

Review

## Open-Pollinated vs. Hybrid Maize Cultivars

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**Abstract:** The history of maize breeding methods in the USA is reviewed to examine the question of types of maize cultivars in sustainable agriculture. The yield potential of OP cultivars was much higher than national average yields prior to 1930, but hybrid cultivars today often out-yield OP cultivars by 50–100% or more. However, rates of gain for yield using recurrent selection on populations appear equal to that recorded for commercial hybrid breeding. The inbred-hybrid method, while successful, was not “the only sound basis” for maize improvement, as evidenced by later experiences in the United States and worldwide. It appears that maize breeders have practiced objective science and achieved concrete goals, although personal interests and goals clearly direct the work at times. As society looks for tools for sustainability based on achieving multiple goals, a special dedication to scientific validation and broad objectivity may be required. The potential for OP cultivars today is evaluated and research questions are identified.

**Keywords:** breeding; composite; hybrid; inbred; maize; OP; open pollinated; synthetic

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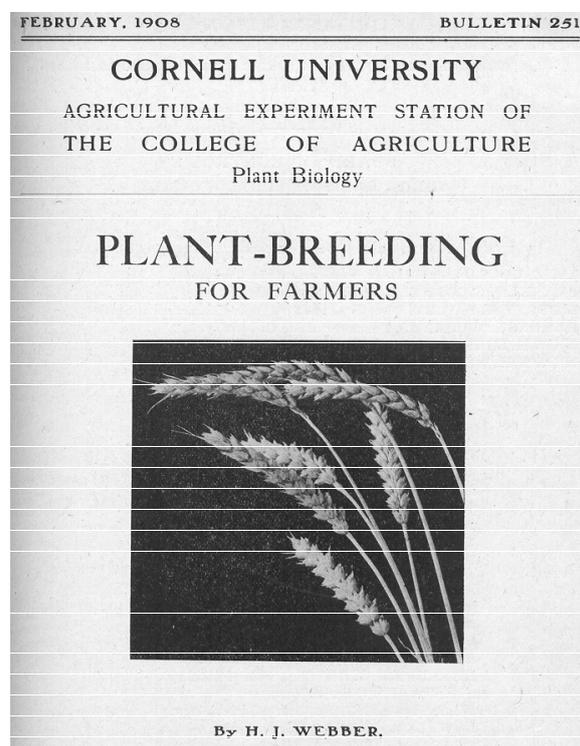
### 1. Introduction

Improved cultivars are a key element among practices used for integrated pest management and other approaches to agricultural sustainability [1-3]. The focus of plant breeders on a broad conception of sustainability has been repeatedly demonstrated. Hayes *et al.* said, “the primary purpose of plant breeding is to obtain or develop varieties or hybrids that are efficient in their use of plant nutrients, that give the greatest return of high-quality products per acre or unit area in relation to cost and ease of production, and that are adapted to the needs of the grower and consumer. It is of great importance also to obtain cultivars that are able to withstand extreme conditions of cold or drought or that have

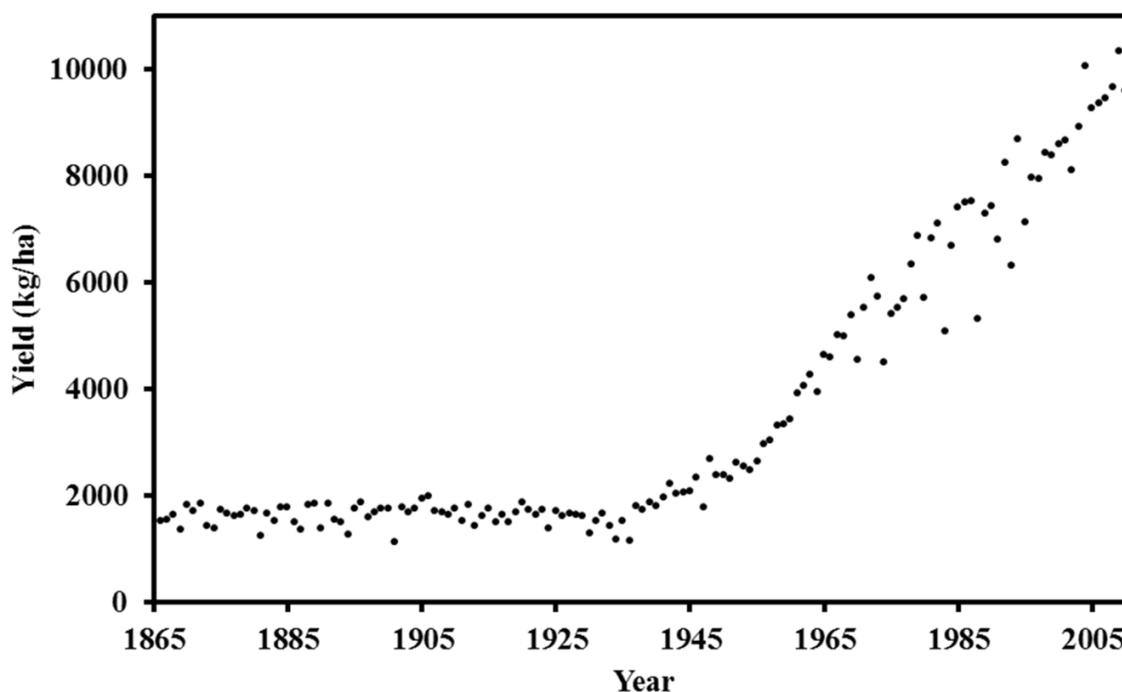
resistance to pathogenic organisms or insect pests. Such qualities help materially to stabilize yields by controlling extreme fluctuations” [4]. This reflects the concerns of farmers and sustainability advocates [5,6]. Plant breeding is also said to be a science, art, and business [3,7,8]. It has had great successes with increasing yields of many species for many systems [4,9,10].

One breeding question that comes up in sustainable agriculture circles in the United States is, “Could someone have bred a high-yielding open-pollinated corn cultivar?” Open-pollinated (OP) maize cultivars are largely farm bred, providing yields of grain that can be saved for seed. After more than eight decades since the commercial introduction of hybrid maize cultivars in the United States, there is still some doubt among some farmers and scientists as to whether OP cultivars had to be given up as inferior to hybrids. The objectivity and goals of hybrid maize breeders as “pure scientists” is either promoted or openly doubted [11,12].

**Figure 1.** USDA and Agricultural Experiment Stations once actively trained farmers on the latest breeding techniques [13]. Unfortunately, the methods promoted were not always very successful for increasing yield.



Maize breeding and seed production by farmers was once the norm (Figure 1). Trade in maize seed and intentional outcrossing with introduced types are ancient practices [14-16]. The result was many OP cultivars [17-21]. However, on-farm maize breeding and efforts to improve on-farm seed production were dropped after the 1930s in most of the United States once successful hybrids were released [10,22-24]. An increase in yield (Figure 2) paid for these annual seed purchases and drove this change largely on economic grounds [25], although farmers were also much impressed with improved standability and the uniform look of the fields. Sometimes the yield increase observed in the USA in the 1940s seems to be attributed almost entirely to the hybrid cultivars themselves [11,26].

**Figure 2.** Average USA maize yields 1866–2010. Data are available from USDA [27].

Those interested in sustainability do not doubt the potential and utility of hybrid maize cultivars. Modern hybrids often yield much more than current OP cultivars [9,28,29] and have often done so since the late 1930s [22,24,30,31]. This has also been true for forage yield [32-34]. Questions remain about the utility of other breeding methods that might allow farmers to produce their own seed, to more effectively breed for their own systems of management, and whether these might be more advantageous for them [35-39]. Also, the benefits of the yield boost from growing hybrid cultivars with high input levels are still debated given the economic and environmental problems with growing continuous maize [23,40-43]. Arguments for helping maize farmers by focusing on yield rather than profit have continued for 100 years [44], regardless of the fact that that this focus has sometimes failed to help farmers meet their economic, environmental or lifestyle needs [40,42,45].

Cleveland suggested that plant breeders were neither scientists in search of objective truths, nor servants within a social construct for existing political and economic interests, but some amalgam thereof [12]. This is a critical issue to consider given the changes to public and private plant breeding, the centralization of seed and gene control in agriculture, and the advent of more intrusive forms of biotechnology [23,37,46]. Were the conclusions of maize breeders presented over the last century well defended by the data or not, as has at times been alleged?

The purpose of this paper is to revisit the history and the current state of OP cultivars and the methods for maize improvement in order to address these questions: Were OP cultivars the cause of low yields in the USA before 1930? Was the inbred-hybrid method the only path to follow for maize improvement? What sort of breeding took place before and after hybrids were released? Is the story we teach agriculture students the real and complete story? Do OP cultivars have a place today?

### 1.1. Approach

I reviewed the maize breeding literature with a focus on the United States, delineating when key changes occurred and by whom. The yield potential of OP cultivars in the United States from the mid-1800s to the early 21st century was then addressed. Reports of multiple cultivar and multi-environment trials, particularly where improved management was more likely to have been practiced, were used to generate yield means under a variety of conditions. Averages for better-adapted cultivars over many environments were sought to best represent the potential of this type of cultivar.

Rates of gain for methods of maize improvement were generated using published summaries [10,47]. Data from the experiments of Weyrich *et al.* with the BS11 maize population were also incorporated [48]. Very high rates of gain (>10%/cycle) observed with some tropical and other populations were ignored for the sake of generating conservative estimates more relevant to potential outcomes for high yielding populations in the higher latitudes.

Conservative estimates of rates of gain from selection, 0.6% annually for gridded mass selection and 1.3% annually for modified ear-to-row selection (based on an average of 83 kg/ha applied to a hypothetical population yielding 6270 kg/ha), were used to predict the yield of OP cultivars had they been bred for 80 years (since 1930), 60 years (since 1950) or 40 years (since 1970) because these two methods do not require controlled pollinations, directly provide seed for planting, and are possibly the most adaptable to on-farm breeding [35,48]. Estimated yields of OP cultivars under modern management, from the review of OP cultivar yields, were multiplied by these generated rates of gain. The predicted yield gain quantity from that first cycle was then added to the base yield for successive years to predict accumulated gains over time: steady gains can continue for many years [29]. I also sought out literature concerning synthetic and composite populations, including tropical maize breeding reports. Published results were used to generate predictions of the potential of this technique to form better OP cultivars.

## 2. Results and Discussion

### 2.1. The Age of On-Farm Selection in Maize—Origins to 1935

Indigenous farmers in the Americas developed maize and methods for seed production; farmers around the world continued this same process of mass selection wherein seeds from good ears or plants were saved each year [14-17,20,21,49]. Selection produced widely used cultivars, such as Improved King Philip Flint, Leaming, and Silver King [18,50,51]. Composite breeding, a technique developed by Native and Immigrant farmers, formed the entire race of Corn Belt Dent and cultivars like Reid's Yellow Dent, Krug's Yellow Dent and Falconer by crossing two racial types [16,26,48-50].

In the early 20th century, maize breeders and extension educators promoted a wide variety of selection techniques that were considered to be an improvement over traditional techniques [13,23,50,52-54]. Most focused on mass selection for ear and seed qualities thought to be related to yield in "pure strains," although some more intensive systems of selection were also being promoted. Universities and associations of corn growers also established corn shows at fairs to exhibit "perfect ears" that were well matured and matched for uniformity. Rist wrote that, "If we are to estimate the value to be derived from corn shows in increased yields alone it probably would not

amount to much, as we know that 'show ears' do not as a rule increase the yield of corn. On the other hand farmers of this state have paid thousands of dollars in tax money for scientific investigation along the line of corn improvement, yet such investigations have resulted in practically no increase in the yield of corn. Therefore, farmers could object to further investigations fully as well as could those who are opposed to corn shows object, as their results have been about the same so far as increased yields are concerned" [55]. In 1921, W.L. Burlison at the University of Illinois wrote that, "from the experiments conducted at this station it appears that while selection has had some effect in increasing the yield of corn, it has not given the results that were anticipated" [23].

Early breeding experiments with maize populations did not often yield impressive results for many breeders at many locations, and breeding based on ear type, though wildly popular and heavily promoted by universities, was even associated with yield reductions over time [13,52,53,56-59]. Datta visited maize breeders across the country and reviewed their techniques [52]. What he found was a mindset of progress through science and the land grant mission, along with a general abhorrence of inbreeding. However, though selection had improved the uniformity and local adaptation of many populations [49,50,60], "scientific" selection techniques promoted before 1920 appear not to have been fully evaluated before their widespread promotion [16].

During the 1920s, the selection program of the University of Illinois Extension Service was apparently successful in increasing yields using mass selection. J.C. Hackleman promoted selection against male plants that appeared barren, against plants with disease, and for high rates of germination. He reported yield gains of 300–600 kg/ha (5–15%) with this method [23]. Given the yields of the day, these were reasonable increases, especially since this was indirect selection for yield.

## 2.2. Yield Potential of OP Cultivars in the United States—1847 to 2005

Reported yields of OP cultivars in university and other scientific trials were usually more than 2000 kg/ha in most parts of the United States when averaged across years, locations, and often times cultivar as well (Table 1), however, it is possible that very poor yields were under-reported [35]. It is clear that the yield potential of many OP cultivars with good management was often over 3000 kg/ha before modern management practices. In recent trials, yields of better-performing OP cultivars were often over 4400 kg/ha, a yield substantially lower than most hybrid checks [9,29,33,61-63].

**Table 1.** Some average yields for open-pollinated maize cultivars in the United States [9,21,24,29,31,33,56-58,61-98]. Average state yields of open-pollinated (OP) cultivars during each test are included when data were available from USDA [27]. Average state yields for the period 1866–1929 for which there are data are marked with an asterisk and are presented to demonstrate changes since this "OP era" for tests carried out after 1930.

Cultivar(s)	Yield kg/ha	State Avg. Yield kg/ha	Area of Evaluation	Year(s) of evaluation
14 cultivars	4890		New York, 1 location	1847
Kingsbury	3060	2350	Vermont, 2 locations	1873
4 flint, 1 dent	3400	2290	Massachusetts, 1 location	1875

Table 1. Cont.

Cultivar(s)	Yield kg/ha	State Avg. Yield kg/ha	Area of Evaluation	Year(s) of evaluation
Stowe Flint	3070	2340	Vermont, 1 location	1878–1879
1 dent	5020	2590	Iowa, cultivation trials	1889
1 dent	2458	1693	Minnesota, 1 location	1889–1891
4 dents	4950	2540	Iowa, single reps, 2 exp.	1891
Leaming	4900	1910	Iowa, 6 locations	1892
3 cultivars	3894	1944	Illinois, 1 rep., 1 location	1887–1894
Minnesota 13	4070	1913	Minnesota, 1 rep., 6 trt.	1895
Silver King	3620	2090	Wisconsin, 749 environ.	1904–1909
Wis. No. 8	2510	2020	N. Wisconsin, 1 location	1907–1910
6 dents	4280	2730	Ohio, several locations	1905–1914
1 dent	4110	1410	Virginia, rotation exp.	1909–1916
2 flint, 2 dent	2870	2410	New York, 4 locations	1910
Reid	4180	2410	Iowa, breeding nursery	1910–1911
Reid	3430	2680	Iowa, Walden farm	1912–1924
Boone County	3730	1480	Virginia, several locations	1913–1916
NE White Prize	3640	1720	Nebraska, 9–14 loc. per year	1914–1917
1 dent	3260	2510	Ohio, 20 yr exp.	pre–1915
Boone County	4550	1520	Virginia, Ag Exp Sta	1916–1917
1 dent	2820	980	Kansas, 8 yr trial	pre–1918
1 dent	4870	1660	Missouri, 17 yr trial	pre–1918
Leaming	4990	2260	Conn., one location	1916–1917
3 dents	3410	2450	New York, 14 environments	1918–1920
Onondaga	4170	2600	New York, 10 environments	1919–1920
2 dents	3190	2160	Minnesota, Ag Exp Sta	1919–1920
5 dents	3270	1810*	Nebraska, coop. trials	1932
3 dents	4110		Midwest, 7 reps, 1 location	1933
3 dents	1919	1354*	E. North Dakota, 1 location	1935–1942
Minn. 13	3130	1910*	Minnesota, 12 environments	1936–1940
Murdock	3470	1910*	Minnesota, 11 environments	1938–1940
3 dents	4170	2330*	Iowa, 15 environments	1939–1941
Clarage	4410	2270*	Ohio, 19 environments	1941–1946
Foster's White	5560	2270*	Ohio, 8 environments	1942–1946
2 dents	3490	1910*	Minnesota, 10 locations	1942–1944
5 dents	2830	1520*	S. Dakota, coop. trials	1942–1944
2 dents	3190	1480*	Kansas, coop. trials	1943–1945

Table 1. Cont.

Cultivar(s)	Yield kg/ha	State Avg. Yield kg/ha	Area of Evaluation	Year(s) of evaluation
Black Hills Sp.	5160	1520*	South Dakota, 1 location	1946–1948
Rainbow Flint	2310	1520*	S. Dakota, 4 environments	1951–1954
Dawes #2	4630	1810*	Nebraska, 2 locations	1953
Cornell 11	3320	2080*	New York, several locations	1953–1954
9 dents	5710	1810*	Nebraska, two locations	1955–1956
Hays Golden	5210	1810*	Nebraska, 1 loc., 20 reps	1956–1959
Reid type	5470	2330*	Iowa, 11 environments	1971–1973
Reid, Lancaster	3940		USA, 11 environments	1980–1981
Reid	5710	2330*	Iowa, 12 environments	1991–1994
Reid	6110	2330*	Iowa, 6 environments	1998, 2000
5 dents	4330	2330*	Iowa, 5 locations	2001
Krug, Reid	5370	2080*	New York, 6 environments	2001–2002
Nokomis Gold	5140		28 Midwest and NE env.	2001–2003
Wapsie Valley	5360		20 Northeast environments	2001–2004

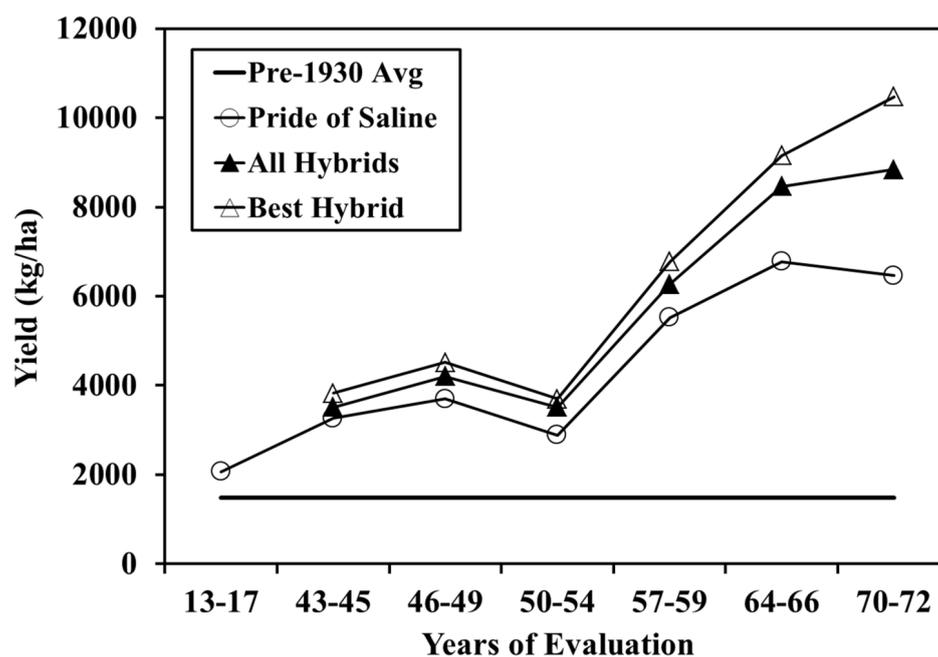
High OP yields were familiar to many before 1930. Yields over 6200 kg/ha were recorded during the mid-1800s [20,21]. Montgomery reported that the four largest yields of maize on record in the United States at that time were over 12542 kg/ha for ears at husking [99], while Bowman reported the largest yield of grain belonged to South Carolina's Z.J. Drake in 1889 (15990 kg/ha) [50]. Hartley wrote that "good farmers frequently raise from 75 to 100 bushels of corn per acre [4700–6270 kg/ha]" and yields this high were regularly observed in Iowa and Wisconsin [51,54]. Cornell University cooperative trials showed average dry grain yields over 3140 kg/ha and at times over 4390 kg/ha, similar to yields reported by notable New York farmers in the 1840s [21,57,73,100,101].

There were two major problems for maize yields prior to 1930. Many farmers were not producing high quality seed (not well dried, freeze damage, not well selected, inbred) and were therefore obtaining poor stands and yields lower than the genetic potential of their cultivars [51,53,54,59,74,102,103]. The other problem was that soil and crop management improvements were not widely adopted, leading to unsustainable production in some cases [34,36]. Kent wrote, "By intense cultivation and proper rotation, most of the farms of Iowa would produce from 75–80 bushels of corn per acre [4700–5020 kg/ha], and under favorable climatic conditions still more" [70]. Yields in Missouri of 4870 vs. 740 kg/ha and in Illinois of 4000 kg/ha vs. 1690 kg/ha were reported for rotated vs. continuous cultivation [78,104]. Still, many farmers did not rotate or fertilize enough because: (1) fertilizers were not always economical [76,77], (2) the value of continuous maize was higher than the value of some alternative crops [105], or (3) for some other reasons. Smith wrote that "the land was corn sick" [104].

One example of the importance of management for yields comes from Kansas where maize yields had fallen steadily, leading to an unsustainable situation before 1920 [79]. At that time one of the highest yielding OP cultivars was Pride of Saline, with an average yield over 1880 kg/ha [78]. In the 1940s, Pride of Saline was yielding 3140–3760 kg/ha and after 1960 it often yielded above 6270 kg/ha

(Figure 3). This is more than three times the Pride of Saline yield from university trials before 1920 with no reported breeding effort.

**Figure 3.** Kansas statewide yields of Pride of Saline and hybrid cultivars from 1913–1972. Data were adapted from reports of the Kansas State University Agricultural Experiment Station [78,79,91,106-113]. The “Best Hybrid” was not the highest performing individual cultivar at each location but the highest yielding cultivar when averaged across test locations.



A complete consideration of the effects of plant breeding during the 20th century includes all of the factors that changed [22,36,114]. No more than 60–70% of the yield gain since 1930 should be attributed to breeding and using hybrid cultivars [29,115]. Hybrid yields in Kansas tests were on average 8–22% higher than Pride of Saline prior to 1960, and this difference increased after 1960 (Figure 2). However, while hybrids often outperformed their OP checks in the 1930s and 1940s [22,30,31,85-88], Reid’s Yellow Dent has yielded about as well as many commercial hybrids from the 1940s and early 1950s, but substantially less than post-1960 hybrids in recent tests in Iowa [9,29]. Also, improvements in standability in hybrids have been more dramatic still, making for greater gains for machine harvested yields and for more flexible grain harvest schedules [9,28-30,97,98]. Could new, more competitive OP cultivars that stand well be bred now?

### 2.3. Adopting the Hybrid Method—1870 to 1935

Farmers had been making crosses among cultivars for thousands of years, and then reselecting new and more vigorous offspring from among the following generations with some success [49,50]. In Michigan, Beal suggested the use of F1 varietal hybrids in the 1870s as did Carrier in Virginia [4,26,116,117]. These new hybrid seeds did find some commercial use in the early 20th

century, although like any hybrid seeds they required annual regeneration and further improvement in these hybrids would require ongoing improvement of each parent population.

Around 1910, some breeders began to think in new ways, to see vigorous cultivars, both uniform and genetically diverse, that had first passed through a period of inbreeding [11,17,44,52,80,114,118]. Early data with inbred hybrids showed great potential in the method, although it would be expensive and removed from the hands of farmers [23,49,94]. Richey said evidence suggested “pure line methods as the only sound basis for real improvement of corn” [119].

Richey reported that F1 varietal hybrids on average did not yield more than the parent cultivars and also noted small or no gains on average from ear-to-row breeding [119]. However, he then expounded on the best yields from Jones’ hybridization work rather than showing that 11 of the 25 Leaming hybrids yielded less than the OP parent [80,119]. Concerning hybridization experiments in Nebraska, Richey wrote, “It is unlikely that all of the crosses yielded equally, and some, therefore, probably exceeded this 0.8 bushel [50 kg/ha] increase” [119]. Had Richey applied the same focus on the best gains from the other breeding methods he would have reported that 2.5% of F1 varietal hybrids outyielded the better parent by 26% or more and would have noted good yield gains in some ear-to-row breeding experiments [119]. Therefore, Richey’s conclusion about pure line methods was only partly correct considering the data presented. On average, hybrids did not yield better than their OP parent cultivars, but some hybrids yielded much better, as is still true today.

At the time, the difficult task of finding the best hybrid combinations provided rapid yield gains in the short run but did not make for long term improvements. However, the method proved wildly successful after years of intensive development when released hybrids often outyielded OP cultivars by 9–40% [10,11,17,22,23,29,31,37,86-88,91,118,120]. From on-farm ear selection and no inbreeding with “pure” populations, breeders appear to have leapt to no population improvement and little farmer involvement. During neither period were decisions fully evaluated through experimentation.

After 1922, most university maize programs in the USA took up inbreeding studies [89]. Some maize breeders moved out of breeding and into different roles [22]. Hartley, the head of USDA’s maize improvement efforts, was pushed from the USDA Bureau of Plant Industry over his conservatism in favor of on-farm seed production and breeding [23]. This parallels changes underway in plant science departments world-wide as molecular and transgenic techniques and courses of study have come into favor and funding for conventional public plant breeding research and education has dwindled even though the approach still works well [7,116,121,122].

#### *2.4. Recurrent Selection Revisited*

Interest among hybrid maize breeders in recurrent or repeated selection rebounded in the 1940s and 1950s when they discovered the need for improved populations from which to select new inbreds [16,47,123], and this time the conclusions were very different. OP cultivars had been thought to lack the genetic variation for successful selection and this was disproven via experimentation [16,124]. Gardner wrote, “mass selection would appear to be as effective as hybridization in increasing yield” [96]. Webel and Lonnquist said of modified ear-to-row selection, “The realized gain suggests the method might be as effective as hybridization in increasing yield” [125]. Lonnquist and Gardner found “that no critical experiments where yield was the main

criterion for selection were reported during the period covered by Richey's report" [95]. Sprague noted "it appears that the ear-to-row method of selection for yielding ability was discredited not because of genetic limitations of the method, but because of the inadequate field plot technique" [16]. Research after Richey's 1922 conclusion showed recurrent selection and varietal hybrids could be very successful at increasing maize yields after all, although they could not provide cultivars with the yields of the best hybrids [35,47,81,95,119,120,126-131].

The Hays Golden OP cultivar from Nebraska showed a yield increase of 40% from several years of recurrent selection for yield alone as compared to the 9–40% yield advantage that many hybrids had over OP cultivars with many years of development [30,47,88,123]. Average gains in yield for gridded mass selection range from 1.8–2.6% annually [10,35,47,120,132]. Modified-ear-to-row selection has demonstrated average gains per year of about 2.1–3.5% [10,35,47,48,133]. These and other recurrent breeding techniques have been very successful in breeding cultivars for farmers in the tropics [120,128,131,132]. Conservative estimates of average potential annual yield gains of 82 kg/ha for mass selection and 83 kg/ha for modified-ear-to-row selection, largely from North American data, are comparable to those experienced in an open-ended inbred hybrid breeding program from the United States, where yields have increased by about 66 kg/ha each year since 1930 [9,29,35]. Both Coors and Duvick provide lists of reasons why these results for recurrent selection might be biased comparisons and might at times favor the results for recurrent selection over the inbred-hybrid method [35,36]. Added to that, recurrent programs rarely if ever achieve the level of selection and evaluation intensity described for commercial hybrid breeding [17]. Regardless of type of cultivar, annual improvements via breeding are essentially about the same. The fastest and cheapest method which best supports sustainable agriculture outcomes will depend on yields in the target agroecosystems, grain prices, and farmer skills and interests.

Gardner's modification to mass selection techniques was to focus on yield among plants in small grids or plots across a seed selection field [96]. This reduces the environmental effects on observed plant phenotypes and improves selection for better genotypes, although it does not allow for evaluation in multiple agroecosystems. The method is easily adapted to farm and garden situations, although it is better for qualitative traits than for yield and may need the two step procedure suggested by Hartley for larger acreages [54]. Modified ear-to-row selection involves replicated evaluation of plant progenies at three locations and is a more intensive technique that would probably require special training for farmers or even a participating breeder [134]. Prior to 1910, some breeders had adopted replication, check rows, detasseling and the use of remnant seed in some ear-to-row breeding trials for better plant evaluations [13,52,58,135]. Use of the triple lattice design for progeny tests (a component of Lonnquist's method) was unlikely before demonstrations of its utility in accounting for finer spatial variation of soils in the early 1940s and the use of bulk seed rows for cross-pollination appears to have originated with Lonnquist [52,134,136,137]. The method often results in rapid gains and the availability of computers makes it and other complex recurrent selection methods a possibility for many farmers, especially those working in groups or when partnering with breeders.

**Table 2.** Predicted yields of maize OP cultivars under modern management after periods of gridded mass selection and modified ear-to-row selection using conservative rates of gain [35,48].

Original Yield Potential, (kg/ha)	Mass Selection			Modified Ear-to-Row Selection		
	80 yrs	60 yrs	40 yrs	80 yrs	60 yrs	40 yrs
6270	9280	8530	7780	12910	11250	9590
5020	7400	6840	6210	10241	8936	7630

What would have happened if these techniques were applied in the past had recurrent selection not been dropped prematurely? Some OP cultivars in the United States have yields of 5020–6270 kg/ha which are not currently economically advantageous [28]. Using conservative estimates of rates of gain, calculations of the predicted gains in yield suggest large gains were and are possible with enough breeding effort (Table 2). Gridded mass selection could have resulted in OP cultivars yielding 9280 kg/ha or more by now had selection begun by 1930. Lonquist's modified ear-to-row method could have resulted in much faster improvements and in fairly competitive OP cultivars even if it had been employed only since its development [134]. Applying recurrent selection now, it would take many years to develop an economically competitive OP cultivar. Competitive commercial OP cultivars for the USA and some other regions were not developed and breeders (and farmers) would have had to overcome the stigma of being old-fashioned and the preference of governments and many farmers for hybrids [23]. Had higher yielding OP cultivars been released prior to 1960, would there have been an advantage? Would many farmers use high yielding OP cultivars today? Would there be an advantage in time, profitability, adaptation, *etc.*?

There are other biological problems to consider. Single plant evaluation in mass selection can increase yield under some circumstances but often results in delayed maturity and no improvement in stalk strength and other critical agronomic traits. Hyrkas and Carena and Bletsos and Goulas were unable to increase yield of improved populations using mass selection and suggested using more intensive recurrent selection techniques that could be more difficult for farmers although predicted rates of gain can be higher [35,48,133,138]. Gardner hit a yield plateau with Hays Golden after 12 cycles of mass selection; modified ear-to-row selection reached the same plateau in only six cycles [47]. Yield plateaus can be overcome by outcrossing, and then proceeding anew with the resulting composite population [131,139]. Eberhart *et al.* promoted the idea of cooperative work with many populations [128]. Such an approach could make available the improved populations and lines needed for outcrossing when breeding plateaus are discovered. At any time inbreds and inbred hybrids could be developed, making for a very comprehensive approach to maize breeding much akin to the successful public program at Iowa State University where theoretical studies of maize breeding technique included selection for agronomic traits as well as yield in both populations and inbreds. There need not be an either or choice with OP and hybrid cultivars.

### 2.5. Composite and Synthetic Populations as OP Cultivars

Hybrid vigor has been harnessed by maize breeders for centuries [14,16,49]. Composite populations (intermated cultivars) and synthetic populations (intermated inbreds), like any maize population with a random mating structure, can be thought of and used as OP cultivars [140] and may offer a rapid approach to increasing OP cultivar performance. Shull and Duvick suggested that the yield of an OP cultivar is a result of all the possible hybrid combinations among the parents [36,44], and Wright demonstrated that the number and yield of parents in a synthetic population determined how much of the hybrid vigor could be retained in the F2 and later generations [141]. The equation based on his work, which was validated for both composites and synthetics by Mochizuki, predicts that as the number of parents increases the amount of retained hybrid vigor increases [142].

$$\text{F2 Synthetic Yield} = H - \frac{(H - P)}{n} \quad (1)$$

H = avg yield of all F1 hybrids, P = avg yield of parents per se,  
n = number of parents

While some saw the potential for synthetic maize cultivars in the USA early on [80,143], little work was done and most results were not promising [16,144,145]. However, many breeders have had synthetic yields at least 15% above that of common OP cultivars and up to 90% of hybrid yields [83,93,97,118,146-149]. It appears that these high yielding synthetic populations never reached farmers in the USA or many other regions for their consideration.

The application of Wright's equation to historical data on maize inbreds and hybrids suggests the possibility of synthetics that yield more than 90% of commercial hybrids if the research were carried out (Table 3), although the work would be intensive with many questions to be answered [36,141,150]. Might such diverse populations open up new ways of dealing with diseases and pests as has worked for multilines of rice [151]? Could synthetics reduce seed costs, provide competitive yields and be further improved via selection on farms? Would many farmers be interested?

**Table 3.** Predicted F2 yields for hypothetical 8-line synthetic cultivars of maize based on average yields of seven single cross hybrids and their inbred parents from different decades [36].

	1930s	1940s	1950s	1960s	1970s	1980s
Single Cross Mean	6717	7033	7960	8171	9098	10492
Midparent or Inbred Mean	2062	3065	3174	3493	4463	5476
Predicted Eight-line Synthetic	6135	6537	7362	7587	8519	9865
Synthetic vs. Single Cross (%)	91.3	92.9	92.5	92.9	93.6	94.0
Planting Density (1000/ha)	30	54	54	54	79	79

Some answers come from the tropics where maize breeding has embraced population improvement and inbreeding and breeders develop inbred hybrids, varietal hybrids, synthetics and other OP cultivars to best fit local needs [120,128,131,152-157]. In those regions synthetic cultivars have proven useful for farmers by providing higher yields and low seed costs, although for long term improvement synthetics may require more genetic diversity than that provided by only 8–10 lines and they may require more intensive selection schemes for further improvement [133,155]. A few farmers in the

United States, especially organic farmers, are looking for good cultivars of maize and other crops from which they could produce their own seed as seed prices have risen sharply in recent years and the number of commercial cultivars without transgenes has diminished [33,140,158,159]. Baltensberger *et al.* suggested that dryland farming and similar regions with climatic stress may be the first agroecosystems to consider for this approach as these lower yielding environments result in similar economic returns for synthetics yielding only 75% of commercial hybrids [147]. Stress environments, and those where hybrids are not economically feasible, are the targets for modern OP cultivar development in the tropics [120,152-154]. Organic farmers may be interested as well, but high organic grain prices could make lost yield opportunities economically detrimental unless cultivars without recombinant DNA were otherwise unavailable [28].

Any type of hybrid is still an option for on-farm seed production. Should sustainable farmers find it economically feasible to produce their own hybrid seed, varietal hybrids might still be a valuable option among several (single cross, top cross, double cross, varietal cross). Improved populations, whether synthetic or otherwise, could be crossed to produce F1 seed each year should those populations demonstrate hybrid vigor when crossed. Advantages of this approach could be higher yields than possible with populations *per se*, cheap hybrid seed given the levels of production that may be possible with populations compared to expected yields of inbred parent lines, and the possibility for ongoing improvement of the parent populations and their hybrids on-farm. Disadvantages could include separate seed production requirements, likely lower yield than single cross hybrids [129], and lower uniformity than that observed in single cross hybrids.

## 2.6. Maize Breeding and Society

Cleveland suggested breeders were neither pure scientists nor only servants to social constructs, and this conclusion appears to be affirmed here [12]. Maize breeders come with their own personal interests for the work to be undertaken and certainly make subjective decisions about specific approaches and goals [8]. The widely promoted selection methods and shows before 1920 and the rejection of recurrent selection from 1922 until the late 1940s show maize breeders and their administrators sometimes got ahead of scientific validation in order to pursue exciting new options. There were some decisions involved in promoting research and development of hybrid cultivars to benefit specific seed businesses [23,37], and most professional maize breeders in the USA ignored the potential of recurrent selection in favor of the task of testing tens of thousands of lines in the 1920s and 1930s [118,119]. There were, however, many promoters of hybrid cultivars who had farmers in mind, and the science behind hybrid breeding methods eventually proved sound and useful to all forms of maize improvement [10,22,160]. Excellent and creative work was carried out that has stood the test of time and provided exceptional new cultivars of many types [10,16,17,89,123,161,162].

In the past thirty years maize breeding has changed further with patents, DNA marker assisted selection, and transgenic techniques joining the process. Public breeding has been fading in favor of breeding by major corporations around the world [116,163]. One might question whether this is once more the promotion of the novel in place of approaches that objectivity might instead focus upon [6,45,105]. Experience tells us that there can be some unanticipated problems with new technologies rushed to market [164], yet sometimes full economic and ecological evaluations are still

unavailable for transgenic maize cultivars until well after commercial release [165-167]. Cox reiterated a calculation from Goodman and Carson comparing conventional hybrid breeding with the more expensive transgenic methods which are apparently no faster to produce new cultivars than conventional methods [168]. This situation is reminiscent of Gardener's favorable comparison of recurrent selection with hybrid breeding decades after the switch to hybrids [96]. At the American Seed Trade Association conference in 2003, John Dudley, then maize breeder from the University of Illinois, asked the audience, "Current corn yield goes up 1.9 Bu/A annually. What [trans]genes would improve this?" Given our experiences, an open and logical discussion of the goals, means, and costs of modern maize breeding appears in order as has always been the case.

Rather than the "March of Progress" from OP cultivars to high yielding hybrids and on to transgenic technologies, perhaps the scientific and social successes and failures of actual maize breeders (e.g., Darrah, Duvick, Hallauer, Hartley, Hayes, Gardner, Goodman, Lonquist, Miranda Filho, Pandey, Paterniani, Richey, Sevilla, Sprague, Stringfield, Troyer, Will, *etc.*) in meeting the needs of farmers and consumers would be more objective and useful for students contemplating breeding for sustainability. And rather than a competition between OP and hybrid cultivars, perhaps it would be most sensible to consider this thought from Pandey *et al.*: "The critical question is not whether hybrids are superior to OPVs, but whether a product is superior to what the farmers grow and which new product they can afford" [152]. Breeding, like any tool with which humanity hopes to derive a better world, requires knowledge, critical thinking, hard work, humility, cooperation, objectivity, and a broad perspective in order to be successful [17,122]. If we are to make the most reasonable choices for a sustainable agriculture, it appears most fruitful to attend to all of them.

#### 4. Conclusions

OP maize cultivars were and are sometimes useful for providing low priced seeds and dependable yields to farmers, although they usually yield less than well adapted hybrid cultivars when those are available. In lower yielding agroecosystems and lower priced markets where OP cultivars appear to be more competitive, farmers need to understand selection and seed production methods and their time investment must be personally and economically satisfying to realize acceptable outcomes. This may not be of interest to farmers with high value maize crops, large enterprises, substantial off-farm activities, or access to hybrid cultivars that meet their needs. It appears that yield gains via breeding are about the same for OP and hybrid cultivars, but starting at a lower yield level, most current OP cultivars would appear to be permanently relegated to lower yield levels compared to most hybrids, although specialty traits might help them be economically competitive anyway. The moment in history when the yield of OP cultivars could have been improved to be competitive with hybrids via recurrent selection alone appears to have passed, although the possibilities of forming competitive OP cultivars using composite/synthetic methods and using more complex recurrent selection methods on-farm remain challenging options that have not been fully investigated in the United States and Europe. These approaches have at times been successful in the tropics. Yields of synthetics 5–10% less than elite hybrids are still theoretically possible but have yet to be achieved. New OP cultivars could be cost competitive in many more agroecosystems than OP cultivars are now and this process could open up more partnerships to breed maize for non-patented traits of importance to sustainable agriculture

(e.g., stress tolerance, insect and disease resistance, nutrient use efficiency, grain quality). There are also existing opportunities for more on-farm development and production of hybrid cultivars. We can approach questions about maize improvement and cultivar choice for sustainable agroecosystems objectively with the most sustainable outcomes for society in mind, an approach often used in maize breeding throughout much of the world.

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### Conflict of Interest

The author declares no conflict of interest.

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