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Genetic analysis of Nile tilapia (*Oreochromis niloticus*) selection line reared in two input environments

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ABSTRACT

Ascertaining the appropriate selection environment for Nile tilapia (*Oreochromis niloticus*) in Africa is a critical issue. Two data sets derived from two selection lines originating from a common base population were analysed in this study. The lines were selected in two different input environments, here named 'low input' and 'high input'. Both data sets were combined and jointly analyzed to estimate the phenotypic and genetic parameters, with a special focus on the examination of genotype by environmental interaction. The data sets included a total of 7640 animals with phenotypic information from three discrete generations. Four different models (in terms of fixed effects) were fitted in univariate (harvest weight) and bivariate (harvest weight in each input line treated as two different traits) animal models to estimate variance and covariance components. The heritabilities estimated from the four different models by univariate analyses ranged from 0.15 to 0.41 (all with standard errors of 0.04). The genetic correlations between harvest weights expressed in the two environments, obtained from the bivariate analyses, ranged from 0.74 to 0.84 (with standard error in the range 0.15 to 0.36). We concluded that there was no significant evidence for genotype by environmental interaction for these two particular input environments.

1. Introduction

Nile tilapia (*Oreochromis niloticus*) is a well known tropical food fish native to Africa. To date several selective breeding programs for Nile tilapia have been established and maintained, for example GIFT (Eknath et al., 1993; Eknath and Acosta, 1998), GET-EXCEL (Tayamen, 2004), FaST (Bolivar, 1998), and GenoMar Supreme Tilapia™ (Zimmermann and Natividad, 2004). These selective breeding programs were implemented in Asia under relatively intensive culture systems where the fish were provided formulated feeds. Nile tilapia has not been developed significantly in Africa with little focus on the prevailing production environments in the continent. This is despite the fact that Africa holds the global wealth of tilapia genetic resources and has a great natural potential for aquaculture development (Pullin, 1988).

In order to have an efficient tilapia production in Africa, ascertaining what is the appropriate environment for selection is important. One approach that may be used for this purpose is to conduct an investigation on growth performance in different culture environments, that is, what is generally called a genotype by environment (G×E) interaction study.

The two data sets used in this study originate from two selection lines from the same base population, progeny of which were maintained and selected in two different input environments, referred to here as 'low input' and 'high input' environments. These two input environments were chosen based on current aquaculture practices and resources in Africa. Tilapia production predominantly takes place under what we here denominate a 'low input environment'. By contrast, the commonly used culture system in selective breeding programs of Nile tilapia has been what we here call 'high input environment'. These two environments are defined in greater detail later in the paper. Results from the data set corresponding to the low input environment have been earlier reported by Charo-Karisa et al. (2006). The objectives of this project were to estimate phenotypic and genetic parameters, selection response, and GxE interaction by combining and jointly analyzing both low and high input selection lines' data.

2. Materials and methods

2.1. The environment

The selective breeding program was carried out at the Regional Research Station of The WorldFish Center in Egypt. The research station

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is located in Abbassa, Abou Hammad, approximately 70 km northeast of Cairo and 80 km inland from the Mediterranean Sea. The average air temperature at Abbassa ranges from 4 °C in winter to 40 °C in summer, while the water temperature varies from 9 °C to 34 °C. Egypt is a climatically dry country with two distinctive seasons, usually referred to as the hot season (May to September), and the cold season (November to March). At Abbassa, the average annual rainfall is between 25 mm and 50 mm, and may occur only once in several years.

2.2. The fish and data structure

The founder population that gave origin to both lines (low input and high input) was established by full diallel-cross mating design from four different local populations of Nile tilapia in Egypt, namely Maryout, Zawia, Abbassa and Aswan. The fish from Abbassa, Zawia and Aswan were from wild populations whereas those from Maryout were collected from a hatchery near Lake Maryout (Rezk et al., 2002; Charo-Karisa et al., 2006). These populations were geographically isolated and the samples were randomly taken in the year 2000. The base population used in this study was produced in 2002 by 87 sires and 115 dams that were randomly selected from the founder population (Charo-Karisa et al., 2006). The mating design was one male mated to two females (known as nested design, each female was mated to only one male) and all the brood stock was identified with Floy Tags® (disc type with alphanumeric code for fingerlings). Approximately 36–40 progeny of each full-sib family from the 2002 Spawning Season (SS02) were evenly divided into two groups: the "high input line" and the "low input line". In a few cases (10) families did not contain enough fry. Those families were only assigned to the high input line.

After SS02, selection and reproduction were carried out separately for the low and high input lines. In other word, the only (genetic) connection between these two selection lines was at the level of the base population (SS02). There was no exchange of fish between the two lines throughout the experiment. For both selection lines (low input and high input), the brooders used to produce progeny in the 2003 spawning season (SS03) and in the 2004 spawning season (SS04) were selected based on the ranking in breeding value for body weight estimated using animal mixed model (Charo-Karisa et al., 2006). The ranking and selection of brooders were performed separately for males and females. During each round of selection, 100 males and 200 females were selected for each line, with an expectation of at least a 50% of successful spawnings. Moreover, to prevent problems from inbreeding depression, mating of full-sibs and half-sibs were avoided (Charo-Karisa et al., 2006). For SS03 and SS04, 20–40 randomly chosen fry from each full sib family were individually identified with Floy Tags® and equally divided over two replicate ponds. This was done for each input line separately. Numbers of fry stocked for each input line in each spawning season are given in Table 1. Numbers of sires and dams used to produce these fry are given in Table 2.

2.3. Rearing of fry

Natural mating and spawning were carried out during summer for one to two months (June to July) in hapas. The fry of each full sib family produced in SS02 were reared in small hapas (1×1×1 m) installed in concrete tanks (6×2×1 m). In SS03 and SS04, fry produced from the low input line were nursed and reared in larger hapas (2×3×1 m) installed in earthen ponds (1000 m^2), whereas fry produced from the high input line were reared in the same concrete tanks until stocking. For the low input line, ponds containing hapas with fry were fertilized with chicken manure (50 kg dm/ha/day) to boost natural productivity. Fry from the high input line were only fed 25% protein pellets. Floy Tags® were used to individually identify the fingerlings when they reached the tagging size of 1.5 to 2.0 g (78 days old on average). After tagging, the fingerlings were returned into the hapas or tanks until stocking in the production environment by September of each spawning year.

Table 1
Numbers of fry stocked (n) and stocking densities (Stk den[a]; per square meter) for each input line (low and high) and for each spawning season (SS).

Spawning season	Low line				High line			
	Pond 1		Pond 2		Pond 8		Pond 9	
	n	Stk den	n	Stk den	n	Stk den	n	Stk den
SS02	1058	1.06	1062	1.06	2110	2.11		
SS03	1058	1.06	1043	1.04	1759	1.76	1734	1.73
SS04	1102	1.10	1104	1.10	1520	1.52	1520	1.52

[a] Pond size: 1000 m^2.

Table 2
Number of sires, dams, progeny at harvest (n), simple mean, standard deviation (SD) and survival rate (S%) of harvest weight (g) by spawning season (SS) and line.

SS	Low input line						High input line					
	Sire	Dam	n	Mean	SD	S%	Sire	Dam	n	Mean	SD	S%
SS02	80	105	1225	67.8	37.7	58	87	115	986	61.2	38.8	47
SS03	50	87	1288	86.0	32.9	61	48	86	1847	53.6	27.6	53
SS04	54	104	1207	129.0	41.0	55	59	101	1087	113.1	51.6	36
Total	184	296	3720				194	302	3920			

2.4. The grow-out system

The two production environments were: (i) the low input environment that only had dry chicken manure (50 kg dry matter/ha/day) as the daily external nutrient source, and (ii) the high input environment where fish received a formulated pellet feed that contained 25% protein (feeding until satiation). Ponds for the high input line were not fertilized. The earthen ponds used were 1000 m^2. Two ponds were used for each input line, except for the high line in SS02 when only one pond was used for grow-out due to small number of fish produced. Stocking densities are given in Table 1. Numbers at harvest and survival rates are given in Table 2. The grow-out period was about eight months, including three to four months of over-wintering. Fish were harvested at the end of April of the following year (usually the harvesting took one to two days).

2.5. Records

The body weight of the fish was recorded at harvest time. Based on the spawning and harvesting dates, age at harvest for each fish was computed. Survival rate was also recorded in each generation. All the corresponding data were collected for three discrete generations with full pedigree. A total of 7640 animals with phenotypic information (harvest weight) were used in the statistical analysis (Table 2).

2.6. Data analysis

2.6.1. General

Variance and covariance components were estimated using restricted maximum likelihood (REML) fitting an animal model. The ASReml computer program was used in all the analyses (Gilmour et al., 2002). The general model used (in matrix notation) was:

$$Y = \mathrm{X}b + \mathrm{Z}_1 a + \mathrm{Z}_2 c + e$$

where,

Y is the vector of observed harvest weights (g);
b is the vector of fixed effects;
a is the vector of random additive genetic effects (pedigree data available on 15,281 animals);

Table 3
Estimates for heritability (h^2) and common full-sib effect (c^2) for harvest weight (g) in different line and spawning season.

Spawning season	Low input line		High input line	
	h^2 (s.e.)	c^2 (s.e.)	h^2 (s.e.)	c^2 (s.e.)
SS02	0.36 (0.28)	0.12 (0.13)	0.71 (0.26)	0.02 (0.12)
SS03	0.37 (0.18)	0.12 (0.07)	0.37 (0.19)	0.21 (0.08)
SS04	0.58 (0.20)	0.05 (0.07)	0.36 (0.15)	0.04 (0.05)

c is the vector of random common full-sib effects (a combination of common environment shared among the full-sibs before communal rearing and/or maternal effect);
e is the vector of residual effects;

X, Z_1 and Z_2 are the design matrices relating observation (Y) to the levels of fixed effects (b), additive genetic effects (a), and common full-sib effects (c).

2.6.2. Estimation of phenotypic and genetic parameters

Univariate analyses were conducted on a within spawning season and line basis, and also combining all the data across spawning seasons and lines. The univariate model for harvest weight was fitted for estimating heritability (h^2), common full-sib effect (c^2) and selection response for harvest weight. The h^2 and c^2 were calculated as:

$$h^2 = \sigma_a^2 / (\sigma_a^2 + \sigma_c^2 + \sigma_e^2); c^2 = \sigma_c^2 / (\sigma_a^2 + \sigma_c^2 + \sigma_e^2)$$

where, σ_a^2 is additive genetic variance; σ_c^2 is common full-sib variance; and σ_e^2 is residual (error) variance.

The six separate analyses were carried out for each of the spawning seasons (3) by line (2) combinations (all available pedigree was used in each analysis). The parameters estimated from the within spawning season and line model served as reference point for other analyses in this study. For this model, sex and pond were fitted as fixed effects; the interaction of age at harvest and sex and the interaction of logarithm of initial body weight (measured during tagging on average age of 78 days) and sex were fitted as linear covariates. Age at harvest within sex was included in the model to correct for the age differences due to asynchronous mating and to account for the different growth curves in males and females. Similarly, initial weight within sex was modeled to correct for growth that happened before communal rearing.

Subsequently, univariate analyses fitting four different models (Models I, II, III and IV) were carried out combining all the data from both lines. The common effects in these four models were sex and the two linear covariates, age at harvest by sex interaction and logarithm of initial body weight by sex interaction. Models I, II, III and IV differed by the presence (or absence) of two fixed environmental effects, namely, pond and spawning season. In this study, low and high input lines were grown out in separate ponds. However, within each line the same ponds were used in consecutive spawning seasons (three discrete spawning seasons).

Pond was the only additional fixed environmental effect in Model I. In this model, we assumed that there were no environmental changes among spawning seasons. In other words, we assume that the fish were managed and handled in an equal manner throughout the three spawning seasons. By contrast, in Model II, spawning season was modeled as the only additional fixed environmental effect, and assumed that pond had no effect on the phenotypes. Pond and spawning season were jointly added as fixed effects in Model III, where we assumed a consistent pond effect across spawning seasons. In Model IV, the pond by spawning season interaction was modeled to reflect that the pond effect could be unique in each spawning season.

The plots of genetic trend and estimated environmental effects (predicted values obtained from ASReml output) for Model I to Model IV were plotted to examine the trend of genetic and environmental effects. The genetic trend was plotted by taking the average of EBV for each spawning season by line.

Finally, bivariate analyses treating the expression of harvest weight in each input environment as two different traits, with the above mentioned four models, were carried out to estimate the genetic correlation between low input and high input harvest weights as a means of examining the GxE interaction.

The genetic change in harvest weight for each line was estimated by taking the difference between mean estimated breeding value (EBV) of progeny from SS02 and SS04 based on Model IV (univariate). The difference was expressed as proportion to the phenotypic least squares mean of body weight (output from ASReml) to obtain the genetic change in percentage units.

3. Results

3.1. Descriptive statistics

After two generations of selection, the phenotypic mean for the low and high input lines increased from 67.8 g to 129.0 g and from 61.2 g to 113.1 g, respectively (Table 2). The standard deviation for harvest weight in Table 2 indicates the presence of a large variation within line and generation. The average survival rate was 58% for low input line and 45% for high input line. These values may be underestimates because the losses include both dead fish and missing fish due to tag losses (2%–11% of the total number of fish stocked).

3.2. Estimation of phenotypic and genetic parameters

The heritability (h^2) and common full-sib effect (c^2) obtained when analyzing data from each spawning season by line combination separately are shown in Table 3. The h^2 for harvest weight ranged from 0.36 to 0.71 with large standard errors (0.15 to 0.28). The estimated c^2 (Table 3) obtained from the high input line were more variable (0.02 to 0.21) compared to c^2 from the low input line (0.05 to 0.12).

Table 4 shows the estimated genetic parameters from univariate analysis across spawning seasons and lines from the four different models. The h^2 estimated from these four models ranged from 0.15 to 0.41 and the c^2 from 0.19 to 0.21 (Table 4). The highest h^2 was estimated from Model I (0.41 ± 0.04), whereas the lowest was from Model II (0.15 ± 0.04). The genetic correlations between harvest weight in both input lines obtained from the bivariate analyses from the four different models varied from 0.74 to 0.84 (Table 4). Again, Model I gave the highest estimate for genetic correlation (0.84 ± 0.15), whereas the lowest was obtained from Model IV (0.74 ± 0.21).

The plots of genetic trend and estimated environmental effects for Model I to Model IV from the univariate analyses are presented in Fig. 1. From the plots of Model IV (Fig. 1g, h), there was a clear positive trend of the pond effects from SS02 to SS04 and a lower genetic trend compared to Model I (Fig. 1a, b). Plots from the other two models (Fig. 1c, d, e, f) also showed positive environmental trends across spawning seasons, and the magnitude of the genetic trends were intermediate between Model I and Model IV.

Table 4
Estimates for heritability (h^2), maternal and common environmental effect (c^2) for harvest weight across spawning seasons and lines from univariate and genetic correlation (r_g) between harvest weight in low and high input lines from bivariate models.

Model number (additional fixed effects)	Univariate		Bivariate
	h^2 (s.e)	c^2 (s.e)	r_g (s.e)
I (Pond)	0.41 (0.04)	0.21 (0.02)	0.84 (0.15)
II (Spawning season)	0.15 (0.04)	0.19 (0.02)	0.83 (0.35)
III (Pond + Spawning season)	0.19 (0.04)	0.19 (0.02)	0.82 (0.36)
IV (Pond * Spawning season)	0.20 (0.04)	0.19 (0.02)	0.74 (0.21)

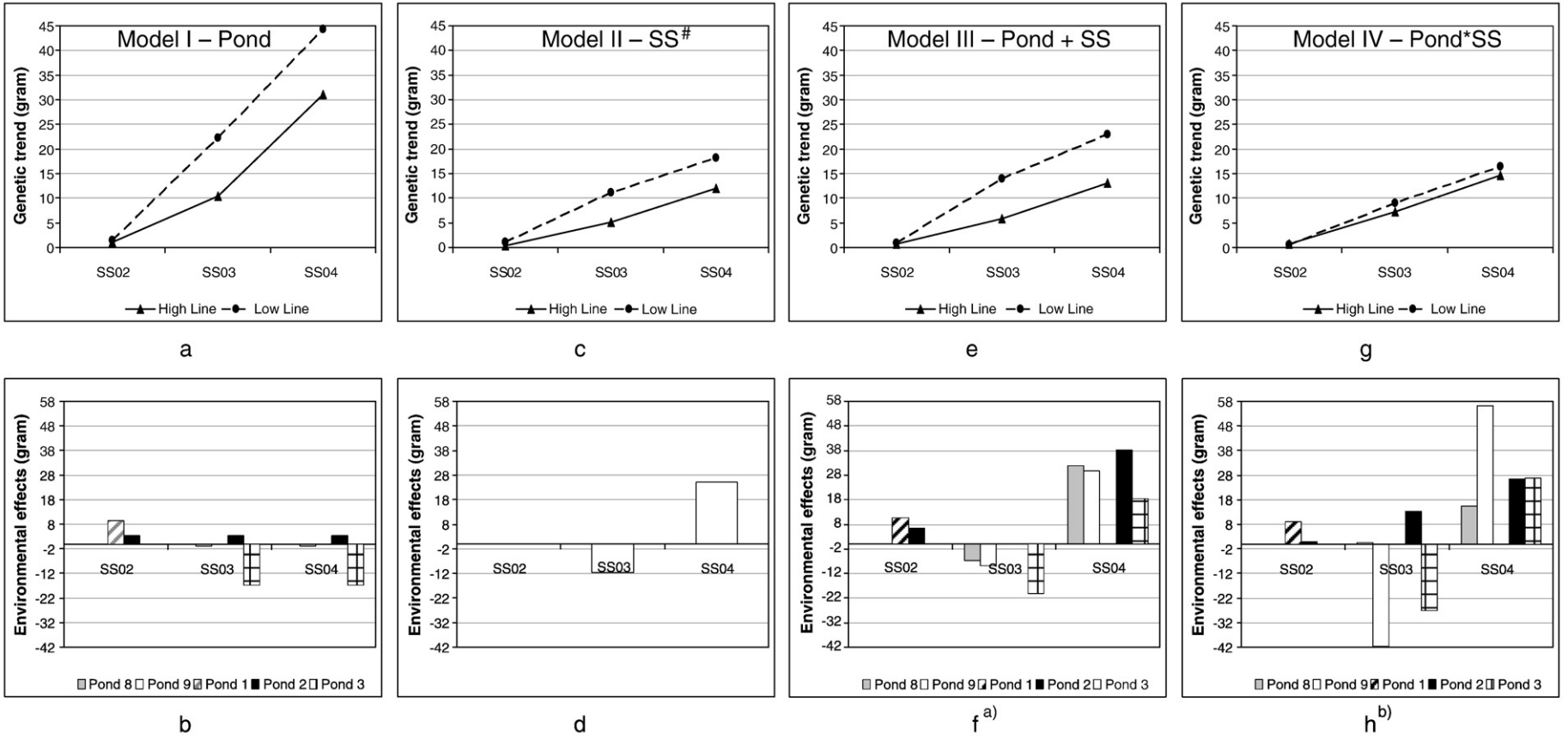

Fig. 1. The genetic trend (a, c, e, g) and estimated systematic environmental effects (b, d, f, h) for harvest weight under univariate analyses. #SS is spawning season effect, a)effects given are (Pond + Season), and b)effects given are (Pond * Season).

The selection response on harvest weight estimated based on the EBVs from Model IV, after two generations of selection, was 7.9 g per spawning season for the low input line and 7.0 g per spawning season for the high input line

4. Discussion

The results from the present study indicated substantial improvement of weight at harvest in both lines. However, this might be partly due to genetic change as well as environmental factors. In Fig. 1, the plots of systematic environmental effects for Models II (Fig. 1d) and IV (Fig. 1h) suggest that the environment improved with time. Comparing the plots from Models I (Fig. 1a, b) and IV (Fig. 1g, h), suggests the presence of confounding between genetic and environmental effects. In this case, genetic change is mainly confounded with spawning season. Although with non-overlapping generations design there is difficulty in separating genetic and environmental effects even when fitting an animal mixed model, h^2 estimated from the four different univariate analyses (0.15–0.41) were still within the range of estimates published in literature (0.24 by Gall and Bakar (1999), 0.20 by Gall and Bakar (2002), 0.26 by Rutten et al. (2005), 0.34 by Ponzoni et al. (2005), and 0.32 by Maluwa et al. (2006)).

The h^2 estimated from the joint univariate analyses across spawning seasons were lower than those estimated within spawning season and line. With a discrete generations design, the connection between generations is mainly through parent–offspring ties. This kind of genetic ties may not be strong enough to effectively separate the environmental from the genetic contributions to performance as suggested by Maluwa et al. (2006). The present study supports this suggestion and it is clearly illustrated by the plots in Fig. 1.

Other than the animal model approach, overlapping generations (Blair and Pollak, 1984; Gall et al., 1993; Ollivier, 1999; Maluwa et al., 2006) and the use of an unselected control line (Blair and Pollak, 1984; Gall et al., 1993; de Rochambeau et al., 1998) are two common approaches used to separate genetic and environmental effects. Both approaches have advantages and disadvantages in terms of their application in fish breeding.

The overlapping generations design has the advantage of enabling the estimation of genetic and environmental effect without the need of maintaining a control line (Gall et al., 1993). This is mainly due to fact that by repeat mating of some sires and dams across generations stronger genetic ties between generations are established (Blair and Pollak, 1984; Ollivier, 1999; Maluwa et al., 2006). However, the difficulty lies in the reproduction of repeat mating sires and dams in subsequent generations. Cryopreservation of sperm or stripping of males and females coupled with in-vitro fertilization methods may overcome the problem, but in any case will be costly and requires skillful technicians. In the present study the intention was to establish overlapping generations but due to mortality, tag losses and difficulties in reproduction of aged fish, the plan did not succeed.

In the unselected control line approach, the usual assumption is that both control and selected lines will be equally affected by environmental changes (Rye and Gjedrem, 2005). Consequently, any difference between two such lines should solely reflect the genetic trend (Rye and Gjedrem, 2005). When both lines are jointly analyzed, the animal mixed model is able to separate the environmental and genetic effects, thus providing a reliable means of estimating selection response. In fish breeding, especially when repeated mating of breeders is difficult, having an unselected control line is easier in term of application and maintenance compared to an overlapping generations design. However, the disadvantage is that the effective population size of the control population has to be relatively large in order to prevent changes due to genetic drift (Gall et al., 1993). Having a large population size for a control line may be deemed not cost effective in some instances by both the research and the commercial sectors, for example the breeding company and farmers. The control line will be competing for space and other resources with the selection line(s).

The estimated c^2 from all the models were in agreement with those reported in other Nile tilapia breeding programs (0.15 by Ponzoni et al. (2005), 0.14–0.21 by Charo-karisa et al. (2006), and 0.21 by Rutten et al. (2005)). A more uniform rearing environment for the fry before the communal rearing would reduce the magnitude of c^2 (Charo-Karisa et al., 2006; Maluwa et al., 2006), but the maternal effects may still be there via egg size and initial mouth brooding for Nile tilapia.

We used Model IV to estimate selection response for harvest weight. We consider this a conservative estimate as we suspect that part of the selection response ended up in the pond by spawning season interaction estimates. Both low and high lines gave very encouraging responses after two generations of selection. However, it should be realized that an unknown degree of confounding between genetic and environmental effects may have caused the estimated responses to deviate upwards or downwards from the true value of the responses.

Several G×E studies on Nile tilapia have been carried out in Asian countries. In Malaysia, a study was carried out to investigate the growth performance of GIFT in two main culture environments, namely, earthen ponds and cages. The study (unpublished authors' results) shows that the genetic correlation for harvest weight between ponds and cages is 0.70 ± 0.11. Eknath et al. (2007) studied G×E for growth performance of the GIFT strain in seven different environments encompassing a range of farming systems and agro-climatic regions in Philippines. Harvest weight expressions in all the environments were positively correlated with each other, and the genetic correlations ranged from 0.36 to 0.99. From the finding of Eknath et al. (2007), the correlations are generally high within the same culture environment (within ponds: 0.76 to 0.99; within cages: 0.99), but are lower and more variable between pond and cage environments (0.36 to 0.82). These results illustrate the notion that the greater the difference between environments, the greater the chance of finding an important G×E. This concept is supported by a recent G×E study with GIFT by Luan et al. (2008) in Vietnam, where the genetic correlation for harvest weight in brackish and freshwater systems was 0.45 ± 0.09.

Robertson (1959) suggested that when the genetic correlation between the trait expression in two different environments was greater than 0.8 the G×E could be considered unimportant. Mulder et al. (2006) concluded that for genetic correlations between two environments of less than 0.7 to 0.8, optimal genetic gain will be achieved by having two environment-specific breeding programs. This strategy is however less appropriate when one of the environments in question has a relative importance of less than 10 to 20% (Mulder et al., 2006). In present study, the genetic correlation for harvest weight between low and high input environments ranged from 0.74 to 0.84 (with high standard error). By taking the lower limit of these estimates, the genetic correlation is smaller than 0.8, which, following Robertson's and Mulder's conclusions would indicate that two different selection programs would be required. Note however, that, for instance, if the selection program were conducted in the low input environment, the genetic correlation indicates that at least 74% of the gain would be captured in the high input environment. Due to the fact that Egypt is a developing country with limited resources, in this situation justifying having two breeding programs for one species would be difficult. In such circumstances, the decision should be made weighing the statistical evidence on GxE, the likely future evolution of the environmental conditions, and economic aspects of the country in question in relation to resources available for genetic improvement programs (Montaldo, 2001).

5. Conclusion

It should be realized that with data from discrete generations and without a control line, even a completely specified animal mixed

model may still suffer from limitations in separating the genetic and environmental effects. The phenotypic and genetic parameters can be estimated from this kind of design but estimates from different models may vary, and result in over- or under-estimating the heritability and genetic correlation. To appropriately address the problem of confounding between genetic and environmental effects, an understanding of the biology of the system and of the limitations of the applied statistical procedures is essential.

The analyses conducted suggest no significant evidence of a G × E interaction large enough to be a serious limiting factor in these production systems. The results could be different if more contrasting environments were involved, as was the case in the G × E study of Nile tilapia in brackish and freshwater environments (Luan et al., 2008). As commented by James (2008), there are no universally applicable rules on how to handle G × E. Therefore, every breeding program should be treated based on its nature and actual situation in the country in question, in addition to the statistical evidence.

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