Microbial Endophyte Mediated Hologenome Manipulation for Enhanced Growth Attributes of Finger Millet

AKSHATA, K. N. NATARAJA AND Y. A. NANJA REDDY Department of Crop Physiology, College of Agriculture, UAS, GKVK, Bengaluru - 560 065 e-Mail : yan_reddy@yahoo.com

AUTHORS CONTRIBUTION

AKSHATA :

Abstract

Conceptualization, design, data analysis and preparation of manuscript

K. N. NATARAJA & Y. A. NANJA REDDY : Conceptualization, design and manuscript editing

Corresponding Author : Akshata

Received : November 2024 *Accepted* : December 2024 Hologenome refers to the combined genome of a plant and its associated microbiome (endophyte) as a functional unit with an interaction between the host plant's genome. It has been postulated that domestication of plants is associated with the loss of beneficial endophytes and their associated benefits in modern-day genotypes. In this context, the relevance of the hologenome concept is examined in the finger millet system using a fungal endophyte (*Fusarium incarnatum*, strain K-23). Suppression of native endophytes using chemical treatments (fungicides and bactericides) caused a significant reduction in root and shoot growth of seedlings. Further, colonizing the external endophyte into the endophyte erased seedlings, recovered the shoot and root growth near to the control level. Hence, the hologenome-enrichment with an endophyte is a sustainable approach to enhance finger millet seedling vigour and thus influence the subsequent plant growth and crop yield.

Keywords : Finger millet, Endophyte, Fusarium incarnatum, Fungicide, Bactericide

TXTENSIVE use of agrochemicals like fungicides, bactericides and herbicides are routine management practices in modern agriculture that have adverse effects on human health, aquatic bodies, soil ecosystem and atmosphere (Basavaraj et al., 2019 and Zubrod et al., 2019). Therefore, there is a need to adopt eco-friendly biological elicitors that would be safe, long-lasting and effective (Nagaraju et al., 2012). Consciously, the present trend in agriculture is towards the use of bio-agents to replace chemical compounds (Gaina and Chhaya, 2024). Hence, colonization of native endophytes or the introduction of external endophytes plays a prominent role in protecting food quality, environmental sustainability and eco-friendly agriculture. Furthermore, endophytes produce a wide range of bioactive compounds with significant biological activity for applications in the fields of medicine, industry, environmental safety, crop protection, and yield improvement

(Bogasa et al., 2024). The endophytes inhabit a diverse group of plant species (Rajamanikyam et al., 2017) and are rich sources of bioactive compounds such as antimicrobial agents, hormones, hydrolytic enzymes (Eid et al., 2019 and Mishra et al., 2019), anti-cancer drugs (Naik, 2019) and anti-diabetic drugs (Dhankhar et al., 2013). Endophytes are often the fungi, bacteria, or actinomycetes that colonize cell walls and cytoplasm of all plant parts (Singh and Dubey, 2015). The beneficial endophytes provide the plants with resistance to biotic and abiotic stresses by emitting volatile compounds that inhibit the fungal pathogens through lethal leakage of proteins and necessary intracellular molecules from fungal pathogens (Santra and Banerjee, 2023) and through increased production of defense-related enzymes like Phenylalanine ammonia lyase (PAL), Peroxidase (POX), Lipoxygenase (LOX) and Glucanase in the plants (Basavaraj et al., 2019).

In agriculture, endophytes can serve as a bio-stimulant and suppressor of plant diseases (Lubna *et al.*, 2018) and weeds (Radhakrishnan *et al.*, 2018) and improve the crop productivity (Lugtenberg *et al.*, 2016). It enhances plant growth directly by enhancing nutrient availability and uptake, phytohormone and organic acids production and indirectly by preventing phytopathogens (Singh *et al.*, 2011; Manasa *et al.*, 2015 and Gouda *et al.*, 2016). Around 9000 different microbial species inhabit the seeds (Shade *et al.*, 2017 and Adam *et al.*, 2018), including crop species like rice, wheat, maize and millets (Mousa *et al.*, 2015; Herrera *et al.*, 2016; Imtiyaz & Eranna, 2021; Kumar *et al.*, 2021 and Hemapriya *et al.*, 2023).

Finger millet (Eleusine coracana) is a climate-resilient cereal crop predominantly cultivated in the semi-arid regions of Africa and Asia as a rainfed crop by >90 per cent of finger millet area (Davis *et al.*, 2019; Nanja Reddy et al., 2021 and Chaturvedi et al., 2022). Its robustness against adverse environments and nutritional richness with a higher yield than other millets made it a promising crop for food security and sustainable agriculture (Hiremath et al., 2018; www.indiaagristat.com). However, in recent years, the productivity of finger millet has decreased due to climate extremes (Nanja Reddy et al., 2022 and Megha et al., 2023). Under rainfed conditions with uneven distribution of rainfall, the early seed germination and seedling establishment are critical for subsequent crop growth and yield (Nanja Reddy et al., 2021). For such a situation, one of the recent, eco-friendly and cost-effective approaches to improve productivity under climate change scenarios could be the use of endophytes (Charisma et al., 2023). Under rainfed conditions, endophytic fungi were found to increase the grain yield and yield attributes of finger millet and other millets (Arunkumar and Shivaprakash, 2017 and Ahmadvand & Hajinia, 2018), in addition to increased grain P, N and protein content (Ahmadvand & Hajinia, 2018). The higher seedling vigour results an adequate plant population, suppresses weed growth and reduces soil evaporation, thus favours water availability for crop growth and productivity under rainfed conditions (Fahad et al., 2017 and Nanja Reddy et al., 2021). Therefore,

integrating the endophytes (fungi/ bacteria) into plants would be a sustainable agricultural practice to reduce the usage of chemical fertilizers, fungicides, pesticides and herbicides so as to reduce environmental pollution. In this study, we attempted to manipulate the hologenome in finger millet, by deleting the native microbiome using fungicide and bactericide treatments. Subsequently, we investigated the introduction of an external fungal endophyte, K-23 and its potential to promote seedling growth.

MATERIAL AND METHODS

Seed Treatment with Fungicide and Bactericide to Erase Seed Native Endophyte

Finger millet seeds were obtained from the All India Coordinated Research Project (AICRP) on Small Millets, University of Agricultural Sciences, GKVK, Bengaluru, India. The seeds were surface-sterilized in 70 per cent (v/v) ethanol for 1 min, then soaked in 4 per cent (w/v) sodium hypochlorite for 1 min and again immersed in 70 per cent (v/v) ethanol for 1 min, followed by washing in sterile distilled water for several times (Arnold et al., 2000 and Kumar et al., 2020). Such disinfected seeds were treated with 0.2 per cent (w/v) bavistin (50WP, Carbendazim) and 200 ppm (w/v) streptomycin sulfate solution for three hours individually and in combination (called as treated) and seeds soaked in sterile distilled water (called as control). After treatment for three hours, seeds were washed thrice with sterile distilled water to remove the traces of the bavistin and streptomycin sulfate. Treated seeds were placed uniformly on germination paper overlaid on plastic sheet, covered with another germination paper, rolled and incubated at room temperature (25-26°C) for seven days and root and shoot lengths were recorded.

Endophyte Enrichment with K-23 after Native Endophyte Removal

K-23 (*Fusarium incarnatum*) inoculum was collected from the endophytes library, Department of Crop Physiology, UASB, GKVK, Bengaluru (Pallavi and Nataraja, 2022). Prior to endophyte enrichment with K-23, seeds were surface sterilized with the standardized protocol as detailed in previous section, surface sterilized seeds were treated with fungicide and bactericide (0.2% Bavistin and 100 ppm streptomycin sulfate, respectively) and were placed for germination for seven days along with the control (explained in earlier section). After seven days of incubation, the seedlings were carefully taken out from the germination paper, the roots were dipped in K-23 fungal endophyte suspension culture for 3 hr. The fungal suspension culture was prepared by growing the fungus on PDA media for nearly 20 days to induce sporulation, the mycelia containing the spores was carefully collected, the concentration of spores (CFU/ ml) was identified by counting the spores using hemocytometer and adjusted to 2x10⁶ CFU/ ml by dilution using sterile water. After treatment the seedlings were kept-back on germination paper for seedling growth for three days. The root and shoot length were measured three days after treatment (10-day old seedlings).

Exploring the Genotype Specificity of Endophyte Enrichment with K-23

Four genotypes of finger millet (GE-845, GE-1309, KMR-630, GPU-28; the GE-845 and GE-1309 were drought tolerant and susceptible, respectively and KMR-630 and GPU-28 are popular varieties; Varsha and Nanja Reddy, 2023) were selected and seeds were surface sterilized by the standardized method. The sterilized seeds were inoculated with K-23 fungal endophyte suspension culture for 3 hours, washed thoroughly with sterilized water and sown in small pots. Plants were grown for up to 30 days and growth parameters were recorded. The design adopted was factorial with two main treatments (control, K-23), sub-treatments with four genotypes in three replications.

Statistical Analysis

The experiments were conducted in completely randomized design, and the data was analyzed for ANOVA using statistical software, OPSTAT and the Duncan Multiple Range Test was applied for testing the significance between the treatments using OPSTAT software (Sheoran *et al.*, 1998).

RESULTS AND DISCUSSION

Several fungi including the Fusarium species cause diseases and decrease the seed germination, seedling growth and seedling vigour in plants (Jain, 2020 and Ahir & Sharma, 2021); however, some fungal stains such as Trichoderma, Pseudomonas and Fusarium sp. are reported to reduce the effect of mycoflora on seedling health (Jain, 2020). Among the Fusarium species, Fusarium incarnatum strain K-23, a beneficial endophyte found in plants including finger millet (Pallavi & Nataraja, 2022 and Hemapriya et al., 2023). Many beneficial endophytes produce various secondary metabolites required for metabolic processes so as to inhibit the growth of disease-causing fungal pathogens and favours the seedling growth (Gouda et al., 2016). In this study, we report the role of native endophytes on seedling growth and the influence of non-native endophytes (K-23) on seedling growth.

Impact of Native Endophytes on Seedling Growth

Seedling growth is hypothesized to be influenced by the native microbiome, which constitutes a substantial portion of the hologenome. The concept of native microbiome influence on seedling growth was investigated by erasing the native microbiome using the fungicide (bavistin), bactericide (streptomycin sulfate) and in combination. Removal of the native endophytes in finger millet suppressed the root and shoot length compared to the control. The reduction in shoot length was higher compared to the root length, inferring that the shoot growth is more dependent on the endophyte population. The decreased root length due to fungicide and bactericide treatment was 13.8 and 24.7 per cent, respectively and the shoot length was by 29.2 and 78.9 per cent, respectively with a distinct phenotypic expression (Table 1 and Plate 1). Among the treatments, the bactericide resulted in a significantly higher reduction of both root and shoot length when compared to the fungicide. The combined effect did not differ statistically from the bactericide alone (Table 1). Further, the root to shoot length ratio was distinctly higher with bactericide or in combination compared to fungicide or control treatments (Table 1).

Treatment	Root length (cm)	% Red. over control	Shoot length (cm)	% Red. over control	Root/ shoot ratio					
Control	6.95 ^a		2.10 ª		3.31					
Bavistin (0.2 %)	5.99 ^b	13.8	1.49 ^b	29.2	4.02					
Streptomycin (200 ppm)	5.23 °	24.7	0.44 °	78.9	11.88					
Bavistin +Streptomycin	4.62 °	33.6	0.64 °	69.7	7.22					
SEm+	0.22	0.08								
C.D @ 5%	0.72	0.26								
C.V. (%)	6.63	11.5								

 TABLE 1

 Effect of fungicide (bavistin) and bactericide (streptomycin) on seedling growth in finger millet (cv. GPU-28)



Plate 1 : Effect of seed treatment with fungicide (bavistin, 0.2%) and bactericide (streptomycin, 200 ppm) on seedling growth of finger millet (Cv. GPU 28)

Similar to the present findings, the fungicide (bavistin, 0.2%) treatment was found to reduce seed germination (23.0%), root length (9.8%), shoot length (6.6%) and chlorophyll content in wheat (Ghurde *et al.*, 2021) and the complete removal of culturable bacterial endophytes by bactericide treatment decreased the seedling growth (Kumar *et al.*, 2020). In another experiment, bio-priming with beneficial bacteria *Trichoderma harzanium* resulted in higher seed germination, seedling length, seedling vigour and test weight in finger millet (Sowmya *et al.*, 2021).

Contrastingly, the general management practice of seed dressing with fungicide or bactericide for a few minutes for removal of seed surface inhabited pathogens might not be a limitation because the colonization of endophyte affected initially due to fungicide treatment; but, with progress in time, the colonization will be recovered (Mohandoss and Suryanarayanan, 2009). Furthermore, although the fungicides and bactericides are crucial for managing plant diseases, these chemicals decrease the density of beneficial native microflora (Gaitan *et al.*, 2005), alter the hologenome and reduce seedling growth. In addition, continuous application of fungicides might lead to chromosomal abnormalities (Pandey and Upadhyay, 1997) and kill the beneficial soil microorganisms. These findings infer that the native microbiome is essential for healthy seedling growth of finger millet, and it appears that finger millet harbors more of bacterial endophytes than the fungal, which needs to be confirmed.

Endophyte Enrichment Alleviates the Growth Inhibition Caused by Fungicide and Bactericide

This study examined the recovery of reduced seedling growth due to removal of endophytes by the fungicide and bactericide treatments through the external application of endophyte. The seedlings in control treatment displayed healthy root and shoot development. Seeds treated with endophyte (K-23) enhanced the seedling growth significantly over the control. Seeds treated with fungicide, bactericide and combination showed a significant reduction in seedling growth over the control or K-23 treatment (Fig. 1). However, treating the seedlings in which the endophytes removed and introduced K-23 externally have recovered the seedling growth significantly over their respective treatments (Fig. 1 and Plate 2). The recovery in root growth treated with bavistin was better over the control, whereas seedlings treated with streptomycin or in combination were close to the control treatment although differed significantly (Fig. 1).

The higher root and shoot growth of K-23 treated seeds could be because, the seed-inhabiting endophyte stimulates the expression of genes in developing seedlings related to root architecture in addition to defense against biotic and abiotic stresses (Imtiyaz & Eranna, 2021 and Gogna et al., 2015), that increases the nutrient solubilization and mobilization (Kumar et al., 2020). The recovery of root and shoot growth of erased endophyte by introducing external endophyte, could be because, the introduced endophyte could be responsible for increased the pigments, nutrient solubilization and production of siderophores, IAA and secondary metabolites (Pandey et al., 2016 and Kumar et al., 2020). The results of the present study and earlier confirm that native endophytes are crucial for seedling establishment (Hemapriya et al., 2023). Furthermore, the seed treatment with K-23 could be effective for seedling establishment under rainfed conditions.







Plate 2 : Effect of seed treatment with endophyte (K-23), fungicide (bavistin, 0.2%) and bactericide (streptomycin, 200 ppm) on seedling growth of finger millet (cv. GPU-28)

Understanding the Dynamics of Endophyte Enrichment on Plant Growth

An experiment was conducted to validate the influence of endophyte on plant growth at the tillering to grand growth stage. The study assessed the impact of fungal endophyte inoculation to the seed on growth parameters across four genotypes (GE-845, GE-1309, KMR-630 and GPU-28) over 30 days. Seed inoculation with fungal endophyte (K-23) resulted in a notable increase in plant height in all the genotypes. Although the genotypes did not differ significantly for plant height, the GPU-28, GE-845, KMR-630 and GE-1309 have showed an increase in plant height by 27.8, 23.0, 12.1 and 8.4 per cent, respectively, with the endophyte treatment over the control. In overall, the fungal endophyte treatment significantly increased the mean plant height by 17.1 per cent across the genotypes (Table 2) and similarly to the extent of

I ABLE 2
Influence of endophyte (Fusarium incarnatum, K-23) colonization on seedling growth
of finger millet at 30 days after sowing

T. 1

Finger millet Genotype	Pl	ant height (cm	l)	Numbe	r of leaves/ se	edling	Leaf area (cm2/ top 3 leaves)			
	Control	Endophyte	Mean	Control	Endophyte	Mean	Control	Endophyte	Mean	
GE-1309	31.0	33.6	32.3	6.2	6.4	6.3	19.0	34.3	26.6 ª	
GE-845	27.0	33.2	30.1	6.0	6.8	6.4	24.9	50.8	37.8 ^b	
KMR-630	28.6	31.4	30.0	6.0	5.8	5.9	40.4	50.5	45.4 °	
GPU-28	30.2	38.6	34.4	5.8	6.8	6.3	35.6	63.7	49.6 ^d	
Mean	29.2 ª	34.2 ^b		6.0	6.5		29.8 ª	49.8 ^b		
	Т	G	T x G	Т	G	T x G	Т	G	T x G	
SEm+	1.2	1.7	2.3	0.2	0.2	0.3	0.9	1.2	1.7	
CD @ 5%	3.4	NS	NS	NS	NS	NS	2.5	3.5	5.0	
CV (%)		16.4			11.7			10.0		

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29.3 per cent (Arunkumar and Shivaprakash, 2017). The bacterial and fungal endophyte enriched seeds reported a significant increase in the root and shoot length over the control (Arunkumar & Shivaprakash, 2017; Kumar *et al.*, 2020; Chaudhary *et al.*, 2023 and Hemapriya *et al.*, 2023). Such increased seedling growth could be due to increased solubilization of micronutrients, increased availability of NPK (Chaudhary *et al.*, 2023) and hormone production like IAA (Eid *et al.*, 2019 and Mishra *et al.*, 2019). The number of leaves per plant did not increase significantly by fungal endophyte treatment in all the genotypes, (Table 2). Interestingly, the leaf expansion

rates were increased significantly due to endophyte treatment in all the genotypes. The leaf area increase was 99.2 per cent (GE-845), 80.5 per cent (GE-1309), 78.9 per cent (GPU-28) and 25.0 per cent (KMR-630), with endophyte treatment as compared to their respective controls (Table 2 and Plate 3). Among the genotypes, the GE-845 and GE-1309 were drought tolerant and susceptible, respectively, in our previous studies (Varsha and Nanja Reddy, 2023). The influence of endophyte was found higher in the tolerant genotype compared to the susceptible ones in terms of plant height and leaf expansion rates. An increase in leaf area with the endophyte treatment has





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also been documented in foxtail millet (Ahmadvand and Hajinia, 2018). The increase in leaf expansion rates with endophyte enrichment is expected to increase the leaf area, plant growth and productivity of finger millet.

Seed treatment with fungal endophyte increased the root length significantly (by 26.3%), root fresh weight (80.2%) and dry weight (121.2%) over the control. Such increased root length would improve soil exploration, water and nutrient absorption in addition to anchorage (Verma *et al.*, 2021 and Chaudhary *et al.*, 2022). With increased root length, the root dry weight was also increased by 29.7 per cent (GE-1309), 57.8 per cent (GE-845), 43.3 per cent (GPU-28) and 42.3 per cent (KMR-630) with endophyte compared to their controls (Table 3). Among the genotypes, GPU-28 showed significantly higher root length and root fresh weight over the other genotypes (Table 3). The drought-tolerant genotype (GE-845) showed a higher percentage increase in root length, fresh weight and dry weight

TABLE 3
Influence of endophyte (Fusarium incarnatum, K-23) colonization on root parameters
at 30 days after sowing (C-Control, E-Endophyte)

Finger millet Genotype	Root length (cm)			Root fresh weight (mg/ seedling)			Root dry weight (mg/ seedling)			Root	Root water content (%)		
	С	Е	Mean	С	Е	Mean	С	Е	Mean	C	Е	Mean	
GE-1309	16.6	19.6	18.1 ª	717	830	775 ^{ab}	133.7	153.3	143.5	81.4	81.4	81.4 a	
GE-845	16.0	22.3	19.2 ª	322	972	647 ª	46.0	218.7	132.4	85.7	77.6	81.7 ª	
KMR-630	16.3	18.7	17.5 ª	544	1043	794 $^{\rm ab}$	52.7	138.7	95.7	90.1	86.3	88.2 ^b	
GPU-28	19.3	25.7	22.5 b	649	1178	914 ^b	77.7	175.0	126.4	88.0	84.8	86.4 ^b	
Mean	17.1 ª	21.6 ^b		558 ª	1006	b	77.5	a 171.4 b		86.3 *	82.5	b	
	Т	G	T x G	Т	G	T x G	Т	G	T x G	Т	G	T x G	
SEm+	0.50	0.71	1.01	41	59	83	8.0	11.4	16.1	0.74	1.04	1.47	
CD @ 5%	1.5	2.2	NS	125	177	250	24.3	NS	48.7	2.2	3.1	NS	
C.V. (%)		9.0			18.3			22.3		-	3.0		

TABLE 4

Influence of endophyte (*Fusarium incarnatum*, K-23) colonization on chlorophyll content in finger millet at 30 days after sowing (C-Control, E-Endophyte)

Genotype	Chorophyll a (mg. g ⁻¹ FW)			Chorop	hyll b (m	g. g ⁻¹ FW)	Total chorophyll (mg. g ⁻¹ FW)			
	С	Е	Mean	С	Е	Mean	С	Е	Mean	
GE-1309	0.70	0.74	0.72	0.19	0.21	0.20	0.89	0.94	0.92	
GE-845	0.68	0.65	0.67	0.15	0.29	0.22	0.83	0.94	0.89	
KMR-630	0.70	0.87	0.79	0.18	0.25	0.22	0.88	1.12	1.00	
GPU-28	0.55	0.75	0.65	0.15	0.18	0.17	0.70	0.93	0.82	
Mean	0.66 a	0.75 b		0.17	0.23		0.83 a	0.98 b		
	Т	G	T x G	Т	G	T x G	Т	G	T x G	
SEm+	0.03	0.04	0.06	0.02	0.04	0.05	0.04	0.06	0.09	
CD @ 5%	0.09	NS	NS	NS	NS	NS	0.13	NS	NS	
CV (%)		14.8		9.2		16.8				

over the susceptible genotype (GE-1309). Interestingly, endophyte treatment significantly reduced the root water content under adequate water conditions (Table 3), suggesting that the endophyte enhances biomass allocation towards root structure development rather than holding water under sufficient water availability. The increased root biomass indicates that the K-23 endophyte promotes root development, increase the surface area available for nutrient uptake and enhancing the stability and resilience of the plant as a whole (Verma *et al.*, 2021).

Furthermore, chlorophyll 'a' and total content increased significantly with the application of endophyte and the chlorophyll contents did not differ between the genotypes (Table 4). However, fungal endophyte enrichment increased the level of total chlorophyll (GPU-28, 32.9%; KMR-630, 27.3%; GE-1309, 5.62%; GE-845, 13.3%) over their respective controls (Table 4). Similarly, endophytes found to increase the chlorophyll content in foxtail millet (Ahmadvand and Hajinia, 2018) and chlorophyll, PS-II activity, carbon assimilation and biomass production (Zhang et al., 2020). The increased chlorophyll 'a', 'b' and total content with endophyte enrichment influences the photosynthesis, crop growth and yield (Setiawati et al., 2021). This increase in chlorophyll content and leaf area due to endophyte enrichment (K-23) indicates the importance of non-native endophytes (Fusariumin carnatum, K-23) on overall seedling growth.

The findings of the present study suggest that the integration of microbial interventions, such as the introduction of adapted fungal endophytes (K-23), into agricultural practices could be a novel strategy to enhance early seedling growth, in addition to reducing the harmful effects of fungicides and bactericides on native endophytes. The hologenome-enrichment approach has the potential to revolutionize crop growth. *Fusarium incarnatum* (K-23) is a potential fungal endophyte in finger millet to improve seedling vigour that would be helpful, especially under rainfed during seed germination and seedling establishment. However, most of the studies pertain to the seedling

level and more research at the whole plant level is necessary for practical applications of endophytes in agriculture.

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