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Trait identification of faba bean ideotypes for Northern European environments

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1 Highlights

- 2 • Trait-based classification reveals distinctiveness of *Vicia faba minor* and *major*.
- 3 • Flowering duration and plant height are key traits of high yielding genotypes.
- 4 • High temperature at flowering is the main yield limitation in North Europe.
- 5 • Latvian landraces are North-Baltic region ideotypes with high yield potential and stability.

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7

8

9 Abstract

10 European pulse production faces a continued loss of cultivated area along with decreasing or stagnant
11 yields. *Vicia faba* is a traditional legume with high genetic diversity cultivated in a wide range of
12 European climates. Therefore *V. faba* is promising to identify stable and high yielding genotypes for
13 specific target environments. The Nordic-Baltic region is challenging for legume growing due to short
14 vegetation period and heat/drought stress in continental climates. Within the pan-European
15 Eurolegume project a set of 18 *V. faba* accessions containing var. *minor* and *major* local landraces and
16 modern cultivars of different geographical origin was evaluated in multi-environmental trials. The aim
17 of this study was to identify ideotypes for Northern Europe and reveal key phenotypic traits conferring
18 high yield potential and stability. Four target environmental clusters represented the range of Nordic
19 growing conditions with yield levels from 128 g m⁻² to 380 g m⁻². Multivariate classification
20 differentiated distinctive groups of var. *minor* and var. *major* accessions with few overlapping
21 genotypes, the former having higher average yield, taller structure, more pods per node and longer
22 flowering duration.

23 Late sowing under long-day conditions above 55° N latitudes resulted in early flowering due to short
24 vegetative development (650 °Cd). Extended flowering duration and tall stature were the most
25 important traits conferring high yields. A negative trade-off between yield potential and yield stability
26 was detected, with yield advantages of stress resistant genotypes only in a limited range of low yielding
27 target environments (<180 g m⁻²). The highest yielding accessions (Latvian var. *minor* landrace Bauska
28 and var. *major* landrace Cēres) represented a favourable combination of yield potential and stability.
29 High temperatures at flowering, within a range of average maximum July temperatures between 20.5-
30 24.5 °C, were identified as most critical environmental variable depressing yield levels between 38.5
31 (var. *major*) and 56.2 (var. *minor*) g m⁻² °C⁻¹.

32 It was concluded that Baltic landraces are promising ideotypes, with adapted flowering phenology and
33 morphological structure, for increased *V. faba* yields in Nordic target environments.

34

35 **Keywords:** adaptation breeding, *Vicia faba* phenology, temperature stress, yield stability, Nordic-Baltic
36 environments
37
38

39 1. Introduction

40 The steady decrease of legume production area in Europe by more than 67 % between 1961 and 2014
41 with the concomitant increase in soybean imports (> 6 fold in the same period) urged European policy
42 makers implement measures to promote cultivation of native legumes. Beside market price
43 considerations, stagnant or decreasing yield levels are a major reason of farmers to abandon
44 traditional legume species from cropping systems. For dry peas, for example, covering 44 % of the area
45 cultivated with pulses in Europe, FAO data reveal a trend towards lower yields ($-54 \text{ kg ha}^{-1} \text{ a}^{-1}$) from
46 1999 onwards (FAOStat, 2017). For winter wheat, Brisson et al. (2010) related decreasing yield trends
47 to more frequent abiotic stresses. Legumes are even considered more sensitive than cereals to a wide
48 range of abiotic stresses (Sultana et al., 2014; Latef and Ahmand, 2015). Ensuring high yield potential
49 and stability under variable environmental conditions should therefore be a main target of legume
50 breeding and management to regain a more prominent role in prevailing crop rotations.

51 Within the FAO strategy of sustainable intensification (FAO, 2011) conservation and use of genetic
52 resources (e.g. wild relatives, landraces, old varieties) is encouraged to broaden the genetic basis of
53 current breeding programs. In faba bean (*Vicia faba* L.) the number of available germplasm worldwide
54 is estimated around 38.000 accessions (Duc et al., 2010). Advances in genotyping methods enable
55 efficient assessment of diversity within existing collections (e.g. Varshney et al., 2009; Link et al., 1995
56 for European and Mediterranean faba bean). Targeted use of novel germplasm for improved varieties
57 however requires linking genetic with phenotypic information (Furbank and Tester, 2011). In spite of
58 advances in high-throughput genotyping and phenotyping, performance of (pre-selected) novel
59 germplasm in multi-environment field testing is still the key criterion for entering the commercial
60 breeding pipeline.

61 In Central to Northern European cropping systems, faba bean is a spring crop sown between March
62 and May and harvested between mid of August to end of September (Jensen et al., 2010); at lower
63 latitudes, frost tolerant varieties also allow faba bean cropping over winter (Sallam et al., 2015).

64 Yield sensitive phenological stages of faba bean to abiotic stresses are between flowering (BBCH scale
65 60; Lancashire et al., 1991) and pod development (BBCH 75) with yield losses up to 50 % during early

66 pod-setting (Duc, 1997; Mwanamwenge et al., 1999). Taking into account that these growing stages
67 coincide with summer months under European cropping conditions, both drought and heat are key
68 stressors influencing faba bean performance. Optimum flowering temperatures are between 20-25°C
69 (Patrick and Stoddard, 2010) with high temperatures, particularly when combined with drought,
70 leading to flower abortion, lower number of pods and reduced seed set (McDonald and Paulsen, 1997).
71 While breeder strive to release cultivars for a broad range of target environments and potential
72 markets (e.g. Braun et al., 1996), this might insufficiently address the adaptation requirements to
73 specific edaphoclimatic conditions (Rannali and Cubero, 1997; Annicchiarico, 2002; Annicchiarico et
74 al., 2005). For such conditions local germplasm (e.g. landraces) can be of particular advantage due to
75 better resistance to biotic and/or abiotic stresses prevailing in the given environment.

76 Phenology is a key factor to align crop development with available growing factors (Blum, 1996; Cleland
77 et al., 2007; Bussel et al., 2015). This is particularly relevant considering the wide latitudinal range of
78 faba bean cultivation in Europe (Jensen et al., 2010) covering dry, temperate and continental climates
79 (Gerstengarbe and Werner, 2009). Northern European environments are characterized by a short
80 growing season with marked seasonality of photo-thermal conditions regulating plant development
81 (Saarikko and Carter, 1996; Zhang et al., 2004) but also prone to temporal heat and drought waves
82 (Teixeira et al., 2013; Spinoni et al., 2015).

83

84 Multi-environment field studies investigating key phenotypic patterns characterizing faba bean
85 germplasm adapted to Northern European growing conditions are virtually absent. Within a pan-
86 European project, *Vicia faba* accessions including *minor* and *major* types, local landraces and modern
87 varieties of different European origins, including northern regions, have been evaluated in field trials
88 at four different Northern European locations. The overall objective was to define high-yielding *V. faba*
89 ideotypes for Nordic-Baltic environments. In particular, this study aimed to identify prevailing
90 environmental constraints and corresponding key phenotypic traits conferring superior crop
91 performance. We hypothesized that local *V. faba* landraces outperform modern varieties, released for
92 broad adaptation, within the specificity of growing condition at above 55°N latitudes. Therefore, they

93 can elucidate yield-determining factors to be selected for faba bean cultivar improvement for Nordic
94 environments.

95

96 **2. Material and Methods**

97 Field experiments for studying the performance of 18 *Vicia faba* genotypes were performed within the
98 EU FP7 EUROLEGUME (www.eurolegume.eu) project over two growing seasons at four Northern
99 European testing sites.

100

101 *2.1 Vicia faba germplasm*

102 The 18 investigated *Vicia faba* genotypes were composed of nine *V. faba* var. *minor* and nine var. *major*
103 accessions (Table 1). The genotypes cover Northern, Central and Southern European origins as well as
104 distinct levels of breeding intensity/history (modern and old varieties, landraces). Throughout the
105 manuscript the following terms are used: accession is the plant material collected in a gene-bank,
106 germplasm describes a set of genetic resources from a species, genotype refers to the member of a
107 species with distinctive genetic constitution (FAO, 2014), landrace defines farmer' selected and locally
108 adapted ecotypes (Zeven, 1998), variety denotes the taxonomic rank between species and form, while
109 cultivar refers to an intentionally human-selected genotype distinctive to others, uniform and stable
110 (Spooner et a., 2003); ideotype defines a hypothetical genotype with optimum trait combinations for
111 adaptation to a specific target environment (Donald, 1968).

112

113 **Table 1.** *Vicia faba* var. *minor* and var. *major* genotypes investigated at four field sites and in two years
114 (EUROLEGUME genotype code, type of accession, local genotype name, country of origin and donor
115 institution).

Genotype	Type	Genotype Name	Country of origin	Donor institutions*
<i>Vicia faba</i> var. <i>minor</i>				
FB01	Modern cultivar	Fuego	Germany	RISE, Sweden
FB07	Landrace	Bauska	Latvia	AREI, Latvia
FB08	Landrace	Priekulu 32	Latvia	PHRC, Latvia

FB12	Old cultivar	Lielplatones	Latvia	PHRC, Latvia
FB15	Landrace	Priekuļu vietejas	Latvia	AREI, Latvia
FB16	Landrace	Valmiera	Latvia	AREI, Latvia
FB21	Modern cultivar	Favel	Portugal	INIAV, Portugal
FB22	Old cultivar	Jõgeva	Estonia	ECRI, Estonia
FB39	Modern cultivar	Gloria	Germany	RISE, Sweden

Vicia faba var. major

FB02	Landrace	Džūkstes	Latvia	PHRC, Latvia
FB03	Landrace	Zaigas	Latvia	PHRC, Latvia
FB05	Landrace	Puntuļa tumšās	Latvia	PHRC, Latvia
FB06	Landrace	Cēres	Latvia	PHRC, Latvia
FB09	Landrace	Puntuļa gaišās	Latvia	PHRC, Latvia
FB10	Landrace	Iras	Latvia	PHRC, Latvia
FB37	Landrace	Gubbestad	Sweden	RISE, Sweden
FB242	Modern cultivar	Aguadulce	Spain	AUA, Greece
FB226	Landrace	Kučānes Sarmītes	Latvia	PHRC, Latvia

116 * AUA Agricultural University of Athens; AREI Institute of Agricultural Resources and Economics; PHRC Pure
 117 Horticultural Research Centre; ECRI Estonian Crop Research Institute; INIAV National Institute for Agricultural
 118 and Veterinarian Research; RISE Research Institute of Sweden.
 119

120 *2.2 Field environments*

121 The genotypes were tested over two growing seasons at four Northern European field sites (Table 2).

122 The Baltic (Latvia, Estonia) testing sites are characterized by a cool temperate climate with increasing
 123 continental character from NEM2 to BOR7, while the Norwegian location near the sea has a temperate
 124 Atlantic climate.

125

126 **Table 2.** Location, altitude, Köppen-Geiger climate and Metzger et al. (2005) environmental
 127 classification of the four experimental sites in 2015 and 2016. See Table 1 for site abbreviations.

Site	Country	Coordinates	Altitude a.s.l. (m)	Koepfen climate class	Metzger environmental class
AREI	Latvia	57°18'57" N, 25°20'19" E	123	Dfb	NEM2
PHRC	Latvia	57°37'43" N, 22°21'36" E	57	Dfb	NEM2
ECRI	Estonia	58°46'15" N, 26°24'18" E	76	Dfb	BOR7
NIBIO	Norway	58°20'24" N, 8°31'22" E	10	Cfb	ATN2

128

129 Soil properties of the experimental fields are given in Table 3. The soils are typical for the Nordic-Baltic
 130 region formed on Quaternary sediments with comparatively high sand content, partially occurrence of
 131 horizons with stagnic or gleyic properties, and moderately to slightly acidic pH-values predominantly
 132 in the silicate buffer range (Jones et al., 2005).

133

134 **Table 3.** Soil properties of experimental fields, including the texture class and particle size distribution,
135 pH (KCl), soil organic matter (SOM) and total Phosphorus (P) and Potassium (K) contents. See Table 2
136 for site abbreviations.

Site	Soil type WRB	Texture class	Sand %	Silt %	Clay %	pH _{KCl}	SOM %	P mg kg ⁻¹	K mg kg ⁻¹
AREI	Stagnic Podzol	Loamy sand	67	3	30	5.7	3.1	68.5	123.7
PHRC	Haplic Podsol	Sandy loam	55	25	20	6.3	2.9	86.2	102.5
ECRI	Stagnic Luvisol	Sandy clay	53	12	35	6.3	3.1	135.9	114.2
NIBIO	Gleyic Dystric Cambisol	Loamy sand	91	7	3	6.0	4.1	295.2	41.9

137

138 2.3 Experimental setup

139 The experimental design in all trials was a randomized complete block design with four (n = 4)
140 replications and a plot size of 3 m². Seeding density was 14 seeds per m² for var. *major* genotypes and
141 40 seeds per m² for var. *minor* genotypes with a seeding depth of 4-6 cm. Seeding time varied between
142 22nd of April (AREI, Latvia; 2015) and 22nd of May (NIBIO, Norway; 2015). Crop management (primary
143 tillage, seedbed preparation, fertilization and plant protection) followed respective local practices and
144 national fertilization recommendations.

145

146 2.4 Trait measurements

147 Measurements covered plant phenology, plant height, yield and yield components as well as protein
148 content. Plant phenological stages were assessed following Meier (1997). Flowering date was
149 registered as Julian day when 50 % of the plants had at least one flower open, date of end of flowering
150 as the Julian day when 80 % of the plants no longer had any flowers open, and maturity date as the
151 Julian day when 80 % of the pods were dry. The vegetative phase duration was obtained as the time
152 from sowing to flowering date, flowering duration as the time from flowering date to date of end of
153 flowering, and generative phase duration as the time from the end of flowering to maturity date.

154 Plant height was measured near maturity (BBCH 71-81) from ground to the tip of the plant for an
155 average of 10 plants in each replication. Yield components comprised number of pods per node,
156 number of seeds per pod and hundred seed weight (HSW). Number of pods per node was defined as
157 average number of pods on the second pod-bearing node of five plants in each replication. Number of
158 seeds per pod was obtained from an average of five dry pods in each replication. HWS was measured
159 for 2 samples of 100 randomly chosen seeds in each replication (BBCH 89). Seed yield from the
160 harvested plots is uniformly given for a seed moisture content of 14 %.

161 Protein content in seeds was measured for a random sample from each replication by near infrared
162 transmittance spectroscopy (Batten, 1998) using an Infratec 1241 Analyser (Foss, Högenäs, Sweden).

163

164 *2.5 Statistical evaluation*

165 Univariate analysis of main effects (genotypes, environments) and their interactions was done by
166 analysis of variance and subsequent comparison of means. We used SAS (version 9.4; SAS Institute
167 Inc., Cary, NC, USA) procedures from the META suite for evaluation of multi-environment breeding
168 trials (Vargas et al., 2013). META uses a mixed model ANOVA with REML to estimate variance
169 components. Years and sites were taken as environments, thus the two seasons and four sites resulted
170 in eight distinct environments, considered as random effects, representing Northern European
171 growing conditions. Genotypes were taken as fixed factor, while replicates (blocks) were considered
172 random and nested within environments. Following Cooper et al. (1996), a distance matrix from
173 genetic correlations between testing environments was calculated with META to highlight
174 differentiation among target environments (displayed as dendrogram).

175 Multivariate methods were applied to identify groups of genotypes sharing common characteristics.
176 Principal component analysis (PCA; SAS procedure PROC FACTOR) was used to reveal key trait groups
177 (principal components) underlying distinctiveness. Common groups of genotypes were identified using
178 Ward clustering method (SAS procedures PROC CLUSTER and PROC TREE) and principal components
179 as composite clustering variables (Bodner et al., 2013).

180 Mutual relations between single traits are provided as heatmaps derived from correlation analysis
181 (Hemedinger, 2013). The main objective of correlation analysis was to identify selection traits that are
182 potential proxies for yield with lower genetic complexity and/or easy to measure in field plots.
183 Yield stability of genotypes was assessed using joint regression, i.e. linear regression of single genotype
184 yield vs. the site mean (Finlay and Wilkinson, 1963; Becker and Leon, 1988; Crossa, 1990). Differences
185 in regression slopes, as an indicator of stability, were compared with linear contrasts in SAS procedure
186 PROC GLM following Sawant (2012); relations to the single traits were analysed (SAS procedure PROC
187 REG).
188 Finally, the response of yield to environmental influences acting as possible abiotic stresses was
189 assessed via regression analysis (PROC REG with RSQUARE selection option). Meteorological variables
190 tested as causal factor were: rainfall, (mean, maximum and minimum) temperatures, solar radiation,
191 evapotranspiration (ET_0 Penman-Monteith; Allen et al., 1998) and climatic water balance deficit
192 (rainfall minus evapotranspiration). Each factor was tested as monthly averages (sums), averages
193 (sums) over the whole growing season as well as over the critical time of flowering/early pod filling
194 (July-August).

195

196 **3. Results**

197 *3.1 Growing conditions*

198 The *V. faba* testing environments differed substantially concerning temperature and humidity (Fig. 1).

199

200

<Figure 1>

201

202 On average the 2016 growing season was about 1 °C warmer than 2015, particularly during spring and
203 early summer months including flowering time. In contrast, higher maximum temperatures in the
204 Baltic counties occurred during early grain filling in August 2015.

205 Rainfall in the oceanic Cfb site in Norway was 1.4x higher compared to the continental Baltic Dfb
206 climates. The driest site was PHRC in Latvia with an average annual rainfall of only 431 mm. The Baltic

207 environments received between 28.6 % (PHRC) to 40.2 % (AREI) less rainfall during the 2015 vegetation
 208 period, while the Norwegian site had a 49.7 % greater precipitation in 2015. Generally, the oceanic
 209 environment of NIBIO did not cause any climatic water balance deficit (Figure 1, right panel; difference
 210 between rainfall and ET_0). At the Baltic sites, a cumulative water balance deficit of up to -191 mm (SD
 211 ± 22 mm) accumulated during the 2015 growing season between May and September. In 2016 a
 212 considerable water balance deficit in the Baltic sites occurred only at PHRC (-131 mm), while incoming
 213 rainfall and ET_0 were balanced at AREI and ECRI.

214 Based on the yield-distance matrix for the eight environments, differentiation among testing sites is
 215 shown in a dendrogram (Fig. 2). The Latvian site at AREI and the Norwegian site formed a common
 216 cluster, with AREI showing higher distance between the two growing seasons. In 2016 the ECRI and
 217 PHRC sites formed a cluster with similar distance as for the AREI-NIBIO group, while PHRC featured the
 218 highest distance to all other environments during the dry and warm growing season 2015.

219

220 <Figure 2>

221

222 3.2 Yield components, quality, phenological and morphological traits

223 Table 4 lists the results of multi-environment ANOVA with best linear unbiased estimates of genotype
 224 means for yield, yield components and protein content. All traits had significant genotype \times
 225 environment interactions, further analysed below (3.5).

226

227 **Table 4.** Results of mixed model multi-environment ANOVA with best linear unbiased estimates,
 228 significance of main effects and their interactions and least significant differences (LSD) for yield, yield
 229 components and protein content of 18 faba bean genotypes (G) tested in eight environments (E). First
 230 part var. *minor*, second part var. *major* with respective means and coefficient of variations (CV).

Genotype name	Genotype number	Yield g m ⁻²	Pods node ⁻¹ number	Seeds pod ⁻¹ number	Seed weight g/100 seeds	Protein %
<i>Vicia faba</i> var. <i>minor</i>						
Fuego	FB01	316.4	1.9	3.2	64.3	29.8

Bauska	FB07	332.9	2.0	3.3	57.9	31.3
Priekulu 32	FB08	304.5	1.7	2.9	77.5	31.3
Lielplatones	FB12	308.0	2.1	3.4	44.9	31.9
Priekulu vietejas	FB15	301.4	1.9	3.3	58.8	31.3
Valmiera	FB16	263.4	1.7	3.2	61.4	31.3
Favel	FB21	78.6	1.5	2.7	95.6	29.9
Jõgeva	FB22	251.8	1.6	2.9	75.6	30.8
Gloria	FB39	236.5	2.1	3.4	52.1	33.3
Mean var. <i>minor</i>		265.9	1.8	3.1	65.3	31.2
CV var. <i>minor</i> (%)		29.0	11.9	8.0	23.4	3.4
<i>Vicia faba</i> var. <i>major</i>						
Džūkstes	FB02	237.0	1.4	2.7	146.1	32.0
Zaigas	FB03	251.8	1.2	2.8	149.4	31.4
Puntuļa tumšās	FB05	225.6	1.4	2.8	125.0	32.1
Cēres	FB06	269.9	1.4	3.3	121.7	31.3
Puntuļa gaišās	FB09	208.5	1.2	2.7	125.6	32.2
Iras	FB10	252.1	1.3	3.0	127.2	30.8
Kučānes Sarmītes	FB226	222.7	1.3	3.3	138.6	32.3
Aguadulce	FB242	32.4	1.2	2.8	127.4	31.2
Gubbestad	FB37	178.2	1.3	2.7	108.1	32.9
Mean var. <i>major</i>		208.7	1.3	2.9	129.9	31.8
CV var. <i>major</i> (%)		34.2	6.7	8.4	9.9	2.1
<i>Genotype</i>		<0.001	<0.001	<0.001	<0.001	<0.001
<i>Environment</i>		0.0398	0.0467	0.0653	0.0557	0.0415
<i>G × E</i>		<0.001	<0.001	<0.001	<0.001	0.0065
LSD		56.5	0.3	0.3	11.6	0.73

231

232 The var. *minor* genotypes were superior in their average yield level (+24.7 % compared to var. *major*):
 233 pods per node were 1.4x and seeds per pod 1.1x those registered in var. *major*. Linear contrasts
 234 between *minor* and *major* types were significant for yield (p=0.012) and pods per node (p=0.002), while
 235 seed per pod did not differ significantly (p=0.219).

236 The var. *minor* genotype with the highest yield was the Latvian landrace Bauska, while the cultivar
 237 Favel from Portugal failed under the Nordic growing conditions. The genotypes of var. *minor*
 238 differentiated more in the yield components pods per node and hundred seed weight compared to
 239 var. *major*. Protein contents were also slightly more variable in var. *minor*—ranging from 29.8 % (min.)
 240 in the German modern cultivar Fuego to 33.3 % (max.) in Gloria (also originating from Germany).
 241 Among var. *major* genotypes, the Latvian landrace Cēres had the highest yield, while the Spanish
 242 modern cultivar Aguadulce and the Swedish landrace Gubbestand produced substantially less average

243 yields. The Spanish genotype was obviously not adapted to the Northern environments, achieving only
 244 marginal yield levels of about one third of the overall genotype mean. Variability in yield components
 245 was highest in hundred seed weight with largest seeds in the Latvian landrace Zaigas and smallest in
 246 the Swedish genotype Gubbestand. Seeds per pod and pods per node differed also significantly among
 247 genotypes; however in absolute terms the ranges of 1.2 to 1.4 for the number of pods per node and
 248 of 2.7 to 3.3 for seeds per pod were rather narrow. Protein content was between 30.8 % (Latvian
 249 landrace Iras) and 33.1 % (Swedish landrace Gubbestand). As expected, protein content showed the
 250 least variability among relevant yield and quality traits.

251 Among phenological traits (Table 5), vegetative and generative duration showed a significant effect of
 252 genotype, environment (vegetative duration) and their interaction, while flowering duration was
 253 significant for the interaction term only. Plant height was influenced significantly by both main effects
 254 and their interaction.

255

256 **Table 5.** Results of mixed model multi-environment ANOVA with best linear unbiased estimates,
 257 significance of main effects and their interactions and least significant differences (LSD) for
 258 phenological and morphological traits of 18 faba bean genotypes (G) tested in eight environments (E).
 259 First part var. *minor*, second part var. *major* with respective means and coefficient of variations (CV).

Genotype name	Genotype number	Duration of phenological stage			Plant height cm
		Vegetative d	Flowering d	Generative d	
<i>Vicia faba</i> var. <i>minor</i>					
Fuego	FB01	50	27	51	95.2
Bauska	FB07	51	30	46	110.7
Priekulu 32	FB08	48	34	46	100.5
Lielplatones	FB12	53	30	44	114.3
Priekulu vietejas	FB15	51	31	47	108.7
Valmiera	FB16	49	29	51	102.8
Favel	FB21	52	22	50	75.0
Jõgeva	FB22	45	29	47	90.2
Gloria	FB39	53	26	48	96.2
Mean var. <i>minor</i>		50	29	48	99.3
CV var. <i>minor</i> (%)		5.2	11.8	5.1	12.1
<i>Vicia faba</i> var. <i>minor</i>					

Džūkstes	FB02	46	25	49	77.0
Zaigas	FB03	44	26	50	80.7
Puntuļa tumšās	FB05	47	27	47	86.2
Cēres	FB06	45	29	50	89.1
Puntuļa gaišās	FB09	46	27	48	87.0
Iras	FB10	45	26	49	76.7
Kučānes Sarmītes	FB226	48	22	56	86.2
Aguadulce	FB242	53	20	58	62.3
Gubbestad	FB37	46	28	53	77.3
Mean var. <i>major</i>		47	26	51	80.3
CV var. <i>major</i> (%)		5.7	11.3	7.3	10.3
<i>Genotype</i>		<0.001	0.2153	0.0279	<0.001
<i>Environment</i>		0.0323	0.1454	0.1639	0.0376
<i>G × E</i>		<0.001	<0.001	0.0004	<0.001
LSD		1.9	9.1	8.6	6.9

260

261 The vegetative and flowering duration in var. *minor* genotypes was on average three days longer, while

262 *major* types possessed a longer generative phase. Phenological contrasts between the two groups

263 were significant for vegetative and flowering duration only ($p_{\text{vegetative}}=0.031$; $p_{\text{flowering}}<0.001$;

264 $p_{\text{generative}}=0.467$). Average plant height was substantially higher (+23.6 %) in *minor* compared to *major*

265 genotypes.

266 Among *minor* types, the overall earliest mature genotypes were the cultivars Favel (Portugal) and

267 Jõgeva (Estonia). This was due to substantially shorter flowering duration in Favel compared to

268 Northern genotypes, while Jõgeva had shortest vegetative phase. The German varieties Fuego and

269 Gloria were in the lower quartile of flowering duration, with long generative and vegetative

270 development stages respectively. Favel and Jõgeva had the most compact canopy stature, while plant

271 height of all Latvian landraces was above average (> 100 cm).

272 Within the var. *major* genotypes, the Southern cultivar Aguadulce presented the latest initiation of

273 flowering and the shortest flowering duration compared to all the other genotypes of this group. With

274 a long generative phase, this genotype was subsequently latest in maturity. Among the other

275 genotypes, phenology was in a similar range, except for a longer generative duration of Gubbestad

276 (Swedish landrace) and Kučānes Sarmītes (Latvian landrace)—being in the upper quartile (≥ 53 days)

277 together with Aguadulce. Plant height varied by 10.3 % around the average, with Latvian landrace
278 Cères being the tallest and Spanish cultivar Aguadulce the most compact genotype.

279

280 3.3 Trait-based genotype differentiation

281 Multivariate approaches, integrating all traits with potential relevance for yield, revealed distinctive
282 groups of genotypes within the investigated germplasm. Direction and length of trait vectors in the
283 PCA biplot (lines in Fig. 3) show inter-trait relations and trait importance. Genotypes are distributed
284 according to their principal component (PC) scores. PC1 captures 55.3 % of overall variability with high
285 loadings for yield components, plant height, and vegetative duration. PC2 explains 19.2 % of variance,
286 with high loadings for protein content and duration of the flowering and generative phases.

287

288 <Figure 3>

289

290 Genotypes belonging to var. *minor* are located at the right side with positive first PC scores, except the
291 Southern cultivar Favel (FB21) with negative PC1 score (similar to var. *major* accessions). The majority
292 group of var. *major*, located in the lower left quadrant, holds negative PC2 scores; in contrast, Spanish
293 cultivar Aguadulce (FB242) and Swedish landrace Gubbestad (in the upper left quadrant) feature
294 positive PC2 scores. The *minor* genotypes Jõgeva (FB22; old cultivar from Estonia) and Latvian landrace
295 Priekulu 32 (FB08) have PC2 scores similar to the main *major* group (Fig. 3).

296

297 The dendrogram (Fig. 4) classifies genotypes according to their PC scores. Two main clusters are
298 distinguished at a semi-partial R^2 value >0.36 , one containing var. *minor* accessions only, while the
299 second contains var. *major* genotypes together with three *minor* types, i.e. two cultivars (FB21 Favel
300 from Portugal, FB22 Jõgeva from Estonia) and the Latvian landrace Priekulu 32 (FB08).

301

302 <Figure 4>

303

304 3.4. Inter-trait relations

305 Understanding relations among single traits is important to highlight potential phenotyping criteria
306 related to faba bean production targets yield and protein content. In addition, allometric relations
307 between easy-to-measure traits and more complex variables can be estimated. Figure 5 gives an
308 overview on inter-trait correlations in the investigated *Vicia faba* germplasm.

309

310

<Figure 5>

311

312 Inter-trait relations were generally weaker in var. *major* genotypes (mean $|R_{\text{Pearson}}|=0.35$) compared
313 to var. *minor* (mean $|R_{\text{Pearson}}|=0.55$). Var. *minor* genotypes showed significant correlations (with
314 $|R_{\text{Pearson}}| \geq 0.75$) of (i) yield with flowering duration (+, positive) and yield with plant height (+), (ii) pods
315 per node with seeds per pod (+) and pods per node with hundred seed weight (-, negative), (iii) seeds
316 per pod with hundred seed weight (-) and plant height (+) and (iv) hundred seed weight with plant
317 height (-). Significant correlations between $0.50 \leq |R_{\text{Pearson}}| < 0.75$ occurred between (i) yield and
318 hundred seed weight (-), (ii) pods per node with plant height (+), (iii) hundred seed weight with protein
319 content (-), and (iv) flowering duration with plant height (+).

320 Within the var. *major* types significant correlations with $|R_{\text{Pearson}}| \geq 0.75$ were found between (i) yield
321 and the duration of the vegetative stage (-) as well as plant height (+). (ii) The length of the vegetative
322 stage correlated negatively with flowering duration. Correlations between $0.50 \leq |R_{\text{Pearson}}| < 0.75$ were
323 found between (i) yield and flowering duration (+) as well as generative duration (-). (iii) Vegetative
324 duration correlated positively with generative duration and negatively with plant height (Fig. 5).

325

326 3.5 Sensitivity to environmental conditions

327 The Southern European genotypes clearly evidenced a lack of adaptation to Northern growing
328 conditions, particularly the Spanish var. *major* genotype Aguadulce (FB242) featured an unusual
329 response pattern at a very low yield level. Swedish landrace Gubbestand (FB37) was the genotype with
330 the steepest slope, i.e. high yield potential under non-stressed environments with limited stability

331 towards lower yielding environments. Most Latvian landraces had similar yield responses within the
332 tested range of environments, with Cēres (FB06) featuring the best combination of a comparatively
333 high yield potential with adaptability to lower yielding environments—resulting in highest average
334 yield (*cf.* Table 4). For *major* type germplasms, slope comparison revealed the narrow range of stability
335 values with statistically significant differences only between Aguadulce and the eight other genotypes.
336 In *Vicia faba* var. *minor* germplasm, the Southern cultivar Favel (FB16) differed from seven others, i.e.
337 except the Latvian landrace Valmiera (FB16). In general, the *minor* genotypes showed more distinct
338 interactions between genotypes and environment (Fig. 6). The old cultivar Lielplatones (FB12) from
339 Latvia possessed the greatest yield under favourable conditions (i.e. non-stressed environments),
340 while being of limited stability, with most severe yield reductions towards low yielding environmental
341 conditions. Valmiera showed the contrary behaviour—least yield potential but greatest yield stability
342 across environments. Statistical comparison of slopes evidenced that Lielplatones and Valmiera
343 constitute the two extreme genotypes of the sample with significantly different yield responses
344 towards adverse environments. A genotype combining comparatively high potential and stability was
345 the Latvian landrace Bauska (FB07) with highest mean yield.

346

347

<Figure 6>

348

349 Excluding the non-adapted Southern genotypes, an analysis of causal relations between plant traits
350 and yield stability quantified via regression slopes indicated a significant relation between yield
351 potential and yield stability: Higher yielding genotypes tended to have a lower yield stability (higher
352 slope) in both *minor* and *major* types ($R^2_{\text{minor}}=0.83$; $p=0.002$; $R^2_{\text{major}}=0.86$, $p<0.001$). Among var. *major*
353 genotypes those with higher protein content tended to higher yield stability ($R^2=0.76$, $p=0.005$). The
354 other traits did not reveal significant influences on yield stability.

355

356 Two key environmental factors significantly influenced yield of *Vicia faba* (Fig. 7): high maximum July
357 temperatures caused a decrease in yield with higher sensitivity of var. *minor* compared to var. *major*.

358 The yield decrease was as high as 73.4 % ($-56.3 \text{ g m}^{-2} \text{ }^{\circ}\text{C}^{-1}$) for var. *minor* and 53.0 % ($-38.5 \text{ g m}^{-2} \text{ }^{\circ}\text{C}^{-1}$)
359 for var. *major*. Yield of var. *minor* also responded stronger to cumulative ET_0 during July to August
360 compared to var. *major* with yield response to ET_0 being positive in the Northern environments.

361

362 **<Figure 7>**

363

364 **4. Discussion**

365 *4.1 Northern European target environments for faba bean production*

366 According to FAO statistics (FAOStat, 2017) faba bean yield variability in Northern and Eastern Europe
367 ranges from around $1,300 \text{ kg ha}^{-1}$ (lower 10 % quantile 2000-2014) to $3,700 \text{ kg ha}^{-1}$ (upper 10 % quantile
368 2000-2014). This range was represented very well in this study with the highest yielding environment
369 at AREI (Latvia) achieving an average yield of $3,796 \text{ kg ha}^{-1}$ in 2015 and the lowest yielding environment
370 at PHRC (Latvia) with $1,281 \text{ kg ha}^{-1}$ in the same year. Yield-based genetic correlations among locations
371 can reveal distinct groups of relevant target environments for cultivar testing (Cooper et al., 1997). In
372 this way three environmental clusters from the sites investigated in this study were identified: one low
373 yielding cluster with PHRC in 2015 representing the most stress prone environments in the region; an
374 intermediate group of environments with similar yield level (average: $2,275 \text{ kg ha}^{-1}$) comprising ECRI
375 (Estonia) and PHRC in wetter 2016; high yielding environments (average: $2,757 \text{ kg ha}^{-1}$) were
376 represented by the oceanic site of Norway and AREI.

377 Areas with continental climates at above 55° N latitudes are most vulnerable agroecosystems to heat
378 stress; areas include the Eastern part of the Baltic countries (Teixeira et al., 2013). Baltic republics,
379 together with Mediterranean countries, were also identified as European drought hotspots for the
380 period 1991–2010 (Spinoni et al., 2015). During the 2015 growing season all Baltic test environments
381 showed a marked water balance deficit between late spring and summer, coinciding with 12-17 days
382 with temperatures $>25^{\circ}\text{C}$ at AREI and PHRC, Latvia respectively, and maximum temperatures up to
383 32.3°C in early August. Furthermore Baltic countries have large areas of comparatively sandy soil with
384 low water storage capacity (Panagos, 2006) accelerating plant water stress during periods of dry spells.

385

386 4.2 Classification and intra-group diversity of faba bean types

387 *V. faba* taxonomy classifies genotypes according to seed size into three groups (*minor*, *equina*, *major*;
388 Nadal et al., 2010). In practice, however, a continuous variation for most morphological, (eco-)
389 physiological and chemical traits has been observed, making discrete differentiation of varieties
390 challenging. Based on a multivariate trait assessment including yield components, phenology, protein
391 content and plant height the two *V. faba* varieties *minor* and *major* were largely identified as distinctive
392 groups. Genotype groups with separate biplot-location than the core of var. *minor* and *major*
393 accessions emerged due to origin (Spanish and Swedish var. *major* genotypes Aguadulce and
394 Gubbenstad, respectively; Portuguese var. *minor* genotype Favel) of the varieties. This led to some
395 overlapping in cluster based distinction, where Favel together with the two Baltic var. *minor* accessions
396 (Jõgeva, old cultivar from Estonia) and Priekulu 32 (Latvian landrace) had similar characteristics to the
397 var. *major* group, particularly due to earliness. The three most distinctive traits between the studied
398 accessions of var. *minor* and var. *major* genotypes were (obviously) seed weight (increased by 50 % in
399 var. *major*), but also number of pods per node (reduced by 39 % in var. *major*), and yield (reduced by
400 27 % in var. *major*). Plants of var. *major* also had about 24 % shorter shoots. Phenological traits differed
401 by only 8 % on average—with flowering duration being the predominant phenological distinction (12
402 % longer in var. *minor*). The average protein content was similar between both groups (31.2-31.8 %).
403 Overall the genotype classification based on field phenotyping data largely confirmed the genetic
404 identification of two distinct groups of small-seeded vs. large-seeded European faba bean varieties
405 (Link et al., 1995).

406

407 However, at the level of single traits, variability within the same group (*minor/major*) can be higher
408 compared to average differences between the two groups resulting in a more continuous variation.
409 Genotyping of faba bean collections has suggested that geographical origin (Polignano et al., 1999;
410 Kwon et al., 2010) and breeding history (landraces vs. advanced varieties; Alghamdi et al., 2012)
411 essentially contribute to high diversity among accessions. This is particularly evident from the distinct

412 position of Southern genotypes per group. Considering the var. *minor* sample only, containing a more
413 balanced number of landraces (n=4) and varieties (n=5), it is demonstrated that the average yield level
414 of landraces is not significantly different from modern varieties (p -value of linear contrasts $p=0.250$),
415 even when excluding the non-adapted Southern genotype Favel. Previous evaluations of genetic
416 resources revealed that crops with less intensive breeding history, such as *Vicia faba* landraces, can
417 even have a superior yield potential compared to commercial cultivars (Karaköy et al., 2014).

418

419

420 *4.3 Phenotypical and phenological characteristics of high yielding faba bean genotypes*

421 Understanding inter-trait-relations is relevant to dissect genetically complex plant characteristics such
422 as yield to underlying components. Advantages of trait-based breeding are potentially greater
423 heritability and improved (e.g. earlier, quicker, more precise) screening of single traits (Link et al., 2007;
424 Reynolds et al., 2009). Thereby relevant determinants underlying superior yield can be identified and
425 selected in a targeted way. The most important plant characteristics in faba bean breeding according
426 to Duc (1997) comprise an early flowering phenology as well as high number of pods per node and
427 seeds per pod as yield components.

428

429 In this experiments, flowering was generally rather early (on average after 650°Cd; 0 °C base
430 temperature; Stützel, 1995; Patrick and Stoddard, 2010) compared to values reported by other studies
431 (e.g. $\approx 1000^\circ\text{Cd}$, Ellis et al., 1990). This probably reflects a photoperiodic sensitivity of faba bean towards
432 long-day conditions: at the average sowing date (6th May ± 8 days SD) day length was already >15 hours
433 at the Nordic-Baltic sites. Under long-day conditions, others previously reported vegetative growth
434 durations similar to our values (Cafalone et al., 2010; Catt et al., 2017). Several studies on phenological
435 differentiation within species collections from distinct geographical origin found early flowering and
436 maturity to be characteristic for accessions with Nordic origin. Regulator genes for photoperiod and
437 temperature optimize developmental adaptation to seasonal availability of growth factors (e.g. pea:
438 Vanhala et al., 2016; Arabidopsis: Lewandowska-Sabat et al., 2017). In this context the recent detection

439 of QTLs for flowering time in response to temperature and photoperiod for faba bean (Catt et al., 2017)
440 is very promising for selecting cultivars with phenological adaptation to a given target environment.
441 Our results thus evidenced a consistent yield advantage of those accessions with prolonged flowering
442 duration for both groups of *V. faba* genotypes. For var. *major* accessions this was in combination with
443 earliness in vegetative and generative stages, which however was strongly driven by the Southern
444 genotype Aguadulce due to high temperature requirements leading to 10 days later maturity and
445 strong yield depression. De Costa et al. (1997) demonstrated that for an indeterminate growth habit
446 in faba bean, a longer flowering duration is increasing yield under favourable environmental
447 conditions. Occurrence of stress during anthesis strongly decreases flowering duration and yield (Xia,
448 1990). A positive relation between flowering duration and seed yield was reported also for other
449 legumes such as mungo bean (Alam Mondal et al., 2011). Overall, our results thus suggested that under
450 Northern conditions an extended flowering duration with early onset of anthesis, driven by the
451 photothermal conditions at higher 55°N latitude, characterizes high yielding genotypes. Interestingly,
452 an indeterminate habit with longer flowering durations was more frequent in the studied landraces
453 than in the six varieties (p -value of linear contrasts $p < 0.001$) demonstrating their potential importance
454 as genetic resource for breeding adapted cultivars.

455

456 Plant height is a trait which allows easy and quickly phenotyping in the field (Busemayer et al., 2013).
457 A positive relation between yield and plant height, demonstrated for both var. *minor* and *major*, was
458 also reported earlier for faba bean (Link et al., 1999; Ulukan et al., 2003; Al-Rifaei et al., 2004) and for
459 other legumes (e.g. chickpea: Toker and Ilhan Cagirgan, 2004). This might be related to a link between
460 height and number of pod bearing nodes along the main stem—an essential component of yield
461 formation (Nagel, 1980; Graf and Rowland, 1987). Still selection for taller plants implies a higher risk
462 of lodging (Link et al., 2010). Concerning other yield components, only a slightly negative relation
463 between seed weight and yield was found in var. *minor*. Previously, Li and Yian (2014) and
464 Neugschwandtner et al. (2015) similarly reported no or only weak correlations of grain yield to seed
465 weight, seeds per pod or pods per plant in faba bean. However, beyond the overall yield effect var.

466 *minor* genotypes exhibited trade-offs between the single yield components, i.e. a negative relation of
467 hundred seed weight with both pods per node and seeds per pod; similar results were reported earlier
468 (López-Bellido et al., 2005; Sadras, 2007). A compensation between seed number and seed size was
469 also reported by Agung and McDonald (1998).

470

471

472 4.4 Yield potential and yield stability

473 Yield stability is of high relevance for agriculture owing to the intrinsic uncertainty in meteorological
474 conditions (Temesgen et al., 2015). Link et al. (1999) showed for faba bean that high yield in favourable
475 (well-watered) environments is correlated with yield under stress (water-limited) conditions. Such a
476 relation between yield potential and stress resistance is frequently reported for moderate stress
477 conditions, while under more severe stress specific resistance traits beyond the generic factors of yield
478 formation become determinant (Blum, 2005). The investigated genotypes in this study showed a
479 significant link between yield potential and stability, pointing to a comparatively narrow environmental
480 adaptation. In terms of yield response, all var. *major* genotypes beside the Southern cultivar Agudulce
481 showed a similar trend. The best combination of yield potential and yield stability in var. *major* was
482 achieved by Latvian landrace Cēres. The best performing genotype among var. *minor* was the Latvian
483 landrace Bauska, also combining yield potential with yield stability to a certain degree.

484 Focussing on the two extremes in var. *minor* with contrasting environmental sensitivity - being the old
485 Latvian cultivar Lielplatones (with high potential and limited yield stability) and the Latvian cultivar
486 Valmiera (with low potential and high yield stability) – two distinctive patterns in phenology and yield
487 components could be detected: Lielplatones was relatively tall in stature with a short generative
488 duration. While the hundred seed weight was lowest among all genotypes, possibly due to a shorter
489 grain-filling phase, high yield was achieved via a greater number of pods per node and seeds per pod.
490 In addition, the protein content was higher compared to the other genotypes. In contrast, Valmiera
491 had a short main stem, a long generative phase with great hundred seed weight, but was low in the
492 other yield components.

493 Within the range of target environments, less stressful conditions evidenced genotype differentiation
494 of faba bean most clearly. For wheat, favourable conditions were previously shown to maximize the
495 phenotypic variance between genotypes (Richards et al., 2010). The crossover-point between stable
496 (Valmiera) and responsive (Lielplatones) faba bean genotypes was determined at 178.2 g m^{-2} , i.e.
497 below the lower yield quartile of all environments (179.8 g m^{-2}). This implies that stable/low yielding
498 genotypes like Valmiera have an advantage only in a limited number of the target environments and
499 selection of promising accessions should be conducted on higher yielding sites based on traits
500 underlying yield potential as suggested earlier (Ceccarelli, 1989).

501

502 *4.5 Response to environmental constraints*

503 Several meteorological variables were considered as potential limiting factors for yield. The two best
504 predictors were average maximum temperatures in July and the sum of evapotranspiration during July
505 and August. While yield decreased with increasing maximum temperatures, evapotranspiration
506 showed a positive influence. The negative effect of high temperatures during flowering is well
507 documented for different crops. For faba bean, Bishop et al. (2016) demonstrated that flowering was
508 mostly affected by heat stress during early stages and that yield decreased linearly with increasing
509 temperatures (from $18/10 \text{ }^{\circ}\text{C}$ to $34/26 \text{ }^{\circ}\text{C}$ day/night). Maximum July air temperatures in the studied
510 Northern environments varied between $20.4 \text{ }^{\circ}\text{C}$ and $24.3 \text{ }^{\circ}\text{C}$ with extremes up to $30.4 \text{ }^{\circ}\text{C}$ (PHRC in
511 2015), resulting in significantly depressed yields (53 % in var. *major* and 73.4 % in var. *minor*). In
512 contrast, the positive influence of cumulative evapotranspiration during flowering and early pod filling
513 (July-August) was unexpected. Generally high ET_0 cause water stress if accompanied by low rainfall.
514 ET_0 is driven by energy balance and mass transfer (Allen et al., 1998) – thus, high ET_0 is the result of
515 high solar radiation and high gradients in water vapour concentration. As the climatic water balance
516 deficit did not significantly influence yield in this study, it is reasonable to interpret the ET influence as
517 related to the radiation component. Under limited duration of the generative phase in the Nordic-
518 Baltic environments, favourable conditions for higher assimilation during early grain filling seem to

519 positively influence yield formation. At the level of yield components, the dual nature of the
520 evapotranspiration effect (water, radiation) was reflected even more clearly. In the earlier var. *major*
521 accessions (i.e. shorter vegetative and flowering duration compared to var. *minor*) seeds per pod were
522 significantly decreased ($R^2=0.78$, $p=0.004$) by ET_0 in June and July, while hundred seed weight tended
523 to increase with higher August ET_0 ($R^2=0.62$, $p=0.020$). However, under low rainfall the ET effect can
524 become negative (i.e. high ET/P; $R^2=0.75$, $p=0.010$). The var. *minor* genotypes showed similar trends,
525 but yield components were less responsive (regressions not significant); however, a direct effect of
526 solar radiation during July could be detected—increasing the number of pods per node ($R^2=0.51$,
527 $p=0.052$). Further in-depth analysis are required to unravel the complex functional interrelation of ET
528 and yield in the studied agroecosystems.

529

530 **5. Conclusion**

531 High yielding *Vicia faba* ideotypes adapted to North European cropping systems must be able to cope
532 with the late initiation of vegetation period, long-day conditions from early vegetative phase, and
533 stress from high temperatures/limited water supply during the sensitive flowering to early pod filling
534 stages. High temperature during flowering was identified as single most critical factor limiting yield.
535 Best yielding genotypes were characterized by a tall stature and a phenological pattern combining
536 earliness (var. *major*) with prolonged duration of anthesis (var. *minor* and var. *major*). The *V. faba*
537 *minor* types had higher yield than the *major* group, with Baltic landraces of var. *minor* outperforming
538 most modern varieties tested. While a negative trade-off between yield potential and yield stability
539 was detected, superior genotypes in high yielding environments performed also better under yield
540 limiting conditions of Nordic target environments. Baltic landraces contained promising accessions,
541 combining yield potential with yield stability, such as Bauska (var. *minor*) and Cēres (var. *major*). These
542 genetic resources provide ideotypes for adapted crop phenology, stature and yield structure to guide
543 crop improvement. Future genotyping of promising accessions from this study should reveal QTLs
544 underling the identified distinctive phenotypic patterns and contribute to effectively exploit *V. faba*
545 genetic resources to breed adapted varieties for Nordic-Baltic environments.

546

547

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552

553

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