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GROWTH RESPONSES OF *ABELMOSCHUS ESCULENTUS* (L.) MOENCH UNDER STRESSES OF DROUGHT AND *MELOIDOGYNE INCOGNITA* INFECTION

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ABSTRACT

Growth and agricultural production of crops including, *Abelmoschus esculentus* (okra), a staple and nutritious vegetable cultivated and consumed in sub-Saharan Africa, is threatened and constrained by abiotic and biotic stresses caused by global climate change. While individual stressors cause devastating impacts to agricultural production, the possible combination of different multiple stresses (either jointly or sequentially), could pose a greater threat to global food production and food security. This study aimed at exploring morphological responses of okra plants cv. 'Meya' subjected to individual, sequential and concurrent stresses of drought and *Meloidogyne incognita* a causative agent of root-knot disease. Results showed both stresses significantly reduced growth and yield components of plants. Individual drought stressed plants significantly reduced growth compared to plants stressed with only nematode infection. Varied morphological differences were observed between plants stressed in sequence and those that received both stresses concomitantly. Plants subjected to dehydration stress prior to nematode infection coped better with the stress combination in comparison to plants that were challenged with nematode infection before dehydration stress and concurrent drought-nematode stress. This okra cultivar was either highly or moderately resistant to nematode infection by moderate formation and establishment of galls and egg masses. Survival mechanisms of this cultivar under both stresses could be primarily linked to its water-use efficiency as well as several cascades of changes in signal transduction pathways.

Keywords: *Meloidogyne incognita*; Nematode; Okra; Pathology; Biotic and Abiotic Stress.

INTRODUCTION

Abiotic and biotic stresses reduce agricultural yields following the exposure of most plants to multiple stresses. Owing to their sessile lifestyle, plants are subjected to various abiotic and biotic stresses in their natural habitat. Different forms of stresses that include drought, heat, salt, and biotic stresses, have been elicited by global climate change and unusual weather events anywhere in the world (Chandra *et al.*, 2021). Altered

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weather patterns such as drought and lack of rainfall; increasing world populations and expansion of irrigated agriculture are some of the main driving forces for the global demand of water, especially in drought-prone region (Ercin and Hoekstra, 2014). The World Economic Forum named the aforementioned stresses as one of the greatest hazards to the world in 2019 because of their potential impact in the past 10 years (The Global Risks Report, 2019). Drought stress has caused a number of morphological and metabolic modifications in plants (Osakabe *et al.*, 2014a; Meena *et al.*, 2017). Root-knot nematodes (RKN) are main vegetable pathogens available in the tropics and sub-tropics. According to research by Hussain *et al.* (2015), the majority of commercial okra types are vulnerable to RKN and result in significant

agricultural losses. In their natural environment, crops frequently encounter both abiotic and biotic stressors at the same time. Studies have demonstrated that plant responses to a variety of combined biotic and abiotic stressors are distinctive and cannot be inferred immediately from the response of each of the several stresses applied separately (Rasmussen *et al.*, 2013; Suzuki *et al.*, 2014; Anwar *et al.*, 2021).

Abelmoschus esculentus (Okra) is a vegetable crop that is a member of the Malvaceae family. It is a herbaceous annual plant that is grown in warm temperate and subtropical climates all over the world. (Akinyele and Osekita 2006; Agba *et al.*, 2011). Being a staple in sub-Saharan regions, the nutritious vegetable can be cultivated on a variety of soil types but some well-drained fertile soil rich in soil organic manure cedes higher productivity (Abidi *et al.*, 2014). Numerous studies have demonstrated that plants, including okra, respond to stressors like drought by changing in a variety of ways that affect their morphology, cellular structure, physiological state, biochemistry, and molecular makeup (Osakabe *et al.*, 2014b; Abdulrahman and Nadir, 2018; Jabborova *et al.*, 2020; Egedigwe *et al.*, 2021). Drought stress on plants has been shown to inhibit plant development throughout vegetative growth phases (plant height, branching, leaf size, expansion, area index and tiller numbers) (Farooq *et al.*, 2009). Plants senesce their leaves under extreme drought stress to decrease transpiration rate and water consumption (Agusti *et al.*, 2012). According to reports, drought accelerates growth and development of plants, shortens the seed-filling phase, and redeploys plant reserves to developing seeds, thereby reducing the time that plants may remain photosynthesis-capable and lowering seed yield (Chadha *et al.*, 2019). Okra has been described as being drought-tolerant (Singh *et al.*, 2014), although most plant species' tolerance to drought is complicated by the interactions between the elements that cause damage and the plant's physiological responses (Manivannan *et al.*, 2008). According to Adejumo *et al.* (2018), the timing, duration, severity, and stage of exposure all had a significant impact on how the okra plants responded to drought.

Thus, okra yield is affected immensely by a number of pathogens such as fungi, bacteria, viruses and nematodes. The obligate, sedentary endo-parasites of the vascular tissues of plant roots are called root-knot nematodes, *Meloidogyne* spp. (Anwar and Mckenry, 2012; Devran *et al.*, 2017) and are universally associated with serious vegetable production losses across the globe (Hallmann

and Meressa, 2018). Although about 100 nominal species of *Meloidogyne* have been reported so far (Wesemael *et al.*, 2013), *M. incognita*, *M. hapla*, *M. javanica* and *M. arenaria* are four species which are especially significant economically. *M. incognita* are so prevalent globally and attack a variety of economically significant crops such that they are regarded as a quiet threat to vegetables (Barbary *et al.*, 2016; Atas *et al.*, 2021). *Meloidogyne* species are thought to cause losses that range from 5% to 43% in total (Gautam *et al.*, 2014; Fabiyi *et al.*, 2018). According to Taylor (1979), RKN decreases plants' tolerance for environmental stress by weakening their defences against pathogens. According to studies, RKNs are directly to blame for okra output declines of up to 27% (Adekunle, 2009; Anwar and Mckenry, 2012; Hussain *et al.*, 2014). These losses were attributed to continuous cropping of okra in same fields year after year (Hussain *et al.*, 2015). Owing to a shift in the global climate, the potential effect of these novel and complex combinations of stresses on growth and productivity of crops has become a major cause of worry. Due to the disastrous impacts of environmental cues on agricultural output, huge attempts, over the past three decades, have been to understand the specific outcomes of these stressors on plants. Current studies are now geared towards understanding plants tolerance to concurrent abiotic and biotic stress combinations (Rivero *et al.*, 2021). This study aimed at exploring morphological responses of okra plants cv. 'Meya' subjected to individual, sequential and concurrent stresses of drought and *Meloidogyne incognita*.

MATERIALS AND METHODS

Plant Material, Preparation of Soil Samples and Experimental bags: This study was conducted at the screen house in the Botanic Garden of the Department of Plant Science and Biotechnology, University of Nigeria Nsukka. Okra seed growers at the Adani-Ojo Ogurugu Agro Centre, Uzouwani LGA, Enugu State provided the "Meya" cultivar's seeds. Sand and composite top layered soil obtained from the Botanical Garden were enriched with cured poultry droppings and mixed in the ratio of 2:1:1 respectively. Using a 250 L metal barrel enriched soil was steam-sterilized for 4.5 hours until it reached 105°C. It was allowed to sit for 7 days before being used. A 2 mm sieve was used to filter an air-dried sample of sterile soil for analysis in the laboratory of the Department of Soil Science, UNN using the standard method of the Association of Official Analytical Chemists (2005). Soil physicochemical properties included pH: 6.4; sandy soil: 64%; silt: 16%;

clay: 11%; organic matter: 8.96%; total nitrogen: 1.43%; phosphorus: 39.1 ppm; exchangeable cations: 24.64 mg/100 g; calcium: 8.2 mg/100 g; magnesium 17.28 mg/100 g; sodium: 0.51 mg/100 g; potassium: 1.45 mg/100 g and hydrogen ion: 1.12 mg/100 g. Eleven kilograms each of sieved sterile soil were weighed into perforated black medium-sized polythene planting bags measuring 25 cm deep and 12 cm in diameter.

Seed Viability Test, Raising Plants in Nursery: All experimental seeds were submerged in water for 24 hours. Only seeds that were submerged were chosen as viable. Three healthy seeds were planted in each nursery planting bag and given enough irrigation for 14 days. Two weeks after sowing, a seedling each, was transferred into experimental bags and they were arranged in the screen house with planting spacing of 40 × 40 cm. Okra plants

Table 1. Treatments used in this study

Treatments	Description
1. Individual drought stress (D)	Okra plants were adequately irrigated at the end of every 10-d water-deficit that lasted for 66 days.
2. Individual root-knot nematode infection (RKN)	Okra plants were infected with <i>M. incognita</i> for 66 days and irrigated at 2-d intervals.
3. Drought-stressed plants challenged with subsequent nematode infection (DBR)	Okra plants were subjected to a 10-day water-deficit prior to a 66-d <i>M. incognita</i> infection. A 2-d irrigation interval was resumed after drought stress.
4. Nematode-infected plants subjected to a subsequent drought stress (RBD)	Okra plants infected with a 66-d <i>M. incognita</i> infection (with a 2-d irrigation interval) prior to a 10-d water-deficit before harvest.
5. Concurrent nematode-drought stressed plants (RAD).	Okra plants received an initial 10-d water-deficit prior to a 66-d <i>M. incognita</i> infection. Plants were adequately irrigated at the end of every 10-d water-deficit interval till termination of experiment.
6. Control plants (Ctrl)	Non-stressed okra plants that were irrigated every 2-d interval for 66 days.

Extraction, Quantification and Inoculation of Nematodes: To inoculate plants with nematodes, an initial population (Pi) of 5000 freshly (within 48 h) hatched second stage juveniles (J₂S) of *M. incognita* (Plate 2D) were used to infect okra plants. J₂S was mass-cultured from single egg mass on infested *Celosia argentea* roots obtained from the Institute of Tropical Agriculture Ibadan, Nigeria. These infested roots were gently uprooted and chopped into smaller pieces (1 – 2 cm) after being rinsed with tap water and shaken vigorously for five minutes in a flask containing 0.5% NaOCl. Eggs were collected on a 38 µm sieve placed over a 25 µm sieve (Hussey and Barker, 1973). From the egg suspension, the juveniles were removed and placed in an extraction tray (Whitehead and Hemming, 1965). Inoculum density was estimated by pouring egg suspension into a measuring cylinder. Estimation of the number of juveniles were made in 10 aliquots of 1 ml in a counting dish under a

were allowed to stabilize for 7 d before treatment applications.

Experimental Design and Treatment conditions and Stress Imposition: Agronomic responses of okra in this study were monitored between the months of February and June, 2022. Experimental bags were arranged in the screen house using a completely randomized design with 6 different treatments replicated 20 times. The experiment was repeated in space, making a total of 240 plants. A description of the six treatments is summarized in Table 1. Prior to treatment applications, irrigation was done every 2-day intervals for this study. All plants were grown under natural conditions and photoperiods between February and June, 2022. Water-proof nylon bags were used to cover soil top surfaces to reduce excessive evaporation of soil water content.

Phillip Harris light microscope at magnification of ×40 and means were calculated (Mukhtar *et al.*, 2013). Using the total volume of nematode suspension, the total number of juveniles was estimated. Juvenile suspension was concentrated by allowing it to settle down for 10 h and supernatant decanted without disturbing the bottom. Inoculation was achieved by adding 3.5 mL into four tiny holes made around the plant and holes were subsequently re-closed with soil.

Growth Assessments of Plant and Nematode: Plants were harvested and growth components evaluated included lengths, of shoots, roots and pods; numbers of surviving leaves, detached leaves, flower buds, adventitious roots and pods per plant, leaf area, stem girth, circumference of pods, 100% days to flowering and total fruit yield. Using the method developed by Kumi *et al.* (2021), the total leaf area was calculated. Fresh weights were obtained after plants

were partitioned into shoots, roots and fruits. Total fruit yield (kg/ha) was calculated as using the method of Firoz *et al.* (2007). Plant tissues were dried at 60°C for 72 h using a Gallenamp oven and their dry weights were recorded. The number of egg masses formed on the complete root system was counted using a hand lens, and the number of galls on the roots were noted. Egg masses were made visible by staining with acid fuchsin (Bybdt *et al.*, 1983) and washed in a solution of acetic acid, lactic acid and water (1:1:1) for 24 h (Petitot *et al.*, 2017), before heating to boiling point in 30 ml of glycerine and few drops of 5N HCL. Photographs of galled roots were taken. The root system was rated for galling (gall index) on a 0 to 5 scale (Taylor and Sasser, 1978) where 0 = no gall, 1 = 1 – 10; 2 = 11 – 20; 3 = 21 – 50; 4 = 51 – 80 and 5 = 81 – 100 galls per root system. The resistance index was rated according to the gall index where 0 = Immune; 1 = Highly resistant (HR); 2 = Resistant (R); 3 = Moderately resistant (MR); 4 = Susceptible (S) and 5 = Highly Susceptible (HS).

STATISTICAL ANALYSIS

All data collected in this study were subjected to one-way analysis of variance (ANOVA). Using SPSS v. 26, least significant difference (LSD) at $P \leq 0.05$ was used to separate means and Pearson correlation was used to evaluate correlation coefficients.

RESULTS

Agro-morphological traits: Figure 1 showed okra plants in the six different treatments used in this study. Both single and combined treatments of drought-nematode infection significantly reduced shoot length of *A. esculentus* in both experiments (Table 2). Okra plants exposed to individual

dehydration stress (D) and *Meloidogyne* infection (RKN) significantly reduced shoot length by 36.2% and 22.3%, respectively. A similar trend was observed in the repeated experiment. Plants under individual drought stress, in the first and repeated experiments, significantly reduced the stem girth by 31.8% and 29.5%, respectively. Significant reductions in SG were recorded in plants of RKN when compared to plants that received stresses in sequence. The production of tap roots and extensive lateral roots were common in plants from all treatments. Apart from plants of RKN in the first experiment, plants in all treatments for both experiments significantly reduced the number of roots compared with control plants. Regarding NOR, a precise trend was seen in both tests. Only okra plants in RKN and RBD significantly reduced the root length in the first experiment, however significant reductions of root length in the repeated experiment were recorded in plants that received treatments of RKN, DBR and RAD. The shortest and longest root length were observed in plants of RKN and control plants respectively for both experiments (Table 2). For both first and repeated experiments, plants in RKN reduced RL by 27.8% and 50.3%, respectively in comparison with control plants. Plants that received RBD and significantly reduced the number of surviving leaves in the first and repeated experiments by 79.4% and 69.9%, respectively and as well induced the detachment of more leaves. Under both experimental conditions and a comparison to control plants, all plants subjected to stress significantly reduced the TLA, with plants in RBD recording significant least reductions of 73.5% and 76.6%, respectively (Table 2).

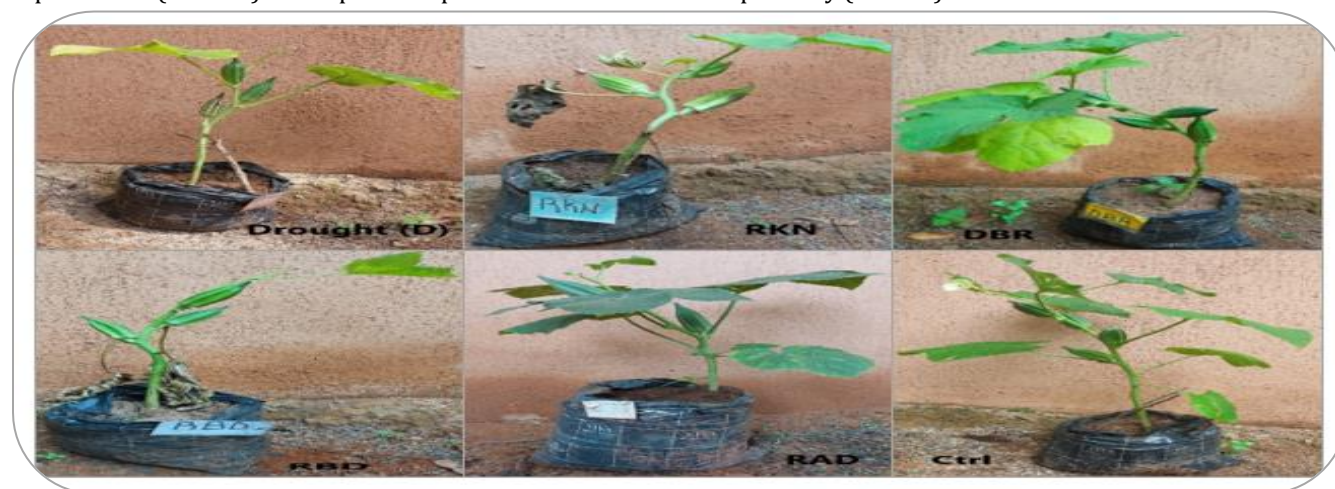


Figure 1. Shoots of *A. esculentus* subjected to individual and combined stresses of drought and *M. incognita* infection. D: Individual drought stress; RKN: Plant inoculated with *M. incognita* only; DBR: Drought stress before nematode infection; RBD: Nematode infection before drought stress; RAD: Concurrent nematode infection and drought stress; CTRL: Control plant.

Table 2. Effect of drought and nematode infection stresses on agro-morphological traits of okra plants

Treatments	Stem				Root				Leaves					
	Length (cm)		Girth (cm)		Number		Length (cm)		Number of surviving		Number of detached		Total area (cm ²)	
	Exp. 1	Exp. 2	Exp. 1	Exp. 2	Exp. 1	Exp. 2	Exp. 1	Exp. 2	Exp. 1	Exp. 2	Exp. 1	Exp. 2	Exp. 1	Exp. 2
D	32.5 ± 1.2 ^{de}	30.83 ± 1.10 ^d	2.90 ± 0.05 ^e	2.91 ± 0.06 ^d	13.90 ± 0.95 ^c	13.95 ± 0.87 ^d	37.79 ± 3.71 ^{ab}	36.15 ± 3.46 ^{ab}	2.40 ± 0.34 ^c	2.25 ± 0.25 ^c	4.10 ± 0.34 ^{ab}	4.10 ± 0.25 ^b	198.83 ± 24.47 ^c	202.24 ± 22.17 ^c
RKN	39.55 ± 1.20 ^b	32.60 ± 0.65 ^{cd}	3.55 ± 0.10 ^c	3.01 ± 0.05 ^{cd}	30.40 ± 1.26 ^a	28.60 ± 0.95 ^b	29.22 ± 2.64 ^c	20.13 ± 1.72 ^c	2.20 ± 0.28 ^c	2.45 ± 0.26 ^c	4.30 ± 0.30 ^a	3.75 ± 0.25 ^{bc}	206.04 ± 19.53 ^c	207.87 ± 18.68 ^c
DBR	39.01 ± 1.59 ^{bc}	36.32 ± 1.69 ^b	3.90 ± 0.07 ^b	3.77 ± 0.08 ^b	23.70 ± 1.18 ^b	23.80 ± 0.85 ^c	34.59 ± 2.19 ^{abc}	29.89 ± 2.71 ^b	3.55 ± 0.32 ^b	4.70 ± 0.47 ^b	3.20 ± 0.27 ^b	3.00 ± 0.32 ^c	288.36 ± 28.01 ^b	301.46 ± 21.39 ^b
RBD	35.64 ± 1.38 ^{cd}	34.52 ± 1.20 ^{bc}	3.90 ± 0.08 ^b	3.87 ± 0.13 ^b	23.40 ± 1.61 ^b	24.30 ± 1.18 ^c	31.20 ± 2.92 ^{bc}	34.14 ± 2.37 ^{ab}	1.35 ± 0.37 ^d	1.70 ± 0.37 ^c	3.80 ± 0.57 ^{ab}	5.45 ± 0.43 ^a	123.51 ± 32.78 ^d	109.21 ± 28.22 ^d
RAD	30.12 ± 1.46 ^e	29.84 ± 1.23 ^d	3.28 ± 0.06 ^d	3.15 ± 0.07 ^c	15.30 ± 1.41 ^c	13.35 ± 1.21 ^d	33.11 ± 2.68 ^{abc}	33.39 ± 2.65 ^b	2.50 ± 0.24 ^c	2.50 ± 0.20 ^c	3.95 ± 0.20 ^{ab}	3.95 ± 0.17 ^b	197.04 ± 25.02 ^c	187.86 ± 21.87 ^c
Ctrl	50.93 ± 0.49 ^a	51.47 ± 0.54 ^a	4.25 ± 0.05 ^a	4.13 ± 0.04 ^a	33.25 ± 0.89 ^a	31.65 ± 0.71 ^a	40.46 ± 0.78 ^a	40.51 ± 0.89 ^a	6.55 ± 0.17 ^a	5.65 ± 0.17 ^a	0.40 ± 0.13 ^c	0.40 ± 0.13 ^d	466.64 ± 9.36 ^a	465.68 ± 7.88 ^a

*Significant means are represented with different alphabets along each vertical array. D- drought; RKN – root-knot nematode; DBR- drought before root-knot nematode; RBD- root-knot nematode before drought; RAD – root-knot nematode and drought; Exp -experiment

Plant biomass: All plants subjected to both individual and combined stresses produced significant reductions in the fresh weight of the shoot when compared to plants in control (Table 3). Under both experimental conditions, plants in D and RAD were the most affected. In a similar trend, the stressed plants significantly reduced the dry weight of the shoots. However, under both experimental conditions, individual drought-stressed plants recorded

the least shoot dry weight (81.1% and 80.5% reductions, respectively). Alternatively, under both experimental conditions, only plants given a sole nematode treatment significantly increased the root fresh weight by 33.6% and 23.9%, respectively, when compared to that in the control. But all plants exposed to either individual or joint drought-nematode stress significantly lowered the root dry weight (Table 3).

Table 3. Okra biomass production under stresses of drought and nematode infection

Treatments	Shoot				Root			
	Fresh weight (g)		Dry weight (g)		Fresh weight (g)		Dry weight (g)	
	Exp. 1	Exp. 2	Exp. 1	Exp. 2	Exp. 1	Exp. 2	Exp. 1	Exp. 2
D	25.89 ± 1.29 ^d	24.91 ± 1.78 ^c	2.11 ± 0.11 ^d	2.11 ± 0.07 ^d	2.22 ± 0.10 ^d	2.22 ± 0.12 ^d	0.57 ± 0.05 ^c	0.49 ± 0.05 ^d
RKN	39.75 ± 2.01 ^b	42.40 ± 1.63 ^b	4.91 ± 0.61 ^c	4.46 ± 0.28 ^c	11.89 ± 0.74 ^a	10.69 ± 0.56 ^a	1.85 ± 0.31 ^b	1.30 ± 0.11 ^b
DBR	41.87 ± 1.41 ^b	42.11 ± 0.88 ^b	7.01 ± 0.42 ^b	7.07 ± 0.17 ^b	8.60 ± 0.56 ^{bc}	7.56 ± 0.65 ^{bc}	1.55 ± 0.14 ^b	1.49 ± 0.10 ^b
RBD	34.41 ± 1.86 ^c	29.00 ± 1.93 ^c	4.94 ± 0.35 ^c	4.26 ± 0.25 ^c	7.39 ± 0.59 ^c	6.83 ± 0.71 ^c	1.01 ± 0.08 ^c	0.91 ± 0.12 ^c
RAD	25.44 ± 2.18 ^d	26.52 ± 2.92 ^c	2.97 ± 0.19 ^d	2.79 ± 0.22 ^d	2.64 ± 0.20 ^d	2.71 ± 0.19 ^d	0.95 ± 0.09 ^c	0.99 ± 0.11 ^c
Ctrl	63.06 ± 1.25 ^a	62.14 ± 1.27 ^a	11.16 ± 0.34 ^a	10.81 ± 0.37 ^a	8.90 ± 0.24 ^b	8.63 ± 0.25 ^b	3.36 ± 0.14 ^a	3.80 ± 0.10 ^a

*Significant means are represented with different alphabets along each vertical array. D- drought; RKN – root-knot nematode; DBR- drought before root-knot nematode; RBD- root-knot nematode before drought; RAD – root-knot nematode and drought; Exp -experiment

Yield and yield-related traits: The number of days to flowering of all stressed plants was significantly

lower in both experimental settings compared to control plants. However, the plants in RAD and those

under individual drought stress produced blooms the fastest. All plants in both experiments significantly reduced the number of pods in comparison to control plants. The least significant reductions in number of pods were recorded in plants of RAD in the first experiment and plants given sole nematode treatment in the repeated experiment. In both experiments, there was a significant reduction in the length of pod across all the treatments as compared to the control

of which RBD treatment group were the most affected. The total yield of okra fruits was significantly reduced by plants under both stresses of drought and nematode infection. Under both experimental conditions, total fruit yield of plants subjected to individual dehydration stress was significantly reduced compared to yield of plants in RKN, DBR and RBD however differed non-significantly from that of plants in RAD (Table 4).

Table 4. Yield and yield components of okra plants under stresses of drought and nematode infection

Traits		Treatments						
		D	RKN	DBR	RBD	RAD	Ctrl	
Flower	Days to flowering	Exp. 1	47.40 ± 0.57 ^d	65.90 ± 0.94 ^b	58.75 ± 1.44 ^c	64.95 ± 1.04 ^b	47.90 ± 0.66 ^d	72.05 ± 0.42 ^a
		Exp. 2	47.75 ± 0.88 ^d	66.30 ± 1.12 ^b	57.55 ± 1.59 ^c	63.60 ± 0.84 ^b	48.65 ± 0.53 ^d	72.55 ± 0.49 ^a
	Number of flower buds	Exp. 1	0.40 ± 0.17 ^c	0.50 ± 0.20 ^c	1.95 ± 0.27 ^b	0.80 ± 0.35 ^c	1.70 ± 0.25 ^b	4.25 ± 0.19 ^a
		Exp. 2	0.35 ± 0.15 ^d	0.15 ± 0.08 ^d	1.20 ± 0.21 ^{bc}	0.65 ± 0.21 ^{cd}	1.25 ± 0.26 ^b	4.35 ± 0.22 ^a
Pods	Number of pods	Exp. 1	2.50 ± 0.14 ^{cd}	2.80 ± 0.16 ^{bc}	3.10 ± 0.23 ^b	2.75 ± 0.20 ^{bc}	2.20 ± 0.14 ^d	4.30 ± 0.15 ^a
		Exp. 2	2.55 ± 0.14 ^{bc}	2.30 ± 0.13 ^c	2.95 ± 0.20 ^b	2.55 ± 0.17 ^{bc}	2.50 ± 0.11 ^{bc}	3.75 ± 0.14 ^a
	Length of pods (cm)	Exp. 1	8.27 ± 0.25 ^c	8.32 ± 0.31 ^c	9.07 ± 0.20 ^b	7.26 ± 0.18 ^d	8.16 ± 0.27 ^c	10.25 ± 0.05 ^a
		Exp. 2	7.83 ± 0.26 ^c	8.12 ± 0.28 ^c	9.33 ± 0.19 ^b	6.92 ± 0.14 ^d	7.99 ± 0.26 ^c	10.30 ± 0.06 ^a
Circumference of pod (cm)	Exp. 1	8.43 ± 0.19	8.53 ± 0.17	9.43 ± 0.14	7.71 ± 0.15	8.26 ± 0.26	10.11 ± 0.05	
	Exp. 2	7.71 ± 0.26	7.14 ± 0.10	8.83 ± 0.19	7.51 ± 0.17	7.62 ± 0.28	10.16 ± 0.05	
Fresh weight of pod (g)	Exp. 1	20.93 ± 0.78 ^d	29.00 ± 1.23 ^c	36.89 ± 2.52 ^b	32.35 ± 2.17 ^{bc}	20.86 ± 2.14 ^d	48.08 ± 1.34 ^a	
	Exp. 2	20.97 ± 0.86 ^e	26.89 ± 1.83 ^{cd}	35.25 ± 2.24 ^b	29.09 ± 1.95 ^c	22.13 ± 2.05 ^{de}	48.10 ± 1.45 ^a	
Dry weight of pod (g)	Exp. 1	3.48 ± 0.15 ^d	4.23 ± 0.19 ^d	7.34 ± 0.51 ^b	5.75 ± 0.42 ^c	3.34 ± 0.19 ^d	10.48 ± 0.30 ^a	
	Exp. 2	3.06 ± 0.15 ^d	3.83 ± 0.16 ^d	6.37 ± 0.63 ^b	5.00 ± 0.27 ^c	3.14 ± 0.19 ^d	10.51 ± 0.28 ^a	
Yield	Total fruit yield (kg/ha)	Exp. 1	1883.97 ± 70.64 ^d	2609.73 ± 110.91 ^c	3320.10 ± 227.05 ^b	2911.28 ± 195.01 ^{bc}	1877.67 ± 192.57 ^d	4326.89 ± 120.42 ^a
		Exp. 2	1887.03 ± 77.04 ^e	2420.51 ± 165.12 ^{cd}	3172.23 ± 201.74 ^b	2618.28 ± 175.67 ^c	1991.70 ± 184.36 ^{de}	4329.36 ± 130.47 ^a

*Significant means are represented with different alphabets along each vertical array. D- drought; RKN – root-knot nematode; DBR- drought before root-knot nematode; RBD- root-knot nematode before drought; RAD – root-knot nematode and drought; Exp -experiment

Root galls and Egg masses: An initial inoculum population of 5000 J₂S of *M. incognita* caused significant formation of galls on roots (Figure 2) while Plate 3 show egg masses and galls stained with acid fuchsin. There were zero galls on roots of plants in individual drought and control treatments, however, a significant number of root galls were formed in all plants infected with

nematodes. Roots of plants in sole drought treatment and the control were void of egg masses under both experimental conditions. Plants infected with only nematodes produced a significant highest number of egg mass in comparison to all nematode-infected treatments, though its number was not significantly different from that of RBD in the repeated experiment (Table 5).

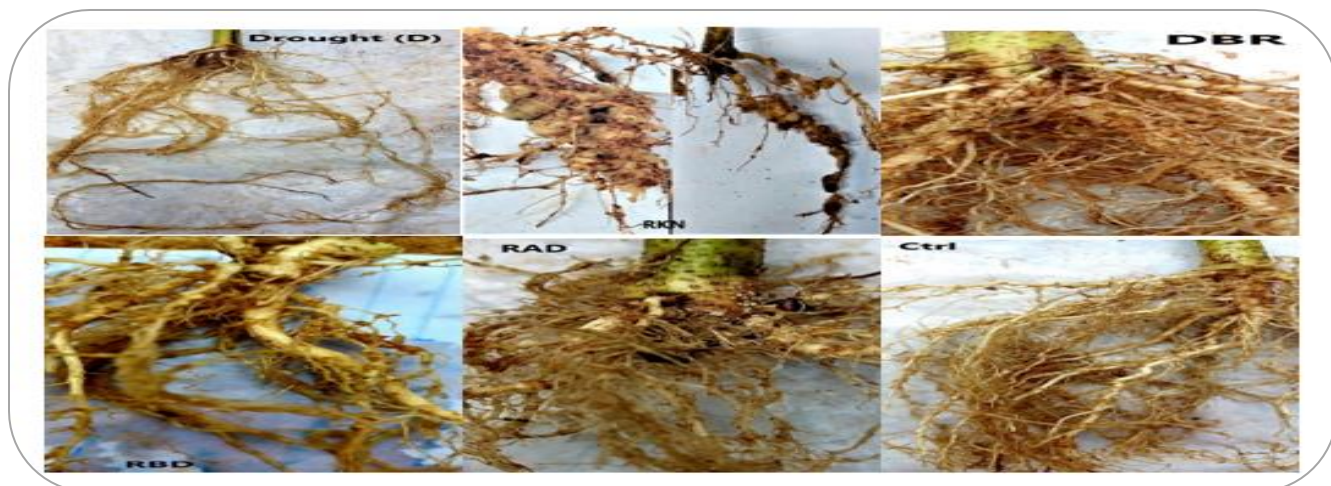


Figure 3. Galled roots of *A. esculentus* under individual, sequentially and concurrently occurring stresses of drought and *M. incognita* infection. D: Individual drought stress; RKN: Roots inoculated with only *M. incognita*; DBR: Drought stress before nematode infection; RBD: Nematode infection before drought stress; RAD: Concurrent nematode infection and drought stress; CTRL: Control plant



Figure 3. Roots of *A. esculentus*, stained with acid fuchsin, showing galls and egg masses

Table 5. Numbers of galls and egg masses of okra plants under stresses of drought and nematode infection

	Number of galls		Number of egg masses	
	Exp. 1	Exp. 2	Exp. 1	Exp. 2
D	0.0 ± 0.0 ^e	0.00 ± 0.00 ^e	0.00 ± 0.00 ^d	0.00 ± 0.00 ^c
RKN	28.4 ± 1.64 ^a	24.00 ± 1.77 ^a	12.55 ± 0.79 ^a	10.15 ± 0.85 ^a
DBR	11.95 ± 1.53 ^c	12.15 ± 1.49 ^c	4.60 ± 0.54 ^c	3.50 ± 0.53 ^b
RBD	21.30 ± 1.56 ^b	20.05 ± 1.77 ^b	10.40 ± 0.89 ^b	10.15 ± 1.08 ^a
RAD	8.05 ± 1.74 ^d	6.75 ± 0.84 ^d	2.90 ± 0.08 ^c	2.25 ± 0.42 ^b
Ctrl	0.00 ± 0.00 ^e	0.00 ± 0.00 ^e	0.00 ± 0.00 ^d	0.00 ± 0.00 ^c

*Significant means are represented with different alphabets along each vertical array. D- drought; RKN – root-knot nematode; DBR- drought before root-knot nematode; RBD- root-knot nematode before drought; RAD – root-knot nematode and drought; Exp -experiment

Relationships among the agronomic traits of *A. esculentus* under stresses of drought and nematode infection:

Correlation coefficients of growth parameters measured are presented in Table 6. The number of detached leaves showed a highly significant negative association with all the parameters except in the case of number of egg masses (a highly significant positive correlation of $r = 0.337$). All growth components, except number of detached leaves and root, showed highly significant positive correlations

with total fruit yield. The number of galls showed highly significant positive and negative correlations with all parameters except in cases of shoot girth and shoot fresh weight. The number of egg mass also had significant positive and negative associations with all parameters but not in cases of shoot length, girth and fresh weight, fresh weight of pod and total fruit yield. Apart from the above exceptions, associations were either highly significant or significantly positive between all growth parameters.

Table 6. Pearson Correlation analysis between Agronomic Traits of Okra under Stresses of Drought and Nematode Infection

	SL	RL	LOP	NSL	NDL	NFB	NOR	NOP	TLA	SG	COP	DF	FWS	FWR	FWP	DWS	DWR	DWP	TFY	NOG	NEM	
SL	1																					
RL	.151*	1																				
LOP	.516**	.209**	1																			
NSL	.526**	.197**	.608**	1																		
NDL	-.502**	-.180**	-.465**	-.749**	1																	
NFB	.583**	.249**	.503**	.589**	-.557**	1																
NOR	.540**	0.078	.326**	.278**	-.300**	.293**	1															
NOP	.541**	.208**	.478**	.448**	-.378**	.427**	.338**	1														
TLA	.513**	.197**	.462**	.568**	-.586**	.542**	.326**	.360**	1													
SG	.549**	0.12	.284**	.369**	-.340**	.536**	.468**	.404**	.304**	1												
COP	.560**	.240**	.556**	.541**	-.473**	.561**	.313**	.479**	.530**	.440**	1											
DF	.559**	-0.013	.273**	.369**	-.398**	.414**	.701**	.384**	.389**	.550**	.305**	1										
FWS	.685**	0.09	.509**	.595**	-.590**	.589**	.579**	.473**	.569**	.512**	.527**	.659**	1									
FWR	.406**	-.138*	.168**	.200**	-.187**	.165*	.621**	.214**	.227**	.416**	.217**	.671**	.502**	1								
FWP	.593**	.148*	.450**	.449**	-.447**	.532**	.518**	.490**	.489**	.552**	.499**	.545**	.660**	.414**	1							
DWS	.700**	.188**	.572**	.618**	-.596**	.651**	.637**	.559**	.602**	.637**	.601**	.633**	.728**	.503**	.682**	1						
DWR	.683**	.148*	.547**	.572**	-.585**	.664**	.541**	.506**	.613**	.526**	.557**	.579**	.708**	.462**	.578**	.775**	1					
DWP	.695**	.184**	.461**	.557**	-.565**	.633**	.527**	.541**	.523**	.657**	.557**	.572**	.675**	.388**	.690**	.765**	.673**	1				
TFY	.593**	.148*	.450**	.449**	-.447**	.532**	.518**	.490**	.489**	.552**	.499**	.545**	.660**	.414**	1.000**	.682**	.578**	.690**	1			
NOG	-.136*	-.284**	-.322**	-.351**	.325**	-.372**	.229**	-.245**	-.369**	0.068	-.319**	.251**	-0.11	.412**	-.135*	-.159*	-.163*	-.226**	-.135*	1		
NEM	-0.097	-.276**	-.351**	-.362**	.337**	-.387**	.243**	-.221**	-.387**	0.081	-.319**	.266**	-0.116	.394**	-0.11	-.174**	-.159*	-.206**	-0.11	.945**	1	

Values in bold are non-significant. SL: shoot length; RL: root length; LOP: length of pod; NSL: number of surviving leaves; NDL: number of detached leaves; NFB: number of flower buds; NOR: number of roots; NOP: number of pods; TLA: total leaf area; SG: stem girth; COP: circumference of pod; DF: days to flowering; FWS: fresh weight of shoot; FWR: fresh weight of root; FWP: fresh weight of pod; DWS: dry weight of shoot; DWR: dry weight of root; DWP: dry weight of pod; TFY: total fruit yield; NOG: number of galls; NEM: number of egg masses. **: Significant at 1%; *: Significant at 5%.

DISCUSSION

Drought is known to initiate several mechanisms in minimizing water loss in plants. Some of these responses include stomata closure, restricted nutrient uptake, and suppression of leaf development. (Gheidary *et al.*, 2017). The significant reductions of plants under dehydration stress could be attributable to the negative and damaging effects of drought stress on plant physiological processes, which may have led to reduced cell division and elongation as a result of declining relative water content and photosynthetic pigments. Significant reductions in number of

surviving leaves and total leaf area decreased chlorophyll content that compromised photosynthetic processes. In turn, reduced photosynthesis leads to poor assimilate production and reduced assimilate movement to the developing fruit that affects total fruit yield. Numerous studies have documented significant decreases in okra morphological features as a result of water shortage (Adejumo *et al.*, 2018; Mueller *et al.*, 2019). One possible reason for substantial reductions in growth of roots under sole drought stress could be the cultivar’s tolerance to drought conditions and hence the production of lesser lateral roots and

formation of more tap roots to access moisture in deeper soil regions. Maintained root growth have been linked to water deficit in plants and such adaptation allowed plants to maximize water uptake (Chaves *et al.*, 2003). The significantly increased number of detached leaves in individually drought-stressed plants possibly explains partial dehydration that leads to increased ABA accumulation in plant tissues. Both stresses may have limiter water and nutrient uptake and this explains the reduced number of days to flowering and total fruit yield. General decreases in both fresh and dry matter content for plants in sole drought treatments

could be attributed to reduced number of leaves as well as reduced photosynthesis (Chadha *et al.*, 2019).

Findings in this study have shown that the okra cultivar, 'Meya' had a gall index of 3 and was moderately resistant to only *M. incognita* after being challenged for 9 weeks. The invasion of plants' roots was evidenced by the formation and establishment of galls indicating the presence of few susceptible genes in this cultivar (Hussain *et al.*, 2016). The non-significant reduction in the number of roots suggests that roots of plants, not capable of penetrating deeper regions of the soil, activated tolerant mechanisms by formation of extensive lateral roots to support growth. Studies have reported significant reduction in growth parameters in okra with increases in inoculum level and shorter nematode infection periods (Hussain *et al.*, 2016; Mukhtar *et al.*, 2017). The hijacking of the root system by gall formation and egg masses accounts for the reduced general growth parameters studied. Possible explanations of significant reductions in root length could be nematodes modified root tissues that limited overall root growth and production. Significant reductions in the number of flower buds and total fruit yield as well as significant increases in the number of detached leaves recorded in individual nematode treatments can be attributed to reduced water use efficiency as well as limited nutrient uptake of the plants. This suggests that nematode infection could simulate drought-like conditions. The significant higher number of galls on infected roots as well as extensive lateral roots accounted for significant increased FWR. The moderate production of root galls and egg masses provides some evidence that resistance mechanisms were involved. Such resistance mechanisms have been linked to both the cultivar and influences from immediate environment (Hussain *et al.*, 2016). More studies are required to support the relationship between J₂S invasion and level of resistance however other scientific evidences suggest that susceptible cultivars are easily invaded compared to resistant ones (Hussain *et al.*, 2014).

CONCLUSION

The climatic conditions that plants are subjected to are constantly changing, and there are more frequent occurrences of various abiotic and biotic stressors. These pressures may manifest either sequentially or simultaneously, affecting the dynamics of the vegetation and consequently restricting plant development and output. Results of this study showed that the okra

cultivar, 'Meya', was either resistant, moderately or highly resistant to *M. incognita* infection through moderate formation and establishment of galls and egg masses, which is an indication of the presence of few susceptible genes. All plants exposed to the individual and combined conditions of drought and nematode infection showed significantly reduced morphological development and agronomic output. For individual stresses, plants subjected to dehydration stress significantly reduced growth and productivity compared to plants challenged with nematode infection. Okra plants responded differently to the combined and sequential impacts of drought stress and nematode infection, which may be explained by a number of variables including the length of the stress, its severity, the stage of plant growth, and the order in which the various stresses were applied. Comparisons of growth between plants in individual treatments and combined treatments showed either significant or insignificant increments and decrements. Growth and yield of plants in concurrent occurring drought-pathogen stress was significantly reduced in comparison with that observed in sequentially occurring stresses. This study suggests that responses to both stresses could be primarily related to water-use efficiencies of okra plants as well as *M. incognita*. Other huge contributing factors may include changes in signal transduction pathways mediated by induced or constitutive stress hormones and genes as well as osmolyte production. Future studies under field conditions, involving holistic approaches of this cultivar's survival mechanisms, are required; giving insights on whether the crosstalk between sequential and concurrent drought-pathogen stresses are agonistic, antagonistic, neutral, synergistic or unpredictable in nature.

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