chromosome of the serotype III strain, no complete temperate phage genomes were identified. Interestingly, three copies of a 47 kb sequence were present that had the characteristics of an integrative plasmid. These elements may also be important for horizontal gene transfer in GBS.

Tettelin and colleagues estimated that 650 proteins encoded by the serotype V genome were surface exposed and therefore were potential virulence factors. They then used a proteomic approach to identify which of these proteins was expressed.

Of 291 recombinant proteins made from this group and used to immunize mice, 139 sera were found to recognize a major GBS protein, 55 of which were shown by fluorescence-activated cell sorter analysis to be expressed on the cell surface. These data are important for understanding the physiology of GBS, as well as identifying new candidate antigens for vaccine development.

A remarkably large number of two-component regulatory systems were found in both new GBS genomes, com-

pared with other bacteria in the Gram-positive group sequenced to date. The type III genome contained 20 histidine kinases and 21 response regulators and the type V genome had 17 of each. By comparison 14 are found in *S. pneumoniae*, 13 in *S. pyogenes*, and only eight in *Lactococcus lactis*.

This finding together with discovery of 107 transcriptional regulators suggests that the GBS have greater flexibility than the other Gram-positive cocci to react and survive in response to fluctuations in the external environment. Such versatility may explain why GBS are able to infect animals such as cattle in addition to humans.

Comparative genome analyses revealed that *S. agalactiae* is more closely related to *S. pyogenes* (group A streptococci, GAS) than *S. pneumoniae*. *S. agalactiae* also shares more orthologous genes with *S. pyogenes* than *S. pneumoniae*. *S. galactiae* or *S. pyogenes* also differ from *S. pneumoniae* in that they are not generally known for their ability to uptake exogenous DNA (transformation). In contrast, *S.*

pneumoniae has a highly developed transformation system.

These new genomes allow important insights into the sequence heterogeneity found among and within GBS serotype strains. Future drug development and identification of candidate antigens for a universal vaccine will critically depend on these data. Ultimately these studies, and similar future ones, will lead to improved prevention and treatment of GBS diseases. ■

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Plant population genetics

What maintains male-sterility factors in plant populations?

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Most flowering plants are hermaphrodites whose flowers have both female parts (ovaries and a style and stigma) and male parts (anthers and stamens). However, 5–10% of species exhibit gynodioecy, ie females as well as hermaphrodites are present (Darwin, 1877). Sexually polymorphic species, such as these gynodioecious species, are particularly useful for studying the advantages and disadvantages of different reproductive modes. There have been many interesting studies of plant breeding systems, and those of gynodioecy have yielded a series of fascinating results. There has been an interplay between theoretical and empirical analyses of gynodioecy that has led to steady progress in understanding, though many puzzles remain. A major question is whether the genetic factors controlling the sexual polymorphism are maintained in gynodioecious species for long time periods or are lost, only to re-evolve again later. Mitochondrial DNA sequence variability data are starting to

shed light on this question (Städler and Delph, 2002).

In most gynodioecious populations, females are in the minority, but female frequencies vary greatly and, surprisingly, sometimes exceed 50% (Olson and McCauley, 2002). The genetics of male sterility can account both for this variability and the high female frequencies. Male sterility is sometimes maternally inherited, and even a slight advantage to a maternally transmitted cytoplasmic male sterility (CMS) factor causing loss of male functions – for instance, some energy saving that could allow higher seed output – allows females to increase in the population until their seed output becomes limited by the pollen supply. CMS is a classic ‘selfish’ genetic element. However, such gynodioecious populations can be invaded by nuclear factors that restore male fertility of individuals with the sterility cytoplasm. Depending on the effects of the genetic factors, the restorer will either spread throughout the population, causing reversion to her-

maphroditism, or the population may remain gynodioecious, with both sterility and fertility cytoplasm present, and both restorers and non-restorers. In theoretical models, such systems behave in complex ways. They can exhibit permanent cycles in the frequencies of the genetic factors (Gouyon *et al.*, 1991), or may approach an equilibrium slowly, with large frequency fluctuations (Charlesworth, 1981).

In maize, where male sterility is used in hybrid breeding, there are three sterility cytoplasm, and several restorers. Many other crop plants have similar systems. In these, male sterility is due to mitochondrial genome rearrangements causing expression of chimaeric proteins, and the genes causing fertility restoration are now starting to be identified.

In natural populations, the genetics is probably similar to that in crops. Since gynodioecious plants often have several different sterility cytoplasm, each with several restorers, analysing these complex polymorphisms is very difficult. However, even without identified CMS genes, sequence variants anywhere in the mitochondrial genome could provide helpful genetic markers, allowing identification of plants’ cytoplasmic genotypes, assuming strictly maternal inheritance, and no (or rare) recombination. Mitochondrial genome variants indeed exist in several gynodioecious plants, and distinct haplotypes coexisting within popu-

lations probably sometimes correspond to different CMS types (Belhassen *et al.*, 1993; DeHaan *et al.*, 1997; Desplanque *et al.*, 2000; Olson and McCauley, 2002). In species whose chloroplasts are maternally transmitted, variants in the chloroplast genome are equally useful, since the mitochondrial and chloroplast genes should be completely linked. Empirical data confirm that variants in the two genomes are indeed strongly associated (Desplanque *et al.*, 2000; Olsen and McCauley, 2002).

The high diversity of organelle genomes of gynodioecious plants is very interesting. If it is higher than in hermaphroditic species (which is not yet known, as few suitable comparisons have been made, and data on DNA sequence diversity in natural plant populations is scarce), this would support models of gynodioecy involving stable or cyclical maintenance of CMS factors, giving time for silent variants to accumulate between and within haplotypes. In contrast, if new male sterility cytoplasms continually arise, but soon spread through the population when restored male fertility evolves (or as frequencies cycle close to zero or one, and chance allele loss occurs) (Frank, 1989), mitochondrial alleles will constantly 'turn over'. Such events should leave little sequence diversity at linked loci, and cytoplasmic diversity will be restricted to variants accumulated since the last mitochondrial genome replacement.

Two recent papers take the next steps

in testing the polymorphism of mitochondrial genotypes of gynodioecious species. By quantifying diversity at individual sites in a mitochondrial DNA sequence within *Silene acaulis* (using the cytochrome b gene), Städler and Delph 2 go beyond merely documenting that haplotypes vary. Quantifying the divergence between haplotypes provides an estimate of how long the different types have persisted. The dating is rough at best, because of our poor current knowledge of molecular clocks in plants (in addition to the well-known irregularity of such clocks), and because it assumes no recombination, which needs further testing, but the data suggest very long times. However, another gynodioecious species, *Silene vulgaris*, seems to give the opposite conclusion (Ingvarsson and Taylor, 2002). This study compared chloroplast and nuclear locus diversity with that in *S. latifolia*, a species with males and females. After correcting for the lower chloroplast mutation rate, and for X-linkage of the nuclear gene, chloroplast diversity seems to be specifically reduced in the gynodioecious species, so in this case a turnover process seems to be supported.

The most striking result in both studies, however, is the surprisingly high cytoplasmic variability. Of course, models in which sterility factors persist for long times predict higher variability in the gynodioecious *S. vulgaris* than the dioecious *S. latifolia*, and this was not found. However, many differences between

species affect diversity. With just one gene sequenced from the nuclear and organelle genomes, one can conclude only that diversity is not extremely low, so a species-wide turnover model is not supported. The contrasting possibilities for male sterility loci are similar to those for host-pathogen systems. Here too, population genetic data sometimes supports sequential turnover of plant resistance alleles, but often suggests long-term maintenance of variability (Bergelson *et al.*, 2001).

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