stem. Basidiospores are **violently discharged**, and the four spores of a basidium are liberated within a few minutes of each other; many reproductive structures of terrestrial fungi are actively liberated using a wide range of mechanical processes for propulsion (Ingold, 1999).

The basidiospore discharge mechanism is a violent (ballistic) discharge that clearly depends on the secretion of a droplet of fluid (water + solutes), which is called **Buller's drop**, close to where the spore is joined to its supporting sterigma. A hydrophobic interaction with the spore surface is also probably important, generating what is known as a **surface tension catapult** (Turner & Webster, 1991; Money, 1998).

This propels the spores directly away from the gill surface over distances ranging from 0.1 to 0.6 mm; spores with the largest Buller's drop are propelled the greatest distance (Stolze-Rybczynski *et al*., 2009). During discharge these spores can be subjected to forces of acceleration several thousand times greater than that experienced by astronauts during the launch of rockets servicing the International Space Station (ISS)! Even more impressive is the fact that while those rockets consume 50% of their mass in fuel during the first 2 minutes of flight, ballistospore discharge is fuelled by metabolites that represent only 1% of the mass of the spore (Money, 1998).

High-speed video analysis suggests that the size and shape of basidiospores affects discharge distance (Stolze-Rybczynski *et al*., 2009), because the asymmetric coalescence of Buller's drop is what produces the ***launching momentum and launch direction*** (Liu *et al*., 2017). There is consequently a close linkage between spore size and morphology and the tube radii and distances between gills; and this close linkage is reflected in the evolution and adaptation of these aspects of the fruit bodies. Liu *et al*. (2017) describe ballistospore discharge as a generic catapulting mechanism for colloidal particles and point out that understanding it has implications for many aspects of both biology and engineering.

The horizontal portion of the basidiospore flight path is halted by air viscosity within one millisecond of the launch and the spores then fall vertically until they clear the gills. Basidiospores are thus 'shot' into the space between adjacent gills, or towards the centre of the pore. They cannot be shot further than about the middle of that space to avoid being impacted onto the other gill (or the other side of the pore). Recent high-speed video analysis suggests that the size and shape of basidiospores affects discharge distance (Stolze-Rybczynski *et al*., 2009), probably by determining the size of Buller's drop. There is consequently a close linkage between spore size and morphology and the tube radii and distances between gills; and this close linkage is reflected in the evolution and adaptation of these aspects of the fruit bodies.

Basidiospores rely on **gravity** to clear the gills or pores and emerge into the turbulent air beneath the fruit body, and this raises another point because the fruit bodies (and gills in many mushrooms) are exquisitely sensitive to gravity and can adjust growth differentials to bring a disturbed stem and gills back to the **vertical**. The shape changes which occur in agaric fruit bodies in response to change in the direction of gravity, usually referred to as **gravitropism** are morphogenetic changes.

When a mushroom fruit body growing vertically, as is normal, is disoriented (say, laid flat on the substratum by a foraging animal or person in a white coat) gravitropic bending results from differential growth of cells in the stem; those on the 'bottom' extend more than those on the 'top' so that the stem bends upwards.

Calcium signalling is involved in regulating these growth differentials and proteomic analysis has revealed that at least fifty-one proteins are differentially-regulated during the response of *Coprinopsis cinerea* to gravity-disorientation (Kim *et al*., 2017; and see Häder, 2018). Gravity perception seems to be dependent on the actin cytoskeleton and nuclear motility; nuclei act as statoliths and interact with the actin cytoskeleton and trigger specific vesicle/microvacuole release from the endomembrane system to effect localised cell growth (Fig. 9.17; Moore *et al*., 1996).

The current interpretation is that this statolith-cytoskeleton interaction is communicated to the transmembrane domains of a sugar transporter located in the plasma membrane to change its substrate specificity and cause an otherwise uniformly distributed growth regulator (***probably a laevorotatory 6-deoxy hexose sugar***) to be asymmetrically transported into the disoriented cells (Moore & Novak Frazer, 2017; and see further discussion in Section 12.9).

The function of all this precision engineering is to get the spores into the turbulent air beneath the cap so they can be distributed by the breeze. But it is another aspect of species diversity because the rate of perception and rate of reaction to changes in the physical environment of this sort are themselves species-specific.

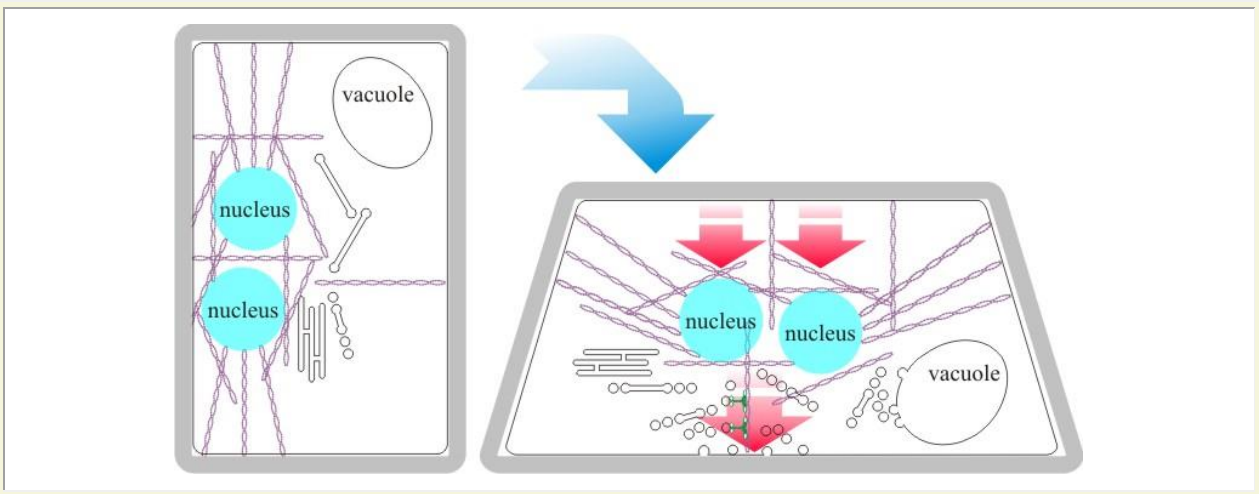

Fig. 9.17. Diagrammatic interpretation of gravity perception in agarics. In Basidiomycota the two nuclei of a dikaryon are enclosed in an F-actin cage in which they are held a particular distance apart (the distance affects patterns of gene expression). Evidence indicates that the nuclei act as statoliths to detect the gravitational field and how this might work is illustrated here. In the vertical orientation (normal for a fruit body stem, for example) the nuclei within their actin cage are positioned within the cell by stressed cables of actin microfilaments (on the left). If the orientation of the tissue is disturbed (for example placed horizontal as on the right), movement of the statoliths (nuclei) within the cage of actin changes the stress on the actin cable connections to the endomembrane system and generates useful directional signals. The current interpretation is that this statolith-***cytoskeleton interaction is communicated to the transmembrane domains of a sugar transporter located in the plasma membrane*** to change its substrate specificity and cause an otherwise uniformly distributed growth regulator (probably a laevorotatory 6-deoxy hexose sugar) to be asymmetrically transported into the disoriented cells (Moore & Novak Frazer, 2017; and see further discussion in Section 12.9). Subsequently, components required for wall modification and resynthesis will be exported when the growth factor induces it. Because the wall resynthesis is localised to the bottom wall, the cell will be curled upwards. This effect, co-ordinated over many cells along the length of tissues like fruit body stems, can reorient them to the vertical if they are subjected to physical disturbance. Modified and redrawn after Moore *et al.*, 1996.

Basidiomycota exhibit **long-term plasmogamy** because the 'sexual' (usually dikaryotic) mycelium has the ability to grow indefinitely. This is not so different from the indeterminate growth of heterokaryons in Ascomycota and it is clear that in both groups the sexually compatible mycelium can have a number of alternative developmental pathways open to it: continuation of hyphal growth, production of asexual spores, and progress into the sexual cycle (Moore, 1998).

Choice between these is often a matter of the impact of very localised environmental conditions on a mycelium which has become competent to embark on a developmental pathway as a result of its capture and accumulation of nutritional resources. The flow chart in Fig. 18 shows an overview of the physiological processes involved in development of fruit bodies and other multicellular structures in fungi and gives some idea of the number of places where species-specific modifications can intervene in a general process to widen diversity.

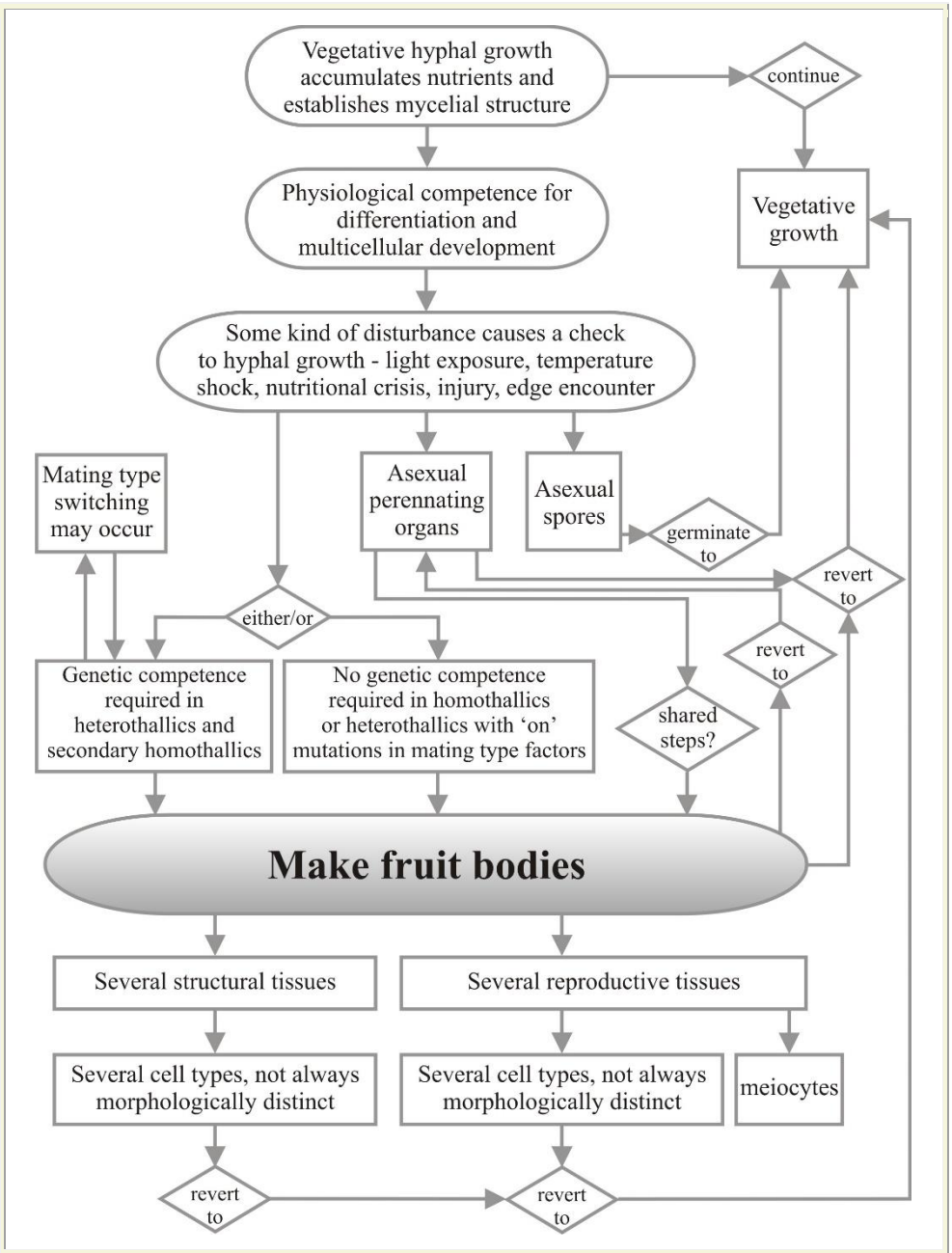

Fig. 9.18. Flow chart showing a summarised view of the processes involved in development of fruit bodies and other multicellular structures in fungi. Modified from Moore & Novak Frazer, 2002.

9.9 Chapter 9 References and further reading

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