Two-Dimensional Electrophoretic Analysis of Kernel Proteins of Triticales and of Their Parental Durum Wheats and Ryes[1]

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ABSTRACT

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Two-dimensional electrophoresis, with nonequilibrium pH gradient electrophoresis in the first dimension and sodium dodecyl sulfate slab gel electrophoresis in the second, was used to examine the proteins in two triticale lines and in their parental lines of wheat (*Triticum durum*) and rye (*Secale cereale*). Kernel proteins were separated into fractions by extractions with water, 0.5 *M* NaCl, and 1% sodium dodecyl sulfate/2% 2-mercaptoethanol. The electrophoregrams of the triticale protein fractions were generally similar but not identical to the electrophoregrams of the corresponding combined fractions of the two parents. Both quantitative and qualitative differences between polypeptides of triticales and their parental durum wheats and ryes were observed. Differences were also found between the polypeptides of the two durum wheats and a hexaploid (Newton) wheat that we have also studied with the same electrophoretic methods (Lei and Reeck 1986).

Triticale is a synthetic cereal species that is a hybrid of wheat (*Triticum*) and rye (*Secale*). An octaploid triticale (genome: AABBDDRR) is synthesized from hexaploid wheat (AABBDD) and diploid rye (RR), whereas tetraploid wheat (AABB) and diploid rye produce hexaploid triticale (AABBRR) (Lorenz 1974, Bushuk and Larter 1980, Muntzing 1979).

Endosperm proteins of triticale have been reported to be composed of 26.4% proteins that are water-soluble, 6.5% salt-soluble, 24.4% alcohol-soluble, 17.3% acetic acid-soluble, and 19.0% nonextracted (Chen and Bushuk 1970a). Thus, the quantitative distribution of the four solubility fractions of triticale proteins is intermediate between those of durum wheat and rye parents (Chen and Bushuk 1970a). By gel filtration of various soluble protein fractions, Chen and Bushuk (1970b) reported that the protein composition of triticale is intermediate between that of the parental species. All the protein bands of triticale in disc gel electrophoresis patterns were present in the parents (Chen and Bushuk 1970c). From the above results, Chen and Bushuk (1970c) concluded that all the proteins of triticale are simply inherited from the parental species. Using sodium dodecyl sulfate (SDS) gel electrophoresis, Orth et al (1974) found that all of the polypeptides of triticale glutenin are present in the glutenins of either or both of the parents. These results are different, however, from those of Yong and Unrau (1964), who observed several new protein bands in triticale by starch gel electrophoresis. Chen and Bushuk (1970c) cautioned that new proteins might be detected by other techniques in the soluble fractions they examined or in the residual proteins not examined in their study. Muntzing (1979) stated that the proteins of triticale possess their own unique characteristics that cannot be regarded as a simple addition of the protein spectra of the parents. Also Chung et al (1983) reported that tryptophan, threonine, cysteine, and glycine contents in two hexaploid triticale grains and milled flour are higher than those of either parent.

We note also that Wrigley and his colleagues have used both one- and two-dimensional electrophoresis to distinguish cereals, including wheat, rye, and triticale (Wrigley et al 1982).

Using a powerful two-dimensional gel electrophoresis technique (O'Farrell et al 1977) to analyze several protein fractions of two triticale lines and the corresponding parents, we reexamine here whether the genomes of durum wheat and rye fully maintain their protein synthesis ability in triticale seeds. Our electrophoretic results also allow comparison of the two durum cultivars with each other and with a hexaploid wheat we have studied (Lei and Reeck 1986).

MATERIALS AND METHODS

Sample Preparation

Kernels of two hexaploid triticale lines (6A580 and 0A1275) and the corresponding parents (durum wheat and rye) of these lines were used in this study. Triticale line 6A580 had shrivelled kernels (18 seeds/g) and was originally produced by crossing durum wheat cultivar Jori (20 seeds/g) and rye cultivar UC90C2 (42 seeds/g). Triticale line 0A1275 had plump kernels (22 seeds/g) and was originally produced by crossing durum wheat cultivar Albidum II

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(40 seeds/g) and rye cultivar Puma (38 seeds/g). The kernels of triticale lines, durum wheats, and ryes were generously provided by J. P. Gustafson, USDA, ARS, University of Missouri.

Single kernels of triticale and durum wheat and two kernels of rye were used for sample preparation. The kernels were ground with a mortar and pestle and transferred into a 1.5-ml Eppendorf tube, extracted with 100 μl of deionized water twice (water-extracted fraction), then with 100 μl of 0.5 M NaCl solution twice (salt-extracted fraction), and finally with 100 μl of 1% sodium dodecyl sulfate (SDS)/2% 2-mercaptoethanol twice (SDS-extracted fraction). After each extraction, samples were centrifuged for 10 min at 15,600 $\times g$ in an Eppendorf model 5412 minicentrifuge at room temperature.

Two-Dimensional Gel Electrophoresis

Samples of water- and salt-extracted fractions were concentrated for electrophoresis by precipitation with four volumes of cold acetone. The precipitation was carried out on a dry ice/ethanol bath for 30 min. SDS was separated from SDS/protein complex (SDS-extracted fractions) by diluting the fraction to a final SDS concentration of 0.1% and then adding four volumes of cold acetone (on dry ice/ethanol bath for 30 min) to precipitate the proteins (Hager and Burgess 1980). Precipitates were collected by centrifugation at 10,000 rpm for 20 min and dissolved directly in lysis buffer (O'Farrell 1975) for the first-dimension electrophoresis.

Nonequilibrium pH gradient electrophoresis (NEPHGE) was used in the first dimension with only slight modifications from the procedures given by O'Farrell et al (1977). The details of the two-dimensional electrophoresis were described elsewhere (Lei et al 1983, Lei and Reeck 1986). Ampholines (LKB) with pH ranges of 5–7, 7–9, and 9–11 (in 1:1:1 ratio) were used for NEPHGE in this study. Total wattage of 6,000 Vhr was used for NEPHGE of water- and salt-extracted proteins, whereas 7,000 Vhr was used for NEPHGE of SDS-extracted proteins. Three percent Nonidet P-40 was used in the first-dimension gels. In the second-dimension SDS slab gels, 10% acrylamide-0.27% bis (acrylamide) was used. The slab gels were stained for 4 hr in 0.2% Coomassie Blue R250/50% methanol/12% acetic acid and destained in 20% methanol/10% acetic acid.

RESULTS

Presentation of Results

We present, in turn, our analyses of water-extracted proteins, then of the salt-extracted proteins, and finally of the major storage proteins (extracted with SDS and 2-mercaptoethanol). For each

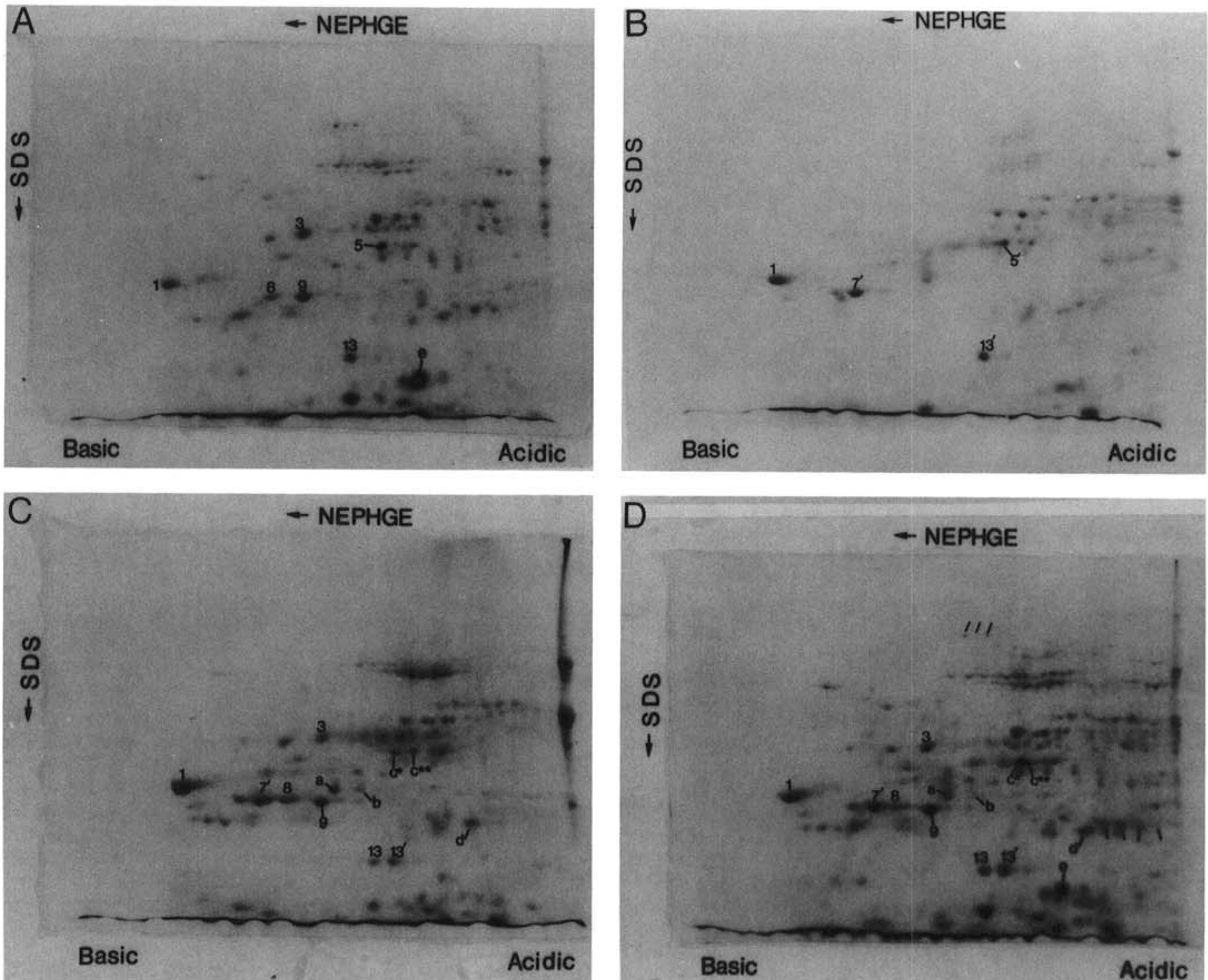

Fig. 1. Two-dimensional electrophoresis of water-extracted protein fractions of Jori durum wheat **(A)**, UC90C2 rye **(B)**, triticale line 6A580 **(C)**, and the mixture of Jori and UC90C2 **(D)**. Loading levels: the entire extracts from 1 wheat seed, 2 rye seeds, 1 triticale seed, and 1 wheat plus 2 rye seeds were loaded for electrophoregrams A through D, respectively. A total of 6,000 Vhr was applied in the nonequilibrium pH gradient electrophoresis. The labeling and comparing of triticale to its parents are discussed in the text.

fraction we examined two triticale lines and their wheat and rye parents.

Each figure shows the results for one type of protein fraction from one triticale line and its parents. Each figure is organized as follows: A, the parental wheat protein fraction; B, the parental rye protein fraction; C, the triticale protein fraction; and D, a mixture of the parental wheat and rye protein fractions.

Some of the interesting features of our results involve faint spots that were clearly visible on the original gels but which are difficult to see on the photographs. The positions of such spots are indicated with lines or arrows on the electrophoregrams. Frequently an electrophoregram has a vertical array of bands near its right edge. The nature of such bands is discussed in Lei and Reeck 1986.

Electrophoretic Analysis of the Water-Extracted Protein Fractions

Two-dimensional electrophoregrams of water-extracted proteins of Jori durum wheat, UC90C2 rye, triticale line 6A580, and the mixture of Jori and UC90C2 are shown in Figure 1 (A, B, C, and D, respectively). Corresponding electrophoregrams for Albidum II durum wheat, Puma rye, triticale line 0A1275, and the mixture of Albidum II and Puma are shown in Figure 2 (A, B, C, and D, respectively).

Comparisons of wheats and ryes. To facilitate comparisons of durum lines to Newton, we numbered several spots in Figures 1 and 2 corresponding to our numbering of components of the albumin fraction of (hexaploid) Newton wheat (Lei and Reeck 1986). Most of the albumin components of the durum wheats appear similar if not identical to those of Newton wheat, but several of the Newton components are apparently absent in the durums. Several of the rye albumin components are apparently identical to wheat albumin components. Some subtle differences are apparent, however. Albumin polypeptide 13 of durum wheat (both Jori and Albidum II) and albumin polypeptide 13′ of rye (both UC90C2 and Puma) are different in charge; the wheat protein is more basic than the rye protein. Polypeptide 7 of Albidum II and 7′ of Puma are different slightly in charge (Fig. 2A and B). Other differences between durum wheat cultivars and between rye cultivars can be found in the electrophoregrams (compare Fig. 1A with 2A, and Fig. 1B with 2B).

Comparisons of triticales with their parental species. The electrophoregrams of triticale albumin fractions are similar but not identical to those of the mixed albumin fractions of the parents. Quantitatively, polypeptide spots a and b of triticale line 6A580 in Figure 1C are more intense than those of the Jori and UC90C2 mixture in Figure 1D. Some qualitative (or extreme quantitative) differences are also apparent. Spot c* is in somewhat different positions in Figure 1C and D. This suggests that the two c* proteins are charge isomers. (Spots c* and c** in Fig. 1D correspond to polypeptide 5 of Jori and polypeptide 5′ of UC90C2, respectively.)

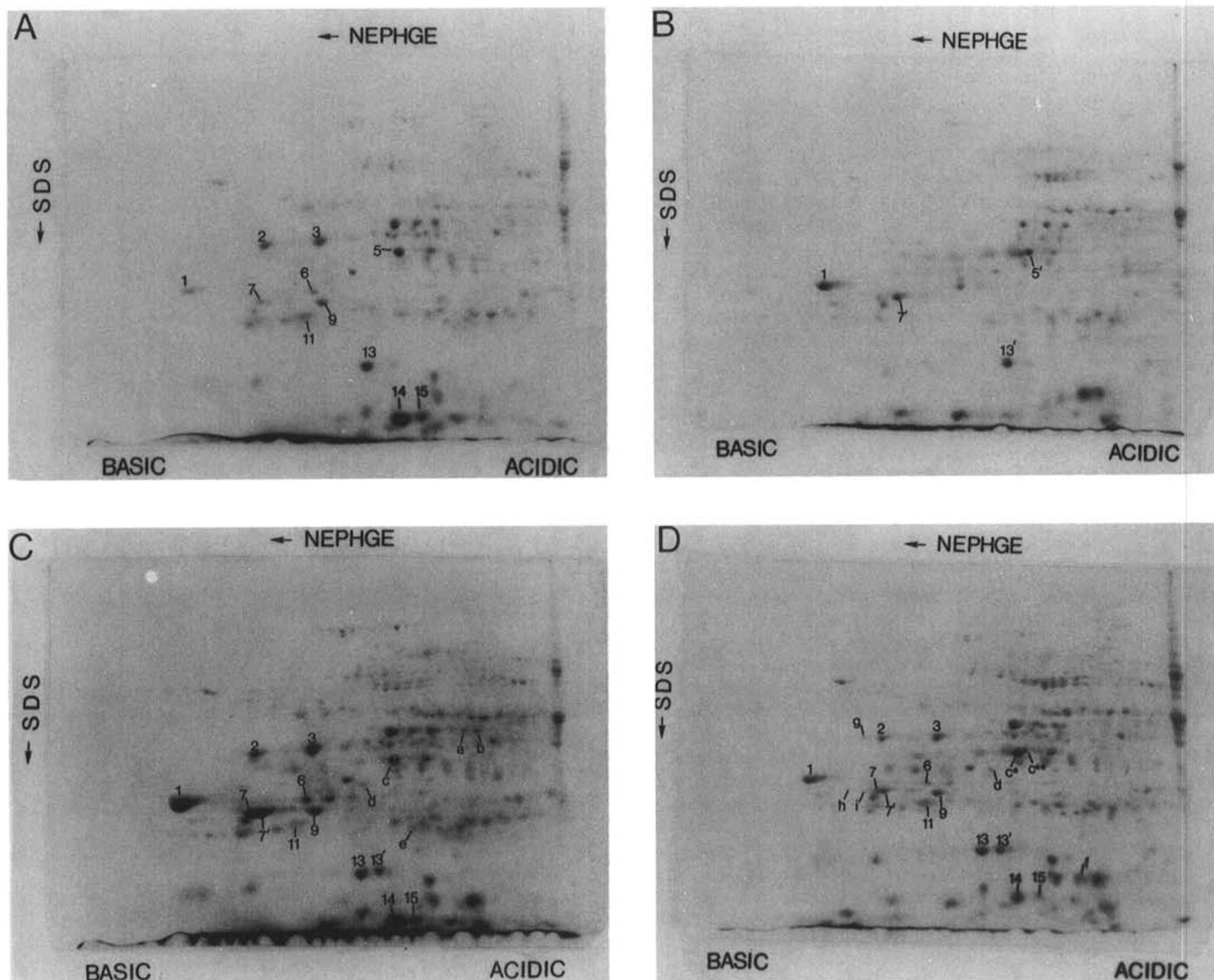

Fig. 2. Two-dimensional electrophoresis of water-extracted proteins of Albidum II durum wheat **(A)**, Puma rye **(B)**, triticale line 0A1275 **(C)**, and the mixture of Albidum II and Puma **(D)**. Loading levels were the same as in Fig. 1. A total of 6,000 Vhr was applied in the nonequilibrium pH gradient electrophoresis. The labeling and comparing of triticale to its parents are discussed in the text.

Spot e and the three faint spots indicated by solid lines on the upper portion of Figure 1D, all of Jori origin, are not found in Figure 1C. Also, four polypeptides to the right of polypeptide d in Figure 1D, indicated by solid lines, are not found in Figure 1C.

In the electrophoregrams of the triticale line 0A1275 albumin fraction (Fig. 2C) are polypeptides a, b, and e, which are not found in either Albidum II or Puma (Fig. 2A, B, and D). Thus, these may be polypeptides synthesized in triticale but not synthesized at detectable levels in either parent. In Figure 2C only one spot c appears, but in Figure 2D we observed two spots (c* and c**). We cannot be certain whether spot c in triticale corresponds to c* or c** in the mixed parental species. Polypeptides c* and c** correspond to polypeptide 5 of Albidum II and polypeptide 5′ of Puma, respectively. This suggests that either polypeptide 5 of Albidum II or polypeptide 5′ of Puma has undergone charge modification in triticale line 0A1275. (Recall that an apparent difference in charge modification was observed for spot c* in Fig. 1 for triticale line 6A580.) Spots d in Figure 2C and D are somewhat different in molecular weight and may actually be different polypeptides. Polypeptides f, g, h, and i in Figure 2D, which are of Puma origin, are absent in Figure 2C.

Electrophoretic Analysis of the Salt-Extracted Protein Fractions Following Water Extractions

The proteins extracted with 0.5 M NaCl (after water extraction) of triticale lines (6A580 and 0A1275) and the corresponding parents are displayed in Figures 3 and 4.

Comparisons of wheats and ryes. The patterns of the two-dimensional gels of the salt-extracted proteins of durum wheat and rye are generally similar to that of Newton wheat (Lei and Reeck 1986), but the spots in GgIV (Lei and Reeck 1986) are less clearly resolved in Figures 3 and 4 than in our study of Newton wheat. It appears that polypeptides 1, 7′, 8, 9, and e on Figure 3D are residual albumin components from either Jori or UC90C2 (Fig. 3A and B). Polypeptides 1, 7′, 8, and 9 of albumin fraction are also present in the salt-extracted fraction of triticale line 6A580 (Fig. 3C). We observed a similar overlap of globulin and albumin fractions in Newton wheat (Lei and Reeck 1986).

Comparisons of triticales with their parental species. The two-dimensional patterns of the polypeptides in the lower right-hand corner of Figure 3C is very different from that of Figure 3D. The four polypeptides with complete arrows in Figure 3C correspond to the polypeptides with complete arrows in Figure 3D. Polypeptide e in Figure 3D is absent from Figure 3C. Arrowheads on Figure 3D spots indicate polypeptides of Jori origin that are not found in triticale line 6A580 (Fig. 3C). Apparently, genes coding for those polypeptides of Jori are not expressed or are expressed less in the triticale. The two heavy arrows in the center of Figure 3C indicate faint polypeptides of triticale line 6A580 that are absent in Figure 3A, B, and D. These two polypeptides are possibly new gene products synthesized in triticale line 6A580.

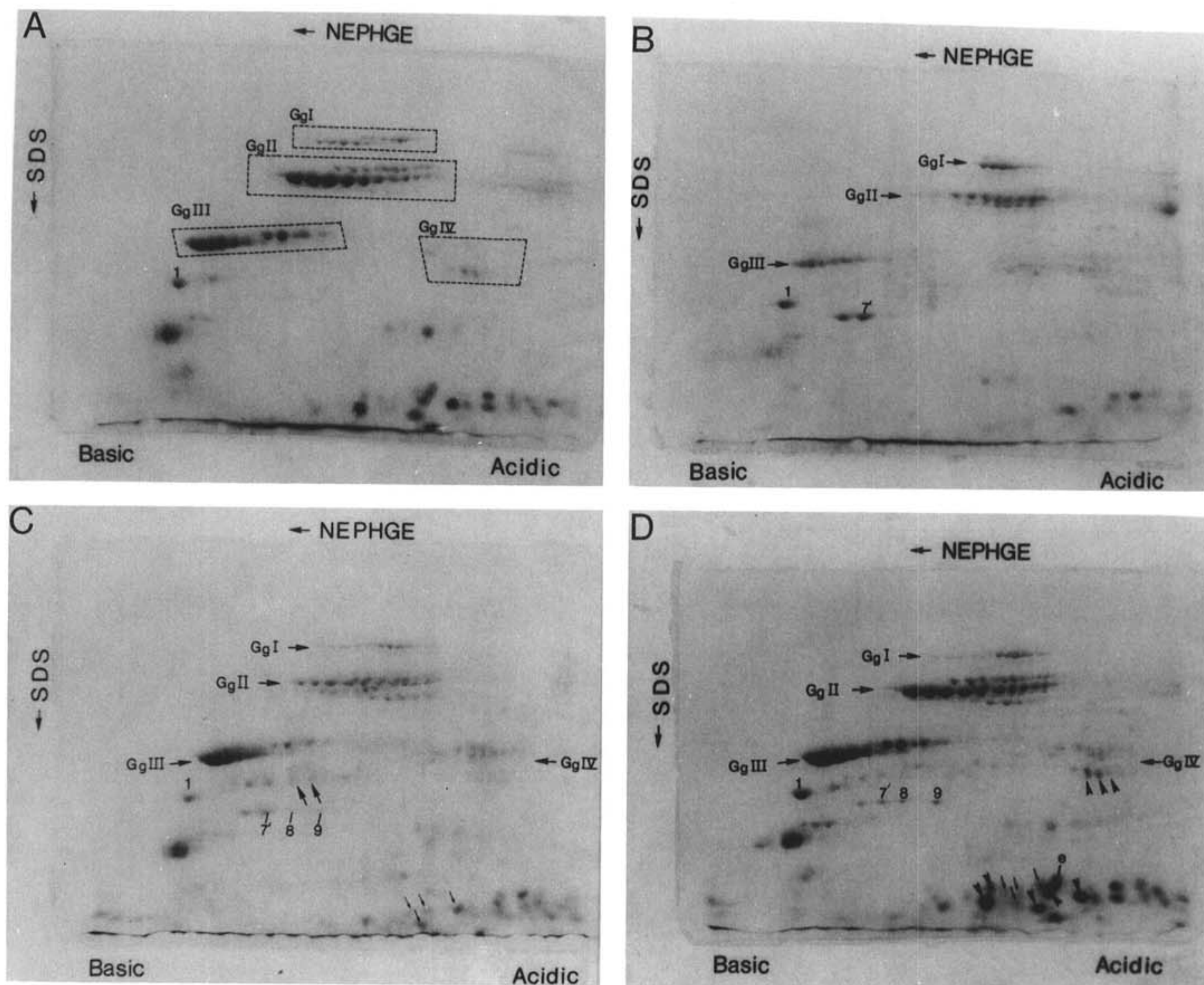

Fig. 3. Two-dimensional electrophoresis of salt-extracted protein fractions (following water extraction) of Jori durum wheat **(A)**, UC90C2 rye **(B)**, triticale line 6A580 **(C)**, and the mixture of Jori and UC90C2 **(D)**. Loading levels were the same as in Fig. 1. A total of 6,000 Vhr was applied in the nonequilibrium pH gradient electrophoresis. The labeling and comparing of triticale to its parents are discussed in the text.

Polypeptides h and i in Figure 4B and D are residual albumin components of rye. They are absent from the salt-extracted fraction (Fig. 4C) as well as the water-extracted fraction (Fig. 2) of triticale line 0A1275. On the other hand, albumin polypeptides 7 and 7′ of triticale line 0A1275 (Fig. 2C) are present in the subsequent salt-extracted fraction (Fig. 4C). The polypeptides between two dotted lines in Figure 4B and D are polypeptides of Puma, which are not found in Figure 4C. The genes coding for this whole group of the polypeptides are apparently silent in the triticale line 0A1275. Two faint polypeptides of Puma indicated by arrowheads in Figure 4B and D are also not found in the electrophoregram of triticale line 0A1275 (Fig. 4C).

Electrophoretic Analysis of the Protein Fraction Obtained by SDS/2-Mercaptoethanol Extraction Following Water and Salt Extractions

The water-and-salt-nonextracted proteins of triticale lines and the corresponding parents were extracted with 1% SDS/2% 2-mercaptoethanol and then analyzed by electrophoresis. Figure 5 shows two-dimensional electrophoregrams of the SDS-extracted proteins of Jori, UC90C2, triticale line 6A580, and the mixture of Jori and UC90C2 (Figure 5A, B, C, and D, respectively). The electrophoregrams of triticale line 0A1275 and its parents are shown in Figure 6.

Comparisons of wheats and ryes. The electrophoretic patterns of major storage proteins of durum wheat (Figs. 5A and 6A) are somewhat similar to that of Newton wheat (Lei and Reeck 1986). Nonetheless, some differences in pattern among Newton, Jori, and Albidum II are clearly apparent in the two-dimensional gels. Interestingly, the electrophoretic pattern of the major storage polypeptides of Albidum II seems more similar to that of Newton than to that of Jori, although Newton is hexaploid and Jori and Albidum II are both tetraploid.

The electrophoretic pattern of major storage proteins of rye is less complicated than that of wheat storage proteins. There are two major polypeptide groups on the rye electrophoregrams (Figs. 5B and 6B). They are 70,000-dalton γ-secalins (70-γ-S) and 40,000-dalton γ-secalins (40-γ-S). (The nomenclature is that of Shewry et al 1983.) Polypeptides above the horizontal dotted lines on Figures 5B and 6B are high-molecular-weight secalins, which are relatively scarce, especially in Puma rye. The 40-γ-S are not easy to identify in the mixed electrophoregram of durum wheat and rye, because some of them coelectrophorese with the storage proteins of durum wheat (Figs. 5D and 6D). Two arrowheads in Figure 5C and D indicate two components of the 40-γ-S.

Comparisons of triticales with their parental species. Most of the polypeptide spots of water-and-salt-nonextracted proteins of triticale on the two-dimensional gels (Figs. 5C and 6C) can be

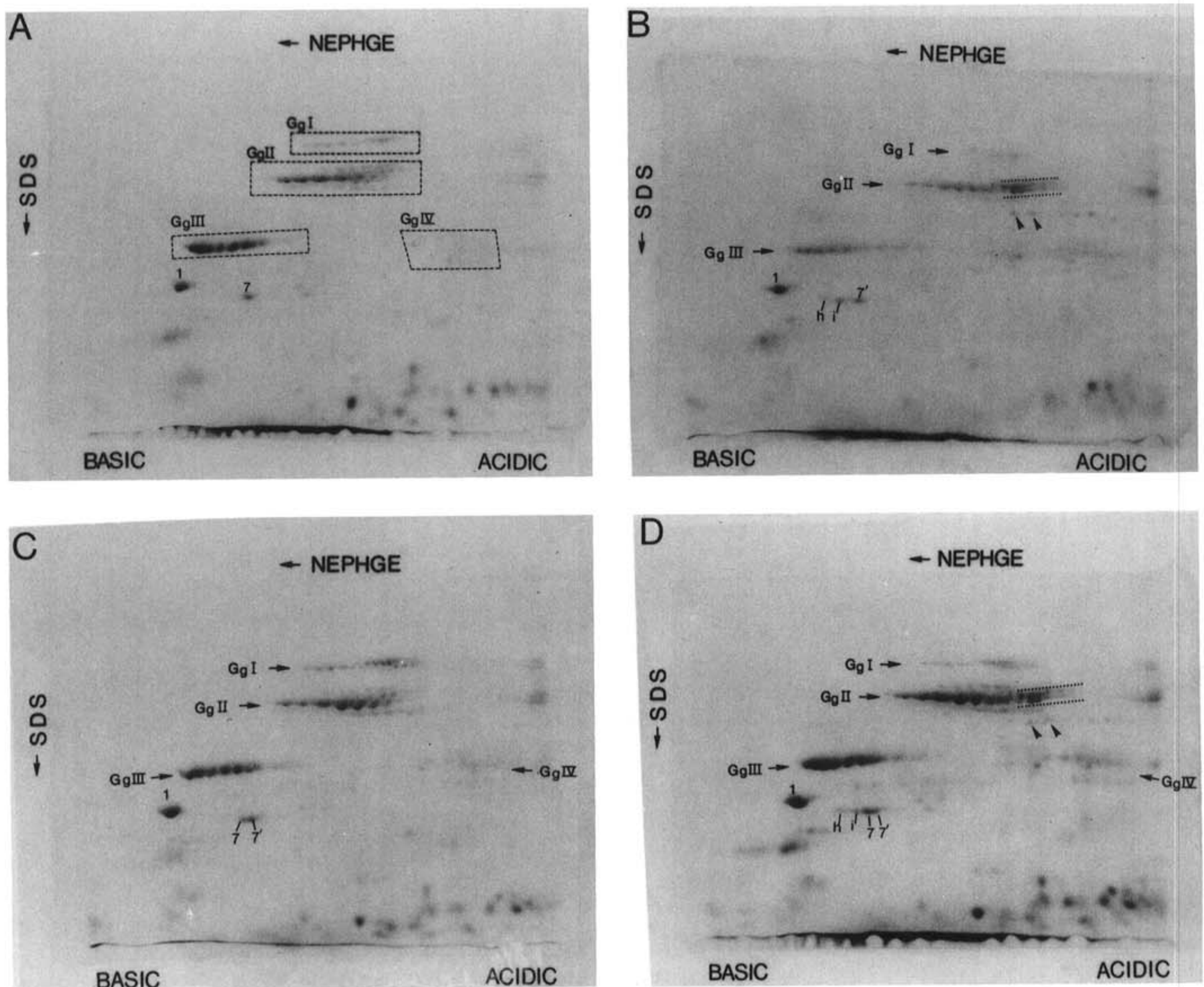

Fig. 4. Two-dimensional electrophoresis of salt-extracted protein fractions of Albidum II durum wheat **(A)**, Puma rye **(B)**, triticale line 0A1275 **(C)**, and the mixture of Albidum II and Puma **(D)**. Loading levels were the same as in Fig. 1. A total of 6,000 Vhr was applied in the nonequilibrium pH gradient electrophoresis. The labeling and comparing of triticale to its parents are discussed in the text.

found in the corresponding parents, but some differences between the triticale and the parents are apparent. The charge of polypeptide a (which is a component of Jori) in Figure 5A and D is different from that of spot a′ in Figure 5C. Polypeptides b and c in Figure 5C are likely the same as polypeptides b and c in Figure 5D, but polypeptides d′, e′, and f′ in Figure 5C are different from polypeptides d, e, and f in Figure 5D. Polypeptides d′, e′, and f′ in Figure 5C may be altered forms of polypeptides d, e, and f or, possibly, they are new gene products of triticale line 6A580. Note that polypeptide f is much more intense than polypeptide f′.

A polypeptide of triticale line 0A1275 (indicated by an arrowhead in Fig. 6C) is absent from its parental species. The molecular weight of this polypeptide is similar to that of 70-γ-S. Although this is a two-kernel analysis, gels analyzing six rye kernels failed to detect this spot. Therefore, it is likely a new product of triticale or a modified 70-γ-S component.

DISCUSSION

Our analyses of proteins in triticale and its parental species by two-dimensional gel electrophoresis clearly show that the large majority of polypeptides in triticale can be accounted for by proteins present in the parental durum wheat or rye cultivars. In this sense our results are consistent with the conclusions from earlier work with one-dimensional gel electrophoresis. A few polypeptides do, however, vary from those of the parental species. Such variations are found in every solubility fraction (water-extracted, salt-extracted, and SDS-extracted fractions) and in both triticale lines. Both quantitative and apparently qualitative variations occur. In Table I we give a summary of the observed differences. The greater resolving power of two-dimensional gels may explain why our results do not agree in detail with those of Chen and Bushuk (1970a,b,c) and of Orth el al (1974).

The fact that rye is a cross-pollinating species cannot be neglected in interpreting our results. This could conceivably account for some of the variation involving those triticale polypeptides coded by the rye genome. Note, however, that we also observe variation in polypeptides coded by the wheat genome.

A secondary aspect of our results is comparison of the proteins of two durum wheats with each other and with the proteins of a hexaploid wheat, Newton (Lei and Reeck 1986). Our electrophoresis methods are able to distinguish the patterns of the major storage protein fractions (i.e., combined gliadin and glutenin fractions) of two durum wheats, Jori and Albidum II (Figs. 5A and 6A). This is potentially important, because it is among durum wheats that the one-dimensional aluminum lactate electrophoresis

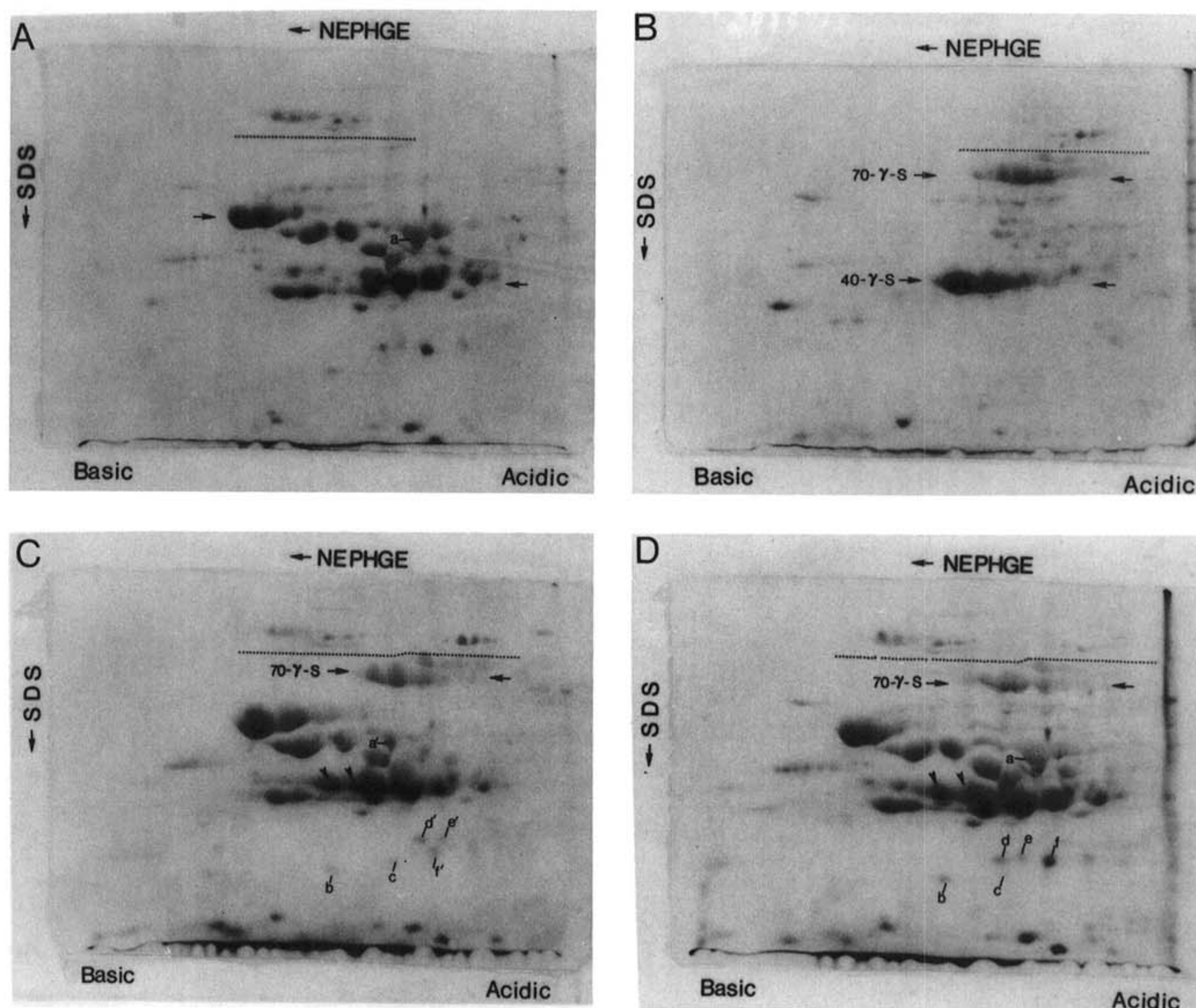

Fig. 5. Two-dimensional electrophoresis of SDS-extracted protein fractions (following water and salt extraction) of Jori durum wheat **(A)**, UC90C2 rye **(B)**, triticale line 6A580 **(C)**, and the mixture of Jori and UC90C2 **(D)**. Loading levels: **A**, half of extract from 1 seed (i.e., 1/2 seed equivalent); **B**, 1 seed equivalent; **C**, 1/3 seed equivalent; **D**, 1/3 seed equivalent of Jori and 4/5 seed equivalent of UC90C2. A total of 7,000 Vhr was applied in the nonequilibrium pH gradient electrophoresis. The labeling and comparing of triticale to its parents are discussed in the text.

TABLE I
Summary of the Differences between Polypeptides of Triticale and Mixed Parental Species

	Extra Spot in Triticale	Missing Spot in Triticale	Difference in Charge	Difference in Molecular Weight
Albumin fractions				
Fig. 1. Triticale 6A580	None	Spot e 7 spots with solid lines	Spot c*	None
Fig. 2. Triticale 0A1275	Spot a Spot b Spot e	Spot f Spot g Spot h Spot i	Spot c	Spot d
Globulin fractions				
Fig. 3. Triticale 6A580	2 spots with arrows	Spot e 8 spots with arrowheads	None	None
Fig. 4. Triticale 0A1275	None	Spots between two dotted lines 2 spots with arrowheads	None	None
Storage protein fractions				
Fig. 5. Triticale 6A580	None	None	Spot a′ Spot d′ Spot e′ Spot f′	Spot f′
Fig. 6. Triticale 0A1275	1 spot with arrow	None	None	None

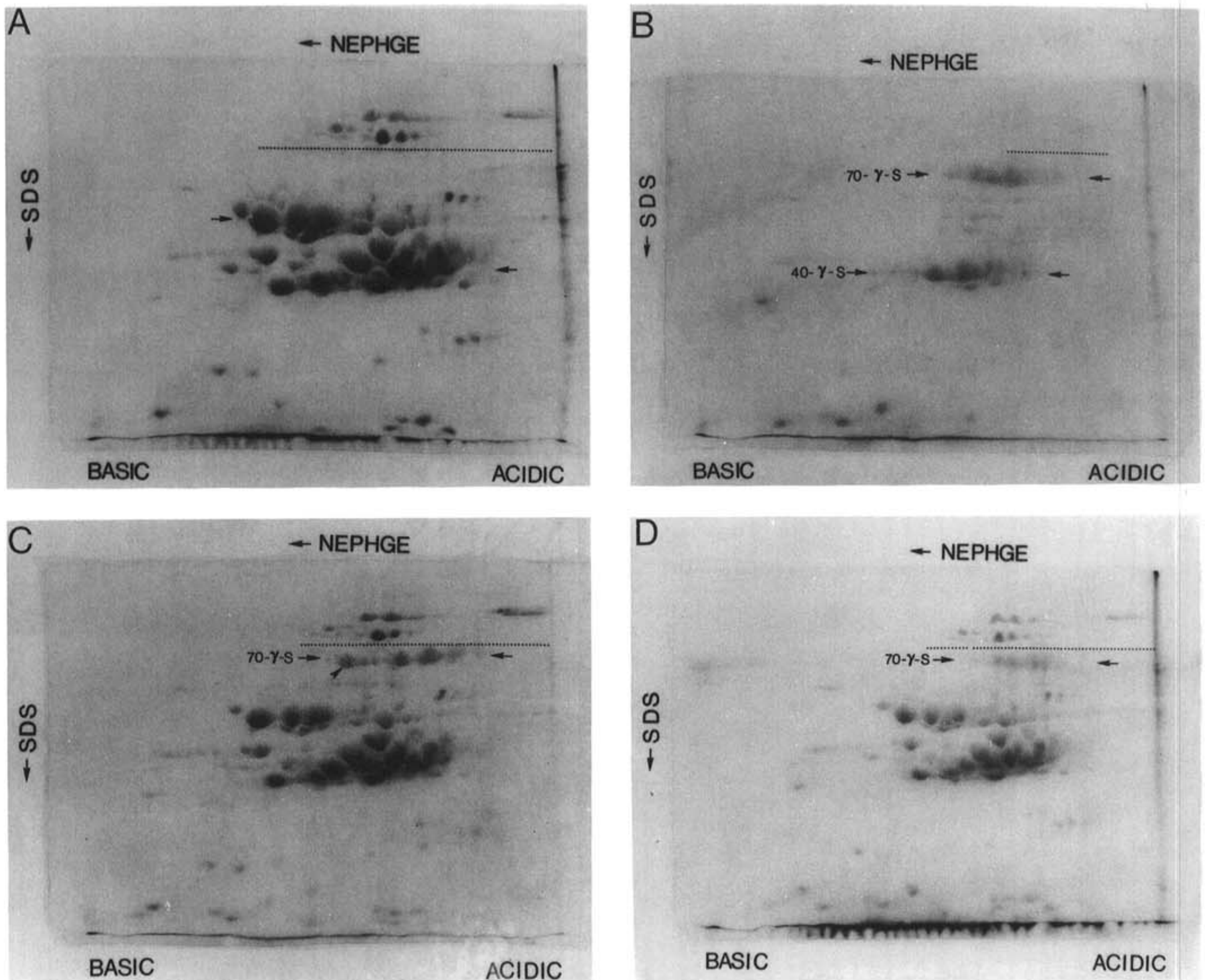

Fig. 6. Two-dimensional electrophoresis of SDS-extracted protein fractions of Albidum II durum wheat **(A)**, Puma rye **(B)**, triticale line 0A1275 **(C)**, and the mixture of Albidum II and Puma **(D)**. Loading levels were the same (in seed equivalents) as in Fig. 5 for **A–C**. For **D**, 1/4 seed equivalent of Albidum II and 4/5 seed equivalent of Puma were loaded. A total of 7,000 Vhr was applied in the nonequilibrium pH gradient electrophoresis. The labeling and comparing of triticale to its parents are discussed in the text.

system is least able to distinguish cultivars. Further, each durum wheat is readily distinguished from the hexaploid wheat (Lei and Reeck 1986). Thus the two-dimensional electrophoresis method we have used in these studies might be a useful supplement to the one-dimensional aluminum lactate gel system for characterization of wheat cultivars, particularly for durum wheats.

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