

Revolutionizing sweetpotato breeding through heterosis exploiting breeding schemes - how far are we?

Exploitation of hybrid vigor is one of the hallmarks of modern plant and animal breeding, but until recently had not been seriously considered by root and tuber breeders. In sweetpotato breeding, we have made exciting progress developing and implementing heterosis exploiting breeding schemes (HEBS) and are now applying this approach at breeding platforms across sub-Saharan Africa and in Peru (Fig. 1). We have completed a full cycle of reciprocal recurrent selection, the method used in heterosis breeding in Peru, and are now applying HEBS to speed up genetic gains in yield and important traits such as virus resistance, earliness, low-sweetness, as well as high iron and zinc.



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Fig 1. Visitors checking out the Satipo heterosis trial with CIP breeder Wolfgang Grüneberg (Credit: J. Low)

What is the problem?

Our traditional approach has been to select for priority traits using polycross or paired cross approaches which have resulted in the sweetpotato varieties grown around the world today. Hybrid breeding was invented by maize breeders, and uses a method called reciprocal recurrent selection (RRS) as follows: a) identify genetically separate populations; b) cross between parents from separate populations and identify parents which produce offspring most superior to the parents; c) within each population, cross (recombine) superior parents with each other, produce offspring from them, and select a new, improved set of parents for crossing between the populations; and d) repeat the process. In maize breeding, inbred lines are derived from the offspring from recombined superior parents in each population, and these inbreds are then used as the parents to produce superior yielding, and uniform hybrids.

It was not obvious how to apply this approach in sweetpotato. Since sweetpotato has six copies of each chromosome, and is mostly self-incompatible, producing inbreds through self-pollination was out of the question. Furthermore, sweetpotato is vegetatively propagated, so we easily get the uniformity unlike the situation for maize which requires development and crossing of inbred lines to produce hybrids. Nevertheless, HEBS are being applied successfully in increasing numbers of crop and animal species. We realized that our current breeding methods were holding back progress in efforts to breed for important recessively inherited traits, such as virus resistance, and low amylase activity.

What do we want to achieve?

We want to achieve large genetic gains for our sweetpotato breeding populations across all key traits by using HEBS in combination with RRS. Using RRS in sweetpotato will allow us to select for desired quality attributes and

resistances in separate, increasingly inbred populations, followed by crossing between the populations. Two critical changes in sweetpotato breeding programs are required to take advantage of the approach: First, we need to identify mutually heterotic populations to be used in RRS, and second, we need to use the offspring information to select the parents for future breeding cycles.

Where are we working?

The HEBS for sweetpotato breeding was conceived of, developed, and continues to be led from the International Potato Center (CIP) headquarters, in Lima, Peru. These activities generated three H1 hybrid populations¹ for: 1) wide adaptation and earliness (Fig. 2), 2) low sweetness after cooking, and 3) high iron. The Regional Sweetpotato Support Platform for Eastern and Central Africa has separated parental genepools and generated a H0 hybrid population, which is undergoing evaluation for SPVD resistance and yield to select the most suitable parents for the first RRS cycle (Fig. 3). The platforms for Southern Africa in Mozambique and West Africa in Ghana are in the process of allocating parental material into genepools.

How are we making it happen?

The key element of the HEBS is the development and improvement of separate mutually heterotic populations, through RRS. At CIP headquarters, a complete RRS cycle was applied for targeting different variety types, namely (1) OFSP for wide adaptation and earliness (WAE), (2) OFSP with non-sweet taste (NSSP), and (3) OFSP with high iron contents (HIFE). In some cases (WAE and NSSP), very strong selection pressure was applied to select the foundation and parental material for the RRS cycle, respectively. The three H1 populations were evaluated together with their parents as well as the foundation of grandparents to estimate the genetic gain. We are demonstrating step by step, that it is in fact possible and highly worthwhile to apply RRS in sweetpotato, first at CIP headquarters, and now - after first tests with 9 x 6 parents from Africa -- we will

¹ In Peru, the foundation of the three populations are clone "grandparents" from two distinct genepools: Population Zapallo (PZ) and Population Jewel (PJ). The first experiments were done in Peru: A total of 49 PJ x 31 PZ clones were recombined to form the first hybrid population, known as H0. This H0 population exhibited heterosis increments of 18.5% for storage root yield. Based on offspring performance in H0 (231 families, 6,898 offspring clones), the parents were selected for the new groups of interest, WAE, NSSP, and HIFE for experiments in SASHA Phase 2. Within each of these 2 partially inbred populations developed—one for the PJ heritage; the other for the PZ heritage. Based on the evaluation of the offspring performance, a new set of PJ and PZ parents were selected to form the H1 hybrid populations, to be used in crossing between population groups.



Fig 2. Planting hybrid population H1 for OFSP wide adaptation and earliness at Canete in Peru with double plots (90 and 120 days harvest) together with parents and grandparents to demonstrate heterosis increments in H1 and genetic gains of a complete reciprocal recurrent selection cycle in HEBS [742 offspring families in H1 (9,881 H1 hybrid clones), parents: 42 PJ' and 42 PZ' clones, foundation and grandparents, respectively: 49 PJ x 31 PZ clones, 2 check clones in Westcott design).



Fig 3. Hybrid population H0 for OFSP with strong virus resistance at Namulonge in Uganda together with parents to demonstrate heterosis increments in H0 [(50 A parents x 80 B parents, number of cross combination / families with at least 6 seed 41.2%, 10,600 entries, 2 check clones in Westcott design).

demonstrate this on large scale at our breeding support platform in Uganda and then at our platforms in Mozambique and Ghana.

What have we achieved so far?

In Peru, two genetically distinct breeding populations, Jewel (PJ) and Zapallo (PZ) were established from 2005 to 2008, and 6,898 genotypes from 231 crosses between 49 PJ and 31 PZ parents formed our first hybrid population (H0). Average heterosis increments of 19% for storage root yield and 20% for number of commercial roots per plant, showed that PJ and PZ are mutually heterotic. Notably, heterosis increments in some offspring for storage root yield were up to 80%. Assessment of genetic diversity of PJ and PZ parents using molecular markers also showed striking separation of the PJ and PZ genepool although both genepools exhibited similar means and genetic variances for key traits.

Best performing parents of the H0 were selected for recombination in each population, with sub-populations selected for wide adaptation and earliness (WAE; 23 PJ and 17 PZ clones), non-sweet quality (NSSP; 5 PJ and 5 PZ clones), and high iron and zinc (HIFE; 5 PJ and 5 PZ clones). Recombination of the 6 sub-populations produced over 14,000 partially inbred clones that were evaluated at locations in jungle (at Satipo) and desert (at Canete) environments of Peru. New PJ (42 WAE, 25 NSSP, 23 HIFE clones) and PZ (28 WAE, 28 PZ, 23 HIFE clones) parents were selected and crossed to form H1 hybrid populations. In 2017, 16,915 H1 clones from 1,315 families were evaluated together with grandparents and parents and standard checks in 2 environments.

Genetic gains in the H1 population over the baseline of grandparents ranged from 68.8 to 110.3% for storage root yield. Heterosis increments for H1 populations compared to parents ranged from 9.3 to 37.6%. Heterosis increments at 90 days (24.2%) were larger than those at 120 days (9.3%) in the WAE H1 population. High selection intensities among baseline NSSP and HIFE foundation grandparents produced larger heterosis increments and genetic gains than the moderate selection intensities applied to the WAE grandparents. Thus, high selection intensities may not create

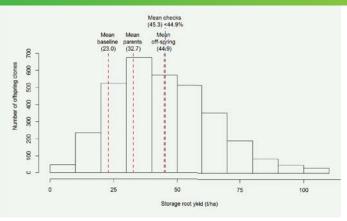


Fig 4: Genetic gains (GG) in storage root yield in H1 for OFSP high iron evaluated across two contrasting environments in Peru (Canete, Satipo) [Mean foundation / grandparents yield (23.0 t/ha), 80 clones each clone in 8 one-meter row plot replications, selected fraction in baseline PJ = 0.10 and PZ = 0.16; mean parents (32.7 t/ha), 46 clones each clone in 8 one-meter row plot replications; mean offspring (44.9 t/ha), 3,292 H1 hybrid clones; total GG: 95.2%; heterosis increment in H1: 37.3%, estimated gain by one reciprocal recurrent selection cycle: 42.2%; 2 check clones (Dagga, Cemsa) in Westcott design.

bottlenecks that could slow genetic gains in sweetpotato (Fig. 4). Based on the frequency of offspring clones being better than the mean of the excellent *check clones*², each of the H1 populations had strong potential to produce new high yielding varieties (Table 1) – iron and zinc results for H1 HIFE will be available soon.

In Uganda, two large populations, UG_A with 50 parents and UG_B with 80 parents, were separate based on using molecular markets to cluster clones with similar genes together. A subset or parents from each population was crossed to produce an H0 population. Heterosis increments averaged 93.2%. However, intra-pool crosses of UG_A x UG_A and UG_B x UG_B also showed high heterosis increments in trials in both Uganda and Mozambique, though not as high as the AxB crosses. Such intra-gene pool heterosis cannot be systematically exploited if the breeder does not operate with two genepools, however. To start applying RRS on a large scale in Uganda, interpopulation crosses among all UG_A and UG_B parents were made and 41.2% produced 6 seeds or more. This H0 population is undergoing evaluation in the field at Namulonge (Fig. 3) and will serve to select parents on basis of offspring performance with emphasis on SPVD and yield. Moreover, a fast track approach has been taken, with a small of UG_A and UG_B parents that have previously exhibited elevated SPVD resistance in progenies. This fast track HEBS approach should allow us to boost the frequency of SPVD resistance from <0.2% to >2% in breeding populations.

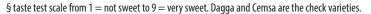
In Mozambique, breeding populations in the north and south are being analyzed using molecular markers to confirm genetic distinctness before commencing systematic implementation of HEBS. HIFE breeding is among the priority traits.

In Ghana, HEBS is being initiated by separating populations using marker assessment of genetic diversity complemented by initial estimates of heterosis increments and general combining ability based on 149 progenies from 22 parents. Results based on 5 plant plots of full-sibs are being compared with those based on 3-plant clonal plots, with at least six clones per family. If the full-sib, mixed plot approach is effective, it would be applied conveniently with larger numbers of progenies and genotypes than the plot-intensive approach being used in Peru and Uganda. In Ghana, sub-populations for HEBS improvement will include NSSP, OFSP, and reduced perishability.

What are the next steps?

Elite H0 combinations identified for WAE in Peru have been used to produce large amounts of seed to be shared with national programs. HEBS implementation at the Sweetpotato Support Platforms in SSA will soon replicate the genetic gains achieved with PJ and PZ in Peru.

Mean H1 sel. breeding lines & checks	Root yield (t/ha)	No. Comm. Roots per plant	Foliage yield (t/ha)	B-carotene (mg / 100 g FW)	Root dry matter (%)	Sweetness taste score§
WAE (N=400)	30.2	3.70	49.0	6.44	26.2	-
Dagga	26.8	2.44	49.1	1.16	26.4	-
Cemsa	15.9	1.53	55.5	0.08	28.4	-
NSSP (N=200)	44.4	3.69	71.6	6.2	25.2	4.1
Dagga	41.1	2.64	72.6	1.11	25.7	5.1
Cemsa	61.7	3.20	115.6	0.88	25.6	6.8





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² A check clone is a released variety that performs well and typically is widespread. One seeks to breed new clones that can surpass the check clone in key traits as part of the rationale for officially releasing the new variety.

Table 1: Mean of selected H1breeding lines for wide adaptationand earliness (WAE) at 90 daysharvest (N = 400) and fornon-sweet sweetpotato aftercooking (NSSP) under normalharvest (N = 200) and check clonesfor observed traits evaluated attwo locations in Peru (Canete andSatipo) after discarding all cloneswith virus symptoms