

## ORIGINAL ARTICLE



# Effect of full-sib and S2-selection on a sweet corn population (*Zea mays* convar. *saccharata*)

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## Abstract

Sweet corn breeding goals differ from grain or silage corn. Sweet corn goals focus on marketable yield including several quality traits. This study explores the effect of a single cycle of full-sib selection and S2 selection on improving the marketable yield of an open-pollinated sweet corn population. The selected populations were subsequently compared in four environments for several plant-, yield- and quality traits relative to the original population. Analysis of variance was used to detect selection progress and indirect effects of selection. Full-sib and S2-selection decreased total yield. Marketable yield was decreased more by S2-selection than by full-sib selection. Flowering time was changed by full-sib selection, but not by S2-selection. Full-sib selection improved ear quality by increasing ear length, the diameter of the ear and the number of kernel rows. S2-selection showed no effect or a negative effect on ear quality. The application of a single cycle of selection using either method seemed inadequate for increasing marketable yield. More cycles might be necessary to make significant improvements.

## KEYWORDS

full-sib selection, marketable yield, open pollinated population, population improvement, S2-selection, sweet corn

## 1 | INTRODUCTION

Sweet corn is an important vegetable which is growing in popularity. Less research has been done on sweet corn than on grain corn or silage corn (Revilla et al., 2021). Furthermore, the breeding goals for sweet corn differ from grain- or silage corn. Sweet corn yield is measured by the weight of the freshly harvested ears or the number of ears. Grain yields are measured for grain corn and above-ground biomass is measured for silage corn. Commercially successful sweet corn varieties should have a high marketable yield. Marketable yield implies high-quality ears. Ears should be long, possess a high number of kernel rows, have good tip-fill, good colour and deep kernels with good taste. Plants should be vigorous and have high rates of germination and

emergence. Clearly, there are parallels between breeding grain- or silage corn and breeding sweet corn, but there are many characteristics specific to breeding sweet corn varieties that have not yet been thoroughly investigated. As sweet corn breeding research is mainly focused on breeding inbreds and hybrids, little information is available on the efficiency of selection methods for the intra-population improvement of specific sweet corn breeding traits.

Open-pollinated varieties (OP-varieties) of sweet corn are of interest in organic production (Desclaux & Nolot, 2014). They are characterized by a large genetic diversity with different genotypes, and different traits. The aim of population breeding for improving open-pollinated varieties is to improve the traits which are important for farmers, the market and the consumers. Other traits remain

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heterogeneous and can contribute to ecosystem services, ecological robustness and buffering capacity (Lammerts Van Bueren et al., 2018). Furthermore, populations are an opportunity for more seed sovereignty, by giving the possibility to farmers to reproduce or improve these open-pollinated cultivars. Traits that are not selected, remain heterogeneous and could evolve differently, giving the possibility to adapt to different environments and growing conditions when farmers continue saving seeds on farms.

Sweetcorn lacks clearly defined heterotic groups (Tracy, 1990). Furthermore, there is a need to supply varieties to farmers which can be easily reproduced. These two factors suggest that intra-population improvement might be useful for improving sweetcorn by increasing general combining ability (GCA), the mean performance of the population and by accumulating favourable alleles.

The genetic control behind the selected traits also affects the selection progress. Initially, higher genetic variance increases the performance of a selection method, while high variance due to the interaction of genotype and environment reduces progress (Hallauer et al., 2011). The initial level of the selected populations is also important for genetic gain. Traits already on a high-performance level are much more difficult to improve (Hallauer et al., 2011). Important factors for population breeding through recombination are genetic relatedness and GCA. Some traits, like the number of marketable ears in sweetcorn, are influenced by specific combining ability (SCA) (Solomon et al., 2012), while for other traits with low heterosis, GCA is much more important (Hallauer et al., 2011). In an open-pollinated population, the yield performance of individual plants relies as well on GCA and SCA, but because of panmixia, the SCA is lost after recombination, so breeding for population improvement is focused on the improvement of GCA.

Other important factors that affect the progress that can be made by selection include selection intensity, the testing capacity of the breeding program, selection on both sexes (on both parents) or only one sex, the heritability of the selected traits and the testing accuracy of the trial.

Different methods such as mass- and full-sib selection, and selection of selfed lines or of their topcrosses have been investigated both in theory and in practice for grain corn. These methods differ in their advantages and disadvantages. These results give hints at which method might be most effective for improving sweet corn, but they are no guarantee which of them would be most efficacious for improving specific traits of sweet corn.

Mass selection could be effective, especially for monogenic or recessive traits and traits with high genetic variance. However, it is less efficient in conditions with high environmental influence and does not offer the possibility to conduct repeated trials in different environments, because the selection is based only on the evaluation of the single plant (Hallauer et al., 2011). However, it is the least extensive selection method, is easy to use and does not require many investments. It has been used for a long time by farmers for on-farm selection. An advantage of this method is also the short cycle of only one year, as selection and recombination occur in the same year. Mass selection offers the possibility of selecting with very high intensity, which could result in efficient selection gains. Selection could be done

in both sexes for those traits which are visible before flowering, but only on the females for the traits visible after flowering, which obviously reduces the selection intensity for these traits. Mass selection is very effective for traits with higher heritabilities ( $>0.6$ ) and traits with higher proportions of additive variance ( $>0.5$ ) (Gallais, 2009).

An advantage of full-sib selection is higher selection intensity by selecting both sexes by choosing the best parents and crossing them. Evaluation of the full-sib crosses is a selection which includes also both sexes and implies selection on GCA. SCA is also selected, but the progress of SCA is neutralized in the recombination of the selected population. The evaluation could be done in several environments to select for more adaptability to different environments as well as a better estimation of genotypic variance.

S2-selection bears several advantages: Selection against deleterious and recessive alleles is possible by selecting inbred lines on per-se performance, which is an advantage compared to mass- and full-sib selection where recessive and deleterious alleles can remain hidden. Selection of S2-lines is effectuated only on one sex: All tested S2-lines are crossed with the same tester which reduces the potential of this selection method because the effect of the tester can hide the genetic effect of the S2-line. Only the remaining seeds of selected mothers (S2-lines) are then recombined. For population breeding, where GCA plays an important role, using a broad tester or the initial population as a tester will result in the selection of lines with high GCA. Using a broad tester, S2-selection improves GCA but not the SCA. As for full-sib selection, the evaluation of S2-Topcrosses could be done in several environments, which gives the opportunity to select for more adaptability to different environments as well as a better estimation of genotypic variance.

Genetic variability in the selected traits is one of the keys to efficient selection gain. Genetic variance of the means of full-sib families is  $\frac{1}{2}$  of the additive variance +  $\frac{1}{4}$  dominance variance with an inbreeding coefficient  $F = 0$ , while in S2-topcrosses it is  $1.5 \cdot \frac{1}{4}$  additive variance +  $0 \cdot$  dominance variance with  $F = .5$ . Additive variance is thus theoretically 0.37 among S2-top crosses vs. 0.5 in full-sibs (Awata et al., 2018; Hallauer et al., 2011). As population breeding is based on exploiting additive variance, full-sib selection might be theoretically slightly more efficient.

Practical aspects such as time, costs and testing capacity are also important for the choice of the best selection method in a commercial population breeding program. Full-sib selection and S2 selection are more time-consuming compared to mass selection and the calculation of the gain of selection per year is reduced by the longer cycle.

Full-sib selection is based on the evaluation of crosses of two plants in a population. Crossing needs one generation and one for evaluation. It could be more time-saving when recombination is done in the same year of evaluation if a winter nursery is available. So the length of the cycle is at minimum 2 years.

S2-line selection is even more time-consuming than full-sib selection because two generations are needed to self-individuals of the populations to obtain S2-lines. The S2-lines must then be topcrossed in a third generation to be evaluated afterwards. An additional generation is needed for the recombination of the selected lines. Thus this

method is the most time-consuming method with five generations included from the first self-pollination to recombination. The utilization of a winter nursery makes it possible to effectuate one cycle in at least 2.5 years in total. If the selection of sublines is considered, the process could take even more time, because the evaluation of sublines and the evaluation of the topcrosses must be done in the environment of interest, and not in the environment of the winter nursery, to select the right environmental conditions.

A winter nursery for two generations per year is costly. Additionally, the evaluation of plots with replicates used for full-sib and S2 selection requires more resources than the evaluation of single plants in mass selection. The necessity to evaluate twice as many S2-families as full-sibs to maintain a constant effective population size should also be considered.

Full-sib selection and S2-line selection have been often tested for their effects in grain corn breeding research (Hallauer et al., 2011). Ten cycles of full-sib selection of two populations were found to increase grain yield (Hallauer, 1988; Moll & Hanson, 1984). Reciprocal full-sib selection between two populations affected the performance of full-sibs and the performance of the corresponding S1 after seven cycles (Hallauer, 1984). High correlations exist between the yield of S2-testcrosses and the yield of later-generation testcrosses (Lile & Hallauer, 1994). This suggests that early testing is an effective tool to breed for good combining abilities (Lile & Hallauer, 1994).

Some studies investigated the effect of full-sib selection on plant development traits: Full-sib family selection was effective in reducing the days-to-silk and plant height and in increasing the number of ears per plant (Hallauer, 1988). Eight cycles of reciprocal full-sib selection had a positive effect on the standability of two populations. (Eyherabide & Hallauer, 1991). Full-sib selection reduced plant height and ear height of grain corn (Pandey et al., 1991).

Weyhrich et al. (1998) compared different selection methods and found that full-sib selection improved per-se performance for grain yield better than mass selection. Pandey et al. (1991) also found that full-sib selection increased grain yield, the number of ears per plant and the 1000-seed weight. After three cycles of full-sib selection in three populations, grain yield was improved with gains of 3.0%, 5.2% and 4.2% per cycle (Coutiño-Estrada et al., 2008). Singh et al. (1986) also reported that full-sib selection increased the number of ears. Hallauer (1988) found that two or three cycles of full-sib selection caused gains in yield ranging from .8 to 9.8% after the first cycle of selection (Hallauer, 1988). However, Ordas et al. (2012) found that full-sib selection failed to improve maize yield while S2 selection was successful.

This study evaluated full-sib selection and S2-selection for their efficiency in improving marketable yield on a super sweet (sh2) sweet corn population with the goal of obtaining improved open-pollinated populations. Selection trials and evaluation trials were conducted under both organic and conventional management to test and adapt the population to growing conditions close to their range of use.

The initial population is compared with populations produced after applying one cycle of full-sib selection or S2-selection. Different plant development traits, yield traits and quality traits were evaluated. The selection was for marketable yield, which implies high quality of

the ears with a long ear, a good tip-fill with a good colour and ear form. Furthermore, the effect of indirect selection on plant, yield and quality traits was explored.

## 2 | MATERIALS AND METHODS

### 2.1 | Full-sib selection

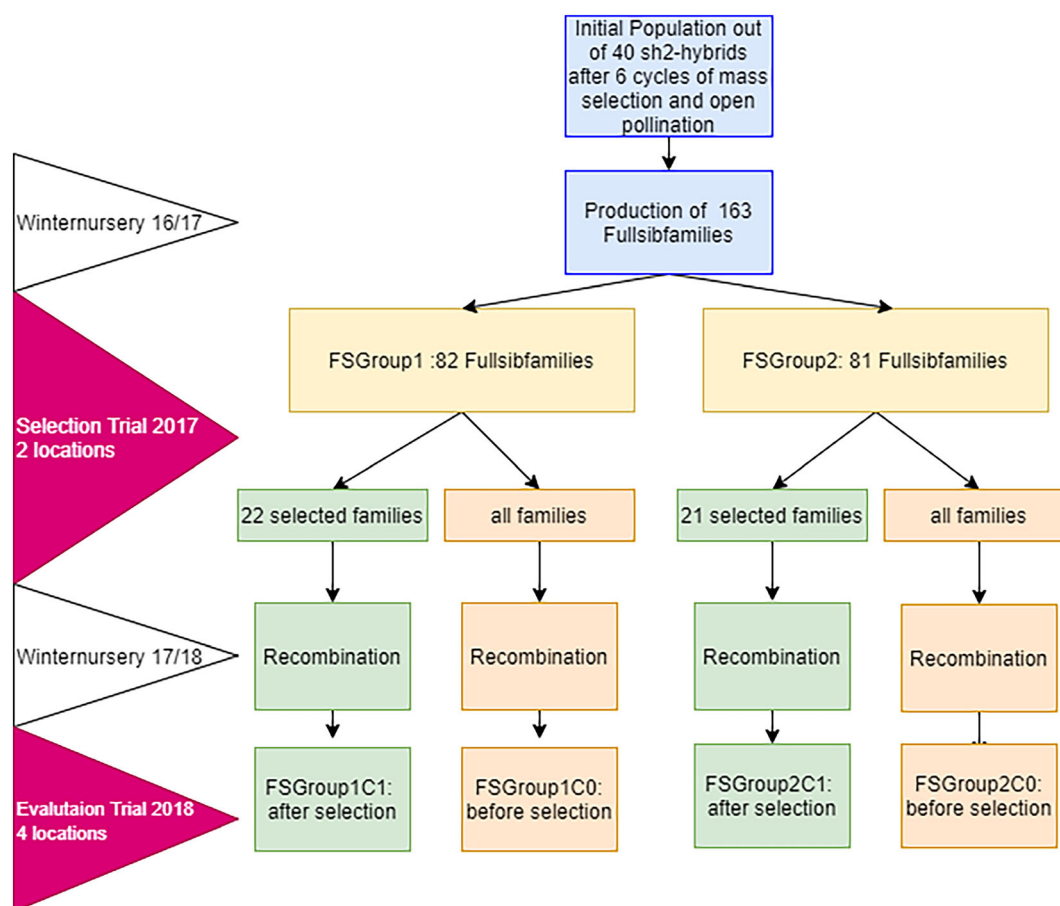
The initial population was developed from 40 yellow “extra sweet” sweet corn hybrid cultivars carrying the *sh2* allele and were free from other mutations as *su* or *se* (Kramer et al., 2015). They were mixed and open-pollinated in 2004 and subsequently selected with negative mass selection for 6 cycles from 2005 to 2016. The selection procedure is described in Figure 1. In The winter nursery near Rancagua, Chile (34° 04' 06.7" S, 70° 43' 48.7" W) in the winter of 2016/17163 full-sib families were produced by crossing 326 plants. The full-sib families were then randomly divided into two groups, FSGroup1 and FSGroup2 with 82 full-sib families in FSGroup1 and 81 in FSGroup2. One cycle of full-sib selection was applied to both groups in 2017 by selecting the best full-sib families. Selection was done on two fields near Göttingen, Germany of which one was under organic and one under conventional management (Table 1). The sum of the temperature was recorded between flowering and harvest and used in combination with regression analysis in order to assess the influence of the weather conditions (temperature) on the marketable yield of individual selections. 22 families in FSGroup1 and 21 in FSGroup2 were selected on marketable yield, based on the adjusted mean across the two fields near Göttingen. Selected and not selected families are represented in Figures 2 and 3.

In each group, three remaining seeds from each of the selected full-sibs were bulked to obtain two bulks, one with 63 seeds in Group 2 and one with 66 seeds in Group 1. The two bulks were grown in the same winter nursery in 2017/18 and each bulk was sib-mated to represent the two populations. Similarly, the initial Group 1 and Group 2 were reproduced in the same winter nursery by taking 1 seed of each of the 82 and 81 full-sib families to obtain two bulks with each of 82 and 81 seeds. Plants within each of these bulks were sib-mated to produce a representative population. For reproduction, a plant was only used once as female or male. Harvested seeds were bulked in equal quantities for each ear and tested as FSGroup1C0 and FSGroup2C0 (before selection) and FSGroup1C1 and FSGroup2C1 (after selection).

Trials to measure the effect of full-sib selection were established in four environments for FSGroup1 and in three environments (without Kleinhohenheim) for FSGroup2 in 2018 in a randomized complete block design with eight replications per environment. Details of the trials are given in Table 1.

### 2.2 | S2-selection

The S2-line selection started on the same population as the full-sib selection. The selection procedure of the S2 selection is described in



**FIGURE 1** Selection process for full-sib selection. [Color figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com/doi/10.1111/pbr.13170)]

Figure 4. In 2015 the first self-pollinations were produced in Rheinau within the initial population. One hundred plants were selfed and seeds from each selfed ear were sown in the winter nursery near Rancagua, Chile in 2015/2016 to conduct the second set of self-pollinations. The S2-lines obtained were all from different mother lines and were sown in 2016 in Rheinau to pollinate them by open pollination with the initial population as testers to increase selection on general combining ability. The seeds of the topcross were then sown in the same two trials near Göttingen, as the plots with full-sib selections. The sum of the temperature was recorded as it was for the full-sib selections.

19 S2-lines were selected for marketable yield based on the adjusted mean across the two fields near Göttingen (Figure 5). Three kernels of each selected line and one kernel of all 100 lines were bulked to create the populations S2C0 (before selection) with 100 kernels and the population S2C1 (after selection) with 57 kernels. Seeds were sent to the same winter nursery in 17/18 for recombination by making full-sib crosses, using each plant only once. The ears coming from the winter nursery were then bulked, by taking the same amount of kernels from each ear.

Trials to measure the effect of S2 selection were established in the same four environments in 2018 in a randomized complete block

design with eight replications per environment, as in full-sib selection (Table 1). The same traits were evaluated, as for full-sib selection.

## 2.3 | Plant vigour, ear quality and yield traits

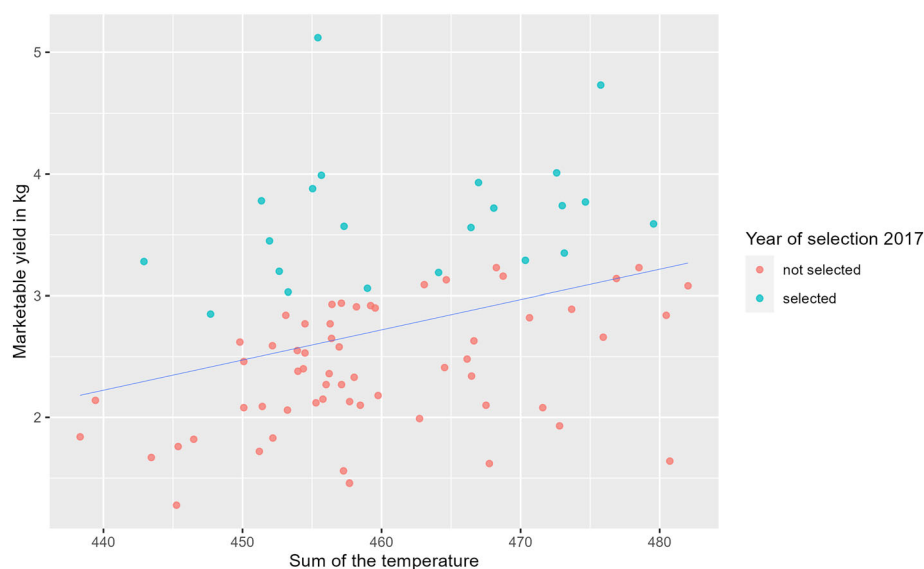
After emergence the number of seedlings was counted and noted as “germination”. Seedlings were thinned out to the same plant density after plants had three leaves, to avoid the influence of unequal germination rates on the performance of the plot. Two visual scorings per plot were carried out before flowering. The first vigour scoring was done when the plants reached BBCH 18 (Lancashire et al., 1991) and the second vigour scoring was done at BBCH 32. The average vigour per plot was scored on a scale of 1–9 (1 = lowest vigour, 9 = highest vigour) based on biomass, plant height, leaf number and leaf width.

Tillering is an undesired trait that can complicate the harvest. Scoring per plot was carried out when the mean height of the plants was about 70 cm (BBCH 34) with 1 = no tillering and 9 = maximum number and size of tillers.

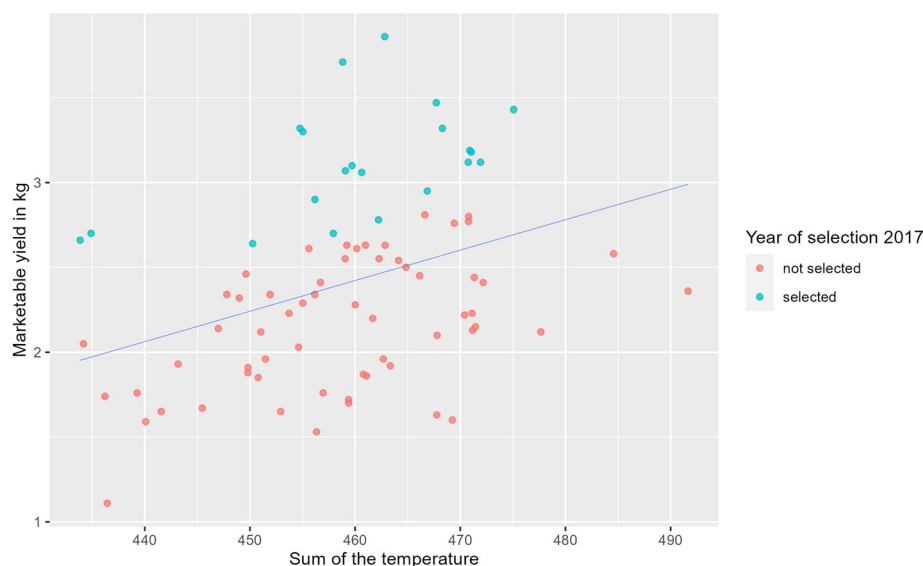
Flowering day was recorded when 50% of the plants of a plot showed silks. Flowering day 1 was the date the first plot in the trial was flowering. A plot flowering one day later was recorded as

**TABLE 1** Experimental sites for selection in Göttingen and for comparing cycles before and after full-sib selection in Rheinau, Göttingen and Kleinhohenheim. Weather stations in <sup>1</sup> Schaffhausen, <sup>2</sup> Göttingen, <sup>3</sup> Kleinhohenheim.

	Rheinau, Switzerland Evaluation trial 2018	Organic field, Göttingen, Germany Selection trial 2017 Evaluation trial 2018	Conventional field, Göttingen, Germany Selection trial 2017 Evaluation trial 2018	Kleinhohenheim, Germany Evaluation trial 2018
Mean temperature/year	9.4 °C <sup>1</sup>	8.7 °C <sup>2</sup>	8.7 °C <sup>2</sup>	11.1 °C <sup>3</sup>
Average temperature may-sept	2018 18.9 °C <sup>1</sup>	2017 16.1 °C <sup>2</sup> 2018 17.9 °C <sup>2</sup>	2017 16.1 °C <sup>2</sup> 2018 17.9 °C <sup>2</sup>	2018 18.4 °C <sup>3</sup>
Precipitation/may-sept	2018 394 mm <sup>1</sup>	2017 388 mm <sup>2</sup> 2018 184 mm <sup>2</sup>	2017 388 mm <sup>2</sup> 2018 184 mm <sup>2</sup>	2018 255 mm <sup>3</sup>
Preceding-crop	Clover grass	2017 clover grass 2018 winter wheat	2017 winter wheat 2018 Faba bean	Winter wheat
Soil conditions	Luvisol, sandy clay	Alluvial loess, silty loam	Alluvial loess, silty loam	Luvisol, loamy clay
Cultivation method	Organic	Organic	Conventional	Organic
Altitude above sea level	395 m	150 m	150 m	435 m
Sowing date	End of April/ beginning of may	8th of June 2017 28th of Mai 2018	12th of June 2017 25th of May 2018	16th of May 2018
Latitude and longitude	47° 38' 1.4244" N, 8° 37' 2.7192" E	51° 29' 53.0664" N, 9° 55' 50.6712" E	51° 29' 53.0664" N, 9° 55' 50.6712" E	48° 44' 14.8272" N, 9.200571
Plot dimensions 2017	-	2 rows, 3 m length, row distance .75 m, 30 plants per plot	2 rows, 3 m length, row distance .75 m, 30 plants per plot	-
Plot dimensions 2018	2 rows, 4.2 m length, row distance .75 m, 42 plants per plot	2 rows, 2 m length, row distance .75 m, 22 plants per plot	2 rows, 2 m length, row distance .75 m, 22 plants per plot	2 rows, 4.2 m length, row distance .75 m, 42 plants per plot
Seeder	Pneumatic single seeder (purpose- built)	Pneumatic single seeder Hege 95 (Hege, Hohebuch)	Pneumatic single seeder Hege 95 (Hege, Hohebuch)	Belt cone seeder (Haldrup, Ilshofen)
Fleece cover to prevent bird damage	No	Yes, removed at BBCH 13	Yes, removed at BBCH 13	No
Irrigation	94 L per plot at BBCH34 in 2018	27 L per plot at BBCH 53 in 2018	27 L per plot at BBCH 53 in 2018	No
Sowing depth	2.5 cm	2.5 cm	2.5 cm	2.5 cm

**FIGURE 2** Selection of full-sibs in FSGGroup1 in 2017 was done by selecting the full-sibs with the best marketable weight. A Pearson correlation was calculated and a line generated from linear regression shows the sum of temperature between flowering and harvest relative to the marketable yield. Blue points represent selected full-sib families and red points non selected ones. [Color figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com)]





**FIGURE 3** Selection of full-sibs in FSGroup2 in 2017 was done by selecting the full-sibs with the best marketable weight. A Pearson correlation was calculated and a line generated from linear regression shows the sum of temperature between flowering and harvest relative to the marketable yield. Blue points represent selected full-sib families and red points non selected ones. [Color figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

flowering day 2 etc. After all plants had been flowering, the heterogeneity of the tassel and the heterogeneity of the plant height was scored visually from 1–9, giving a 1 for homogenous plants as in an F1-hybrid.

Harvesting took place at flowering day + 32 days in Göttingen 2017 and flowering day + 31 days in Göttingen 2018 in both management systems and at +33 days in Rheinau and Kleinhohenheim. Plants showing symptoms of *Ustilago maydis* were counted (number of smut) at harvest of the cobs. To take into account different climatic conditions during ripening, temperature was recorded between flowering and harvest and the sum of the temperature was calculated.

Tassel heterogeneity and plant height heterogeneity were scored in 2018 following a scale 1 = very homogeneous to 9 = very heterogenous.

The largest ear on every plant was harvested. Immature ears (silk not browning) were discarded. The number of plants per plot was counted at harvest. Ears were husked, weighed and counted (Total yield, Number of ears) and visually classified into marketable ears and non-marketable ears. Ears shorter than 12 cm or longer than 23 cm were counted as non-marketable. Ears with odd shapes, with pollination less than 50%, and with unripe kernels were discarded as non-marketable. Marketable yield was weighed and the number of marketable ears was counted. Only the marketable ears were used to score quality traits.

Tip fill was scored 1 (=tips without seeds) to 9 (=fully filled). Ratings under 5 were sorted out as non-marketable ears. The mean ear length was scored in cm. Colour was scored 1 = least intense in colour (whitish) and 9 = most intense colour. Ear shape was scored 1 = ears with a pointed shape to 9 = cylindrical ears. Five marketable ears were chosen randomly to count the number of kernel rows at the centre of the ear. The diameter of the ear and the diameter of the cob of 5 cobs were measured in the middle of the ear to calculate the kernel length. The heterogeneity of the ear shape and the ear length was scored visually from 1 to 9 with cobs homogenous as in an F1-Hybrid = 1.

## 2.4 | Statistical analysis

Data adjustment for full-sib- and S2-selection was done with Plapstat (Utz, 2001) to adjust data on the incomplete Block design in the trials of 2017. Data analysis was done with R (R Core Team, 2024), and figures were generated with the packages ggplot2 (Wickham, 2016) and ggrepel. The package agricolae (de Mendiburu & Yaseen, 2020) was used for Tukey tests. Outliers were identified by calculating the inter-quartile range (IQR) for each trait separately on every location and removing data outside the interval of  $[Q_1 - 1.5 \cdot IQR, Q_3 + 1.5 \cdot IQR]$  with  $Q_1$  = first quartile and  $Q_3$  = third quartile.

To compare C0 and C1, the analysis of variance was done separately in each full-sib group and for S2-selection with the following model:

$$Y_{ijk} = \mu + g_i + l_j + b_{kj} + g_{lj} + e_{ijk}$$

in which  $Y_{ijk}$  or  $Y_{ijkl}$  are the observations of a plot,  $\mu$  is the general mean, with the effects  $g_i$  for genotype  $i$ ,  $l_j$  for location  $j$ ,  $b_{kj}$  for block  $k$  within location  $j$  and with the respective interactions and the error terms  $e_{ijk}$ .

The Anova is described in Table 2 for four locations for full-sib- and S2-selection:

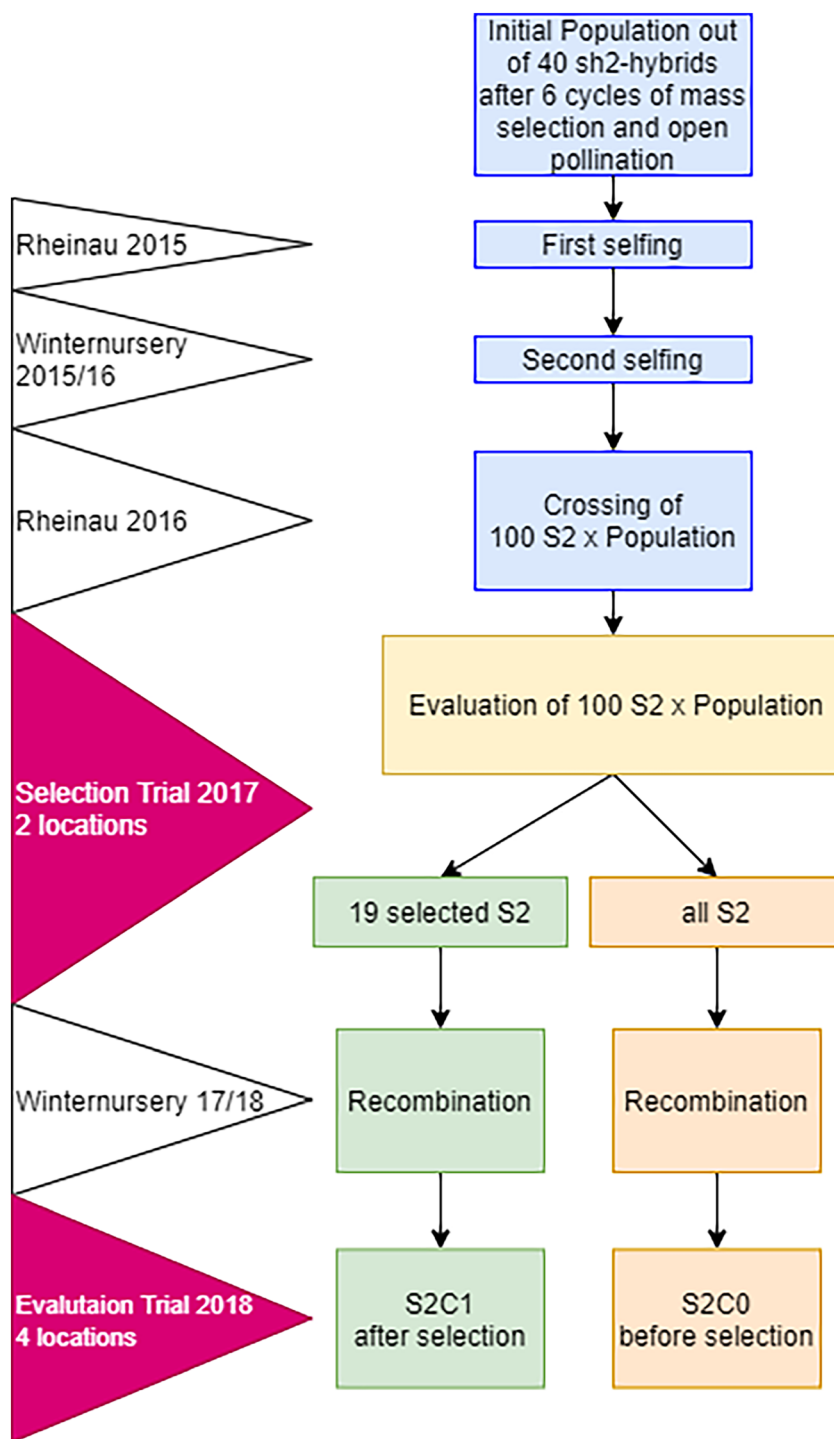
For the overall comparison of C0 and C1 on both full-sib groups the Anova on the means of the locations was done with the following model:

$$Y_{ij} = \mu + g_i + l_j + g_{lj} + e_{ij}$$

in which  $Y_{ij}$  is the mean of all blocks in a location,  $\mu$  is the general mean, with the effects  $g_i$  for genotype  $i$  before or after selection,  $l_j$  for location  $j$  and with the respective interactions and the error terms  $e_{ij}$ .

Data adjustment, cleaning and calculation for S2-selection were the same as for full-sib selection. For S2-selection the Anova was calculated for four environments, except for tillering where data from Rheinau was missing.

**FIGURE 4** Selection process S2-selection.  
[Color figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com/doi/10.1111/pbr.13170)]



### 3 | RESULTS

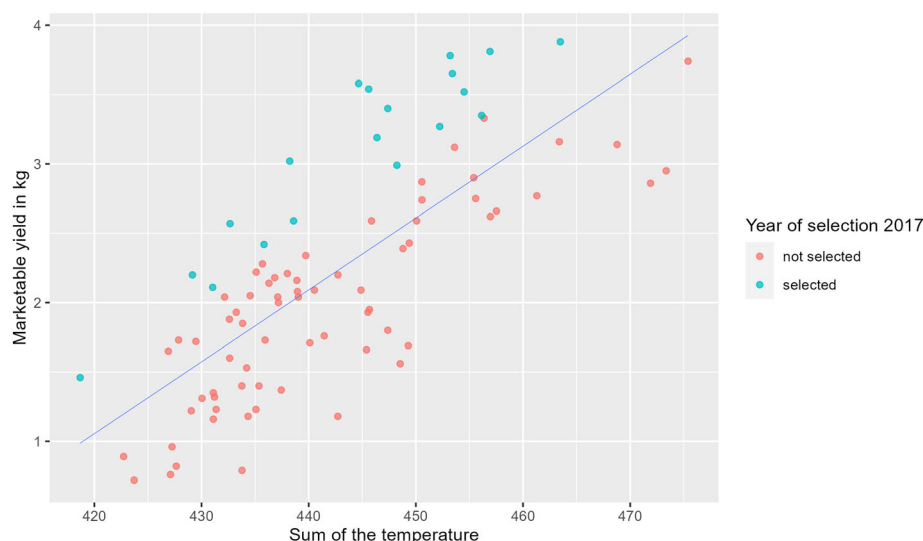
#### 3.1 | Full-sib selection

##### 3.1.1 | Anova

Comparing the means per location shows, that most of the traits did not change significantly over selection (Table 3).

The sum of the temperature increased for the selected populations, which indicates a higher amount of temperature from flowering day = 1 until harvest (Figures S1 and S2). The number of plants decreased over selection (Figures S3 and S4).

In full-sib group 2 the selected families were slightly earlier flowering after selection, while in full-sib group 1 selected families were slightly later. Observing both groups, selected families were slightly later flowering.



**FIGURE 5** Selection of topcrosses of S2-lines in the year of selection 2017. The red points represent non-selected topcrosses of S2-lines with the population as tester and the blue points represent the selected topcrosses. The regression line (blue) was calculated over all topcrosses and was used to select by shifting the line parallel to the y-axis. [Color figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

**TABLE 2** Anova on three locations for full-sib group2 and on four locations for full-sib group1 and S2-selection. The compared genotypes are C0 and C1;  $I$  = number of locations.

Anova	Degrees of freedom
Genotype	2-1
Location	$I-1$
Block nested in location	$I(8-1)$
Interaction: GenotypexLocation	$(I-1)(2-1)$
Residual interaction BlockxGenotyp*location	$I(8-1)(2-1)$
Total	$(I*2*8)-1$

The effect of selection was visible in the ear length, which showed an increase of 0.64 cm. Some significant changes could be observed in the following unselected traits: The Heterogeneity of the tassels decreased by 1.13 scores (Figures S5 and S6). The diameter of the ear increased very slightly through selection by 0.13 cm. The number of kernel rows increased by 1.07 rows, which is a big change for one selection cycle.

### 3.1.2 | Yield was mostly decreased by selection

There were few significant changes in yield traits despite the fact that marketable yield was a selection criterion. Selection did affect total yield, which decreased slightly, but significantly by 0.46 kg. Separate analysis of both groups reveals that total yield is decreased by selection (Figures 6 and 7) in both groups. The change was significant for group 2. The total number of ears decreased in both groups in tendency, but not significantly.

A decrease of the marketable yield in kg could be observed in both groups but this change was not significant (Figures 8 and 9). Looking at the number of marketable ears (Figures 10 and 11), the decrease was less pronounced than in the marketable yield, but this

change was not significant either. In full-sib group 2 there were more but smaller marketable ears after selection because the number of marketable ears increases, but the weight decreases.

The % of marketable yield did not show a sign. Change in both groups. However, there are slightly increasing means in both groups. Changes are opposed in both groups for the % of the number of marketable ears. In full-sib group1 means decreased slightly but contrarily full-sib group2 increased significantly the percentage of the number of marketable ears.

### 3.1.3 | The number of kernel rows and the ear diameter were increased by the selection

The two quality traits where changes are most obvious are the number of kernel rows (Figures 12 and 13) and the diameter of the ear (Figures 14 and 15). Both traits were increased by selection in both groups, while the changes were only significant in full-sib group1 for both traits.

### 3.1.4 | Different reactions to selection in tip fill, the length of the ear and ear colour

Some traits showed a less clear reaction to selection as one of the groups showed a change, but the other one did not. So, for example, tipfill decreased in full-sib group1 but showed no clear change in full-sib group2. The length of the ear increased significantly in full-sib group 1, but not in group2 (Figures 16 and 17). A change towards lighter colour was observed as an effect of selection in both groups, but the changes were not significant.

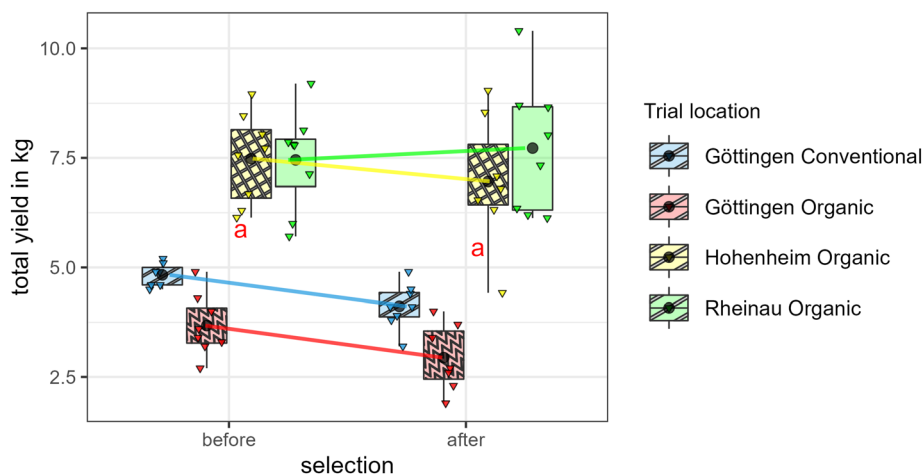
The changes were dis-similar in both groups for ear shape, kernel length and heterogeneity of the ear length and the ear shape. For the shape of the ear, full-sib group 1 changed to a more cylindrical shape but group 2 shows a change to a more conical shape. The changes

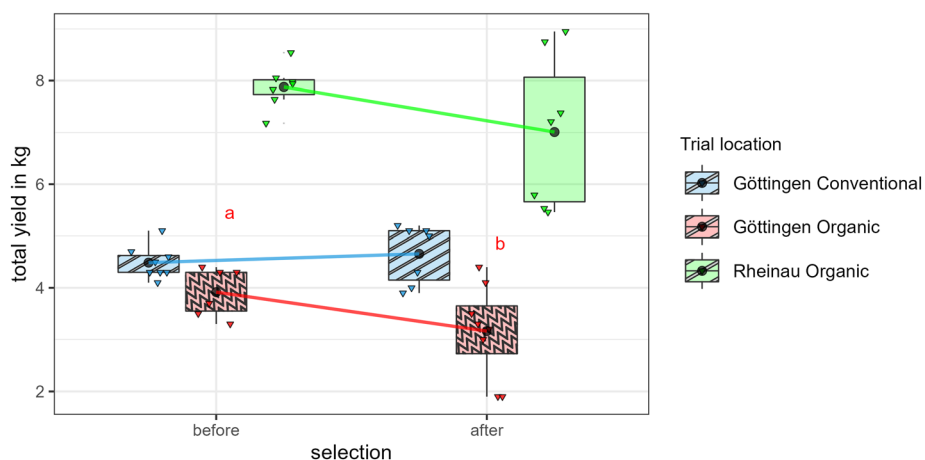


**TABLE 3** Overall comparisons of C1 and C0 of full-sib selection with a Tukey test on means over locations for all observed traits. Direct selection was done on marketable yield. The groups of the Tukey test on the factor selection (before/after selection) are indicated. Traits with significant changes through selection are printed in bold.

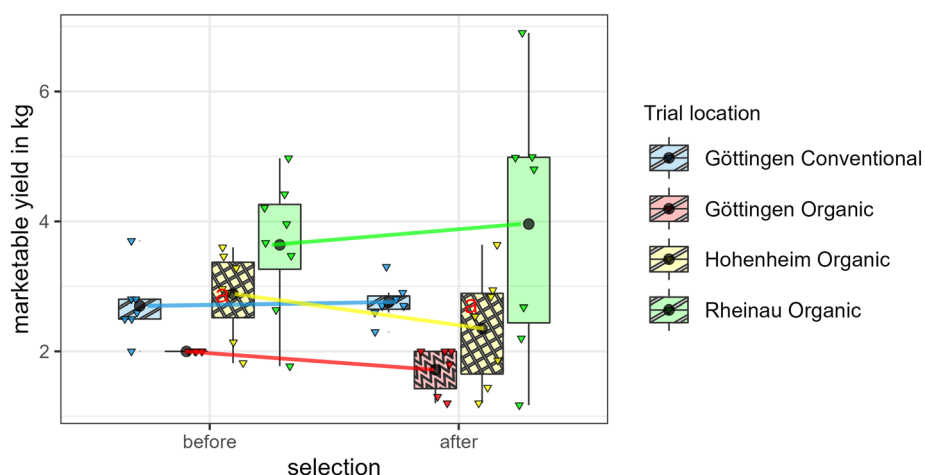
Mean over all locations before selection	Mean over all locations after selection	Trait	Unit
Plant development			
6.84 a	6.83 a	First vigour scoring	Score
5.29 a	4.55 b	<b>Flowering day</b>	<b>Count</b>
68.64 a	67.25 a	Germination	Count
7.99 a	7.84 a	Heterogeneity of the plant height	Score
6.36 a	5.23 b	<b>Heterogeneity of the tassel</b>	Score
30.80 a	30.1 a	Number of plants	Count
3.76 a	4.00 a	Number of smut	Count
7.72 a	7.45 a	Second vigour scoring	Score
653.65 b	661.08 a	<b>Sum of the temperature</b>	<b>°C</b>
1.88 a	2.00 a	Tillering	Score
Yield			
5.67 a	5.21 b	<b>Total yield</b>	<b>Kg</b>
2.96 a	2.84 a	Marketable yield	Kg
26.13 a	25.05 a	Number of ears	
10.29 a	10.10 a	Number of marketable ears	
.34 a	.35 a	Fraction of ears that were marketable	%
.57 a	.58 a	Fraction of yield that was marketable	%
Quality			
4.99 b	5.12 a	<b>Diameter of the ear</b>	<b>Cm</b>
6.92 a	6.77 a	Ear colour	Score
18.43 b	19.07 a	<b>Ear length</b>	<b>Cm</b>
7.27 a	7.03 a	Ear shape	Score
6.35 a	6.36 a	Heoterenogeneity of the ear shape	Score
6.76 a	6.97 a	Heterogeneity of the ear length	Score
1.60 a	1.58 a	Kernel length	Cm
14.19 b	15.26 a	<b>Number of kernel rows</b>	
8.05 a	7.91 a	Tip fill	Score

**FIGURE 6** Total yield of full-sib group 1 before and after selection with colours and shading representing the four locations in the evaluation year. Boxplots for each location show the quantiles and the black round points represent mean values for each location. Location values are connected with coloured lines. The letters indicate the result of the Tukey test and are plotted on the mean value over all locations. [Color figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com)]

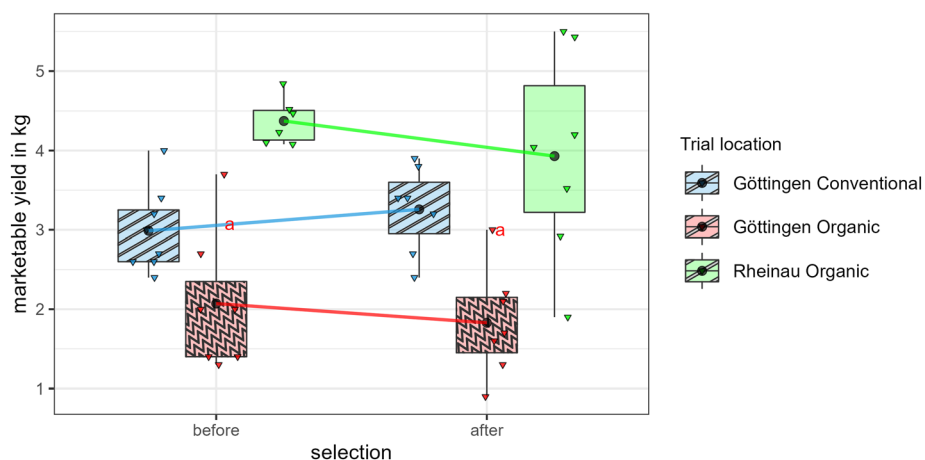




**FIGURE 7** Total yield of full-sib group 2 before and after selection with colours and shading representing the 3 locations in the evaluation year. Boxplots for each location show the quantiles and the black round points represent mean values for each location. Location values are connected with coloured lines. The letters indicate the result of the Tukey test and are plotted on the mean value over all locations. [Color figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com/doi/10.1111/pbr.13170)]



**FIGURE 8** Marketable yield in full-sib group 1 before and after selection with colours and shading representing the 4 locations in the evaluation year. Boxplots for each location show the quantiles and the black round points represent mean values for each location. Location values are connected with coloured lines. The letters indicate the result of the Tukey test and are plotted on the mean value over all locations. [Color figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com/doi/10.1111/pbr.13170)]

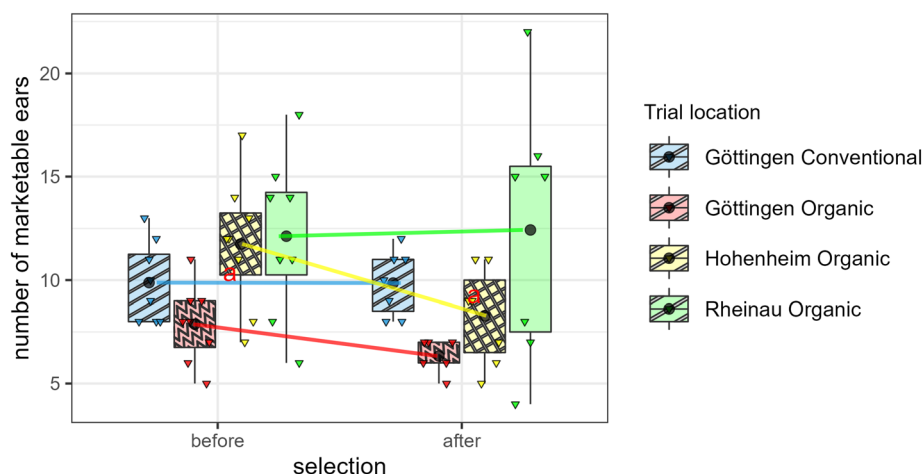


**FIGURE 9** Marketable yield in full-sib group 2 before and after selection with colours and shading representing the 3 locations in the evaluation year. Boxplots for each location show the quantiles and the black round points represent mean values for each location. Location values are connected with coloured lines. The letters indicate the result of the Tukey test and are plotted on the mean value over all locations. [Color figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com/doi/10.1111/pbr.13170)]

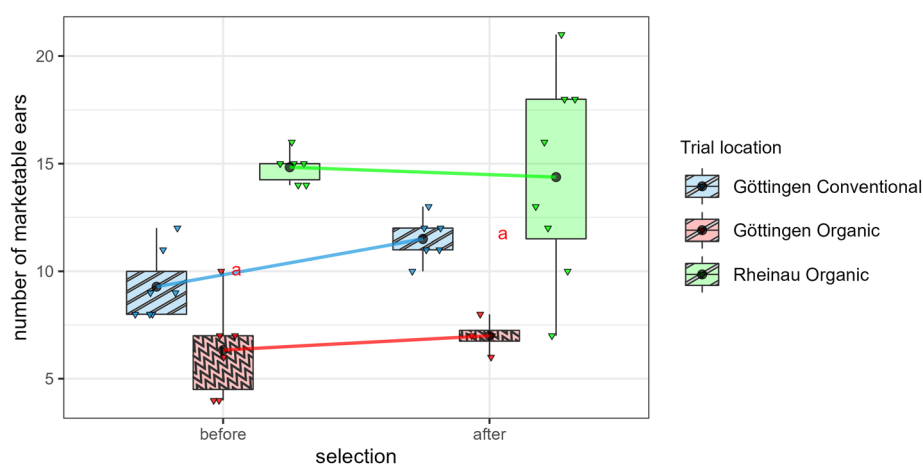
were not significant but contradictory. The kernel length did not show a clear reaction to selection. While there was a significant change towards shorter kernels in the full-sib group 1, a change for longer kernel length could be observed in group 2 (not significant). In both groups, no significant change occurred for the heterogeneity of the

ear length. While means increased slightly in full-sib group 1, which indicates more homogeneity after selection, in group 2 the means decreased with more heterogeneity after selection. The heterogeneity of the ear shape did not show significant changes and both groups showed contradictory changes in the means.

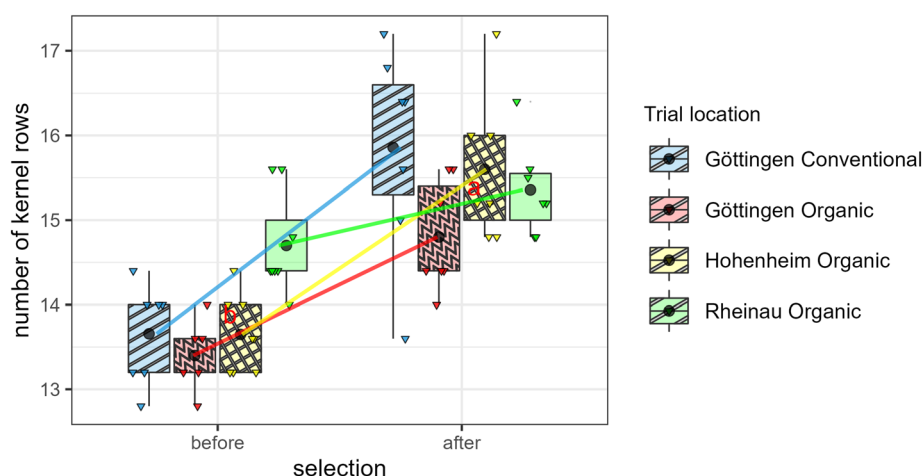
**FIGURE 10** Number of marketable ears in full-sib group 1 before and after selection with colours and shading representing the four locations in the evaluation year. Boxplots for each location show the quantiles and the black round points represent mean values for each location. Location values are connected with coloured lines. The letters indicate the result of the Tukey test and are plotted on the mean value over all locations. [Color figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com/doi/10.1111/pbr.13170)]



**FIGURE 11** Number of marketable ears in full-sib group 2 before and after selection with colours and shading representing the 3 locations in the evaluation year. Boxplots for each location show the quantiles and the black round points represent mean values for each location. Location values are connected with coloured lines. The letters indicate the result of the Tukey test and are plotted on the mean value over all locations. [Color figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com/doi/10.1111/pbr.13170)]



**FIGURE 12** Number of kernel rows in full-sib group 1 before and after selection with colours and shading representing the four locations in the evaluation year. Boxplots for each location show the quantiles and the black round points represent mean values for each location. Location values are connected with coloured lines. The letters indicate the result of the Tukey test and are plotted on the mean value over all locations. [Color figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com/doi/10.1111/pbr.13170)]



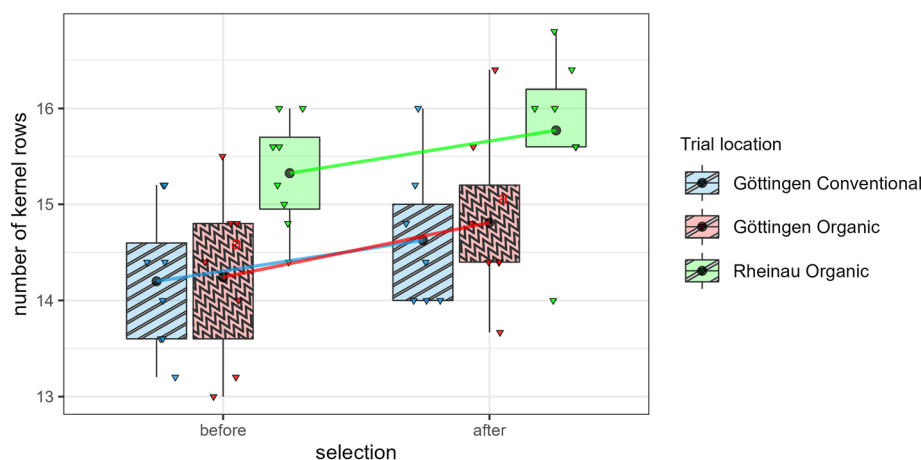
## 3.2 | S2-selection

### 3.2.1 | Anova

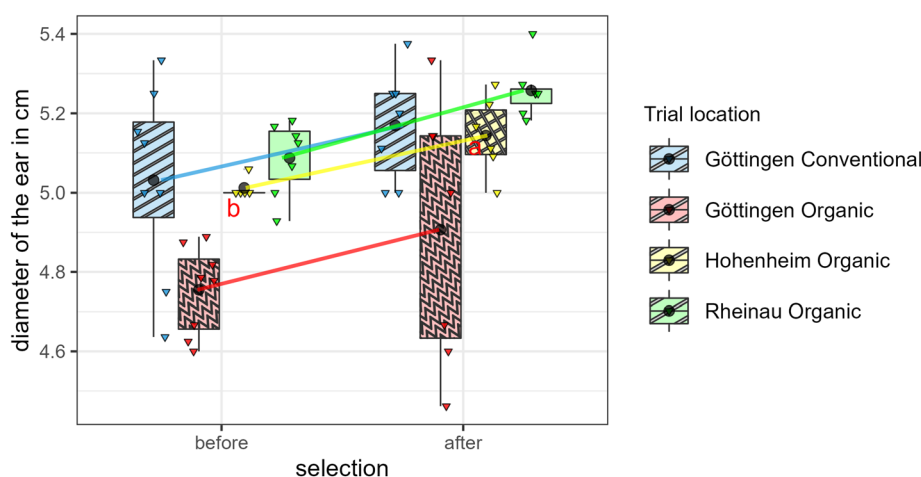
The comparison of the means over all locations before and after selection is represented in Table 4 and data of the locations separately is shown more in detail for some traits in Figures 18–23.

### 3.2.2 | No clear changes in several plant development traits

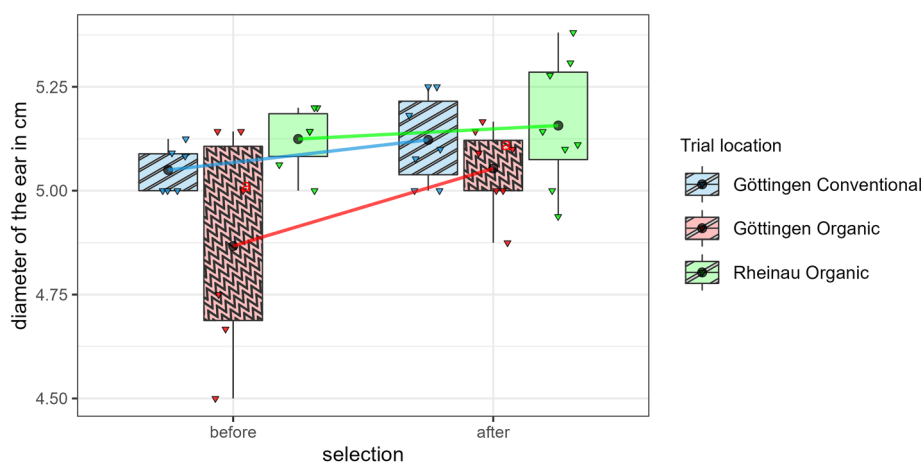
No significant change is observable for all plant development traits in S2-selection (Table 4). The flowering day increased slightly (Figure S7), which means that selection might have caused later flowering. Nevertheless, this change is very small and not



**FIGURE 13** Number of kernel rows in full-sib group 2 before and after selection with colours and shading representing the three locations in the evaluation year. Boxplots for each location show the quantiles and the black round points represent mean values for each location. Location values are connected with coloured lines. The letters indicate the result of the Tukey test and are plotted on the mean value over all locations. [Color figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com/doi/10.1111/pbr.13170)]



**FIGURE 14** Diameter of the ear in full-sib group 1 before and after selection with colours and shading representing the four locations in the evaluation year. Boxplots for each location show the quantiles and the black round points represent mean values for each location. Location values are connected with coloured lines. The letters indicate the result of the Tukey test and are plotted on the mean value over all locations. [Color figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com/doi/10.1111/pbr.13170)]

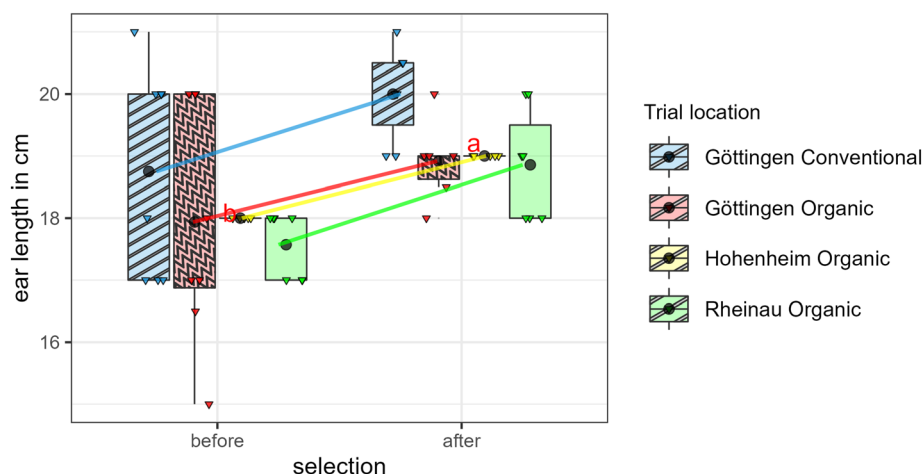


**FIGURE 15** Diameter of the ear in full-sib group 2 before and after selection with colours and shading representing the three locations in the evaluation year. Boxplots for each location show the quantiles and the black round points represent mean values for each location. Location values are connected with coloured lines. The letters indicate the result of the Tukey test and are plotted on the mean value over all locations. [Color figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com/doi/10.1111/pbr.13170)]

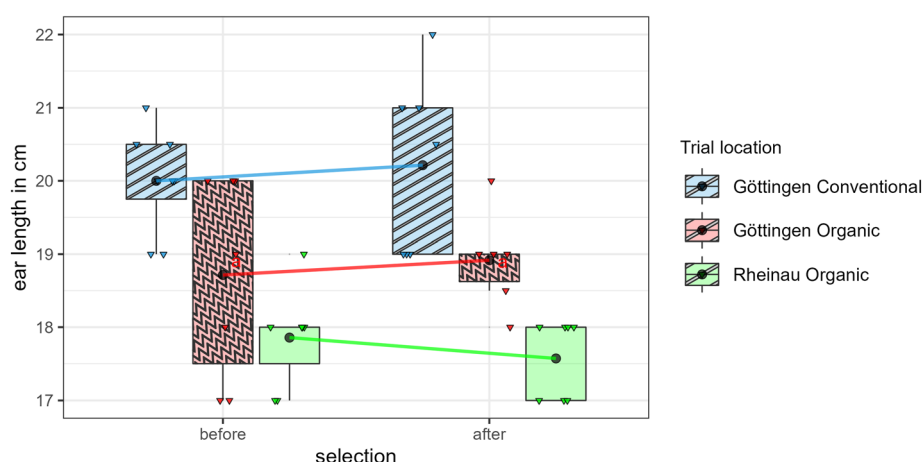
significant. The sum of the temperature decreased as well, but not significantly. This indicates that the selected population was harvested after slightly less warm weather. The heterogeneity of the tassel (Figure S8) and the heterogeneity of the plant height did not show a clear change at the first vigour scoring. However, the

second vigour scoring (Figure S9) indicated a slight decrease in vigour through selection, which was not significant. Traits which decreased, without significant change were the number of plants (Figure S10) showing symptoms of smut and tillering as well as germination.

**FIGURE 16** Ear length in full-sib group 1 before and after selection with colours and shading representing the 3 locations in the evaluation year. Boxplots for each location show the quantiles and the black round points represent mean values for each location. Location values are connected with coloured lines. The letters indicate the result of the Tukey test and are plotted on the mean value over all locations. [Color figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com)]



**FIGURE 17** Ear length in full-sib group 2 before and after selection with colours and shading representing the three locations in the evaluation year. Boxplots for each location show the quantiles and the black round points represent mean values for each location. Location values are connected with coloured lines. The letters indicate the result of the Tukey test and are plotted on the mean value over all locations. [Color figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com)]



### 3.2.3 | Less yield after selection

Yield showed significant changes. Almost all yield traits were decreased by S2-selection (Table 4). The total number of ears and the total yield (Figure 18) decreased slightly, but not significantly. But the decrease in the number of marketable ears is significant. Here the population after selection showed fewer marketable ears in all locations, but Göttingen on the organic field (Figure 19) with a decrease of the mean of  $-2.04$  ears through selection. The same reduction is observed for the marketable yield in kg (Figure 20). The decrease in the percentage of the marketable yield and fraction of marketable ears is significant. Interestingly the organic Göttingen location did not show this decrease.

### 3.2.4 | Tipfill and ear shape improved by selection

Selection improved tipfill significantly with a gain of 0.37 score value. The selection also improved the shape of the ear towards a cylindrical shape in the selected population with a gain of 0.6 score value. The length of the ears (Figure 21) was increased through selection, but this change was not significant.

### 3.2.5 | The number of kernel rows, kernel length and ear diameter declined

But there were also traits that were decreased by selection. The number of kernel rows was clearly reduced by selection with a loss of 0.8 (Figure 22). The length of the kernels was also clearly reduced ( $-0.16$  cm) by selection, as well as the diameter of the ears (Figure 23), which became slenderer ( $-0.14$  cm). No clear changes could be seen in the heterogeneity of the ear shape and for ear length and colour.

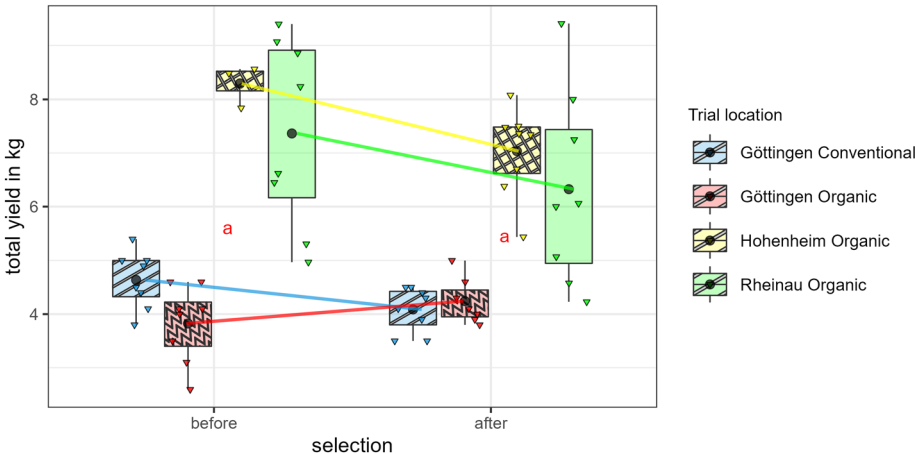
## 4 | DISCUSSION

### 4.1 | No clear effect of both methods on yield traits

We would have expected larger positive changes in yield and marketable yield, which was the directly selected trait in this study. However, our study shows that both methods failed to improve marketable yield. Surprisingly, we did observe mostly decreasing values for yield traits including significantly decreased total yield following full-sib

**TABLE 4** Overall comparison of C1 and C0 of S2-selection with a Tukey test for all observed traits. Direct selection was done on marketable yield. The groups of the Tukey test on the factor selection (before/after selection) are indicated. Traits with significant changes through selection are printed in bold.

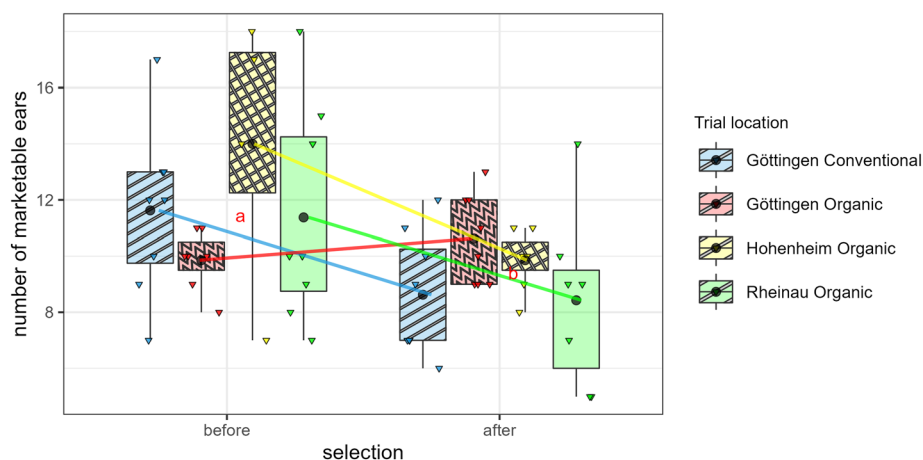
Mean over all locations before selection	Mean over all locations after selection	Trait	Unit
Plant development			
6.13 a	6.31 a	First vigour scoring	Score
7.03 a	7.12 a	Flowering day	Count
72.17 a	71.29 a	Germination	Count
7.92 a	7.29 a	Heterogeneity of the plant height	Score
6.56 a	6.31 a	Heterogeneity of the tassel	Score
31.12 a	32.13 a	Number of plants	Count
3.50 a	2.84 a	Number of smut	Count
7.46 a	7.07 a	Second vigour scoring	Score
637.89 a	637.07 a	Sum of the temperature	°C
2.39 a	2.10 a	Tillering	Score
Yield			
5.61 a	5.46 a	Total yield	Kg
3.30 a	2.61 b	<b>Marketable yield</b>	Kg
27.00 a	27.26 a	Number of ears	
11.44 a	9.40 b	<b>Number of marketable ears</b>	
.40 a	.34 b	<b>Fraction of ears that were marketable.</b>	%
.62 a	.52 b	<b>Fraction of yield that was marketable</b>	%
Quality			
5.10 a	4.96 b	<b>Diameter of the ear</b>	Cm
6.69 a	6.72 a	Ear colour	Score
18.54 a	19.02 a	Ear length	Cm
6.82 b	7.42 a	<b>Ear shape</b>	Score
5.95 a	6.19 a	Heoterogeneity of the ear shape	Score
6.67 a	7.00 a	Heterogeneity of the ear length	Score
1.71 a	1.55 b	<b>Kernel length</b>	Cm
15.01 a	14.21 b	<b>Number of kernel rows</b>	
7.77 b	8.14 a	<b>Tip fill</b>	Score



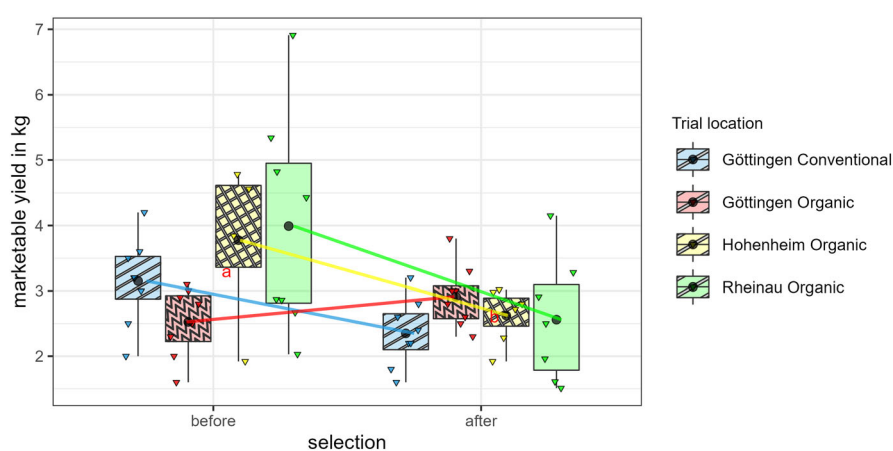
**FIGURE 18** The total yield in S2-selection before and after selection with colours and shading representing the four locations in the evaluation year. Boxplots for each location show the quantiles and the black round points as means of every location which are connected with coloured lines. The letters indicate the result of the Tukey test and are plotted on the mean value over all locations. [Color figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com/doi/10.1111/jbr.13170)]



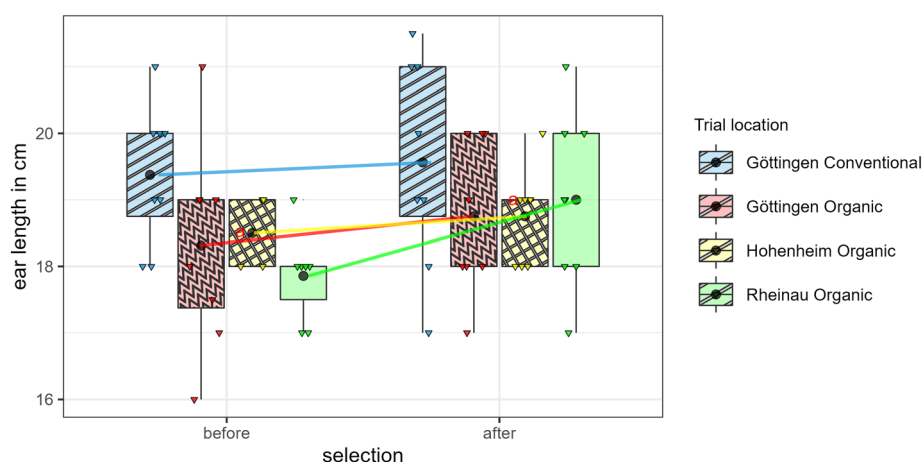
**FIGURE 19** The number of marketable ears in S2-selection before and after selection with colours and shading representing the four locations in the evaluation year. Boxplots for each location show the quantiles and the black round points as means of every location which are connected with coloured lines. The letters indicate the result of the Tukey test and are plotted on the mean value over all locations. [Color figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com/doi/10.1111/pbr.13170)]



**FIGURE 20** The marketable yield in S2-selection before and after selection with colours and shading representing the four locations in the evaluation year. Boxplots for each location show the quantiles and the black round points as means of every location which are connected with coloured lines. The letters indicate the result of the Tukey test and are plotted on the mean value over all locations. [Color figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com/doi/10.1111/pbr.13170)]



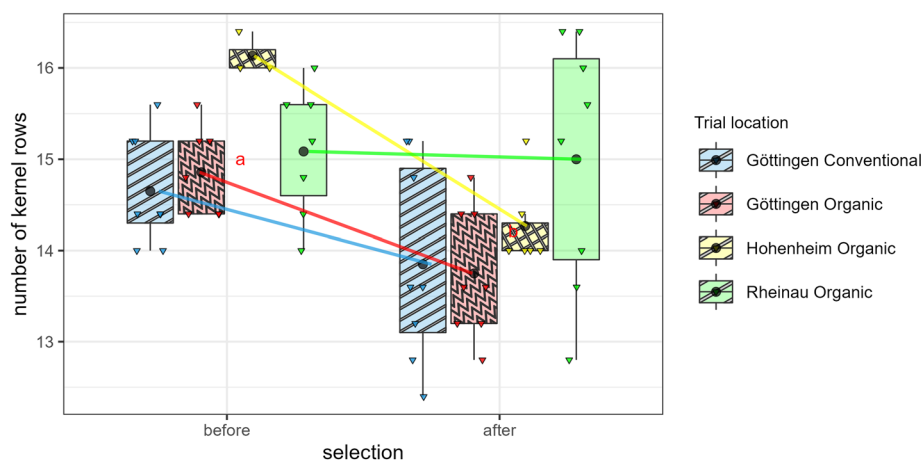
**FIGURE 21** The ear length in S2-selection before and after selection with colours and shading representing the 4 locations in the evaluation year. Boxplots for each location show the quantiles and the black round points as means of every location which are connected with coloured lines. The letters indicate the result of the Tukey test and indicate the mean of all locations. The letters indicate the result of the Tukey test and are plotted on the mean value over all locations. [Color figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com/doi/10.1111/pbr.13170)]



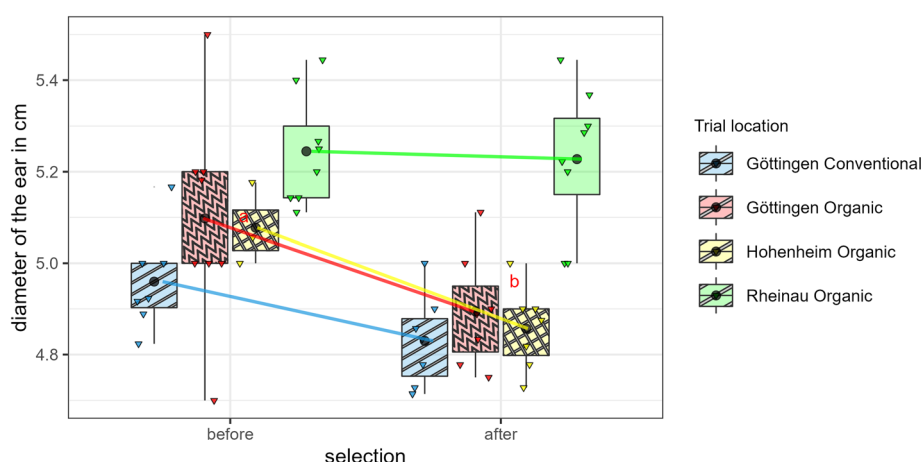
selection. S2-selection shows as well decreasing yield even clearer than full-sib selection in our study.

Results in the literature on heritabilities of yield traits and selection gain in sweet corn are contradictory: Grain yield in sweet corn showed low heritabilities in Asgh's study (Jawad Asgh & Sadaqat Me, 1999). But in contrast, Ojo et al. (2020) found high heritabilities for grain yield for 106 full-sib families ( $h^2 = .88/.98$ . Other

researchers found that yield was decreased by full-sib selection and by selfing, which is consistent with our study (Treenoo & Amnueysit, 2012). However, that same study showed positive effects of full-sib selection and selection of inbred lines on the number of ears per plant. Another study, (Saleh et al., 1993), showed the effects of full-sib and S1-selection on two populations. In this study, S1-selection was superior to full-sib selection for improving yield.



**FIGURE 22** The number of kernel rows in S2-selection before and after selection with colours and shading representing the four locations in the evaluation year. Boxplots for each location show the quantiles and the black round points as means of every location which are connected with coloured lines. The letters indicate the result of the Tukey test and are plotted on the mean value over all locations. [Color figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com/doi/10.1111/pbr.13170)] [wileyonlinelibrary.com](https://onlinelibrary.wiley.com/doi/10.1111/pbr.13170)]



**FIGURE 23** The diameter of the ears in S2-selection before and after selection with colours and shading representing the four locations in the evaluation year. Boxplots for each location show the quantiles and the black round points as means of every location, which are connected with coloured lines. The letters indicate the result of the Tukey test and are plotted on the mean value over all locations. [Color figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com/doi/10.1111/pbr.13170)] [wileyonlinelibrary.com](https://onlinelibrary.wiley.com/doi/10.1111/pbr.13170)]

These differing results in the literature show that there is no clear effect of these selection methods on sweet corn yield traits. Our study indicates that other factors might be important for the success of selection.

An explanation for the yield loss could be, that the marketable yield might be a trait that strongly depends on heterotic effects, having no significant GCA- but a significant SCA effect (Solomon et al., 2012). These results would support our findings, that it is difficult to improve marketable yield within only one cycle, using two selection methods that aim to improve mainly GCA-effects.

Decreased genetic variability, or even inbreeding, could explain the loss of yield. Uncontrolled inbreeding means a reduction in yield and vigour. But while yield traits decreased, no clear change was observable for the vigour scores in both methods. Inbreeding was kept to a minimum by a selection of a sufficient number of selection entities. So a yield reduction by inbreeding is rather unclear, but cannot be excluded.

Increasing selection intensity is related to a decrease in effective population size. Selection gain can be increased by increasing selection intensity while keeping an acceptably large effective population size. In our experiment, selection intensity was 0.25 and 0.26 for full-sib selection and it was 0.19 for S2 selection. These correspond to

standardized selection differentials  $k = 1.271$  and  $k = 1.248$  for full-sib selection and  $k = 1.428$  for S2-selection (Gallais, 2009) which are relatively low standardized selection differentials (Brhane, 1989). Selection intensity was slightly higher in S2-selection than in full-sib selection which should give higher selection gains, but probably higher selection intensities might have led to bigger effects of both selection methods. On the other hand, the number of selected entities should not be too small, to avoid the loss of genetic variability for long-term breeding goals. In this case, higher selection intensities should have been achieved by testing more full-sibs or S2-topcrosses.

Hallauer et al. (2011) reported that the effect of selection can depend also on the performance level of the initial population. As our initial population was selected for several years by mass selection, the additive variance for traits with high heritability might have been exploited already well and further improvement would be only possible by selection under environments with greater diversity.

## 4.2 | Effect on earliness of full-sib selection

Maize-flowering time is a highly heritable trait (Hemavathy, 2020; Ojo et al., 2020; Saboor Khan et al., 2018; G. Saleh et al., 1993; G. B. Saleh

et al., 2002). An effect of full-sib selection on earliness was visible in our study, where the selected population flowered earlier. This was more obvious in full-sib group 1. But S2-selection did not change flowering time.

The change caused by full-sib selection could be due to an indirect effect of selection on marketable yield if yield and flowering time are correlated. In one study, no correlation was found in 12 Populations between days of silking and the yield (Saleh et al., 2002). But days to silking were found negatively correlated to the yield in other studies (Chavan et al., 2020; Dagla et al., 2015; Gonçalves et al., 2018; Hemavathy, 2020). Dickert and Tracy (2002) reported that yields are reduced in very early material by reduced plant height and less photosynthetic surface. Thus in early populations, selection for later flowering can probably increase yields by delaying flowering dates. However, the population studied in our article is not extremely early. Thus, the selection pressure on later full-sibs might be rather due to genetic drift effects or assortative mating caused by crossing full-sib parents that flower at the same time. Possibly, plants flowering at the same time are also genetically related, which could have an inbreeding effect in the resulting full-sibs and in the recombined population. Crosses between early flowering parents, resulting in even earlier full-sibs might have also disadvantages in the productivity of marketable yield. In S2-topcrosses the earliness of the lines might have less influence because it may be hidden by the tester.

### 4.3 | Effect on ear quality

Full-sib selection effectively increased ear length. This could be observed mainly in full-sib group 1. S2-selection did not effectively improve ear quality in our study. The diameter of the ear was significantly increased by full-sib selection significantly, but S2-selection decreased it. The same pattern was observed for the number of rows. This may have been due to the high correlation between ear diameter and kernel row (Hallauer et al., 2011).

High heritability was reported in sweet corn for the number of kernel rows and the ear length which makes selection more efficient (Hallauer et al., 2011; Jawad Asgh & Sadaqat Me, 1999; Ojo et al., 2020). Solomon et al. (2012) found that the ear length and the ear diameter are significantly influenced by GCA. Gonçalves et al. (2018) found that ear diameter and ear length contributed the most to ear yield. Full-sib selection had an influence on quality in our study because selection for ear length is an important criterion for marketability. But, while the quality of the marketable ears increased through selection the quantity of marketable ears did not increase. S2 selection had a rather negative influence on all these quality traits. It is not clear why positive effects were observed in Full-sib selection and not in S2-selection.

Contradictory results were also found by Treenoo and Amnueysit (2012) where full-sib selection did not improve ear length but decreased the diameter of the ears in the first generation and in the second generation no change occurred. The number of rows was not improved significantly in that study.

## 5 | CONCLUSION

Full-sib selection had positive effects on ear length and the diameter of the ear and even larger effects on the number of rows. S2-selection did not show a positive effect on ear length but it decreased the number of rows and the diameter of ears. Full-sib selection increased flowering time. Neither method was efficient for improving marketable yield. Our results show, that marketable yield of sweet corn is a very complex trait, which cannot easily be improved by one cycle of full-sib or S2-selection. Probably the effect of the year has also a bigger influence in only one selection cycle than selection in more cycles and the environmental conditions in the evaluation year would have an influence as well. The effect of more cycles of selection should be investigated in more than one evaluation year.

### AUTHOR CONTRIBUTIONS

BH and HB conceived and planned the project. CA carried out experiments and data analysis. CA wrote the manuscript and all authors reviewed it.

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### CONFLICT OF INTEREST STATEMENT

On behalf of all authors, the corresponding author states that there is no conflict of interest.

### DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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## SUPPORTING INFORMATION

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