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Performance evaluation of Nile tilapia (*Oreochromis niloticus*) improved strains in Ghana

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ABSTRACT

Growth performance and survival to harvest of the Akosombo strain generation 10 and the GIFT strain generation two (derived from GIFT generation 11 in Malaysia) were evaluated in Ghana. The fish were from 96 families of the Akosombo selected line (AKOS), 30 of the Akosombo control line (AKOC), and 22 of the GIFT strain (GIFT). In total, 11,812 tagged fingerlings were stocked at a density of 3 fish.m^{-2} into two ponds, each 2000 m^2. Fish were fed 38% crude protein pelleted feed, twice daily at a rate of 5% body weight, for 120 days. Harvest weight of GIFT (150.1 ± 58.5 g) was 2.2 times larger than AKOC (67.6 ± 28.4 g) and 1.8 times larger than the AKOS (85.2 ± 32.0 g) strains. The least-squares mean weight of male GIFT were 98.6 g more than AKOC and 82.7 g more than AKOS. The corresponding ratios for females were even greater, with female GIFT weighing 106.5 g more than AKOC, and 89.9 g more than AKOS. The AKOS grew larger than the AKOC, 15.9 g larger for males and 16.6 g for females. All differences were highly significant ($P < 0.001$). Male fish were significantly larger than females for all three strains ($P < 0.001$). Overall, individual survival rate at harvest was 53.6% and not significantly different between strains, with GIFT survival being 55.2%, AKOS 54.5% and AKOC 50.0%. The results of the present study demonstrated: 1) marked differences in the growth performance of GIFT and Akosombo strains, and 2) the strong growth performance of GIFT in an equatorial West African environment, with similar survival to that of the local strain.

1. Introduction

Tilapias comprise one of the most important groups of aquaculture species. In 2018, of the 82.1 million tonnes (MT) of aquaculture food-fish production, 5.5 MT was accounted for tilapia production (FAO, 2020), 81% of which was Nile tilapia (*Oreochromis niloticus*) (FAO, 2020). Several genetic improvement programs have been developed for Nile tilapia (Komen and Trong, 2014). These include the Genetically Improved Farmed Tilapia (GIFT) developed in the 1980s by ICLARM (now known as WorldFish) with other institutional partners and the Akosombo strain developed at the Aquaculture Research and Development Centre (ARDEC) of the Water Research Institute (WRI) of the Council for Scientific and Industrial Research (CSIR), in Ghana, since 2000.

The base population for selection of GIFT was composed from four wild African strains (including a Ghanaian strain) and four farmed Asian strains (of which three originated from Ghana) (Eknath et al., 1993; Bentsen et al., 2017). GIFT has shown a remarkable genetic gain in growth rate and has out-performed other strains in a variety of farming systems in Asia (Bentsen et al., 2017). Several studies have identified the socioeconomic benefits arising from farming of GIFT, including improved rural income and employment (Dey et al., 2000; Gupta and Acosta, 2004; Yuan et al., 2020). According to the Asian Development Bank (2005) "the economic internal rate of return on investments in GIFT development and dissemination was more than 70% over a period from 1988 to 2010, with an estimated net present value of US$ 368 million in constant 2001 prices". In 2001, the base population of the Akosombo strain was composed of fish from three agro-ecological zones (Nawuni in the Northern Region, Yeji in the Brong Ahafo Region and Kpando in the Volta Region) and one farmer's stock (a fish farm at Nsawam in the Eastern Region) in Ghana (Attipoe et al., 2013; CSIR - Water Research Institute, 2013). The collected specimens were held in a quarantine facility at ARDEC and used to form the base population for a full-pedigreed breeding program. After the first two generations of selection (2002 to 2004), heritability for harvest

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weight was found to be 0.039 ± 0.014, and estimated cumulative response to selection ranged from 4.36 to 5.34% (Attipoe et al., 2013). After a decade of selection, the Aksombo strain was reported to have 30% faster growth than other farmed tilapia strains in the West African sub-region, resulting in improved tilapia production in Ghana (CSIR - Water Research Institute, 2013). The Akosombo strain enabled farmers to shorten harvest time from eight to six months and was also reported to have higher survival rate than other unimproved strains (CSIR - Water Research Institute, 2013).

In 2004, the Nairobi Declaration institutionalized the WorldFish (then WorldFish Center) policy of non-introduction of GIFT to African countries where Nile tilapia is indigenous (Gupta, 2002; Gupta and Acosta, 2004). Instead, WorldFish helped these countries to develop their own selective breeding programs for indigenous Nile tilapia using the GIFT methodology. However, in 2007, WorldFish Center (2007) approved the ‘Policy on the Transfer of GIFT from Asia to Africa’, recognizing that the genetic risk of introducing GIFT is comparable to those associated with the genetic improvement of indigenous Nile tilapia strains.

Critical data required for assessing risks and benefits of introduction include that on performance of the strain to be introduced with that of the local strains. As part of a project on aquaculture in the Volta basin (i.e. the ‘TIVO project’), the performance of Nile tilapia genetic resources was assessed in Benin, Burkina Faso, Côte d'Ivoire, Mali, and Togo (Lind et al., 2019). The GIFT strain (generation 11 in Malaysia) was introduced to Ghana (CSIR - Water Research Institute, 2013) on an experimental basis, with the purpose of comparing its growth performance with the locally improved Akosombo strain.

The present paper reports the results of an experiment comparing pond growth performance and survival to harvest of the Akosombo strain generation 10 and the second generation of the GIFT strain in Ghana. This work on the two Nile tilapia strains, which have been genetically improved under equatorial conditions, provides rare benchmarking information on performance of these strains in West Africa.

2. Materials and methods

2.1. Experimental facilities and experimental design

The animals used in the experimental set up from breeding populations at ARDEC, Ghana, were humanely handled and managed in conformity with national guidelines on ethics and animal welfare (https://csir.org.gh/index.php/r-d/research-ethics-intellectual-property-rights/irb-iacuc/item/432-iacuc-standard-operating-procedure-sop).

The experiment was conducted at quarantine facilities that had been developed to maintain the introduced GIFT strain at ARDEC, Akosombo, Ghana from December 2013 to December 2014. Facilities for fry production were limited, as was space within the quarantine facility for fish rearing, and only two ponds were available for the experiment. This meant that family production had to be carried out over an extended period (Table 1). The number of available GIFT broodstock (58 males and 116 females, allowing 58 matings at a ratio of 1 male to 2 females) limited the number of families produced and fry subsequently tested for growth performance. The Akosombo strain (selected AKOS and control AKOC line) families were produced in immediately adjacent facilities outside the quarantine area. These facilities had larger hatchery capability, resulting in larger numbers of families produced as part of the routine selection program.

The two replicate grow-out ponds available for the experiment were each 2000 m^2. For testing growth performance in ponds under normal farming conditions with standard stocking density of 3 $fish.m^{-2}$, a total of 12,000 fish (6000 per pond) was required. Given the limited number of fry available with 22 GIFT and 30 AKOC families, 96 AKOS families were needed to provide the overall stocking density of 3 $fish.m^{-2}$.

2.2. Strains used

The GIFT strain (1852 fingerlings from 60 families of generation 11) was imported from WorldFish in Malaysia to ARDEC in Ghana during May 2012. Broodstock from both the AKOC and AKOS lines from generation nine of the Akosombo strain, and of the first GIFT generation in Ghana were used to produce experimental fish for this study. Therefore, the performance of generation 10 of the Akosombo strain (both AKOS and AKOC lines, of which the control line was made up of male and female breeders with average estimated breeding values) and generation two of GIFT in Ghana were compared.

2.3. Production of fish

Eggs or fry from both strains were collected in 11 batches from 26th December 2013 until 8th April 2014 (Table 1) and were incubated in down-welling jars until hatching. Fry were initially stocked at a density of 200 $fry.m^{-2}$ in 1-m^2 (1 × 1 m) nursing hapas (two per family) and fed a fine powdered feed (38% crude protein) for six weeks. Thereafter, they were transferred into 3-m^2 (3 × 1 m) hapas until the fingerlings reached approximately 5 g. Fish were from 96 families of generation 10 of AKOS, 30 of AKOC, and 22 of GIFT. All the fish were tagged with Passive Integrated Transponder (PIT) tags in May 2014. Prior to tagging, the fish were anesthetized with Tricaine mesylate (Tricaine methanesulfonate, MS-222) at a concentration of 0.33 $g.l^{-1}$ and placed in freshwater to recover after tagging. Tagged fish were conditioned in 1-m^2 (1 × 1 m) hapas for 10 days. Dead fish were replaced with newly tagged fish from the same family.

The two 2000-m^2 ponds (pond 1 and pond 2) located in the biosecure facility at ARDEC were prepared for stocking of the tagged fish. For both strains (including the AKOC), 80 tagged fingerlings per family were stocked equally into two ponds (40 each) on 17th July 2014. A total of 12,043 tagged fingerlings were stocked at a density of approximately 3 $fish.m^{-2}$. Fish were fed with 38% crude protein pelleted feed twice daily and at a rate of 5% body weight for 120 days. A sample of fish was weighed every two weeks, and the amount of feed given was adjusted accordingly.

Fish from pond 1 were harvested from 27th November to 2nd December 2014, while those from pond 2 were from 9th to 16th December 2014. They were transferred to hapas (5 × 2 m) and maintained for seven days. Thereafter individual PIT tag code, sex, and harvest weight were recorded for each fish.

Table 1
Numbers of families collected from the three strains (11 batches).

Strain[1]	Year											Total
	2013					2014						
	26/12	14/1	17/1	26/1	28/1	11/2	12/2	25/2	11/3	12/3	8/4	
AKOC	14	7		1	5	1		1	1			30
AKOS	62	20			5	5		2	1		1	96
GIFT	2		5				11			3	1	22
Total	78	27	5	1	10	6	11	3	2	3	2	148

[1] AKOC = Akosombo control line, AKOS = Akosombo selected line, GIFT = GIFT strain.

Table 2
Number of fish, mean stocking and harvest weights ± standard deviations, and coefficient of variation (CV) by pond, strain, and sex.

Pond	Strain[1]	Sex	# of fish		Stocking weight (g)		Harvest weight (g)	
			Stocking[*]	Harvest	Mean ± SD	CV	Mean ± SD	CV
Pond 1	AKOC	Female		304	8.3 ± 4.4	53.1	52.6 ± 14.5	27.6
		Male		403	8.7 ± 4.2	48.8	92.6 ± 22.8	24.6
		Total	1180	707	8.5 ± 4.3	50.6	75.4 ± 28.0	37.1
	AKOS	Female		1203	8.3 ± 3.5	42.1	75.1 ± 21.1	28.1
		Male		1310	9.8 ± 4.0	40.9	112.4 ± 27.4	24.4
		Total	3872	2513	9.1 ± 3.8	42.2	94.5 ± 30.8	32.6
	GIFT	Female		245	6.0 ± 3.6	60.5	165.1 ± 43.6	26.4
		Male		179	6.4 ± 3.5	54.5	191.1 ± 50.3	26.3
		Total	851	424	6.2 ± 3.6	57.9	176.1 ± 48.3	27.4
Total	pond 1		5904	3644	8.6 ± 4.0	46.4	100.3 ± 43.5	43.3
Pond 2	AKOC	Female		161	8.7 ± 4.5	51.9	36.7 ± 22.0	59.9
		Male		313	9.4 ± 4.8	51.4	65.9 ± 20.1	30.5
		Total	1184	474	9.2 ± 4.7	51.6	56.0 ± 25.0	44.6
	AKOS	Female		630	8.2 ± 3.5	43.0	50.4 ± 16.9	33.6
		Male		1064	10.5 ± 4.6	43.7	83.9 ± 26.8	32.0
		Total	3865	1694	9.6 ± 4.4	45.3	71.4 ± 28.6	40.1
	GIFT	Female		260	6.0 ± 3.8	63.1	111.1 ± 48.5	43.6
		Male		260	7.3 ± 3.8	51.5	146.6 ± 60.5	41.3
		Total	860	520	6.7 ± 3.8	57.6	128.8 ± 57.6	44.7
Total	pond 2		5909	2688	9.0 + 4.5	50.0	79.8 ± 43.3	54.3
2 ponds	AKOC		2364	1181	8.8 ± 4.5	51.2	67.6 ± 28.4	42.0
	AKOS		7737	4207	9.3 ± 4.1	43.7	85.2 ± 32.0	37.6
	GIFT		1711	944	6.4 ± 3.7	57.8	150.1 ± 58.5	39.0
Total			11,812	6332	8.8 ± 4.2	48.1	91.6 ± 44.6	48.7

[1] AKOC = Akosombo control line, AKOS = Akosombo selected line, GIFT = GIFT strain.
[*] Sexes cannot be identified at stocking.

2.4. Data analysis

Data were analyzed using R software version 3.6.3 (R Core Team, 2020). The different weights of fish at the start of the experiment (Table 2) were accounted for by including the total age at harvest (total age from spawning until harvesting) as a covariate. Harvest weight was analyzed using the following mixed-effects model (Model 1) using package 'nlme' (Pinheiro et al., 2020)

$\boldsymbol{harw_{ijklm} = \mu + \beta_1 \times harage_{ijklm} + (strain \times sex)_i + pond_j + sire_k + dam_l + e_{ijklm}}$ (**Model 1**) where, $\boldsymbol{harw_{ijklm}}$ is harvest weight of the $\boldsymbol{m^{th}}$ fish, $\boldsymbol{\mu}$ is the population mean, $\boldsymbol{\beta_1 \times harage_{ijklm}}$ is the fixed regression on total age at harvest, $\boldsymbol{harage}$, $\boldsymbol{(strain \times sex)_i}$ is the fixed effect of the $\boldsymbol{i}$ combination of strain (the two Akosombo lines and the GIFT) and sex (male and female), $\boldsymbol{pond_j}$ is random effect of pond $\boldsymbol{j}$, $\boldsymbol{sire_k}$ is random effect of sire $\boldsymbol{k}$, $\boldsymbol{dam_l}$ is random effect of dam $\boldsymbol{l}$, and $\boldsymbol{e_{ijklm}}$ is the random residual term.

Individual survival at harvest (alive = 1, dead = 0) was analyzed using the following generalized (logistic regression) mixed-effects model (Model 2) using package 'lme4' (Bates et al., 2015)

$\boldsymbol{y_{ijkl} = \mu + strain_i + pond_j + sire_k}$ (**Model 2**) where, $\boldsymbol{y_{ijkl}}$ is the logit link function of survival at harvest of individual $\boldsymbol{l}$ (alive = 1, dead = 0), $\boldsymbol{\mu}$ is the population mean, $\boldsymbol{strain_i}$ is fixed effect of the $\boldsymbol{i}$ strain (the two Akosombo lines and the GIFT), $\boldsymbol{pond_j}$ is random effect of the $\boldsymbol{j}$ pond (2 ponds), and $\boldsymbol{sire_j}$ is random effect of sire $\boldsymbol{j}$.

For harvest weight, p-values in type III Sum of Square ANOVA were calculated using package 'lmerTest' (Kuznetsova et al., 2017). For both harvest weight and individual survival at harvest, least squares means (LSM) for strains and sexes, and their pairwise comparisons of means were calculated using package 'emmeans' (Lenth et al., 2020). For individual survival at harvest, all values were transformed from the logit scale to the response scale.

3. Results

3.1. Descriptive statistics

In total, there were 6332 fish from 148 full-sib families (148 sires and 148 dams) harvested from the two ponds, of which pond 1 had more fish (3644, 58% of the total number of fish in the two ponds) than pond 2 (2688, 42%) (Table 2).

The mean harvest weight of the GIFT strain over both ponds (150.1 ± 58.5 g) was 2.2 times larger than that for AKOC (67.6 ± 28.4 g) and 1.8 times larger than that for the AKOS strain (85.2 ± 32.0 g), and this trend was consistent for both ponds (Table 2). The mean harvest weight of GIFT in pond 1 (176.1 ± 48.3 g) was 37% larger than that in pond 2 (128.8 ± 57.6 g). For the Akosombo lines, it was similar: AKOC fish in pond 1 (75.4 ± 28.0 g) were larger than in pond 2 (56.0 ± 25.0 g), and for AKOS it was 94.5 ± 30.8 g in pond 1 and 71.4 ± 28.6 g in pond 2. For all the three groups, males were significantly heavier than females, most noticeably with AKOC (males 72.3% larger) and AKOS (males 49.5% larger), but less so in GIFT (20.0%).

Overall survival rate of the three groups was 54%, with 55% for GIFT, 54% for AKOS, and 50% AKOC, and the differences were not statistically significant. The number of surviving fish in pond 1 was higher than in pond 2, but relative survival among strains differed between ponds. However, the overall percentages of the numbers of fish in each strain at harvest (65% AKOS, 20% AKOC, and 15% GIFT) were similar to those at stocking (66% AKOS, 20% AKOC, and 14% GIFT) (Table 3).

3.2. Fixed effects and covariate

For harvest weight, two fixed effects (strain and sex), their interactions, and one covariate (total age at harvest) were all significant (Table 4). For individual survival at harvest, strain as the only fixed effect was not significant ($P = 0.08$).

3.3. Strain comparisons

GIFT outperformed AKOC and AKOS by large margins for growth. The analysis took account of the differences in stocking weight by the inclusion of age at harvest as a covariate (Table 2). The LSM of male GIFT individually was 98.6 g more than AKOC and 82.7 g more than AKOS. The corresponding differences for females were greater; where

Table 3
Numbers (and percentages) of surviving fish at harvest by strain.

Strain[1]	Pond 1	Pond 2	Total
AKOC	707 (19%)	474 (18%)	1181 (19%)
AKOS	2513 (69%)	1694 (63%)	4207 (66%)
GIFT	424 (12%)	520 (19%)	944 (15%)
Total	3644 (100%)	2688 (100%)	6332 (100%)

[1] AKOC = Akosombo control line, AKOS = Akosombo selected line, GIFT = GIFT strain.

Table 4
ANOVA for fixed effects (strain and sex), interaction, and covariate (total age-at -arvest) on harvest weight.

Effect	DF (num)	DF (den)	*F*-value	*p*-value
(Intercept)	1	6037	14.9	< 0.0001
Strain	2	287	471.1	< 0.0001
Sex	1	6037	505.9	< 0.0001
Strain × sex interaction	2	6037	7.9	0.0004
Total age-at-harvest	1	6037	72.1	< 0.0001

female GIFT individually weighed 106.5 g more than AKOC, and 89.9 g more than AKOS. The AKOS performed better than AKOC, 15.9 g better for males and 16.6 g for females. All differences in terms of harvest weight between different groups of fish were highly significant ($P < 0.001$). Male fish were found to be significantly larger than females for all three strains ($P < 0.001$). For AKOC, the difference (35.7 g) was similar to that of AKOS (35.0 g). The difference between male and female GIFT was smaller (27.8 g) (Table 5).

The odds for AKOC survival was 83.8% compared to AKOS and 80.2% compared to GIFT, while the odds of survival for AKOS was 95.7% compared to GIFT. However, all pairwise differences in LSM for survival were not significant ($P = 0.09$ to 0.89) (Table 6).

4. Discussion

The objective of this study was to compare growth performance and survival of the Akosombo strain developed in Ghana with those of the GIFT strain developed in Asia, both of which had been selected for performance in equatorial environments. In the present study, GIFT grew faster than the Akosombo strain and AKOS faster than AKOC. GIFT grew to a larger size, despite being smaller in size when stocked. However, some aspects of the experimental design may have differentially biased the estimates of growth of the different strains. First, the numbers of fish in each strain were unequal throughout the experiment, with the AKOS strain having more families and individual fish than the GIFT and AKOC strains (Tables 2 and 3). Where there are marked differences in abundance of two groups, assuming no restriction for food, the rarer group might have a growth advantage as a result of reduced numbers (or density) relative to the more common group (Brett, 1979), although this is debated as being dependent on the natural schooling and feeding relations of the species or groups (Yamagishi, 1963, 1969). The second issue is the co-rearing of the three groups means that there will be direct competition for food and space between them. Selection for growth in GIFT has been found to increase competitiveness (e.g., for feed) or aggressiveness (e.g., the ability to suppress growth of other individuals) (Khaw et al., 2016). Observations of the Akosombo and GIFT fingerlings in separate hapas reported common gathering of GIFT fish to the surface with mouths gaping open at feeding times, but rarely by Akosombo strain. Given those observations, fingerlings were sampled during the pond experiments. The identity of the tagged fish showed that the majority (80–90%) near the feeders at the start of the feeding periods were GIFT fingerlings. GIFT success in direct competition for food and space, may have contributed to its being able to grow faster and depress the growth of the Akosombo strains relative to situations in which the strains were reared separately.

One way to test whether or not these effects occurred is to compare the relative performance of the strains when reared separately. This was done by comparing the growth of the fish used in the experiment with that of the previous generation, accessing data from the breeding program where the GIFT and Akosombo lines were reared separately. Given that the period over which growth was measured was similar (approximately 230 days), the comparison is most simply made using the daily growth rate for each strain (Table 7). These results showed slower growth rate in the pond experiment relative to those in the breeding program for all strains. This may be due to a number of differences in the environmental circumstances between the two sets of measurements. However, the pertinent issue is comparison of the relative growth rates among strains. The reduction in growth rate in the pond experiment relative to the breeding program was greater for male AKOS (35%) and AKOC (39%) than for male GIFT (22%) suggesting an effect of competition between the males accounting for around 10–15% of the growth difference between the Akosombo strains and GIFT in the pond experiment. Since AKOS was more abundant than both AKOC and GIFT, these results suggest no obvious effects of density differences in the pond experiment. Although the pattern of change was somewhat different for females, there was no evidence that any growth differences were related to density. Growth rates for females were reduced to a lesser degree than males, with AKOC having a greater decline (29%) than either AKOS (16%) or GIFT (18%), between which there was little difference. Thus, the female data suggested no competitive effect. Overall, these results provide limited evidence for an effect of direct competition, perhaps restricted to males, but no effect of differences in relative density in the current experiment.

Table 6
Least-square means of survival to harvest for each strain (on the diagonal, value = logit scale = estimate ± standard error) and pairwise comparison (off diagonal, value = response scale). The pairwise comparisons indicate the differences of the estimate for the given strain and sex in the column relative to that on the diagonal (e.g., AKOS estimates were 0.838 those of AKOC).

	AKOC	AKOS	GIFT
AKOC	**0.003 ± 0.251**	0.838 (*P* = 0.09)	0.802 (*P* = 0.13)
AKOS		**0.180 ± 0.243**	0.957 (*P* = 0.89)
GIFT			**0.224 ± 0.255**

Table 5
Least-square means of harvest weight for each sex in each strain (on the diagonal, value = estimate ± standard error) and pairwise comparisons (off diagonal). Differences on the diagonal are in grams. The pairwise comparisons indicate the differences of the estimate for the given strain and sex in the column relative to that on the diagonal (e.g., AKOC female estimates were 35.7 g less than AKOC males). All pairwise comparisons were significant ($P < 0.001$).

	AKOC, female	AKOC, male	AKOS, female	AKOS, male	GIFT, female	GIFT, male
AKOC female	**43.2 ± 15.8**	−35.7	−16.6	−51.6	−106.5	−134.3
AKOC male		**78.9 ± 15.8**	19.1	−15.9	−70.9	−98.6
AKOS female			**59.8 ± 15.7**	−35.0	−89.9	−117.7
AKOS male				**94.8 ± 15.7**	−54.5	−82.7
GIFT female					**149.7 ± 15.9**	−27.8
GIFT male						**177.5 ± 15.9**

Table 7
Daily growth rate (g day^{-1}) of three strains (GIFT, AKOS, and AKOC) in the current experiment and previous generation of the breeding program in Ghana, and the difference in growth rate between the two expressed as a percent of the breeding program growth rate. The period of growth for both the experimental and the breeding-program fish was approximately 230 days. Daily growth rate = harvest weight/total age from spawning until harvest.

Strain	Daily growth rate (g day^{-1})	
	Males	Females
Experiment (reared together)		
GIFT G2 Ghana experiment	0.56	0.47
AKOS G10 experiment	0.30	0.21
AKOC G10 experiment	0.25	0.15
Breeding program (reared separately)		
GIFT G1 Ghana	0.72	0.57
AKOS G9	0.46	0.25
AKOC G9	0.41	0.21
Differences (%) of experiment compared to breeding program		
GIFT	−22	−18
AKOS	−35	−16
AKOC	−39	−29

This interpretation agrees with the first assessment from data calculated in 2012, where GIFT was reported to grow 1.6 times faster than Akosombo strain after 122 days (CSIR - Water Research Institute, 2013). As noted, the present experiment may have overestimated the differences between GIFT and AKOS, but it is clear that GIFT grows 1.6 to 1.9 times faster than AKOS.

It is pertinent for this discussion to consider the results of studies during the initial testing of populations used to create the base population of the GIFT strain. The wild Ghanaian strain tested in the 1980s (220 fingerlings collected from the Volta River System in October 1988) was the poorest performer during the inter-strain comparison that preceded to establishment of the base population of GIFT (Eknath et al., 1993). In addition, the farmed strains from Israel, Singapore, and Taiwan, all of which originated from Ghana, were intermediate- to slow-growing (Eknath et al., 1993, 2007). All four were the slowest-growing strains in all environments (cage, pond, and rice-fish cultures) in which the fish were tested, thus, all strains derived from Ghana contributed only 2.6 to 8.5% each to the founding population of GIFT. The representation of all these strains was reduced over time following selection for faster growth in the presence of other superior genetic material, and after five generations of selection provided only 0.6 to 5.3% of the GIFT population (Bentsen et al., 2017). The extent to which bottlenecks and consequent inbreeding may have affected the Ghanaian strain(s) introduction into Asia, and into GIFT, is unknown. However, the numbers of individuals included in the GIFT program from the strains including the Ghanaian strains were comparable to that for other sources. Therefore, these results suggest a fundamental genetic difference with respect to growth rates between the Ghanaian strain and the other source populations of GIFT compared more than 30 years ago.

This study, however, does not suggest that Ghanaian stocks will not respond to selection. It is clear that the Akosombo program has successfully produced, over 10 years of selection, a strain that grows about 30% faster than unimproved Ghanaian stocks (CSIR - Water Research Institute, 2013). The present experiment found AKOS grew 26% faster than AKOC, with males 22% and females 42% faster. However, the GIFT strain was reported to show a 67% improvement in growth compared to the base population or 88% improvement compared to the control group after only five generation of selection (Bentsen et al., 2017).

When transferred to Ghana in 2012, GIFT had been selected for seven generations in the Philippines and thereafter 11 generations in Malaysia, a total of 18 generations of selection, with Ponzoni et al. (2011) reporting more than 10% improvement per generation sustained over more than six generations. While there were likely differences in the management of Akosombo and GIFT programs in terms of number of families per generation, the approaches in these two programs were the same (i.e., pedigree-based BLUP calculation for breeding values and a mating scheme designed to maintain inbreeding at an acceptable level of ~0.5% per generation). There were factors that might have hindered the response to selection in the Akosombo strain. Although three wild stocks were collected from three ecological zones in Ghana, the fourth was from a fish farm at Nsawam where the fingerlings were introduced by the Institute of Aquatic Biology in 1982 and had not been replenished for 24 years according to anecdotal data in Attipoe et al. (2013). After the first two generations of selection, Attipoe et al. (2013) reported that the heritability was 0.039 ± 0.014. Despite experimental difficulties that may have affected accuracy of heritability estimation, such as tag loss and high mortalities (Attipoe et al., 2013), this value indicated that the genetic variation for growth was low in the Akosombo strain. These data also suggest a fundamental genetic difference with respect to growth rates between the Akosombo and GIFT strains.

It is well known that sexual dimorphism exists in Nile tilapia populations, with males growing faster than females (Beveridge and McAndrew, 2000). The same trend was reported in GIFT (Bentsen et al., 2017). It has been assumed that growth of both males and females of the GIFT strain was simultaneously improved, although the difference between two sexes over time caused by long-term selection has not yet been quantified. In from the present work, the difference between GIFT male and female fish was smaller than those of AKOS and AKOC, and that of AKOS significantly smaller than of AKOC (Tables 2 and 5), indicating that selection improved growth for both sexes and at the same time reduced the difference between the two sexes.

Individual survival at harvest was not significantly different between the Akosombo strains and GIFT (Tables 3 and 6). For GIFT, survival remained the same after nine generations of selection (Ponzoni et al., 2011). Given that both programs used the same breeding approach, the same trend would be expected for the Akosombo strain and is suggested by the similar survival rates observed in the experiment.

There are debates about the use of indigenous or imported elite strains with respect to balancing conservation and development, and differences in views of the extent to which these strains are adapted to local ecosystems and to ecological and their economic sustainability (Ansah et al., 2014; Anane-Taabeah et al., 2019). These issues will be debated in respect of the choice of strain for use in the development of the aquaculture industry in Ghana and the Volta basin at large. The results of the present study demonstrated marked differences in the performance of GIFT and Akosombo strains relative to growth, and strong growth performance of GIFT in an equatorial West African environment, with survival similar to that of the local strain.

Significant gains achieved in the Akosombo genetic improvement program over ten years are less than those achieved in the GIFT program, even after taking account of the longer period of selection for GIFT. The data suggest that it would require more than 20 years of selection for the Akosombo strain to achieve similar levels of growth to the GIFT strain generation tested, during which time continued selection of GIFT would result in even greater improvement in performance. Use of GIFT would be expected to provide a huge boost in commercial tilapia production in Ghana and the sub-region. In the absence of a formal and transparent process for responsible introduction and management of improved strains, the possibility of the risk of illegal or uncontrolled introduction and mismanagement of stocks of unverified origins with potential deteriorative effects can be expected. Genetic characterization of tilapia purchased in Ghana (Anane-Taabeah et al., 2019) suggested that there may have been informal introductions to Ghana contrary to Ghanaian policy at the time. There could be significant consequences for the development of the aquaculture industry in Ghana and the sub-region depending on choice of strains and corresponding responsible management.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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