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RESEARCH ARTICLE

EFFECT OF EXTRACTS OF AZADIRACHTA INDICA, KHAYA SENEGALENSIS AND BOSWELLIA DALZIELII ON THE DEVELOPMENT OF THE ANGULAR LEAF SPOT, GROWTH AND DEVELOPMENT PARAMETERS OF RICE (ORYZA SATIVA L).

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Abstract

Rice is one of the most widely grown and consumed cereals in Chad. However, its production decreases over the years due to bio-aggressors. This situation pushes farmers to use chemical synthetic plant protection products to remedy insect and disease attacks. These chemicals expose them to risks of poisoning and environmental pollution. To reduce the use of these chemical pesticides, extracts of *Azadirachta indica*, *Khaya senegalensis* and *Boswellia dalzielii* were used to treat rice seeds. These seeds were soaked separately in the different extracts used at a concentration of 50 mg/ml for one hour before sowing. The incidence and severity of the angular spot, growth and development parameters were assessed. The three types of plant extracts showed a high reduction in the incidence and severity of the disease, and improved certain growth and development parameters. These plant extracts could be used as bio-fungicides in rice cultivation.

Introduction:-

Rice (Oryza sativa L.) is the third most consumed cereal in the world after maize and wheat with a production of 740.9 million tons (FAOSTAT, 2016). It is used in the manufacture of starch, health foods, alcohol and pharmaceuticals (Webster and Gunnell, 1992). In Chad, its production in 2018 was 257,701.23 tons for an area of 182,403,587 ha or 1.4 t/ha (ONDR, 2018). This yield is low compared to other producing countries such as Burkina Faso (1.9t/ha) and Nigeria (2t/ha) (FAOSTAT, 2017). Among these diseases, those caused by fungi are the most important because they cause severe damage to rice plants and considerably reduce field rice yields compared to viral or bacterial diseases (Habib et al., 2012). Ora et al. (2011) have shown that most fungal diseases are seed-borne to seedlings. The angular leaf spot caused by Alternaria padwickii is responsible for discoloration and seedling meltdown (Naeimi et al., 2003). It considerably reduces photosynthetic activity and therefore disrupts the growth and development of plants in the field (Ou, 1985). Chemical control is generally used to control this disease (Ibian et al., 2006). However, improper handling of chemical fungicides leads to soil microflora degradation, environmental pollution and resistance development in some fungal species (Schillberg et al., 2001; Arcury et al., 2002). On the other hand, plant-extract-based bio-fungicides would be an effective and inexpensive alternative for fungal disease control (Kuri et al., 2011). Herbal fungicides are biodegradable and less toxic (Delvin and Zettel, 1999). The studies

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of Mansur et al. (2013); Nguefack et al. (2013) and Serferbe et al. (2015) have shown that seed treatment (Triticum eastivum, Zea mays, Oryza sp and Gossypium barbadense) with plant extracts result in giving healthy and vigorous seedlings. The work of Khan et al. (1991) showed that Neem leaves and seeds have the ability to prevent the development of fungi. The purpose of this study is to evaluate the antifungal activity of Azadirachta indica, Khaya senegalensis and Boswellia dalzielii extract on the angular spot and their effect on improving rice yield.

Materials and Methods:-

Seed source and plant material:-

The rice seeds were obtained from the National Rural Development Agency (ANADER) in Bongor, Mayo - Kebbi East province, Chad. Eight (08) rice varieties were collected (TOX, CH3, CH8, WITA9 D6, D4, D3 and D1).
The plant organs (Azadirachta indica fruits, Khaya senegalensis seeds and Boswellia dalzielii bark) were harvested in Pala, Chad.

Preparation of extracts:-

These harvested plant organs (fruits, seeds and bark) were dried in an oven at a temperature of 45°C for 7 days and ground to powder using a SEVEN 7 STAR GERMANY brand grinder. One hundred grams of powder from each plant was macerated separately in 500 ml of distilled water for 48 hours. The mixture was filtered using No. 1 Wattman paper and the resulting filtrate was dried in an oven at a temperature of 45° C until the water completely evaporated.

Seed treatment:-

The seeds of the 8 rice varieties (CH3, CH8, D1, D3, D4, D6, TOX and WITA9) were dipped separately in different extract solutions including Azadirachta indica, Khaya senegalensis and Boswellia dalzielii at a concentration of 50 mg/ml for one hour. Distilled water and MANCOZEBE 80 WP (1 mg/ml) were used as negative and positive controls respectively. The treated seeds were then stored in blotting paper to remove excess moisture from the surface and dry in the open air.

Evaluation of the different extracts:-

Field trial was conducted at the Institute of Agricultural Research for Development (IRAD) in Dschang (5°26 N and 10°26 W) from June to October (2016 and 2017). Eight rice varieties were sown in a Split Plot Device over an area of 609 m^2 with three replicates. Each block consisted of eight (8) 13 m^2 (13 m x 1 m) elementary plots. The elementary plots formed by five (5) subplots of 2 m^2 each. The number of infected tillers in each elementary plot was counted and then examined during the tillering, heading and maturity stage on 10 random plants. The impact was determined by the following formula:

$$I = \frac{\text{Number of infected talles}}{\text{Total number of tillers per poke}} \times 100$$

Severity of the angular leaf spot was determined on a scale from 0 to 9 (IRRI, 1996).

For growth parameters, plant size was measured using a graduated ruler from the crown, and the number of leaves per plant and the number of tillers per plant were counted. The leaf area (cm2) was determined according to the formula of Winter & Coll (1956).

SF = L × W × K

(with K = 0.754, L = length of the sheet and l = width of the sheet).

With regard to development parameters, the number of panicles per plant and the number of seeds per panicle were recorded and the weights of 1000 seeds (g) were measured using a 0.01g Mettler precision balance. The yield (t/ha) of paddy rice seed was calculated according to the formula of Lacharme (2001).

Yield = NP/m^2 × NT/P × Npa/T × NG/Pa × PG

NP/m^2 = number of plants/m^2 - NT/P = number of tillers / foot - NPa/T = number of panicle / ball - NG/Pa = number of grains/panicles and PG= weight of a grain.

Statistical analysis:-

The data collected were subjected to an analysis of variance (ANOVA) using the SPSS Software version 17 in order to detect significant differences between the averages. The Duncan Test Comparison Test was used to analyze the significance of the results at a probability threshold of 5 %.

Results:-

All rice plants from seeds treated with Azadirachta indica extract, Khaya senegalensis and Boswellia dalzielii and MANCOZEBE had significantly lower incidence ($P \leq 0.05$) than those from negative controls (Table 1). The antifungal efficacy of these extracts varied depending on the treatment and phenological phase of the rice. During the tillering stage, plants of variety D6 from seeds treated with Azadirachta indica extract (50 mg/ml) showed the lowest incidence (0.1 %). In contrast, the incidence of angular spot in negative control plants was significantly high (9.11 %). The incidence of angular spot of CH8 variety plants whose seeds have been treated with Boswellia dalzielii extract was 0.6 % compared to 9.11 % for negative control plants of the same variety. Treatment with Khaya sengalensis extract resulted in an incidence of 0.17 % in the TOX variety compared to 8.5 % for control plants. During the heading stage, the TOX, WITA9 and D4 varieties treated with Azadirachta indica extract showed low incidences of 0.15 %, 0.78 % and 1.51 % respectively, while they were high at 17.68 %, 13.92 % and 6.11 % for negative control plants. The same is true for the incidence of the angular spot on rice plants treated with Boswellia dalzielii extract, which were 0.29 % (TOX), 0.37 % (D6), 0.75 % (WITA9), and 0.6 % (CH8), lower than those of negative control plants. The extract of Khaya senegalensis recorded a low incidence of 2.37 % compared to 12.1 % for negative control plants and 3.17 % for positive control plants. No angular spot manifestations were observed in variety D3. During the maturity stage, the incidence of the angular spot on plants of the CH8 variety treated with Azadirachta indica, Boswellia dalzielli and Khaya senegalensis extract was 14.83 %, 10.75 % and 14.8 % respectively, while that of negative control plants reached 100 %.

Table 1:-Variation in the incidence of the angular spot of rice according to treatments with of extracts Azadirachta indica Khaya senegalensis and Boswellia dalzielii

Treatment at 50 mg/ml	**TOX**	**D6**	**CH3**	**D1**	**WITA9**	**D4**	**CH8**	**D3**	**Mean**
	Tillering phase								
A. indica	0,11b	0,1d	0,8d	0,5d	0,13d	0,78e	4,44b	-	0,84±1,4b
B. dalzielii	0,29b	0,37cd	1,67c	1,75cd	0,75cd	1,83cde	0,6d	-	0,91±0,73b
K. senegalensis	0,17b	0,26d	2,68b	4,53bc	9,53ab	3,89bc	4,44b	-	3,18±3,2b
Positive control	0,1b	1,08b	0,05d	1,17d	0,11d	0,09f	1,43c	-	0,5±0,6b
Negative control	8,5a	9,11a	3a	10,35a	10,35a	6,05a	62,5a	-	13,73±20,04a
	Heading phase								
A. indica	0,15c	3,26bc	5,33bc	0,78d	0,78c	1,51e	12,5bc	2,05b	3,29±4,07b
B. dalzielii	1,67b	0,83d	5,33abc	5,5b	5,5bc	4,23bc	7,58cde	0,33d	3,87±2,6b
K. senegalensis	6,67b	2,37cd	9,61ab	4,64bc	11,64a	4,16c	13,5b	2,5bc	6,88±4,24b
Positive control	0,02c	3,17bc	0,09c	5,9b	5,9bc	1,9de	3,48de	1,66bcd	2,7±2,28b
Negative control	17,68a	12,1a	7,02a	13,92a	13,92b	6,11a	79,16a	3,27a	19,14±2,71a
	Maturity phase								
A. indica	2,3de	5,59bc	6bc	3,51c	3,51f	2,32ef	14,83cd	2,3bcd	5,04±4,2b
B. dalzielii	6,3cd	2,66d	7,66b	9,23b	9,23bcd	5,08bcd	10,75d	3,16b	6,75±2,9b
K. senegalensis	13,6bc	5,22bc	11,67cd	9,08b	12,66bc	4,5bcde	14,8cd	2,5bcd	9,25±4,6b
Positive control	0,7f	4,37c	0,1d	9,19b	9,19cde	1,9fg	19,66b	2,16cde	5,9±0,5b
Negative control	27,02a	13,96a	11a	14,11a	16,11a	8,33a	100a	5,16a	24,46±3,19a

Two results read (phenological phase) in the same column are significantly different if they are not followed by the same letters according to Duncan's test ($P \leq 0.05$).

Seed treatment of different rice varieties with extracts of Azadirachta indica, Khaya senegalensis, Boswellia dalzielii revealed that the severity of the angular spot was significantly lower than that of negative control plants (Table 2). The antifungal efficacy of these extracts varied according to the treatments and the phenological stage (tillering, heading and maturity). During the tillering phase, the average severity of the angular spot ranged from 0.04 to 2.04. It was significantly lower for plants whose seeds were treated with extracts of Azadirachta indica, Boswellia dalzielii, Khaya senegalensis and mancozebe. Indeed, the TOX variety treated with Azadirachta indica, Khaya senegalensis and Boswellia dalzielii extract had a low severity of 0.09, 0.04 and 0.12 respectively. On the other

hand, the positive control (mancozebe) had a severity of 0.001 and the negative control had a severity of 1.33. During the heading phase, the effect of Azadirachta indica, Khaya senegalensis and Boswellia dalzielii extract was illustrated by a weak severity of the angular spot. The average severity of the angular spot ranged from 0.83 to 4.01. Indeed, the variety WITA9 revealed a severity of 1.32 for treatments with Azadirachta indica extracts, 1.08 for treatments with Khaya senegalensis extracts, 1.5 for treatments with Boswellia dalzielii extracts, 0.92 for mancozeb, and 4.12 for the negative control. During the maturity phase, the lowest severity (1) was recorded for the TOX variety whose seeds were treated with Azadirachta indica extract and the mancozeb positive control (0.22) compared to 5 for the angular spot severity in negative controls.

Table 2:-Variation in the severity of the angular spot of rice according to treatments with extracts of Azadirachta indica, Khaya senegalensis and Boswellia dalzielii

Treatment at 50 mg/ml	**TOX**	**D6**	**WITA9**	**D4**	**CH8**	**D3**	**CH3**	**D1**	**Mean**
	Tillering phase								
A. indica	0,09b	0,009c	0,001d	0,24cd	1,5bc	-	0,03d	1,07b	0,36±0,58bc
B. dalzielii	0,04b	0,15b	0,08cd	1bc	0,08e	-	1,67c	0,08c	0,38±0,6bc
K. senegalensis	0,12b	0,03c	1,87bc	2,01ab	1,5bc	-	3b	2,01b	1,3±1,13ab
Positive control	0,001c	0,23ab	-	0,02e	0,05de	-	0,002d	0,03d	0,04±0,078c
Negative control	1,33a	0,33a	2,33a	2,08a	3,87a	-	4,05a	2,33a	2,04±1,47a
	Heading phase								
A. indica	0,6d	1c	1,32bcd	0,66c	2,93bc	2,16b	1,70c	2,32cd	1,58±0,83b
B. dalzielii	1,67b	0,33d	1,08cde	2,04bc	1,76cd	1,08bc	2,28b	5,08b	1,9±1,4b
K. senegalensis	0,67c	1,06ab	1,5bc	3,1b	2,93bc	0,05de	1,07cd	4,5bc	1,86±1,4b
Positive control	0,04d	1,01bc	0,92e	0,75c	1,33cd	0,66cd	0,08d	1,92d	0,83±0,62b
Negative control	2,36a	2a	4,12a	3,5a	4,17a	3,57a	5,03a	7,33a	4,01±1,6a
	Maturity phase								
A. indica	1d	1,89cd	1,42de	1,25c	3,5def	4,5b	3,09b	2,24c	2,36±1,23bc
B. dalzielii	2,67b	1,76cde	3,26bc	1,83bc	4,15cde	1,25cd	2,9bc	5,6a	2,9±1,42b
K. senegalensis	1,75c	2b	3,2bc	2,35b	6,5bc	1,9d	2,82bcd	3,2b	2,96±1,5b
Positive control	0,22e	1,5de	1,56de	1,5d	2,17fg	1,16e	1,7de	1,56d	1,42±0,56c
Negative control	5a	3,18a	5,08a	5,48a	8,27a	4,84a	6,04a	8,08a	5,74±1,7a

Two results read (phenological phase) in the same column are significantly different if they are not followed by the same letters according to Duncan's test ($P \leq 0.05$).

Some growth parameters independent of rice varieties have been significantly improved compared to the negative control (Table 3). The variety WITA09 whose seeds were treated with Azadirachta indica extract had the largest size (56.05 cm) compared to the negative control rice plants (48.38 cm). The number of shoots of variety CH8 was significantly higher (36.88) for plants whose seeds were treated with Boswellia dalzielii extract compared to the negative control (30.66). Rice plants of variety D6 whose seeds were treated with Khaya sengalensis extract had significantly higher leaf counts (8.03) than negative control plants (5.09).

Table 4 shows that treatment with Azadirachta indica extract of the TOX variety resulted in the most significantly high number of panicles (16.12) compared to negative control panicles (11.5). The treatment of variety D3 with Azadirachta indica extract showed a significantly higher number of seeds per panicle (142.6) compared to the negative control (118.6). The weight of a thousand seeds of variety D1 whose seeds have been treated with Khaya senegalensis extract is significantly higher (40.34 g) than that of the negative controls (19.33 g). The most significantly high yields were obtained with Khaya senegalensis extract treatment in the TOX (5.69 t/ha), CH8 (3.95 t/ha) and D1 (4.16 t/ha) varieties. Also, variety D6 treated with Boswellia dalzielii extract had a significantly higher yield (4.84 t/ha) compared to the negative control (1.51 t/ha).

Table 3:-Variation in growth parameters of the different rice varieties according to treatments with extracts of Azadirachta indica, Khaya senegalensis and Boswellia dalzielii

Treatment at 50 mg/ml	**TOX**	**WITA9**	**CH8**	**CH3**	**D6**	**D4**	**D3**	**D1**
	Height (cm)							
A. indica	45,99ab	56,05a	55,88bc	53,55a	45,24a	48,33a	50,3abc	47,16a

B. dalzielii	52,63a	52,22b	62,61a	45,33b	42,14a	45,16a	56,05a	44,36ab
K. senegalensis	45,52ab	51,16b	56,84bc	47,44ab	37,75b	49,38a	52ab	41,22b
Positive control	40,81c	54,22a	55,11bc	53,38a	37,66b	46,22a	47,27bc	45,83ab
Negative control	42,38b	48,38c	50d	42,66c	38,11b	50,61a	46c	46,69a
	Number of leafs/plant							
A. indica	7,01a	7,17a	7,02a	9,16a	5,29bc	6,97a	6,98ab	6,85ab
B. dalzielii	7a	7,1a	6,14b	7,77ab	6,54b	6,98a	7,05a	7,01a
K. senegalensis	7a	7,04a	6,58b	7ab	8,03a	6,96a	6,97ab	6b
Positive control	7a	7,04a	7,01a	6,94bc	5,57bc	6,73a	7,09a	6,79ab
Negative control	7a	6,58b	6,95b	6c	5,59bc	6,28a	6,37b	6,97ab
	Number of talle/plant							
A. indica	24,19a	25,88a	35,66a	22,44ab	5,29bc	6,97a	26,16ab	21,77ab
B. dalzielii	20,11ab	20,55b	36,88a	19,6abc	6,54b	6,98a	30,11a	19,66b
K. senegalensis	22,11ab	19,83c	33,28ab	13,11c	8,03a	6,96a	21,5ab	17,11c
Positive control	20,22ab	24,27a	34,77ab	26,88a	5,57bc	6,73a	26,33a	23,58a
Negative control	17,33b	20,5bc	30,66c	24,66ab	5,59bc	6,28a	28,72a	20,55ab
	Leaf area (cm^2)							
A. indica	20,75b	31,65a	26,38a	17,38ab	20,46a	20,8a	20,54ab	18,64a
B. dalzielii	21,3b	23,9b	24,64ab	18,29a	17,03b	19,1ab	23,52a	19,57a
K. senegalensis	23,68a	20,42c	26,04a	11,19c	15,88b	19,2ab	19,56b	15,29b
Positive control	19,12bc	26,7ab	21,1abc	17,48ab	14,97c	11,43b	21,68a	18,64a
Negative control	18,15c	17,4d	19,62c	10,01c	13,74c	12,54b	19,36b	15,94b

Two results read in the same column are significantly different if they are not followed by the same letters according to the Duncan Test ($P \leq 0.05$).

Table 4:-Variation in the development parameters of the different rice varieties according to the treatments with extracts of Azadirachta indica, Khaya senegalensis and Boswellia dalzielii

Treatment at 50 mg/ml	**TOX**	**WITA9**	**CH8**	**CH3**	**D6**	**D4**	**D3**	**D1**
	Number of panicles per plant							
A. indica	16,12a	16,48ab	23,7ab	22a	15,55a	16,22cd	21,44a	14,5b
B. dalzielii	13,4cd	13,7bc	24,59a	19,44de	13,37c	17,18bc	20,07ab	13,11bc
K. senegalensis	14,74bc	13,48c	22,19b	21,44bc	12,09d	20a	16,33cde	13,4bc
Positive control	13,48cd	17,25a	23,18ab	19,56cd	14,33b	18,07b	16,88cd	15,72a
Negative control	11,55de	13,7bc	20,44c	21,8abc	12,14d	15,77e	15,14e	12,7c
	Number of seeds per panicle							
A. indica	118a	138,66b	84def	120a	102,6a	75,3abc	142,6a	109,67ab
B. dalzielii	110,3ab	123,6cd	94,66bc	90,67bc	95bc	85,66ab	136b	60,67cd
K. senegalensis	105,3bcd	105,6de	122,3a	79de	98,33b	52c	120,3cd	110,33a
Positive control	118,3a	140,18a	90cd	84cde	84,33d	96a	126bc	107abc
Negative control	99d	95,33ef	91,66bcd	71f	95,66c	71bc	118,6d	68,33c
	Weight of 1000 seeds (g)							
A. indica	34,28ab	37,57bc	30,01bcd	27,57d	27,59cd	23,2bcd	38,66a	31,72b
B. dalzielii	32,37bc	32,91cd	33,34bc	32,9abc	30,92bc	30,27b	28,6cde	30,33bc
K. senegalensis	35,99a	38,57ab	39,01a	38,56a	43,92a	39,94a	37,66b	40,34a
Positive control	28,66c	39,91a	29,68de	29,56cd	27,9cd	20,6d	29,6cd	30,33bc
Negative control	26,66cd	17,57e	20,68f	18,9e	17,59de	23,2bcd	17,66ef	19,33d
	Yield (t/ha)							
A. indica	4,91ab	5,11a	2,27bcd	4,71a	2,62bc	3,43ad	5,97a	3,36ab
B. dalzielii	3,71abc	3,18bc	2,93ab	2,93cd	4,84a	4,24a	5,12ab	2,5bcd
K. senegalensis	5,69a	4,38a	3,95a	2,83cd	2,57bc	3,17bcd	5,05bc	4,16a
Positive control	3,67bc	3,5b	2,27bcd	3,84bc	2,2cd	3,06bcd	4,94c	3,53ab
Negative control	1,88d	2,36c	1,42d	2,65e	1,51e	2,26de	2,67d	2,95bcd

Two results read in the same column are significantly different if they are not followed by the same letters according to the Duncan Test ($P \leq 0.05$).

Discussion:-

Treatment of rice seeds with Azadirachta indica, Khaya senegalensis and Boswellia dalzielii extract had a positive effect in improving growth and development parameters. Rice plants whose seeds were treated with extracts of Azadirachta indica, Khaya senegalensis and Boswellia dalzielii showed significantly higher growth parameters and development compared to the controls. This improvement in growth and development parameters was due to the active compounds present in the various extracts of Azadirachta indica, Khaya senegalensis and Boswellia dalzielii such as phytohormones (auxins, cytokinins), flavonoids, terpenoids (Shamshad and Naqvi, 2002; Marinov et al., 2005). These active compounds would affect the cellular metabolism of rice plants and thus promote good growth and development of rice plants. The work of Idu et al. (2014) has shown that the macro-elements (potassium) and trace elements (sodium, calcium, magnesium, iron, zinc and manganese) contained in the extract of Khaya senegalensis grains can contribute to facilitating photosynthesis and regulating water for greater resistance to temperature variations. Neem seeds are very rich in fatty acids (oleic acid, stearic acid, palmitic acid) amounting to about 50% of the weight of its seed. These substances would act as growth regulators. The work of Alemika & Oluwole (1991) and Adelakun et al. (2001) showed that Boswellia dalzielii extract contains saponins, tannins, flavonoids, steroids and terpenes. They facilitate growth and resistance to abiotic stresses. The results obtained in this study with the treatments of Boswellia dalzielii and Azadirachta indica extract are similar to those of Hasan et al. (2005). They showed that the extracts of these two plants improve the growth and development of wheat and cotton. Similarly, the work of Faruq et al. (2015) showed that treating rice seed with Azadirachta indica extracts produced plants with higher yields after germination than the control plants.

The treatment of the different rice varieties with extracts of Azadirachta indica, Khaya senegalensis and Boswellia dalzielii and mancozeb resulted in a reduction in the incidence and severity of the angular spot compared to the negative controls. The inhibitory effect of the extracts of these three plants varied from one extract to another and was similar to that of the mancozebe fungicide (positive control). Similar antifungal activity results of Azadirachta indica and Khaya senegalensis extract on fungi (Fusarium moniliforme, Aspergillus flavus, Aspergillus niger,and Botryodiplodia theobromae) have been reported by Nwachukwu and Umechuruba, (2001); Lakshman and Ahir, (2011). Similarly, Mothana et al. (2011) have demonstrated that Boswellia spp. extract had inhibited the growth of plant pathogenic fungi. Inhibition of Alterania padwickii growth is a consequence of the substances contained in the extracts of Azadirachta indica, Khaya senegalensis and Boswellia dalzielii. Also, the work showed that incidence and severity gradually increased with phenological stages. These results corroborates those of Klomp (1977), who showed that disease sensitivity increased with the age of the plants.

Conclusion:-

Rice seed treatments with extracts of Azadirachta indica, Khaya senegalensis and Boswellia dalzielii have significantly increased rice growth and development parameters. The extracts of the three plants used gave a significant reduction in the incidence and severity of the angular spot.

The use of extracts from these plants in the control of fungal pathogens in rice can reduce the use of environmentally toxic chemicals. These results provide an alternative for chemical control of fungal diseases. They will allow farmers to reorient the phytosanitary treatments of rice seeds by using plants extracts as sources of pesticides.

Conflict of interest:-

The authors state that there is no conflict of interest.

Authors' contributions:-

This work was carried out in collaboration with all the authors. The SS author designed the experiment, performed the statistical analysis and wrote the manuscript; GRTN and KJR supervised the work, reviewed the manuscript and made suggestions. All authors have read and approved the final version of the manuscript.

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