

over one's genes? Perhaps it is because this notion resonates with a public that in the eighties and nineties the same press have bullied into believing that there is 'a gene for everything'. In that sense, the debate is remarkably similar to the one on whether we humans (or animals in general) have such a thing as a free — or conscious — will. Much like with the idea of the vulgarised genetic determinism, the scientific data that, at the very least, question the case for a clear free and conscious will are viewed as handcuffing the basic human freedom, the very essence of being human. But, while free will is being mainly defended on philosophical and psychological grounds, epigenetics seems to offer solid scientific proof — DNA modification as a kind of liberation. Structurally, then, this is the same reason why Lysenko's ideas thrived in a Marxist system.

Apart from that, the reason for why epigenetics is so intensely and tendentiously covered in the press may simply be a journalistic one. Science journalism, where it still exists, is part of the news industry, and thus needs to be newsy; ironically, that the environment can influence the phenotype and the genes is terribly old news, no news at all, really. So, at the very least, such a story will need a human-interest factor. This is easy for fossil ancestors or cute chimpanzees, but not so easy for molecular genetics. Therefore, a larger frame has to be invoked, far-fetched as it may be. Building around the story is a legitimate literary technique to some extent, but becomes dangerous when the frame interferes with the presentation and interpretation of empirical data. In effect, it's not far from what Lysenko did, and makes the whole purpose of science journalism questionable. It won't cost lives as Lysenko's mad ideas — after all, it's only molecular biology — but the public have a right to be informed correctly. First, because they pay for the research. Second, because at the very least they need to know that science, and genetics in particular, cannot give them simple answers about who they are and how they should live, and neither can epigenetics. They'll have to work that out for themselves and let Lysenko lie.

Florian Maderspacher is Current Biology's Senior Reviews Editor.
E-mail: florian.maderspacher@current-biology.com

Quick guide

Grasses

John Raven¹ and Howard Thomas²

What is a grass? A member of the Gramineae (Poaceae), the fifth largest family of flowering plants and the second largest family of monocotyledons, with over 700 genera and about 10,500 species. Lawns, cow pastures and cereal fields are, to an extent depending on the success of weed control, mainly or entirely composed of grasses. As well as these herbaceous forms, the woody bamboos are also grasses. Not every plant commonly prefixed 'grass' is a member of the Poaceae; grasslands are, however, dominated by true grasses. Closely related families which might be mistaken for grasses are the sedges (Cyperaceae), rushes (Juncaceae) and gondwanan Restionaceae. The Poaceae is the largest family of purely wind-pollinated seed plants.

What use are grasses? Grasses provide four of the five major crops by annual global production, and there are five grasses in the top ten. These grasses are, in decreasing order of production: sugarcane, maize, wheat, rice and barley. Grasses supply over half of the energy in human food through direct consumption and through products of grass-fed animals, as well as providing major inputs to beers and of many spirits, and, alas, gluten-related diseases. Other direct human uses of grasses include sporting and other amenity areas. Less readily quantified in monetary terms are the ecosystem services provided by the remaining semi-natural grasslands and savannas. The cultivated grasses and semi-natural grasslands together account for about 15% of global (marine and continental) primary productivity. Grasses with the C₄ photosynthetic pathway constitute about 45% of total grass species, and account for about two-thirds of grass productivity or about 10% of global primary productivity.

When did grasses evolve? Grasses originated in the Late Cretaceous about 70 million years ago: some

of the last dinosaurs ate the first grasses. The earliest grasses had C₃ photosynthetic physiology; C₄ grasses evolved over 30 million years ago as atmospheric CO₂ was decreasing, although other environmental factors were also involved in the radiation of C₄ grasses in the late Paleogene and Neogene. The expansion of grasslands as a major biome began about eight million years ago, with dominance of C₄ photosynthesis in tropical to warm temperate grasslands. The semi-natural and agricultural pastures of temperate regions, based on cool-season grasses, date from establishment of human migration and trade routes over recent tens of millennia. Identifying the relative significance of the various traits that contribute to the dominance of grasslands, and of a limited number of species in grasslands, will involve further integration of phylogenetic and palaeoenvironmental studies.

How did domestication of wild grasses give rise to cereals and their weeds? Agriculture began with the domestication of wild grasses, a decisive step in the evolution of human civilization. Domestication selected variants with self-fertility, annual habit, hypertrophied grains and foliage, non-shattering seedheads, rapid establishment and growth and high harvest-index.

Wheat and barley originated in the pan-Mediterranean/Southwestern Asia region (sometimes called the Fertile Crescent). The earliest cultivated forms of wheat were einkorn (*Triticum monococcum*) and emmer (*T. dicoccum*). Modern bread wheat has a complex hexaploid genome as a result of interspecific hybridization between wild relatives. The first hybridization event combined the genomes of *T. urartu* and a probably extinct close relative of *Aegilops speltoides* into the tetraploid *T. turgidum* subsp. *dicoccoides*. Then, during the early stages of human agriculture, about 10,000 years ago, a second hybridization introduced the genome of the diploid *Aegilops tauschii*. Barley is a diploid species and there is evidence of a history of much gene flow between wild and domesticated forms. The ancestor of maize is teosinte, a group of five species of large grasses native to Central America. Teosinte was domesticated around 8,000 years ago,

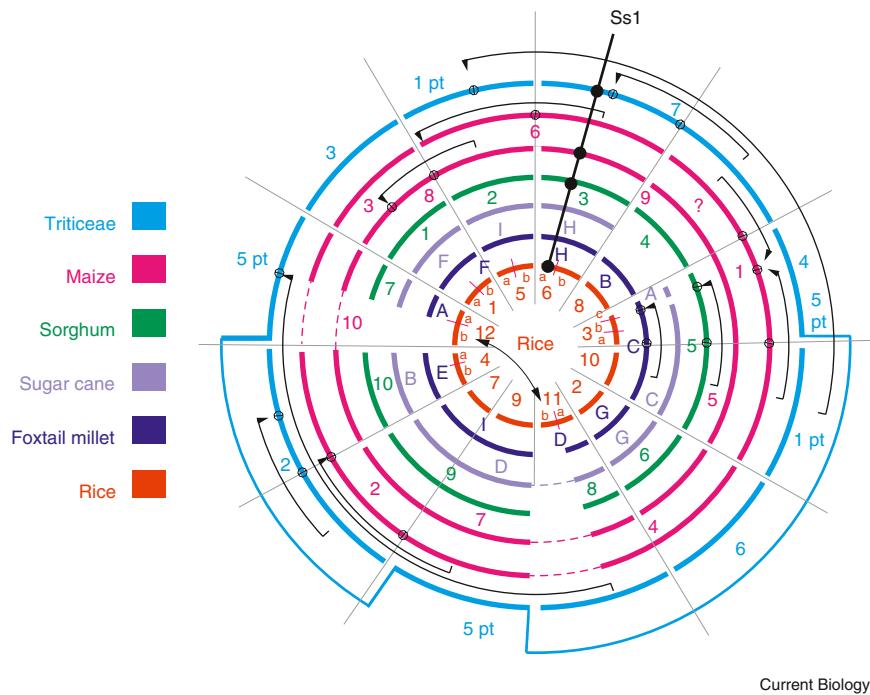


Figure 1. Conservation of gene order allows the genomes of graminaceous species to be concentrically aligned, forming so-called ‘crop circles’.

The locus *Ss1* encodes the enzyme sucrose synthase-1. Image source: <http://tinyurl.com/37vmwut>. Reproduced courtesy of Graham Moore and Tracie Foote, John Innes Centre, Norwich, UK.

probably in the area of present-day central Mexico whence agriculture based on maize spread south. The earliest evidence of cultivated rice comes from sites in the Yangtze river valley in China and date from 10,000 years ago. Certain grass weeds of cereals have acquired domestication traits by co-selection, and some former weed species — notably oat and rye — have even become adopted as crops in their own right. Other weeds, such as the poisonous ryegrass darnel (*Lolium temulentum*), persist as cereal mimics and in non-intensive agricultural systems can enter the food-chain with harmful consequences.

Why are grasses so successful?

The ancestral monocotyledon lacked a vascular cambium (a tissue layer that generates cells for secondary growth); some monocotyledons have independently evolved some form of secondary growth, but the grasses have not. Despite this, bamboos are woody and some species grow to heights of 30 m — one-third the height of the tallest conifer or dicotyledon tree. However, it is the perennial herbaceous habit which

underlies the success of grasses in producing the grassland biome. One clear attribute of grasses that helps resist vertebrate grazers is the capacity for basal growth of leaves and intercalary growth of stems, as well as the gravitropic differential growth of nodes that allows vertical growth after trampling or lodging by storms. Grazing is also restricted by more extensive silicification in grasses than in most vascular plants other than horsetails. The C₄ syndrome can include lower leaf nitrogen content, with a larger fraction of this nitrogen in the bundle sheaths than in C₃ plants. While these attributes of C₃ and C₄ plants are not confined to grasses, it is the diversification and spread of C₄ grasses that parallels the evolution of more complex tooth structure (hypodonty) from the simpler brachydonty in several clades of large mammalian herbivores.

Can conservation of gene organisation between grass species be identified and exploited? The genetic map of an organism locates genes relative to one another on each of the chromosomes. As genetic maps for the major cereal and forage

grasses were established, it became clear that the genes of one grass species occur in more or less the same order in the genome as the equivalent (orthologous) genes in another species. Conservation of gene order between genomes is called colinearity or synteny and is a feature of the genetics of grass species that has many theoretical and practical implications. One way of displaying the colinear organisation of grass genomes is to arrange genetic maps concentrically. In Figure 1, maps of each of the 12 chromosomes of rice (the species with the smallest genome) form the innermost circle. If we line up orthologous DNA sequences in the progressively larger genomes of millet, sugar cane, sorghum, maize and wheat, a series of ‘crop circles’ emerges.

In many cases colinearity is not perfect because regions of particular genomes have undergone duplication, or inversion, or deletion, or translocation to new positions. Such rearrangements give direct insights into the evolutionary histories of the different grasses as they diverged during speciation. Conservation of gene order between different species presents the crop geneticist with a powerful tool. If the position of a particular gene on the genetic map of one species is known (Figure 1 shows the example of a maize sucrose synthase gene, *Ss1*), one can use the synteny relationship to read between maps to the corresponding location and pinpoint the orthologous gene in another species. Plant breeders employ this method to find useful new sources of genetic variation and associated DNA markers, while molecular geneticists exploit it for map-based cloning, rapidly zeroing in on the DNA sequence of the genomic region encoding any mapped trait.

Can grass crop productivity be increased? Increasing human population, pressure on agricultural land from other uses, and increasing fertilizer prices are among the challenges facing world agriculture. Rice is the major food for a third of humanity, and the yields of widely used rice varieties are limited by the rate at which the crop can photosynthesise, in that there is unused capacity for grain production. Photosynthesis will increase as a result of increasing atmospheric CO₂,

but rice will not make as effective use of the additional CO₂ as would other C₃ crops — those plants that, like 55% of grass species, have the basic mechanism of photosynthetic CO₂ assimilation. An alternative is to change rice into a C₄ plant, which could increase yield by up to 50% while using little or no more nitrogen or water. Although the challenges to such a venture are many and large, the reward for success would also be large. Rice genes will need to have their site(s) of expression changed, and additional genes from other plants introduced and expressed in the appropriate sites in a modified rice leaf anatomy. Research in this area is still at an early stage.

Can and should grass crops be produced for biofuels? As well as increasing problems with food security, we can look forward to a future with a scarcity of fuel, and especially the portable fuel currently used to power land, sea and air transport. Biofuels from grasses clearly can play a role in supplementing fossil fuels and energy from renewable sources, since ethanol from sugarcane has been used in fuels for motor vehicles in Brazil for almost 20 years, with the importance of bioethanol varying in parallel with the world price of oil. Least controversial as a means of increasing use of grasses in producing biofuels is the conversion of unused parts of grasses grown for human or animal food into biofuel, although not returning the unused part of grass crops to the soil will certainly deplete soil of organic matter. More contentious is the growth of highly productive grasses, usually perennial C₄ grasses such as *Miscanthus*, specifically as fuel crops. Such uses will ultimately bring them into competition for land and resource inputs with food crops, and more generally with conservation areas and wilderness. All biofuel projects, and not just those involving grasses, need to be rigorously evaluated in terms of their lifetime carbon balance to avoid the possibility that unsuspected production of CO₂, for example in land use change, does not negate their role in CO₂ mitigation.

¹Division of Plant Sciences, University of Dundee at SCRI, Scottish Crop Research Institute, Invergowrie, Dundee DD2 5DA, UK.

²IBERS, Edward Lloyd Building, Aberystwyth University, Ceredigion SY23 3DA, UK.

E-mail: j.a.raven@dundee.ac.uk

Correspondence

Dogs showing separation-related behaviour exhibit a ‘pessimistic’ cognitive bias

Michael Mendl¹, Julie Brooks¹, Christine Basse¹, Oliver Burman^{1,2}, Elizabeth Paul¹, Emily Blackwell¹, and Rachel Casey¹

Up to five million pet dogs in the UK (~50% of the population) may, at some stage of their lives, perform undesirable separation-related behaviour (SRB) when left home alone [1], including vocalising, destruction and toileting [2]. Some owners perceive their dog to be ‘fine’ or even ‘happy’ when performing SRB [3], a few seek professional help [1], and others relinquish the dog [4]. Given the magnitude of the issue and the varied perceptions and behaviour of owners, the underlying emotional (affective) states of dogs showing SRB, and hence their welfare, requires elucidation. Whilst most dogs are believed to be anxious when showing SRB [1,2], it is uncertain whether their background affective state (mood) when they are not separated is also negative [1]. Here we use a new ‘cognitive bias’ measure of animal affect to show that dogs which exhibit high levels of SRB in a separation test also appear to have a more negative underlying mood.

The subjects were 24 dogs (50% male; estimated age range: 9–108 months) at two UK animal re-homing centres. Seven to twelve days after entering the centres, each dog took part in a previously validated SRB test [5] designed to measure its response to being left alone. Each dog was taken to a room where a researcher interacted with it for 20 minutes. The following day the dog was taken back to the room by the researcher who, after a short period of interaction, left it alone for five minutes during which the total time that the dog spent performing SRB was determined from video recordings and calculated as a ‘SRB score’ (for full details of the experimental procedures, see the Supplemental Information available online).

One to two days after the SRB test, each dog was subjected to a cognitive bias (CB) test of affective state, based on theoretical and empirical findings that an individual’s background affective state, or mood, biases its decision-making and, specifically, that individuals in negative states make more negative (‘pessimistic’) judgements about ambiguous stimuli than happier individuals [6–8]. Dogs were trained to move from a start position to a food bowl on each trial of the CB test [9]. When the bowl was on one side of the room (‘positive’ location, P) it contained a small quantity of food, and when on the opposite side (‘negative’ location, N) it was empty (Figure 1A). When dogs were deemed to have discriminated P and N locations (see Supplemental Information), testing began. In test trials the bowl (empty) was placed at one of three ambiguous locations between P and N (near-positive (NP), middle (M), or near-negative (NN); Figure 1A). Three test trials were presented at each location with each test trial separated by four standard training (P, N) trials. Test trials allowed us to measure whether dogs ran quickly to the ambiguous locations (indicating anticipation of food: an ‘optimistic’ judgement) or more slowly (a ‘pessimistic’ judgement). We could thus investigate whether dogs showing higher levels of SRB also behaved more ‘pessimistically’, indicating an underlying negative affective state [6–9]. Mean latencies to get to the bowl during each of the three types of test trial (NP, M, NN), and during training trials (P, N) were calculated for each dog. To control for differences in dog size and running speed, we adjusted each dog’s test trial latencies according to its mean ‘baseline’ latencies during training trials (for full details of the experimental procedures, see Supplemental Information).

Time spent performing separation-related behaviour in the SRB test ranged from 0–169 seconds. SRB score was not affected by sex, neuter status, breed category, or animal centre and did not correlate with estimated age (see Supplemental Information). Figure 1B shows mean latencies to get to the bowl during training (P, N) and test (NP, M, NN) trials for all dogs. Bowl location affected latency (Friedman test, $\chi^2 = 68.15$, $n = 24$, $p < 0.001$), reflecting a clear generalisation response with