# **Development of soft kernel durum wheat**

Craig F. MORRIS (☑)

USDA-ARS Western Wheat Quality Laboratory, Washington State University, Pullman, WA 99164, USA

**Abstract** Kernel texture (grain hardness) is a fundamental and determining factor related to wheat (Triticum spp.) milling, baking and flour utilization. There are three kernel texture classes in wheat: soft and hard hexaploid (T. aestivum), and very hard durum (T. turgidum subsp. durum). The genetic basis for these three classes lies with the Puroindoline genes. Phenotypically, the easiest means of quantifying kernel texture is with the Single Kernel Characterization System (SKCS), although other means are valid and can provide fundamental material properties. Typical SKCS values for soft wheat would be around 25 and for durum wheat≥80. Soft kernel durum wheat was created via homeologous recombination using the ph1b mutation, which facilitated the transfer of ca. 28 Mbp of 5DS that replaced ca. 21 Mbp of 5BS. The 5DS translocation contained a complete and intact Hardness locus and both Puroindoline genes. Expression of the Puroindoline genes in durum grain resulted in kernel texture and flour milling characteristics nearly identical to that of soft wheat, with high yields of break and straightgrade flours, which had small particle size and low starch damage. Dough water absorption was markedly reduced compared to durum flour and semolina. Dough strength was essentially unchanged and reflected the inherent gluten properties of the durum background. Pasta quality was essentially equal-to-or-better than pasta made from semolina. Agronomically, soft durum germplasm showed good potential with moderate grain yield and resistance to a number of fungal pathogens and insects. Future breeding efforts will no doubt further improve the quality and competitiveness of soft durum cultivars.

**Keywords** soft durum wheat, grain hardness, Puroindolines, milling, baking, pasta, noodles

## 1 Introduction

Kernel texture (grain hardness) is a fundamental and

Received March 6, 2019; accepted March 22, 2019

Correspondence: craig.morris@ars.usda.gov

Treffice tentare (Stain maraness) is a randamental an

determining factor related to wheat (*Triticum* spp.) milling, baking and flour utilization<sup>[1]</sup>. Generally speaking, there are three kernel texture classes: soft and hard hexaploid (*T. aestivum*), and very hard durum (*T. turgidum* subsp. *durum*). The genetic basis for these three classes lies with the Puroindoline genes, Puroindoline a and Puroindoline b (*Pina* and *Pinb*, respectively)<sup>[2,3]</sup>. A fourth class exists, "Super Soft," but it has not been commercialized and its genetic basis is incompletely understood<sup>[4–6]</sup>. This paper focuses on the development of soft kernel durum wheat, an endeavor led by the author at the USDA Western Wheat Quality Laboratory, but one that required the talents and contributions of numerous collaborators.

# 1.1 Measurement of kernel texture phenotype

Before discussing further the development of soft kernel durum wheat, it is useful to consider the techniques of measuring wheat kernel texture. Each technique exploits an aspect of the underlying material properties of the endosperm, and encompasses particle size distribution of meals after grinding and flours after milling, the effect of particle size on near infrared light reflectance, and the resistance of the endosperm to crushing/fracture. Clearly, the most relevant has to do with producing alimentary meals and flours. In this regard, various means of grinding wheat or producing flour have direct meaning<sup>[7]</sup>. Among the earliest standardized methods was the Particle Size Index, which simply sieved a sample of ground meal and expressed the amount that passed through the sieve as a proportionality<sup>[8]</sup>. Softer wheats due to their finer particle size, had a greater proportion that would pass through. On a simple laboratory test mill, which attempts to emulate commercial flour milling, the parameter known as "break flour yield" may provide a better estimate of kernel texture (especially softness). The fact that greater kernel hardness translates into meals of coarser (greater) mean particle size was exploited by Norris and coworkers[9] who used the reflectance of light in the near infrared to assess kernel texture. Upon scanning the reflectance spectra of a group of soft and of hard wheats, wavelengths at 1680 and 2230 nm were used to develop an algorithm that arbitrarily

assigned a value of 25 to soft wheats, and 75 to hard wheats. These values have no units and also no particular limits, although values less than, say 10, and greater than 110 are rarely encountered; the highest values are associated with very hard, vitreous, and high protein durum wheat [10,11]. Regarding crushing strength, the most fundamental approach involves preparing a specimen of defined dimensions and applying a stress until the specimen fails. Typical response variables include failure stress, failure strain, failure energy (area), and Young's modulus [12–16]. Specimens may be parallelepipedal ("brick") or cylindrical. Although specimen preparation is somewhat tedious, the analysis expresses texture in universally understood material properties.

A variation on the crushing approach that is much simpler involves using the Single Kernel Characterization System (SKCS) 4100 (Perten Instruments). With this device, kernels are individually crushed but no specimen preparation is required. A computer algorithm adjusts for kernel weight, dimension and moisture<sup>[17]</sup>.

#### 1.2 Role of Puroindolines in kernel texture

As mentioned above, the Puroindoline genes and proteins are the underlying genetic basis of soft kernel texture. Early on, before the discovery of the Puroindolines, a small ill-defined group of small proteins termed "friabilin" were consistently found associated with the surface of starch isolated from soft wheat. When hard wheat was examined, the occurrence was much reduced, and friabilin was absent in durum wheat [18–20].

The nature of this friabilin–starch association was complex, but clearly involved on some level bound polar lipids<sup>[21–23]</sup>. Eventually, the fields of friabilin research and kernel texture coalesced with a largely unrelated field, that of lipid binding proteins from wheat flour<sup>[2]</sup>. Through this work, friabilin was resolved into *Pina*, *Pinb* and a third closely related gene/protein, Grain softness protein-1 (*Gsp-1*/*GSP-1*, respectively). Although *Pina*, *Pinb* and *Gsp-1* clearly share an evolutionary history<sup>[24,25]</sup>. Somewhat surprising, an additional paralog, Puroindoline b-2 (*Pinb-2*), although polymorphic across multiple loci, similarly shows no distinct association with kernel texture<sup>[26–32]</sup>.

The significant breakthrough regarding the genetics of kernel texture came with the discovery of sequence variants (mutations) in *Pina* and *Pinb*<sup>[33,34]</sup>. These reports set off a number of searches for new Puroindoline sequences in wheat germplasm from Northern Europe<sup>[35]</sup>, North America<sup>[28,36]</sup>, China<sup>[37-41]</sup>, and Eastern Asia<sup>[42]</sup>. These and other studies showed that all wheats of the 'soft' phenotype class possessed *Pina* and *Pinb* in unaltered forms, which were derived from *Aegilops tauschii* during the initial hexaploidization event(s)<sup>[24,43]</sup>. Conversely, all hard kernel hexaploid wheats were shown to possess one (rarely two) mutation in *Pina* or *Pinb*, most often in

Pinb<sup>[2,3,44]</sup>. The discovery of these mutant sequences has continued and they have been assigned a systematic nomenclature based on the guidelines of the Catalogue of Genes Symbols for Wheat<sup>[45]</sup>, which involves an abbreviation of the gene, Pina and Pinb, the sub-genome location first in a series of loci, Pina-D1 and Pinb-D1, and lastly a lowercase letter assigned to the allele/sequence. The wild-type alleles/sequences are assigned 'a', Pina-D1a and Pinb-D1a. This is also, as noted above, the soft kernel haplotype. Each of these unique mutant sequences has the potential to increase the hardness of the endosperm through partial loss of the softening function of the Puroindolines. Since not all mutations have an equal effect, different levels of kernel texture phenotype result<sup>[17,46–49]</sup>.

# 2 Development of soft kernel durum wheat

#### 2.1 Homeologous recombination

The development of soft kernel durum wheat was aimed at removing its primary limitation to milling, processing and utilization, that is, its very hard kernel texture<sup>[50]</sup>. And although uncertain at the outset, the transfer of the Puroindolines effectively converted durum into the equivalent of the soft class of hexaploid wheat. (In fact, since all commercial durum cultivars possess white bran, soft durum is a 'soft white spring wheat'). The transfer of the Puroindolines was accomplished through the use of a mutation in the Pairing homeologous-1 gene (Ph1) (the mutation is variously identified as ph1b or Ph1b), which allows non-homologous chromosomes to pair. The stepwise sequence and details of crossing, cytology and selection are described in Morris and coworkers<sup>[51]</sup>. Essentially, a small portion of the distal tip of chromosome 5D short arm (5DS) was transferred to chromosome 5BS. It has recently been resolved that ~28163252 bp of 5DS replaced ~20742425 bp of 5BS, and that the crossover occurred in a 39-bp region in the middle of a putative gene<sup>[52]</sup>. Although this fragment of 5DS carries an entire and intact Hardness locus with promoters, etc. [53,54], the Puroindolines alone can function effectively as transgenes in wheat, rice and maize<sup>[55–57]</sup> to soften the endosperm of these cereals. Conversely, silencing the Puroindolines<sup>[58]</sup> or deleting the Ha locus<sup>[59]</sup> results in an endosperm texture similar to that of durum wheat.

## 2.2 Milling and baking quality

Durum wheat is recognized as having variable but limited baking quality<sup>[60]</sup>. A major factor in both the commercial use of durum wheat and the laboratory assessment of durum wheat milling and baking quality relates, inescapably, from its very hard kernel texture. Flours (or semolina) will be coarser (larger particle size distribution) and may have greater levels of starch damage, which greatly affects

dough water absorption and rheology. The creation of soft durum impacted nearly every aspect of milling, baking, pasta and noodle quality. SKCS hardness, break flour yield and flour yield were similar to commercial soft white wheat cultivars, and tempering response was also consistent with the soft kernel trait [61,62]. On a per unit weight of flour produced, soft durum required only from one-fifth to one-third the energy as hard durum<sup>[63]</sup>. Soft durum flours had low starch damage and low solvent retention capacity (SRC) water and SRC carbonate. Dough water absorption was also reduced relative to hard kernel durum<sup>[64–66]</sup>; cookie quality in some ways surprisingly performed better than soft hexaploid wheat<sup>[64]</sup>. Given the caveat of altered dough water absorption, dough strength was essentially unchanged and reflected the inherent gluten properties of the durum background.

### 2.3 Pasta and noodles

Pasta and noodle quality of soft durum were either improved or unchanged relative to hard durum cultivars. The smaller particle size (flour vs. semolina) and low starch damage contributed to faster and more uniform hydration. A lower hydration requirement was considered a positive feature from a drying and energy standpoint. Although there is little consensus on laboratory evaluation of pasta<sup>[67]</sup>, fresh pasta made from soft durum exhibited lower cooking loss, lower water uptake, higher firmness, and lower stickiness. Color ( $L^*$  and  $b^*$ ) was comparable to semolina. For sheeted noodles, white salted, alkaline and egg, soft durum exhibited low darkening over time ( $\Delta L^*$ ), which is likely related to its low level of polyphenol oxidase. At neutral pH, the soft durum noodles were, not surprisingly, much yellower than the hexaploid wheat noodles. At alkaline pH, although hexaploid wheat flours show a dramatic increase in yellow color, the soft durum did not<sup>[68-70]</sup>

# 2.4 Agronomics

One question was whether the soft kernel trait either directly or as a consequence of the 5BS-5DS translocation would alter agronomic traits, including resistance to pests. In a broad study spanning multiple crop years, the answer appears to be 'no'<sup>[71]</sup>. Soft durum lines were compared to commercial hard red spring wheat cultivars and proved to be relatively competitive for grain yield, exceeding by > 90% the yield of the hard red spring wheat cv. Buck Pronto at over half of 34 locations. The soft durum lines exhibited moderate-to-strong resistance to stripe rust (*Puccinia striiformis* f. sp. *tritici*), good resistance to stem rust (*Puccinia graminis* f. sp. *tritici*), and near complete resistance to dwarf bunt (*Tilletia controversa*). Variable levels of resistance to cereal cyst nematode (*Heteroderma filipievi*) were observed among lines, some

being highly resistant. Resistance to Hessian fly (*Mayetiola destructor*) was observed in some of the plants, which were selected and re-screened. Increasing the seeding rate up to two-times the local management levels did not significantly impact grain yield. The soft durum lines showed no tolerance to acid soils with high levels of aluminum, and appear to be highly susceptible to fusarium crown rot (*Fusarium pseudograminearum*). Regardless of these studies, a more detailed analysis of the genes lost and gained, respectively, with the replacement of the original ~20.7 Mbp of 5BS of cv. Svevo with the ~28.2 Mbp of Chinese Spring is worthwhile.

These studies show that there is good agronomic potential in the current soft durum lines for moderate grain yield and good pest resistance. (Current germplasm is all derived from Soft Svevo, although high backcross derived lines have been obtained from commercial durum cultivars, and crosses have been made with CIMMYT lines). Further breeding efforts and germplasm introgression will likely improve the competitiveness of soft durum wheat with currently-grown hard red spring wheat and commercial durum cultivars. From a technological standpoint, soft kernel durum shows equal-to-or better end-use quality compared to normal hard kernel durum; milling is essentially equal to soft hexaploid wheat. Considering the breadth of studies, no disadvantage related to the soft kernel trait nor the 5BS-5DS translocation has been observed.

## 3 Conclusions

Homoeologous recombination successfully transferred a small amount of chromosome 5DS containing the Hardness locus from bread wheat to durum wheat. The result was soft kernel durum. Expression of the Puroindoline genes in durum grain resulted in kernel texture and flour milling characteristics nearly identical to that of soft wheat, with high yields of break and straight grade flours, which had small particle size and low starch damage. Dough water absorption was markedly reduced compared to durum flour and semolina. Dough strength was essentially unchanged and reflected the inherent gluten properties of the durum background. Pasta quality was essentially equalto-or-better than pasta made from semolina. Agronomically, soft durum germplasm showed good potential with moderate grain yield and resistance to a number of fungal pathogens and insects. Future breeding efforts will no doubt further improve the quality and competitiveness of soft durum cultivars.

Acknowledgements The assistance of Stacey Sykes, Shawna Vogl, and the entire staff of the Western Wheat Quality Laboratory, especially Doug Engle, Gail Peden, Mary Baldridge, Bill Kelley, Mishelle Lenssen and Eric Wegner are gratefully acknowledged. Numerous collaborators made contributions to

the development and evaluations of soft durum; please note the co-authors cited in the References. Of particular thanks, the contributions of Leonard Joppa, Alecia Kiszonas, Marco Simeone, Domenico Lafiandra, Jessica Murray, Jeff Boehm Jr., and Maria Itria Ibba are warmly acknowledged.

Compliance with ethics guidelines Craig F. Morris declares that he has no conflict of interest; as a co-inventor of soft durum wheat, he receives some licensing royalties from USDA.

This article is a review and does not contain any studies with human or animal subjects performed by the author.

## References

- Morris C F. Impact of blending hard and soft white wheats on milling and baking quality. *Cereal Foods World*, 1992, 37: 643– 648
- Morris C F. Puroindolines: the molecular genetic basis of wheat grain hardness. *Plant Molecular Biology*, 2002, 48(5–6): 633–647
- Bhave M, Morris C F. Molecular genetics of Puroindolines and related genes: allelic diversity in wheat and other grasses. *Plant Molecular Biology*, 2008, 66(3): 205–219
- Morris C F, Anderson J A, King G E, Bettge A D, Garland-Campbell K, Allan R E, Fuerst E P, Beecher B S. Characterization of a unique "super soft" kernel trait in wheat. *Cereal Chemistry*, 2011, 88(6): 576–583
- Ibba M I, Kiszonas A M, See D R, Skinner D Z, Morris C F. Mapping kernel texture in a soft durum (*Triticum turgidum* subsp. durum) wheat population. Journal of Cereal Science, 2019, 85: 20– 26
- Kumar N, Orenday-Ortiz J M, Kiszonas A M, Boehm J D Jr, Morris C F. Genetic analysis of a unique 'super soft' kernel texture phenotype in soft white spring wheat. *Journal of Cereal Science*, 2019, 85: 162–167
- Morris C F, DeMacon V L, Giroux M J. Wheat grain hardness among chromosome 5D homozygous recombinant substitution lines using different methods of measurement. *Cereal Chemistry*, 1999, 76(2): 249–254
- 8. Williams P C, Sobering D C. Attempts at standardization of hardness testing of wheat. I. The grinding/sieving (particle size index) method. *Cereal Foods World*, 1986, **31**: 359–364
- Norris K H, Hruschka W R, Bean M M, Slaughter D C. A definition of wheat hardness using near infrared reflectance spectroscopy. *Cereal Foods World*, 1989, 34: 696–705
- Morris C F, Massa A. Puroindoline genotype of the U.S. National Institute of Standards & Technology Reference Material 8441, Wheat Hardness. *Cereal Chemistry*, 2003, 80(6): 674–678
- Sissons M J, Osborne B G, Hare R A, Sissons S A, Jackson R. Application of the single-kernel characterization system to durum wheat testing and quality prediction. *Cereal Chemistry*, 2000, 77(1):
- 12. Morris C F, Pecka K, Bettge A D. A device for the preparation of cereal endosperm bricks. *Cereal Chemistry*, 2007, **84**(1): 67–69
- Morris C F, Bettge A D, Pitts M J, King G E, Pecka K, McCluskey P J. Compressive strength of wheat endosperm: comparison of endosperm bricks to the single kernel characterization system. Cereal Chemistry, 2008, 85(3): 359–365

- Morris C F, Delwiche S R, Bettge A D, Mabille F, Abecassis J, Pitts M J, Dowell F E, Deroo C, Pearson T. Collaborative analysis of wheat endosperm compressive material properties. *Cereal Chemistry*, 2011, 88(4): 391–396
- Delwiche S R, Morris C F, Mabille F, Abecassis J. Influence of instrument rigidity and specimen geometry on calculations of compressive strength properties of wheat endosperm. *Cereal Chemistry*, 2012, 89(1): 24–29
- Morris C F, Pitts M J, Bettge A D, Pecka K, King G E, McCluskey P J. Compressive strength of wheat endosperm: analysis of endosperm bricks. *Cereal Chemistry*, 2008, 85(3): 351–358
- Martin J M, Frohberg R C, Morris C F, Talbert L E, Giroux M J.
  Milling and bread baking traits associated with Puroindoline sequence type in hard red spring wheat. *Crop Science*, 2001, 41(1): 228–234
- Morris C F, Greenblatt G A, Malkawi H I. Enhanced electrophoretic detection and isolation of friabilin, a starch granule protein. *Cereal Chemistry*, 1992, 69: 467–468
- 19. Morris C F, Greenblatt G A, Bettge A D, Malkawi H I. Isolation and characterization of multiple forms of friabilin. *Journal of Cereal Science*, 1994, **21**(2): 167–174
- Bettge A D, Morris C F, Greenblatt G A. Assessing genotypic softness in single wheat kernels using starch granule-associated friabilin as a biochemical marker. *Euphytica*, 1995, 86(1): 65–72
- Greenblatt G A, Bettge A D, Morris C F. Relationship between endosperm texture and the occurrence of friabilin and bound polar lipids on wheat starch. *Cereal Chemistry*, 1995, 72: 172–176
- Finnie S M, Jeannotte R, Morris C F, Faubion J M. Variation in polar lipid composition within near-isogenic wheat lines containing different Puroindoline haplotypes. *Journal of Cereal Science*, 2010, 51(1): 66–72
- 23. Finnie S M, Jeannotte R, Morris C F, Giroux M J, Faubion J M. Variation in polar lipids located on the surface of wheat starch. *Journal of Cereal Science*, 2010, **51**(1): 73–80
- Massa A N, Morris C F. Molecular evolution of the Puroindoline-a, Puroindoline-b, and Grain Softness Protein-1 genes in the tribe Triticeae. *Journal of Molecular Evolution*, 2006, 63: 526–536; erratum 63: 718
- Morris C F, Geng H, Beecher B S, Ma D. A review of the occurrence of Grain softness protein-1 genes in wheat (*Triticum aestivum L.*). *Plant Molecular Biology*, 2013, 83(6): 507–521
- 26. Chen F, Beecher B S, Morris C F. Physical mapping and a new variant of Puroindoline b-2 genes in wheat. *Theoretical and Applied Genetics*, 2010, **120**(4): 745–751
- 27. Chen F, Zhang F, Cheng X, Morris C F, Xu H, Dong Z, Zhan K, He Z, Xia X, Cui D. Association of Puroindoline b-2 variants with grain traits, yield components and flag leaf size in bread wheat (*Triticum aestivum* L.) varieties of Yellow and Huai Valley of China. *Journal of Cereal Science*, 2010, 52(2): 247–253
- 28. Geng H, Beecher B S, He Z, Kiszonas A M, Morris C F. Prevalence of Puroindoline D1 and Puroindoline b-2 variants in U.S. Pacific Northwest wheat breeding germplasm pools, and their association with kernel texture. *Theoretical and Applied Genetics*, 2012, 124(7): 1259–1269
- Geng H W, Beecher B S, He Z, Morris C F. Physical mapping of Puroindoline b-2 genes in wheat using 'Chinese Spring' chromo-

- some group 7 deletion lines. Crop Science, 2012, 52(6): 2674-2678
- Chen F, Shang X, Morris C F, Zhang F, Dong Z, Cui D. Molecular characterization and diversity of Puroindoline b-2 variants in cultivated and wild diploid wheat. *Genetic Resources and Crop Evolution*, 2013, 60(1): 49–58
- 31. Chen F, Zhang F, Li H, Morris C F, Cao Y, Shang X, Cui D. Allelic variation and distribution independence of Puroindoline b-B2 variants and their association with grain texture in wheat. *Molecular Breeding*, 2013, **32**(2): 399–409
- 32. Geng H W, Beecher B S, Pumphrey M, He Z H, Morris C F. Segregation analysis indicates that Puroindoline b-2 variants 2 and 3 are allelic in *Triticum aestivum* L. and that a revision to Puroindoline b-2 gene symbolization is indicated. *Journal of Cereal Science*, 2013, 57(1): 61–66
- Giroux M J, Morris C F. A glycine to serine change in Puroindoline b is associated with wheat grain hardness and low levels of starchsurface friabilin. *Theoretical and Applied Genetics*, 1997, 95(5–6): 857–864
- 34. Giroux M J, Morris C F. Wheat grain hardness results from highly conserved mutations in the friabilin components Puroindoline a and b. Proceedings of the National Academy of Sciences of the United States of America, 1998, 95(11): 6262–6266
- Lillemo M, Morris C F. A leucine to proline mutation in Puroindoline b is frequently present in hard wheats from Northern Europe. *Theoretical and Applied Genetics*, 2000, 100(7): 1100– 1107
- Morris C F, Lillemo M, Simeone M C, Giroux M J, Babb S L, Kidwell K K. Prevalence of Puroindoline grain hardness genotypes among historically significant North American spring and winter wheats. *Crop Science*, 2001, 41(1): 218–228
- Chen F, He Z, Xia X, Lillemo M, Morris C F. A new Puroindoline b mutation present in Chinese winter wheat cultivar Jingdong 11. *Journal of Cereal Science*, 2005, 42(2): 267–269
- 38. He Z H, Chen F, Xia X C, Xia L Q, Zhang X Y, Lillemo M, Morris C F. Molecular and biochemical characterization of Puroindoline A and B alleles in Chinese improved cultivars and landraces. In: Proceedings of the 7th International Wheat Conference, Mar del Plata. Argentina: Springer, 2005, 441–448
- Xia L, Chen F, He Z, Chen X, Morris C F. Occurrence of Puroindoline alleles in Chinese winter wheats. *Cereal Chemistry*, 2005, 82(1): 38–43
- 40. Chen F, He Z H, Xia X C, Xia L Q, Zhang X Y, Lillemo M, Morris C F. Molecular and biochemical characterization of Puroindoline a and b alleles in Chinese landraces and historical cultivars. Theoretical and Applied Genetics, 2006, 112(3): 400–409
- 41. He Z H, Chen F, Xia X C, Xia L Q, Zhang X Y, Lillemo M, Morris C F. Molecular and biochemical characterization of Puroindoline A and B alleles in Chinese improved cultivars and landraces. In: Buck H T, Hisi J E, Saloman N, eds. Wheat Production in Stressed Environments. The Netherlands: *Springer*, 2007, 441–448
- Tanaka H, Morris C F, Haruna M, Tsujimoto H. Prevalence of Puroindoline alleles in wheat varieties from eastern Asia including the discovery of a new SNP in Puroindoline b. *Plant Genetic Resources*, 2008, 6(2): 142–152
- 43. Massa A N, Morris C F, Gill B S. Sequence diversity of Puroindoline-a, Puroindoline-b and the grain softness protein

- genes in Aegilops tauschii Coss. Crop Science, 2004, 44(5): 1808–1816
- Pasha I, Anjum F M, Morris C F. Grain hardness: a major determinant of wheat quality. Food Science & Technology International, 2010, 16(6): 511–522
- 45. Morris C F, Bhave M. Reconciliation of D-genome Puroindoline allele designations with current DNA sequence data. *Journal of Cereal Science*, 2008, **48**(2): 277–287
- Morris C F, King G E. Registration of hard kernel Puroindoline allele near-isogenic line hexaploid wheat genetic stocks. *Journal of Plant Registrations*, 2008, 2(1): 67–68
- 47. Gedye K R, Morris C F, Bettge A D. Determination and evaluation of the sequence and textural effects of the Puroindoline a and Puroindoline b genes in a population of synthetic hexaploid wheat. *Theoretical and Applied Genetics*, 2004, 109(8): 1597–1603
- 48. Boehm J D Jr, Ibba M I, Kiszonas A M, See D R, Skinner D Z, Morris C F. Identification of genotyping-by-sequencing sequence tags associated with milling performance and end-use quality traits in elite hard red spring wheat (*Triticum aestivum L.*). *Journal of Cereal Science*, 2017, 77: 73–83
- Boehm J D Jr, Ibba M I, Kiszonas A M, See D R, Skinner D Z, Morris C F. Genetic analysis of kernel texture (grain hardness) in a hard red spring wheat (*Triticum aestivum* L.) bi-parental population. *Journal of Cereal Science*, 2018, 79: 57–65
- Morris C F, Casper J, Kiszonas A M, Fuerst E P, Murray J, Simeone M C, Lafiandra D. Soft kernel durum wheat—a new bakery ingredient? *Cereal Foods World*, 2015, 60(2): 76–83
- 51. Morris C F, Simeone M C, King G E, Lafiandra D. Transfer of soft kernel texture from *Triticum aestivum* to durum wheat, *Triticum turgidum* ssp. *durum*. *Crop Science*, 2011, **51**: 114–122
- Boehm J D Jr, Zhang M, Cai X, Morris C F. Molecular and cytogenetic characterization of the 5DS-5BS chromosome translocation conditioning soft kernel texture in durum wheat. *Plant Genome*, 2017, 10(3): 1–11
- Lillemo M, Cosimo Simeone M, Morris C F. Analysis of Puroindoline a and b sequences from *Triticum aestivum* cv. 'Penawawa' and related diploid taxa. *Euphytica*, 2002, 126(3): 321–331
- 54. Simeone M, Gedye K R, Mason-Gamer R, Gill B S, Morris C F. Conserved regulatory elements identified from a comparative Puroindoline gene sequence survey of *Triticum* and *Aegilops* diploid taxa. *Journal of Cereal Science*, 2006, 44(1): 21–33
- Martin J M, Meyer F D, Morris C F, Giroux M J. Pilot scale milling characteristics of transgenic isolines of a hard wheat over-expressing Puroindolines. *Crop Science*, 2007, 47(2): 495–504
- Zhang J, Martin J M, Beecher B, Morris C F, Curtis Hannah L, Giroux M J. Seed-specific expression of the wheat Puroindoline genes improves maize wet milling yields. *Plant Biotechnology Journal*, 2009, 7(8): 733–743
- Krishnamurthy K, Giroux M J. Expression of wheat Puroindoline genes in transgenic rice enhances grain softness. *Nature Biotechnol*ogy, 2001, 19(2): 162–166
- 58. Xia L, Geng H, Chen X, He Z, Lillemo M, Morris C F. Silencing of Puroindoline a alters the kernel texture in transgenic bread wheat. *Journal of Cereal Science*, 2008, **47**(2): 331–338
- 59. Morris C F, Beecher B S. The distal portion of the short arm of

- wheat (*Triticum aestivum* L.) chromosome 5D controls endosperm vitreosity and grain hardness. *Theoretical and Applied Genetics*, 2012, **125**(2): 247–254
- 60. Ammar K, Kronstad W E, Morris C F. Breadmaking quality of selected durum wheat genotypes and its relationship with high molecular weight glutenin subunits, allelic variation and gluten protein polymeric composition. *Cereal Chemistry*, 2000, 77(2): 230–236
- Murray J C, Kiszonas A M, Wilson J D, Morris C F. Effect of soft kernel texture on the milling properties of soft durum wheat. *Cereal Chemistry*, 2016, 93(5): 513–517
- Boehm J D Jr, Ibba M I, Kiszonas A M, Morris C F. End-use quality of CIMMYT-derived soft-kernel durum wheat germplasm: I. Grain, milling and soft wheat quality. *Crop Science*, 2017, 57(3): 1475– 1484
- 63. Heinze K, Kiszonas A M, Murray J C, Morris C F, Lullien-Pellerin V. Puroindoline genes introduced into durum wheat reduce milling energy and change milling behavior similar to soft common wheats. *Journal of Cereal Science*, 2016, 71: 183–189
- 64. Murray J C, Kiszonas A M, Morris C F. Influence of soft kernel texture on the flour, water absorption, rheology, and baking quality of durum wheat. *Cereal Chemistry*, 2017, **94**(2): 215–222
- 65. Quayson E T, Atwell W, Morris C F, Marti A. Empirical rheology and pasting properties of soft-textured durum wheat (*Triticum*

- turgidum ssp. durum) and hard-textured common wheat (T. aestivum). Journal of Cereal Science, 2016, 69: 252–258
- 66. Boehm J D Jr, Ibba M I, Kiszonas A M, Morris C F. End-use quality of CIMMYT-derived soft-kernel durum wheat germplasm: II. Dough strength and pan bread quality. *Crop Science*, 2017, 57(3): 1485–1494
- Murray J C, Kiszonas A M, Morris C F. Pasta production: complexity in defining processing conditions for reference trials and quality assessment methods. *Cereal Chemistry*, 2017, 94(5): 791– 797
- 68. Kiszonas A M, Ma D, Fuerst E P, Casper J, Engle D A, Morris C F. Color characteristics of white salted, alkaline, and egg noodles prepared from *Triticum aestivum* L. and a soft kernel durum *T. turgidum* ssp. durum. Cereal Chemistry, 2018, 95(6): 747–759
- Murray J C, Kiszonas A M, Morris C F. Influence of soft kernel texture on fresh durum pasta. *Journal of Food Science*, 2018, 83 (11): 2812–2818
- Morris C F. Determinants of wheat noodle color. *Journal of the Science of Food and Agriculture*, 2018, 98(14): 5171–5180
- 71. Kiszonas A M, Higginbotham R, Chen X M, Garland Campbell K, Bosque-Perez N A, Pumphrey M, Rouse M N, Hole D, Wen N, Morris C F. Agronomic traits in durum wheat germplasm possessing Puroindoline genes. *Agronomy Journal*, 2019. [Epub ahead of print] doi: 10.2134/agronj2018.08.0534