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Interrelationships between seed yield and 20 related traits of 49 canola (*Brassica napus* L.) genotypes in non-stressed and water-stressed environments

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Abstract

Development of new canola (*Brassica napus* L.) cultivars requires efficient tools to monitor trait association in a breeding program. The efficiency of a breeding program depends mainly on the direction of the correlation between yield and its components and the relative importance of each component involved in contributing to seed yield. This research uses sequential path analysis to determine the interrelationships among seed yield and 20 related traits. Forty nine canola genotypes were grown in two environments (non-stressed and water-stressed conditions) to determine the important components of seed yield. Observations were recorded on 20 other canola traits. Correlation coefficient analysis revealed seed yield was positively correlated with all the traits except stem diameter and days to flowering in the non-stressed environment. Seed yield was significantly positively correlated with all measured traits except first pod height, first lateral branch height, number of lateral branches pod^{-1}, number of pods plant^{-1} and stem diameter in the water-stressed environment. Sequential path analysis identified the 1,000-seed weight (TSW) and main stem length as important first order traits that influenced seed yield in the non-stressed environment. Plant height and the TSW were important first order traits that influenced seed yield in the water-stressed environment. All direct effects were significant, as indicated by bootstrap analysis. The results suggest that TSW could be used as a selection criterion in selecting for increased seed yield in canola in both non-stressed and water-stressed conditions.

Additional key words: bootstrap analysis, conventional path analysis, drought tolerance.

Resumen

Interrelación entre el rendimiento de las semillas y veinte caracteres asociados de 49 cultivares de colza (*Brassica napus* L.) en entornos sin estrés y con estrés hídrico

En los programas de mejora, el desarrollo de nuevos cultivares de colza (*Brassica napus* L.) requiere herramientas eficaces para analizar la correlación entre el rendimiento de las semillas y sus componentes genéticos. La presente investigación utiliza un análisis secuencial para determinar las interrelaciones entre el rendimiento de las semillas y 20 caracteres relacionados. Se cultivaron 49 genotipos de colza en dos ambientes (sin estrés y con estrés hídrico) para determinar los componentes más importantes del rendimiento de las semillas y se realizaron observaciones sobre otros 20 caracteres. El análisis del coeficiente de correlación reveló que el rendimiento de las semillas está positivamente correlacionado con todos estos caracteres, excepto con el diámetro del tallo y días hasta la floración en condiciones sin estrés, y con la altura de la primera vaina, altura de la primera rama lateral, número de ramas laterales por vaina, número de vainas por planta y diámetro del tallo, en condiciones de estrés hídrico. Del análisis secuencial se dedujo que el peso de 1.000 semillas (TSW) y la longitud de tallo principal son los caracteres que más influyen sobre el rendimiento de las semillas en condiciones sin estrés hídrico, y la altura de la planta y el TSW en condiciones de estrés hídrico. En un análisis *bootstrap*, todos los efectos directos fueron significativos. El estudio sugiere que podría utilizarse el carácter TSW en la selección para aumentar el rendimiento de semillas de colza, tanto en condiciones sin estrés como con estrés hídrico.

Palabras clave adicionales: análisis *bootstrap*, análisis convencional, tolerancia a la sequía.

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Introduction

Improvement of seed yield in canola (*Brassica napus* L.) has been the primary objective of canola breeders for many years. Seed yield is a quantitative trait, which is largely influenced by the environment and hence has a low heritability (Duhoon *et al.,* 1982; Brandle and McVetty, 1989). As a result, the response to direct selection for seed yield may be unpredictable, unless there is good control of environmental variation. Plant breeders are seldom interested in a single trait and therefore, there is the need to examine the relationships among various traits, especially between seed yield and other traits. As the number of independent variables influencing a particular dependent variable is increased, a certain amount of interdependence is expected. In such situations, correlations may be insufficient to explain the associations in a way that will enable breeders to decide on a direct or indirect selection strategy (Ofori, 1996).

Different statistical techniques have been used in modelling crops yield, including correlation, regression, path analysis, factor analysis, factor components and cluster analysis (Leilah and Al-Khateeb, 2005). Determination of correlation coefficients is an important statistical procedure to evaluate breeding programs for high yield, as well as to examine direct and indirect contributions to yield variables (Mohammad *et al.,* 2002). Path coefficient analysis is a statistical technique for partitioning correlation coefficients into direct and indirect effects, so the contribution of each trait, to seed yield, can be estimated (Dewey and Lu, 1959; Duarte and Adams, 1972).

Most of those investigators ignored the importance of the causal relationship, as stressed by Wright (1921), and they used a model similar to that of Dewey and Lu (1959), in which bidirectional causation, among yield components, is assumed. Path analysis requires determination of causal relationships among variables, based on either *a priori* evidence or a postulated hypothesis. Plant yield components develop sequentially (Fisher and Palmer, 1983) with later-developing components under the control of earlier-developing components (Thomas *et al.,* 1970; Dofing and Knight, 1992). Analysis of values of the correlation coefficients, of different characters, with yield assists in deciding their relative importance and their value as selection criteria for yield. Path coefficient indicates the relative importance of each component (Wright, 1921; Dewey and Lu, 1959; Tyagi *et al.,* 1988; Dofing and Knight, 1992).

This conventional approach might result in multicollinearity for variables, particularly when correlations among some of the traits are high (Hair *et al.,* 1995). There may be difficulties in interpretation of the actual contribution of each variable (since the effects are mixed or confounded because of collinearity) and supplementation of unique explanatory predictions from additional variables. Samonte *et al.* (1998) adopted sequential path analysis for determining relationships among yield and related traits in rice (*Oryza sativa* L.) by organizing and analyzing various predictor variables in first, second, and third order paths. The sequential path model has distinct advantages over the conventional path model in discerning actual effects of different predictor variables and can provided a better fit for various datasets (Mohammadi *et al.,* 2003). However, collinearity of predictor variables was not tested before organization of the variables into different path orders. Recently sequential path analysis was used in maize (*Zea mays* L.) by Mohammadi *et al.* (2003) and in potato (*Solanum tubersum* L.) by Asghari-Zakaria *et al.* (2007). Although, there are several reports on correlation and path coefficient analysis in canola (Degenhart and Kondra, 1984; Engqvist and Becker, 1993; Ozer *et al.,* 1999; Ali *et al.,* 2003; Khan *et al.,* 2006, 2008; Ivanovska *et al.,* 2007; Marjanovic-Jeromela *et al.,* 2007; Basalma, 2008), detailed cause and effect relationships using sequential path analysis have not been examined in canola.

The main objectives of this research were to analyze the correlation between seed yield and related traits in canola by applying sequential path analysis and identifying traits, of genotypes, which may be useful in breeding higher-yielding genotypes in non-stressed and water-stressed environments.

Abbreviations used: CPA (conventional path analysis), DFS (days to flowering starting), DPM (days to physiological maturity), FP (flowering period), HFB (height of the first lateral branch), HFP (height of the first pod), HI (harvest index), LBP (length lateral branch pod), LMP (length main pod), LP (length pod of plant), MSL (main stem length), NBP (number of lateral branches per pod), NPB (number of pods lateral branch^{-1}), NPM (number of pods main stem^{-1}), NPP (number of pods plant^{-1}), NSP (number of seeds pod^{-1}, plant), NSPB (number of seeds pod lateral branch^{-1}), NSPM (number of seeds pod^{-1} main stem), PH (plant height), SD (stem diameter), SPA (sequential path analysis), SY (seed yield), TSW (thousand-seed weight), VIF (variance inflation factor).

Material and methods

A nine by nine diallel cross, without reciprocals (half diallel), was made in the growing season of 2006-2007 at the Seed and Plant Improvement Institute (SPII), Karaj, Iran. Three drought tolerant genotypes, SLM046, Okapi and Orient, three moderately tolerant genotypes, Fornax, Colvert and Zarfam, and three susceptible genotypes, Opera, Modena and Talaye were used as parents. The nine canola genotypes were chosen based on their considerable variability in yield, yield components and drought tolerance. Thirty six hybrids from a half diallel cross, excluding reciprocals were used in the current study. In 2007-2008, the subsequent season, two sets of material consisting of the parents, their 36 F_1 hybrids and four control genotypes Hayola 401, RGS003, Licord and Opera genotypes were grown in the field at Tarbiat Modares University, Iran.

Plots of non-stressed (optimal conditions) and water-stressed (drought conditions) plants were established separately using a 7×7 simple lattice design with two replicates. Sowing was done at the bottom of a furrow in a 30-60 cm system (one pair of rows in each furrow at 30 cm spacing, with 60 cm between the two paired rows) in the third week of October. There were four pair of rows 2 m long and 0.60 m apart, plot size was 4.8 m^2. Plots were overplanted and thinned to a distance between plants in the row of 10 cm for an established plant density of 16.7 plants m^{-2}. Nitrogen fertilizer was hand applied across all treatments [50 kg N ha^{-1} at sowing as urea (46% N), a further 50 kg N ha^{-1} was top-dressed at the start of flowering and 50 kg N ha^{-1} more at the start of podding]. The other fertilizers were applied prior to ploughing at the recommended rates of 16 and 70 kg ha^{-1} of P and K respectively. Weeds were controlled by hand as needed.

The non-stressed and water-stressed trials were sown adjacent to each other in the same field separated by 10 m to reduce lateral water infiltration from the non-stressed to the water-stressed trial. Water-stress was applied by control of irrigation during the pod lengthening stage. Thus, drought was applied by withholding water when the first pod appeared at the beginning of pod filling and seed-filling. Also in these stages total leaf water potential was used as the index of soil water status according to Williams and Araujo (2002) and Pellegrino *et al.* (2005). Total leaf water potential was measured using a pressure chamber (PMS, Instrument Company, Corvallis, Oregon). Two-thirds of top leaf lamina was excised and placed immediately into a rubber stopper, and used to read water potential according to Fischer *et al.* (1977) and Singh *et al.* (1982). Five plants $plot^{-1}$ were used to determine water potential. Water potential was measured, at all growth stages, during the middle of the day between 12:00 and 13:00 hours. The average total leaf water potential during the above stages was –18 bars in the water-stressed environment.

Twenty one traits canola traits were measured on 49 genotypes of the two trials. Fifteen traits were measured on 10 random (vying plant) points $plot^{-1}$. The traits were plant height (PH), number of lateral branches pod^{-1} (NBP), number of pods main $stem^{-1}$ (NPM), number of pods lateral $branch^{-1}$ (NPB), main stem length (MSL), number of pods $plant^{-1}$ (NPP), height of first pod (HFP), height of first lateral branch (HFB), number of seeds pod^{-1} of main stem (NSPM), number of seeds pod^{-1} of lateral branch (NSPB), length main stem pod (LMP), length lateral branch pod (LBP), number of seeds pod^{-1} of plant (NSP), length pod of plant (LP) and stem diameter (SD). Days to flowering (DFS), flowering period (FP) and days to physiological maturity (DPM) were recorded. The 1,000-seed weight (TSW) was measured on a sub-sample of seed harvested from each plot. The area harvested was 2.7 m^2. Only the middle six rows were harvested and weighed to determine biological yield. Seed yield (SY) was measured at physiological maturity and yield was adjusted to 12.5% seed moisture content. Harvest index (HI) was calculated from the biological and seed yield.

The datasets were first tested for normality by the Anderson and Darling normality test using Minitab version 14 (2005) statistical software. Data from each trial were subjected to analysis of variance (ANOVA) using appropriate models. Phenotypic linear correlation coefficients were calculated for all possible comparisons using the Pearson correlation coefficient. Correlation coefficients were partitioned into direct and indirect effects using conventional path coefficient analysis (Dewey and Lu, 1959).

Sequential stepwise multiple regression was performed to organize the predictor variables into first, second and third order paths on the basis of their respective contributions to total variation in seed yield and minimal collinearity using SPSS 13 (SPSS, 2004). The sequential path model consisted of predictor and response variables. The level of multicollinearity in each component path was measured from two common measures, the tolerance value and its inverse and the variance inflation factor (VIF) as suggested by Hair *et* *al.* (1995). The tolerance value is the amount of variability of the selected independent variable not explained by other independent variables (1-R^2), where R^2 is the coefficient of determination for the prediction variable by the predictor variables. The VIF indicates the extent of effects of other independent variables on the variance of the selected independent variable [VIF = 1/(1/R^2)]. Thus, very small tolerance values (much lower than 0.1) or high VIF values (> 10) indicate high collinearity (Hair *et al.,* 1995; Mohammadi *et al.,* 2003).

Partial coefficients of determination (analogous to linear regression) were calculated from the path coefficients for all predictor variables. To estimate the standard error path coefficients, bootstrap analysis (Efron and Tibshirani, 1993) was performed using the S-Plus 2000 (MathSoft, 1999) statistical package.

Results

Simple correlations

The analysis of variance results indicated highly significant differences in canola genotypes for all traits under study (data not shown). To determine in the most precise manner the interrelation of direct and indirect seed yield components simple correlations were established and path coefficient analysis performed. The simple correlation coefficients in the non-stressed environment (Table 1) showed there were high positive correlations between seed yield and all of the measured traits except for SD and DFS.

As shown in Table 1, all traits were positively, and significantly, correlated with NPP, except for MSL and DFS. There was a statistically significant and positive correlation between HI and other canola characters except for MSL and DFS (Table 1). The 1,000-seed weight (TSW) had significant positive correlations with all other measured traits except for SD and FP (Table 1).

In the water-stressed environment, seed yield was significantly positively correlated with all measured traits except for HFP, HFB, NBP, NPP and SD (Table 2). However, seed yield had a significant negative correlation with DPM. Seed yield had significant positive correlations in similar traits in the non-stressed and water-stressed environments, but seed yield was not a significant positive correlation with DFS in the non-stressed environment. Seed yield was significantly positively correlated in NBP, NPP, HFB and HFP in the non-stressed environment while these traits did not have a significant correlation in the non-stressed

Table 1. Pairwise correlation coefficients between 21 traits of 49 canola genotypes measured in a non-stressed environment

Trait[a]	PH	NBP	NPM	NPB	MSL	NPP	HFB	HFP	NSPM	NSPB	LMP	LBP	NSP	LP	HI	TSW	SD	DFS	FP	DPM
NBP	0.88[b]																			
NPM	0.53	0.43																		
NPB	0.61	0.40	0.77																	
MSL	0.07	0.16	0.24	0.13																
NPP	0.80	0.75	0.86	0.86	0.23															
HFB	0.86	0.94	0.48	0.38	0.20	0.72														
HFP	0.86	0.84	0.20	0.29	0.08	0.53	0.83													
NSPM	0.45	0.35	0.34	0.49	0.23	0.45	0.41	0.40												
NSPB	0.47	0.32	0.37	0.54	0.12	0.49	0.36	0.38	0.79											
LMP	0.64	0.49	0.51	0.53	0.02	0.57	0.56	0.47	0.53	0.49										
LBP	0.35	0.28	0.49	0.29	0.16	0.40	0.44	0.19	0.34	0.24	0.44									
NSP	0.35	0.22	0.41	0.50	0.19	0.43	0.29	0.27	0.91	0.94	0.48	0.32								
LP	0.46	0.34	0.60	0.42	0.13	0.51	0.5	0.26	0.45	0.37	0.74	0.92	0.44							
HI	0.62	0.53	0.76	0.71	0.13	0.78	0.59	0.32	0.47	0.59	0.71	0.58	0.55	0.72						
TSW	0.45	0.36	0.53	0.57	0.29	0.58	0.39	0.30	0.50	0.55	0.40	0.42	0.54	0.47	0.54					
SD	0.32	0.52	0.55	0.33	0.21	0.57	0.48	0.03	–0.02	–0.06	0.27	0.20	–0.07	0.25	0.55	0.19				
DFS	–0.46	–0.30	0.04	–0.19	–0.01	–0.18	–0.29	–0.50	–0.47	–0.52	–0.26	–0.02	–0.44	–0.08	–0.09	–0.33	0.28			
FP	0.41	0.29	0.42	0.47	–0.12	0.47	0.27	0.22	–0.16	0.11	0.35	0.21	–0.06	0.30	0.59	0.23	0.27	0.11		
DPM	0.39	0.32	0.52	0.49	0.48	0.53	0.34	0.26	–0.02	0.18	0.29	0.25	0.07	0.31	0.55	0.53	0.28	0.12	0.71	
SY	0.58	0.45	0.62	0.65	0.32	0.67	0.52	0.41	0.60	0.61	0.56	0.47	0.62	0.56	0.76	0.68	0.25	–0.16	0.39	0.56

[a] For trait abbreviations refer to text. [b] Critical values of correlation $P < 0.05$ and $P < 0.01$ (df 47) are 0.37 and 0.29, respectively.

Table 2. Pairwise correlation coefficients between 21 traits of 49 canola genotypes measured in a water stressed environment

Trait	PH	NBP	NPM	NPB	MSL	NPP	HFB	HFP	NSPM	NSPB	LMP	LBP	NSP	LP	HI	TSW	SD	DFS	FP	DPM
NBP	0.13[a]																			
NPM	0.56	0.39																		
NPB	0.63	0.32	0.86																	
MSL	0.48	0.31	0.80	0.61																
NPP	0.25	0.38	0.77	0.46	0.65															
HFB	0.15	0.16	0.51	0.25	0.45	0.46														
HFP	0.25	0.17	0.52	0.33	0.38	0.37	0.86													
NSPM	0.41	0.22	0.38	0.52	0.35	0.16	0.05	0.06												
NSPB	0.43	0.13	0.44	0.70	0.32	0.20	–0.07	0.01	0.51											
LMP	0.28	0.14	0.38	0.38	0.26	0.05	0.08	0.11	0.09	0.07										
LBP	0.24	0.05	0.29	0.38	0.19	0.20	–0.18	–0.11	0.08	0.41	0.26									
NSP	0.45	0.15	0.37	0.65	0.33	0.08	–0.11	–0.06	0.82	0.87	0.07	0.28								
LP	0.29	0.07	0.29	0.42	0.19	0.03	–0.17	–0.13	0.10	0.30	0.66	0.83	0.28							
HI	0.03	0.11	0.32	0.33	0.16	0.11	0.00	0.00	0.24	0.06	0.44	–0.11	0.17	0.20						
TSW	0.05	0.19	0.25	0.35	0.11	0.19	–0.14	–0.20	0.56	0.34	0.04	0.21	0.48	0.21	0.38					
SD	0.35	0.09	0.02	0.18	–0.17	–0.12	–0.17	–0.01	–0.23	0.02	–0.09	–0.05	–0.12	–0.13	–0.24	–0.22				
DFS	0.29	0.07	0.24	0.42	0.18	–0.05	–0.17	–0.14	0.18	0.36	0.67	0.40	0.36	0.65	0.14	0.06	0.03			
FP	0.09	0.03	0.26	0.14	0.06	0.16	0.22	0.32	–0.34	–0.20	–0.12	–0.15	–0.34	–0.22	–0.18	–0.39	0.38	–0.29		
DPM	0.08	0.03	0.20	0.06	0.07	0.12	0.27	0.29	–0.33	–0.29	–0.08	–0.25	–0.39	–0.29	–0.17	–0.42	0.37	–0.29	0.75	
SY	0.40	0.12	0.48	0.65	0.37	0.19	–0.09	–0.06	0.59	0.58	0.42	0.41	0.67	0.54	0.48	0.67	–0.17	0.45	–0.41	–0.43

[a] Critical values of correlation $P < 0.05$ and $P < 0.01$ (D.F. 47) are 0.37 and 0.29, respectively.

environment. The HI was significantly positively correlated with PH, NPP, NPB and seed yield in the water-stressed environment.

Conventional and sequential path analysis

To determine the relative importance of the traits the data were subjected to conventional path analysis. This allows separation of the correlation coefficient with components of direct and indirect effects. The results pertaining to direct effects of components traits on canola seed yield, where yield-related traits were considered as first order variables, with seed yield as the response variable, are presented in Table 3. The results of two measures of multicollinearity analysis (Tolerance and Variance Inflation Factor) for conventional path analysis are given in Table 3. According to the conventional path analysis and multicollinearity analysis, there are inconsistent relationships among the variables. Results from this analysis in the non-stressed environment, where all traits were considered as first-order variables (Model I) with seed yield as the response variable, indicated high multicollinearity for some traits, particularly for those showing a high direct effects such as the number of seeds pod^{-1} of plant (VIF = 822), harvest index (VIF = 33.2) length of lateral branch pod (VIF = 179.5), length of main pod (VIF = 78) and plant height (VIF = 29). These traits were therefore removed as first-order variables from the analysis in the non-stressed environment. In the water-stressed environment (Table 3), the traits number of pods main stem^{-1} (VIF = 165.9), number of pods lateral branch^{-1} (VIF = 29.6) and number of seeds pod^{-1} of plant (VIF = 95.5) showed high multicollinearity when all traits were considered as first-order variables with seed yield as the response variable and were removed as first-order variables from the analysis in the water-stressed environment. This strategy for the evaluation of different trait correlations and path analysis was used by Samonte *et al.* (1998) in rice and Mohammadi *et al.* (2003) in maize.

Estimation of direct effects by sequential path analysis (Table 4), were considered where yield-related traits, as grouped into first, second, and third-order variables, with seed yield (Model II). Analysis of multicollinearity indicated a better understanding of the interrelationships among the various traits and their relative contribution to seed yield. The results of tolerance and VIF values for predictor variables in non-stressed and water-stressed environments indicated a remarkable reduction of VIF values in Model I compared

Table 3. Direct effects of first-order predictor variables on the seed yield of 49 canola genotypes in a non-stressed and water stressed environments and two common measures of collinearity in conventional path analysis

Trait	Non-stressed environment			Water stressed environment		
	Direct effet	Tolerance	VIF[a]	Direct effect	Tolerance	VIF
PH	0.522	0.034	29.0	0.133	0.264	3.8
NBP	0.088	0.005	211.0	–0.085	0.681	1.5
NPM	–0.162	0.017	60.1	0.698	0.006	165.9
NPB	0.050	0.007	150.9	0.527	0.034	29.6
MSL	0.291	0.156	6.4	–0.133	0.068	14.8
NPP	–0.052	0.003	349.1	–0.280	0.052	19.4
HFB	0.359	0.036	28.1	–0.314	0.082	12.2
HFP	–0.371	0.018	54.7	0.034	0.151	6.6
NSPM	–0.652	0.004	222.5	–0.352	0.032	31.7
NSPB	–1.507	0.003	291.4	–0.341	0.023	43.0
LMP	0.730	0.013	78.0	0.126	0.063	15.8
LBP	0.896	0.006	179.5	0.004	0.029	34.1
NSP	1.899	0.001	822.0	0.365	0.010	95.5
LP	–1.792	0.003	325.5	–0.101	0.020	50.6
HI	0.997	0.030	33.2	–0.087	0.100	10.0
TSW	0.446	0.147	6.8	0.278	0.178	5.6
SD	–0.662	0.038	26.2	–0.222	0.152	6.6
DFS	0.281	0.207	4.8	–0.126	0.176	5.7
FP	0.090	0.104	9.6	–0.390	0.080	12.6
DPM	–0.193	0.046	21.8	–0.138	0.259	3.9

[a] VIF: variance inflation factor.

with Model II. Stepwise regression in this study minimized collinearity measures (tolerance and VIF) of all variables, thus facilitating detection of the actual contribution of each predictor variables in different path components, with negligible confounding effects and interference. The advantage of sequential path procedure over conventional path analysis in minimizing collinearity problems and identifying actual contributions of each component in different path components are similar to those found in other crop studies (maize: Agrama, 1996; Mohammadi *et al.,* 2003; rice: Samonte *et al.,* 1998; and potato: Asghari-Zakaria *et al.,* 2007), indicating that it should be very effective in achieving favourable results.

In statistical analysis, researchers are usually interested in obtaining not only a point estimate of a statistic but also an estimate of the variation in the point estimate and a confidence interval for the true value of the parameter. Resampling techniques, such as the bootstrap, provide estimates of the standard error, confidence interval, and the distribution of any statistic. To use these procedures, the mean direct effects, estimated from a set of 1,000 bootstrap samples were in close agreement with observed direct effects of the various traits (Table 5). The low standard error of all the direct effects and the low bias also indicated the robustness of sequential path analysis. The T-test of significance, using standard error values, obtained through bootstrap resampling, indicated that all the direct effects were significant (data not shown).

The adjusted coefficient of determination (Adj. $R^2 = 0.45$) represents the influence of the MSL and TSW traits as first-order variables involved in the study of total variability of seed yield in the non-stressed environment while the PH and TSW traits, as first-order variables, accounted for nearly 56% of the variation in seed yield in the water-stressed environment (Table 5). In the non-stressed environment among the MSL and TSW traits, the TSW had the greater direct effect (0.65) than MSL on seed yield. The Indirect effect to the TSW was low and positive (0.037) via MSL but the indirect effect on the MSL was relatively high and positive (0.187) via TSW.

Many attempts have been made to graphically present statistical outputs. The diagram of sequential path analysis for the non-stressed environment (Fig. 1) gives a better understanding of the interrelationships among the various variables and their relative contribution to seed yield. The results of sequential path analysis, when the second-order variables were used

Table 4. Measures of collinearity values (tolerance and variance inflation factor, VIF) for predictor variables in conventional path analysis (CPA, all predictor variables as first-order variables) and sequential path analysis (SPA, predictors grouped into first-, second-, and third-order variables)

Predictor variable	Response variable	Tolerance		VIF	
		CPA	SPA	CPA	SPA
Non-stressed environment					
MSL	SY	0.156	0.916	6.4	1.1
TSW		0.147	0.916	6.8	1.1
DPM	MSL	0.046	0.496	21.8	2.0
FP		0.104	0.496	9.6	2.0
NPP	TSW	0.003	0.563	349.1	1.8
NSP		0.001	0.783	822.0	1.3
DPM		0.046	0.686	21.8	1.5
NPB	NPP	0.007	0.844	150.9	1.2
NBP		0.005	0.844	211.0	1.2
NSPM	NSP	0.004	0.374	222.5	2.7
NSPB		0.003	0.374	291.4	2.7
NSPM	DPM	0.004	0.730	222.5	1.4
NPB		0.007	0.461	150.9	2.2
HI		0.030	0.476	33.2	2.1
NSPM	FP	0.004	0.674	222.5	1.5
HI		0.030	0.470	33.2	2.1
SD		0.038	0.601	26.2	1.7
Water stressed environment					
PH	SY	0.264	0.997	3.8	1.0
TSW		0.178	0.997	5.6	1.0
NPB	PH	0.034	0.397	29.6	2.5
SD		0.152	0.716	6.6	1.4
MSL		0.068	0.541	14.8	1.8
NSPM		0.032	0.618	31.7	1.6
NSPM	TSW	0.032	0.938	31.7	1.1
HI		0.100	0.942	10.0	1.1
HFP		0.151	0.996	6.6	1.0
NPM	NPB	0.006	0.861	165.9	1.2
NSP		0.010	0.861	95.5	1.2
FP	SD	0.080	1.000	12.6	1.0
NPM	MSL	0.006	1.000	165.9	1.0
NSP		0.010	0.234	95.5	4.3
NSPB	NSPM	0.023	0.225	43.0	4.4
NPP		0.052	0.917	19.4	1.1
LMP	HI	0.063	1.000	15.8	1.0
HFB	HFP	0.082	1.000	2.2	1.0

as predictors, and the first-order variables as response variables, indicated that NPP, NSP and DPM positively influenced the TSW (Table 6) and accounted for more than 52% of the observed variation in the non-stressed environment (Fig. 1). The FP positively and the DPM negatively influenced MSL and accounted for more than 64% of the observed variation while HI positively, NSPB and HFP negatively influenced the DFS and accounted for more than 43% of the observed variation in the non-stressed environment (Table 5). When the third-order variables were used as predictors and second-order variables as response variables the results indicated NPB and NBP positively influenced the NPP and accounted for about 94% of observed variation while NSPM and NSPB positively influenced NSP and accounted for about 95% of the observed variation in the non-stressed environment. Also NSPM negatively and NPB and HI positively influenced DPM and accounted for about 45% of observed variation while NSPM and SD negatively and HI positively influenced

Table 5. Estimation of standard error values of path coefficients using bootstrap analysis

Predictor variable	Response variable	Adj. R^2	Direct effect	Bootstrap		
				Bias	Mean	SE
Non-stressed environment						
MSL	SY	0.45	0.13	–0.0022	0.13	0.113
TSW			0.65	0.0056	0.65	0.097
DPM	MSL	0.64	1.14	0.0158	1.15	0.129
FP			–0.92	–0.0110	–0.94	0.118
NPP	TSW	0.52	0.18	0.0057	0.18	0.134
NSP			0.43	0.0031	0.44	0.13
DPM			0.40	0.0013	0.40	0.124
NPB	NPP	0.94	0.67	–0.0011	0.67	0.039
NBP			0.49	–0.0056	0.48	0.049
NSPM	NSP	0.95	0.44	–0.0049	0.43	0.063
NSPB			0.60	0.0025	0.60	0.053
NSPM	DPM	0.45	–0.43	–0.0048	–0.43	0.113
NPB			0.34	0.0025	0.34	0.139
HI			0.50	0.0023	0.50	0.165
NSPM	FP	0.66	–0.69	0.0019	–0.69	0.096
HI			1.11	–0.0041	1.11	0.126
SD			–0.36	0.0024	–0.36	0.116
Water stressed environment						
PH	SY	0.56	0.37	–0.0021	0.37	0.091
TSW			0.65	–0.0042	0.64	0.087
NPB	PH	0.51	0.20	0.0401	0.24	0.179
SD			0.44	–0.0041	0.43	0.136
MSL			0.33	–0.0163	0.31	0.149
NSPM			0.29	–0.0480	0.25	0.166
NSPM	TSW	0.40	0.52	0.0260	0.54	0.130
HI			0.26	–0.0142	0.24	0.097
HFP			–0.24	–0.0059	–0.24	0.110
NPM	NPB	0.87	0.72	–0.0015	0.72	0.092
NSP			0.39	–0.0004	0.38	0.066
FP	SD	0.12	0.37	–0.0137	0.36	0.162
NPM	MSL	0.64	0.80	–0.0004	0.80	0.067
NSP	NSPM	0.88	1.63	–0.0197	1.61	0.114
NSPB			–0.95	0.0208	–0.93	0.123
NPP			0.23	–0.0019	0.23	0.050
LMP	HI	0.18	0.44	–0.0006	0.44	0.112
HFB	HFP	0.74	0.86	–0.0029	0.86	0.060

FP and accounted for about 66% of observed variation in the non-stressed environment (Table 5).

In the water-stressed environment (Table 5), both PH and TSW had a relatively equal direct effect on seed yield (0.56 and 0.51 respectively). Marjanovic-Jeromela *et al.* (2008) concluded that the strongest effect on seed yield was estimated for PH which differs from the findings of Tak (1976) who estimated the strongest direct effect of NPP and NSP on seed yield and Yadav and Kumar (1984) who estimated the strongest direct effect of NPM and NBP on seed yield. The indirect effect of the TSW on seed yield via PH and indirect effect of PH on seed yield via the TSW were low. Results of sequential path analysis in the water-stressed environment, when second-order variables were used as predictors and first-order variables as response variables, showed that NPB, SD, MSL and NSPM positively influenced PH (Table 7) and accounted for more than 51% of observed variation (Fig. 2). The NSPM and HI positively and HFP negatively influenced TSW and accounted for more than 40% of observed variation. Results of sequential path analysis when the third-order variables

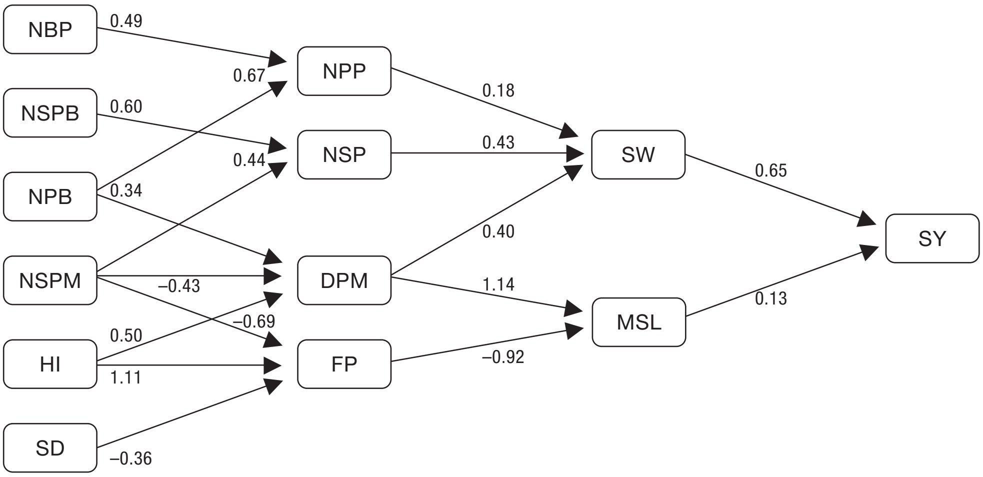

Figure 1. Sequential path analysis diagram illustrating the interrelationships among various traits contributing to seed yield in a non-stressed environment. For trait abbreviations refer to text.

were used as predictors, and second-order variables as response variables, showed that NPM and NSP positively influenced NPB and accounted for more than 87% of observed variation in the water-stressed environment (Fig. 2). Also NSP and NPP positively and NSPB negatively influenced NSPM and accounted for more than 88% of the observed variation. The FP positively influenced SD and accounted for about 12% of the observed variation, in the non-stressed environment. The NPM positively influenced MSL, LMP positively influenced HI and HFB positively influenced HFP and accounted for about 64%, 18% and 74% of observed variation respectively in the non-stressed environment (Table 5). Yield component studies, in both environments, indicated that only the TSW was positively associated with seed yield and had an important direct

Table 6. Direct and indirect effects in a non-stressed environment for the predictor variables in sequential path analysis (grouped into first, second and third order variables)

SY

	MSL	**TSW**
MSL	0.129	0.187
TSW	0.037	0.646

MSL

	DPM	**FP**
DPM	1.136	–0.656
FP	0.806	–0.924

NPP

	NPB	**NBP**
NPB	0.671	0.192
NBP	0.265	0.485

NSP

	NSPM	**NSPB**
NSPM	0.437	0.471
NSPB	0.346	0.595

TSW

	NPP	**NSP**	**DPM**
NPP	0.179	0.186	0.213
NSP	0.077	0.433	0.03
DPM	0.096	0.033	0.399

FP

	NSPM	**HI**	**SD**
NSPM	–0.687	0.521	0.006
HI	–0.322	1.114	–0.198
SD	0.011	0.613	–0.360

DPM

	NSPM	**NPB**	**HI**
NSPM	–0.425	0.167	0.235
NPB	–0.209	0.340	0.357
HI	–0.199	0.242	0.502

Table 7. Direct and indirect effects in a water-stressed environment for predictor variables in sequential path analysis (grouped into first, second and third order variables)

SY

	PH	TSW
PH	0.368	0.035
TSW	0.020	0.646

NPB

	NPM	NSP
NPM	0.720	0.144
NSP	0.269	0.385

TSW

	NSPM	HI	HFP
NSPM	0.515	0.062	–0.015
HI	0.124	0.257	0.000
HFP	0.033	0.000	–0.238

NSPM

	NSP	NSPB	NPP
NSP	1.626	–0.823	0.017
NSPB	1.413	–0.946	0.046
NPP	0.123	–0.192	0.228

PH

	NPB	SD	MSL	NSPM
NPB	0.199	0.079	0.200	0.152
SD	0.036	0.436	–0.055	–0.067
MSL	0.121	–0.073	0.327	0.103
NSPM	0.103	–0.099	0.114	0.293

effect on seed yield in both the non-stressed and water-stressed environments. Conventional path analysis and yield component studies in both the non-stressed and water-stressed environments gave conflicting results.

Discussion

For future breeding and selection, it is important to ascertain the variation available for plant structure and yield components in a species. A better understanding of how yield components influence yield formation in field crops can be obtained by using path analysis to determine the direct and indirect effects of primary, secondary and tertiary traits on yield formation. The main advantage is that path analysis not only identifies the most important factor directly affecting a trait, but also indicates how factors affect the trait indirectly through other factors (Kang *et al.,* 1983, 1989; Kozak and Kang, 2006). Previous research indicated that path

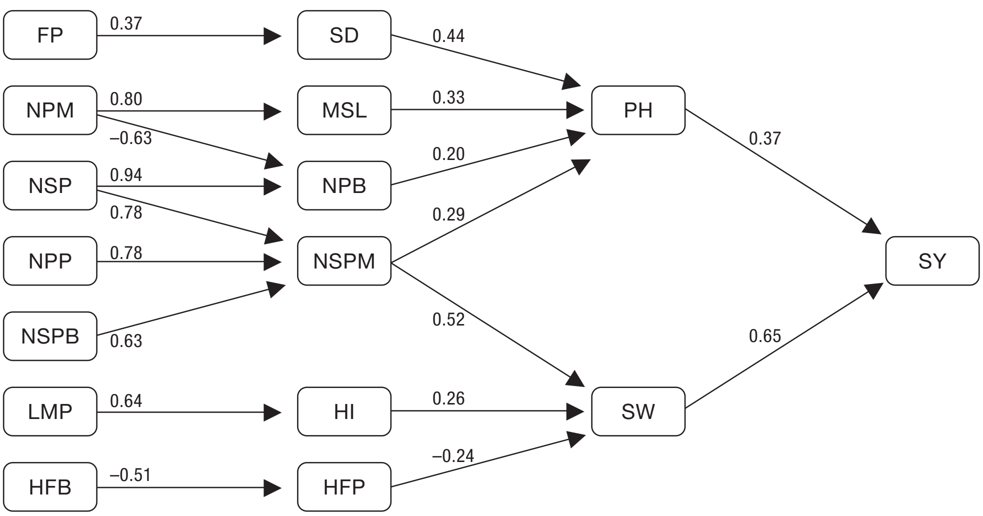

Figure 2. Sequential path analysis diagram illustrating the interrelationships among various traits contributing to seed yield in a water-stressed environment.

coefficient analysis provides more information on the interrelationships between yield components and yield than correlation coefficients (Dewey and Lu, 1959; Kang *et al.,* 1983; Gravois and McNew, 1993; Board *et al.,* 1997; Kozak and Kang, 2006). Path analysis helps to determine if yield component compensation is occurring. Yield component compensation occurs when two, or more, yield components affecting yield or any other yield component act inversely in their effects.

Many authors have reported similar results. Significant correlations between the number of pods plant^{-1} and seed yield, TSW and seed weight pod^{-1} were reported by Olsson (1960), Thurling and Vijendra-Das (1979), Ozer *et al.* (1999) and Ivanovska *et al.* (2007). Leilah and Al-Khateeb (2005) found high positive, significant, correlation between number of pods plant^{-1} with PH, stem diameter, NBP, number of seeds pod^{-1} of plant, TSW, harvest index and seed yield. The present results showed that the number of seeds pod^{-1} of plant (NSP) had no significant correlation with NBP, flowering period (FP), DPM, and MSL and SD traits (Table 1). Correlations between all the other traits were positive and significant. Singh and Singh (1995) and Khan *et al.* (2006) found similar results with regard to correlations between number of seeds pod^{-1} of plant with number of pods plant^{-1}, pod length of plant and seed yield.

Similar to these results, Sadaqat *et al.* (2003) reported strongly positive correlations between HI with the number of pods plant^{-1} and seed yield in canola. Degenhart and Kondra (1984) also found highly significant, positive correlation between HI and seed yield. The most interesting trait to use as an indirect means of selecting for yield is the TSW. This character is a yield component and is easier to determine than yield and generally has a high heritability (Engqvist and Becker, 1993). Leiah and Al-Khateeb (2005) and Ivanovska *et al.* (2007) reported a high, positive, significant, correlation between TSW and seed yield. Further, Marjanovic-Jeromela *et al.* (2008) reported a moderate, positive, significant correlation and Tuncturk and Ciftci (2007) reported a low positive, significant correlation between TSW and seed yield. In contrast Lee *et al.* (1977), Richards and Thurling (1979), Lefort-Buson and Dattee (1985), Engqvist and Becker (1993) and Basalma (2008) found no significant correlation between these two traits.

Like these results for PH, HI, NPP, and seed yield, Sadaqat *et al.* (2003) reported strongly positive correlations between seed yield and PH, HI, NPP and NBP in canola grown under drought conditions. Yadav and Kumar (1984) also found a highly significant, positive correlation between MSL and seed yield under water-stressed conditions. In an evaluation of water stressed Indian mustard (*Brassica juncea* L.) correlation analysis showed that seed yield was correlated positively with NPM and NPB (Yadav and Singh, 1996). The result of this study showed a significant negative correlation between seed yield and DPM, but Morrison and Stewart (2002) found no significant correlation between these two traits.

To construct a path diagram it is necessary to arrange the traits in order of their natural sequential development. The amount that a trait contributes to yield is influenced by the different traits through different paths. Imprecise assessment of a trait's contribution through incorrect pathways may misdirect breeding attempts, thus limiting the efficiency in selecting favourable cultivars (Agrama, 1996). Also the conventional approach for path analysis might result in a multicollinearity of variables, particularly when the correlations among some of the variables are high (Samonte *et al.,* 1998). To avoid the problems of conventional path analysis and multicollinearity of variables, sequential path analysis was used. On the other hand, the basic assumption while carrying out multiple regression is that the traits used as predictor variables are independent of each other, In reality yield-related traits are intricately interrelated, often leading to high multicollinearity. Thus a novel approach of organizing the variables into a different order path, based on trait relationships indicated by earlier studies, was adopted and used in different crops by Samonte *et al.* (1998), Mohammadi *et al.* (2003) and Asghari-Zakaria *et al.* (2007).

Sadaqat *et al.* (2003) reached similar inferences regarding the correlation between HI and NPB but the other traits did not show significant correlations. They also reported that, HI was significantly, positively correlated with NPM, length of main pod, TSW and seed yield. The relationship of NPP with NBP, NPM, NPB, MSL, HFB and HFP in a water-stressed environment was positive and significant (Table 2). Clarke and Simpson (1978) reported a significant negative correlation between NPP and number of seeds pod^{-1} of plant under a water deficit. The present study did not show significant correlation between these traits.

Seifert and Boelcke (1977), Ozer *et al.* (1999), Algan and Aygun (2001), and Tuncturk and Ciftci (2007) all also reported the highest direct effect of TSW on seed yield in non-stressed environments but differ from the findings of Thurling (1974), Ali *et al.* (2002), Ivanovska *et al.* (2007) and Marjanovic-Jeromela *et al.* (2008). Marinkovic *et al.* (2003) estimated the strongest direct effect of DFS and days to flowering ending (DFE) on seed yield. Generally, but not in all cases, NPP, NSP, NPM and NBP were associated with seed yield and had a direct effect on seed yield under drought conditions (Tak, 1976; Yadav and Kumar, 1984). The traits NPP, NSP, HI and TSW were associated with seed yield and had a direct effect on seed yield under normal conditions (Zuberi and Ahmad, 1973; Campbell and Kondra, 1978; Ozer *et al.,* 1999; Algan and Aygun, 2001; Marjanovic-Jeromela *et al.,* 2008). This study demonstrated the utility of sequential path analysis over conventional path analysis in discerning the direct and indirect effects of various yield-related traits. The traits FP, HI, MSL, NPB, NPP, NSP, NSPB, NSPM, SD and TSW were identified as the first, second and third order variables in both the non-stressed and water stressed environments (Figs. 1, 2). Number of seeds (pod^{-1}, pod of main stem and pods on lateral branch) and the TSW had direct and indirect effects on seed yield in both environments and many authors have estimated similar relationships in canola Tak (1976) under drought conditions and Degenhart and Kondra, 1984; Khan *et al.,* 2000; Ali *et al.,* 2003; Akbar *et al.,* 2007 under normal conditions). These results revealed the importance of the number of pods plant^{-1} and TSW as a criterion for canola yield improvement. Therefore, selection for increasing seed yield through these traits might be successful. Engqvist and Becker (1993) considered TSW as most interesting trait to use as an indirect selection criteria for yield. Therefore direct selection through the TSW should be effective. Similar reports have been made by Seifert and Boelcke (1977), Ozer *et al.* (1999), Algan and Aygun (2001) and Tuncturk and Ciftci (2007) which support the results of this study.

Many authors have estimated significant positive correlations between seed yield and other morphological traits. Ivanovska *et al.* (2007) and Tuncturk and Ciftci (2007) reached similar inferences regarding the correlations between seed yield with PH, number of pods plant^{-1}, number of seeds pod^{-1}, number of branches plant^{-1}, and the TSW. In contrast, Basalma (2008) reported that seed yield did not show any significant association with PH, number of branches plant^{-1}, number of pods on main stem, number of seeds pod^{-1} and the TSW. Finally, correlations between yield and yield-determining traits have been repeatedly analysed in rapeseed (Olsson, 1960; Thurling, 1974; Richards and Thurling, 1979; Degenhart and Kondra, 1984; Lefort-Buson and Dattee, 1985; Ozer *et al.,* 1999; Ivanovska *et al.,* 2007; Dehghani *et al.,* 2008).

As detected by path analysis flowering period and HI affected seed yield (Table 5), for breeding, selection based on pod length and seed number pod^{-1} is very important. Pod length can be easily determined and may serve as an indirect selection trait (Leon and Becker, 1995). Diepenbrock (2000) stated that the duration of growth, rate of production and HI are crucial for enhancing biomass and seed yield. During the growth cycle, establishment of the stand, flower initiation, the use of radiation and the availability of assimilates for pod set and seed filling are decisive factors influencing yield. Sequential path analysis showed that selection for new canola lines should be based on the number of pods plant^{-1} and seeds pod^{-1} (Arunachalam and Amirthadevarathinam, 1977; Guo *et al.,* 1987; Jiang and Guan, 1988; Ozer *et al.,* 1999) and HI (Diepenbrock, 2000) to raise seed yield per unit area.

According to simple correlation and sequential path analyses, in this experiment, there were very close relationships with seed yield and with NBP and DPM in the non-stressed environment. However, these two traits had no effect on seed yield in the water-stressed environment. In contrast results from the water-stressed environment indicated an effect of HFB, HFP, LMP, NPM and HI on seed yield. The positive direct effect of HI, on yield per plant, established in here supports the statement of Djakov (1982), cited by Ali *et al.* (2003) that breeding for increased HI remains the most effective method of breeding for high yield. It was concluded that selection of tall plants on the basis of a high NPM and longer main pods would raise the seed yield potential (Basalma, 2008). Height to the first lateral branch is an important trait, especially during harvesting, which makes rapeseed breeders eager to develop high yielding cultivars with a desirable plant architecture (Marjanovic-Jeromela *et al.,* 2008). With regard to this trait, breeding for drought tolerance with high values of HFB could also be useful at harvest.

Generally, both simple correlation and sequential path analyses, in this research, demonstrated very close interrelationships among seed yield, and other observed traits, with TSW as the first order variable in both environments and FP, HI, NPB, NPP, NSP, NSPB, NSPM, SD traits as second and third order variables. On the other hand, the most important yield components which did not differ under different moisture conditions were FP, HI, MSL, NPB, NPP, NSP, NSPB, NSPM, SD and TSW in the breeding research to increase seed yield. The importance of NBP and DPM can be seen for selection, in breeding programs, with the goal of improved canola seed yield under the normal condition. Selection for HFB, HFP, LMP, NPM and HI should be emphasized in lines in breeding programs with the aim of improved canola seed yield under arid and semi-arid conditions. The traits which mostly accounted for high yield under drought stress were HFB, HFP, LMP, NPM and HI, which produced consistent direct and indirect effects on seed yield.

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