Biological Differences Between the Evolutionary Lineages Within *Phytophthora ramorum* and *Phytophthora lateralis.* Should the Lineages Be Formally Taxonomically Designated?[1]

Clive Brasier[2]

Abstract

It is now generally accepted that the four evolutionary lineages of *Phytophthora ramorum* (informally designated NA1, NA2, EU1, and EU2) are relatively anciently divergent populations, recently introduced into Europe and North America from different, unknown geographic locations; that recombinants between them are genetically unstable and probably unfit to survive, indicating reproductive isolation; and that they differ in growth rates and aggressiveness. EU1 lineage, for example, is on average faster growing in culture and more pathogenic on *Quercus rubra* bark than the NA1 lineage. Our recent studies show that all four lineages can be readily discriminated in simple G x E stress tests on colony and growth behavior alone. Furthermore, the EU2 lineage is, on average, more aggressive than EU1 on larch stems, but EU1 may produce more sporangia than EU2 on larch needles.

Among *Phytophthora* tree pathogens, multiple evolutionary lineages are not unique to *P. ramorum*. Our studies have revealed four lineages within *P. ramorum's* closest known relative - *P. lateralis* (informally designated TWK, TWJ, PNW, and UK). They have distinctive colony types; exhibit considerable differences in growth rate; and differ in sporangial size and shape, chlamydospore size, and in aggressiveness on *C. lawsoniana.* Overall, these differences may be greater than those seen among the *P. ramorum* lineages. Other Phytophthoras exhibiting multiple lineages include *P. cinnamomi* and possibly also *P. austrocedri* and *P. kernoviae.*

Within *P ramorum* or within *P lateralis*, the lineages tend to share characteristics, such as their basic spore morphology, a common host range, a common breeding system (potentially outcrossing heterothallic and inbreeding homothallic, respectively), and phylogenetic relatedness. These are broadly consistent with being conspecific and sharing a common ancestor. Equally, the morphological, behavioral, and genetic differences between the lineages suggest they have become adapted (via selection, drift, and reproductive isolation) to somewhat different biogeographic environments. Some evolutionary biologists might consider them equivalent to sibling or cryptic species. Taxonomists may view their phenotypic differences as sufficiently large to warrant formal taxonomic recognition. In *P. lateralis*, for example, the differences between the lineages are probably as large as those between some described *Phytophthora* species.

---

[1] A version of this paper was presented at the Sixth Sudden Oak Death Science Symposium, June 20-23, 2016, San Francisco, California.

[2] Forest Research, Farnham, Surrey, GU10 4LH, UK.
Corresponding author: clive.brasier@forestry.gsi.gov.uk.

Should such lineages in *Phytophthora*, therefore, be formally recognized as subspecies or even as species? 'Lineage' is an informal term. It has no formal taxonomic status. In the author's view, while the term 'lineage' was helpful during earlier 'fact finding' stages of scientific understanding, it no longer adequately conveys the extent of the biological differences between the 'lineages.' In view of their pathological differences, it can certainly be argued that a more formal designation would be advantageous for plant health regulation and communication. The rest of the world might do well, for example, to regulate definitively against the importation of the *P. ramorum* EU2 lineage from the UK. By consolidating the biological realities, formal designation could also help remove some popular misconceptions regarding the status of the lineages, for example, that they are roughly equivalent only to genotypes.