0.487 \cdot S_t \cdot \epsilon_i \cdot \epsilon_c \cdot \epsilon_p$$

59 Where Y is yield, S_t is the total amount of incident solar radiation with 0.487 being the fraction which
60 is photosynthetically active, ϵ_i the efficiency of the plant in intercepting the fraction of
61 photosynthetically active radiation, ϵ_c the efficiency of the photosynthetic processes converting light
62 to energy and ϵ_p the proportion of energy produced which is partitioned into harvestable product.
63 Whilst ϵ_p has largely been optimised there is still potential to improve ϵ_i and ϵ_c through optimisation
64 of light interception and photosynthetic reactions (Farquhar et al., 2001; Raines, 2011). Rate of canopy
65 development, amount and arrangement of chlorophyll and the leaf canopy architecture are all
66 characters which can contribute towards ϵ_i which may be targets for optimisation.

67 The rate of canopy development is one of the major factors affecting ϵ_i (Flood et al., 2011; Long et al.,
68 2006; Nunes-Nesi et al., 2016). Early and rapid canopy establishment can allow crops to take
69 advantage of shorter growing seasons in Northern latitudes where the greatest amount of radiation
70 is available in early spring (Murchie et al., 2009; Parry et al., 2011; Richards, 2000; Zhu et al., 2010).
71 Extending the duration of canopy maintenance with slower loss of chlorophyll content during the grain
72 filling phase in 'Stay-green' varieties is associated with an increase in grain weight in barley, maize and
73 wheat and can lead to increased yields (Diaz et al., 2005; Emebiri, 2013; Parry et al., 2011; Zheng et
74 al., 2009).

75 The chlorophyll arrangement throughout the canopy will also affect the ϵ_i as canopy with a more even
76 distribution of chlorophyll throughout the leaf layers along with a greater total volume of chlorophyll
77 may increase total light captured by reducing the number of leaves becoming saturated in the upper
78 layers of the canopy (Ort et al., 2011; Yin and Struik, 2015). Saturation of upper leaf layers is a limiting
79 factor in light interception as the electron transport systems fall at relatively low light levels (Björkman
80 and Demmig, 1987). A horizontal leaf arrangement leads to saturation of the upper canopy whereas
81 a canopy with an upper leaf angle of 75° from the horizontal can have double the efficiency of energy

82 capture of a horizontal canopy at midday (Long et al., 2006). Leaf size also affects light interception
83 and there is a trade-off between leaf size and self-shading (Amanullah et al., 2007; Long et al., 2006).
84 The primary aim of this study was to assess a collection of European spring barley landraces for
85 variation in traits associated with light interception efficiency including the timing of canopy
86 development, chlorophyll content and arrangement, leaf canopy architecture and HI. The secondary
87 aim of the study was to relate any variation found in light interception traits to environmental
88 conditions from the locations which the landraces originated in order to understand the factors that
89 may have led to their local adaptation. From these tests, results are put into context of how trait
90 variation can be considered for improvements in plant breeding and resilience to climate change.

91 **2. Methods**

92 **2.1 Seed source and Experimental Design**

93 The field experiment was carried out at Scotland's Rural College's Boghall farm in Midlothian,
94 Scotland, UK (55°52'26"N 3°12'26"W) in spring and summer of 2014 and 2015. The soil type at these
95 sites is a sandy loam (Macmerry Series). The farm is situated on the south-east slope of the Pentland
96 hills at an elevation of 190m and the previous crop in the fields on both years was spring barley.

97 The barley landrace material was collected from gene banks (Table 1) prior to the start of this project
98 and the landraces were specifically chosen to represent a wide latitudinal range across Europe which
99 encompasses a spread of different climatic conditions and season lengths. The latitude and longitude
100 of their original collection was used for collection of climatic data (Table 2). The landraces were a
101 mixture of 2 and 6 row types dependent on the number of rows of seeds present on each ear. The
102 modern cultivar Concerto was included to represent modern pedigree bred germplasm as a
103 comparison to the landraces and was included as it was the main variety in Scotland during the
104 experimental years.

105 The experimental design was a fully randomised, blocked design with three blocks in 2014 and four in
106 2015 and twelve plots per block(Plots measured 0.5m²). Four replicate plants per plot were used as
107 technical replicates. Plots were sown on 09/04/14 and 23/04/15 and each plot was treated with
108 120kg/hectare of nitrogen by hand with 60kg applied on 26/04/14 and 25/04/15 for respective years
109 and an additional 60kg two weeks after the first application. An herbicide treatment was applied
110 when the plants reached GS23 (Harmony 70g/ha + Oxytril 0.5L/ha + High load micra.m 1.0L/ha).

111 **2.2 Climate**

112 The climate in the location of original collection for each of the landraces was included as a possible
113 factor influencing the canopy structure. Climate data were obtained from the national meteorological
114 offices in each country of origin (Table 2). The area over which the weather data was collected varies
115 between countries from local weather data to regional data depending on the scale of reporting. It
116 was always taken as the closest reported point to the latitude and longitude of origin of the landraces.
117 The climatic variables reported are the total rainfall (mm) for spring/summer, the total number of
118 sunlight hours for spring/summer and the average daily temperature (°C) for spring/summer. The data
119 are long-term averages with FRA1, FIN1, BRI1 and SPN1 (Table 2) being from 1981-2010. GER2, NOR1,
120 NOR2, CZE1 and GER3 and from 1961-1991 and ITA1 (Table 2) is from 1971-2000.

121 **2.3 Crop Measurements**

122 **2.3.1 Canopy establishment**

123 The Growth Stage (GS) of the plants were recorded weekly throughout the growth season and was
124 assessed using the HGCA (AHDB) growth stage guide which is based on the Zadoks 100 point growth
125 scale (HGCA (The Scottish Executive), 2006; Zadoks et al., 1974). The plot was deemed to have reached
126 a specific growth stage when at least 50% of the plants in the plot had reached that growth stage.
127 Additional, in depth, assessment of four replicate plants per block of the canopy structure including
128 leaf angle, length and chlorophyll content (by proxy with SPAD readings) were measured at GS24,
129 GS39 and GS59. At GS24 the plant is made up of the main shoot and four tillers and is in the

130 establishment phase of its lifecycle. By GS39 stem extension is underway and the flag leaf is fully
131 emerged meaning that canopy establishment is complete. At GS59 the ear has fully emerged from the
132 boot and the plant has progressed from vegetative growth to reproductive growth.

133 **2.3.2 Chlorophyll content, Distribution and Leaf Dimensions**

134 The leaf chlorophyll content was assessed by proxy using of a SPAD meter (Minolta Corp, Ramsay, NJ).
135 SPAD readings were taken on the uppermost leaf excluding the flag leaf on a weekly basis midway
136 along the length of the leaf blade. SPAD readings at GS39 and 59 are reported here.

137 Leaf area was measured by detaching the leaves where they meet the stem and immediately passing
138 them through a leaf area meter (Li-3100 are meter, LiCor Inc., Lincoln, NE) which calculated leaf area
139 in cm². Leaves were passed through the meter three times and the readings averaged. The leaves that
140 had been used for leaf area measures were then placed in individual paper bags and dried in an oven
141 (Ecocell, MMM Medcenter, Munich, Germany) at 80°C for 48 hours. The leaves were then weighed
142 using a precision balance (Kern PLJ, D-72336, Kern & Sohn Gontbl, Balingen, Germany) in grams. The
143 specific leaf area (SLA) was calculated as leaf area divided by leaf dry weight. The leaf area, dry weight
144 and SLA were all measured at GS39 on the uppermost leaf excluding the flag leaf.

145 **2.3.3 Leaf canopy architecture**

146 Leaf angle was measured at GS39 and 59 in relation to the stem directly above it using a Helix Oxford
147 protractor (Maped Helix, West Midlands, UK) to the nearest 5⁰. Care was taken to avoid bending the
148 leaf away from the stem by minimising handling prior to this measure being taken.

149 **2.3.4 Allocation of resources**

150 Harvest took place on 12/08/14 and 04/09/15. The ears on the shoots used for the earlier structural
151 measurements were individually hand threshed and the grain number, row count and grain weight
152 recorded and the 1000grain weight calculated. Grain weight was measured using a precision balance

153 (Kern PLJ, D-72336, Kern & Sohn Gontbl, Balingen, Germany). The ear and the straw were harvested
154 to allow calculation of harvest index. The straw was dried in an oven (EcoCell, MMM Medcenter,
155 Munich, Germany) at 80°C for 48 hours and weighed using a precision balance (Kern PLJ, D-72336,
156 Kern & Sohn Gontbl, Balingen, Germany). Harvest index was then calculated by dividing the grain
157 weight by the combined weight of the grain plus the straw plus the chaff. A total yield in tonnes per
158 hectare was not calculated for the lines as the experimental design limited the amount of material
159 that could be collected for each plot.

160 **2.4 Statistical Analysis**

161 We used an Analysis of Variance (ANOVA) model to determine whether there was a significant amount
162 of variation among the landraces in each trait of interest at a significance level of $p=0.05$. Year was
163 included as a factor to see if differences between the two years of the trial were present and if there
164 was an interaction between the year of the trial and variation between the landraces in the trait of
165 interest. The results of the ANOVA are reported as the test statistic F-value to show the ratio of
166 between to within group variability with the degrees of freedom as a subscript followed by the p-
167 value. Effects of year of the trial are also reported if significant. Regression analysis of climate and
168 latitude with each measure of canopy structure was carried out to see if there was a relationship
169 between traits and local climatic conditions of each landrace line. A multiple regression of leaf angle
170 with latitude and temperature was used to examine if both factors regressed significantly with leaf
171 angle. The linear regression of leaf angle with temperature is reported below as this was the significant
172 factor. Results of the regression are reported as the test statistic t-value to show if the slope of the
173 regression is significantly different from zero with the upper degree of freedom as a subscript followed
174 by the p-value which is taken as significant at a level of $p=0.05$. In the regression analysis year was
175 included in a factor to see if the response differed between years and this is reported where
176 significant. All figures report an average of all data between the years. Correlation analysis was carried
177 out on allocation of resources factors to assess if relationships were present between the variables.

178 The correlation coefficient of significant relationships is given followed by the p-value. All statistical
179 analysis was carried out using GenStat 16th Edition (VSN International Ltd, Hemel Hempstead, UK).

180 **3. Results**

181 **3.1 Growing conditions in experiments**

182 In 2014 the average daily temperature at Boghall ranged from 7°C to 16°C. The average monthly
183 rainfall was 107mm and the average monthly hours of sunlight was 119 hours. In 2015 the average
184 daily temperature ranged from 5.5°C to 14.5°C. The average monthly rainfall was 130mm and the
185 average monthly hours of sunlight was 119 hours.

186 **3.2 Canopy Establishment**

187 Landraces differ significantly in their development rate between GS24 and GS39 ($F_{10,52}=9.36$, $p<0.001$)
188 (Figure 1) ranging from 12-20 days. Year was included as a factor in the analysis and there was a
189 difference between the two years of the trial ($F_{10,52}=19.78$, $p<0.001$) but there was no interaction
190 effect between the landraces and the year. GS24-GS39 is the stage in the plant leading up to full
191 canopy establishment where GS24 consists of a plant with the main shoot and four tillers. It then
192 moves through stem extension until it reached GS39 where the flag leaf is fully emerged. The length
193 of time spent between these growth stages declines significantly in length in landraces from higher
194 latitudes ($t_{20}=34.5$, $p<0.001$, $R^2=0.65$) with a significant effect when year was included as a factor
195 ($p<0.001$) in the regression analysis. The modern cultivar Concerto spent longer than the landraces to
196 reach GS24 and a similar amount of time in the canopy establishment stage between GS24 and GS39
197 to the Southern European landraces.

198 **3.3 Chlorophyll Content, Distribution and Leaf Dimensions**

199 There were significant differences in SPAD readings between the lines at all three growth stages: GS24
200 ($F_{11,57}=6.97$, $p<0.001$), GS39 ($F_{11,57}=4.45$, $p<0.001$) and GS59 ($F_{11,57}=2.07$, $p=0.037$) (Figure 2) with SPAD
201 values ranging from 32.5-43.4, 35.2-45.4 and 41.1-48.7 respectively. When year was included as a

202 factor in the ANOVA analysis it was seen that there was a significant difference between the years at
203 GS24 ($F_{1,57}=35.04$, $p<0.001$) and GS59 ($F_{1,57}=5.22$, $p=0.026$). There was no relationship between either
204 climate or latitude and leaf chlorophyll content. Concerto had higher SPAD readings than the landraces
205 at all growth stages.

206 The length of the second leaf showed significant differences between the landraces at both GS39
207 ($F_{11,57}=6.38$, $p<0.001$) and GS59 ($F_{11,57}=8.17$, $p<0.001$) (Table 3) with leaf length between 23.2-30.3 and
208 20.8-29.7cm respectively. When year of trial was included as a factor in the analysis significant
209 differences were present at both GS39 ($F_{1,57}=53.32$, $p<0.001$) and GS59 ($F_{1,57}=34.71$, $p<0.001$). There
210 were no significant differences between the landraces in SLA (Table 3).

211 **3.4 Leaf Canopy Architecture**

212 Landraces differ significantly in their leaf angle at GS39 ($F_{11,57}=10.48$, $p<0.001$) (Table 3) where the
213 final leaf of the canopy has fully emerged and GS59 ($F_{11,57}=14.74$, $p<0.001$) (Table 3) where the ear has
214 fully emerged and the plant is switching from the vegetative to reproductive phase of its lifecycle
215 (Table 3). The leaf angles from vertical range from 18-45 degrees and 31-84 degrees respectively.
216 When year of trial was included as a factor in the analysis significant effects were seen at GS39 only
217 ($F_{1,57}=14.69$, $p<0.001$). Leaf angle increases significantly with average temperature and Fig. 3 shows
218 this relationship at GS59 (which is when the ear is fully emerged and the canopy size is at its maximum)
219 ($t_{20}=28.47$, $p<0.001$, $R^2=0.56$) (Table 3) at the location of origin. The same relationship is present at the
220 earlier GS39 where the flag leaf is fully emerged ($t_{20}=12.31$, $p=0.002$, $R^2=0.35$) (Table 3). Concerto
221 fitted into the pattern of the landraces when temperature of the trial site was used as their origin
222 location.

223 **3.5 Allocation of resources**

224 The HI showed significant differences among the landraces in the 2 row lines ($F_{7,37}=23.72$, $p<0.001$).
225 The 1000 grain weight showed a significant difference between the landraces in both the 2 ($F_{7,37}=8.12$,

226 $p < 0.001$) and 6 row lines ($F_{3,17} = 7.57$, $p = 0.002$). When year was included as a factor in the analysis there
227 was a significant difference in 1000 grain weight between the years of the trial ($F_{1,37} = 4.99$, $p = 0.032$).
228 The number of grains per ear showed a significant difference between the landraces in the 2 row lines
229 ($F_{7,37} = 5.88$, $p < 0.001$) (Table 4). When year was included as a factor in the analysis there was a
230 significant difference in number of grains per ear between the years of the trial ($F_{1,37} = 48.57$, $p < 0.001$).
231 There was a significant positive correlation of number of grains per ear with 1000 grain weight with a
232 correlation coefficient of $r = 0.934$, $p = 0.001$ (Figure 4).

233 **4. Discussion**

234 The data collected in this study will allow a picture of the variation present in traits associated with
235 photosynthetic efficiency in spring barley landraces to be assessed. It will also allow the variation seen
236 to be examined for local adaptation to environmental conditions and how this variation can be
237 subsequently used in pre-breeding programs. It was found that differences in rate of canopy
238 development, chlorophyll content and canopy leaf angle all varied significantly between the landraces.
239 Canopy development rate and leaf angle both varied with climatic conditions at the location of origin
240 with shorter duration at higher latitudes and more planophile leaves at lower temperatures,
241 suggesting adaptation to local condition. The traits looked at in this study were assessed out with the
242 local climatic conditions where they originated which suggests that the variation found is under strong
243 genetic control and this could be very beneficial to breeding programs.

244 **4.1 Canopy Establishment**

245 The Scandinavian landraces progressed quickly through stem extension to canopy closure (Figure 1)
246 which would be advantageous for light interception, biomass production and grain development
247 during the early phase of a shorter growing season. There were differences in the time spent in this
248 phase of development between the years of the trial showing that the environment has an effect on
249 development rate but there were also differences between the landraces which showed genetic
250 variation is present between the lines. This has been seen in barley and other cereals including wheat
251 and oats (Goyne et al., 1993; Kemanian et al., 2004; Muurinen and Peltonen-Sainio, 2006; Peltonen-

252 Sainio, 1997). Landraces from Northern latitudes will likely contain the photoperiod non-responsive
253 polymorphism in the *Ppd-H1* gene (Jones et al., 2011; Turner et al., 2005) allowing them to move into
254 flowering irrespective of day-length. This polymorphism has been linked to leaf size caused by changes
255 in duration of leaf growth (Digel et al., 2016). Reaching full canopy establishment quicker may also be
256 an advantage in out-competing weeds, shading out possible (weed) competitors in organic systems or
257 allowing reduced herbicide application under conventional management (Sim et al. 2007; Kruk et al.
258 2006). The modern cultivar Concerto spent more time reaching GS24 than the landraces but
259 progressed from GS24-GS39 at the same rate as the landraces from Southern European latitudes
260 reaching full canopy closure later than the landraces. The early development of the Scandinavian
261 landraces may be a trait of interest in developing new varieties which are able to take advantage of
262 early light in a short growing season.

263 **4.2 Chlorophyll Content, Distribution and Leaf Dimensions**

264 During leaf emergence and through canopy closure there were differences in chlorophyll content
265 between the landraces (Figure 2). Variation has been observed in modern varieties in a study of
266 Sardinian wheat, barley and triticale (Giunta et al., 2002) with the varieties showing high levels of
267 variation in chlorophyll content caused by a strong genetic and weak environmental and G*E
268 components suggesting that chlorophyll content has not been driven in a particular direction as a side
269 effect of breeding for other traits such as plant height. An environmental effect was seen in this study
270 as differences in chlorophyll content were seen at some growth stages between the years of the trial.
271 The modern cultivar Concerto was included in this study and had higher SPAD readings than the
272 landraces present. Sufficient variation may already exist for altering the volume of chlorophyll in
273 barley in the current pool of parents but having landraces as an alternative allows options for wider
274 genetic material to be introduced to the breeding programs. Maintaining chlorophyll content for
275 longer may be of benefit, as in rice it was seen that for each extra day of canopy maintenance there
276 was an increase of 0.2 tonnes per hectare in yield (Akita, 1989). Compared to modern cultivars, wheat
277 landraces have been seen to begin to senesce quicker once they have reached grain filling which

278 suggests a potential negative side effect in using landraces in breeding (Gaju et al., 2016). This was
279 visually observed in this study although senescence was not measured directly. This is something pre-
280 breeding programs would need to be taken into account when using landraces.

281 The distribution of chlorophyll will be affected by the size and shape of the leaves and there were
282 differences between the landraces in regard to leaf length at both GS39 and 59 but not in SLA
283 suggesting that lines with a larger leaf surface area are thinner and *vice versa* (Table 3). This is
284 supported by research in barley which showed no differences in SLA between cultivars (Giunta et al.,
285 2002) in contrast to their findings in wheat and triticale which showed variation in SLA. Unfortunately
286 due to experimental constraints caused by the small size of the trial plots it was not possible to
287 measure the leaf area index or light interception. This would have completed the picture of how leaf
288 size and shape is affecting the light capture of the landraces throughout different phases of growth
289 and is something to be explored in future work. Selection for seedling leaves with a larger surface area
290 has occurred in wheat and it was accompanied by an increased early plant biomass and vigour (Zhang
291 et al., 2015). If a similar approach could be applied in barley then light interception efficiency could be
292 increased early in the growth cycle especially in Northern latitudes where the growth season is short
293 (Mukula and Rantanen, 1837).

294 **4.3 Leaf Canopy Architecture**

295 Leaf angle had been associated with cereal yields and our study showed significant variation in leaf
296 angle among barley landraces (Table 3). Early studies in Maize showed a yield increase of 40% with a
297 10° leaf inclination from vertical (Pendleton et al., 1968). High yielding rice varieties such as 'Takanari'
298 have been reported to have higher photosynthetic rates per leaf than other varieties (Taylaran et al.,
299 2011) and an erect leaf posture (Nan Su San et al., 2018) along with decreased levels of photo-
300 inhibition (Horton et al., 1999; Kumagai et al., 2014). The optimal crop ideotype has previously been
301 that of an overall erect canopy (Donald, 1968) but it is now suggested that decreasing leaf angle from
302 the bottom leaf layer of the canopy to the top would be more efficient in maximising light interception

303 (Ku et al., 2010; Long et al., 2006; Zhu et al., 2010). Rice hybrids are being developed with 5⁰, 10⁰ and
304 20⁰ flag, 1st and 2nd leaves respectively (Peng et al., 2008). Canopies could be developed not only with
305 variation in leaf angle but also with differential volumes of chlorophyll through leaf layers tailored to
306 local environmental conditions (Ort et al., 2015).

307 The landraces from Southern latitudes were characterised by an erectophile leaf angle which has a
308 negative relationship with latitude and temperature (Table 3, Figure 3). As latitude and temperature
309 may be related a multiple linear regression was used to try to untangle if leaf angle was responding to
310 one or both of the factors and this showed that leaf angle was responding to temperature. In other
311 work an erectophile canopy structure has been seen to be beneficial in coping with heat stress and
312 increasing water-use- and photosynthetic-efficiency through reduction in heat loads (Ryel et al., 1993;
313 Valladares and Pugnaire, 1999; Werner et al., 2001) reducing excess light levels causing
314 photosynthetic saturation at midday (Falster and Westoby, 2003). This suggests a degree of local
315 adaptation to climatic temperature and light levels in canopy structure although more work would be
316 needed to confirm this. The modern cultivar Concerto which has been developed for a climate midway
317 in the range seen for the landraces fitted well with the regression seen in the landraces with
318 temperature possibly indicating that this pattern has been retained in new breeding material.

319 **4.4 Allocation of resources**

320 Variation among landraces in yield components and resource partitioning was observed (Table 4) and
321 studies have found relationships between numbers of grain and grain weight (Acreche and Slafer,
322 2006; Calderini and Reynolds, 2000) with wheat showing a reduction in average grain weight with
323 increasing numbers of grain (Acreche and Slafer, 2006). There is uncertainty over whether competition
324 between grains for resources reduces weight when there are more grains present (Borrás et al., 2004).
325 In the barley landraces, an increase in grain weight with grain number in the 2-row lines (Figure 4)
326 may be a consequence of lower tiller numbers and more resources allocated per ear. Landrace total
327 yields were not obtained on an area basis due to constraints created by the small plot size. This would

328 have been informative in understanding how canopy structure traits affects final yield. However, as
329 landraces would need to enter a pre-breeding program to introduce traits of interest into new
330 varieties high yields could be maintained through careful trait selection. Source-sink limitations will
331 need to be considered when improving traits associated with photosynthetic efficiency as yields have
332 been shown to be sink limited with the number of grain per m² being the major contributor to yield
333 as opposed to grain weight (Burnett et al., 2016; Lynch et al., 2017; Madani et al., 2010; Serrago et al.,
334 2013). In order for greater photosynthetic efficiency to enhance yields sink strength must be increased
335 with higher number of floret production, higher numbers of productive tillers and the capacity for
336 larger grains (Reynolds et al., 2009).

337 **5. Acknowledgements**

338 The authors would like to thank the technical and trials staff at SRUC for their assistance with this
339 work.

340 **6. References**

- 341 Acreche, M.M., Slafer, G.A., 2006. Grain weight response to increases in number of grains in wheat
342 in a Mediterranean area. *F. Crop. Res.* 98, 52–59. <https://doi.org/10.1016/j.fcr.2005.12.005>
- 343 Akita, S., 1989. Improving yield potential in tropical rice, in: *Progress in Irrigated Rice Research*. IRRI,
344 Los Banos, pp. 41–73.
- 345 Amanullah, Hassan, M.J., Nawab, K., Ali, A., 2007. Response of specific leaf area (SLA), leaf area index
346 (LAI) and leaf area ratio (LAR) of Maize (*Zea mays*, L.) to plant density, rate and timing of
347 nitrogen application. *World Appl. Sci. J.* 2, 235–243.
- 348 Bailey-Serres, J., Fukao, T., Ronald, P., Ismail, A., Heuer, S., Mackill, D., 2010. Submergence Tolerant
349 Rice: SUB1's Journey from Landrace to Modern Cultivar. *Rice* 3, 138–147.
350 <https://doi.org/10.1007/s12284-010-9048-5>
- 351 Bellucci, E., Bitocchi, E., Rau, D., Nanni, L., Ferradini, N., Giardini, A., Rodriguez, M., Attene, G., Papa,

352 R., 2013. Population structure of barley landrace populations and gene-flow with modern
353 varieties. *PLoS One* 8, e83891. <https://doi.org/10.1371/journal.pone.0083891>

354 Björkman, O., Demmig, B., 1987. Photon yield of O₂ evolution and chlorophyll fluorescence
355 characteristics at 77 K among vascular plants of diverse origins. *Planta* 170, 489–504.
356 <https://doi.org/10.1007/BF00402983>

357 Borrás, L., Slafer, G.A., Otegui, M.E., 2004. Seed dry weight response to source-sink manipulations in
358 wheat, maize and soybean: A quantitative reappraisal. *F. Crop. Res.* 86, 131–146.
359 <https://doi.org/10.1016/j.fcr.2003.08.002>

360 Burnett, A.C., Rogers, A., Rees, M., Osborne, C.P., 2016. Carbon source–sink limitations differ
361 between two species with contrasting growth strategies. *Plant. Cell Environ.* 39, 2460–2472.
362 <https://doi.org/10.1111/pce.12801>

363 Calderini, D.F., Reynolds, M.P., 2000. Changes in grain weight as a consequence of de-graining
364 treatments at pre- and post-anthesis in synthetic hexaploid lines of wheat. *Aust. J. Agric. Res.*
365 27, 187–191. <https://doi.org/10.17700/jai.2015.6.1>

366 Diaz, C., Purdy, S., Christ, A., Morot-Gaudry, J.-F., Wingler, A., Masclaux-Daubresse, C., 2005.
367 Characterization of Markers to Determine the Extent and Variability of Leaf Senescence in
368 *Arabidopsis*. A Metabolic Profiling Approach. *Plant Physiol.* 138, 898–908.
369 <https://doi.org/10.1104/pp.105.060764>

370 Digel, B., Tavakol, E., Verderio, G., Tondelli, A., Xu, X., Cattivelli, L., Rossini, L., von Korff, M., 2016.
371 Photoperiod-H1 (Ppd-H1) Controls Leaf Size. *Plant Physiol.* 172, 405–415.
372 <https://doi.org/10.1104/pp.16.00977>

373 Donald, C.M., 1968. The breeding of crop ideotypes. *Euphytica* 17, 385–403.
374 <https://doi.org/10.1007/BF00056241>

375 Dwivedi, S.L., Ceccarelli, S., Blair, M.W., Upadhyaya, H.D., Are, A.K., Ortiz, R., 2016. Landrace
376 Germplasm for Improving Yield and Abiotic Stress Adaptation. *Trends Plant Sci.* 21, 31–42.
377 <https://doi.org/10.1016/j.tplants.2015.10.012>

378 Emebiri, L.C., 2013. QTL dissection of the loss of green colour during post-anthesis grain maturation
379 in two-rowed barley. *Theor. Appl. Genet.* 126, 1873–84. <https://doi.org/10.1007/s00122-013->
380 2102-0

381 Evans, L.T., 1997. Adapting and improving crops: the endless task. *Philos. Trans. R. Soc. B Biol. Sci.*
382 352, 901–906. <https://doi.org/10.1098/rstb.1997.0069>

383 Falster, D.S., Westoby, M., 2003. Leaf size and angle vary widely across species: What consequences
384 for light interception? *New Phytol.* 158, 509–525. <https://doi.org/10.1046/j.1469->
385 8137.2003.00765.x

386 Farquhar, G.D., von Caemmerer S, Berry, J.A., 2001. Models of photosynthesis. *Plant Physiol.* 125,
387 42–45. <https://doi.org/10.1104/pp.125.1.42>

388 Fischer, R.A., Edmeades, G.O., 2010. Breeding and Cereal Yield Progress. *Crop Sci.*
389 <https://doi.org/10.2135/cropsci2009.10.0564>

390 Flood, P.J., Harbinson, J., Aarts, M.G.M., 2011. Natural genetic variation in plant photosynthesis.
391 *Trends Plant Sci.* <https://doi.org/10.1016/j.tplants.2011.02.005>

392 Gaju, O., DeSilva, J., Carvalho, P., Hawkesford, M.J., Griffiths, S., Greenland, A., Foulkes, M.J., 2016.
393 Leaf photosynthesis and associations with grain yield, biomass and nitrogen-use efficiency in
394 landraces, synthetic-derived lines and cultivars in wheat. *F. Crop. Res.* 193, 1–15.
395 <https://doi.org/10.1016/j.fcr.2016.04.018>

396 Giunta, F., Motzo, R., Deidda, M., 2002. SPAD readings and associated leaf traits in durum wheat,
397 barley and triticale cultivars. *Euphytica* 125, 197–205.

398 <https://doi.org/10.1023/a:1015878719389>

399 Goynes, P.J., Milroy, S.P., Lilley, J.M., Hare J M, 1993. Radiation Interception, Radiation Use Efficiency
400 and Growth of Barley Cultivars. *Aust. J. Agric. Res.* 44, 1351–1366.

401 HGCA (The Scottish Executive), 2006. The barley growth guide.

402 Horton, P., Murchie, E.H., Chen, Y., Hubbart, S., Peng, S., Horton, P., 1999. Interactions between
403 Senescence and Leaf Orientation Determine in Situ Patterns of Photosynthesis and
404 Photoinhibition in Field-Grown Rice¹. *Plant Physiol.* <https://doi.org/10.1104/pp.119.2.553>

405 Jones, H., Civián, P., Cockram, J., Leigh, F.J., Smith, L.M., Jones, M.K., Charles, M.P., Molina-Cano, J.-L.,
406 Powell, W., Jones, G., Brown, T.A., 2011. Evolutionary history of barley cultivation in Europe
407 revealed by genetic analysis of extant landraces. *BMC Evol. Biol.* 11, 320.
408 <https://doi.org/10.1186/1471-2148-11-320>

409 Kemanian, A.R., Stöckle, C.O., Huggins, D.R., 2004. Variability of Barley Radiation-Use Efficiency. *Crop*
410 *Sci.* <https://doi.org/10.2135/cropsci2004.1662>

411 Kruk, B., Insausti, P., Razul, A., Benech-Arnold, R., 2006. Light and thermal environments as modified
412 by a wheat crop: effects on weed seed germination. *J. Appl. Ecol.* 43, 227–236.
413 <https://doi.org/10.1111/j.1365-2664.2006.01140.x>

414 Ku, L.X., Zhao, W.M., Zhang, J., Wu, L.C., Wang, C.L., Wang, P.A., Zhang, W.Q., Chen, Y.H., 2010.
415 Quantitative trait loci mapping of leaf angle and leaf orientation value in maize (*Zea mays* L.).
416 *Theor. Appl. Genet.* 121, 951–959. <https://doi.org/10.1007/s00122-010-1364-z>

417 Kumagai, E., Hamaoka, N., Araki, T., Ueno, O., 2014. Dorsoventral asymmetry of photosynthesis and
418 photoinhibition in flag leaves of two rice cultivars that differ in nitrogen response and leaf
419 angle. *Physiol. Plant.* <https://doi.org/10.1111/ppl.12145>

420 Long, S.P., Marshall-Colon, A., Zhu, X.-G., 2015. Meeting the Global Food Demand of the Future by

421 Engineering Crop Photosynthesis and Yield Potential. *Cell* 161, 56–66.
422 <https://doi.org/10.1016/j.cell.2015.03.019>

423 Long, S.P., Zhu, X.-G., Naidu, S.L., Ort, D.R., 2006. Can improvement in photosynthesis increase crop
424 yields? *Plant. Cell Environ.* 29, 315–330. <https://doi.org/10.1111/j.1365-3040.2005.01493.x>

425 Lynch, J.P., Doyle, D., McAuley, S., McHardy, F., Danneels, Q., Black, L.C., White, E.M., Spink, J., 2017.
426 The impact of variation in grain number and individual grain weight on winter wheat yield in
427 the high yield potential environment of Ireland. *Eur. J. Agron.* 87, 40–49.
428 <https://doi.org/https://doi.org/10.1016/j.eja.2017.05.001>

429 Mackay, I., Horwell, A., Garner, J., White, J., McKee, J., Philpott, H., 2011. Reanalyses of the historical
430 series of UK variety trials to quantify the contributions of genetic and environmental factors to
431 trends and variability in yield over time. *Theor. Appl. Genet.* 122, 225–238.
432 <https://doi.org/10.1007/s00122-010-1438-y>

433 Madani, A., Rad, A.S., Pazoki, A., Nourmohammadi, G., Zarghami, R., 2010. Wheat (*Triticum aestivum*
434 L.) grain filling and dry matter partitioning responses to source:sink modifications under
435 postanthesis water and nitrogen deficiency. *Acta Sci. - Agron.* 32, 145–151.
436 <https://doi.org/10.4025/actasciagron.v32i1.6273>

437 Meseka, S., Fakorede, M., Ajala, S., Badu-Apraku, B., Menkir, A., 2013. Introgression of Alleles from
438 Maize Landraces to Improve Drought Tolerance in an Adapted Germplasm. *J. Crop Improv.* 27,
439 96–112. <https://doi.org/10.1080/15427528.2012.729259>

440 Meseka, S., Menkir, A., Obeng-Antwi, K., 2015. Exploitation of beneficial alleles from maize (*Zea*
441 mays L.) landraces to enhance performance of an elite variety in water stress environments.
442 *Euphytica* 201, 149–160. <https://doi.org/10.1007/s10681-014-1214-1>

443 Monteith, J.L., Moss, C.J., 1977. Climate and the Efficiency of Crop Production in Britain [and

444 Discussion]. *Philos. Trans. R. Soc. B Biol. Sci.* <https://doi.org/10.1098/rstb.1977.0140>

445 Mukula, J., Rantanen, O., 1837. Climatic risks to the yield and quality of field crops in Finland: I. Basic
446 facts about Finnish field crops production. *Ann. Agric. Fenn.* 26, 1–18.

447 Murchie, E.H., Pinto, M., Horton, P., 2009. Agriculture and the new challenges for photosynthesis
448 research. *New Phytol.* 181, 532–552. <https://doi.org/10.1111/j.1469-8137.2008.02705.x>

449 Muurinen, S., Peltonen-Sainio, P., 2006. Radiation-use efficiency of modern and old spring cereal
450 cultivars and its response to nitrogen in northern growing conditions. *F. Crop. Res.* 96, 363–
451 373. <https://doi.org/10.1016/j.fcr.2005.08.009>

452 Nan Su San, Ootsuki, Y., Adachi, S., Yamamoto, T., Ueda, T., Tanabata, T., Motobayashi, T., Ookawa,
453 T., Hirasawa, T., 2018. A near-isogenic rice line carrying a QTL for larger leaf inclination angle
454 yields heavier biomass and grain. *F. Crop. Res.* 219, 131–138.
455 <https://doi.org/10.1016/j.fcr.2018.01.025>

456 Nunes-Nesi, A., Nascimento, V. de L., de Oliveira Silva, F.M., Zsögön, A., Araújo, W.L., Sulpice, R.,
457 2016. Natural genetic variation for morphological and molecular determinants of plant growth
458 and yield. *J. Exp. Bot.* 67, 2989–3001. <https://doi.org/10.1093/jxb/erw124>

459 Ort, D.R., Merchant, S.S., Alric, J., Barkan, A., Blankenship, R.E., Bock, R., Croce, R., Hanson, M.R.,
460 Hibberd, J.M., Long, S.P., Moore, T.A., Moroney, J., Niyogi, K.K., Parry, M.A.J., Peralta-Yahya,
461 P.P., Prince, R.C., Redding, K.E., Spalding, M.H., van Wijk, K.J., Vermaas, W.F.J., von Caemmerer,
462 S., Weber, A.P.M., Yeates, T.O., Yuan, J.S., Zhu, X.G., 2015. Redesigning photosynthesis to
463 sustainably meet global food and bioenergy demand. *Proc. Natl. Acad. Sci.* 112, 8529–8536.
464 <https://doi.org/10.1073/pnas.1424031112>

465 Ort, D.R., Zhu, X., Melis, A., 2011. Optimizing Antenna Size to Maximize Photosynthetic Efficiency.
466 *Plant Physiol.* 155, 79–85. <https://doi.org/10.1104/pp.110.165886>

467 Parry, M.A.J., Reynolds, M., Salvucci, M.E., Raines, C., Andralojc, P.J., Zhu, X.G., Price, G.D., Condon,
468 A.G., Furbank, R.T., 2011. Raising yield potential of wheat. II. Increasing photosynthetic capacity
469 and efficiency. *J. Exp. Bot.* 62, 453–467. <https://doi.org/10.1093/jxb/erq304>

470 Peltonen-Sainio, P., 1997. Leaf Area Duration of Oat at High Latitudes. *J. Agron. Crop Sci.* 178, 149–
471 155. <https://doi.org/10.1111/j.1439-037X.1997.tb00483.x>

472 Pendleton, J.W., Smith, G.E., Winter, S.R., Johnston, T.J., 1968. Field Investigations of the
473 Relationships of Leaf Angle in Corn (*Zea mays* L.) to Grain Yield and Apparent Photosynthesis1.
474 *Agron. J.* 60, 422. <https://doi.org/10.2134/agronj1968.00021962006000040027x>

475 Peng, S., Khush, G.S., Virk, P., Tang, Q., Zou, Y., 2008. Progress in ideotype breeding to increase rice
476 yield potential. *F. Crop. Res.* <https://doi.org/10.1016/j.fcr.2008.04.001>

477 Raines, C.A., 2011. Increasing photosynthetic carbon assimilation in C3 plants to improve crop yield:
478 current and future strategies. *Plant Physiol.* 155, 36–42.
479 <https://doi.org/10.1104/pp.110.168559>

480 Ray, D.K., Ramankutty, N., Mueller, N.D., West, P.C., Foley, J. a, 2012. Recent patterns of crop yield
481 growth and stagnation. *Nat. Commun.* 3, 1293. <https://doi.org/10.1038/ncomms2296>

482 Reynolds, M., Bonnett, D., Chapman, S.C., Furbank, R.T., Manès, Y., Mather, D.E., Parry, M.A.J., 2011.
483 Raising yield potential of wheat. I. Overview of a consortium approach and breeding strategies.
484 *J. Exp. Bot.* 62, 439–452. <https://doi.org/10.1093/jxb/erq311>

485 Reynolds, M., Foulkes, M.J., Slafer, G.A., Berry, P., Parry, M.A.J., Snape, J.W., Angus, W.J., 2009.
486 Raising yield potential in wheat. *J. Exp. Bot.* 60, 1899–1918.
487 <https://doi.org/10.1093/jxb/erp016>

488 Richards, R.A., 2000. Selectable traits to increase crop photosynthesis and yield of grain crops. *J. Exp.*
489 *Bot.* 51, 447–458. https://doi.org/10.1093/jexbot/51.suppl_1.447

490 Rodriguez, M., Rau, D., Papa, R., Attene, G., 2008. Genotype by environment interactions in barley
491 (*Hordeum vulgare* L.): different responses of landraces, recombinant inbred lines and varieties
492 to Mediterranean environment. *Euphytica* 163, 231–247. <https://doi.org/10.1007/s10681-007->
493 9635-8

494 Ryel, R.J., Beyschlag, W., Caldwell, M.M., 1993. Foliage orientation and carbon gain in two tussock
495 grasses as assessed with a new whole-plant gas-exchange model. *Funct. Ecol.*
496 <https://doi.org/10.2307/2389874>

497 Serrago, R.A., Alzueta, I., Savin, R., Slafer, G.A., 2013. Understanding grain yield responses to source-
498 sink ratios during grain filling in wheat and barley under contrasting environments. *F. Crop. Res.*
499 150, 42–51. <https://doi.org/10.1016/j.fcr.2013.05.016>

500 Sim, L.C., Froud-Williams, R.J., Gooding, . J, 2007. The influence of winter oilseed rape (*Brassica*
501 *napus* ssp. *oleifera* var. *biennis*) canopy size on grass weed growth and grass weed seed return.
502 *J. Agric. Sci.* 145, 313–327. <https://doi.org/10.1017/S0021859606006721>

503 Taylaran, R.D., Adachi, S., Ookawa, T., Usuda, H., Hirasawa, T., 2011. Hydraulic conductance as well
504 as nitrogen accumulation plays a role in the higher rate of leaf photosynthesis of the most
505 productive variety of rice in Japan. *J. Exp. Bot.* 62, 4067–4077.
506 <https://doi.org/10.1093/jxb/err126>

507 The Scottish Government, 2018. Cereal and oilseed rape harvest: 2018 final estimates.

508 Turner, A., Beales, J., Faure, S., Dunford, R.P., Laurie, D.A., 2005. The pseudo-response regulator Ppd-
509 H1 provides adaptation to photoperiod in barley. *Science* (80-.). 310, 1031–1034.
510 <https://doi.org/10.1126/science.1117619>

511 Valladares, F., Pugnaire, F.I., 1999. Tradeoffs between irradiance capture and avoidance in semi-arid
512 environments assessed with a crown architecture model. *Ann. Bot.*

513 <https://doi.org/10.1006/anbo.1998.0843>

514 Villa, T.C.C., Maxted, N., Scholten, M., Ford-Lloyd, B., 2005. Defining and Identifying Crop Landraces.
515 *Plant Genet. Resour.* 3, 373–384. <https://doi.org/10.1079/PGR200591>

516 Werner, C., Ryel, R.J., Correia, O., Beyschlag, W., 2001. Structural and functional variability within the
517 canopy and its relevance for carbon gain and stress avoidance. *Acta Oecologica*.
518 [https://doi.org/10.1016/S1146-609X\(01\)01106-7](https://doi.org/10.1016/S1146-609X(01)01106-7)

519 Xu, K., Mackill, D.J., 1996. A major locus for submergence tolerance mapped on rice chromosome 9.
520 *Mol. Breed.* 2, 19–224. <https://doi.org/10.1007/BF00564199>

521 Yahiaoui, S., Cuesta-Marcos, A., Gracia, M.P., Medina, B., Lasa, J.M., Casas, A.M., Ciudad, F.J.,
522 Montoya, J.L., Moralejo, M., Molina-Cano, J.L., Igartua, E., 2014. Spanish barley landraces
523 outperform modern cultivars at low-productivity sites. *Plant Breed.* 133, 218–226.
524 <https://doi.org/10.1111/pbr.12148>

525 Yin, X., Struik, P.C., 2015. Constraints to the potential efficiency of converting solar radiation into
526 phytoenergy in annual crops: from leaf biochemistry to canopy physiology and crop ecology. *J.*
527 *Exp. Bot.* 66, 6535–6549. <https://doi.org/10.1093/jxb/erv371>

528 Zadoks, J.C., Chang, T.T., Konzak, C.F., 1974. A decimal code for the growth stages of cereals. *Weed*
529 *Res.* 14, 415–421. <https://doi.org/10.1111/j.1365-3180.1974.tb01084.x>

530 Zhang, L., Richards, R.A., Condon, A.G., Liu, D.C., Rebetzke, G.J., 2015. Recurrent selection for wider
531 seedling leaves increases early biomass and leaf area in wheat (*Triticum aestivum* L.). *J. Exp.*
532 *Bot.* 66, 1215–1226. <https://doi.org/10.1093/jxb/eru468>

533 Zheng, H.J., Wu, a. Z., Zheng, C.C., Wang, Y.F., Cai, R., Shen, X.F., Xu, R.R., Liu, P., Kong, L.J., Dong,
534 S.T., 2009. QTL mapping of maize (*Zea mays*) stay-green traits and their relationship to yield.
535 *Plant Breed.* 128, 54–62. <https://doi.org/10.1111/j.1439-0523.2008.01529.x>

536 Zhu, X.-G., Long, S.P., Ort, D.R., 2010. Improving photosynthetic efficiency for greater yield. *Annu.*
537 *Rev. Plant Biol.* 61, 235–261. <https://doi.org/10.1146/annurev-arplant-042809-112206>

538