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RESEARCH ARTICLE

Evaluation of Cultivated and Wild *Allium* Accessions for Resistance to *Fusarium oxysporum* f. sp. *cepae*

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Abstract *Fusarium* basal rot (FBR) caused by *Fusarium oxysporum* f. sp. *cepae* (FOC) is a highly destructive soil borne disease incurring heavy damage in pre and post harvest onion and garlic crops worldwide. Only a few onion lines exhibit partial resistance against the pathogen and there is a need for identification of more effective resistance sources for use in breeding programmes. Selected sets of wild onion and garlic accession and seven related *Allium* species were screened for resistance to *Fusarium* basal rot using three FOC isolates. FOC infection revealed significant variation among the evaluated *Allium* species (at $P = 0.001$). *A. sativum* accession 'CBT-As153' showed high level of resistance to each isolate while *A. cepa* accession 'CBT-Ac77' exhibited intermediate resistance. Among related *Allium* species, *A. fistulosum, A. roylei* and *A. schoenoprasum* were highly resistant, *A. tuberosum* had mixed response while *A. griffithianum* was susceptible. Further, the root density of *Allium* species negatively correlated with disease incidence for different FOC isolates. Thus, the present study suggests that besides related *Allium* species, *A. sativum* 'CBT-As153' can be used as a potential donor of FBR resistance for genetic improvement of onion and garlic in India.

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Introduction

Onion *(Allium cepa* L.) also called as "queen of kitchen" is a high value spice cum bulbous vegetable crop cultivated in almost all parts of the world. Besides high food value, it is attributed with several medicinal properties and is used in treatment of chickenpox, influenza, measles and cardiovascular diseases, etc. It acts as a source for anticancerous drugs [1, 2]. On a worldwide basis, onion ranks as one of the five most important fresh market vegetable crops [3]. Garlic (*Allium sativum* L.) is also a unique member of the family Alliaceae and used throughout history for both culinary and medicinal purposes. Currently, garlic is often categorized as a stimulant, diaphoretic, expectorant and diuretic due to the presence of allicin and essential oils in the bulb and leaves [4]. India has the second largest land area next only to China under onion and garlic production [5]. The International Trade Centre (ITC), Geneva has recorded an enormous rise in the global demand for onion and garlic in recent times. However, with only 10.16 t/ha and 4.32 t/ha, India ranks only 102nd for onion and 74th for garlic in terms of global productivity [5]. Among several factors, diseases are the most important cause associated with low productivity.

Fusarium basal rot (FBR) caused by *Fusarium oxysporum* f. sp. *cepae* (FOC) is a highly destructive root and bulb disease of onion and related *Allium* species in the temperate and subtropical regions of the world [6]. As many as 18 FOC isolates have been recorded under field conditions [7]. It is responsible for causing severe loss in productivity at

both pre- and post- harvest stage [3]. FOC is a soil borne necrotrophic fungus that infects primarily through the root tip, secondary root formation points, gradually spreading into the basal plate thereby colonizing the entire plant through the vascular system. This causes basal plate discoloration and necrosis, wilting up of the whole plant and ultimately leading to rot of the bulb scales [3].

Currently practiced application procedures for controlling FOC with fungicides such as Carbendazim and Mancozeb is time-consuming and costly and often gets ineffective through emergence of resistant races of the pathogen. Biological control of *Fusarium* basal rot by inoculation of antagonistic fungi and bacteria such as *Trichoderma* and *Pseudomonas* has been considered as an alternative approach to chemical control [8, 9]. However, this technique only controls FBR to a certain extent and is not 100 % effective. Under these circumstances, the most effective way to minimize the damage of FBR in onion and garlic would be to grow resistant cultivars [10]. But the sources of naturally available host plant resistant to FBR are very limited. Although considerable level of FOC resistance has been reported in a few related *Allium* species such as *A. fistulosum* and *A. roylei* [11, 12], they are yet to be utilized for successful improvement of cultivated onion and garlic. *Allium* genotypes largely differ in their level of resistance to FOC [13]. A few onion lines have been identified to exhibit moderate resistance against FOC in both laboratory and field screening conditions in different regions of the world [7, 13–17]. However, most of these lines could exhibit only partial reduction in infection and post-harvest yield losses. Hence, there is a need for further identification of more effective resistance sources to solve the economically important FOC infection problem. Further, recent developments in the field of genetic transformation [18] and somatic hybridization [19] suggest constructive characterization of resistance traits through molecular cloning approaches. In the present study, the authors screened selected set of onion and garlic accessions as well as seven related *Allium* species for levels of resistance to FOC and trace suitable donor for FBR resistance.

Material and Methods

The plant materials used in the study are listed in Table 1. Eight accessions of onion (*Allium cepa*) and seven accessions of garlic (*Allium sativum*) were collected from the wild forest areas across the western and south western regions of Odisha state in India. The distance between collection sites varied from 48 km, between the forest areas of Titlagarh and Khariar, to 355 km between Nuapada and Athmallik. Plants at least 30 m apart were sampled from each collection sites. Flower heads were collected for the source of seeds in case of *A. cepa* while bulbs were collected for *A. sativum.* Four accessions of *A. tuberosum* and one accession each of *A. roylei, A. fistulosum, A. clarkei* and *A. griffithianum* were obtained from National Bureau of Plant Genetic Resources (NBPGR), New Delhi. One accession each of *A. schoenoprasum*, *A. ampeloprasum* and *A. tuberosum* were secured from GRIN, USDA, USA. Two cultivars each of garlic (Yamuna Safed and Bhima Omkar) and onion (Arka Kirtiman and Arka Kalyan) were used as control plant types. All the plant materials used in this study are maintained at Centre of Biotechnology, Siksha O Anusandhan University.

The seeds and bulbs were surface sterilized with 10 % commercial bleach (Sodium hypochlorite) for 10 min followed by twice submersion and washing with 70 % alcohol for 30 s. Seedlings were grown in sterilized pots and transplanted into fresh pots with the same soil substrate (one plant per pot) 40 days after sowing. Three virulent isolates of *F. oxysporum* f. sp. *cepae* (FOC-CBT3 collected from Acharya NG Ranga Agricultural University, Guntur, Andhra Pradesh, FOC-CBT7 collected from Mahatma Phule Krishi Vidyapeeth, Rahuri, Maharashtra and FOC-CBT12 collected from Indian Institute of Horticultural Research, Bangalore) were used for inoculation studies. The experimental setup involved ten plants per accession-isolate combination, and as many non-inoculated controls. Each assay was conducted in triplicate and ten plants were used for each replicate. Due to less availability of germplasm, the related *Allium* species involved eight plants per accession-isolate combination. The experiment was conducted with randomized plants within each treatment to avoid cross-contamination. The pathogen inoculation was done according to Galvan et al. [12]. Mycelial plugs from Potato-Dextrose Agar plates were transferred to potato-dextrose broth and grown at 26 °C for 5 days on a rotary shaker. The mycelium and broth were comminuted with a blender and centrifuged at 3500 rpm for 10 min. The spore-containing pellet was resuspended in potato-dextrose broth, filtered through cheese cloth and adjusted to 3×10^5 conidia/ml. For pathogen infection, all plants were twice inoculated 10 and 21 days post transplanting by pouring 40 ml of conidial suspension to each pot. Control plants were inoculated with distilled water. The inoculated pots were maintained in a growth chamber with average daily temperature of 25–27 °C and 12 h photoperiod. Disease incidence and severity was evaluated 90 days after transplantation on maturity. Plants were harvested by carefully washing the soil from the roots with water. The number of roots per plant was determined to study its influence on *Fusarium* infection. The percent disease incidence was recorded and resistant plants were defined by the presence of healthy primary and secondary roots. The level of basal plate damage (Disease Index) was recorded by using a 0–3

Table 1 *Allium* accessions included in the screening of resistance to *Fusarium* basal rot

Allium accessions	Accn no.	Source or origin
Allium cepa	CBT-Ac17	Bhawanipatna, Odisha, India
A. cepa	CBT-Ac46	Titlagarh, Odisha, India
A. cepa	CBT-Ac77	Sonepur, Odisha, India
A. cepa	CBT-Ac96	Baliguda, Odisha, India
A. cepa	CBT-AAc128	Kuchinda, Odisha, India
A. cepa	CBT-Ac132	Padmapur, Odisha, India
A. cepa	CBT-Ac169	Nuapada, Odisha, India
A. cepa	CBT-Ac176	Athmallik, Odisha, India
Allium sativum	CBT-As11	Sonepur, Odisha, India
A. sativum	CBT-As23	Sonepur, Odisha, India
A. sativum	CBT-As63	Nuapada, Odisha, India
A. sativum	CBT-As83	Bhawanipatna, Odisha, India
A. sativum	CBT-As103	Bhawanipatna, Odisha, India
A. sativum	CBT-As153	Bolangir, Odisha, India
A. sativum	CBT-As171	Bargarh, Odisha, India
Allium tuberosum	IC-353524	[a]NBPGR, India
A. tuberosum	IC-353536	NBPGR, India
A. tuberosum	IC-353535	NBPGR, India
A. tuberosum	N-151	NBPGR, India
A. tuberosum	W66751	[d]USDA, USA
Allium ampeloprasum	PI576881	Netherlands
Allium schoenoprasum	PI664902	United Kingdom
Allium roylei	IC-353540	NBPGR, India
Allium fistulosum	NIC 20231	NBPGR, India
Allium clarkei	IC-383446	NBPGR, India
Allium griffithianum	IC-255676	NBPGR, India
Allium sativum cv. Yamuna safed	–	[b]OUAT, Odisha, India
A. sativum cv. Bhima Omkar	–	OUAT, Odisha, India
Allium cepa cv. Arka kirtiman	–	[c]IIHR, Bangalore, India
A. cepa cv. Arka kalyan	–	IIHR, Bangalore, India

[a] NBPGR: National Bureau of Plant Genetic Resources

[b] OUAT: Orissa Institute of Agriculture and Technology

[c] IIHR: Indian Institute of Horticultural Research

[d] USDA: United States Department of Agriculture

'*Fusarium* rot score', where: 0 = no symptoms (>10 infection); 1 = slight infection (10–20 % of the basal plate infected); 2 = moderately infected (20–50 %); 3 = highly infected (>50 % in both foliar region and bulbs). The disease severity index (DSI) was calculated using the following formula:

$$\mathrm{DSI} = \sum_{n=0}^{3}\{(n \times \text{number of plants with score n}) / \text{total number of plants})\},$$

where n is the number on '*Fusarium* rot score' scale [9].

The statistical analysis was carried out with SAS version 9.1 (SAS Institute, Inc. Cary, NC, USA). The possible two-way interaction between and among the 3 FOC isolates and 30 garlic accessions were tested with a general linear model approach. A mean separation test was done using Fisher's distribution analysis at $p = 0.001$ for both *Allium accessions* and FOC isolates. Pearson's Correlation analysis was performed to assess the influence of root density over FBR incidence by calculating the Pearson's product-moment correlation coefficient using following formula:

$$r = \sum(xy)/\mathrm{sqrt}\left[\left(\sum x^2\right) \times \left(y^2\right)\right],$$

where $x = x_i - \dot{X}$, x_i represents the number of roots per plants, $\dot{X}$ is the mean x value, $y = y_i - \dot{Y}$, y_i represents the percentage of disease infection.

Results and Discussion

Three *F. oxysporum* f. sp. *cepae* isolates and seven related *Allium* species were used to screen for determining the level of resistance in onion and garlic accessions. Although *F. oxysporum* f. sp. *cepae* strains are host specific and have largely evolved towards pathogenicity in onion, they are also reported to cause *Fusarium* wilt in numerous other plant species [15]. The *Fusarium* isolates used in the present study also showed a wide host range across different related *Allium* species. Statistical analysis revealed large and significant variation in the degree of disease incidence in the overall distribution of the number of plants in all *Allium* accessions (Table 2). The distinctive morphological structures and physiological factors of different *Allium* species might be involved in their variable response to *Fusarium* basal rot. However, the three FOC isolates reported no significant differences over the disease index scores. The three isolates were found to be equally aggressive/ineffective and exhibited similar disease index (DI) score for any given isolate-accession combination. This may be because of the fact that the three FOC isolates might have high genetic similarity. Genetically similar *F. oxysporum* isolates have been found from different countries and collection sites exhibiting similar level of pathogenicity [12].

Table 2 Analysis of variance for the distribution over percentage of infection

Sources of variation	*df*	Sum of squares	Mean squares	F
Between *Fusarium* isolates	2	346.86	173.43	2.28
Between *Allium* accessions	29	71,531.07	2466.59	32.41
Residual	58	4414.46	76.11	
Total	89	76,292.4		

The onion and garlic cultivars 'Yamuna Safed', 'Bhima Omkar', 'Arka Kirtiman' and 'Arka Kalyan' exhibited a consistently high disease index (DI) scores (Fig. 1; supplementary Table S1). The basal plate of these plants was completely wilted and the roots entirely damaged within 8 weeks after inoculation. Six of the seven garlic accessions showed high DI scores with infection ranging from 67 to 96 %. Among them, garlic accn. CBT-As11 showed the highest infection rate. On the other hand, garlic accn.

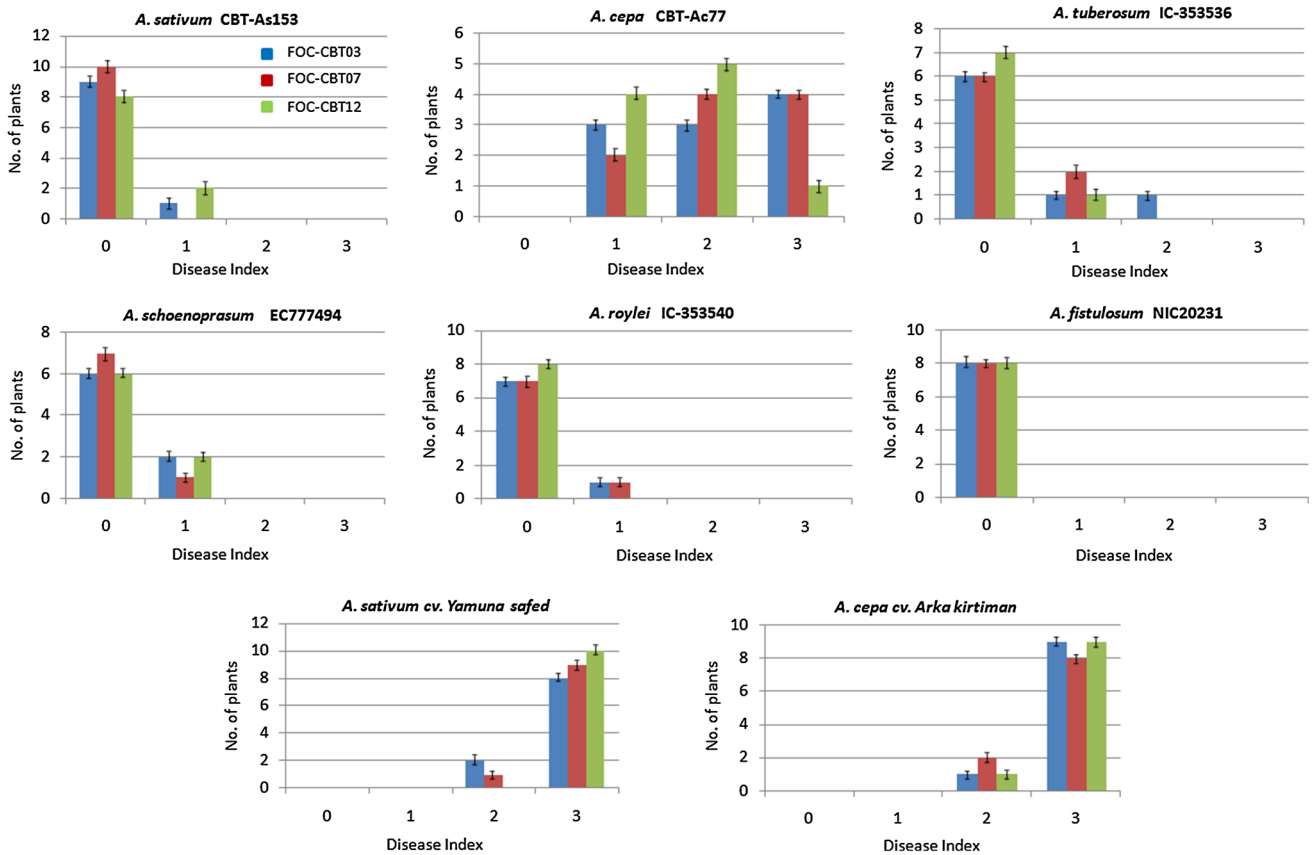

Fig. 1 Distribution of plants of *Allium* accession in each disease index class after inoculation with three *F. oxysporum f.* sp. *cepae* isolates FOC-CBT03, FOC-CBT07 and FOC-CBT12. The DI classes ranged from 0 to 3 as indicated in the "Material and Methods" section

CBT-As153 had the lowest DI scores when evaluated for resistance to the three *Fusarium* isolates (supplementary Table S1). Only 6 % of disease infection was noticed in CBT-As153 even after 90 days post inoculation and 27 of 30 inoculated plants were grouped in the first disease index class (DI = 0) (Fig. 1). The phenotypic variation with respect to disease incidence among garlic accessions suggests the involvement of genetic variables towards FOC resistance. Further, the garlic accessions were collected from different agroclimatic zones and alienated conditions. The adaptability of the garlic accession to specific environmental conditions, together with poor accessibility of specific vegetative compatibility groups of FOC isolates might have resulted in resistance development. The accessions showing resistance to FOC could be subjected to continual growth for the development of populations with greater proportions of resistant plants as has been reported with some onion selections in America [20].

All the tested onion accessions were found susceptible to *Fusarium* basal rot. Seven out of eight onion accessions had high levels of infections (DI = 3) with all the three *Fusarium* isolates. One onion accession CBT-Ac77 was moderately resistant to infection ranging from 25 to 45 %. The roots were completely decayed after 90 days, although the basal plate was found intact. Onion being an out crossing crop has a greater tendency of variation resulting in differential response to infection. Moreover, the low infection in CBT-Ac77 can be attributed to the high number of roots (21 per plant on average) which may have allowed the plant to survive *Fusarium* infection. Similar results were also reported by Galvan et al. [12] and Ozer et al. [21]. Then again, screening assay conditions may have also resulted in the partial infection of the experimental plant types.

Among the related *Allium* species, the three fungal isolates had the lowest level of infection against *A. fistulosum, A. roylei* and *A. schoenoprasum.* All the *A. fistulosum* plants examined with the three fungal isolates in the present study were categorized within the first DI class. Holz and Knox-Davies [22], Dissanayake et al. [7] and Galvan et al. [12] has separately reported significant resistance of *A. fistulosum* to different virulent FOC isolates from Europe and America as compared to a set of onion cultivars and related *Allium* species. Poor or no infection of FOC isolates in *A. fistulosum* could be attributed to the unique underground morphology of the plant. *A. fistulosum* does not have modified bulb stems, they are highly dormant and possess continuously growing roots and basal plate system. This may allow the plant to overcome *Fusarium* infection as the wilted root and plate tissues could be replaced regularly. Alternatively, the presence of qualitative resistance related genes against FOC isolates may also be responsible for *A. fistulosum* to be resistant to *Fusarium* basal rot. Similarly, *A. roylei* and *A. schoenoprasum* had 22 and 20 plants respectively within the first DI class and exhibited poor disease incidence. Earlier report also suggests high to intermediate level of resistance in *A. schoenoprasum* and *A. roylei* [12]. *A. tuberosum* accession IC-353536 also had the lowest DI scores with an average infection of only 3.63 % restricted largely to the primary and secondary roots. On the other hand, *A. griffithianum* and *A. tuberosum* accession IC-353524 were found completely susceptible. Nineteen of 24 plants of *A. griffithianum* were grouped within the third DI class. In addition, *A. ampeloprasum, A. clarkei* and three accessions of *A. tuberosum* 'IC-353535', 'N-151', 'EC777493' had moderate infection with the three *Fusarium* isolates and their DI scores were intermediate between those of *A. fistulosum, A sativum* accn 'CBT-As153' and those of susceptible onion and garlic accessions. High variability and wide geographic distribution may be responsible for differential response of *A. tuberosum* to Fusarium wilt similar to the response of *Zingiber zerumbet* against soft rot pathogen, *Pythium aphanidermatum* reported earlier [23]. Moreover, resistance response could be linked to the biochemical combinations. Chinese chives or *A. tuberosum* are rich in volatiles and organosulphur compounds, which have inhibitory effect on pathogenic microbes. Zhang et al. [24] have reported that crop rotation of banana with Chinese chives causes inhibition of *Fusarium oxysporum f.* sp. *cubense* growth and spore germination.

A. fistulosum had the maximum root development under controlled as well as diseased condition with an average of 31 roots per plant. A. *schoenoprasum* and *A. roylei* narrowly followed with an average of 25 and 24 roots per plant respectively. On the other extreme, *A. cepa* cv 'Arka Kirtiman' (7 roots per plant) and *A. cepa* accn CBT-Ac96 (8 roots per plants) had the lowest root density. The root density in control *Allium* accessions exhibited strong negative correlation with the disease incidence for the three isolates (FOC-CBT03, r = −0.87; FOC-CBT07, r = −0.88; FOC-CBT12, r = −0.83). *A. sativum* CBT-As153, *A. fistulosum, A. roylei* and *A. schoenoprasum* with least DI scores had 25, 31, 24 and 26 roots per plant respectively. Similarly, *A. sativum* CBT-As103, *A. cepa* CBT-Ac132, *A. cepa* cv. 'Arka Kirtiman' and *A. sativum* cv 'Yamuna Safed' with high DI scores (80 % infection and above with three isolates) had produced only an average of 8, 7, 7 and 10 roots per plant respectively. However, *A. griffithianum* and *A. tuberosum* accession IC-353524 had an exceptionally large root system (average 24 and 19 roots per plant respectively) suggesting that denser rooting system may not be an absolute criterion for basal rot resistance. Galvan et al. [12] also reported that *A. vavilovii*, a closely related species of onion was largely susceptible to FOC isolates inspite of having a denser rooting system.

The host response of the three *Fusarium* isolates distinctly varied among the species examined. While, *A. fistulosum* and *A. sativum* accn CBT-As153 were completely resistant with uninfected basal plate and roots, *A. ampeloprasum* and *A. clarkii* were partially affected with decayed roots but uninfected basal plate. Likewise, *A. griffithianum* with complete susceptibility had both basal plate and root system destroyed. This suggests that FOC isolates invade and infect diverse species at different stages. Similar host response has been reported with *Phytopthora infestans* against *Solanum* species [25] and *P. aphanidermatum* against *Zingiber* species [23]. However, the host response of FOC is yet to be reported from tribes other than Alliaceae. An extensive resistance screening involving species from different tribes will only throw light on the actual host range of *F. oxysporum* f. sp. *cepae* within the subfamily Allioideae.

Conclusion

In conclusion, none of the *A. cepa* accessions were found resistant against any of the FOC isolates used in the study. However, *A. sativum* accn 'CBT-As153', *A. fistulosum* and *A. schoenoprasum* exhibited complete resistance and can be used as potential source for donating FBR resistance to cultivated garlic and onion. Earlier report showed that interspecific hybridization between onion and *A. schoenoprasum* did not result in viable offspring [26]. Due to genetic similarity and high taxonomic affinity, *A. fistulosum* can be exploited for interspecific hybridization with cultivated onion for generating viable FOC resistant progenies. The same has also been predicted for *A. roylei* and *A. galanthum* [11]. Although, commercially produced garlic is asexually propagated, a few reports also suggest the possibility of sexual reproduction for incorporation of traits into cultivated varieties [27, 28]. Alternatively, molecular isolation and transfer of resistance trait from 'CBT-As153' to the cultivated backgrounds of onion and garlic through somatic hybridization and genetic engineering approaches may also be attempted for developing broad spectrum FBR resistance.

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Conflict of interests The authors declare no conflict of interest.

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