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Induction and Characterization of Mutations Related to Dwarf Habit in Hardy *Hibiscus* (*Muenchhusia* section)

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Abstract. **Hybrids between various species of *Hibiscus* in the *Muenchhusia* section are popular in commercial markets due to their colorful, floriferous blooms. However, many commercial cultivars are too vigorous for use in smaller garden spaces and often have only a few flowers in bloom. Stable, heritable mutants exhibiting dwarf stature and better branching architecture will be valuable to the commercial production of hardy *Hibiscus*. The goal of this project was to induce stable, heritable mutations using ethyl methanesulfonate that result in increased branching and a dwarf compact phenotype and introgress the compact phenotypes into lines of hardy *Hibiscus* to generate a series of diverse compact cultivars for use in commercial markets. Multiple mutations associated with dwarf, compact phenotypes were successfully induced. Hybridizations were made between M2 plants displaying a dwarf phenotype and hybrids developed through conventional breeding that do not possess the dwarf mutation in their background to develop diverse selections of dwarf plants. Inheritance patterns of the dwarf genes were determined through the segregation ratios of the dwarf phenotype in the F_1 and F_2 generations of these hybrids. Compared with wild-type progeny, dwarf progeny had shorter internode lengths and a greater number of primary branches.**

Although there are many cultivars of hardy *Hibiscus* (*Muenchhusia* section), there is the continual need for cultivars with improved growth habits and flowering characteristics (Kuligowska et al. 2016). Interspecific hybrids between various species of *Hibiscus* in the *Muenchhusia* section are prized for their numerous, large flowers, which have led them to commercial markets. However, hybrids are still too vigorous for use in smaller garden spaces. Dwarf mutants would allow for the use of cultivars in smaller or confined gardening spaces. Induced mutation provides an effective way of generating genetic variability in ornamentals, provided that the desired characteristics are possible within the genetic potential of a given species (Kuligowska et al. 2016; Schum 2003). Mutation breeding has proven to be a very effective tool for ornamental plant improvement (Schum 2003). Many of the traits that are economically important in ornamentals, such as novel flower color or patterning and plant growth habits, are phenotypes that are easily selected after treatment (Schum 2003). Because most cultivars of hardy *Hibiscus* are clonally propagated, a single mutant plant with desirable traits can represent a significant cultivar improvement effort. Several hormones are known to be associated with control of plant height, including gibberellic acids (GA), brassinosteriods (BR), auxins, and cytokinins (Fernandez et al. 2009; Werner et al. 2001). Although many hormones are associated with plant height, it has been shown that genes associated with auxins, GA, and BR have the most direct effects on plant height with the least adverse pleiotropic side effects on other traits (Cline 1991; Fernandez et al. 2009). Mutants defective in either GA or BR biosynthesis or signaling pathways display dwarf phenotypes (Fernandez et al. 2009). These dwarf phenotypes exhibited by mutants defective in GA or BR biosynthesis or signaling pathways could be used to develop more compact cultivars of hardy *Hibiscus* for use in more confined spaces. GAs are a large family of diterpene compounds that promote stem elongation (Fernandez et al. 2009). Mutants defective in GA biosynthesis or signaling pathways often exhibit decreased internode length (Fernandez et al. 2009). The BR family of plant hormones promotes plant growth through cell elongation (Fernandez et al. 2009). Mutants defective in BR biosynthesis or signaling pathways are typically characterized by short stems, reduced apical dominance, and male sterility (Yin et al. 2002). Cytokinins are a class of plant hormones that play a key role in plant morphogenesis. Cytokinin-deficient plants have been associated with stunted shoots and smaller apical meristems (Werner et al. 2001). Auxins are a family of plant hormones that suppress the generation of lateral shoots, and mutants defective in auxin biosynthesis or signaling pathways are characterized by a bushy phenotype with little to no presence of apical dominance (Cline 1991).

Ethyl methanesulfonate (EMS) is known to generate point mutations effectively in various species of plants (Stevens and Rick 1986). Chemical mutagens typically are less invasive than irradiation, which can cause chromosome disruption and fragmentation (Sleper and Poehlman 2006). The goal of this project was to induce stable, heritable mutations resulting in increased branching and a dwarf compact phenotype and introgress the compact phenotypes into lines of hardy *Hibiscus* to generate a series of diverse compact cultivars for use in commercial markets. EMS was chosen over irradiation for the induction of mutations because of its proficiency in inducing point mutations. Due to the importance of growth habits in this crop, the efficiency of mutation breeding in the improvement of ornamental plants, and the effectiveness of EMS as a mutagen, an experiment to induce mutations associated with hormone dwarfism and compact habit in hardy *Hibiscus* was conducted to improve this crop as an ornamental plant.

Materials and Methods

Determination of optimal EMS treatment rate for hardy Hibiscus hybrids. A rate study comparing the viability of hardy *Hibiscus* seeds treated with varying concentrations of EMS was conducted to determine the optimal concentration for EMS treatment of hardy *Hibiscus* seeds on a large scale. The effect on viability of the following concentrations of EMS diluted in distilled water (v/v) was examined: no treatment, 0%, 0.12%, 0.25%, 0.37%, 0.5%, and 1.0% EMS. Seeds were treated for 24 h at room temperature. The half-life of EMS is 93 h at 20 °C and 26 h at 30 °C (Kodym and Afza 2003). The treatment duration was shorter than the half-life of the mutagenic agent, therefore no buffering agent was used. Twenty self-pollinated seeds of the inbred cultivar *H. moscheutos* Honey Moon White w/ Eye were collected. Forty-eight seeds were randomly chosen and assigned to each of the seven treatment groups. Before EMS treatment, all seeds were scarified by treatment with 99% H_2SO_4 for 15 min and then treated with their respective concentrations of EMS. After soaking in the EMS concentration for 24 h, seeds were removed from the solution and washed three times with distilled water sown in 48-cell trays and placed on a mist bench (misting for 5 s every 5 min) to germinate. Seeds were allowed to germinate on the mist bench for 1 week, after which they were moved to the greenhouse, and germination was evaluated.

Plant material for mutation induction. The group of seeds treated with EMS consisted of various families of hardy *Hibiscus* hybrid seeds generated for evaluation in 2019 through the hybridization of popular commercial cultivars. Seeds from inbred lines were unavailable, so

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high-vigor hybrid seeds were used instead. The pedigrees of the hybrid seed families used in this treatment group are shown in Table 1.

Seed scarification and germination of treatment group. All seeds of hardy *Hibiscus* were scarified by treatment with H_2SO_4 for 15 min based on previously established successful methods (Barrios and Ruter 2019; Sakhanokho 2009). After treatment, seeds were washed three times with DIH_2O, sown in 40-cell flats, and placed in a greenhouse to germinate. Seeds were misted four times per day for 1 week to assist germination.

Induction of mutations and identification of individuals carrying dwarfism-associated alleles. All seeds were scarified and then treated with a solution of 0.5% EMS for 24 h. After the seeds were removed from the EMS solution, they were washed three times with DIH_2O, sown in 40-cell trays and placed on a mist bench (misting for 5 s every 5 min) to germinate. Seeds were allowed to germinate on the mist bench for 1 week then moved to the greenhouse, where germination was evaluated. Forty seeds from each family treated were soaked in 0% EMS as a control for germination percentage and identification of mutants based on phenotypic differences. M2 seed, the second generation following mutagenic treatment, was generated through the self-pollination of M1 *Hibiscus* to isolate recessive mutants. These M2 progenies were grown out under greenhouse conditions and evaluated for height, internode length, and number of primary branches. Data on internode length, height, and the number of primary branches were taken while these plants were growing in 4.5-inch pots.

Data collection. Throughout various stages of this research, plants were assessed for height, internode length, and the number of primary branches. Height was measured in centimeters from the base of the plant to the highest point of the plant. Internode length was measured in centimeters by selecting and measuring three internodes best representative of the plant at least five nodes down from the meristem of the selected branch. The three internode lengths were then averaged. Primary branches were defined as the number of branches stemming from the base or primary stem of a plant.

Hybridization of Hibiscus. Plants designated for hybridization were forced into flowering using nighttime interruption with incandescent lights for 1 hour at midnight each night. Plants designated as maternal parents were emasculated in the early morning before anthesis at ~7:00 AM each day. At ~9:00 AM each day, crosses were made by applying pollen from paternal plants onto the stigmas of the emasculated flowers using a Q-tip. When self-pollination was required, plants were not emasculated; instead, they were self-pollinated by applying pollen from the anthers to the stigmas of the same flower.

Introgression of dwarfism-associated alleles to elite breeding lines of hardy Hibiscus. Four superior dwarf selections from the mutant group (MA20-34-7, MA20-42-13, MA20-42-25, and MA20-107-4) were reciprocally crossed to 21 plants present in a hardy *Hibiscus* hybrid breeding block. Thirty-nine F_1 families were generated through these crosses. It was assumed that selection for the mutant allele would be made in the F_2 generation if the allele was recessive. Therefore, eight plants of each of the F_1 families were grown in a greenhouse. Three self-pollinations were made on each of the plants, and these self-pollinated seeds were collected. In total, 225 F_2 families were generated, and seeds from the 225 F_2 families were germinated. Eighteen seedlings of each family were planted in the field at the University of Florida Plant Science Research and Education Unit in Citra, FL, USA (lat. 29.40836659543007°N, long. –82.17175527248554°W) where sufficient plant numbers were available. Data were taken for the segregation ratios of these F_2 families.

Assessment of the effect of the qualitatively inherited mutant gene on branching parameters. After determining that MA20-34-7 possessed a desirable recessive mutation for increased branching, data were taken on six families possessing MA20-34-7 with differing hybrid selections in their backgrounds to quantify the effect of the mutation. The variables measured were height from the base of the plant, number of primary branches, defined as the number of branches stemming from the base of the plant and primary stem, and internode length.

Data analysis. Data analysis was performed in SAS software (SAS version 9.4; SAS Institute Inc., Cary, NC, USA). Calculation of means, standard errors, and mean separations were analyzed using the PROC GLM function of the program. Significant differences between means of the variables measured were identified using *t* tests.

Results and Discussion

Determination of optimal EMS treatment concentration for hardy Hibiscus hybrids. Before the treatment of a large number of seeds, a dose–response study using inbred seeds was conducted to determine EMS concentration that had sufficient effects on the genome of *Hibiscus* to generate noticeable mutations but were not lethal. Consequently, a 0.5% EMS solution was chosen for treatment because it was a sufficient EMS concentration to induce mutations, and the germination percentage at that concentration was still greater than 50%.

Induction of mutations and identification of individuals carrying dwarfism-associated alleles. The group of seeds treated with EMS consisted of various families of hardy *Hibiscus* hybrid seeds generated for evaluation through the hybridization of popular commercial cultivars. The pedigrees of the hybrid seed families used in this treatment group and their germination percentages are shown in Table 1.

A total of 2278 seeds from 20 families were treated, with 265 of the treated seeds germinating. Germination percentages for this treatment group were dramatically lower than

Table 1. The pedigrees of the hybrid hardy *Hibiscus* seed and family germination percentages when treated with 0.5% ethyl methanesulfonate (EMS) for 24 h compared with the 0% EMS control.

Family	Maternal parent	Paternal parent	0.5% EMS treatment germination (%)	Control germination (%)
MA-19-1	*H. moscheutos* 'Honey Moon White w/ Eye'	*H. moscheutos* 'Honey Moon White w/ Eye'	0.00	67.50
MA-19-3	*H. moscheutos* 'Honey Moon White w/ Eye'	*H. moscheutos* 'Honey Moon Deep Red'	0.63	33.33
MA-19-5	*H. moscheutos* 'Honey Moon White w/ Eye'	*H. hybrida* 'Summer Spice Cordon Bleu'	0.00	87.50
MA-19-10	*H. moscheutos* 'Honey Moon White w/ Eye'	Open pollination	1.88	75.00
MA-19-11	*H. moscheutos* 'Honey Moon Light Rose'	*H. moscheutos* 'Honey Moon Deep Red'	0.00	50.00
MA-19-17	*H. moscheutos* 'Honey Moon Light Rose'	Open pollination	1.36	40.00
MA-19-19	*H. moscheutos* 'Honey Moon Deep Red'	*H. moscheutos* 'Honey Moon Light Rose'	70.63	85.00
MA-19-25	*H. moscheutos* 'Honey Moon Rose'	*H. moscheutos* 'Honey Moon White w/ Eye'	1.25	72.50
MA-19-26	*H. moscheutos* 'Honey Moon Rose'	*H. moscheutos* 'Honey Moon Light Rose'	0.00	15.00
MA-19-27	*H. moscheutos* 'Honey Moon Rose'	*H. moscheutos* 'Honey Moon Deep Red'	22.50	0.00
MA-19-28	*H. moscheutos* 'Honey Moon Rose'	*H. moscheutos* 'Honey Moon Rose'	0.00	2.50
MA-19-29	*H. moscheutos* 'Honey Moon Rose'	*H. hybrida* 'Summer Spice Cordon Bleu'	3.13	57.50
MA-19-30	*H. moscheutos* 'Honey Moon Rose'	*H. hybrida* 'Summer Spice Amaretto'	25.63	7.50
MA-19-34	*H. moscheutos* 'Honey Moon Rose'	Open pollination	0.00	52.50
MA-19-40	*H. hybrida* 'Summer Spice Amaretto'	*H. moscheutos* 'Honey Moon Deep Red'	38.75	72.50
MA-19-43	*H. hybrida* 'Summer Spice Amaretto'	*H. hybrida* 'Summer Spice Amaretto'	0.00	50.00
MA-19-48	*H. hybrida* 'Summer Spice Brady Bleu'	*H. moscheutos* 'Honey Moon Light Rose'	0.00	90.00
MA-19-50	*H. hybrida* 'Summer Spice Brady Bleu'	*H. moscheutos* 'Honey Moon Rose'	0.00	7.50
MA-19-53	*H. hybrida* 'Summer Spice Brady Bleu'	*H. hybrida* 'Summer Spice Brady Bleu'	19.38	67.50
MA-19-55	*H. grandiflorus*	*H. grandiflorus*	0.00	35.00

was expected from the treatment rate study (Table 1). These decreased germination rates could be due to the hybrid nature of the seeds compared with the seeds from the inbred lines used in the rate study. It was noted that families with *H. moscheutos* 'Honey Moon Deep Red' in their pedigree tended to have higher germination percentages when treated; however, a controlled experiment is required for accurate assessment of the effect of genotype on germination percentage in response to EMS treatment. M1 seedlings were allowed to grow out in a greenhouse for 8 weeks and then were planted in the field in Citra, FL, USA. Putative mutants were then selected from the remaining plants, clonally propagated, and brought back to the greenhouse, where they were self-pollinated to generate M2 seed. No dwarf plants were present in this M1 generation of treated seed. This result was anticipated because mutations generated with EMS treatment tend to be recessive, and the probability of phenotypic mutants in the M1 generation is extremely low (Arisha et al. 2015; Roychowdhury and Tah 2013). Ultimately, 114 unique M2 families were generated through self-pollination of these M1 plants.

A total of 2443 M2 plants from 114 families were evaluated in the greenhouse throughout the summer. Data were taken on 2-month-old plants for plant height, internode length, and the number of primary branches. Plant height ranged from 0.7 to 37.5 cm, with an average plant height of 19.6 cm. Internode length ranged from 0.2 to 11.3 cm, with an average internode length of 1.5 cm. The number of primary branches ranged from 1 to 9, with an average number of primary branches being 2.6 (data not shown).

When evaluating M2 plants for branching at this relatively juvenile stage, the data points assessed were efficient in predicting plants that would end up exhibiting a dwarf phenotype when grown out to maturity at 3 months. The most efficient data point for identifying dwarf hardy *Hibiscus* at this young plant stage was the number of primary branches (Fig. 1). Internode length was an inappropriate parameter to measure at this growth stage due to significant variability in internode length at the young plant stage (data not shown). Plant height was also inappropriate because the shortest plants tended to be weak plants that were not well-branched. Initially, 75 M2 plants were selected based on the number of primary branches, and branching quality was assessed visually in the greenhouse. These 75 selections were potted into 1-gallon pots and further evaluated in the greenhouse. Ultimately, these 75 selections were narrowed down to four final M2 plants. All four selections had the most primary branches of all the M2 plants evaluated. These selections were used to cross reciprocally to plants in a hardy *Hibiscus* breeding block to introgress the dwarf genes into elite breeding lines of UF hardy *Hibiscus*.

Introgression of dwarfism-associated alleles to elite breeding lines of hardy Hibiscus. The four superior dwarf selections (MA20-34-7, MA20-42-13, MA20-42-25, and MA20-107-4) were reciprocally crossed to 21 elite plants that were developed through conventional breeding efforts to generate a hardy *Hibiscus* hybrid population. All the M2 selections were used as both maternal and paternal parents in the generation of these hybrids, with the exception of MA20-34-7, which made nonviable pollen. Thirty-nine F_1 families were generated through these crosses. Eight plants of each of the F_1 families were grown in a greenhouse for 4 months. No phenotypic dwarf mutants were observed in this F_1 generation. Three self-pollinations were made on each of the plants, and seeds were collected and combined for each plant. In total, 225 F_2 families were generated.

Seeds from the 225 F_2 families were germinated. Eighteen seedlings of each family were planted in the field in Citra, FL, USA. These plants were grown in the field to assess branching habit and to identify dwarf plants. Dwarf plants were easily identified by their compact structure and noticeable lack of apical dominance (Fig. 2). It was expected that families would segregate in a 3:1 nondwarf-to-dwarf ratio because the mutations generated were expected to be single gene recessive in nature.

All 64 families with MA20-107-4 in their background did not produce any dwarf individuals. As a result, it is believed that the desirable branching characteristics exhibited by MA20-107-4 were due to quantitatively inherited branching genes as opposed to an induced dwarf gene, which would have been inherited qualitatively in nature. Families with MA20-42-25 in their background segregated in a 1396:72 wildtype-to-dwarf ratio. A chi-square test comparing this observed segregation ratio to the expected 3:1 wildtype-to-dwarf ratio yielded a χ^2 of 316.167 12 (1, N = 1468, $P = 0.05$) allowing us to reject the hypothesis that families with MA20-42-25 in their background would segregate in a 3:1 ratio as expected. If the phenotype observed was the result of two recessive alleles, a 15:1 segregation ratio would be expected (Sleper and Poehlman 2006). When comparing the segregation ratio to a 15:1 nondwarf to dwarf ratio, the chi-square test yielded a value of 4.64 (1, N = 1468, $P = 0.05$), allowing us to reject the hypothesis that families with MA20-42-25 in their background segregate at a 15:1 ratio. Families with MA20-42-13 in their background did not segregate in the expected 3:1 ratio either. These families were segregated in a 491:44 wildtype-to-dwarf ratio. A chi-square test comparing this observed segregation ratio to the expected 3:1 wild-type to dwarf ratio yielded a χ^2 of 80.3 12 (1, N = 535, $P = 0.05$), allowing us to reject the hypothesis that families with MA20-42-13 in their background would segregate in a 3:1 ratio as expected. Likewise, when comparing the segregation ratio to a 15:1 wildtype to dwarf ratio, the chi-square test yielded a value of 3.9 (1, N = 535, $P = 0.05$), allowing us to reject the hypothesis that families with MA20-42-13 in their background segregate at a 15:1 ratio.

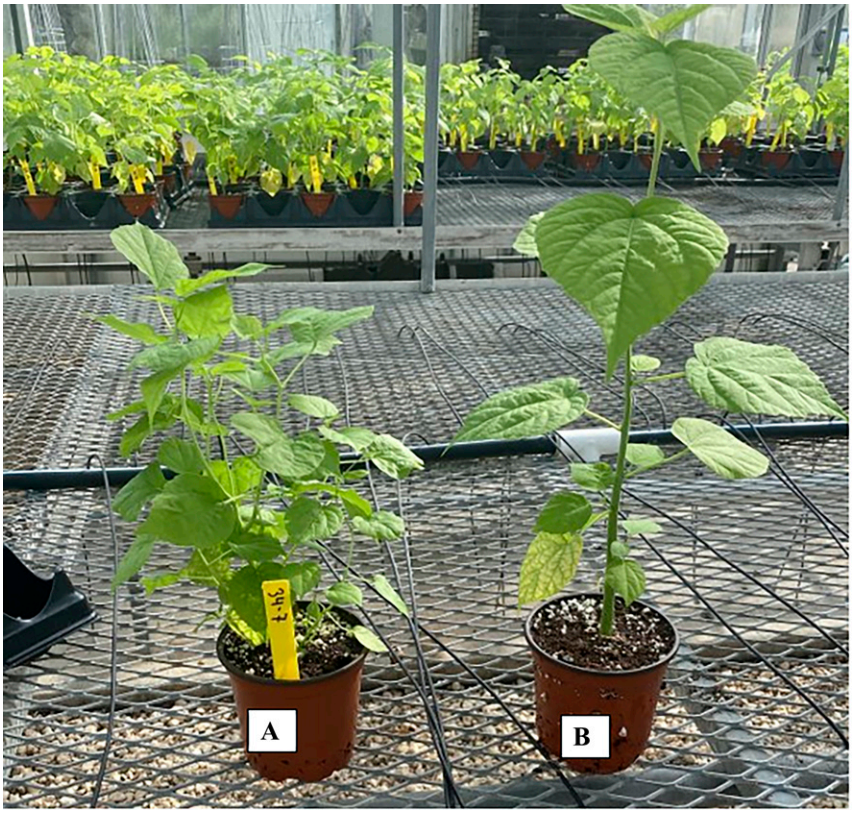

Fig. 1. Two M2 siblings with identical pedigrees segregating for different numbers of primary branches. Plant A possesses nine primary branches and a notably better branching habit compared with plant B with only one primary branch.

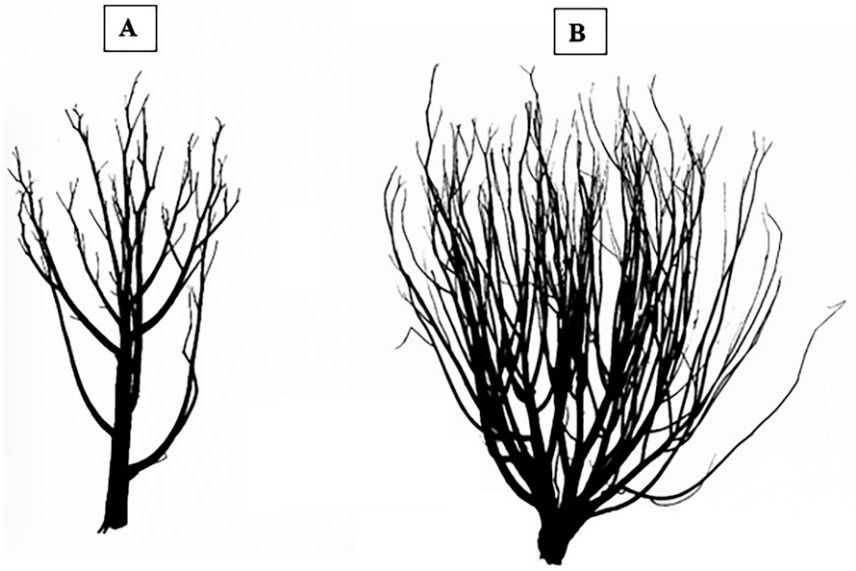

Fig. 2. Scanned images of two siblings from the same F2 family, where mutant genes from MA20-34-7 were introgressed into elite lines of hardy *Hibiscus*. Both of these plants contain MA20-34-7 in their background; however, they are segregating for the dwarfism-associated mutation. Plant B on the right is homozygous for the recessive mutation.

MA20-34-7 was determined to possess the most desirable qualitatively inherited dwarfism-associated gene. In total, M2 families with MA20-34-7 in their backgrounds segregated in a 996:336 wildtype-to-dwarf ratio. A chi-square test comparing this observed segregation ratio to the expected 3:1 nondwarf-to-dwarf ratio yielded a χ^2 of 2.12 (1, N = 1359, $P = 0.05$), suggesting that we cannot reject the null hypothesis that families with MA20-34-7 in their background segregated in a 3:1 ratio for the dwarfism-associated allele. A photo of two plants from the same family containing MA20-34-7 in their background segregating for the dwarfism mutation is shown in Fig. 2.

Effect of a qualitatively inherited mutant dwarf gene on branching parameters. To assess the effect of the mutant dwarf gene induced in MA20-34-7 on parameters that influence branching, the internode length, plant height, and number of primary branches were evaluated on five F2 families that possessed MA20-34-7 in their pedigree but had differing lineages otherwise. Internode length, plant height, and the number of primary branches were all observed to be significantly different between dwarf and wildtype plants. On average, wildtype plants were 55 cm tall, whereas dwarf plants were 41.6 cm tall (Table 2). Dwarf plants had an average internode length of 3.18 cm, whereas wildtype plants had an average of 3.59 cm (Table 2). The most pronounced parameter assessed between dwarf and wildtype plants was the number of primary branches. Wildtype plants had 11.3 primary branches on average, whereas dwarf plants had an average of 27.1 primary branches (Table 2). Significant differences between dwarf and wildtype plants for internode length suggest a decrease in plant cell elongation in these dwarfs, whereas an increase in primary branches suggests a decrease in apical control and apical dominance.

In summary, multiple mutations associated with dwarf, well-branched phenotypes were successfully induced in *Hibiscus* using EMS. This was the first report of dwarf mutants within the Muenchhusia section of *Hibiscus*. These mutations were heritable through successful hybridization with clones of interspecific hybrid hardy *Hibiscus*. Through segregation ratios of the dwarf phenotype in the M1 and M2 generations of hybrids between the initial M2 dwarf plants and plants that do not possess the dwarf mutation in their background, inheritance patterns of the dwarf genes were determined. The dwarf phenotype identified in MA20-34-7 was controlled by a single recessive gene and displayed a qualitative inheritance pattern. The inheritance pattern of the dwarf phenotype identified in MA20-42-13 and MA20-42-25 could not be identified. Due to the single recessive gene inheritance pattern displayed for dwarf habit by the progeny of MA20-34-7, this parent was determined to be the most ideal for breeding purposes as a greater number of dwarf progeny would be present in F_2 segregating populations for selection.

Table 2. Mean height (cm), internode length (cm), and numbers of primary branches between dwarf and wildtype plants with MA20-34-7 in their background.

Habit	Ht (cm)	Internode length (cm)	Primary branches
Wild-type	55.0 ± 0.81 a[1]	3.59 ± 0.06 a	11.3 ± 0.45 b
Dwarf	41.6 ± 1.24 b	3.18 ± 0.09 b	27.1 ± 0.68 a

[1] Any two means not followed by the same letter are significantly different at $\alpha \leq 0.05$.

Dwarf mutants recovered from EMS treatment were expected to have shorter internode length compared with their siblings not displaying the dwarf phenotype. Although a significantly shorter internode length was displayed between dwarf and wildtype progeny of MA20-34-7, this difference was slight. Plants exhibiting the dwarf phenotype associated with this mutation had a significantly greater number of primary branches as well.

Mutants defective in BR biosynthesis or signaling pathways are characterized by short stems due to decreased cell elongation, reduced apical dominance, and male sterility (Yin et al. 2002). The production of nonviable pollen by MA20-34-7 suggests the possibility that the dwarf phenotype exhibited by MA20-34-7 is related to the biosynthesis or signaling of BR because mutants deficient in BR biosynthesis or signaling pathways, have been associated with male sterility (Yin et al. 2002). Although the phenotypes of decreased internode length and reduced apical dominance exhibited by MA20-34-7 and its dwarf progeny suggest that the mutation induced and identified in this plant could likely be associated with the biosynthesis or signaling of BR or auxin. Further experiments to analyze BR and auxin synthesis and signaling in this mutant and its progeny are warranted to determine whether hormone-related pathways are affected by this mutation.

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