Phenotype, Inheritance, and Regulation of Expression of a New Virescent Mutant in Watermelon: Juvenile Albino

X.P. Zhang, B.B. Rhodes, and W.V. Baird

Department of Horticulture, Clemson University, Clemson, SC 29634

H.T. Skorupska

Department of Agronomy and Soils and Department of Biological Sciences, Clemson University, Clemson, SC 29634

W.C. Bridges

Department of Experimental Statistics, Clemson University, Clemson, SC 29634

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Abstract. Juvenile albino, gene symbol *ja*, is a spontaneous virescent mutant, first observed in 'Dixielee' and an F₂ population of 'G17AB' (*msms*) x 'Dixielee' in 1992. Hypocotyls, new young leaves, shoot tips, tendrils and flowers on the main shoot of the *ja* mutant are all albino during early spring. The interior portions of albino leaves gradually become green, while the margins remain albino. Fruit rind color of the mutant is variegated. Growth of the *ja* mutant is severely impaired in the early spring. However, the mutant grows at a rate comparable to wild-type in the summer, and produces fruit of almost normal size. Genetic analysis of F₁, F₂, and BC₁ populations derived from the *ja* mutant showed that the gene for the *ja* mutant is inherited as a single, recessive, nuclear gene. Segregation ratios in the F₂ and BC₁ progenies derived from the cross between the previously reported delayed green virescent mutant and the *ja* mutant indicate independent inheritance of the genes *dg* and *ja*. Temperature and red/far-red light had no differential effect on mutant and the wild-type plants. An increase of daylength from 8 to 15 hours increased fresh weight and chlorophyll content more in the *ja* mutant than in the wild-type. The mutant had a higher chlorophyll a : b ratio than the wild-type under long days. Chlorophyll synthesis or accumulation in the mutant is severely impaired under short days. This is the only virescent mutant in the family *Cucurbitaceae* whose expression is regulated by daylength.

A virescent mutant is a pigment-deficient mutant in which deficiencies or alterations in the photosynthetic apparatus may be modified by environmental factors (Hopkins et al., 1980). Virescent mutants are useful for studying photosynthesis (Somerville, 1986), interactions between nuclear and plastid genomes (Taylor, 1989; Wetzel et al., 1994), gene flow in experimental populations (Handel, 1982), and for developing linkage maps (McCreight and Bohn, 1979; Whelan et al., 1975; Zink, 1977). Also, virescent mutants can be used as seedling markers for hybrid seed production and backcross breeding without hand-pollination (Nugent and Hoffman, 1981; Nugent, 1994; Zhang et al., 1996).

Four spontaneous chlorophyll-deficient mutants have been described in watermelon (Provvidenti, 1994; Rhodes, 1986; Rhodes and Zhang, 1995; Robinson et al., 1976). Delayed-green (*dg*) (Rhodes, 1986), is characterized by pale-green cotyledons and new leaves that turn green as development progresses. The *dg* mutation is inherited as a single recessive gene, *dg* (Zhang et al., 1996). *Spotted* mutation, inherited as a single dominant gene, *Sp*, results in yellow spots on cotyledons, leaves and fruit (Rhodes, 1986). *Yellow* (*Yl*), an incompletely dominant gene, produces yellow leaves with reduced chlorophyll content (Warid and Abd-El-Hafez, 1976). *Seedling leaf variegation* (*slv*), a single recessive gene, causes whitish-green cotyledons and mosaic-like variegated leaves at the seedling stage under low temperature (<20 °C). This

type of chlorophyll deficiency at low temperature is common in cultivated watermelons (Provvidenti, 1994).

In 1992, we observed a new virescent mutant, juvenile albino (*ja*) in two populations, the self-pollinated 'Dixielee' and an F₂ population of 'G17AB' (*msms*) x 'Dixielee' (Zhang and Rhodes, 1994). The mutation *ja* is believed to be spontaneous, originating in 'Dixielee'. This is substantiated by the fact that *ja* plants existed in an F₂ population of 'R309' x 'Dixielee', which was tested in 1995, but the crosses were initiated at the same time as the 'G17AB' (*msms*) x 'Dixielee' cross. 'R309' is a selection belonging to *Citrullus colocynthis* (Rhodes et al., 1992).

Dramatic seasonal differences in albino phenotype expression were observed in the *ja* mutant. A *ja* plant of 'Dixielee' produced three fruit, each about 10 kg, during Summer 1993. However, this plant was nearly albino when grown in the greenhouse in early February and was moved into a growth chamber to rescue it. Understanding the regulation of *ja* expression is, therefore, as important as understanding the inheritance of the mutation. We report here the phenotypic characteristics of the *ja* mutant; inheritance of the *ja* mutation; the genetic relationship between *ja* and *dg*; and the regulation of *ja* expression. Potential applications of the *ja* mutant to watermelon genetics and breeding are also discussed.

Materials and Methods

Phenotype characterization of the *ja* mutant was conducted from Spring 1992 to Fall 1994 in the field at Edisto Research and Education Center (EREC) of Clemson Univ., Blackville, S.C., and in the greenhouse on the main campus of Clemson Univ. The *ja* mutant and the wild-type of cultivar 'Dixielee' were used primarily for phenotype characterization. To study the consistency of *ja*

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phenotype in different genetic backgrounds, *ja* mutants derived from the F₂ populations of 20J57 (*JaJa*) × ‘Dixielee’ (*jaja*) and ‘Sweet Princess’ (*JaJa*) × ‘Dixielee’ (*jaja*), and the population with pedigree [G17AB × (G17AB × ‘Dixielee’)] × (G17AB × ‘Dixielee’) and genotypes *msmsJaja* × *MsmsJaja*, were examined in the field along with the wild-type in Spring–Summer 1993 at EREC.

Genetic studies were conducted to understand the inheritance of the *ja* mutation and the genetic relationship between *ja* and the previously reported virescent mutation *dg*, which has some phenotypic similarities to *ja*. Eight populations were examined for inheritance of the *ja* trait (Table 1). A population of self-pollinated heterozygous (*Jaja*) ‘Dixielee’ was tested in the greenhouse during Fall 1993. G17AB is a male-sterile line developed in China (Zhang and Wang, 1990; Zhang et al., 1994).

The genetic relationship between *ja* and *dg* was investigated using five populations grown in the greenhouse during late fall of 1993 (Table 2). Comparison of the observed segregation ratio and the expected ratio was accomplished using a chi-square analysis.

Three experiments were conducted to assess the effect of temperature, daylength, and end of day (EOD) light on juvenile albino phenotypic expression. Seeds of ‘Dixielee’ (normal) and *ja* mutant were planted in Todd planter flats (no. 14-2574; A.H. Hummert Seed Co., St. Louis) containing premoistened commercial soilless potting mix (Mix No. 2. Fafard, Inc., Anderson, S.C.) and placed into a growth chamber (model E15; Controlled Environments Ltd., Winnipeg, Manitoba, Canada) with photosynthetic photon flux (PPF) of 40 to 300 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ for a 15-h period and temperatures of 23 (night) to 32 °C (day). The light ramp was programmed to increase the PPF from 40 to 300 and to decrease from 300 to 40 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ in a period of 2.5 h, respectively. A completely randomized design with four replications was used for each of these three experiments. Uniform seedlings of each genotype were selected from those raised in the growth chamber, and assigned to the experiment units, each consisting of four seedlings. Two days before the initiation of treatments, seedlings were transplanted into 5.6 × 5.6 × 5.6-cm Kord Inserts (no. 6761-8, Park Seed Wholesale, Greenwood, S.C.) containing a sterilized mix of vegetable garden topsoil and fine sand (3:1).

The first experiment was designed to determine if temperature affects *ja* expression. Ten-day-old seedlings were used for this experiment. All seedlings were kept in the growth chamber with a daytime (15 h) temperature of 25 to 32 °C and PPF of 40 to 300

$\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$. Nighttime (9 h) temperature treatments were low (5 ± 2 °C) or high (23 ± 2 °C). The high temperature treatment was conducted in the growth chamber, and the cold treatment was conducted in a dual-program illuminated incubator (Precision Scientific Group, GCA Cooperation, Chicago). After 10 days, total fresh weight and seedling height were determined.

The second experiment was conducted to determine if daylength affects *ja* expression. Two-week-old growth chamber-grown seedlings were used for this experiment. Two alternative photoperiods, but with balanced total energy input, were used. The long-day treatment consisted of 8 h high PPF (200 to 300 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) and 7 h below the accepted compensation point, with a PPF of 20 to 40 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$. The short-day treatment consisted of 8 h of the high PPF only. After 10 days, shoot fresh weight and leaf chlorophyll content were determined. Chlorophyll content was assayed on a spectrophotometer (SPECTRONIC 1001; Bausch & Lomb, Rochester, N.Y.). Chlorophyll was extracted in 80% acetone as described by Witham et al. (1971). Total chlorophyll, chlorophyll a, and chlorophyll b content of the extract were calculated according to the formulae of Witham et al. (1971). One gram of leaf tissue was collected from each seedling, and six seedlings were randomly sampled for each treatment and genotype.

The third experiment was conducted to determine if phytochrome is involved in the regulation of *ja* expression. Seven-day-old seedlings of ‘Dixielee’ *ja* mutant and the wild-type were used in this experiment. The treatment methods and conditions were similar to those described by Decoteau and Friend (1991). Plants were provided 300 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ PPF during an 8-h period of day in the laboratory equipped with a multi-vapor HID light (General Electric Corp.). The day/night temperature cycle averaged 27/21 °C. At the end of this daily 8-h photoperiod, the seedlings were briefly (15 min each light type) exposed to red (R), far-red (FR), R + FR (i.e., 15 min R followed by 15 min FR light treatment), FR + R (i.e., 15 min FR followed by 15 min R light treatment), or directly placed in dark (control). R light exposure (2.8 W·m⁻² in the 600 to 700 nm waveband) was obtained by filtering radiation from six cool-white, 40-W fluorescent lamps through a Roscolux no. 19 acetate filter (Rosco, Port Chester, N.Y.). FR light exposure (10 W·m⁻² in the 700 to 780 nm waveband) was obtained by filtering radiation from two 150-W internal-reflector, incandescent lamps through a polyacrylic sheet of cast acrylic no. 2711, dark red (Rohm and Haas, Bristol, Pa.). After 10 days, fresh weight, hypocotyl length, and petiole length were determined.

Table 1. Summary of juvenile albino mutant inheritance study^z.

Pedigree	Genotype	Generation	Season ^y	Phenotype		Expected ratio	χ^2	P value
				Normal	Juvenile albino			
Dixielee	<i>jaja</i>	P ₁	Sp	0	100			
20J57	<i>JaJa</i>	P ₂	Sp	25	0			
20J57 × Dixielee	<i>JaJa</i> × <i>jaja</i>	P ₁ × P ₂	Sp	25	0			
(20J57 × Dixielee) × Dixielee	(<i>JaJa</i> × <i>jaja</i>) × <i>jaja</i>	F ₁ × P ₁	Sp	117	119	1:1	0.02	0.90
(20J57 × Dixielee) ⊗	(<i>JaJa</i> × <i>jaja</i>) ⊗	F ₂	Sp	457	147	3:1	0.04	0.71
Heterozygous Dixielee ⊗	(<i>Jaja</i>) ⊗	---	F; Sp	96	34	3:1	0.09	0.76
(Sweet Princess × Dixielee) ⊗	(<i>JaJa</i> × <i>jaja</i>) ⊗	F ₂	SS	209	64	3:1	0.35	0.55
[G17AB × (G17AB × Dixielee)] × (G17AB × Dixielee)	<i>msmsJaja</i> × <i>MsmsJaja</i>	---	SS	128	42	3:1	0.01	0.93

^zPhenotypes of progenies of ‘Dixielee’, 20J57, 20J57 × ‘Dixielee’, (20J57 × ‘Dixielee’) × ‘Dixielee’ and (20J57 × ‘Dixielee’) F₂ were tested in the greenhouse at seedling stage. Phenotypes of progenies of self-pollinated heterozygous ‘Dixielee’ (*Jaja*), (Sweet Princess × ‘Dixielee’) F₂, and [G17AB × (G17AB × ‘Dixielee’)] × (G17AB × ‘Dixielee’) were determined from seedlings grown in the field.

^ySeason: spring = Sp; spring–summer = SS; fall = F.

Table 2. Inheritance of *ja* and *dg* loci.^z

Pedigree	Genotype	Generation	Phenotype			Expected ratio	χ^2	<i>P</i> value
			Normal	Delayed green	Juvenile albino			
Dixielee	(<i>jaja</i>)	P ₁	0	0	36			
Pale90	(<i>dgdg</i>)	P ₂	0	38	0			
Pale90 x Dixielee	(<i>dgdg</i> x <i>jaja</i>)	F ₁	35	0	0			
(Pale90 x Dixielee) x Dixielee	(<i>dgdg</i> x <i>jaja</i>) x <i>jaja</i>	BC ₁	37	0	39	1:1	0.05	0.82
(Pale90 x Dixielee) ⊗	(<i>dgdg</i> x <i>jaja</i>) ⊗	F ₂	206	74	86	9:3:4	0.75	0.59

^zPhenotypes of individuals involved in this study were determined at seedling stage. Phenotypes of individuals with *jajadgdg* and *jajaDg₋* were indistinguishable.

Temperature, daylength, and EOD light treatment were subjected to an ANOVA using the GLM procedure in SAS (SAS Institute, 1988).

Results and Discussion

Phenotype. The *ja* mutant is apparent as early as seedling emergence. Cotyledons are yellowish to light cream (Fig. 1) when seedlings first emerge from the soil and gradually turn greenish-yellow. Variation in the expression of cotyledon color was observed among progeny seedlings in our homogeneous populations. The hypocotyl of the *ja* mutant is always pure white; in contrast, the wild-type hypocotyl is light green. Young leaves of the mutant, grown in spring/early summer in South Carolina, are yellowish to white. These albino leaves gradually become green as development progresses, but the margins of the leaves remain white, resulting in a chimeric appearance to mature leaves (Fig. 2). Shoot tips, tendrils, petioles, stems (Fig. 2) and flower petals (Fig. 3) of the mutant are white to light cream with a slight hint of green. Pollen grains from albino flowers are colorless, but viable. The stigmas are orange, apparently lacking chlorophyll. The ovary color varies from light green to pure white. Some portions of the fruit rind are unevenly yellow (Fig. 4), showing that rind color of mature fruit is also affected by the *ja* gene.

Fig. 1. Seedlings of the *juvenile albino* watermelon mutant and the wild-type.

In addition to these chlorophyll differences, the flower petals of the *ja* mutant are considerably smaller than those of the wild-type. The petals of some flowers are not large enough to cover the stigma or anthers. Female fertility and fruit setting of the mutant is the same as that of the wild-type. No effect of the *ja* gene on flesh color has been observed. Soluble solids content in the fruit of the *ja* mutant is comparable to that of wild-type (data not shown). The phenotypic characters of the *ja* mutant are very similar to the *virescent* (*v*) mutant described by Hoffman and Nugent (1973) in melon. However the *v* gene in melon also affects flesh color, producing salmon-like streaks in bright yellow flesh.

Growth of the *ja* mutant in early spring is severely impaired. Seedlings of the *ja* mutant grow very slow when they are planted in February and March in the greenhouse, and many of them die when it is cloudy and/or they receive too much water. Growth of the mutant plants improves as the season progresses, and in the summer they grow comparably to the wild-type. Branches produced from the main shoots in the summer are almost normal green (Fig. 2). Flowers produced by these branches are normal in color and size. Typical *ja* phenotypic characteristics were not observed from the homozygous 'Dixielee' *ja* seedlings planted in August in the greenhouse until later in September. Modification of *ja* expression in different seasons has been observed in all genetic stocks where *ja* was introduced. Seasonal variation of *virescent* expression was not noted in the *v* melon mutant (Hoffman and Nugent, 1973).

Color modifications of cotyledon, hypocotyl, leaf, stem, flower, pollen and fruit rind in the *ja* mutant are most likely the result of chlorophyll deficiencies caused by the *ja* gene. Our current hypothesis is that the function of the *ja* gene is probably limited to impairing chlorophyll synthesis or accumulation.

Inheritance of juvenile albino. A cross between homozygous juvenile albino line and homozygous normal green produced a normal green F₁ hybrid. Backcrossing the F₁ to the juvenile albino parent produced BC₁ progeny that segregated 1 normal : 1 juvenile albino. The F₂ progeny segregated 3 normal : 1 juvenile albino. Three other populations, segregated in the expected ratio of 3 normal : 1 juvenile albino (Table 1). These results suggest that juvenile albino is controlled by a single recessive nuclear gene, designated *ja*. This confirms our previous suggestion based on preliminary data (Zhang and Rhodes, 1994).

Relationship between juvenile albino and delayed green. The previously described *virescent* mutant *dg* (Rhodes, 1986; Zhang et al.,

Fig. 2. A shoot of a *juvenile albino* watermelon plant grown in the field in early June. Note the color difference between primary and secondary shoot.

1996) is the only chlorophyll deficiency mutant in watermelon that is similar to the *ja* mutant. F_1 progeny between homozygous *ja* and *dg* were normal green. Backcrossing F_1 to the *ja* parent 'Dixielee' produced progeny that segregated 1 normal : 1 *ja*. The F_2 progeny segregated in the ratio of 9 normal : 3 delayed-green : 4 *ja* (Table 2). Individuals with genotype *jajadgdg* were indistinguishable from individuals with genotype *jajaDg_*. These results are consistent with the hypothesis that the two watermelon virescent genes *ja* and *dg* are inherited independently.

Regulation of juvenile albino expression. Under conditions that activate the expression of the *ja* gene, the mutant grows very poorly or even senesces. However, under conditions that inhibit *ja* gene expression the mutant grows almost as normally as the wild-type. Understanding the regulation of *ja* gene expression is important for maintaining and using this mutant in genetic studies and breeding.

Fig. 3. Flowers of the *juvenile albino* mutant (**top**) and the wild-type (**bottom**).

There are chlorophyll mutants that are light or temperature sensitive in maize (Hopkins et al., 1980; Hopkins and Elfman, 1984; Millerd and McWilliam, 1968), cotton (Benedict and Kohel, 1968), cucumber (Whelan, 1972) and watermelon (Provvidenti, 1994). We first speculated that the *ja* mutant was sensitive to low temperature because mutant seedlings were always severely albino in the early spring when it was cold, especially at night. When the mutant seedlings were provided a 15-h photoperiod, neither low ($5 \pm 2^\circ\text{C}$) nor high ($23 \pm 2^\circ\text{C}$) night temperature resulted in *ja* phenotype in seedlings of the mutant (Table 3). The mutant was almost as green as the wild-type. Like the wild-type, the mutant plants exposed to low night temperature were slightly greener than those exposed to high night temperature. As shown in Table 3, temperature affected seedling growth of the mutant and the wild-type in the same manner. Low night temperature significantly reduced seedling fresh weight and height of both mutant and wild-type. The insignificant genotype and treatment interaction ($P = 0.6045$ for fresh weight and $P = 0.1232$ for seedling height) confirms that temperature does not differentially affect the *ja* mutant and its wild-type. Temperature, therefore, is not likely the environment factor that regulates the expression of the *ja* gene.

The *ja* mutant responded to daylength very differently than did the wild-type. Although leaf color of the wild-type appeared the same under short and long days, the typical *ja* phenotype occurred under short days and produced almost normal seedlings under long days. As shown in Table 4, the *ja* mutant produced only half the fresh weight of the wild-type under short days. However, the mutant produced as much tissue as the wild-type under long days. Chlorophyll a was not increased in the wild-type when a longer photoperiod was provided. However, chlorophyll a was almost doubled in the seedlings of the *ja* mutant under long days. A slight increase in chlorophyll b was also observed in the *ja* mutant when long days were provided, but no changes were observed in the wild-type. The seedlings of the *ja* mutant had a higher chlorophyll a:b ratio than the wild-type when expression of *ja* was inhibited under long days. In contrast to our results, Hopkins et al. (1980) observed a significantly higher chlorophyll a : b ratio in the maize *Oy-yg* mutant than in the wild-type when expression of *Oy-yg* was enhanced under high light intensity conditions. Overall, daylength did not influence chlorophyll a : b ratio of the *ja* mutant and the wild-type. As indicated by the significant genotype and treatment interaction ($P = 0.0001, 0.0004$, and 0.0474 for fresh weight, chlorophyll a, and chlorophyll b, respectively), the *ja* mutant responded to daylength very differently from the wild-type. Daylength, therefore, is one environmental factor regulating the expression of the *ja* gene. Expression of the *ja* gene is activated in the mutant by a short photoperiod. The current study did not determine the minimum daylength that significantly inhibits the expression of *ja* gene and allows normal development of the mutant. Based on field observations made over the last 3 years, the minimum daylength required for normal growth of the *ja* mutant is about 14 h. Controlled experiments are needed to define more precisely the minimum photoperiod and determine if there is quantitative expression of the *ja* gene and/or the *ja* phenotype.

There are chlorophyll mutants whose expres-

Fig. 4. Fruit of the *juvenile albino* mutant (left) and the wild-type (right).

sion is regulated by light intensity in maize (Hopkins et al., 1980), cotton (Benedict and Kohel, 1968) and cucumber (Whelan, 1972). The expression of *ja* is not likely regulated by light intensity because the mutant produced the typical albino phenotype in the greenhouse and field in the early spring, where the light intensity varied several fold. The typical albino phenotype was also observed in the mutant plants grown in the greenhouse in the winter, where the light intensity was often very low because of the cloudy weather. No other chlorophyll-deficiency mutations whose expression is regulated by daylength have been reported for cucurbit crops or other plant species. Therefore, the *ja* watermelon mutant described here is a very rare, if not unique, virescent mutant where gene expression is regulated by daylength.

The possibility of phytochrome involvement in the regulation of *ja* expression was investigated after the role of daylength in *ja* expression was documented. In this experiment, no evidence of the involvement of phytochrome in the regulation of the *ja* expression was found. Brief exposures (15 min) of seedlings of the *ja* mutant and wild-type to irradiances of monochromatic R (the treatments R and FR + R) or FR (the treatments FR and R + FR) light at the end of the 8-h photoperiod did not alter the albino phenotype of the *ja* mutant. Phytochrome-regulated seedling growth in both geno-

types was similar to that described by Decoteau and Friend (1991) in 'Sugar Baby' watermelon seedlings. As shown in Table 5, the seedlings receiving R + FR light treatment had greater fresh weight. Both the *ja* mutant and wild-type had similar response to the treatments where fresh weight was measured, as indicated by insignificant interaction between genotype and treatment ($P = 0.6130$). Also, the hypocotyl and petiole of the first and second true leaf were longer in seedlings receiving FR and R + FR light treatments regardless of the genotype. However, more elongation of hypocotyl and leaf petiole was stimulated by FR and R + FR treatments in wild-type than in mutant seedlings as indicated by significant interaction between genotype and treatment. This was probably due to an insufficient supply of carbohydrates to support FR stimulated elongation growth in the *ja* mutant. In fact, 3 out of 16 *ja* seedlings receiving FR treatment were dead or close to death by the end of the experiment.

The *ja* mutant is useful for genetic studies and watermelon breeding. The *ja* mutant is an ideal seedling marker in genetic studies because it is unambiguously differentiated from the wild-type with green cotyledons and greenish hypocotyl, as soon as the seedling emerges from soil. When this mutant is used to study gene flow in watermelon populations, large progeny tests can be accomplished in a short time in limited space. If the *ja* gene is introduced into the seed parent of a hybrid variety, genetic purity of the hybrid seed can be tested in the greenhouse or laboratory in about 10 days instead of in the field, which requires two months or longer. This gene will also be helpful for detecting and eliminating off-types existing in an inbred line before the off-type produces pollen, resulting in further genetic contamination. Combining *ja* and *ms* (Zhang and Wang, 1990; Zhang et al., 1994) should permit commercial hybrid seed production without hand-pollination. We have been working on the development of a male-sterile line with the *ja* seedling marker since the discovery of *ja* in one of the populations related to male-sterility breeding in 1992 (Zhang and Rhodes, 1994). Unpublished data indicate that this male-sterile line with the *ja* seedling marker produced a higher frequency of true hybrids than the male-sterile line with the *dg* seedling marker under open-pollination conditions (Zhang et al., 1996).

In summary, juvenile albino is a new virescent mutant in

Table 3. Effects of night temperature, low ($5 \pm 2^\circ\text{C}$) vs. high ($23 \pm 2^\circ\text{C}$), on seedling growth of *ja* 'Dixielee' and its wild-type watermelon.^z

Treatment	Genotype	Fresh wt (g)y	Seedling ht (cm) ^y
Low temperature	<i>ja ja</i>	4.4 ± 1.5	7.8 ± 2.4
	<i>Ja Ja</i>	8.0 ± 1.2	14.5 ± 2.2
	Mean	6.2 ± 2.3	11.2 ± 4.1
High temperature	<i>ja ja</i>	6.4 ± 1.1	14.5 ± 3.4
	<i>Ja Ja</i>	10.3 ± 1.1	23.7 ± 4.0
	Mean	8.3 ± 2.3	19.2 ± 5.9
Factor		<i>P</i> value	
Genotype		0.0001	0.0001
Treatment		0.0001	0.0001
Genotype $\times$ treatment		0.6043	0.1232

^zTreatments started on 10-day-old seedlings in a growth chamber with PPF of 40 to 300 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ for a 15-h period and temperature 25 to 32 $^\circ\text{C}$ during day in the experiment period.

^yMean $\pm$ SD.

Table 4. Effects of day length, short day (8 h) vs. long day (15 h)^z, on shoot fresh weight (FW), chlorophyll a (a, mg·g⁻¹ leaf), chlorophyll b (b, mg·g⁻¹ leaf), and chlorophyll a : b ratio (a : b) of seedlings of juvenile albino 'Dixielee' and its wild-type watermelon.^y

Treatment	Genotype	FW (g) ^w	a ^w	b ^w	a : b ^w
Short day	<i>ja ja</i>	4.9 ± 1.6	0.7 ± 0.1	0.3 ± 0.05	2.7 ± 0.3
	<i>Ja Ja</i>	9.4 ± 1.8	1.7 ± 0.1	0.7 ± 0.06	2.6 ± 0.1
Long day	<i>ja ja</i>	11.2 ± 1.9	1.3 ± 0.2	0.4 ± 0.07	2.9 ± 0.1
	<i>Ja Ja</i>	12.5 ± 0.9	1.8 ± 0.1	0.7 ± 0.07	2.5 ± 0.1
Factor			<i>P value</i>		
Genotype		0.0001	0.0001	0.0001	0.0008
Treatment		0.0001	0.0001	0.0001	0.8443
Genotype × treatment		0.0001	0.0004	0.0474	0.1251

^zLong day consisting of 8 h high PPF (200 to 300 μmol·m⁻²·s⁻¹) and 7 h low PPF (20 to 40 μmol·m⁻²·s⁻¹), short day consisting of 8 h high PPF only.

^yTwo-week-old seedlings grown in the growth chamber were used for this experiment.

^wMean ±SD.

Table 5. Effects of end-of-day light, red (R), far-red (FR), R + FR, FR + R and dark (control), on seedling growth (shoot fresh weight = FW, hypocotyl length = HL, first leaf petiole length = 1st PL, and second leaf petiole length = 2nd PL) of *ja* 'Dixielee' and wild-type watermelon.^z

Treatment	Genotype	FW (g) ^y	HL (cm) ^y	1st PL (cm) ^y	2nd PL (cm) ^y
Control	<i>ja ja</i>	0.7 ± 0.1	6.2 ± 0.7	0.7 ± 0.3	0.4 ± 0.2
	<i>Ja Ja</i>	2.2 ± 0.7	7.6 ± 0.7	2.9 ± 0.4	2.4 ± 0.4
R	<i>ja ja</i>	0.9 ± 0.3	5.2 ± 1.1	0.9 ± 0.4	0.5 ± 0.3
	<i>Ja Ja</i>	2.5 ± 0.6	6.7 ± 1.0	3.2 ± 0.4	2.5 ± 0.7
FR + R	<i>ja ja</i>	0.7 ± 0.3	5.7 ± 0.8	0.7 ± 0.3	0.4 ± 0.2
	<i>Ja Ja</i>	2.4 ± 0.3	7.8 ± 0.8	3.0 ± 0.3	2.5 ± 0.4
FR	<i>ja ja</i>	0.6 ± 0.4	7.6 ± 1.1	0.5 ± 0.2	0.2 ± 0.1
	<i>Ja Ja</i>	2.6 ± 0.6	12.4 ± 1.3	5.4 ± 0.9	3.6 ± 1.1
R + FR	<i>ja ja</i>	1.2 ± 0.4	10.1 ± 3.2	1.6 ± 0.9	0.9 ± 0.9
	<i>Ja Ja</i>	3.0 ± 0.8	13.4 ± 1.4	5.6 ± 1.2	4.1 ± 1.6
Factors			<i>P value</i>		
Genotype		0.0001	0.0001	0.0001	0.0001
Treatment		0.0121	0.0001	0.0001	0.0003
Genotype × treatment		0.6130	0.0129	0.0001	0.0227

^zSeven-day-old seedlings grown in the growth chamber were used in this experiment. Plants were provided PPF of 300 μmol·m⁻²·s⁻¹ during a 8-h period of day. The day/night temperature cycle averaged 27/21 °C.

^yMean ±SD.

watermelon that is controlled by a single, recessive, nuclear gene. A gene symbol *ja* is proposed for this mutation. The mutants *ja* and *dg*, the previously reported virescent mutant, are located at independent loci. Expression of the *ja* gene is regulated by daylength. Long days inhibit the expression of *ja*, and therefore, the mutant grows almost normally when long days are provided. Under short days, chlorophyll synthesis and/or accumulation in the *ja* mutant is severely impaired, and the mutant grows very poorly or even senesces. Knowledge of involvement of daylength in the regulation of *ja* expression is useful for properly maintaining and propagating the mutant. This mutant can be maintained and propagated in areas where long days (longer than 14 h) are available. The *ja* mutant provides a useful seedling marker for watermelon genetic study and breeding, as well as unique material for studying photosynthesis in plants.

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