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Variance components and heritability of yield and yield components of wheat under drought-stressed and non-stressed conditions

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Abstract

This study estimated the variance components and heritability of yield and yield related traits of a population of 96 diverse bread wheat genotypes under drought-stressed and non-stressed conditions. The genotypes were evaluated across eight testing environments during the 2014/2015 and 2015/2016 growing seasons using an alpha lattice design with two replications. Combined analysis of variance and variance components were analysed following the General Linear Model (GLM)'s procedure. Results indicated the presence of significant effects of genotypes, seasons, sites, and water regimes and their interactions. From the eight testing conditions, high levels of genotypic variance ($\sigma2g$) were estimated for spike length (73%), number of spikelets per spike (44.19%), plant height (51.26%), number of kennels per spike (32.98%), number of days-to-heading (44.24%) and thousand seed weight (22.98%), resulting in high broad-sense heritability estimates of > 0.50. Conversely, genotypic variation was relatively moderate for the number of days to maturity, grain yield and number of productive tillers per plant, contributing to 15.03%, 8.46% and 6.13% of the total variation, respectively. The heritability estimates of the later traits were $20\% \le H2 < 50\%$ which may limit their selection gains under drought-stressed environments. Further, quantitative trait loci analysis and progeny testing are required to discern the number of genes and associated genetic effect and to pinpoint genomic regions in the tested wheat genetic resources for effective breeding for drought tolerance.

Keywords: drought stress; heritability; variance components; wheat; yield components.
Abbreviations: DTH_days to 50% heading; PH_plant height; TN_number of productive tillers; DTM_days to maturity; SL_spike length; SPS_number of spikelets per spike; KPS_number of kennels per plant; TSW_thousand seed weight; GY_gain yield.

Introduction

Global wheat (*Triticum aestivum.* L; 2n=6x=42, AABBDD) production and productivity is challenged by periodic drought and heat stresses associated with climate change (Alexandratos and Bruinsma, 2012; Daryanto et al., 2016). A decreasing trend is witnessed in the total production area and productivity of wheat and other long cycle cereal crops under dryland production conditions globally (Simelton et al., 2012; Lesk et al., 2016). This has been attributed to the combined effects of biotic and abiotic constraints, mainly drought and heat stresses (Jha et al., 2014). Wheat is a C3 crop that is sensitive to drought stress and high temperature conditions, especially during the post-anthesis growth stages, when the crop is often faced by erratic rainfall and prolonged dry spells (Alain et al., 2011; Ilker et al., 2011). Breeding wheat cultivars with drought and heat tolerance is considered to be an economic and sustainable drought mitigation strategy, notably under low input farming systems in sub-Saharan Africa (Kotir, 2011). Suitable genetic resources with complementary drought adaptive traits are required to speed-up breeding of wheat cultivars that are better adapted to marginal rainfall conditions (Manes et al., 2012). Consequently, various national and international wheat improvement programs mainly the International Maize and Wheat Improvement Center (CIMMYT) are developing candidate wheat germplasm with considerable abiotic and biotic stress tolerance for breeding or direct production through rigorous evaluations under the target production environments.

Grain yield of wheat is a complex trait consisting of various components such as the number of productive tillers per plant, number of spikelets per spike, number of kernels per spike and grain weight. Other complementary traits affecting yield response include the number of days- to-heading and -maturity, plant height and spike length (Lopes et al., 2012; Slafer et al., 2014). Partitioning of the effect of genotype (g), environment (e) and g x e interaction (GEI) provides reasonable estimates of their relative contribution to phenotypic variation during selection. Genotype x environment interaction leads to differential response of genotypes due to polygenic effect and the influence of the growing environment (Hall, 2000; Sanchez-Garcia et al., 2012; Rad et al., 2013). This requires evaluation of diverse candidate genotypes across representative testing environments to select promising lines for further breeding or for cultivar recommendation. Selection response for grain yield can be achieved through direct or indirect selection of yield components, which have complementary effects, contributing to enhanced crop productivity.

The magnitudes of genetic variance components and heritability affect selection response of a trait (Falconer and Mackay, 1996). Heritability is the proportion of genetic variation to the total phenotypic variation, which is one of the useful parameters to estimate the likelihood of genetic gain after selection in a given population and environment. Further, heritability values estimate the likelihood of tracing genes or quantitative trait loci (QTL) affecting particular traits. Several studies have attempted to estimate the heritability of important economic traits that directly affect yield response in wheat, particularly under drought-stressed and non-stressed conditions (Aycicek and Yildirim, 2006; Eid, 2009; Abdolshahi et al., 2015). Aycicek and Yildirim (2006) reported heritability estimates as low as 2.07%, 1.01%

and 0.1% for days-to-heading, plant height and grain yield, respectively, due to high genotype by environment interaction. Heritability estimates are specific to the test population or individuals evaluated under the prevailing environments. Therefore, heritability values should be determined in a given breeding population to estimate the response to selection.

In an attempt to select drought tolerant wheat genotypes, diverse germplasm were acquired from CIMMYT. These genetic resources were found to be tolerant to drought and heat stresses. The lines were screened for drought tolerances based on phenotypic and proline analyses (Mwadzingeni et al., 2016b). The germplasm needs to be further evaluated for genetic worthiness and selection response towards improved grain yield and it component traits. Improving these traits will allow selection of lines with high breeding values under the prevailing growth conditions to maximize their genetic potential for drought tolerance breeding or for direct production since the currently cultivated wheat genotypes are vulnerable to recurrent droughts. Therefore, the objective of this study was to determine variance components and heritability of yield and yield related traits of 96 diverse bread wheat genotypes under drought-stressed and non-stressed conditions.

Results

Influence of genotypes, water regimes, seasons and testing environments on trait variability

Table 1 summarises the combined analysis of variance (ANOVA) for the studied traits. Highly significant differences ($P < 0.01$) were observed among the main effects of the genotype, site, season and water regime for most of the studied traits. The number of days-to-heading and number of productive tillers per plant is non-significantly affected by the water regime; while thousand seed weight was non-significantly affected by seasonal variability. Most of the interaction effects were significant ($P < 0.05$). Grain yield response was not affected by the genotype by site, genotype by season, genotype by site by water regime and genotype by site by season by water regime interactions.

Variance component analysis and heritability estimates

The variance component estimates for the nine phenotypic traits of the 96 wheat genotypes evaluated across the two test sites in two seasons under two water regimes are presented in Table 2. Generally marked genotypic variation existed among the studied traits, except for the number of days to maturity, number of productive tillers and grain yield that were considerably influenced by the environment. The mean values of traits, the least significant differences (LSD) and the coefficient of variation (CV) were presented by Mwadzingeni et al. (2016b). Spike length, number of spikelets per spike, plant height, number of kennels per spike, number of days-to-heading and thousand seed weight had moderate to high genotypic variances (σ^2_g) of 73%, 44%, 51%, 32.98%, 44.24% and 22.98%, respectively, largely due to genotypic differences, hence, had high heritability estimates above 50% (Table 2). Moderate heritability values ($20\% \geq H^2 < 50\%$) were observed for the number of days-to-maturity (47.29%), grain yield (38.93%) and number of productive tillers per plant (28.83%). For the later traits, much of the variation was explained by the residual component (σ^2_e) as compared to the interactions of the genotype by other components. Variation in grain yield (σ^2_g =8.46) was considerably influenced by the genotype by environment interaction.

Discussion

Global climate change presents a major threat to wheat production and productivity, particularly due to increased drought frequencies and intensities, hence, the need to breed drought tolerant and better adapted varieties for the changing environments (Budak et al., 2013). Possibly, the susceptibility of modern wheat varieties to water stress is magnifying the effects of drought on the crop's poor production and productivity under severe drought-stress condition. Achievement of significant genetic advances from phenotypic selection is hindered by the differential responses of genotypes to target test or production environments. This study partitioned variance components and estimated their influence on heritability values of yield and yield related traits in a set of candidate wheat germplasm. The lines were selected from CIMMYT pre-breeding nurseries for drought and heat tolerance and found to be useful for drought tolerance breeding (Mwadzingeni et al., 2016b). The significant genotypic differences ($P < 0.001$) observed for the studied traits reflects that the germplasm pool from which the sampled lines were selected contains a broad genetic base (Table 1). Some of these genetic resources could, therefore, be useful in breeding the locally cultivated varieties to marginal growing conditions. Significant differences due to the water regime observed on all traits except days-to-heading is expected since drought stress is known to negatively affect yield and its components (Fischer and Maurer, 1978). Water stress is reported to influence tissue elongation, resulting to reduced plant height and spike length (Moayedi et al., 2010; Sanjari Pireivatlou and Yazdansepas, 2010). The non-significant effect ($P > 0.5$) of water regime on the number of days-to-heading was expected since the genotypes were stressed at 50% heading. Drought stress shortens the grain filling period, resulting in a significant reduction of the number of days-to-maturity, which could explain the significant differences, observed among genotypes due to water regimes (Kilic and Yagbasanlar, 2010). Shortening of effective grain filling period may result in shriveled kernels and; hence, reduced seed weight with a subsequent yield penalty. It is also worth noting that genotype by water regime interaction had non-significant effects on the number of days-to-maturity, as well as on spike length and number of spikelets per spike, which could explain the capacity of respective genotypes to maintain their rankings under different water regimes. The high influence of the environment on the phenotypic variation for the number days-to-maturity, grain yield and number of productive tillers indicate the existence of considerable variation due sites, seasons and water regimes singly or in combinations. Low heritability estimates are reported for polygenic traits studied under varying conditions, particularly involving drought stress (Eid, 2009). The high heritability estimates of spike length (94.61%), number of spikelets per spike (87.28%), plant height (86.33%), number of kennels per spike (78.43%), number of days-to- heading (76.26%) and thousand seed weight (68.15%) may suggest the effect of some major genes or QTL on these traits under both water-stressed and non-stressed conditions.

Table 1. Mean squares and significant tests after combined analysis of variance for nine phenotypic traits of 96 wheat genotypes evaluated in two localities over two seasons, under two water regimes and two replications.

		Traits								
Source	DF	DTH	DTM	PH	TN	SL	SPS	KPS	TSW	GY
Genotype (Gen)	95	344.606***	199.43***	728.957***	3.115***	18.549***	30.677***	331.134***	186.037***	8631.239***
Gen*Site	95	37.272***	47.964***	49.566***	0.465ns	0.451***	2.597***	25.188ns	55.38***	2045.785ns
Gen * Season	95	67.301***	80.449***	81.983***	1.582***	0.756***	3.604***	55.57***	33.155***	3345.954***
Gen * Water Regime (WR)	95	8.825ns	18.368ns	40.419***	1.634***	0.243ns	1.572ns	43.257***	26.791**	4066.003***
Gen*Site * Season	95	25.616***	30.912*	32.934*	0.498ns	0.521***	2.993***	21.728ns	40.848***	2262.287*
Gen*Site * WR	95	7.54ns	14.1ns	32.462*	0.362ns	0.308ns	1.919ns	23.443ns	19.081ns	1425.247ns
Gen * Season * WR	95	10.547ns	21.376ns	30.266ns	1.148***	0.196ns	1.565ns	39.592***	26.725**	2726.462***
Gen*Site * Season * WR	95	10.113ns	20.717ns	24.678ns	0.444ns	0.343ns	1.66ns	26.342ns	20.469ns	2010.68ns
Site	1	16318.39***	128214.9***	6164.719***	341.128***	604.201***	3546.493***	86899.79***	775.639ns	3342901***
Season	1	2405.143***	5077.068***	6955.221***	0.048ns	214.505***	3018.38***	419.758***	932.91***	26429.13***
WR	1	42.684ns	6628.792***	7762.736***	455.257***	7.053***	82.78***	4992.579***	6887.799***	1922719***
Error	760	9.584	22.542	25.384	0.648	0.279	1.717	26.483	20.056	1755.159

DTH days to 50% heading, DF degrees of freedom, PH plant height, TN number of productive tillers, DTM days to maturity, SL spike length, SPS number of spikelets per spike, KPS number of kennels per plant; TSW thousand seed weight, GY gain yield, * $P < 0.05$ (2-tailed), ** $P < 0.01$ level (2-tailed), *** $P < 0.001$ level (2-tailed), ns non-significant.

Table 2. Variance components for nine phenotypic traits of 96 wheat genotypes evaluated in two localities over two seasons, under two water regimes and two replications.

	Traits																	
	DTH		DTM		PH		TN		SL		SPS		KPS		TWS		GY	
Component	Var	%	var	%	var	%	var	%	var	%	var	%	var	%	var	%	var	%
Genotype (Gen)	16.58	44.24	6.16	15.03	39.27	51.26	0.06	6.13	1.12	73.00	1.75	44.19	16.77	32.98	8.74	22.98	229.09	8.46
Gen*Site	1.78	4.75	2.97	7.24	1.11	1.44	0.01	0.58	0.00[1]	0.00[1]	0.00[1]	0.00[1]	0.80	1.58	2.00	5.26	46.97	1.73
Gen*Season	5.17	13.79	6.13	14.95	5.44	7.10	0.05	4.67	0.05	3.12	0.09	2.25	2.60	5.11	0.00[1]	0.00[1]	45.48	1.68
Gen*Water regime (WR)	0.11	0.28	0.45	1.11	0.00	0.00[1]	0.07	6.91	0.01	0.65	0.00[1]	0.00[1]	0.83	1.63	0.18	0.47	248.40	9.17
Gen*Site*season	3.89	10.37	2.56	6.25	2.07	2.70	0.01	1.36	0.05	2.93	0.34	8.54	0.00[1]	0.00[1]	5.24	13.77	63.59	2.35
Gen*Site*WR	0.00[1]	0.00[1]	0.00[1]	0.00[1]	1.95	2.54	0.00[1]	0.00[1]	0.00[1]	0.00[1]	0.07	1.67	0.00[1]	0.00[1]	0.00[1]	0.00[1]	0.00[1]	0.00[1]
Gen*Season*WR	0.11	0.29	0.17	0.41	1.40	1.83	0.18	17.23	0.00[1]	0.00[1]	0.00[1]	0.00[1]	3.37	6.63	1.62	4.25	186.21	6.87
Gen*Site*Season*WR	0.27	0.71	0.00[1]	0.00[1]	0.00	0.00[1]	0.00[1]	0.00[1]	0.03	2.15	0.00[1]	0.00[1]	0.00[1]	0.00[1]	0.21	0.56	133.86	4.94
Residual	9.58	25.57	22.54	55.02	25.38	33.13	0.65	63.10	0.28	18.15	1.72	43.36	26.49	52.08	20.06	52.72	1755.16	64.80
Total variance	37.48	100.00	40.97	100.00	76.61	100.00	1.03	100.00	1.54	100.00	3.96	100.00	50.85	100	38.04	100.00	2708.76	100.00
Phenotypic variance (V*p*)	21.74		13.03		45.49		0.21		1.18		2.01		21.38		12.83		588.40	
Heritability (H^2)	0.76		0.47		0.86		0.29		0.95		0.87		0.78		0.68		0.39	
Heritability (%)	76.26		47.29		86.33		28.83		94.61		87.28		78.43		68.15		38.93	

DTH days to 50% heading, PH plant height, TN number of productive tillers, DTM days to maturity, SL spike length, SPS number of spikelets per spike, KPS number of kennels per plant; TSW thousand seed weight, GY gain yield, Var variance, [1]the value was negative.

Table 3. Partial analysis of variance and expected mean squares among 96 selected bread wheat genotypes evaluated in two sites, two seasons, under two water regimes using two replications.

Source of variation	Degrees of freedom	Expected mean square
Genotype (g)	g – 1	$\sigma^2_e + r\sigma^2_{gwls} + rw\sigma^2_{gls} + rs\sigma^2_{glw} + rl\sigma^2_{gsw} + rwl\sigma^2_{gs} + rls\sigma^2_{gw} + rsw\sigma^2_{gl} + \sigma^2_g$
Site (l)	l – 1	–
Season (s)	s – 1	–
Water regime (w)	w – 1	–
gl	(g – 1)(l – 1)	$\sigma^2_e + r\sigma^2_{gwls} + rw\sigma^2_{gls} + rs\sigma^2_{glw} + rsw\sigma^2_{gl}$
Gs	(g – 1)(s – 1)	$\sigma^2_e + r\sigma^2_{gwls} + rl\sigma^2_{gws} + rw\sigma^2_{gls} + rwl\sigma^2_{gs}$
Gw	(g – 1)(w – 1)	$\sigma^2_e + r\sigma^2_{gwls} + rl\sigma^2_{gws} + rs\sigma^2_{glw} + rsl\sigma^2_{gw}$
gls	(g – 1)(l – 1)(s – 1)	$\sigma^2_e + r\sigma^2_{gwls} + rw\sigma^2_{gls}$
glw	(g – 1)(l – 1)(w – 1)	$\sigma^2_e + r\sigma^2_{gwls} + rs\sigma^2_{glw}$
gws	(g – 1)(w – 1)(s – 1)	$\sigma_e^2 + r\sigma^2_{gwls} + rl\sigma^2_{gws}$
glws	(g – 1)(l – 1)(w - 1)(s - 1)	$\sigma^2_e + r\sigma^2_{gwls}$
Replication within water regime, seasons and sites	lws (r – 1)	–
ME_e	lws (g – 1)(r - 1)	σ^2_e

σ^2_e environmental variance, σ^2_g genotypic variance, σ^2_{gl} genotype by site interaction variance, σ^2_{gs} genotype by season interaction variance, σ^2_{gw} genotype by water regime interaction variance, σ^2_{gls} genotype by site by season interaction variance, genotype by site by water regime interaction (glw), σ^2_{gws} genotype by water regime by site interaction variance, σ^2_{gws} genotype by site by water regime by season interaction, r replication.

Previous studies identified some of the major QTL encoding for functional genes that control most agronomic traits in wheat under drought-stressed conditions (Spielmeyer et al., 2007; Mathews et al., 2008; Li et al., 2015; Mwadzingeni et al., 2016a). Some of the genetic components affecting plant height could also influence spike length since the two traits are highly correlated, and both have high heritability estimates (Mwadzingeni et al., 2016b). Owing to the high heritability estimates observed in this study, association mapping based on the studied set of germplasm and traits could probably identify genetic determinants influencing these traits under contrasting environments. Moderate heritability values (20% > H^2 < 50%) that were observed for the number of productive tillers (28.83%), number of days-to-maturity (47.29%) and grain yield (38.93%) could also reflect the presence of some major or minor genes and QTL controlling these traits (Table 2). The results from this study concurs with the findings of Abdolshahi et al. (2015) who reported high heritability estimates for several morphological traits of wheat evaluated under drought-stressed and non-stressed conditions, including plant height (79%), thousand seed weight (85%) and days to flowering (85%), and moderate heritability for grain yield (45%).

Grain yield is a polygenic trait that is highly influenced by the environment under drought-stressed condition; hence, the moderate heritability estimate of this trait was expected. Genetic gains in grain yield is achieved through selection of component traits. Selection for highly heritable traits that positively correlate with other quantitative traits enhances the efficiency of selection (Shimelis and Shiringani, 2010). Heritability for grain yield was estimated at 38.93% which is in agreement with the moderate value of 45% reported by Abdolshahi et al. (2015). However, the heritability estimates obtained in this study are higher than moderate and low values (H^2 < 50%) reported by Yagdi and Sozen (2009) from a set of durum wheat genotypes tested under different environmental conditions. This confirms that heritability values are subject to the particular set of genotypes being evaluated and the target testing environments. Such differences in a set of populations and test environments could explain variable heritability estimates for similar key traits obtained in various studies (Eid, 2009; Mohsin et al., 2009).

The tested germplasm pool is a vital source of genetic variation for drought tolerance breeding. The lines exhibited high levels of genotypic and phenotypic variability for the studied traits. Under the test environments, selection based on the studied traits can result in significant genetic advances for drought tolerance owing to high heritability values. The number of days-to-maturity, number of productive tillers per plant and grain yield showed moderate heritability values. The tested wheat germplasm are useful genetic resources which will be shared among wheat breeding programs in sub-Saharan Africa to exploit their genetic variation and potential for drought adaptation across marginal rainfall growing environments. It is recommended to explore the variability existing within the germplasm through molecular markers, quantitative trait loci (QTL) analysis or progeny testing to pinpoint the number of genes and their gene action for effective breeding for drought tolerance.

Materials and Methods

Plant materials and study site

Ninety-six diverse bread wheat genotypes comprising of 88 lines that were received from CIMMYT's heat and drought tolerance nurseries and eight locally grown drought-susceptible cultivars were evaluated in this study. These genotypes were targeted since they were pre-bred specifically to concentrate drought tolerance traits and their performance under stress conditions experienced locally had not been explored. The list of genotypes, their sources and pedigrees are summarized by Mwadzingeni et al. (2016b). The experiments were conducted at the University of KwaZulu-Natal (UKZN), Ukulinga Research Farm that is located at latitude 29° 40' S and longitude 30° 24' E; and at an altitude of 806 meters above sea level. Concurrent greenhouse experiments were carried out at UKZN's greenhouse facilities. The day/night temperatures in the greenhouse were maintained at $30^oC/20^oC$, and the humidity was kept in the range of 45% to 55%. Field testing conditions during the study period were summarized by Mwadzingeni et al. (2016b).

Experimental design and data collection

Genotypes were evaluated across eight testing environments during the December 2014 to April 2015 and December 2015 to April 2016 growing seasons using an alpha lattice design with two replications. Test genotypes were evaluated under two contrasting water regimes involving drought-stressed and non-stressed conditions, where post-anthesis drought stress was imposed from 50% heading to maturity through withholding irrigation until the moisture content dropped to 35% of the field capacity based on tensiometer readings. Plot of 1.5 m long rows were used. Under the greenhouse experiments, seven plants were raised in five litre capacity plastic pots filled with composited pine bark media. Standard agronomic practices recommended for wheat production in the areas were followed. Data on nine agronomic traits were collected from each experiment. These included the number of days from sowing to heading (DTH) which were recorded when 50% of the spikes had extruded above the flag leaf. The number of productive tillers per plant (TN) was determined by counting tillers with spikes that had successfully set seeds. Plant height (PH) was measured from the ground level to the tip of the spike in centimeters at maturity using a meter rule. Days-to-maturity (DTM) were counted from sowing to the day when 50% of the peduncle had turned yellow or dried. The spike length (SL) was measured in centimeters using a 30 cm ruler after harvesting. This was followed by counting of the number of spikelets per spike (SPS) and the number of kennels per spike (KPS). Lastly, thousand seed weight expressed in gram 1000^{-1} seeds from a randomly sampled kernels (TSW) and grain yield per plot (GY) were determined by weighing the seeds in grams (g) on a digital scale.

Data analysis

Combined analysis of variance and variance components were analyzed following the General Linear Model (GLM)'s variance component analysis procedure of Agrobase (Agrobase, 2005) and GenStat® version 17, VSN, International (Payne, 2014) by considering the seasons and water regimes as fixed factors, while the genotypes and sites were treated as random factors. Negative variances were adjusted to zero (Robinson et al., 1955; Borojevic, 1990). Partial analysis of variance and expected mean of squares (EMS) were calculated following Borojevic (1990), Gordon et al. (1972) and Shimelis and Shiringani (2010) as presented in Table 3. The broad sense heritability (H^2) estimates were calculated from the phenotypic variance (σ^2_p) and the genotypic variance (σ^2_g) according to Allard (1999) as;

$$H^2 = \sigma^2_g / (\sigma^2_g + \sigma^2_{gwls} / wls + \sigma^2_{gls} / ls + \sigma^2_{glw} / lw + \sigma^2_{gsw} / sw + \sigma^2_{gs} / s + \sigma^2_{gw} / w + \sigma^2_{gl} / l + \sigma^2_e / rlsw) = \sigma^2_g / (\sigma^2_g + \sigma^2_{gxe} / e + \sigma^2_e / re) = \sigma^2_g / \sigma^2_p.$$

Conclusion

The tested germplasm pool is a vital source of genetic variation for drought tolerance breeding. The lines exhibited high levels of genotypic and phenotypic variability for the studied traits. Under the test environments, selection based on the studied traits can result in significant genetic advances for drought tolerance owing to high heritability values. The number of days to maturity, number of productive tillers per plant and grain yield showed moderate heritability values. The tested wheat germplasm constitutes a useful resource which could be used by wheat breeding programs in sub-Saharan Africa to exploit their genetic variation and potential for drought adaptation across marginal rainfall growing environments. It is recommended to explore the variability existing within the germplasm through molecular markers, QTL analysis or progeny testing to pinpoint the number of genes and their gene action for effective breeding for drought tolerance through population structure analysis and marker trait association studies.

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