

Full Length Research Paper

Assessment of water yam (*Dioscorea alata* L.) landrace varieties for resistance to anthracnose disease

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Received 19 May, 2021; Accepted 22 September, 2021

Yam anthracnose disease (YAD), caused by the fungus *Colletotrichum gloeosporioides* Penz, is the most damaging fungal disease of *Dioscorea alata* yam worldwide. Local yam varieties, which sustain Côte d'Ivoire's farmers and other end-users livelihoods, are highly susceptible to this pathogen. Thus, there is a need for developing new yam cultivars to sustain yam production in Côte d'Ivoire. To achieve such objective, identifying and selecting sources of resistance within the existing germplasm is crucial prior to the establishment of a breeding program. This study, therefore, aimed at determining the field resistance to *C. gloeosporioides* of 115 *D. alata* landrace varieties. Field experiments were conducted at the Research Station for Food Crops (SRCV) of the CNRA, Bouaké City, in Central Côte d'Ivoire, for three growing seasons. Results showed that symptoms of the anthracnose disease were more noticeable four months after planting (P3): high disease severity and incidence scores. At this period, 'Betebete' group (DSS = 3.40 and DI = 99.81%) was the most sensitive to anthracnose disease across years. In contrast, 'Brazo' (DSS = 2.24 and DI = 94.81%) and 'Florido' (DSS = 2.59 and DI = 97.23%) groups were the least sensitive. This finding indicates that local yam accessions from Côte d'Ivoire have different sensitivity levels to anthracnose disease attacks. Therefore, the genetic diversity from this work should be further exploited by yam breeding and genetic improvement programs for developing cultivars, combining resistance to YAD, high yield potential, and superior tuber quality to meet producers and consumers' needs.

Key words: Anthracnose, Côte d'Ivoire, disease resistance, environment, *Dioscorea alata*, plant breeding.

INTRODUCTION

Yam (*Dioscorea* spp.) is an economically important staple food crop for over 300 million people in tropics and

subtropics (Kutama et al., 2013; Reddy et al., 2015; Adifon et al., 2019). It is a perennial herbaceous vine,

mainly cultivated for its starchy underground tubers. Yam plays an essential role in nutrition and social cultural life of millions of people in West Africa, where its cultivation is extensively practiced (Amani et al., 2004; Tostain et al., 2005; Jayakody et al., 2007; Andres et al., 2017). Yam is also an important source of income for farmers and significantly contributes to achieving food security in the yam production areas of West Africa (Sartie and Asiedu, 2014; Mulualem et al., 2018). Besides, it represents the most energy-rich food crop compared to other root and tuber crops such as cassava, sweet potato, and cocoyam (Onyenobi et al., 2014).

In 2018, the global yam production was ~72.6 million metric tonnes. About 70.5 million tonnes (~97%) originated from African countries, and of which, 66.8 million tonnes (92%) came from West Africa (FAOSTAT, 2020). Yam cultivation in Africa is mainly concentrated around the areas referred to as “yam civilization” or “yam belt” (Coursey, 1976). In this area, yam production is dominated by Nigeria, Ghana, Côte d'Ivoire, Benin, Cameroon, and Togo (FAOSTAT, 2020). Two cultivated yam species are dominant for their economic importance: *Dioscorea rotundata* Poir. and *Dioscorea alata* L. (Mignouna et al., 2008).

Yam is the largest food crop in Côte d'Ivoire. The country's 2018 production volume exceeded seven (~7.2) million tonnes (FAOSTAT, 2020). Yam cultivation is mainly practiced in the savannah areas of the central and the northern parts of the country. Cultivation is dominated by the *D. alata* species, which accounts for 60 to 70% of the total yam production (Doubmbia, 1995; Kouakou et al., 2007). Compared to other edible yam species, *D. alata* exhibits superior agronomic qualities such as high yield potential, ease of propagation, rapid growth to overcome weeds, and long post-harvest storage period of the tubers (Mignouna et al., 2002; Thiele et al., 2020).

Despite the agronomic, nutritional and economic qualities of *D. alata*, numerous biotic and abiotic constraints threaten its production worldwide. According to Winch et al. (1984) and Abang et al. (2002), one of the most damaging biotic constraints to *D. alata* production is the anthracnose disease, caused by a microscopic fungus referred to as *Colletotrichum gloeosporioides* (Penz.). On yams, noticeable symptoms of this pathogen include a significant reduction of tuber yield and quality because of plant necrosis and the reduction of the photosynthetic surface area. When weather conditions are conducive, this disease can lead to 80-90% tuber yield loss (Emehute et al., 1998).

The management of the yam anthracnose disease focuses on the use of cultural techniques based on the

destruction of infected plant debris, the introduction of resistant varieties and the use of chemicals (Ano et al., 2005). Compared with the above techniques, variety selection through plant breeding and the use of resistant or tolerant cultivars to anthracnose disease is the most cost-effective and sustainable control measure. It limits amounts of pesticides applied and, thus, ensures low production costs and less harm to environment (Brun et al., 2010). In West Indies, *D. alata* cultivars with resistant to anthracnose disease were identified through observations under field conditions or tests carried out on whole plants derived from tissue culture (Degras et al., 1984; Onyeka et al., 2006). In Africa and the Solomon Islands, differences in the susceptibility of several yam cultivars have been reported, and among which, TDa291 and DAN087 were identified as moderately resistant (Emehute et al., 1998). Kouakou et al. (2007) carried out similar studies in Côte d'Ivoire using a set of 43 accessions from the core collection of the Centre National de Recherche Agronomique (CNRA). Of these yam accessions, 67% were resistant and 5% were severely attacked. This pioneering work revealed differences in the response of the CNRA's *D. alata* varieties to the attack by the *C. gloeosporioides*. However, the CNRA collection was further enriched by introduction of new accessions from country-wide collections between 2008 and 2013. The CNRA now has over 200 accessions made of local landraces, improved and introduced varieties but, the susceptibility of local varieties to anthracnose disease is not well documented.

The present work aimed to determine the level of resistance to anthracnose disease in a set of 115 local landrace accessions from the CNRA *D. alata* collection in Côte d'Ivoire. It focused on establishing homogeneous groups which would be used in plant breeding programs for the selection of new clones or resistant cultivars. It is also a preliminary work to the determination of quantitative trait loci (QTLs) that control anthracnose disease resistance in *D. alata* varieties.

MATERIALS AND METHODS

Experimental site

The experiment was conducted at the Research Station for Food Crops (SRCV) of the National Center of Agronomic Research (CNRA) located in the Bouaké City, in central Côte d'Ivoire (7°44' N latitude and 5°04'W longitude). The region is characterized by a Boualean-type climate and constitutes a transition zone between the humid forests (with a short dry season) and the dry savannas (with a long dry season) (N'Goran, 2008). It is characterized by a bimodal rainfall regime (March to June and September to October)

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Table 1: Anthracnose disease severity rating scale for *D. alata*.

Rated scale	Areas covered (%)	Disease symptoms observed on the plants	Susceptibility to anthracnose disease
1	0	No symptoms	Highly resistant (HR)
2	1-25	Some small spots on leaves	Resistant (R)
3	25-50	Many spots or blight symptoms on leaves	Moderately resistant (MR)
4	50-75	Many spots or blight symptoms on leaves and stems	Susceptible (S)
5	< 75	Occurrences of symptoms from the bottom to the top on leaves, stems and shoots	Highly susceptible (HS)

and two dry seasons (November to February and July to August) (N'zi et al., 2010). Precipitation is irregular in the study site and often reaches an annual amount of ~1,100 mm. The mean annual temperature is 27°C, with variations of 3- 5°C. The Station's soils are shallow, ferritic, and gravelly and result from a weathering of a material of granitic origin (Kouamé, 1992). Regularly exploited, soils are relatively degraded.

Plant materials

The plant material used for the anthracnose disease resistance assessment consisted of 115 landrace accessions of *D. alata* sourced out of 228 accessions from the CNRA collection. These accessions were partly the result of prospecting and collection missions carried out between 2008 and 2013 in the major yam production areas of the Southern, Central and Northern Côte d'Ivoire. They were divided into different variety groups, including 'Betebete' (46 accessions), 'Brazo' (8 accessions), 'Douoble' (13 accessions), 'Florido' (31 accessions), and 'Nza' (17 accessions) (Table S1).

Experimental design for screening accessions

The above-described *D. alata* accessions were screened for anthracnose resistance under natural conditions for three (3) successive years, from 2017 to 2019. The tuber planting was done on ridges made using a ridging machine attached to a tractor in a previously cleared and plowed plot. The trials were set according to a randomized complete block design with five replications per accession in each of the two blocks (5x2 per accession). The total plot size was 60 m x 42 m, representing 0.2520 ha. The blocks were separated by 2 m apart and contained each 115 accessions. Each plot was composed of five cuttings of ~300 to 400 g from tuber fragments or whole tubers of a single accession, at spacing of 1 m within and between rows.

Each year, planting was done at the beginning of the rainy season and harvesting when the plants had completely wilted. The planting dates were different from year to year due to a variation in the return of the rains. Thus, in 2017, planting took place in May, whereas in 2018 and 2019, it was done in July and June, respectively.

Trial management

Regular weeding of the trials was manually carried out using a hand hoe depending on the level of grass cover. Stakes made of wood (Chinese bamboo, teak or other plants) or iron were brought to the yam plants two months after planting to facilitate individual plant assessment for the disease occurrence and evolution. No fertilizer

was used.

Observation and anthracnose disease scoring

Observation of anthracnose disease symptom occurrences started two months after planting at the plant growth phase and then monthly until complete senescence of the plants. Thus, three observations were made each year following regular periods. In this work, these are referred to as P1 (2 months after planting, MAP), P2 (3 MAP), and P3 (4 MAP), corresponding to the first, second and the third observation periods, respectively (Table 2). The observations mainly concerned the appearance of anthracnose symptoms on leaves, stems or young shoots and their evolution over time on each plant for all accessions. Plants were observed from bottom to top, and disease intensity/severity was rated using a 1-5 rating scale (Table 1) as described by Asala et al. (2012) and Kolade et al. (2018).

From this scale, the disease severity and the average disease incidence were determined for all accessions in each replication as follows:

- Disease severity scores or DSS:

$$DSS = \frac{\text{sum of scores of infected plant units} > 1}{\text{Total number of infected plants units}}; \text{ (IITA, 1998)}$$

- Disease incidence or DI (%):

$$DI = \frac{\text{Number of infected plant units}}{\text{Total number of plant units assessed}} \times 100; \text{ (Cooke, 1998)}$$

Weather conditions at Bouake during the study periods

Data on the amount of rainfall (mm), number of rainy days, and temperature (°C) were collected and provided by the CNRA (Source: GDSME, CNRA). The wind speed and relative humidity for the study periods were obtained through the online site "www.histoire-meteo.net". Table 2 summarizes weather data information during the study periods.

Statistical analysis

Disease severity and incidence scores were used to assess the response of *D. alata* accessions to the anthracnose disease. Severity score and incidence data were subjected to non-parametric analysis of variance using the Kruskal-Wallis test with the R software 3.6.3 package. When a significant variety group

Table 2. Weather parameters per year and per observation periods in Bouaké, Côte d'Ivoire.

Observation period	Weather parameter	Year		
		2017	2018	2019
2 months after planting (P1)	Rainfall (mm)	81.00	234.70	253.60
	Number of rainy days	9.00	13.00	7.00
	Temperature (°C)	23.70	24.10	23.70
	Wind speed (km/h)	12.00	9.00	14.00
	Relative humidity (%)	79.00	93.00	88.00
3 months after planting (P2)	Rainfall (mm)	33.10	82.00	116.10
	Number of rainy days	8.00	8.00	9.00
	Temperature (°C)	23.70	24.30	24.10
	Wind speed (km/h)	11.00	8.00	10.00
	Relative humidity (%)	85.00	82.00	87.00
4 months after planting (P3)	Rainfall (mm)	143.80	0.00	147.70
	Number of rainy days	10.00	0.00	10.00
	Temperature (°C)	24.10	26.20	24.30
	Wind speed (km/h)	10.00	8.00	10.00
	Relative humidity (%)	88.00	73.00	85.00

Source: GDSME, CNRA and www.historique-meteo.net

effect was observed at an evaluation period or year at 5% p -value threshold, the Wilcoxon test allowed pairwise comparison of means. The Holm-Bonferroni correction method was carried to constitute homogeneous groups. K-proportion comparison test using the Chi^2 test of the Monte Carlo method with 5000 simulations was also performed to compare the proportions of accessions identified as resistant, moderately resistant, susceptible and highly susceptible in different variety groups, using the XLSTAT 2016 software. In the case of significant differences, the test was supplemented by the Marascuilo procedure to identify the proportions causing the differences. Besides, the mean anthracnose severity scores of different accessions at the most discriminating observation period, that is, P3 (4 MAP) in all three years, were subjected to a hierarchical clustering analysis to classify the accessions according to their sensitivity to disease. The dendrogram construction was performed using the ward.D2 method with cluster packages of R software from a distance matrix, which was generated using the Euclidean method with library stats implemented in R packages.

RESULTS AND DISCUSSION

Characteristics of anthracnose symptoms observed on the leaves of *D. alata* accessions

The most noticeable symptoms were on the leaves. Two main types of leaf necrotic spots were common: i) the presence of numerous tiny spots throughout the leaf area, including the main and secondary veins (Figure 1A) and ii) the presence of large and irregularly-shaped spots on the leaves (Figure 1B). These spots were surrounded by a yellow halo and particularly concentrated on the leaf veins (Figure 1D). These spots were often strongly

present on one edge of the leaf blade (Figure 1C) and their coalescence was leading, at an advanced stage of the disease, to complete necrosis of the infected leaf edge. Characteristic symptoms of the anthracnose disease were observed on *D. alata* plants during the study period (2017-2019) at Bouaké in central Côte d'Ivoire. These symptoms showed a strong similarity with those described on yam by Baudin (1966) and Reddy (2015). In general, symptoms on older leaves were marked by the occurrence of large spots and many tiny spots, simultaneously or not on the same plant. Jackson et al. (2002) reported similar observations on the same yam species.

Effect of the year of assessment and variety groups on the anthracnose disease severity scores and disease incidence on *D. alata*

The anthracnose disease severity scores and disease incidence among *D. alata* variety groups varied significantly with the growing season (year) ($p < 0.05$) (Table 3). Disease severity scores and disease incidence were higher in 2017 and 2019 than they were in 2018 for all tested variety groups. However, the anthracnose disease incidence in 'Brazo' variety group was not statistically different across years. The highest disease severity score (2.37) was observed in 2019, while the highest disease incidence value was 71.57% in 2017.

There was a significant difference ($p < 0.05$) in

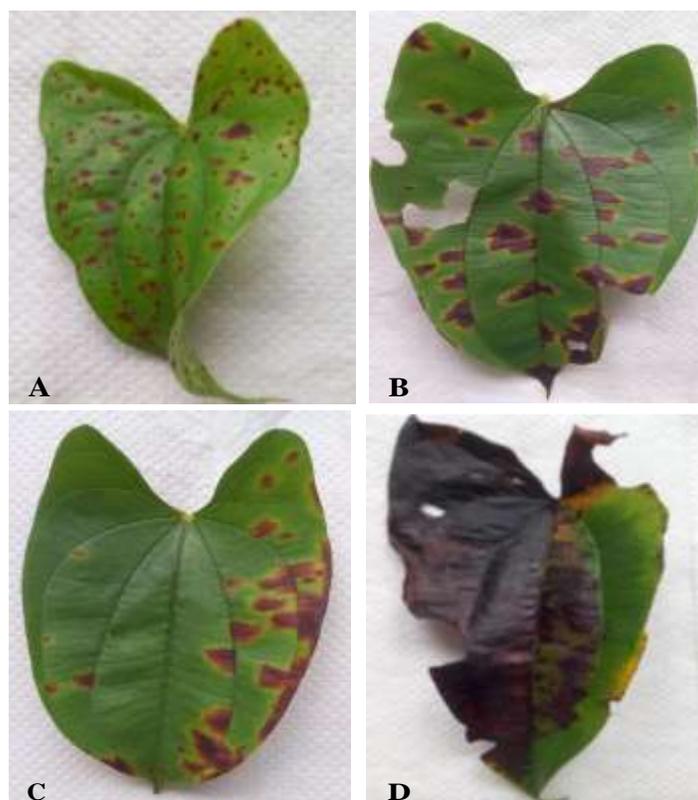


Figure 1. Key symptoms of the anthracnose disease on *D. alata* leaves. A: presence of numerous tiny spots throughout the leaf area, including the main and secondary veins; B: presence of large and irregularly-shaped spots on the leaves; C: spots surrounded by a yellow halo and particularly concentrated on the leaf veins; D: spots on one edge of the leaf blade and their coalescence leading to complete necrosis of the infected leaf edge.

anthracnose disease severity scores among variety groups within years, except for the disease incidence. In 2017, the highest disease severity score was observed on the 'Betebete' variety group (2.42), while it was 1.95 and 2.65 in 2018 and 2019, respectively. Conversely, the lowest scores were obtained on the 'Florida' variety group across the three years of observation. These low values were 2.01 in 2017, 1.54 in 2018, and 2.11 in 2019. In addition, the disease incidence has not allowed a significant discrimination among accessions of different variety groups over time, indicating that the occurrence frequencies of the anthracnose disease symptoms did not vary with variety groups (Table 3). The accession responses to anthracnose disease over years would be related to two main factors: environmental or external factors and intrinsic characteristics of the accessions or internal factors. Environmental conditions play a key role in the development and spread of a disease. High rainfall and high relative humidity, coupled with relatively high temperatures and wind, provide favourable conditions for

the growth and dispersal of fungi such as *C. gloeosporioides* (Roberts et al., 2001). Such favourable conditions were predominant at Bouaké during the study period. The growing year 2019 was marked by high rainfall, high relative humidity, and high wind speeds, in contrast to 2018 and 2017, a condition that favoured high pathogen pressure. The annual fluctuations of these environmental parameters would be at the origin of the instability in the response of some accessions to anthracnose disease. For instance, accessions that were identified as resistant, moderately resistant, or susceptible in one year had been moderately resistant, susceptible or highly susceptible in another year, and vice-versa. This instability in accession responses would also be due to several biotic and abiotic factors such as leaf age, pathogen strain, time of infection, and cultural conditions (Egesi et al., 2007; Pwajem, 2015). In yam, young leaves are more susceptible to anthracnose disease. When the period of high rainfall coincides with the stage of plant development where more young leaves

Table 3. Anthracnose disease severity scores (DSS) and disease incidence (DI) in different variety groups of *D. alata* across years.

Variety group	DSS			Statistical tests		DI (%)			Statistical tests	
	2017	2018	2019	Chi 2	P	2017	2018	2019	Chi 2	P
Florido	2.01±0.73 ^a	1.54±0.61 ^b	2.11±0.80 ^a	27.08	<0.001	67.23±43.61 ^a	38.61±43.32 ^b	65.05±44.79 ^a	22.24	<0.001
Brazo	2.00±0.62 ^a	1.57±0.50 ^b	1.95±0.75 ^a	7.02	0.029	68.32±41.94	42.66±43.95	64.83±45.53	3.50	0.173
Nza	2.24±0.93 ^a	1.55±0.73 ^b	2.46±1.08 ^a	21.73	<0.001	72.63±41.50 ^a	32.63±45.73 ^b	70.83±44.16 ^a	21.73	<0.001
Douable	2.23±0.91 ^a	1.79±0.82 ^b	2.30±0.9 ^a	10.49	<0.010	68.11±43.88 ^a	38.61±43.59 ^b	71.11±44.45 ^a	13.31	<0.010
Betebete	2.42±1.03 ^b	1.95±0.98 ^c	2.65±1.02 ^a	37.36	<0.001	75.47±38.89 ^a	49.31±44.57 ^b	71.28±42.72 ^a	32.24	<0.001
Means	2.22±0.95 ^b	1.73±0.86 ^c	2.37±1.01 ^a	1132.4	<0.001	71.57±42.28 ^a	40.74±45.12 ^c	70.03±43.22 ^b	198.49	<0.001
				Means					Means	
Florido	2.01±0.73 ^c	1.54±0.61 ^c	2.11±0.80 ^c	1.88±0.75 ^b		67.23±43.61	38.61±43.32	65.05±44.79	57.15±45.62	
Brazo	2.00±0.62 ^c	1.57±0.50 ^b	1.95±0.75 ^c	1.76±0.59 ^b		68.32±41.94	42.66±43.95	64.83±45.53	56.21±45.08	
Nza	2.24±0.93 ^b	1.55±0.73 ^b	2.46±1.08 ^b	2.04±0.95 ^{ab}		72.63±41.50	32.63±45.73	70.83±44.16	58.34±47.04	
Douable	2.23±0.91 ^b	1.79±0.82 ^b	2.30±0.91 ^b	2.19±0.96 ^a		68.11±43.88	38.61±43.59	71.11±44.45	60.06±45.89	
Betebete	2.42±1.03 ^a	1.95±0.98 ^a	2.65±1.02 ^a	2.32±1.04 ^a		75.47±38.89	49.31±44.57	71.28±42.72	65.53±43.58	
Statistical tests	Chi 2	9.81	11.65	30.59	38.11	2.12	7.05	3.11	7.80	
	P	0.043	0.020	<0.001	<0.001	0.713	0.132	0.538	0.099	

Experimental data represent the means ± standard deviation with n=10, (*): For a given parameter, means followed by the same letter are not statistically different at the threshold $\alpha=0.05$.

are present, the disease spreads rapidly and black spots and necrosis appear on leaves and stems (Reddy et al., 2015). In addition, *C. gloeosporioides* strains with varying levels of virulence have been identified in *D. alata* (Abang et al., 2002). Each year, the abundance of the most virulent strains in a plantation could lead to a severe attack of *C. gloeosporioides*. According to Eynard (1975), the fungal flora could undergo strong annual fluctuations and be abundant in some years while in other years, the number is significantly reduced. Moreover, the trials were established on different plots at the CNRA station and thus could also be the source of the disparity among accessions depending on the year. This observation is supported by the results of Chakraborty et al. (2002) which showed strong

spatial variations in populations of *C. gloeosporioides* in Brazil. Planting carried out late in July 2018, due to a lack or delay of rainfall at the appropriate planting periods (March, April or May) led to low disease severity scores and incidence in contrast to years 2017 and 2019. Egesi et al. (2007) reported similar results. Indeed, these authors found that yams planted early in March showed much more severe symptoms of anthracnose disease than plantations made in April and May. Late plantations in August showed a much lower level of anthracnose disease. However, this result contrast with that of Emehute et al. (1998) who reported that late planting of yams would favour the development of anthracnose symptoms. Despite changes in environmental conditions,

some accessions exhibited consistently a low disease severity scores and disease incidence, while other expressed higher values of anthracnose disease parameters. Some of these accessions remained stable across years, showing that accessions of *D. alata* in Côte d'Ivoire can differently react to anthracnose disease. Internal factors would be related to this kind of responses in accessions. Indeed, plants have a natural defense system that protects them against attacks by pathogens (Jones and Dangl, 2006). During a pathogenic attack, this system activates and mobilizes various types of molecules, including resistance proteins encoded by specific genes (McDowell and Woffenden, 2003). These resistance genes are capable of conferring plants a resistance against attacks from

Table 4. Anthracnose disease severity scores (DSS) and disease incidence (DI) in different variety groups of *D. alata* at different symptom assessment periods.

Variety group	DSS			Statistical tests		DI (%)			Statistical tests	
	P1	P2	P3	Chi 2	P	P1	P2	P3	Chi 2	P
Florida	1.16±0.29 ^c	1.91±0.59 ^b	2.59±0.53 ^a	175.99	<0.001	7.82±17.01 ^c	65.20±41.07 ^b	97.23±12.66 ^a	185.85	<0.001
Brazo	1.18±0.30 ^b	1.97±0.43 ^{ab}	2.24±0.35 ^a	53.53	<0.001	10.49±24.91 ^c	70.00±38.25 ^b	94.81±13.11 ^a	55.11	<0.001
Nza	1.21±0.29 ^c	2.02±0.74 ^b	2.96±0.80 ^a	83.02	<0.001	12.63±26.36 ^c	66.25±46.29 ^b	99.30±4.81 ^a	81.17	<0.001
Douoble	1.31±0.39 ^c	2.01±0.68 ^b	2.99±0.65 ^a	75.60	<0.001	15.77±27.59 ^c	62.57±45.55 ^b	99.04±6.17 ^a	66.94	<0.001
Betebete	1.40±0.41 ^c	2.22±0.71 ^b	3.40±0.78 ^a	25.34	<0.001	23.54±32.10 ^c	73.84±40.05 ^b	99.80±2.21 ^a	22.30	<0.001
Means	1.27±0.45 ^c	2.06±0.72 ^b	2.98±0.82 ^a	605.7	<0.001	14.65±27.91 ^c	68.78±42.51 ^b	98.91±7.47 ^a	586.37	<0.001
				Means					Means	
Florida	1.16±0.29 ^c	1.91±0.59 ^c	2.59±0.53 ^c	1.88±0.75 ^b		7.82±17.01 ^e	65.20±41.07	97.23±12.66 ^c	57.15±45.62	
Brazo	1.18±0.30 ^c	1.97±0.43 ^{bc}	2.24±0.35 ^d	1.76±0.59 ^b		10.49±24.91 ^d	70.00±38.25	94.81±13.11 ^d	56.21±45.08	
Nza	1.21±0.29 ^c	2.02±0.74 ^b	2.96±0.80 ^b	2.04±0.95 ^{ab}		12.63±26.36 ^c	66.25±46.29	99.30±4.81 ^c	58.34±47.04	
Douoble	1.31±0.39 ^b	2.01±0.68 ^b	2.99±0.65 ^b	2.19±0.96 ^a		15.77±27.59 ^b	62.57±45.55	99.04±6.17 ^b	60.06±45.89	
Betebete	1.40±0.41 ^a	2.22±0.71 ^a	3.40±0.78 ^a	2.32±1.04 ^a		23.54±32.10 ^a	73.84±40.05	99.80±2.21 ^a	65.53±43.58	
Statistical tests	<i>Chi 2</i>	25.87	14.33	91.46	38.11	20.19	3.45	14.85	7.80	
	<i>P</i>	<0.001	0.006	<0.001	<0.001	<0.001	0.484	<0.01	0.099	

Experimental data represent the means ± standard deviation with n=10, (*): For a given parameter, means followed by the same letter are not statistically different at the threshold $\alpha=0.05$. P1 (2 months after planting; 2 MAP), P2 (3 MAP) and P3 (4 MAP).

external origins. In general, plant resistance is governed by R genes that can individually act through major genes or joint action through genes called QTL (Quantitative Trait Loci) or QRL (Quantitative Resistance Loci) (Lindhout, 2002; Stuthman et al., 2007; Brun et al., 2010). The presence or absence of these genes in plants could be responsible for the resistant or susceptible character of accessions in *D. alata*.

Effects of the assessment periods and variety groups on anthracnose disease severity score and disease incidence in *D. alata*

Anthracnose disease severity scores and disease

incidence increased significantly ($p<0.05$) from period one (P1) to period three (P3) in all the studied variety groups of *D. alata*. The disease severity scores and disease incidence in different variety groups were higher at P3 (four months after planting) and lower at period P1 (two months after planting).

The highest values of disease severity scores and disease incidence at P3 were reported in the 'Betebete' variety group (3.40 and 99.80%, respectively), followed by 'Douoble' (2.99 and 99.04%), 'Nza' (2.96 and 99.30%), 'Florida' (2.59 and 97.23%), and 'Brazo' (2.24 and 94.81%) variety groups. The mean disease severity scores were 1.27, 2.06, and 2.99 with disease incidences

of 14.65, 68.78, and 98.91% at periods P1, P2, and P3, respectively. At P3, all the selected yam accessions showed symptoms of anthracnose disease and an average disease incidence of 98.9% (Table 4).

The anthracnose disease severity scores and disease incidence were significantly different ($p<0.05$) among *D. alata* variety groups at P1 and P3, except the disease incidence at P2 (Table 4). The average disease severity scores of anthracnose were higher in 'Betebete' variety group at all three assessment periods (P1, P2, and P3). The average disease severity scores were 1.40, 2.22, and 3.40, respectively. Lower disease severity scores were observed in 'Florida'

at P1 (1.16) and P2 (1.91) and in 'Brazo' at P3 (2.24). The disease incidence was higher in 'Betebete' at P1 and P3. It was 23.54% at P1 and 99.80% at P3. On the other hand, the lowest average values for disease incidence were observed in 'Florido' and 'Brazo' variety groups. Corresponding values were 7.82% in 'Florido' at period P1 and 94.81% in Brazo at P3. In this study, *D. alata* landrace accessions from the CNRA collection responded differently to *C. gloeosporioides* attacks depending on the periods when the disease symptoms were observed. Some accessions expressed the disease symptoms at earlier stages while others showed symptoms much later. It was the case for accessions from the same variety group. The accessions from 'Betebete' variety group exhibited the symptoms of the anthracnose disease earlier than those from other groups. The variation in accession responses according to observation periods could be explained by the progression and spread of the disease under environmental conditions that favour *C. gloeosporioides* development. Indeed, anthracnose disease attacks all parts of the yam at all stages of its development (Akem, 1999). However, the symptoms are most visible on aerial organs such as leaves and stems. Attacks start with small brown spots with 2 to 5 mm in diameter, often surrounded by a yellow halo (Emehute et al., 1998).

These spots grow, enlarge, and then become coalescent and much larger with irregular shapes over large areas, resulting in wilting, dieback and death of the infected plant tissue (Gautam, 2014). During its progression, the disease gradually spreads from one plant to another by wind and rainwater from specialized structures such as spores or conidia produced in large quantities (Pwakem, 2015).

Anthracnose disease severity scores in accessions of *D. alata* and frequencies according to periods of symptom observation in each of the years

Based on a semi-quantitative scale, anthracnose disease severity scores 1 and 2 were recorded on *D. alata* accessions at P1 of each year. At this period, accessions with a score 1 were the most frequent in each of the years. The period P2 was characterized by the presence of scores 1, 2, and 3 with a predominance of score 2, except in 2019, when accessions with score 1 were most frequent. P3 was the period with four levels of anthracnose disease sensitivity: scores 2, 3, 4, and 5. Accessions with a score 3 were predominant at this period across all years. The four levels of accession sensitivity to anthracnose disease in each of the assessment year corresponded to the scores for resistant (R), moderately resistant (MR), susceptible (S) and highly susceptible (HS), respectively. Thus, the period P3 seemed to be the most discriminating period among *D.*

alata accessions for yam anthracnose disease (Figure 2).

Anthracnose disease severity scores and disease incidence among *D. alata* variety groups four months after planting (P3) across assessment years

Anthracnose disease severity scores varied significantly ($p < 0.05$) among *D. alata* variety groups at P3 of each year (Table 5). However, apart from 2019, the disease incidence was not different among variety groups in 2017 and 2018. The 'Betebete' variety group exhibited the highest disease severity scores across years. Corresponding disease severity values were 3.58, 3.08, and 3.55 in 2017, 2018, and 2019, respectively. Lower disease severity scores were observed in 'Brazo' and 'Florido' across years. In 'Brazo', disease severity scores were 2.31 in 2017, 2.09 in 2018, and 2.34 in 2019. The disease incidence was 95.55% in 'Brazo' and reached 100% in other variety groups in 2019. Across years, the highest disease severity score (3.40) and disease incidence (99.81%) were recorded in 'Betebete' variety group while the lowest values were recorded in 'Brazo'.

This assessment period, corresponding to four months after planting, coincided in 2017 and 2019 with the months of September and October, respectively. On the other hand, following a delay in yam planting in 2018, the third disease observation period was in November, a period corresponding to the beginning of the fading phase of the plants and marked by an almost total absence of rainfall. In 2017 and 2019, months of September and October were marked by high rainfall in Bouaké. The coincidence of the yam active development phase and periods of high rainfall favoured the growth of the pathogenic fungi. This coincidence could explain the severe attacks of *C. gloeosporioides* observed in these periods (Gnago et al., 2004; Mbaye et al., 2008; Dossa et al., 2019). In the West Indies, where similar observations were made, the disease develops at the beginning of September, a period when temperature and humidity levels are high, and the disease damages continue until November (Ano et al., 2005).

Hierarchical clustering of 115 *D. alata* landrace accessions using mean disease severity scores four months after planting (P3)

Mean disease severity score was calculated using disease scores at P3 across the three years of assessment. From these mean disease severity scores, hierarchical clustering analysis using ward. D2 aggregation method was carried out. It clearly showed four (4) main groups of accessions for the sensitivity to anthracnose disease. The groups were identified about 4 Euclidean distance units (Figure 3). Cluster 1, comprising

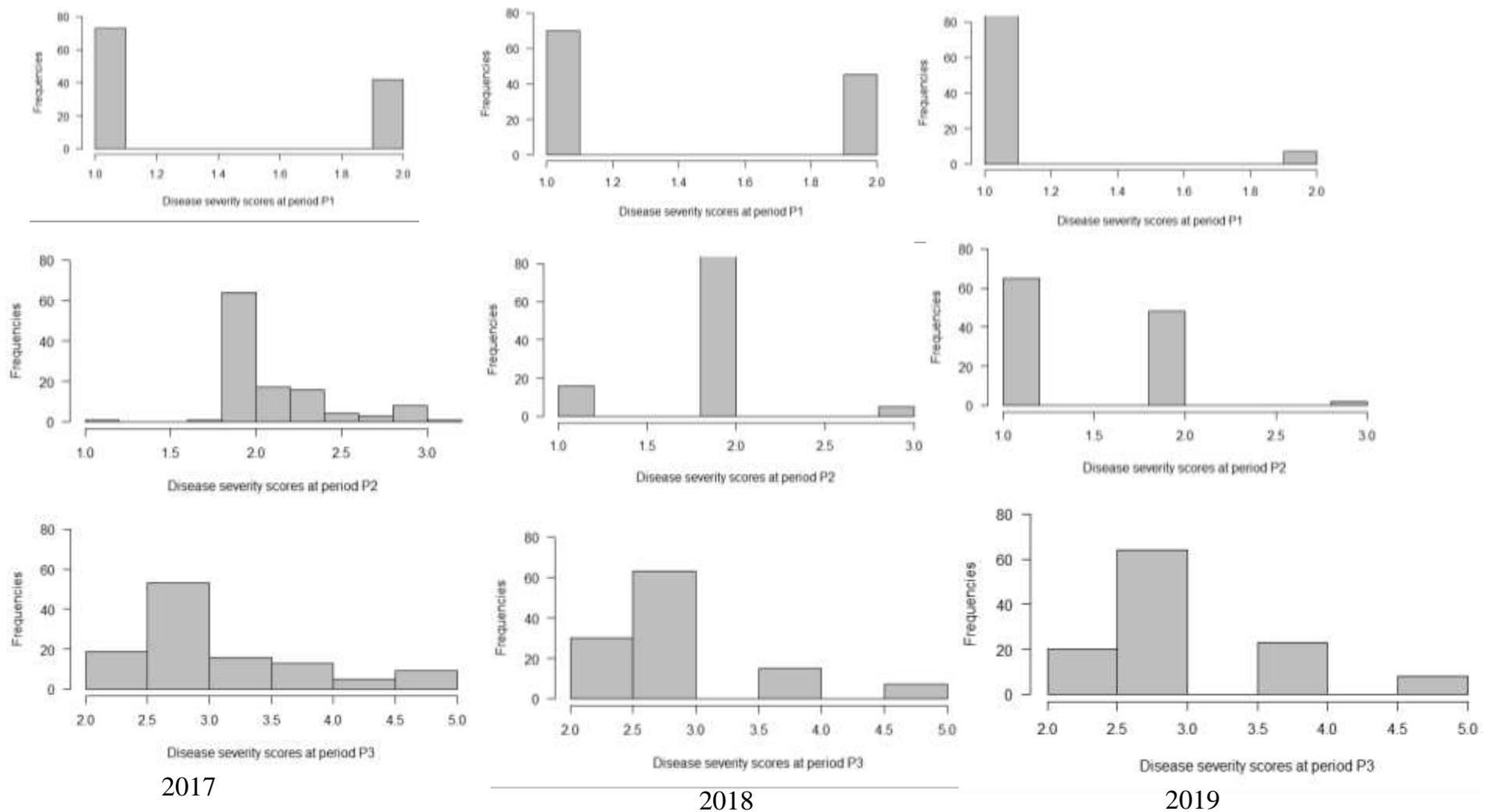


Figure 2. Anthracnose disease severity scores in *D. alata* accessions from different variety groups at periods of disease symptom observations across the study years.

of 60.87% of accessions, had disease severity scores ranging from 2.42 to 3.18 and represented

the moderately resistant accession group. On the other hand, the cluster 2 (14.78% of accessions),

scoring from 2.00 to 2.17, was identified as a resistant accession group (Table 6). Susceptible

Table 5. Anthracnose disease severity scores (DSS) and disease incidence (DI) among *D. alata* variety groups at period P3 of each assessment year.

Varietal group	DSS			DI (%)			Means		
	2017	2018	2019	2017	2018	2019	DSS	DI (%)	
Betebete	3.58±0.78 ^a	3.08±0.80 ^a	3.55±0.67 ^a	100.00±0.00	99.43±3.76	100.00±0.00 ^a	3.40± 0.78 ^a	99.81±2.17 ^a	
Brazo	2.31±0.38 ^c	2.09±0.23 ^c	2.34± 0.38 ^b	97.77±6.67	91.11±20.27	95.55±8.81 ^b	2.24± 0.35 ^d	94.81±13.11 ^d	
Douable	3.32±0.63 ^{ab}	2.72±0.46 ^{ab}	3.20±0.90 ^a	100.00±0.00	97.14±10.69	100.00±0.00 ^a	3.08± 0.72 ^b	99.04±6.17 ^b	
Florido	2.75±0.51 ^c	2.28± 0.42 ^c	2.72±0.54 ^b	99.21±4.41	92.50±20.90	100.00±0.00 ^a	2.59± 0.53 ^c	97.23±12.66 ^c	
Nza	3.15±0.77 ^b	2.46±0.51 ^{bc}	3.25±0.87 ^a	100.00±0.00	97.91±8.33	100.00±0.00 ^a	2.96± 0.80 ^b	99.30±4.81 ^b	
Statistical tests	<i>Chi 2</i> <i>P</i>	37.23 <0.001	37.80 <0.001	41.41 <0.001	6.16 0.187	6.48 0.165	23.76 <0.001	97.47 <0.001	19.53 <0.001

Experimental data represent the means ± standard deviation with n=10, (*): For a given parameter, means followed by the same letter are not statistically different at the threshold $\alpha=0.05$.

(15.65%) and highly susceptible (8.70%) accessions belonged to clusters 3 and 4, respectively. They scored from 3.25 to 3.89 and from 4.15 to 5.00, respectively. The memberships of each cluster are shown in supplementary file (Table S1). Cluster characterization, using mean disease severity scores and disease incidence in an analysis of variance, indicated significant differences ($p<0.05$) among groups (Table 6). Distinction among clusters was clearly established with mean disease severity scores. However, it was partially established with disease incidence information. The average disease severity scores were higher in cluster 4 and lower in cluster 2. Thus, anthracnose disease score appears to be a pertinent parameter in discriminating *D. alata* accessions for anthracnose disease sensitivity under field conditions.

Proportions of accessions from different variety groups for each level of anthracnose disease sensitivity four months after planting (P3) across the three years

Proportions of resistant (R), susceptible (S), and

highly susceptible (HS) accessions were significantly different ($p<0.05$) among and within *D. alata* variety groups. 'Brazo' (0.58) and Florido (0.45) had the highest proportions of resistant accessions, while the 'Betebete' had the lowest proportion (0.08). However, the proportions of susceptible (0.21) and highly susceptible (0.13) accessions were higher in the 'Betebete' than in other variety groups. Proportions of these reaction categories were lower in 'Brazo' and 'Florido'. None of the accessions in 'Brazo' was susceptible or highly susceptible. It was the same in 'Florido' for the highly susceptible category. The proportions of moderately resistant (MR) accessions did not significantly differ ($p>0.05$) among variety groups (Table 7).

In other yam growing regions, particularly in the West Indies, studies had also identified four response groups (R, MR, MS and S) on the same yam species, based on laboratory tissue inoculation tests (Onyeka et al., 2006). In contrast, previous studies conducted in Côte d'Ivoire, using a sample set of 43 accessions, identified three response groups based on the disease severity scores: R, S, and HS (Kouakou et al., 2007).

In Nigeria, Amusa (2000) also grouped yam accessions into three main groups (R, MS and S) based on observations in field conditions. These differences in the classification of *D. alata* accessions would be due, on one hand, to the methods used in disease severity rating which varied from one study to another. On the other hand, differences in results could be attributed to testing conditions (natural field/culture or laboratory testing conditions).

Conclusion

The results from this study showed that the 115 *D. alata* local accessions responded differently to severe attacks by *C. gloeosporioides*, which usually coincided with high rainfall periods. Based on their responses to disease attacks, four (4) main groups were identified and designated as resistant (R), moderately resistant (MR), susceptible (S), and highly susceptible (HS). Resistant accessions belonged mainly to the 'Brazo' and 'Florido' groups, while susceptible accessions were mostly from the 'Betebete'

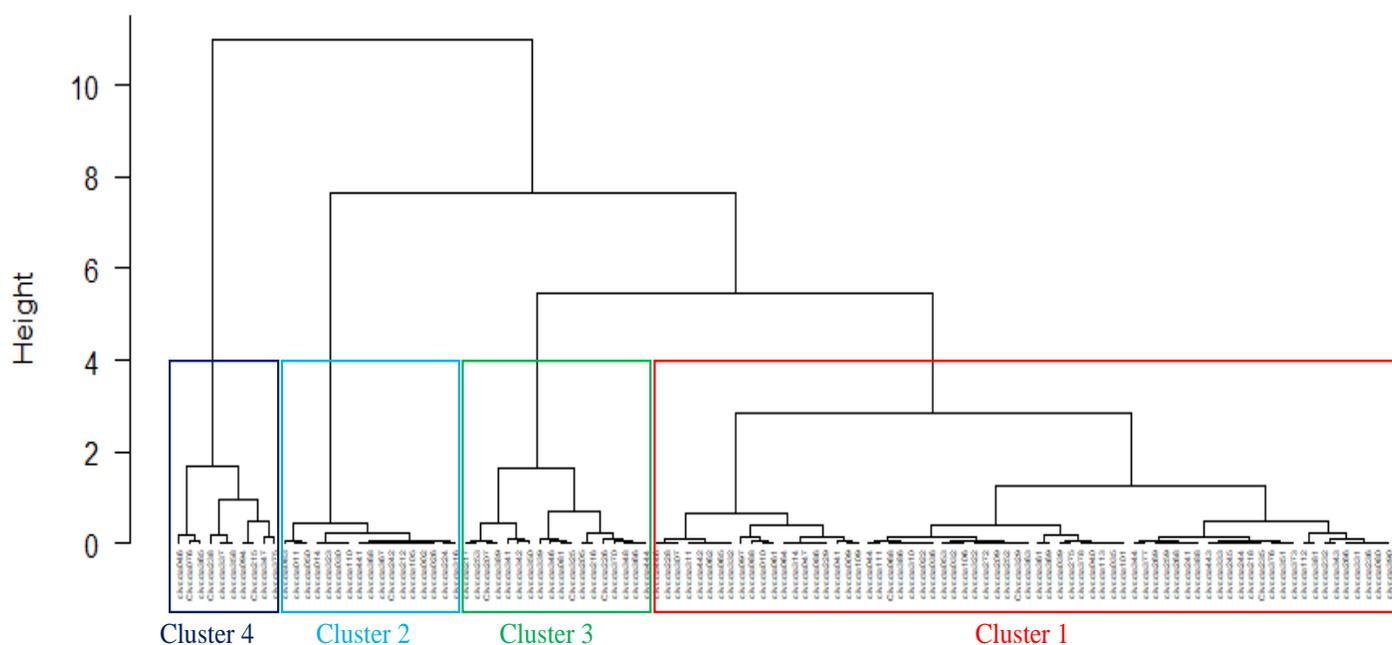


Figure 3. Hierarchical clustering of 115 *D. alata* landrace accessions based on disease severity scores four months after planting (P3).

Table 6. Characteristics of clusters using anthracnose disease severity scores (DSS) and disease incidence (DI).

Clusters	Proportions (%)	DSS			DI (%)			Resistance classes
		Min	Max	Means	Min	Max	Means	
Cluster 1 (N = 70)	60.87	2.42	3.18	2.85 ± 0.18 ^c	92.12	100	99.53 ± 1.61 ^a	MR
Cluster 2 (N = 17)	14.78	2.00	2.17	2.04 ± 0.05 ^d	86.67	100	96.99 ± 4.57 ^b	R
Cluster 3 (N = 18)	15.65	3.25	3.89	3.53 ± 0.21 ^b	88.88	100	99.01 ± 2.97 ^{ab}	S
Cluster 4 (N = 10)	8.70	4.15	5.00	4.55 ± 0.31 ^a	94.44	100	99.44 ± 1.75 ^{ab}	HS
Statistical tests	<i>Chi 2</i> <i>P-value</i>	-	-	87.45 <0.001	-	-	12.69 <0.01	

(*) For a given parameter, average values followed by the same letter are not statistically different at the threshold $\alpha=0.05$; Min: Minimum; Max: Maximum.

Table 7. Proportions of accessions in variety groups according to anthracnose disease susceptibility levels across years.

Variety group	Susceptibility levels of <i>D. alata</i> accessions to anthracnose disease				
	R	MR	S	HS	
Betebete	0.08 ^b	0.56	0.22 ^a	0.14 ^a	
Brazo	0.58 ^a	0.42	0.00 ^c	0.00 ^b	
Douoble	0.10 ^{bc}	0.67	0.15 ^{abc}	0.08 ^{ab}	
Florida	0.45 ^a	0.50	0.05 ^{bc}	0.00 ^b	
Nza	0.35 ^{ab}	0.43	0.16 ^{ab}	0.06 ^{ab}	
Statistical tests	<i>Chi 2</i> <i>P</i>	61.722 < 0.001	7.295 0.122	16.488 0.004	18.026 0.002

(*) For a given parameter, average values followed by the same letter are not statistically different at the threshold $\alpha=0.05$; Resistant (R), moderately resistant (MR), susceptible (S) and highly susceptible (HS)

variety group. However, most resistant and moderately resistant accessions were stable across year. This study's results suggest that there is a genotypic effect that controls anthracnose disease resistance in *D. alata* accessions. The presence of resistant accessions within the water yam collection of Côte d'Ivoire shows that some varieties are tolerant to natural fungal pathogens, in particular *C. gloeosporioides*. These accessions could, therefore, be used in genetic improvement programs for the creation and selection of new clones or cultivars.

CONFLICT OF INTERESTS

The authors have not declared any conflict of interests.

ACKNOWLEDGEMENTS

The field activities of this study were supported by the Africa Yam project of IITA (International Institute of Tropical Agriculture) and funded by the Bill and Melinda Gates Foundation (BMGF). We also thank the National Agronomic Research Centre (CNRA), a partner in the project, for carrying out the work in Côte d'Ivoire.

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Table S1. Classification of 115 landrace accessions of *D. alata* based on the anthracnose disease severity scores at period P3 for each assessment year.

Accessions	Variety group	Years of assessment of anthracnose disease symptoms in <i>D. alata</i>						Means	
		2017		2018		2019		DSS ± Sd	Group
		DSS ± Sd	Group	DSS ± Sd	Group	DSS ± Sd	Group		
civcda 002	Brazo	2.00 ± 0.00 ^d	R	2.00 ± 0.00 ^d	R	2.00 ± 0.00 ^d	R	2.00 ± 0.00 ^d	R
civcda 026	Betebete	2.00 ± 0.00 ^d	R	2.00 ± 0.00 ^d	R	2.00 ± 0.00 ^d	R	2.00 ± 0.00 ^d	R
civcda 105	Forido	2.00 ± 0.00 ^d	R	2.00 ± 0.00 ^d	R	2.00 ± 0.00 ^d	R	2.00 ± 0.00 ^d	R
civcda 212	Nza	2.00 ± 0.00 ^d	R	2.00 ± 0.00 ^d	R	2.00 ± 0.00 ^d	R	2.00 ± 0.00 ^d	R
civcda 242	Florido	2.00 ± 0.00 ^d	R	2.00 ± 0.00 ^d	R	2.00 ± 0.00 ^d	R	2.00 ± 0.00 ^d	R
civcda 367	Nza	2.00 ± 0.00 ^d	R	2.00 ± 0.00 ^d	R	2.00 ± 0.00 ^d	R	2.00 ± 0.00 ^d	R
civcda 368	Florido	2.00 ± 0.00 ^d	R	2.00 ± 0.00 ^d	R	2.00 ± 0.00 ^d	R	2.00 ± 0.00 ^d	R
civcda 441	Nza	2.00 ± 0.00 ^d	R	2.00 ± 0.00 ^d	R	2.00 ± 0.00 ^d	R	2.00 ± 0.00 ^d	R
civcda 224	Florido	2.00 ± 0.00 ^d	R	2.07 ± 0.99 ^d	R	2.00 ± 0.00 ^d	R	2.02 ± 0.04 ^d	R
civcda 316	Florido	2.00 ± 0.00 ^d	R	2.09 ± 0.12 ^d	R	2.00 ± 0.00 ^d	R	2.03 ± 0.05 ^d	R
civcda 014	Brazo	2.00 ± 0.00 ^d	R	2.14 ± 0.20 ^d	R	2.00 ± 0.00 ^d	R	2.05 ± 0.08 ^d	R
civcda 030	Florido	2.20 ± 0.28 ^a	R	2.28 ± 0.00 ^d	R	2.00 ± 0.00 ^d	R	2.07 ± 0.12 ^d	R
civcda 110	Brazo	2.00 ± 0.00 ^d	R	2.00 ± 0.00 ^d	R	2.20 ± 0.28 ^d	R	2.07 ± 0.12 ^d	R
civcda 323	Florido	2.00 ± 0.00 ^d	R	2.20 ± 0.28 ^d	R	2.00 ± 0.00 ^d	R	2.07 ± 0.12 ^d	R
civcda 083	Florido	2.00 ± 0.00 ^d	R	2.00 ± 0.00 ^d	R	2.40 ± 0.57 ^d	R	2.13 ± 0.23 ^d	R
civcda 011	Florido	2.25 ± 0.35 ^d	R	2.14 ± 0.20 ^d	R	2.10 ± 0.14 ^d	R	2.16 ± 0.08 ^d	R
civcda 050	Brazo	2.50 ± 0.00 ^c	MR	2.00 ± 0.00 ^d	R	2.00 ± 0.00 ^d	R	2.17 ± 0.29 ^d	R
civcda 097	Brazo	2.75 ± 0.35 ^c	MR	2.00 ± 0.00 ^d	R	2.50 ± 0.71 ^c	MR	2.42 ± 0.38 ^c	MR
civcda 088	Betebete	2.70 ± 0.42 ^c	MR	2.00 ± 0.00 ^d	R	2.70 ± 0.42 ^c	MR	2.47 ± 0.40 ^{ac}	MR
civcda 061	Brazo	2.50 ± 0.71 ^c	MR	2.00 ± 0.00 ^d	R	3.00 ± 0.00 ^c	MR	2.50 ± 0.50 ^c	MR
civcda 010	Brazo	2.96 ± 1.00 ^c	MR	2.00 ± 0.00 ^d	R	2.58 ± 0.25 ^c	MR	2.51 ± 0.48 ^c	MR
civcda 064	Florido	2.80 ± 0.28 ^c	MR	2.20 ± 0.00 ^d	R	2.67 ± 0.47 ^c	MR	2.56 ± 0.32 ^c	MR
civcda 314	Florido	2.60 ± 0.57 ^c	MR	2.07 ± 0.99 ^d	R	3.00 ± 0.00 ^c	MR	2.56 ± 0.47 ^c	MR
civcda 086	Bêtêbêtê	2.70 ± 0.42 ^c	MR	2.00 ± 0.00 ^d	R	3.00 ± 0.00 ^c	MR	2.57 ± 0.51 ^c	MR
civcda 229	Nza	3.00 ± 0.00 ^c	MR	2.00 ± 0.00 ^d	R	2.70 ± 0.42 ^c	MR	2.57 ± 0.51 ^c	MR
civcda 047	Florido	2.88 ± 0.18 ^c	MR	2.00 ± 0.00 ^d	R	2.85 ± 0.49 ^c	MR	2.58 ± 0.50 ^c	MR
civcda 041	Florido	2.90 ± 0.70 ^c	MR	2.00 ± 0.00 ^d	R	2.90 ± 0.14 ^c	MR	2.60 ± 0.52 ^c	MR
civcda 009	Douoblé	2.90 ± 0.14 ^c	MR	2.00 ± 0.00 ^d	R	3.00 ± 0.00 ^c	MR	2.63 ± 0.55 ^c	MR
civcda 109	Florido	2.90 ± 0.70 ^c	MR	2.00 ± 0.00 ^d	R	3.00 ± 0.00 ^c	MR	2.63 ± 0.55 ^c	MR
civcda 228	Florido	3.00 ± 0.00 ^c	MR	2.00 ± 0.00 ^d	R	3.00 ± 0.00 ^c	MR	2.67 ± 0.58 ^c	MR
civcda 307	Douoblé	3.00 ± 0.00 ^c	MR	3.00 ± 0.00 ^d	MR	2.00 ± 0.00 ^d	R	2.67 ± 0.58 ^c	MR
civcda 355	Florido	3.00 ± 0.00 ^c	MR	2.00 ± 0.00 ^d	R	3.00 ± 0.00 ^c	MR	2.67 ± 0.58 ^c	MR
civcda 311	Nza	3.00 ± 0.00 ^c	MR	2.34 ± 0.47 ^d	R	2.73 ± 0.74 ^c	MR	2.69 ± 0.33 ^c	MR
civcda 442	Florido	3.00 ± 0.00 ^c	MR	2.07 ± 0.99 ^d	R	3.00 ± 0.00 ^c	MR	2.69 ± 0.54 ^c	MR
civcda 062	Brazo	2.60 ± 0.57 ^c	MR	2.71 ± 0.00 ^c	MR	2.80 ± 0.00 ^c	MR	2.70 ± 0.10 ^c	MR
civcda 065	Florido	3.00 ± 0.00 ^c	MR	2.14 ± 0.20 ^d	R	3.00 ± 0.00 ^c	MR	2.71 ± 0.50 ^c	MR
civcda 332	Florido	2.50 ± 0.71 ^c	MR	2.64 ± 0.51 ^c	MR	3.00 ± 0.00 ^c	MR	2.71 ± 0.26 ^c	MR
civcda 361	Nza	3.00 ± 0.00 ^c	MR	2.29 ± 0.40 ^d	R	3.00 ± 0.00 ^{bc}	MR	2.76 ± 0.41 ^c	MR
civcda 369	Florido	3.00 ± 0.00 ^c	MR	2.43 ± 0.60 ^d	R	2.88 ± 0.18 ^c	MR	2.77 ± 0.30 ^c	MR
civcda 378	Florido	2.80 ± 0.28 ^c	MR	2.67 ± 0.49 ^c	MR	3.00 ± 0.00 ^c	MR	2.82 ± 0.18 ^c	MR
civcda 035	Douoblé	3.00 ± 0.00 ^c	MR	2.50 ± 0.71 ^c	MR	3.00 ± 0.00 ^c	MR	2.83 ± 0.29 ^c	MR
civcda 101	Betebete	2.50 ± 0.71 ^c	MR	2.00 ± 0.00 ^d	R	4.00 ± 0.00 ^b	S	2.83 ± 0.29 ^c	MR
civcda 113	Douoblé	3.00 ± 0.00 ^c	MR	2.50 ± 0.71 ^c	MR	3.00 ± 0.00 ^c	MR	2.83 ± 0.29 ^c	MR
civcda 040	Florido	3.25 ± 0.35 ^c	MR	2.28 ± 0.00 ^d	R	3.00 ± 0.00 ^c	MR	2.84 ± 0.50 ^c	MR
civcda 039	Florido	3.00 ± 0.00 ^c	MR	2.55 ± 0.07 ^c	MR	3.00 ± 0.00 ^c	MR	2.85 ± 0.26 ^c	MR
civcda 275	Betebete	3.00 ± 0.00 ^c	MR	2.57 ± 0.00 ^c	MR	3.00 ± 0.00 ^c	MR	2.87 ± 0.25 ^c	MR

Table S1. Contd.

civcda 068	Betebete	3.00 ± 0.00 ^c	MR	2.50 ± 0.71 ^{ab}	MR	3.10 ± 0.42 ^c	MR	2.87 ± 0.32 ^c	MR
civcda 386	Betebete	3.00 ± 0.00 ^c	MR	2.63 ± 0.29 ^c	MR	3.00 ± 0.00 ^c	MR	2.88 ± 0.07 ^c	MR
civcda 036	Florido	3.00 ± 0.00 ^c	MR	2.84 ± 0.23 ^c	MR	2.80 ± 0.00 ^c	MR	2.88 ± 0.07 ^c	MR
civcda 022	Florido	2.80 ± 0.28 ^c	MR	2.93 ± 0.11 ^{ab}	MR	2.92 ± 0.59 ^c	MR	2.88 ± 0.07 ^c	MR
civcda 310	Nza	3.25 ± 0.35 ^c	MR	2.30 ± 0.42 ^d	R	3.10 ± 0.42 ^c	MR	2.88 ± 0.07 ^c	MR
civcda 044	Betebete	3.00 ± 0.00 ^c	MR	2.57 ± 0.61 ^c	MR	3.10 ± 0.42 ^c	MR	2.89 ± 0.28 ^c	MR
civcda 111	Douoblé	3.00 ± 0.00 ^c	MR	2.71 ± 0.00 ^c	MR	3.00 ± 0.00 ^c	MR	2.90 ± 0.17 ^c	MR
civcda 272	Betebete	3.00 ± 0.00 ^c	MR	2.63 ± 0.53 ^c	MR	3.10 ± 0.42 ^c	MR	2.91 ± 0.08 ^c	MR
civcda 322	Nza	3.00 ± 0.00 ^c	MR	2.43 ± 0.60 ^d	R	3.30 ± 0.42 ^c	MR	2.91 ± 0.08 ^c	MR
civcda 209	Nza	3.33 ± 0.47 ^b	S	2.40 ± 0.57 ^d	R	3.00 ± 0.00 ^c	MR	2.91 ± 0.47 ^c	MR
civcda 252	Betebete	3.00 ± 0.00 ^c	MR	2.84 ± 0.23 ^c	MR	2.90 ± 0.14 ^c	MR	2.91 ± 0.08 ^c	MR
civcda 329	Betebete	3.00 ± 0.00 ^c	MR	2.75 ± 0.35 ^c	MR	3.00 ± 0.00 ^c	MR	2.92 ± 0.14 ^c	MR
civcda 363	Florido	2.75 ± 0.00 ^c	MR	2.00 ± 0.00 ^d	R	4.00 ± 0.00 ^b	S	2.92 ± 1.01 ^c	MR
civcda 032	Florido	3.80 ± 0.57 ^b	S	3.00 ± 0.00 ^c	MR	2.00 ± 0.00 ^d	R	2.93 ± 0.90 ^c	MR
civcda 106	Douoblé	2.80 ± 0.28 ^c	MR	3.00 ± 0.00 ^c	MR	3.00 ± 0.00 ^c	MR	2.93 ± 0.90 ^c	MR
civcda 053	Betebete	3.00 ± 0.00 ^c	MR	2.84 ± 0.23 ^c	MR	3.00 ± 0.00 ^c	MR	2.94 ± 0.10 ^c	MR
civcda 373	Betebete	3.00 ± 0.00 ^c	MR	2.90 ± 0.14 ^c	MR	3.00 ± 0.00 ^c	MR	2.97 ± 0.34 ^{cc}	MR
civcda 351	Florido	3.20 ± 0.28 ^c	MR	2.59 ± 0.02 ^c	MR	3.13 ± 0.18 ^c	MR	2.97 ± 0.34 ^{cc}	MR
civcda 376	Florido	3.84 ± 0.23 ^b	S	2.10 ± 0.14 ^d	R	3.00 ± 0.00 ^c	MR	2.98 ± 0.87 ^{cc}	MR
civcda 443	Betebete	3.20 ± 0.28 ^c	MR	2.79 ± 0.30 ^c	MR	3.00 ± 0.00 ^c	MR	2.99 ± 0.20 ^c	MR
civcda 218	Douoblé	3.00 ± 0.00 ^c	MR	3.00 ± 0.00 ^c	MR	3.00 ± 0.00 ^c	MR	3.00 ± 0.00 ^c	MR
civcda 235	Douoblé	4.00 ± 0.00 ^b	S	3.00 ± 0.00 ^c	MR	2.00 ± 0.00 ^d	R	3.00 ± 0.00 ^c	MR
civcda 244	Betebete	3.00 ± 0.00 ^c	MR	3.00 ± 0.00 ^c	MR	3.00 ± 0.00 ^c	MR	3.00 ± 0.00 ^c	MR
civcda 245	Betebete	3.00 ± 0.00 ^c	MR	2.00 ± 0.00 ^d	R	4.00 ± 0.00 ^b	S	3.00 ± 0.00 ^c	MR
civcda 333	Florido	3.00 ± 0.00 ^c	MR	2.00 ± 0.00 ^d	R	4.00 ± 0.00 ^b	S	3.00 ± 0.00 ^{cc}	MR
civcda 388	Nza	3.00 ± 0.00 ^c	MR	2.21 ± 0.10 ^d	R	3.83 ± 0.24 ^b	S	3.01 ± 0.81 ^c	MR
civcda 241	Betebete	3.00 ± 0.00 ^c	MR	2.79 ± 1.11 ^c	MR	3.27 ± 0.09 ^c	MR	3.02 ± 0.24 ^c	MR
civcda 268	Betebete	3.45 ± 0.07 ^b	S	2.93 ± 0.11 ^c	MR	2.70 ± 0.42 ^c	MR	3.03 ± 0.10 ^c	MR
civcda 259	Betebete	2.95 ± 0.63 ^c	MR	3.14 ± 0.20 ^c	MR	3.00 ± 0.00 ^c	MR	3.03 ± 0.10 ^c	MR
civcda 269	Betebete	3.00 ± 0.00 ^c	MR	3.00 ± 0.00 ^c	MR	3.10 ± 0.42 ^c	MR	3.03 ± 0.10 ^c	MR
civcda 377	Betebete	3.00 ± 0.00 ^c	MR	2.21 ± 0.10 ^d	R	3.90 ± 0.14 ^b	S	3.04 ± 0.85 ^c	MR
civcda 344	Betebete	3.00 ± 0.00 ^c	MR	3.14 ± 0.20 ^c	MR	3.00 ± 0.00 ^c	MR	3.02 ± 0.08 ^c	MR
civcda 331	Douoblé	3.00 ± 0.00 ^c	MR	3.00 ± 0.00 ^c	MR	3.67 ± 0.24 ^c	MR	3.06 ± 0.66 ^c	MR
civcda 266	Nza	3.00 ± 0.00 ^c	MR	2.43 ± 0.60 ^c	R	3.75 ± 0.35 ^b	S	3.06 ± 0.66 ^c	MR
civcda 080	Betebete	3.00 ± 0.00 ^c	MR	3.00 ± 0.00 ^c	MR	3.20 ± 0.28 ^c	MR	3.07 ± 0.12 ^c	MR
civcda 390	Nza	3.20 ± 0.28 ^c	MR	3.00 ± 0.00 ^{ab}	MR	3.00 ± 0.00 ^c	MR	3.07 ± 0.12 ^c	MR
civcda 236	Douoblé	3.65 ± 0.21 ^b	S	2.60 ± 0.57 ^c	MR	3.00 ± 0.00 ^c	MR	3.08 ± 0.53 ^c	MR
civcda 343	Nza	3.25 ± 0.35 ^c	MR	3.07 ± 0.99 ^c	MR	3.00 ± 0.00 ^c	MR	3.11 ± 0.13 ^c	MR
civcda 232	Betebete	3.00 ± 0.00 ^c	MR	2.84 ± 0.23 ^c	MR	3.50 ± 0.35 ^b	S	3.12 ± 0.33 ^c	MR
civcda 381	Betebete	3.00 ± 0.00 ^c	MR	2.50 ± 0.71 ^c	MR	4.00 ± 0.00 ^b	S	3.17 ± 0.76 ^c	MR
civcda 112	Betebete	3.00 ± 0.00 ^c	MR	3.43 ± 0.60 ^c	MR	3.13 ± 0.18 ^b	MR	3.18 ± 0.22 ^c	MR
civcda 226	Nza	3.50 ± 0.71 ^b	S	2.00 ± 0.00 ^d	R	4.25 ± 0.00 ^a	HS	3.25 ± 1.15 ^b	S
civcda 348	Betebete	4.00 ± 0.00 ^b	S	2.25 ± 0.00 ^d	R	3.60 ± 0.85 ^b	S	3.28 ± 0.92 ^b	S
civcda 366	Betebete	3.80 ± 0.57 ^b	S	3.07 ± 0.99 ^c	MR	3.00 ± 0.00 ^c	MR	3.29 ± 0.44 ^b	S
civcda 444	Betebete	4.17 ± 0.23 ^b	S	2.71 ± 0.00 ^c	MR	3.00 ± 0.00 ^c	MR	3.29 ± 0.77 ^b	S
civcda 370	Betebete	3.60 ± 0.85 ^b	S	2.61 ± 0.15 ^c	MR	3.75 ± 0.35 ^b	S	3.32 ± 0.62 ^b	S
civcda 216	Betebete	4.80 ± 0.28 ^a	HS	2.28 ± 0.00 ^d	R	3.00 ± 0.00 ^c	MR	3.36 ± 1.30 ^b	S
civcda 205	Florido	3.25 ± 0.35 ^c	MR	3.90 ± 0.14 ^b	S	3.00 ± 0.00 ^c	MR	3.38 ± 0.46 ^b	S
civcda 339	Douoblé	3.65 ± 0.21 ^b	S	2.79 ± 0.30 ^c	MR	4.00 ± 0.00 ^b	S	3.48 ± 0.63 ^b	S
civcda 081	Betebete	4.75 ± 0.35 ^a	HS	2.80 ± 0.00 ^c	MR	3.00 ± 0.00 ^c	MR	3.52 ± 1.07 ^b	S

Table S1. Contd.

civcda 328	Betebete	3.50 ± 0.71 ^b	S	4.00 ± 0.00 ^b	S	3.10 ± 0.42 ^c	MR	3.53 ± 0.45 ^b	S
civcda 346	Betebete	3.50 ± 0.71 ^b	S	3.34 ± 0.47 ^b	S	3.83 ± 0.24 ^b	S	3.56 ± 0.25 ^b	S
civcda 389	Doublé	3.80 ± 0.57 ^b	S	2.25 ± 0.00 ^d	R	5.00 ± 0.00 ^a	HS	3.68 ± 1.38 ^b	S
civcda 207	Betebete	3.00 ± 0.00 ^c	MR	3.07 ± 0.99 ^c	MR	5.00 ± 0.00 ^a	HS	3.69 ± 1.14 ^b	S
civcda 253	Betebete	5.00 ± 0.00 ^a	HS	2.00 ± 0.00 ^d	R	4.13 ± 0.18 ^a	HS	3.71 ± 0.50 ^b	S
civcda 217	Betebete	4.00 ± 0.00 ^b	S	3.14 ± 0.20 ^c	MR	4.00 ± 0.00 ^b	S	3.71 ± 0.50 ^b	S
civcda 342	Nza	3.84 ± 0.23 ^b	S	3.17 ± 0.00 ^c	MR	4.25 ± 0.07 ^a	HS	3.82 ± 0.64 ^b	S
civcda 350	Betebete	3.80 ± 0.57 ^b	S	3.76 ± 0.06 ^b	S	4.00 ± 0.00 ^b	S	3.85 ± 0.13 ^b	S
civcda 341	Betebete	4.17 ± 0.23 ^a	HS	3.52 ± 1.68 ^b	S	4.00 ± 0.00 ^b	S	3.89 ± 0.34 ^b	S
civcda 358	Nza	4.00 ± 0.00 ^b	S	3.71 ± 0.00 ^b	S	4.75 ± 0.35 ^a	HS	4.15 ± 0.54 ^a	HS
civcda 337	Nza	5.00 ± 0.00 ^a	HS	2.50 ± 0.71 ^c	MR	5.00 ± 0.00 ^a	HS	4.17 ± 1.44 ^a	HS
civcda 238	Betebete	4.55 ± 0.07 ^a	HS	4.07 ± 0.99 ^b	S	4.17 ± 0.24 ^a	HS	4.26 ± 0.25 ^a	HS
civcda 215	Doublé	5.00 ± 0.00 ^a	HS	3.75 ± 1.77 ^b	S	5.00 ± 0.00 ^a	HS	4.42 ± 1.01 ^a	HS
civcda 094	Betebete	4.25 ± 0.35 ^a	HS	5.00 ± 0.00 ^a	HS	4.50 ± 0.35 ^b	HS	4.58 ± 0.52 ^a	HS
civcda 375	Betebete	5.00 ± 0.00 ^a	HS	3.99 ± 1.20 ^b	S	4.80 ± 0.28 ^a	HS	4.60 ± 0.53 ^a	HS
civcda 347	Betebete	5.00 ± 0.00 ^a	HS	4.14 ± 1.22 ^b	S	5.00 ± 0.00 ^a	HS	4.71 ± 0.50 ^a	HS
civcda 365	Betebete	5.00 ± 0.00 ^a	HS	4.86 ± 0.21 ^a	HS	5.00 ± 0.00 ^a	HS	4.85 ± 0.95 ^a	HS
civcda 046	Betebete	5.00 ± 0.00 ^a	HS	5.00 ± 0.00 ^a	HS	4.60 ± 0.57 ^a	HS	4.87 ± 0.23 ^a	HS
civcda 076	Betebete	5.00 ± 0.00 ^a	HS						
Tests statistiques	χ ² P	96.35 <0.001		6.12 <0.001		24.82 <0.001		87.45 <0.001	

For a given parameter, means followed by the same letter are not statistically different to the *p*-value threshold $\alpha=0.05$. R: Resistant; MR: Moderately Resistant; S: Susceptive and HS: Highly susceptible; civcda: Côte d'Ivoire, collection *Dioscorea alata*, Sd: Standard deviation.