Inheritance of Phosphoglucumutase Isozymes in Pecan

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Abstract. Six phosphoglucumutase phenotypes were observed in pecan [*Carya illinoensis* (Wangenh.) K. Koch] progeny after controlled pollinations. At least one locus (*Pgm-1*) is present that controls polymorphism of phosphoglucumutase (PGM) isozymes in pecan. The inheritance appears simple with three observed alleles. However, progeny produced from two crosses resulted in significant deviation from the expected segregation ratios. Out of 65 named cultivars, 61 were of a single phenotype, and two of six possible phenotypes were not observed. Only one region of PGM activity was consistently expressed by gel electrophoresis from pecan tissue.

Three traits in pecan are known to be simply inherited. Two traits include the biochemical markers malate dehydrogenase (EC 1.1.1.37) and phosphoglucose isomerase (EC 5.3.1.9) (Marquard, 1987) and the other is floral heterodichogamy (Thompson and Romberg, 1985). Characterization of other pecan genes would enhance genetic understanding of and research on this species. This report documents polymorphism and inheritance of phosphoglucumutase (EC 2.7.5.1; PGM) in pecan.

Leaf or cotyledon tissue from individual plants or nuts was homogenized in an appropriate buffer. Crude enzyme extracts were loaded onto 12.5% horizontal starch gels. Proteins were separated by electrophoresis that was completed in ≈ 1.5 h at 350 constant volts at 4C. Gels were sliced horizontally and PGM was detected in a 50-ml solution of 0.2 M Tris buffer (pH 8.0) to which 25 mg of fructose-6-phosphate, 10 units of glucose-6-phosphate dehydrogenase, 10 mg NADP, 10 mg MTT, 10 mg phenazine methosulfate, and 10 mg magnesium chloride were added. Extraction and run buffers have been previously reported (Marquard and Skorpenske, 1989).

Initially, only three PGM phenotypes were observed among several hundred mature pecan clones. Controlled crosses were made as described by Smith and Romberg (1940) among individuals of each of the three available phenotypes. Mature fruit from each controlled pollination were hand harvested and the PGM phenotype was determined from seed cotyledon tissue to verify inheritance. Each parental combination was evaluated by χ^2 analysis for homogeneity to expected segregation ratios. Linkage between *Mdh-1* and the putative gene (*Pgm-1*) controlling PGM was evaluated from progeny derived from a cross between the U.S. Dept. of Agriculture clone 58-3-51 and 'Osage'.

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Leaf tissue was used to characterize PGM of 65 named cultivars. PGM expression in pecan is identical among various plant parts, including cotyledons, leaves, shoots, and roots (Marquard and Skorpenske, 1989).

Table 1. Segregation and χ^2 statistic for inheritance of phosphoglucumutase (*Pgm-1*) in pecan.

Parental genotypes (<i>Pgm-1</i>) parental clone		Year of cross	Progeny segregation						Test ratio	χ^2	Probability (%)
			aa	ab	ac	bb	bc	cc			
aa	×	aa									
Western	×	Western	1989	24	---	---	---	---	---	---	---
aa	×	ab									
Western	×	58-3-51 ^z	1987	90	54	---	---	---	1:1	9.0	<0.5
Western	×	58-4-21 ^z	1989	79	49	---	---	---	1:1	7.0	<1.0
aa	×	ac									
Western	×	Riverside	1987	49	---	57	---	---	1:1	0.6	25-50
ab	×	aa									
58-3-51	×	Osage	1987	45	46	---	---	---	1:1	0.01	>90
58-3-51	×	Western	1987	28	31	---	---	---	1:1	0.15	>90
58-3-51	×	N-1-62 ^z	1987	49	60	---	---	---	1:1	1.11	25-50
ab	×	ab									
58-3-51	×	58-3-51	1987	19	36	21	---	---	1:2:1	0.32	75-90
ab	×	ac									
58-3-51	×	Riverside	1987	46	52	40	---	44	1:1:1:1	2.8	25-50
ac	×	aa									
Riverside	×	Western	1987	21	---	26	---	---	1:1	0.5	25-50
ac	×	ab									
Riverside	×	58-3-51	1987	92	47	76	---	53	1:1:1:1	19.4	<0.5
Riverside	×	58-4-21	1989	29	14	26	---	11	1:1:1:1	11.7	<1.0
ac	×	ac									
Riverside	×	Riverside	1987	14	---	33	---	10	1:2:1	1.9	25-50

^zClone 58-3-51 was parented by ('Curtis' and 'Stuart'); 58-4-21 by ('Desirable' and 'Curtis'); and N-1-62 by ('Nugget' and 'Western Schley').

Table 2. *Pgm-1* genotype of 65 pecan cultivars.

<i>Pgm-1</i> genotype	Pecan cultivars
aa	Alley, Apache, Barton, Brooks, Burkett, Caddo, Candy, Cape Fear, Carmichael, Cherokee, Cheyenne, Chickasaw, Choctaw, Colby, Comanche, Delmas, Dependable, Desirable, Evers, Forkert, Giles, Gloria Grande, GraBohls, GraCross, GraKing, Halbert, Harper, Hirschi, Ideal, Johnson, Kincaid, Kiowa, Mahan, Maramec, Melrose, Mobile, Mohawk, Moneymaker, Norton, Nugget, Odom, Osage, Pabst, Pawnee, Podsednik, Posey, Rincon, Risien #1, San Saba, San Saba Improved, Shawnee, Shoshoni, Sioux, Squirrels Delight, Success, Sullivan, Sumner, Teche, Tejas, Van Deman, Western Schley
ab	Brake, Elliott
bc	Riverside Curtis

Fig. 1. Banding patterns observed for phosphoglucumutase in pecan, relative mobilities, and associated genotypes for *Pgm-1*.

Six PGM phenotypes were observed from nuts produced from controlled crosses, and resolution of PGM isozymes was excellent (Fig. 1). Phenotypes and segregation of the progeny are consistent with one codominant gene controlled PGM in pecan and that gene is designated as *Pgm-1*. Phenotypes include three single-band types and three double-banded types. Genotype aa is arbitrarily assigned to the fastest single-banded type, and the other genotypes and corresponding phenotypes follow (Fig. 1). Heterozygous individuals produced a two-banded phenotype, suggesting PGM in pecan is a monomer, which is consistent with other plant species,

including walnut (Arulsekhar et al., 1986). Segregation ratios support simple inheritance of PGM, controlled by at least three alleles at a single locus (Table 1). However, progeny produced when *ab* pollen was used in combination with an *aa* or *ac* maternal parent resulted in significant deviation from the expected segregation ratio. Fewer individuals with an *ab* genotype were observed than expected, and this was observed in 2 years of controlled crosses with various pollen parents (Table 1). However, an *ab* × *ab* cross conformed to the expected segregation ratio, and this inconsistency remains unexplained.

Progeny from a cross between the U.S. Dept. of Agriculture clone 58-3-51 and 'Osage' cosegregated for *Mdh-1* and *Pgm-1*. 'Osage' is homozygous at both loci and the progeny segregated into four classes. The observed frequencies were 18:25:27:21, which agrees closely with the expected ratio (1:1:1:1) for independent assortment ($\chi^2 =$

2.14, $0.5 < P < 0.75$) suggesting *Mdh-1* and *Pgm-1* are not closely linked.

The majority (> 90%) of named cultivars that were characterized for *Pgm-1* had an *aa* genotype and none possessed a *bb* or *cc* genotype (Table 2). Presumably, this distribution of genotypes reflects allelic frequencies in native populations of pecan and not linkage to an undesirable trait that is being selected against. Seed collected from five native populations in five states produced seedlings that had 58 *aa* and seven *ac* genotypes (unpublished).

Gottlieb (1982) reported plants generally have two genes controlling PGM. In pecan, a second region of PGM activity, with slower migration and much fainter bands than *Pgm-1*, is infrequently observed. Whether these faint bands represent a second gene product that is poorly extracted or an artifact remains unknown. *Pgm-1* in pecan is controlled by at least three alleles and is the third gene

identified that controls a biochemical trait in pecan.

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