



# Stomatal development: focusing on the grasses

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The development and patterning of stomata in the plant epidermis has emerged as an ideal system for studying fundamental plant developmental processes. Over the past twenty years most studies of stomata have used the model dicotyledonous plant *Arabidopsis thaliana*. However, cultivated monocotyledonous grass (or Gramineae) varieties provide the majority of human nutrition, and future research into grass stomata could be of critical importance for improving food security. Recent studies using *Brachypodium distachyon*, *Hordeum vulgare* (barley) and *Oryza sativa* (rice) have led to the identification of the core transcriptional regulators essential for stomatal initiation and progression in grasses, and begun to unravel the role of secretory signaling peptides in controlling stomatal developmental. This review revisits how stomatal developmental unfolds in grasses, and identifies key ontogenetic steps for which knowledge of the underpinning molecular mechanisms remains outstanding.

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## Introduction

Stomata function as the interface between plants and atmosphere, exerting control over gaseous diffusion and balancing the uptake of carbon dioxide with the loss of water vapour [1]. Regulation of stomatal development is of critical importance in allowing plants to adjust their gaseous exchange to suit the prevailing environmental conditions [2–4]. Stomatal development has been extensively studied, and has emerged as an excellent system for investigating cell-fate specification and cellular differentiation [5,6\*\*]. The distribution of stomata on the leaf

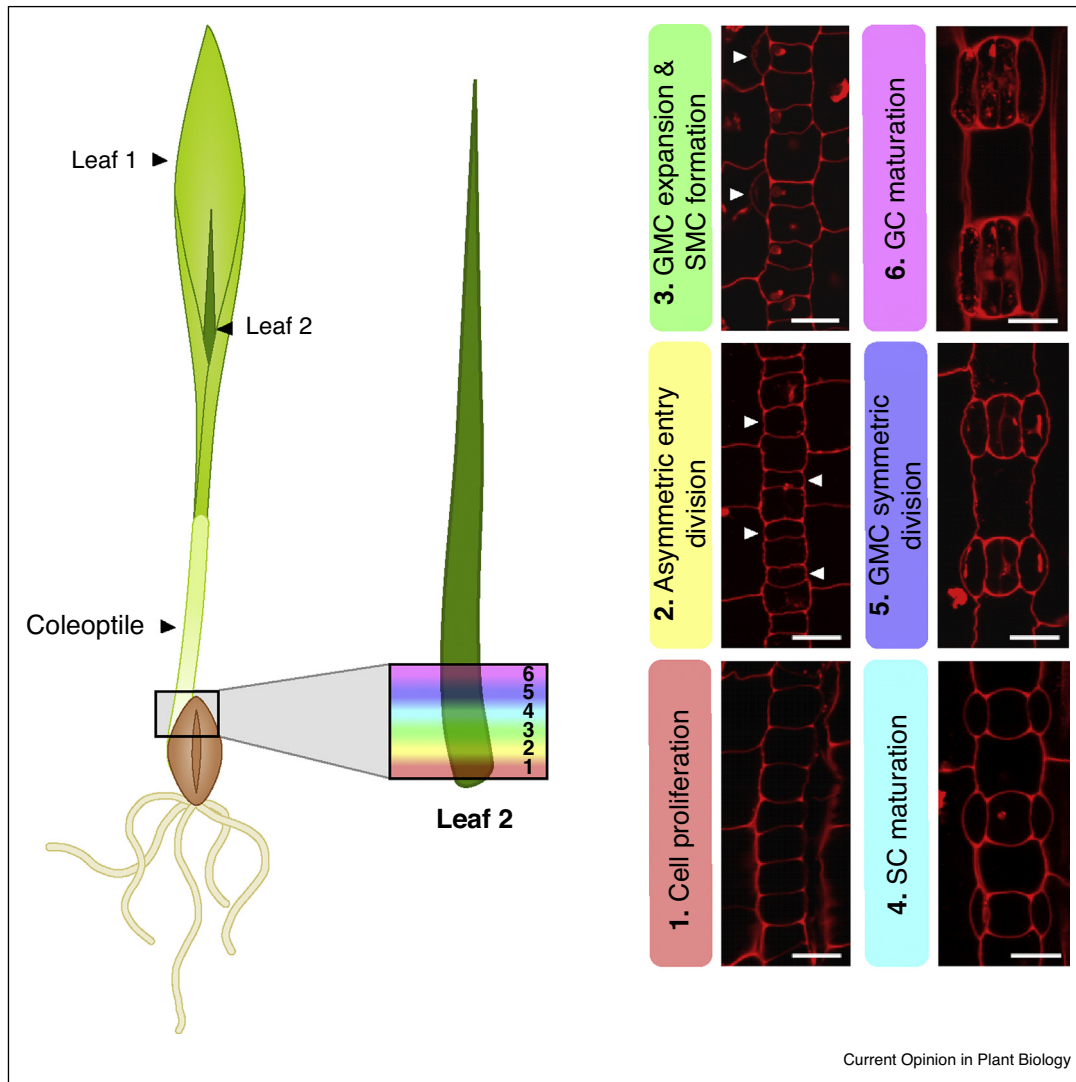
surface is a highly regulated process with a level of plasticity, and components regulating stomatal development continue to be identified [7,8]. Much of our current understanding stems from work conducted on the model dicot *Arabidopsis thaliana* and many comprehensive reviews are available [9,10].

Although cereal grasses provide the majority of human nutrition we still know surprisingly little about their stomata. As scientific focus moves towards the engineering of ‘climate ready crops’ that will be better suited to predicted warmer, drier, higher carbon dioxide environments, understanding the regulatory mechanisms of grass stomatal development and patterning could prove key to future success. In this review, we outline recent advances emerging from studies of grasses and discuss the outstanding questions.

## The grass stomatal lineage

The development of stomatal complexes in grasses differs to that of the dicots in a number of ways. Most notably, grass stomata are formed from dumbbell-shaped guard cells (GCs) that are flanked by subsidiary cells (SC) which develop in parallel rows within defined and specific epidermal cell files. In contrast, the GCs of dicots are kidney-shaped and form stomata that are scattered throughout the epidermis in a less orderly pattern. In nascent leaves, grass stomatal development occurs along a spatiotemporal gradient with the earliest stages occurring basally, and proceeding as cells move upwards as the leaf expands [11,12]. This developmental pathway can be broken down into 6 stages and is illustrated using barley (*Hordeum vulgare*) in Figure 1. Initially, close to the leaf base, prior to stomatal-lineage cell specification, potential precursor cells proliferate in particular files (Stage 1). As undifferentiated cells are pushed further up the leaf blade alternate cells enter the stomatal development pathway via an asymmetric ‘entry’ division leading to a smaller guard mother cell (GMC) and a larger sister cell (Stage 2). Cells from files on either side of a newly formed GMC then also divide asymmetrically to form subsidiary mother cells (SMCs) (Stage 3). After the cells have increased in size, mature GMCs are flanked by two nascent SCs (Stage 4), a final symmetric division of the GMC leads to the formation of two immature GCs (Stage 5). The stomatal complex matures and expands to form a pair of dumbbell-shaped GCs, which separate to form the stomatal pore (Stage 6). Thus, each mature grass stomatal complex includes a central pore, a dumbbell-shaped GC pair and two flanking SCs. Each complex overlies an airspace,

Figure 1



Six stages of grass stomatal development. **(1)** Selection of stomatal lineage cells within defined rows. **(2)** Asymmetric entry divisions generate smaller guard mother cells (GMCs), depicted by white arrows, and larger epidermal cells. **(3)** GMCs then expand and laterally induce subsidiary mother cell (SMC) formation (see white arrows) via asymmetric divisions. **(4)** Subsidiary cell maturation. **(5)** GMCs divide symmetrically. **(6)** GMC elongation and maturation to form the guard cell (GC) complex. All confocal images were taken from the base of leaf 2 of 6-day-old barley seedlings (cv. Golden Promise) stained with propidium iodide. Scale bar = 5  $\mu\text{m}$ .

or ‘sub-stomatal cavity’, which forms between the mesophyll cells of the underlying layer, to facilitate efficient gaseous diffusion in and out of the leaf. Several recent studies provide insights into the transcriptional and regulatory mechanisms underpinning grass stomatal development. These make use of grass genome sequences and build on knowledge gained from Arabidopsis.

#### Brachypodium: A model for recent discovery

Despite differences in morphology and patterning, the basic helix-loop-helix transcription factors underpinning stomatal fate in Arabidopsis, SPEECHLESS (SPCH), MUTE and FAMA together with heterodimeric partners

INDUCER OF CBF EXPRESSION1 (ICE1) and SCREAM2 (SCRM2) are highly conserved, with origins which predate the divergence of the mosses and hornworts from ancestral land plants [5,6<sup>\*\*</sup>,13,14<sup>\*\*</sup>]. The discovery of functionally orthologous grass genes [15–18] has shed light on the mechanisms responsible for stomatal development and patterning in grasses. Liu *et al.* [12] investigated putative orthologues of SPCH, MUTE and FAMA in both rice and maize (*Zea mays*) and revealed at least one SPCH and a FAMA gene that are required for stomatal development in rice. More recently, Raissig *et al.* [14<sup>\*\*</sup>] used the wheat relative *Brachypodium distachyon* (Brachypodium), to dissect the roles of grass SPCH and

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