Genetics of Apical Dominance in Plantain (*Musa* spp., AAB Group) and Improvement of Suckering Behavior

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Abstract. Apical dominance, i.e., the inhibition of lateral bud growth due to growth substances released by the terminal bud, has been considered as a limiting factor for the perennial productivity of plantains (*Musa* spp., AAB group). Segregation ratios in F₁ and F₂ plantain–banana hybrids suggest that inheritance of apical dominance is controlled by a major recessive gene, *ad*. The dominant *Ad* allele improved the suckering of plantain–banana hybrids, as measured by the height of the tallest sucker at flowering and harvest. At harvest, the ratoon crop of the diploid and tetraploid hybrids had completed 70% to 100% of its vegetative development, whereas the ratoon of the plantain parents, due to high apical dominance, was only at 50% of total pseudostem growth. Sucker growth rates are generally the result of gibberellic acid (GA₃) levels, and it is suggested that the *Ad* gene regulates GA₃ production. However, the *Ad* gene has incomplete penetrance, genetic specificity, and variable expressivity. Increased frequency of the *Ad* gene and a commensurate improvement in the suckering behavior of the diploid populations may be achieved by phenotypic recurrent selection.

Plantain and banana (*Musa* spp.) are important food crops in the humid forest and mid-altitude agroecologies of sub-Saharan Africa. They are high-yielding and form an integral component of the farming systems in these ecologies. In addition to being a staple food for rural and urban consumers, plantain and banana provide an important source of rural income. The crop is mainly produced by smallholders in compound or home gardens as well as in large fields (Swennen, 1990; Swennen and Vuylsteke, 1991).

Cultivated *Musa* are mostly triploids ($2n = 3x = 33$). Being almost completely sterile, they develop fruit by parthenocarpy. The most important cultivars vary in their genomic constitution and are generally classified as follows: dessert bananas (AAA), East African highland bananas (AAA), plantains (AAB), and starchy bananas. The genome of the cultivated types is derived from the diploid wild species *M. acuminata* Colla and *M. balbisiana* Colla, which contributed the A and B genomes, respectively (Simmonds, 1966). Different types are cultivated in distinct ecoregions. Thus, the AAB plantains are predominant in the humid lowlands of West and Central Africa, while AAA cooking and beer bananas prevail in the East African highlands (Vuylsteke et al., 1993a).

Pest and disease pressure on the crop has been increasing for the past 15 years. Major production constraints in sub-Saharan Africa are fungal diseases (black sigatoka leaf spot, *Fusarium* wilt), pests (banana weevil), nematodes, and the phenomenon of yield decline (mainly in plantains). Declining soil fertility also accounts for decreased yields.

Vigorous sucker growth is required for perennial productivity of plantains. A sucker is a lateral shoot produced from the underground stem (corm), which can form roots and become a separate individual plant. Sucker development consists of three distinct stages: peeper (young sucker bearing scale leaves only), sword

sucker (sucker bearing narrow sword leaves), and maiden sucker (large but nonfruiting ratoon with foliage leaves) (Simmonds, 1966; Swennen et al., 1984). These stages are influenced by growth substances produced by the “mother plant” (Swennen et al., 1984). The inability of plantains to produce tall and strong sword or maiden suckers during flower initiation of the mother plant is considered a major cause of the poor ratooning and the relatively short productive life span of the crop (Braide and Wilson, 1980). Conversely, well-developed suckers are often observed on banana (*Musa* spp., AAA group) plants (Barker and Steward, 1962).

Poor ratooning of plantains results from the strong apical dominance exhibited by the main plant and the competition between suckers (Swennen et al., 1984; Swennen and Wilson, 1983). Apical dominance is controlled by growth substances released by the terminal bud, which inhibit growth of lateral buds (De Langhe et al., 1983). Thus, sword suckers of plantains remain small until after flowering of the mother plant, because their demand sink for assimilates is too weak under the influence of apical dominance.

One of the main goals in plantain breeding is the development of cultivars with improved ratooning. At the International Institute of Tropical Agriculture (IITA), wild and cultivated bananas are used as a source of alleles to improve plantain ratooning. This paper describes the utilization of a wild non-edible banana to improve the suckering behavior of plantain and presents the genetic analysis of apical dominance in *Musa* spp.

Materials and Methods

The triploid plantain cultivars Obino l'Ewai (OL), Bobby Tannap (BT), and 'French Reversion' (FR); the improved diploid banana 'SH-3362' from the Fundacion Hondureña de Investigacion Agricola (FHIA, Honduras); and the parthenocarpic diploid banana 'Pisang lili' (PL) were used as females in crosses with the wild diploid bananas 'Calcutta 4' (C4) and 'Long Tavoy' (LT). 'Calcutta 4' has been considered a true-breeding line (Simmonds, 1952). The plantain parents have strong apical dominance, whereas the diploid bananas have no apical dominance. A diploid progeny without apical dominance, derived from the 'FR' x 'C4' cross, was

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selfed to produce the F_2 . 'Calcutta 4' was also selfed to produce a self-generation.

More than 1000 bunches of the female parents were pollinated with either 'C4' or 'LT'. Several hundred hybrid seeds were obtained and germinated by in vitro embryo culture (Vuylsteke et al., 1990). Seedlings were transferred to the nursery and sorted into putative ploidies based on their gross morphological characteristics (Simmonds, 1948). Chromosome counts using root-tips or pollen mother cells confirmed the ploidy level in a sample of these hybrids (K. V. Bai, IITA, personal communication). Diploid, triploid, and tetraploid progenies were then established in selection fields for preliminary evaluation (Vuylsteke et al., 1993b). Seedlings exhibiting grossly abnormal foliage typical of aneuploids, and hyperpolyploids were rogued.

At the High Rainfall Station of the International Institute of Tropical Agriculture at Onne (southeastern Nigeria), parents and segregating populations were evaluated for apical dominance, plant height, and height of tallest sucker at flowering and harvest. Hybrids were randomly distributed in the field. A maximum of four clonal plants were evaluated for each hybrid in the plant crop, i.e., the first production cycle. Plants were spaced at 3m x 2m and fertilized at a rate of 550 kg K_2O and 300 kg N/ha per year, split over six applications at six weekly intervals. For selection purposes, the plantain hybrids were compared with their plantain parents, which were planted at the same density in replicated plots.

Apical dominance was scored at plant crop flowering. Clones with high apical dominance showed inhibited sucker development, while clones with low apical dominance had one or two well-developed suckers (regulated suckering behavior) or many developing suckers (nonregulated suckering behavior). Plant height

(cm) and height of tallest sucker (cm) at flowering and harvest of the mother plant were recorded according to the method of Swennen and De Langhe (1985).

A chi-square test for goodness of fit was used to test the critical segregation ratio in the F_2 . Similarly, chi-square analysis was carried out to test whether the observed segregation ratios in the test crosses 'BT' x 'C4' and 'OL' x 'C4' were the result of lack of penetrance of the *Ad* gene or of residual heterozygosity at the *Ad* locus of 'C4'. The expected ratio of the cross *ad/ad/ad* x *Ad/ad* is 1:1 for individuals with apical dominance relative to those without apical dominance. Thus, the χ^2 test was used for testing the homogeneity of a binomial distribution with $p=0.5$ and $q=0.5$. For any sample of N size, the expected minimum number of individuals with apical dominance in the sample should be $Np - 2(Npq)^{1/2}$ at the 95% confidence level. A lack of significance suggests that the cross was not of the *ad/ad/ad* x *Ad/ad* type. The observed number of individuals in the smaller number class should be higher than the expected minimum from the binomial distribution when the assignment of genotypes is correct (Ortiz and Peloquin, 1991). Therefore, if the observed number of individuals with apical dominance is less than the expected minimum, the cross may be of the *ad/ad/ad* x *Ad/Ad* type, suggesting that there is incomplete penetrance of the *Ad* gene.

Nested ANOVAs (plants within clones within ploidy) were carried out to analyze plant height and height of tallest sucker at flowering and harvest of the mother plant. Total phenotypic variance was partitioned according to the following sources of variation: between crosses, between ploidy within crosses, between clones within ploidy within crosses, and within clones (environmental). The contribution to total phenotypic variation

Table 1. Segregation ratios for apical dominance in intraspecific AA x AA and interspecific-interploidy AAB x AA crosses of plantain and banana (*Musa* spp.).

Cross	Probable genotype of cross	Apical dominance		Expected ratio	Statistics
		Yes	No		
Calcutta 4 (C4) selfed	<i>Ad/Ad</i> x <i>Ad/Ad</i>	0	46	0:1	
AAcv ^z x AAw ^y					
Pisang lilin x C4	<i>Ad/Ad</i> x <i>Ad/Ad</i>	0	46	0:1	
SH-3362 x C4	<i>Ad/Ad</i> x <i>Ad/Ad</i>	0	42	0:1	
SH-3362 x Long Tavoy	<i>Ad/Ad</i> x <i>Ad/Ad</i>	0	18	0:1	
AAB ^x x AAw					
French Reversion x C4	<i>ad/ad/ad</i> x <i>Ad/Ad</i>				
F ₁ -2x		0	8	0:1	
F ₁ -3x		0	1	0:1	
F ₂ -2x	<i>Ad/ad</i> x <i>Ad/ad</i>	4	30	1:3	$\chi^2 = 3.18^{NS}$
Bobby Tannap x C4	<i>ad/ad/ad</i> x <i>Ad/Ad</i>				
2x		7 ^w	52	0:1	EM ^v = 21.82
3x		0	1	0:1	
4x		1 ^w	7	0:1	EM = 1.18
Obino l'Ewai x C4	<i>ad/ad/ad</i> x <i>Ad/Ad</i>				
2x		2 ^w	16	0:1	EM = 4.76
3x		0	1	0:1	
4x		3 ^w	12	0:1	EM = 3.62

^zCultivated 2x *M. acuminata*.

^yWild 2x *M. acuminata*.

^xCultivated 3x plantain.

^wHigh apical dominance at flowering but one sucker develops freely during fruit-filling time.

^vEM = expected minimum according to binomial distribution and assuming that the 2x parent is heterozygous. If *Ad* has incomplete penetrance, the EM should be higher than the observed value in a cross between a recessive homozygous and a dominant homozygous (Ortiz and Peloquin, 1991).

^{NS}Nonsignificant at $P = 0.05$.

was measured by the sum of squares of each source of variation. Mean comparisons were done using critical values of the Student's *t* distribution based on Sidak's multiplicative inequality (Sokal and Rohlf, 1981) at the significance level $P' = 1 - (1 - P)^{1/k}$, where *P* is the Type I error rate and *k* is the number of intended comparisons.

Results and Discussion

The segregation ratios for apical dominance in intraspecific crosses between diploid *M. acuminata* clones and interspecific crosses between triploid AAB plantains and diploid *M. acuminata* clones are presented in Table 1. All AA parents have uninhibited and nonregulated suckering behavior, and their progenies behave similarly, showing no apical dominance. This suggests that the gene(s) for nonapical dominance could be fixed in this AA gene pool.

The *F*₁ progenies obtained by crossing the AAB plantain 'French Reversion' with the AA wild banana 'Calcutta 4' did not show apical dominance. All progenies showed better suckering than their plantain parent. The *F*₂ segregated for apical dominance, with 30 *F*₂ progenies showing no apical dominance and 4 *F*₂ progenies exhibiting strong apical dominance (Table 1). This fits a ratio of 3 nonapical dominance : 1 apical dominance ($\chi^2 = 3.18^{NS}$, $0.10 < P < 0.05$), suggesting that apical dominance may be controlled by a major recessive gene in the *Ad* locus.

The tetraploid and diploid *F*₁ progenies obtained from crosses between the AAB plantains 'Bobby Tannap' and 'Obino l'Ewai' with 'Calcutta 4' segregated for apical dominance. The hypothesis that 'Calcutta 4' could be a heterozygous genotype for the *Ad* locus was rejected because the expected minimum values were higher than the observed numbers of diploids and tetraploids with apical dominance in both *F*₁ progenies (Table 1). The fact that the expected minimum was higher than the observed number in both crosses between two homozygous parents for the *Ad* locus (*ad/ad*/

ad × *Ad/Ad*) would indicate that the *Ad* gene exhibits incomplete penetrance, i.e., the frequency with which the dominant gene manifests itself in the phenotype of the carriers is lower than expected (Vogt, 1926). Moreover, penetrance depends both on genotype and environment. For example, penetrance was complete in progenies of the 'French Reversion' × 'Calcutta 4' cross and, thus, it did not affect the segregation ratio in its *F*₂.

The few plantain-derived hybrids with high apical dominance at flowering had one sucker that developed freely during the fruit-filling period, i.e., the time between flowering and harvest. It is important to note that there is no sink competition between ratoon and main pseudostem growth before plantain flowering. However, after flowering, competition occurs between the fructifying inflorescence, the preferential sink, and the ratoon (Swennen and De Langhe, 1985). An indication of the genetic specificity of the *Ad* allele is the suckering behavior of the plantain hybrids that exhibited a high apical dominance at flowering but had one sucker showing continuous development during the fruit-filling period.

The genetic regulation of the activity of the *Ad* gene probably involves selective transcription of different regions of the genome in response to stimuli, varying temporally and more or less permanently. According to Swennen et al. (1984), gibberellic acid (*GA*₃) is the single hormone that regulates the suckering mechanism in plantain and banana. They suggested that *GA*₃ is antagonistic to the inhibition factor (apical dominance). Swennen et al. (1984) also mentioned that sword sucker development of plantains responds to *GA*₃ flushes, which only stimulate peepers that are physiologically sensitive to *GA*₃ at the time of the flush. Our hypothesis is that the *Ad* gene controls the production of *GA*₃ in the suckers of the plantain-banana hybrids. Presence of the dominant allele results in improved ratooning of the hybrids as compared with their plantain parents.

The diploid and tetraploid hybrids had taller suckers than their plantain parents at harvest (Table 2). In the diploid hybrids, height of the tallest sucker at harvest of the plant crop was the same as the plant crop's height at flowering. At harvest of the tetraploid hybrids, their tallest sucker had completed almost 3/4 or more of the ratoon's vegetative development. Conversely, the plantains' suckers showed only 50% of total pseudostem growth due to strong apical dominance of the mother plant. Therefore, the plantain-banana hybrids had a shorter production cycle and faster sequences of generations than their plantain parents, which will eventually result in a higher yield potential per unit area and time.

The lack of significant differences between the diploid and tetraploid hybrids in both families indicates that ploidy itself does not affect height of the tallest sucker. However, pseudostems of tetraploid hybrids were taller than those of diploid hybrids (Table 2). Ortiz and Vuylsteke (1992) found that a single recessive *dw* gene controls dwarfism in plantain. These data indicate that gene action of the *Ad* alleles does not affect pseudostem height, suggesting that the *Ad* and *dw* genes are genetically independent. The former affects sucker development, which is measured as height of tallest sucker at harvest, whereas the latter influences plant height.

There were highly significant differences for height of tallest sucker at flowering ($P < 0.01$) and at harvest ($P < 0.01$) between clones within the same ploidy and the same cross. Variation between clones accounts for 68.1% and 72.6% of total phenotypic variation for height of tallest sucker at flowering and harvest, respectively. This provides evidence that the *Ad* gene has variable expressivity, i.e., the kind or degree of phenotypic expression exhibited by a penetrant gene varies (Vogt, 1926). The second most important component of total variation for height of tallest sucker was the variance within clones. This variance component

Table 2. Plant height and height of tallest sucker at harvest of the plant crop of plantain parents and their 2x and 4x plantain-banana (*Musa* spp.) hybrids, obtained from crosses with the wild banana 'Calcutta 4' (C4).

	Pseudostem ht (1)	Ht of tallest sucker (2)	Ratio (2:1)
Plantain parent/hybrid	(cm)		(%)
Bobby Tannap (<i>BT</i>)	340	171	50
BT x C4 2x (BT2x)	233	235	101
BT x C4 4x (BT4x)	281	249	89
Obino l'Ewai (<i>OL</i>)	370	188	51
OL x C4 2x (OL2x)	254	238	94
OL x C4 4x (OL4x)	336	243	72
<i>Comparisons^c</i>			
BT2x vs. BT4x	**	NS	
BT vs. BT4x	**	**	
BT vs. BT2x	**	**	
OL2x vs. OL4x	**	NS	
OL vs. OL4x	**	**	
OL vs. OL2x	**	**	
BT vs. OL	**	NS	
BT4x vs. OL4x	**	NS	
BT2x vs. OL2x	NS	NS	

^cMean comparisons using critical values of Student's *t* distribution based on Sidak's multiplicative inequality at the significance level $P' = 1 - (1 - P)^{1/k}$, where *P* is the Type I error rate and *k* is the number of intended comparisons.

NS,**Nonsignificant or significant at $P = 0.01$, respectively.

accounts for 24.2% and 25.5% of total phenotypic variation for height of tallest sucker at flowering and harvest, respectively. This suggests that the variable expressivity for height of tallest sucker depends on genotype (between clone variance) and environment (within clone variance).

In conclusion, apical dominance in plantain is genetically controlled by a major recessive *ad* gene. Most bananas have the alternative dominant allele, *Ad*, which improves the suckering behavior of the plantain–banana hybrids. The *Ad* allele has incomplete penetrance, genetic specificity, and variable expressivity, which affect the height of the tallest sucker at both flowering and harvest of the mother plant.

The frequency of the *Ad* allele can be increased in the diploid plantain–banana population by phenotypic recurrent selection. In fact, if the genotypic proportions *Ad/Ad* : *Ad/ad* : *ad/ad* are equal to p^2 : $2pq$: q^2 with fitness of 1:1:1-s and selection against *ad/ad* is complete, then only *Ad/Ad* and *Ad/ad* genotypes contribute to the next generation by p^2 and $2pq$, respectively. During the recurrent selection process, the *Ad* allele frequency will always increase. However, the rate of change in *Ad* allele frequency will decrease with subsequent selection cycles.

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