



Full Length Article

Evaluating Factors Affecting Cotton Tolerance to Potassium Deficiency Stress using Path Analysis

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ABSTRACT

Plant nutritionists advocate potassium (K) uptake as an essential aspect administering biomass production under K deficiency stress. In this solution culture study, we evaluated twenty-five cotton (*Gossypium hirsutum* L.) genotypes under deficient K (0.3 mm) condition to evaluate factors affecting cotton tolerance to K deficiency stress. For the first time in the literature, path analysis was conducted through structural equation modeling (SEM) methodology to assess the direct and indirect effects of root dry weight (RDW), leaf area (LFA), total K concentration (KCT), K use efficiency (KUE) and total K uptake (KUT) on shoot dry weight (SDW) of cotton under K deficiency stress. The SDW was directly governed by the KUT followed by the KUE, under K deficiency stress, while the direct contribution of LFA was lower than these two. The indirect contribution of LFA to SDW, followed by the RDW and the KCT, was more pronounced than any other plant characters. All the plant characters indirectly affected SDW by directly enhancing KUT. A direct negative effect of the KUE was observed on the KUT. In conclusion, under the K deficiency stress, the efficient cotton genotypes sustained their SDW by displaying enhanced K uptake, due to their well developed photosynthetic apparatus and efficient root system. Thus, breeding programs for developing K-use efficient cotton genotypes under low K supply should involve leaf area and root biomass as important physiological markers.

Key Words: *Gossypium hirsutum* L; K deficiency; K uptake; K-use efficiency; Path analysis; Structural equation modeling

INTRODUCTION

Soils deficient in nutrients are widespread all over the agricultural regions in the world and the developing countries are worse affected, because of their low fertilizer use (Snapp *et al.*, 2002; Rengel & Damon, 2008). Currently, the emphasis has been given to develop nutrient-use efficient genotypes that could perform well under nutrient deficient environments, because of elevating awareness of the bad impacts of chemical fertilizers to the environments, scorching fertilizer prices and increased use of poor quality land (Rengel & Marschner, 2005). Nutrient use efficient genotypes have ability to offer maximum dry matter or yield for each increment of accumulated nutrient (Swaidar *et al.*, 1994).

Nutrient-use-efficiency (NUE) is dependent on two interrelated groups of plant factors: uptake efficiency – nutrient uptake relative to its supply and utilization efficiency – plant yield relative to nutrient uptake or accumulation (Zhang *et al.*, 1999). The differences in nutrient-use-efficiency are attributed to both differential uptake and utilization (Giordano *et al.*, 1982). Plant genotypes vary in their uptake, translocation, accumulation and use of mineral elements (Clark, 1983). Efficient genotypes show enhanced extraction of nutrients from stress

environments and hence are better adapted to nutrient deficiencies (Vose, 1984). Crop cultivars vary in terms of their response to the potassium (K) nutrition (Nawaz *et al.*, 2006; Clement-Bailey & Gwathmey, 2007; Minjian *et al.*, 2007). The ability of plants to uptake and efficiently utilize the K varies widely among inter-and intra-species over a wide range (Glass & Perley, 1980). Crop species possess particular K absorption and utilization mechanisms to maintain high vegetative and reproductive growth (Chen & Gabelman, 1999).

In many studies, K uptake was correlated with biomass production under K deficiency stress (Siddiqi & Glass, 1983a & b; Mengel & Stephen, 1985; Cassman *et al.*, 1989; Gill *et al.*, 1997; Nawaz *et al.*, 2006). The enhanced K uptake under K deficiency stress is an excellent marker to select K-efficient genotypes that could better adapt in low K input agriculture.

For evaluating the nature and magnitude of association between two variables, considered to be interdependent, correlation analysis is used (Steel *et al.*, 1997). Nonetheless, the associations determined through correlation coefficients may be attributed to a number of interdependent variables. Hence, the conclusions drawn exclusively on the basis of correlation coefficients may be misleading, because of the provision of insufficient information in relation to what may

truly be a diverse association between variables (Kang, 1994). Further partitioning of correlation coefficients into direct and indirect effects for a certain set of relationships (Gravois & Helms, 1992) through path analysis can be very helpful to find a casual mechanism lying behind a perceived biological relationship (Kozak *et al.*, 2008). In case two variables are indirectly associated, path analysis helps determine to what magnitude other variables influence the association (McGiffen *et al.*, 1994) and identifies the variables contributing more significance to an observed relationship (Ssango *et al.*, 2004).

The importance of subject matter demands for a serious data analysis to confirm the relative contribution of various factors that enhance the adaptability of cotton under K deficient condition. Such studies may prove beneficial for plant breeders in developing the K-efficient cotton genotypes for low K input agriculture. For this purpose, various advance statistical modeling techniques can be used, such as path analysis through structural equation modeling (SEM) methodology (Zia-ul-hassan & Arshad, 2008).

SEM is a very general, mostly linear and cross-sectional statistical modeling technique, which is largely confirmatory and used to determine the validity of certain model. It involves a structure of the covariance matrix of the measures. After estimating the model's parameters, the resulting model-implied covariance matrix are compared to an empirical or data-based covariance matrix. If the two matrices are consistent with one another, then the structural equation model can be considered a plausible explanation for relations between the measures (Anonymous, 2008).

In this study, we aimed at confirming the hypothesis that K uptake chiefly governs SDW production of cotton and envisages the factors that contribute to SDW directly or indirectly by augmenting K uptake under K deficiency stress.

MATERIALS AND METHODS

The solution culture experiment was conducted in a rain-protected glass house of the Institute of Soil and Environmental Sciences, University of Agriculture, Faisalabad, Pakistan (Latitude: 31°–26' N, Longitude = 73°–06' E, Altitude: 184.4 m). Average temperature, relative humidity and net radiation ranged from 24 to 39°C, 29 to 78% and 6.0 to 14 MJ m⁻² day⁻¹ during the study (Source: Agricultural Meteorology Cell, University of Agriculture, Faisalabad, Pakistan). The experiment involved 25 cotton genotypes, viz. BH-163, Chandi, CIM-473, CIM-496, CIM-499, CIM-506, CIM-707, CRIS-9, Desi okra, FH-2006, Hari Dost, Karishma, NIAB-78, NIAB-824, NIAB-884, NIBGE-2, PB-899, Qalandri, Rehmani, Reshmi, Sarmast, Shahbaz, Shaheen, Sohni and TS-30/2K. The seeds of all the cotton genotypes were germinated in sand and one-week-old comparable plants were transplanted to foam plugged holes of polystyrene thermopore sheets (Ahmad *et al.*, 2001). The twice-replicated experiment was

conducted with four repeats following completely randomized design and the results were pooled. The genotypes were grown in half strength modified Johnson's solution (Johnson *et al.*, 1957), containing deficient level of K (0.3 mm K) for four weeks and harvested. The leaf area (LFA) was recorded using area meter (Delta-T Devices Ltd., Cambridge, England). The dry weights of shoots (SDW) and roots (RDW) were recorded on a digital top-loaded balance (Setra BL-4100S, USA). For analyzing K concentration (KC), 0.5 g portion of ground shoots or roots were digested in 3:1 ratio of diacid mixture composed of nitric and perchloric acids (Miller, 1998). The KC was determined using Jenway PFP-7 flame photometer (Jenway, Dunmow, Essex, UK). The total KC (KCT) was calculated by adding KC of shoot (KCS) and root (KCR). The K use efficiency (KUE) was calculated by dividing the SDW with KCS. The K uptake of shoot (KUS) and root (KUR) were calculated by multiplying the KCS and KCR with SDW and RDW, respectively. The total K uptake (KUT) was the sum of KUS and KUR. All these calculations were performed by using the formulae suggested by Nawaz *et al.* (2006).

The SEM statistical software package AmosTM 7.0 and SPSS® for Windows version 15.0 were integrated to assess the direct and indirect effects of various parameters in enhancing SDW production under K deficiency stress. AmosTM (Analysis of Moment Structures) is a powerful SEM statistical software package specially used for path analysis to specify, estimate, assess and present models in an intuitive path diagram to show hypothesized relationships or confirm complex relationships among variables (Arbuckle, 2006). The SEM appeared as path diagram with a particular casual flow from a set of exogenous variables (RDW, LFA, KCT & KUE) through an intervening variable (KUT) and an outcome variable (SDW). KUT was considered as an intervening variable, because earlier studies frequently reported that K uptake was correlated well to biomass production under K deficiency stress (Siddiqi & Glass, 1983a & b; Mengel & Stephen, 1985; Cassman *et al.*, 1989; Gill *et al.*, 1997; Nawaz *et al.*, 2006). The single-headed arrows were used to imply a direction of assumed casual influence, while the double-headed arrows were used to represent covariance between two variables. The overall model fit was determined using a variety of fit measures as described by Arbuckle (2006).

Primarily a full model was developed without deleting any path to SDW. Afterwards, a reduced model was selected by individually deleting non-significant paths to SDW. The final reduced model contained no direct path from RDW to SDW (Fig. 1). The reduced model was recursive (n = 100) i.e., no variable in the model had an effect on itself. The full model contained 21 parameters (6 variances one for each variable & 15 path coefficients). The reduced model had 20 parameters (the path from RDW to SDW was dropped). The independence model (with no paths) contained 6 parameters (the variances of 6 variables).

RESULTS

Before implying a path analysis, the elements of the model were checked to determine whether they were related significantly to each other. As presented in Table I, all the correlations among the plant characters were significant ($p < 0.01$), except for KCT with SDW, RDW with LFA and KUT with KUE. However, due to highly significant correlations ($p < 0.01$) of KCT and KUE with all other plant characters, we considered both these parameters for inclusion in the model to explore their direct and indirect effects on cotton SDW production.

A path analysis was conducted with a series of multiple regressions to test the fit between the data and the reduced model. The SDW was significantly correlated with the four exogenous variables (KUT, KCT, KUE & LFA), $R^2 = 0.93$, $F(4, 95) = 313.5$ ($p < 0.01$). The predictors of SDW explained 93% of its variance and the error variance of SDW was only 7% of the variance of SDW itself. All the path coefficient loadings to SDW from the four exogenous variables were significant ($p < 0.01$). An increase in KUT, KUE, KCT and LFA by 1 standard deviation respectively increased the SDW by 0.58, 0.50, -0.10 and 0.15 standard deviation. Similarly, KUT was also significantly correlated with four exogenous variables (RDW, KCT, KUE & LFA), $R^2 = 0.66$, $F(4, 95) = 45.85$ ($p < 0.001$). The predictors of KUT explained only 66% of its variance and the error variance of KUT was about 34% of the variance of KUT itself. All the path coefficient loadings to KUT from the four exogenous variables were highly significant (0.01 level), except for a comparatively less significant path from KUE ($p < 0.05$). An increase in RDW, KCT, KUE and LFA by 1 standard deviation increased KUT by 0.45, 0.26, -0.20 and 0.53 standard deviation, respectively.

The reduced model was a modified version of the full or saturated model (Fig. 1). We have dropped the direct path from RDW to SDW in the reduced model due to its being non-significant ($p = 0.45$) in the full model. For the full model, SDW was significantly related to the five exogenous variables (RDW, LFA, KCT, KUE & KUT), $R^2 = 0.93$, $F(5, 94) = 249.82$, $p < 0.001$. As we already mentioned, except from RDW all the direct paths to SDW were significant either beyond 0.01 level (in case of KUE & KUT) or 0.05 level (in case of LFA & KCT). Dropping RDW from the regression model did not affect the R^2 value of the reduced model. Hence, the fit between the model and the data did not significantly reduce.

A highest regression weight estimate was obtained for the loading from RDW to KUT, indicating that when RDW goes up by 1, KUT goes up by 198.8 ± 5.8 ($p < 0.001$). Similarly, highest regression weight estimate was noted for loadings from KUE to SDW, revealing that when KUE goes up by 1, SDW goes up by 8.3 ± 0.6 ($p < 0.001$) (Table II). Table III presents model fit summary for the reduced model and compares it with the full and the independence models. The chi-square static, CMIN, for the reduced model was

Table I. Simple correlation coefficients among plant characters of cotton genotypes under K deficiency stress

Parameter	SDW	RDW	LFA	KCT	KUE
RDW	0.674**				
LFA	0.806**	0.573**			
KCT	-0.152NS	0.024NS	-0.149NS		
KUE	0.725**	0.444**	0.541**	-0.371**	
KUT	0.742**	0.659**	0.636**	0.267**	0.185NS

** : significant beyond $p < 0.01$, NS: non-significant, SDW: shoot dry weight, RDW: root dry weight, LFA: leaf area, KCT: total K concentration, KUE: K use efficiency, KUT: total K uptake

Table II. Standardized regression weights of the reduced model

Loading		Estimate	S.E.	Significance
To	From			
KUT	RDW	198.8	34	***
KUT	LFA	0.349	0.05	***
KUT	KCT	0.449	0.11	***
KUT	KUE	-139.3	54	NS
SDW	KUE	8.3	0.57	***
SDW	KUT	0.014	0.001	***
SDW	LFA	0.002	0.001	***
SDW	KCT	-0.004	0.001	NS

***: significant at $p < 0.001$, NS: non-significant, S.E.: Standard error, SDW: shoot dry weight, RDW: root dry weight, LFA: leaf area, KCT: total K concentration, KUE: K use efficiency, KUT: total K uptake.

Table III. Model fit summary for the reduced, full and independence models

Model Fit Test	Reduced Model	Full Model	Independence Model
CMIN	0.612	0.000	467.0
DF	1.000	0.000	15.00
P	0.434	-	0.000
RMR	0.000	0.000	547.0
GFI	0.998	1.000	0.421
NFI	0.999	1.000	0.000
CFI	1.000	1.000	0.000
RMSEA	0.000	-	0.552

CMIN: Chi-square, DF: degrees of freedom, P: probability, RMR: root mean square residual, GFI: goodness of fit index, NFI: normed fit index, CFI: comparative fit index, RMSEA: root mean square error of approximation

non-significant ($p = 0.43$), which revealed that the reduced model fits the data as well as does the full model. Hence, deleting a direct path from RDW to SDW did not affect model fit. The root mean square residual (RMR), in case of reduced model is perfectly equal to that of full model. It indicated that the estimated variances and covariances did not differ from the observed ones and the model fit was better. The goodness of fit index (GFI) of the reduced model was greater than 0.9. Its closeness to the GFI of the full model indicated good fitting of the reduced model. The goodness of fit indices: normed fit index (NFI) and comparative fit index (CFI) compared the reduced model with the independence model. Values of both these indices (> 0.9) indicated a good fit. CFI is said to be a good index

Fig. 1. Structural equation modeling results, indicating the relationship among exogenous variables (RDW: root dry weight, LFA: leaf area, KCT: total K concentration, KUE: K use efficiency), intervening variable (KUT: total K uptake) and outcome variable (SDW: shoot dry weight). e1 and e2: error associated with KUT and SDW, respectively). Coefficients shown are standardized values. The single-headed arrows imply a direction of assumed casual influence, while the double-headed arrows represent covariance between two variables

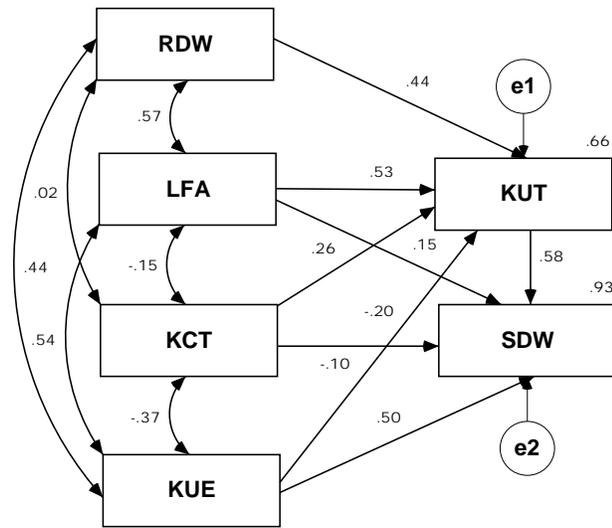
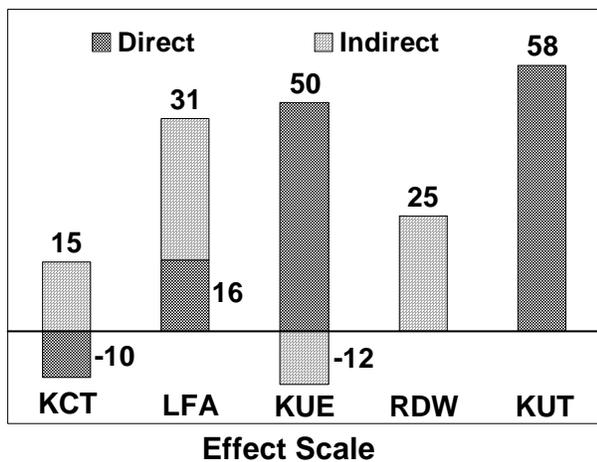


Fig. 2. Direct and indirect effects of various plant characters (KCT: total K concentration, LFA: leaf area, KUE: K use efficiency, RDW: root dry weight, KUT: total K uptake) affecting shoot dry weight of cotton genotypes under K deficiency stress



for use even with small samples. CFI of the reduced model is identical with that of full model. The root mean square error of approximation (RMSEA), estimated lack of fit compared to the saturated model. The RMSEA of 0.000 for default model indicated a good fit of the model to the data.

DISCUSSION

The uptake of K appeared to be the major factor contributing cotton biomass production under K deficiency stress, followed by KUE, while the direct contribution of LFA was lower than both of them. Nonetheless, the indirect contribution of LFA to SDW was more than any other character, followed by RDW and KCT. These all characters enhanced KUT directly, and indirectly affected SDW (Fig. 2). K deficiency stress activates K uptake in plants (Fernando *et al.*, 1990; Ashley *et al.*, 2006), which is usually associated with the induction of expression of high affinity transporters and is considered a key mechanism of adaptation to K starvation (Ashley *et al.*, 2006). Higher uptake rates and greater accumulation of K are attributed to K efficient cotton cultivars (Cassman *et al.*, 1989).

Siddiqi and Glass (1983a & b) found correlation between K uptake and SDW of barley under K deficiency stress. Higher K uptake rates were also correlated well with absolute and relative growth rates and higher root weight. Similarly, Mengel and Stephen (1985) reported significant correlation between total K uptake and root fresh weight and root length of rye grass and red clover in a field experiment on low K soil. Cassman *et al.* (1989) attributed high SDW production and K use efficiency of field grown cotton under low soil K to higher K uptake rate during fruit development and greater total K accumulation. In wheat, the most efficient, high SDW producing genotype–Dirk had high K uptake and utilization efficiency under K deficiency stress (Gill *et al.*, 1997). Recently, Nawaz *et al.* (2006), in a solution culture experiment involving 15 maize genotypes, elucidated that high SDW production was a function of high K uptake under K deficiency stress.

In this study, KUT had strong relationship with LFA and RDW (Table I). The direct effect of LFA on SDW was more than RDW (Fig. 2). Leaf growth is the most susceptible physiological process to K deficient conditions (Reddy *et al.*, 2000). It is reported that K deficiency reduces cotton leaf area, leaf weight (Cassman *et al.*, 1989) and leaf area index (Cassman *et al.*, 1989; Pettigrew & Meredith, 1997). By the time leaves display K deficiency symptoms, all other plant parts are already affected (Rosolem & Mikklsen, 1991). A K deficient cotton leaf possesses relatively lesser intercellular air space and fewer chloroplasts in mesophyll tissue than the control plants; their chloroplasts are filled with large starch granules, and contain apparently more and greater plastoglobuli and fewer grana (Zhao *et al.*, 2001). A moderate K deficiency drastically reduces the photosynthetic rate of a single leaf (Bednarz *et al.*, 1998; Bednarz & Oosterhuis, 1999; Wright, 1999; Zhao *et al.*, 2001) or a canopy (Gwathmey & Howard, 1998; Pettigrew, 1999) of cotton. Dong *et al.* (2004) concluded that leaf photosynthesis reduction induced by K-deficiency are closely associated with decreased stomatal conductance, increased mesophyll resistance, low chlorophyll content, poor chloroplast ultrastructure,

restricted saccharide translocation and decreased synthesis of RuBP carboxylase.

Root dry biomass also affected SDW by enhancing KUT, under K deficiency stress. K is a diffusion-supplied nutrient and hence the efficiency of plants to uptake K under its deficiency stress largely depends upon root morphology, root hairs, root exudates and release of K from non-exchangeable pool (Rengel & Damon, 2008). Nawaz *et al.* (2006) also reported strong correlation between K uptake of maize genotypes and root biomass accumulation. Genotypes that had high root/shoot ratio were K-use efficient.

CONCLUSION

Under the K deficiency stress, the enhanced shoot dry weight of cotton genotypes was a function of their enhanced leaf area and root dry biomass, due to their positive direct effect on the K uptake. The enhanced K uptake followed by the KUE proved to be the major contributing factors to cotton biomass production under the K deficiency stress. Hence, leaf area and root dry biomass could be considered as important physiological markers to breed K-efficient cotton genotypes for low-K-input sustainable agriculture.

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