Inheritance of Dwarfiness and Erect Growth Habit in Progenies of *Jatropha curcas* × *Jatropha integerrima*

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ABSTRACT. *Jatropha* (*Jatropha curcas*) is one of the most popular tree crops for seed production as a source of oil for biodiesel. However, currently grown cultivars are too large in canopy size and thus have very low harvest index. Alteration of canopy height and size can lead to identification of a desirable plant architecture for jatropha. A study was conducted to determine genetic control of dwarfiness and erect growth habit in jatropha populations derived from an interspecific cross between *J. curcas* with tall-erect (TL-ER) plant type and *J. integerrima* with dwarf-spreading (DW-SP) plant type. Crosses were made between both species to develop F₁, F₂, BC₁F₁, and BC₁F₂ generations. The F₂ plants segregated at a 1:2:1 ratio for tall (TL), intermediate (ID), and dwarf (DW) plant types as well as for spreading (SP), upright (UP), and erect (ER) canopy angles. Both characters segregated independently producing nine phenotypes including TL-ER, TL-UP, TL-SP, ID-ER, ID-UP, ID-SP, DW-ER, DW-UP, and DW-SP at a 1:2:1:2:4:2:1:2:1 ratio. The BC₁F₁ (*J. curcas* × F₁) plant segregated into TL-ER, TL-UP, ID-ER, and ID-UP at a 1:1:1:1 expected ratio. Six BC₁F₂ lines were also evaluated to confirm the results by selfing two trees each of BC₁F₁ showing TL-ER, TL-UP, and ID-ER growth habits. The progenies of TL-ER trees were all TL-ER; the progenies of TL-UP trees segregated into TL-ER, TL-UP, and TL-SP at an expected 1:2:1 ratio, whereas the progenies of ID-ER trees segregated into TL-ER, ID-ER, and DW-ER at an expected 1:2:1 ratio. The results indicated that dwarfiness and erect growth habit were each controlled by independent genes with incomplete dominant action. The knowledge and progenies obtained from this study can be used in breeding jatropha for desirable canopy size and shape.

Jatropha curcas (jatropha, physic nut) is a shrub producing seeds with high oil for biodiesel production. The center of origin of jatropha is in the Central American region around Mexico. It was introduced to Africa and Asia and cultivated worldwide in the tropics and subtropics, largely on waste lands under harsh climatic conditions (Openshaw, 2000). Most of the current jatropha cultivars were obtained from naturally grown plants; thus, they are still wild and giving low seed yield with uneven fruit maturity. Progress in jatropha breeding is still limited, attributed mainly to its low genetic diversity (Tar et al., 2011). Germplasm improvement is initially the main pre-breeding work before an effective jatropha breeding program can be launched. Presently, most jatropha trees are medium-sized bushes with canopy height of 3 to 6 m and canopy diameter

of 2 to 4 m when fully grown. The farmers need to regularly prune them to reduce the plant size to ease fruit harvesting. Decreasing the canopy size to facilitate production and increase seed yield per unit area is an important objective to domesticate this shrub species.

Jatropha curcas has a shorter juvenility period (≈1 to 2 months shorter) in plants grown from stem cuttings than those grown from seedlings. Jatropha can flower 4 to 6 months after transplanting with profuse fruit set. The fruits mature 2 to 3 months after flowering and the seeds contain ≈35% to 45% oil content. *J. integerrima* (peregrina) is a strictly ornamental species bearing bright red flowers in inflorescences. The plants grown from cuttings can flower within 6 to 8 months with very few fruits set giving a similar seed oil content as *J. curcas*. *J. integerrima* seeds have ≈40% oil but the quality is inferior to jatropha oil as a result of lower oleic-linoleic acid ratio (Popluechai, 2010).

A number of scientists have reported inheritance of plant architecture such as basal branching type in guar [*Cyamopsis tetragonoloba* (Liu et al., 2006)], compact dwarf plant in pigeonpea [*Cajanus cajan* (Dhanasekar et al., 2007)], and pillar (columnar), compact, and dwarf plants in peach [*Prunus persica* (Hu and Scorza, 2009; Scorza et al., 2002)]. Plant height and columnar (canopy angle) in peach were each

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independently controlled by a single gene (Hu and Scorza, 2009). For *Jatropha*, there has been no report on inheritance of plant type, possibly as a result of low variability of this character available in its germplasm. However, genetic and phenotypic variability in *Jatropha* can be created, particularly through interspecific hybridization between *Jatropha* with a dwarf *J. integerrima*. Crossing between the two species can produce hybrid seeds (Dhillon et al., 2009; Muakrong et al., 2014; Parthiban et al., 2009; Sujatha and Prabakaran, 2003). Among these four reports, Muakrong et al. (2014) produced the hybrids for woody purpose, whereas Sujatha and Prabakaran (2003) produced ornamental hybrids. The other two articles reported the success in obtaining the interspecific hybrids without further pursuit.

In this study, we made interspecific crosses between tall-erect *J. curcas* and dwarf-spreading *J. integerrima* and obtained several F_1 , F_2 , BC_1F_1 , and BC_1F_2 plants. The progenies were observed on canopy height and canopy angle with the objective to determine the inheritance of these two traits.

Materials and Methods

PLANT MATERIALS. Hand pollination was made in 2008 between a tall-erect plant from *J. curcas* (Jc) collected from a naturally grown plant in Chai Nat province, Thailand, and a dwarf-spreading plant of *J. integerrima* (Jid). Hybrid seeds were obtained only when Jc was the female parent. Nine F_1 seedlings were sown but plant No. 4 set more seeds and thus was chosen for self-pollination and backcrossing to produce F_2 and BC_1F_1 (Jc $\times$ F_1) seeds for study on the inheritance of canopy height and shape. Two BC_1F_1 plants each of distinct plant types, viz. tall-erect, tall-upright, and intermediate-erect, were self-pollinated to obtain six BC_1F_2 families for confirmation of the F_2 and BC_1F_1 results. In each generation, seedlings were sown from seed and raised in a nursery until 3 months old before transplanting into a field of the Department of Agronomy, Kasetsart University, Kamphaeng Saen campus, Nakhon Pathom, Thailand.

Cuttings were also prepared from both parents and the F_1 plant No. 4 using branches of 1 to 2 cm diameter and cut into pieces 20 to 25 cm long. Each cutting was planted in a 15-cm diameter plastic bag filled with 1 kg commercial soil.

FIELD STUDY OF F_2 AND BC_1F_1 . Seedlings of 183 F_2 and 139 BC_1F_1 , together with 20 cuttings each of the parents and F_1 plant No. 4, were

transplanted to the field at a spacing of 1×1.5 m in May 2010. Each plant was fertilized with 50 g/plant of 15N–6.5P–12.5K twice, once at 4 months and another at 8 months after transplanting. At 1 year old, the plants naturally shed leaves so their plant architecture could easily be recorded (Fig. 1).

FIELD STUDY OF BC_1F_2 . To confirm the inheritance of growth habit, two BC_1F_2 lines from each distinct BC_1F_1 phenotype were evaluated. This included plants derived from two BC_1F_1 plants with tall-erect character, two with tall-upright, and two with intermediate-erect. The BC_1F_2 seedlings were transplanted into the field in Dec. 2011.

DATA COLLECTION. Plant architecture was evaluated 8 months after transplanting, when most leaves dropped off on approaching the dry season (Fig. 1). Plant height was measured

Fig. 1. Nine growth habits of 1-year-old F_2 plants from an interspecific cross between *Jatropha curcas* and dwarf *Jatropha integerrima* observed in dry season 2011, (A) tall-spreading, (B) tall-upright, (C) tall-erect, (D) intermediate-spreading, (E) intermediate-upright, (F) intermediate-erect, (G) dwarf-spreading, (H) dwarf-upright, and (I) dwarf-erect. The standing ruler in the picture is 3 m long.

from the ground to crown height by a meter ruler, whereas canopy shape was measured from degree of canopy angle by a giant protractor and presented following the equation of Thakur et al. (2010). A canopy angle is obtained from $\theta_1 + \theta_2$ where θ_1 and θ_2 are the angles of inclination of the widest position of canopy from the vertical orientation on both sides (Fig. 2). Each plant was measured once from north–south direction of the canopy and another time from east–west direction to determine an average canopy angle of that plant. Upright canopy angle is wider than the erect type but narrower than the spreading type.

STATISTICAL ANALYSIS. The differences between the parents and F_1 for canopy height and canopy angle were examined by F -test in an analysis of variance (ANOVA) performed in a completely randomized design with unequal replications. The goodness-of-fit in segregation ratio of the growth habits in each family as well as heterogeneity among families sharing the same expected ratio were tested by χ^2 (Russell, 1996). Both ANOVA and χ^2 were analyzed using the R freeware program (R Development Core Team, 2010).

Fig. 2. Measurement of canopy angle (degrees) in *Jatropha* plant as suggested by Thakur et al. (2010). θ_1 and θ_2 are the angles of inclination of the widest position of canopy from vertical orientation on both sides.

Table 1. Mean canopy height and degree of canopy angle in parents and F_1 hybrid from an interspecific cross between *Jatropha curcas* (Jc) and dwarf *Jatropha integerrima* (Jid).

Genotype	Canopy ht [mean $\pm$ SE (cm)]	Phenotype	Canopy angle [mean $\pm$ SE (degrees)]	Phenotype
Jc	273 $\pm$ 2.60 a ^z	Tall	68 $\pm$ 1.96 c	Erect
Jid	140 $\pm$ 1.62 c	Dwarf	170 $\pm$ 1.67 a	Spreading
F_1	215 $\pm$ 5.22 b	Intermediate	115 $\pm$ 1.29 b	Upright

^zMeans within a column followed by different letters are significantly different at $P \leq 0.01$ using Duncan’s multiple range test.

Results and Discussion

Canopy height and degree of canopy angle were different between the parents, whereas the F_1 plants exhibited intermediate canopy height and upright canopy angle (Table 1). The tall plant showed incomplete dominance to the dwarf plant, whereas spreading showed incomplete dominance to erectness. The number of plants showing different canopy height and degree of canopy angle in parents, F_1 , F_2 , and BC_1F_1 ($Jc \times F_1$) are given together with appropriate χ^2 tests (Table 2). The frequency distribution in different classes is also depicted in Figure 3. Canopy height in the F_2 population segregated as 55 TL:76 ID:52 DW, which fit with a 1:2:1 ratio at a χ^2 value of 5.35 ($P = 0.07$, $df = 2$). BC_1F_1 seeds were obtained only when Jc was the female parent pollinated by the F_1 and the progenies segregated as 63 TL:76 ID, which agreed to a 1:1 ratio with a χ^2 value of 1.22 ($P = 0.27$, $df = 1$). Degree of canopy angle among the F_2 plants showed 40 ER:93 UP:50 SP, which was acceptable at a 1:2:1 ratio with a χ^2 value of 1.14 ($P = 0.56$, $df = 2$). BC_1F_1 plants were 66 ER and 73 UP, which agreed with a 1:1 ratio at a χ^2 value of 0.35 ($P = 0.55$, $df = 1$).

Nine phenotypic combinations of plant height and growth habit in the F_2 population are depicted in Figure 1. The number in each class were 16 TL-SP:29 TL-UP:10 TL-ER:16 ID-SP:44 ID-UP:16 ID-ER:18 DW-SP:20 DW-UP:14 DW-ER, giving a χ^2 against a 1:2:1:2:4:2:1:2:1 ratio of 12.54 ($P = 0.13$, $df = 8$) (Table 3). In the BC_1F_1 population, the observed data were 32 TL-ER:31 TL-UP:34 ID-ER:42 ID-UP, which fit well with a 1:1:1:1 ratio at a χ^2 value of 2.15 ($P = 0.54$, $df = 3$). Both F_2

Table 2. Chi-square test for goodness-of-fit of segregation ratios in F_2 and BC_1F_1 populations from an interspecific cross between *Jatropha curcas* (Jc) and dwarf *Jatropha integerrima* (Jid).

Generations	No.	Canopy ht ^z			Expected ratio	χ^2	P
		TL	ID	DW			
P_1 (Jc)	20	20	0	0			
P_2 (Jid)	20	0	0	20			
F_1	20	0	20	0			
F_2	183	55	76	52	1:2:1	5.35	0.07
BC_1F_1 ($Jc \times F_1$)	139	63	76	0	1:1	1.22	0.27

Generations	No.	Canopy angle ^z			Expected ratio	χ^2	P
		ER	UP	SP			
P_1 (Jc)	20	20	0	0			
P_2 (Jid)	20	0	0	20			
F_1	20	0	20	0			
F_2	183	40	93	50	1:2:1	1.14	0.56
BC_1F_1 ($Jc \times F_1$)	139	66	73	0	1:1	0.35	0.55

^zTL = tall; ID = intermediate; DW = dwarf; ER = erect; UP = upright; SP = spreading.

and BC_1F_1 populations showed no association between canopy height and degree of canopy angle (Table 3).

The segregation pattern for plant types in BC_1F_2 families (Table 4) confirmed that the progenies of BC_1F_1 plants with tall-erect were all tall-erect, whereas the tall-upright plants gave BC_1F_2 progenies that fitted with a 1 TL-ER:2 TL-UP:1 TL-SP within individual families as well as pooled data. The segregation number also agreed across families, giving heterogeneity

Fig. 3. Frequency histograms of canopy height and degree of canopy angle in parents, F₁, F₂, and BC₁F₁ from an interspecific cross between *Jatropha curcas* (Jc) and dwarf *Jatropha integerrima* (Jid).

Table 3. Chi-square test for independent segregation between canopy height and canopy angle in F₂ and BC₁F₁ plants from an interspecific cross between *Jatropha curcas* (Jc) and dwarf *Jatropha integerrima* (Jid).

Generations	No.	Plant growth habits ^z									Expected ratio	χ^2	P
		TL-ER	TL-UP	TL-SP	ID-ER	ID-UP	ID-SP	DW-ER	DW-UP	DW-SP			
P ₁ (Jc)	20	20											
P ₂ (Jid)	20									20			
F ₁	20					20							
F ₂	183	10	29	16	16	44	16	14	20	18	1:2:1:2:4:2:1:2:1	12.54	0.13
BC ₁ F ₁ (F ₁ × Jc)	139	32	31		34	42					1:1:1:1	2.15	0.54

^zTL-ER = tall-erect; TL-UP = tall-upright; TL-SP = tall-spreading; ID-ER = intermediate-erect; ID-UP = intermediate-upright; ID-SP = intermediate-spreading; DW-ER = dwarf-erect; DW-UP = dwarf-upright; DW-SP = dwarf-spreading.

among families of 0.04 ($P = 0.98$). The BC₁F₂ families derived from two plants with ID-ER were TL-ER, ID-ER, and DW-ER, which fell into a 1:2:1 ratio without heterogeneity among families ($\chi^2 = 0.27$, $P = 0.88$).

The two gene loci for growth habits in jatropha are designated here as Dw_1/Dw_2 for canopy height and Er_1/Er_2 for degree of canopy angle. Each locus expresses incomplete dominant gene action and segregates independently. A suitable

Table 4. Chi-square test for independent segregation between canopy height and canopy angle in BC₁F₂ jatropha families.^z

BC ₁ F ₁ phenotype and plant no.	No.	BC ₁ F ₂ plant growth habit ^y					Expected ratio	χ^2	<i>P</i> (df = 2)	
		TL-ER	TL-UP	TL-SP	ID-ER	DW-ER				
TL-ER										
Plant #1	14	14								
Plant #2	12	12								
TL-UP										
Plant #1	25	4	14	7			1:2:1	1.08	0.58	
Plant #2	22	4	12	6			1:2:1	0.55	0.76	
Pooled	47	8	26	13			1:2:1	1.60	0.45	
Heterogeneity								0.04	0.98	
ID-ER										
Plant #1	33	9			18	6	1:2:1	0.82	0.66	
Plant #2	30	8			15	7	1:2:1	0.07	0.97	
Pooled	63	17			33	13	1:2:1	0.65	0.72	
Heterogeneity								0.27	0.88	

^zAgreement between families in each BC₁F₁ phenotype was tested by a χ^2 for heterogeneity.^yTL-ER = tall-erect; TL-UP = tall-upright; TL-SP = tall-spreading; ID-ER = intermediate-erect; DW-ER = dwarf-erect.

molecular marker analysis could reveal whether they are located on different chromosomes. Intermediate or semidwarf plant height has the heterozygous *Dw₁Dw₂* genotype, whereas upright canopy angle carries the heterozygous *Er₁Er₂* genotype. Our results are in line with those reported in peach by Gradziel and Beres (1993), Hu and Scorza (2009), and Scorza et al. (2002) that plant height and canopy angle were controlled by a single gene with an incomplete dominant action. This information is useful for jatropha breeding and genetic studies.

The F₂ plants from this interspecific cross comprise nine plant type combinations from the genotypes *Dw₁Dw₁Er₂Er₂* of Jc and *Dw₂Dw₂Er₁Er₁* of Jid. Some novel growth habits, especially dwarf-erect and dwarf-upright, can have a commercial value for jatropha production under high plant density, for machine harvesting, and for ornamental purposes. Tall-erect and tall-upright characters have a potential in breeding jatropha for high biomass (Muakrong et al., 2014). These novel plant types are being used in breeding jatropha for fuel and feed by Kasetsart University.

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