



Effective population size (N_e) of organically and conventionally grown composite cross winter wheat populations depending on generation

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ABSTRACT

Effective Population Sizes (N_e) of three winter wheat composite cross populations (CCPs) that had been maintained under organic and conventional conditions from the F_7 to the F_{12} were analysed. The number of plants (N) needed to maintain an N_e of 5000 for each population was calculated based on the mean variation in the number of gametes per parent (S_k^2).

Variability in kernel number per plant was high, leading to large variations in the contribution of single plants to the next generation. Also, N required for an N_e of 5000 individuals was somewhat variable among the CCPs, but changed little from the F_7 (mean N of 11,955) to the F_9 (mean N 11,854) under the assumption of 2% outcrossing. There was, however, an increase to a mean N of 14,374 between the F_9 and the F_{12} , most likely due to an extreme winterkill in the F_{11} . The calculation of N using demographic data can only give general estimations but was well suited to show changes in the populations over time as affected by generation and year. Results show that drift was limited even under disruptive climatic events.

1. Introduction

Increased levels of biodiversity have been shown to provide for more resilience as defined by Döring et al. (2014) in the face of perturbations and can buffer extreme climatic events and adverse growing conditions to a wider extent than large monocultures do (Newton et al., 2009; Fa0, 2011; Altieri et al., 2015). These findings are in conflict with the fact that since the early 20th century trends in agriculture, plant breeding and breeding legislation have been towards an increased use of genetically uniform varieties, narrowing the genetic base of crop plants in farmers' fields (Harlan, 1975; Tanksley and McCouch, 1997; Haussmann et al., 2004; Finckh and Wolfe, 2006; Brumlop et al., 2013). The majority of current crop breeding is focused on crop ideotypes that provide high yields, are well adapted to farming systems with regular external inputs and will cope well in a monocultural system (Yapa, 1977, 1993; Murphy et al., 2005; Lamichhane et al., 2018). There is increasing concern that such uniform cultivars are inappropriate for dealing with unpredictable environmental changes because they may have limited ability to evolve in response to environmental fluctuations and they have limited capacity to react to novel stress factors (Newton et al., 2009; Döring et al., 2011; Murphy et al., 2013). Also, the ability of crops to buffer extreme climatic events or unexpected pathogen

exposure is limited in uniform cultivars as the uniformity of genotypes in the field allows no variability of reactions within the crop. Beneficial effects of crop genetic diversity on productivity, population recovery from disturbances have been reviewed by Dawson et al. (2012) and by Finckh and Wolfe (2015) and agrobiodiversity has been ranked high on the list of potential solutions to the problem of a growing demand for food (Jacobsen et al., 2013) and feed (Himanen et al., 2013).

The composite cross breeding approach is supposed to help broaden the genetic base of crops (Finckh, 2008; Döring et al., 2011; Wolfe and Döring, 2016) and is at the same time an efficient strategy for the dynamic conservation and management of genes and genotypes. Composite cross populations (CCPs) are genetically heterogeneous and segregating populations, which result from the intercrossing of large numbers of parental genotypes from diverse origins. Exposing these populations to the forces of natural selection allows their stepwise adaptation to the prevailing growing conditions. This is because plants with better adaptation to the local growing conditions will contribute more seed to the next generation than plants less well adapted (Suneson, 1956; Döring et al., 2011). While genetic variability is expected to decrease in each population over time under the combined effects of drift and selection, overall diversity is supposed to be maintained through the differentiation between populations (Goldringer

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et al., 2001b). Over time, composite cross populations adapt to the conditions under which they are grown because their genetically heterogeneous nature allows for micro evolutionary processes (Le Boulc'h et al., 1994; Paillard et al., 2000; Rhoné et al., 2010; Bertholdsson et al., 2016). At the same time, a large degree of genetic diversity is maintained in the populations, allowing the populations to deal with abiotic and biotic stresses and variable growing conditions. This flexibility is seen as a major advantage under the predicted threats of climate change (Döring et al., 2011; Murphy et al., 2013).

After several years of natural selection, populations can be used in further breeding activities as they usually provide well adapted material for further selection work (Finckh and Wolfe, 2015). Goldringer et al. (2001a) assume that wheat lines with high agronomic potential can be developed from wheat populations after only few selection cycles of breeding work after the phase of natural selection in the population is finished. They compared yielding abilities of the best lines selected from several populations that had reached the F_{10} with current reference varieties and found that the selected lines yielded just as well. Another strategy for exploiting CCPs could be to mix the populations with elite pure lines (Döring et al., 2015).

Managing CCPs under different environmental conditions and under natural selection promotes the emergence of new genotypes through recombination (Goldringer et al., 2001a). Results from various experiments growing CCPs under different environments and subject to different selective pressures have shown that CCPs usually maintain a large degree of genetic diversity within populations (Allard, 1988; David et al., 1997; Enjalbert et al., 1999; Goldringer et al., 2006). This means that CCPs are an effective means of dynamic genetic resource conservation (Allard, 1990; Goldringer et al., 2006).

As the maintenance of genetic variability in crops is a key purpose in wheat population breeding it is crucial to understand the degree of variation that will be maintained in this strongly inbreeding crop over time as this affects the “evolutionary potential” of a population (Goldringer and Bataillon, 2004; Espeland and Rice, 2010). Observations on conventional spring and winter wheat cultivars indicate that maximum outcrossing rates can range between 4 and 6.1% (Griffin, 1987; Martin, 1990; Hucl, 1996), under heat stress even 30% have been reported (Lukac et al., 2012). In genetically diverse wheat populations outcrossing rates of up to 10.1% have been reported (Enjalbert et al., 1998). Such high outcrossing rates could help to maintain diversity much longer than one would expect with strict selfing. Heterozygous genotypes offer additional phenotypes to the selection forces and their recombination and segregation creates new diversity. A valuable tool to evaluate the evolutionary potential is the estimation of the effective population size (N_e). Population size is perhaps – besides the factors mating system, mutation rate and gene flow – the most important factor when determining the evolutionary potential of a population as this determines how vulnerable a population is to genetic drift. Goldringer et al. (2001b) point out the importance of effective population size in order to “predict the evolution of genetic diversity within a system”. Inbred populations display lower levels of genetic diversity in comparison to outcrossing species and as such have lower effective population sizes and effective recombination rates (Porcher et al., 2004). These lower effective population sizes and the reduced recombination rates lead to a more marked effect of genetic drift and selection, as well as reduced quantitative genetic variation within such inbred populations (Charlesworth and Charlesworth, 1995). Smaller effective population sizes may tend to increase the inbreeding coefficient, resulting in a further loss of genetic variability and decreasing population fitness (Buza et al., 2000). Even in medium-sized populations, important and beneficial genetic variability can be lost through genetic drift and through the hitchhiking of deleterious alleles through selection (Goldringer et al., 2001a).

Despite the recent great interest in the composite cross breeding approach in wheat, no systematic studies on the temporal changes of N_e in wheat CCPs have been conducted and thus it is unclear, how many

plants should be used for the maintenance of CCPs to limit genetic drift. Saghai Maroof et al. (1994), working with barley CCPs, maintained populations of over 15 000 individual plants. The populations Goldringer et al. (2001a) studied, consisted of 10,000–15,000 plants. They state that a population of a “few thousand individuals” is necessary to limit genetic drift. In another experiment, Goldringer et al. (2001b) maintained an original population size of 5000 individual plants and had an estimated demographic N_e of 2800 individual plants. They stress the importance of maintaining larger population sizes, especially in populations displaying high variation among the individuals in their seed contribution to the next generation.

The variance effective size of a population and the inbreeding effective size are two complementing ways to specify the risk of random drift for a given population (i.e., of random loss of diversity across generations). For populations with relatively stable numbers of individuals across generations, the two concepts collapse. For populations with changing size, the variance effective population size focusses on allele-frequency drift resulting from the sampling of gametes, hence reflects the number of offspring produced. Populations that possess a large between-individuals variance in offspring number have a small effective population size (Falconer and Mackay, 1996; Hartl and Clark, 2007; Espeland and Rice, 2010).

We assessed the variance effective size and phenotypic variation in the F_7 to F_{12} grown between 2008 and 2013 in twelve winter wheat CCPs based on three different genetic backgrounds and maintained as parallel non-mixing populations in an organic and in a conventional farming system. The following questions were addressed: 1. What is the variation in number of tillers, kernel weight and kernel number per plant within the different populations between the different growing systems and over time, i.e. generations \times year? How variable is the contribution of single plants to the next generation? 2. Has there been an overall change of variation in tillering capacity, kernel numbers per tiller and per plant, or in TKW of the different populations over time? 3. Assuming that an N_e of 5000 individual plants should be present in each population and every year in order to limit the effects of genetic drift (Goldringer et al., 2001b), what is the required number of individuals per population and in each generation in order to maintain this N_e ?

2. Materials and methods

2.1. Setting up, maintenance and adaptation of the CCPs at the University of Kassel, Germany

The winter wheat CCPs created in 2002 in the UK are suitable for European growing conditions and were created by the John Innes Centre (JIC, Norwich, UK) in cooperation with Elm Farm Research Centre (Newbury, UK). The parental varieties were 20 successful European varieties, released between 1934 and 2000, with a focus on varieties of British origin, approximately representing the breeding progress at the end of the 20th century. Key criteria for selection of this set were its diverse genetic base and its potential for stable performance under low input growing conditions. One group of 12 high baking quality parental varieties (Bezostaya, Hereward, M. Widgeon, Mercia, Monopol, Pastiche, Renan, Renesansa, Soissons, Spark, Thatcher) were crossed in a half-diallel to form the Q-CCP (66 crosses, 2 unsuccessful). A second half-diallel of 9 high yielding varieties (Bezostaya, Buchan, Claire, Deben, HTL, Norman, Option, Tanker, Wembley) formed the Y-CCP (36 crosses, 3 unsuccessful). The variety Bezostaya was contained in both. The YQ-CCP was created using the 11×8 Q \times Y intercrosses plus Bezostaya crossed with all 19 other parents (total = 88 + 19 crosses, 14 unsuccessful). All seed of the F_2 generations of the successful crosses were bulked. Despite of some unsuccessful crosses, progenies of all intended varieties were contained in each population, however, the frequencies of the progenies varied between 2 and 12%. In addition to the parental crosses with the exception of Bezostaya each variety was crossed with a male sterile line and

aliquots of 8, 11 or all 19 of the F_2 generations of these crosses were mixed into the three CCPs described above to enhance early generation outcrossing (Döring et al., 2015). A comprehensive analysis of the performance of the individual parental varieties was published by Jones et al. (2010) and the initial setting up and maintenance of the European CCPs established at the John Innes Centre, UK, in 2002 was described in detail by Döring et al. (2015).

After two years of multiplication at two organic and two conventional sites in the south and east of the UK, F_4 seed of the four sites was bulked and about 2 kg each was sent to the Department of Ecological Plant Protection, Faculty of Organic Agricultural Sciences, University of Kassel, Germany in autumn 2005, where they have been maintained since under contrasting agronomic conditions.

Each F_4 population was divided into two and sown into an organically managed trial site and into a conventional trial site (resulting in three CCP_{org} and three CCP_{conv}). In autumn 2006, enough seed was available to split each population one more time to create two parallel populations of each. Since then within both systems (organic, conventional), two Y, two Q, and two YQ populations have been maintained as parallel populations. This allows for the comparison of changes in the populations over time within and between systems. Random changes in the populations and changes that occurred due to effects of the environment (e.g. organic vs. conventional growing conditions) can be distinguished. Thus, since generation F_6 a total of twelve CCPs (six CCP_{org} and six CCP_{conv}) have been maintained at the two trial sites with no artificial selection applied apart from the removal of the tallest plants (> 130 cm) in the early generations to prevent the populations from gaining too much in plant height as tall plants may have a disproportional advantage in the populations (Le Boulc'h et al., 1994; Goldringer et al., 1998). Popular commercial winter wheat varieties were grown next to the CCP plots every year to allow for comparison (see Table 1). Every year, the current generation of each population was sown with 52,500 viable seeds in a plot of at least 150 m² (350 seeds/m²) in the hopes to ensure an N_e of at least 5000. Considering the size of the populations maintained by other researchers (Saghai Maroof et al., 1994; Goldringer et al., 2001a, 2001b) and taking note of the high variation in contribution to the next generation recorded in the different populations of this study, an effective population size (N_e) of 5000 individual plants was deemed reasonable and should be sufficient to avoid genetic drift in the populations.

Table 1
Reference varieties planted in the two agricultural systems (harvested 2008–2010 and 2013).

Generation/Year	Conven-tional	Organic
F_7 – 2008		Achat Batis Bussard Capo Tamaro
F_8 – 2009	Capo Cubus Hermann Impression	Achat Batis Bussard Capo Tamaro
F_9 – 2010	Batis Capo Impression Skagen	Achat Astaro Batis Capo Skagen Tamaro
F_{12} – 2013	Achat Akteur Butaro Capo	Achat Akteur Butaro Capo Naturastar Scaro

2.2. Field sites and experimental design

The populations were grown every year at the Research Station of the University of Kassel in Neu-Eichenberg, located 51°22' N and 9°54' E at an altitude of 247 m above sea level. Mean annual precipitation (2000–2013) was 684 mm, and mean annual temperature 9.3 °C. Weather data were collected by a local automated weather station that is part of the official German Weather monitoring and professionally supervised.

The soil in the organic fields is a deep Haplic Luvisol with 76 soil points (Wildhagen, 1998) and has been organically-managed since 1984. No mineral fertilizers, fungicides, insecticides or herbicides were applied, weeds were controlled mechanically through harrowing and/or hoeing at the tillering stage. The CCPs were integrated into the crop rotation, usually wheat followed after two years of a grass-clover mixture. The conventional field was located within 750 m distance to the organic field, but the soil of the conventionally managed field was generally poorer than that of the organic area (Stagnic Luvisol with 52 soil points (Wildhagen, 1998)). There, the CCPs were rotated yearly with grass-clover and mineral nitrogen fertilizer was applied at a rate of 180 kg/ha in two split applications during the growing season (90 kg/ha at each application). Growth regulators were applied in 2008 and 2009, but not thereafter. Herbicide was applied once a year in early spring, but no fungicides or insecticides were used to allow for natural disease and pest pressure.

All populations were bordered by 3 m of non-wheat or the populations themselves to prevent outcrossing between the different populations. In most years, several reference varieties were planted next to the populations in plots of about 30 m² each (Table 1).

2.3. Assessments

From the F_7 to the F_9 (2008–2010) and in the F_{12} (2013), 50 individual plants, including roots, were randomly taken from the beginning, middle and end of each plot. Plants were harvested shortly before threshing the plots. The soil was carefully removed from the roots and individual plants were separated and dried for an additional two weeks. Plants were threshed individually and the number of tillers, kernel number and kernel weight were recorded per plant. In 2008 (F_7), 30 individual plants from each reference variety were additionally harvested and threshed together. The collective kernel number and weight were recorded and from this data the kernel number and weight for each individual plant could be calculated, but no information of the variation was available. In 2009 (F_8), 2010 (F_9), and 2013 (F_{12}), 30 plants were harvested from the reference varieties, but were processed as single plants as described above.

2.4. Calculation of effective population size (N_e)

Using the data collected for the seed number of the individual plants in each population, the effective population size (variance effective size) of non-random mating populations was calculated using the formula by Kimura and Crow (1963):

$$N_e = \frac{4N}{2(1 - \alpha) + S_k^2(1 + \alpha)} \quad (1)$$

where N is the number of plants needed in order to maintain a given N_e (such as $N_e = 5000$) (see Appendix B for details of calculation). From this equation, the number of individuals N which are required to achieve a desired minimum N_e can be derived as:

$$N = \frac{1}{4} [N_e \{2(1 - \alpha) + S_k^2(1 + \alpha)\}] \quad (2)$$

The basis for deducing N_e was the degree of self-fertilization and the variance of the number of gametes per parent which entered into the next generation. For the cross-fertilization, three scenarios were

assumed, 0%, 2%, and 8% of cross-fertilization, with no variation for this value among plants and generation. For the variance of reproductive success, there are two sources of variance. To visualize the first source, we suppose that all plants produced the same number of seeds. To keep the number of individuals per CCP population constant, only a small fraction of the total harvest will be used for sowing the next CCP generation, with on average one seed per plant of the previous generation. Not every plant will donate exactly one seed to the next generation, because the procedure is not single-seed-descent, but bulk breeding. The number of seeds donated per plant should follow a Poisson distribution. With this, not only the mean, but the variance of number of seeds contributed per plant to the next generation will be 1 (variance equals mean for the Poisson distribution). If the plants do not produce the same number of seed, then the variance of the number of gametes per parent entering the next generation will be inflated by this second source of variation. Hence, it was a necessity to assess the initial variance of seed number per plant, which existed before the above-mentioned sampling variance occurred. For this purpose, the experimental variance of the number of seeds per plant as assessed in the F_7 to the F_9 and in the F_{12} was taken. The average number of seeds per plant as measured across all populations and generations was 61; the variance of the number of seeds per plant was, on average, 1020. This variance of number of seeds per plant, had, for each population and generation, to be transformed to a level of variance as would have resulted with a constant average of 1 seed per plant. We follow the rule: $var(c x) = c^2 var(x)$. Let x be the number of seeds per plant in a population, $\mu(x)$ is the mean and $var(x)$ is the variance, both as assessed experimentally. We need $var(x')$ for $\mu(x') = 1$. We write $x = cx'$ (with on average 61 seeds per plant, as an example, $c = 61$). Thus, $var(x) = var(cx') = c^2 var(x')$. Hence, $var(x') = var(x)/c^2$. Hence, the variances as assessed in each of the CCPs were divided by the squares of their means, resulting in the sought-for variance at a level of (an average of) one seed per plant. This second source of variation was added to the first source to quantify the CCP-specific variance for seeds per plant that entered the next generation. With this, variance of number of seeds donated to the next generation (if it was on average one seed) was deduced. Yet, the algebra of Kimura and Crow (1963, Eqs. (1) and (2)) deals with S^2_k , where k is the number of gametes donated per plant, not the number of seeds. With two gametes making one seed, the variance for the number of gametes per parent was calculated by multiplying the variance of number of seeds with $2^2 = 4$.

The degree of self-fertilization, assumed to be 100% or 98% or 92%, were used to calculate the equilibrium inbreeding coefficient α following Haldane (1924) and Wright and Cockerham (1985) as:

$$\alpha = \frac{s}{2 - s} \quad (3)$$

where s is the rate of self-fertilization. Hence, the CCPs were assumed to be near to their inbreeding equilibrium. In a scenario with single seed descent breeding, the sampling variance of the number of gametes produced per parent, S^2_k , would be zero. In combination with $s = 1$, this would result in $N_e = \infty$, meaning that drift would be zero (Vencovsky and Crossa, 1999). Hence, random drift will here mainly be caused by the variation of number of seeds per plant and to a lesser extent by selfing not being complete.

The plot size required for an N_e of 5000 individuals was calculated assuming a plant density of 350 plants/m². This is identical to the sowing rate because the exact germination rate and overwintering rate were not known.

2.5. Data evaluation and statistical analysis

In order to identify relevant extreme weather conditions such as prolonged drought or wet conditions or extreme heat and cold periods, precipitation sums over four months as well as weekly temperatures were scrutinized in detail.

The statistical calculations were performed using IBM SPSS Statistics (Version 22). Descriptive statistical parameters such as the mean, variance, standard deviation and range were calculated for kernel number per plant, kernel number per tiller, tiller number per plant and TKW.

A Kruskal-Wallis test and a post-hoc pairwise Wilcoxon test with Bonferroni correction were used to calculate the significance of the differences in the mean number of tillers per plant and kernel number per tiller and per plant (count data, no normal distribution), among populations in each generation and between generations. For TKW (normal distribution) an analysis of variance (ANOVA) and a post-hoc Tukey-B or Games-Howell test (in the case of no homogeneity of variance) were used to make all possible two-way comparisons. Neither the Kruskal-Wallis test, nor ANOVA, were performed across the different growing systems (i.e. organic and conventional), but only within growing systems.

3. Results

3.1. Weather conditions during population evolution

Comparing the mean annual temperatures and total annual precipitation (September to August in the wheat growing seasons 2007/08–2012/13) at the experimental farm (Table 2), results in rather similar overall conditions. The growing season of 2012/13 was coldest and at the same time driest. The growing season of 2011/12 was warmest and the precipitation was close to 800 mm, while it was little more than 600 mm in the driest year.

Despite these overall similar values there were some distinct differences amongst years, especially during the winters, which might have contributed to differences between CCP generations (Fig. 1). The winter 2007/08 was unusually warm with hardly any frost. The winters 2008/09, 2009/10, and 2010/11 were characterized by continuously declining temperatures during fall with the lowest temperatures in December or January/February. The winter of 2012/13 was relatively warm, but lasted longer with temperatures around freezing point into the first days of April. In contrast, 2011/12 was frost free and warm until the end of January 2012 when temperatures dropped from a 24 h average of around 0 °C to an average of -12 °C within less than a week. There was frost without snow cover for two weeks, minimum temperatures at night reached down to -20 °C and maximum day temperatures stayed below -5 °C for more than a week resulting in frozen soil down to a depth of 50 cm. This period was followed by a warmer and dry second half of February and a warm and dry March (mean temperature in March 7.5 °C, total precipitation 15 mm). These relatively warm weeks of drought following the extreme cold worsened the effect of the cold and put surviving plants in the frozen soil under severe water stress (Brumlop et al., 2017).

3.2. Variability of tiller number per plant

Mean numbers of tillers per plant were quite similar over time, the conventional CCPs in the F_7 (2008) were the only exception (Fig. 2).

Table 2

Mean annual temperatures and total annual precipitation (September to August in the wheat growing seasons 2007/08–2012/13) at the experimental farm.

Wheat growing season (Sept – Aug)	2007/2008 (F ₇)	2008/2009 (F ₈)	2009/2010 (F ₉)	2010/2011 (F ₁₀)	2011/2012 (F ₁₁)	2012/2013 (F ₁₂)	mean
Mean annual temperature [°C]	9.6	9.1	8.8	9.0	9.7	8.5	9.1
Total annual precipitation [mm]	785	659	791	626	779	615	709

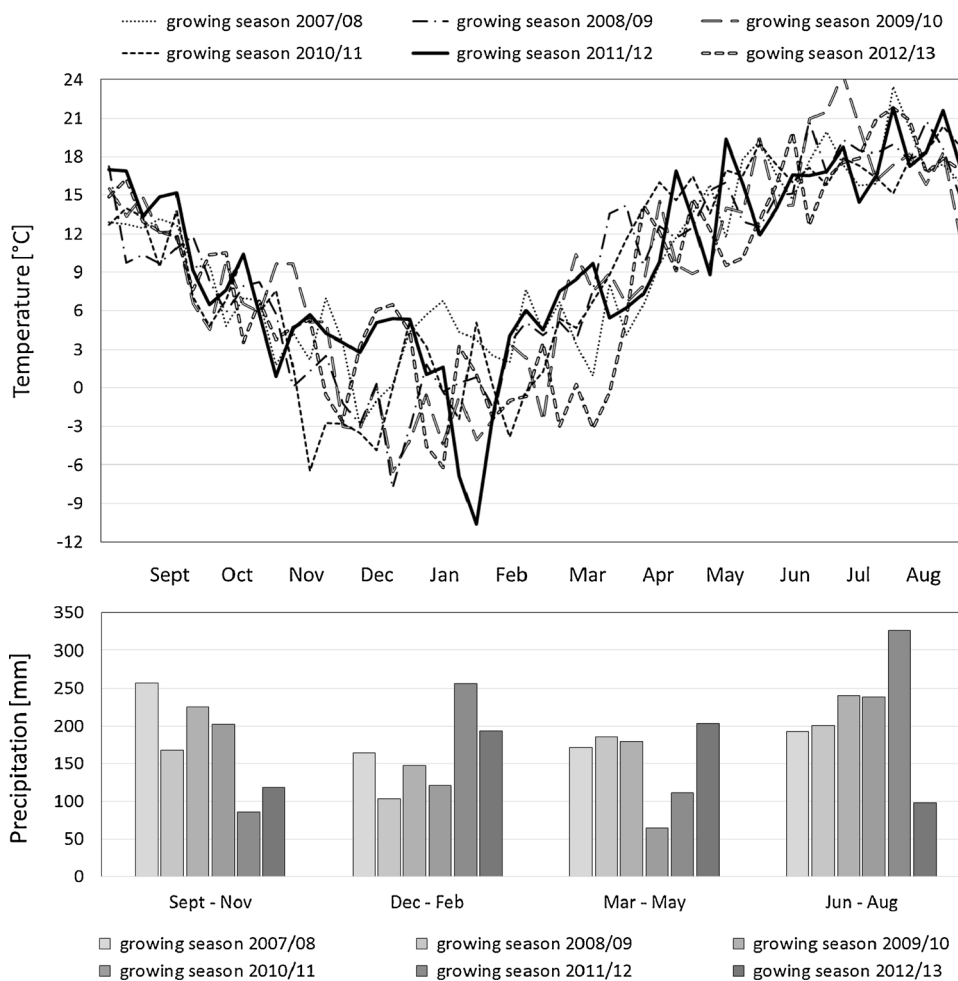


Fig. 1. Mean weekly temperatures and total quarterly precipitation from September 2007 to August 2013 at the experimental farm.

They had, on average, significantly fewer tillers per plant (1.13) than the conventional F₁₂ in 2013 (1.51). Tillers per plant in the F₈ (2009) and the F₉ (2010) populations were significantly higher than in the F₇ (2008) and F₁₂ (2013) (chi² = 162.33, df = 3, p ≤ 0.001).

Also in the organic populations, for which mean tiller number ranged between 1.53 and 1.74, significant generation x year effects were found (chi² = 18.10, df = 3, p ≤ 0.001). The F₉ had significantly more tillers per plant (1.74) than the F₇ (2008) and F₁₂ (2013) (1.53

and 1.61 respectively). There were no consistent differences in number of tillers per plant among the populations within system and year nor over time (Fig. 2). Within the years no clear subgroups of the parallel Q, Y, and YQ populations formed; also, tiller numbers per plants varied considerably between the parallel populations. For example, OY II had the second lowest number of tillers per plant (1.40) in the F₇ (2008), but the highest (2.06) in the F₉ (2010).

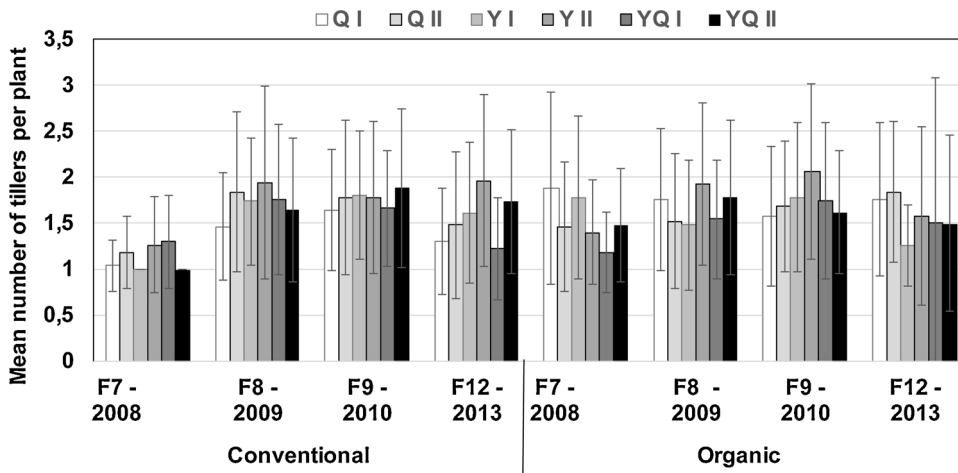


Fig. 2. Mean tiller number per plant for all populations grown under both conventional and organic conditions from the F7 to the F9 and F₁₂. The error bars denote SD for each population (n = 50 plants per population).

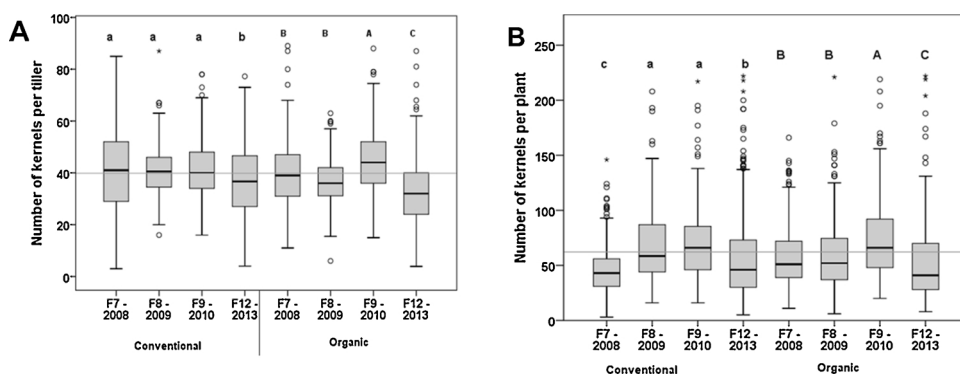


Fig. 3. A) Kernel number per tiller produced in the conventional and organic wheat populations from the F₇ to the F₉ and F₁₂. B) Kernel number per plant produced in the conventional and organic wheat populations from the F₇ to the F₉ and F₁₂. The median, minimum and maximum, 25% and 75% quantiles and out and extreme values are given (○ = outlier between 1.5 x interquartile range and 3 x interquartile range; * = extreme value > 3 x interquartile range). Horizontal line indicates mean number of kernels per tiller/plant in the trial. Generation means within system marked with different upper- or lower-case letters differed significantly (Kruskal Wallis test with post hoc pairwise Wilcoxon test with Bonferroni correction) at $p \leq 0.05$. $n = 50$ plants per population.

3.3. Variability of kernel number per tiller and per plant

Kernel number per tiller varied among generations x years in the conventional ($\chi^2 = 23.06$, $df = 3$, $p \leq 0.001$) and in the organic system ($\chi^2 = 142.94$, $df = 3$, $p \leq 0.001$). The conventional F₁₂ populations in 2013 had the significantly lowest number of kernels per tiller (Fig. 3A) and mean kernel numbers per tiller varied considerably. The CCP CY II had significantly more kernels per tiller than CQ I ($p \leq 0.001$) and CQ II ($p \leq 0.003$) (Appendix Table A1).

In the organic system, the F₉ in 2010 had significantly more kernels per tiller than the other three generations, while the F₁₂ in 2013 had fewer (Fig. 3A). Significant differences among populations within the generations were not found (Appendix Tables A1 and A2).

The mean number of kernels per plant increased significantly from the F₇ (2008) to the F₉ (2010) in both systems (generations x year under conventional conditions: $\chi^2 = 139.48$, $df = 3$, $p \leq 0.001$; generations x year under organic conditions: $\chi^2 = 97.56$, $df = 3$, $p \leq 0.001$). In the F₁₂ (2013), kernel numbers per plant were again significantly lower than in the F₉ in both systems (Fig. 3B).

Among the CCP_{conv}, the F₇ (2008) and F₁₂ (2013) had some populations that differed significantly from each other with no clear pattern. Similarly, some organic populations within the F₉ and F₁₂ were significantly different from each other, again with no pattern (Table 3).

The mean kernel numbers per plant in the reference varieties were in the same range as in the populations with similar standard deviations (Table 3). The means of the reference varieties were in most years similar to each other within systems. However, ‘Capo’ in particular reacted strongly to the system. Although the same seeds were used, mean kernel numbers varied considerably, but inconsistently between the two systems. In 2009 and 2013, ‘Capo’, formed more seeds per plant in the conventional plots, in 2010 more seeds were formed in the organic plots. Seed numbers in ‘Achat’ grown organically changed consistently from year to year (Table 3). Like for the CCPs, the varieties had the highest number of kernels per plant in 2010. However, in 2009, the CCPs had higher kernel numbers per plant than the references. In 2013 the numbers were lower, especially in the organic CCPs, however, this was due to the extremely high number of kernels per plant in Scaro (Table 3). Unfortunately, no data on the number of tillers per plant are available for the reference varieties as these were threshed in bulk.

3.4. Variability of thousand kernel weight (TKW)

The TKW followed the same yearly pattern in the conventional and organic system with highest TKW in 2008, lowest in 2009 and 2010, and 2013 in between (Fig. 4). Although the reference varieties were not the same every year, the changing varieties followed the same yearly pattern as the populations (data not shown). In contrast to the number of kernels per plant, there were consistent differences between the

CCP_{conv} within years with the Q II populations producing the highest TKW in the F₇ to F₉ (2008–2010), followed by the Q I, YQ and Y populations (Appendix Table A3). In the F₁₂ in 2013, Q II and YQ I produced the highest TKW (41.9 and 43.4 g respectively). Among the CCP_{org} there were no consistent differences for TKW (Appendix, Table A4).

3.5. Effective population size (N_e)

The number of plants (N) for all CCPs needed to maintain an N_e of 5000 individuals was calculated using the variance in the number of gametes contributed per parent, which is based on the variance and mean of kernel number per plant found in these populations. Three scenarios were accounted for in the calculations. In the first scenario (Table 4 and Appendix B1), no outcrossing was accounted for in the calculation and so the inbreeding coefficient (α) used was 1. In the second scenario (Table 4 and Appendix B1), some degree of allogamy within the populations was assumed and an outcrossing rate of 2% was used in order to calculate the inbreeding coefficient as $\alpha = 0.96$. This outcrossing rate was a conservative estimation based on results from previous studies on wheat outcrossing rates. The third scenario (Table 4 and Appendix B1) took the more extreme outcrossing rates into account which were found in studies (Griffin, 1987; Martin, 1990; Hucl, 1996; Enjalbert et al., 1998) and an outcrossing rate of 8% and an inbreeding coefficient of $\alpha = 0.85$ was used in the calculations. Plant numbers required to maintain an N_e of 5000 individuals are slightly reduced with increasing outcrossing rates, although not very much (Table 4). Assuming the populations were completely autogamous (Scenario 1), number of plants (N) needed to maintain an N_e of 5000 individuals were highest. At an outcrossing rate of 2%, N was on average 190 plants smaller (= 1.3%), at an outcrossing rate of 8% the required N was further reduced by an average of 528 plants (= 3.6%) with all populations following proportionate patterns. No difference between the farming systems or the populations within generations were observed.

Little if any variation in the required N occurred from F₇ to F₉ from 2008 to 2010 and no pattern could be found in the populations as some increased and some decreased over time (Table 4 and Fig. 5). However, in most populations the required N increased considerably between the F₉ and the F₁₂. Only the three populations CQ I, CYQ I and OQ II were similar in the F₁₂ to the years before.

The increase in N for maintaining an N_e of 5000 in the population CQ II is disproportionately high. An N of 11,974 in 2010 in the F₉ contrasts with an N of 17,791 in 2013 in the F₁₂. A repeated resampling with random subsampling of 30 plants from the available 50 plants resulted in disproportionately high increases in N in the CQ II population only (details not reported here), thus supporting the reported result.

Table 3

Descriptive summary of the kernel number per plant for all wheat populations ($n = 50$ per population) and reference varieties ($n = 30$ plants per variety) for each generation x year.

Year	Populations				Reference varieties								
	CCP	Conventional		Organic		Conventional			Organic				
		Kernels/plant mean (SD)	Min – Max (range)	Kernels/plant mean (SD)	Min – Max (range)	Variety	Kernels/plant mean (SD)	Min – Max (range)	Variety	Kernels/plant mean (SD)	Min – Max (range)		
F ₇ - 2008	Q I	37 (17)	b ^{a)}	53 – 64	64 (34)	a	11 – 145		Achat	57			
	Q II	47 (17)	a	12 – 84	53 (26)	a	14 – 121		Batis	76			
	Y I	42 (15)	b	12 – 70	67 (35)	a	22 – 166		Bussard	72			
	Y II	52 (29)	a	8 – 146	57 (25)	a	21 – 135		Capo	86			
	YQ I	58 (27)	a	8 – 124	49 (20)	a	16 – 103		Tamaro	61			
	YQ II	39 (17)	b	4 – 82	58 (24)	a	22 – 136						
	mean	46 (22)		3 – 146	58 (28)	11 – 166			mean	69			
F ₈ - 2009	Q I	58 (23)	a	27 – 118	62 (27)	a	25 – 133	Capo	66 (31)	15 – 132	Achat	45 (22)	20 – 106
	Q II	70 (33)	a	16 – 190	55 (27)	a	20 – 151	Cubus	66 (29)	36 – 146	Batis	46 (22)	22 – 110
	Y I	69 (30)	a	27 – 146	53 (24)	a	21 – 119	Hermann	55 (28)	19 – 131	Bussard	47 (27)	21 – 126
	Y II	79 (42)	a	22 – 208	68 (34)	a	25 – 221	Impression	47 (20)	18 – 213	Capo	40 (18)	21 – 106
	YQ I	70 (30)	a	36 – 163	52 (22)	a	18 – 131				Tamaro	56 (25)	22 – 111
	YQ II	65 (33)	a	33 – 193	67 (38)	a	6 – 179						
	mean	69 (33)		16 – 208	60 (30)	6 – 221	mean	58 (28)	15 – 213	mean	47 (23)	20 – 126	
F ₉ - 2010	Q I	67 (29)	a	22 – 177	65 (29)	b ^{c)}	20 – 154	Batis	74 (29)	28 – 142	Achat	78 (35)	9 – 156
	Q II	68 (31)	a	32 – 164	63 (23)	b	34 – 137	Capo	69 (36)	32 – 152	Astardo	89 (32)	44 – 181
	Y I	79 (32)	a	30 – 157	82 (41)	ab	24 – 219	Impression	73 (34)	36 – 158	Batis	74 (29)	35 – 125
	Y II	68 (30)	a	16 – 191	90 (42)	a	32 – 208	Skagen	65 (36)	26 – 149	Capo	82 (35)	33 – 188
	YQ I	66 (25)	a	31 – 138	76 (35)	ab	34 – 161				Skagen	102 (42)	48 – 206
	YQ II	73 (39)	a	24 – 217	72 (31)	ab	20 – 149				Tamaro	72 (31)	35 – 134
	mean	70 (31)		16 – 217	75 (35)	20 – 219	mean	70 (33)	26 – 158	mean	83 (35)	9 – 206	
F ₁₂ - 2013	Q I	44 (22)	b ^{b)}	6 – 105	56 (41)	ab ^{d)}	8 – 204	Achat	43 (22)	11 – 106	Achat	46 (37)	9 – 139
	Q II	54 (48)	b	11 – 222	63 (32)	a	13 – 143	Akteur	70 (39)	19 – 165	Akteur	65 (48)	17 – 213
	Y I	67 (50)	a	6 – 208	42 (28)	b	10 – 129	Butaro	44 (38)	16 – 232	Butaro	48 (27)	21 – 134
	Y II	74 (48)	a	17 – 200	54 (39)	ab	13 – 219	Capo	96 (42)	20 – 192	Capo	65 (33)	12 – 145
	YQ I	44 (23)	b	10 – 145	56 (39)	ab	12 – 222				Naturastar	60 (34)	17 – 139
	YQ II	63 (40)	ab	5 – 192	47 (34)	ab	13 – 188				Scaro	109 (95)	19 – 332
	mean	57 (41)		5 – 222	53 (36)	8 – 222	mean	63 (42)	11 – 232	mean	65 (54)	9 – 332	

^{a)} $\chi^2 = 22.88$, $df = 5$, $p \leq 0.001$ ^{b)} $\chi^2 = 18.80$, $df = 5$, $p = 0.002$ ^{c)} $\chi^2 = 17.17$, $df = 5$, $p = 0.004$ ^{d)} $\chi^2 = 15.90$, $df = 5$, $p = 0.007$.

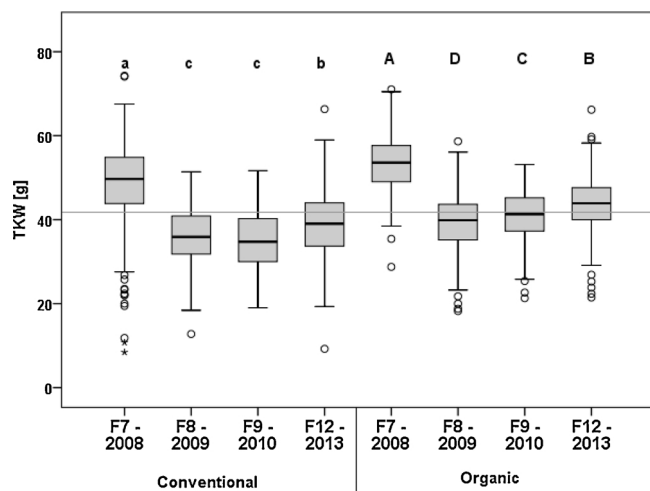


Fig. 4. Thousand kernel weight (TKW) for individual plants in the conventional and organic wheat populations from the F₇ to the F₉ and F₁₂. The median, minimum and maximum, 25% and 75% quantiles and out and extreme values are given (○ = out value between 1.5 x interquartile range and 3 x interquartile range; * = extreme value > 3 x interquartile range). Horizontal line indicates mean TKW in the trial. Generation means within system marked with different upper- or lower-case letters differed significantly (ANOVA and a post-hoc Tukey-B/Games-Howell test) at $p \leq 0.05$. $n = 50$ plants per population.

4. Discussion

The CCPs under both growing systems and in each generation revealed a high degree of variability in kernel number per plant and TKW.

The highest variance was found in the TKW, which had the highest number of statistically significant differences in the mean TKW among the populations and between generations. Also, the contribution of single plants to the next generation varied greatly. The range of kernel number per plant under the conventional system spread from a minimum of 3 seeds per plant in 2008 in the F₇ CQ I population to a maximum of 222 kernels per plant in 2013 in the F₁₂ CYQ II population. In the organic system, the plant with the lowest number of seeds (6) was found in 2009 in the F₈ OYQ II population and the plant with the highest number of seeds (222) in 2013 in the F₁₂ OYQ I population. The tiller number per plant did not vary much among populations, although the CCP_{conv} in the F₇ (2008) exhibited very low tiller numbers per plant in comparison to the other generations in both growing systems. Variability of kernel number per tiller was also not very high. N_e , which was calculated using the variance in the number of gametes contributed per parent (based on the variance and mean of kernel number per plant) was somewhat variable among the CCPs as was the mean number of kernels per plant. The plot sizes required for an N_e of 5000 individuals, which were calculated based on N changed little over time from the F₇ to the F₉ but in most cases were considerably higher in 2013 in the F₁₂.

Differences in weather in the years of the study could explain some of the significant differences among the generations x years. The process of generative development in wheat starts in early spring. During the mid- to late tillering stages the maximum number of spikelets per head is fixed. The number of kernels produced by each spikelet is set during the initiation and maturation of the florets just before and during early booting (April to May). At the anthesis stage, the spikelet has reached full size and kernel development begins (Cook and Veseth, 1991). Thus, the critical stages of wheat development in order to maximize yield are mid- to late tillering and floret initiation and

Table 4

Number of plants (N) for all CCPs needed to maintain an N_e of 5000 individuals with an outcrossing rate of 0, 2, and 8% for organic and conventional CCPs (F7, F8, F9 and F₁₂).

CCP	Conventional			Organic			
	no outcrossing	2 % outcrossing	8 % outcrossing	no outcrossing	2 % outcrossing	8 % outcrossing	
F ₇ – 2008	Q I	12040	11902	11518	12867	12713	12284
	Q II	11355	11231	10884	12306	12163	11765
	Y I	11358	11233	10887	12668	12518	12100
	Y II	13045	12888	12450	11917	11782	11405
	YQ I	12229	12087	11693	11670	11539	11176
	YQ II	11966	11829	11450	11705	11573	11208
	mean	11999	11,862	11480	12189	12048	11656
F ₈ – 2009	Q I	11520	11392	11037	11882	11747	11373
	Q II	12205	12064	11671	12445	12299	11894
	Y I	11838	11704	11331	11975	11838	11458
	Y II	12873	12718	12289	12522	12375	11965
	YQ I	11871	11736	11362	11781	11648	11279
	YQ II	12578	12429	12017	13181	13021	12575
	mean	12147	12007	11618	12298	12155	11757
F ₉ – 2010	Q I	11865	11730	11356	12063	11924	11540
	Q II	12114	11,974	11587	11322	11198	10853
	Y I	11631	11501	11140	12435	12289	11884
	Y II	11961	11825	11445	12218	12076	11683
	YQ I	11401	11275	10927	12116	11977	11589
	YQ II	12872	12717	12288	11790	11657	11287
	mean	11,974	11837	11457	11991	11854	11473
F ₁₂ – 2013	Q I	12623	12474	12058	15251	15050	14492
	Q II	18047	17,791	17081	12674	12523	12105
	Y I	15418	15214	14647	14371	14187	13677
	Y II	14130	13951	13453	15323	15120	14558
	YQ I	12801	12648	12223	14847	14654	14118
	YQ II	14079	13901	13407	15166	14966	14413
	mean	14516	14330	13812	14605	14417	13894

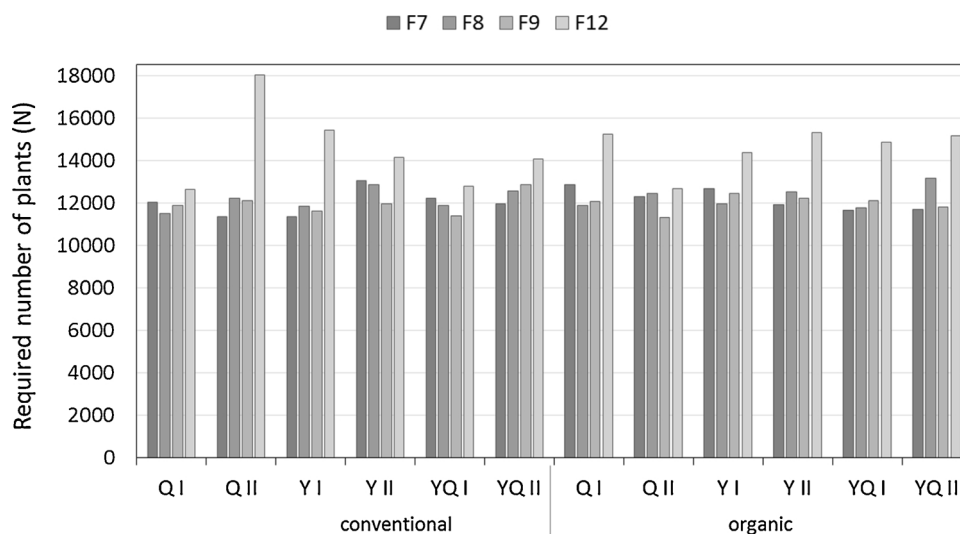


Fig. 5. Number of plants (N) needed in order to maintain an N_e of 5000 in the F7, F8, F9 and F₁₂ of 12 CCPs harvested in 2008, 2009, 2010, and 2012, respectively, with an outcrossing rate of 2%.

maturation before and during early booting. Each development phase of wheat from emergence through to grain-fill is dependent on accumulated heat units or temperature. Availability of water is another factor that plays an important role in attainable yields, and, within the range of adaptation, any increase in the amount of water available to the wheat crop will translate into increased yield (Cook and Veseth, 1991).

Variation in mean annual temperatures in the wheat growing seasons (September to August) was moderate and is unlikely directly responsible for the yearly variations in kernel numbers per tiller, per plant or TKW. It is more informative to focus on temperature and precipitation in April and May i.e. the period where maximum yield obtainable

is set each year.

The cold April temperatures in 2008 together with a total monthly precipitation of 73 mm (accumulated precipitation from January to April 250 mm) resulted in low kernel numbers per plant in the conventional F₇ CCPs and a high TKW, but this was not the case in the organic CCPs. As the conventional field was located on a slope resulting in cold air flows and thus an overall colder microclimate, it is possible that this difference was critical in spring 2008.

In contrast, the rather warm April month of 2009 was accompanied by a very dry spring (total monthly precipitation in April of 33 mm, total accumulated precipitation from January to April 151 mm) and resulted in low kernel numbers per tiller and plant and also in low TKW

in the organic F_8 CCPs, but not in the conventional ones. It is likely that mineralization of nutrients in the organic system was restricted due to the drought during the critical phase for wheat. Such problems are much less common when inorganic N is provided to the plants (Finckh and van Bruggen, 2015). In 2013, all F_{12} populations were clearly different from the F_7 to F_9 during 2008–2010 regarding kernels per tiller, kernels per plant and consequently N_e . With the exception of the variety Scaro, the reference varieties also had quite low numbers of kernels per plant in that year pointing to a specific year effect. The winter 2012/13 was long and cold into late March followed by a very warm April (Fig. 1). This likely reduced the number of florets per spikelet (Cook and Veseth, 1991) and thus led to rather low number of seeds in general as described above. The extreme case of the conventional CQ II population requiring > 17,000 plants in the F_{12} compared to around 12,000 in the F_9 , three years earlier, also points to a random event that acted independent of the genetics on this population.

Besides these possible effects of the weather in spring, the single most extreme climatic event between 2007 and 2013 was as described above the period from December 2011 to April 2012 resulting in serious winter kill. In a two-year study taking place in the growing seasons 2011/12 and 12/13, the F_{11} of the organic and conventional CCPs were compared in a field trial, using the F_{10} seed in both seasons. The extreme winter kill in 2011/12 was especially damaging for the populations with Y genetics (Brumlop et al., 2017). The rooting patterns of the populations also changed dramatically after the winter kill but these changes were not persistent over time indicating that the overall genetic variation was not affected by this single extreme event (Vijaya Bhaskar et al., 2019). If the demographic population size had not been large enough, the winter kill could have caused a bottle neck in that year. However, this cannot be shown with our data due to the confounding effects of generation \times year.

Wheat populations under dynamic management over several generations were also studied in a French study, where two wheat populations were assessed for fitness related traits such as plant height, kernel number per plant, kernel weight per plant and kernel number per tiller. Populations of the 1st, 5th and 10th generations were studied and an increase in plant height was observed over generations while kernel number and kernel weight per plant decreased. This was thought to be due to re-allocation of reproductive resources to vegetative functions in the taller plants (Goldringer et al., 2001b). As the generations were grown in different years with strong yearly variation in weather potentially affecting kernel numbers, changes in kernel numbers in our data cannot be directly compared to the data from Goldringer et al. (2001b). The potential for compensation among genetically diverse plants overall leads to lower variation in total yield among diversified cereal stands than among pure stands resulting in greater yield stability in cultivar mixtures (Finckh et al., 2000). The CCPs studied in our study also show overall greater yield stability than pure stands (Weedon and Finckh, 2018).

Plant height was not assessed in the present study and during the early generations the tallest plants had been removed to prevent the CCPs to gain too much height, which might explain the discrepancy to the study of Goldringer et al. (2001a), who suggest that "competition in heterogeneous populations selects for the highest plants although this induces a decrease in the global grain production of the populations." They also mention that the estimated heritability of the studied phenotypic traits was highest for plant height and TKW, medium for kernel number per tiller, tiller number per plant, kernel number per plant and kernel weight per plant. Our data for the yield components are in line with this observation. Also, plant height in the twelve CCPs was measured in several generations (Finckh et al., 2009; Bertholdsson et al., 2016; Brumlop et al., 2017). In general, the YCCPs are shorter than the QCCPs and the YQCCPs are intermediate. This can be explained by the genetic makeup of the populations. Effects of the genetic makeup and the growing system on the CCPs were also demonstrated for changes in traits of early development between the F_6 and F_{11} (Bertholdsson et al.,

2016) and up to the F_{15} (Vijaya Bhaskar et al., 2019). With respect to N_e , however, no effects of genetic background are evident. Instead, it appears that different random processes acted in each population leading to differences even between parallel populations. One reason for these divergent processes may be that the CCPs were still very diverse and heterozygous in the F_5 when they were split. For example, a study of leaf rust (*Puccinia triticina*) resistance in the CCPs revealed that 22 out of 23 single seed progenies from the F_5 CCPs segregated for resistance to leaf rust indicating that the expected degree of homozygosity for an F_5 inbreeding crop had not yet been realized (Finckh et al., 2009, 2010). Comparing the F_4 and F_5 generation of these same CCPs, the resistance frequency to one rust isolate increased significantly between the F_4 and the F_5 generation, while the resistance frequency for another isolate decreased between the two generations, suggesting a high potential for random change in the CCPs (Stange et al., 2006). This is in line with other studies reporting large degrees of genetic diversity between and within experimental CCPs (Allard, 1988; David et al., 1997; Enjalbert et al., 1999; Goldringer et al., 2006).

Goldringer et al. (2001b) reported a tendency for smaller variances in the CCPs in later generations. This indicates a stabilizing effect within the populations in later generations. This is in line with Qualset (1968), who reported that the genetic changes within CCPs due to selective pressures tended to be dramatic in the early generations, but that later generations experienced a loss of overall diversity, an increased selection for improved genotypes and slower and less dramatic evolutionary changes. As we only assessed generations from the F_7 onwards it is likely that the phase of dramatic changes mentioned by Qualset (1968) had already passed before this study started. The results on F_4 studies in the CCPs presented by Stange et al. (2006), reporting large variability of various traits indicate that this was the time of significant changes.

To understand the nature of the changes in the later generations it would be helpful to know the outcrossing rates. Outcrossing rates from generation to generation may change and be reduced, unless the populations have turned into a mixture of homozygous lines due to the inbreeding nature of wheat. If the populations had already reached an inbreeding equilibrium, the outcrossing rate would not change over the subsequent generations (Enjalbert and David, 2000). However, molecular marker analyses from the F_{12} (after the frost event) revealed up to 5% heterozygosity in our CCPs (Weedon et al., unpublished).

The calculation of the number of plants (N) needed to maintain an N_e of 5000 using demographic data only can give a general estimate about the effective size of a population that varies depending on the assumed outcrossing rate. It is likely that every population under both agricultural systems and in each generation has a different outcrossing rate. Such varying outcrossing rates would again give different results for the number of plants which are necessary to meet a given N_e criterion. Another factor that could not be taken into account when calculating N is the success of germination and the subsequent survival of all individual plants to the reproductive stage. In general, it seems that a plot size of about 150 m² for the CCPs maintained at the University of Kassel since 2005 was sufficient to avoid genetic drift in the populations (Enjalbert et al., 1999; Goldringer et al., 2001b) and to minimize the loss of genetic variability. This was even true for the extreme case of the F_{12} CQ II in the conventional system where the combination of a high variance in the original kernel number and a rather low original mean kernel number led to an N of > 17,000. Assuming that at least 300 plants ensued from the 350 kernels m⁻² sown this, for the first time, required a plot size greater than 50 m². Attempts to test the validity of the result by removing single outliers from the data did not make the population much more similar to the others; suggesting that this high variance was immanent to the sample. In order to determine whether the population CQ II underwent evolutionary processes, which were different to the other CCPs between the F_9 and F_{12} , molecular analyses will be required.

Considering the 20 initial varieties, a rare gene which might be a

private allele for one of them will initially hold on average 5% frequency in the CCP. Taking, for simplification, 0% outcrossing, and number of individuals such as $N = 12.000\text{--}14.500$ (i.e., $N_e = 5000$; cf. Table 5), the probability that in one generation such an allele is lost is $P = 0.95^N$ which is (practically) zero ($P = 0.95^N$ is the probability that all of the N plants of the next generation do not have the rare allele). Following Kimura and Ohta (1969) and applying $N_e = 5000$, an allele with 5% frequency would, on average, be lost due to drift only after as many as 3153 generations of maintaining the population at that effective population size. In contrast, for example, an allele present initially at 5% would be lost after an average of 100 generations through drift if N_e is 159. Considering these populations, we have to anticipate that there will be tens of thousands of genes present; thus, our expectation is that with so many genes some rare alleles could already have been lost in earlier generations: As nothing is granted in nature, even within the generations of the study and even if drift was extremely unlikely, some of the wheat genes in the plants of the CCPs could theoretically have lost a rare allele.

In conclusion, the first research question addressed in this study about the variation among populations and between generations and years can be clearly answered. Not only in the F_7 , but also five years later in the F_{12} , variation in number of tillers, kernel weight and kernel number per plant among the different populations and between generations was still high and the high initial variability of contribution of single plants to the next generation even increased after the extreme winterkill 2011/12 and the winter 2012/13. While genetic effects of these events are likely, the fact that the demographic population size

had been very large suggests that no bottleneck effect but a year effect has influenced the populations.

The second question, about changes in the variability of yield components of the populations over the six years of study and whether a loss of diversity or a stabilizing effect can be observed, cannot be clearly answered. Nevertheless, the large degree of diversity still present within the CCPs ensures the adaptability of the populations to changing environmental conditions, as was reported by Brumlop et al. (2017). The inconsistent differences among populations, including those between parallel populations, clearly suggest that random changes are of great importance in evolutionary breeding. The calculation of N needed to achieve an N_e of 5000, using the variance in the number of gametes contributed per parent based on the variance and mean of kernel number per plant is a useful tool to determine the number of individuals required to limit genetic drift in the populations. The calculation of this value using demographic data can only give general estimations. Nevertheless, it was well suited to show differences among the populations over generations and years and results show that the CCPs maintained at the University of Kassel in plots of at least 150 m^2 are large enough to limit genetic drift even under such disruptive climatic events as described for the winter of 2011/12.

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Appendix A

Table A1

Descriptive summary of the kernel number per tiller for all conventional wheat populations and for each generation ($n = 50$ plants per population).

	CCP	Mean kernel no. per tiller		Standard deviation (SD)	Min – Max (range)
F_7 - 2008	CQ I	36	a*	16.5	3 – 64
	CQ II	43	a	19.1	12 – 84
	CY I	42	a	15.3	12 – 70
	CY II	41	a	15.3	8 – 84
	CYQ I	45	a	15.8	8 – 85
	CYQ II	39	a	17.1	4 – 82
	mean	41	A**	16.7	3 – 85
	F_8 - 2009	CQ I	40	a	8.9
CQ II		39	a	9.1	16 – 66
CY I		40	a	7.9	25 – 59
CY II		42	a	13.3	22 – 87
CYQ I		42	a	9.4	24 – 61
CYQ II		41	a	8.2	24 – 62
mean		41	A	23.2	15 – 186
F_9 - 2010		CQ I	42	a	12.0
	CQ II	40	a	10.2	18 – 67
	CY I	45	a	11.8	27 – 69
	CY II	40	a	12.6	16 – 78
	CYQ I	41	a	8.4	23 – 57
	CYQ II	40	a	10.4	17 – 58
	mean	41	A	11.0	16 – 78
	F_{12} - 2013	CQ I	34	b	12.4
CQ II		34	b	15.3	11 – 73
CY I		38	ab	14.0	6 – 69
CY II		44	a	12.8	17 – 73
CYQ I		36	ab	12.8	10 – 73
CYQ II		34	ab	12.2	5 – 58
mean		36	B	13.5	5 – 73

* Within generation populations followed by different lower-case letters are significantly different at $p \leq 0.05$ using a Kruskal-Wallis test and a post-hoc pairwise Wilcoxon test with Bonferroni correction.

** Generations followed by different upper-case letters are significantly different at $p \leq 0.05$ using a Kruskal-Wallis test and a post-hoc pairwise Wilcoxon test with Bonferroni correction.

Table A2

Descriptive summary of the kernel number per tiller for all organic wheat populations and for each generation (n = 50 plants per population).

	CCP	Mean kernel no. per tiller		Standard deviation (SD)	Min – Max (range)
F ₇ - 2008	OQ I	36	a	13.8	11 – 87
	OQ II	37	a	10.9	14 – 62
	OY I	38	a	8.2	22 – 58
	OY II	42	a	13.6	21 – 80
	OYQ I	42	a	13.0	16 – 89
	OYQ II	41	a	11.3	22 – 68
	mean	39	B**	12.1	11 – 89
F ₈ - 2009	OQ I	36	a	8.0	23 – 63
	OQ II	37	a	9.5	19 – 56
	OY I	37	a	9.2	18 – 59
	OY II	36	a	9.1	17 – 57
	OYQ I	35	a	9.4	16 – 60
	OYQ II	37	a	9.1	6 – 60
	mean	37	B	9.0	6 – 63
F ₉ - 2010	OQ I	43	a	15.2	15 – 88
	OQ II	40	a	10.2	21 – 60
	OY I	47	a	11.1	23 – 71
	OY II	45	a	11.0	24 – 72
	OYQ I	46	a	12.3	21 – 79
	OYQ II	46	a	13.5	20 – 78
	mean	45	A	12.5	15 – 88
F ₁₂ - 2013	OQ I	30	a	11.9	8 – 68
	OQ II	34	a	11.5	13 – 66
	OY I	32	a	13.7	10 – 81
	OY II	35	a	12.3	12 – 74
	OYQ I	37	a	13.5	12 – 87
	OYQ II	32	a	9.2	13 – 51
	mean	33	C	12.3	8 – 87

* Within generation populations followed by different lower-case letters are significantly different at $p \leq 0.05$ using a Kruskal-Wallis test and a post-hoc pairwise Wilcoxon test with Bonferroni correction.

** Generations followed by different upper-case letters are significantly different at $p \leq 0.05$ using a Kruskal-Wallis test and a post-hoc pairwise Wilcoxon test with Bonferroni correction.

Table A3

Descriptive summary of thousand kernel weight (TKW) for all conventional wheat populations and for each generation (n = 50 plants per population).

	CCP	Mean TKW [g]		Standard deviation (SD)	Min – Max [g]
F ₇ - 2008	CQ I	48.4	abc*	10.2	20.0 - 67.6
	CQ II	53.5	a	8.0	36.9 - 74.3
	CY I	48.6	bc	7.2	27.9 - 63.6
	CY II	45.3	c	10.2	11.8 - 60.3
	CYQ I	51.3	ab	6.7	29.6 - 67.1
	CYQ II	45.6	bc	12.7	8.4 - 67.4
	mean	48.8	A**	9.8	8.4 - 74.3
F ₈ - 2009	CQ I	35.5	ab	6.0	22.4 - 51.4
	CQ II	38.0	a	6.9	18.4 - 50.0
	CY I	34.7	ab	6.0	23.9 - 46.8
	CY II	36.3	ab	5.7	12.8 - 48.1
	CYQ I	34.3	b	6.1	22.8 - 44.2
	CYQ II	37.3	ab	6.8	21.6 - 50.8
	mean	36.0	B	6.4	12.8 - 51.4
F ₉ - 2010	CQ I	36.0	bc	9.4	19.1 - 50.9
	CQ II	41.9	a	9.1	23.8 - 49.1
	CY I	32.1	c	6.4	19.0 - 48.9
	CY II	33.9	bc	5.4	23.8 - 50.2
	CYQ I	36.4	b	5.7	22.4 - 46.1
	CYQ II	35.5	bc	6.7	23.2 - 51.7
	mean	35.1	C	7.8	19.0 - 51.7
F ₁₂ - 2013	CQ I	39.9	ab	7.8	24.7 - 66.3
	CQ II	41.9	a	9.3	23.8 - 52.6
	CY I	34.3	c	8.3	9.2 - 46.6
	CY II	36.3	bc	4.5	27.7 - 46.2
	CYQ I	43.4	a	7.5	24.1 - 58.9
	CYQ II	38.7	bc	6.9	21.4 - 50.7
	mean	39.1	B	8.1	9.2 - 66.3

* Within generation populations followed by different lower-case letters are significantly different at $p \leq 0.05$ using an analysis of variance (ANOVA) and a post-hoc Tukey-B/Games-Howell test.

** Generations followed by different upper-case letters are significantly different at $p \leq 0.05$ using an analysis of variance (ANOVA) and a post-hoc Tukey-B/Games-Howell test.

Table A4

Descriptive summary of thousand kernel weight (TKW) for all organic wheat populations and for each generation (n = 50 plants per population).

	CCP	Mean TKW [g]		Standard deviation (SD)	Min – Max [g]
F ₇ - 2008	OQ I	51.6	b	7.3	35.4 - 66.6
	OQ II	53.7	ab	5.7	42.9 - 70.5
	OY I	53.3	ab	5.6	41.1 - 68.9
	OY II	55.4	a	5.7	44.5 - 68.3
	OYQ I	53.8	ab	7.3	28.8 - 71.0
	OYQ II	52.9	ab	6.8	40.0 - 68.2
	mean	53.4	A**	6.5	28.8 - 71.0
F ₈ - 2009	OQ I	40.6	a	6.1	23.5 - 51.9
	OQ II	40.9	a	7.7	18.2 - 56.1
	OY I	39.4	a	4.9	28.9 - 51.1
	OY II	36.0	b	6.3	20.0 - 51.1
	OYQ I	39.1	a	6.2	18.8 - 51.6
	OYQ II	40.2	a	6.4	24.3 - 58.7
	mean	39.4	D	6.5	18.2 - 58.7
F ₉ - 2010	OQ I	43.5	a	5.0	30.5 - 51.9
	OQ II	40.2	b	4.9	25.8 - 49.6
	OY I	41.5	ab	5.8	28.7 - 53.1
	OY II	40.0	b	6.2	21.3 - 52.7
	OYQ I	40.4	ab	7.0	22.6 - 51.4
	OYQ II	41.1	ab	4.8	29.3 - 52.4
	mean	41.1	C	5.7	21.3 - 53.1
F ₁₂ - 2013	OQ I	43.6	ab	7.1	21.5 - 66.2
	OQ II	41.9	b	6.2	22.4 - 53.2
	OY I	42.9	ab	5.7	29.1 - 53.0
	OY II	44.3	ab	5.9	25.3 - 59.1
	OYQ I	45.6	a	5.1	34.6 - 57.4
	OYQ II	43.8	ab	6.8	30.3 - 59.7
	mean	43.7	B	6.2	21.5 - 66.2

* Within generation populations followed by different lower-case letters are significantly different at $p \leq 0.05$ using an analysis of variance (ANOVA) and a post-hoc Tukey-B/Games-Howell test.

** Generations followed by different upper-case letters are significantly different at $p \leq 0.05$ using an analysis of variance (ANOVA) and a post-hoc Tukey-B/Games-Howell test.

Appendix B

Table B1Transformation of data to Poisson distribution and calculation of N required for all CC populations to achieve the desired N_e of 5000 with an inbreeding coefficient of $\alpha = 1, 0.96, \text{ and } 0.85$, respectively.

CCP	Experimental results for number of kernels per plant		Adjustment to a mean of 1 kernel per plant ^{a)}	Adjusted variance plus sampling variance ^{b)}	S ² _k ^{c)}	N ^{d)} $\alpha = 1$	N ^{d)} $\alpha = 0.96$	N ^{d)} $\alpha = 0.85$
	Variance	Average	Adjusted variance					
F7-CQ-I	271.7	36.5	0.2040	1.2040	4.816	12040	11902	11518
F7-CQ-II	298.3	46.9	0.1355	1.1355	4.542	11355	11231	10884
F7-CY-I	235.4	41.6	0.1358	1.1358	4.543	11358	11233	10887
F7-CY-II	817.7	51.8	0.3045	1.3045	5.218	13045	12888	12450
F7-CYQ-I	742.1	57.7	0.2229	1.2229	4.892	12229	12087	11693
F7-CYQ-II	292.8	38.6	0.1966	1.1966	4.786	11966	11829	11450
F7-OQ-I	1185.3	64.3	0.2867	1.2867	5.147	12867	12713	12284
F7-OQ-II	651.8	53.2	0.2306	1.2306	4.923	12306	12163	11765
F7-OY-I	1204.8	67.2	0.2668	1.2668	5.067	12668	12518	12100
F7-OY-II	618.2	56.8	0.1917	1.1917	4.767	11917	11782	11405
F7-OYQ-I	397.0	48.8	0.1670	1.1670	4.668	11670	11539	11176
F7-OYQ-II	579.4	58.3	0.1705	1.1705	4.682	11705	11573	11208
F8-CQ-I	505.0	57.6	0.1520	1.1520	4.608	11520	11392	11037
F8-CQ-II	1087.3	70.2	0.2205	1.2205	4.882	12205	12064	11671
F8-CY-I	884.1	69.4	0.1838	1.1838	4.735	11838	11704	11331
F8-CY-II	1784.6	78.8	0.2873	1.2873	5.149	12873	12718	12289
F8-CYQ-I	909.3	69.7	0.1871	1.1871	4.748	11871	11736	11362
F8-CYQ-II	1097.9	65.3	0.2578	1.2578	5.031	12578	12429	12017
F8-OQ-I	724.1	62.0	0.1882	1.1882	4.753	11882	11747	11373
F8-OQ-II	742.3	55.1	0.2445	1.2445	4.978	12445	12299	11894
F8-OY-I	557.3	53.1	0.1975	1.1975	4.790	11975	11838	11458
F8-OY-II	1165.7	68.0	0.2522	1.2522	5.009	12522	12375	11965
F8-OYQ-I	482.7	52.1	0.1781	1.1781	4.712	11781	11648	11279

(continued on next page)

Table B1 (continued)

CCP	Experimental results for number of kernels per plant		Adjustment to a mean of 1 kernel per plant ^{a)}	Adjusted variance plus sampling variance ^{b)}	S_k^2 ^{c)}	N_e ^{d)} $\alpha = 1$	N_e ^{d)} $\alpha = 0.96$	N_e ^{d)} $\alpha = 0.85$
F8-OYQ-II	1442.6	67.3	0.3181	1.3181	5.273	13181	13021	12575
F9-CQ-I	843.5	67.3	0.1865	1.1865	4.746	11865	11730	11356
F9-CQ-II	986.1	68.3	0.2114	1.2114	4.846	12114	11,974	11587
F9-CY-I	1008.8	78.6	0.1631	1.1631	4.652	11631	11501	11140
F9-CY-II	908.9	68.1	0.1961	1.1961	4.784	11961	11825	11445
F9-CYQ-I	608.0	65.9	0.1401	1.1401	4.560	11401	11275	10927
F9-CYQ-II	1514.4	72.6	0.2872	1.2872	5.149	12872	12717	12288
F9-OQ-I	864.0	64.7	0.2063	1.2063	4.825	12063	11924	11540
F9-OQ-II	516.6	62.5	0.1322	1.1322	4.529	11322	11198	10853
F9-OY-I	1655.1	82.4	0.2435	1.2435	4.974	12435	12289	11884
F9-OY-II	1785.9	89.7	0.2218	1.2218	4.887	12218	12076	11683
F9-OYQ-I	1219.8	75.9	0.2116	1.2116	4.847	12116	11977	11589
F9-OYQ-II	931.7	72.1	0.1790	1.1790	4.716	11790	11657	11287
F12-CQ-I	499.1	43.6	0.2623	1.2623	5.049	12623	12474	12058
F12-CQ-II	2308.7	53.6	0.8047	1.8047	7.219	18047	17,791	17081
F12-CY-I	2463.5	67.4	0.5418	1.5418	6.167	15418	15214	14647
F12-CY-II	2270.8	74.2	0.4130	1.4130	5.652	14130	13951	13453
F12-CYQ-I	543.7	44.1	0.2801	1.2801	5.120	12801	12648	12223
F12-CYQ-II	1623.2	63.1	0.4079	1.4079	5.632	14079	13901	13407
F12-OQ-I	1670.8	56.4	0.5251	1.5251	6.100	15251	15050	14492
F12-OQ-II	1045.7	62.5	0.2674	1.2674	5.069	12674	12523	12105
F12-OY-I	768.8	41.9	0.4371	1.4371	5.748	14371	14187	13677
F12-OY-II	1555.6	54.1	0.5323	1.5323	6.129	15323	15120	14558
F12-OYQ-I	1527.7	56.1	0.4847	1.4847	5.939	14847	14654	14118
F12-OYQ-II	1147.9	47.1	0.5166	1.5166	6.066	15166	14966	14413

a) (Experimental variance for number of kernels per plant)/(Experimental mean number of kernels per plant)².

b) Adjusted variance plus Poisson-derived sampling variance (which is 1.0).

c) Multiplication by 2² to find S_k^2 .

d) Number of individuals required to achieve $N_e = 5000$ is: $N = \frac{1}{4} [N_e \{2(1-\alpha) + S_k^2(1 + \alpha)\}] - \square$.

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