Isozyme Variation Among California Almond Cultivars: II. Cultivar Characterization and Origins

R. Hauagge¹, D.E. Kester², S. Arulasekar³, D.E. Parfitt⁴, and L. Liu⁵
University of California, Davis, CA 95616

Additional index words: germplasm, electrophoresis, Prunus dulcis

Abstract. Horizontal starch gel electrophoresis was used to study the variation of aspartate aminotransferase (AAT-1), glucose phosphate isomerase (GPI-2), leucine aminopeptidase (LAP-1) and phosphoglucomutase (PGM-1 and PGM-2) isozymes in 76 cultivars and accessions of almond. Cultivars could be separated into 40 classes for identification.

Six major commercial almond cultivars have been grown since the early 1900s. The principal cultivar has been 'Nonpareil' (60–65% of the crop) and 'Texas Prolific', since named 'Mission' (~25%). 'Ne Plus Ultra', 'Peerless', 'Drake’s Seedling', 'Ne Plus Ultra', 'Peerless', 'Drake’s Seedling', and 'Nonpareil' are among the most popular cultivars in California. These cultivars have been selected and propagated for over a century, resulting in a diverse range of genetic variation. Allozymes also can be used to study variation within specific populations of organisms and to show relationships among them.

The cultivated almond (Prunus dulcis D.A. Webb syn. P. amygdalus Batsch.) is represented in California by a group of cultivars that were from seedling selections made prior to 1900 or their descendents (9, 13, 21). The original introduction of almonds to California was made during the latter part of the 19th century. The almonds were either scions of European cultivars or seeds from which seedling orchards were grown. Superior seedlings were selected, named, and propagated by observant pioneer horticulturists.

Six major commercial almond cultivars have been grown since the early 1900s. The principal cultivar has been 'Nonpareil' (60–65% of the crop) and 'Texas Prolific', since named 'Mission' (~25%). 'Ne Plus Ultra', 'Peerless', 'Drake’s Seedling',...
and ‘I.X.L.’ were grown to a lesser extent in combination with the main cultivars for cross-pollination. These six accounted for about 95% of the commercial acreage by 1940 (9). Beginning in 1938, additional cultivars have been introduced from breeding programs (6). More significant, chance seedlings along roads or ditchbanks near commercial orchards or ungrafted rootstocks became a source of new cultivars. Beginning about the 1950s, these chance seedlings have been selected and patented by orchardists and nurserymen and have been planted extensively in commercial orchards. Between 1958 to the present, about 50 cultivars have been patented and introduced, many of which have unknown or incompletely known parentage (6, 13).

Phenotypic observations, pollen incompatibility studies, and inheritance studies (10) suggest that most of the recent California cultivars are offspring of ‘Nonpareil’ and ‘Mission’. A knowledge of cultivar origin could improve our understanding of the source of certain genetic traits among this group of cultivars, including noninfectious bud-failure (12), pollen incompatibility (9, 13), and graft incompatibility to Marianna 2624 plum rootstock (9, 10).

The inheritance of four different isozyme systems [i.e., aspartate aminotransferase (AAT), glucose phosphate isomerase (GPI), leucine aminopeptidase (LAP), and phosphoglucomutase (PGM)] has been established in almond (7, 8) and provides the basis for the present study.

This paper describes the isozyme patterns for 73 cultivars and selections and their possible origins (11).

**Materials and Methods**

Sources of plant materials were cultivars growing in orchards of the Univ. of California, Davis, or in cultivar test plots (11). The youngest fully expanded leaves from mature trees of each almond cultivar were collected from healthy, vigorous shoots of terminal buds that were still growing. At least three samples collected at different times during the growing season were assayed for each cultivar. Leaves were stored at 2°C until used for protein extraction. Protein extraction, gel running, and assay conditions have been described elsewhere (8).

Genetic control for the isozymes of ATT, GPI, LAP, and PGM have been established using starch gel electrophoresis (7, 8). The nomenclature used to denote isozymes is based on Wendel and Parks (19). The allelic designation based on the observed genotype with a possible null allele was checked only for the cultivars ‘Mission’ and ‘Padre’.

**Results and Discussion**


The above cultivars were divided into five main classes according to origin (Tables 1, 2, and 3). Their parentage is discussed on the basis of their isozyme constitution. General plant and nut phenotypes and relationships among pollen incompatibility alleles are also important in origin analysis of almond cultivars (D.E. Kester, unpublished data).

**Group 1: Original California genotypes.** Twenty-two cultivars originating prior to 1900 represent the original isozyme gene pool available in California and include both imported cultivars (e.g., ‘Almendro de la Pie’, ‘Marcona’, ‘Jordan’, and ‘Tarragona’) and named seedling selections (Table 1). These cultivars are grouped in a system that allows classification according to genotype. Fourteen of the 15 possible genotypes are represented. These include two of the three possible genotypes of GPI-2 and all three genotypes of LAP-2, AAT-1, PGM-1, and PGM-2. In addition, ‘Mission’ has possibly a null allele at the Lap-1 locus (8). The genotypes of the two major commercial cultivars in California (‘Nonpareil’ and ‘Mission’) are shown and the percent alleles common to them are given (Table 1).

‘Nonpareil’, ‘Ne Plus Ultra’, ‘I.X.L.’, and ‘LaPrima’ are a significant subgroup that originated from a single seedling orchard planted by A.T. Hatch, Suisun, Calif. in 1879 (20, 21). Three of these cultivars became major cultivars. ‘Nonpareil’ and ‘LaPrima’ have the same genotypes for the five isozymes. ‘Ne Plus Ultra’ differs by one and ‘I.X.L.’ by three.

The Gpi-2ab genotype is unique and separates ‘Mission’—‘Languedoc’—‘Walton’ and ‘Tarragona’ from others in Group 1, which are homozygous for Gpi-2aa. Their uniqueness also is shown by a low percentage of common alleles with the other cultivars. ‘Languedoc’ was the ancestral early (=1850s) cultivar, supposedly imported from France, although it is different from similarly named cultivars currently grown there (C. Grassely, personal communication). ‘Texas Prolific’, originating in Houston, Texas, is presumably a seedling of ‘Languedoc’ reintroduced to California about 1900 (20) and eventually renamed ‘Mission’. The Gpi-2ab genotype and the null allele of Lap-1 are important markers for ‘Mission’ parentage.

Other groups with similar genotypes among this original population include ‘Peerless’ and ‘Smith XL’, ‘Drake’ differing by one allele, as does ‘Eureka’ and ‘Long IXL’.

Four Spanish cultivars (‘Marcona’, ‘Jordan’, ‘Almendro de la Pie’, and ‘Tarragona’) show a range of isozyme genotypes that parallel the range of isozymes of California-originated cultivars.

**Group 2: Controlled crosses.** Isozyme patterns of nine cultivars of known parentage (Table 2) show the large extent to which ‘Nonpareil’ was used as a parent in breeding programs. A large number of alleles present in ‘Nonpareil’ are also shown in their offspring with 70% to 100% of the alleles being identical.

F.W. Anderson (private breeder) used ‘Mission’ as the dominant parent in his breeding program. ‘Nonpareil’ was probably the other parent or grandparent in these cultivars. These cultivars show a range of isozyme variability—some being similar to ‘Nonpareil’, others to ‘Mission’. Others came from seedlings of ‘Tardy Nonpareil’, a late-blooming mutation of ‘Nonpareil’ with the same isozyme genotype. Isozyme analysis provides
Table 1. Isozyme genotypes for four polymorphic isozymes in the population of California almond cultivars introduced before 1900 (20).

<table>
<thead>
<tr>
<th>Cultivar</th>
<th>Isozyme designation</th>
<th>Percent alleles common to</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Gpi-2</td>
<td>Lap-1</td>
</tr>
<tr>
<td>Peerless®, Smith XL</td>
<td>aa</td>
<td>bb</td>
</tr>
<tr>
<td>Drake®</td>
<td>aa</td>
<td>bb</td>
</tr>
<tr>
<td>I.X.L.®</td>
<td>aa</td>
<td>bb</td>
</tr>
<tr>
<td>Almendro de la Pie®</td>
<td>aa</td>
<td>bc</td>
</tr>
<tr>
<td>Bigelow, Golden State</td>
<td>aa</td>
<td>bc</td>
</tr>
<tr>
<td>LaMarie</td>
<td>aa</td>
<td>bc</td>
</tr>
<tr>
<td>Eureka, Long IXL</td>
<td>aa</td>
<td>bc</td>
</tr>
<tr>
<td>Nonpareil®, Ne Plus Ultra®</td>
<td>aa</td>
<td>bc</td>
</tr>
<tr>
<td>hatch origin (see text).</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Languedoc</td>
<td>ab</td>
<td>bc</td>
</tr>
<tr>
<td>Walton</td>
<td>ab</td>
<td>cc</td>
</tr>
<tr>
<td>Nonpareil, 'La Prima'</td>
<td>aa</td>
<td>bc</td>
</tr>
<tr>
<td>Ne Plus Ultra</td>
<td>aa</td>
<td>bc</td>
</tr>
<tr>
<td>Lewelling</td>
<td>aa</td>
<td>bc</td>
</tr>
<tr>
<td>Standard</td>
<td>aa</td>
<td>bc</td>
</tr>
<tr>
<td>Harriot</td>
<td>aa</td>
<td>cc</td>
</tr>
<tr>
<td>Jordan®</td>
<td>aa</td>
<td>cc</td>
</tr>
<tr>
<td>Marcona®</td>
<td>aa</td>
<td>cc</td>
</tr>
<tr>
<td>Tarragona®</td>
<td>ab</td>
<td>bc</td>
</tr>
<tr>
<td>Mission®</td>
<td>ab</td>
<td>nc</td>
</tr>
<tr>
<td>Languedoc</td>
<td>ab</td>
<td>cc</td>
</tr>
<tr>
<td>Walton</td>
<td>ab</td>
<td>cc</td>
</tr>
<tr>
<td>Nonpareil, 'La Prima'</td>
<td>aa</td>
<td>bc</td>
</tr>
<tr>
<td>Ne Plus Ultra</td>
<td>aa</td>
<td>bc</td>
</tr>
<tr>
<td>hatch origin (see text).</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Languedoc</td>
<td>ab</td>
<td>cc</td>
</tr>
<tr>
<td>Walton</td>
<td>ab</td>
<td>cc</td>
</tr>
<tr>
<td>Nonpareil, 'La Prima'</td>
<td>aa</td>
<td>bc</td>
</tr>
<tr>
<td>Ne Plus Ultra</td>
<td>aa</td>
<td>bc</td>
</tr>
<tr>
<td>hatch origin (see text).</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Languedoc</td>
<td>ab</td>
<td>cc</td>
</tr>
<tr>
<td>Walton</td>
<td>ab</td>
<td>cc</td>
</tr>
<tr>
<td>Nonpareil, 'La Prima'</td>
<td>aa</td>
<td>bc</td>
</tr>
<tr>
<td>Ne Plus Ultra</td>
<td>aa</td>
<td>bc</td>
</tr>
<tr>
<td>hatch origin (see text).</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Languedoc</td>
<td>ab</td>
<td>cc</td>
</tr>
<tr>
<td>Walton</td>
<td>ab</td>
<td>cc</td>
</tr>
<tr>
<td>Nonpareil, 'La Prima'</td>
<td>aa</td>
<td>bc</td>
</tr>
<tr>
<td>Ne Plus Ultra</td>
<td>aa</td>
<td>bc</td>
</tr>
<tr>
<td>hatch origin (see text).</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Languedoc</td>
<td>ab</td>
<td>cc</td>
</tr>
<tr>
<td>Walton</td>
<td>ab</td>
<td>cc</td>
</tr>
<tr>
<td>Nonpareil, 'La Prima'</td>
<td>aa</td>
<td>bc</td>
</tr>
<tr>
<td>Ne Plus Ultra</td>
<td>aa</td>
<td>bc</td>
</tr>
<tr>
<td>hatch origin (see text).</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Languedoc</td>
<td>ab</td>
<td>cc</td>
</tr>
<tr>
<td>Walton</td>
<td>ab</td>
<td>cc</td>
</tr>
<tr>
<td>Nonpareil, 'La Prima'</td>
<td>aa</td>
<td>bc</td>
</tr>
<tr>
<td>Ne Plus Ultra</td>
<td>aa</td>
<td>bc</td>
</tr>
<tr>
<td>hatch origin (see text).</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Languedoc</td>
<td>ab</td>
<td>cc</td>
</tr>
<tr>
<td>Walton</td>
<td>ab</td>
<td>cc</td>
</tr>
<tr>
<td>Nonpareil, 'La Prima'</td>
<td>aa</td>
<td>bc</td>
</tr>
<tr>
<td>Ne Plus Ultra</td>
<td>aa</td>
<td>bc</td>
</tr>
<tr>
<td>hatch origin (see text).</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Languedoc</td>
<td>ab</td>
<td>cc</td>
</tr>
<tr>
<td>Walton</td>
<td>ab</td>
<td>cc</td>
</tr>
</tbody>
</table>

Supporting evidence that 'Mission' is the other putative parent. 'Ripon', 'Titan', and 'Tioga' have the Gpi-2ab genotype, which indicates a direct relationship to 'Mission'. 'Ripon' and 'Titan' also have the Lap-1bb genotype, which could result from segregation of the null allele Lap-1cn in 'Mission' when crossed to 'Nonpareil' with a Lap-1bc genotype.

Group 3: Chance seedlings. The genotypes of a large number of cultivars of chance seedling origin are presented (Table 3).

Table 2. Isozyme genotypes from four polymorphic isozymes in almond cultivars derived from controlled crosses in California breeding programs.

<table>
<thead>
<tr>
<th>Cultivar</th>
<th>Isozyme designation</th>
<th>Percent common alleles with</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Gpi-2</td>
<td>Lap-1</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Harpareil</td>
<td>aa</td>
<td>cc</td>
</tr>
<tr>
<td>Jordanolo</td>
<td>aa</td>
<td>bc</td>
</tr>
<tr>
<td>Nonpareil x Harriott</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Davey</td>
<td>aa</td>
<td>bc</td>
</tr>
<tr>
<td>Nonpareil x Sans Faute</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Vesta</td>
<td>aa</td>
<td>bc</td>
</tr>
<tr>
<td>Solano</td>
<td>aa</td>
<td>bc</td>
</tr>
<tr>
<td>Kapareil</td>
<td>aa</td>
<td>bc</td>
</tr>
<tr>
<td>Milow</td>
<td>aa</td>
<td>cc</td>
</tr>
<tr>
<td>Sonora</td>
<td>aa</td>
<td>cc</td>
</tr>
<tr>
<td>Tardy Nonpareil x OP (probably 'Mission')*</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Planada</td>
<td>aa</td>
<td>bc</td>
</tr>
<tr>
<td>Ripon</td>
<td>ab</td>
<td>bb</td>
</tr>
<tr>
<td>Titan</td>
<td>ab</td>
<td>bb</td>
</tr>
<tr>
<td>Tioga</td>
<td>ab</td>
<td>cc</td>
</tr>
<tr>
<td>Mission x Nonpareil</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Yosemite</td>
<td>aa</td>
<td>bc</td>
</tr>
<tr>
<td>Butte</td>
<td>aa</td>
<td>cc</td>
</tr>
</tbody>
</table>

*Came from orchard where 'Mission' was pollinator.
<table>
<thead>
<tr>
<th>Cultivar</th>
<th>Gpi-2</th>
<th>Lap-1</th>
<th>Aat-1</th>
<th>Pgm-1</th>
<th>Pgm-2</th>
<th>Percent common alleles with Nonpareil</th>
<th>Percent common alleles with Mission</th>
</tr>
</thead>
<tbody>
<tr>
<td>Nonpareil</td>
<td>aa</td>
<td>bb</td>
<td>aa</td>
<td>bb</td>
<td>ab</td>
<td>70</td>
<td>30</td>
</tr>
<tr>
<td>Mission</td>
<td>aa</td>
<td>bc</td>
<td>ab</td>
<td>bb</td>
<td>aa</td>
<td>70</td>
<td>30</td>
</tr>
<tr>
<td>Spencer</td>
<td>aa</td>
<td>bb</td>
<td>ab</td>
<td>bb</td>
<td>aa</td>
<td>70</td>
<td>30</td>
</tr>
<tr>
<td>Kutsch</td>
<td>aa</td>
<td>bc</td>
<td>ab</td>
<td>aa</td>
<td>ab</td>
<td>70</td>
<td>30</td>
</tr>
<tr>
<td>Bonita</td>
<td>aa</td>
<td>bc</td>
<td>aa</td>
<td>aa</td>
<td>ab</td>
<td>70</td>
<td>30</td>
</tr>
<tr>
<td>Mono e</td>
<td>aa</td>
<td>bc</td>
<td>ab</td>
<td>bb</td>
<td>ab</td>
<td>70</td>
<td>30</td>
</tr>
<tr>
<td>Thompson</td>
<td>aa</td>
<td>bc</td>
<td>ab</td>
<td>bb</td>
<td>ab</td>
<td>70</td>
<td>30</td>
</tr>
<tr>
<td>Profuse</td>
<td>aa</td>
<td>bc</td>
<td>ab</td>
<td>aa</td>
<td>ab</td>
<td>70</td>
<td>30</td>
</tr>
<tr>
<td>Selectian 88-66</td>
<td>aa</td>
<td>bc</td>
<td>ab</td>
<td>aa</td>
<td>ab</td>
<td>70</td>
<td>30</td>
</tr>
<tr>
<td>Moneytree</td>
<td>aa</td>
<td>bc</td>
<td>ab</td>
<td>aa</td>
<td>ab</td>
<td>70</td>
<td>30</td>
</tr>
<tr>
<td>Harvey, Merced</td>
<td>aa</td>
<td>bc</td>
<td>ab</td>
<td>ab</td>
<td>aa</td>
<td>70</td>
<td>30</td>
</tr>
<tr>
<td>Sans Faute</td>
<td>aa</td>
<td>bc</td>
<td>ab</td>
<td>ab</td>
<td>ab</td>
<td>70</td>
<td>30</td>
</tr>
<tr>
<td>Ruby</td>
<td>aa</td>
<td>bc</td>
<td>ab</td>
<td>ab</td>
<td>ab</td>
<td>70</td>
<td>30</td>
</tr>
<tr>
<td>Carrion</td>
<td>aa</td>
<td>cc</td>
<td>ab</td>
<td>ab</td>
<td>bb</td>
<td>70</td>
<td>30</td>
</tr>
<tr>
<td>Monterey, Tokyo</td>
<td>aa</td>
<td>cc</td>
<td>ab</td>
<td>ab</td>
<td>bb</td>
<td>70</td>
<td>30</td>
</tr>
<tr>
<td>Heart, Elsie,</td>
<td>aa</td>
<td>cc</td>
<td>ab</td>
<td>ab</td>
<td>bb</td>
<td>70</td>
<td>30</td>
</tr>
<tr>
<td>LeGrand d</td>
<td>aa</td>
<td>cc</td>
<td>ab</td>
<td>ab</td>
<td>bb</td>
<td>70</td>
<td>30</td>
</tr>
<tr>
<td>Carmel, Godde,</td>
<td>aa</td>
<td>cc</td>
<td>ab</td>
<td>ab</td>
<td>bb</td>
<td>70</td>
<td>30</td>
</tr>
<tr>
<td>Janice, Arbuckle</td>
<td>aa</td>
<td>cc</td>
<td>ab</td>
<td>ab</td>
<td>bb</td>
<td>70</td>
<td>30</td>
</tr>
<tr>
<td>Sydney Special,</td>
<td>aa</td>
<td>cc</td>
<td>ab</td>
<td>ab</td>
<td>bb</td>
<td>70</td>
<td>30</td>
</tr>
<tr>
<td>Livingston</td>
<td>aa</td>
<td>cc</td>
<td>ab</td>
<td>ab</td>
<td>bb</td>
<td>70</td>
<td>30</td>
</tr>
<tr>
<td>Fritz</td>
<td>ab</td>
<td>bb</td>
<td>aa</td>
<td>ab</td>
<td>bb</td>
<td>70</td>
<td>30</td>
</tr>
<tr>
<td>Granada</td>
<td>ab</td>
<td>bb</td>
<td>aa</td>
<td>ab</td>
<td>ab</td>
<td>70</td>
<td>30</td>
</tr>
<tr>
<td>Monarch</td>
<td>ab</td>
<td>bb</td>
<td>aa</td>
<td>ab</td>
<td>ab</td>
<td>70</td>
<td>30</td>
</tr>
<tr>
<td>Pioneer</td>
<td>ab</td>
<td>cc</td>
<td>ab</td>
<td>ab</td>
<td>ab</td>
<td>70</td>
<td>30</td>
</tr>
<tr>
<td>Hoover, LeGrand e</td>
<td>ab</td>
<td>cc</td>
<td>ab</td>
<td>ab</td>
<td>ab</td>
<td>70</td>
<td>30</td>
</tr>
<tr>
<td>Price</td>
<td>ab</td>
<td>cc</td>
<td>aa</td>
<td>ab</td>
<td>bb</td>
<td>70</td>
<td>30</td>
</tr>
<tr>
<td>Rosbon</td>
<td>ab</td>
<td>cc</td>
<td>aa</td>
<td>ab</td>
<td>bb</td>
<td>70</td>
<td>30</td>
</tr>
<tr>
<td>Ballico</td>
<td>ab</td>
<td>cc</td>
<td>ab</td>
<td>aa</td>
<td>ab</td>
<td>70</td>
<td>30</td>
</tr>
<tr>
<td>Padre, Valenta</td>
<td>ab</td>
<td>cc</td>
<td>ab</td>
<td>ab</td>
<td>ab</td>
<td>70</td>
<td>30</td>
</tr>
<tr>
<td>Sauret #1</td>
<td>ab</td>
<td>cc</td>
<td>ab</td>
<td>aa</td>
<td>ab</td>
<td>70</td>
<td>30</td>
</tr>
<tr>
<td>Grace, Norman</td>
<td>ab</td>
<td>cc</td>
<td>ab</td>
<td>aa</td>
<td>ab</td>
<td>70</td>
<td>30</td>
</tr>
</tbody>
</table>

To establish possible parents of these chance-seeding cultivars, isozyme combinations for the progeny of all possible crosses of the six potential parents were calculated (not shown) and possible parental combinations for each of the cultivars are given (Table 4). The cross 'Nonpareil' x 'I.X.L.' is not included because these cultivars are pollen cross-incompatible and should not produce any progeny (10). 'Nonpareil' could have been one of the parents in all 34 cultivars, 'Mission' in 31, 'Ne Plus Ultra' in 23, 'Peerless' in 14, 'Drake' in 11, and 'I.X.L.' in five. The most probable parental combinations for all of these cultivars were 'Nonpareil' x 'Mission' (91%), 'Nonpareil' x 'Ne Plus Ultra' (50%), and 'Ne Plus Ultra' x 'Mission' (59%). The latter cross is less-likely because of difference in time of bloom. One reason that 'Ne Plus Ultra' may appear as a frequent parental potential is the close similarity of its isozyme pattern with 'Nonpareil', which differs by only one allele. Cultivars were ranked in order of numbers of possible parental combinations with which they were related.

Group 3.1 includes 'Merced' and 'Harvey', which have identical isozyme genotypes with 'Nonpareil', and 'Sans Faute', which differs from 'Nonpareil' by one allele. Although these data show other parental possibilities, 'Nonpareil', 'Mission', and 'Ne Plus Ultra' dominate as likely parents. The next group (3.2) includes 'Sauret #2', 'Thompson', and 'Mono'. These differ from Group 3.1 by one allele and one less possible cross. ‘Ruby’ (Group 3.3) has the same isozymes as ‘Planada’ (Table 2) and differs from group 3.2 since only four cultivars are possible parents.

Group 3.4 includes seven cultivars that have the same possible parents, with only three possible crosses ('Nonpareil' x 'Mission', 'Nonpareil' x 'Ne Plus Ultra', and 'Mission' x 'Ne Plus Ultra'). ‘Butte’ (Table 2) also has the same allelic combination as this group and is a descendant of ‘Nonpareil’ and ‘Mission’ (16).

Group 3.5 includes five cultivars, with the only possible parents being either 'Nonpareil' x 'Mission' or 'Mission' x 'Ne Plus Ultra'. ‘Padre’ is a cross of ‘Mission’ x ‘Swanson’. The latter is an unknown chance selection present in a grower orchard and likely to be ‘Nonpareil’ x ‘Mission’. ‘Norman’ and ‘Tioga’ also have the same alleles as this group (Table 3). Group 3.6 has seven cultivars for which the only possible parentage is ‘Nonpareil’ x ‘Mission’.

Group 3.7 is a miscellaneous group. ‘Monarch’ and ‘Granada’ have ‘Mission’ for one of the parents because of the b allele of the Gpi-2 genotype. Other parents than ‘Nonpareil’ are suggested, such as ‘Peerless’, ‘Drake’, or ‘I.X.L.’. ‘Granada’ nuts are morphologically similar to ‘I.X.L.’, suggesting that it is the other parent.

Group 3.8 is a miscellaneous group where the origin is less clear. Although all could have arisen from ‘Nonpareil’ x ‘Miss-
Table 4. Possible origins of various cultivars based on inheritance of five isozyme systems.

<table>
<thead>
<tr>
<th>Cultivar</th>
<th>Nonpareil</th>
<th>Mission</th>
<th>NPU</th>
<th>Peerless</th>
<th>Group</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>M</td>
<td>Ne</td>
<td>P</td>
<td>D</td>
<td></td>
</tr>
<tr>
<td>1. Merced</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td></td>
</tr>
<tr>
<td>2. Harvey</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td></td>
</tr>
<tr>
<td>3. Sans Faute</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td></td>
</tr>
<tr>
<td>4. Säuret #2</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td></td>
</tr>
<tr>
<td>5. Thompson</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td></td>
</tr>
<tr>
<td>6. Mono</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td></td>
</tr>
<tr>
<td>7. Ruby</td>
<td>X</td>
<td>X</td>
<td>O</td>
<td>X</td>
<td></td>
</tr>
<tr>
<td>8. Janice</td>
<td>X</td>
<td>X</td>
<td>O</td>
<td>O</td>
<td></td>
</tr>
<tr>
<td>9. Carmel</td>
<td>X</td>
<td>X</td>
<td>O</td>
<td>O</td>
<td></td>
</tr>
<tr>
<td>10. Carrion</td>
<td>X</td>
<td>X</td>
<td>O</td>
<td>O</td>
<td></td>
</tr>
<tr>
<td>11. Godde</td>
<td>X</td>
<td>X</td>
<td>O</td>
<td>O</td>
<td></td>
</tr>
<tr>
<td>12. Monterey</td>
<td>X</td>
<td>X</td>
<td>O</td>
<td>O</td>
<td></td>
</tr>
<tr>
<td>13. Livingston</td>
<td>X</td>
<td>X</td>
<td>O</td>
<td>O</td>
<td></td>
</tr>
<tr>
<td>14. Tokyo</td>
<td>X</td>
<td>X</td>
<td>O</td>
<td>O</td>
<td></td>
</tr>
<tr>
<td>15. Padre</td>
<td>X</td>
<td>O</td>
<td>O</td>
<td>O</td>
<td></td>
</tr>
<tr>
<td>16. Robson</td>
<td>X</td>
<td>O</td>
<td>O</td>
<td>O</td>
<td></td>
</tr>
<tr>
<td>17. Grace</td>
<td>X</td>
<td>O</td>
<td>O</td>
<td>O</td>
<td></td>
</tr>
<tr>
<td>18. Norman</td>
<td>X</td>
<td>O</td>
<td>O</td>
<td>O</td>
<td></td>
</tr>
<tr>
<td>19. Valenta</td>
<td>X</td>
<td>O</td>
<td>O</td>
<td>O</td>
<td></td>
</tr>
<tr>
<td>20. Ballco</td>
<td>X</td>
<td>O</td>
<td>O</td>
<td>O</td>
<td></td>
</tr>
<tr>
<td>21. Elsie</td>
<td>X</td>
<td>O</td>
<td>O</td>
<td>O</td>
<td></td>
</tr>
<tr>
<td>22. Heart</td>
<td>X</td>
<td>O</td>
<td>O</td>
<td>O</td>
<td></td>
</tr>
<tr>
<td>23. LeGrand</td>
<td>X</td>
<td>O</td>
<td>O</td>
<td>O</td>
<td></td>
</tr>
<tr>
<td>24. Hoover</td>
<td>X</td>
<td>O</td>
<td>O</td>
<td>O</td>
<td></td>
</tr>
<tr>
<td>25. Säuret #1</td>
<td>X</td>
<td>O</td>
<td>O</td>
<td>O</td>
<td></td>
</tr>
<tr>
<td>26. Price</td>
<td>X</td>
<td>O</td>
<td>O</td>
<td>O</td>
<td></td>
</tr>
<tr>
<td>27. Monarch</td>
<td>X</td>
<td>O</td>
<td>O</td>
<td>O</td>
<td></td>
</tr>
<tr>
<td>28. Granada</td>
<td>X</td>
<td>O</td>
<td>O</td>
<td>O</td>
<td></td>
</tr>
<tr>
<td>29. Moneytree</td>
<td>X</td>
<td>O</td>
<td>X</td>
<td>O</td>
<td></td>
</tr>
<tr>
<td>30. Bonita</td>
<td>X</td>
<td>O</td>
<td>X</td>
<td>O</td>
<td></td>
</tr>
<tr>
<td>31. Fritz</td>
<td>X</td>
<td>O</td>
<td>O</td>
<td>X</td>
<td></td>
</tr>
<tr>
<td>32. Spencer</td>
<td>O</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td></td>
</tr>
<tr>
<td>33. Profuse</td>
<td>O</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td></td>
</tr>
<tr>
<td>34. Kutsch</td>
<td>O</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td></td>
</tr>
</tbody>
</table>

Total: 31 17 11 9 20 11 8 2 9 3 3 1 0 0 ---

Percent: 91 50 32 26 59 32 24 6 26 9 9 3 0 0 ---

'M = 'Mission', Ne = 'Ne Plus Ultra', N = 'Nonpareil', D = 'Drake', P = 'Peerless', and I = 'I.X.L.'.

*X = Possible origin, O = impossible origin.

'sion', other possibilities are likely partly because of tree or nut characteristics. 'Moneytree' and 'Bonita' show a possible relationship to 'Peerless'. 'Fritz' must be an offspring of 'Mission' because of the Gpi-2ab combination. However, its Lap-lbb genotype could only be possible if the null allele segregates from 'Mission'. The other parent could be 'Ne Plus Ultra', 'Peerless', or 'Drake', but phenotypic tree and nut comparisons suggest 'Drake'.

'Spencer', 'Profuse', and 'Kutsch' (Group 3.9) differ from all others in being the only cultivars on the list that could not be offspring of both 'Nonpareil' and 'Mission'. Both have a strong similarity to 'Nonpareil', but 'Peerless' also could be a likely parent for 'Spencer' and 'Ne Plus Ultra' for 'Profuse'.

Group 4: Mutations. A number of budsports or alleged mutations were examined. Five of them had the identical genotype of the parental cultivar from which they were derived. They are
crinkled ‘Peerless’ and ‘Bitter Merced’ (bud-mutations of ‘Peerless’ and ‘Merced’, respectively) and ‘Jeffries’, ‘Tardy Nonpareil’, and ‘Weststeyn’ (bud mutations of ‘Nonpareil’). Two cultivars (‘Monterey’ and ‘Carmel’) (Table 3) are alleged to be bud-mutations of ‘Nonpareil’ because they were discovered as separate trees in commercial ‘Nonpareil’ orchards (6). However, isozyme differences indicate that origin by mutation is not possible (Tables 1 and 3). Furthermore, there are significant phenotypic differences between both of these cultivars and ‘Nonpareil’.

**Group 5: Unique genotypes.** ‘Pioneer’ and ‘Selection 88–66’ are two clones that had unique alleles not found in the other almond cultivars (Table 3). ‘Pioneer’ has been assumed to be an interspecific hybrid between peach and almond. The isozyme pattern of LAP supports the origin, since the same pattern has been reproduced in controlled crosses of almond and peach (8).

Isozyme analysis not only provides genetic markers for identification purposes but is also a procedure for analyzing the origin of cultivars. The almond cultivars grown in California show a wide range of polymorphisms and a unique opportunity for cultivar identification. Analysis of other isozyme systems would further refine the system.

Evidence is provided that the gene pool in California is dominated by descendants of two major cultivars—‘Nonpareil’ and ‘Mission’ (‘Texas’). This analysis alone does not prove that these two cultivars are the only possible parents in all instances. However, when combined with other information, including pollen incompatibility studies, historical analysis, phenotype comparison, and genetic studies, isozyme analysis provides strong supporting evidence (D.E. Kester, unpublished data).

**Literature Cited**