

## In Memoriam

Professor John Philip  
Grime, FRS  
(1935–2021)

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Professor John Philip ('Phil') Grime FRS, who has died at the age of 85 (Figure 1), developed the field of plant functional ecology and was among the most influential scientists to have studied the Earth's vegetation. During an especially formative period for plant ecology in the 1970s, Phil established the conceptual framework of plant strategy theory that would revolutionize our understanding of plant adaptation by emphasizing function over form: that is, as an economy of resource use (particularly mineral nutrients) that would unite the dynamics of communities and ecosystems. Phil was an early champion of the idea that ecosystems function according to the chemistry and behavior of their dominant plants, which shifted the paradigm from simple environmental determinism to one of species driving ecosystem processes through their functional traits. As human alterations of the global environment would come to increasingly dominate ecological studies in the later stages of Phil's career, his approach to understanding vegetation structure would become a key component to earth system science and efforts to protect biodiversity globally.

Phil's scientific impact has been felt worldwide for generations of ecologists interested in applying general laws to diverse organisms. Remarkably, it was based almost entirely on his personal experiences within the relatively small confines of managed grasslands surrounding Sheffield, UK. After a wartime childhood in nearby Manchester, Phil began his career-long association with the University of Sheffield as an undergraduate, ultimately obtaining his PhD there in 1960. After a brief stint in the USA as a postdoc at the Connecticut

Agricultural Experiment Station (the only time in his life he would drive a car), Phil returned to Sheffield to join the recently formed Unit of Comparative Plant Ecology (UCPE), becoming its director in 1989. Phil was instrumental in developing the reputation of the UCPE as a hotbed of plant functional ecology and training an international cast of young ecologists that would go on to develop his work in other biomes. But the theory that made 'Grime' a famous (and occasionally infamous) name in ecology was based on day-trip field excursions that Phil and colleagues would make into the lime and gritstone pasturelands in the late 1960s, rarely more than an hour or two from the university.

Two seminal publications of the early 1970s would come to define Phil's approach to finding universal patterns in the structure of vegetation. 'Competitive exclusion in herbaceous vegetation' [1] introduced the 'hump-backed' model, which predicted that plant species richness peaks in communities that produce an aboveground biomass of about 600 g m<sup>-2</sup> year<sup>-1</sup>. The model was one of the first to make specific recommendations about the management of local biodiversity. 'Vegetation classification by reference to strategies' [2] introduced 'competition-stress-disturbance' (CSR) theory. CSR would become synonymous with Phil's approach to studying vegetation; because he chose to present the concept as a triangle of three opposing selection pressures, many would come to refer to CSR theory as Grime's triangle. Although not obvious from these papers, each was based on extensive vegetation datasets of the Sheffield region compiled by the UCPE team (particularly longtime associate John Hodgson). Although many would come to know Phil as a theorist and provocateur (a role he would assume often in the 1980s and 1990s), Phil would always argue that his insights were born of detailed field observations and a UCPE research team with expertise in both field botany and physiology.

As UCPE director, Phil focused the team's efforts on two types of controlled environment studies, each of which would set new standards for empirical work. On the one hand, Phil championed an approach to testing community theories in experimental 'microcosms', in which multiple species of plants, and sometimes animals and various microbes, were carefully manipulated in small containers to test aspects of community organization. A series of influential studies would result, including among the first demonstrations of the role of mycorrhizal networks in community diversity [3], plant responses to CO<sub>2</sub> fertilization in relation to functional type [4], and the role of intra-specific genetic diversity in community dynamics [5]. At the other extreme, to test CSR theory Phil invented an inductive laboratory approach called trait screening, in which species of contrasted habitats were subjected to systematic phenotypic measurements under standardized growing conditions. Among many traits to emerge as predictive of overall functional strategy from this work was specific leaf area (leaf area per unit dry mass), which has become ubiquitous in plant studies as an indicator of the leaf economics spectrum. Indeed, the emergence of plant resource-use economics as a dominant mode of ecological inquiry since the early 2000s is based in large degree on Phil's work; he not only predicted the economics spectrum as the main driver of trait variation in plants in the 1970s but had already established the main empirical patterns by the late 1980s. With John Hodgson and Rod Hunt he would publish the incomparable *Comparative Plant Ecology* in 1988, a book that introduced an entirely new way of studying a local flora from the perspective of function rather than taxonomy.

Phil was a fierce defender of his ideas and relished debate. Those who were graduate students in the 1980s may remember conference exchanges between Phil and John Harper, two giants of British ecology with strongly different world views (Harper



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Figure 1. Phil on the slope of the Buxton climate change experiment in 2013. (Credit: Jason Fridley.)

coming from a more agricultural background that focused on population dynamics). In the 1990s Phil's nemesis would become David Tilman of the University of Minnesota, whose own theory of plant communities based on the principle of low resource tolerance (R-star) would rival Phil's views on the limited role of competition in stressful habitats. The debate intensified when Tilman published results from an experiment purporting to show that more diverse plant communities were more productive, igniting the 'biodiversity and ecosystem functioning debate' that, for a time, divided plant ecologists into two camps. Embedded in the opposition, Phil countered with the 'mass ratio hypothesis' [6], arguing that ecosystems function according to the traits of dominant plants rather than the number of species. What is sometimes lost in the acrimony of this debate is that, perhaps for the first time, plant ecologists were put on the world stage as arbiters of a global sustainability dilemma, a perspective that Phil infused in his work more than a decade before such concerns were the norm in academic ecology.

Phil was also a pioneer in climate change research. As global warming became a pressing issue in the ecological community in the late 1980s, the UK Natural Environmental Research Council (NERC) established two large climate change experiments, one across a steep, infertile daleside near Buxton in Derbyshire. Phil would lead the effort at Buxton to show that plants on infertile soils were resistant to climate warming [7] and show how CSR theory could be used to predict which communities are most vulnerable to shifts of temperature and rainfall. When NERC stopped funding the Buxton experiment at the end of the grant cycle, Phil invested his own time and money to continue the manipulations (with the help of long-time associate Andrew Askew) and eventually succeeded in renewed support for the experiment through a US collaborator. Today, at nearly 30 years old, the Buxton Climate Change Impacts Lab is run by a consortium of UK researchers and is one of the longest running climate manipulations in the world.

Phil leaves behind a discipline transformed by his search for universal principles.

His many awards include the inaugural Alexander von Humboldt medal from the International Association of Vegetation Science, given in recognition of a scientist who perhaps more than any other transformed how ecologists think about plants: that most plants are not selected to grow fast but rather protect their store of meager resources; that plants of fertile habitats achieve dominance through rapid growth and resource preemption; and that simple traits can indicate both evolutionary pressures operating on individuals and rates of key ecosystem processes. Phil trained several generations of ecologists and inspired scores more to seek general patterns in what often appear to be irreducibly complex communities. Although often seen as a fire-brand, Phil showed extraordinary patience with young scientists and always pushed students and collaborators to consider the global ramifications of their work. His passing closes a chapter in the history of plant ecology that marks its transition from the careful study of local vegetation to the dominant role of plants in the functioning of ecosystems worldwide.

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