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Genetic Variances, Heritability and Traits Association of Early Maturing Maize Hybrids under Induced Drought at Seedling and Flowering Stages

S. A. Adewale [a] and R. O. Akinwale [a*]

[a] *Department of Crop Production and Protection, Obafemi Awolowo University, Ile-Ife, Osun State, Nigeria.*

Authors' contributions

This work was carried out in collaboration between both authors. Authors SAA and ROA conceived, designed and executed the study and as well drafted the manuscript. Author SAA collected the data, performed the statistical analysis, and wrote the first draft. Authors SAA and ROA critically reviewed the manuscript. Both authors read and approved the final manuscript.

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ABSTRACT

Aims: Information on traits association and inheritance are crucial to designing appropriate breeding strategies for improving maize production and productivity in drought-prone ecologies. The objectives of this study were to investigate inter-trait relationships among maize hybrids and estimate genetic variances and heritability of drought tolerance parameters under seedling and flowering drought conditions.

Methodology: Sixty-six single cross hybrids generated using diallel mating design plus nine hybrid checks were evaluated using a 5 x 15 alpha lattice and randomized complete block designs in three replicates on the field and in the screenhouse respectively, during 2015 cropping season. Data were collected on grain yield, ears per plant, anthesis-silking interval, seedling aspect, chlorophyll content and leaf area and these data were subjected to analysis of variance as well as correlation and path coefficient analyses.

**Corresponding author: E-mail: akinrichie2002@yahoo.com;*

Results: Significant mean squares (*P* = .05) were observed for all measured traits except leaf area and shoot fresh weight. Narrow-sense heritability estimate for grain yield was moderate (33.4%) on the field and low (0 – 25%) for all the seedling traits. The low narrow-sense heritability estimates observed for most seedling traits implied that the scope for improvement of these traits in the genotypes is limited. Seedling traits under drought stress were not directly correlated with grain yield on the field except number of dead leaves relative to the total number of leaves. Results of the path analysis revealed that number of leaves, number of dead leaves and chlorophyll content under the screenhouse conditions had significant direct effects on grain yield on the field.

Conclusion: Number of leaves, and chlorophyll content under drought at seedling stage could therefore be used as indicator traits for grain yield improvement in maize exposed to drought stress at flowering stage.

Keywords: Drought; heritability; genetic variance; path analysis; maize hybrids; screenhouse conditions.

1. INTRODUCTION

“Maize is an important staple food, animal feed and industrial crop in sub-Saharan Africa (SSA). The savannas of the sub region offer ideal environments for maize production because they are characterized by high solar radiation, low night temperatures, low incidence of pests, and diseases. Over 85% of the population of people in the rural areas in Africa grows maize due to its suitability in diverse farming systems and its ability for increased yield under improved management practices as compared to other cereal crops” [1]. Auta et al. [2] recommended that “the development and accelerated deployment of maize hybrids would increase maize yields in the major maize producing countries of West and Central Africa”. Studies have demonstrated that “hybrids can increase farmers’ maize yields by more than 40% in favourable growing environments and by more than 30% even under stressful conditions” [3].

Drought is a major constraint in boosting maize production in Africa especially in the SSA, coupled with other abiotic stresses it has resulted in maize displacement by high value crops to marginal areas [4]. “Drought exerts its effects on yield through its effects on physiological processes, and through losses in plant stand when such stress occurs during emergence and at the seedling stage. The extent of grain yield reduction in maize due to drought stress depends on the stage of crop development at the time of the stress and its severity. However, the flowering period in maize is the most sensitive to drought. The most economically feasible and sustainable way to boost maize production and productivity in SSA is to develop drought tolerant varieties for the farmers. Earlier studies conducted in the rainforest agro-climatic zone showed that maize planted early significantly out-yielded those planted later in the season primarily because grain filling coincided with the period of relatively high incident solar radiation” [5]. Maize plants with excellent adaptive response to drought at seedling stage will help in combating the effect of early season drought in the rainforest agro-ecology of southwestern Nigeria. Therefore, the evaluation of maize crop at the seedling stage is an important aspect of crop breeding program with the objective to evolve drought tolerant varieties. Developing specific maize genotypes which can tolerate drought at seedling stage, especially in southwestern Nigeria where the rainfall pattern is bimodal, will offer the farmers in this region the opportunity of planting maize earlier in the year (that is, late February to early April), immediately after the first few rains and by extension West Africa. Therefore, development of high yielding cultivars that combine tolerance to drought at both seedling and flowering stages could be a coping strategy to combat detrimental effects of climate change on maize production and productivity in the sub-region.

“Grain yield is a complex trait and it is collectively influenced by various component traits, besides being polygenically inherited and highly influenced by environmental variation. The appropriate knowledge of interrelationships between grain yield and its contributing components can significantly improve the efficiency of breeding programs using appropriate selection indices” [6]. In making selection for improved genotypes in maize, yield is the primary trait but selection under drought based on grain yield alone is inefficient due to low heritability of grain yield and the complexity of genotype-environment interactions [7]. “Genetic variance and heritability of maize grain yield are reduced under drought whereas secondary traits have relatively high genetic variance and heritability" [8,9]. However, the relative usefulness of secondary traits as indirect selection criteria for grain yield is often inconclusive for all experiments because of the nature of the genetic materials and different conditions of experiments [10]. In the past years, the use of secondary traits with grain yield in making selection has increased selection breeding efficiency in maize grown under stress conditions by 20 to 50% [11, 12]. Badu-Apraku et al. [13] reported that the most reliable traits for selection for improved grain yield under drought stress in the early maturing germplasm were ear aspect, ears per plant, anthesis-silking interval, and plant aspect. There is dearth of information on reliable seedling drought traits for predicting improved grain yield under flowering drought conditions.

"Correlation analysis helps to measure the level of relationships among traits and to establish the level at which these traits are mutually different" [14]. "Path coefficient analysis helps to know the nature, extent and direction of selection; it is the most valuable tool commonly used to establish the exact relationships in terms of cause and effect, identifying the direct, indirect and total (direct plus indirect) causal effects, as well as to remove any spurious effect that may be present" [15]. Studies had reported that tolerance to drought stress at seedling stage and at flowering stage has no relationship, using correlation analysis [16]. However, correlation analysis, being a bivariate analysis only detect linear relationships between two variables while it assumes no significant influence of interrelationship of other variables. Therefore, the use of multivariate techniques such as path coefficient analysis, which considers the effect of several independent traits on a target (dependent) trait by partitioning the total correlation into direct and indirect effects (effects exerted through other independent variables) is necessary. In such analysis, traits with significant direct effect on a target trait are identified while those with indirect effect through other traits are also detected. Information obtained from such analysis is more important than mere correlation and would not only help in identifying important secondary traits that could be used as indirect selection criteria for improving maize genotypes for a desired trait, but will provide adequate information useful to formulate base index which will in turn improve the efficiency of selection for the target trait.

The primary objectives of this present study were to (i) estimate genetic variance and heritability of traits for drought tolerance at seedling and flowering stages of maize hybrids; and (ii) investigate the inter-trait relationships under seedling and flowering drought stress conditions, using simple correlations and path co-efficient analyses.

2. MATERIALS AND METHODS

2.1 Generation of Crosses

Twelve inbred lines were planted in breeding nursery in a single-row plot, 5 m long at a spacing of 0.75 m x 0.25 m. Standard agronomic practices were employed to ensure good crop stand. At flowering, the twelve inbred parents were crossed in a diallel fashion to generate 66 single-cross hybrids. The different crosses were harvested separately, processed and packaged into trials for evaluation.

2.2 Field Performance Evaluation

Drought stress at flowering stage was achieved in the field. The experiment was conducted at the Crop Science Unit of the Teaching and Research Farm, Obafemi Awolowo University, Ile Ife ($7^{0}28^{'}$N $4^{0}33^{'}$E, 244 m, 1200 mm rainfall) during the 2015 cropping season. The planting was done on the 21st September, such that flowering could coincide with a period of no rainfall (drought). A trial composed of the sixty-six (66) single cross hybrids plus nine checks was laid out using a 5 x 15 alpha lattice design with three replications. Each entry was planted into a single-row plot, 5 m long with 0.75 m spacing between rows and 0.50 m spacing between plants within a row. Three seeds were sown per hole and later thinned to two plants per hill to attain a population density of 53,333 plants ha^{-1}. A compound fertilizer of NPK 15:15:15 was applied at the rates of 60 kg N, 60 kg P and 60 kg K_2O ha^{-1} at two weeks after planting. An additional 60 kg N ha^{-1} was also applied as side dressing at four weeks after planting using urea (46% N). On each plot on the field, data were collected on days to anthesis, days to silking, number of ears per plant (EPP), plant and ear heights. Plant aspect was rated on a scale of 1 to 9, where 1 = excellent overall phenotypic appeal and 9 = poor overall phenotypic appeal. Ear aspect was scored on a scale of 1 to 9, where 1 = clean, uniform and large ears and 9 = rotten, variable and small ears. Stay-green characteristic (leaf death score) was scored per plot at 70 days after planting, on a scale of 1 to 9, where 1 = almost all leaves green and 9 = virtually all leaves dead. Harvested ears from each plot were shelled to determine the percentage grain moisture. Grain yield in kg ha^{-1} was adjusted to 15% moisture content and computed from the shelled grain weight.

2.3 Screenhouse Evaluation

Drought stress at seedling stage was imposed in the screenhouse. The sixty-six single-cross hybrids plus nine hybrid checks were planted under drought stress imposed at the seedling stage at the screen house, Department of Crop Production and Protection, Obafemi Awolowo University, Ile Ife in 2015. The trial was laid out in a randomized incomplete block design with three replications. Six seeds of each inbred were sown per pot. The methodology proposed by Akinwale et al. [17] for screening maize genotypes for tolerance to drought at seedling stage was adopted, water was applied to each pot at the rate of 0.6 litres daily for 7 days, after which watering stopped. Data were collected at two-day intervals from 3 days after watering had stopped (DAWS) till 9 DAWS on the following: plant height, number of leaves, number of dead leaves, leaf length and breadth, leaf area, and number of dead leaves relative to the total number of leaves (RDL) in percentage. In addition, seedling aspect was scored on a scale of 1 to 9, where 1 = absence of visible symptoms of stress: vigorous plants, no wilting, no dead leaves, no chlorosis, no height reduction and unrolled turgid leaves and 9 = total collapse or 100% death of seedlings, dried leaves and stem, as described by Akinwale et al. [17].

2.4 Data Analysis

Data collected were subjected to analysis of variance using PROC general linear model (GLM) procedure of Statistical Analysis Software (SAS), version 9.2 [18]. In the analysis, genotype was considered as a random factor and to achieve that, random statement option in GLM was used. Genetic variances were estimated using Proc Varcomp procedure of SAS. Estimate of narrow-sense heritability was performed as the proportion of additive variance over phenotypic variance expressed in percentage and this was done on plot mean basis for all traits under the two study conditions. In addition, path coefficient analysis was carried out to partition total correlation among traits into direct and indirect effects considering grain yield as the dependent variable. Pearson correlation (phenotypic correlation) was first calculated and then the correlation coefficients were partitioned into direct and indirect effects through path coefficient analysis using PATHSAS program developed by Cramer et al. [19].

3. RESULTS AND DISCUSSION

Results of analysis of variance (ANOVA) showed significant (*P* = .05) differences among the genotypes for all seedling traits evaluated in the screenhouse except leaf area and fresh shoot weight (Table 1). Similarly, significant (*P* = .05) effects were observed for genotype for all measured traits under stress conditions on the field (Table 2). The significant mean squares observed among the genotypes under the different stress conditions indicated presence of wide genetic variability within the genetic materials, which implies that genetic progress could be achieved from selection for improvement for drought tolerance at both growth stages. The coefficients of variation (CVs) associated with the stressed environments are usually higher and the coefficients of determination (R^2) lower than those associated with the non-stressed environments. Thus, CVs of less than 30% was obtained only for seedling aspect score, chlorophyll content and plant height under seedling drought conditions and for all traits measured under flowering drought conditions except ear aspect. In addition, the proportion of variation explained by the ANOVA model (R^2) is greater than 50% for chlorophyll content, dry shoot weight and number of dead leaves and greater than 60% for all the flowering drought traits, indicating the reliability of the model.

The additive variance measures the variation due to the average effects of alleles (additive effects) and the variation in the effects that are transmitted from one generation to another while the dominance variance is the variance due to interaction of average effects of alleles (dominance effects) [20]. The dominance variance is a function of allele frequencies and the level of dominance. In our present study, the additive variance was greater than non-additive (dominance) variance for all traits except number of ears per plant under the flowering drought conditions (Table 3). In contrast, the dominance variance was greater than the additive variance for all traits under the seedling drought conditions, which implied that tolerance to drought involves different genes or combination of genes depending on the stage at which the drought set in the crop cycle. Estimates of additive genetic variance were significantly different from zero for all traits under field drought conditions and for all traits under the screenhouse conditions except seedling aspect, dry shoot weight and fresh shoot weight. Dominance variances were significantly different from zero for all measured traits except seedling fresh shoot weight. Due to negative estimates, additive variance of dry shoot weight and dominance variance of fresh shoot weight were equated to zero. Thus, their dominance to additive genetic variance ratio could not be estimated. The dominance to additive genetic variance ratios were greater than 0.5 for four out of the eight traits under drought at the flowering stage and for seven out of the nine traits under seedling drought conditions.

Narrow-sense heritability estimate for grain yield was moderate (33.4%). The values of narrow-sense heritability for the traits ranged from 7.3% for ears per plant to 50% for plant height under drought at flowering and 0.38% for fresh weight to 25% for number of leaves under seedling drought conditions. Heritability estimates provide information on how probable a trait could be transmitted from parents to their offspring [20]. Low narrow-sense heritability estimate observed for most measured traits, especially under drought at seedling stage is an indication that the scope for improvement of these traits in the parents is limited. However, it might be desirable to increase the number of replications and locations to increase the accuracy of estimated entry means, and thus the heritability.

Adequate knowledge on the inter-relationship among traits is important in designing effective selection programs for crop improvement. Results showed that seedling traits were not directly correlated with grain yield except number of dead leaves relative to the total number of leaves which displayed significant negative relationship (Table 4). Ears per plant showed significant negative relationship with number of dead leaves and number of dead leaves relative to the total number of leaves. This implied that a hybrid with high number of dead leaves under drought at seedling stage will possibly give lower number of ears harvested per plot under drought conditions at flowering. Plant aspect had significant negative relationship with leaf area, number of leaves, shoot fresh weight and shoot dry weight. This suggests that maize hybrids under drought stress at seedling stage with high number of leaves, leaf area, shoot fresh weight and shoot dry weight would give rise to plants with excellent physical appearance under the same condition at flowering stage. In addition, stay green characteristic showed significant positive relationship with number of dead leaves and number of dead leaves relative to the total number of leaves. Though some of the seedling drought traits were found to be significantly correlated with traits taken on the field under flowering drought conditions, the strength of the relationships was generally low. Therefore, the results of this study showed that seedling drought tolerance traits cannot be used as the main criteria for predicting grain yield in the hybrids under flowering drought conditions. This corroborates the findings from the study of Meeks et al. [16] who reported that the seedling drought conditions were independent of drought responses at flowering on the field, possibly due to the type of screening environments used and the high genetic diversity that segregated for traits conditioning drought tolerance. Even though low values of correlation coefficients (r) were obtained, *r* measures only linear relationship, which path analysis helps to decompose among the studied characters, thereby enhancing better interpretation of relationships as well as pattern of the effects of one trait on the other.

An important objective of this study was to identify seedling drought traits with greatest influence on grain yield for use in future breeding programs. Thus, the correlation coefficients of the seedling drought traits with grain yield were further partitioned into direct and indirect effects through path analysis (Table 5). The low residual effect (0.25) indicates that the seedling traits altogether contributed substantially to grain yield. Among the seedling traits, path analysis identified number of leaves (0.294), and number of dead leaves (-0.242), chlorophyll content (0.052) as traits with significant direct contributions to grain yield, whereas number of leaves had the highest direct effect. This result was not surprising since leaf synthesizes the photosynthates, which are stored in plant tissues and culminate in yield for the crop. Number of leaves was related to the number of photosynthetic components such as chloroplasts and therefore an increase in the number of leaves improves photosynthetic capacity. Path coefficient analysis showed that number of seedling leaves was the most important trait for grain yield improvement through its direct and indirect effects on grain yield. Number of leaves, relative number of dead leaves to the total number of leaves is contributing indirectly to the

Table 1. Mean squares of seedling aspects and other seedling traits of 66 hybrids plus 9 checks evaluated under induced drought at seedling stage at the screen house, 2015

SV	Df	Seedling aspect score	Chlorophyll content (μmol L^{-1})	Plant height (cm)	Leaf area, (cm^2)	Number of dead leaves	Number of leaves	RDL	Fresh shoot weight (g)	Dry shoot weight (g)
Rep	2	12.20**	25.39	102.09**	90.15	5.32	39.66	854.30	9.07**	0.16*
Entry	74	1.83*	55.62**	29.04*	94.20	10.00**	55.56**	717.58**	0.26	0.05**
Error	148	1.27	16.39	19.34	79.73	3.17	35.91	416.36	0.26	0.03
R^2		0.46	0.63	0.45	0.37	0.62	0.44	0.47	0.49	0.53
CV		20.65	11.95	18.61	40.84	37.11	30.95	41.90	50.95	41.68

***significant at 0.05 probability level, ** s**ignificant at 0.01 probability level*
RDL = number of dead leaves relative to the total number of leaves

Table 2. Mean squares for grain yield and other agronomic traits of 66 hybrids plus 9 hybrid checks evaluated under drought at flowering stage, at the teaching and research Farm Obafemi Awolowo University, Ile Ife, 2015

Source of variation	Df	Grain yield	Ears per plant	Plant aspect	Ear Aspect	Anthesis - silking interval	Plant height	Ear height	Stay green characteristics
Block (Replicate)	12	652613.3**	0.16**	6.91**	5.64**	9.55**	1223.52**	388.68**	3.99**
Replicate	2	977096.1**	0.47**	9.76**	21.63**	9.75**	2628.29**	882.79**	13.26**
Genotype	74	318140.3**	0.112**	2.24**	2.73**	4.69**	455.57**	162.38**	2.17**
Error	136	120633.0	0.06	0.77	1.59	1.65	124.48	50.26	0.93
R^2		0.68	0.62	0.75	0.63	0.71	0.79	0.75	0.68
CV		27.26	33.22	15.35	16.7	31.69	11.35	16.35	16.3

**significant at 0.05 probability level, ** significant at 0.01 probability level*

Table 3. Additive ($\hat{\sigma}^2{}_A$) and non-additive ($\hat{\sigma}^2{}_{NA}$) variances, narrow-sense heritability estimates (h^2), for grain yield and other agronomic traits of hybrids generated from diallel crosses evaluated under terminal drought in the field and under imposed drought in the screen house

Traits	$\hat{\sigma}^2{}_A$ ± SE	$\hat{\sigma}^2{}_{NA}$ ± SE	$\hat{\sigma}^2{}_{NA}$ /$\hat{\sigma}^2{}_A$	h^2 (%)
Flowering drought environment				
Grain yield	40465.76±3512.730	36639.40±2026.930	0.91	33.4
Ears per plant	0.02±0.001	0.02±0.001	1.00	7.3
Plant aspect	0.35±0.030	0.22±0.020	0.63	35.7
Ear aspect	0.53±0.040	0.06±0.020	0.11	46.0
Anthesis-silking interval	0.90±0.070	0.37±0.030	0.41	45.0
Plant height	99.55±7.380	30.60±2.590	0.31	49.9
Ear height	17.70±1.590	13.58±1.010	0.77	31.1
Stay green characteristic	0.436±0.030	0.20±0.020	0.45	44.0
Seedling drought environment				
Seedling aspect	0.002±0.010	0.140±0.015	61.670	0.39
Chlorophyll content	3.154±0.390	15.270±0.360	4.840	17.0
Plant height	2.000±0.240	2.080±0.230	1.040	18.7
Leaf area	1.520±0.540	4.970±0.910	3.270	4.3
Number of dead leaves	0.412±0.070	2.080±0.060	5.060	11.6
Number of leaves	6.870±0.690	12.200±0.500	1.770	25.0
RDL	5.320±1.190	30.060±1.630	5.650	7.6
Fresh weight	0.001±0.001	0±0.003	0	0.38
Dry weight	0±0.0002	0.011±0.001	0	0.0

Table 4. Pearson correlation of traits evaluated under drought induced at the seedling at the screenhouse, faculty of agriculture and under drought at flowering stage at the teaching and research Farm, Obafemi Awolowo University, Ile Ife, 2015

		Traits under drought at flowering stage							
		Anthesis-silking interval	**Ears per plant**	**Plant height**	**Ear height,**	**Plant aspect**	**Stay green characteristics**	**Ear aspect**	**Grain yield,**
Traits under drought at seedling	Number of dead leaves	0.15*	-0.15*	0.07	0.03	0.01	0.30**	0.17**	-0.07
	Leaf area	0.02	0.08	0.06	0.02	-0.14*	-0.08	-0.02	-0.02
	RDL	0.14*	-0.18**	-0.03	-0.06	0.11	0.28**	0.24**	-0.14*
	Number of leaves	0.06	-0.11	0.11	0.10	-0.18**	0.09	0.05	0.12
	Seedling aspect	0.02	-0.13	-0.03	-0.05	0.12	0.13	0.07	-0.02
	Chlorophyll content	0.06	0.07	-0.09	-0.03	0.08	0.05	-0.03	0.09
	Shoot fresh weight	-0.03	0.03	0.10	0.08	-0.20**	-0.12	-0.09	0.04
	Shoot dry weight	-0.09	0.09	0.17**	0.16**	-0.22**	-0.10	-0.11	0.06

***significant at 0.05 probability level, ** s**ignificant at 0.01 probability level*

Table 5. Estimates of direct (diagonal values in bold) and indirect (off-diagonal values) effects based on path analysis of yield attributing characters on grain yield, evaluated under drought induced at the seedling stage in the screenhouse, and under drought that coincided with flowering stage

	Seedling height	**Number of dead leaves**	**Leaf area**	**RDL**	**Number of leaves**	**Seedling aspect**	**Chlorophyll content**	**Shoot fresh weight**	**Shoot dry weight**
Seedling height	**-0.051**	-0.055	0.003	0.001	0.108	-0.002	-0.005	-0.006	-0.018
Number of dead leaves	-0.011	**-0.242**	0.001	0.149	0.169	0.003	0.001	0.006	-0.002
Leaf area	-0.021	-0.023	**0.008**	-0.007	0.069	-0.001	-0.009	-0.005	-0.020
RDL	0.000	-0.183	-0.003	**0.196**	0.035	0.003	-0.001	0.005	0.005
Number of leaves	-0.019	-0.139	0.002	0.023	**0.294**	0.001	-0.001	-0.001	-0.013
Seedling aspect	0.012	-0.109	-0.001	0.086	0.055	**0.007**	0.006	0.013	0.019
Chlorophyll content	0.005	-0.003	-0.001	0.001	-0.007	0.001	**0.052**	0.002	0.008
Shoot fresh weight	-0.013	0.068	0.002	-0.047	0.008	-0.004	-0.004	**-0.022**	-0.034
Shoot dry weight	-0.013	-0.007	0.002	-0.014	0.052	-0.002	-0.006	-0.011	**0.073**

Residual effect = 0.2517

number of dead leaves. For number of leaves, number of dead leaves recorded the highest indirect effect. Under seedling drought conditions, in our study, number of leaves, chlorophyll content and leaf area were identified as the most important traits contributing to the variation in grain yield, suggesting that they are reliable secondary traits under drought stress conditions. In addition, these traits can be used as criteria for selecting for drought-tolerant genotypes under seedling stress conditions in early maturing maize hybrids. Under the field conditions, the path analysis identified ear aspect (-0.48), ears per plant (0.331), ear height (0.283), plant height (-0.255) and plant aspect (-0.219) as traits with the highest direct effect on grain yield (Table not shown). These results are similar with those of Badu-Apraku et al. [9], who identified plant and ear aspects and plant and ear heights as the most reliable traits for the simultaneous selection in the extra-early inbreds for improved yield under low-N and drought stress environments.

4. CONCLUSION

There was narrow genetic base for seedling drought tolerance traits in the early-maturing maize germplasm studied and this might limit the scope of improvement of the traits under drought stress. In addition, low additive variances and heritability estimates were obtained for most traits. Number of leaves and number of dead leaves under seedling drought stress had the highest direct effects on grain yield under field conditions, indicating that these seedling traits are reliable predictors of grain yield of early maize hybrids.

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COMPETING INTERESTS

Authors have declared that no competing interests exist.

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