

NEWS AND COMMENTARY

Consequences of meristematic growth

A definitive demonstration of fitness effects due to somatic mutation in a plant

DG Scofield

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The open, meristematic development of plants, in which there is no separation between somatic and germline tissues and cell lineages can become highly ramified while growing great distances, results in bodies that can span wide ranges of size and age while sustaining heavy physical damage. This comes at a cost relative to nearly all animals, in which somatic mutations that accumulate in shoot apical meristems during growth are transmissible to gametes.

Edward J Klekowski Jr, over the course of many papers and a rich book (1988), argued that many features of plants have evolved to mitigate against somatic mutations. We still have a very limited understanding of how this violation of Weismann's Doctrine may affect the course of plant ecology and evolution. In a recent issue, Bobiwash *et al.* (2013) made an important step forward by directly demonstrating fitness effects of *de novo* somatic mutations transmitted through gametes and estimating the rate of somatic mutations in a large set of controlled crosses in clonal blueberry.

A handful of studies over the past few decades have been designed to test for fitness declines due to somatic mutations. Two examples are Klekowski's (1984) demonstration of an increased frequency of nonviable spores in larger fern clones, while more recently Ally *et al.* (2010) showed that *Populus trichocarpa* clones gradually lost pollen viability with increasing clone size. As suggestive as these and similar results are, they could also be interpreted as a nontransmissible phenotypic 'aging' (Kearsley and

Whitham, 1998; Ally *et al.*, 2010), or as architectural effects, in which resource delivery to sporogenic tissue is mediated by plant size (Diggle, 1995).

Bobiwash *et al.* (2013) avoided these complications by testing a contrast suggested by Klekowski (1988), autogamy depression (Klekowski, 1988; Schultz and Scofield, 2009). Autogamy depression compares the fitness of inbred progeny produced by two different types of self-crosses: (1) autogamous crosses, in which pollen from a flower is used to fertilize the ovules of that flower or a closely neighbouring flower; and (2) geitonogamous crosses, in which pollen is used to fertilize ovules from a different and widely separated flower in the same individual plant. In general, inbreeding depression due to exposure of heterozygous recessive deleterious alleles as homozygous is expected to reduce the fitness of progeny arising from both types of self-crosses relative to an outcrossed progeny (Charlesworth and Charlesworth, 1987). Autogamy depression makes the additional prediction that with *de novo* somatic mutation, the number of such alleles susceptible to exposure will depend on the amount of growth away from the nearest phenotypic ancestral location common to the pollen and ovule involved in each self-cross. Thus, to a degree dependent upon growth distances, inbred progeny of an autogamous cross should have greater inbreeding depression than inbred progeny, resulting from a variety of geitonogamous crosses (Schultz and Scofield, 2009).

As these crosses can be made reciprocally between any two locations, the autogamy depression test avoids confounding the fitness effects of *de novo* somatic mutations with those due to developmental or architectural effects. One expects nonmutational

factors to affect flowers at each location equally. If there is no somatic mutation, there should be no difference in inbreeding depression between autogamous and geitonogamous crosses, and this is manifestly contradicted by the results of Bobiwash *et al.* (2013).

Supplementing their experimental fieldwork, Bobiwash *et al.* (2013) also reviewed the literature and found further empirical support for autogamy depression (their Table S1). Given the wealth of controlled-pollination studies over the last several decades, it seems likely that similar data have been gathered but simply have not been published. Notably, Bobiwash *et al.* (2013) have deposited their data in DataDryad (datadryad.org). Data from all published studies should be placed in such permanent public archives to avoid 'file-drawer effects'; these data can find new life and new citations by helping to test questions never previously considered.

Bobiwash *et al.* (2013) have shown that there are consequences of *de novo* somatic mutations *within* a generation. Their estimate of overall mutation rate exceeds rate estimates in annual plants by an order of magnitude or more. This result makes a powerful case for the need to produce theory and data which help us understand what happens to such mutations *between* generations. A theoretical study by Morgan (2001) concluded with the provocative suggestion that the observed distribution of mating systems in large plants could best be explained if relative rates of meiotic and transmissible somatic mutation scaled such that, for large plants, the within-generation somatic mutation rate was at least several times greater than the meiotic mutation rate. This seemed an unlikely high somatic mutation rate, but at lower rates the theory

Dr DG Scofield is at the Department of Evolutionary Biology, Evolutionary Biology Centre, Uppsala University, Uppsala, Sweden
E-mail: douglas.scofield@ebc.uu.se

showed that the selective cost of a single episode of meiotic mutation could be discounted with a longer lifetime, leading to the prediction of increased selfing with increased generation time; needless to say, this has no support (Scofield and Schultz, 2006). Now Bobiwash *et al.* (2013) have produced an estimate of somatic mutation rate having roughly the order required for Morgan's theory to produce sensible predictions, suggesting that the scaling of somatic mutation rate with plant size—its 'annual renewal'—is an important evolutionary feature.

Curiously, on longer time scales, the net effect of somatic mutation might actually be to lower the rate of evolution. Smith and Donoghue (2008) demonstrated that woody clades have lower rates of molecular evolution than sister herbaceous clades. One possibility for resolution is the existence of more efficient between-generation selection against somatic mutation. A meta-analysis showed that survival of inbred progeny to adulthood was dependent upon plant size and was essentially nil within populations of large-statured plants (Scofield and Schultz, 2006).

Carefully designed next-generation sequencing experiments, which reveal rates and spectra of somatic mutations within

individual plant crowns, should provide considerable insight, but we will still need convincing links to the phenotype to truly gain insight into the evolutionary impact of somatic mutations. Whatever the data ultimately show, it is clear that a comparatively low long-term molecular evolutionary rate in woody taxa in no way implies a lack of explanatory power due to somatic mutation.

Finally, this work demonstrates the benefits that an evolutionary perspective can bring to applied sciences. Bobiwash *et al.* (2013) carried out this work as part of a larger assessment of pollination service and pollinator effectiveness within commercially important blueberry populations. Incorporating these inbreeding and autogamy depression results into models of population and clonal structure can provide important guidance for spatial management of this pollination-dependent agricultural resource.

Klekowski's (1988) multifaceted conceptual model emphasises a fundamental evolutionary tension between the flexibility of meristematic development and its potential deleterious consequences, and in doing so raises many fundamental questions regarding the trajectories of plant evolution. No doubt there is much more insight to come.

CONFLICT OF INTEREST

The author declares no conflict of interest.

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