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Variance Components, Correlation and Path Coefficient Analysis of Morpho-Physiological and Yield Related Traits in Spider Plant (*Gynandropsis gynandra* (L.) Briq.) under Water-Stress Conditions

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Abstract: Drought is the most complex abiotic stress for crop production at the global level. Therefore, developing new African spider plant genotypes tolerant to drought stress is one of the best approaches to achieving and optimizing high yield potential with water use efficiency. Advances in the selection of this crop can be determined by an understanding of genetic variability, heritability, and the associations that exist among different traits. The aim of this study was to gather information that will aid in the breeding of African spider plant cultivars with improved drought tolerance. A randomized complete block design (RCBD) experiment with eighteen genotypes and four replications was carried out across three water regimes: severe drought (30% field capacity), intermediate drought (50% field capacity), and well-watered (100% field capacity), in two seasons. Data on twelve morpho-physiological traits were recorded. The analysis of variance showed significant differences among genotypes ($p < 0.05$) in leaf yield and yield-related traits. The phenotypic coefficient of variation (PCV) was greater than the genotypic coefficient of variation (GCV) for all 12 traits evaluated. High to moderate heritability estimates combined with a high to moderate genetic advance were observed for number of leaves, leaf width, plant height and stem diameter under drought stress conditions, indicating that these traits are controlled by additive gene action. Because of their predominant additive gene effects, correlation with leaf yield and favorable direct and indirect effects via the other yield-attributing traits, number of leaves per plant, plant height, days to 50% flowering, relative water content, net photosynthesis and leaf length could be used as target traits to improve spider plant leaf yield under drought-stressed conditions.

Keywords: morpho-physiological traits; water regimes; variance components; trait association; heritability; genetic advance

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1. Introduction

Spider plant (*Gynandropsis gynandra* (L.) Briq.), also known as cat's whiskers, is a semi-wild indigenous African leafy vegetable (ALV) that has its natural habitat in Sub-Saharan Africa where it grows as a volunteer weed [1]. The crop is among the most essential primary food sources for several millions of people, particularly in the developing world. However, spider plant has received little or no effort in cultivation and domestication [2]. Despite less effort on domestication and cultivation, spider plant has been reported to be rich in essential nutrients that include vitamins A and C, magnesium, calcium, iron and

antioxidant enzymes (which include catalase, peroxidases, superoxide dismutase) together with non-enzymatic antioxidants (which include ascorbic acid, flavonoids, glutathione, tocopherols, and carotenoids) [3]. This makes it a good candidate for fighting several diseases and tackling malnutrition [4]. Equally important, spider plant is valuable as it can adapt to climate variability. Thus it is resilient to unfavorable environmental conditions and can effortlessly be cultivated in drought-prone areas [5]. As a result, the leafy vegetable plays a vital role in the nutrition, livelihood and health of populations residing in peripheral and marginal areas of Africa [6]. *Gynandropsis gynandra* has been reported to be mainly cultivated and commercialized by women, thus contributing to income generation and the improvement of livelihoods [7–9].

Nevertheless, to realize high leaf yields of spider plant, improved varieties are necessary. These varieties should be able to produce high yields even under stress conditions such as drought. Drought remains a problem of global magnitude that influences the production and quality of many crops. It occurs when an area experiences below-average rainfall leading to reduced moisture in the soil, decreased streamflow, and crop damage [10]. Drought stress is an outcome of water loss from plants eclipsing the ability of roots to imbibe water when the plant's water content decreases enough to interrupt normal plant processes [11]. Drought adversely affects crops resulting in yield reduction by influencing their anatomy, morphology, physiology and biochemistry [12,13]. Drought tolerance is, therefore, an essential breeding objective in most crop breeding programs. However, breeding for yield, which is also a complex quantitative trait, under drought stress is not easy. It has been reported that when moisture stress increases, the heritability and genetic variance of yield decrease [14–16]. Drought stress, thus, complicates the task of achieving genetic progress by intrinsically selecting for yield per se, hence the utilization of secondary traits is highly recommended [17].

Drought tolerance in crops can be improved through direct or indirect selection. However, it is challenging to make genetic improvements under drought conditions by selecting for yield per se, and thus the use of secondary traits is recommended [18,19]. These secondary traits are plant attributes, apart from yield, that give breeders additional knowledge on how the plant functions in a particular environment [20]. Ideal secondary traits should have a high heritability and genetic correlation with yield under water stress conditions [21]. These secondary traits or yield components can be characterized into morphological and physiological components and are all under genetic and environmental influences [22]. Thus, it is imperative to classify the total variation due to these traits into non-heritable and heritable components. This can be achieved with the aid of genetic parameters, namely, phenotypic and genotypic coefficients of variation, variance components and heritability estimates [23–25]. These estimates are important as they inform plant breeders on strategies that increase genetic gain during selection. Although correlation studies are useful in breeding programs, they do not provide adequate information and knowledge on the interrelationships of heritable traits. This, in turn, can result in inaccurate information. However, a combination of correlation studies and path coefficient analysis enables the determination of significant traits that influence economic traits such as yield. Path coefficient analysis estimates the direct and indirect effects of a parameter over the other and thus shows traits that can be used for the selection of yield either directly or indirectly [26].

Some studies have been conducted to establish the genetic diversity and genetic parameters of the spider plant to lay a scientific base for the preservation, evaluation and varietal enhancement of the species. Secondary morphological and physiological traits are presumed to be under simple genetic control compared with yield and are strongly correlated to it. This hypothesis has not been tested on the spider plant, especially under drought stress. Therefore, the objectives of this study were to (i) estimate variance components and heritability for yield and yield components under drought conditions, (ii) determine the relationship between yield and associated traits through correlation and path coefficient analysis under drought conditions and (iii) determine the secondary morpho-physiological traits to be used for selection in spider plant under drought situations.

2. Materials and Methods

2.1. Plant Material

This study looked at 18 African spider plant accessions from East Africa (5), West Africa (5), Southern Africa (4), and Asia (4). The accessions were obtained from the Laboratory of Genetics, Biotechnology, and Seed Science of the University of Abomey-Calavi in Benin, the World Vegetable Center, the Kenya Resource Center for Indigenous Knowledge (Kenya) and the University of Ouagadougou (Burkina Faso) as indicated in Table 1. The selected accessions are grown primarily under rain-fed conditions by smallholder farmers and are frequently exposed to prolonged drought stress. These accessions were also selected based on germination percentage and ability to produce high leaf yield under optimum conditions.

Table 1. List of genotypes used in the present study.

Genotype	Genebank of Origin	Country of Origin	Region
L01	KENRIK *	Kenya	East Africa
L02	University of Ouagadougou	Burkina-Faso	West Africa
L03	GBioS/UAC	Benin	West Africa
L04	GBioS/UAC	Benin	West Africa
L05	GBioS/UAC	Togo	West Africa
L06	University of Ouagadougou	Burkina-Faso	West Africa
L07	World Vegetable Center	Thailand	Asia
L08	World Vegetable Center	Zambia	Southern Africa
L09	World Vegetable Center	South Africa	Southern Africa
L10	World Vegetable Center	Malaysia	Asia
L11	World Vegetable Center	Uganda	East Africa
L12	World Vegetable Center	Malaysia	Asia
L13	KENRIK	Kenya	East Africa
L14	World Vegetable Center	Uganda	East Africa
L15	LUANAR	Malawi	Southern Africa
L16	Otjiwarongo	Namibia	Southern Africa
L17	World Vegetable Center	Laos	Asia
L18	KENRIK	Kenya	East Africa

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2.2. Growing Environments, Experimental Design and Agronomic Practices

Experiments were conducted at the University of KwaZulu-Natal, School of Agricultural, Earth, and Environmental Sciences in Pietermaritzburg, South Africa, in the Controlled Environment Research Unit (CERU). The experiments were carried out over two seasons from October 2020 to December 2020 (Season 1) and from February 2021 to April 2021 (Season 2).

The 18 accessions were evaluated under three varying water regimes in each of the two seasons. The water regimes were: severe stress (30% field capacity), moderate stress (50% field capacity) and well-watered (100% field capacity), defined based on the findings of Masinde et al. [27]. The seeds of each accession were sown in dedicated seedling trays and nurtured into seedlings before transplanting into individual pots, two weeks after sowing, under each water regime. In each water regime, the 18 genotypes were laid in a randomized complete block design with four replications, and each plot constituted three plants for both experiments. The seedlings were irrigated to keep the soil moisture of the pots at 100% field capacity for the first seven days after transplanting. Drought stress was applied from the eighth day after transplanting by stopping the irrigation to 21 days after transplanting, coinciding with the harvest maturity stage. The quantity of water applied in the pots was determined by calculating the optimum amount of water (field capacity, FC) of the potting mixture using the procedure described by Kesiime et al. [28]. The pots used for the experiment were medium-sized plastic pots with three plants per plot, one plant in

each plot, and each pot with a capacity of 4.5 kg. Composted pine bark was used as the potting medium. During the transplanting process, (N:P:K) (2:3:2) fertilizer was applied to seedlings in the pots using the basal application technique at a rate of 140 kg ha^{-1}.

2.3. Data Collection

2.3.1. Phenological and Morphological Traits

Days to 50% flowering (Fl) were determined as the number of days between the planting date and the date when 50% of the plants began flowering. Plant height (Ph) in cm was measured using a meter rule from the surface of the soil to the tip of the flower for the three plants in each plot, and an average was recorded. Leaf length (Ll) was measured in cm using a ruler as the length per each leaf from the pointy part at one end to the point at which the leaf joins the stalk at the other end; an average of three leaves per plant was recorded. Leaf width (Lw) in cm was measured using a ruler as the longest extension of any two points on the blade edge perpendicular to the leaf length axis. Stem diameter (Sd) was measured in mm on the base of the plant stem using a digital vernier caliper, and an average of three plants was recorded.

2.3.2. Physiological Traits

Most of the physiological traits were recorded from 08:00 to 12:00 midday to prevent a sizable possibility of diurnal variation in stomatal conductance [29].

2.3.3. Leaf Gas Exchange Parameters

During the planting season, the following parameters were recorded three times: net photosynthesis (Photo), transpiration rate (Trans, mmol m^{-2} s^{-1}) and stomatal conductance (Cond, mol m^{-2} s^{-1}) with an LI-6400XT Portable Photosynthesis System (Licor Bioscience, Inc., Lincoln, NE, USA) fully equipped with an infrared gas analyzer (IRGA) connected to a leaf chamber fluorometer (LCF). The outward leaf CO_2 concentration (C_a) and formulated saturating photosynthetic active radiation (PAR) were set to 400 µmol^{-1} and 1000 μmol^{-2} m^{-2} s $^{-1}$, respectively. The leaf temperature was kept constant at 25 °C. The water flow rate and relative humidity were both held constant at 500 μmol and 43%, respectively. The leaf-to-air vapor pressure deficit in the cuvette was kept constant at 1.7 kPa to avoid stomatal closure due to low air humidity. Leaf gas exchange parameters were measured on the third half-formed leaf from the plant's tip by attaching the leaf inside the sensor head. For each accession, measurements were taken from three plants in both non-stressed and drought-stressed conditions.

2.3.4. Chlorophyll Content and Relative Water Content

Chlorophyll content (Spad) was measured for three flag leaves in each plot using a Biobase portable chlorophyll meter (Bio-Base, Jinan, China). To obtain an accurate estimate of relative water content, 6 fully expanded relatively young leaves from each treatment were collected (*RWC*). After thoroughly drying the leaf's surface with tissue paper, everything was wrapped in polythene bags and transported to the laboratory. The leaf samples were weighed to determine the fresh weight of the leaf (*FW*). The samples were set in Petri dishes with distilled water and left in the dark for the entire night. Excess water from the leaves was blotted with blotting paper and turgid weight was measured (*TW*). The leaves were then dried in an oven at 80–85 °C for 24 h, and the dry weight was measured (*DW*).

Relative water content (*RWC*) was estimated based on the following formula:

$$(\%)\ RWC = \frac{FW - DW}{TW - DW} \times 100 \quad (1)$$

where *FW* = sample of fresh leaf weight, *TW* = sample of turgid leaf weight and *DW* = sample of dry leaf weight.

2.3.5. Yield and Yield-Related Component Traits

The number of leaves per plant (Nl) was determined by counting all the leaves per plant, and an average for three plants was recorded. Leaf yield (Ly) was obtained by weighing the leaf yield per plot with a scale.

2.4. Data Analysis

2.4.1. Analysis of Variance

Analysis of variance (ANOVA) for the recorded traits in each water regime across seasons was computed in R software version R-4.1.1 using restricted maximum likelihood (REML) analysis with linear mixed models [30]. The ANOVA model in each water regime, and in each season can be presented as in Equation (2). For combined analysis, seasons were treated as random effects, whereas accessions were treated as fixed effects. The *F* statistic ($p < 0.05$) was used to test the significance of different items in the ANOVA, which is the ratio of the sum of mean squares to the mean square error.

$$y_{ij} = \mu + t_i + b_j + e_{ij}\ i = 1,\ 2,\ \cdots,\ 18,\ j = 1,\ 2 \tag{2}$$

where i is the general mean, t_i is the effect of the ith genotype, b_j is the effect of the jth block and e_{ij} is the random error term.

2.4.2. Evaluating Genotypic and Phenotypic Variances

Genotypic V_G, genotype by environment interaction V_{GE} and error/environmental variances (V_E) were estimated by employing the lmer package in R software version R-4.1.1 [30]. Phenotypic variances (σ_p^2) were estimated using the following formula

$$V_p = V_G + \frac{V_{GE}}{l} + \frac{V_E}{rl} \tag{3}$$

where, l is the number of growing environments and r is the number of replications.

2.4.3. Evaluating Genotypic and Phenotypic Coefficient of Variation

These components were estimated based on the formula proposed by Burton [31].

Genotypic coefficient of variation,

$$\text{GCV\%} = \frac{\sqrt{V_G}}{\bar{x}} \times 100 \tag{4}$$

where V_G = genotypic variance and $\bar{x}$ is the mean for the population.

Phenotypic coefficient of variation,

$$\text{PCV\%} = \frac{\sqrt{V_P}}{\bar{x}} \times 100 \tag{5}$$

where V_P = phenotypic variance and $\bar{x}$ is the population mean.

The coefficients of variation (GCV and PCV) were classified as low: less than 10%, moderate: 10% to 20%, and high: greater than 20% as suggested by Sivasubramanjan and Menon [32].

2.4.4. Evaluation of Heritability

Broad sense heritability (H^2) was determined for various traits as per the formula suggested by Allard [33]. The estimates for heritability for a single environment were performed using the formula

$$H^2 = \sigma_g^2/\sigma_p^2 \times 100 \tag{6}$$

where σ_p^2 is the phenotypic variance and σ_g^2 is the genotypic variance.

Heritability percentage was classified as low: less than 30%, medium: 30–60% and high: greater than 60% according to Robinson et al. [34].

2.4.5. Determination of Genetic Advance (GA) and Genetic Advance as Percent of the Mean (GAM)

The genetic advance for different characteristics was determined with the use of the formula proposed by Johnson et al. [35] using the formula in Equation (7).

$$\text{Genetic advance GA} = H^2 \cdot i \cdot \sigma_p \quad (7)$$

where H^2 is broad-sense heritability, i is the selection differential at 5% selection intensity and σ_p is the phenotypic standard deviation.

The genetic advance as a percent of the mean was estimated using the following formula:

$$\text{GA \% mean} = \frac{\text{GA}}{\overline{x}} \times 100 \quad (8)$$

where GA = genetic advance and $\overline{x}$ = population mean.

Following Falconer and Mackay [36], the genetic advance (GA percent) values were classified as low: less than 10%, moderate: 10–20% and high: greater than 20%.

2.4.6. Correlation Analysis

Phenotypic correlation analysis was conducted following the Pearson's correlation coefficient method using ("corrplot") package in R software version R-4.1.1 [30,32].

$$r_p = \frac{p\ cov\ x\ .\ y}{\sqrt{\delta^2\ px\ .\ \delta^2 py}} \quad (9)$$

where r_p is phenotypic correlation coefficients, $p\ cov\ x\ .\ y$ is phenotypic covariance between variables x and y, $\delta^2\ px$ is the phenotypic variance for variable x and $\delta^2 py$ is the phenotypic variance for variable y.

2.4.7. Path Coefficient Analysis

Path coefficient analysis was performed using correlation coefficients as suggested by Dewey and Lu [26].

$$r_{ij} = p_{ij} + \sum r_{rk} p_{kj} \quad (10)$$

where r_{ij} = mutual relationship between independent character i and the dependent character j as can be seen by the phenotypic correlation coefficients. p_{ij} = elements of direct effects of the independent trait i on the dependent character j as evident by the path coefficients. $\sum r_{rk} p_{kj}$ = summation of indirect effects of a given independent character i on a given dependent character j via all other independent characters k.

A path analysis scale suggested by Lenka and Mishra [37] was used to categorize the estimates as negligible with values ranging from 0.00 to 0.09, low with values ranging from 0.10 to 0.19, moderate with values ranging from 0.20 to 0.29, high with values ranging from 0.30 to 0.99 and more than 1.00 as very high path coefficients.

The involvement of additional unknown characters in the analysis is estimated as the residual P_R using the formula:

$$P_{R=}\sqrt{(1 - \sum P_{ij} r_{ij})}. \quad (11)$$

3. Results

3.1. Analysis of Variance

The mean squares, means and coefficient of variations (CV) for morpho-physiological traits and yield components across two growing seasons under well-watered, mild stress and severe stress conditions are presented in Table 2a–c, respectively. From the analysis

of variance, highly significant differences ($p < 0.05$) were noted between the main effects of seasons, genotypes, replications and their interactions for a good number of traits (Table 2a–c). Under well-watered conditions (Table 2a), the seasonal effect was significant ($p < 0.05$) for a large number of traits including days to 50% flowering (Fl), plant height (Ph), leaf length (Ll), stomatal conductance (Cond), net photosynthesis rate (Photo) and transpiration rate (Trans). Under mild stress conditions, most traits were non-significant for the seasonal effect except for days to 50% flowering, leaf length, chlorophyll content and transpiration rate. Similarly, under severe stress conditions, the seasonal effects were non-significant on most traits except for days to 50% flowering, leaf width, stem diameter, chlorophyll content, stomatal conductance and leaf yield.

The mean squares for genotypes varied significantly ($p < 0.05$) in almost all the traits under the three water regimes. The mean squares for genotypes were highly significant ($p < 0.01$) for all the traits studied under well-watered conditions (Table 2a). Under mild stress conditions, the genotype effect was significant ($p < 0.05$) for the majority of traits with chlorophyll content as the only non-significant trait (Table 2b). Similarly, under severe stress conditions (Table 2c), the genotype effect was significant on most traits except for chlorophyll content (Spad), stomatal conductance (Cond) and transpiration rate (Trans).

3.2. Variance Components and Heritability Estimates

The variance components estimates, heritability and genetic advances of 18 spider plant genotypes evaluated under three water regimes are presented in Table 3a–c. Under well-watered conditions, genotypic variances ranged from 0.00 for transpiration rate (Trans) to 1020.20 for leaf yield (Ly). In addition to the above, the genotypic variance ranged from 0.00 for stomatal conductance (Cond) to 182.91 for leaf yield (Ly) under mild stress conditions and 0.00 for stomatal conductance (Cond) to 76.02 for number of leaves (Nl) under severe stress. The phenotypic variances observed ranged from 0.00 for stomatal conductance (Cond) to 1022.43 for leaf yield (Ly) under well-watered conditions, 0.00 for stomatal conductance to 184.74 for leaf yield (Ly) under mild stress conditions and 0.00 for stomatal conductance to 77.06 for number of leaves under severe stress conditions. For all yield and yield-contributing traits, phenotypic variance was greater than genotypic variance across the three water regimes.

The genotypic coefficient of variation estimates (GCV) ranged from 0.10% (relative water content) to 46.86% (leaf yield) under well-watered conditions, 0.11% (relative water content) to 54.42% (leaf yield) under mild stress conditions, and 0.00% (stomatal conductance) to 74.22% (leaf yield). In this study, it was observed that well-watered conditions had a phenotypic coefficient of variation (PCV) ranging from 0.10% (relative water content) to 46.91% ((leaf yield), whereas mild stress conditions had a PCV ranging from 0.11 (relative water content) to 46.86% (leaf yield) and lastly, severe stress conditions had a PCV ranging from 0.00% (stomatal conductance) to 74.34% (leaf yield). High GCV and PCV values of >20% were recorded for leaf yield (46.86% and 46.91%, respectively) and number of leaves (34.85% and 35.02, respectively), under well-watered conditions. The same traits, leaf yield and number of leaves, also showed a high (>20%) GCV (54.42% and 28.55%, respectively) and PCV (54.70% and 28.85%, respectively) under mild stress. Under severe stress conditions, GCV and PCV were high for leaf yield (74.22% and 74.34%, respectively), number of leaves (39.63% and 39.90%, respectively) and plant height (21.95% and 26.54%, respectively). As shown in Table 3a–c, moderate (10–20%) GCV and PCV values were recorded for leaf length (15.04% and 11.40%, respectively), leaf width (13.39% and 10.67%, respectively), stem diameter (14.01% and 11.92%, respectively) and stomatal conductance (18.37% and 13.63%, respectively) under well-watered conditions. Under mild stress conditions, moderate values were observed for plant height (18.67%, GCV) and (16.55%, PCV), stem diameter ((15.31%, GCV) and (12.75%, PCV)) and stomatal conductance (23.05%, GCV) and (11.95%, PCV). Leaf width (11.98%) and (10.15%) together with stem diameter (17.19%) and (11.48%) had moderate (10–20%) GCV and PCV values, respectively, under severe stress conditions.

Table 2. Mean squares from analysis of variance of 12 traits under three water regimes.

Source	Df	Fl	Ph	Ll	Lw	Sd	Spad	*RWC*	Cond	Photo	Trans	Nl	Ly
(a) Well-watered													
Season	1	220.03 ***	511.51 **	3.55 *	4.41	1.54	19.43	0.30	0.05 ***	350.91 ***	0.00 ***	10.6	3.5
Genotype	17	113.12 ***	223.22 ***	6.43 ***	8.37 ***	7.15 ***	19.88 ***	430.73 ***	0.01 ***	225.71 ***	0.00 **	6438.5 ***	8179.6 ***
Rep	3	18.06	333.62 ***	2.70 *	4.62 *	8.53 ***	14.75	12.48	0.02 ***	12.24	0.00 ***	284.8 **	435 ***
Season × Rep	3	336.68 ***	330.48 ***	3.94 **	8.98 ***	1.98	1.08	6.21	0.00	149.38 ***	0.00 ***	122.4	194.3 ***
Season × Genotype	17	7.23	83.80 *	2.76 ***	3.09 **	2.00 **	12.74 *	1.38	0.01 **	28.51 **	0.00	37.4	7.1
Residuals	102	17.97	47.41	0.75	1.20	0.83	6.52	3.54	0.00	11.67	0.00	68.4	19.6
Mean		58	52.78	5.96	7.64	6.75	40.49	74.38	0.2310	75.43	0.0178	81	68.16
CV		8.65	13.05	14.57	14.36	13.51	6.31	2.53	21.31	4.53	17.66	10.21	6.50
(b) Mild stress													
Season	1	300.44 ***	60.32	2.56 *	0.93	1.36	45.68 *	0.11	0.00	0.19	0.00 ***	0.69	16.07
Genotype	17	31.48 ***	332.39 ***	2.52 ***	3.75 ***	3.61 ***	10.09	293 ***	0.01 ***	73.6 ***	0.00 *	1231.52 ***	1477.94 ***
Rep	3	80.15 ***	91.62	0.72537	0.79	2.28	10.34	1.26	0.01 *	5.36	0.00	42.35	34.89
Season × Rep	3	5.64	163.81 **	0.42796	0.56	2.00	2.51	1.39	0.01	347.42 ***	0.00	11.82	14.56
Season × Genotype	17	14.65	72.2 *	1.45 ***	2.00 **	1.11	5.34	1.19	0.01 *	24.76 *	0.00	5.55	1.61
Residuals	102	9.83	39.81	0.47	0.75	0.95	6.63	1.26	0.00	14.21	0.00	29.27	16.8
Mean		38	34.53	4.27	5.41	4.39	34.64	53.14	0.15	59.83	0.0124	43	24.85
CV		8.36	18.27	16.04	16.06	22.28	7.44	2.11	40.08	6.30	20.87	12.58	16.49
(c) Severe stress													
Season	1	637.56 ***	142.80	0.56	4.03 **	7.47 ***	42.25 *	4.59	0.03 ***	64.66	0.00	0.44	7.27 *
Genotype	17	52.66 ***	295.30 ***	1.07 ***	1.99 ***	2.42 ***	14.20	196.32 ***	0.00	157.34 ***	0.00	616.47 ***	432.45 ***
Rep	3	38.53 *	167.82 **	0.27	0.50	0.25	8.72	3.27	0.01 *	21.88	0.00 *	14.28	25.86 ***
Season × Rep	3	81.69 ***	19.66	0.05	0.30	0.92	57.42 ***	1.57	0.00	70.12 *	0.00 ***	5.31	0.49
Season × Genotype	17	6.47	93.47 **	0.98 ***	0.56	1.34 ***	5.05	0.96	0.00	37.57 *	0.00	1.53	0.23
Residuals	102	12.41	37.36	0.28	0.44	0.46	9.26	4.28	0.00	17.98	0.00	9.43	1.61
Mean		29	22.89	3.36	4.16	3.20	30.15	39.20	0.1213	44.64	0.0094	22	9.89
CV		12.15	26.71	15.61	16.01	21.24	10.10	5.28	36.79	9.50	27.75	13.96	12.83

* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$, Df = Degrees of freedom, Fl = Days to 50% flowering, Ph = Plant height, Ll = Leaf length, Lw = Leaf width, Sd = Stem diameter, Spad = Chlorophyll content, *RWC* = Relative water content, Photo = Net photosynthesis rate, Cond = Stomatal conductance, Trans = Transpiration rate, Nl = Number of leaves per plant, Ly = Leaf yield.

Table 3. Variance components estimates and genetic parameters of eighteen spider plant genotypes evaluated over two seasons, under three water regimes (a) well-watered; (b) mild stress; (c) severe stress.

Trait	V_G	$V_{G\,x\,E}$	V_E	V_P	PCV	GCV	H^2	GA	GAM (%)
(a) Well-watered									
Fl	12.09	0.00	16.44	14.14	6.48	5.99	85.47	6.62	11.42
Ph	17.43	9.10	47.41	27.90	10.01	7.91	62.46	6.80	12.88
Ll	0.46	0.50	0.75	0.80	15.04	11.40	57.43	1.06	17.80
Lw	0.66	0.46	1.20	1.05	13.39	10.67	63.49	1.34	17.51
Sd	0.65	0.29	0.83	0.89	14.01	11.92	72.39	1.41	20.89
Spad	0.89	1.55	6.52	2.48	3.89	2.33	35.90	1.17	2.88
RWC	0.01	0.00	0.00	0.01	0.10	0.10	99.25	0.15	0.20
Photo	24.65	4.21	11.67	28.21	7.04	6.58	87.37	9.56	12.67
Cond	0.00	0.00	0.00	0.00	18.37	13.63	55.04	0.05	20.83
Trans	0.00	0.00	0.00	0.00	9.59	6.51	46.06	0.00	9.10
Nl	796.82	0.00	63.96	804.82	35.02	34.85	99.01	57.86	71.43
Ly	1020.20	0.00	17.83	1022.43	46.91	46.86	99.78	65.73	96.43
(b) Mild stress									
Fl	2.10	1.20	9.84	3.94	5.22	3.82	53.47	2.19	5.75
Ph	32.67	7.79	39.87	41.55	18.67	16.55	78.63	10.44	30.24
Ll	0.13	0.25	0.47	0.32	13.15	8.56	42.39	0.49	11.49
Lw	0.23	0.30	0.75	0.47	12.66	8.78	48.14	0.68	12.55
Sd	0.31	0.04	0.96	0.45	15.31	12.75	69.43	0.96	21.89
Spad	0.45	0.00	6.45	1.26	3.24	1.95	36.04	0.83	2.41
RWC	0.00	0.00	0.00	0.00	0.11	0.11	99.58	0.12	0.23
Photo	6.13	2.58	14.22	9.20	5.07	4.14	66.65	4.16	6.96
Cond	0.00	0.00	0.00	0.00	23.05	11.95	26.86	0.02	12.75
Trans	0.00	0.00	0.00	0.00	10.14	6.17	37.08	0.00	7.74
Nl	150.72	0.00	25.74	153.94	28.85	28.55	97.91	25.02	58.20
Ly	182.91	0.00	14.63	184.74	54.70	54.42	99.01	27.72	111.56
(c) Severe stress									
Fl	5.14	0.00	11.56	6.58	8.85	7.82	78.05	4.13	14.22
Ph	25.25	13.99	37.37	36.91	26.54	21.95	68.40	8.56	37.40
Ll	0.01	0.17	0.27	0.13	10.89	3.61	10.96	0.08	2.46
Lw	0.18	0.03	0.44	0.25	11.98	10.15	71.89	0.74	17.73
Sd	0.14	0.22	0.46	0.30	17.19	11.48	44.64	0.51	15.81
Spad	0.69	0.00	8.66	1.77	4.42	2.76	38.99	1.07	3.55
RWC	0.00	0.00	0.00	0.00	0.13	0.13	98.10	0.10	0.26
Photo	14.97	4.89	17.98	19.67	9.93	8.67	76.13	6.96	15.58
Cond	0.00	0.00	0.00	0.00	15.77	0.00	0.00	0.00	0.00
Trans	0.00	0.00	0.00	0.00	10.91	4.89	20.06	0.00	4.51
Nl	76.02	0.00	8.30	77.06	39.90	39.63	98.65	17.84	81.09
Ly	53.88	0.00	1.41	54.06	74.34	74.22	99.67	15.10	152.64

V_G = genotypic variance, $V_{G\,x\,E}$ = genotype x environment interaction variance, V_E = error variance, V_P = phenotypic variance, PCV = phenotypic coefficient of variation, GCV = genotypic coefficient of variation, H^2 = heritability, GA = genetic advance, GAM = genetic advance as a percentage of the mean, Fl = days to 50% flowering, Ph = plant height, Ll = leaf length, Lw = leaf width, Sd = stem diameter, Spad = chlorophyll content, *RWC* = relative water content, Photo = net photosynthesis rate, Cond = stomatal conductance, Trans = transpiration rate, Nl = number of leaves per plant, Ly = leaf yield.

Although most of the traits had minor differences between PCV and GCV values across all water regimes, a few traits showed a significant difference between the PCV and GCV values. Stomatal conductance (23.05–11.95) showed a significant difference between the PCV and GCV values under mild stress conditions. Under severe stress conditions, leaf length (10.89–3.61), stem diameter (17.19–11.48), stomatal conductance (15.77–0.00) and transpiration rate (10.91–4.89) exhibited large differences between the PCV and GCV values. The PCV was higher than its corresponding GCV for all the traits across water regimes.

Heritability estimates for all the studied traits varied from high (>60%), moderate (30–60%) and low (<30%) across all the water regimes (Table 3a–c). Under well-watered conditions, high heritability values (>60%) were observed for the vast majority of traits except for the transpiration rate (30–60%), chlorophyll content rate (30–60%), stomatal conductance (30–60%) and leaf length (30–60%). Plant height (78.63%), stem diameter (69.43%), relative water content (99.58%), net photosynthesis rate (66.65%), number of leaves (97.91%) and leaf yield (99.01%) exhibited high heritability (>60%) under mild stress conditions. Furthermore, days to 50% flowering (53.47%), leaf length (42.39%), leaf width (48.18%), chlorophyll content (36.04%) and transpiration rate (37.08%) showed moderate (30–60%) heritability estimates under mild stress conditions. In contrast, stomatal conductance (26.86%) showed a low heritability value under mild stress conditions. Under severe stress conditions, most traits had a high heritability (>60%), and these included leaf yield (99.67%), number of leaves (98.65%), plant height (68.40%), days to 50% flowering (78.05%), photosynthesis rate (76.13%), relative water content (98.10%) and leaf width (71.89%). In addition to the above, moderate heritability estimates (30–60%) were recorded for stem diameter (44.64%) and chlorophyll content (38.99%). Stomatal conductance (0.00%), transpiration rate (20.06%) and leaf length (10.96%) recorded low heritability (<30%) under severe stress.

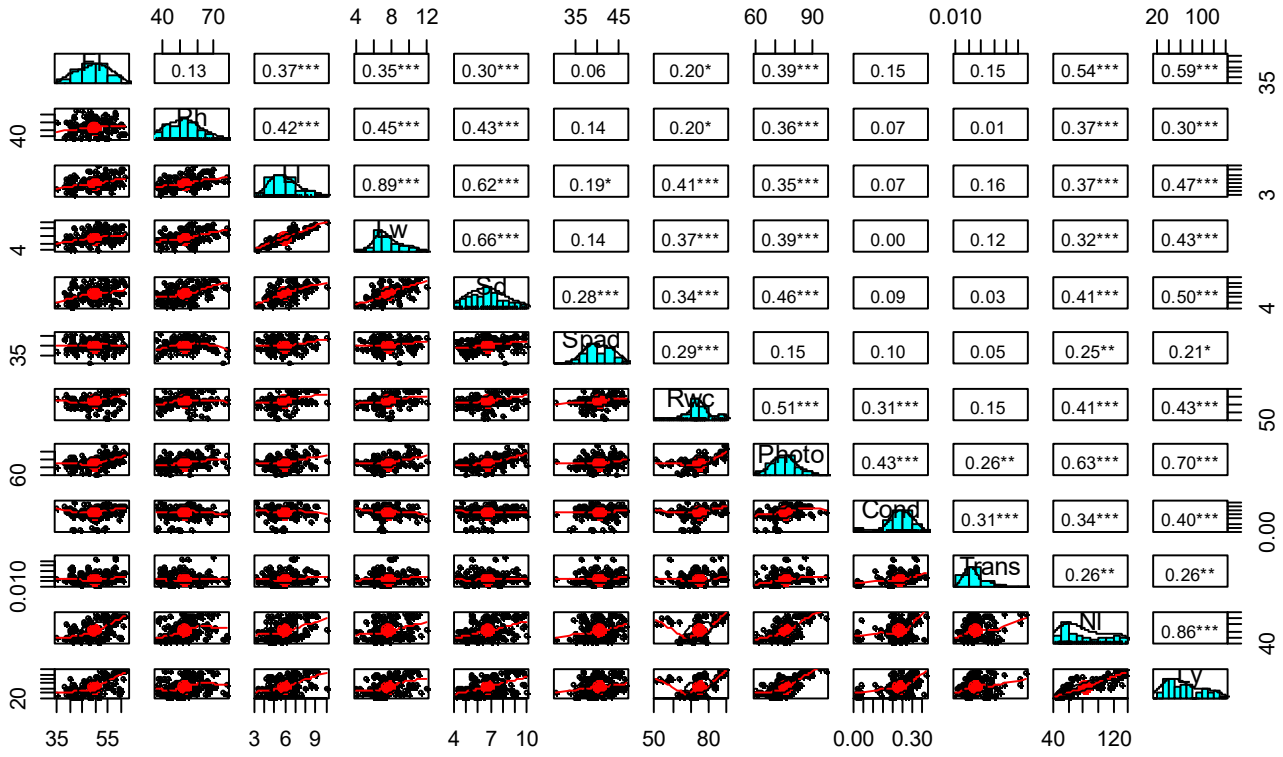
Genetic advance as a percentage of the mean varied from low (0–10%) to moderate (10–20%) to high (20% and above) (Table 3a–c). High values of genetic advance (20% and above) were reported for stem diameter (20.89%), number of leaves (71.43%), stomatal conductance (20.83%) and leaf yield (96.43%) under well-watered conditions. Moderate GAM values (10–20%) were also noted for days to 50% flowering (11.42%), plant height (12.88%), leaf length (17.80%), leaf width (17.51%) and net photosynthesis rate (12.67%) under well-watered conditions. Under mild stress conditions, high genetic advance estimates (20% and above) were observed for leaf yield (111.56%), number of leaves (58.20%), stem diameter (21.89%) and plant height (30.24%). In addition to high GAM values, moderate values (10–20%) were also observed for leaf length (11.49%), leaf width (12.55%) and stomatal conductance (12.75%) under mild stress conditions. Plant height (37.40%), number of leaves (81.09%) and leaf yield (152.64%) exhibited a high GAM (20% and above) values under severe stress. Furthermore, days to 50% flowering (14.22%), leaf width (17.73%) and stem diameter (15.81%) and net photosynthesis rate (15.58%) showed moderate (10–20%) GAM values under severe stress conditions.

A high heritability coupled with high genetic advance was observed for stem diameter, stomatal conductance, number of leaves and leaf yield under well-watered conditions. Moderate heritability coupled with high genetic advance was also noted for stomatal conductance under well-watered conditions. In addition, high to moderate heritability estimates accompanied with moderate genetic advance were observed for days to 50% flowering, photosynthesis, plant height, leaf length and leaf width under well-watered conditions. Additionally, a high heritability estimate coupled with a low genetic advance was observed for relative water content. Plant height, stem diameter, number of leaves and leaf yield had high heritability estimates coupled with high genetic advance under mild stress conditions. Furthermore, high heritability estimates coupled with low genetic advance were observed for relative water content and net photosynthesis under mild stress conditions. Moderate heritability accompanied with moderate genetic advance were observed for leaf length and leaf width under mild stress conditions. Under severe stress conditions, plant height, number of leaves and leaf yield showed a high heritability accompanied by high genetic advance. High to moderate heritability accompanied with moderate genetic advance were observed for days to 50% flowering, leaf width, stem diameter and net photosynthesis under severe stress. In addition, a high heritability coupled with a low genetic advance was also observed for relative water content.

3.3. Correlation Coefficient Estimates

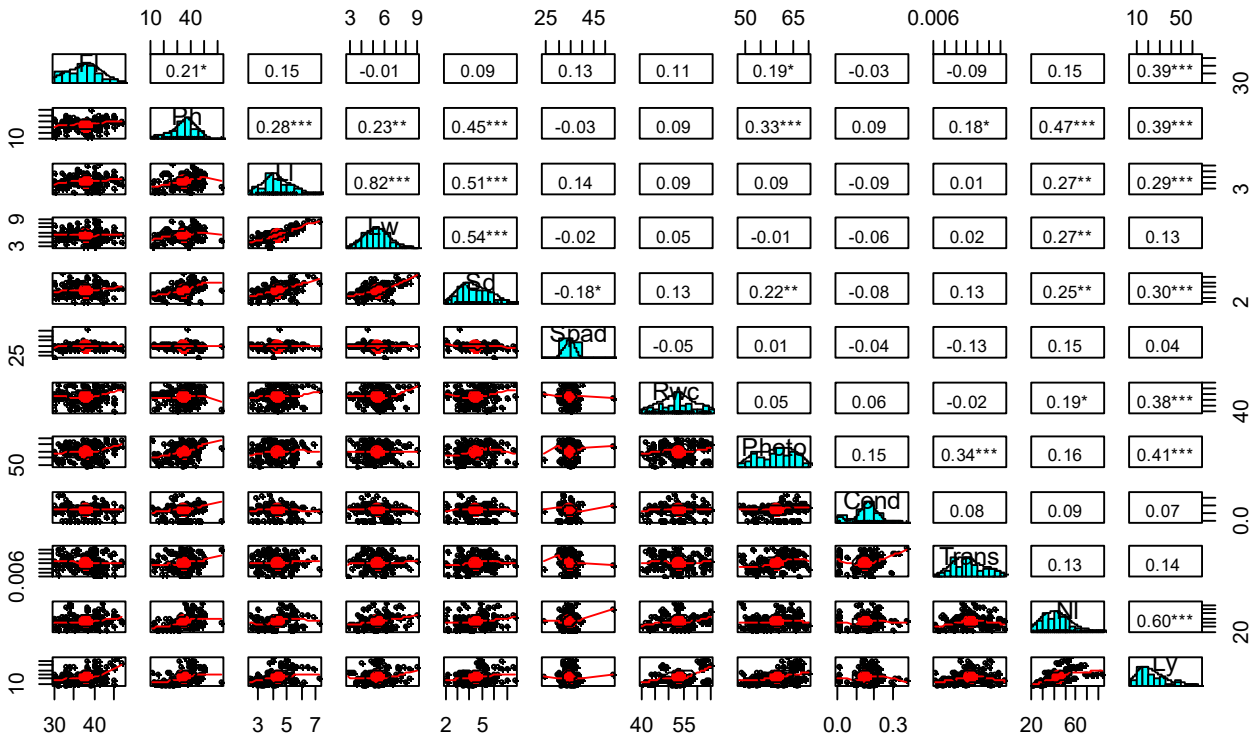
Figure 1a–c shows Pearson's correlation coefficients (r) among morphological and physiological traits of 18 spider plant accessions in non-stressed and water-stressed conditions. In this study, the degree of association was divided into three categories: weak (0–0.3), moderate (0.3–0.7) and strong (0.7+). Under well-watered conditions, leaf yield showed a strong positive correlation with the number of leaves (r = 0.86 ***), moderate positive association with net photosynthesis rate (r = 0.70 ***), stem diameter (r = 0.50 ***), days to 50% flowering (r = 0.59 ***), leaf length (r = 0.47 ***), leaf width (r = 0.43 ***), relative water content (r = 0.43 ***) and stomatal conductance (r = 0.40 ***). Weak and positive correlations were observed between leaf yield and plant height (r = 0.30 ***), transpiration rate (r = 0.26 ***) and chlorophyll content (r = 0.21 *). A strong and positive correlation was also observed between leaf length and leaf width (r = 0.89 ***) under well-watered conditions (Figure 1a).

Under mild stress conditions, leaf yield showed a moderate and positive correlation with the number of leaves per plant (r = 0.60 ***), net photosynthesis rate (r = 0.41 ***), plant height (r = 0.39 ***), days to 50% flowering (r = 0.39 ***) and relative water content (r = 0.38 ***). Weak and positive associations were observed between leaf yield and stem diameter (r = 0.30 ***) and leaf length (r = 0.29 ***). Leaf length and leaf width also showed a strong and positive correlation (r = 0.82 ***) under mild stress conditions.

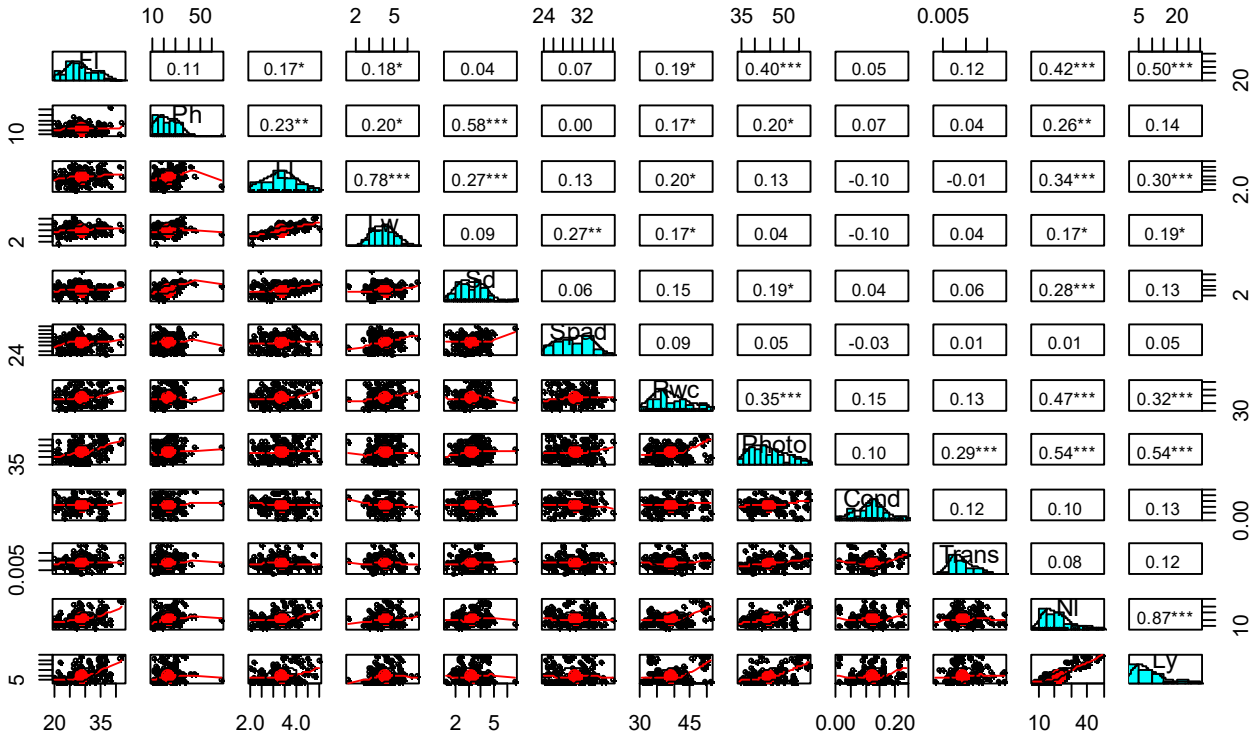


(**a**) Well-watered

Figure 1. *Cont.*



(**b**) Mild stress



(**c**) Severe stress

Figure 1. Pearson correlation coefficients among twelve morpho-physiological traits of 18 eighteen

African spider plant accessions evaluated under three water regimes (**a**) well-watered (**b**) mild stress (**c**) severe stress. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$, Fl = days to 50% flowering, Ph = plant height, Ll = leaf length, Lw = leaf width, Sd = stem diameter, Spad = chlorophyll content, Rwc = relative water content, Photo = net photosynthesis rate, Cond = stomatal conductance, Trans = transpiration rate, Nl = number of leaves per plant and Ly = leaf yield.

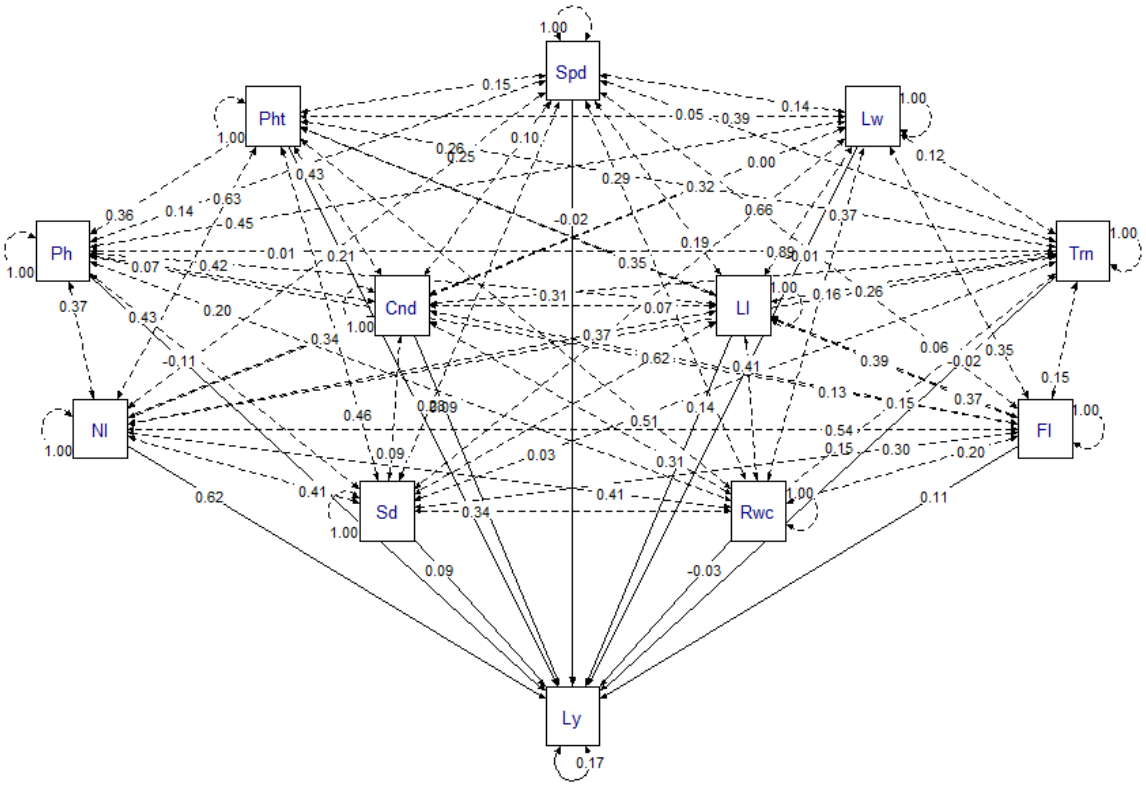
Strong and positive correlations were also observed between leaf yield and number of leaves per plant (r = 0.87 ***), moderate and positive correlations with net photosynthesis rate (r = 0.54 ***), days to 50% flowering (r = 0.50 ***), relative water content (r = 0.32 ***) and leaf length (r = 0.30 ***) under severe stress. A weak and positive correlation was also noted between leaf yield and plant height (r = 0.21 *). Leaf length and leaf width had a strong and positive association (r = 0.78 ***) under severe stress.

3.4. Path Coefficient Analysis

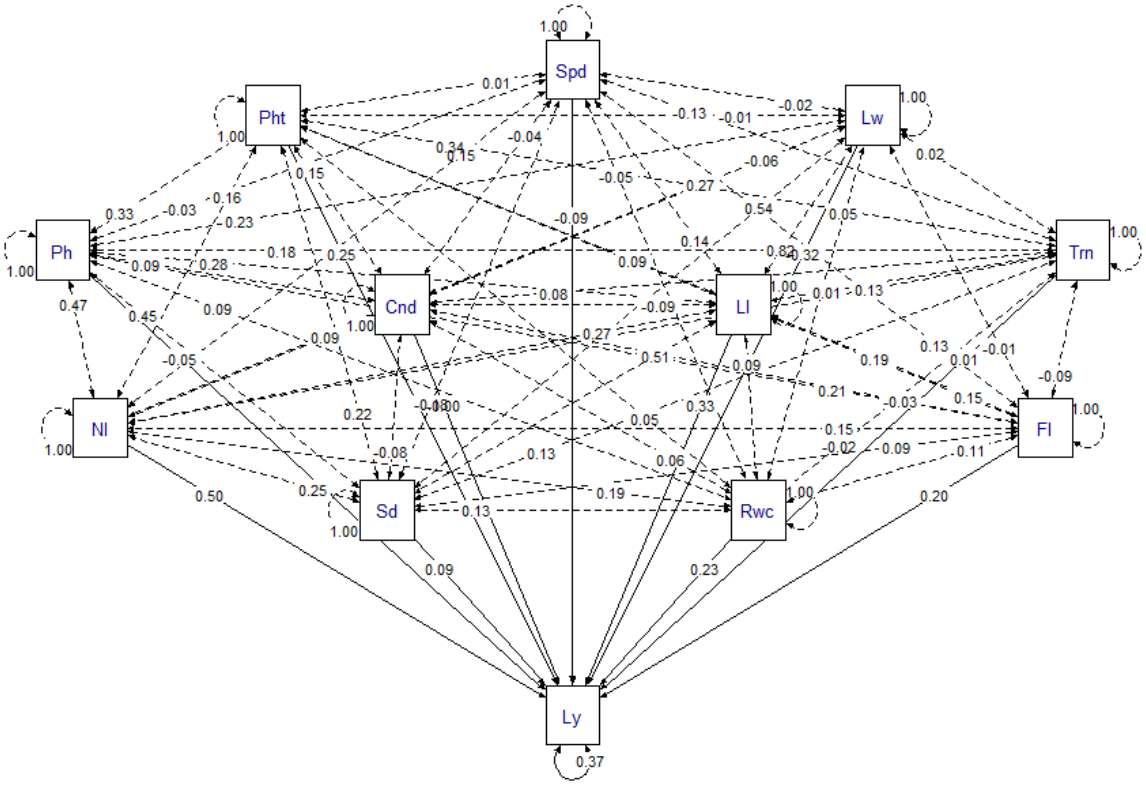
Path analysis was used to assess the direct and indirect effects of yield attributing traits on leaf yield across all three water regimes as reported in Figure 2a–c. A scale for path analysis was used to categorize the estimates into negligible with values ranging from 0.00 to 0.09, low from 0.10 to 0.19, moderate from 0.20 to 0.29 and high from 0.30 to 0.99. The residual effects were 0.17 for well-watered conditions (Figure 2a), 0.37 for mild stress conditions (Figure 2b), and 0.18 for severe stress conditions (Figure 2c). Under well-watered conditions, the number of leaves (0.62) showed a high positive direct effect on leaf yield (Figure 2a). The net photosynthesis rate (0.21) showed a moderate direct effect on leaf yield whereas leaf length (0.14) and days to 50% flowering exhibited (0.11) a low but positive direct effect on leaf yield. However, plant height (−0.11) had a negative direct effect on leaf yield. The remaining traits were recorded as negligible with some positive, stem diameter (0.09) and stomatal conductance (0.09). Chlorophyll content (−0.02), relative water content (−0.03) and transpiration rate (−0.02) were negatively negligible under well-watered conditions.

Under well-watered conditions, the indirect effects of several traits observed were mostly positive and high through the number of leaves. Net photosynthesis rate (0.39) had a high and positive indirect effect on leaf yield through the number of leaves. The indirect effects of relative water content (0.25), stem diameter (0.25) plant height (0.23), leaf length (0.23), leaf width (0.20), and stomatal conductance (0.21) through the number of leaves were positive and moderate. Transpiration rate (0.17) and chlorophyll content (0.16) showed a low and positive indirect effect on leaf yield through the number of leaves. Under mild stress conditions (Figure 2b), the number of leaves (0.50) and leaf length (0.33) showed a high positive direct effect on leaf yield. Net photosynthesis rate (0.25), relative water content (0.23) and days to 50% flowering (0.20) exhibited a moderate direct effect on leaf yield. Leaf width (−0.32) showed a very high but negative direct effect on leaf yield. Plant height (0.24) showed a moderate indirect effect whereas leaf length (0.14), stem diameter (0.13), and relative water content (0.10) showed a positive and low indirect effect via the number of leaves.

The results for path coefficient analysis estimates under severe stress conditions are presented in Figure 2c. Number of leaves (0.86) had a high and positive direct effect on leaf yield. Days to 50% flowering (0.11) had a low and positive direct effect on leaf yield. In addition to the above, relative water content (−0.14) and stem diameter (−0.09) had a negative but direct effect on leaf yield. Net photosynthesis rate (0.46), relative water content (0.40), leaf length (0.31) and days to 50% flowering (0.36) exhibited a high and positive indirect effect via the number of leaves. A positive and moderate indirect effect via number of leaves was observed for plant height (0.26) and stem diameter (0.24).

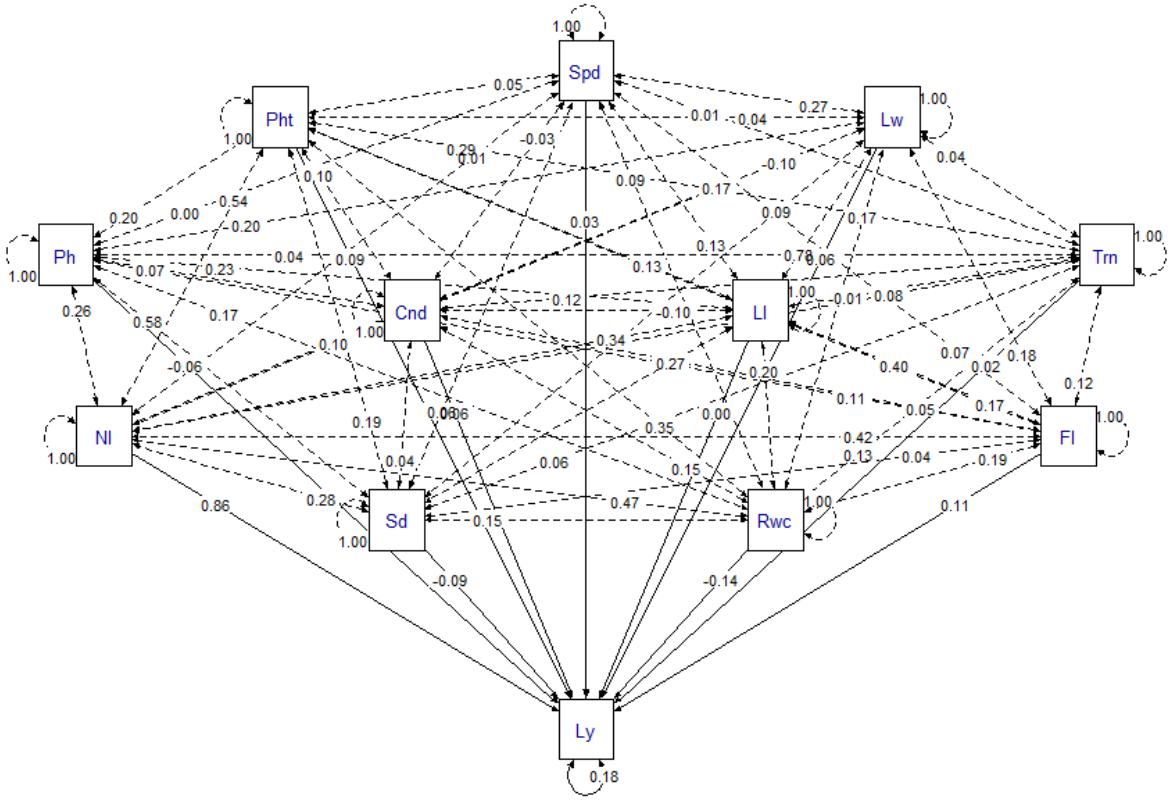


(**a**) Well-watered conditions



(**b**) Mild stress conditions

Figure 2. *Cont.*



(**c**) Severe stress conditions

Figure 2. Direct and indirect effects of different metrical traits on leaf yield in African spider plant accessions., Fl = days to 50% flowering, Ph = plant height, Ll = leaf length, Lw = leaf width, Sd = stem diameter, Spd = chlorophyll content, Rwc = relative water content, Pht = photosynthesis, Cnd = stomatal conductance, Trn = transpiration rate, Nl = number of leaves per plant, Ly = leaf yield.

4. Discussion

4.1. Performance of Accessions under Different Water-Regimes

The analysis of variance of the spider plant revealed that genotypic effects were highly significant ($p < 0.01$) for leaf yield and yield components under well-watered conditions which showed that genotypes differed significantly for yield and all yield-contributing traits. Under mild stress, genotypic effects were highly significant for all traits except for chlorophyll content. Under severe stress conditions, only chlorophyll content, stomatal conductance and transpiration rate were not significant ($p < 0.05$) indicating the existence of genetic variation among the spider plant accessions studied. According to Mosenda et al. [38], a wide and varied source of tolerance to water stress has been discovered in various African spider plant genotypes. In any plant breeding program, variability is critical for selecting superior genotypes. This also reaffirms that the concept of single-trait selection is not the most reliable way to improve a trait in any crop improvement program.

Under stressed conditions, the significantly large genotype mean squares obtained for the number of leaves, plant height and leaf yield revealed that the accessions varied widely in their potential for these traits. [39]. According to the findings of this study, the selection for leaf yield improvement under drought stress conditions should include simultaneous selection for several traits such as photosynthesis, number of leaves, days to 50% flowering, relative water content, plant height and leaf length. As evidenced by the results, this can be attributed to the influence of the accessions on the interaction with the water treatment. The considerably higher CV% for some traits could be attributed to the higher variability of genotype x treatment in accession performance. This appears to suggest that evaluating

the drought tolerance traits in African spider plant populations under varying levels of water stress rather than just one level was satisfactory [39–41].

4.2. Variance Components and Heritability

The selection of genotypes on the basis of their phenotypic variation (mean and range) is often complicated by environmental factors that may obscure the actual genetic variation. Therefore, apportioning phenotypic variation into genotypic and environmental factors is critical for genotype selection. In Table 3a–c, phenotypic variance estimates were higher than genotypic variance estimates across all the water regimes, which indicates the impact of environmental factors on these traits [42]. Zakaria et al. [43] reported similar findings in all the traits studied in spider plant. The genetic element is fundamental for breeding purposes because it influences the amount of variation passed down to offspring during the breeding process. High genotypic variance and phenotypic estimates were recorded for the number of leaves per plant and leaf yield under all three water regimes. The high genotypic and phenotypic variance of the abovementioned traits revealed that there was more variability, indicating a greater scope of selection for the traits [44].

Estimates of genotypic and phenotypic coefficients of variation are required to determine the magnitude of environmental influence on various traits. The genotypic coefficient of variation (GCV) determines the best relative amount of genetic variation. The number of leaves per plant and leaf yield had higher PCV and GCV values (>20%) under all three water regimes. In addition, plant height had higher PCV and GCV values (>20%) under severe drought stress. These traits with the highest PCV and GCV values have a high level of genetic variability, whereas traits with the lowest PCV and GCV values have a low level of genetic variability [45]. The moderate (10–20%) GCV and PCV values recorded for leaf length, leaf width, stem diameter and stomatal conductance under well-watered conditions, plant height, stem diameter and stomatal conductance under mild stress conditions and leaf width and stem diameter severe stress conditions suggests that selection based on these traits could be effective and their phenotypic expression can be a favorable indicator of genotypic potential [46]. In general, selection will be beneficial for the development of traits related to the degree of preferable variation. Lower PCV and GCV (<10%) values of traits indicate that environmental factors influenced the expression of these traits more than genetic factors. As a result, development through selection cannot be effective based on these traits [46].

The magnitude of the differences between genotypic and phenotypic coefficients of variation indicates the environmental effect on any trait. Large differences indicate a strong environmental influence, whereas small differences indicate a strong genetic influence. Stomatal conductance showed a significant difference between the PCV and GCV values under mild stress conditions. Under severe stress conditions, leaf length, stem diameter, stomatal conductance and stomatal conductance exhibited large differences between the PCV and GCV values in this study. This suggests that the environmental effect on the expression of those characteristics is greater and that selection based on these traits would be ineffective for further yield improvement [47].

Heritability assessment calculates the relative influence of genetic and non-genetic discrepancies to overall phenotypic variance in a population. It is a vital feature in quantitative genetics, especially in selective breeding. High heritability values (>60%) were observed for the vast majority of traits except for the transpiration rate, chlorophyll content rate, stomatal conductance and leaf length under well-watered conditions. Plant height, stem diameter, relative water content, photosynthesis rate, number of leaves and leaf yield exhibited high heritability (>60%) under mild stress conditions. Under severe stress conditions, most traits had a high heritability (>60%), and these included leaf yield, number of leaves, plant height, days to 50% flowering, photosynthesis rate, relative water content and leaf width. In this study, relatively high heritability (>60%) was noted in drought stress environments for leaf yield and yield-related traits such as plant height, number of leaves, leaf yield, days to 50% flowering and photosynthesis rate when compared to the non-stress environment.

This suggests that environmental variability had less impact on these traits. This inferred that these characteristics were expressed more clearly under drought stress conditions, and therefore, phenotypic selection for such traits would be favorable, as also explained by Zakaria et al. [43]. Furthermore, the high heritability estimates for those characters demonstrate a strong selection response in these characters. Similar findings were reported by Houdegbe et al. [48] under well-watered conditions, which support the current study.

High estimates of genetic advance as a percentage of the mean (20% and above) were recorded for leaf yield, number of leaves per plant, stomatal conductance, and stem diameter under well-watered conditions. Under mild stress conditions, leaf yield, number of leaves per plant, stem diameter, and plant height had a high GAM. Plant height, number of leaves per plant and leaf yield also recorded high genetic advance as a percent of the mean values under severe stress. Under both mild and severe stress conditions, plant height, stem diameter, number of leaves per plant and leaf yield showed high to moderate heritability and genetic advance. High genetic advance as a percentage of the mean values indicate additive gene action, whereas low values indicate non-additive gene action [49].

Heritability and genetic advance estimates are critical in predicting the reliability of phenotypic value as a breeding value guide. Stem diameter, stomatal conductance, number of leaves per plant, plant height, leaf length, leaf width, photosynthesis and stomatal conductance had high/moderate heritability with a high/moderate genetic advance as a percentage of the mean under normal conditions. Under mild stress conditions, plant height, stem diameter, number of leaves per plant, leaf length and leaf width recorded a high/moderate heritability with a high/moderate genetic advance as a percentage of the mean values. Under severe stress conditions, plant height, number of leaves per plant, leaf width, stem diameter, days to 50% flowering and photosynthesis showed a high/moderate heritability accompanied with a high/moderate genetic advance. This suggests that these traits were influenced by additive genes favoring their improvement through direct selection even under water stress conditions [42,50]. High heritability in combination with low genetic advance as a percentage of the mean indicates the presence of non-additive gene effects in the inheritance of the specific trait. Traits with low heritability estimates and poor genetic advance as a percentage of the mean are difficult to select directly and should be selected indirectly through related traits.

4.3. Correlation Coefficients and Path Coefficient Analysis

Knowledge of correlation coefficients among traits is useful to breeders because it indicates which traits should be targeted for selection to increase yield under certain environmental conditions. The correlation coefficient results (Figure 1a–c) revealed that traits such as number of leaves per plant, photosynthesis, and days to 50% flowering had a high to moderate positive correlation with leaf yield under all three water regimes. This suggests that an increase in leaf yield can be obtained by an increase in the number of leaves per plant, leaf photosynthesis rate and late flowering. As a result, these traits could be used as indirect selection criteria to improve leaf yield in African spider plant under both stressed and non-stressed conditions [43,48].

Under both mild and severe stress conditions, days to 50% flowering, relative water content, photosynthesis and number of leaves had moderate to high positive correlation with leaf yield. The correlations varied between water regimes, indicating that the level of association between the traits is influenced by environmental factors such as drought stress. Selection strategies must therefore account for such variations in trait association [51]. Correlation findings between yield and yield-attributing traits revealed that selecting for photosynthesis rate, number of leaves per plant, relative water content and days to 50% flowering would be effective in achieving higher leaf yield in African spider plant under drought stress environments.

However, correlation coefficients do not provide precise information about the interrelationship between the causal and resultant variables. Path coefficient analysis is thus an effective method for determining direct and indirect bases of correlations through the use of correlation coefficients of various plant traits. Therefore, the correlation coefficient estimates were partitioned into direct and indirect effects to determine the intensity of independent variables' effects on dependent variables. The residual effects in the study were 0.17 for well-watered conditions, 0.37 for mild stress conditions, and 0.18 for severe stress conditions. This indicates that the causal traits explained approximately 83% of the variability in leaf yield, leaving 17% unexplained under well-watered conditions. Under mild stress, 63% of the variability was explained by the casual traits leaving 37% unexplained. Furthermore, under severe stress, 82% of the variability was explained by the characters studied leaving 18% of the variability unexplained. According to Hasan-Ud-Daula et al. [44], these residual effects on leaf yield could be due to other factors not studied such as environmental errors or sampling errors. The number of leaves per plant had a high and positive direct effect on leaf yield across all water regimes.

Under well-watered conditions, the photosynthesis rate had a moderate and positive direct effect on leaf yield. In the mildly stressed environment, leaf length had a high and positive direct effect on leaf yield. Relative water content and photosynthesis rate had a moderate and positive direct effect. This suggests that more attention should be placed on the genetic improvement of these traits in order to increase leaf yield through indirect selection [52,53]. Plant height had a negative direct effect on leaf yield across all water regimes, but this trait had a positive correlation with leaf yield. Belay [54] reported similar findings in maize. The positive correlation of this trait with leaf yield was because of the positive indirect effect of this trait through other traits.

Plant height had a moderate and positive indirect effect on leaf yield via the number of leaves per plant in all three water regimes. The photosynthesis rate had a high and positive indirect effect on leaf yield under well-watered conditions. Plant height, stem diameter, leaf length, leaf width, relative water content and stomatal conductance all had a moderate and positive indirect effect on leaf yield via the number of leaves per plant under well-watered conditions. Plant height had a moderate and positive indirect effect on leaf yield via the number of leaves per plant under mild stress conditions. In the severe stress regime, relative water content, photosynthesis rate and leaf length had a high and positive indirect effect on leaf yield via the number of leaves per plant. Stem diameter and plant height had a moderate and positive indirect effect on leaf yield via the number of leaves per plant. This suggests that selecting for traits such as plant height, days to 50% flowering, relative water content, net photosynthesis and leaf length under stress conditions could be effective and can improve leaf yield indirectly by influencing the number of leaves per plant.

5. Conclusions

The accessions used in this study showed significant genetic variation for all traits measured, providing essential genetic resources for African spider plant improvement and opportunities to identify genotypes and traits with water regime stability. Traits with high to moderate genetic variance, heritability, and genetic advances, such as the number of leaves per plant, plant height and stem diameter could be improved through direct selection under drought stress conditions. These traits can also be used to indirectly select for yield under water stress conditions. The number of leaves per plant had the highest positive direct effect and strongest positive correlation with leaf yield, providing a foundation for leaf yield selection and improvement under drought stress conditions. Other traits including plant height, days to 50% flowering, relative water content, net photosynthesis and leaf length should also be considered for selection for leaf yield improvement especially under drought stress. In addition to data generated in this study, molecular genotyping of the accessions with selected molecular markers is essential to select complementary accessions for drought tolerance breeding.

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