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O. Chloupek · P. Hrstkova

Adaptation of crops to environment

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Abstract Adaptability is defined as the ability of a crop (or variety) to respond positively to changes in agricultural conditions. The trait is genetically controlled and provides an ability to exploit environmental attributes, both natural and agronomic. Values of relative adaptability can be determined by the regression of the yield of the tested crop over the average yield of compared crops from several environments. We evaluated relative adaptability of 12 staple crops in 12 European countries and compared the yield data over a 43-year period from 1961 to 2003. An additional set of average yield data was also available for the 15 European Union (EU15) member countries. A wider range of 26 crop species was investigated that allowed comparisons between Europe and the USA between 1961 and 2003. Adaptability was closely related to the annual yield increases of the crops studied ($r^2=0.999$ both in the EU15 and the USA). However, the adaptability of certain crops differed between the two regions. Pulse, maize, millet, wheat and sorghum showed the highest adaptability in the EU15 region, whereas strawberry, pear, tomato, walnut and maize were highest in the USA. The lowest adaptability was found for walnut, pear, apple, cauliflower and hop in the EU15 and for mustard, hop, sugar beet, millet and oat in the USA. In European countries, crops with similar biology, environment and agronomical practices (like the amount of fertilizers and pesticides applied) tended to have similar adaptability values. The data indicate that high adaptability is an important prerequisite for continued yield gains in the best environments.

Keywords Adaptability · Crops · Europe environment · US environment · Response to environment · Genotype × environment · Yield

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O. Chloupek (✉) · P. Hrstkova
Mendel University, Zemedelska 1, 613 00 Brno, Czech Republic
E-mail: chloupek@mendelu.cz

Introduction

Agricultural crops originated from nine homelands (Fertile Crescent, China, Eastern US, etc.) and became adapted to new environments as they advanced across the world (Diamond 2002). The spread exposed the crops to selection pressures, which were absent from their origins. Human selection favoured characteristics of low selective value in the wild and a dependence on man-made habitats (Harlan 1992). Variability in adaptability to different environments has been reported at both the species and the variety levels (e.g. Dencic et al. 2000; Banziger and Cooper 2001). Adaptability generally falls into two classes: (1) the ability to perform at an acceptable level in a range of environments, general adaptability (e.g. Dencic et al. 2000; Farshadfar and Sutka 2003) and (2) the ability to perform well only in fertile environments, specific adaptability (Chloupek et al. 2003).

Adaptability is the result of genotype × environment interactions. The genetic component involves both major and minor genes. Single genes for vernalisation requirement, photoperiod insensitivity and semidwarfism played a major role in adapting wheat and rice to new environments, including high input systems. Minor genes for adaptability have been discovered by quantitative traits locus (QTL) analysis. QTLs responsible for general adaptability (rainfed and irrigated conditions) and for specific adaptability to rainfed conditions were also identified in wheat (Farshadfar and Sutka 2003; Kato et al. 2000). AFLP markers were identified separately for yield, adaptability (evaluated by regression slope) and stability (Kraakman et al. 2004). For example two QTLs for adaptability in treated variant were mapped on chromosome 1 of barley linked to QTLs for yield and its stability. Environmental effects include natural factors such as geography, climate, season and human factors such as agronomy (Chloupek et al. 2004; Dencic et al. 2000; Farshadfar and Sutka 2003).

Breeding for general or specific adaptability is a serious issue in the development of commercially viable cultivars. Recent studies (e.g. white clover) have shown that yield of a new variety with higher yield potential was only realised in the most favourable environments (Chloupek et al. 2003). The objective of this article was to investigate the phenomenon and its implications further. Adaptation of a wide range of crops was investigated using publicly available yield data for several countries over several seasons. The data allowed us to make comparisons between crops and between countries/regions (Europe and the USA) over a 43-year period.

Materials and methods

Adaptability of crops was determined by the linear regression of yield (dependent variable) on years (independent variable). A similar method has been used widely in the evaluation of varieties within a crop (Finlay and Wilkinson 1963). The regression coefficient (slope) of each variety can then be compared among varieties and in different environments. Adaptability can be interpreted as follows: (a) slope <1, indicates a low response (adaptability for non-favourable environments); (b) slope $=1$, average response; (c) slope >1, high response (adaptability for fertile environments). The regression coefficient is compared over different favourable environments (years and locations), given by the average yield of the varieties compared. Average yield level of an environment for each year was determined as the average yield potential for all the crops (without regard to their area or importance) in a particular year. The yield potential for a crop was given as an index: $i = x_i/\bar{x}$, where x_i was the yield of the crop in 1 year and $\bar{x}$ the average yield of the crop over the whole studied period. Hierarchical cluster analysis was used for the evaluation, and dendrograms were constructed based on Euklid distances and *average between groups clustering procedure* (UNISTAT 5.1). Absolute (not relative) yields were used for the evaluation.

Adaptability was calculated for two purposes: (a) to determine the adaptability of various crops within a particular country/region and (b) to determine which country/region was most suited to a particular crop. For the approach (a), adaptability was evaluated for 26 fields, vegetables and fruit tree crops in the USA and the EU15. The EU15 comprised the 15 member countries of the EU between 1961 and 2003: Austria, Belgium, Denmark, Finland, France, Germany, Greece, Ireland, Italy, Luxembourg, Netherlands, Portugal, Spain, Sweden and the UK. Data for 12 staple crops in a different set of 12 European countries were also analysed: Austria, the Czech Republic (CZ), France, Germany, Hungary, Italy, the Netherlands, Poland, Romania, the former Soviet Union (SU), Spain and the UK. The average yield of the 15 European Union (EU15) countries was also included as an additional 13th "country".

In the first approach, the independent variable was the average yield of the 26, or 12, crops in a particular country and in the second approach the average yield of each of the 12 crops over all the countries. The dependent variable was the yield of a particular crop in one country during 1961–2003, for which data were available. The crops investigated are given in Table. 1 and 2. The values of adaptability in a particular country were compared with relative yield increment of the crop in the country by linear correlation. Statistical data were obtained from the Web site of the Food and Agriculture Organization (FAO) of the United Nations, 1961–2003 (http://www.fao.org).

Results

Adaptability of crops within countries

Table 1 gives yield data for 26 crops in the EU15 and the USA over the 43-year period (1961–2003). From the table, it can be seen that the greatest increases in yields were found for pulse, maize, millet and wheat (3.83, 2.78, 2.53 and 2.43% per year, respectively; column C in Table 1) in the EU15, and for strawberry, tomato, pear and walnut (4.18, 2.24, 2.21 and 2.04% per year, respectively) in the USA. Yield declines were greatest for walnut, pear, apple and cauliflower (2.86, 0.90, 0.75 and 0.20% per year) in the EU15. No decline was found for any crop in the USA, but mustard yields were static (0.00) and increases in yields of hop, millet and sugar beet were marginal (0.30, 0.51 and 0.53% yearly, respectively).

Similar adaptability values between the EU15 and the USA crops were found for barley, cabbage, carrot, hop, mustard, oat, peach, potato, sunflower and tomato (zero values in column E of Table 1). However, the adaptability of the crops in the EU15 and the USA was not always mutually correlated; significantly higher values in the EU15, compared to the USA, were found for maize, millet, pea, pulse, rye, sorghum, soybean, sugar beet and wheat. Conversely, the USA had higher adaptability values for apple, cauliflower, pear, rice, spinach, strawberry and walnut.

Linear correlation coefficients between the relative average yield increase per year (column C) and adaptability (columns D) of the crops were the same for both the EU15 and the USA (0.999, Table 1). Diversity of adaptability in the EU15 was greater than in the USA since the standard deviation for the average adaptability was greater (1.123 compared to 0.634).

Correlations between adaptability and increasing yield were found for particular European countries: Austria, CZ, France, Germany, Hungary, Italy, the Netherlands, Poland, Romania, the former SU, Spain and the UK (0.933, 0.830, 0.998, 0.995, 0.538, 0.992, 0.975, 0.981, 0.982, 0.933, 0.972 and 0.997, respectively). However, only 9–12 staple crops could be evaluated, as not all crops were grown in all countries. All the values, with the exception of Hungary, were highly significant.

Table 1 Yield increases and adaptability of 26 crops to the EU15 and the USA environments over a 43-year period (1961–2003)

Crop	EU15				USA				E
	A	B	C	D	A	B	C	D	
Apple	29.14	−219	−0.75	-0.49^{bc}	21.16	314	1.48	1.20^{hij}	−
Barley	3.66	46	1.27	1.09^{hi}	2.64	32	1.21	0.99^{fgh}	0
Cabbage	25.30	174	0.69	0.60^{ef}	19.99	149	0.75	0.59^{cd}	0
Carrot	36.01	460	1.28	1.09^{ghi}	31.00	360	1.16	0.93^{efg}	0
Cauliflower	16.85	−34	−0.20	-0.17^{c}	12.77	183	1.43	1.13^{ghij}	−
Hop	1.60	−1	0.00	-0.03^{cd}	1.96	6	0.30	0.23^{b}	0
Maize	5.92	164	2.78	2.35^{m}	6.40	110	1.72	1.41^{j}	+
Millet	2.59	66	2.53	2.19^{lmn}	1.36	7	0.51	0.49^{bcd}	+
Mustard	1.39	3	0.24	0.24^{de}	0.95	1	0.00	-0.01^{a}	0
Oat	2.93	27	0.94	0.82^{fg}	1.92	13	0.68	0.57^{cd}	0
Peach	13.11	147	1.12	0.99^{ghi}	15.24	117	0.77	0.62^{cde}	0
Pear	20.28	−182	−0.90	-0.66^{b}	23.88	529	2.21	1.78^{k}	−
Pea	3.17	70	2.22	1.91^{klm}	2.09	26	1.26	1.05^{defghi}	+
Potato	25.66	442	1.72	1.46^{jk}	31.10	479	1.54	1.21^{ij}	0
Pulse	1.81	69	3.83	3.16^{n}	1.61	14	0.87	0.70^{de}	+
Rice	5.56	42	0.75	0.64^{ef}	5.67	69	1.21	0.94^{fg}	−
Rye	3.14	65	2.06	1.74^{jkl}	1.60	11	0.69	0.58^{cd}	+
Sorghum	4.34	98	2.25	1.93^{l}	3.59	27	0.75	0.67^{cdef}	+
Soybean	2.43	49	2.02	1.69^{jkl}	2.07	25	1.20	0.99^{fgh}	+
Spinach	15.00	90	0.60	0.50^{e}	13.69	197	1.44	1.12^{ghi}	−
Strawberry	14.09	124	0.88	0.78^{fg}	23.66	989	4.18	3.26^{l}	−
Sugar beet	46.31	643	1.39	1.18^{i}	44.48	234	0.53	0.45^{bc}	+
Sunflower	1.29	17	1.35	1.18^{fghij}	1.26	12	0.96	0.82^{defg}	0
Tomato	41.06	941	2.29	1.91^{l}	47.03	1054	2.24	1.76^{k}	0
Walnut	4.39	−126	−2.86	-2.17^{a}	2.38	48	2.04	1.62^{jk}	−
Wheat	4.08	99	2.43	2.07^{lm}	2.28	26	1.14	0.92^{efg}	+
Average adaptability	1.00 +/−1.123				1.00 +/−0.634				

Pulse is rather a heterogeneous group (consisting of different legumes in different countries), but used in the FAO statistics
A Average yield during 1961–2003 (t/ha)
B Average yield increment per year (kg/ha) as a regression coefficient with time (all the values were significant with the exception of hop in the EU and mustard in the EU and the USA)
C Per cent of the yields' increment per year of the average yield (B as a per cent of A)
D Adaptability of the crops (regression coefficient) within the EU15 and the USA, respectively. The figures in the columns followed by the same letters are not significantly different ($P = 0.05$)
E Comparison of adaptability in the EU15 with the USA [+, significantly ($P = 0.05$) higher value in the EU15; −, significantly lower in the EU15 than in the USA; 0, without significant difference]

The level of adaptability of crops within Europe was also evaluated. Analysis of variance showed significant differences between the 12 crops evaluated. Average values of adaptability of a crop within the countries, including the EU15, were used for this purpose (Table 2).

Table 2 Average adaptability of crops within European countries (given in Table 3)

Crop	Number of countries	Average adaptability
Pulse	13	1.34 c
Maize	11	1.30
Wheat	13	1.26 bc
Rye	13	1.20 abc
Pea	13	1.18 abc
Barley	13	1.08 abc
Oat	13	0.97 abc
Potato	13	0.89 ab
Sugar beet	13	0.79 a
Rapeseed	12	0.78
Wine grape	9	0.65
Hop	10	0.31

It can be seen from Table 2 that the adaptability of pulse, maize and wheat in Europe was significantly higher than that of sugar beet and probably also of rapeseed, wine grape and hop. Adaptability for particular crops was similar when the crops shared similar biology and agronomy (barley and oats, rye and wheat, potato and sugar beet).

Adaptability comparisons for the 12 European countries and the EU15 (without regard to the adaptability of crops in the particular countries)

Thirteen European 'countries' (EU15 included here as a 'country') with the highest and lowest adaptability values are given in Table 3. Average yield of a particular crop over all evaluated 'countries' was used to compare adaptability among the 'countries'. The values are given in Table 3.

While Table 3 provides comparisons for 12 crop species, Fig. 1 gives an example of adaptability of wheat over the 13 countries. Wheat was found to be best adapted in the Netherlands, the UK and France, where

Table 3 Countries with the highest and the lowest adaptability values for 12 crops in 1961–2003 (over the 13 European 'countries', including the EU15)

Crop	Number of countries	Countries with the highest daptability for the crop	Countries with the lowest adaptability for the crop
Wheat	13	N 1.71, UK 1.62, F 1.62	SU 0.26, I 0.45, R 0.45
Rye	13	UK 1.91, F 1.58, G 1.55	P 0.41, S 0.45, SU 0.53
Barley	13	F 1.82, G 1.44, I 1.32	SU 0.30, S 0.57, R 0.67
Oat	13	UK 2.07, F 1.66, G 1.50	SU 0.36, R 0.41, S 0.51
Maize	11	S 1.65, EU 1.46, I 1.44	SU 0.13, R 0.29, H 0.73
Pulse	13	F 3.08, EU15 2.04, G 1.22	S 0.04, SU 0.30, I 0.56
Pea	13	F 2.04, EU15 2.01, I 1.68	R 0.11, SU 0.26, S 0.30
Rapeseed	12	F 1.82, CZ 1.62, G 1.61	R 0.08, SU 0.14, I 0.39
Sugar beet	13	F 2.04, S 1.96, EU15 1.35	SU 0.07, R 0.12, P 0.58
Potato	13	F 1.83, G 1.69, UK 1.61	SU 0.07, P 0.15, R 0.43
Hop	10	S 1.78, G 1.42, EU15 1.34	SU −0.69, CZ 0.81, R 0.89
Wine grape	9	CZ 1.34, H 1.26, I 1.22	S 0.59, SU 0.63, EU15 0.78

Average adaptability for each crop amounts to 1
A Austria, *CZ* Czech Republic; EU15: *F* France, *G* Germany, *H* Hungary, *I* Italy, *N* The Netherlands, *P* Poland, *R* Romania, *SU* previous Soviet Union, *S* Spain, *UK* United Kingdom

the values of adaptability were >1 and reached 1.71, 1.62 and 1.62, respectively (Table 3). On the other hand the lowest values (and <1) for wheat were found in the former SU, Italy and Romania (0.26, 0.45 and 0.45, respectively). Real yield data for wheat are plotted in Fig. 1 (t/ha); adaptability is shown by the inclination of the regression lines, and it is obvious that the values of adaptability are associated to the yield level.

General adaptability for wheat was found, most notably, in the Netherlands and in Germany, where it produced high yields in favourable as well as in non-favourable years. Comparison of the EU15 with the CZ showed that whereas the wheat crop responded to favourable environments (years) in the EU, in the CZ wheat was able to produce similar yields in less favourable conditions (4.08 and 4.01 t/ha), which could be regarded as specific adaptability to that environment.

Average values of the relative growth in yield of a crop (with the exception of hop and wine grape, where quality is more important than yield) were found to be correlated with adaptability ($r = 0.712$*).

Comparison of crop adaptability among European countries based on eight staple crops

Eight of the 26 crops studied are staple crops, grown in all 13 European 'countries' on a large scale: wheat, barley, oat, rye, potato, sugar beet, pea and pulse. These important crops were selected to compare adaptability across Europe (Fig. 2).

Figure 2 shows that the adaptability of the eight staple crops within countries was similar when the countries had comparable environmental, agronomic

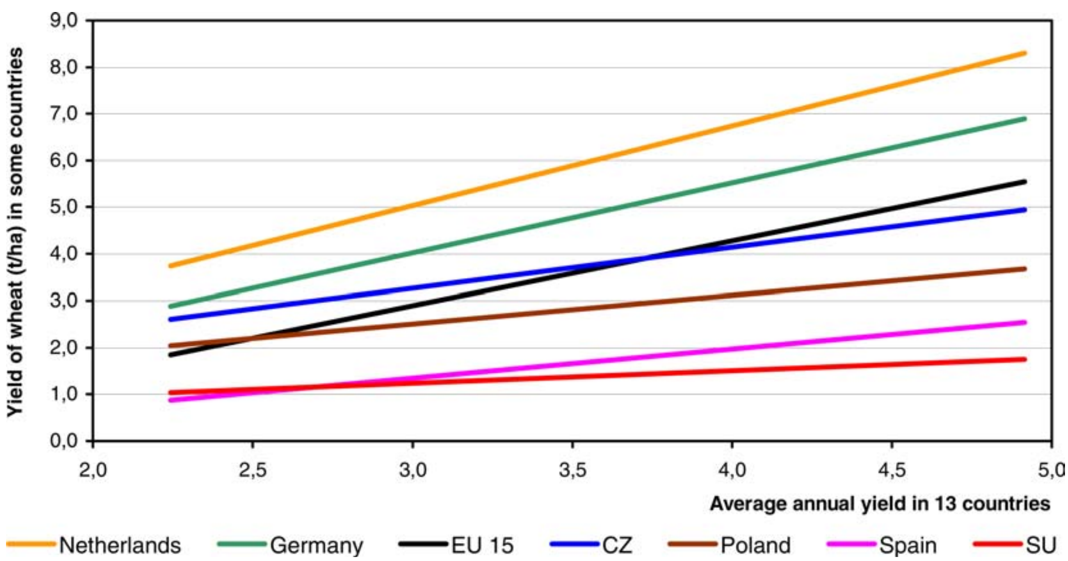

Fig. 1 Adaptability of wheat over the 13 European countries assessed (including EU15)

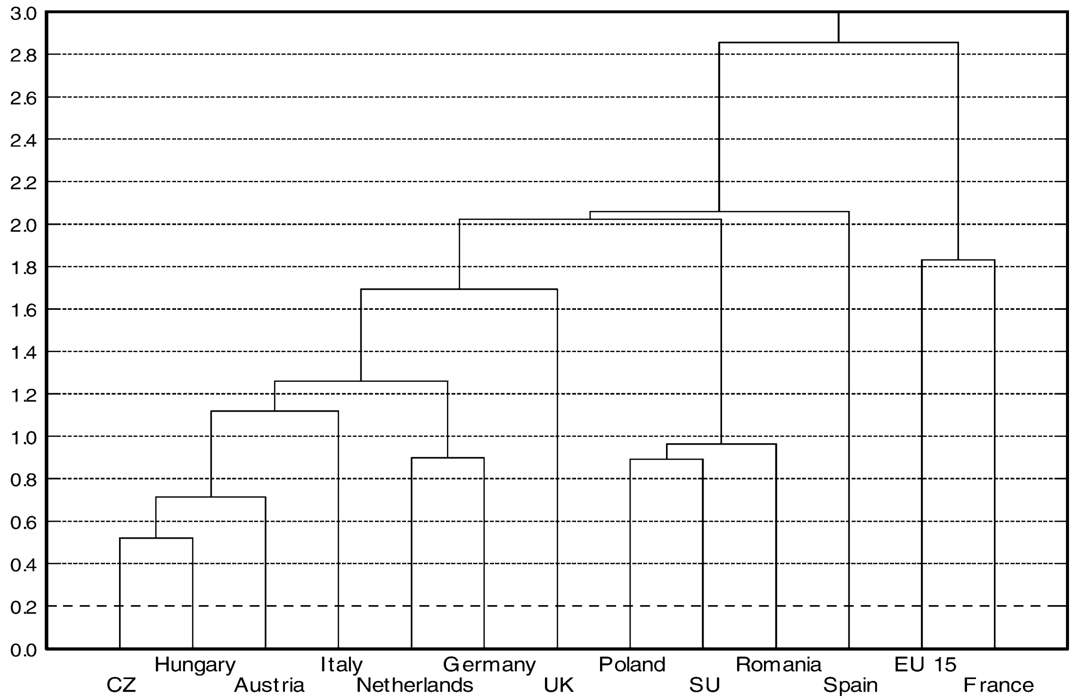

Fig. 2 Similarity of environment based on adaptability values of eight staple crops (shown in Fig. 1) grown in 13 European countries (including the EU15) between 1961 and 2003

and crop handling conditions, e.g. groupings of: the Czech Republic, Hungary and Austria; the Netherlands and Germany; Romania, the former Soviet Union and Poland, etc.

Discussion

We studied the adaptability of 26 crops over a 43-year period from 1961 to 2003. Adaptability over time is controlled by:

– Weather (large variation over years)
– Agronomical practices (smaller variations from year to year)
– Differences in phenotypic expression, due to different genotype × environment interactions

Location, year and their interactions are major factors influencing yield in poly-factorial field experiments. This assumption is supported by the values obtained for adaptability. Adaptability values were also influenced by other inputs (suitable varieties, agronomical practices, etc.) since the adaptability of the same crops was higher in the countries where the yields grew more rapidly ($r = 0.712^*$). The correlation of the level of yield with adaptability of crops can be explained by the results, e.g. of Kraakman et al. (2004) who found linkage between yield and its adaptability in barley.

Table 1 shows that adaptability to the environment was not pre-determined by the origin of the crop. For example, maize which traces its origin to America was significantly better adapted to European environments. This observation, however, was most pronounced in the cases of high adaptability of pea, pulse, rye, sugar beet and wheat to European environments (these crops originate from Eurasia).

Higher adaptability in the EU15 was found for crops, which have been cultivated in Europe for some time, in particular pulse and cereal crops. In contrast the USA showed higher adaptability in crops with a much shorter history of cultivation, in particular horticultural crops. Variation of adaptability of the 26 crops in the EU was greater than in the USA, by nearly two times (Table 1, last row). Grain legumes and cereals have been grown for many thousands of years in Europe. According to Hanus (1997) barley and pea have been in cultivation for more than 9,000, wheat more than 7,000, oat, rapeseed and grape more than 6,000 and potato more than 5,000 years. Sugar beet, however, is an exception and has only be grown for about 200 years (Hanus 1997). In contrast most of the 26 crops have been adapting to conditions in the USA only for several hundred years.

It is possible that the crops, which are more intensively bred (which have more registered varieties) and/or have been in cultivation longer and/or generatively propagated, have higher adaptability in Europe. However, this analogy is not generally valid. We compared the adaptability of spring and winter barley varieties grown in the Czech Republic. Although spring barley is more prevalent than winter types in the Czech Republic, winter varieties were found to be more adapted and gave higher yields, even though winter types did not survive each winter.

The correlation between yield, growth of yield and adaptability of crops can be indicative of the country/region a particular crop is best adapted to. They are mostly countries with high yield levels. Conversely low adaptability was associated with countries with low yield levels. Therefore suitable varieties and suitable agronomy have the potential to improve adaptability. However, more adapted crops were found to be more sensitive to changes in environment, agronomy, new varieties and their interactions.

Selecting crops for adaptation to environmental conditions and to improved agronomy will increase yield over the next decade (Troyer 2003; Denison et al. 2003). Breeding for general adaptation involves the screening of segregating populations in multilocation environments, including an optimal environment to determine yield potential, and screening for tolerance to abiotic and biotic stresses (Braun et al. 1996). Plant breeding for specific adaptability has also been suggested as an addition to the identified constraints, e.g. to low input agronomy (Banziger and Cooper 2001). The data presented suggest that crops adapted to evaluated environments showed higher increases in yield over 1961–2003. Crops (and varieties) with higher adaptability should be grown in higher input conditions.

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