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Evaluating Soybean Cultivars for Low- and High-Temperature Tolerance During the Seedling Growth Stage

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Received: 1 December 2018; Accepted: 22 December 2018; Published: 1 January 2019

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Abstract: Soybean (*Glycine max* L.) seedlings may be exposed to low or high temperatures under early or conventional soybean production systems practiced in the US Midsouth. However, a wide range of soybean cultivars commonly grown in the region may inherit diverse tolerance to degrees of temperatures. Therefore, a study was conducted in a controlled-environment facility to quantify 64 soybean cultivars from Maturity Group III to V, to low (LT; 20/12 °C), optimum (OT; 30/22 °C), and high (HT; 40/32 °C) temperature treatments during the seedling growth stage. Several shoot, root, and physiological parameters were assessed at 20 days after sowing. The study found a significant decline in the measured root, shoot, and physiological parameters at both low and high temperatures, except for root average diameter (RAD) and lateral root numbers under LT effects. Under HT, shoot growth was significantly increased, however, root growth showed a significant reduction. Maturity group (MG) III had significantly lower values for the measured root, shoot, and physiological traits across temperature treatments when compared with MG IV and V. Cultivar variability existed and reflected considerably through positive or negative responses in growth to LT and HT. Cumulative stress response indices and principal component analysis were used to identify cultivar-specific tolerance to temperatures. Based on the analysis, cultivars CZ 5225 LL and GS47R216 were identified as most sensitive and tolerant to LT, while, cultivars 45A-46 and 5115LL identified as most tolerant and sensitive to HT, respectively. The information on cultivar-specific tolerance to low or high temperatures obtained in this study would help in cultivar selection to minimize stand loss in present production areas.

Keywords: cumulative stress response indices; conventional soybean production system; early soybean production system; maturity groups; root morphology

1. Introduction

Soybean is an important oilseed crop in the US Midsouth, where an average air temperature of 30 °C is considered ideal for germination and seedling emergence [1]. However, soybean planting dates vary from early March to late May depending upon the type of production system followed, namely, early soybean production system (ESPS) and conventional soybean production system (CSPS) [2,3]. The CSPS involves May and later plantings of soybean varieties belonging to maturity group (MG)

V-VIII, which allows rapid seed germination and emergence [4]. Whereas ESPS involves planting early-maturing varieties, MG III and IV, from late-March to early-April [5]. Soybean acres and yields are consistently increased in the US Midsouth since the shift from CSPS to ESPS, which provides benefits of early season rainfall, avoids reproduction stage from mid-summer drought and high temperatures, prevents late-season insect-attack, and potential early harvest [1]. However, farmers may risk the exposure of early-growth (seed germination and seedling emergence) of soybean to chilling injury under ESPS, leading to uneven and poor stand establishment [5]. Thus, planting too early under EPSP and too late under CSPS could expose soybean seedling growth to both low- and high-temperatures, respectively, in the US Midsouth.

During the early germination process of soybean, low temperatures can significantly reduce the rate of imbibition, the ability of embryo tissue to expand, and mitochondrial respiration [6,7]. Further, susceptibility to chilling injury increases with decreasing initial moisture content in the embryo [6]. The rate of hypocotyl elongation significantly decreases with decreasing temperature below 30 °C [8]. Interestingly, after effects of low temperatures during the seedling stage can substantially extend the vegetative growth rate, and increase number of axillary branches, the rate of dry weight per plant and pod setting [9]. Whereas, the effects of high temperatures are mostly studied and considered damaging on the reproductive growth and yield potential in soybean, especially under the CSPS system [5,10,11]. Many argue that the success of the ESPS system was due to continuously increasing global air temperatures over the years [10,12,13] and they emphasize the importance of determining heat/cold tolerance among the available soybean cultivars during early-growth stages. Also, southernmost states of the US with higher spring temperatures are deprived of the ESPS [12].

Currently, numerous soybean varieties are available that are recommended for a given region that may differ in their tolerance to low and high temperatures [1]. Therefore variety selection along with other planting decisions (i.e., planting date, seed rate, and row spacing) is a key to profitable soybean production in a specific environment [4,14]. Temperature and photoperiod predominantly affect morphological and physiological growth and development of soybean plant among other environmental variables [15]. While the phenological response to temperature can primarily determine soybean variety selection for cultivation in a given geographical location during early growth-stages with little interaction of photoperiod [15,16], however, photoperiod modifies the response to temperature with changing geographical locations and therefore serves as a basis for classifying the cultivars by maturity group [17]. Studies in the past have determined genotypic variability in phenological responses to temperatures for the traits such as germination, plant height, node number, net photosynthesis, leaf area, and fruit number per plant by either varying the planting date in the field [2,18–21] or utilizing controlled-environment facilities [10,22–26]. However, photoperiod can become a confounding factor when using planting date as a variable to determine the cultivar response to temperature [16]. Therefore, soybean cultivars tolerance to low or high temperatures within or across MGs at constant photoperiods can be best achieved by utilizing controlled-environment facilities.

Also, root architecture is increasingly studied in US Midsouth crops such as rice, corn, and cotton in identifying responses involved in stress tolerance during seedling growth [22,23,27,28], however, little is known about the soybean root system under stressful conditions [3]. Early assessments of whole-root systems without breaking off the finer parts was nearly impractical in the past [29]. For this reason, previous studies mostly screened cultivars for abiotic stress tolerance based on above-growth traits, like height, leaf area, and node numbers [18,19,29]. However, the introduction of root phenotype systems, like hydroponics, gels, wax-petroleum layers, and WinRHIZO root scanner, have offered plant and soil scientists to evaluate root system architecture traits with minimal destruction [23,30,31]. Recent studies have successfully exploited the above technologies to define the relationship between temperature stress tolerance and root traits, including root length, diameter, thickness, surface area, and lateral root numbers [27,28,31]. Further, differences in correlation between root and shoot traits to different abiotic stresses were also found during the seedling stage [27]. Therefore, combined analysis of above- and belowground growth and developmental traits are important in identifying cultivars for abiotic stress tolerance.

The overall objective of this study was to quantify the temperature effects on root and shoot growth of 64 soybean cultivars during the early-growth stage using the sunlit controlled-environment facility. The specific objective was to classify the soybean cultivars for their degree of tolerance to low- and high-temperatures.

2. Materials and Methods

This experiment was conducted in Soil-Plant-Atmosphere-Research (SPAR) units, a sunlit controlled-environmental facility located at the Environmental Plant Physiology Laboratory, Mississippi State University, MS, USA during the 2016 growing season [32]. The experiment consisted of a collection of 64 soybean cultivars from maturity groups (MG) III, IV, and V (Table 1) that are most commonly grown in the US Midsouth and were evaluated under three different day/night temperature treatments (TTs) namely, low temperature (LT; 20/12 °C), optimum temperature (OT; 30/22 °C), and high temperature (HT; 40/32 °C). The experiment was organized in completely randomized design with two factorial arrangements (64 cultivars × 3 TTs) replicated three times spatially using nine different SPAR units such that three replications of each treatment combination (cultivar and TT) were represented by three SPAR units. Treated seeds of sixty-four soybean cultivars were sown in 576 polyvinyl chloride (PVC) plastic pots (10 cm diameter and 45.5 cm tall), each filled with sandy soil and 250 g of gravel at the bottom. The pots were placed in the SPAR units at the time of sowing. Immediately after sowing, TTs were imposed and continued until harvesting, 20 days after sowing (DAS). Initially, four seeds were seeded in each pot at a depth of 2 cm and then thinned to 1 plant after emergence. Plants were irrigated three times per day through an automated, computer-controlled drip system with full-strength Hoagland's nutrient solution at 0700, 1200 and 1700 h. All SPAR units were maintained at 400 ppm CO_2 throughout the experiment.

Table 1. Cultivars name, and maturity group of sixty-four soybean cultivars along with temperature, low (LT), optimum (OT), and high (HT), effects on shoot parameters, total plant dry weight, and physiological parameters, measured at 20 days after sowing. The mean value for each parameter related to maturity group (MG) presented below in Italic format.

Company	Cultivar	MG	Plant Height, cm			Mainstem Nodes, no. plant^{-1}			Leaf Area, cm^2			Leaf Weight, g			Stem Weight, g			Total Plant Weight, g			Chlorophyll Content as SPAD Units			Canopy Temperature, °C		
			LT	OT	HT	LT	OT	HT	LT	OT	HT	LT	OT	HT	LT	OT	HT	LT	OT	HT	LT	OT	HT	LT	OT	HT
Dyna-Gro Seed	32y39	III	5	13	15	1	3	4	26	206	232	0.13	0.82	0.81	0.04	0.37	0.44	0.22	1.44	1.48	25	37	41	25	30	34
Mycogen Seeds	5N393R2	III	4	12	12	1	3	5	46	227	316	0.19	0.81	1.04	0.04	0.28	0.38	0.34	1.32	1.72	29	37	43	25	30	36
Syngenta United States	S39-T3	III	4	10	11	1	3	5	26	215	260	0.11	0.83	0.89	0.03	0.31	0.36	0.18	1.41	1.53	31	40	45	25	29	35
Syngenta United States	S39-C4	III	4	11	11	1	3	4	29	*257*	263	0.11	1.00	0.97	0.02	0.36	0.35	0.19	1.73	1.65	29	40	47	26	31	36
REV Brand Seeds	38 R10	III	4	12	13	1	4	4	43	290	230	0.19	1.19	0.89	0.05	0.43	0.36	0.33	2.04	1.53	28	37	43	25	31	35
	Mean	*III*	*4*	*11*	*12*	*1*	*3*	*4*	*34*	*239*	*26*	*0.15*	*0.93*	*0.92*	*0.04*	*0.35*	*0.38*	*0.25*	*1.59*	*1.58*	*28*	*38*	*44*	*25*	*30*	*35*
Go Soy Genetics Optimized	IREANE	IV	5	15	14	1	4	5	40	265	302	0.18	0.88	1.04	0.03	0.37	0.44	0.29	1.54	1.86	24	34	40	24	30	35
Go Soy Genetics Optimized	483.C	IV	5	17	18	1	4	5	60	286	266	0.32	0.96	1.16	0.06	0.43	0.48	0.49	1.78	1.90	26	33	42	25	32	35
UniSouth Genetics Inc.	ELLIS	IV	5	13	15	1	4	4	33	237	277	0.15	0.91	0.96	0.04	0.35	0.40	0.25	1.54	1.65	26	36	39	25	31	34
REV Brand Seeds	48L63	IV	4	12	14	1	3	5	29	209	231	0.11	0.85	0.88	0.04	0.35	0.43	0.21	1.46	1.59	27	35	44	26	30	34
Delta Grow Seeds Com. Inc.	DG 4781LL	IV	5	14	16	1	4	4	38	265	228	0.18	0.93	0.70	0.05	0.40	0.38	0.31	1.60	1.35	26	34	40	25	29	38
Go Soy Genetics Optimized	4714LL	IV	5	13	16	1	4	4	43	273	251	0.15	1.04	0.86	0.04	0.43	0.41	0.29	1.79	1.61	26	33	39	25	28	34
Progeny Ag Products	P 4247LL	IV	5	11	12	1	3	5	44	284	327	0.16	0.98	1.15	0.03	0.40	0.46	0.28	1.79	2.07	27	37	41	25	30	35
Bayer Credenz	CZ 4044 LL	IV	5	13	15	1	4	5	30	257	360	0.16	0.96	1.15	0.03	0.39	0.51	0.23	1.63	2.01	27	38	43	25	29	35
Dyna-Gro Seeds	S49LL34	IV	4	14	16	1	3	5	42	245	259	0.34	0.79	0.85	0.04	0.34	0.36	0.47	1.41	1.48	26	35	40	25	28	35
DuPont Pioneer	P41T33R	IV	5	11	10	1	4	4	40	278	218	0.15	1.10	0.80	0.02	0.40	0.33	0.24	1.84	1.46	28	37	40	26	31	35
Delta Grow Seeds Com. Inc.	DG 4680RR2	IV	5	12	13	1	3	4	40	258	235	0.22	1.05	0.93	0.03	0.42	0.39	0.32	1.82	1.62	27	36	42	26	31	35
REV Brand Seeds	45A46	IV	6	12	15	1	3	5	29	174	340	0.14	0.63	1.23	0.04	0.24	0.49	0.25	1.09	2.05	24	35	43	25	29	33
Mycogen Seeds	5N424R2	IV	5	11	11	1	4	4	28	274	281	0.13	0.94	0.89	0.04	0.37	0.37	0.24	1.70	1.58	28	37	41	25	31	35
Dyna-Gro Seed	31RY45	IV	4	11	12	1	4	4	27	282	285	0.15	1.18	1.03	0.04	0.48	0.48	0.27	2.10	1.85	28	36	44	24	30	34
AGSouth Genetics	GS45R216	IV	5	13	14	1	4	4	41	242	248	0.24	0.85	0.79	0.02	0.36	0.40	0.35	1.53	1.49	28	36	42	25	30	36
Asgrow	AG4632	IV	4	12	13	1	4	4	37	279	287	0.13	1.14	1.01	0.03	0.43	0.47	0.23	1.97	1.80	28	38	44	26	29	34
Progeny Ag Products	P 4588RY	IV	5	14	13	1	4	4	28	340	237	0.15	0.92	0.68	0.03	0.36	0.26	0.23	1.55	1.19	28	35	40	24	30	36
Syngenta United States	S45-W9	IV	4	10	11	1	3	4	28	303	157	0.08	0.71	0.62	0.03	0.28	0.20	0.15	1.26	1.03	29	39	39	25	30	33
Bayer Credenz	CZ 4181 RY	IV	5	11	12	1	3	4	40	238	350	0.21	0.80	1.32	0.04	0.36	0.53	0.31	1.42	2.27	26	36	42	26	31	34
Delta Grow Seed Com. Inc.	DG 825RR2/STS	IV	5	12	12	1	4	4	46	278	225	0.26	1.10	0.88	0.06	0.48	0.37	0.41	1.93	1.54	29	40	45	24	27	36
DuPont Pioneer	P47T36R	IV	5	12	11	1	3	4	37	192	187	0.10	0.80	0.69	0.04	0.32	0.31	0.21	1.39	1.24	28	36	41	25	29	36
Syngenta United States	S47-K5	IV	5	11	10	1	3	4	31	234	158	0.08	0.88	0.57	0.03	0.33	0.25	0.15	1.51	1.05	26	39	44	24	29	35
AGSouth Genetics	GS47R216	IV	6	15	15	1	4	5	36	310	313	0.06	1.08	0.93	0.04	0.48	0.44	0.20	1.92	1.73	26	38	40	25	30	34
Armor Seeds	47-R70 (AR4705)	IV	4	13	12	1	3	4	42	268	308	0.22	0.98	1.01	0.03	0.41	0.48	0.34	1.72	1.84	27	38	43	25	30	34
Mycogen Seed	5N490R2	IV	4	13	13	1	3	5	37	230	263	0.17	0.80	0.88	0.04	0.40	0.43	0.28	1.48	1.61	29	37	42	25	30	35
REV Brand Seeds	48A26	IV	5	13	15	1	4	5	37	217	311	0.20	0.86	1.14	0.04	0.38	0.50	0.32	1.58	1.98	26	36	44	25	30	36
Progeny Ag Products	P 4757RY	IV	6	12	13	1	3	4	29	249	254	0.15	2.69	0.79	0.03	0.38	0.38	0.23	3.44	1.48	28	37	40	24	29	36
Dyna-Gro seeds	S48RS53	IV	5	15	13	1	4	4	41	285	259	0.24	1.10	0.91	0.04	0.47	0.43	0.39	1.92	1.62	31	40	46	26	30	35
Go Soy Genetics Optimized	4814GTS	IV	4	11	11	1	4	4	35	331	247	0.21	0.81	0.80	0.03	0.34	0.31	0.31	1.44	1.35	27	37	42	25	30	35
Croplan WinField United	R2C4775	IV	4	11	12	1	3	4	30	239	251	0.19	1.04	1.00	0.02	0.40	0.39	0.28	1.77	1.78	28	35	41	25	30	35
Bayer Credenz	CZ 4898 RY	IV	5	12	13	1	3	4	33	240	266	0.19	0.78	0.91	0.03	0.37	0.39	0.27	1.43	1.60	23	34	40	25	30	36
Dixie Belle	DB 4911	IV	5	15	14	1	4	4	30	294	271	0.10	1.16	1.00	0.02	0.36	0.33	0.18	1.83	1.64	26	39	44	25	30	35
Great Heart Seed Co.	GT-476CR2	IV	4	12	12	1	4	4	40	321	246	0.14	1.18	0.96	0.03	0.52	0.36	0.26	2.11	1.57	29	28	41	25	31	37
NC State University	PI 471938	IV	4	15	15	1	4	5	38	364	330	0.24	1.25	1.10	0.04	0.55	0.53	0.34	2.14	1.96	29	40	42	25	30	32
University of Missouri	R01-416F	IV	5	12	12	1	4	4	47	287	254	0.19	1.17	0.96	0.05	0.47	0.38	0.30	2.01	1.60	26	41	45	24	31	35
	Mean	*IV*	*5*	*13*	*13*	*1*	*4*	*4*	*37*	*266*	*265*	*0.17*	*1.01*	*0.93*	*0.04*	*0.39*	*0.40*	*0.28*	*1.73*	*1.64*	*27*	*36*	*42*	*25*	*30*	*35*
Asgrow	AG5332	V	5	11	11	1	3	4	39	254	271	0.16	0.87	0.89	0.04	0.35	0.33	0.33	1.50	1.53	30	40	43	25	31	35
Progeny	P5333 RY	V	4	14	14	1	4	4	37	305	317	0.16	1.20	1.16	0.04	0.48	0.56	0.27	2.08	2.06	24	36	38	26	31	34
USDA-ARS	JTN-5110	V	4	12	12	1	4	4	35	352	337	0.17	1.57	1.26	0.05	0.66	0.43	0.30	2.69	2.09	27	38	42	25	29	34

Table 1. *Cont.*

Company	Cultivar	MG	Plant Height, cm			Mainstem Nodes, no. plant^{-1}			Leaf Area, cm^2			Leaf Weight, g			Stem Weight, g			Total Plant Weight, g			Chlorophyll Content as SPAD Units			Canopy Temperature, °C		
			LT	OT	HT	LT	OT	HT	LT	OT	HT	LT	OT	HT	LT	OT	HT	LT	OT	HT	LT	OT	HT	LT	OT	HT
Go Soy Genetics Optimized	LELAND	V	5	14	14	1	4	4	32	283	258	0.17	1.02	0.88	0.02	0.39	0.38	0.26	1.69	1.53	24	38	44	25	30	34
Delta Grow Seeds Co Inc	DG5067LL	V	4	11	13	1	3	5	40	225	311	0.20	0.96	1.09	0.05	0.31	0.44	0.35	1.57	1.84	28	38	45	25	30	35
Go Soy Genetics Optimized	5115LL	V	5	11	12	1	3	4	49	276	209	0.26	1.01	0.70	0.05	0.37	0.30	0.40	1.77	1.19	26	35	39	25	29	36
Dyna-Gro Seed	S55LS75	V	5	14	15	1	3	5	34	248	282	0.16	1.03	0.87	0.03	0.47	0.48	0.25	1.78	1.71	25	35	39	24	29	35
Bayer Credenz	CZ 5242 LL	V	5	11	12	1	3	4	34	200	287	0.15	0.65	0.89	0.03	0.28	0.40	0.24	1.13	1.57	26	35	41	25	30	36
Bayer Credenz	CZ 5225 LL	V	5	15	15	1	4	4	27	218	269	0.15	0.78	0.82	0.03	0.39	0.42	0.22	1.41	1.50	28	36	40	26	30	35
Delta Grow Seeds Com. Inc.	DG 5170RR2/STS	V	5	11	13	1	4	4	38	339	299	0.19	1.33	1.09	0.04	0.46	0.44	0.30	2.14	1.87	29	38	43	25	29	34
REV Brand Seeds	51A56	V	5	12	13	1	4	4	47	239	280	0.20	0.96	0.97	0.05	0.35	0.46	0.32	1.60	1.69	27	35	38	25	29	34
DuPont Pioneer	P52T50R	V	4	13	13	1	4	4	39	290	276	0.12	1.12	1.03	0.03	0.41	0.44	0.23	1.84	1.78	24	37	43	25	30	35
Syngenta United States	S55-Q3	V	5	14	15	1	4	4	47	231	273	0.18	0.77	0.89	0.07	0.30	0.36	0.32	1.30	1.54	26	37	44	25	30	37
Syngenta United States	S56-M8	V	5	14	13	1	3	4	39	198	201	0.10	0.66	0.66	0.03	0.19	0.26	0.17	1.05	1.15	24	36	44	25	29	36
Go Soy Genetics Optimized	5214GTS	V	5	17	15	1	4	5	37	315	365	0.15	1.18	1.14	0.03	0.54	0.52	0.24	2.04	1.98	27	36	45	23	28	35
Armor	55-R68	V	4	14	13	1	4	4	36	307	330	0.17	1.18	0.95	0.05	0.47	0.44	0.28	1.99	1.70	24	33	39	24	31	36
Progeny Ag Products	P 5226RYS	V	4	12	13	1	4	5	45	322	280	0.25	1.07	0.98	0.03	0.42	0.40	0.37	1.84	1.63	26	36	42	25	30	35
Mycogen Seeds	5N523R2	V	4	12	12	1	3	4	32	277	231	0.17	1.03	0.92	0.02	0.39	0.36	0.28	1.77	1.59	29	38	42	25	29	35
Dyna-Gro seed	S56RY84	V	5	16	15	1	4	5	51	306	322	0.25	1.04	1.02	0.05	0.51	0.48	0.41	1.89	1.87	24	35	38	25	29	35
Croplan WinField United	R2C5225S	V	4	12	12	1	3	5	41	335	282	0.26	1.16	1.03	0.03	0.51	0.46	0.38	2.04	1.84	27	37	40	25	29	33
Bayer Credenz	CZ 5375 RY	V	5	11	12	1	3	4	34	244	330	0.18	0.87	1.07	0.04	0.30	0.43	0.28	1.45	1.87	26	35	42	25	31	36
REV Brand Seeds	57R21	V	5	15	13	1	4	4	46	293	278	0.21	1.03	1.08	0.04	0.46	0.36	0.30	1.80	1.77	26	34	46	25	30	35
Syngenta United States	S58-Z4	V	5	12	12	1	3	4	28	203	247	0.17	0.70	0.81	0.03	0.28	0.36	0.24	1.19	1.45	28	34	40	25	28	35
Dyna-Gro Seed	S57RY26	V	6	14	15	1	4	4	43	303	350	0.22	1.12	1.20	0.03	0.47	0.47	0.35	1.94	2.02	27	36	45	25	31	34
	Mean	*V*		13	13	1	4	4	39	274	287	0.18	1.01	0.98	0.04	0.41	0.42	0.30	1.73	1.70	26	36	42	25	30	35
Mean			5	13	13	1	4	4	37	267	273	0.18	1.00	0.95	0.04	0.40	0.41	0.29	1.72	1.66	27	36	42	25	30	35
† ANOVA																										
MG				† ***			ns			***			ns			ns			ns			***			ns	
CUL			† ns	***	***	ns	ns	ns	***	***	***	***	***	ns	ns	***	ns	***	***	ns	***	***	***	ns	ns	ns
TT				***			***			***			***			***			***			***			***	
LT				***			***			ns			***			ns			ns			***			***	
HT				***			***			***			***			***			***			***			***	
MG × TT				ns			ns			***			ns			ns			ns			***			ns	
CUL × TT				***			ns			***			***			† *			***			ns			ns	

† *, ***, and ns representing significance at the $p \leq 0.05$, $p \leq 0.001$, and non-significant ($p \geq 0.05$), respectively. CUL, cultivar; MG, maturity group; TT, temperature treatment; LT, low-temperature treatment; HT, high-temperature treatment; OT, optimum temperature treatment.

2.1. Measurements

Physiological parameters such as chlorophyll content were measured using chlorophyll estimates measured and presented as Soil-Plant-Analysis-Development (SPAD) units (SPAD-502, Minolta Camera Co. Ltd., Osaka, Japan) and canopy temperature using an infrared thermometer (MI-230, Apogee Instruments, Inc., Logan, UT, USA) were measured on the day before the harvest between 10:00 to 12:00 a.m. Shoot parameters such as plant height (PH), mainstem node number (NN), and leaf area (LA) using leaf area meter (Li-3100, Li-COR Inc., Lincoln, Nebraska, USA) were measured at the time of harvest. Root parameters such as cumulative root length (CRL), root surface area (RSA), root diameter (RD), lateral root numbers (i.e., numbers of root tips (RT), forks (RF), crossings (RC)), and root volume (RV) were measured and analyzed using the Win-RHIZO optical scanner according to the methods described previously [27,28,30,31]. After that, plant-component dry weights, stems, leaves, and roots, were obtained by oven-drying at 80 °C, and root/shoot ratio was calculated accordingly.

2.2. Cumulative Stress Response Indices

Cumulative stress response indices for LT (CLTRI) and HT (CHTRI) were calculated to classify soybean cultivars based on their degree of tolerance to LT and HT, respectively. Koti et al. [33] defined cumulative stress response index (CSRI) as the sum of relative individual component responses under each treatment. Accordingly, individual stress response indices for LT (ILTRI) and HT (IHTRI) for each cultivar were obtained by dividing the value of parameter obtained at LT or HT by the value of the same parameter obtained at OT. The calculations were done for all measured parameters. Then, CLTRI and CHTRI were calculated for each cultivar by summing ILTRI and IHTRI, respectively. Finally, soybean cultivars were classified as sensitive, moderately sensitive, moderately tolerant, and highly tolerant to LT or HT based on CLTRI or CHTRI values, and an increment of one standard deviation, respectively, as described by Koti et al. [33].

2.3. Data Analysis

Considering all SPAR chambers have the same growth conditions, except temperature, the assignment of temperature treatments to a given SPAR unit was randomized and cultivars were completely randomized within each unit, therefore, the study was treated as a completely randomized design for statistical analysis purposes. Proc ANOVA analysis procedure (ANOVA) was performed on the replicated values of the measured parameters using PROC GLM procedure in SAS (SAS Institute, Inc., Cary, NC, USA) to determine the effect of cultivar, TT, MG, and their interaction. Post ANOVA means comparison was made using least significant difference (LSD = 0.05). Pearson's correlation coefficients for pairs of shoot, root, and physiological traits were calculated at α level of 5%. Sigma plot 13.0 (Systat Software, Inc., San Jose, CA, USA) was used to generate graphs and correlations using best-fitted regression functions.

2.4. Principal Component Analysis (PCA)

The principal component analysis was performed to identify the parameters that best describe either low or high-temperature tolerance to response variables and to classify cultivars into different temperature tolerant groups. The analysis was conducted with the PRINCOMP procedure of SAS (SAS Institute, Inc., Cary, NC, USA) and the results were summarized in biplots using SigmaPlot 13 (Systat Software, Inc., San Jose, CA, USA), which are the plots of the mean principal component scores (PC scores) for the treatments of first two principal components. PCA was performed on the correlation matrix of 64 soybean cultivars and 16 response variables comprising plant height (PH), mainstem nodes number (NN), leaf area (LA), stem weight (SW), leaf weight (LW), root weight (RW), total weight (TW), root length (RL), root surface area (RSA), root average diameter (RAD), root volume (RV), canopy temperature (CT), root tips (RNT), root forks (RNF), root crossings (RC), and root-shoot ratio (RS). The superimposed biplot was developed by plotting eigenvectors for the 16 responses as solid circles and cultivars as open stars projecting from the origin into various positions. The values of eigenvectors and PC scores were used to classify soybean cultivars into LT and HT tolerant groups.

3. Results

3.1. Growth and Development

3.1.1. Shoot Parameters

The study revealed significant cultivar, TT, MG, and their interaction effects on most of the measured parameters (Tables 1 and 2). Among shoot parameters, TTs significantly affected PH, NN, and LA ($p < 0.001$). On an average across cultivars, the values for PH and NN significantly increased ($p < 0.001$) with increasing temperatures from low to high, but LA was significantly reduced under LT effects with no differences were observed between OT and HT ($p > 0.05$). Maturity groups significantly differed for PH and LA ($p < 0.001$), while MG × TT interactions were only significant for LA (Table 1). However, cultivars showed significant variability for PH and LA ($p < 0.001$) under the TTs, except under LT effects (Table 1). Further, no variations among the cultivars were observed for NN ($p > 0.05$). Also, interaction effect (cultivar × TT) was significant for PH and LA ($p < 0.001$), but not for NN. The averaged PH increased from 5 to 13 cm, LA from 1 to 4 cm^2, and NN from 37 to 273, respectively, when compared between OT and HT. Cultivars 4714, 48L63, and 45A46 showed a greater increase in PH among other cultivars with increasing temperatures from optimum to high (Table 1).

In contrast, cultivars P41T33R, P 4588RY, and AR4705 grown at OT were taller than at HT. The maximum and minimum values for PH were observed in cultivar 483C at HT and cultivar 55-R68 at LT, respectively. Overall, cultivars belonging to MG III had significantly lower values for PH (Figure 1A), while differences were not significant between MG IV and V (Table 1). At low temperature, 11% reduction was observed in plant height for cultivars from MG III when compared to MG IV and V (Figure 1A). The highest and lowest percent increase in LA was observed in cultivar JTN-5110 and P47T36R, respectively, when compared between LT and OT effects (Table 1). Cultivars like CZ 4044 LL, 45A46, and CZ 4181 RY showed greater values for LA with increasing temperatures from optimal to high, while LA of cultivars like S45-W9, and P41T33R was smaller under OT than HT. Similar to plant height, cultivars belonging to MG V, showed 9 and 12% increase in leaf area at high and low temperature compared to the cultivars from MG III (Figure 1B). Moreover, some cultivars like S47-K5, S48RS53, R01-416F, and JTN-5110 showed lower values for both PH as well as LA under HT than OT (Table 1). Cultivar 5214GTS at HT showed highest, and cultivar S39-T3 at LT showed the lowest value for LA, respectively. On an average across TTs, MG V cultivars had greater LA than MG III and IV (Table 1).

Table 2. Cultivars name, and maturity group of sixty-four soybean cultivars along with temperature, low (LT), optimum (OT), and high (HT), effects on root growth and development traits, measured at 20 days after sowing. The mean value for each parameter related to maturity group (MG) presented below in Italic format.

Company	Cultivar	MG	CRL, cm plant^{-1}			RSA, cm^2 plant^{-1}			RAD, cm			RV, cm^3 plant^{-1}			RNT, no. plant^{-1}			RNF, no. plant^{-1}			RNC, no. plant^{-1}			R/S			RW, g plant^{-1}		
			LT	OT	HT	LT	OT	HT	LT	OT	HT	LT	OT	HT	LT	OT	HT	LT	OT	HT	LT	OT	HT	LT	OT	HT	LT	OT	HT
Dyna-Gro Seed	32y39	III	414	2251	1987	72	312	274	0.5	0.4	0.4	1.0	3.4	3.0	2189	3703	4220	1141	6706	6570	80	830	781	1.23	0.66	0.54	0.1	0.2	0.2
Mycogen Seeds	5N393R2	III	717	2026	2389	125	296	346	0.6	0.5	0.5	1.8	3.5	4.0	1371	4021	4998	1332	5871	8860	165	688	1082	2.58	0.84	0.80	0.1	0.2	0.3
Syngenta United States	S39-T3	III	372	2340	2213	67	337	302	0.6	0.5	0.4	1.0	3.9	3.3	2028	6284	4782	659	7544	8507	65	801	1049	1.10	0.90	0.79	0.0	0.3	0.3
Syngenta United States	S39-C4	III	560	2609	2407	98	403	341	0.6	0.5	0.5	1.4	5.0	3.8	1571	5994	5323	1108	9101	9813	126	966	1154	2.43	1.02	0.97	0.1	0.4	0.3
REV Brand Seeds	38 R10	III	743	3092	2384	117	465	333	0.5	0.5	0.4	1.5	5.6	3.7	1621	3768	4687	1485	11,861	9018	200	1373	1070	1.80	0.95	0.79	0.1	0.4	0.3
	Mean	III	561	2464	2276	96	363	319	0.6	0.5	0.4	1.3	4.3	3.6	1756	4754	4802	1145	8217	8554	127	932	1027	1.8	0.9	0.8	0.1	0.3	0.3
Go Soy Genetics Optimized	IREANE	IV	644	2752	3090	102	356	435	0.5	0.4	0.4	1.3	3.7	4.9	1367	7271	7120	1414	9787	15,723	162	1189	1659	2.78	0.80	0.86	0.1	0.3	0.4
Go Soy Genetics Optimized	483.C	IV	998	3558	2359	156	488	320	0.5	0.4	0.4	2.0	5.3	3.5	2756	5599	5694	2717	15,255	9192	290	1908	961	2.00	0.91	0.53	0.1	0.4	0.3
UniSouth Genetics Inc.	ELLIS	IV	679	2115	2938	100	277	382	0.5	0.4	0.4	1.2	3.0	4.0	1320	4358	5918	1229	7234	13,986	215	861	1641	1.64	0.78	0.73	0.1	0.3	0.3
REV Brand Seeds	48L63	IV	502	2188	2475	82	324	350	0.5	0.5	0.4	1.1	3.8	3.9	1405	3446	5861	918	7742	8929	107	846	1005	1.55	0.74	0.66	0.1	0.3	0.3
Delta Grow Seeds Com. Inc.	DG 4781LL	IV	754	2393	2606	133	331	360	0.6	0.4	0.4	1.9	3.6	4.0	1871	9450	6631	1379	7623	9744	180	814	1123	1.86	0.68	0.70	0.1	0.3	0.3
Go Soy Genetics Optimized	4714LL	IV	742	2691	2565	122	390	362	0.5	0.5	0.5	1.7	4.5	4.1	2458	5725	5700	1667	9090	11,462	165	1010	1116	2.33	0.74	0.82	0.1	0.3	0.3
Progeny Ag Products	P 4247LL	IV	714	3333	3337	120	491	486	0.5	0.5	0.5	1.7	5.8	6.0	1346	5959	6628	1748	12,758	14,741	222	1406	1459	3.11	1.01	1.01	0.1	0.4	0.5
Bayer Credenz	CZ 4044 LL	IV	510	2873	2629	78	394	346	0.5	0.4	0.4	1.0	4.3	3.6	1481	4804	5072	1048	9815	10,136	135	1205	1321	1.33	0.73	0.69	0.0	0.3	0.4
Dyna-Gro Seeds	S49LL34	IV	555	2238	2553	94	330	355	0.5	0.5	0.4	1.3	3.9	3.9	2240	3097	6125	1083	7387	9296	121	868	1053	2.55	0.82	0.74	0.1	0.3	0.3
DuPont Pioneer	P41T33R	IV	659	3186	2751	106	417	391	0.5	0.4	0.5	1.4	4.4	4.4	1407	5592	4015	1220	11,865	11,868	142	1598	1288	3.14	0.85	0.99	0.1	0.3	0.3
Delta Grow Seeds Co Inc	DG 4680RR2	IV	639	2659	2361	102	380	306	0.5	0.5	0.4	1.3	4.3	3.2	1939	6207	5670	1586	9585	9512	188	1069	1150	2.63	0.86	0.77	0.1	0.4	0.3
REV Brand Seeds	45A46	IV	492	1887	2951	82	275	406	0.5	0.5	0.4	1.1	3.2	4.4	2478	4987	6708	1472	6456	12,079	113	593	1408	1.83	0.92	0.66	0.1	0.2	0.3
Mycogen Seeds	5N424R2	IV	642	3141	2335	99	420	327	0.5	0.4	0.4	1.2	4.5	3.6	1558	6653	5363	1282	10,741	9416	183	1396	1057	1.83	1.07	0.89	0.1	0.4	0.3
Dyna-Gro Seed	31RY45	IV	597	3474	3067	105	509	423	0.6	0.5	0.4	1.5	5.9	4.7	1553	7162	8533	1036	13,543	13,046	115	1541	1454	2.00	0.89	0.73	0.1	0.4	0.4
AGSouth Genetics	GS45R216	IV	753	2895	2007	124	409	261	0.5	0.5	0.4	1.6	4.6	2.7	1483	6759	4221	2023	9841	8267	209	1126	1024	4.00	0.90	0.74	0.1	0.3	0.3
Asgrow	AG4632	IV	564	2936	2264	95	440	314	0.5	0.5	0.4	1.3	5.3	3.5	1546	5053	4335	923	11,514	9375	107	1158	1044	1.90	0.95	0.66	0.1	0.4	0.3
Progeny Ag Products	P 4588RY	IV	480	2493	2273	81	317	309	0.5	0.4	0.4	1.1	3.2	3.3	1263	9315	7881	918	8437	8340	100	1026	930	2.00	0.73	0.92	0.1	0.3	0.2
Syngenta United States	S45-W9	IV	393	2011	1561	72	281	216	0.6	0.4	0.4	1.0	3.1	2.4	1191	8656	4932	790	5721	5300	80	626	592	1.63	0.95	1.05	0.0	0.3	0.2
Bayer Credenz	CZ 4181 RY	IV	660	2221	3362	99	305	449	0.5	0.4	0.4	1.2	3.3	4.8	1696	5495	6228	1192	6991	16,099	204	881	1996	1.42	0.72	0.78	0.1	0.3	0.4
Delta Grow Seed Com. Inc.	DG 4825RR2/STS	IV	710	3250	2499	121	447	346	0.5	0.4	0.4	1.6	4.9	3.8	2894	6166	4988	1613	12,772	10,034	172	1513	1184	1.44	0.74	0.77	0.1	0.4	0.3
DuPont Pioneer	P47T36R	IV	631	2222	1859	109	311	257	0.6	0.4	0.4	1.5	3.5	2.8	2377	5081	4612	1530	7189	6342	139	845	678	1.92	0.86	0.76	0.1	0.3	0.2
Syngenta United States	S47-K5	IV	444	2700	1716	69	371	245	0.5	0.4	0.5	0.9	4.1	2.8	1549	5477	4102	949	8912	5749	111	1144	659	1.75	0.94	0.96	0.0	0.3	0.2
AGSouth Genetics	GS47R216	IV	748	2836	2521	122	417	352	0.5	0.5	0.4	1.6	4.9	3.9	1591	5252	5759	1380	10,628	9321	191	1182	1170	2.23	0.76	0.81	0.1	0.4	0.4
Armor Seeds	47-R70 (AR4705)	IV	672	2689	2199	112	348	305	0.5	0.4	0.4	1.5	3.9	3.4	1640	7078	5881	1141	9556	8432	159	1263	826	2.60	0.79	0.73	0.1	0.3	0.4
Mycogen Seed	5N490R2	IV	651	2207	2348	101	296	288	0.5	0.4	0.4	1.3	3.2	2.8	2495	3797	6651	1157	6614	9039	137	861	1157	1.62	0.70	0.68	0.1	0.3	0.3
REV Brand Seeds	48A26	IV	591	2974	2869	94	424	399	0.5	0.5	0.4	1.2	4.8	4.4	1790	5246	6305	1259	10,112	12,486	149	1232	1385	1.77	0.88	0.69	0.1	0.3	0.3
Progeny Ag Products	P 4757RY	IV	512	2676	2384	77	361	312	0.5	0.4	0.4	0.9	3.9	3.3	2115	7402	5672	1073	9354	8884	112	1087	1048	1.50	0.99	0.79	0.1	0.4	0.3
Dyna-Gro seeds	S48RS53	IV	762	2808	2013	131	381	289	0.6	0.4	0.4	1.8	4.1	2.6	1353	3518	4320	2169	10,220	7872	214	1335	970	2.54	0.74	0.65	0.1	0.3	0.3
Go Soy Genetics Optimized	4814GTS	IV	482	2155	2413	86	313	306	0.6	0.5	0.4	1.2	3.6	3.1	1219	5046	6238	974	6611	8911	98	817	1194	2.44	0.85	0.77	0.1	0.3	0.2
Croplan WinField United	R2C4775	IV	508	2769	2771	82	408	390	0.5	0.5	0.4	1.0	4.8	4.4	3047	4911	5292	1301	10,823	11,150	123	1143	1339	2.57	0.82	1.03	0.1	0.3	0.4
Bayer Credenz	CZ 4898 RY	IV	538	2256	2785	88	305	369	0.5	0.4	0.4	1.2	3.3	3.9	2052	4975	8320	1019	6800	11,555	107	863	1324	1.30	0.74	0.74	0.0	0.3	0.3
Dixie Belle	DB 4911	IV	600	2828	3209	83	372	418	0.4	0.4	0.4	0.9	3.9	4.3	1387	6270	6249	1299	10,877	15,688	213	1404	1868	2.83	0.85	0.95	0.1	0.3	0.3
Great Heart Seed Com.	GT-476CR2	IV	631	2637	2310	98	370	265	0.5	0.4	0.4	1.2	4.2	2.4	1362	4816	7214	1513	10,388	9250	179	1179	1156	3.22	0.77	0.73	0.1	0.4	0.3
NC State University	PI 471938	IV	657	3505	2933	104	482	406	0.5	0.4	0.4	1.3	5.3	4.5	2756	6232	8144	1615	14,331	14,341	179	1714	1512	1.50	0.64	0.62	0.1	0.4	0.3

Table 2. *Cont.*

Company	Cultivar	MG	CRL, cm plant^{-1}			RSA, cm^2 plant^{-1}			RAD, cm			RV, cm^3 plant^{-1}			RNT, no. plant^{-1}			RNF, no. plant^{-1}			RNC, no. plant^{-1}			R/S			RW, g plant^{-1}		
			LT	OT	HT	LT	OT	HT	LT	OT	HT	LT	OT	HT	LT	OT	HT	LT	OT	HT	LT	OT	HT	LT	OT	HT	LT	OT	HT
University of Missouri	R01-416F	IV	635	3828	3110	88	515	422	0.4	0.4	0.4	1.0	5.5	4.6	1879	5635	5029	1869	16,496	14,412	199	1952	1660	1.43	0.79	0.70	0.1	0.4	0.3
	Mean	IV	621	2725	2555	100	379	348	0.5	0.4	0.4	1.3	4.2	3.8	1825	5785	5926	1357	9802	10,571	158	1162	1212	2.1	0.8	0.8	0.1	0.3	0.3
Asgrow	AG5332	V	771	2660	2245	125	355	313	0.5	0.4	0.4	1.6	3.8	3.5	2007	6025	4339	1402	8549	8272	164	1052	975	2.77	0.77	0.96	0.1	0.3	0.3
Progeny	PR 5333	V	675	3501	2683	100	480	345	0.5	0.4	0.4	1.2	5.2	3.5	2589	5115	6602	1714	14,145	11,916	199	1823	1456	1.92	0.82	0.61	0.1	0.4	0.3
USDA-ARS	JTN-5110	V	792	3676	2936	117	514	405	0.5	0.4	0.4	1.4	5.8	4.5	2800	6792	6115	1900	17,403	13,616	231	1853	1227	1.64	0.69	0.92	0.1	0.5	0.4
Go Soy Genetics Optimized	LELAND	V	681	3814	3105	111	522	398	0.5	0.4	0.4	1.4	5.7	4.1	1747	7842	9836	1192	16,821	13,978	140	1816	1704	2.86	0.71	0.73	0.1	0.3	0.3
Delta Grow Seeds Com. Inc.	DG5067LL	V	802	3313	2232	122	436	317	0.5	0.4	0.4	1.5	4.6	3.6	2005	6564	7167	1892	12,744	9638	247	1635	941	2.14	1.01	0.70	0.1	0.3	0.3
Go Soy Genetics Optimized	5115LL	V	615	3417	1848	117	484	277	0.5	0.5	0.5	1.4	5.5	3.3	1143	8448	5117	1166	11,630	6408	142	1408	647	2.00	1.04	0.63	0.1	0.4	0.2
Dyna-Gro Seed	S55LS75	V	589	2689	3081	93	373	438	0.5	0.4	0.5	1.2	4.1	5.0	1303	4594	6105	1206	9725	12,816	174	1158	1437	1.60	0.59	0.78	0.1	0.3	0.4
Bayer Credenz	CZ 5242 LL	V	612	2388	2676	92	310	367	0.5	0.4	0.4	1.1	3.2	4.0	1617	6525	5050	1230	8460	10,822	148	923	1320	1.89	0.72	0.71	0.1	0.2	0.3
Bayer Credenz	CZ 5225 LL	V	424	2426	2552	61	317	351	0.5	0.4	0.4	0.7	3.3	3.9	1303	6817	5478	909	9166	9809	100	960	1085	1.50	0.62	0.61	0.0	0.2	0.3
Delta Grow Seeds Com. Inc.	.DG 5170RR2/STS	V	530	3219	2985	87	456	441	0.5	0.4	0.5	1.1	5.1	5.2	1544	6606	6300	877	11,589	13,906	103	1313	1333	1.62	0.79	0.77	0.1	0.4	0.3
REV Brand Seeds	51A56	V	677	2747	2386	109	368	296	0.5	0.4	0.4	1.4	3.9	2.9	1405	8443	10,390	1771	9838	7798	190	1230	873	1.57	0.81	0.55	0.1	0.3	0.3
DuPont Pioneer	P52T50R	V	625	2963	2928	98	391	372	0.5	0.4	0.4	1.2	4.1	3.8	1211	6504	7084	1276	11,012	12,055	158	1391	1481	2.88	0.76	0.69	0.1	0.3	0.3
Syngenta United States	S55-Q3	V	445	2347	2562	70	298	328	0.5	0.4	0.4	0.9	3.0	3.4	1742	7492	7220	1155	8729	10,726	115	1011	1247	0.86	0.80	0.81	0.1	0.2	0.3
Syngenta United States	S56-M8	V	761	2736	2298	113	349	301	0.5	0.4	0.4	1.3	3.6	3.2	1534	10,121	8450	1770	10,547	9242	235	1222	1049	1.10	1.05	0.90	0.0	0.2	0.2
Go Soy Genetics Optimized	5214GTS	V	491	2581	2986	76	353	379	0.5	0.4	0.4	0.9	3.9	3.8	1864	3850	5892	877	9461	12,930	116	1129	1610	1.80	0.59	0.61	0.1	0.3	0.3
Armor	55-R68	V	659	3108	2961	99	399	388	0.5	0.4	0.4	1.2	4.1	4.1	2160	5362	4301	1193	10,938	13,484	164	1486	1671	1.43	0.72	0.69	0.1	0.3	0.3
Progeny Ag Products	P 5226RYS	V	717	3336	2889	112	469	395	0.5	0.4	0.4	1.4	5.3	4.3	1441	4898	6982	1660	11,885	11,445	217	1505	1274	3.00	0.82	0.66	0.1	0.3	0.3
Mycogen Seeds	5N523R2	V	692	2981	2039	115	441	293	0.5	0.5	0.5	1.5	5.2	3.4	3097	3801	5335	1791	9946	7093	164	1257	780	3.43	0.88	0.87	0.1	0.3	0.3
Dyna-Gro seed	S56RY84	V	864	3195	3028	132	457	433	0.5	0.5	0.5	1.6	5.2	5.0	1292	4672	6125	1973	12,079	15,097	293	1440	1553	2.33	0.65	0.77	0.1	0.3	0.4
Croplan WinField United	R2C5225S	V	737	3008	2750	120	430	379	0.5	0.5	0.4	1.6	4.9	4.2	1729	5019	5144	1654	10434	10,673	186	1266	1190	2.78	0.72	0.76	0.1	0.4	0.4
Bayer Credenz	CZ 5375 RY	V	594	3017	3530	104	428	486	0.5	0.5	0.4	1.5	4.8	5.3	1782	5153	7038	1214	11,698	16,497	130	1312	1861	1.46	0.90	0.87	0.1	0.3	0.4
REV Brand Seeds	57R21	V	553	2342	2450	83	310	333	0.5	0.4	0.4	1.0	3.3	3.6	1815	10,931	6604	1303	8993	9743	166	907	1103	1.25	0.70	0.93	0.1	0.3	0.3
Syngenta United States	S58-Z4	V	395	2424	2092	63	323	282	0.5	0.4	0.4	0.8	3.4	3.0	1345	6649	4403	684	7774	7873	81	933	934	1.63	0.77	0.79	0.0	0.2	0.3
Dyna-Gro Seed	S57RY26	V	914	3488	3736	134	485	493	0.5	0.4	0.4	1.6	5.4	5.2	1487	4933	7876	2420	15,177	20,092	359	1740	2150	3.00	0.76	0.73	0.1	0.4	0.3
	Mean	V	651	2974	2707	102	406	367	0.5	0.4	0.4	1.3	4.4	4.0	1748	6382	6456	1426	11,198	11,497	176	1324	1288	2.0	0.8	0.8	0.1	0.3	0.3
Mean			628	2798	2590	101	388	353	0.5	0.4	0.4	1.3	4.3	3.8	1791	5928	6037	1367	10,202	10,761	162	1204	1226	2.06	0.81	0.77	0.1	0.3	0.3
† ANOVA																													
MG				***			***			***			ns			***			***			***			ns			ns	
CUL			***	***	***	***	***	***	*	**	**	ns	***	***	***	***	***	***	***	***	***	***	***	***	***	***	**	ns	ns
TT				***			***			***			***			***			***			***			***				***
LT				***			***			***			***			***			***			***			***				***
HT				***			***			***			***			***			***			***			***				ns
MG x TT				ns			ns			ns			ns			***			***			**			ns				ns
CUL x TT				***			***			ns			***			***			***			***			*				ns

† *, **, ***, and ns representing significance at the $p \leq 0.05$, $p \leq 0.01$, $p \leq 0.001$, and non-significant ($p \geq 0.05$), respectively. CUL, cultivar; MG, maturity group; TT, temperature treatment; LT, low-temperature treatment; HT, high-temperature treatment; OT, optimum temperature treatment; R/S, root to shoot ratio.

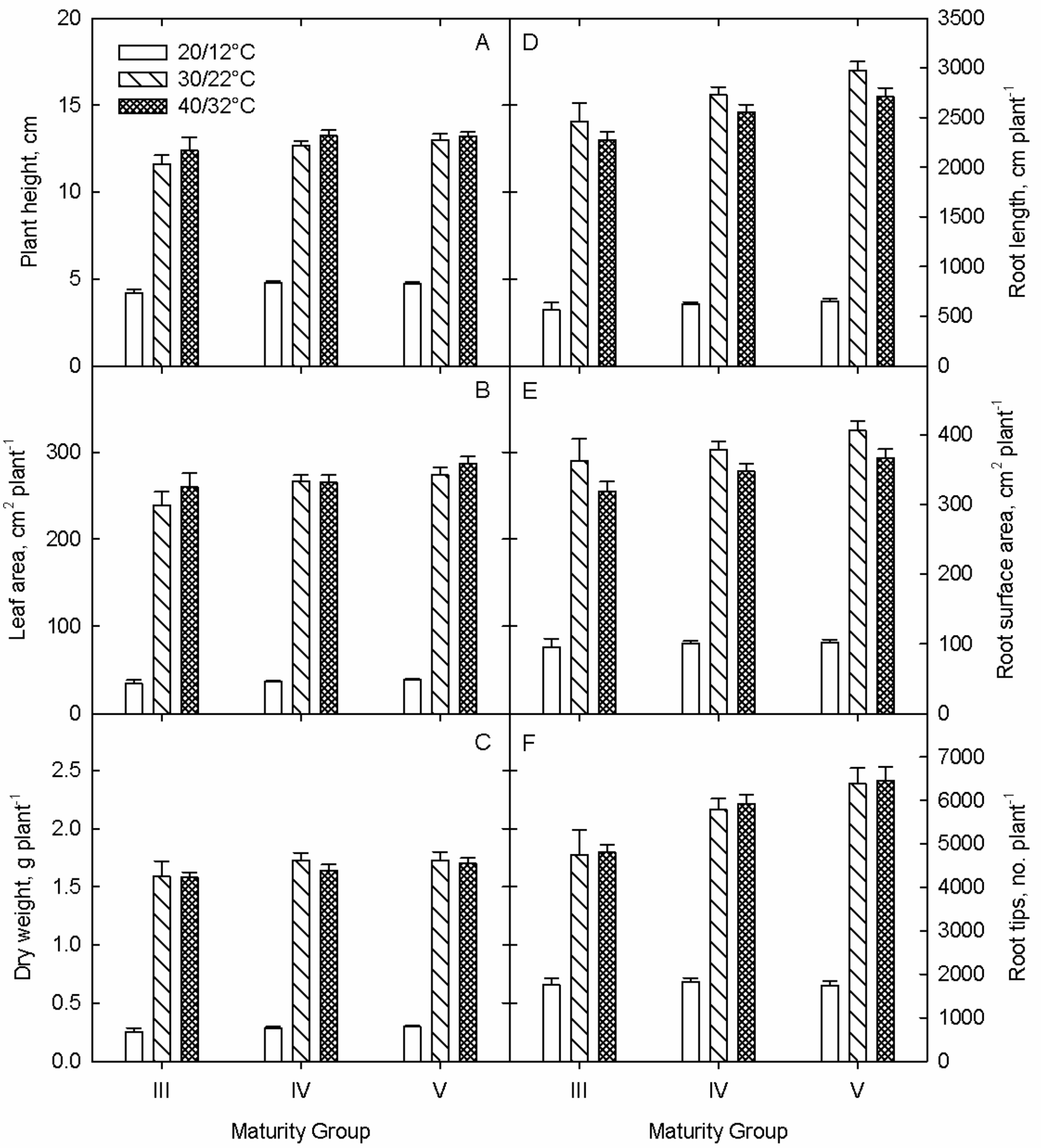

Figure 1. Temperature and maturity group interaction for (**A**) plant height, (**B**) leaf area, (**C**) dry weight, (**D**) root length, (**E**) root surface area, and (**F**) root tips for soybean 64 cultivars harvested 20 days after sowing. Data shows mean + SE.

3.1.2. Root Parameters

The effects of TTs were significant in all the measured root parameters (Table 2). Further, cultivars varied significantly across TTs for all the measured root parameters, except root volume (RV) at LT, and root weights (RW). Cultivar x TT interaction was also significant ($p < 0.001$) for all the root parameters, except root average diameter (RAD) and RW (Table 2). Maturity groups significantly differed for root traits, except for RV, RW, and R/S, while interaction effect of MG with TTs was significant only for lateral root development (i.e., RNF, RNC, and RNT) (Table 2).

Root Growth

Unlike shoot growth, root growth parameters, including CRL, RSA, and RV showed decline under stress conditions than control (Table 2). The mean CRL was obtained highest at OT (2798.06 cm), followed by HT (2590.36 cm), and LT (627.65), respectively (Table 2). The percent decline in mean CRL was higher at LT (77.5%) than HT (7.4%). Among 64 soybean cultivars, S39-T3 showed significantly highest (84.09%), and 5N393R2 showed significantly lowest (64.6%) decline in CRL at LT when compared to OT (Table 2). Overall, the mean CRL was significantly higher for MG V (2110.72 cm) followed by MG IV (1973.84 cm) and MG III (1766.79 cm). On an average across cultivars, the percent decline in RSA at LT and HT were 74% and 9%, respectively. The highest and lowest value for RSA were obtained in LELAND at OT, and CZ 5225 LL at LT, respectively (Table 2). Unlike LT effects, some cultivars including 5N393R2, IREANE, and ELLIS had greater values for CRL and RSA under HT when compared to OT. The cultivars belonging to MG V had significantly higher RSA on an average (Figure 1E), with no differences observed between MG III and IV ($p > 0.05$). The percent increases of RSA were 6, 11, and 13% for the cultivars from MG V compared to MG III at low, optimum, and high temperature conditions (Figure 1E). Interestingly, the mean value of RAD was significantly greater at LT (0.51 mm) than OT (0.44 mm) or HT (0.43 mm) across the tested cultivars (Table 2). Contrasting to CRL, MG III showed significantly higher mean RSA (0.49 mm) followed by MG 4 (0.46 mm) and MG5 (0.45 mm), respectively (Table 2).

Root Development

In contrast to root growth, the mean values of root development parameters, including RNT, RNF, and RNC, significantly increased with increasing temperatures from low to high (Table 2). On an averaged across cultivars, the values for RNF, RNT, and RNC ranged from 1791 to 6037, 1367 to 10,761, and 165 to 1226, respectively, across TTs (Table 2). Cultivars 51A56 and 5115LL showed maximum and minimum values for RNT, while cultivars S57RY26 and S39-T3 showed maximum and minimum values for RNF as well as RNC, respectively, across TTs (Table 2). Likewise observed for shoot parameters, the study observed a reduction in root development (i.e., RNT, RNF, and RNC) with an increase from optimum to high temperatures in some cultivars, including GS45R216, S45-W9, P47T36R, and AR4705 (Table 2). Also, the strong effect of MG was observed in lateral root development, such that MG V cultivars showed greater lateral root numbers than MG III and IV (Figure 1F). However, the effects were modified with increasing temperatures.

3.1.3. Plant-Component Dry Weights

The study observed significant effects of LT and HT on leaf dry weight (LW), while stem dry weights (SW) and root dry weights (RW) were only affected under LT (Tables 1 and 2). No effects of MG or MG × TT were found on dry weights (Tables 1 and 2). The decline in LW was higher under LT effects (82.5%) than under HT effects (5.7%) compared to OT when averaged across cultivars. However, cultivars varied significantly for LW under LT and OT, but not under HT (Table 1). The LW ranged from 0.05 g in GS47R216 at LT to 2.67 g in P 4757 RY at OT. The mean SW and RW showed a reduction of 90.6% and 77% under LT stress, respectively when compared to OT. Among tested cultivars, the maximum reduction was observed in R2C4775 (94.2%) and S39-T3 (86.7%) for SW and RW, respectively under LT effects (Tables 1 and 2). Total dry weight (TW) calculated by summation of LW, SW, and RW was significantly reduced under LT effects by 83.4%. Further, cultivar × TT interaction was significant for TW such that TW varied between 0.14 g in S45-W9 at LT and 3.43 g in P 4757 RY at OT (Table 1).

3.1.4. Physiological Parameters

The study observed significant cultivar, MG, and TT effects on chlorophyll measured and expressed as SPAD values ($p < 0.001$). The SPAD values significantly increased from LT to HT, ranging from 26.86 to 41.93, on an average across the cultivars (Table 1). Among tested cultivars, the maximum and minimum SPAD values were observed in S48RS53 (38.7) and 55-R68 (31.7), respectively across TTs. Overall, MG III showed significantly higher SPAD values than MG IV and V. However the interaction effects were not significant for SPAD value ($p > 0.05$). Similarly, mean canopy temperatures were significantly ($p < 0.001$) highest under HT (34.9 °C), followed by OT (29.8 °C), and LT (24.9 °C), respectively, across cultivars, with no difference ($p > 0.05$) observed among cultivars and maturity groups.

3.2. Cumulative Stress Response Indices

Cumulative stress response indices for high temperature (CHTRI) varied from 13.02 (heat sensitive) to 26.28 (heat tolerant) across 64 soybean cultivars. Based on CHTRI values and an increment of 1.0 SD, nine cultivars were identified as highly sensitive, 30 were moderately sensitive, 17 were moderately tolerant, and eight were highly tolerant to HT, among the tested cultivars (Table 3). Cultivar 45A-46 showed the highest tolerance, and 5115LL showed the highest sensitivity to HT effects, respectively. Further, CHTRI showed a positive and significant correlation ($p > 0.001$) to CHTRI calculated for root parameters (r^2 = 0.91) and shoot parameters (r^2 = 0.70) separately (Figure 2).

Table 3. Classification of soybean cultivars into high-temperature tolerance groups based on cumulative high-temperature response index (CHTRI; unitless), along with individual scores in parenthesis.

Heat Sensitive (CHTRI = 13.20 to 15.32)	Moderately Heat-Sensitive (CHTRI = 15.33 to 17.62)	Moderately Heat-Tolerant (CHTRI = 17.63 to 19.91)	Heat Tolerant (CHTRI > 19.92)
5115LL (13.02)	GS45R216 (15.47)	DG4781LL (17.75)	IREANE (20.25)
S47-K5 (14.00)	5N424R2 (15.05)	S39-T3 (18.01)	CZ 4898 RY (20.59)
S45-W9 (14.77)	GT-476CR2 (15.58)	S56RY84 (18.03)	CZ 5242 LL (20.84)
483C (14.91)	AG4632 (15.66)	CZ 5225 LL (18.03)	CZ 5375 RY (20.88)
38 R10 (14.92)	5N523R2 (15.66)	S58-Z4 (18.04)	ELLIS (21.16)
R01-416F (15.06)	P47T36R (15.94)	DB 4911 (18.07)	5N393R2 (21.21)
JTN-5110 (15.16)	P 4588RY (15.97)	R2C4775 (18.10)	CZ 4181 RY (24.17)
S48RS53 (15.24)	P41T33R (16.03)	P 4247 LL (18.69)	45A46 (26.28)
DG 4825RR2/STS (15.25)	P 5333 RY (16.09)	S57RY26 (18.79)	
	LELAND (16.25)	CZ 4044 LL (18.83)	
	GS47R216 (16.38)	5214GTS (18.91)	
	DG 4680RR2 (16.41)	48A26 (19.09)	
	31RY45 (16.46)	S55-Q3 (19.25)	
	PI 471938 (16.50)	5N490R2 (19.35)	
	P 5226 RYS (16.57)	S49LL34 (19.54)	
	R2C5225S (16.61)	48L63 (19.73)	
	51A56 (16.71)	S55LS75 (19.81)	
	P 4757 RY (16.38)		
	AR4705 (16.90)		
	AG5332 (16.93)		
	55-R68 (17.06)		
	S39-C4 (17.10)		
	DG 5170 RR2/STS (17.27)		
	P52T50R (17.38)		
	57R21 (17.44)		
	4814GTS (17.51)		
	DG 5067 LL (17.52)		
	S56-M8 (17.54)		
	32y39 (17.54)		
	4714LL (17.59)		

Cumulative stress response indices for low temperatures classified 21 cultivars as cold sensitive, 32 cultivars as moderately cold sensitive, six cultivars as moderately cold tolerant, and five cultivars as cold tolerant, based on the means and SD. Cultivars CZ 5225 LL and GS47R216 were identified as most sensitive and tolerant to LT, respectively (Table 4). Unlike CHTRI, CLTRI has had a poor correlation to CLTRI calculated for the shoot (r^2 = 0.05) and root parameters (r^2 = 0.38) separately (Figure 3). However, CLTRI had a significant and positive correlation with CHTRI ($p < 0.001$; r^2 = 0.96) (Figure 4).

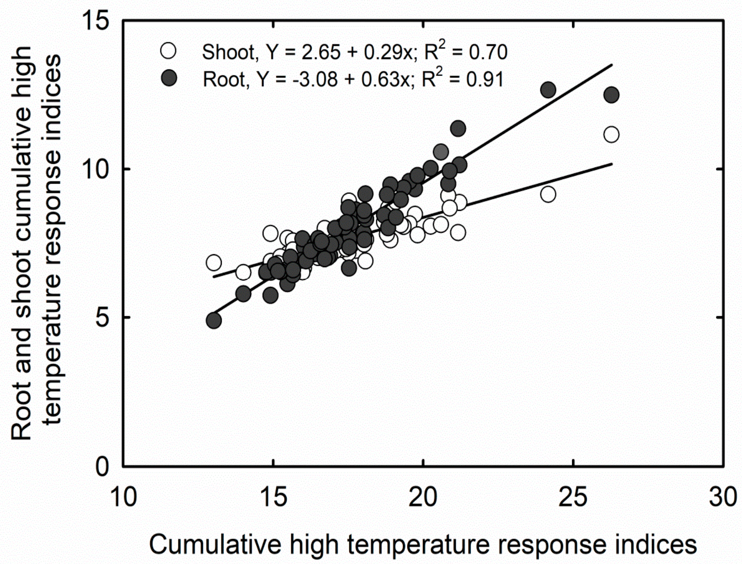

Figure 2. Correlation between cumulative high-temperature response indices and cumulative high-temperature response indices calculated for root and shoot parameters separately among 64 soybean cultivars, measured at 20 days after sowing.

Table 4. Classification of soybean cultivars into cold tolerance groups based on total low-temperature response index (CLTRI; unitless), along with individual scores in parenthesis.

Cold-Sensitive	Moderate Cold Sensitive	Moderate Cold Tolerant	Cold Tolerant
(CLTRI = 6.12 to 6.94)	**(CLTRI = 6.95 to 7.76)**	**(CLTRI = 7.77 to 8.58)**	**(CLTRI > 8.59)**
CZ 5225 LL (6.12)	S47-K5 (6.95)	5N523R2 (7.94)	4714LL (8.68)
CZ 4044 LL (6.16)	DG 4680RR2 (6.98)	P52T50R (7.99)	5N393R2 (8.94)
R01-416F (6.21)	R2C4775 (6.99)	S48RS53 (8.10)	AG5332 (9.42)
57R21 (6.29)	CZ 5375 RY (7.00)	45A46 (8.15)	GT-476CR2 (9.83)
PI 471938 (6.32)	P 5226 RYS (7.00)	DG4781LL (8.29)	GS47R216 (10.34)
S39-T3 (6.39)	S58-Z4 (7.00)	P47T36R (8.56)	
48A26 (6.54)	R2C5225S (7.01)		
AG4632 (6.63)	38 R10 (7.02)		
CZ 4898 RY (6.63)	S55-Q3 (7.03)		
5115LL (6.66)	483C (7.12)		
DG 5170 RR2/STS (6.67)	CZ 4181 RY (7.13)		
S39-C4 (6.75)	S56-M8 (7.15)		
P 4588RY (6.76)	5214GTS (7.16)		
P 5333 RY (6.77)	S45-W9 (7.20)		
LELAND (6.78)	DB 4911 (7.21)		
S55LS75 (6.81)	32y39 (7.25)		
5N424R2 (6.83)	GS45R216 (7.25)		
JTN-5110 (6.86)	51A56 (7.28)		
4814GTS (6.86)	AR4705 (7.29)		
31RY45 (6.90)	IREANE (7.30)		
55-R68 (6.91)	P 4247 LL (7.37)		
	DG 4825RR2/STS (7.38)		
	48L63 (7.40)		
	S57RY26 (7.40)		
	P 4757 RY (7.42)		
	CZ 5242 LL (7.51)		
	DG 5067 LL (7.53)		
	ELLIS (7.61)		
	P41T33R (7.61)		
	5N490R2 (7.65)		
	S56RY84 (7.66)		
	S49LL34 (7.71)		

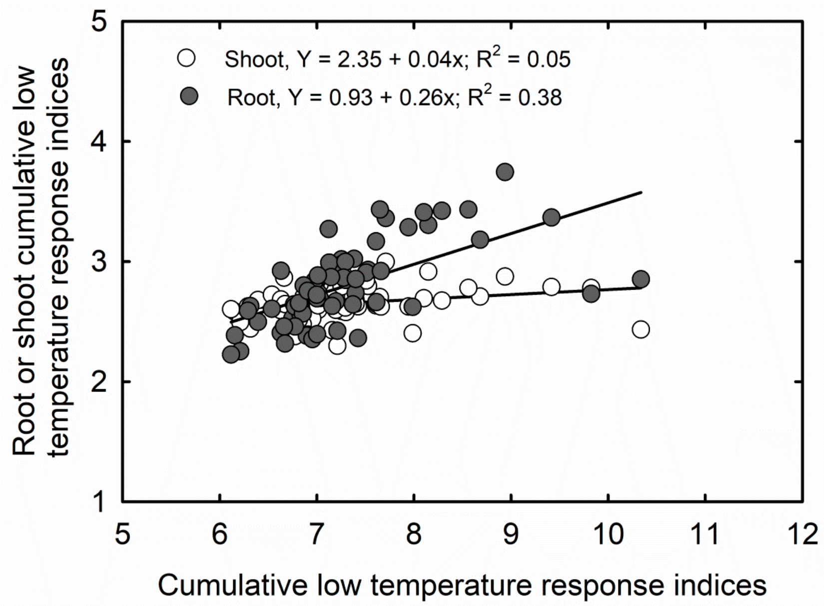

Figure 3. Correlation between cumulative low-temperature response indices and cumulative low-temperature response indices calculated for root and shoot parameters separately among 64 soybean cultivars, measured at 20 days after sowing.

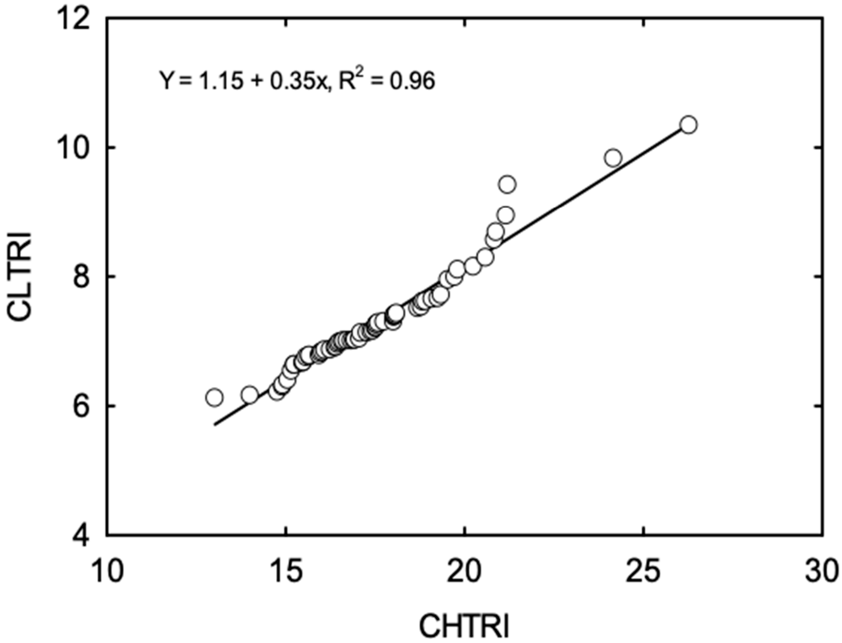

Figure 4. Correlation between cumulative high-temperature response indices (CHTRI) and cumulative low-temperature response indices (CLTRI) among 64 soybean cultivars, measured at 20 days after sowing.

3.3. Principal Component Analysis (PCA)

According to the PCA analysis, the first two principal components (PCs) accounted for 56% of the total variance at low temperature (Figure 5A) while 60% of the variability was expressed under high temperature (Figure 5B). PC1 accounted for 44 and 49% of the variance among the cultivars for LT and HT with higher positive loadings for LW, RV, RW, and TW at LT and RL, RSA, RC, and TW at HT (Figure 5). PC2 accounted for an additional 12 and 11% of the variation with the AD, SPAD, and CT at low temperature and AD, CT, and RV at high temperature. Proceeding from both positive and negative loadings of PC1 and PC2, 64 soybean cultivars were classified into three main groups as tolerant, moderate, and sensitive. Within this classification, GT476CR2 and 4714LL represented tolerance, 483C, S56RY84, S57RY26, 45A46, and DG4781LL as moderate, and S47K5 and CZ5225LL as sensitive for low temperature (Figure 5). On the other hand, CZ5242LL and 45A46 came under high-temperature tolerant group followed by S56M8, AG5332, PI471938, DB4911, CZ5225LL, and S39T3 as intermediate and 38R10 and S48RS53 as high temperature sensitive.

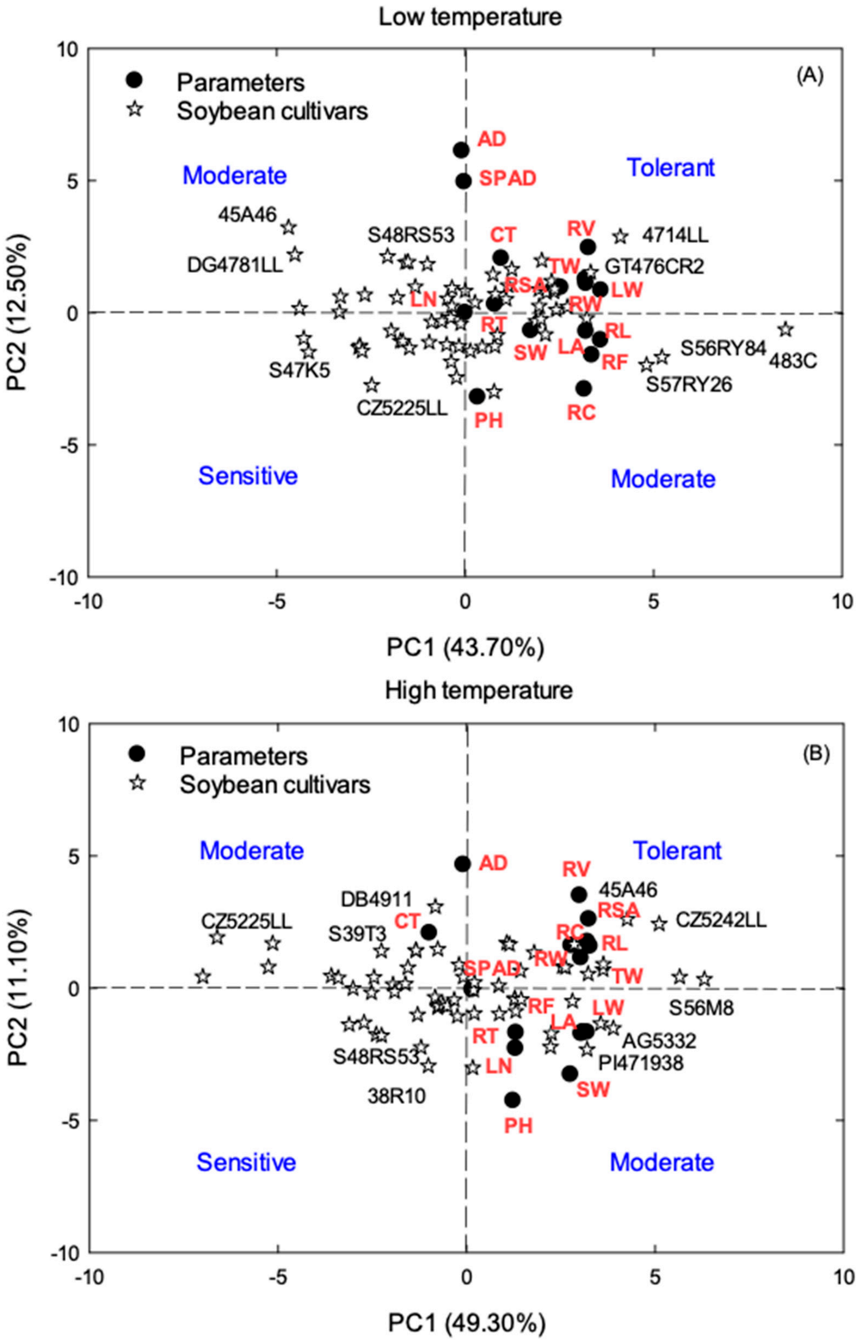

Figure 5. Principal component analysis (PCA) biplot for the first two principal component (PC) scores, PC1, and PC2, related to the classification of 64 soybean cultivars (open stars) for low (**A**) and high-temperature (**B**) tolerance. The eigenvectors for the crop traits (solid circles) are superimposed with the PC biplot scores at the similar scale that reflect the contribution of each parameter in the determination of tolerance or the susceptibility towards heat or cold. The eigenvector values were multiplied by ten to obtain a clear and superimposed figure.

4. Discussion

The identification of LT and HT tolerance in soybeans is vital for effective management and production under ESPS and CSPS in US Midsouth. Further, information on cultivar-specific tolerance to a degree of temperatures can be exploited in breeding programs to develop tolerant genotypes that are highly suited for cold or hot environments. Most of the studies in the past have utilized planting date as a criterion to evaluate cultivar's ability to grow under a given production system [2,18–21]. However, several confounding weather factors co-vary during the growing season that limits the results of such studies to validate cultivar's tolerance to low or high-temperature tolerance [16]. The present study is distinct in that it utilizes controlled conditions to identify cultivar-specific tolerance to LT or HT during early-growth, keeping other environments constant. Secondly, this study characterized both shoots as well as root growth and development to determine the temperature tolerance in the soybean cultivars. The present study evaluated soybean cultivars belonging to MG III, IV, and V, which are recommended ideal for the US Midsouth environments based on previous literature describing the interactive effects of agronomic practices, environments, and MG [2,16,19,20,34–36]. The present study showed vigorous seedling growth in cultivars belonging MG IV and V when compared to MG III, which supports recent studies that favored MG IV and V to utilize under ESPS in the US Midsouth [2,19].

Among TTs, LT caused more severe reductions in the shoot, root, and physiological parameters of soybean seedlings than HT. This was expected because, in general, soybean is regarded a warm season crop [9], and considered sensitive to chilling that may occur within a certain range of temperatures during most of the stages of life cycle [7,16,25]. The highest damage from chilling injury was observed during germination and seedling emergence of soybean, which showed the severity of damage increase linearly with decreasing temperatures, and finally leading to the death of seedlings [6–8]. Also, chilling injury during seedling growth of soybean has been identified as a major constraint in the success of ESPS in the US Midsouth [5]. Cool and wet conditions developed from early season rainfall may hinder germination of April-planted soybeans under ESPS [4,5]. According to Wuebker et al. [26], seeds flooded for one day after the start of imbibition showed 18% decrease in germination at 15 °C than at 25 °C. Similar to the present study, the findings on early-season planting (April–May) of other crops grown in US Midsouth such as cotton and corn reported LT as most damaging for seedling growth among various abiotic stress factors [27,28,30,31]. The lesser degree of damage from imposed levels of HT further suggests that like most species, soybean also have a higher temperature optimum for vegetative development than reproductive development [11]. Higher mean values for chlorophyll content as well as canopy temperatures under HT effects than LT further strengths the arguments mentioned above. SPAD values and canopy temperatures are important parameters to evaluate plant photosynthetic efficiency and acclimation [37,38]. The higher chlorophyll content attributed to higher photosynthetic rate might have positively contributed to greater plant component dry weights observed under HT treatments in this study.

Interestingly, the present study found varied response of shoot and root parameters to the effects of TTs. The shoot growth was more adversely affected under LT but showed rapid increases under HT effects, when compared to OT. This supports previous reports of rapid germination and emergence on late-season planting (May or later) of soybean under CSPS [2–4]. Little is known on the effects on abiotic on the root system of soybeans compared to other major crops such as corn, rice, and cotton of US Midsouth during seedling growth [27,28,30]. Root hydraulic conductivity is considered most sensitive to low temperatures irrespective of soil moisture status [39]. The low temperatures can induce assimilate partitioning regarding higher RAD, and lower CRL and RSA to maintain root hydraulic conductivity in plants [3,27,28]. Higher mean RAD observed under LT effects in this study was in agreement with Singh et al. [27] and Wijewardana et al. [28] that found significantly greater mean RAD in cotton and corn seedlings under LT effects, respectively. Moreover, in agreeing with previous findings, RAD was negatively correlated with all the other shoot and root parameters (Table S1). Similar to RAD, RS also exhibited a negative correlation (Table S1), however, all the correlations were significantly different ($p < 0.001$). Further, increased lateral root numbers (RNF, RNC, and RNT) under HT corroborate the findings of Khaled et al. [3] that showed mean lateral root numbers in soybeans were significantly increased (12.7%) in CSPS (June planting) compared to ESPS (April planting). Further, increased lateral root number may have positively contributed to increased root biomass (canopy temperatures) observed under HT effects in this study.

According to PCA, RL, RV, TW, and LA were identified as the traits that best described the temperature tolerance in soybean. Similar to the CLTRI and CHTRI procedure, PCA also identified 4714LL and GT476CR2 as cold tolerant, S47K5 and CZ5225LL as cold sensitive, 45A46 and CZ5242LL as heat-tolerant, and S48RS53 as heat sensitive. Therefore, the findings from PCA were in reasonable agreement with the CLTRI and CHTRI methods where all traits were used in the analysis and the classification of soybean cultivars for low- and high-temperature tolerance. Both positive and negative response in the shoot and root parameters under HT effects supports a positive correlation obtained between CLTRI and CHTRI calculated for a shoot or root parameters separately. The cultivars are showing a reduction in a shoot or root parameters under high temperatures ascribed to their low tolerance to imposed levels of HT or vice versa. A strong and positive correlation between CHTRI and CLTRI indicates that temperature treatments operate likewise on seedling growth and development. For instance, cultivars like 5115LL and JTN-5110 were found sensitive to both LT and HT, while cultivars like 5N393R2 and 45A46 showed tolerance to both HT and LT. The identified tolerance among the tested cultivars based on CHTRI and CLTRI will help farmers in selecting cultivars suited best for a specific region as well as a production system followed, with an aim to maximize benefits regarding temperature tolerance.

5. Conclusions

Soybean cultivars varied markedly in their response to high and low temperatures during seedling growth stage, however, modified by maturity group. The reduction in growth and development were more pronounced under LT than under at HT during the seedling growth stage of all soybean cultivars. Significant variability existed in the tested cultivars, from same or different MGs, in responses to imposed TTs for the measured parameters. The changes in morphological and physiological growth characteristics can be ascribed to cultivar's degree of tolerance to the imposed level of temperature stresses. Also, the differential response in the shoot and root parameters to TT and MG signifies the importance of understanding both shoot and root system under stress conditions as well production system followed.

Further, cumulative stress response indices and principal component analysis developed to score the cultivars for high or low-temperature tolerance could be exploited in breeding programs to develop genotypes for temperature tolerance. The LT and HT scores of the cultivars along with region-specific yield data would be helpful for producers' to select cultivars best suited for their production system. Additional research in the field is warranted to investigate the relevance of this study and possibly predicting cultivars tolerance to low and high-temperature conditions under ESPS and CSPS, respectively. Also, testing the cultivars for reproductive tolerance to high temperatures will also be needed to identify tolerance to yield-related parameters.

Supplementary Materials: The following are available online at http://www.mdpi.com/2073-4395/9/1/13/s1, Table S1: Pearson correlation matrix showing the relationship among plant height (PH), leaf area (LA), leaf weight (LW), stem weight (SW), root weight (RW), total weight (TW), canopy temperature (CT), chlorophyll content (SPAD), Cumulative root length (RCL), root surface area (RSA), root diameter (RAD), root volume (RV), number of root tips (RT), number of forks (RF), number of crossings (RC), and root/shoot ratio (RS) of 64 soybean cultivars.

Author Contributions: Conceptualization, K.R.R.; Methodology, K.R.R., F.A.A. and C.W.; Software and Formal Analysis, F.A.A., K.R.R. and C.W.; Investigation, K.R.R. and F.A.A.; Resources, K.R.R.; Data Curation, K.R.R.; Writing-Original Draft Preparation B.S. and F.A.A.; Writing-Review & Editing, F.A.A., B.S., C.W., J.T.I., W.G. and K.R.R.; Supervision, K.R.R.; Project Administration, K.R.R.; Funding Acquisition, K.R.R., J.T.I. and W.G.

Funding: This research was funded by Mississippi Soybean Promotion Board and National Institute Food and Agriculture, NIFA (2016-34263-25763 and MIS 043040) and Mississippi Soybean Promotion Board and MAFES-SRI.

Acknowledgments: We thank David Brand for technical assistance and graduate students of the Environmental Plant Physiology Lab at Mississippi State University for their support during data collection. This article is a contribution from the Department of Plant and Soil Sciences, Mississippi State University, Mississippi Agricultural, and Forestry Experiment Station.

Conflicts of Interest: The authors declare no conflict of interest

Abbreviations

CSPS	conventional soybean production system
CLTRI	cumulative stress response indices for low temperature
CHTRI	cumulative stress response indices for high temperature
CT	canopy temperatures
CRL	cumulative root length
DAS	days after sowing
ESPS	early soybean production system
HT	high temperature
ILTRI	individual stress response index for low temperature
IHTRI	individual stress response index for high temperature
LA	leaf area
LW	leaf weight
NN	mainstem node number
LT	low temperature
MG	maturity group
PH	plant height
RAD	root average diameter
RNC	number of root crossings
RF	number of root forks
RSA	root surface area
CT	canopy temperature
RNT	number of root tips
R/S	root and shoot ratio
RV	root volume
RW	root weight
SW	stem weight
RNT	number of root tips
TW	total weights
TT	temperature treatments

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