FACTORS AFFECTING GRAIN SHRIVELLING IN SECONDARY HEXAPLOID TRITICALE

by

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INTRODUCTION

Apart from the hybridization used to introduce advantageous genes into cereals that already serve as human food sources, interspecific and intergeneric hybridization is used also to produce new crops to supplement existing food and feed resources. Some of the most interesting intergeneric crosses that fall in the latter category are triticale, hybrids produced by crosses between the genera Triticum (wheat) and Secale (rye). Triticales were produced to move the wheat-belt northward, to increase the protein nutritional quality, and to improve disease resistance of wheat-like crops. Commercial acceptance of these new hybrid species is predicated on their agronomic and post-harvest quality characteristics compared to existing cereal grains. More specifically, triticale is compared to wheat, its major genome donor, with the desire to improve any number of agronomic, nutritional, or functional quality characteristics.

The significant successes achieved so far with triticale are still obscured by the overshadowing, inherent shrivelled pericarp and endosperm depression problems that classify the grains as "shrivelled." The mechanism of, and factors influencing grain shrivelling, need more intensive study, considering the many inconsistencies reported (1, 21, 34, 53, 65, 91, 96, 98, among others). These experimental variations are primarily attributed to genotypically different triticale materials.

This study investigated the grain shrivelling problem in 8 triticale cultivars of known wheat parentage and rye chromosomal composition.

Grains from each cultivar were categorized as plump, medium shrivelled, and highly shrivelled. Bulk grain samples of each cultivar were used to estimate protein, starch, soluble sugars, and α-amylase activity. Additionally, baking performance was estimated in flour from bulk samples of each cultivar. Grain morphology of categorized samples was observed by scanning electron microscopy (SEM). Seed from each of the three morphological categories of the Rahum cultivar was planted and seed morphology at different developmental stages (5, 10, 15, 20, 26, and 35 days post-anthesis) was studied under light microscopy. At weekly intervals from 7 to 35 days post-anthesis, starch, soluble sugars, moisture, and α-amylase activity were determined also in the same developing seed.

Because many ideas and hypotheses of triticale grain shrivelling conflict due to genetic and environmental differences, this work was designed to test earlier hypotheses and unify the concepts of seed shrivelling.

REVIEW OF LITERATURE

Nomenclature

Triticale is the commonly accepted name for crosses between wheat and rye and includes octaploid and hexaploid forms, both primary and secondary types, as well as tetraploid forms (30, 124). X Triticosecale Wittmack is the presently accepted generic name (7). The various types are indicated in Table 1.

Table 1. Types of triticale, their genomic constitution and origin.

Triticale type (genomic constitution)	Origin (genomic constitution)
Tetraploid (AARR or BBRR)	6x triticale (ABR) X 2x rye (R)
Primary hexaploid (AABBRR)	4x wheat (AB) X 2x rye (R) 6x triticale (ABR) X 6x triticale (ABR)
Primary octaploid (AABBDDRR)	6x wheat (ABD) X 2x rye (R) 8x triticale (ABDR) X 8x triticale (ABDR)
Secondary hexaploid (AABBRR)[a]	8x triticale (ABDR) X 6x triticale (ABR) 6x triticale (ABR) X 6x wheat (ABD)
Secondary octaploid (AABBDDRR)	8x triticale (ABDR) X 6x wheat (ABD) 8x triticale (ABDR) X 6x triticale (ABR)
Wheat-rye addition lines	
Wheat-rye substitution lines	

[a]Assume no chromosome substitutions or translocations.

Origin and Evolution of Triticale

In 1876 Wilson reported the first wheat-rye hybrid. Rimpau (1891) subsequently obtained the first fertile amphidiploid which Muntzing (1936) proved to be a pure triticale with 2n = 56 chromosomes. In 1931 Muntzing began his research on octaploid triticale in Sweden but it was not until the late 1930's, with the establishment of colchicine as a technique for doubling the chromosome number of sterile hybrids, that triticale became important as a potential crop. More variable octaploid and hexaploid triticales were obtained by Sanchez-Monge and Tijo (93) and Sanchez-Monge (92) in Spain. Sanchez-Monge and co-workers concluded that 42 chromosome triticales with acceptable agronomic characteristics could be obtained by recombination and selection of primary triticales.

In 1954 the University of Manitoba in Canada started a triticale breeding program. The initial material used was a hexaploid triticale produced by O'mara. Several additional hexaploid and octaploid triticales were obtained subsequently with more improvements through selection being obtained in hexaploid triticales than in the octaploid forms.

A significant advance in triticale development occurred in 1960 when it was demonstrated that hybridization between octaploid and hexaploid triticales produced secondary hexaploids that were superior to their parents (81); a finding confirmed by Kiss (47) and Jenkins (37). Sisodia (101) suggested that the improved characteristics of secondary triticale might be due to a more harmonious relationship between hexaploid wheat cytoplasm and the hexaploid triticale nucleus

than between tetraploid wheat cytoplasm and the hexaploid triticale nucleus. This relationship is not expected to be absolute due to differences in genotypic responses.

In 1964, a cooperative program between the University of Manitoba in Canada and the International Maize and Wheat Improvement Center (CIMMYT) in Mexico was initiated. Both germ plasm and information were exchanged to speed up the production of widely varied germ plasm. Nature cooperated too with a spontaneous backcross of bread wheat to triticale (119) to produce the highly fertile armadillo types and mark an important advance in triticale improvement. Some of the advantageous characters that armadillo types expressed were: (1) development of triticale lines with full fertility that were high yielding; (2) lines with improved test weight as a result of improved grain plumpness; (3) lines insensitive to photoperiod; and (4) introduction of one gene for dwarfness.

In 1971, the Canadian International Development Agency (CIDA), contributed as a major sponsor for the initiation of an international triticale development program in which CIMMYT and the University of Manitoba were directly involved. The original idea of this program, still operative today, is the development of triticale with applications for human consumption in developing countries.

Marked yield improvement of triticales during the early 1970's resulted from the wide use of the armadillo germ plasm in Canada (56), in some United States locations (57), in Europe (28, 48), in Africa (80), and in Mexico (121). Since 1974, triticale strains have been developed that are of wide environment adaptability, exhibit adaptation/tolerance to acidic and aluminum toxic (to wheat) soils in Brazil, and

carry greater resistance than wheat to Septoria tritici that is advantageous in Brazil, Argentina, Ethiopia, and the Mediterranean region (13).

More recently, several spring triticale lines that had exhibited good adaptation and higher yields in previous trials (15) were tested in 110 locations in different cereal producing regions of the world. Results from the 56 reporting locations showed that average grain yield was 4018 kg/ha in the 1975-1976 yield nursery and 3590 kg/ha in the 1976-1977 yield nursery. Some of the triticale lines outyielded the local wheat checks (Table 2).

Table 2. Average yield (kg/ha) over all locations.[a]

Variety name	1975-1976	1976-1977
Mapache	4483	4057
Rahum	4451	3847
Bacum	4311	3618
Yoreme	4250	3527
Lince	4217	3817
Siete cerros (bread wheat)	3656	3217
Jupateco (bread wheat)	4078	3316

[a]From CIMMYT, Information Bulletin No. 41 (15).

Despite the overall poor performance of the triticales in 1976-77, grain yield was higher in general than the 2 wheat checks.

Grain Morphology

Light microscopy (98) and SEM (23, 65, 82) studies have shown that the basic surface morphological characteristics of triticale are similar to those of wheat, rye, and barley. However, in most of the cases, triticale has a wrinkled appearance that ranges from slight to severe. In the latter case, the pericarp appears papery and shrivelled with endosperm depressions.

Cross sections of several cereals under SEM (82) indicated that the structure, arrangement, size of the pericarp and aleurone layers of triticale grain were basically similar to the same characteristics of wheat and rye. The starch granules in the central endosperm of triticale varied in size with an average diameter of about 20 microns while those in the sub-aleurone layer had an average diameter of about 12 microns. In this characteristic, triticale resembled more closely rye than wheat (82).

Dronzek et al. (23) observed triticale 6A190 and its specific rye and wheat parents. Their observations were generally in agreement with those of Pomeranz (82); however, they found that the starch granules of triticale have a diameter of about 30-35 microns, representing an intermediate size when compared to the parental starch granules.

Dronzek et al. (23) and Lorenz et al. (65) by SEM, and Simmonds (98) by light microscopy, found that developmental changes in the pericarp, aleurone, and endosperm of triticale occurred in a manner similar to those in wheat and rye during grain maturation.

Important morphological changes in the developing triticale grain have been described as follows: 1) Degeneration of the pericarp begins at about 3-4 days post-anthesis (p.a.) (98); at about 6-8 days p.a. tube and cross cells originate probably from the outer integument, while the seed coat is derived from the inner integument. Simmonds and Campbell (99), however, suggested that in triticale, as well as in rye, the large and oval tubular cells are the ones that give rise to tube and cross cells that at maturity compose the inner epidermis. They did not find the outer integument visible at 4 to 5 days p.a. whereas the inner integument remained visible as a layer until maturity. At about 7-10 days p.a. the cell walls of the inner integument become thickened while the cell contents started to degenerate. Approximately 18 days p.a. the walls collapse to form the testa or seed coat (99). 2) Simmonds (98) observed that the cambial cell layer of the endosperm (meristematic cells) differentiate at about 10 days p.a. to form the aleurone layer. Lorenz (65) found aleurone cells to be clearly discernible at approximately 16-18 days p.a. as has been reported for wheat (24, 78). 3) Endosperm cellularization by cytokinesis occurs at about 4-6 days p.a. in triticale, wheat and rye, forming regular radial columns of cells in wheat (24), and rye (99). The endosperm cells in triticale were found (98) to form in an irregular and disturbed way. 4) Cell division termination has been reported to occur during 12-14 days p.a. in triticale (98), during 10-16 days p.a. in wheat (24, 78), and at about 18 days p.a. in rye (99). 5) After cell division terminates in the endosperm, subsequent development is by cell elongation and deposition of storage materials.

Starch granules were first observed in triticale and rye at about 10 days p.a. being initially deposited in the periphery around the endosperm cell walls. Starch deposition subsequently spread to the center of the cell with storage protein being deposited concurrently at about 12-14 days p.a. in the cytoplasm of the subaleurone cells (98, 99). These observations were in agreement with the results obtained by Percival (78) and Evers (24) for the same developmental changes in wheat endosperm. 6) The mature state of the triticale grain is finally characterized by a wrinkled pericarp attached to the endosperm with the seed coat and nucellar epidermis compressed between them and the endosperm cells full of starch granules embedded in a protein matrix (65, 98). However, in some cases, when shrivelling affects the triticale grain, some developmental abnormalities occur. These abnormalities will be described in a later section concerning the problem of grain shrivelling and its possible causes.

Protein and Amino Acid Composition

Protein. One of the major reasons to incorporate rye germ plasm into wheat was to obtain a higher crude protein content and indeed the earlier triticale lines showed a higher content than wheat (55, 111, 114, 117). A second consideration was to maintain high protein in the flour for baking. The protein content of hexaploid triticales in grain and flour ranged between 16.1 to 19.8% and 15.1 to 18.8%, respectively. For 2 octaploid triticales it was 17.9% and 19.2% in grain and 16.6% and 18.0% in flour (111). These high protein values have been positively related to kernel shrivelling, with Villegas and Bauer (113) finding considerably decreased protein contents of 13.4 to 13.7% in improved grain type

triticales. This finding was confirmed by Tarkowski et al. (107) who observed that shrivelled grains from secondary hexaploid triticales contained at least 5 percent more protein than the plump ones. Ruckman et al. (89), in their experiments, conducted at several California locations, found spring triticales to contain an average of 16.3% protein, and Khristova (46) in Europe, reported that the protein content of octaploid and hexaploid triticales ranged between 15.8 to 19.2%. These results suggest that both groups tested triticales with some kernel shrivelling.

At present, the average protein content of triticale lines at CIMMYT is between 13.0 to 13.5% (14), while in India it has been reported that high yielding triticale protein contents range from 13.2 to 18.5% (70). Because recently developed triticales do not exhibit the common earlier problems of partial sterility, excessive seed shrivelling and others, the relationship between protein content and grain shrivelling is no longer clearly evident (personal experience with CIMMYT materials).

Amino acids. The amino acid composition of total endosperm proteins and various protein fractions in the hexaploid triticale 6A190, was intermediate between that of the parental species (16, 22, 118) and was interpreted by Chen and Bushuk (17) as the result of simple parental protein inheritance. Yong and Unrau (118), however, suggested that a decrease in one individual amino acid of one of the triticale protein fractions was, in general, compensated by an increase of the same amino acid in another fraction to produce intermediate levels of amino acids in triticale compared to those in its parents.

Due to a wide variability in the genotype of the different triticales, it has been reported that the amino acid composition of triticale was equally varied. Thus glutamic acid has been reported to be in higher levels in wheat than in triticale (16, 55, 106, 113, 118), as well as higher in triticale than in wheat (2). Aspartic acid has been reported higher in wheat than in triticale (85, 117, 118) and lower in wheat than in triticale (2, 16, 55, 113). Cystine was reported higher in wheat than in triticale by Haber et al. (31), and in similar concentration in both wheat and triticale by others (85, 113). The same situation can be found in the literature for most of the rest of the amino acids. Only arginine (2, 16, 85, 113) and lysine (2, 16, 31, 55, 89, 107, 113, 114) are reported consistently lower in wheat than in triticale.

Riley and Ewart (85) studied the amino acid composition of wheat (Holdfast), rye (King II), and of the triticale and addition lines produced from the cross between these progenitors. Among the addition lines, there were quantitative differences in amino acid composition. The rye chromosome (rc) I disomic addition line increased cystine and lysine by 10.7 and 8.7%, respectively; rc II, increased proline by 9.1% and reduced aspartic acid by 8.6%; rc IV, increased and rc VI reduced arginine by 11.7 and 8.0%, respectively; rc VI increased proline by 11.8%; and rc VII reduced threonine by 10.4%. It appears that rye chromosome I produces potentially significant changes for nutritional quality improvement of wheat protein, whereas rc VII seems to be unfavorable because it reduces the threonine content. Riley and Ewart (85) concluded that threonine, serine, glutamic acid, alanine, proline and

tyrosine levels in the triticale amphiploid could be the result of interchromosomal interaction, while simple additivity could account for the remaining amino acids.

Besides genotypic variability, other factors also affect the amino acid levels in triticale. Lorenz et al. (60) found that lysine levels varied considerably depending on variety and location of winter triticales grown in Colorado. The authors also found that winter triticales grown at high elevations did not show a lysine advantage as reported for spring triticales (89, 114). Hraska (35) studied the content of several triticales suggesting that 60% of the amino acid content control factor(s) resided in the genotype, 20% in environmental conditions, and 20% in environment-genotype interactions. In all cases, amino acid composition must be considered as shifts in protein synthesis because free amino acid levels cannot account for the wide variations reported and are not consistent with current knowledge of genetic control of protein biosynthesis (74).

Nutritional value. Nutritional quality of triticale has been found superior in many cases to wheat, corn, barley, sorghum, and rye (27, 36, 49, 50, 51, 54, 69). However, shrivelled grain effects confound the results. Both chemical and biological assays have indicated that triticale protein superiority is due primarily to its higher contents of lysine and sulfur-containing amino acids and to a lesser extent to a slightly better amino acid balance. Therefore, it is generally accepted that triticale, as food and feed, provides slightly better nutritional quality than some other cereals.

Carbohydrates

Starch. Chemical, physical and structural characteristics of starches from wheat, rye, and triticale, have been reported to be similar (12, 33, 52, 58). The starch content in various triticale lines ranged from 49.1 to 57.1% and correlated ($r = 0.746$) with grain density and grain shrivelling (53). A significant correlation, however, was not obtained between starch content and α-amylase activity. The lower amylograph viscosity of triticale flour, and in some studies of triticale starch, compared to similar wheat and rye products, can be attributed to a higher α-amylase activity in triticale than in its parental species (53). From grain development studies, Klassen et al. (53) suggested that an early termination of starch deposition in the endosperm occurred in shrivelled-grain triticale lines.

Sugars. Total alcohol-soluble carbohydrates were determined by Vaisey and Unrau (112) from a group of hexaploid, octaploid and tetraploid triticales. They found total soluble sugars generally to be slightly higher in triticale than in bread wheat and durum wheat, but lower than in rye. Higher sucrose and glucose contents were suggested to be responsible for the increased soluble sugars in triticale although the major proportion of the total soluble sugars was due to oligosaccharides in all the materials studies (53.7 to 78.6% of total sugars), of which glucose was the only monomeric component.

Klassen et al. (53) found that the reducing sugars content of several triticales was highly correlated with α-amylase activity ($r = 0.093$). Thus, the authors suggested that in some shrivelled

triticale lines high ∝-amylase activity produced a breakdown of starch that was subsequently manifested by increased reducing sugars in the grain. However, that same phenomenon was not observed by Becker et al. (8), Agrawal (1), Noll (75), and Singh et al. (100). It appears possible also that in shrivelled triticales, the mechanism(s) of sucrose hydrolysis and incorporation of glucose for starch synthesis fail in certain instances and lead to sucrose and glucose accumulation (8, 112) and result in an early termination of starch synthesis (34, 53). Additional evidence that supports the latter contention was the presence of maltose and maltotriose in small amounts in triticale grain (8). If starch breakdown had occurred, larger amounts of these two oligosaccharides should have occurred. In general, the oligosaccharide composition of maturing wheat, rye and several triticale grains, was similar (8).

Pentosans. Grain pentosans of triticale 6A190, its durum wheat and rye parents, and of hard red spring were determined by Heinrich and Hill (32). Water-soluble pentosan content was similar in triticale and its durum parent although the triticale pentosans (both water-soluble and insoluble) had the highest arabinose: xylose ratios among the samples studied. Four pentosan fractions that differed in carbohydrate contents were identified but no correlations were established between the pentosan fractions of the materials studied (32).

Enzymatic Activity

Alpha-amylase. Higher ∝-amylase activity in triticale than in wheat and rye was first reported by Muntzing (72) and later confirmed by

several authors (18, 21, 34, 38, 53, 61, 84, 100). However, α-amylase activity varied widely among different triticale lines. This phenomenon is not yet well understood since, while some workers suggest that the higher α-amylase activity is related to the degree of kernel shrivelling (18, 34, 75, 100), other investigators were not able to obtain a clearly evident relationship between the same parameters (53), or to establish a relationship at all (1). Therefore, it may be more likely that the major factors responsible for the levels of α-amylase activity reside in the genomic composition of the specific triticale cultivar under study, as well as in the environment and environment-genotype interactions. For example, Welsh and Lorenz (115) observed that the winter triticale cultivar TR131 grown at different Colorado locations, produced amylograph values ranging from 20 to 840 BU.

The high α-amylase activity characteristic of triticale, has been attritubed to inheritance of high α-amylase activity from its rye parent (98), and/or as a sign of precocious germination (in some lines). This last statement is based on the observations of Hill et al. (34) and Dedio et al. (21) who noted that a remarkable increase in α-amylase activity occurred in endosperm and aleurone at about 25-30 days post-anthesis. Even more, amylase attack on starch granules occurred during grain development of the triticale endosperm (cv. 6A190) (21). Further characterization studies of α-amylase (97) and inmunochemical identification of α-amylases of developing, mature and germinated triticale grains of the same cultivar (20), confirm that at least in the triticale line 6A190, and probably in other cultivars of the same shrivelled types,

germination-type α-amylase is present during grain development, suggesting that these amylases may be due to lack of dormancy that results in de novo synthesis of α-amylase (20).

Protease. Madl and Tsen (67), by comparative studies of the proteolytic activity of wheat and rye grown in Kansas and triticales grown in Kansas and Mexico, found that proteolytic activity of triticale flours is higher than that of wheat flour, and approximates that of rye flour. Moreover, flours from Mexican triticales showed higher proteolytic activity than rye flour. These authors suggested that proteolytic activity in triticale flours increases as the proportion of the outer endosperm increases in the flour.

Lorenz and Welsh (61) studied proteolytic activity during grain development on triticale and their parental species. They found proteolytic activity decreased as maturation proceeded in all the material studied. The greatest drop in proteolytic activity was observed in durum wheat while the smallest occurred in rye. Even though marked differences occurred in the proteolytic activity among triticales, they remained with intermediate proteolytic activity at maturity. This wide variation among triticale lines was also observed by Noll (75), who found that proteolytic activity was higher in shrivelled-grained than in plump-grained triticales. He found too that the four protease isozymes identified were present in all the triticales studied, and no protease isozyme pattern differences were observed among shrivelled-grained and plump-grained triticales.

Peroxidase. Rao et al. (84) studied peroxidase activity during grain development in wheat, rye, and two triticales (one plump-grained and another shrivelled-grained). Triticale showed the highest peroxidase activity while rye had the lowest. They found also that the shrivelled triticale had two times as much peroxidase activity as the plump one. Moreover, the peroxidase activity changes during development differed among the triticales, as well as between triticale and parental species. Thus, Rao et al. (84) suggested a possible interaction between the genomes forming triticale. On the other hand, Noll (75) observed that peroxidase activity fluctuated at early stages of grain development in relation to later grain shrivelling but was definitely higher in shrivelled triticales at maturity. Noll (75) found too that shrivelled and plump-grained triticales differed in the presence of one peroxidase isozyme from developing to mature grain. One peroxidase isozyme is present in triticales that yield plump grains but absent in the ones that yield shrivelled grains.

Food Uses of Triticale

Milling. The milling characteristics of different triticale types have been studied in various experimental mills by a number of workers (4, 25, 42, 58, 67, 88, 104, 111). The findings of all the above studies showed that triticale had poor milling performance and produced flour yields of 50.0 to 69.0% compared to 66.8 to 73.0% yields from wheat. The low triticale yields have been attributed to low grain test weight as a function of grain shrivelling problems. This suggestion was in agreement with the results of Pinto (80) who milled

52 triticale lines conditioned at 12.5% moisture and obtained flour yields of 54.0 to 72.0%. Pinto (80) concluded that the wide range in milling performance resulted from the equally wide range of shrivelling in his materials. More recently high-yielding, plump-grained triticales at CIMMYT have yielded an average flour per cent of approximately 65 (14, 77).

Breadmaking. Wheat is the most widely used cereal around the world. The unique rheological characteristics of its flour makes it very suitable for the production of a varied number of baking goods of which bread is the most valuable product. The rheological characteristics of triticale flours have been studied and compared with those of wheat flour.

Mixing properties in the farinograph (42, 88, 110, 111) and in the mixograph (63), revealed that the triticale flours studied exhibited lower water absorption and considerably shorter mixing times and mixing tolerances than bread-wheat flours. Lower gluten content (2, 16) along with higher sulfhydryl content (66) than in wheat may be the main factors affecting strength and water absorption.

The weakness of triticale flours was further confirmed when breadmaking performance of triticale was observed to be quite inferior to that of wheat flours (2, 42, 63, 88, 111). When 80:20 blends of wheat and triticale flours were used, however, overall breadmaking characteristics of 100% wheat flours were improved. They suggested that triticale flour provided the diastatic power, lacking in the wheat flour, necessary for satisfactory levels of CO_2 production during fermentation.

Satisfactory breads produced by 100% triticale flours were obtained when modifications in the breadmaking procedures, such as lower mixing speed and short- or non-fermentation time, were made (62, 63, 109). Satisfactory performance was explained to be due to a combination of better breadmaking practices for triticale, along with the actual improvement of the rheological characteristics of certain triticale types. Thus, the short- or non-fermentation time procedures eliminate excessive enzymatic hydrolysis (at least due to high α-amylase and protease activity) that weaken the dough structure during fermentation. On the other hand, baking quality of new triticale strains have been attained by intensive selection from crosses between triticales and bread wheats (14).

The utilization of dough conditioners such as sodium stearoyl lactylate, sucrose tallowate, or ethoxylated monoglycerides, has been observed to improve the baking performance of triticale flours (110).

Miscellaneous products. The rheological characteristics of triticale flours are more critical for the production of loaves of bread from fermented doughs and for cakes from chlorinated flours (108), than for other types of cereal products. Thus, the utilization of triticale to obtain products such as white rye bread and hard rolls (58); pancake and waffle mixes (87); cookies (109); chapaties, flat bread consumed in India (102); extruded breakfast cereals (36, 64); noodles (59); malts for brewing (83); and protein concentrates (95, 116) has been reported to be satisfactory.

Grain Shrivelling

Cytogenetical factors. Darvey (19) studied the influence of individual rye chromosomes as addition lines to hexaploid wheat (Imperial to Chinese Spring, King II to Holdfast, and Dakold to Kharkov), as substitution lines (Imperial in Chinese Spring, King II in Holdfast, and Dakold in Kharkov), and in aneuploid lines (Chinese Spring aneuploids). He found that all rye chromosomes, with the possible exception of chromosome 2R, caused from minor to major effects on grain shrivelling. Added or substituted rye chromosomes 4R/7R, 5R, and 6R caused the major effects. By aneuploid analysis of the three homoelogous groups, he found chromosomes 5A and 5B to have a major effect on grain shrivelling. He suggested nuclear instability in triticale at meiosis and in young endosperm resulted in grain shrivelling due to genome interaction and different developmental rates of wheat and rye.

Kaltsikes (41) studied the early seed development of several hexaploid triticale lines representing a wide range of grain shrivelling. Although there were differences in the rates of embryo development among lines, no mitotic abnormalities were observed. Thus he suggested that embryo development is not related to grain shrivelling even though he found that antipodal disintegration started and terminated first (72 h post-anthesis) in the triticale line with the higher incidence of shrivelling. He did conclude that the duration of the integrity of the antipodals and the rate of endosperm development seemed to be positively related with the degree of shrivelling observed in the lines studied.

Bennett (9) studied the early events of endosperm development in the triticale cv. Rosner. He found that at 2 days post-anthesis some endosperms showed pronounced asynchronous nuclear development manifested as aberrant polyploid nuclei containing up to four times the normal DNA content. He found failure of anaphase during mitosis to be the most frequent phenomena producing aberrant nuclei; however, omission of mitosis (endomitosis) between successive phases of DNA synthesis was also observed to occur. Once the aberrant nuclei was produced, it continued to undergo DNA synthesis at normal intervals creating increasingly abnormal products which remained unisolated from normal endosperm nuclei until cell wall formation occurred. Bennett (9) suggested that the time at which the abnormality occurs (at the coenocytic stage) may be the determinant for subsequent endosperm development. Thus, if the initial miss-division occurs early in the coenccytic stage, giant polyploid nuclei are produced followed by the death of the endosperm. If the abnormality occurs late during the coenocytic stage, so that only a few cycles of DNA synthesis are completed before ceil walls form, then it is not so likely that the entire endosperm will die. He suggested perhaps only the cells with polyploid endosperm nuclei would die and confirmed his idea by fixing endosperm at 5 days post-anthesis wherein dead cells or aborting aberrant nuclei were found in otherwise normal endosperm. The author concluded that dead masses of cells with aberrant nuclei were formed late in the coenocytic stage and may be related to the degree of grain shrivelling in triticale.

Kaltsikes et al. (44) studied endosperm development during the first 7 days after fertilization of primary triticales and triticales

product of intercrossing and selection compared to two hexaploid and one tetraploid wheats, and one rye. The authors' observations were as follows: at 4 days post-anthesis all four triticale showed the same number of endosperm nuclei. Cellularization was general until the 13th endosperm nuclei division stage. Cellularization was observed to begin at no fixed point.

A low frequency of aberrant endosperm nuclei was observed at the 6th nuclei division stage in both primary triticales; in latter stages the number of aberrant nuclei increased to a greater proportion in the more shrivelled triticale (6A190), while the frequency of aberrants in the plump triticale (6A250) remained low up to the 14th nuclei division stage. More aberrant nuclei were observed near the embryo than anywhere else in both primary triticales.

In the other group of triticales, a low frequency of aberrant nuclei was observed up to the 11th nuclei division stage in both the more (2ITSN52) and less (2ITSN73) shrivelled triticale lines. During the next two division stages, an increase in the number of aberrant nuclei occurred in both triticales being much more pronounced in 2ITSN52 than in 2ITSN73 and followed by a slight decrease during the 13th nuclei division stage. In both triticales, more aberrant nuclei occurred near the micropylar end of the embryo sac.

Among all the materials studied, durum wheat exhibited the lowest frequency of aberrant nuclei at all the studied stages; rye presented the highest among the parents and the triticales were intermediate with 6A250 and 2ITSN73 much lower than 6A190 and 2ITSN52. Aberrant nuclei

were not found to be located predominantly near the embryo in all the parental materials.

On the other hand, Kaltsikes et al. (44) also observed that up to the 10th nuclei division stage, the rate of antipodals degeneration was faster in 6A190 and 2ITSN52 than in 6A250 or 2ITSN73. However, at the 11th nuclei division stage, half or more of the antipodals were degenerate in 6A190, 6A250, and 2ITSN52 while in 2iTSN73 this stage of the antipodals was delayed until the 12th nuclei division stage. Antipodals in bread and durum wheat materials behave more or less similarly to those of 2ITSN73 while antipodals in rye behave similarly to 6A190 and and 2ITSN52. Therefore, Kaltsikes et al. (44) suggested that the rye parent alone or in combination with wheat is responsible for the higher number of aberrant endosperm nuclei and earlier degeneration of antipodals as observed in shrivelled-grained triticales.

Kaltsikes and Roupakias (43) studied several disomic substitution and addition lines (Holdfast King II and Kharkov Dakold) to identify the rye chromosome(s) and, for some chromosomes, the arm responsible for the production of aberrant endosperm nuclei and kernel shrivelling. Their findings agreed with Darvey (19) in that all rye chromosomes, when added to wheat, have from minor to major effect in the production of aberrant endosperm nuclei. However, while Darvey (19) found that chromosome 2R may have no effect in this phenomenon, Kaltsikes and Roupakias (43) found that besides 2R, the rye chromosome 7R as well as the short arms of 4R, 5R, and probably 6R, may have no effect in the production of aberrant nuclei. Rye chromosomes with a major influence on the number of aberrant

nuclei were, in descending order of magnitude, 5R, 4R, 6R, 3R, $6R^{1}$ ($6R^{1}$: long arm), and 1R.

While Bennett (9) found that the most common abnormality was bridges formed due to the presence of late-replicating telomeric heterochromatin in some rye chromosomes, Kaltsikes and Roupakias (43) suggested that certain combinations of wheat and rye chromosomes leading to interactions that either prevent spindle formation, or induce late replication in certain chromosome regions which need not necessarily be heterochromatin, are the abnormalities more likely to produce aberrant endosperm nuclei. Early antipodals degeneration and delayed endosperm cellularization in both substitution and addition lines were not observed to be correlated with grain shrivelling in this study. Kaltsikes and Roupakias (43) concluded that the number of aberrant endosperm nuclei was correlated with grain shrivelling in the addition and substitution lines with the exception of the 6R/6B substitution line in which there were few aberrants but severe kernel shrivelling. They suggested that there may be more than one way in which grain shrivelling can be induced.

Bennett (10) studied the early stages of grain development in 21 genotypes including 6 hexaploid triticales, 7 wheat-rye disomic addition lines (Holdfast-King II), 7 wheat-rye monosomic addition lines (Chinese Spring-King II), and 1 rye (Petkus Spring). The results obtained by Bennett (10) supported findings from his previous work (9) in that most of the aberrant endosperm nuclei originated from late replicating telomeric heterochromatin that failed to separate and formed bridges

between nuclei. He observed also that aberrant nuclei were positively related with the degree of grain shrivelling in triticale. The latter relationship, is in agreement with the findings of Kaltsikes et al. (44) and Kaltsikes and Roupakias (43).

Morphological factors. Morphological characteristics associated as a cause and/or manifestation of grain shrivelling in triticale have been studied in some extent by different investigators. Dronzek et al. (23) by SEM, studied morphological characteristics of the mature grain of the triticale 6A190. These authors observed some empty regions where no starch or endosperm formation occurred in the grain. Furthermore, some starch damage, apparently due to α-amylase activity, near the aleurone and crease of the grain was also observed. Dronzek et al. (23) suggested that a probable relationship between α-amylase activity and kernel shrivelling could be related with anomalous endosperm development.

Shealy and Simmonds (96) studied the early developmental morphology of several triticale lines representing severe shrivelled- to plump-grained triticales. These authors observed aleurone malformation to be first recognized at 6 days post-anthesis and well established by 10 days post-anthesis. Invagination and malformation of aleurone and endosperm were suggested to be associated with precocious release of α-amylase in adjacent endosperm areas leading to shrivelled kernels.

Simmonds (98) observed, with light microscopy, the morphological changes during grain development of the triticale line 6A190. He found that an interference with the meristematic function of the peripheral

endosperm could be observed at about 6-7 days post-anthesis, later to be manifested as an invagination of the outer meristematic layer. This was produced apparently by a thickening and intrusion of the nucellar epidermis between adjacent endosperm cells that distorted the aleurone layer. Simmonds (98) suggested that distorted aleurone cells released enzymes that degraded the meristematic layer, producing empty areas beneath the nucellar epidermis that finally resulted in malformation and shrivelling in the grain. He suggested also that premature release of α-amylase and subsequent digestion of starch granules is a phenomenon that contributes to grain shrivelling in triticale. He found that shrivelling was clearly manifested in the grain surface at about 34 days post-anthesis when the grain started to lose moisture.

Lorenz (65) studied grain development of the triticale line 6TA204 and found that the morphological changes during maturation were similar to those occurring in normal wheat and rye. The only abnormality that produced shrivelled appearance was a separation of the pericarp from the endosperm in some places. The results obtained by Lorenz (65) may be explained by the highly fertile and cytologically stable characteristics of 6TA204 (90) and its plump grains.

Biochemical factors. According to Klassen et al. (53), triticale has been observed to have a short dormancy period resulting in premature α-amylase activity and precocious germination that may produce kernel shrivelling.

In studies of the carbohydrate content and α-amylase activity at different stages of triticale grain development in lines with different

degrees of grain shrivelling, he found ∝-amylase activity high at the beginning (10 days post-anthesis) which then decreased rapidly during early stages of maturity. At about 50-55% grain moisture, the more shrivelled lines showed rapid, high increases in ∝-amylase activity until maturity. In contrast, only slight increases were observed in the less shrivelled lines. Klassen et al. (53) found that at maturity, with the exception of one triticale line (cv. Beaver "s"), ∝-amylase activity was highly correlated with the degree of grain shrivelling. Similar studies carried out with different triticale genotypes (34, 61, 75. 84, 100) showed that ∝-amylase activity decreased during the early stages of maturation but increased rapidly at about 50-55% moisture or 22 to 28 days post-anthesis in triticale lines with high degree of kernel shrivelling. Only small increases occurred in plump-grained lines. However, although Chojnacki et al. (18) found that grain shrivelling "caused" high levels of ∝-amylase activity in several triticale lines, they did not observe the pattern of enzyme changes during grain development. They found instead that the experimental materials were heterogeneous in terms of ∝-amylase activity changes and could be divided into three different groups. Chojnacki et al. (18) concluded that triticale may be bred with ∝-amylase levels similar to that found in rye and discarded the idea that high levels of ∝-amylase activity were, in general, related to precocious germination. Their idea was supported by Jenkins and Meredith (38) who suggested that the weather during the maturation and post-maturation stages was not conducive to to sprouting as reflected in the very low ∝-amylase activity (higher though than in wheat) for the pre- and post-ripe periods in triticale and rye. Furthermore, Agrawal (1) found that a triticale line with

shrivelled grains had almost identical low α-amylase activity as in wheat while the plump-grained triticale had higher α-amylase activity at certain stages of grain development than the shrivelled-grained triticale. Agrawal (1) concluded that amylases and hence sprouting, were not related to grain shrivelling in the materials studied.

On the other hand, the levels of some carbohydrates have been found to be related to the degree of shrivelling in triticale grain. Thus, Klassen et al. (53) observed that starch accumulation during grain development terminates earlier in shrivelled-grained triticales than in plump-grained triticales, and remained constant until maturity. They observed also that reducing sugars remained higher at maturity in the more shrivelled-grained triticales than in the plump-grained triticales. Similar results were obtained by Singh et al. (100) who found that total alcohol-soluble sugars were higher when the starch content was lower in the shrivelled-grained triticale. Noll (75) also observed similar relationships between starch, total soluble sugars, and grain shrivelling in triticale, but no significant difference in reducing sugars between shrivelled- and plump-grained triticales. Besides the controversial relationship that could exist between α-amylase activity, starch content and grain shrivelling, Hill et al. (34) carried out sucrose-^{14}C feeding experiments in the triticale cultivars 6A190 and 6531 and found that the shrivelled triticale 6A190 was less efficient in transporting sucrose to the head than the plump triticale 6531. In addition, 6A190 deposited more transported sucrose to the pericarp than did 6531 and that the rate of starch deposition was slower than in 6531. Hill et al. (34) concluded that nutrient transport to the head may also be involved in the production

of grain shrivelling in triticale which agrees with Jenner and Rathjen's (39) observations of an active barrier against nutrient transport in some wheats.

MATERIALS AND METHODS

Hexaploid triticale, wheat, and rye samples were grown under uniform environmental conditions at Cd. Obregon, Sonora, Mexico, during the winter of 1977-78 as part of the CIMMYT's triticale yield trials. The triticale lines, which are advanced products of intercrossing and selection, were chosen to obtain material with different degrees of grain shrivelling while minimizing genetic and environmental variables. Variety or cross name, and identification number to be used throughout this work, are presented in Table 3.

Meal/Flour Preparation

To obtain whole-meal flours, the samples were ground as received in a UDY-Cyclone pulverizer to pass a 0.5 mm screen.

Flours were obtained from triticale samples tempered at 12.5% moisture for 24 hr; wheat samples, at 15% moisture for 24 hr; and the rye sample, at 14% moisture for 24 hr. All flours were milled in a Brabender Quadrumat Senior experimental mill to pass a 10xx-mesh sieve.

Moisture, Ash, and Protein

Moisture, ash, and protein were determined by the official methods (13.004, 13.006, and 38.012, respectively) of the AOAC (5).

Mixograms and Sedimentation Test

Mixograms and sedimentation tests were determined as described in the approved methods of the AACC (3).

Table 3. Triticale, wheat, and rye samples studied.

Variety No.	Variety or cross name	Identification No.
Triticale		
424	Rahum	P-1
430	Mapache	P-2
823	PM 28 Bulk-Cml "s" X-21349-2N-0Y	P-3
827	IA-M_2A X Pi62/Bgl "s" X-116304-110-1M-0Y	P-4
1628	Drira-Arm "s" X-21367-4N-0Y	P-5
2427	IRA^2 X M_2A X-11308-B-2M-3Y-2Y-4M-0Y	P-6
1303	IA-Kla X Cal X-14920-2Y-0M	P-7
1401	Bgc-Bulk e2 X-11066-A-6M-100Y-101B-100Y-0Y	P-10
Wheat		
	Calidad	P-8
	Hermosillo	P-9
Rye		
	Snoopy	P-11

Bread Baking

Two baking systems were used--the straight dough method described in the approved methods of the AACC (3) as a long-fermentation time system and the straight dough method described by Finney et al. (26) and designated as a short-fermentation time system. In the last system, the formula and procedure were used as follows: 100 g flour (14% moisture basis), 3 g shortening, 3 g nonfat milk solids, 5 g sugar, 7.2% of yeast (flour basis), 1.0 g NaCl. Absorption and mixing time were optimized for each dough. The doughs were punched after 40 and 60 minutes and molded and panned after 70 minutes. Proof time was 25 min and oven time was 25 min at 218°C. Loaf volume and weight were measured immediately after baking. Loaves were scored after cooling.

Alpha-amylase Activity

Alpha-amylase activity was determined by the method of Barnes and Blakeney (6). This method includes a partially hydrolyzed potato starch, crosslinked by 1,4 butanodioldiglycidether and labelled with Cibacron Blue by covalent bonds. This substrate, available commercially as Phadebas tablets (Pharmacia Laboratories, Inc., Piscataway, N.Y.), is resistant to degradation by β-amylase, and liberates water-soluble dye-labelled products upon α-amylase hydrolysis. A partially purified triticale (P-10) α-amylase was prepared according to Greenwood and Milne (29), and its activity determined as follows: 10 mg of the partially purified α-amylase was dissolved in 10 ml of 0.1M acetate buffer, pH 5.5, containing .001M $CaCl_2$. One ml of the properly diluted enzyme solution (20, 40, 60, 80, 100/ml aliquots) was incubated in the

presence of a starch solution, prepared according to Strumeyer (105), at 30°C for 10 min. Reducing products were measured by the Nelson colorimetric copper procedure as described by Robyt and Whelan (86). The activity was determined as International Enzyme Units (EU). One EU is equal to 1 µmole of maltose produced for 1 ml of enzyme solution in 1 min.

The Phadebas ∝-amylase activity method was performed as follows: ∝-amylase was extracted from 100 to 500 mg of triticale whole meal and/or flour, and from 2 g of wheat and rye whole meal and/or flour, with 20 ml of 0.05M maleate buffer, pH 6.0, containing calcium chloride 0.2 g/l. The suspension was gently shaken for 5 min on a vortex mixer or a magnetic stirrer and then centrifuged at 5000 rpm for 10 min. Five ml of the properly diluted supernatant were transferred to a 10-ml graduated test tube and placed in a water bath at 50°C until equilibrated (10 min). A timer was started on the addition of one Phadebas tablet which was completely dispersed by shaking gently on a vortex mixer. The digest was incubated for 15 min, with a gentle vortex mix each 5 min. On completion of the incubation, 1.0 ml of 0.5M NaOH was added, mixed thoroughly in the vortex, and the volume made up to 10 ml with distilled water. The colored solution was filtered and the absorbance read against a nonenzyme blank at 620 nm with a 1 cm lightpath cuvette. Alpha-amylase activity was obtained by converting absorbance values into EU by using the calibration curve obtained from the action of partially purified triticale ∝-amylase in the Phadebas substrate.

Starch

Starch content was determined with the Dreywood's anthrone reagent as described by McCready et al. (68) as follows:

a) Sugars extraction. Fifty to 200 mg of sample were placed in a 50-ml polypropylene centrifuge tube, mixed with 20 ml of 80% ethanol and immediately stoppered with a marble. The tube was placed in a water bath at 60°C for 45 min and stirred thoroughly during the first 20 min (to avoid sample adhering to the tube walls). After 45 min, the sample was placed in an ice-water bath (5 min) and then centrifuged (14,000 rpm, 15 min). The supernatant was decanted in a 50-ml Erlenmeyer flask. The residue was extracted again as described above. The supernatant solutions were combined and stored at 5°C for total and reducing sugars determinations.

b) Starch solubilization. To the residue from the sugars extraction, 5 ml of distilled water were added and 6.5 ml of 52% perchloric acid were added while stirring. The contents were stirred continuously for 5 min with a glass rod and occasionally thereafter for 15 min. Subsequently 20 ml of distilled water were added and the whole mixture centrifuged (5000 rpm, 15 min). The starch supernatant was transferred to a 100-ml volumetric flask. The residue was again extracted with 5 ml of distilled water and 6.5 ml of 52% perchloric acid added as above. The extraction continued for 30 min followed by washing the contents into the supernatant containing 100-ml volumetric flask. The volume was made up to 100 ml with distilled water and filtered.

c) Starch determination. Five ml of the properly diluted starch solution were transferred to a test tube (18 X 150 mm) and kept in an ice-water bath. Ten ml of fresh anthrone reagent were added slowly, the tube was stoppered with a marble, and the whole mixed thoroughly on a vortex mixer. The solution was heated for 7.5 min in a boiling-water bath and immediately cooled to room temperature in an ice-water bath. The reaction mixture was thoroughly stirred on the vortex and the absorbance measured at 630 nm. A glucose standard curve (0, 15, 30, 60, 90, 120, and 150 µg of glucose) was prepared with each set of samples. Glucose (µg) multiplied by 0.92 was used to convert to starch µg.

Total Soluble Sugars

Total soluble sugars were determined in the sugars solution obtained by ethanol extraction above in the starch determination procedure. A portion of the alcoholic sugars solution (depending on total sugars expected) was evaporated in an oven at 50-55°C, and then resuspended in 10 ml of distilled water. Ir necessary, a further dilution was made in order to obtain the proper amount of sugar in 5 ml of the solution to be tested by the Dreywood's anthrone reagent described above for starch determination. Total sugars were reported as percent of dry matter.

Reducing Sugars

Reducing sugars were determined with the Nelson procedure (73) as follows:

Reagent A. Twenty-five g of anhydrous sodium carbonate, 25 g sodium potassium tartrate, 20 g sodium bicarbonate, and 200 g of sodium sulfate were dissolved in 800 ml of distilled water, diluted to 1000 ml and filtered. The solution was stored in an amber container above 20°C.

Reagent B. Thirty g of cupric sulfate pentahydrate were dissolved in 200 ml of distilled water containing 4 drops of concentrated sulfuric acid. The reagent was kept in an amber bottle at 5°C.

Reagent C. Twenty-five g of ammonium molybdate were dissolved in 450 ml of distilled water to which 21 ml of concentrated sulfuric acid were slowly mixed. Three g of sodium arsenate heptahydrate dissolved in 25 ml of distilled water were added slowly and the whole was diluted to 500 ml and warmed 24 hr at 37°C in an amber container.

Reagent D. One ml of reagent B was added to 25 ml of reagent A. This reagent was prepared fresh daily.

The aqueous sugars solution obtained after the evaporation of alcoholic sugar extract, described above in the total soluble sugars determination procedure, was utilized. One ml of the properly diluted sugar solution was mixed with 1 ml of freshly prepared reagent D, the test tube (18 X 150 mm) stoppered with a marble, and incubated in a

boiling-water bath. After 20 min of incubation, the tube was cooled to room temperature in an ice-water bath, 1 ml of reagent C was added, and the contents shaken on a vortex mixer until carbon dioxide was no longer evolved. Finally, 10 ml of distilled water was added, the whole solution mixed thoroughly, and the absorbance measured at 630 nm. A standard curve of glucose (0, 5, 10, 15, 20, and 25 µg of glucose) was prepared with each set of samples. Reducing sugars were reported as percent of dry matter.

Scanning Electron Microscopy (SEM)

All triticale samples were categorized into three classes as follows: a = plump; b = medium shrivelled; and c = highly shrivelled. Wheat, rye, and categorized triticale grains were fractured with a razor blade to obtain median transverse cross-sections. The sections were mounted on specimen stubs using silver paste (Pelco Industries, Tustin, California). The stubs were vacuum coated with carbon and gold-palladium to approximately 200 Å thickness. Sections were viewed with an ETEC Autoscan electron microscope operating at 10 KV.

Grain Developing Study

Seeds of the three classes, representing different degrees of grain shrivelling (categorized above in the SEM procedure) within a secondary hexaploid triticale (cv. Rahum) were grown separately under controlled environmental conditions. As the heads emerged, each was bagged, and the anthesis date recorded.

For the biochemical study, the spikes were harvested in the afternoon at each of 5 different stages of maturity (7, 14, 21, 28, and 35 days post-anthesis). Number of spikelets per spike and number of grains per spike were recorded. The grains were removed from 3 to 5 spikes, immediately weighed, and freeze-dried for 36 hr to obtain the moisture content. The freeze-dried samples were ground initially in a "Super Junior Moulinex" coffee grinder and pulverized finely in a Wig-L-Bug dental amalgamotor. Alpha-amylase activity, starch, total soluble sugars, and reducing sugars were determined as described above.

For the study of morphological changes during grain development, 2 spikes were harvested at 5 different stages of maturity (5, 10, 15, 20, 26 and 35 days post-anthesis) and fixed in glacial acetic acid-formaldehyde-picric acid (Bouins fixative) or formaldehyde-propionic acid - 70% ethanol (FPA fixative). Dehydration, infiltration, and embedding were effected according to an ethanoltertiary butanol-paraffin schedule of Sass (94). Transverse sections of 10 microns thickness were prepared on a Spencer no. 815 rotary microtome (American Optical Co., Buffalo, N.Y.), stained with Safranin and Fast Green FCF, and permanent slides prepared in Preservaslide (Curtin Matheson Scientific).

RESULTS AND DISCUSSION

All triticale lines studied contained 2n=6x=42 chromosomes (71), and were advanced secondary triticales as products of intercrosses among triticales and between triticales and hexaploid wheats.

Meal/Flour Preparation

The tempering and milling procedures used were chosen to produce flour (or meal) simulating those commercially accepted in terms of bran content as reflected by flour ash content. No attempts to maximize flour yield were made for two reasons: (a) milling performance of triticale was not the concern of this study and, (b) triticale produces lower flour yields than wheat due to grain shrivelling (14, 62, 77, 104, 116).

Protein and Ash Content

Moisture, protein, and ash content of the experimental grains are given in Table 4. Triticale protein varied from 11.8 to 13.7% with an average of 12.6%, while wheat (P-8 and P-9) and rye (P-11) samples contained 14.8, 13.0 and 12.6%, respectively. When grain samples were converted to flour, an average drop of 1.95% protein occurred in triticale, while for wheat (P-8 and P-9) and rye (P-11) the component decrease was of 1.8, 0.8, and 4.6%, respectively. Thus, flour protein among triticales varied from 9.6 to 11.7% with an average of 10.6%, while wheat (P-8 and P-9) and rye flour samples contained 13.8, 12.2, and 8.0%, respectively. Ash content of triticale (except P-6 and P-7) and rye flours was slightly higher than that of wheat flours. Protein and ash values indicated that triticale endosperm protein is intermediate between wheat and rye.

Table 4. Moisture, protein and ash content of triticale, wheat and rye.[a]

Sample no.	Grain[b]		Flour[c]		
	Moisture %	Protein %	Moisture %	Protein %	Ash %
P-1	10.2	12.4	12.2	10.8	0.53
P-2	9.7	12.3	11.8	10.7	0.52
P-3	9.4	12.7	12.0	10.6	0.57
P-4	10.0	11.8	12.2	9.6	0.57
P-5	9.6	12.0	12.0	10.3	0.56
P-6	10.0	12.6	12.0	10.0	0.46
P-7	9.7	13.5	12.0	11.3	0.46
P-8	10.6	14.8	13.6	13.0	0.47
P-9	10.3	13.0	14.3	12.2	0.39
P-10	10.4	13.7	12.6	11.7	0.53
P-11	9.4	12.6	11.8	8.0	0.51

[a]Protein and ash on a 14% moisture basis.

[b]Grain protein (N X 5.83).

[c]Triticale and rye flour protein (N X 5.83); wheat flour protein (N X 5.7).

Sedimentation Value

Sedimentation values of the triticale and wheat flours are given in Table 5. In the sedimentation test, the volume of the sediment consists mainly of swollen gluten and occluded starch although the sedimentation value is influenced primarily by the quality and quantity of gluten. Sedimentation values of triticale flours (except P-10) varied from 14 to 26 cc (characteristic of weak flours) with an average of 20 cc. The triticale flour P-10 had 43 cc (characteristic of medium strong flours) and the wheat flours (P-8 and P-9) had 66 and 52 cc (characteristic of strong flours), respectively. It is of importance to point out that among bread wheats, within certain limits, as the flour protein increases the gluten content increases, resulting in an increase in sedimentation value. However, the same relationship was not observed to occur among triticale flours. For example, triticale P-7 with a protein content of 11.3%, had a sedimentation value of 14 cc (the lowest here obtained for triticale), while the triticale P-1 and P-10 with protein contents of 10.8 and 11.7%, respectively, had sedimentation values of 26 and 43 cc, respectively. The high sedimentation value observed for triticale P-10 indicated that this line would be expected to have the best breadmaking quality among the triticale lines under study.

Mixographic Characteristics

The mixograph data is presented in Table 5. From mixograph curves, the mixing time required to obtain an optimum developed dough,

Table 5. Sedimentation, mixograph, and baking data of triticale and wheat flours.

Sample no.	Sedimentation value (cc)	Mixograph			Baking quality[d]					
		H_2O abs (%)	Peak height (cm)	Time to maximum ht (min)	H_2O abs (%)	Mix time[a] (min)	Loaf wt (g)	Loaf vol (cc)	Crumb color[b]	Grain texture[c]
P-1	26	59.7	3.7	1.92	58.0	1.0	150	670	3	S
P-2	20	59.7	3.4	1.50	57.0	5/6	148	640	2	U
P-3	22	59.7	3.4	1.33	58.0	1.0	150	570	3	U
P-4	16	58.8	3.3	1.33	57.5	4.5/6	150	500	2	VU gummy
P-5	23	59.4	3.4	1.50	58.5	1.0	153	510	2	VU gummy
P-6	22	59.1	3.6	1.25	58.0	5/6	151	620	3	U gummy
P-7	14	60.3	3.4	0.50	58.8	4/6	150	510	1	VU gummy
P-8	66	62.3	6.8	2.66	69.3	2 1/6	150	1005	4	VS
P-9	52	61.3	7.7	1.83	67.1	1 5/6	152	955	4	VS
P-10	43	61.3	4.2	1.75	60.0	1.0	145	820	4	VS

[a]Mixing adjusted to produce better dough consistency and handling characteristics.

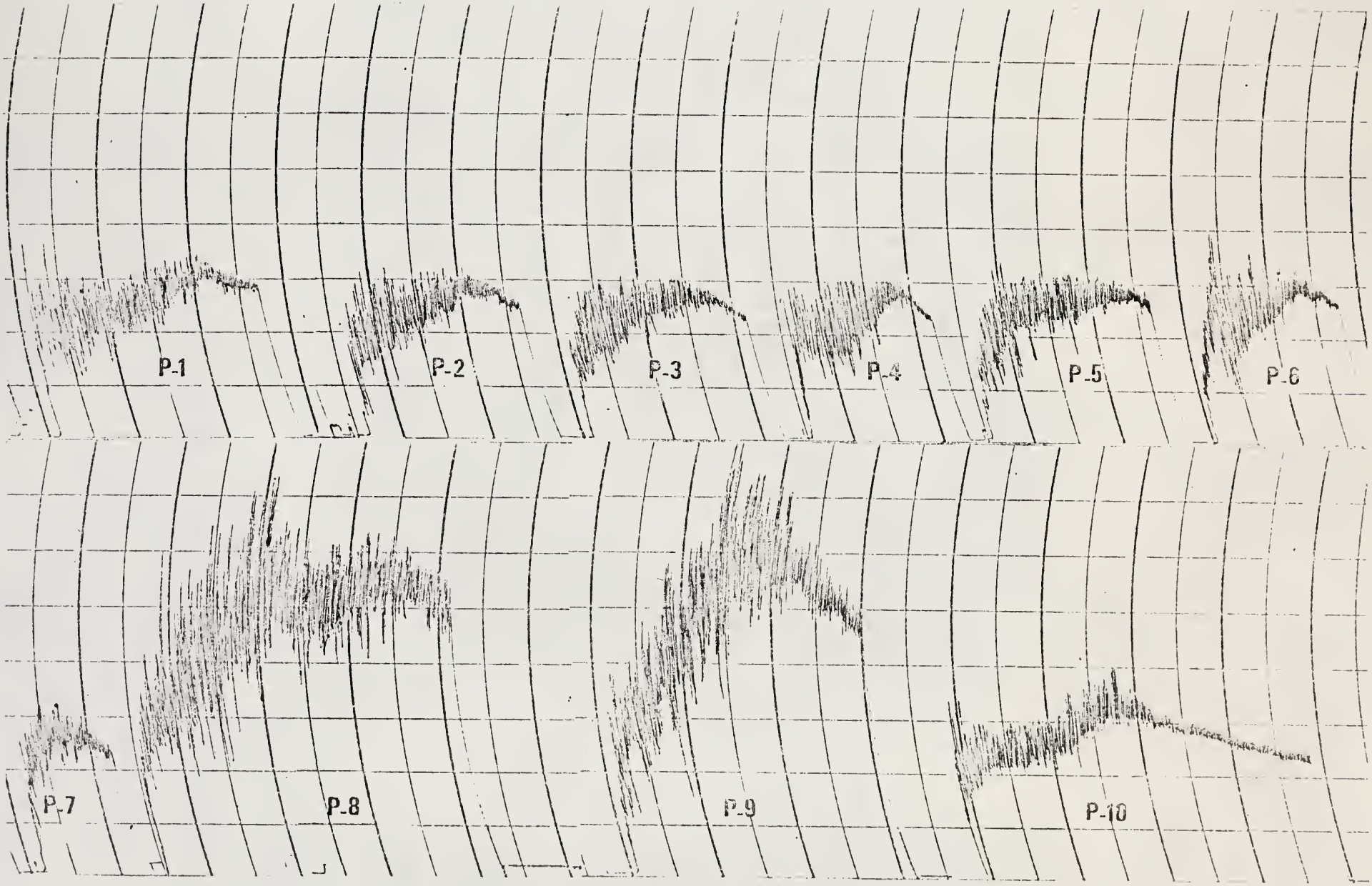
[b]4-creamy bright; 3-creamy pale; 2-dark; 1-very dark.

[c]VS=very satisfactory; S=satisfactory; U=unsatisfactory; VU=very unsatisfactory.

[d]Average value from 3 replicates.

its tolerance to overmixing, and the interrelation between flour absorption and protein content as influenced by gluten quantity and quality (represented by the curve peak height) can be determined. Triticale flours were observed to vary widely in mixing time and, except for P-1 and P-10, to develop faster than the wheat flours. As shown in Fig. 1, all triticales showed shorter stability or tolerance to overmixing, and shorter peak height than wheat flours. Similar results were obtained by Lorenz et al. (63) with the mixograph, and by Tsen et al. (110) and Lorenz and Welsh (62) with the farinograph. Among bread wheats, flour absorption has been found to be directly influenced to a great extent by the flour protein content in which, according to Kasarda et al. (45), about 85% is gluten. This interrelation is manifested in the mixogram characteristics of wheat flours. Thus, considering the results obtained, it might be possible that the water used exceeded the actual flour absorption of triticales, leading to a more fluid dough that developed fast and provided only low resistance to the rotating mixing forces resulting in low peak-height curves. Therefore, it may be suggested that the interrelation between flour absorption and flour protein observed in wheat did not appear to be true for triticale due, perhaps, to lower gluten content and strength in the total protein as indicated by the sedimentation values obtained. Triticale P-10 as judged by its protein content, sedimentation value, and its mixing time, may result in a satisfactory loaf of bread as suggested earlier.

Figure 1. Mixograms of triticale and wheat flours.


P-1
P-2
P-3
P-4
P-5
P-6
P-7
P-8
P-9
P-10

Baking Quality

It has been claimed (26) that no differences in baking quality can be detected when wheat doughs are baked with the long fermentation time or the short fermentation time systems described above. This statement was made in regard to increased oxidation requirements (by a factor of three) as the fermentation time decreased from 180 to 70 min (26). Because short fermentation time produces triticale loaves with improved quality (63, 110) and the short fermentation time system produces baking characteristics comparable to those produced by the long fermentation time system, it seemed that baking quality of wheat and triticale flours could be compared simultaneously with the short fermentation time system that does not affect wheat and could be favorable for triticale baking performance. To confirm this suggestion, a check wheat flour was baked with both baking systems. No detectable differences in baking characteristics were found between the breads produced by either baking systems. Therefore, the short fermentation time was used to evaluate the baking quality of triticale flours. Baking data are presented in Table 5.

In order to obtain doughs with acceptable consistency and handling characteristics, water and mixing time, based on mixograph data, were reduced in all triticale flours. However, as the fermentation time increased, the triticale doughs varied in their consistency. With the exception of P-1 and P-10, all the triticale samples became sticky and difficult to handle. This characteristic was ultimately reflected in the loaves of bread, as shown in Table 5 and Fig. 2, where it can

be observed that most of the triticales (except P-1 and P-10) gave poor baking performance. These breads had low volume, open and nonuniform grain, dark crumb color, and gummy texture. The triticale P-1 showed potential to be a very satisfactory breadmaking triticale. In fact, Lorenz and Welsh (62) found that the same triticale line produced very satisfactory loaves of bread when 20 ppm of potassium bromate (an oxidant) and 0.5% of sodium stearoyl-2-lactylate were added to the formula. The triticale P-10 exhibited baking characteristics that could be considered very satisfactory to produce bread.

Although all the triticales studied are considered advanced secondary hexaploid triticales, they exhibited extremes of sedimentation, mixograph and baking characteristics. Factors that may influence this variability are as follows: a) The numbers of rye and wheat chromosomes in a triticale cultivar may vary from one to another considering that chromosome substitutions occur (30). If a pair of rye homologous chromosomes is substituted for a pair of homologous wheat D-genome chromosomes, this substitution would have a strong effect on the synthesis of gluten protein. Therefore, the number of rye and D-genome chromosomes, their identity, and the interaction between them would influence the composition and the physical and baking characteristics of the secondary hexaploid triticales (16, 76). b) Alpha-amylase and protease activity vary widely among triticales. However, this enzymatic activity is generally higher in triticale than in wheat (21, 61, 67, 75). This high enzymatic activity in triticale would be expected to have a detrimental effect on breadmaking since, during fermentation, it weakens the dough structure by decreasing the gas retention capacity and producing undesirable gummy crumb.

Figure 2. Loaves of bread baked from different triticale flours and one wheat flour.

It is concluded that among secondary hexaploid triticales, a few lines (P-1 and P-10) have now acquired the baking performance that previously had been considered a unique characteristic of wheat. However, further effort should be made to increase the number of triticales with baking quality, improved grain type, and decreased enzymatic activity.

Alpha-amylase Activity

Grain and flour α-amylase activity varied widely among triticales but in general was many-fold higher than in wheat and rye (Table 6). These observations are in full agreement with those reported by several previous workers (21, 53, 61, 84, 100). Most of the flour samples (except P-6 and P-11) had lower α-amylase activity than their corresponding grain sample. This latter result could be explained by the fact that most of the grain α-amylase activity is located in the aleurone and endosperm cells immediately below the aleurone (21) and was not obtained in the low extraction flour of the triticales under study (as indicated by their ash content, Table 4). In the case of samples P-6 and P-11, the slightly higher α-amylase activity in flour than in grain indicated that α-amylase activity in the aleurone was lower than in the endosperm as observed also by Dedio et al. (21) and Simmonds and Campbell (99) when studying the rye cv. prolific.

Although a relationship between α-amylase activity and extent of grain shrivelling in triticale has been suggested (18, 53, 75, 84, 96), no relationship could be found in these advanced secondary triticales. Because a range of plump to highly shrivelled grains could be observed

Table 6. Biochemical and chemical composition of grain and flour samples.[a]

Sample no.	Grain				Flour			
	α-amylase activity EU/g	Starch %	Total soluble sugars %	Reducing sugars %	α-amylase activity EU/g	Starch %	Total soluble sugars %	Reducing sugars %
P-1	283.1	59.6	3.7	0.20	163.1	79.3	2.1	0.20
P-2	179.4	59.4	4.1	0.23	102.0	74.0	2.1	0.27
P-3	211.0	59.0	4.8	0.23	128.1	77.8	2.2	0.23
P-4	181.7	62.3	3.9	0.17	133.1	79.0	2.0	0.16
P-5	613.9	59.2	5.2	0.24	418.8	73.9	3.6	0.23
P-6	46.7	65.3	4.8	0.19	54.6	74.0	2.6	0.21
P-7	212.6	57.0	5.6	0.25	105.2	70.9	5.0	0.34
P-8	2.4	58.5	2.6	0.16	0.8	72.5	1.8	0.28
P-9	1.4	66.2	3.0	0.20	0.9	75.1	1.8	0.31
P-10	182.3	61.2	4.2	0.16	131.1	68.2	2.7	0.25
P-11	2.3	54.5	5.0	0.21	7.3	76.2	4.4	0.16

[a]Dry weight basis.

in each cultivar bulk sample (Fig. 3), a subjective visual classification of plump, medium shrivelled, and highly shrivelled grains (designated class -a, -b, and -c, respectively) within each of the 8 triticale cultivars was established. Grain quality was ranked by the frequency of plump grains in each cultivar (Fig. 3 and Table 7). Still no evident relationship between ∝-amylase activity and extent of grain shrivelling could be observed despite the consideration that whole meal and flour triticale samples might not have included the grain classes in the same proportions estimated by visual selection. In order to draw firm conclusions, each of the 3 visual grain classes of all 8 triticale cultivars (P1a, P1b, P1c, P2a,....., P10c) was analyzed (Table 8). The results were consistent within triticale cultivars in that plumpest grain had the lowest ∝-amylase activity, class b had an intermediate and class c had the highest ∝-amylase activity. However, this relationship was not observed among samples. When ∝-amylase activity of plump (class-a) and medium shrivelled (class-b) grains of different triticales were compared to each other, no relationship could be seen. For example, P-10a had 4.5 times the ∝-amylase activity of P-2a and P-5a had 1.9 times the activity of P-2b. The ∝-amylase activity of the highly shrivelled class c varied widely from one triticale to another. However, the lowest ∝-amylase activity of any highly shrivelled classes was higher than the ∝-amylase activity of any -a or -b class of all the 8 triticale cultivars. These results provide additional evidence virtually to eliminate any contention that ∝-amylase activity is a major factor influencing grain shrivelling in triticale, which is in agreement with the earlier results of Agrawal (1) and Klassen et al. (53).

Figure 3. Photograph showing the actual size and characteristics of categorized and bulk samples of seven triticales under study (triticale P-10 grain type is represented here by triticale P-5).

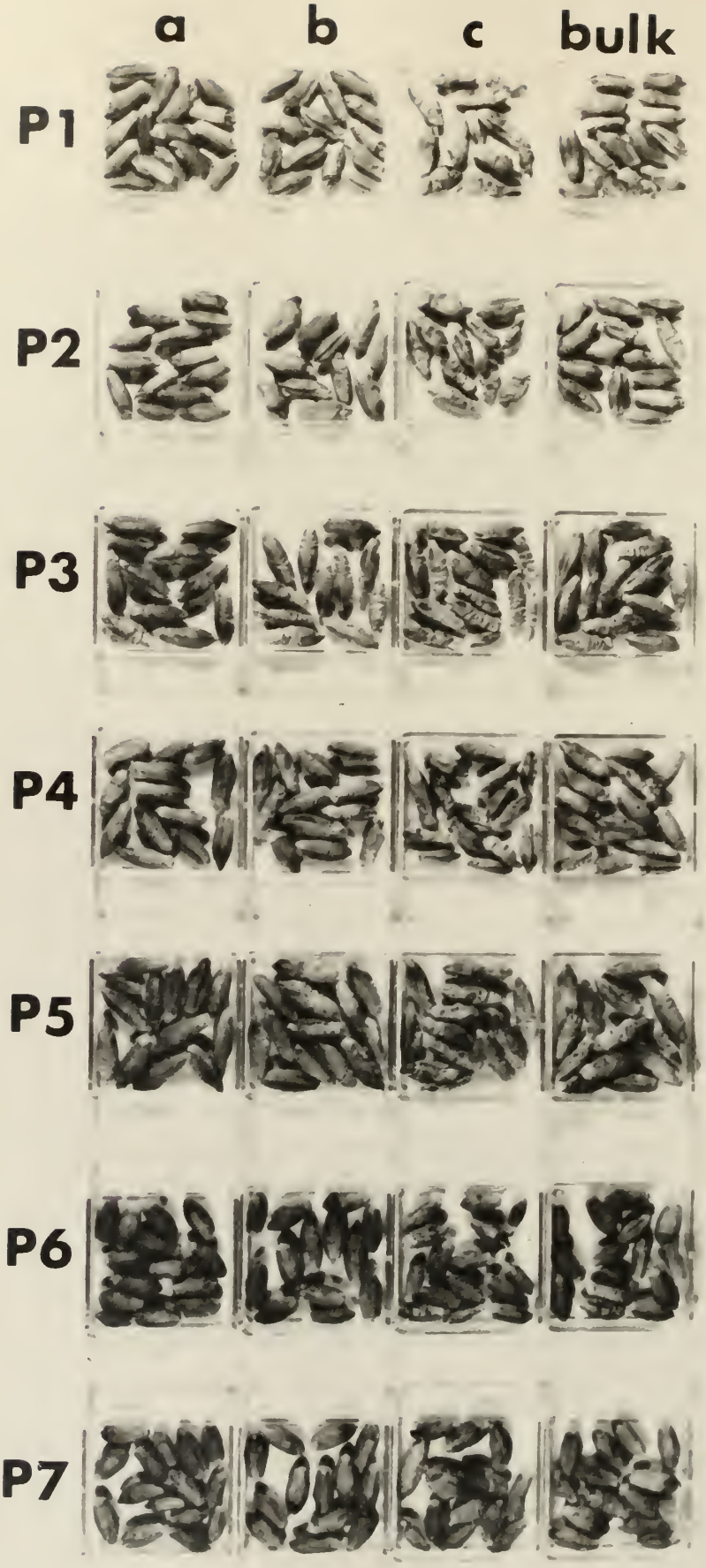

a
b
c
bulk
P1
P2
P3
P4
P5
P6
P7

Table 7. Ranking of the triticale samples based on frequency of plump-(a); medium shrivelled-(b) and highly shrivelled-(c) grains.[a]

Sample no.	Grain class a %	b %	c %	Grain quality ranking[b]
P-1	39.0	47.6	13.4	3
P-2	28.6	56.5	14.9	4
P-3	18.0	62.3	19.7	6
P-4	20.0	69.9	10.1	5
P-5	14.2	65.6	20.2	8
P-6	49.8	42.8	7.4	1
P-7	46.2	44.1	9.7	2
P-10	17.1	56.8	26.1	7

[a]Average percent of 3-replicate determinations.

[b]1 = highest frequency of plump grains; 8 = the lowest.

Table 8. Biochemical and chemical composition of categorized triticale grain samples.

Sample no.	∝-amylase activity EU/g	Starch %	Total soluble sugars %	Reducing sugars %
P-1a	68.3	64.3	3.2	0.12
P-1b	168.3	59.8	3.0	0.16
P-1c	1047.8	55.8	5.5	0.29
P-2a	20.5	68.0	4.2	0.09
P-2b	42.1	68.0	4.7	0.10
P-2c	485.1	61.5	7.7	0.21
P-3a	27.9	66.6	4.4	0.08
P-3b	112.2	64.8	5.0	0.09
P-3c	402.4	60.2	5.8	0.25
P-4a	42.8	68.2	4.3	0.07
P-4b	141.5	67.2	5.0	0.10
P-4c	737.2	58.8	8.5	0.24
P-5a	80.3	67.8	4.4	0.09
P-5b	171.0	64.6	4.7	0.11
P-5c	765.9	59.0	5.0	0.46
P-6a	35.4	69.6	4.3	0.04
P-6b	55.6	68.5	4.7	0.07
P-6c	367.2	59.2	7.3	0.12
P-7a	49.6	62.0	5.1	0.05
P-7b	75.3	58.7	5.6	0.08
P-7c	794.5	54.2	8.8	0.48
P-10a	92.2	63.9	4.7	0.07
P-10b	257.3	60.8	4.4	0.07
P-10c	275.9	57.7	5.2	0.08

[a]Dry weight basis.

Starch

Triticale grain and flour starch content ranged from 57.0 to 65.3% and from 68.2 to 79.3%, respectively (Table 6). The starch content of wheat grain and flour essentially fell within the respective range of starch content of triticale (P-9 grain at 66.2 was slightly high). Rye grain had the lowest starch content while rye flour starch was within the triticale flour range. No relationships between starch content (in grain and flour) and extent of shrivelling could be established using ranked triticale (Table 7 ranking). When the visually categorized classes of all the 8 triticales were analyzed, the starch content was observed consistently higher in the plump -a class within a cultivar (Table 8). However, this relationship was not observed when starch contents of different grain classes of various triticales were compared. These observations may be explained partially by collapses to fill empty spaces in the endosperm (as suggested by Simmonds, 98), by variations due to packing of contents within the endosperm, variations in grain size (Fig. 3) and total dry matter accumulation (as suggested by Salminen and Hill, 91), as well as by variations in α-amylase activity among the triticales studied. The relationship between starch content and extent of grain shrivelling is in agreement with the results of several investigators (34, 53, 75) but contrary to those of Agrawal (1) who compared only two triticale lines (one plump and one shrivelled).

Total Soluble Sugars

Total soluble sugars ranged from 3.7 to 5.6% and from 2.0 to 5.0% for triticale grain and flour, respectively (Table 6). Wheat grain and flour had lower total soluble sugars than the respective triticale materials, while rye grain and flour total soluble sugars fell within the respective ranges of total soluble sugars in triticale. In ranked triticales (Table 7), no relationship between total soluble sugars (in grain and flour) and extent of grain shrivelling was found. When the three classes of all the 8 triticales were analyzed, the highly shrivelled grain class within cultivars exhibited the highest total soluble sugars content although in some cultivars, P-3, P-5 and P-10 for example, the highly shrivelled grain class did not have considerably higher total soluble sugars than the plump one (Table 8). This relationship was not observed to occur consistently for the plump and medium shrivelled grain classes and a larger variation even was found when the total soluble sugars of grain classes of different triticales were compared to each other. Similar results were obtained by Noll (75). Therefore, it is suggested that total soluble sugars is not a parameter that could indicate strongly the extent of grain shrivelling in triticale.

Reducing Sugars

Reducing sugars in triticale grain and flour ranged from 0.16 to 0.25% and from 0.16 to 0.34%, respectively (Table 6). Wheat and rye (grain and flour) fell within the respective range of reducing sugars observed in triticale. In ranked triticales, no relationship between

reducing sugars and extent of shriveling was observed. The same lack of relationship resulted when the three grain classes of all the eight triticales were analyzed and reducing sugars content compared within and between triticales. Similar results were obtained by Noll (75) who found no significant difference, in reducing sugars, between shrivelled- and plump-grained triticales.

SEM-Morphological Relationships to Grain Shrivelling

Cross section, aleurone and pericarp detail, and starchy endosperm detail SEM photographs of mature grain of all three visually categorized classes of the eight triticales, as well as wheat and rye, are presented in Plates 4 to 12. Plump class -a of all the triticale lines showed aleurone and starchy endosperm cells similar to those in wheat and rye (Figs. b and c in Plates 4 to 12). The pericarp is attached tightly to the grain as in wheat; however, in some few points, the pericarp separated from the seed coat, to produce a slightly shrivelled appearance (Fig. a in Plates 4, 6, 8, and 11). This observation is in agreement with Dronzek et al. (23) and Lorenz et al. (65). Separation of the pericarp from most of the seed coat surface is a common characteristic in rye (Fig. d in Plate 12). It is of particular interest in most of the triticale lines to note that in the area where the seed coat and the pigment strand join, an empty space--varying from small to large--can be observed between the pericarp and either the seed coat or nucellar epidermis (Fig. a in Plates 5, 7, 8, 10, 11). This is a factor to be considered when grain density is used as a criterion for selection of

Plate 4. Cross section of triticale grain classes:

P-1a (Figures a, b, and c)

P-1b (Figures d, e, and f)

P-1c (Figures g, h, and i)

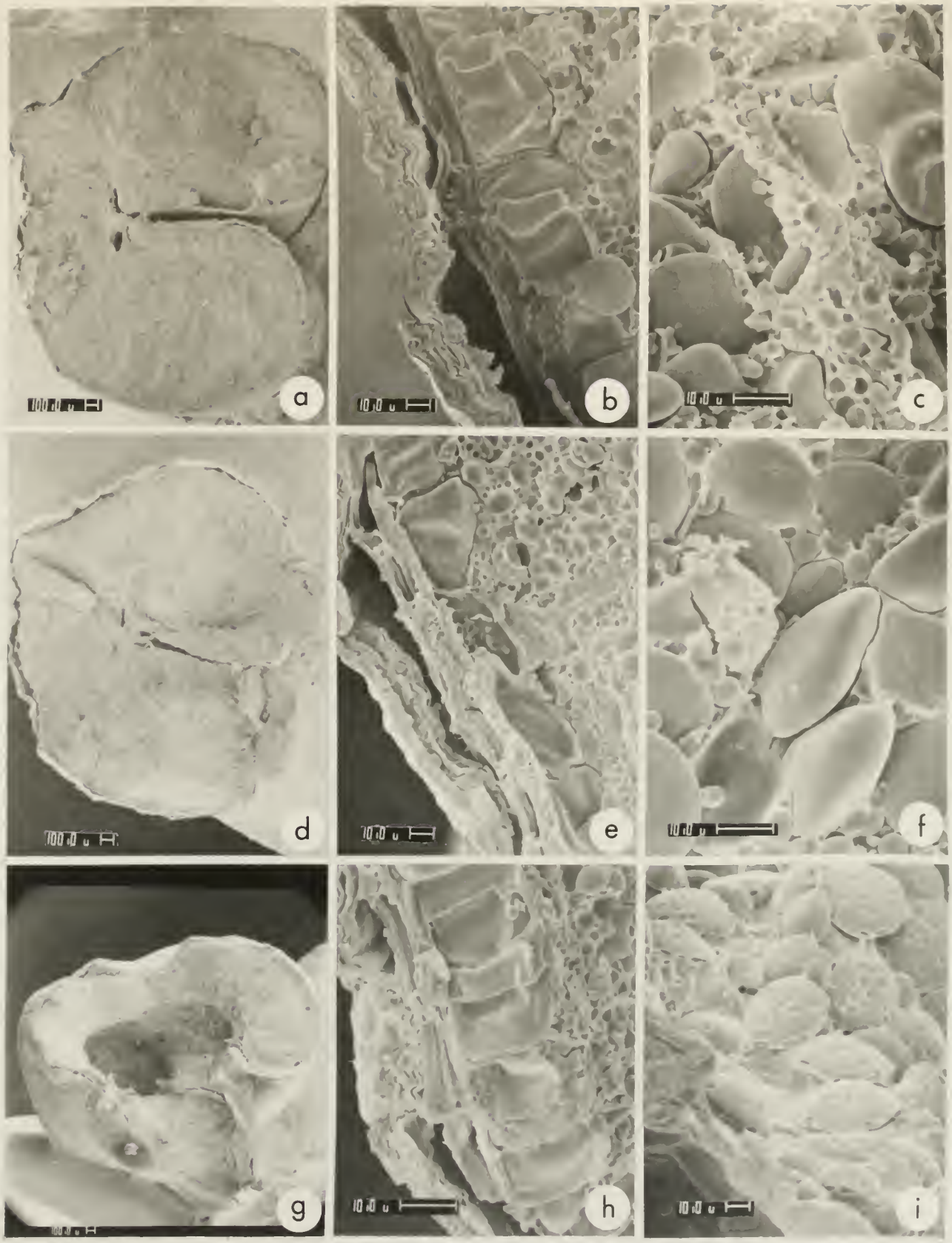

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Plate 5. Cross section of triticale grain classes:

P-2a (Figures a, b, and c)

P-2b (Figures d, e, and f)

P-2c (Figures g, h, and i)

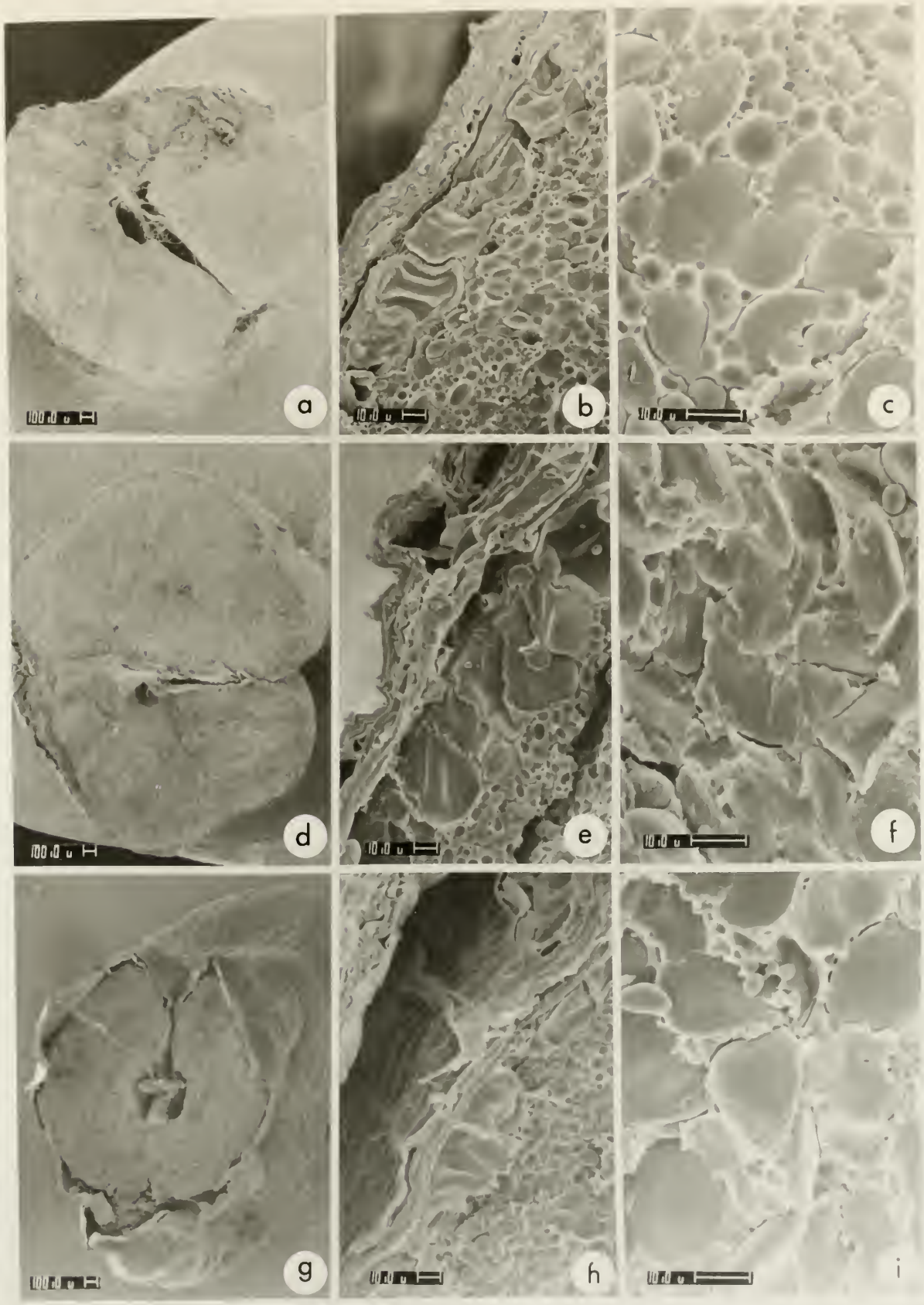
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Plate 6. Cross section of triticale grain classes:

P-3a (Figures a, b, and c)

P-3b (Figures d, e, and f)

P-3c (Figures g, h, and i)

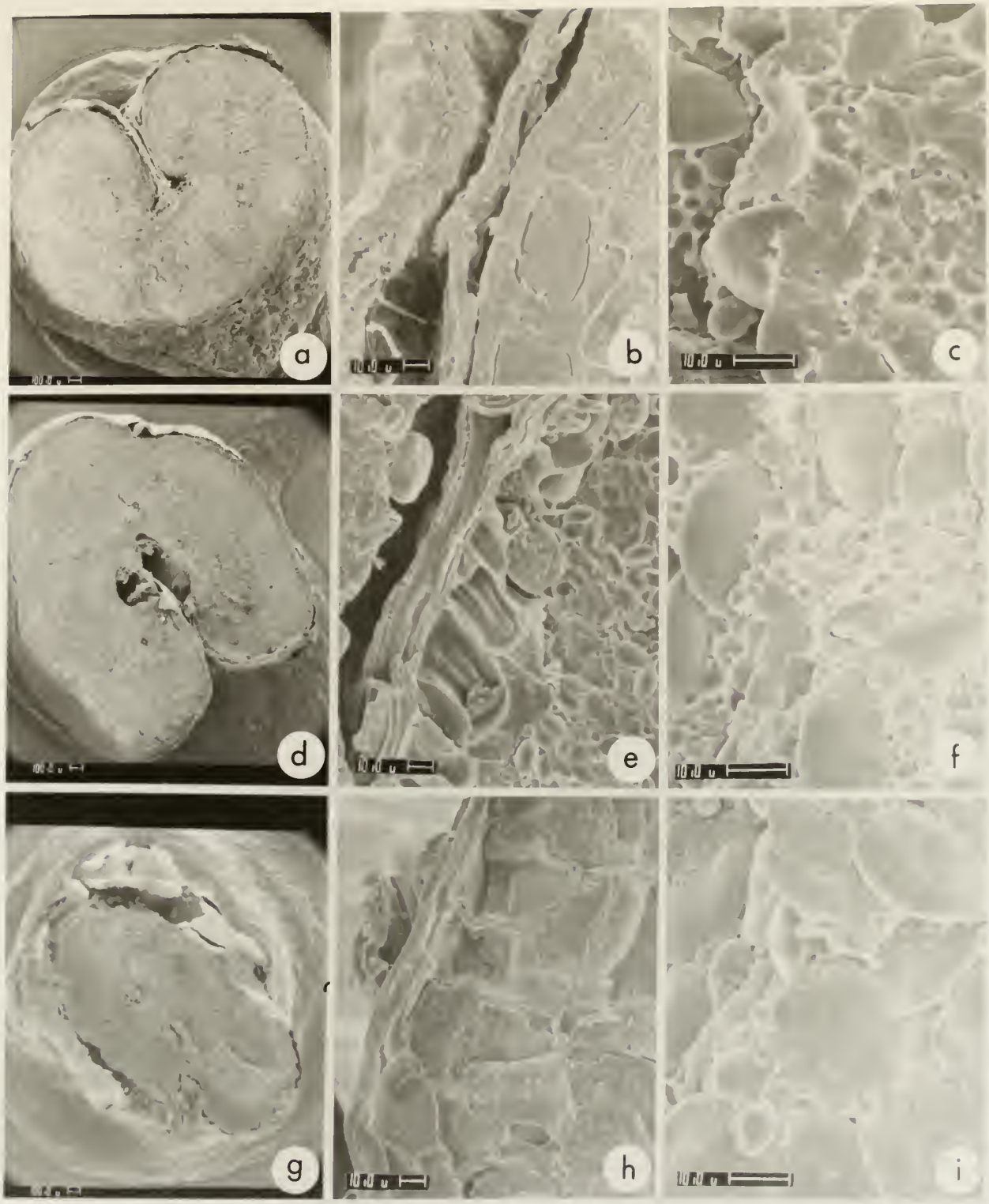
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Plate 7. Cross section of triticale grain classes:

P-4a (Figures a, b, and c)

P-4b (Figures d, e, and f)

P-4c (Figures g, h, and i)

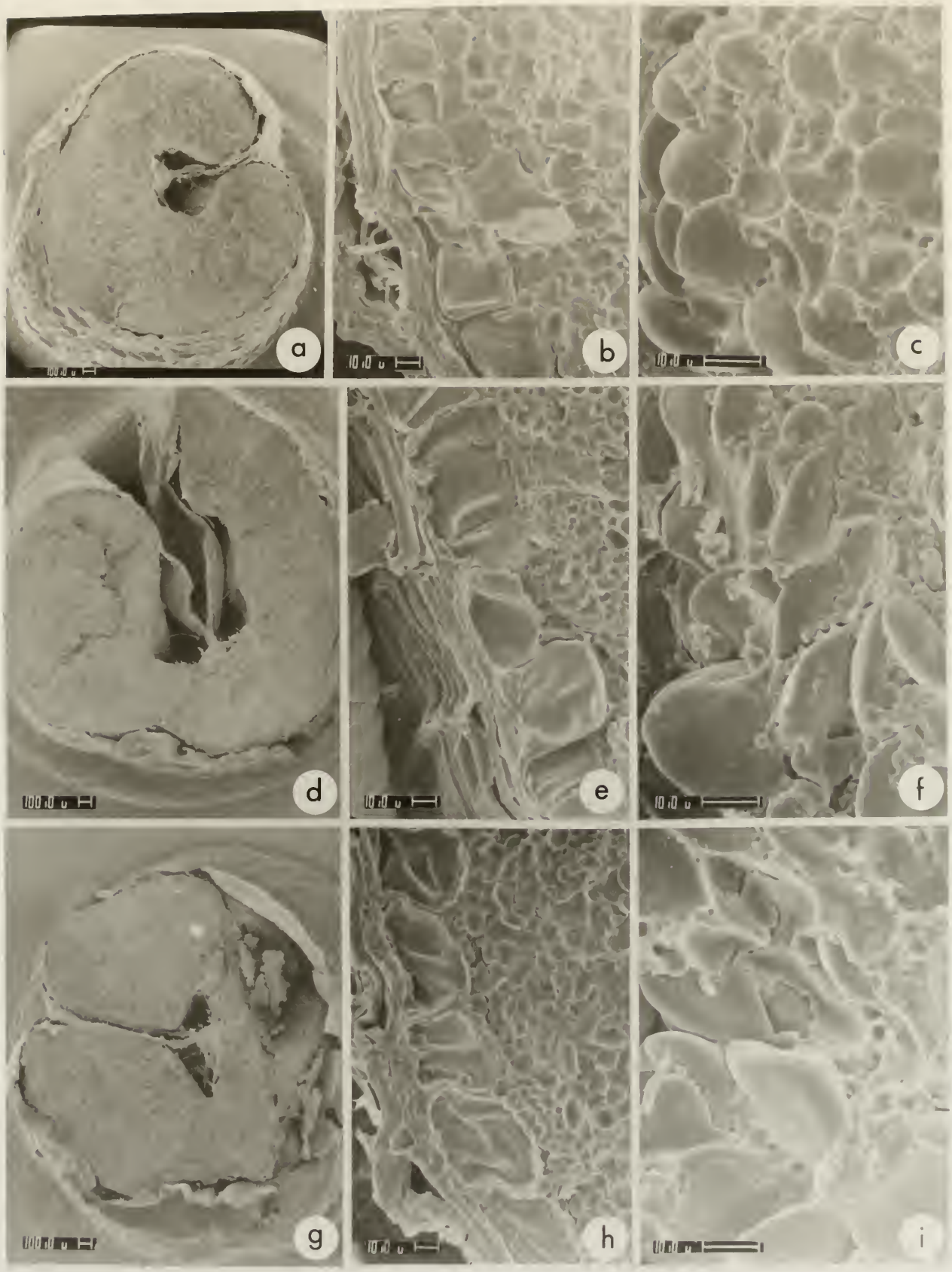
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Plate 8. Cross section of triticale grain classes:

P-5a (Figures a, b, and c)

P-5b (Figures d, e, and f)

P-5c (Figures g, h, and i)

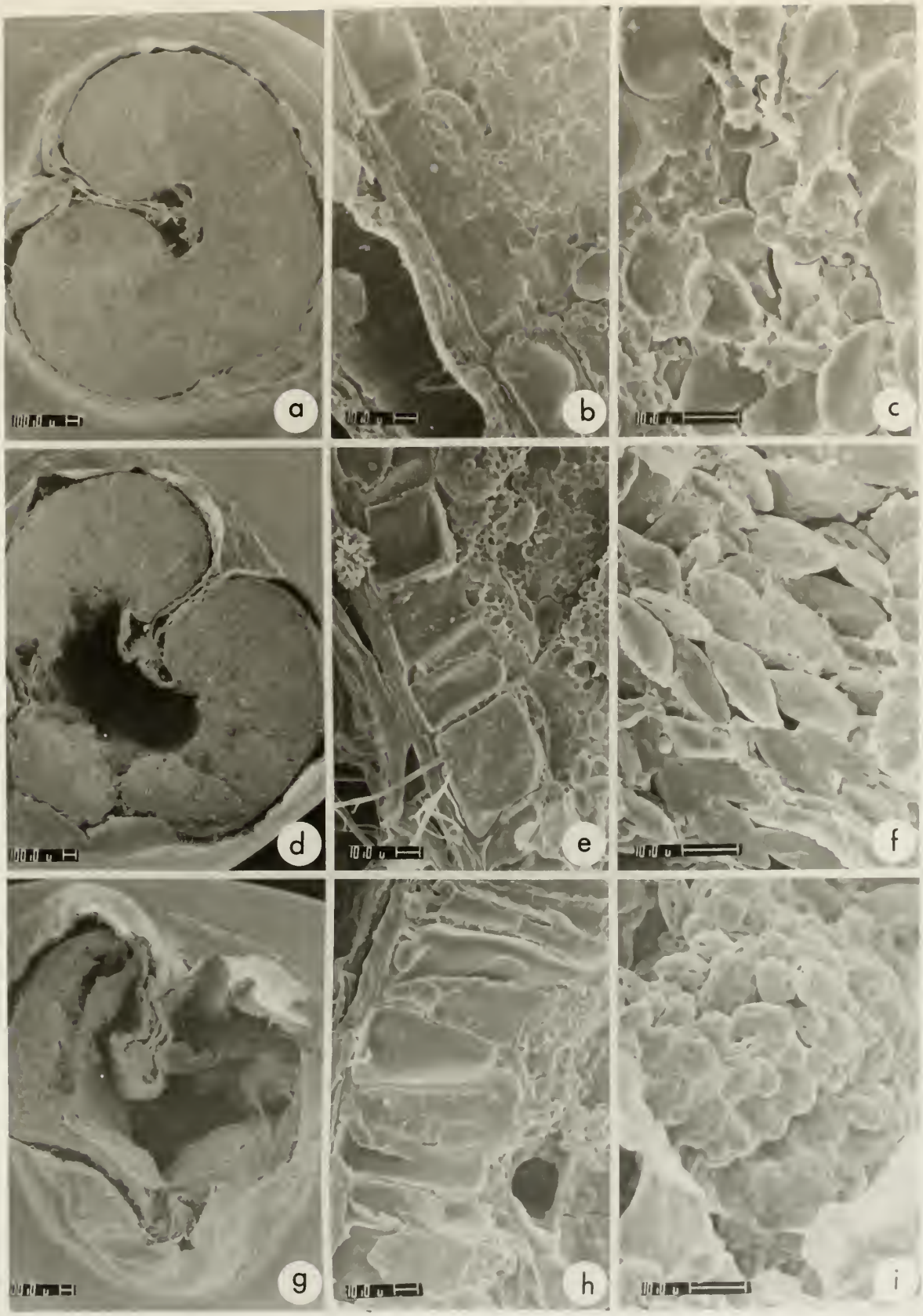
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Plate 9. Cross section of triticale grain classes:

P-6a (Figures a, b, and c)

P-6b (Figures d, e, and f)

P-6c (Figures g, h, and i)

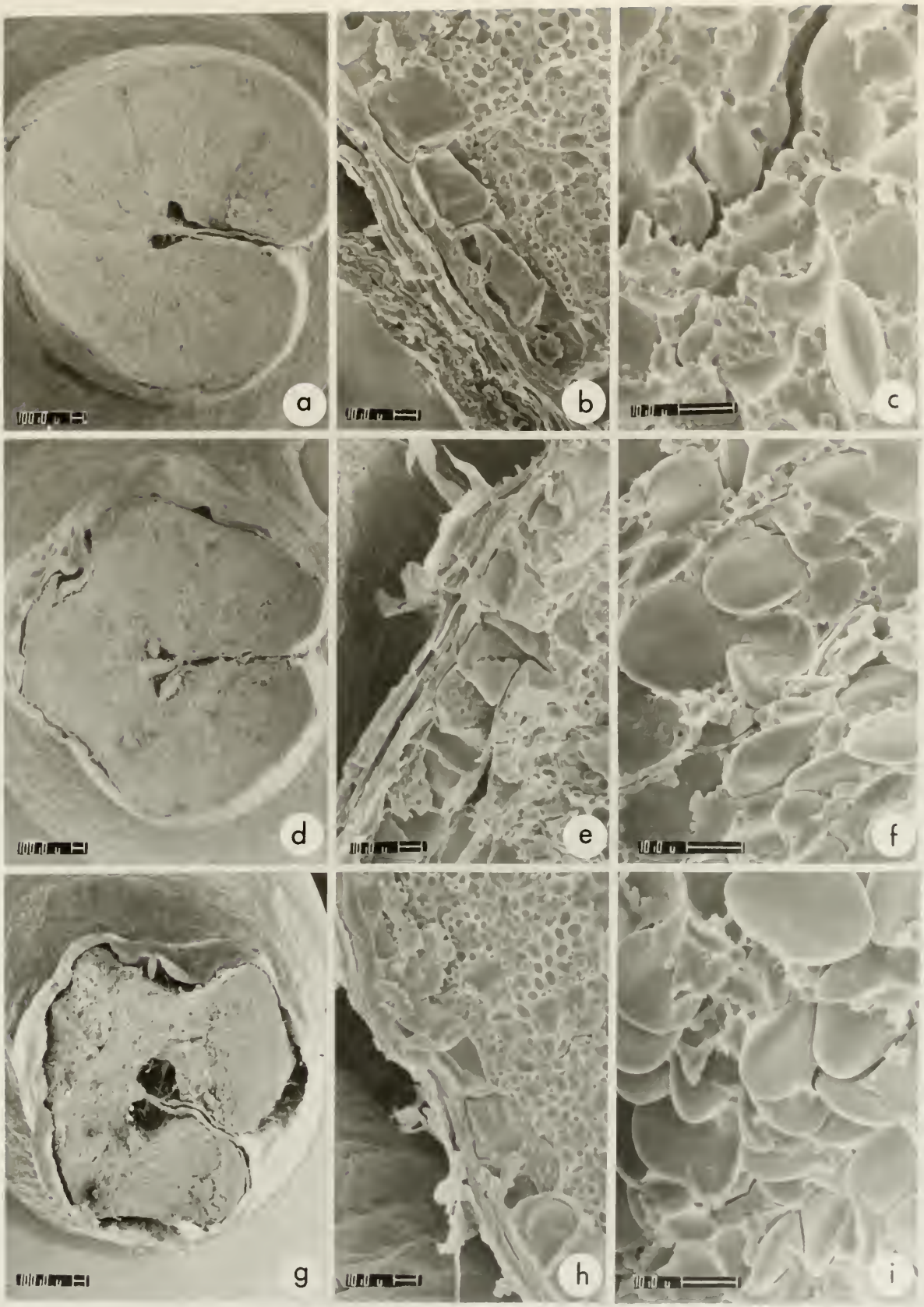
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Plate 10. Cross section of triticale grain classes:

P-7a (Figures a, b, and c)

P-7b (Figures d, e, and f)

P-7c (Figures g, h, and i)

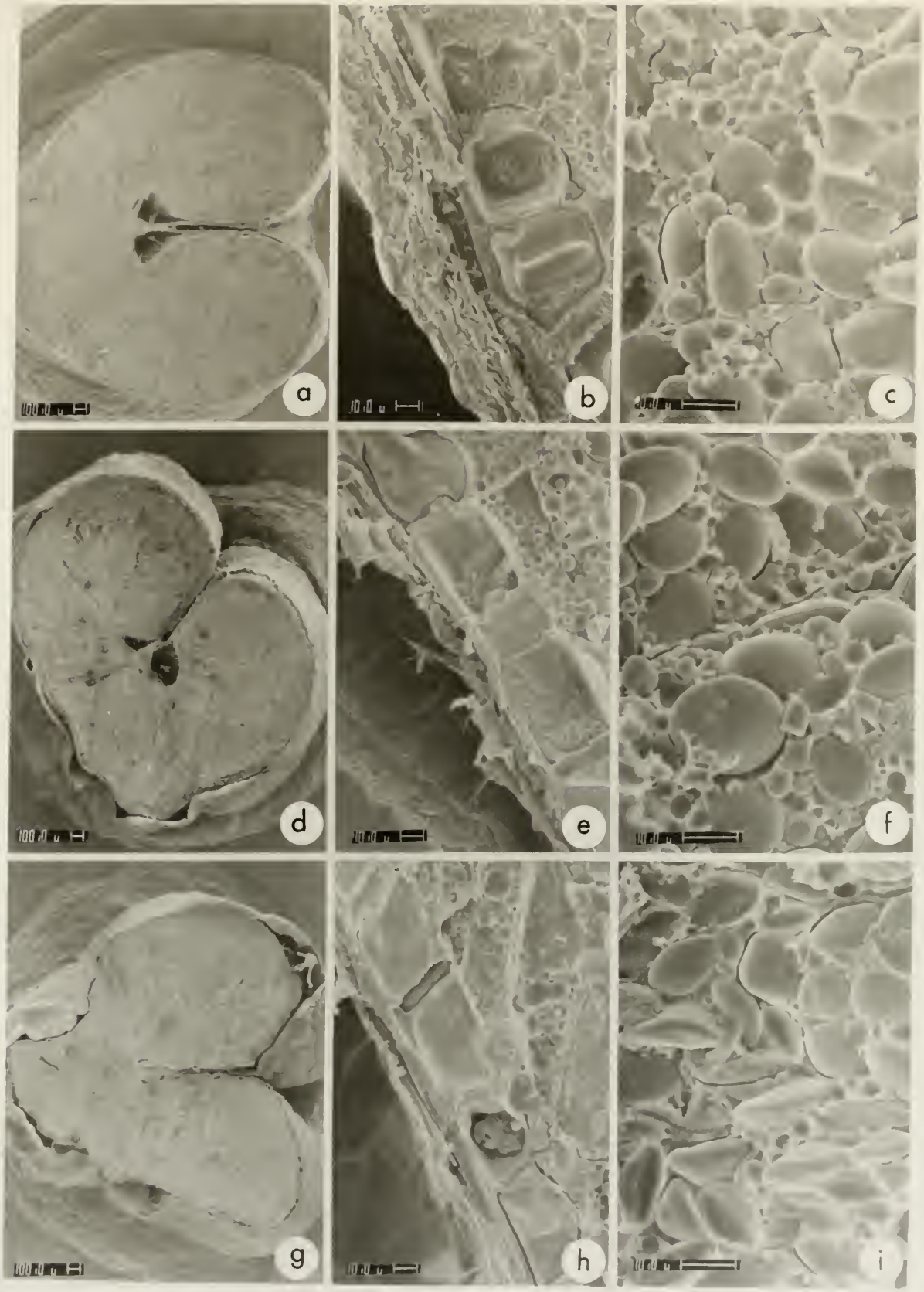
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Plate II. Cross section of triticale grain classes:

P-10a (Figures a, b, and c)

P-10b (Figures d, e, and f)

P-10c (Figures g, h, and i)

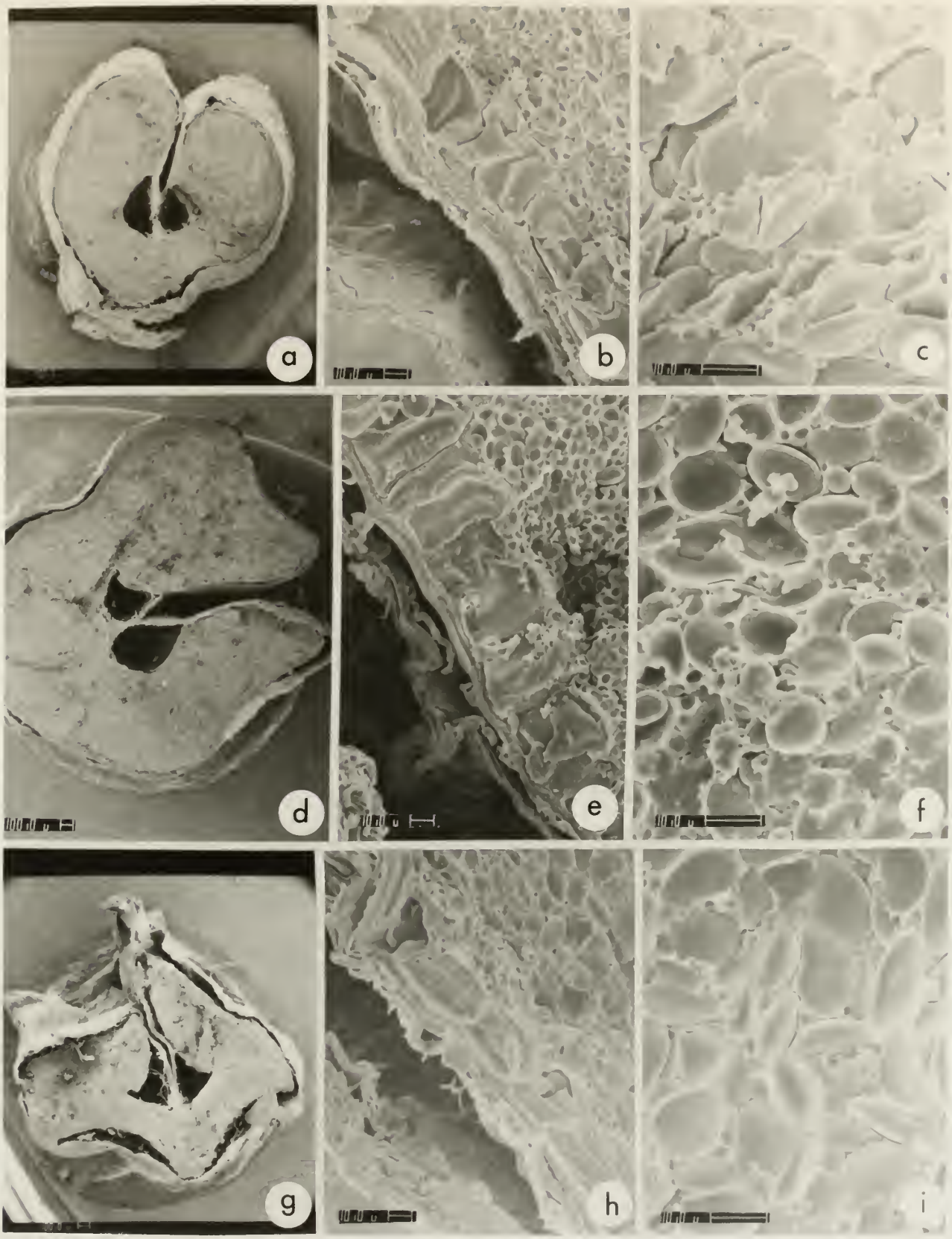
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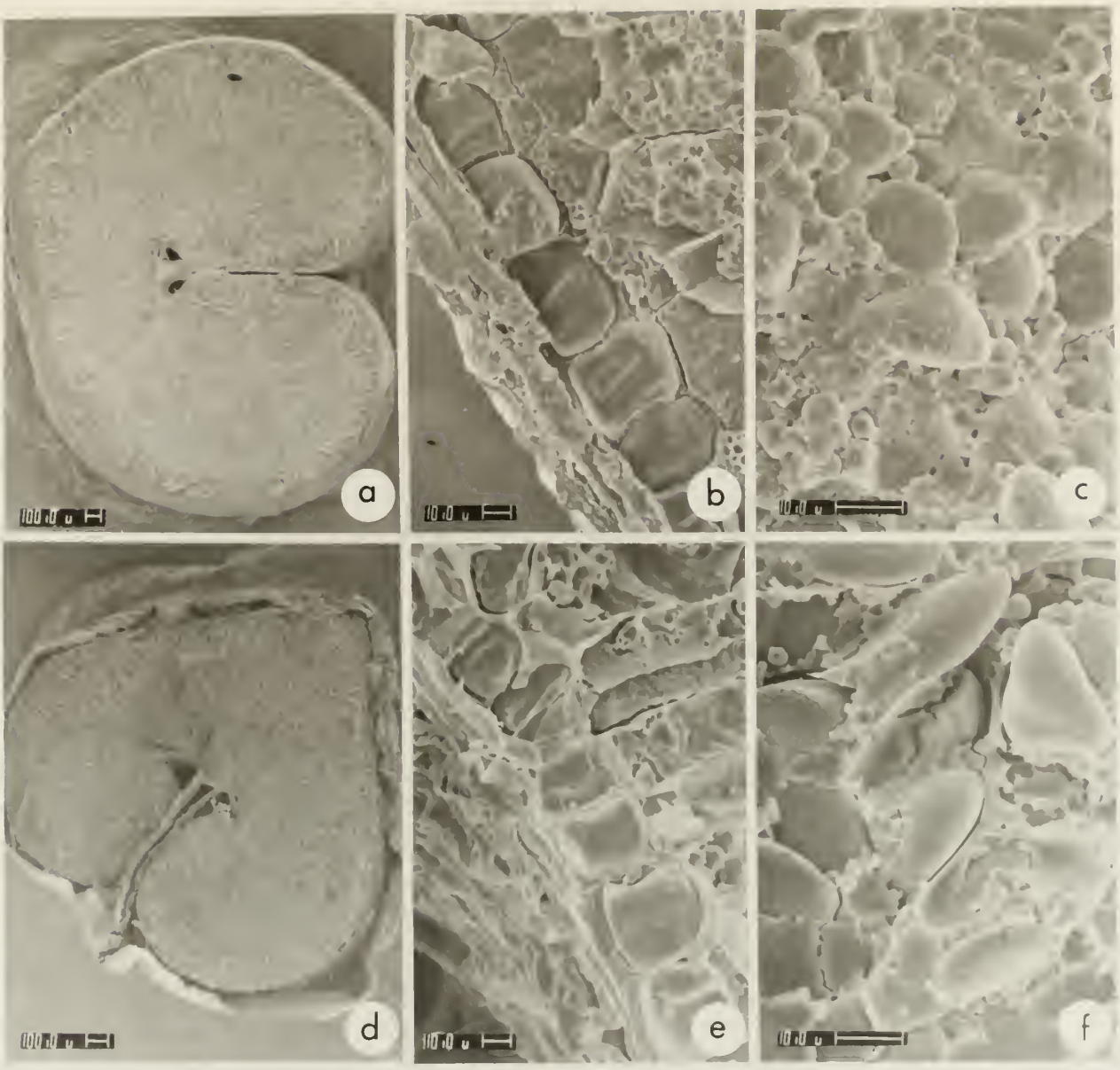
Plate 12. Cross section of wheat and rye grains:

Wheat P-8 (Figures a, b, and c)

Rye P-11 (Figures d, e, and f)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grain plumpness in triticale because the volume of the grain could not be conpletely filled with starchy endosperm and the selection would be erroneous. The suggestion agrees also with observations of Salminen and Hill (91) that masked diffences between shrivelled- and plump-grained triticale lines could result from variability in sink size and total dry matter production among the lines.

Medium shrivelled class -b of all the triticale lines (except P-5b) showed aleurone cells and starchy endosperm similar to normal as compared to the plump class grains (Figs. e and f in Plates 4 to 11). The pericarp separation from the seed coat was more pronounced and at more points than in the plump class which enhanced the shrivelling appearance (Fig. d in Plates 4 to 11). For this particular characteristic, the medium shrivelled triticale grain class resembled more its rye than its wheat parents (Figs. a and d in Plate 12). The shrunken aspect of the medium shrivelled grains was observed to be even more intensified by the occurrence of depressions at some points of the endosperm surface (Fig. d in Plates 4 to 11). No depressions were observed in the rye or wheat endosperms (Figs. a and d in Plate 12) indicating that endosperm depressions in triticale grain are morphological abnormalities rather than inherited characteristics. The voids between the pericarp and seed coat observed previously in the plump grain class were observed to occur also in a similar way in the medium shrivelled grain classes (Fig. d in Plates 6, 7, 10, and 11). In two of the samples, the cheeks of the grain were separated uncommonly from each other (Fig. d in Plates 7 and 11), a characteristic that could result from early developmental

problems (10, 43, 44). Grains of the triticale P-5b exhibited characteristics that differed from those in all others of the same grain class. Aleurone cells were observed to be normal all around the endosperm except for the dorsal side of the grain where aleurone cells were disrupted at points of depressions in the starchy endosperm (Fig. d in Plate 8). Perhaps the endosperm had a weak structure produced by a void that extended from the head of the crease to the depression points. Perhaps, too, that as the grain lost moisture during maturation, an invagination of nucellar epidermis and seed coat crushed and disrupted the aleurone cells which, in turn, could have initiated some catabolic hydrolysis of proteinaceous membranes and starch granules of the endosperm (Fig. f in Plate 8).

In the highly shrivelled class -c, five of the triticale accessions (P-2c, P-3c, P-6c, P-7c, and P-11c) had aleurone cells apparently intact. Compression of aleurone cells at various points along the endosperm surface was the only abnormality observed (Figs. g and h in Plates 5, 6, 7, 10, and 11). In another two lines (P-1c and P-4c), the aleurone was crushed and disrupted at specific points of the endosperm resulting from either a cavity in the endosperm extending from the crease to a large portion of the central endosperm (Fig. g in Plate 4) or by a localized collapse of a large area of the endosperm (Fig. g in Plate 7). In the remaining triticale (P-5c), aleurone cells were crushed and disrupted at several points along the endosperm surface. Only about half of the grain sink was filled (Fig. g in Plate 8). Starch granules attacked by α-amylase were observed in three (P-1c, P-3c and P-5c)

of the eight triticale lines (Fig. i in Plates 4, 6, and 8). The extent of starch damage was slight in P-3c (Fig. i in Plate 6) increasing in P-1c (Fig. i in Plate 4) and severe in P-5c (Fig. i in Plate 8). In the endosperm of the remaining triticale lines, the starch granules appeared intact (Fig. i in Plates 5, 7, 9, 10, and 11), suggesting that α-amylase attack did not occur in the endosperm of these highly shrivelled triticales. The highly shrivelled appearance of the grains of this class was due primarily to pericarp shrivelling and pericarp separation from the seed coat because depressions were greater in number and in depth than those in grains of classes -a and -b (Fig. g in Plates 4 to 9). The endosperm depressions could result from a collapse of nucellar and seed coat into an insufficiently filled portion of the starchy endosperm perhaps dependent on how the starchy endosperm was packed (Fig. i in Plates 4 to 10). This suggestion is demonstrated better by the morphological characteristics observed in the samples P-1c, P-3c, P-5c, and P-10c. The sample P-1c showed a cavity about one third the size of the total cross section with the walls composed of starchy endosperm (Figs. g and i in Plate 4). Sample P-3c showed a narrowed, enlarged profile in which one cheek was missing and most of the pericarp had separated from the grain mass composed of compact endosperm surrounded by the nucellus and the seed coat (Figs. g and h in Plate 6). Sample P-5c showed a compact endosperm that formed a rim around only about two-thirds of the grain periphery. More than half of the grain was composed of a cavity subdivided by the seed coat. The seed coat outlined the

internal cavity while the pericarp and seed coat enclose the external cavity (Fig. g in Plate 8). Finally, sample P-10c exhibited an endosperm of polyhedrical shape outlined by the seed coat and in which the pericarp was mostly separated from the seed coat-endosperm mass. At the center of the grain, the crease head falls, separating two cavities enclosed between the seed coat and pericarp (Fig. g in Plate 11).

Enzymatic damage of starch granules has been reported commonly. Sheally and Simmonds (96) and Simmonds (98) suggested that an early release of α-amylase, as also observed by Klassen et al. (53), could be related to grain shrivelling in triticale. However, enzymatically damaged starch granules observed here occurred in only 3 out of 8 triticale lines. Furthermore, the extent of starch damage in the sample P-5c is the only one that could even be considered to affect grain shrivelling (Fig. i in Plate 8). In the other two samples, the extent of starch damage cannot be considered large enough to result in a collapse of endosperm cells (Fig. i in Plates 4 and 6). Therefore, it is more likely that failure of the endosperm cells to completely fill its grain sink is a phenomenon responsible for the grain shrivelling in triticale. To further support some findings of this work, compositional and morphological changes during development of grains produced by the three grain classes of the triticale P-1 were examined.

Compositional Changes During Grain Development as Influenced by Grain Shrivelling

Changes in composition during the development of grains were derived from the three different grain classes (P-1a, P-1b and P-1c)

of the triticale cultivar Rahum and are presented in two ways in Table 9 and Figs. 13 to 18. For comparison and discussion purposes, the results are reported as mg/kernel and EU/kernel.

Water. Changes in water content occurred in a similar manner in all grain samples during the first 28 days post-anthesis (p.a.). Loss of water was first manifested at 21 days p.a. This was observed similarly by Agrawal (1). From 28 to 35 days p.a., grains from P-1a and P-1b kept losing water at about the same rate. In contrast, a dramatic drop in water content occurred in grains from P-1c to levels characteristic of post-harvested mature grains. Thus, at 35 days p.a., the highest water content corresponded to grains from P-1b (15.5 mg/kernel) and the lowest to grain from P-1c (2.2 mg/kernel).

Alpha-amylase activity. In all grain samples, α-amylase activity increased from anthesis to 14 days p.a., followed by a decrease in the next 7 days. However, the rate of α-amylase activity increase varied among the samples. At 21 days p.a. the highest α-amylase activity occurred in grains from P-1c (3.97 EU/kernel) and the lowest corresponded to P-1a (3.58 EU/kernel). From 21 to 28 days p.a., α-amylase activity decreased at a similar rate in grains from P-1a and P-1b but, in contrast, increased very rapidly in P-1c. Thus at 28 days p.a., grains from P-1c had an α-amylase activity 6 times higher than that in grains from P-1a and P-1b. In the next 7 days α-amylase activity increased in grains from both P-1a and P-1b, but at a lower rate in P-1a than P-1b, and decreased in grains from P-1c. Subsequently at 35 days post-anthesis,

Table 9. Compositional changes during grain development as influenced by degree of shrivelling within a triticale line (P-1).

Sample no.	Days post-anthesis	Moisture		∝-amylase activity		Starch		Total soluble sugars		Reducing sugars	
		%	H_2O mg/kernel	EU/g[a]	EU/kernel	%[a]	mg/kernel	%[a]	mg/kernel	%[a]	mg/kernel
P-1a	7	75.0	8.4	896.4	2.50	22.1	0.62	38.7	1.08	12.2	0.34
	14	69.2	20.5	766.1	7.00	29.8	2.72	24.0	2.19	10.5	0.96
	21	67.0	23.7	307.8	3.58	39.4	4.58	8.8	1.02	4.5	0.52
	28	66.3	18.4	315.0	2.94	37.6	3.51	4.6	0.42	2.1	0.20
	35	43.4	12.9	499.5	8.38	41.4	6.95	3.3	0.55	0.7	0.12
P-1b	7	75.4	6.0	871.0	1.69	17.6	0.34	33.7	0.66	14.2	0.28
	14	72.1	21.2	752.6	6.17	30.2	2.47	23.4	1.92	10.8	0.88
	21	68.3	30.0	283.5	3.94	45.6	6.34	7.7	1.07	3.3	0.46
	28	64.2	26.6	188.6	2.80	48.1	7.14	4.3	0.64	1.9	0.28
	35	51.6	15.5	907.2	13.15	35.0	5.07	3.4	0.49	0.8	0.12
	35[b]	45.8	25.0	180.0	5.33	52.3	15.48	3.0	0.89	0.6	0.18
P-1c	7	74.2	6.0	900.0	1.87	25.1	0.52	40.6	0.84	14.5	0.30
	14	73.6	16.2	709.0	4.11	24.5	1.42	18.6	1.08	5.2	0.30
	21	69.3	23.9	375.2	3.97	31.1	3.29	6.6	0.72	3.4	0.36
	28	64.3	21.4	1566.0	18.59	38.9	4.62	5.7	0.68	3.0	0.36
	35	16.7	2.2	1404.0	15.43	34.2	3.76	7.2	0.79	0.8	0.09

[a]Dry weight basis.

[b]Better grain type (less shrivelled) than samples from other spikes at 35 days post-anthesis.

Figures 13 to 18. Changes in moisture (or water) (■); α-amylase activity (▲); starch (●); total soluble sugars (□); and reducing sugars (○) during grain development, as influenced by grain shrivelling (P-1a from plump seeds, P-1b from medium shrivelled seeds, and P-1c from highly shrivelled seeds).

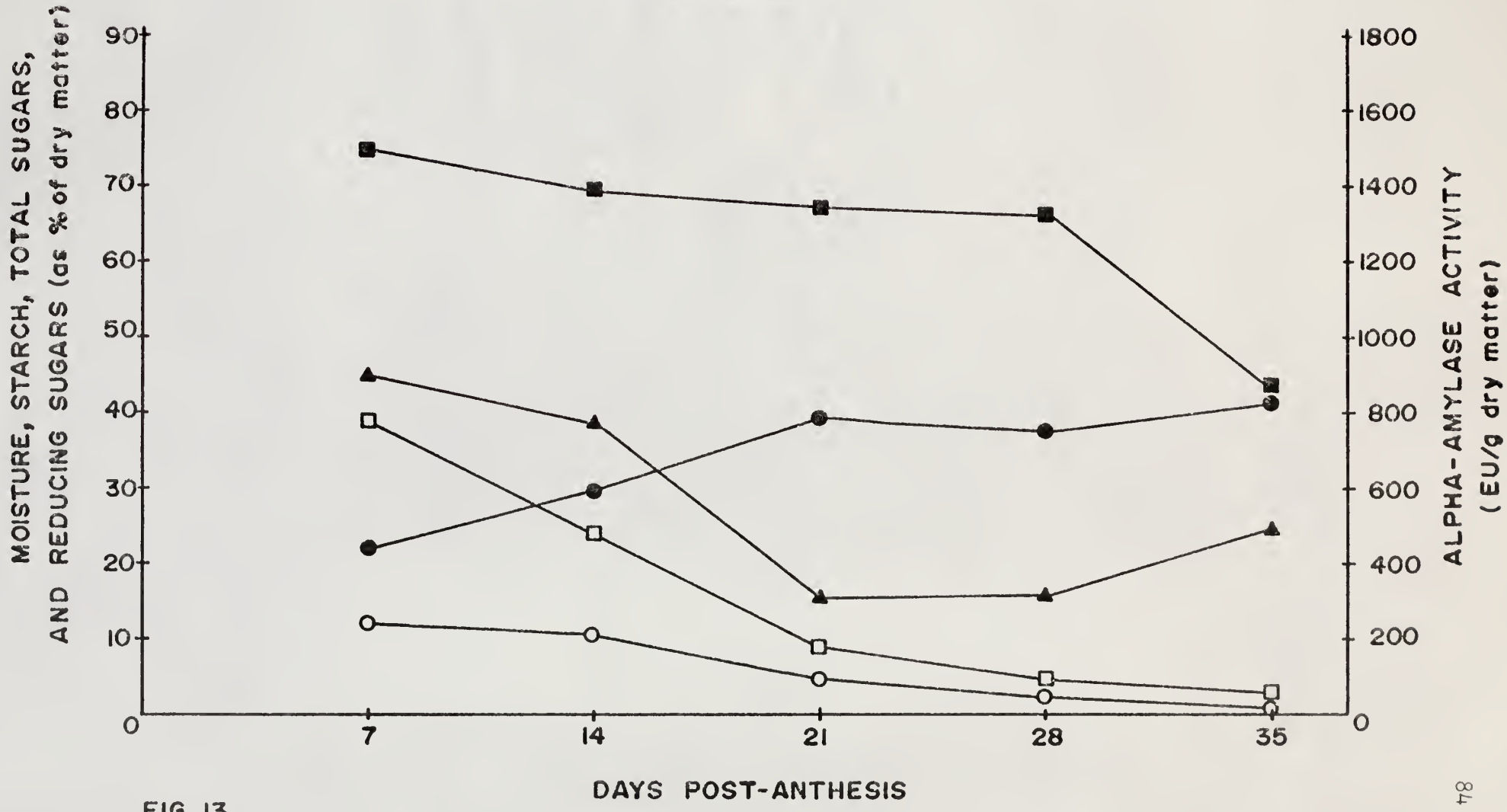

P-1a
(DRY WEIGHT BASIS)
MOISTURE, STARCH, TOTAL SUGARS,
AND REDUCING SUGARS (as % of dry matter)
ALPHA-AMYLASE ACTIVITY
(EU/g dry matter)
0
10
20
30
40
50
60
70
80
90
0
200
400
600
800
1000
1200
1400
1600
1800
7
14
21
28
35
DAYS POST-ANTHESIS

FIG. 13

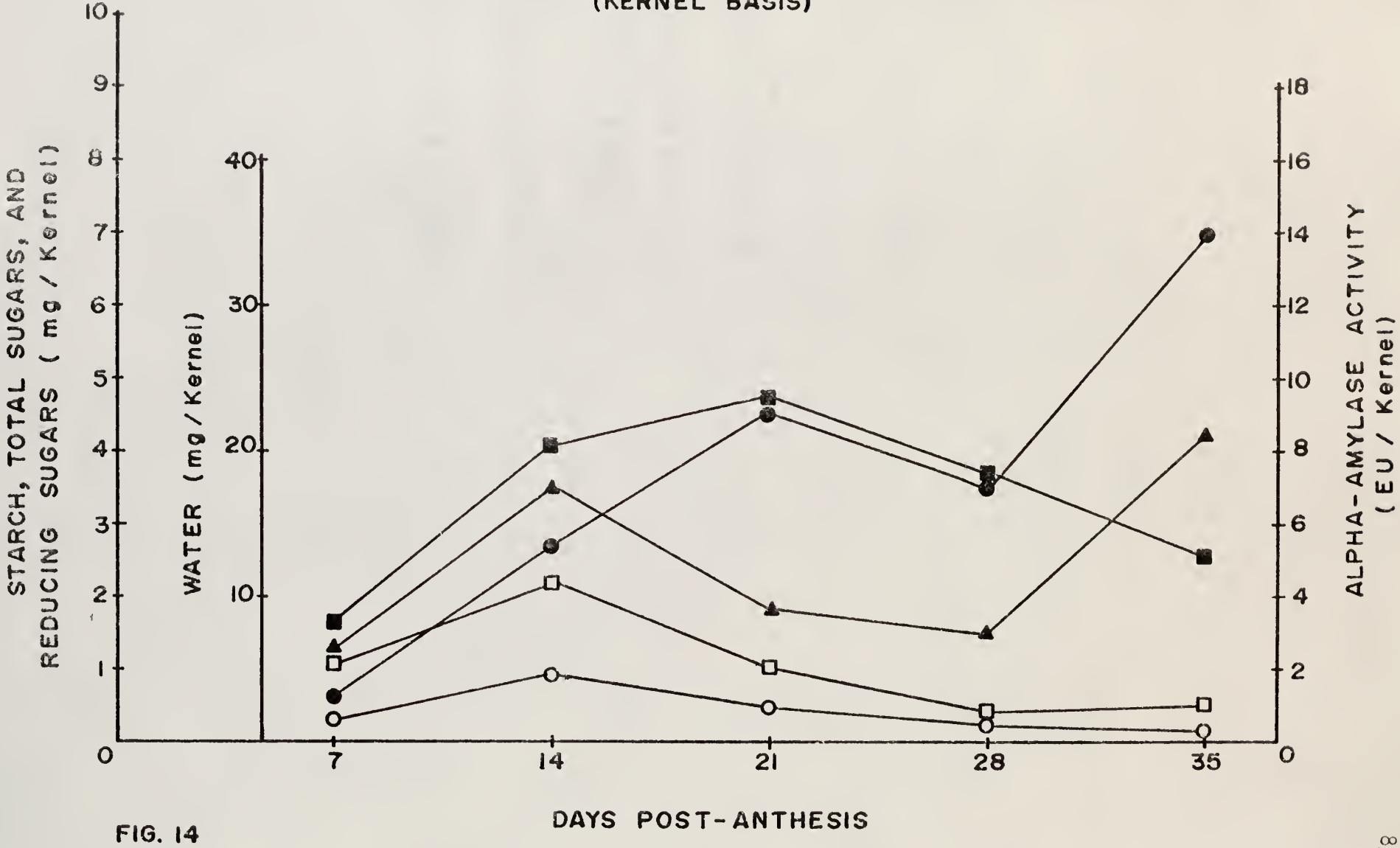

P-1a
(KERNEL BASIS)
STARCH, TOTAL SUGARS, AND
REDUCING SUGARS (mg / Kernel)
WATER (mg / Kernel)
ALPHA-AMYLASE ACTIVITY
(EU / Kernel)
0
1
2
3
4
5
6
7
8
9
10
0
10
20
30
40
0
2
4
6
8
10
12
14
16
18
7
14
21
28
35
DAYS POST-ANTHESIS

FIG. 14

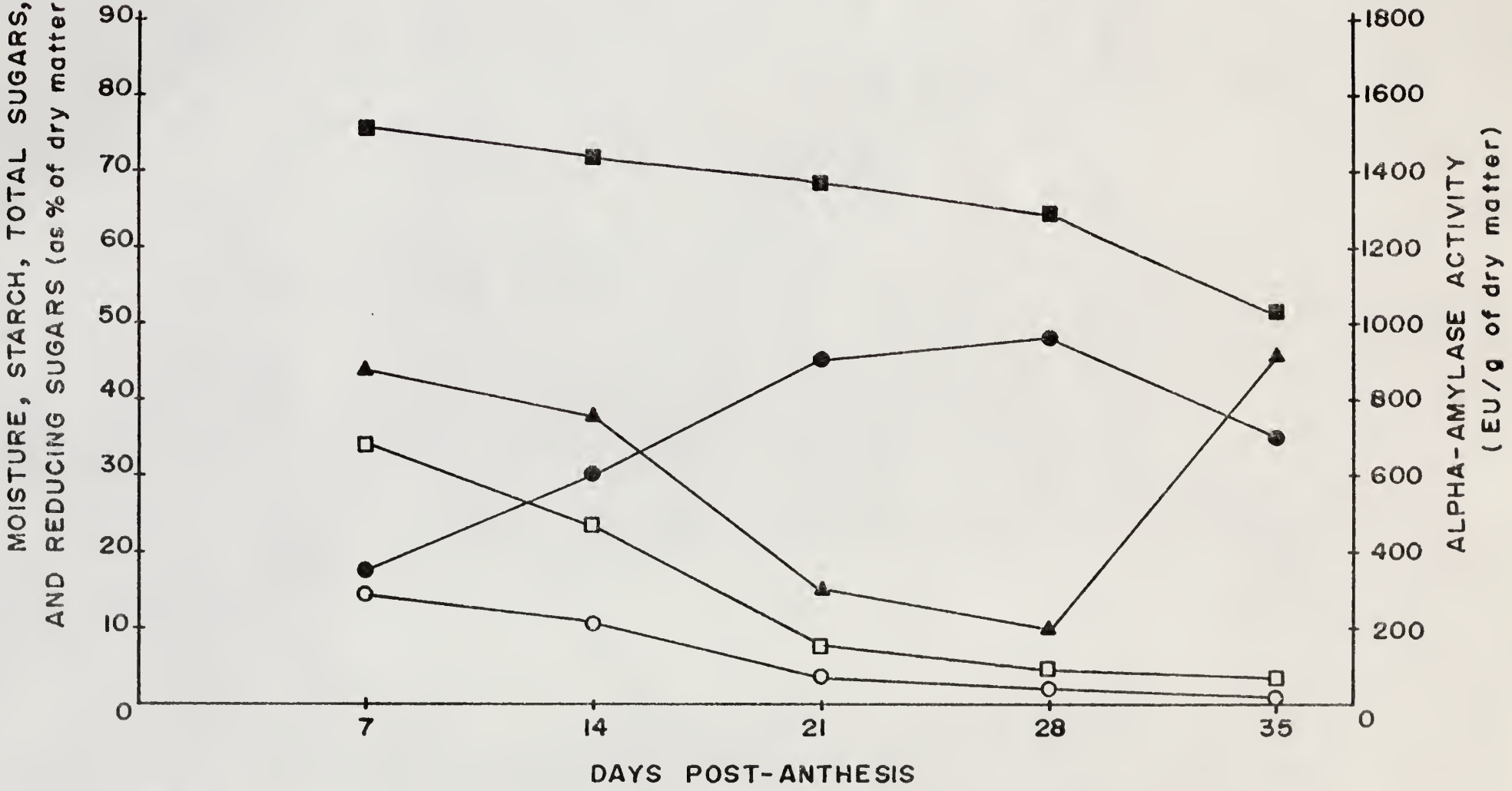

P-1b
(DRY WEIGHT BASIS)
MOISTURE, STARCH, TOTAL SUGARS, AND REDUCING SUGARS (as % of dry matter)
ALPHA-AMYLASE ACTIVITY (EU/g of dry matter)
0
10
20
30
40
50
60
70
80
90
0
200
400
600
800
1000
1200
1400
1600
1800
7
14
21
28
35
DAYS POST-ANTHESIS

FIG. 15

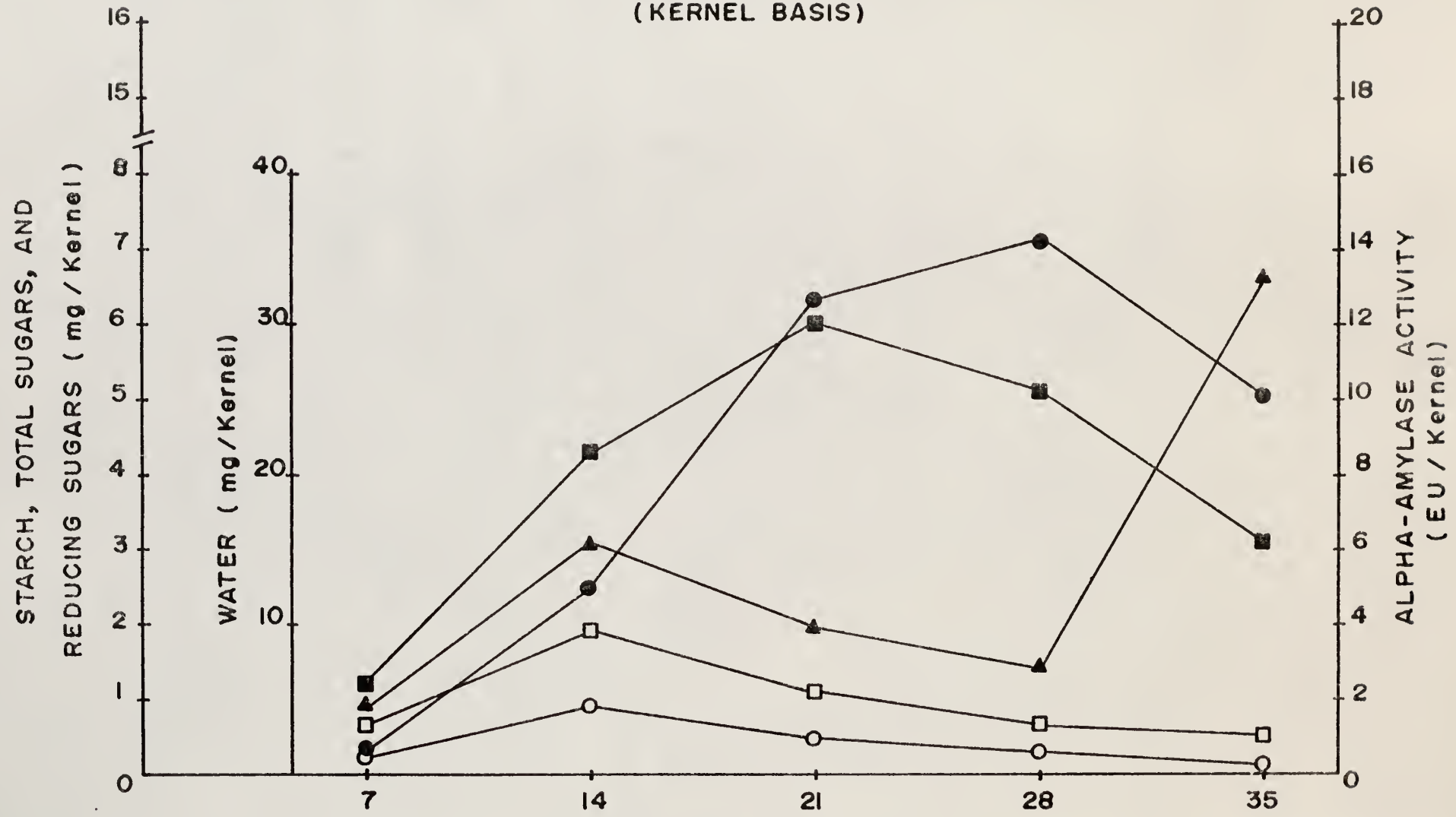

P-1b
(KERNEL BASIS)
STARCH, TOTAL SUGARS, AND
REDUCING SUGARS (mg / Kernel)
WATER (mg / Kernel)
ALPHA-AMYLASE ACTIVITY
(E U / Kernel)
DAYS POST-ANTESIS
7
14
21
28
35

FIG. 16

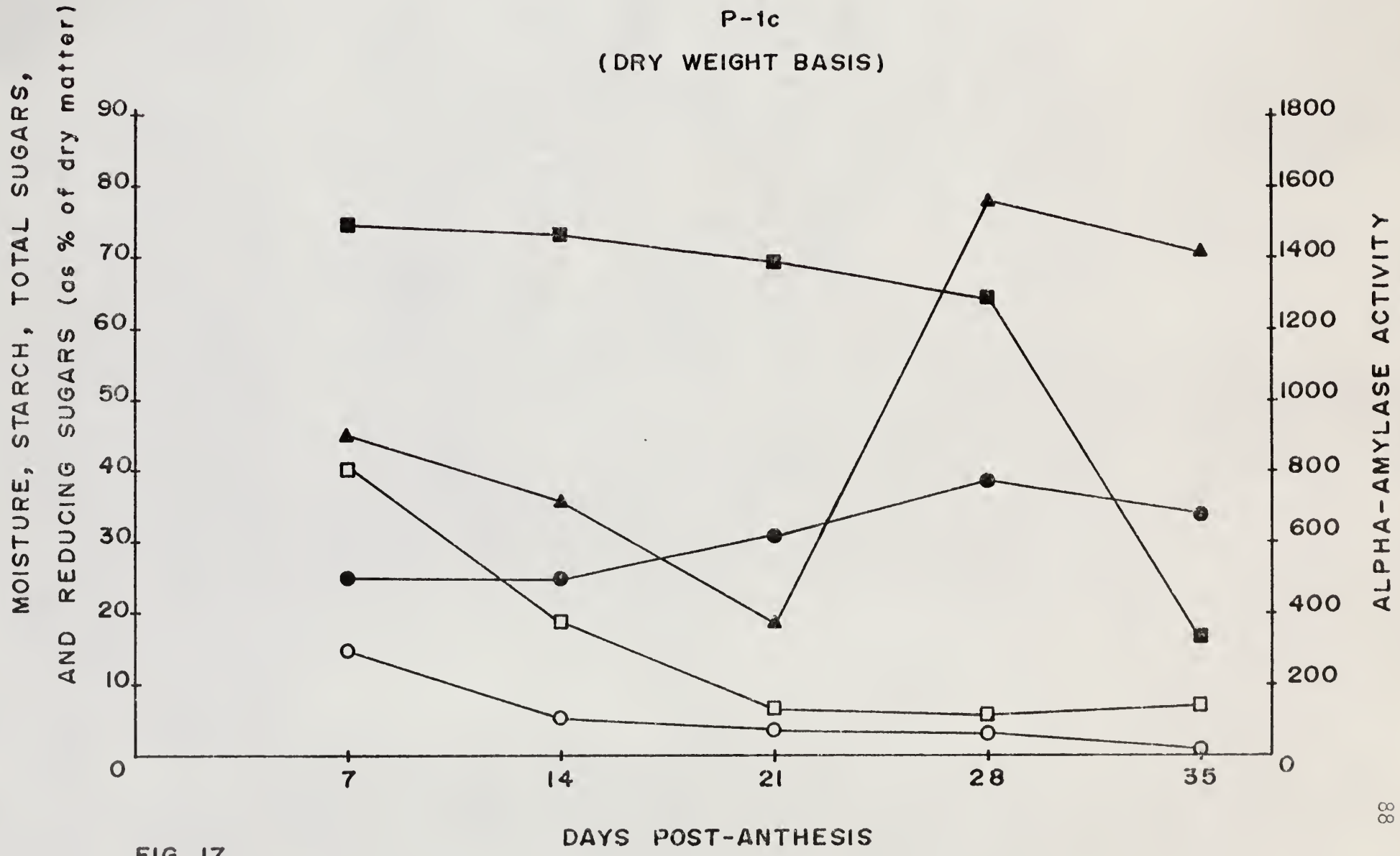

P-1c
(DRY WEIGHT BASIS)
MOISTURE, STARCH, TOTAL SUGARS,
AND REDUCING SUGARS (as % of dry matter)
ALPHA-AMYLASE ACTIVITY
(EU/g of dry matter)
0
10
20
30
40
50
60
70
80
90
0
200
400
600
800
1000
1200
1400
1600
1800
7
14
21
28
35
DAYS POST-ANTHESIS

FIG. 17

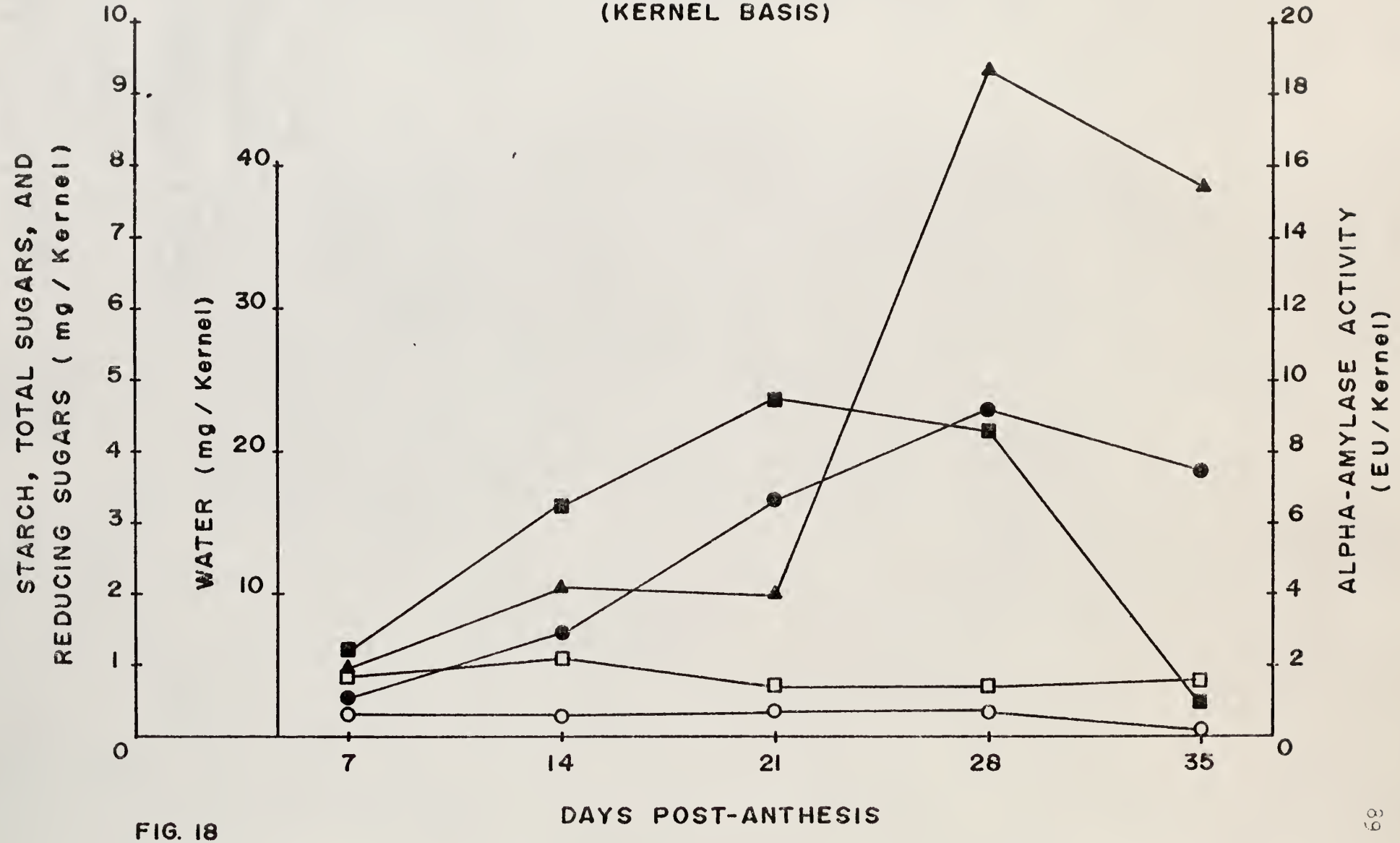

P-1c
(KERNEL BASIS)
STARCH, TOTAL SUGARS, AND REDUCING SUGARS (mg / Kernel)
WATER (mg / Kernel)
ALPHA-AMYLASE ACTIVITY (EU / Kernel)
DAYS POST-ANTHESIS
0
1
2
3
4
5
6
7
8
9
10
10
20
30
40
0
2
4
6
8
10
12
14
16
18
20
7
14
21
28
35

FIG. 18

the highest α-amylase activity corresponded to grains from P-1c (15.43 EU/kernel) followed by the α-amylase activity in grains from P-1b (13.15 EU/kernel), and the lowest corresponding to grains from P-1a (8.38 EU/kernel). The pattern of changes in α-amylase activity observed for the highly shrivelled triticale grains, was similar to that observed by Hill et al. (34) in the shrivelled triticale 6A190. The results here obtained, suggested that the factor(s) producing grain shrivelling also affect, in parallel, the α-amylase activity in the grain.

Starch. In all three grain samples, the starch content was observed to increase from anthesis to 21 days p.a. although the rate of accumulation differed among the three samples. At 21 days p.a., grains from P-1b had the highest starch content (6.34 mg/kernel) and grains from P-1c had the lowest one (3.29 mg/kernel). Thereafter the pattern of starch changes differed among the three samples. In grains from P-1a starch content decreased between 21 to 28 days p.a., followed by a rapid increase from 28 to 35 days post-anthesis. In contrast, the starch content of P-1b and P-1c increased until 28 days p.a. followed by a drop in the next 7 days.

At 35 days p.a., grains from P-1a had the highest starch content (6.95 mg/kernel) while grains from P-1c had the lowest one (3.76 mg/kernel). This trend was observed also by Noll (75). These results indicate that the factor(s) producing grain shrivelling also affect the accumulation of starch in the grain or, perhaps, that the extent

of accumulation of starch influences the degree of grain shrivelling in triticale. This latter suggestion could be supported by the results of Klassen et al. (53) who found no accumulation of starch in later developmental stages in the shrivelled triticale 6A190.

Total soluble sugars. The pattern of changes in total soluble sugars appeared to be more or less similar in all three samples, although the rate of increase or decrease varied among them. The highest level of total soluble sugars in all samples occurred at 14 days p.a., followed by a gradual decrease. Thus, at 35 days p.a., the highest total soluble sugars content corresponded to grains from P-1c (0.79 mg/kernel) and the lowest corresponded to grains from P-1b (0.49 mg/kernel). These results indicated no clearly evident relationship between total soluble sugars and grain shrivelling in triticale.

Reducing sugars. The amount of reducing sugars increased slightly in grain from P-1a and P-1b until the 14th day p.a. Thereafter there was a gradual decrease to equivalent low levels at 35 days p.a. In grains from P-1c, the amount of reducing sugars was fairly constant throughout grain maturation until 28 days p.a., followed by a dramatic drop in the next 7 days. At 35 days p.a. the amount of reducing sugars in all the three samples was more or less equivalent (0.09 to 0.12 mg/kernel). One can conclude that no real differences occurred in reducing sugars content--a finding similar to that of Noll (75).

In general, there was no evident relationship between either α-amylase activity and starch content or sugars (total and reducing) and α-amylase activity or starch content.

Developmental Morphology and its Relationship to Grain Shrivelling

Light microscope observations of general morphological characteristics of developing grains produced by plants from P-1a, P-1b and P-1c seeds are presented in Plates 19 and 20. At 5 days post-anthesis (p.a.), morphological characteristics of all three samples were similar (Fig. a in Plate 19). At this stage, the innermost pericarp cells were degenerated at the ventral part of the grain (Fig. a in Plate 19). Several layers of cells, outer and inner integuments and nucellar tissue, surrounded the enlarging embryo sac in which the antipodal cells were centrally located. Endosperm cellularization had begun and was observed from the periphery inwards (Fig. a in Plate 19). Similar developmental morphology of triticale grains had been reported earlier (21, 96, 98).

In the next developmental stages, a progressively increased lysis of pericarp cells occurred, so that 26 days p.a. onward, only 2 or 3 pericarp cell layers were observed to occur in all samples (Fig. c in Plate 20).

Outer and inner integuments were observed to develop in a similar manner in all samples. At 20 days p.a. the outer integument was no longer observed while the inner one remained as a thin layer of crushed cells (Fig. a in Plate 20), that at maturity is recognized as the seed coat of the grain (98).

The nucellar tissue, composed initially of several cell layers, remained as a single celled-layer (nucellar epidermis) until 15 days p.a. At this stage, crushed cells of the nucellar epidermis were observed only in areas in which they were in intimate contact with the

Plate 19. Cross section of triticale grain classes at several developmental stages.

a = antipodals
oi = outer integument
ii = inner integument
p = pericarp
ne = nucellar epidermis
al = aleurone
en = endosperm

Figure a: P-1b at 5 days post-anthesis. 149X.

Figure b: P-1b at 10 days post-anthesis. 45X.

Figure c: P-1c at 10 days post-anthesis. 29X.

Figure d: P-1b at 15 days post-anthesis. 114X.

Figure e: P-1c at 15 days post-anthesis. 149X.

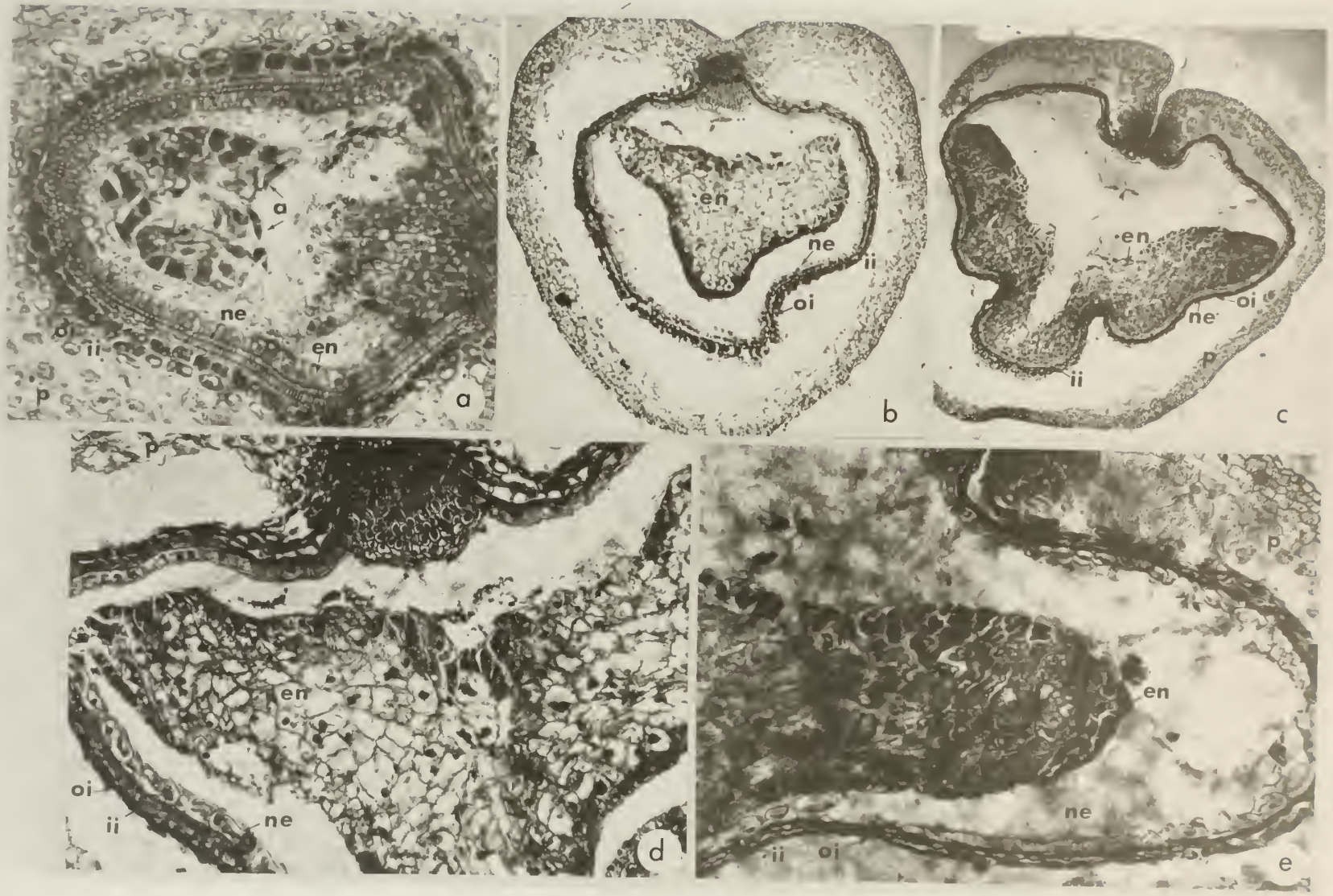

a
ne
oi
ii
en
p
a
en
ne
ii
oi
b
en
ne
oi
p
ii
c
p
en
oi
ii
ne
d
p
en
ne
ii
oi
e

Plate 20. Cross section of triticale grain classes at several developmental stages.

a = antipodals
oi = outer integument
ii = inner integument
p = pericarp
ne = nucellar epidermis
al = aleurone
en = endosperm

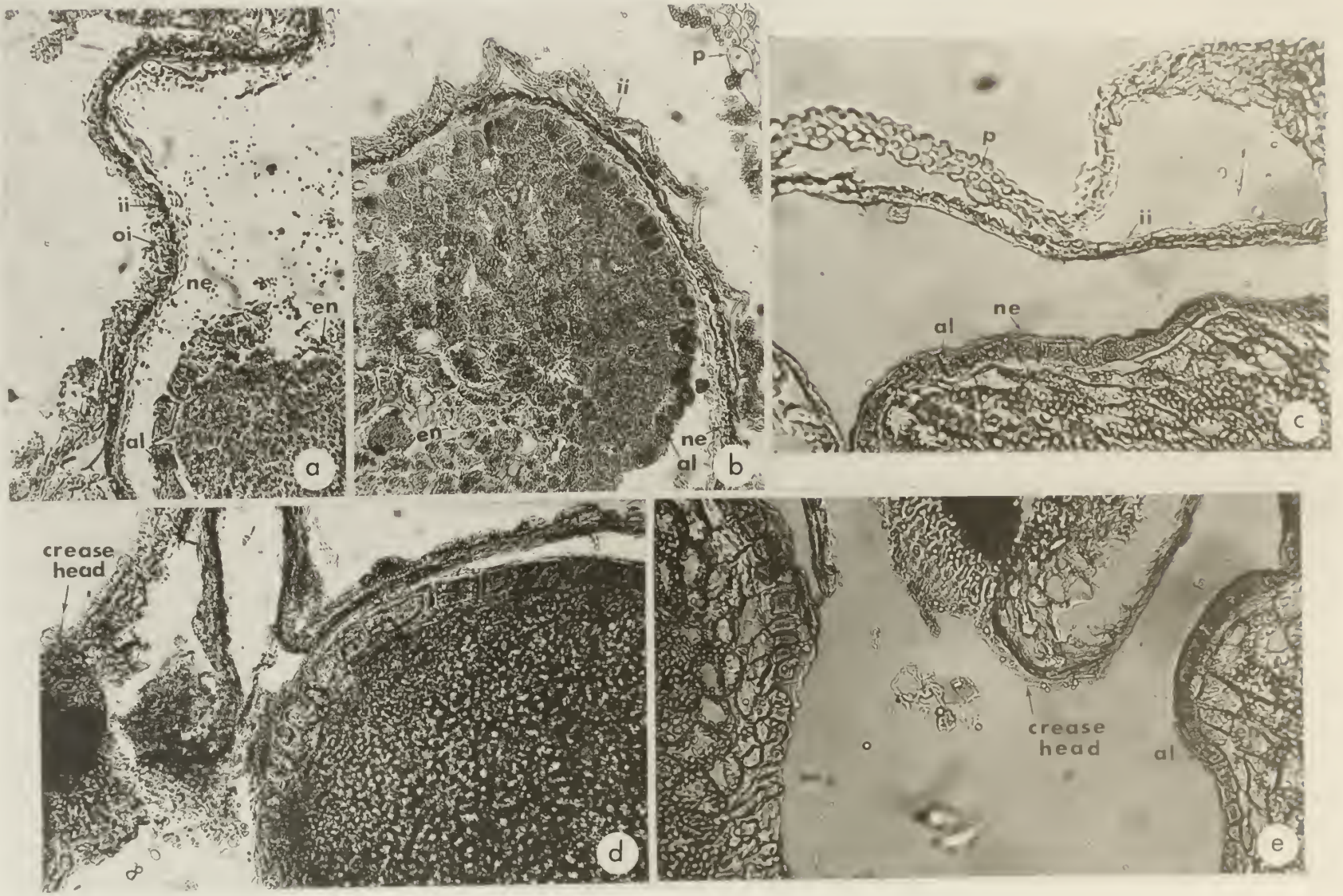
Figure a: P-1c at 20 days post-anthesis. 114X.

Figure b: P-1b at 26 days post-anthesis. 114X.

Figure c: P-1c at 26 days post-anthesis. 149X.

Figure d: P-1b at 35 days post-anthesis. 114X.

Figure e: P-1c at 35 days post-anthesis. 181X.


ii
oi
ne
en
al
a
p
ii
en
ne
al
b
p
ii
al
ne
c
crease
head
d
crease
head
al
e

endosperm cells (Fig. e in Plate 19). The same phenomenon was observed by Simmonds (98) to occur soon after 7 days p.a. From 20 days p.a. onward, the nucellar epidermis was recognized as a thin layer surrounding the endosperm. No significant differences in this structural component were found among grains from all three samples.

Meristematic characteristics of the outermost endosperm cells continued in all samples until 15 days p.a. (Fig. d in Plate 19), similarly observed by Simmonds (98), and perhaps until a few days later. Subsequent endosperm development resulted from cell enlargemant and deposition of starch and protein as suggested by the clearly recognized aleurone cell layer surrounding the endosperm. In some areas a pronounced empty space between the endosperm and the rest of the seed coat occurred (Figs. a and c in Plate 20).

Development of the starchy endosperm from 5 days p.a. until 35 days p.a. differed among grains produced by P-1a, P-1b and P-1c. At 10 days p.a. the mass of cellularized endosperm did not fill the grain sink; this characteristic was much more pronounced in grains from P-1c (Fig. b in Plate 19 represents P-1a and P-1b grains, and Fig. c in Plate 19 represents grains from P-1c). Thereafter, the failure of grain sink filling resulted in the endosperm lining only a certain extent of the total volume, leading to an empty space between the endosperm and the crease area of the grain. This empty space was always of lesser extent in grains from P-1a and P-1b (Fig. d in Plate 20) than from P-1c (Fig. e in Plate 20). Aleurone cells were disrupted in most of the area surrounding the cavity (Fig. a in Plate 20). When the mass of endosperm

did not fill the grain sink, enlargement or expansion of seed coat did not take place as occurs under normal conditions. Thus at 26 days p.a., the pericarp cells remained separated from the rest of the grain (except at the crease head) and to a greater extent in grains from P-1c (Fig. c in Plate 20) than in those of P-1a and P-1b (Fig. b in Plate 20). At 35 days p.a., grains from P-1c showed surface depressions, due to water loss and the way the endosperm had filled, and the pericarp and seed coat had collapsed to produce a wrinkled appearance (Fig. d in Plate 20). Grains from P-1a and P-1b (Fig. d in Plate 20) showed the same abnormal characteristics but to a much lesser extent than in those from P-1c.

Based on SEM observations at maturity and on 35 days p.a. sections, endosperm depressions and pericarp shrivelling as well as invagination of the seed coat in the crease area, would increase due to loss of water.

These developmental morphology observations support the findings of Kaltsikes et al. (44) and Bennett (10), in that the frequency of aberrant endosperm nuclei at the earliest endosperm development stages lead to reduced numbers of endosperm cells and limited the capacity of the endosperm to fill the sink of the grain. The final result of all these related processes is grain shrivelling of triticale.

Rye Chromosome Constitution

Rye chromosome composition is important because: a) Among secondary hexaploid triticales, rye chromosomes are commonly substituted by D-genome chromosomes of bread wheat (30). Thus it would be possible

to have 7 or less pairs of rye chromosomes present in the 8 triticales studied. D-genome chromosomes contribute greatly to baking quality which would explain in part the baking performance of the 8 triticales. b) Darvey (19) found that chromosomes 5R, 6R, and 7R/4R have major effects on seed shrivelling in triticale, while Kaltsikes and Roupakias (43) reported 5R, 4R, and 6R have major effects in the production of aberrant endosperm nuclei--a phenomenon related to grain shrivelling in triticale. Therefore the identification of rye chromosomes in our triticales would give some information about the possible grain shrivelling relationships. c) All 8 triticales produced grains that could be categorized from plump to highly shrivelled. If the differences in grain shrivelling within a triticale cultivar originated from genotypic differences between plump and shrivelled grains, part of the answer to our question would reside in the rye-D-genome substitutions. The cytogenetic information from the 8 triticales was provided by Dr. Joseph Pilch from CIMMYT (79). Random samples from the 8 triticale lines were analyzed and the chromosomes identified by Giemsa banding. The best seed types of all the triticale lines (except P-1) were used. Triticale P-1 was analyzed as its three classes (P-1a, P-1b, and P-1c). Rye chromosome identification of the 8 triticale cultivars is presented in Tables 10 and 11.

Table 10. Number and identity of rye chromosomes present in the secondary hexaploid triticale cv. Rahum.[a]

Sample	Frequency of plants	Rye chromosomes 1R	2R	3R	4R	5R	6R	7R	No. of rye chromosome pairs
P-1a	15	--L +		+		-- +	+	+	5
P-1b	10	+		+		-- +	+	+	5
	5	--L +		+	**S +	*- +	* +	+	6
P-1c	8	+		+	**S +	-- +	+	+	6
	5	+		+	**S +	+	+	+	6
	3	+		+	**S +	+	+	+	6
	2	+		+	**S +	*- +	+	+	6

[a]From Pilch (79).

*No terminal heterochromatin on one chromosome.

**No terminal heterochromatin on both chromosomes.

\- Reduced terminal heterochromatin on one chromosome.

-- Reduced terminal heterochromatin on both chromosomes.

L Chromosome long arm.

S Chromosome short arm.

Table 11. Number and identity of rye chromosomes present in 7 secondary hexaploid triticale.[a]

Sample	No. of plants analyzed	Rye chromosomes							No. rye chromosome pairs
		1R	2R	3R	4R	5R	6R	7R	
P-2	10	+	+			+	+	+	5
P-3	10	--L +	+	+	+	--L +	+	+	7
P-4	10	+	+	+	**S +	+	+	+	7
P-5	10	+	+	+	+	+	+	--L +	7
P-6	10	+	+			+	+	+	5
P-7	10	+	+			+	+	+	5
P-10	10	+	+			+	+	+	5

[a]From Pilch (79).

**No terminal heterochromatin on both chromosomes.

-- Reduced terminal heterochromatin on both chromosomes.

L Chromosome long arm.

S Chromosome short arm.

GENERAL DISCUSSION

The biochemical and morphological results from developing and mature grain strongly suggest that abnormal endosperm development is the major factor responsible for grain shrivelling in triticale.

The α-amylase activity results (Table 8) and SEM-morphological observations (Plates 4 to 11) definitely proved that α-amylase activity does not affect shrivelling. Although α-amylase activity increases within a triticale cultivar as shrivelling increases, that can be explained by two alternative reasons. First, the quantity of starchy endosperm in the highly shrivelled grains is less than in plump grains, as observed by SEM and light microscopy, which results in a smaller ratio of starchy endosperm to aleurone. Thus α-amylase concentration increases as does α-amylase activity on a per kernel basis. Secondly, it is also possible that the same mechanism(s) that affect(s) grain shrivelling may also increase α-amylase activity but it is of a secondary nature because the attacked starch granules maintain their shape and do not collapse.

The observed relationship between grain shrivelling and starch content (Tables 8 and 9) is interpreted as starch accumulation being influenced by the factor(s) producing grain shrivelling. This statement is based on SEM and light microscopy observations, as well as by changes in starch in developing grains (Table 9). It is supported further by the high frequency of aberrant endosperm nuclei observed to occur in highly shrivelled triticales (44, 10). Theoretically, only 4 aberrant nuclei at the 32 cell stage could result in a 12% reduction

in the number of endosperm cells in 4 days. Because Jenner and Rathjen (39, 40) observed that an unidentified mechanism(s) limits the accumulation of sucrose in wheat, it is logical to extend this, as a part of the maturation/senescence mechanisms, to triticale. As such, developing triticale with limited endosperm cell numbers--i.e., the endosperm sink--should "turn off" the flow of nutrients earlier than plump grains and hence reach physiological maturity earlier. This was observed in the dramatic drop in moisture content that occurred at 35 days post-anthesis in grains from P-1c while in grains from P-1a and P-1b the loss of water occurred at a much slower rate (Table 9). P-1a and P-1b would be expected to reach physiological maturity several days later and would accumulate more starch during the 28 to 35 days post-anthesis period than in the more shrivelled grain sample from P-1c. This was seen also in the two P-1b samples (Table 9). These observations are supported by Hill et al. (34) who found a shrivelled triticale to transport less labeled sucrose to the head than a plump one; by Agrawal (1) who observed maximum starch content at 35 days post-anthesis in a shrivelled triticale and at 42 days post-anthesis in a plump one; and by Srivastava (103) who suggested that a starch decline after 30 days post-anthesis could be related to a decrease in the capacity of shrivelled triticale grains to accept and/or metabolize nutrients.

The high levels of α-amylase activity found in mature grain and in its flour (Tables 6 and 8), regardless of the extent of grain shrivelling, indicate that the levels of total soluble sugars and reducing sugars should have been higher than what was observed. A possible explanation

for this is that the grain utilizes free sugars (both total and reducing) for either energy, and/or polymerization into other carbohydrates/starch in the grain.

Although the triticales that baked satisfactorily (P-1 and P-10) had 2 pairs of D-genome chromosomes (Table 10 and 11), no relationship between baking quality and the presence of D-genome chromosomes was obtained.

When the number and identity of rye chromosomes present in each of the triticale genotypes (Table 11) was compared to its extent of grain shrivelling, no evident relationship was found.

Grain classes of the triticale P-1 showed differences in rye chromosome composition. The plump grain class had 5 rye chromosome pairs--2R and 4R were missing. The medium shrivelled class had two groups of genotypes--one similar to P-1a grains and the other to that of P-1c grains that had one additional rye chromosome (4R). Some morphological differences in chromosome 5R separated the P-1c class into 4 subclasses (Table 10). The absence of the 4R chromosome in plump grains could be a significant influence in grain shrivelling as suggested by Darvey (19) and Kaltsikes and Roupakias (43). Different triticale genotypes originating from a single cultivar could be explained only as partial sterility and consequent illegitimate outcrossing in the experimental fields where several different cultivars are grown in the same plot. This could also explain the observations that plump and shrivelled grains are randomly distributed in a single spike and that different plants from the same cultivar can

produce different seed types as observed in the class P-1b at 35 days post-anthesis during the developmental study (Table 9).

From these overall observations and supplementary rye chromosome data with additional supporting earlier event findings of Kaltsikes and Roupakias (43) and Bennett (10), it is concluded that grain shrivelling in triticale has its origin in incongruity problems between wheat and rye chromosomes in the triticale genotype. The extent of grain shrivelling is established at the earliest stages of endosperm development when aberrant nuclei are formed. As a consequence, the number of cells that will remain at maturity is reduced. The reduced number of endosperm cells leads to an early termination of dry matter accumulation because no sink area for storage exists. Consequently, physiological maturity occurs early. Since the embryo sac was prepared to be completely filled by the expanding endosperm cells, and it cannot do so as a result of reduced number of endosperm cells, the pericarp, seed coat and aleurone layers collapse due to empty spaces that occur at the later stages of grain maturation. The final result is endosperm voids and depressions that can disrupt aleurone cells facilitating enzymatic attack (primarily α-amylase) on starch granules in adjacent cells, and the pericarp shrivelling that characterizes most mature triticale grains.

SUMMARY

Satisfactory loaves of bread were obtained from some secondary hexaploid triticales containing chromosomes from the D-genome of bread wheat, when 7.2% yeast and 70 minutes fermentation time were used in the baking procedure.

Because a range of plump to highly shrivelled grains could be observed in each cultivar bulk sample, a subjective visual classification of plump, medium shrivelled, and highly shrivelled grains (designated class -a, -b, and -c, respectively) within each of the 8 triticale cultivars was established.

The α-amylase activity of all the triticales (as bulk, as flour from the bulk, and as classified grain samples) were higher than that of wheat and rye grain and flour.

Starch content of plump and medium shrivelled triticale grains was similar to that of wheat, and higher than that of rye while the starch content of highly shrivelled grains was lower than that of wheat and similar to that of rye.

Total soluble sugars and reducing sugars showed no significant difference between triticale bulk samples, wheat, and rye. However, the highly shrivelled triticale grain samples were higher, in these two components, than wheat and rye.

Alpha-amylase activity, starch, total soluble sugars, and reducing sugars determination in classified triticale samples, indicated that no

evident relationship between these parameters and degree of grain shrivelling exist in secondary hexaploid triticales.

Changes in composition during the development of grains produced from the three grain classes of triticale Rahum (P-1) showed that, from 21 to 35 days post-anthesis, grains from highly shrivelled seeds had the highest α-amylase activity while grains from plump seeds had the lowest one. Thus, indicating that the factor(s) producing grain shrivelling also affect, in parallel, the α-amylase activity in the grain.

Changes in water and starch content during development suggested that shrivelled grains reached physiological maturity earlier than plump grains, perhaps due to a lower capacity of the shrivelled grains to store dry matter.

The pattern of changes in total soluble sugars in grains from the three classified seeds was similar throughout development, although the rate of increase or decrease varied among them. At 35 days post-anthesis, the highest level of total soluble sugars corresponded to grains from highly shrivelled seeds and the lowest to those from medium shrivelled ones. Thus, a relationship between grain shrivelling and total soluble sugars was not evidently observed.

Reducing sugars decreased with maturation in grains from plump and medium shrivelled seeds. In contrast, this component was fairly constant in grains from highly shrivelled seeds, until 28 days post-anthesis when a decrease during the next 7 days was observed. At 35 days post-anthesis, the reducing sugars content showed no significant difference among all samples.

Morphology of classified mature and developing grains (observed under SEM and light microscopy, respectively), showed that grain shrivelling in triticale resulted from failure of the starchy endosperm cells to completely fill the grain sink. Even though enzymatically damaged starch granules were observed (under SEM) in the highly shrivelled grains of 3 triticales, the extent of damage could not be considered to cause grain shrivelling.

No evident relationship between grain shrivelling and the number and identity of rye chromosomes present in each of the 8 triticale cultivars was observed.

Different genotypes detected in the single triticale Rahum (P-1), indicated that partial sterility and consequent outcrossing occurred in this cultivar.

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FACTORS AFFECTING GRAIN SHRIVELLING IN SECONDARY HEXAPLOID TRITICALE

by

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Eight secondary hexaploid triticales containing from 5 to 7 rye chromosome pairs were selected for variation in degree of grain shrivelling. Among the triticales with chromosomes from the D-genome of bread wheat, two presented satisfactory breadmaking quality. All triticale grain and flour samples had higher α-amylase activity than wheat and rye. Alpha-amylase activity, starch, total soluble sugars and reducing sugars of each cultivar (classified in plump, medium shrivelled and highly shrivelled grain classes) were not observed to be related to grain shrivelling in triticale. Compositional changes during the development of grains produced from the three grain classes of the triticale cultivar Rahum indicated that the factor(s) producing grain shrivelling also affect, in parallel, the α-amylase activity in the grain. Changes in water and starch content indicated that the highly shrivelled grains reached physiological maturity earlier than plump grains. Total and reducing sugars did not reflect the high α-amylase activity of highly shrivelled grains, suggesting that the grain is capable of eliminating (by catabolizing or relocating mechanisms) excessive levels of soluble carbohydrate. SEM and light microscopy examination of mature developing triticale grains showed that grain shrivelling resulted from failure of endosperm cells to fill their grain sink. Although enzymatically damaged starch grains were observed in 3 out of 8 triticales, the extent of damage could not be considered large enough to cause grain shrivelling. No evident relationship between grain shrivelling and the number and identity of rye chromosomes present in each of the 8 triticale cultivars was observed.