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Embryo Development and Germination of *Cycas* Seeds

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Abstract. **Germination of *Cycas revoluta* seed is slow and erratic when planted immediately after collection, and most lose viability in a few months. In a 2 × 4 × 4 factorial experiment, seeds were stored at 5° and 22°C for 24 weeks and subsequently treated with H_2SO_4 (18 M) for 0, 1, 2, or 3 hr followed by GA_3 (1000 ppm) for 0, 24, 48, or 72 hr. Morphophysiological complex dormancy contributes to the lengthy germination process. Removal of the fleshy, water-repellant sarcotesta (containing inhibitors), scarification of the thick water-impermeable sclerotesta, and maturation of the embryo, which is in very early stages of development at the time of seed abscission, all enhance germination. At 5°, 92% of the seeds survived, but only 42% of the seeds stored at 22° were viable after 24 weeks, the result of desiccation. Under all but 72 hr of GA_3 exposure time, response surface shapes lead to the expectation that germination will be better without H_2SO_4 or with higher levels of H_2SO_4 than with intermediate levels. The response to GA_3 at any given exposure to H_2SO_4 is similar in both cold- and warm-stored seeds: for a given GA_3 level, one optimum H_2SO_4 exposure gives the best germination percentage, peak value (PV), or germination value (GV). Optimal GV results when seeds are stored at 5° for 24 weeks to allow embryo maturation followed by removal of the sarcotesta, 1 hr of H_2SO_4 exposure, and 36 hr of GA_3 exposure.**

Comparatively little is known about germination requirements or dormancies in gymnosperm seeds (13). Cycads, an interesting and endangered group of gymnosperms, have been particularly neglected. Unavailability of seeds in sufficient quantities for experimental purposes has been largely responsible for lack of research. With the keen interest in commercial production of cycads in warmer climates, seeds of the more commonly cultivated species are now available. Fast and uniform germination is essential because of the relatively rapid loss of viability (6).

Seeds of most cycads require several months to germinate (6, 7). At least three, and possibly four, concomitant dormancy mechanisms contribute to their delayed germination: a fleshy sarcotesta, which apparently contains unspecified inhibitors (3); a thick and very hard sclerotesta; and, in some species, an immature embryo at the time of seed abscission (6, 8–10). It was reported that seed germination of cycads may be enhanced by mechanical removal of the sarcotesta and scarification of the sclerotesta with H_2SO_4 for various lengths of time (6–8). Germination of seeds was also shown to be significantly enhanced with GA_3 treatment (8, 9). Improved seed germination when GA_3 is used has been attributed to breakdown of physiological dormancy (16, 17). Nicolaeva (21) has referred to such a multiple dormancy as "morphophysiological complex dormancy". When methods that had proven successful with other species of cycads were attempted with the commonly cultivated species of *Cycas*, including *C. revoluta* Thunb. (king sago palm) and *C. circinalis* L. (queen sago palm), they did not improve germi-

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nation. The purpose of this research was to determine the cause(s) of delayed germination and methods that would allow the storage and rapid germination of these important ornamental plants.

Materials and Methods

Fresh seeds of *Cycas revoluta* were obtained in Feb. 1984. These were floated in water to determine their viability before starting the experiment (10). Viable seeds, which had sunk, were stored for 24 weeks in permeable bags in a cooler at a constant 5°C or at 22°. Five randomly selected seeds were examined for development of the embryo beginning at the outset of the experiment and once every 4 weeks thereafter. The seeds were freehand-sectioned and the embryo removed, stained with acetocarmine for ease of observation, and photographed with a Wild–Heerbrugg stereomicroscope with photographic attachments. After 24 weeks, when the embryo appeared morphologically mature, seeds were once again subjected to the flotation test. Floating seeds were discarded. The sarcotesta was then removed and, in a 4 × 4 factorial experiment, the seeds were scarified with 0, 1, 2, or 3 hr of concentrated (18 M) H_2SO_4, rinsed with water for about 2 hr, and then soaked in 1000 ppm GA_3 for 0, 24, 48, or 72 hr. Seeds then were planted at one-half depth (one-half of the seed length exposed) in trays filled with coarse sand (20 mesh, 0.85 mm), and placed randomly in a greenhouse maintained at 28° ± 3°/20° ± 1° day/night temperatures under mist (5 sec/5 min). There were five replications of 15 seeds each of the cold-stored seeds and three replications of 15 seeds each for seeds stored at 22°. Number of seeds that germinated was recorded once every 2 days for a total of 90 days. Germination value (GV), which combines speed and total germination, was calculated using Czabator's (5) method. These were fitted to a full quadratic model with multiple linear regression (19, 23).

Results and Discussion

Only 8% of the seeds stored at 5°C had lost their viability after 24 weeks, but 58% of the seeds stored at 22° were no longer viable. Because of the fewer number of seeds, replications of seeds stored at 22° were limited to three lots of 15 seeds, as compared to five lots of 15 seeds per treatment for the cool-stored seeds. The sarcotesta of seeds stored at 22° had dried, and, for the most part, was falling away, whereas those of seeds stored at 5° were intact and turgid. Loss of viability in *Cycas* seeds was reported (10) to be caused by dehydration, resulting in shrinkage and subsequent separation of the female gametophyte from the sclerotesta. When seeds are stored at 22°, the sarcotesta dries out relatively quickly, directly exposing the sclerotesta, resulting in rapid water loss. The significantly lower viability (42%) can be directly attributed to dehydration. Unlike most other seeds, viability is not restored by rehydration, despite the seemingly normal embryo. The sarcotesta of seeds stored at 5° remained intact and turgid for the entire storage period, preventing excessive dehydration of the female gametophyte and maintaining viability of the seed. Nishida (22) noted a consistent increase (13.25 g to 18.00 g) in weight of developing *C. revoluta* seeds from August through November. Dry matter content in the same time period increased from 6.6% to 49.6%. This was accompanied by a reduction in water content from August through February (93.4% to 50.4%). Cycad seeds, however, do not appear to undergo metabolic reduction and enter a quiescent or dormant phase, as do seeds of many other plants (15). Any additional loss of water is detrimental and results in loss of viability. Separation of the female gametophyte from the sclerotesta is symptomatic of the decrease in water content (10). Seeds of cycads may be classified as recalcitrant because these cannot be dried below a critical moisture level without irreversible damage (14, 24).

Examination of the embryo at the outset of the experiment indicated a pair of archegonia in a relatively advanced stage of development, where one of the two was beginning to degenerate (Fig. 1A). An embryo with a distinct suspensor but undifferentiated cotyledons developed from the remaining archegonium in about 4 weeks (Fig. 1B). The cotyledons were fully differentiated at the end of the 12th week (Fig. 1C). Several more weeks were required before the embryo was actually mature, as determined by loss of the suspensor and presence of the coleorrhiza (Fig. 1D). Embryo development of seeds stored at 22°C appeared asynchronous; some were larger and more ma-

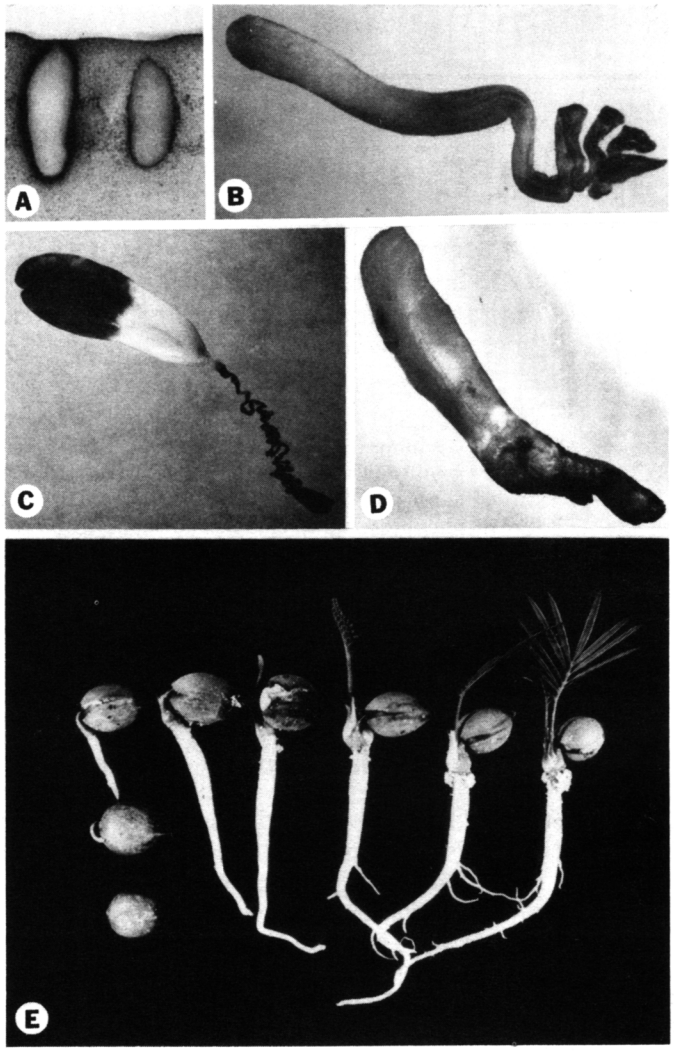

Fig. 1. Development of the embryo in *Cycas revoluta*. (**A**) Developing (**left**) and degenerating (**right**) archegonia at the time of seed abscission. (**B**) Development of the embryo with a suspensor and undifferentiated cotyledons in 4 weeks. (**C**) Embryo with suspensor but differentiated cotyledons in 12 weeks. (**D**) Fully developed embryo at the end of 24 weeks—length of the embryo nearly equals length of the seed. (**E**) Stages of germination, beginning with protrusion of the coleorrhiza from the sclerotesta (**left**), growth of the stem from apical portion of the root (**center**), and fully developed seedling (**right**).

ture than others after 24 weeks. Embryos of cold-stored seeds appeared equally well-developed. Despite the apparent maturity of the embryo, seeds did not germinate as rapidly as those treated with H_2SO_4–GA_3 (Fig. 2 A and D). Response surface models of all three germination parameters [absolute percentage, peak value (PV), and germination value (GV)] differed under the two temperature storage regimes. The response surfaces for seeds stored at 22° are dome-shaped (Fig. 2 A–C). While holding either GA_3 or H_2SO_4 exposure constant, varying the other is expected to produce one optimum germination percentage, PV, or GV. Cold-stored seeds are not predicted to behave in this manner. The response surface for percent germination under all but the 72-hr GA_3 exposure time shows that germination is expected to be better either without H_2SO_4 exposure or with higher levels of H_2SO_4 exposure than with intermediate levels. In the case of GV (Fig. 2E) and PV (Fig. 2F) response surfaces, the same phenomenon occurs, but only at or near 72 hr of exposure to GA_3. The response to GA_3 at any given exposure to H_2SO_4 is similar in both the cold- or 22°-stored seeds. For a given GA_3 level, one optimum H_2SO_4 exposure gives the best germination percentage, PV, or GV.

Monnier and Norstog (18) have shown that embryos of the related genus *Zamia* did not differentiate properly when excised early, whereas those excised several months later, although immature, immediately entered a period of organogenesis. They concluded that, during their more prolonged stay in the ovule, the embryo seemed to have received an "inductive stimulus" that permitted subsequent differentiation. Seeds of *C. revoluta* followed the same pattern, except that, when stored at 22°C, they appeared developmentally asynchronous with embryos of some seeds maturing earlier than others. Those with relatively more advanced embryos may be more subject to loss of viability under prolonged storage at room temperature because of the greater moisture loss. Had these seeds been stored under cool temperatures for a period of time and then moved to warmer storage, they might not only have remained viable, but perhaps would have been first to germinate. This possibility is most evident in the model for PV at the highest H_2SO_4 exposure with

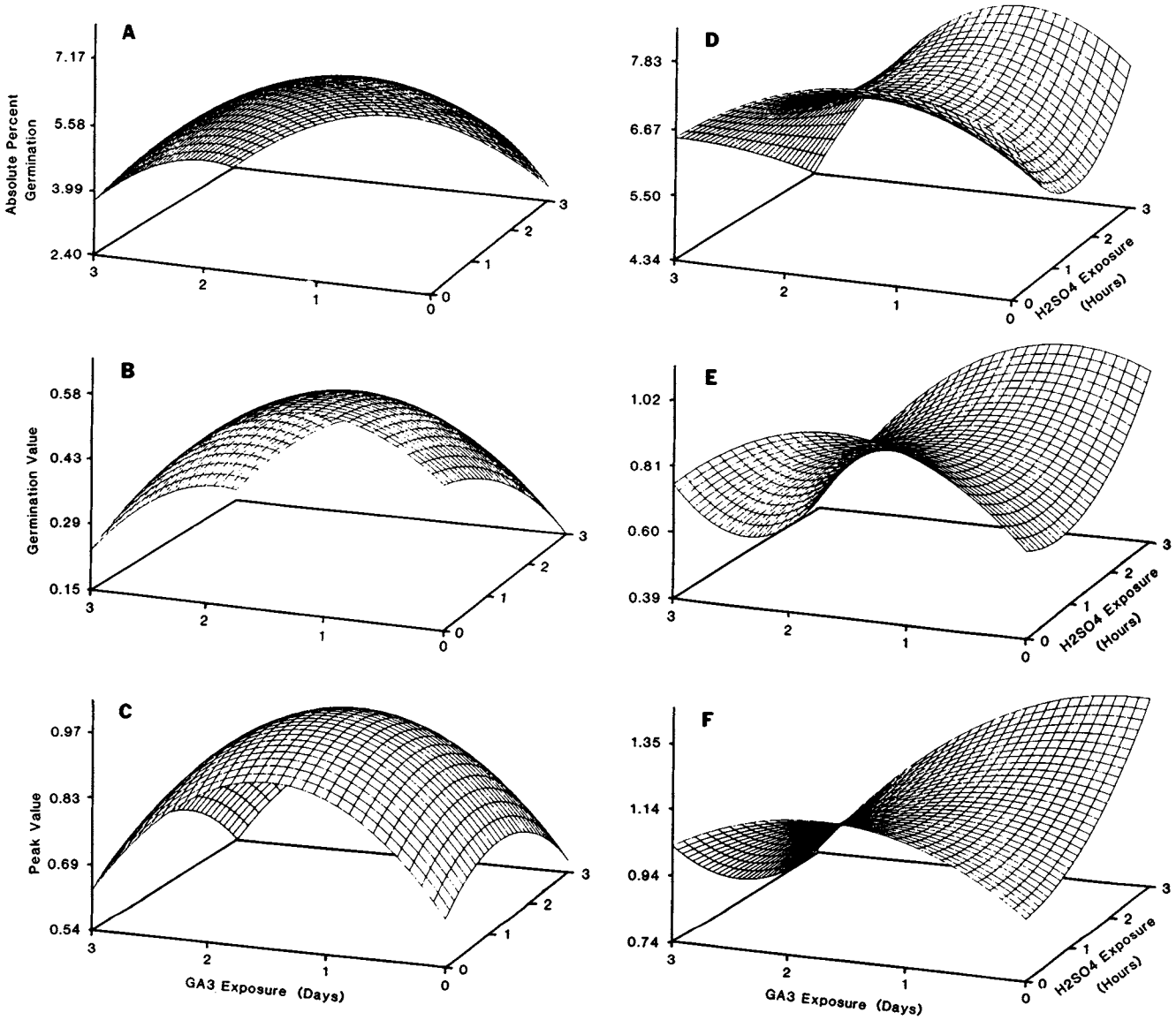

Fig. 2. Response surface models for germination of *C. revoluta* seeds. Seeds stored at 22°C (**A–C**) or 5° (**D–F**) and treated with H_2SO_4 and GA_3. (**A** and **D**) Absolute percent germination. (**B** and **F**) Germination value. (**C** and **F**) Peak value.

no GA_3 (Fig. 2 C and F). The main effect of stratification is on speed of germination or "germination synchronization" (12), which results in an increase in the total number of seeds that germinate and reduction in germination time. Cold stratification of *C. revoluta* seeds resulted in retention of viability, increased percentage, and uniformity of germination. As noted by Evenari (13), the environmental conditions under which seeds mature affects their final physiological constitution. Maintenance of seed moisture content is the most important factor in cold-stratified, synchronous germination (12). The relatively faster germination speed of cold-stored seeds indicates normal development of the embryo and a lack of "chilling shock" reported to occur with cold storage in some warm-temperate-subtropical seeds (20).

The difference between innate and imposed dormancy is that innate dormancy cannot be overcome by conditions favorable for germination (17). In cycads, growth of the embryo is a slow but continuous process without a resting period (11); it proceeds from fertilization to archegonial development and subsequent initiation of the embryo, the gradual elongation of the embryonic axis, and finally, protrusion of the coleorrhiza from the seed coat followed by the unique development of the seedlings (see Fig. 1 A–E). Thus, germination is hindered not so much by physiological dormancy as it is by slow morphological development of the embryo, by the mechanical dormancy imposed by the thick sclerotesta, and the water-impermeable outer layer of the sarcotesta. Although the seeds will eventually germinate under proper environmental conditions, the actual process of germination is influenced by GA_3, indicating the need for a promotor.

Hormones have long been recognized as a triggering factor in the germination process. It has been suggested that germination, which is sporadic or altogether lacking, may result from the absence of appropriate stimulators such as gibberellins or kinetins (17). In cycads, GA_3 does not appear to affect embryo development, but functions rather as a germination "promotor", a term used by Kahn (16) for the primary role of GAs in germination regulation and release of physiological dormancy. Endogenous GAs in cycads, as in other seeds, probably occur in the nutritive tissue before the seeds mature, but are absorbed by the developing embryo and diminish as the seeds mature (2). Exposure to exogenous GA is necessary for induction of the enzymes at sites that regulate germination. Numerous enzymes are activated as a result of hormone treatment (25). It is possible that, at a given concentration or exposure time, the effect on activation of enzymes may be negative, while at higher or lower levels the results may be positive. Nevertheless, while occurrence of anomalous germination is not uncommon (4), the reasons for this anomalous behavior are not readily apparent. The germination rate predicted for seeds cold-stratified and treated with H_2SO_4 was more than 50% faster than the seeds stored at room temperature and similarily treated.

Morphophysiological dormancy complexes are known to occur in herbaceous species (1) and have been reported in such woody taxa as *Nandina domestica* (7) and *Zamia* spp. (8, 9). *Cycas* species differ in their germination behavior. Although data are not presented for *C. circinalis* due to insufficient number of seeds in the experiments, results were very similar to those presented for *C. revoluta*. This is surprising because the latter taxon is of tropical origin. Such similarity in the germination mode of a tropical and a warm-temperate species would not be expected. These two species differ in one major respect, which is of considerable practical significance. While seeds of *C. revoluta* and *C. taiwaniana* Carruth. sink in water when viable, those of *C. circinalis* and related taxa float due to the presence of air-filled spongy tissue (10). Hence, the assumption that all viable seeds sink is not valid and caution must be exercised when determining viability in species of this genus. Other species, such as *C. media* R. Br., *C. normanbyana* F. Muel., and *C. wadei* Merr., require no treatment other than removal of the sarcotesta, and germinate without difficulty when collected soon after abscission. In fact, under natural conditions, a small percentage of seeds of all species germinate several months after abscission when left undisturbed.

Abscisic acid (ABA) or substances with similar properties have been reported to arise from the carotenoid violaxanthin via production of xanthoxin in various parts of mature seeds (2). Sarcotesta of the seed in *C. revoluta* lacks chlorophyll but contains a mixture of carotenoids (β-carotene, β-cryptoxanthin, and zeaxanthin) in tubulous chromoplasts, giving the seed an orange color (26). The inhibitory effect of the sarcotesta, as noted by Brown (3) and by our observations, may be the result of ABA or other such substances that arise from these carotenoids. Seeds germinate only when the sarcotesta is removed or naturally decomposed.

Based on the trends indicated by the response surfaces, optimal germination value occurs when *C. revoluta* seeds are stored at 5°C for 24 weeks, which is necessary for embryo maturity, followed by removal of the sarcotesta. Our observations indicate faster embryo maturity at 22°, followed rapidly by desiccation and death. It may be beneficial to store the seeds first at low, and then relatively high, temperatures. This parallels the sequence of seed development under natural conditions. Seeds abscise in January–February and remain on the ground until summer, when some germinate.

Subsequent treatments to be used also are influenced by storage temperatures. Cold-stored seeds are positively affected by exposure to GA_3 when H_2SO_4 is used, but, after a certain threshold, the combination of both is detrimental. Thus, relatively fast, uniform germination is possible when seeds are treated with H_2SO_4 for $\approx$1 hr, followed by GA_3 for $\approx$36 hr. However, actual experimental data somewhat contradict the model; the highest germination percentages recorded in both 22° and 5°C treatments (54.7% and 51.1%, respectively), were with 24 hr of exposure to GA_3 and without H_2SO_4 treatment. Despite prediction of the models that use of H_2SO_4 produces the fastest germination in all treatments irrespective of storage temperature (1.55 seeds/day and 1.12 seeds/day, respectively), we recommend use of H_2SO_4 for relatively short periods of time to avoid any possible damage to seeds.

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Studies of Three New Genes, Linkage, and Epistasis in Lettuce

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Additional index words. *Lactuca sativa*, leaf color, flower color, achene color, plump involucre, early flowering, male sterility

Abstract. **Three new lettuce (*Lactuca sativa* L.) genes were described and named: *shiny green (Sgsg), salmon (Sasa),* and *apple green (Agag). Plump involucre* and *male sterile* are linked, with $p = 0.345$. *Plump involucre* and *Early flowering* are linked closely, with p approaching zero. Twenty-five gene pairs tested for linkage were independently inherited. In achene color, the order of recessive epistasis is *white* > *yellow* > *brown*. The double-recessive combination *vivicd-2cd-2 (virescent* and *chlorophyll deficient)* is phenotypically *virescent* and partially lethal.**

Among the goals of lettuce genetics research at the U.S. Agricultural Research Station have been the identification of major genes, construction of the genetic map, and elucidation of relationships among genes and between genes and the environment. This paper continues the description of major genes, linkage, epistasis, and other interactive relationships among the genes of lettuce. I report three new genes, two linkages, and two epistatic relationships.

Materials and Methods

Seven experiments were conducted. The three inheritance studies were based on the following crosses: Shiny green—'Amaral 78' x 'Salinas' and 'Amaral 78' x 'Vanguard 75'; Salmon flower—'Golden Bibb' x 'Salinas' and 'Golden Bibb' x 'Australian'; Apple green—82-1061-1 x 'Vanguard 75'. In each cross, the mutant form is the female parent.

'Amaral 78' is a 'Salinas'-type crisphead lettuce released by Quali-Sel Seeds (Salinas, Calif.) in 1978. The Plant Variety Protection certificate describes 'Amaral 78' as differing from 'Salinas' in the glossy green color of the foliage and seed stalk, as compared to the duller green of 'Salinas'. Color value, based on the Royal Horticultural Society Colour Chart (RHS), is 143B for 'Amaral 78' and 143C for 'Salinas'. Plants of 'Amaral 78' grown in the greenhouse showed the same glossy or shiny color, which also extended to the involucre bracts.

'Summer Bibb', a butterhead lettuce cultivar, normally has yellow flowers. A variant obtained from Scattini Seeds (Salinas, Calif.) has salmon-colored flowers. Modifications of yellow previously reported are: *pale (papa)* and *golden (gogo)* (Ryder, 1971). Plants of the three variant color types were grown at the

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