Variability for Critical Photoperiod for Tuberization and Tuber Yield Among Monoploid, Anther-derived Genotypes of Solanum phureja

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Abstract. Monoploid genotypes (2n = x = 12), derived by anther culture of a diplandrous (2n pollen-producing) clone of Solanum phureja Juz. & Buk., a South American diploid potato species, were examined for their use in germplasm development. Nine monoploid genotypes and the anther-donor genotype were grown in three chambers (10-, 14-, and 18-hr daylengths) to examine the effect of photoperiod on tuber yield and to determine the variability for critical photoperiod for tuberization. Significant differences were found among the monoploid genotypes for tuber weight and tuber number. Longer photoperiod treatments decreased and delayed tuberization. Axillary tuber formation from single-node cuttings was used to estimate the onset of tuber induction and demonstrated variability among monoploid genotypes for critical photoperiod for tuberization.

Tuberization of potato is a critical process by which photosynthates are redirected from above-ground growth to storage tissues. Many factors have been shown to affect its induction and degree, including regulation by a symbiotic fungus (2), the carbon : nitrogen ratio (17), and photoperiod (3). An interaction between photoperiod and temperature on endogenous substances that regulate tuberization has been demonstrated (6). Many growth substances, including cytokinins and abscisic acid, gibberellins, and ethylene, have been implicated in tuberization (14). The role of Ca and Ca inhibitors has also been examined (1). The exact controlling mechanism, however, has not been determined and probably consists of a combination of exogenous and endogenous factors, many of which are affected by genotypic predispositions.

Solanum spp. have exhibited a wide range of photoperiodic behaviors, from those that will tuberize even under very long days, characteristic of S. tuberosum L. cultivars, to those that will only tuberize under short photoperiods, illustrated by many diploid species, both wild and cultivated. Conventional breeding methods have met with limited success because of the narrow genetic base of S. tuberosum cultivars, compounded by their tetraploidy, the highly heterozygous nature of the species, and the multigenic nature of tuber yield (10, 11). The use of exotic germplasm, in spite of its photoperiodic requirement, has been viewed as an essential step in the introduction of new allelic forms that might allow potato breeders to surpass current thresholds for characters of economic importance (7).

Monoploid clones may simplify selection efforts because their phenotypes are a direct reflection of their genotypes. In our study, variability among nine monoploid genotypes, derived from anther culture of a diplandrous (2n pollen-producing) clone of S. phureja Juz. & Buk., was examined with regard to critical c:ia; · photoperiod for tuberization. A modification of Ewing's screening technique (4) was used to determine the critical photoperiod for each genotype. By this technique, single-node cuttings are taken from plants grown under successively shorter photoperiods, placed in moist sand under long days, and scored for shoot, stolon, axillary tuber formation, or no growth. Cuttings that tuberize indicate that the mother plants were grown under photoperiods shorter than the critical photoperiod necessary for tuber induction. In our study, plants were grown under one of three photoperiods (10-, 14-, and 18-hr daylengths) for their entire life cycle to eliminate the confounding effects of plant age on tuberization in response to photoperiod. Cuttings were scored for vegetative growth, formation of storage tissue, or no growth.
The two main objectives of this study were to determine 1) variability among monoploid genotypes extracted from a single, heterozygous, diploid clone for multigenic traits, namely tuber yield and plant height; and 2) segregation in both directions from the anther-donor (i.e., some higher, some lower) among the monoploid genotypes for a yield characteristic, namely, critical photoperiod for tuberization.

Materials and Methods

Nine monoploid genotypes (AM2, AM3, AM4, AM6, AM?, AM20, AM21, AM26, and AM27) and the anther-donor genotype [PP5, selected from S. phureja P.I. 225669 (15)] were grown under greenhouse conditions, harvested simultaneously to minimize any effects of the mother tubers, and stored at 6°C for at least 1 month to break dormancy. The tubers were transferred to the Southeastern Plant Environment (Phytotron) Laboratories of North Carolina State Univ., planted in flats containing one-third peat-lite (Redi Earth, W.R. Grace) and two-thirds coarse gravel, and placed in three walk-in controlled environment ~ooms (chamber size B "'='1.2 x 2.7 m).

After the minimum 10-hr day length (650 J.Lmol·s - I.m - 2 photosynthetic photon flux, PPF), low-intensity incandescent lights (50 J.Lmol·s · 1·m· 2 PPF) were used to extend photoperiods in two of the chambers to 14 and 18 hr. All chambers were main tained at 18°C for the minimum 10-hr light period and at 14° for the remaining 14 hr. A nutrient solution containing 106 mg·liter - 1 N, 10 mg·liter - 1 P, and 111 mg·liter - 1 K was applied three times weekly throughout the experiment (12).

Six weeks after planting, sprouted tubers were transplanted into individual 150-mm-diameter pots (six plants per genotype per chamber). Eight weeks after experiment initiation, measurements of node number and plant height were taken for all plants. At 8 weeks, the plants were decapitated and three singlenode cuttings containing a young, but fully expanded, leaf were taken from each plant. The cuttings were placed in moist sand and transported to the greenhouse at Virginia Polytechnic Institute and State Univ., Blacksburg (18 cuttings per genotype per sampling date). At 10, 12, and 14 weeks, axillary branches were decapitated and cuttings taken in a similar manner. Ambient autumn light conditions were supplemented with incandescent lights to extend the photoperiod to 20 hr and the cuttings were placed under intermittent mist. After 3 weeks, each cutting was scored to indicate a vegetative (rooting with or without axillary shoot formation) response (-1), no response (0), or axillary tuber formation (+ 1). Tuber formation included axillary tubers exclusively as well as tubers with connecting stolons and/or roots. Tubers from each original plant were harvested at 16 weeks. Total tuber weight and tuber number (> 10 mm in diameter) were recorded for each plant.

Data were analyzed using the General Linear Models procedure of the Statistical Analysis System (13). Mean separation of tuber weight, tuber number, and internode length was by Student-Newman-Keuls' test, 5% level.

Results

Response of single-node cuttings. Single-node cuttings of eight of the monoploid genotypes, as well as the anther-donor genotype, taken from the 10-hr photoperiod, produced axillary tubers (Fig. 1 top). Therefore, as expected, it can be concluded that most of the genotypes had a critical photoperiod for tuberization that was longer than 10 hr. Only AM26 did not demonstrate consistent tuberization at this photoperiod.

Segregation for critical photoperiod for tuberization among the monoploid genotypes was more apparent at the 14-hr photoperiod (Fig. 1 center). At 8 weeks, cuttings from most of the genotypes demonstrated mostly a vegetative response, although many formed axillary tubers at later sampling dates. PP5 and AM4 showed a strong vegetative response at this photoperiod, suggesting that their critical photoperiods for tuberization were shorter than 14 hr. AM26 even more strongly demonstrated only a vegetative response or no response than under the 10-hr photoperiod. AM21 was the only monoploid genotype that demonstrated a strong tuberizing response at all sampling dates. Under an 18-hr photoperiod, AM2, AM3, and AM27 had switched to a predominantly vegetative response, which placed their crit- · ical photoperiods for tuberization between 14 and 18 hr (Fig. 1 bottom). By contrast, cuttings from AM6, AM7, AM20, and AM21 still were able to demonstrate a strong tuberization response at one sampling date under this photoperiod, which suggested a longer critical photoperiod for these genotypes.

Tuber yield. With the exception of AM4 grown under an 18-hr photoperiod, all of the monoploids exhibited measurable tuber yield by 16 weeks, regardless of their critical photoperiod, as indicated by cuttings. The monoploid genotypes varied significantly for tuber weight per plant at all photoperiods (Fig. 2 top). PP5 was consistently higher in tuber weight per plant than the monoploid genotypes, but decreased to such an extent under 18 hr that it no longer significantly differed from AM21, one of the monoploids that showed a

tuberization response under an 18-hr photoperiod. In addition, AM21 showed the greatest tuberization response among the monoploids in all photoperiods and its yield was least affected by increasing photoperiods. The anther-donor (PP5) produced many tubers per plant at 10 hr and all monoploid genotypes produced similar numbers of tubers per plant as PP5 (Fig 2 center), although some monoploids differed significantly from others. However, at longer photoperiods, segregation for tuber number among the monoplaids was evident by low (AM4 at 14 hr) and high (AM21 at 18 hr) tuber numbers compared with their anther-donor genotype.

Plant height. As with critical photoperiod for tuberization, segregation for mean internode length was most apparent at the 14-hr photoperiod (Fig. 2 center). Mean internode legnth of PP5 was reduced at the 10-hr photoperiod, under which AM6 had significantly longer internodes than PP5. At 14- and 18-hr photoperiods, however, the monoploids generally had shorter internodes than PP5, although there were significant differences among them.

Discussion

Segregation for a multigenic trait, such as tuberization, may be exposed directly by analysis of monoploid genotypes produced through anther culture and examined under strict environmental control. By this method, the influence of dominance is eliminated and environmental influences are minimized. Tuber initiation is believed to be a multigenic trait (8, 10, 11). S. phureja is a heterozygous, self-incompatible, diploid species and would be expected to produce a heterogeneous array of genotypes via androgenesis. Results of this experiment confirm the inherent variability of the anther-donor genotype.

Response of single-node cuttings. Single-node cuttings have been used to estimate the onset of tuberization in a potato plant while allowing the plant to continue its growth (4, 5, 9). This method of assessment, however, is not expected to be absolute, especially with only a small number of cuttings. For example, AM26 exhibited a consistent vegetative response over four sampling dates, even under the 10-hr photoperiod (Fig. 1 top), yet it produced a reasonable tuber crop compared to other monoploid genotypes that exhibited strong axillary tuber formation (Fig. 2 top). In general, however, genotypes that formed many axillary tubers from cuttings of plants exposed to a given photoperiod also produced relatively high tuber yields at that photoperiod. Single-node cuttings of AM21 formed tubers, even when taken from plants grown under a 18-hr photoperiod, and the mother plant correspondingly produced a consistently high mean tuber yield.

Physiological age of the plant also affects tuber induction. Plants grown under noninductive photoperiods will tuberize eventually, but much later than plants grown under inductive conditions. This response is mirrored by the tendency for older single-node cuttings to begin forming axillary tubers even if taken from plants grown under noninductive photoperiods (see Fig. 1 bottom). Cuttings from AM6, AM7, and AM20 under 14- and 18-hr photoperiods began to form axillary tubers only when taken from plants that were at least 14 weeks old, suggesting that tuber induction in these genotypes occurred much later than on similar plants grown under shorter photoperiods. By contrast, cuttings taken from AM21 8 weeks after planting already had been induced to tuberize. This tuberization response of AM21, however, was not demonstrated by subsequent cuttings. Regardless, for this method to be effective in selecting genotypes possessing longer critical photoperiods for tuberization, cuttings should be taken before the plants have reached physiological maturity.

Tuber yield. Variability for mean tuber yield was apparent among the monoploid genotypes; however, all monoploid genotypes, with the exception of AM21 grown under the 18-hr photoperiod, had lower mean tuber yield than their anther-donor.This was expected, since tuber yield is affected by both ploidy level and genotype (10). In addition, monoploid genotypes are expected to exhibit considerable inbreeding depression. Segregation in both directions was better illustrated by mean tuber number (Fig. 2 center), where PP5 exhibited an intermediate phenotype. Ideally, improvement of marketable tuber yield would require high tuber weight per plant and low tuber number, even under a long photoperiod. Unfortunately, the monoploid genotype producing the highest yield at the longest photoperiod (AM21) also produced a mean tuber number that was significantly higher than PP5. It is important, therefore, to assess genotypes for both characteristics simultaneously and at the photoperiod for which the crop is being developed.

Plant height. Photoperiod has been shown to affect internode elongation in tuber-bearing Solanum spp. (16). Potato plants grown under short photoperiods have exhibited a corresponding reduction in internode length, which may or may not influence tuberization (6). In this experiment, mean internode length was reduced under

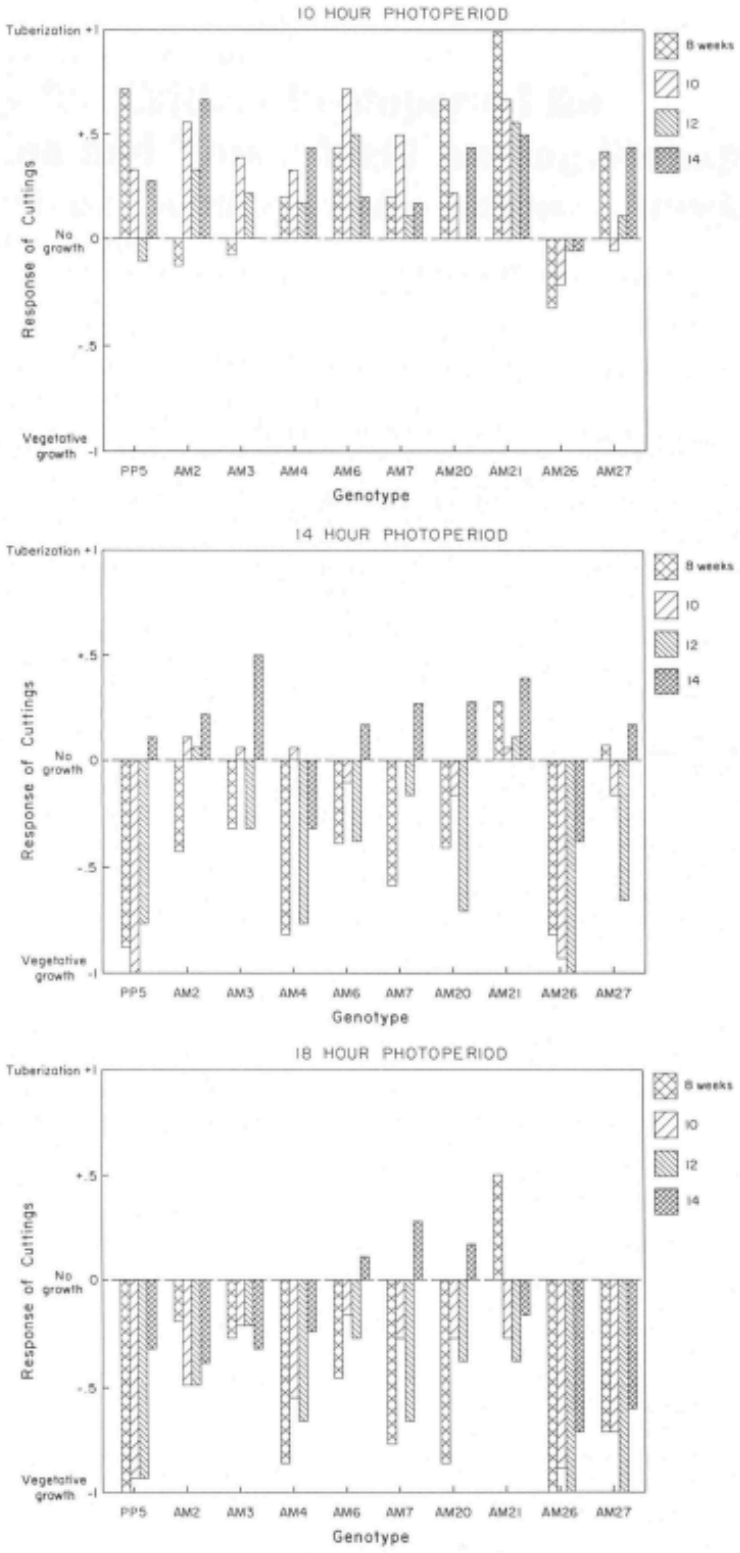

Fig. 1. Vegetative growth (-1) vs. axillary tuber formation (+ 1) of single-node cuttings from nine monoploid (AM) genotypes and their diploid, anther-donor genotype (PPS) of Solanum phureja taken from plants after 8 (i:8l), 10 (IZJ), 12 (~, and 14 (DJ weeks of growth under a 10-hr (top), 14-hr (center), or 18-hr (bottom) photoperiod. Zero values indicate equal response; n = 18.

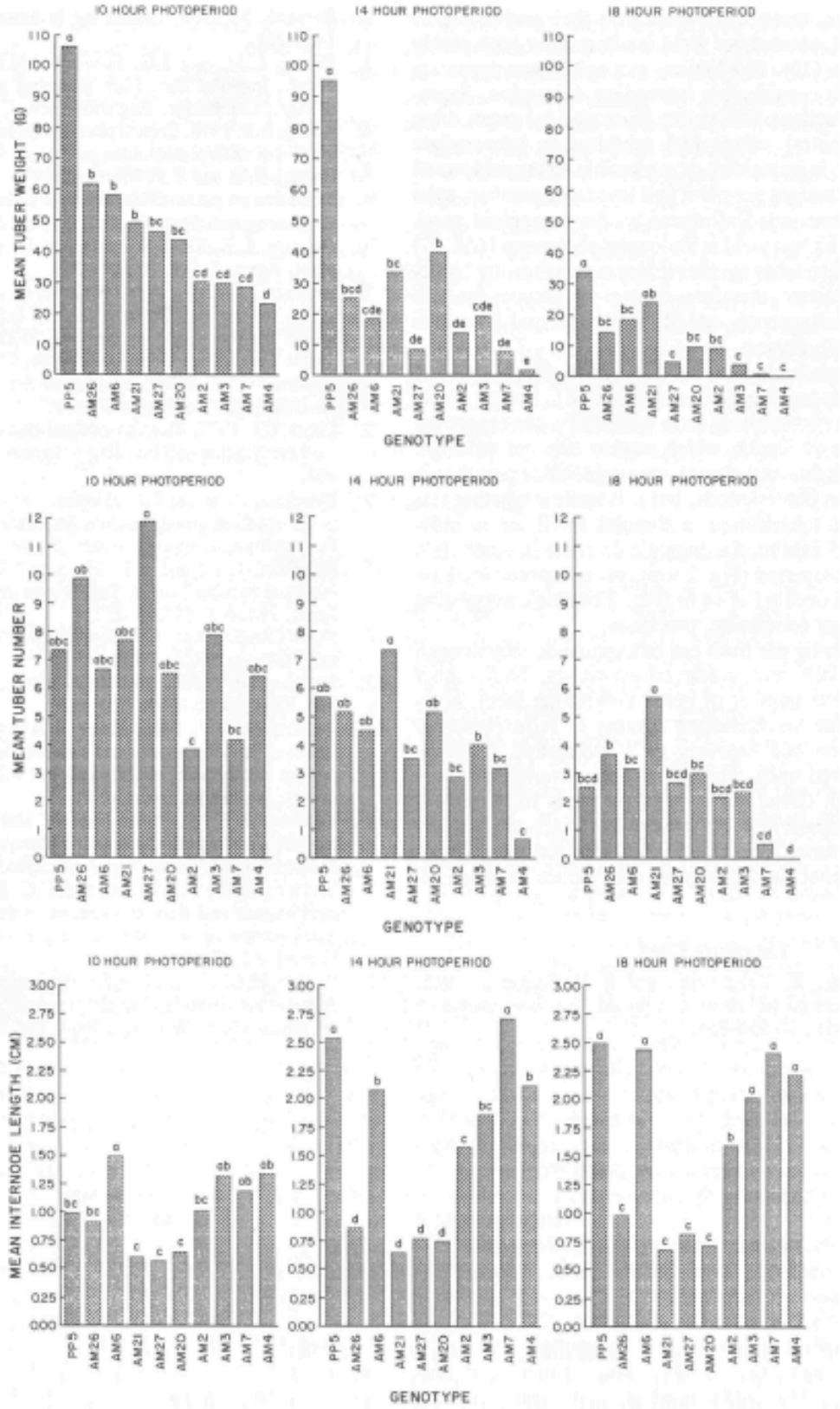

Fig. 2 Means for tuber yield per plant (g) (top), tuber number per plant (center), and internode length (em) (bottom) of nine monoploid (AM) genotypes and their anther-donor genotype (PPS) grown under 10-, 14-, and 18-hr photoperiods for 16 weeks. Mean separation by Student-Newman-Keuls test, 5% level; n = 6.

short photoperiods, but it is unclear whether this was in response to tuberization, a stimulus for it, or an independent event. PP5 exhibited a dramatic decrease in tuber yield under an 18-hr photoperiod (Fig. 2 top), yet its marked increase in internode length occured at 14 hr (Fig. 2 bottom), suggesting independent, though competing, processes.

Variability for multigenic traits can be exposed directly through the use of monoploid, anther-derived genotypes. The number of characters and the number of genes controlling them, however, will determine the minimum number of regenerants required for detection and recovery of a monoploid genotype possessing all desired traits. This is true for conventional selection efforts as well. Given the segregation ratios for tetraploid cultivars, the incompatibility and sterility that characterize many of them, and the time, space, and labor required for conventional screening, monoploid genotypes may reduce selection efforts considerably.

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