numerical studies of an accepted model of thermal convection. They use their results to reveal, for the first time, the mechanism by which the chaotic dynamics is generated. A key concept needed to understand chaos is its sensitive dependence on current conditions (Fig. 1). When the history of the system is plotted in multidimensional phase space, two trajectories or paths that differ slightly at some instant will separate exponentially fast from each other along certain directions (while approaching each other exponentially fast along other directions).

Understanding the dynamics means understanding this exponential growth, which can be characterized by parameters known as Lyapunov exponents. The number of Lyapunov exponents is equal to the dimensionality of the phase space. Egolf et al. determine the first 100 or so of these exponents for their convecting system, and show that the pattern of exponents is independent of the size of the system in the sense that doubling the system size causes new exponents to appear between the old ones. Furthermore, the largest exponents correspond to the creation of localized defects in the convection pattern — that is, places where the pattern of rising and falling motion of the fluid changes its topology — not unlike the appearance of defects in a disordered crystal lattice when it is deformed.

The implication of this work[3] is that the origin of the unpredictable motion, at least in this particular form of spatiotemporal chaos, lies in what happens in small regions of space and over short timescales. These local changes in the organization of the flow affect the surrounding regions in such a way that the entire future evolution is affected. This is something akin to Ed Lorenz's famous remark that the localized flapping of a butterfly's wings might change the weather dramatically over the entire world a few weeks later, except that here the localized events occur naturally; they are not external interventions. Although such sensitivity to localized fluctuations has never been confirmed as the source of the weather's unpredictability, it is apparently the origin of chaotic dynamics in thermal convection.

The methods used by Egolf et al. should apply to many other forms of chaos in spatially extended systems (physical, chemical and biological) for which reliable model equations are available, so that the key processes leading to the complex dynamics can be identified. Applications to areas as diverse as cardiology and atmospheric dynamics might be expected eventually. Moreover, it is not unreasonable to imagine that insight into the processes leading to unpredictability will also lead to progress in modifying or controlling the dynamics of these systems. ■

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Plant biology

Shattering developments

Günter Theißen

Imagine a world without fruits: there would be no apples and oranges, of course, but also no bread, no noodle and rice meals, and (oh my God!) no wine and beer. An improved understanding of the genetic control of fruit development should help us to design better fruits for various purposes. On page 766 of this issue[1], Liljegren et al. report advances which provide a starting point to do just that. At the same time, the authors' data give an exciting glimpse of the role of developmental control genes in fruit evolution.

Fruits mediate seed maturation and dispersal, and are derived from flowers. So they are unique to flowering plants, the angiosperms (as opposed to the gymnosperms, which produce unprotected, or 'naked', seeds). The model plant *Arabidopsis thaliana*, a tiny weed from the mustard family Brassicaceae, produces dry, dehiscent fruits — that is, they burst open at maturity to release the seeds. *Arabidopsis* fruits are composed of two valves (carpel walls) separated by a thin structure termed the replum[1,2] (see Fig. 1 of the paper on page 767). At the valve–replum boundary, a narrow band of cells develops into the dehiscence zone. Late in fruit development, cells in the 'dehiscence zone' separate from one another, the valves detach from the replum, and the seeds can disperse.

Liljegren et al. have generated *Arabidopsis* plants in which two very similar genes, *SHATTERPROOF1* (*SHP1*) and *SHATTERPROOF2* (*SHP2*), have both lost their
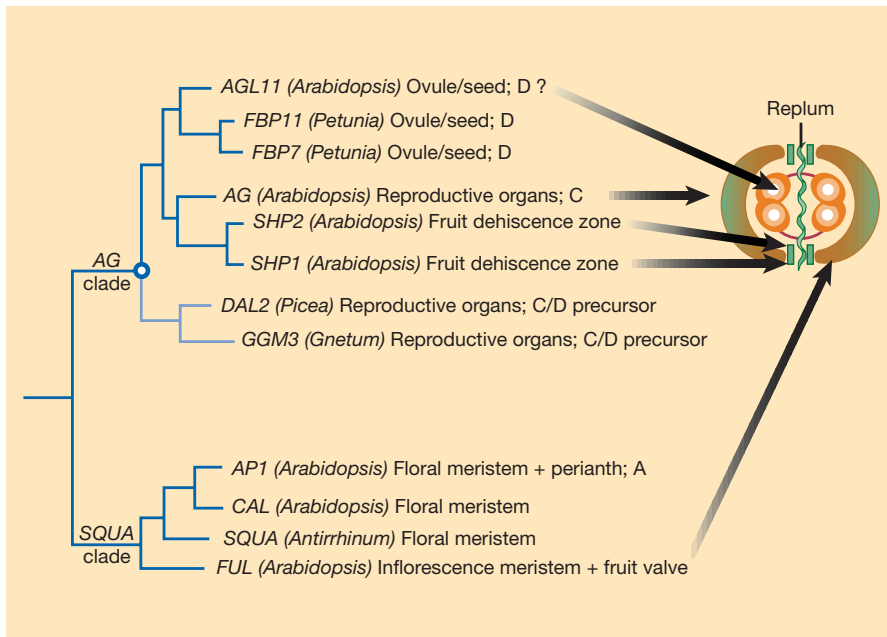
Figure 1 MADS-box genes and fruit evolution. The cladogram shows the relationship between some examples of MADS-box genes. A, C and D indicate gene functions involved in specifying the identity of particular parts of the flower: sepals and petals (A), stamens and carpels (C), and ovules (D)[7,8,10]. DAL2 and GGM3 are genes from two gymnosperm species; all the others are from flowering (angiosperm) plants[8]. The separation of angiosperm and gymnosperm members of the AG clade occurred about 300 million years ago (dot at the base of the AG clade). SHP1, SHP2 and FUL are the SHATTERPROOF1 and 2 and FRUITFULL genes investigated by Liljegren et al.[1]; AG, AGAMOUS; SQUA, SQUAMOSA; AGL11, AG-like11; FBP7/11, FLORAL BINDING PROTEIN7/11; AP1, APETALA1; CAL, CAULIFLOWER.

function. In mature fruits of these double mutants, the dehiscence zones are absent, so the fruits fail to break open. The authors have complemented their loss-of-function analyses by examining transgenic plants that express the *SHP* genes constitutively (that is, all the time and in all tissues of the plant), and also by using putative downstream targets of these genes as molecular markers to monitor the cellular differentiation of valve margins.

To cut a long story short, it turns out that *SHP1* and *SHP2* ensure correct development of the cells in the dehiscence zone and of adjacent cells at the valve margin. Liljegren *et al.* also report evidence that another gene, *FRUITFULL* (*FUL*), interacts antagonistically with the *SHP* genes during development of the valve margin; *FUL* is required for valve-cell differentiation and expansion after fertilization[2].

These findings are agronomically important because *Arabidopsis* is closely related to oilseed crop plants, such as canola (*Brassica napus* and *Brassica rapa*) in which premature fruit dehiscence — pod shatter — causes considerable yield losses. Knocking out *SHP*, or overexpressing *FUL*, could result in shatter-resistant canola plants. Such plants might be generated either by genetic engineering (possibly the fast way, but not fashionable in Europe at the moment), or by random mutagenesis and marker-assisted breeding.

The studies of Liljegren *et al.*[1] will also help us to understand fruit evolution. Some reproductive characters[3], including fruit indehiscence, evolved independently several times within the Brassicaceae, for example in close relatives of the genus *Lepidium* (pepper cresses) (K. Mummenhoff, personal communication). Because loss of *SHP* function (which in other plants is not necessarily provided by two different genes) has little effect apart from its influence on fruit dehiscence, it may represent a simple mechanism by which indehiscent fruits originated from dehiscent fruits.

Moreover, *SHP1*, *SHP2* and *FUL* (formerly known as *AGL1*, *AGL5* and *AGL8*, respectively[4,5]) belong to the family of so-called MADS-box genes, which encode gene transcription factors in plants, animals and fungi[6–8]. MADS-box genes are involved in many developmental processes in the plant life cycle. But they became famous, at least among plant biologists, because some of them specify the identity of the different floral organs during flower development. These organs are the leaf-like sepals; the often colourful and attractive petals; the stamens (the male reproductive organs); and the carpels (the female reproductive organs), inside which the ovules develop into seeds.

The MADS-box gene family is composed of several defined gene clades — sets of genes that share a most recent common ancestor not shared with any of the other MADS-box genes[7–9]. *SHP1* and *SHP2* are members of a group of closely related genes termed the *AGAMOUS* (*AG*) clade[7,8] (Fig. 1). This clade also includes the genes known to specify stamen and carpel identity during flower development (such as *AG* itself), and those that specify ovule identity[10]. Members of the *AG* clade have also been found in gymnosperms (Fig. 1), but not in ferns, implying that the first member of this clade arose 300–400 million years ago[8]. At that time, flowers and fruits were not yet established — flowering plants probably originated not much more than 200 million years ago.

The ancestral function of members of the *AG* clade was probably to specify the primary identity of reproductive organs[8]. So it seems that the *SHP* genes have a highly specialized function (control of dehiscence-zone development) in a structure (the fruit) that originated relatively late in evolution and which itself serves a quite specialized function (seed maturation and dispersal) (Fig. 1). This provides a pretty good example of the involvement of new genes, generated by gene duplication, sequence divergence and fixation within the *AG* clade[7,8], in the evolution of reproductive devices within the past 200 million years.

Another striking example of functional gene recruitment is provided by the *FUL* gene. This belongs to the clade of *SQUAMOSA*-like genes, whose members operate in specifying meristem — proliferative tissue — identity[7,8]. *FUL* itself still works in determining meristem identity in inflorescences[2,8]. But it was obviously recruited during the course of fruit evolution for its additional function in the fruit valves (Fig. 1).

We are just at the beginning of understanding the role of MADS-box genes in fruit development and evolution. Clearly, however, fruiterers, as well as florists and evolutionary biologists, owe a lot to this dynamic gene family. ∎

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