Effects of the Physiological Age of Bananas on Their Susceptibility to Wound Anthracnose Due to *Colletotrichum musae*

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ABSTRACT

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Wound anthracnose, caused by *Colletotrichum musae*, and early ripening are the main problems affecting the quality of export bananas (*Musa* AAA Cavendish) from the Caribbean. These problems generally concern bananas grown in lowland plantations during the rainy season. Three experiments were carried out to study the influence of the physiological age of bananas, calculated on the basis of mean daily temperature sums, on their susceptibility to anthracnose. Stressful growing conditions, especially soil flooding, slowed fruit growth but had no direct effect on fruit susceptibility to *C. musae* or on the green life. However, fruit that had accumulated lower temperature sums were less susceptible to wound anthracnose. By varying the source-sink ratio, we show that bananas of the same grade but different physiological ages had markedly different susceptibility to *C. musae*. Bananas with the same temperature sum accumulation but grown in different soil-climate conditions had different levels of susceptibility. Fruit grown in cooler, highland areas were less susceptible to *C. musae* than fruit of the same physiological age from lowland plantations. Our results suggest that temperature sum accumulation rate is a critical factor affecting the susceptibility of bananas to the pathogen.

Additional keywords: postharvest disease, wound disease

Wound anthracnose and early ripening of fruit are serious problems that decrease the quality of export bananas (*Musa* AAA Cavendish) from the West Indies (16). Anthracnose is caused by the fungus *Colletotrichum musae*, which spreads from the floral parts and senescent bracts to contaminate fruit in plantations (9). Conidia reach the fruit surface in runoff rainwater on the banana bunch (8). They quickly germinate and form melanized appressoria, which are quiescent structures of the pathogen (28). These appressoria germinate during fruit maturation and form infection hyphae that colonize the peel and then penetrate into the fruit pulp (37). When fruits are wounded, rot develops long before the fruit ripens, and lesions expand quickly (26). This form of the disease, called wound anthracnose, can trigger early fruit ripening, sometimes seriously damaging fruit when it develops during container transport (29).

Early ripening of fruit can be due to physiological factors independent of post-harvest disease development. Banana is a

climacteric fruit, but must be harvested green and remain in a preclimacteric phase until reaching the ripening room, where it undergoes an ethylene treatment to induce ripening. Harvesting fruit too late will reduce the length of the preclimacteric phase, which is also called the green life (30). Moreover, harvesting physiologically old fruit can induce ripening of all boxed bananas in a container due to the triggering effect of ethylene release by such bananas on maturation (25).

These qualitative problems generally arise during the hot rainy season and especially affect fruit growing in lowland plantations. Previous studies revealed that bananas grown in lowland areas are more susceptible to wound anthracnose than those grown in highland zones (4). These susceptible bananas were from banana plants with high foliar Mn concentration, a feature that is typical of plants grown under stressful conditions, e.g., in poorly drained plots and/or under anoxic soil conditions (10). Moreover, such bananas produce more ethylene in response to wounding than highland-grown bananas, especially during the rainy season (3). In these studies, however, only commercial grade diameter bananas were harvested without consideration of their physiological age. This fruit grade-oriented harvesting method is adopted by most banana growers. However, basing a harvesting strategy solely on this criterion overlooks

the physiological age of the fruit, i.e., a development stage calculated as the temperature sum accumulated by the fruit (using 14°C as the base temperature). Ganry (13) showed that commercial grade bananas have accumulated approximately 900 degree-days (dd) under normal growth conditions in Guadeloupe (FWI). It has also been demonstrated that banana growth rates are dependent on growing conditions (6,21). For example, fruit growth rate differs according to the source-sink ratio. In addition, the flowering-to-harvest time and the temperature sum accumulated by the fruit can differ substantially between bananas of the same commercial grade. The physiological ages of bananas harvested at the same commercial grade can thus vary markedly. Hence, it is possible that the high anthracnose susceptibility of lowland bananas during the rainy season occurs when they are harvested at an older physiological age. Fruit from stressed banana plants could also be more susceptible to anthracnose due to the plant's physiological responses to adverse conditions, such as a slowdown in growth (21).

We examined the relationship between the physiological age of the fruit and the susceptibility to wound anthracnose induced by *C. musae*. Three experiments were conducted to analyze: (i) the effects of flooding, a stressful growing condition, on bananas harvested at the same physiological age, (ii) the effects on fruit quality of early harvesting of bananas from two distinctly different soil-climate zones, and (iii) the effects of modifying the source-sink ratio on bananas harvested at a constant commercial grade and physiological age.

MATERIALS AND METHODS

Plant material. All experiments were conducted in Guadeloupe (French West Indies: 16°N, 62°W) with *Musa acuminata* (AAA, cv. Grande Naine, Cavendish subgroup). Micropropagated banana plants in their first growth cycle were planted in a greenhouse to test for effects of flooding or in the field for the source-sink ratio test. For the test of age and susceptibility, banana plants grown in two locations were in their third growth cycle.

Experimental design. To test the effects of flooding on banana susceptibility to *C. musae*, 27 banana plants were grown in a greenhouse (30 m length, 8 m width, 6 m high, temperature between 25 and 31°C) in individual pots (1.2 m high, 1 m diame-

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ter) filled with 1 m³ of alluvial soil. The plants were fertilized weekly (17 g KNO₃ and 4 g urea per plant), and irrigation was controlled by measurement of the water status in the soil every day (water potential measured at 30 cm depth with tensiometers [SMS 2500 S (sensor) and SMS 2000 (tube)] and RedOx potential measured with RedOx probe [Eijkelkamp probe – Paltin International Inc. (USA)]). Nine replications of each of two stress treatments and one control treatment were placed arbitrarily in the greenhouse. In treatment 1 (9 banana plants), pot drainage was stopped at the flowering stage, about 6 months after planting, and watering was continued until soil saturation; soil water potential ranged from –2 kPa to 0 kPa, and RedOx potential was around –300 mV. In treatment 2 (9 banana plants), pot drainage was stopped 3 months after planting, and watering was continued until soil saturation as above; soil water potential ranged from –2 kPa to 0 kPa, and RedOx potential was around –300 mV. In the control (9 banana plants), irrigation was regulated so that the banana plants would not be under water deficit; the soil water potential ranged from –10 to –20 kPa, and the RedOx potential was above 200 mV. Bunches were harvested when the temperature sum reached 900 dd.

To test the effects of harvesting bananas at an early physiological age on susceptibility to *C. musae*, 20 banana plants at the flowering stage within each of two contrasting soil-climate conditions, named lowland plain zone (altitude: 50 m, halloysitic soil [11], mean daily temperature during experiment: 25.5°C [max: 29°C, min: 22°C]) and highland mountain zone (altitude: 700 m, soil classified as Umbric Andosol [11], mean daily temperature during experiment: 21.5°C [max: 25°C, min: 19°C]), were chosen on the basis of homogeneity in plant size and number of hands per bunch. The plants were separated ran-

domly into two groups based on a temperature sum of 700 dd during the flowering-to-harvest period (early harvest) and of 900 dd during the flowering-to-harvest period (standard harvest) (14). Thus, there were 10 plants for each treatment. This experiment was repeated three times, in May 2002, December 2003, and June 2004 (harvest date), with the same number of plants and the same number of repetitions.

The effects of the source-sink ratio on banana susceptibility to *C. musae* were tested on plants grown in the lowland zone (altitude: 30 m, soil classified as Ferral sol [11], mean daily temperature: 25.5°C [max: 29°C, min: 22°C]). Sixty homogeneous banana plants at the flowering stage were chosen for each replication of the experiment. These plants were divided arbitrarily into three treatments. The first one was a “High source-sink ratio treatment” (14 leaves and 2 hands per bunch). At the flowering stage, six of the eight hands on the bunches of 20 plants were trimmed so that only hands II and III (second and third hand from the top of the bunch) remained on the floral stalk. The second treatment was a “Low source-sink ratio treatment” (3 leaves, 8 hands on the bunch). At the flowering stage, 20 banana plants were severely defoliated so that only the three youngest leaves remained. The control was a “Normal source-sink ratio treatment” (14 leaves and 8 hands per bunch) without bunch trimming or defoliation performed on the final 20 banana plants. Two harvest techniques have been practiced in this experiment, the first one based on temperature sum (900 dd) and the second one on fruit diameter on the third hand reach (34 mm). Thus, there are 10 plants for each treatment. This experiment was repeated three times, in July 2002, January 2004, and October 2004 (harvest date).

Fruit inoculation. Suspensions of conidia (*Colletotrichum musae*/strain 46-12 from Guadeloupe [7], stored as frozen

conidial suspensions at –80°C in 30% glycerin) were prepared from 7- to 10-day-old cultures grown on modified Mathur’s medium (35). The cultures were maintained at 25°C in the dark. Conidia were recovered by washing the cultures with sterile distilled water. The conidial suspensions were filtered through a 10-µm sieve to eliminate mycelial fragments. In order to eliminate germination inhibitors contained in the conidial matrix (27), three successive 10-min washings were carried out by centrifugation at 4,000 rpm (JOUAN M 1400, Saint Nazaire, France).

At the flowering stage (horizontal finger stage), two bananas in hand III were inoculated according to the technique described by Chillet and de Lapeyre de Bellaire (2) with 25-µl droplet of a conidial suspension (10⁶ conidia per ml). Then, bunches were enclosed in blue plastic covers by the technique commonly implemented in commercial plantations to improve fruit growth by elevating temperature around the bunch and to limit damage caused by thrips (1).

Calculation of fruit age. Temperature probes (Tiny Tag Ultra - Gemini Data Loggers UK Ltd.) were placed under a meteorological shelter on the experimental plots and in the greenhouse. Mean daily temperature was calculated on the basis of hourly temperatures. The physiological age of the fruit (expressed in dd) was calculated by the mean daily temperature sums accumulated by fruit at the 14°C threshold during the flowering-to-harvest period (14).

Fruit harvest. Table 1 presents the harvest criteria considered for the different treatments in the three types of experiment. Bananas of hand III on each experimental bunch were separated at harvest.

Physiological characteristics of fruits. Fruit length and diameter were measured on a median finger in the outer row of hand III (18). The green life of bananas in each experimental hand was

Table 1. Locations, treatments, and design of the experiments conducted

Growth cycle	Location	Exp. ^z	Treatment	No. of plants per replicate	No. of replicates	Harvest criteria
1st	Greenhouse	1	Control	9	1	TS = 900 dd
			Flooding at flowering	9		TS = 900 dd
			Flooding after 3.5 months	9		TS = 900 dd
3rd	Changy (lowland)	2	Lowland early	10	3	TS = 700 dd
			Lowland standard	10		TS = 900 dd
	Matouba (highland)		Highland early	10		TS = 700 dd
			Highland standard	10		TS = 900 dd
1st	Douville	3	High So/Si, (TS)	10	3	TS = 900 dd
			High So/Si, (diameter)	10		Fruit diameter = 34 mm
			Low So/Si, (TS)	10		TS = 900 dd
			Low So/Si, (diameter)	10		Fruit diameter = 34 mm
			Control, (TS)	10		TS = 900 dd
			Control, (diameter)	10		Fruit diameter = 34 mm

^z Exp. 1: Effect of flooding on banana susceptibility to *Colletotrichum musae* / Banana plants in their first cycle of growth have been planted in a greenhouse in individuals pots / Harvest at 900 degree-days (dd). Exp. 2: Effect of harvesting bananas at an early physiological age on susceptibility to *C. musae* / Two harvest stages (700 and 900 dd) / Two locations (lowland and highland); Exp. 3: Effect of the source-sink ratio (So/Si) on banana susceptibility to *C. musae* / High So/Si corresponds to the treatment with 14 leaves functional and only 2 hands per bunch / Low So/Si corresponds to the treatment with 3 leaves and 8 hands per bunch / Control correspond to the treatment with 14 leaves and 8 hands per bunch / Harvest at 900 dd and when fruit diameter reaches 34 mm. TS = mean daily temperature sum at the 14°C threshold.

determined at 20°C using the method described by Chillet and de Lapeyre de Bellaire (2). This analysis was performed on a banana cut from the inner row of each hand, after a treatment with a postharvest fungicide (thiabendazole 500 ppm).

Characterization of fruit susceptibility to *C. musae*. Bananas inoculated at flowering were wounded at harvest using a TA-XT2 penetrometer (SMS) (bruising by calibrated compression of 15% of the fruit diameter) and stored at 13.5°C for 10 days to simulate maritime transport conditions, then stored for a further 10 days at 20°C to allow natural ripening.

The length (L) and width (w) of the necrotic tissue was measured after the storage period. The rotted area was then calculated by the ellipse area formula (Length × width × $\pi/4$). Thus, for each bunch, there are two measurements (because of 2 inoculated fruits). Data were averaged to obtain a single value per bunch.

Statistical analysis. Data were subjected to analysis of variance and means separated by the Newman-Keuls test (at the 5% probability level). These statistical analyses were performed for each separate experiment using the STAT-ITCF software package.

RESULTS

Effects of growing conditions on banana susceptibility to *C. musae*. Flooding at the flowering stage or at the vegetative stage had a very clear effect on fruit diameter and length (Table 2). At morphological stage 900 dd (70 days), the mean diameter of flooded bananas was 3 or 4 mm less than the control, a reduction of

10%. The mean difference between length of the control bananas and of the most stressed bananas ("Stress after 3.5 months") was 4.2 cm. Flooded conditions therefore caused an overall decrease in fruit length of about 30%.

Although flooding had a major impact on fruit morphology, it had no detectable effects on fruit susceptibility to *C. musae* or on the green life.

Effects of harvesting bananas at an early physiological age on susceptibility to *C. musae*. In both lowland and highland zones, harvesting bananas at an earlier physiological age (700 dd instead of 900 dd) reduced the susceptibility of bananas to *C. musae* and significantly increased their green life (Table 3), but there was a substantial concomitant decrease in fruit diameter in both zones and in finger length in the lowland zone in all experiments. These results also highlighted differences in the behavior of highland bananas as compared with those grown in lowland areas. At the same physiological age, fruit diameter and length were significantly greater in highland bananas. A highland banana that had accumulated 700 dd in 77 days of growth had almost the same diameter as a lowland banana that had accumulated 900 dd in 78 days of growth. Highland bananas also had significantly lower susceptibility to anthracnose compared with lowland bananas. Lowland bananas harvested at 900 dd were significantly more susceptible to *C. musae* than highland bananas harvested at 900 dd and lowland bananas harvested at 700 dd. These three groups were significantly more susceptible to

C. musae than highland banana harvested at 700 dd.

Effects of the source-sink ratio on banana susceptibility to *C. musae*. Modifying the source-sink ratio by bunch trimming and defoliation had a marked effect on banana diameter and length in the three replicates of the experiment (Table 4). At physiological age 900 dd, the mean diameter of bananas from the treatment where the bunch was trimmed and fruits harvest at 900 dd was 8.7 mm greater than that of bananas from the treatment where the plant was defoliated and the fruits harvested at 900 dd. Bananas from the defoliated treatment and fruits harvested at diameter 34 mm took 24 days longer and consequently had accumulated a supplementary 320 dd compared with bananas from the treatment where the bunch was trimmed and the fruits harvested at the same diameter.

Modifications in the source-sink ratio had a highly significant effect on fruit susceptibility to *C. musae* and on the green life of bananas when harvested at a constant diameter (34 mm). Bananas from the treatment (Low So/Si [diameter]) had a threefold greater rotted area in comparison with bananas from the treatment (High So/Si [diameter]). Moreover, when bananas were harvested at 900 dd irrespective of the diameter (31.1 to 39.8 mm), no significant differences were noted with respect to rotted area and green life (Table 4).

DISCUSSION

The first experiment revealed that flooding had a marked impact on fruit diameter and length at harvest. Soil flooding is known to have effects on plant physiology, such as a reduction in root respiration (33), stomatal closure (31), a reduction in photosynthetic activity (32), and development of chlorosis (22). Stress also led to an increase in foliar Mn levels of 700 ppm in leaves in the treatment "Stress after 3.5 months" and 244 ppm in control plant leaves when measured at the flowering stage (data not shown). This clearly confirmed the known phenomenon whereby Mn uptake is high in plants growing in waterlogged anoxic soil as Mn is chemically reduced (15) and highly assimilated (10,23).

Flooding stress of the root systems of plants is known to have an impact on the

Table 2. Effect of flooding on the morphological characteristics, green life, and anthracnose susceptibility of bananas

	FHP (days) ^y	Fruit diam. (mm)	Finger length (cm)	Green life (days)	Rotted area (mm ²)
Control	70	31.2 a ^z	18.0 a	35.0 ns	1,237 ns
Stress at flowering	70	27.0 b	15.2 b	34.9 ns	1,138 ns
Stress after 3.5 months	70	28.4 b	13.8 c	35.7 ns	1,391 ns
F value	-	10.70	45.54	0.17	0.43
Probability	-	<0.01	<0.01	0.85	0.66

^y FHP = flowering-to-harvest period.

^z Means followed by the same letter are not statistically different according to the Newman-Keuls test ($P = 0.05$). ns = not significant. Eighteen fruits (from the third hand of the 9 bunches) contribute to each mean value.

Table 3. Morphological, physiological characteristics and anthracnose susceptibility of lowland and highland bananas

	FHP (days) ^y	Temperature sum accumulation rate (dd/day)	Fruit diam. (mm)	Finger length (cm)	Rotted area (mm ²)	Green life (days)
Lowland 700 dd	58	12.1	27.9 c ^z	12.9 b	742.9 b	41.3 a
Lowland 900 dd	78	11.5	32.0 b	14.4 a	979.7 c	22.8 b
Highland 700 dd	77	9.1	32.3 b	15.9 a	333.8 a	41.4 a
Highland 900 dd	106	8.5	35.5 a	15.7 a	820.3 b	22.4 b
F value	-	-	57.33	11.54	16.62	226.13
Probability	-	-	<0.01	<0.01	<0.01	<0.01

^y FHP = flowering-to-harvest period.

^z Means followed by the same letter are not statistically different according to the Newman-Keuls test ($P = 0.05$). Twenty fruits (from the third hand of the 10 bunches) contribute to each mean value for each experiment. Data presented are combined from three experiments after testing for homogeneity of variance.

aboveground parts (34), especially fruit growth, for example in kiwifruit (36). This reduction in fruit diameter and length at harvest in bananas is the result of a decrease in the fruit pulp filling rate and in cell multiplication (20,21). Banana fingers from plants that have grown under anoxic soil conditions since the vegetative stage are shorter than those that have been subjected to anoxia from the flowering stage. Hence, stress can have a substantial impact on fruit size when it is applied at an early growth stage, especially during the cell division phase which begins a long time before the onset of flowering (24).

This marked effect on fruit morphology was not correlated with any physiological changes in susceptibility to *C. musae*. In addition, flooding of the soil had no effect on fruit green life. However a close relationship between the temperature sum accumulated by fruit during growth, its physiological age, and green life was observed. Regardless of their diameter, bananas were found to have the same green life when harvested at the same temperature sum.

Early harvesting of fruit, i.e., at physiological age 700 dd rather than 900 dd, reduced banana susceptibility to *C. musae* and increased the green life under the two soil-climate conditions tested. These experiments indicate that the physiological age of the fruit is a key factor in its susceptibility to *C. musae*. Our results, however, suggest that this is not the sole factor involved in this susceptibility, because at the same physiological age and thus the same green life, highland bananas were always significantly less susceptible than lowland bananas. It should be noted that temperature accumulation was faster in lowland zones than in the highlands. Our results showed that it took 106 days for highland bananas and 78 days for lowland bananas to accumulate 900 dd. Thus, the physiological development of lowland fruit was temporally faster. It is possible that accelerated development boosts its susceptibility to pathogens. For instance, bananas harvested in the greenhouse, which had also accumulated a 900 dd temperature

sum very quickly (mean 70 days), were found to be highly susceptible to wound anthracnose.

Our results suggest that the susceptibility of bananas to wound anthracnose is closely linked with their physiological age based on temperature sums. However, the temperature sum accumulation rate also seems to be involved. Under the same soil-climate conditions, we found that only the physiological age was involved since the temperature conditions were identical for all bananas. A comparison of the susceptibility of bananas from two separate zones, with different temperature conditions, indicated that the temperature sum accumulation rate (temperature sum/number of days) was also a key factor (around 12 dd/day in lowland and 8.7 dd/day in highland). In contrast, the green life seemed to be closely linked with the temperature sum. In lowland and highland areas, fruit harvest at a given physiological age resulted in the same fruit green life.

The effects of modifying the source-sink ratio on fruit morphology have already been studied through different degrees of bunch trimming, by shading the leaves to reduce photosynthesis, by defoliating plants or covering the bunches to increase fruit temperature (5,12,17,19,21). Our present results agree with these studies on fruit morphology, and are original concerning fruit susceptibility to postharvest disease. Modifying the source-sink ratio clearly confirmed that the physiological age of bananas is a crucial factor in their susceptibility to *C. musae*. At the same physiological age, bananas from the same plot but of completely different diameters were found to have the same susceptibility and green life. Conversely, at the same diameter, bananas from the same plot sometimes had very different susceptibility levels, varying by one- to threefold, when the physiological ages of the bananas differed. Bananas that had accumulated the highest temperature sum were always the most susceptible to anthracnose. These results clearly confirmed the dissociation between fruit diameter and physiological age, and that the temperature sum is a valid

indicator of the physiological development of bananas.

The results of the present experiments provide a partial explanation for common problems that are detrimental to the quality of bananas grown in lowland plantations during the rainy season, especially wound anthracnose and early ripening. Anoxic conditions can arise under such soil-climate conditions in conjunction with high rainfall and poor drainage. When this occurs, stressed banana plants undergo a slowdown in vegetative development, with a concomitant decline in the diameter growth rate of the fruit. The prevailing strategy is to harvest bananas once they have reached commercial diameter, irrespective of their physiological age. Then, such bananas have a short green life, an older physiological age, and are therefore highly susceptible to *C. musae*. These bananas are thus more susceptible to the development of wound anthracnose infection and to storage disorders associated with early ripening.

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Table 4. Effects of modifying the source-sink ratio on physiological characteristics of fruits

Treatment ^x	Harvest criteria ^y	Flowering-to-harvest period (days)	Physiological age (in dd)	Fruit diameter (mm)	Finger length (cm)	Green life (days)	Rotted area (mm ²)
FR	dd	73	898	39.8 a ^z	20.1 a	25.7 b	1,245 b
	FD	63	746	34.9 b	18.8 b	37.3 a	693 c
D	dd	73	898	31.1 c	14.6 d	22.7 b	1,557 b
	FD	87	1,066	34.0 b	15.7 cd	12.7 c	2,057 a
C	dd	73	898	34.9 b	17.3 c	25.6 b	1,286 b
	FD	72	887	34.5 b	17.0 c	24.0 b	1,313 b
F value	-	-	-	7.93	16.65	5.87	12.37
Probability	-	-	-	<0.01	<0.01	<0.01	<0.01

^x FR = fruit removal, D = defoliation, C = control.

^y dd = degree-days, FD = fruit diameter.

^z Means followed by the same letter are not statistically different according to the Newman-Keuls test ($P = 0.05$). Twenty fruits (from the third hand of the 10 bunches) contribute to each mean value for each experiment. Data presented are combined from three experiments after testing for homogeneity of variance.

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