Path analysis of genotype × environment interactions in rainfed durum wheat

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Introduction

The development of high-yielding cultivars requires a thorough knowledge of the existing genetic variation for yield and its components (Shukla et al., 2006). Grain yield is a result of the combined effects of genotype, environment, and their interaction. The importance of the genotype × environment (GE) interaction is that it causes different reactions of genotypes when they are grown in different environments. The efficiency of a breeding program depends mainly on the direction and magnitude of the association between yield and its components and also the relative importance of each factor involved in contributing to grain yield (Agrama, 1996). The GE interaction is induced by differential responses of genotypes to environmental factors present during the development for component traits (Ehdaei et al., 1999).

Environmental stresses that occur during the sequential development of yield components constitute the major ingredients of GE interaction of yield. Several researchers (Ehdaei et al., 1999; Grafius, 1969; Lynch & Tai, 1989; Tai, 1975; Tai et al., 1994; Thomas et al., 1971) presented the concept of a sequential developmental process of yield components. Tai (1971) developed a statistical model based on the path analysis approach (Wright, 1934), which has been used successfully to study GE interaction of yield and its components for a set of genotypes evaluated in a range of environments. There are two important assumptions of the model: (i) the chronological sequence in the development in yield components is X1 to X2 to X3 to X4 and yield, Y, is final multiplicative product of sequential development process i.e. $Y = X1 \times X2 \times X3 \times X4$; and (ii) the environmental response can be separated into independent groups i.e. R1, R2, R3, and R4, where each group supports the development of a component trait. The path analysis method has been used to investigate GE interaction in potato under water stress (Lynch & Tai, 1989) and heat stress conditions (Tai et al., 1994) and in wheat under different level of nitrogen (Ehdaei et al., 1999).

The main objectives were to (i) study GE interaction for grain yield and its components in durum wheat under diversified rainfed environments and (ii) identify superior genotypes to environmental constraints in the highland rainfed conditions of Iran.
To study the relationship between yield and the components of yield, the model proposed by Tai (1975) was used. The causal relationship between the grain yield and its four components is diagrammed in Figure 1. The multiplicative product of the yield components resulted in total yield. The $u_1, u_2, u_3, \text{and } u_4$ are the path coefficient from $R_1$ to $X_1$, $R_2$ to $X_2$, $R_3$ to $X_3$, and $R_4$ to $X_4$, respectively, and $a_1, a_2, \ldots, a_9$ are the path coefficients between $X_1, X_2, X_3, X_4, \text{and } Y$.

The path coefficients which measure directly the effects of $R_1, R_2, R_3, \text{and } R_4$ on yield ($Y$) can be determined by calculating at first the products of path coefficients along each of the possible compound paths connecting the $R$'s to yield ($Y$) and then adding up the products of all the compound paths from $R_1, R_2, R_3, \text{or } R_4$ to $Y$.

The model separates environmental components into independent groups and estimates their contribution to the development of individual component traits. In Tai’s model, the yield of the $i\text{th}$ genotype ($i = 1 \ldots l$) in the $j$th environment ($j = 1 \ldots m$) is composed of a mean genotypic effect, $\mu$; four multiplicative terms of the GE interaction formed by four genotypic components, $v_1i, v_2i, v_3i, \text{and } v_4i$; four environmental components, $r_1j, r_2j, r_3j, \text{and } r_4j$; and an experimental error, $e_{ij}$. It can be expressed as:

$$Y_{ij} = \mu + v_1i r_1j + v_2i r_2j + v_3i r_3j + v_4i r_4j + e_{ij}$$

The environmental components are measured in standard deviation units and genotypic components represent the efficiency of the genotype to utilize one standard unit input of the four environmental components during the ontogeny of yield development. The genotypic components are estimated by path analysis (Wright, 1921). The environmental components are then estimated by least squares using the observed yields and estimates of the genotypic components. For details see Tai (1975). The validity of the path analysis model to represent the observed results was assessed by the degree of correlation between observed and fitted data of each of the genotypes for each of the traits. This was carried out by calculating correlation coefficients between observed and fitted data.
data for individual genotypes across three replicates over three seasons. Shukla’s (1972) stability variance was estimated based on grain yield for each genotype. The yield stability information was then used to compare the results of the genetic and environmental component estimates of the GE interactions.

## Results

### Variance components

The results of combined ANOVA for grain yield and its components are given in Table 1. Highly significant differences (p < .01) were observed among genotypes, environments and GE interaction effects for yield and its components (Table 1). Depending on trait, the environments accounted for the 64.1–99.6% of total sum of squares (SS), followed by GE interaction which captured .4–24.1% and genotype accounted for .05–18.0%. This indicates that for all traits, the environment accounted for most of the variation followed by GE and genotype effects. The linear regression of GE interaction accounted for 2.5–18.2% of GE interaction variation, depending on trait, whereas the residual of the variation around regression slope explained 81.8–97.5% of variation. Large portion of GE interactions was due to a non-linear component which can be regarded as a very important parameter for selection of stable genotypes.

The mean, minimum, maximum, and coefficient of variation (CV%) for yield and its components (X1, X2, X3, and X4) also are presented in Table 1. The mean yield for genotypes was 1542 kg ha⁻¹ and ranged from 1289 to 1969 kg ha⁻¹ across 21 environments. The values for DTH (X1) varied from 191 to 197 days, for DTM (X2) ranged from 220 to 224 days, for PLH (X3) was varied from 57.9 to 83.8 cm and for 1000-TKW (X4) varied from 30.4 to 37.3 g across 21 environments. The coefficient of variation (CV%) was the least for components X2 followed by X1

### Estimates of genotypic components of GE interaction

The genotypic components of GE interaction for 25 tested genotypes are presented in Table 2. The validity of the estimations was verified by the high correlation between observed and fitted yields of individual genotypes. The correlations between observed mean yields and the values fitted by the model for 25 genotypes was high except for genotype G24, although was significant (r = .50; p < .01). This genotype was late in flowering, had the highest PLH, and low yield productivity. The genotype G25 (bread wheat old variety) gave the highest mean yield across environments. The breeding lines G8, G2, and G3 were in the group of second highest yield. Old durum variety (G24) and breeding lines (G18, G19) were poor in yield productivity.

The range of component $v_1$ was larger than those of $v_2$, $v_3$, and $v_4$. Thus, the genotypes showed more varied responses to the environmental stresses for the flowering time which is the most important trait under rainfed condition. All genotypes showed negative estimates of $v_1$ component, indicating all genotypes used a negative unit of this component to escape from terminal drought and heat stresses. Breeding lines G2 and G9 had the highest value for $v_1$, indicating early flowering had the highest impact in yield productivity of these promising durum wheat breeding lines and, in contrast, this component with $v_1 = −0.077$ had the least impact on yield productivity of old bread wheat cultivar (G25). In contrast to $v_1$, the all genotypes showed positive estimates of $v_3$ and $v_4$, thus the yield productivity of all genotypes was positively more influenced by $v_3$ and $v_4$ components. Breeding lines G2 and G9 had the

| Source       | df  | MS          | %§ | MS          | % | MS          | % | MS          | % | MS          | % | MS          | % |
|--------------|-----|-------------|----|-------------|---|-------------|---|-------------|---|-------------|---|-------------|---|
| Genotype     | 24  | 393,304**   | 2.5| 46.9**      | .3| 15.6**      | 0 | 1027.7**    | 18| 80.0**      | 10.2| 1027.7**    | 18|
| Environment  | 20  | 15,187,400**| 81.2| 97.8**      | 99.6| 4400.5**    | 64.1| 615.4**     | 65.7| 615.4**     | 65.7|
| GE          | 480 | 127,016**   | 16.3| 5.2**       | 6.3**| 4.7         | 23.1**| 18.2       | 51.2**| 17.9       | 9.4**| 17.9       | 9.4**|
| Linear       | 24  | 278,359**   | 11.4| 19.09**    | 8.7| 21.3**     | 18.2| 185.7**   | 18.1| 185.7**    | 18.1| 185.7**    | 18.1|
| Deviation    | 456 | 119,051     | 8.9| 9.53         | 95.3| 4.4       | 81.8| 44.1      | 81.9| 9.6       | 97.5| 9.6       | 97.5|
| Total        | 524 |             |    |             |    |             |    |           |    |           |    |           |    |
The breeding lines G8, G2, and G3 had slightly lower mean yields than G25 but with lower \( \nu_1 \) and higher \( \nu_4 \) estimates. The new cultivar (G22) had moderate mean yield and moderate estimates of the four genotypic components. In contrast, G2 and G25 were the only two genotypes showing a high level of responses to all genotypic components of the GE interaction except for \( \nu_4 \) component. However, their reactions to the first and fourth environmental components were in opposite directions.

The genotypes G18, G14, G23, G4, and G2 with the lowest stability variance values were stable, while the genotypes G25 followed by G24, G3, G17, and G15 with the highest stability variance were unstable (Table 2). Correlation coefficients were calculated between mean yield and the four genotypic components of the GE interactions and stability variance (Table 3). Mean yield and stability variance were significantly correlated (\( r = .397; p < .05 \)), indicating a positive trend between high yielding and stability performance in genetic materials. Stability variance negatively correlated with \( \nu_1 \) component and positively with \( \nu_4 \) component, indicating the importance of plant stature and kernel weight components in stabilizing grain yield across diverse environments. An interesting result was the highly positive correlation between the \( \nu_1 \) and \( \nu_4 \) indicating early in flowering which resulting in increasing kernel weight. The negative correlation between \( \nu_1 \) and \( \nu_2 \) showing that earlier in flowering essentially not resulting

### Table 2. Mean grain yield, genotypic components of GE interaction, and stability variance for 25 genotypes across 21 rainfed environments, and correlation coefficients between observed and fitted data for each of the genotypes.

| Code | Type | Mean grain yield (kg/ha) | \( \nu_1 \) | \( \nu_2 \) | \( \nu_3 \) | \( \nu_4 \) | \( \sigma^2 \times 10^{-4} \) | Correlation Coefficient |
|------|------|--------------------------|------------|------------|------------|------------|-------------------|-------------------------|
| G1   | Breeding line | 1476bcde | -371 | .307 | .701 | -1.149 | 27.1 | .79** |
| G2   | Breeding line | 1676b   | -715 | .471 | .61 | -1.173 | 25.2 | .76** |
| G3   | Breeding line | 1648b   | -5   | .354 | .528 | -1.012 | 39.6 | .62** |
| G4   | Breeding line | 1418bcd | -338 | .366 | .666 | .014 | 23.9 | .72** |
| G5   | Breeding line | 1546bcd | -489 | .368 | .716 | -0.053 | 27.0 | .78** |
| G6   | Breeding line | 1475bcd | -385 | .284 | .65 | -0.093 | 26.1 | .72** |
| G7   | Breeding line | 1594bc  | -382 | .28 | .61 | -0.17 | 28.7 | .71** |
| G8   | Breeding line | 1690b   | -466 | .192 | .598 | -1.148 | 25.4 | .69** |
| G9   | Breeding line | 1529bcd | -715 | .482 | .613 | -0.098 | 25.6 | .72** |
| G10  | Breeding line | 1407bcd | -465 | .266 | .64 | -2.22 | 27.2 | .79** |
| G11  | Breeding line | 1559bcd | -54  | .315 | .553 | -2.18  | 35.0 | .73** |
| G12  | Breeding line | 1504bcd | -587 | .322 | .635 | -2.09 | 32.6 | .77** |
| G13  | Breeding line | 1467bcd | -5   | .327 | .463 | -1.76 | 35.6 | .61** |
| G14  | Breeding line | 1590bc  | -39  | .366 | .733 | .031  | 20.2 | .78** |
| G15  | Breeding line | 1623b   | -484 | .299 | .584 | -0.087 | 37.5 | .70** |
| G16  | Breeding line | 1469bcd | -651 | .449 | .642 | -0.096 | 31.6 | .79** |
| G17  | Breeding line | 1509bc  | -541 | .33  | .619 | -1.129 | 38.9 | .77** |
| G18  | Breeding line | 1357cd  | -413 | .359 | .666 | -2.258 | 18.9 | .81** |
| G19  | Breeding line | 1358cd  | -418 | .356 | .745 | -1.32 | 29.3 | .85** |
| G20  | Breeding line | 1538bcd | -218 | .289 | .569 | .032  | 35.2 | .62** |
| G21  | Breeding line | 1507bcd | -133 | .176 | .646 | .077  | 29.0 | .67** |
| G22  | New cultivar | 1506bc  | -561 | .428 | .585 | -1.17 | 33.8 | .75** |
| G23  | Old variety  | 1642bc  | -342 | .267 | .591 | -1.15 | 22.4 | .69** |
| G24  | Old variety  | 1289d   | -216 | .308 | .456 | -0.036 | 50.0 | .53** |
| G25  | Old variety  | 1969a   | -077 | .207 | .514 | .19 | 64.4 | .50** |
| Mean |         | 1542    | -436 | .325 | .613 | -0.094 | 31.6 | .72** |

**Means in same column followed by common letters are not significant based on Duncan’s test at 5% level of probability.

*Significant at \( p = .01 \).
in earlier maturity. The $v_4$ component showed positive correlation ($r = .417; p < .05$) with mean yield, indicating the importance of kernel weight in yield productivity under rainfed condition.

**Estimates of environmental components of GE interaction**

The agroclimatic characteristics, environmental index (EI), and estimates of the 4 environmental components ($r_1, r_2, r_3,$ and $r_4$) of the 21 environments are given in Table 4. The correlations of EI with $r_1, r_2, r_3,$ and $r_4$ were, respectively, $-.118, -.098, -.568,$ and $.085.$ Both $r_1$ and $r_2$ had a much greater absolute sizes than $r_3$ and $r_4$ in most environments. Only in few occasions were the influences of $r_3$ or $r_4$ smaller than or similar to that of $r_1$ and $r_2.$ The $r_3$ component did not show a clear trend that could be associated with the environmental stresses, and the values for $r_4$ were slightly greater than the corresponding values for $r_2, r_3,$ and $r_4.$ Like $r_1, r_2,$ and $r_3$ also did not show a clear trend with environmental stresses, but there was a general trend for $r_4$ which showed a negative values for moderate cold and warm environments (except for I12) and positive values for cold environments (except for A12 and S11). However, the third environmental component was apparently the most influential on grain yield productivity which had a significant negative correlation with the EI ($r = -.568; p < .01$) (Table 5). A moderate correlation ($r = .535; p < .01$) was observed

| Table 4. Agroclimatic characteristics, environmental index, and environmental components of GE interaction for 21 test environments. |
|---|
| Code* | Status | Cropping season | Rainfall (mm) | Temperature (°C) | YLD (kg/ha) | DTH (Day) | DTM (Day) | PLH (cm) | TKW (g) | $r_1$ | $r_2$ | $r_3$ | $r_4$ |
| K11 | MC | 2010–11 | 342.5 | 11.8 | 1840 | 194 | 228 | 78 | 19 | 298 | -.69 | .288 | -.322 | .09 |
| K12 | MC | 2011–12 | 302.9 | 11.0 | 2360 | 181 | 213 | 62 | 25 | 818 | -.554 | .153 | -.219 | .003 |
| K13 | MC | 2012–13 | 394.3 | 13.4 | 774 | 181 | 218 | 48 | 34 | -768 | -.529 | .129 | -.194 | .035 |
| Mean in absolute size | | | 346.6 | 12.1 | 1658 | 185 | 220 | 63 | 26 | | .59 | .19 | .25 | .04 |
| M11 | C | 2010–11 | 351.4 | 5.6 | 1979 | 220 | 252 | 65 | 36 | | .59 | .19 | .25 | .04 |
| M12 | C | 2011–12 | 251.0 | 4.0 | 859 | 217 | 242 | 42 | 31 | | -.363 | .146 | .215 | .014 |
| M13 | C | 2012–13 | 351.1 | 6.4 | 1824 | 210 | 247 | 61 | 32 | | .59 | .19 | .25 | .04 |
| Q11 | C | 2010–11 | 346.6 | 6.6 | 1565 | 220 | 251 | 63 | 29 | | -.206 | -.29 | .185 | .396 |
| Q12 | C | 2011–12 | 313.3 | 6.5 | 788 | 156 | 195 | 43 | 40 | | -.216 | -.750 |** | .477 |
| Q13 | C | 2012–13 | 256.1 | 8.4 | 2708 | 193 | 235 | 74 | 38 | | .049 | -.021 | .555 | -.032 |
| Mean in absolute size | | | 287.7 | 7.9 | 1388 | 206 | 234 | 61 | 34 | | .26 | .2 | .32 | .26 |
| I11 | W | 2010–11 | 384.3 | 13.5 | 3537 | 140 | 170 | 90 | 27 | 1995 | .189 | -.193 | -.729 | .241 |
| I12 | W | 2011–12 | 328.9 | 12.9 | 974 | 121 | 142 | 54 | 37 | | -.542 | -.104 | .049 | -.181 |
| I13 | W | 2012–13 | 396.1 | 13.6 | 2063 | 162 | 192 | 71 | 36 | | -.435 | -.661 | -.045 | .099 |
| Mean in absolute size | | | 369.8 | 13.4 | 2191 | 141 | 168 | 72 | 33 | | .39 | .32 | .27 | .17 |

*Code represent for the environments (combination of location-year). The initial letters in codes are stand for first letter of locations name and numbers of 11, 12 and 13 in environments codes are stand for 2011, 2012 and 2013 cropping seasons. K: Kermanshah; M: Maragheh; Q: Qamloo; U: Uromieh; A: Ardabil; S: Shirvan and I: Ilam. MC: moderate cold; C: cold; W: moderate warm; this classification is based on the regions of Iran, which the locations are located. The locations of Maragheh, Qamloo, Uromieh, Ardabil and Shirvan are located in highland rainfed areas of Iran with winter temperature less than <5 °C, while Kermanshah location is located in moderate cold region of Iran with winter temperature between 5 and 10 °C and Ilam location is located in the warm region of Iran with winter temperature more than 8 °C. EI: environmental index; YLD: mean yield; DTH: days to heading; DTM: days to maturity; PLH: plant height; TKW: 1000-kernel weight.
Discussion

Environmental variations seemed to be of importance in determining performance, and therefore, evaluation based on several years and locations is a necessary strategy to be pursued in the breeding program (Yue et al., 1997). Year-to-year climatic variation has a great impact on the degree of stress experienced by crops, hence the use of testing environments to represent stressed target environments. Since each environment consists of a combination of various factors, in other words, cold and drought stresses that influence adaptation and stability performance, it is difficult to specify all the differences between environments in relation to these factors. (Chapman et al., 1997). High yield of durum wheat under fluctuation environments requires not only high yield in a unique environment, but also the stability of relatively high yield across varied environments. The data from this experiment revealed a trend toward improved yield stability, as evidenced by the correlation of kernel weight and PLh with stability variance of yield. This indicates that the key strategies for yield stability improvement are most likely to be the kernel weight and PLh under rainfed conditions. High yielding breeding lines at warm and moderate cold locations had good tolerance ability throughout the whole stress season especially to terminal drought and heat stresses. The cold stress was more dominant than drought stress at cold locations, as none of the breeding lines did not surpass the bread wheat old variety (a bread wheat cultivar with good tolerance to cold stress and widely adapted to highland rainfed regions of Iran) indicating no genetic gain for cold tolerance in breeding lines compared to this popular cultivar.

The mean yield of five top yielding breeding lines at warm location was 2469 kg ha$^{-1}$ and at moderate location was 1930 kg ha$^{-1}$ and top old variety (G25) at warm and moderate cold locations produced 1884 and 1624 kg ha$^{-1}$, respectively. These results indicated yield improvements equal to 40 and 18% for first five top yielding breeding lines and new cultivar; solid circles: old cultivars.

Table 5. Pearson correlation coefficients between environmental components of mean yield and environmental index.

| Environmental components | EI      | $r_1$ | $r_2$ | $r_3$ | $r_4$ |
|--------------------------|---------|-------|-------|-------|-------|
| $r_1$                    | −.118   |       |       |       |       |
| $r_2$                    | −.098   | −.262 |       |       |       |
| $r_3$                    | −.568** | .298  | .049  |       |       |
| $r_4$                    | .085    | .535**| −.168 | −.044 |       |

**Significant at $p = .01$.**

between the $r_1$ and $r_4$ indicating positive trend between flowering date and grain weight in tested environments. This leads to the conclusion that the impact on yield of this environmental component is associated with the magnitude of the genotypic component. In moderate and warm locations the $r_1$ component which supported the process of flowering was larger in absolute size than $r_2$, $r_3$, and $r_4$ components, while in cold locations the $r_3$ component which represents the plant stature was larger than other three components (Table 4). These results, however, indicate the importance of early flowering ($r_1$) to escape from drought and heat terminal stresses in moderate and warm locations than cold locations. The highest mean yield was obtained in warm (2191 kg ha$^{-1}$) followed by moderate (1658 kg ha$^{-1}$) and cold (1388 kg ha$^{-1}$) locations. In cold locations, the $r_4$ component which supported the process of kernel weight was greater in absolute size than other three components.

Analysis of mean yields in test locations differing in winter temperature (consisting of December, January and February months) revealed a significantly positive association between the yield potential in moderate and warm locations (Figure 2). Therefore, it would be desirable to combine high yield with heat tolerance so that the varieties could be used in both locations with differing winter temperatures. No significant relationship was observed between genotypic mean yield in cold location with those in warm and moderate locations.
lines relative to top old variety (G25) in warm and moderate cold locations, respectively, while under cold stress conditions no yield improvement for breeding lines was observed. This result indicates that the cold stress is the most limiting factor than drought for durum production under highland rainfed conditions of Iran (Mohammadi et al., 2014). This supports this idea that positive genetic gains in breeding programs more limited in environments with more stresses. This agrees with the findings of Ceccarelli (1996), Munoz et al. (1998), Donmez et al. (2001), Voltas et al. (2002) and Pswarayi et al. (2008). However, achieving genetic gains in yield in stressful environments has been recognized to be a difficult challenge for plant breeders, while progress in yield gains has been much higher in non-stressed environments (Richards et al., 2002; Villegas et al., 2007).

The negative $v_1$ values for all genotypes and its values larger than $v_2$, $v_3$, and $v_4$ in absolute size suggests the genotypes showed more divergent responses to the changes in environmental effects influencing flowering than the other components for yield productivity. Variation in $v_1$ values among the genotypes was greatest, followed by $v_2$, $v_3$, and $v_4$, suggesting that genotypic differences in response to rainfed conditions associated more with flowering than other genotypic components. Most genotypes were more sensitive to a unit change of the first environmental component supporting flowering than the other components. These results, accompanied by the fact that the estimates of $r_1$ were larger and more variable than those of $r_2$, $r_3$, and $r_4$ over the environments, lead to the conclusion that the flowering time played a more important role in GE interactions of grain yield than other traits in durum wheat.

Positive association ($p < .05$) between mean yield and stability variance indicated a positive trend between high yielding and stability performance in genetic materials. This relation supports that genotype's performance responds in a consistent fashion to changes in the environments resulting in dynamic stability in genetic materials. This is in agreement with earlier reports on the correlations between mean yield and stability variance (Cross, 1977; Eagles et al., 1977; Eberhart & Russell, 1966; Mühleisen et al., 2014). Stability in grain yield under stress environments could be provided by a better ability of compensation in yield components (Matsuo, 1975). Many researchers have shown that grain yield of wheat depends on several grain yield components in different crop species (Aggarwal et al., 1987; Bansal & Sinha, 1991; Khanna-Chopra & Viswanathan, 1999; Klomsa-ard et al., 2013). This study indicated that kernel weight and flowering provided stability to the breeding lines G3 and G13, whereas plant stature contributed towards the stability of breeding lines G9, G10, G5, and G18.

Our findings clearly indicated that breeding lines as a group were more heat and drought tolerant than old varieties and, in contrast, old varieties were more cold tolerant than breeding lines. The results also clearly indicated that higher grain yields are associated with higher kernel weight ($v_4$), which resulted from early flowering ($v_1$), and so more emphasis should be given to these traits for the improvement of yield in durum wheat under rainfed conditions of Iran. Selection for high value kernel weight resulting from early flowering will enhance yield stability in breeding lines which is a major step towards facilitating the increasing abiotic stress expected from the predicted climate change. In conclusion, path analysis provided a useful picture for understanding GE interaction and grain yield components compensation in rainfed durum wheat, and hence these traits may be taken as indices of selection purposes. The responses of the individual genotypes did not reveal a common structure that would explain genotypic differences in tolerance to environmental stresses. However, the determination of genotypic strategies that maximize tolerance to environmental stresses deserves further research.

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No potential conflict of interest was reported by the authors.

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