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Refining breeding methods for organic and low-input agriculture: analysis of an international winter wheat ring test

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Abstract An increasing interest in sustainable forms of agriculture exists worldwide and the demand for varieties specifically adapted to organic and low-input agriculture is rising. As a consequence, breeding methods need to be refined accordingly. In order to get better insight into needs and possibilities with this regard, a comprehensive ring test was performed from 2006 to 2008 with 14 winter wheat varieties in 36 environments in major cropping regions of Austria, France, Romania and Switzerland. Environments were grouped into 9 different subsets according to input systems, years, and countries. Input system N0 consisted of 13 organic and 6 no-input trials; 17 trials in input system N received various levels of synthetic nitrogen. For grain yield (YLD) and protein yield (PYLD), significant G × E was detected. Countries had a stronger effect on both traits than systems. Overall, it was more efficient to select YLD and PYLD in N, for targeting both systems N and N0. For PYLD, direct testing within a given country was always more efficient than indirect selection. Many traits could be scored equally well in both systems, N and N0, but for some traits particularly important for organic agriculture, such as soil coverage, better differentiation was observed under organic conditions. Therefore, we agree with other authors that a commercially sustainable breeding program for organic and low-input agriculture should combine information from high and low-input levels and from diverse regions. Local testing of varieties, however, remains indispensable.

Keywords Breeding · Genotype by environment interaction (G × E) · Low-input agriculture · Organic agriculture · Relative efficiency of indirect selection · *Triticum aestivum*

Abbreviations

H	Broad sense heritability
LI	Low-input (conventional) trials
N0	Without synthetic nitrogen supply
N	With synthetic nitrogen supply

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NI	No-input (conventional) trials
OA	Organic trials
PROT	Protein content
PYLD	Protein yield
RE	Relative efficiency of indirect selection
YLD	Grain yield

Introduction

During the last two decades, organic and low-input sustainable forms of agriculture became of increasing interest worldwide (Willer and Kilcher 2013). In Europe, organic agriculture is particularly successful in Austria and Switzerland and is supported with direct payments and production oriented subsidies (BLW 2013). Both, organic and low-input plant production systems are extensive production methods and try to minimise external inputs: Organic agriculture excludes the use of synthetic plant protection products and mineral fertiliser, while low-input agriculture seeks to reduce the use of both by applying economic threshold levels. In contrast to conventional production systems, organic and low-input wheat production have to cope with major constraints regarding plant pests and diseases, weeds and limited nutrient supply, which require an integrated control approach. Such an approach includes the use of well adapted and suitable wheat varieties, in addition to appropriate cropping techniques (Lammerts van Bueren et al. 2008; Lammerts van Bueren and Myers 2012). Besides the ability to efficiently make use of available nitrogen, important characteristics of these varieties are high disease resistance and competitiveness with weeds (Mason and Spaner 2006; Baenziger et al. 2011; Lammerts van Bueren et al. 2011; Cormier et al. 2013; Kamran et al. 2013). A series of implementable traits for the breeding of wheat varieties well suited for organic use has been compiled by Löschenberger et al. (2008).

Wheat varieties perform differently under conventional and organic systems (Reid et al. 2009, 2011; Baenziger et al. 2011; Kirk et al. 2012). Accordingly, several countries in Europe—namely Austria, France and Germany—introduced official Value of Cultivation and Use assessments (VCU). Nowadays, a large number of wheat varieties adapted to organic production conditions are available, the majority of which, however, were selected indirectly under conventional conditions for organic use (Löschenberger et al. 2008; Rolland et al. 2012; AGES 2013). The question of whether direct selection of organic varieties could be beneficial is controversial. Several studies conducted on spring wheat (Reid et al. 2009, 2011) and winter wheat (Brancourt-Hulmel et al. 2005; Murphy et al. 2007) conclude that direct selection for organic and low-input systems is more efficient than indirect selection, while indirect selection for organic use is only partially or not at all successful (Baenziger et al. 2011). Therefore, most authors suggest that separate breeding programs targeting organic production systems are necessary. Other studies suggest that breeding programs should at least include also organic besides conventional environments to maximise selection gains (Kirk et al. 2012). In fact, we can learn from CIMMYT maize breeding programs that the selection of genotypes with a very broad adaptation to mega-environments can be of advantage: The heritability of traits within a given test region determines the relative efficiency of indirect selection for performance in another target region (Falconer and Mackay 1997; Weber et al. 2012; Kebede et al. 2013).

We conducted a comprehensive ring test with a well selected, orthogonal set of high quality winter wheat genotypes over 36 diverse environments (i.e. trial by year combinations) in major cropping regions of Austria, France, Romania and Switzerland. Organic trials and conventional trials without and with various levels of synthetic nitrogen fertilization were combined in the ring test to get a broad and general picture on genotype by environment interaction (G $\times$ E) with respect to performance under organic and low-input conditions. The diverse set of data was explored post hoc to gain new insights regarding selection strategies for organic and low-input agriculture, some of which we share in this paper. Common experimental guidelines and uniform scoring methods allowed us to evaluate genotype performance, association of traits and a comparison of relative efficiencies of direct and indirect selection under different cropping systems. Furthermore, we investigated the possibility of reducing the number of selection years in a given test region by including additional environments outside the target region. Based on the results of the ring test, we draw conclusions regarding the improvement of breeding methods for organic and low-input cultivars and their assessment.

Materials and methods

Setup of ring test

We tested a set of 14 high quality winter wheat varieties which were similar in plant height and heading date. These varieties represent the outcome of breeding programs for low-input and organic agriculture in their respective countries of origin. Three varieties were contributed by each ring test partner: Aurolus, Bitop and Cornelius from Austria; Skerzzo, Renan and breeding line DI9714 from France; Ardeal, Jupiter and Junona from Romania; Siala, Titlis and Zinal from Switzerland; and two additional cultivars, Format and Naturastar, from Germany.

Table 1 Description of winter wheat ring test environments: trial ID, country, year, location, system, synthetic nitrogen supply, average temperature and sum of precipitation for the growing season

	Country[a]	Year	Location	System[b]	N_{syn} (kg/ha)	Temp. (°C)	Precip. (mm)
A1	AT	2006	Probstdorf	N	130	9.2	434
A2	AT	2007	Probstdorf	N	130	12.1	377
A3	AT	2008	Probstdorf	N	130	9.9	771
A4	AT	2006	Dörfles	OA	0	8.9	442
A5	AT	2007	Dörfles	OA	0	11.9	348
A6	AT	2008	Dörfles	OA	0	10.1	683
C7	CH	2006	Changins	N	180	9.4	767
C8	CH	2007	Changins	N	170	11.1	848
C9	CH	2006	Changins	N	100	9.4	767
C10	CH	2007	Changins	N	90	11.1	848
C11	CH	2006	Changins	NI	0	9.4	767
C12	CH	2007	Changins	NI	0	11.1	848
F13	FR	2006	Rennes	N	40	11	556
F14	FR	2008	Rennes	N	40	10.8	697
F15	FR	2006	Rennes	OA	0	11	556
F16	FR	2007	Rennes	OA	0	12.1	809
F17	FR	2008	Rennes	OA	0	10.8	697
F18	FR	2006	Le Moulon	N	100	12	372
F19	FR	2007	Le Moulon	N	100	12.4	573
F20	FR	2006	Le Moulon	OA	0	12	372
F21	FR	2007	Le Moulon	OA	0	12.4	573
F22	FR	2006	Lusignan	N	90	10.9	624
F23	FR	2007	Lusignan	N	150	11.8	1,008
F24	FR	2006	Lusignan	OA	0	10.9	624
F25	FR	2007	Lusignan	OA	0	11.8	1,008
R26	RO	2006	Fundulea	N	100	8.6	717
R27	RO	2007	Fundulea	N	100	12.9	200
R28	RO	2008	Fundulea[c]	N	100	11.6	346
R29	RO	2007	Fundulea	N	100	12.9	200
R30	RO	2006	Fundulea	NI	0	8.6	717
R31	RO	2007	Fundulea	NI	0	12.9	200
R32	RO	2007	Fundulea[c]	NI	0	12.9	200
R33	RO	2008	Fundulea	NI	0	11.6	346
R34	RO	2006	Fundulea	OA	0	8.6	717
R35	RO	2007	Fundulea	OA	0	12.9	200
R36	RO	2008	Fundulea	OA	0	11.6	346

[a] *AT* Austria, *CH* Switzerland, *FR* France, *RO* Romania

[b] *N* conventional trials with synthetic nitrogen, *NI* conventional trials without synthetic nitrogen and *OA* organic trials

[c] Irrigated trials in Romania 2007: 3 × 25 mm

In total, 36 orthogonal ring test environments (i.e. trial by year combinations) in Austria, France, Romania and Switzerland were analysed and are characterised in Table 1: 13 trials were conducted under certified organic agriculture (OA) conditions, 6 trials were conducted without synthetic nitrogen supply (NI), and 17 trials were supplied with varying levels of synthetic nitrogen (N). None of the trials received foliar fungicide.

Average precipitation during vegetation was 380 and 509 mm for Romania and Austria and 650 and 807 mm for France and Switzerland, respectively. Average temperature during vegetation varied more among trial sites in Romania (8.6–12.9 °C) and in Austria (8.9–12.1 °C) than in France (11.0–12.4 °C) and Switzerland (9.4–11.1 °C). Austrian trials were situated in the very East of the country, which like Romania belongs to the continental climate zone.

Various traits were scored routinely or whenever proper differentiation could be observed. A list of the traits scored in at least 50 % of the environments is given in Table 2. All data were recorded per plot, with the exception of protein content and hectolitre weight, where bulk samples were analysed in Austria and Romania. Soil coverage and leaf inclination at developmental stage EC32 were each scored at minimum in four N and OA environments.

Environments were split into two major subsets, termed N and N0, according to management systems. Subset N comprised the 17 trials performed with synthetic nitrogen (N_{syn}) supply; subset N0 comprised 19 trials performed without N_{syn} supply. Subset N0 consisted of 13 OA trials and 6 conventional NI trials. Since NI trials were grown exclusively in Switzerland (instead of OA trials) and in Romania, the original classification of trials into N, NI and OA (Table 1) could not be used for further analysis due to high heterogeneity within classes, which was caused by confounding country effects (Fig. 1). NI trials were therefore combined with OA trials resulting in subset N0. Additional trial subsets were formed comprising years (2006, 2007 and 2008), countries (Austria, France, Switzerland and Romania) and yield level (upper and lower yielding half of trials). These subsets were used to calculate differences in variety performance, broad sense heritability as well as relative efficiency of indirect selection (RE) for selected traits.

In order to investigate the possibility of replacing years in a testing region by including additional trial sites outside the target region, REs for grain yield (YLD) were calculated with 3 trial subsets, each composed of 12 out of the original 36 environments. Austria plus Romania were grouped as a target region based on climate data, GGE biplots (Fig. 2) and high genetic correlation values for both YLD and protein yield (PYLD) (Table 6). One N and one OA trial for years 2006, 2007 and 2008 from both Romania and Austria together served as "3 years at 4 locations" target set, and 12 environments chosen randomly from 2006 and 2007 were used to create two different "1 year at 12 locations" test sets for calculating REs under various test and target scenarios.

Table 2 Description of traits: scoring details and number of environments in which a trait was scored for systems N, NI and OA[a]

Trait	Description	Scoring details	n_N	n_{NI}	n_{OA}
YLD	Grain yield	dt/ha	17	6	13
PROT	Protein content in dry matter	%	17	6	11
PYLD	Protein yield	dt/ha; PYLD = YLD × PROT/100	17	6	11
HLW	Hectolitre weight	kg/hl	16	6	11
HD	Heading date	Days from January 1st	16	5	9
PH	Plant height	Plant height final, cm	17	6	10
LOD	Lodging susceptibility	1 (resistant)–9 (susceptible)	13	2	9
LR	Leaf rust susceptibility	1 (resistant)–9 (susceptible)	10	2	7
COV32	Soil coverage at EC 32	% soil covered	4	2	6
INCL32	Leaf inclination at EC 32	1 (upright)–9 (flag leaf curved)	5	1	4

[a] *N* conventional trials with synthetic nitrogen, *NI* conventional trials without synthetic nitrogen and *OA* organic trials

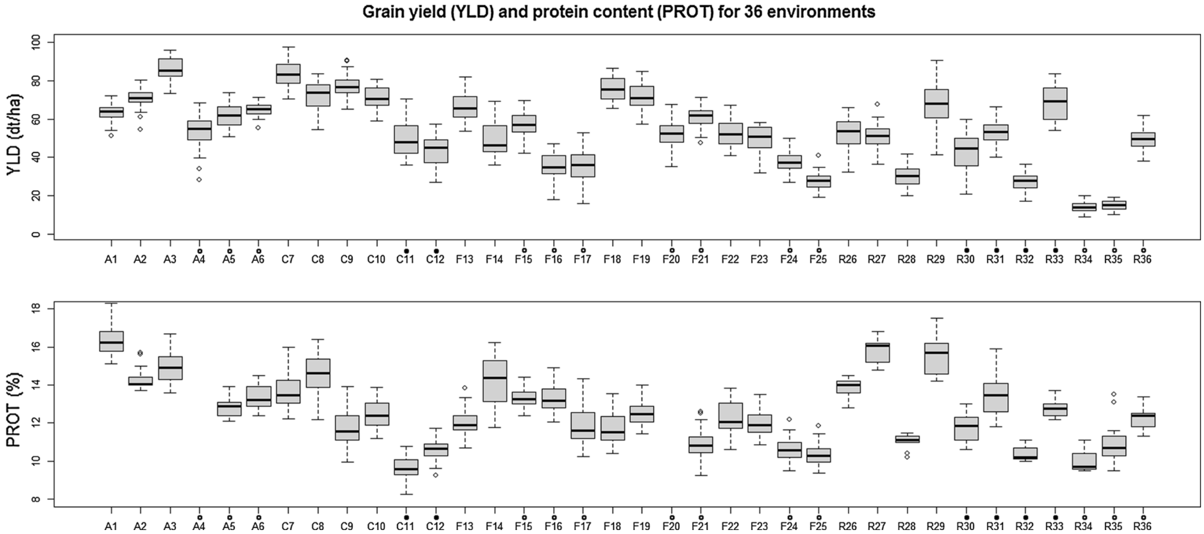

Fig. 1 Mean grain yield (YLD) and protein content (PROT) for 36 environments located in Austria (*A1–A6*), Switzerland (*C7–C12*), France (*F13–F25*) and Romania (*R26–R36*). Organic (OA) and conventional no input (NI) trials are marked with a *circle* and *filled circle*, respectively

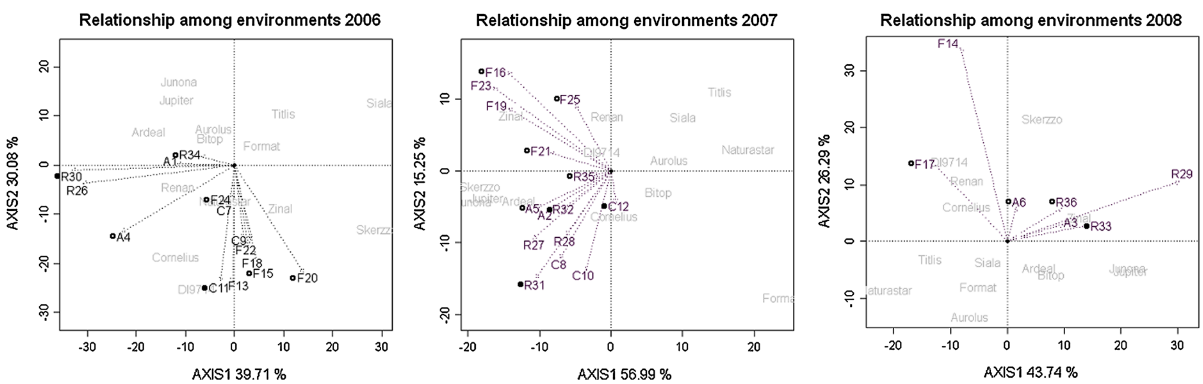

Fig. 2 Relationship among environments for 2006, 2007, 2008. GGE biplots for mean grain yield (YLD) in 36 environments located in Austria (*A1–A6*), Switzerland (*C7–C12*), France (*F13–F25*) and Romania (*R26–R36*). The angle between two vectors approximates the correlation between two environments. Organic (OA) and conventional no input (NI) trials are marked with a *circle* and *filled circle*, respectively

Statistical analysis

All trials were analysed as randomised complete blocks, with two to four blocks (replications) depending on the environment. Genotype means for phenotypic traits were estimated for each environment separately. These values were subsequently used to calculate Pearson‘s correlation coefficients between different subsets as described above. Protein content was not recorded for each plot but compiled samples per genotype for 14 out of 36 environments. Therefore, ANOVA was performed for YLD and PYLD only, and differences between management systems, years, and countries were established using Tukey‘s multiple comparison test. Variance components and broad sense heritability (H) of YLD and PYLD were calculated for each subset individually, using the model $Y_{ijkl} = \mu + g_i + e_j + ge_{ij} + r_k(e_j) + \varepsilon_{ijkl}$, where μ denotes the overall mean, g_i the genetic effect of genotype i, e_j the effect of environment j, ge_{ij} the interaction between genotype i and environment j, $r_k(e_j)$ the effect of the replication k nested in the environment j, and ε_{ijkl} the residual effect. While the genotype means in each subset were calculated by considering the genotype as fixed effect, all factors were treated as random effects for estimating the variance components. Variance components for genotype (σ^2_g), genotype by environment interaction (σ^2_{ge}), and residual (σ^2_ε) effects were expressed as a percentage of the total phenotypic variance ($\sigma^2_p = \sigma^2_g + \sigma^2_{ge} + \sigma^2_\varepsilon$). For each subset, H of YLD and PYLD was calculated as $H = \sigma^2_g/[\sigma^2_g + (\sigma^2_{ge}/e) + (\sigma^2_\varepsilon/er)]$, with e denoting the number of environments and r the number of replications.

Statistical analyses were performed with Plabstat (V3, H.Utz, Hohenheim) and SAS software version 9.2 (SAS Institute Inc. 2001; Cary, NC, USA). Boxplots and GGE biplot analysis were performed with R 3.0.1 (RDC Team 2014), the latter with the package GGE biplot GUI (Bernal and Villardon 2013).

Relative efficiency of indirect selection

The genotype means for each subset were used to calculate the genetic correlation (rg) for the different pairs of subsets as ratios between the phenotypic correlation (rp) and the square roots of YLD and PYLD H in the test (H1) and target (H2) environments: $rg = rp/(H1 \times H2)^{1/2}$. As suggested by Weber et al. (2012), the estimates of rg were allowed to exceed the upper limit of 1 but were subsequently restricted to ≤ 1 to get reasonable estimates of indirect selection: (Restricted) rg estimates were used together with H of YLD and PYLD in the test (H1) and target (H2) environments to predict the relative efficiency of indirect selection for each pair of subsets as $RE = rg\ (H1/H2)^{1/2}$. Indirect selection is recommended whenever the ratio of the correlated response (selection in the non-targeted environments) to the direct response (selection in the targeted environments) is greater than one (Baenziger et al. 2011; Weber et al. 2012).

GGE biplots and correlations

GGE biplots were used to explore the relationship between genotypes, countries, and years. Environments are displayed in column metric view without scaling of values. GGE biplots are based on mean values no matter how exact they are and do not provide any statistical evaluation (Yan and Holland 2009). In the case of metric environment means, the angle of the vectors approximately reflects the correlation coefficients between environments and hence facilitates their grouping (Yan et al. 2007; Gauch et al. 2008; Yang et al. 2009).

Pearson's coefficients of correlation were calculated for selected traits in addition to YLD and PYLD: Protein content (PROT), hectolitre weight (HLW), plant height (PH), lodging susceptibility (LOD), leaf rust resistance (LR), soil coverage (COV32) and leaf inclination (INCL32).

Results

Characterisation of environments

The performance of 14 wheat varieties was evaluated in 36 environments (Fig. 1), which show great heterogeneity for mean grain yield (YLD) and protein content (PROT).

GGE biplots were used to visualise the relationship between environments and genotypes for the years 2006, 2007 and 2008 (Fig. 2). 'Relationship among environments' plots were helpful to display the similarity between environments, as the angle between two vectors approximates the correlation coefficient between two environments. For 2006, two clusters were detected: One comprising Austrian and Romanian, the other comprising French and Swiss trials. For 2007, Romanian, Austrian and Swiss trials clustered together, whereas French trials formed a separate group. For 2008, which did not contain any Swiss trials, Romanian and Austrian trials formed one cluster, while French trials formed a separate group. For all years, organic (OA) as well as conventional no-input (NI) trials dispersed among all trial clusters.

ANOVA was performed for YLD and protein yield (PYLD) but not for PROT *per se*, because PROT data were partly measured on bulked replicates. Significant differences were found between genotypes, input systems and countries (Table 3). For both YLD and PYLD, genotype by year and genotype by country interactions were found to be significant. A significant genotype by system interaction was detected for YLD only. A grouping of the 36 environments according to their YLD level (and ignoring their system affiliation) revealed significant differences between genotypes

Table 3 ANOVA results for variables grain yield (YLD) and protein yield (PYLD): separate ANOVAs were calculated for different subsets of environments to test the impact of factors genotype (GEN), subset and interaction between genotype and subset

Variable	*F* value[a]			LSMeans[b]			
	GEN	SYS	GEN × SYS	N	N0		
YLD	8.77**	14.37**	1.57*	64.09[a]	44.74[b]		
PYLD	4.81**	18.94**	0.77 ns	8.66[a]	5.22[b]		
	GEN	YIELD	GEN × YIELD	HIGHYLD	LOWYLD		
YLD	8.19**	58.67**	1.46 ns	67.2[a]	38.95[b]		
PYLD	4.63**	57.39**	0.78 ns	9.07[a]	4.54[b]		
	GEN	YEAR	GEN × YEAR	2006	2007	2008	
YLD	8.51**	0.95 ns	2.76**	55.42[a]	49.42[a]	60.27[a]	
PYLD	4.60**	1.22 ns	1.99**	6.99[a]	6.27[a]	8.3[a]	
	GEN	COUTRY	GEN × COUTRY	AT	CH	FR	RO
YLD	8.82**	4.28**	3.31**	66.63[a]	66.07[a]	51.49[ab]	43.03[b]
PYLD	4.18**	4.18**	2.33**	9.99[a]	8.17[ab]	6.24[b]	5.65[b]

Subsets were formed according to system (SYS) with (N) and without (N0) synthetic N supply, yield level (YIELD) of upper (HIGHYLD) and lower (LOWYLD) yielding half of environments, year (2006, 2007 and 2008), and country (AT, CH, FR and RO)

[a] *ns* not significant; * $p < 0.1$; ** $p < 0.05$

[b] LSMeans followed by different letters between columns are significantly different ($p < 0.05$) according to Tukey‘s HSD test

and YLD level, but no significant interaction between these two factors (Table 3). Therefore, OA and NI trials (located in Switzerland and Romania only) were combined into N0 in order to avoid the confounding of any system effects by a country bias.

Mean performance for all three traits YLD, PROT, PYLD is clearly higher in N and similar for OA, NI and N0 conditions: Mean values for PROT were 13.5, 11.8, 11.4 and 11.7 % for N, OA, NI and N0 trials, respectively. Mean PYLD was 8.3 dt/ha for N trials, and 5.1, 5.5 and 5.2 dt/ha for OA, NI and N0 trials, respectively. For PROT the best ranking genotypes were the same in all systems.

Trait associations in systems N and N0

As expected, for all combinations of management systems, a strong positive correlation between YLD and PYLD and a negative correlation between PROT and YLD was found. PROT was positively correlated with hectoliter weight (HLW) only in N systems. Late heading date (HD) and leaf rust susceptibility (LR) had a negative impact on PYLD in both systems. Like YLD, PROT and PYLD, genotype means for lodging susceptibility (LOD), soil coverage (COV32) and leaf inclination (INCL32) at EC stage 32 were also highly correlated ($r > 0.8$) among systems N and N0 (Table 4). LOD was correlated with INCL32 within N ($r = 0.75$), but not within N0 trials. Taller genotypes were more prone to lodging under both N and N0 conditions. While tall cultivars yielded less under N supply, no such effect was found for N0, not even when OA and NI data were processed separately (data not shown). In contrast to what was observed for LOD, COV32 and INCL32 were strongly correlated with each other under N0 ($r = 0.84$) but not under N management conditions. COV32 was scored in 6 OA, 2 NI and in 4 N trials, standard deviation and thus discrimination ability of genotype mean COV32 results was about double in OA and N0 as compared to the NI and N systems (13.0 and 10.4 for OA and N0 vs. 5.4 and 4.3 for NI and N, respectively).

Relative efficiency of indirect selection for different test and target environments

For YLD and PYLD, variance components for genotype, genotype by environment (e.g. system N/N0) interaction and residual variance as well as broad sense heritability (H) are shown for systems, years and countries in Table 5. H for both YLD and PYLD was markedly higher for N compared to N0. Within N0, H

Table 4 Correlation coefficients r[a] for genotype means of grain yield (YLD), protein content (PROT), protein yield (PYLD), heading date (HD), final plant height (PH), lodging susceptibility (LOD), leaf rust susceptibility (LR), soil coverage (COV32) and leaf inclination at EC32 (INCL32) in systems with (N) and without (N0) synthetic nitrogen supply

	YLD		PROT		PYLD		HLW		HD		PH	
	N	N0	N	N0	N	N0	N	N0	N	N0	N	N0
YLD												
N	1.00	0.80	−0.81	−0.85	0.75	0.56	ns	ns	−0.49	−0.54	−0.60	−0.65
N0	0.80	1.00	−0.59	−0.76	0.64	0.80	ns	ns	ns	ns	ns	ns
PROT												
N	−0.81	−0.59	1.00	0.88	ns	ns	0.55	0.57	ns	ns	0.52	0.61
N0	−0.85	−0.76	0.88	1.00	ns	ns	ns	ns	ns	ns	ns	ns
PYLD												
N	0.75	0.64	ns	ns	1.00	0.82	ns	0.49	−0.81	−0.84	ns	ns
N0	0.56	0.80	ns	ns	0.82	1.00	0.50	0.54	−0.66	−0.69	ns	ns
HLW												
N	ns	ns	0.55	ns	ns	0.50	1.00	0.98	−0.58	−0.56	ns	ns
N0	ns	ns	0.57	ns	0.49	0.54	0.98	1.00	−0.63	−0.60	ns	ns
HD												
N	−0.49	ns	ns	ns	−0.81	−0.66	−0.58	−0.63	1.00	1.00	ns	ns
N0	−0.54	ns	ns	ns	−0.84	−0.69	−0.56	−0.60	1.00	1.00	ns	ns
PH												
N	−0.60	ns	0.52	ns	ns	ns	ns	ns	ns	ns	1.00	0.99
N0	−0.65	ns	0.61	ns	ns	ns	ns	ns	ns	ns	0.99	1.00
LOD												
N	ns	ns	ns	ns	ns	ns	0.51	ns	ns	ns	0.79	0.77
N0	ns	ns	ns	ns	ns	0.50	0.61	0.54	ns	ns	0.53	0.54
LR												
N	−0.52	−0.46	ns	ns	−0.67	−0.64	ns	ns	0.46	0.48	ns	ns
N0	−0.55	−0.52	ns	0.47	−0.65	−0.63	ns	ns	ns	ns	ns	ns
COV32												
N	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	0.51	0.49
N0	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	0.60	0.58
INCL32												
N	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	0.70	0.70
N0	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	0.63	0.61

	LOD		LR		COV32		INCL32	
	N	N0	N	N0	N	N0	N	N0
YLD								
N	ns	ns	−0.52	−0.55	ns	ns	ns	ns
N0	ns	ns	−0.46	−0.52	ns	ns	ns	ns
PROT								
N	ns	ns	ns	ns	ns	ns	ns	ns
N0	ns	ns	ns	0.47	ns	ns	ns	ns
PYLD								
N	ns	ns	−0.67	−0.65	ns	ns	ns	ns
N0	ns	0.50	−0.64	−0.63	ns	ns	ns	ns

Table 4 continued

	LOD		LR		COV32		INCL32	
	N	N0	N	N0	N	N0	N	N0
HLW								
N	0.51	0.61	ns	ns	ns	ns	ns	ns
N0	ns	0.54	ns	ns	ns	ns	ns	ns
HD								
N	ns	ns	0.46	ns	ns	ns	ns	ns
N0	ns	ns	0.48	ns	ns	ns	ns	ns
PH								
N	0.79	0.53	ns	ns	0.51	0.60	0.70	0.63
N0	0.77	0.54	ns	ns	0.49	0.58	0.70	0.61
LOD								
N	1.00	0.86	ns	ns	0.48	0.73	0.75	0.64
N0	0.86	1.00	ns	ns	ns	0.60	0.52	ns
LR								
N	ns	ns	1.00	0.97	ns	ns	ns	ns
N0	ns	ns	0.97	1.00	ns	ns	ns	ns
COV32								
N	0.48	ns	ns	ns	1.00	0.80	ns	0.56
N0	0.73	0.60	ns	ns	0.80	1.00	0.74	0.84
INCL32								
N	0.75	0.52	ns	ns	ns	0.74	1.00	0.90
N0	0.64	ns	ns	ns	0.56	0.84	0.90	1.00

[a] Significance levels for Pearson‘s correlation coefficient $r > 0.458$ $p < 0.1$; for $r > 0.532$ $p < 0.05$; for $r > 0.661$ $p < 0.01$ and for $r > 0.780$ $p < 0.001$

of YLD was higher for the 13 OA trials (H = 0.61) than for the 6 NI trials (H = 0.44). With respect to different years and countries, H varied greatly: The lowest values for H were observed for year 2008 and Austria, the highest for year 2007 and France (Table 5).

Phenotypic (rp) and genetic (rg) correlation, as well as relative efficiency of indirect selection (RE) values are depicted in Table 6 for the test and target environments subject to investigation. For both traits, YLD and PYLD, it was more efficient to test in system N in order to select for target system N0 or N.

Using 2006 as a test environment for years 2007 and 2008 was not sufficient for YLD and even misleading for PYLD. Correspondingly, indirect selection in both 2007 and 2008 gave false results for 2006. Indirect selection in 2007 for 2008 was more efficient than direct selection in the year 2008 for YLD and PYLD. Testing in year 2008 for 2007 was only about half as efficient as testing directly in 2007. However, one has to take into account that the number of trial sites used in 2008 was half that of 2007.

Most REs for YLD calculated between countries were poor or even detrimental (due to low rg values), with the exceptions of Austria and Romania, and Austria and Switzerland: Due to low H of YLD in Austria, indirect selection in Romania or Switzerland was slightly more efficient. Indirect selection for PYLD was inefficient or even erroneous in all cases of country comparisons.

With an equal number of 12 trials, mimicking identical trialling costs, replacement of testing years by including additional trial sites from outside the Austrian-Romanian target region gave good results for the year 2007, but poor results for 2006 (Table 7). Even when we chose both the yearly test group and target environment group randomly, or by eliminating the trials with the worst repeatability (data not shown), results were similar to those in Table 7.

Table 5 Variance components and broad sense heritability (H) for (a) grain yield (YLD) and (b) protein yield (PYLD) for different subsets of environments: subsets were formed according to system with (N) and without (N0) synthetic nitrogen supply, year (2006, 2007 and 2008), and country (AT, CH, FR and RO)

(a) YLD (dt/ha)									
Test environment	n environments					Variance components[a]			
System	n_{env}	n_{AT}	n_{CH}	n_{FR}	n_{RO}	σ_g^2	σ_{ge}^2	σ_{re}^2	H
N	17	3	4	6	4	21.2	49.2	29.5	0.86
N0	19	3	2	7	7	7.7	64.6	27.7	0.67
Year	n_{env}	n_{AT}	n_{CH}	n_{FR}	n_{RO}	σ_g^2	σ_{ge}^2	σ_{re}^2	H
2006	14	2	3	6	3	16.8	54.1	29.1	0.79
2007	15	2	3	5	5	31.2	33.5	35.2	0.91
2008	7	2	0	2	3	9.8	71.9	18.3	0.47
Country	n_{env}	n_{AT}	n_{CH}	n_{FR}	n_{RO}	σ_g^2	σ_{ge}^2	σ_{re}^2	H
AT	6	6				15.7	55.7	28.6	0.59
CH	6		6			22.2	29.6	48.2	0.74
FR	13			13		27.5	46.7	25.8	0.87
RO	11				11	28.1	50.9	21.0	0.84

(b) PYLD (dt/ha)									
Test environment	n environments					Variance components[a]			
System	n_{env}	n_{AT}	n_{CH}	n_{FR}	n_{RO}	σ_g^2	σ_{ge}^2	σ_{re}^2	H
N	17	3	4	6	4	8.2	51.1	40.7	0.68
N0	17	2	2	6	7	5.0	58.8	36.2	0.58
Year	n_{env}	n_{AT}	n_{CH}	n_{FR}	n_{RO}	σ_g^2	σ_{ge}^2	σ_{re}^2	H
2006	13	1	3	5	3	6.1	51.7	42.2	0.56
2007	15	2	3	5	5	21.7	32.9	45.4	0.86
2008	7	2	0	2	3	3.9	71.1	25.0	0.26
Country	n_{env}	n_{AT}	n_{CH}	n_{FR}	n_{RO}	σ_g^2	σ_{ge}^2	σ_{re}^2	H
AT	5	5				8.9	41.4	49.7	0.47
CH	6		6			14.9	27.5	57.6	0.66
FR	12			12		16.8	46.8	36.3	0.79
RO	11				11	16.4	57.9	25.7	0.73

[a] Variance components expressed as a percentage of the total phenotypic variance including the genotype (g), genotype x environment (ge), and the residual (re) variance

Discussion

Selection of environments, genotypes, and traits

We investigated a set of 36 diverse environments for selection of varieties suitable for organic and low-input agriculture, in order to account for the tremendous diversity of organic and other low-input environments to which organic and low-input varieties need to be adapted to. Trial sites and their exact management, in particular with regard to the amount of synthetic N supplied, were chosen by each partner. Higher N input trials according to local agricultural practice were also included (Table 1), but none of the trials received foliar fungicides. Test environments were highly variable, as shown by climate data and environment mean results for YLD, PROT and PYLD (Table 1; Fig. 1).

The genotypes chosen for this study were 14 wheat varieties. This is a limited number compared to the potentially large field of application of the below stated conclusions. However, this set was applied orthogonally and hence results are comparable across environments. All varieties have high baking quality,

Table 6 Phenotypic correlation, genetic correlation and relative efficiency of indirect selection for grain yield (YLD) and protein yield (PYLD) for different subsets of environments: subsets were formed according to system with (N) and without (N0) synthetic nitrogen supply, year (2006, 2007 and 2008), and country (AT, CH, FR and RO)

(a) YLD (dt/ha)

Test environment	Target environment											
	Phenotypic correlation (rp)				Genetic correlation (rg)				Selection efficiency (RE)[a]			
System	N	N0			N	N0			N	N0		
N	1.00	0.79			1.16	1.04			1.00	1.14		
N0	0.79	1.00			1.04	1.50			0.88	1.00		
Year	2006	2007	2008		2006	2007	2008		2006	2007	2008	
2006	1.00	0.27	0.26		1.27	0.31	0.43		1.00	0.29	0.55	
2007	0.27	1.00	0.83		0.31	1.10	1.27		0.34	1.00	1.39	
2008	0.26	0.83	1.00		0.43	1.27	2.13		0.33	0.72	1.00	
Country	AT	CH	FR	RO	AT	CH	FR	RO	AT	CH	FR	RO
AT	1.00	0.65	0.22	0.73	1.69	0.97	0.30	1.04	1.00	0.87	0.25	0.84
CH	0.65	1.00	0.59	0.27	0.97	1.34	0.73	0.34	1.09	1.00	0.68	0.32
FR	0.22	0.59	1.00	−0.01	0.30	0.73	1.15	−0.01	0.37	0.79	1.00	−0.01
RO	0.73	0.27	−0.01	1.00	1.04	0.34	−0.01	1.19	1.19	0.36	−0.01	1.00

(b) PYLD (dt/ha)

Test environment	Target environment											
	Phenotypic correlation (rp)				Genetic correlation (rg)				Selection efficiency (RE)[a]			
System	N	N0			N	N0			N	N0		
N	1.00	0.79			1.48	1.26			1.00	1.08		
N0	0.79	1.00			1.26	1.73			0.92	1.00		
Year	2006	2007	2008		2006	2007	2008		2006	2007	2008	
2006	1.00	0.24	−0.11		1.78	0.34	−0.30		1.00	0.27	−0.44	
2007	0.24	1.00	0.73		0.34	1.16	1.54		0.42	1.00	1.84	
2008	−0.11	0.73	1.00		−0.30	1.54	3.89		−0.20	0.54	1.00	
Country	AT	CH	FR	RO	AT	CH	FR	RO	AT	CH	FR	RO
AT	1.00	0.15	−0.05	0.37	2.11	0.26	−0.08	0.62	1.00	0.22	−0.07	0.50
CH	0.15	1.00	0.33	0.29	0.26	1.52	0.45	0.42	0.31	1.00	0.41	0.39
FR	−0.05	0.33	1.00	0.14	−0.08	0.45	1.27	0.19	−0.11	0.50	1.00	0.20
RO	0.37	0.29	0.14	1.00	0.62	0.42	0.19	1.37	0.77	0.44	0.18	1.00

[a] Calculation of RE was based on rg estimates restricted to ≤1

similar heading date (earliness), and plant height. Similarity in earliness among the test varieties avoids interference with the other morphological and physiological traits (Cormier et al. 2013). The genetic background of the tested varieties is broad, despite the restriction to 14 genotypes, i.e. it covers the whole testing region and involves a strong accent on contrasting local adaptation.

The main agronomic traits analysed in our study with regard to selection efficiency in N and N0 systems were YLD and PYLD. Use of PYLD is an evasion of the strong negative correlation that was observed between YLD and PROT (Table 4). Furthermore, PYLD is important in agricultural practice, since throughout Europe organic farmers obtain premiums for high PROT. PYLD is also used by breeders as a simple selection index for ranking genotypes with regard to yield and quality simultaneously. Similarly, PYLD of a given variety can serve as an approximation for its nitrogen use efficiency

Table 7 Phenotypic correlation, genetic correlation and relative efficiency of indirect selection for grain yield (YLD) for different subsets of test and target environments: 2006 and 2007 represent "1 year at 12 locations" test sets, 2006–2008 represents a "3 years at 4 locations" test set

Test environment					Target environment								
					Phenotypic correlation (rp)			Genetic correlation (rg)			Selection efficiency (RE)		
	Country	n_{env}	n_{total}	*H*	2006	2007	2006–2008	2006	2007	2006–2008	2006	2007	2006–2008
2006	AT	*2*	*12*	0.74	1.00	0.23	0.41	1.35	0.28	0.56	1.000	0.259	0.560
	CH	*2*											
	FR	5											
	RO	3											
2007	AT	*2*	*12*	0.89	0.23	1.00	0.86	0.28	1.12	1.07	0.311	1.000	1.180
	CH	*3*											
	FR	3											
	RO	4											
2006–2008	AT	6	12	0.73	0.41	0.86	1.00	0.56	1.07	1.37	0.553	0.968	1.000
	RO	6											

2006 and 2007 include environments from all 4 countries (AT, CH, FR and RO) whereas environments chosen for 2006–2008 represent AT and RO only. For 2006–2008, two environments for both AT and RO were chosen for each of the 3 years

(Oberforster and Werteker 2009; AGES 2013). Moreover, in Austria, PYLD is used as decision criterion for variety release (AGES 2013).

Beyond investigation of the relative efficiency of indirect selection of these main traits, the here presented ring test allowed for exploration of secondary traits more relevant to low-input and organic varieties, e.g. soil coverage and leave inclination at early growth stages, in contrasting environments.

Relative efficiency of indirect selection

Indirect selection is recommended whenever the ratio of the correlated response (selection in non-target environments) to the direct response (selection in the target environments) is greater than one (Baenziger et al. 2011; Weber et al. 2012). Predicted response to selection in one region compared to response in another is mainly determined by genetic correlation (rg) between regions—with a high rg accounting for broad adaptation (Przystalski et al. 2008)—and broad sense heritability of a given trait (Weber et al. 2012).

The presented post hoc investigation aimed to determine the REs regarding different systems, years and countries. Overall, countries and years had a markedly larger effect than systems, which was shown by higher genotypic variance components within countries and years as compared to systems. The comparison of systems, grouped into N and N0, showed that selection in N was more effective for N0 than vice versa. When considering years, 2007 proved very effective for the selection of superior genotypes with respect to YLD and PYLD for 2008, whereas indirect selection in—and also for—2006 was not efficient. These specific results are explained by severe frost damage prevalent only in 2006 in Romania and Austria, showing that a single limiting factor can cause very specific adaptation needs. For PYLD direct selection in the target country was always more effective than indirect selection in any other country (Table 6). We conclude that local adaptation plays a major role and is more important than specific adaptation to a specific cropping system.

In this context, we investigated the possibility of replacing years in a given testing region by including additional environments from outside that region by combining information of GGE biplots with that of REs. Such a posteriori clustering was also used by Baenziger et al. (2011). This approach allowed us to group East Austrian and Romanian trials together into one target region, as, in all 3 years, trials from East Austria and Romania cluster more closely to each other than to those of France and Switzerland. The validity of this grouping is supported by similar local temperature and precipitation data (Table 1), and high rg values for both YLD and PYLD (Table 6).

However, selection efficiency for this continental East Austrian-Romanian target region was best in 2007 when Switzerland and France were included, and better than 3 years of testing in the target region alone. Again, testing in the target region in 2006 was not representative for other trial subsets, neither for 2007 nor for 3 years testing. We conclude from our data that strong local and specific year events (e.g. frost damage) can reduce selection efficiency. This may be countered by simultaneously selecting in distinct geographical regions.

Breeding wheat for organic and low-input systems

Our results support the hypothesis that selection efficiency can be increased by combining N and N0 environments. For specific traits that are mainly relevant in organic agriculture (e.g. soil coverage), this work gave evidence that direct selection in organically managed fields provides a better differentiation of these traits. Interestingly, inter-trait correlation among COV32 and INCL32 is systematically better in N0 than in N trials. The same holds true for scoring of tillering capacity, where differentiation is lower in N trials than in N0 (data not shown). In N fertilised trials, tillering is promoted by readily available nitrogen in early spring for all genotypes, thus leading to higher tiller numbers and less differentiation among genotypes. This finding gives evidence that traits conferring weed suppression capacity are more efficiently scored under organic or N0 conditions, even in the absence of weed. This is in line with long year practical experience of breeding in organic conditions (Löschenberger 2009). Several authors confirm that combining information from both organic and non-organic systems is beneficial when breeding for low input and organic systems. Reid et al. (2011) suggest that selection for grain yield in organic systems should be conducted within organic systems. It was evident however in their study that data obtained from conventional yield trials also had some relevance for breeding for organic environments. Baenziger et al. (2011) suggest selection in the early generations for highly heritable traits in either the conventional or organic system. However, in later generations when the number of testing sites is increased, G $\times$ E is larger and less heritable traits are studied, separate testing programs in conventional and organic (Baenziger et al. 2011) or on nitrogen deficient systems are recommended (Stagnari et al. 2013). Przystalski et al. (2008) argue that based on the assumption that the ranking of varieties for key plant traits differs between an organic and a conventional cropping system, an independent system of organic variety trials may be required for selection. Genotype by system interaction was found by Hildermann et al. (2010) and Wortman et al. (2013).

Our data let us assume two classes of traits: Those, where available nitrogen increases differentiation (e.g. YLD, PH); and those where it blurs differentiation (e.g. COV32, INCL32). Therefore, it may be promising to work with both types of environments (N and N0). If traits are highly correlated among systems, it does not matter under which conditions selection is performed. Equally, special attention should be given to limiting factors, like winter hardiness, causing strong GxE.

Conclusion

The results of the here presented ring test provide evidence that breeding for organic and low-input agriculture can benefit from a higher selection efficiency achieved by combining data from organic and conventional trials. Specific adaptation to a region or country, however, is more important than adaptation to the cropping system and makes local testing of a variety indispensable. Direct selection can be advantageous for some traits that are mainly relevant in organically managed fields, e.g. soil coverage, due to better differentiation under low or no-input conditions. Taken together, we suggest that a commercially sustainable breeding program for organic and low-input agriculture should combine information from diverse input levels and from diverse regions.

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