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Relationship between Malate Dehydrogenase Isozyme Genotype and Plant Vigor in Peach

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***Abstract.* The relationship between malate dehydrogenase (MDH) isozyme genotype and plant vigor in peach *[Prunus persica* (L.) Batsch] was examined in two F_2 populations (selfed 'Belle of Georgia' and 'Cresthaven') segregating at the *Mdh1* locus. Total progeny examined were 1610 and 998 in the 'Belle of Georgia' and 'Cresthaven' populations, respectively. In both populations, plant vigor (as defined by total height and trunk caliper after 1 year of growth) was significantly less in *Mdh1-1/Mdh1-1* homozygotes. Homozygous *Mdh1-2/Mdh1-2* individuals showed the greatest vigor, and were significantly different in vigor from *Mdh1-1/Mdh1-1* homozygotes in both populations and from *Mdh1-1/Mdh1-2* heterozygotes in the 'Belle of Georgia' population. A significant deviation from the expected 1 *Mdh1-1/Mdh1-1* : 2 *Mdh1-1/Mdh1-1* : 1 *Mdh1-2/Mdh1-2* ratio was observed in the 'Belle of Georgia' population, suggesting moderate lethality of homozygous *Mdh1-1/Mdh1-1* genotypes.**

Isozyme polymorphism at the *Mdh1* locus in peach has been described by various authors. Arulsekar et al. (1986) and Durham et al. (1987) demonstrated that the variability observed for MDH in peach could be explained by the presence of two alleles (S and F) interacting at a single locus, designated *Mgh1*. Mowrey et al. (1990) reported the presence of a third allele *(Mdh1-3)* at the *Mdh1* locus, and proposed the designation of *Mdh1-1* and *Mdh1-2* for the F and S alleles, respectively. Characterization of peach cultivars, breeding lines, and plant introductions for MDH has shown that *Mdh1-1/Mdh1-1* homozygotes are very rare. Of 290 cultivars tested by Arulsekar et al, (1986), only six were *Mdh1-1/Mdh1-1.* Durham et al. (1987) found only one *Mdh1-1lMdh1-1* homozygote among 59 cultivars and breeding lines surveyed. Mowrey et al. (1990) found only one *Mdh1-1/Mdh1-1* homozygote among 56 peach plant introductions. This is noteworthy, because the cultivar 'Chinese Cling', introduced into the United States in 1850 (Scorza et al., 1985), is homozygous *Mdh1-1/Mdh1-1* (Arulsekar et al., 1986). This cultivar served as the base for cultivar improvement in most state and federal peach breeding programs. Most commercial peach cultivars grown today in the eastern United States can be traced back to 'Chinese Cling' (Scorza et al., 1985). Thus, the *Mdh1-1* allele has been rapidly eliminated from breeding populations. Arulsekar et al. (1986) and Mowrey et al. (1990) have suggested that the *Mdh1-1* allele in the homozygous state may have some selective disadvantage, or is closely linked to an undesirable character.

During routine electrophoretic analysis of various F_2 populations in support of our gene linkage studies in peach, an apparent association between MDH isozyme genotype and plant vigor was observed. This study was initiated to determine the relationship between MDH isozyme genotype and plant vigor in peach using two F_2 populations segregating at the *Mdh1* locus.

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Materials and Methods

Two F_2 populations (selfed 'Belle of Georgia' and 'Cresthaven') segregating for the *Mdh1-1* and *Mdh1-2* alleles at the *Mdh1* locus were used to examine the relationship between MDH isozyme genotype and plant vigor. Seed from selfed plants was obtained from each cultivar in 1988 by enclosing trees in screen cages during bloom to exclude pollinating insects. Fruit were harvested when mature, and pits were removed from the fruit. Pits containing the seed were planted directly in the field in Oct. 1988 in methyl bromide-fumigated soil at the Sandhills Research Station, Jackson Springs, N.C. Seeds were spaced ≈10 cm apart in rows 6 m apart. Seeds germinated in Mar. 1989 after exposure to natural stratification. Actively growing plants in both populations were characterized for MDH on morpholine-citrate (pH 6.1) starch gels using standard electrophoretic techniques described by Mowrey et al. (1990). Plant vigor was determined by measuring total height and trunk caliper of each plant at the end of the first growing season. Total progeny examined were 1610 and 998 in the 'Belle of Georgia' and 'Cresthaven' populations, respectively. Mean plant height and caliper were calculated for each MDH isozyme genotype class within each population, and means were compared using the Waller–Duncan K-ratio *t* test (Wailer and Duncan, 1969).

Results and Discussion

Plant height and caliper were strongly correlated; only the plant height data are presented. Mean height of F_2 trees from 'Belle of Georgia' (135.0 cm) was significantly greater than that from 'Cresthaven' (121.6 cm). In both populations, mean plant height was significantly less in *Mdh1-1/Mdh1-1* homozygotes when compared to the other genotypes (Table 1).

Table 1. Mean plant height of three malate dehydrogenase isozyme genotype groups in two F_2 peach populations after 1 year of growth.

	Plant ht (cm)	
	F_2 population[z]	
MDH genotype	Belle of Georgia	Cresthaven
Mdh1-1/Mdh1-1	108.3 a	110.0 a
Mdh1-1/Mdh1-2	139.4 b	125.5 b
Mdh1-2/Mdh1-2	148.1 c	125.2 b

[z]Mean separation within column by Waller–Duncan K-ratio *t* test, (K = 100).

Homozygous *Mdh1-2/Mdh1-2* individuals showed the greatest vigor and were significantly different from *Mdh1-1/Mdh1-1* homozygotes in both populations and from *Mdh1-1/Mdh1-2* heterozygotes in the 'Belle of Georgia' population. The association between MDH genotype and plant vigor was greater in the 'Belle of Georgia' population than in 'Cresthaven', as shown by the frequency distribution data (Figs. 1 and 2). The additive effect [calculated as: *(Mdh1-2/Mdh1-2* mean height - *Mdh1-1/Mdh1-1* mean height)/2] associated with the *Mdh1-2* allele was 19.9 and 7.8 cm in the 'Belle of Georgia' and 'Cresthaven' populations, respectively. Mean height of *Mdh1-1/Mdh1-1* homozygotes was 27% and 12% less than that of *Mdh1-2/Mdh1-2* homozygotes in the 'Belle of Georgia' and 'Cresthaven' populations, respectively (Table 1). A significant deviation from the expected 1 *Mdh1-1lMdh1-1* : 2 *Mdh1-1/Mdh1-2* : 1 *Mdh1-2/Mdh1-2* ratio was observed in the 'Belle of Georgia' population (χ^2 = 10.6, $P < 0.01$), but not in the 'Cresthaven' population ($\chi^2 = 2.08$, $P = 0.25 - 0.50$) (Table 2). This result suggests that moderate lethality of *Mdh1-1/Mdh1-1* homozygotes may

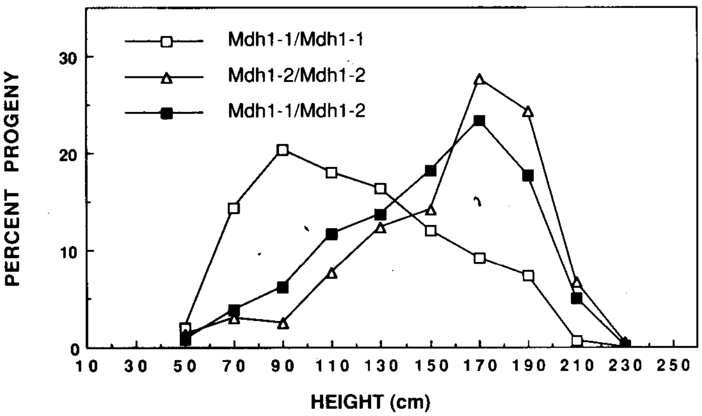

Fig. 1. Frequency distribution of three malate dehydrogenase isozyme classes (*Mdh1-1/Mdh1-1, Mdh1-2/Mdh1-2,* and *Mdh1-1/Mdh1-2*) in an F_2 population of 'Belle of Georgia' peach. Data points represent the percentage of total progeny within MDH class contained in the height interval defined by that x axis height value and the prior labeled value.

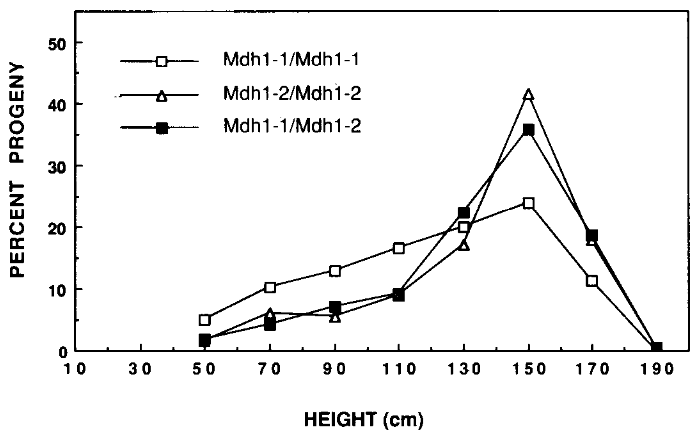

Fig. 2. Frequency distribution of three malate dehydrogenase isozyme classes (*Mdh1-1/Mdh1-1, Mdh1-2/Mdh1-2,* and *Mdh1-1/Mdh1-2*) in an F_2 population of 'Cresthaven' peach. Data points represent the percentage of total progeny within MDH class contained in the height interval defined by that x axis height value and the prior labeled value.

Table 2. Phenotypic ratios and goodness-of-fit for segregation at the *Mdh1* isozyme locus in two peach F_2 populations.

	Segregation classes					
F_2 population	*Mdh 1-1/1-1*	*Mdh 1-1/1-2*	*Mdh 1-2/1-2*	Test ratio	χ^2	*P* value
Belle of Georgia	350	820	440	1:2:1	10.6	<0.01
Cresthaven	246	483	269	1:2:1	2.1	0.25–0.50

occur in certain genetic backgrounds and may explain partially the rarity of this genotype.

It is noteworthy that other homozygous *Mdh1-1/Mdh1-1* peach cultivars exhibit low vigor. 'Chinese Cling' and 'Siberian-C', both *Mdh1-1/Mdh1-1* (Arulsekar et al., 1986), are low to modcrate in vigor (characterization of 'Siberian C' by R.E.C. Layne, personal communication). As early as 1932, Blake (1932) characterized the cultivar J.H. Hale *(Mdh1-1/Mdh1-2)* as "slightly dwarf" in habit. Blake (1933) further reported that 'Elberta' (heterozygous *Mdh1-1/Mdh1-2),* a seedling of 'Chinese Cling' (Hedrick, 1917), produced numerous "semi-dwarf" and "full dwarf" seedlings. These reports further support the relationship between the homozygous *Mdh1-1/Mdh1-1* genotype and low vigor in peach.

Our results clearly show that *Mdh1-1/Mdh1-1* homozygotes are low in vigor, and that the relationship was greater in the 'Belle of Georgia' population as compared to 'Cresthaven'. 'Belle of Georgia' is a direct descendent of 'Chinese Cling', having originated as an open-pollinated seedling from it (Hedrick, 1917). Conversely, 'Cresthaven' has a more complex pedigree (Brooks and Olmo, 1972), and is about four generations removed from 'Chinese Cling'. Differences in the two populations regarding the relative effect of the *Mdh1-1* allele on plant vigor may be attributed to differences in genetic backgrounds. It is possible that other genes affecting vigor, either in unlinked regions of the genome or in the region near the *Mdh1* locus, also are segregating in the F_2 population of 'Cresthaven', thus obscuring the relationship between vigor and MDH genotype.

We propose that one explanation for the rarity of homozygous *Mdh1-1/Mdh1-1* genotypes among commercial peach cultivars and breeding lines is due to the marked reduction in vigor of these individuals, and their subsequent loss through natural competition in seedling rows and through culling by breeders during selection. Moderate lethality of *Mdh1-1/Mdh1-1* homozygotes further reduces their numbers in breeding populations. Peach breeders have long lamented the production problems faced due to the undesirably high vigor of most commercial peach cultivars, and the lack of appropriate dwarfing rootstock and appropriate dwarf and semi-dwarf scion cultivars to address this concern. This study suggests that a full range in plant vigor can be obtained in young seedling populations segregating at the *Mdh1* locus, and that this association between vigor and MDH genotype provides a convenient marker that can be characterized as early as the seed stage, if desired.

The basis for the relationship between MDH genotype and plant vigor cannot be determined from these data. Low vigor of *Mdh1-1/Mdh1-1* homozygotes could be due directly to the kinetics and cellular function of the actual variant isozyme itself. Alternatively, the *Mdh1* locus may be closely linked to a gene with a major influence on plant vigor, and this gene may have been introduced with the *Mdh1-1* allele into current commercial germplasm from 'Chinese Cling'. The existence of some *Mdh1-1/Mdh1-1* homozygotes exhibiting normal vigor in the two populations examined in this study lends support to the gene linkage hypothesis. Also, the presence of *Mdh1-2/Mdh1-2* homozygotes showing low vigor supports this hypothesis, in that such individuals may represent recombinant. These alternatives warrant further investigation.

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