

the Y chromosome in a single fly strain (ensuring an otherwise common genetic background). They then screened a nearly genome-wide set of genes and looked for differences in gene expression in response to the substituted Y chromosome. Because of high statistical error rates when thousands of genes are scored simultaneously, it is difficult to estimate the exact number of affected genes, but the estimates are surprisingly high, ranging from around 100 up to about 1000 (*D. melanogaster* is estimated to have ~13,000 genes).

Lemos *et al.* also detected several coherent patterns among the Y-regulated genes. The Y chromosome influences the expression of genes that are more strongly expressed in males. Genes regulated by the Y chromosome are also more strongly influenced by environmental stress (heat shock), and many are associated with sperm development. Genes that influence the mitochondria are also overrepresented in the pool of genes regulated by the Y chromosome. In addition, affected genes are more evolutionarily dynamic in terms of polymorphisms for gene expression within the species, and more diverged from a closely related congener (*Drosophila simulans*).

It is now well established that a large proportion of the genome is expressed at different levels in males and females in many organisms (3), and the patterns found by Lemos *et al.* fit well with what would be expected for Y-linked regulatory genes. Whereas the Y chromosome spends every generation in males, the X chromosome and autosomes alternate between the sexes across generations. A mutation favoring males that is located on the X chromosome or autosomes can therefore only accumulate when selection in females is concordant, absent, or not too strongly discordant (4). However, this restriction is removed for Y-linked mutations because there can be no counterselection in females. Even when a mutation results in a phenotype that is exclusive to males, it will have an advantage if Y-linked because, unlike the X chromosome and autosomes, the Y chromosome is expressed (and hence selected) in males every generation (see the figure). The Y chromosome therefore represents a favorable platform for mutations that improve male gene expression.

As many Y-linked genes have degenerated, should we expect the Y chromosome to inevitably be lost altogether? Not necessarily. As the number of functional genes on the Y chromosome declines, the efficacy of natural selection increases on the remaining genes. Decay of the Y chromosome therefore slows down over time and can ultimately stop altogether. The fitness advantage of a highly degenerated Y chromosome is illustrated by

Drosophila affinis in which the Y chromosome is not required for fertility. In this species, males with no Y chromosome (XO) sire 25 to 38% fewer offspring when competing with XY males (5). The study by Lemos *et al.* provides a mechanism for the large fitness advantage of XY males, even when vital fertility factors are absent on the Y chromosome: The Y chromosome has evolved to become a major regulator of gene expression in males.

If the Y chromosome is such a strong regulator of genes in males, then why have past studies found so few Y-linked traits in humans and flies? The Y chromosome may have evolved to modulate rather than turn on or turn off gene expression. Its effects may therefore be continuous rather than discrete and thus more difficult to detect than the more distinct phenotypes associated with loss-of-function mutations. As the power of quantitative trait locus analysis increases, the phenotypic manifestations of the genes regulated by the Y chromosome discovered by Lemos *et al.* may become more apparent.

The next stage in understanding the newly discovered regulatory powers of the *Drosophila* Y chromosome will be to characterize the genetic mechanism(s) underlying their influence. It will also be interesting to see, in flies and other species, whether genomic components that are only transmitted through the matriline (mitochondria and cytoplasmic endosymbionts) have evolved to strongly influence gene expression in females. The study by Lemos *et al.* further suggests that it will be important to test whether the human Y chromosome also has evolved to become a regulatory giant.

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ENVIRONMENTAL SCIENCE

How Green Are Biofuels?

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Many biofuels are associated with lower greenhouse-gas emissions but have greater aggregate environmental costs than gasoline.

Global warming and escalating petroleum costs are creating an urgent need to find ecologically friendly fuels. Biofuels—such as ethanol from corn (maize) and sugarcane—have been increasingly heralded as a possible savior (1, 2). But others have argued that biofuels will consume vast swaths of farmland and native habitats, drive up food prices, and result in little reduction in greenhouse-gas emissions (3–5). An innovative study by Zah *et al.* (6), commissioned by the Swiss government, could help to resolve this debate by providing a detailed assessment of the environmental costs and benefits of different transport biofuels.

To date, most efforts to evaluate different biofuel crops have focused on their merits for reducing greenhouse-gas emissions or fossil fuel use. Some studies suggest that corn-derived ethanol in the United States (7) and

Europe (8) consumes more energy than it produces; others suggest a modest net benefit (2). Relative to petroleum, nearly all biofuels diminish greenhouse-gas emissions, although crops such as switchgrass easily outperform corn and soy (9). Such comparisons are sensitive to assumptions about local growing conditions and crop by-products, but even more important, their focus on greenhouse gases and energy use is too narrow.

The arguments that support one biofuel crop over another can easily change when one considers their full environmental effects. A key factor affecting biofuel efficacy is whether native ecosystems are destroyed to produce the biofuels. For example, regardless of how effective sugarcane is for producing ethanol, its benefits quickly diminish if carbon-rich tropical forests are being razed to make the sugarcane fields, thereby causing vast greenhouse-gas emission increases (4). Such comparisons become even more lopsided if the full environmental benefits of tropical forests—for example, for biodiversity

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conservation, hydrological functioning, and soil protection—are included (10, 11).

Another environmental cost that varies among biofuels is trace-gas emissions. For example, crops that require nitrogen fertilizers, such as corn or rapeseed, can be a significant source of nitrous oxide, an important greenhouse gas that also destroys stratospheric ozone. When nitrous oxide emissions are compared among ethanol-producing crops, grasses and woody coppice become more favorable, whereas corn or canola may be worse for global warming than simply burning fossil fuels (3).

In the debate about different biofuels, one can easily be overwhelmed by the “apples and oranges” problem: Each biofuel has certain benefits and potential costs, and there is no common currency for comparing them. This is where Zah *et al.* have broken new ground by devising a conceptual scheme to evaluate different biofuels using just two criteria: greenhouse-gas emissions and overall environmental impact.

The authors compare gasoline, diesel, and natural gas with 26 different biofuels produced from a wide range of “crops.” They assess the total environmental impact of each fuel by aggregating natural resource depletion and damage to human health and ecosystems into a single indicator, using two different methods (12). The second key criterion for each fuel is its greenhouse-gas emissions relative to gasoline.

The findings of Zah *et al.* are striking (13). Most (21 out of 26) biofuels reduce greenhouse-gas emissions by more than 30% relative to gasoline. But nearly half (12 out of 26) of the biofuels—including the economically most important ones, namely U.S. corn ethanol, Brazilian sugarcane ethanol and soy diesel, and Malaysian palm-oil diesel—have greater aggregate environmental costs than do fossil fuels (see the figure, top panels). Biofuels that fare best are those produced from residual products, such as biowaste or recycled cooking oil, as well as ethanol from

Emissions versus other impacts. Although most biofuels reduce greenhouse gas emissions relative to gasoline, many, including soy (top right) and corn (top left), do not fare well in terms of other environmental impacts (6). Second-generation biofuels produced from non-food plants such as switchgrass (bottom) may perform better in environmental terms.

grass or wood. The findings highlight the enormous differences in costs and benefits among different biofuels.

Despite its apparent advantages, the scheme of Zah *et al.* is not perfect. Collapsing disparate environmental costs into a single number is risky, although it is reassuring that the two different methods used yielded similar results. A bigger worry is that their analyses fail to capture the potentially important indirect effects of different biofuels. For example, U.S. government subsidies to encourage corn-based ethanol production are prompting many American farmers to shift from growing soy to growing corn. This is helping to drive up global soy prices, which in turn amplifies economic incentives to destroy Amazonian forests and Brazilian tropical savannas for soy production (14). Furthermore, Zah *et al.* rely on relatively old (2004) data sets and fail to consider the social consequences of large-scale biofuel production, especially rising food cost.

Zah *et al.* excluded from their analysis so-called second-generation biofuels, such as those made from the breakdown of plant cellulose or lignin, because of insufficient data. Such biofuels could be produced from nonfood

plants—such as prairie grasses or trees grown on marginal land (15), or algae cultivated in aquaculture (16)—reducing the use of food crops for biofuels (see the figure, bottom panel). Some second-generation biofuels appear particularly promising in terms of their benefits and costs for biofuel production (5).

Not all biofuels are beneficial when their full environmental impacts are assessed; some of the most important,

such as those produced from corn, sugarcane, and soy, perform poorly in many contexts. There is a clear need to consider more than just energy and greenhouse-gas emissions when evaluating different biofuels and to pursue new biofuel crops and technologies. Governments should be far more selective about which biofuel crops they support through subsidies and tax benefits. For example, multibillion-dollar subsidies for U.S. corn production appear to be a perverse incentive from a rational cost-benefit perspective.

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Supporting Online Material

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Fig. S1
Reference

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