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An integrated study of grain development of wheat (cv. Hereward)

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ABSTRACT

We have carried out a detailed study of grain development of wheat cv. Hereward in order to provide a reference source for researchers and to obtain new information on aspects of development that relate to end use quality. This has included published reports of transcriptome analysis using Affymetrix wheat GeneChip oligonucleotide arrays, the expression profiles of transcription factors, the deposition of starch and storage proteins and the deposition and metabolism of endosperm cell walls. The present review brings together data from these studies with new analyses of grain structure and metabolic profiling to provide the most detailed description that is currently available of wheat grain development using a single series of samples.

1. Introduction

Although the preparation of foods for human consumption is the major use of wheat worldwide, significant amounts are used for other purposes. For example, a greater amount of wheat is used in the UK for livestock feed (about 6 m tonnes pa) than for milling (about 5 tonnes pa), and significant amounts for distilling (about 0.7 m tonnes pa) and bioethanol (estimated to increase to 1.5–2 m tonnes pa). Although these end uses have different quality requirements in terms of grain composition and properties, in all cases the quality is largely determined by events occurring during grain development. Understanding grain development and how it is regulated is therefore of fundamental importance for the improvement of grain quality, whether by conventional breeding or genetic engineering.

The development of the wheat grain has been well described at the microscopic level, as reviewed by Bechtel et al. (2009). By contrast, events at the biochemical and molecular levels are less well understood with most studies focussing on a specific developmental phase (notably grain filling), a specific part of the grain (often the endosperm) (eg Drea et al., 2005) or a specific group of components (notably proteins, starch and cell walls) (see for example Carceller and Aussenac, 2001; Dupont and Altenbach, 2003; Gupta et al., 1996; Johansson et al., 1994; Mecham et al., 1981; Philippe et al., 2006; Toole et al., 2007, 2009).

We therefore initiated a detailed study of biochemical, molecular and spatial aspects of grain development of the wheat cultivar Hereward, in order to provide a more comprehensive view of events occurring, and focussing particularly on the grain filling and maturation period.

This study was intended to provide a reference source for researchers as well as to provide new information on aspects of development that relate to end use quality and has so far resulted in separate reports on transcriptome analysis and transcription factors (Wan et al., 2008), deposition of starch and storage proteins (Shewry et al., 2009) and the deposition and metabolism of endosperm cell walls (Toole et al., 2010). The present review brings together data from these studies and provides additional data on other aspects of grain structure, metabolism and composition in order to provide an integrated description of grain development.

The wheat cultivar Hereward was selected because of its unique position in UK wheat production. Whereas most UK wheat cultivars become outclassed and cease being grown within a few years, Hereward is still grown over a limited area despite having been released in 1991. This is because it is favoured by millers and

Abbreviations: AX, arabinoxylan; AXAH, arabinoxylan arabinofuranohydrolase; AXOS, arabinoxylan oligosaccharide; BAHD, a family of acyltransferases named after the four first characterised members; β-glucan, (1,3:1,4) β-D-glucan; *CSLF6*, cellulose synthase-like; DP, degree of polymerisation; FT-IT, Fourier-transform infra-red; GABS, gamma-amino butyric acid; GT, glucosyl transferase; HP-AEC, high-performance anion exchange chromatography; NMR, nuclear magnetic resonance; Pfam, protein family; PCA, principal component analysis; WE-AX, water-extractable arabinoxylan; WU-AX, water-unextractable arabinoxylan.

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processors due to its high and stable quality. The basis for this quality is still not understood although it is known that Hereward does not have a favourable combination of high molecular weight subunits of glutenin. Hence, a second aim of the project was to provide information on the basis for the quality of Hereward. Finally, the project has focused on the endosperm as this is the major tissue which determines the end use properties of the grain.

In order to ensure that the results from the various parts of the study were comparable they were carried out on samples prepared at the same time. These comprised four sets of approximately 100 developing caryopses at each stage of development, each being taken from the central third of ten heads. Two of these samples were used for transcriptome analysis (Wan et al., 2008) and the other two freeze dried and used for biochemical analysis (Shewry et al., 2009; Toole et al., 2010). A fifth set of samples were taken at the same time and stored in 70% ethanol for FT-IR micro-spectroscopy (Toole et al., 2010). The only analyses which were not carried out on these sample sets are the micrographs shown in Fig. 1. These were carried out on samples grown in the field at Rothamsted in 2011 to provide a background for the changes during grain filling which are discussed below.

1.1. Pattern of grain development

The early stages of grain development have been reviewed by Bechtel et al. (2009) and will only be briefly described here. The first event is “double fertilisation”, with one pollen reproductive nucleus fusing with two female polar nuclei within the embryo sac to give a triploid endosperm nucleus and the second pollen reproductive nucleus fusing with the egg nucleus to give the diploid zygote. These are surrounded by several tissues (nucellus, nucellar epidermis, inner integument, outer integument, tube cells, cross cells and maternal pericarp) which are of maternal origin.

1.2. The endosperm

Fertilisation is followed by numerous mitotic divisions which are not accompanied by cell division, leading to the formation, after one or two days, of a single multinucleate cell with a peripheral zone of cytoplasm (syncytium) and a large central vacuole. Cellularisation is then initiated by the appearance of anticlinal cell walls which separate the nuclei in the endosperm syncytium to form the so called “alveoli”. The walls are first observed in the syncytium

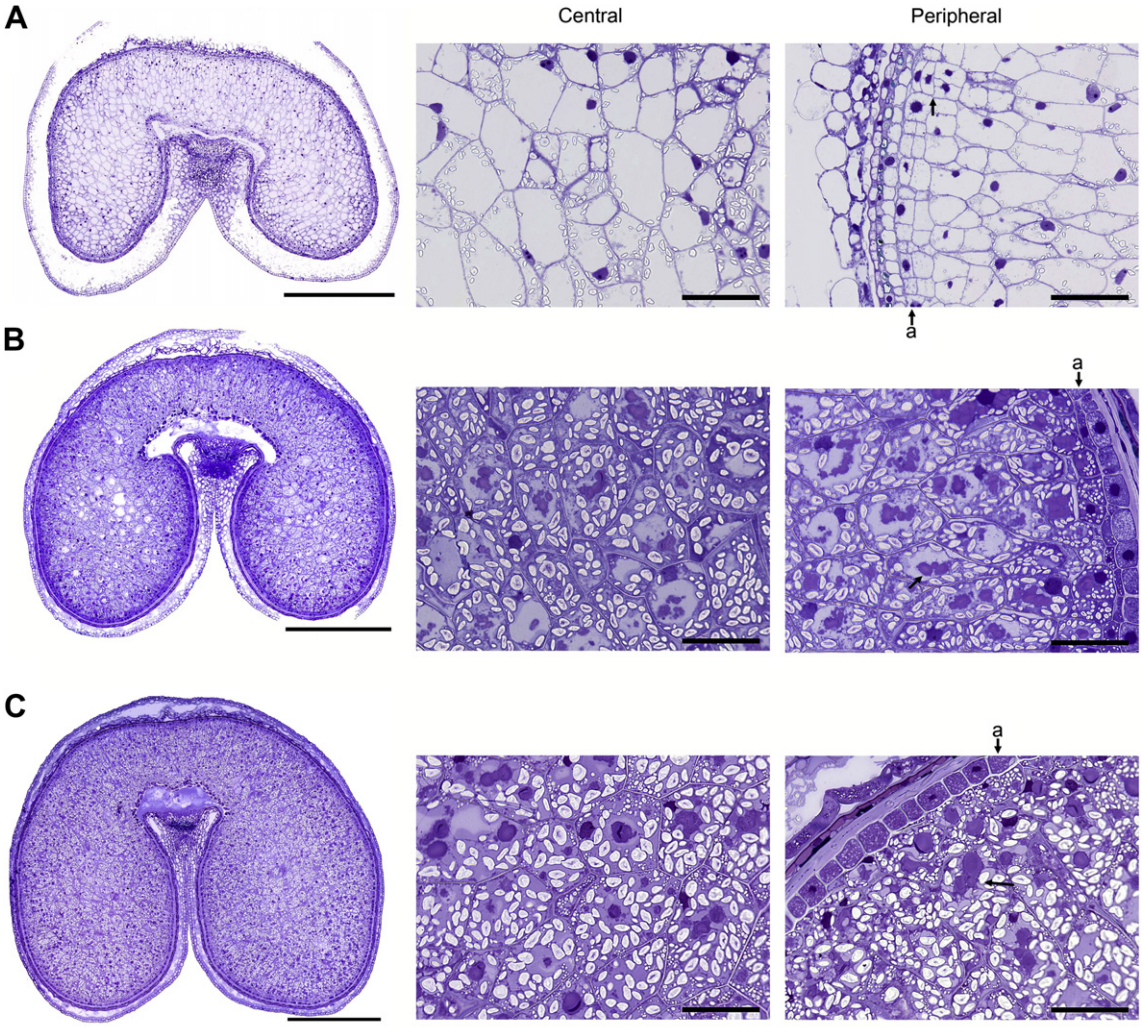

Fig. 1. Transverse sections of developing caryopses of wheat cv. Hereward before and during grain filling. The left hand panels show whole sections and the central and right hand panels show higher magnification images of areas of the central and peripheral endosperm, respectively. A, 10 daa (initiation of protein accumulation). The arrow indicates sub-aleurone cells which have recently undergone division; B, 18 daa (end of cell division phase, linear rate of grain filling). The arrow indicates protein deposits within the vacuole of a sub-aleurone cell; C, 22 daa (maximum rate of grain filling). The arrow indicates a sub-aleurone cell which is essentially full of protein. Sections are stained with toluidine blue. The aleurone layer is indicated by “a”. The bar is 1 mm in the left hand panel, 100 nm in the central and right hand panels. Previously unpublished data of Paola Tosi (Rothamsted Research).