JOHN PHILIP GRIME

30 April 1935 — 19 April 2021

Elected FRS 1998

BY SIMON PIERCE¹,* AND JASON D. FRIDLEY²

¹Department of Agricultural and Environmental Sciences, University of Milan, via Celoria 2, 20133 Milan, Italy
²Department of Biology, Syracuse University, 107 College Place, Syracuse, NY 13244, USA

John Philip ‘Phil’ Grime developed fundamental theory in plant ecology that emerged from a lifetime of fieldwork and experimental studies in the Sheffield region, South Yorkshire, UK. His approach was an unusual combination of observation, experiment and theory: he conducted detailed, intensive observations of natural communities, alongside experimental manipulation of those communities and simulated ‘microcosms’ in the service of formulating general rules (‘strategies’) by which plants evolve with respect to their environment. In this way, Grime was one of several key figures that propelled plant ecology away from descriptive methods focusing on vegetation composition and toward a science more integrated with other fields, including evolutionary biology and Earth science. Grime’s investigative approach was an inspiration for the modern field of global change biology, and, by focusing on understanding the contrasting roles species and their traits play in the functioning of ecosystems, marked the beginning of the field of plant functional ecology. For much of his career Grime held the post of full professor (and in retirement, emeritus professor of ecology) at the University of Sheffield, where he also served as the director of the Unit of Comparative Plant Ecology and of the Buxton Climate Change Impacts Laboratory. Awarded an honorary doctorate by Radboud University (Nijmegen, The Netherlands) and a foreign membership of the Royal Netherlands Academy of Arts and Sciences, Grime was the first person awarded the Alexander von Humboldt Award of the International Association for Vegetation Science.

* simon.pierce@unimi.it

© 2021 The Author(s)
https://doi.org/10.1098/rsbm.2021.0021 3 Published by the Royal Society
John Philip Grime was born on 30 April 1935, at Denison House (63 Denison Road, Victoria Park, Manchester, UK) to Robert Grime, a bank manager from nearby Middleton, and Gertrude Grime, née Burns. An unusual surname, Grime is a Medieval derivation of the Norse-Viking name Grímr, meaning ‘grim or fierce one’, meant to evoke the Norse god Odin (the surname had become established in northern England by the time of the Domuesday Book of 1086; Hanks et al. 2016).

When Grime was still very young, the family moved to 29 Bentley Avenue, north of Middleton, a rural location where a single line of houses had been constructed near to the Manchester/Rochdale canal, embedded within farmland. The back garden fence was adjacent to an area of mature, species-rich wetland known locally as ‘The Dip’, and, by Grime’s own account, played an important role in developing his enthusiasm for botany.

Grime’s childhood and school years (figure 1) were spent in this rural setting, although his childhood was not untouched by the wider world, and in particular by the Second World War. His father was often absent throughout this period, having been posted to Italy, and one of Grime’s earliest memories was of standing on his front doorstep watching a WWII bomber roaring overhead. Following the war, Grime and his father were able to transform the borders of their garden into a source of natural colour as whole-hearted adherents of the British passion for gardening that emerged from the wartime necessity for victory gardens.

As a young man, Grime would frequent the city of Manchester accompanied by his father’s brother, Ernest, to support Manchester City football club, of which he remained a life-long and ardent follower. With a canal practically on his doorstep, Grime was also a keen angler (figure 1).

Grime first arrived at the University of Sheffield in October 1953 after winning an undergraduate scholarship, which also allowed him to defer his national service. His thesis work involved studying the limestone grasslands to the east of Sheffield. In 1956, he enrolled again at Sheffield for doctoral studies involving investigation of the nutrient requirements of grassland plants. Graduating in 1960, Grime then held a two-year postdoctoral position with
John Philip Grime

Figure 2. (a) Phil Grime as a young man was a dedicated botanist. (b) He is shown here embarking on the Carinthia, a Cunard steamship, and departing for (c) a two-year postdoctoral position at the Connecticut Agricultural Experiment Station, USA, in 1963. Photographs courtesy S. Grime. (Online version in colour.)

the Nature Conservancy Grassland Research Unit of the Department of Botany at Sheffield (figure 2). During these early Sheffield years, he was active in the University Staff Cricket Club and fund-raising activities, particularly during the traditional student rag-week, being ‘particularly serious’ about winning the boat races (T. C. Hutchinson, pers. comm.; figure 3).

In 1963, he embarked for an overseas position as a postdoctoral researcher at the Department of Soils and Climatology of the Connecticut Agricultural Experiment Station (New Haven, Connecticut, USA; figure 2)—incidentally, the only time in his life that he drove a car. On his return in 1964, he joined the Unit of Comparative Plant Ecology (UCPE), founded in 1961 by Professor Roy Clapham FRS and led by Professor Ian H. Rorison, then part of the Botany department of the University of Sheffield. By 1967, two of Grime’s long-term collaborators, John G. Hodgson and Rod Hunt, had arrived at the UCPE, both of whom would continue publishing with Grime throughout the following decades. Hunt’s 1967–1970 PhD work on plant growth rate with Grime was important to the development of Grime’s seminal ‘CSR theory’ (see ‘Scientific contributions’ section below). Prior to this quantitative analysis, Grime had relied on an intuitive sense of plant communities ‘derived from his own explorations as a young man of the natural and semi-natural herbaceous vegetation of the north of England’ (R. Hunt, pers. comm.).

During this period, in 1966, Grime married Jean Carol Sorenson, and in July 1968 their son Frank, who became a musician, was born. The marriage with Jean was dissolved in 1982.

From 1989 onwards, Grime took on the role of director of the UCPE (he became deputy director in 1971), which at the time was funded by the UK’s Natural Environment Research Council (NERC). He also played a primary role in the development of the Buxton Climate Change Impacts Laboratory, which in 1992 was among the first established climate change manipulations of natural vegetation, manipulations still ongoing at the time of this writing. Although a productive time for the UCPE, it was also marked by increasing friction with regard to funding and management. Grime, ever passionate about his work, had a reputation as overly assertive in his promotion of the UCPE, which fostered a more competitive than collaborative relationship with some UK research groups. This included ecologists at Silwood
Figure 3. Fully participant in all aspects of university life: (a) Phil Grime helping to draw crowds and raise money for charity at the University of Sheffield raft race on the river Don (indicated by the yellow arrow); (b) on the winning side as captain of the University Staff Cricket Club (sitting far left). Photographs courtesy S. Grime. (Online version in colour.)

Park, who were also promoting ecology at the level of national funding under the umbrella of population rather than functional ecology, which may have contributed to the termination of NERC support of the UCPE during the late 1990s.

At the same time, Grime encouraged fruitful interchange of both people and ideas between the UCPE and many other institutions, particularly at the international level. Rosemary Booth, UCPE technician and later PhD graduate with Grime, remembers:
Some of my most enduring memories of my time at UCPE came from the wonderful visitors who came from around the globe to work with Phil, taking the ecological theory and the experimental techniques developed in the Unit back to every continent. By night we had theatre and opera visits with our visitors, and I hosted many evening gatherings where firm and long-lasting friendships were cemented forming a strong foundation from which the ecological research developed in UCPE could be disseminated via the many long-term collaborative research projects devised during the visit.

Indeed, longer-term visits by researchers such as Sandra Díaz, Lauchlan H. Fraser, Hans Cornelissen and Bruno Cerabolini would later prove instrumental in developing functional plant ecology in other parts of the world. During this period, the authors of the present article were also inspired by personal experiences of Grime as a patient listener, willing to spend time explaining when others were disinclined. Former PhD graduate and UCPE colleague Ken Thompson states: ‘I’ve never known anyone less likely to set out deliberately to make another ecologist (however young, ignorant, or ill-informed) look stupid. Phil was always willing to listen patiently to questions and explain his point of view; he had time for everyone.’

To his Sheffield colleagues, Grime is also remembered for his incessant push for discovery by means of experimental manipulation. Andrew Askew, his long-time research associate, remembers Grime first and foremost as a restless experimentalist: ‘Any spare space anywhere was soon filled with an experiment, at Tapton, at Buxton and on the ground floor in the main department. There was no point in keeping anywhere clear as you would find an experiment there by next morning!’

A substantial number of experiments did not meet Grime’s threshold for novelty and were never published. Indeed, his insistence on realism in experiments sometimes made what would otherwise be straightforward projects into complex affairs. For example, on several occasions many cubic yards of soil would be dug and hauled up steep dalesides in Derbyshire to get the soil substrate ‘just right’—including construction of a custom winch-powered railway bed. In other microcosm studies Grime would insist on creating deep and shallow microsites with wood blocks to create conditions that he perceived as essential to plants living in limestone substrate.

On 14 October 2000 Grime married colleague Sarah M. Buckland at Nercwys Church in Flintshire, North Wales, which was followed two years later by the arrival of Lucy and, after two more years, Matthew (figure 4).

Grime remained highly active in research throughout the early decades of the twenty-first century (see ‘Scientific contributions’ section below), actively publishing scientific work for 58 years and well into retirement. During this time, he continued to mentor Sheffield undergraduates and graduate students from many universities; hosted visiting scholars from China, Switzerland, Libya and the US; delivered plenary talks at international conferences; and maintained the Buxton climate manipulation. Indeed, Grime once commented that the UK’s principal experimental investigation of climate change impacts on natural ecosystems—a subject of crucial importance to future generations—was being led by a retired gentleman in his free time, who used the bus to arrive at the field site over an hour away (J. P. Grime, pers. comm.; figure 4). Although perhaps intended as a comment on the national funding of ecology, at a personal level it also reveals Grime’s dedication and life-long passion for his work. He was conferred the title of emeritus professor of ecology by the University of Sheffield and, always a tenacious and active hands-on researcher, continued working into the last year of his life, even tending microcosms on the back patio of his home. On 19 April 2021, at the
Figure 4. (a) The Grime family (wife Sarah, Phil, daughter Lucy and son Matthew) relaxing at a cricket match; (b) Phil Grime working at the Buxton Climate Change Impacts Laboratory. Photographs courtesy Jason D. Fridley. (Online version in colour.)

age of 85, Grime passed away at the Seven Hills Nursing Home, Sheffield, after a brief but debilitating battle with dementia.

**Scientific contributions**

Grime’s main contribution as a researcher was to introduce ‘genuinely new ways of looking at things rather than just tweaking existing paradigms’ (D. Wardle, pers. comm.). His ability to see generalities where others only saw endless complexity and detail, and the recognition that just a few principal factors can determine the character of vegetation, have been described as Grime’s genius (R. Hunt, pers. comm.).

The pursuit of generalities was inspired by Robert MacArthur’s (MacArthur 1968) suggestion that ‘general events are only seen by ecologists with rather blurred vision’, which Grime quoted on numerous occasions. He described this pursuit as a search for ‘the truth’ (J. P. Grime, pers. comm.). From anyone else this might seem a pretentious affirmation, but Grime, being a very practical and direct person, meant that observed natural phenomena should take centre-stage in ecological study. Indeed, the theoretical work for which he was renowned emerged from patient observation and experimental comparison of natural systems, carried through to his large-scale experimental manipulations of grassland microcosms and natural vegetation. He often spoke of the interplay between observation, experiment and hypothesis.

If one could use a single word to summarize Grime’s approach to ecology, it might be ‘function’: how organisms and communities work and interact with each other and with the environment. Seen through an evolutionary lens, Grime’s work underlined that convergent evolution reflected similarities not simply in form, but fundamentally in terms of how plants operate. One could say that Grime’s work started with the goal of ascertaining, in his words, ‘why plants grow where they do’. As his career progressed, he gradually built the case that it
is not simply that plants fit a particular habitat; their traits, by governing ecosystems, play a key role in shaping and maintaining the habitat in which they live. These have become central themes of modern plant ecology.

Plant functional trade-offs and resource use

Grime’s scientific publishing career began in 1961 with a paper in *Nature* reporting a non-destructive method for estimating leaf chlorophyll contents of grassland plants (1)*. Subsequent papers investigated the adaptation of species to calcareous and siliceous substrates, particularly in Derbyshire where wind-deposited acid soil overlays limestone (2, 3). The dual approach of observation and manipulative experimentation of microcosms used in these studies would lay the foundations of much of Grime’s empirical method for the rest of his career.

His subsequent study of seedling growth responses to light intensity gradients (4) was crucial in placing resource availability at the heart of the study of wild plant survival and mortality; this theme would be expanded during Grime’s career and investigated widely by plant ecologists. The early 1960s were also the start of Grime’s quantification of functional traits such as dry mass accumulation (growth rate), plant height, leaf size and seed mass. Indeed, Grime (4) discovered a positive correlation between seed mass and plant height (although limited to seedlings), which more than 50 years later would be recognized as a global feature of plant size variability (Díaz *et al.* 2016).

By 1965 Grime had started to distil his observations into general observations of plant functional types, recognizing different ‘susceptibilities’, or modes of response to natural selection pressures (5). Although a general framework had yet to be presented, these observations represent a clear attempt to link the natural selection of species to their occupation of particular habitats. This was bolstered by his second *Nature* paper (6), where Grime introduced the theme of trade-offs, or the investment of resources in one capacity at the expense of another, in this case adaptations to sun and shade environments. Resource use trade-offs would become a hallmark of Grime’s approach to plant strategy theory, and would eventually coalesce into what he called the ‘resource axis’ separating ‘fast’ (or resource-acquisitive) and ‘slow’ species (low growth rate, long tissue longevity). A further key insight arising from work in the late 1960s was that acquisitive versus conservative growth strategies were evident not just in the plant community, but also for associated organisms, including herbivorous snails (7, 8).

The humped-back model of species richness/productivity

The 1970s were characterized by extensive field survey campaigns, originally published as an analysis of 630 quadrats in grassland habitats throughout a 2400 km² area mainly to the west of Sheffield (9). Constant addition to this database, alongside long-term collaborator and fellow cricketer John G. Hodgson, meant that by 1973 over 3000 quadrats had been conducted in 57 habitat types—several decades later, the number of quadrats would swell to over 13 000 (J. G. Hodgson, pers. comm.).

Furthermore, cultivation of 135 prominent herbaceous species in controlled conditions allowed measurement of relative growth rate, and greenhouse experiments allowed the relative growth performance and competition between species to be investigated. From this,

* Numbers in this form refer to the bibliography at the end of the text.
Grime drew general conclusions (10) about the mechanisms regulating ‘species density’ (the number of species per unit area, now more commonly known as species richness). Low species richness was recorded in two environmentally opposed places: on highly acidic, nutrient-poor substrates, interpreted as the operation of environmental ‘stress’; and in habitats dominated by tall species with expansive life forms, high growth rates and extensive litter accumulation, underpinning ‘competitive exclusion’. Grime provided further data (11) from transects showing that species richness is greatest at intermediate intensities of factors that limit productivity: stress (in this case, along a gradient of soil lead concentrations) or management promoting ‘defoliation and damage’ (mowing, grazing, trampling). He referred to ‘a fundamental dichotomy in the adaptive strategy of herbaceous plants’ as ‘the result of the conflicting selection pressures exerted, in productive habitats, by competition and, in unproductive habitats, by environmental stress’ (10). Essentially, this linked a suite of functional traits (attributes affecting organism fitness) to habitat preference. Discussing this work, Grime also provided a definition of competition in terms of resource pre-emption that would become a hallmark of his views of species interactions and adaptive strategies: ‘competition between plants may be defined as the tendency of neighbouring plants to utilize the same quanta of light, ions of mineral nutrients, molecules of water or volume of space’ (12).

The 1973 publications (10, 11) were the first to present a theoretical bell-shaped (unimodal) or ‘humped-back’ biodiversity–productivity curve supported by data from transects conducted in a range of ecosystems. Transect data would later be supplemented by measurements of biomass (‘standing crop’, or the amount of biomass that can be harvested, plus accumulated litter) plotted against species richness measured across a range of habitats, confirming a general humped-back model for species richness along a broad productivity gradient. This provided empirical support for Eugene Odum’s (Odum 1963) observation that ‘the greatest diversity occurs in the moderate or middle range of a physical gradient’ and pre-dated by five years Connell’s (1978) intermediate disturbance hypothesis (IDH), which also describes a unimodal species richness relationship, albeit focusing on disturbance gradients and originally drawing from examples in tropical rainforests and coral reefs.

Both the humped-back model and the IDH have generated considerable debate, mostly centred around the arguments that a relationship may not always be evident, and that, as a complex upper boundary or ‘unimodel envelope’ relationship (Grace 2001), it is not useful for predicting species richness values directly from productivity data (Adler et al. 2011; Grace et al. 2014). However, this perhaps misses the point. As an upper limit to species richness, it shows where high richness can emerge (with a sufficiently large local pool of species), but most importantly the conditions in which it unequivocally cannot, which is of great interest to vegetation managers and conservationists (Pierce 2014). It is also consistent with global-scale richness data across a large biomass range (Fraser et al. 2015). This illustrates one of the remarkable aspects of Grime’s work: while it focused on one specific geographic region, it was comprehensive enough to find relevance at the global scale.

**CSR plant strategy theory**

Competitor, stress-tolerator, ruderal (CSR) theory is one of Grime’s most well-known contributions to ecology, and was introduced in a *Nature* paper in 1974 (13) (summarized in figure 5). The CSR model was originally intended as a means of classifying and comparing vegetation types according to the relative importance of contrasting growth strategies and as a method for describing vegetation processes such as succession. Grime suggested that
this was necessary owing to the 'subjectivity' of phytosociology and difficulty applying phytosociology to 'recent or unstable' vegetation influenced by human impacts (13). In other words, the CSR model was not introduced explicitly as a formal theory, but as a conceptual model and quantitative classification method.

A key assertion of the CSR model involves standing crop. This can either be high, when biomass is produced in large amounts by species exhibiting rapid vegetative expansion to pre-empt resources (competition), or low, in situations where biomass either accumulates slowly owing to environmental stress or is periodically removed by damage (disturbance). This suggests that three principal selection pressures act on the species forming communities, with the character of the community and properties of the ecosystem, such as biomass production, reflecting the relative importance of the various strategies that comprise it. This forms the basis of what is often referred to as ‘Grime’s triangle’ or erroneously as ‘triangle theory’ (it is not a theory about triangles).

This model would initially prove controversial, common criticisms being that it was not empirically well supported, that the scheme artificially constrained plant variability into a rigid framework and that it was not easily applicable (Westoby 1998). Indeed, the method originally used by Grime (13) required labour intensive growth analysis to determine inherent growth rates for each species—developed with Rod Hunt (14)—and was not applicable directly to individual plants growing in the field. Another criticism was that plant survival might depend on alternative mechanisms, such as differential competitive abilities for above- and below-ground resources (Tilman 1988).

Grime would also express his models as conceptual diagrams rather than equations, and this was perhaps misinterpreted as a lack of rigour. (In private, Grime admitted admiration for researchers, such as Tilman, that could express their ideas in this manner.) In retrospect, some
of the controversy may have been due to the impression from the initial paper (13) that CSR was an assertion based on few data, rather than thousands of vegetation quadrats.

Grime developed the CSR model further (15), notably with greater detail surrounding the definitions of stress and disturbance, the shared effect of different types of stress factor (all of which limit metabolic rates and thus biomass production) and the survival of stress-tolerators via inherently ‘slow-but-steady’ growth in limiting and variable habitats. In this paper, Grime introduced the terms ‘C-, S- and R-selection’, and related this to MacArthur and Wilson’s r/K-selection theory (MacArthur & Wilson 1967). According to r/K-selection theory, organisms achieve fitness either by maximizing the ‘intrinsic rate of natural increase’ (r) and reproduction during phases of population expansion or, when the habitat reaches its carrying capacity and the population reaches its maximum size (K), species exhibit robust adult life forms. Grime argued that while the traits of r-selected organisms are unambiguous, the traits of K-selected organisms are inconsistent, ranging from large size achieved via rapid growth in productive habitats to slow growth (perhaps eventually to large size) and hardiness in limiting habitats. Grime’s first book (16) provided an expanded discussion and justification for splitting K-selection into C- and S-selection. In this first edition, emphasis was placed on explaining the processes governing vegetation composition, but little was said regarding the wider ecosystem.

Functional trait screening and the Integrated Screening Programme

By the start of the 1980s, one of the main goals of plant ecology was to explain vegetation composition across environmental and disturbance gradients, but there was a growing realization of the importance of global change and the participation of vegetation in the wider ecosystem. Several schools of thought were prominent at that time. In addition to Grime’s approach, focused on plant resource use, Peter Grubb’s regeneration niche concept described vegetation composition in terms of opportunities for establishment (Grubb 1977), while the demographic approach of John Harper (FRS 1978) also emphasized seedling establishment but in the context of life history theory (Harper 1977). In private, Grime would remark that the regeneration niche was an idea he wished he had had (M. J. Crawley (FRS 2002), pers. comm.). Indeed, despite the debate that grew around the details of each approach, perhaps fuelled by conflicting personalities, these are not mutually exclusive ideas, each dealing with different aspects of ecology that all potentially influence vegetation composition. However, the Grimean approach based on resource use and adaptive strategies inherently links vegetation with ecosystem properties such as resource availability and biomass production, and is of direct relevance to ecosystem functioning.

As the field shifted to global change ecology, Grime’s theory was one of the few existing frameworks for making ecosystem-level predictions, and in this sense he was not only insightful but also fortunate to expound his ideas at this time. Grime would later point out, in perhaps one of his most important and least controversial insights, that there is a clear need, in a world impacted by anthropogenic environmental forcing, to understand how ecosystem properties are influenced by plant functioning. A corollary of this argument was the need to identify the plant traits and life history characters that affect survival and govern ecosystem properties.

The 1970s and 1980s were characterized by large-scale screening of plant traits, alongside numerous collaborators (see the full list of publications in the supplementary material). This included the characterization of seasonal variation in soil seed banks of contrasting habitats.
(17) and measurement of germination characteristics for 403 species (18), representing standardized comparative studies of the relationship between taxonomy, seed morphology, physiological responses and germination for wild plants. A fifth Nature paper (19) would relate genome size variation in 162 species to the seasonal timing of plant growth, showing that species that emerge in early spring do so by means of cell expansion rather than division, and consequently are selected to maintain large nuclear genomes that promote larger cell sizes. This contrasts with species that grow in warmer periods where genome size rather than temperature limits the rate of mitosis and thus potential growth rate.

Other experimental studies in this period focused on the plasticity of root and shoot system responses to resource availability (20, 21) and a further Nature paper showed that grazing and mycorrhizal associations alter floristic diversity by favouring subordinate species relative to dominants (22). One of the outcomes of this concerted research effort was the publication of Grime, Hodgson and Hunt’s authoritative Comparative plant ecology (23). This unique ‘functional catalogue of plants’ aimed to translate academic insights concerning the ecology of single species into a format useful for management, intended as an accessible database of ‘standardized accounts of the biology and ecology of common vascular plants of the British flora’.

In 1987, the Unit of Comparative Plant Ecology formally launched the Integrated Screening Programme (ISP) to: ‘1) establish the range of variation in selected plant traits, 2) recognise recurring patterns of ecological and evolutionary specialisation, and thus 3) devise a functional classification of plants relevant to the analysis of communities and ecosystems and the management of vegetation’ (K. Thompson, pers. comm.). Forty-three species representative of all major landscape components of mainland Britain were chosen, and adult and juvenile plants subjected to measurement of 63 traits. The ISP screening work, conducted throughout the late 1980s and 1990s, included investigations of the role of plasticity of root and shoot growth in resource acquisition in patchy, heterogeneous environments, demonstrating that competition is relatively unimportant for species growing on infertile soils (24–32), and also writing (with G. A. Hendry) the practical laboratory manual Methods in comparative plant ecology (33). A further Nature paper investigated the feedbacks between elevated CO₂ concentrations and plant growth responses (34).

The synergy of field and lab work in this period was particularly powerful, as Ken Thompson (pers. comm.) points out:

an early example, and still one of my favourites, is MacGillivray et al. (1995) [(35)], which tested the ability of the pivotal axis of stress tolerance to predict resistance and resilience of five types of herbaceous vegetation to three types of extreme event (frost, drought and fire). The results confirmed that the syndrome of plant traits associated with stress tolerance was positively correlated with resistance to extreme events, but negatively correlated with resilience. In other words, if you know enough about the traits of enough species, you can predict how the world works.

Work in this period would also investigate the relationship between productivity and herbivore impacts in the context of plant defence theory (36), and continue work on wild plant responses to elevated CO₂ (37).

An outcome of the ISP (38) was to firmly establish the existence of resource investment trade-offs in vascular plants. A principal axis of variability involved strong linkages between
leaf nutrient concentrations, growth rate, root and shoot foraging responses, the longevity, tensile strength and palatability of leaves and the rate of decomposition of leaf litter, all traits heavily involved in ecosystem functioning. This firmly established the plant resource axis as ‘a trade-off between attributes conferring an ability for high rates of resource acquisition in productive habitats and those responsible for retention of resource capital in unproductive conditions’ (38), which in the final decades of Grime’s career would become known as the plant economics spectrum (Wright et al. 2004; Reich 2014).

Mass ratio theory and the early 2000s

By the late 1990s debate emerged surrounding the views that species richness promotes ecosystem processes such as productivity (arising from microcosm experiments at Silwood Park and Cedar Creek, championed in part by David Tilman (ForMemRS 2017)) versus Grime’s mass ratio theory that dominant species, contributing proportionally greater biomass and particular trait values, largely determine productivity (39).

While the former camp argued for a direct positive relationship between biodiversity and ecosystem productivity and stability, Grime argued that dominant species are particularly important, with subordinates and transient species having intermittent roles affecting opportunities for the establishment and regeneration of dominants. This view is intertwined with the humped-back model and CSR theory, in which high productivity is associated with dominance by small numbers of $C$-selected species: a view ultimately borne out by joint measurement of biomass and CSR strategies across a wide range of vegetation types (Cerabolini et al. 2016). Grime’s view has also found extensive support in independent large-scale experimental manipulations of grassland vegetation designed specifically to test mass ratio theory (Smith et al. 2019; Sonkoly et al. 2019), and mass ratio effects are implicit in the widely adopted measurement of community-weighted mean trait values (Bílá et al. 2014; Tardif et al. 2014). However, recent results (Jochum et al. 2020) also suggest that experiments supporting a simple biodiversity/ecosystem relationship can represent plant communities in an ecologically realistic way, and for many the debate remains open.

In another key development during this period, the CSR classification tool was developed to provide a more practical method (40), also introducing the concept of investigating ‘hard’ traits (i.e. fundamental physiological characters that are too labour intensive to investigate widely) using proxy ‘soft’ traits (traits correlated with hard traits but that are easy and rapid to measure, from large sample sizes of plants in nature). Experimental work in the early 2000s would continue to produce a range of key discoveries: that productive ecosystems are more responsive to climate change (41); that during plant invasions, invasion depends mainly on nutrient availabilities (42, 43); and that species invasions are driven by net resource availability, as determined by both environmental qualities and the competitive intensity of native vegetation (44). The importance of Grime’s CSR strategies to plant invasion has recently been confirmed at the global scale (Guo et al. 2018, 2019). As a summary of work to date, Grime would publish the second edition of Plant strategies, vegetation process and ecosystem properties (45), now with emphasis on the links between species traits and ecosystem processes.

Arguably, the culmination of the screening work at Sheffield was the involvement of Grime and UCPE co-workers in two studies that laid the foundation of the plant economics
In 2002, Grime and Mackey (46) would explicitly refer to ‘a spectrum of plant functional types which in terms of resource processing range from “the acquisitive” to “the retentive” and correspond respectively to highly productive and chronically unproductive vegetation’—a spectrum later to be confirmed worldwide for leaves (Wright et al. 2004). Involvement of UCPE in the collaborative study that collated ISP-style trait screening from three continents (47) confirmed linkages between ‘soft’ and ‘hard’ traits over large scales and found ‘a fundamental trade-off in plant design between a set of plant attributes that allow rapid acquisition of resources (“acquisitive type”), and another set that permits conservation of resources within well protected tissues (“conservative/retentive types”). This would provide inspiration for Diaz et al. (2016) to analyse worldwide variation in soft traits and confirm the existence of a global spectrum of plant form and function, characterized by trade-offs in resource economics and the size of plants and their parts.

Later career contributions: the twin filter model and universal adaptive strategy theory

Perhaps one of Grime’s most important papers was published in 2006, entitled ‘Trait convergence and trait divergence in herbaceous plant communities: mechanisms and consequences’ (48). This attempted to explain the apparent paradox that species coexisting in a community must be functionally similar in order to occupy the same habitat, but sufficiently different to allow coexistence. Grime suggested that the local species pool (all species that could potentially occupy a given habitat) is subjected to two filters that operate simultaneously. In the first, site productivity was proposed as a general, convergent filter, restricting fitness to a subset of possible trait values. Acting within this subset, specific events and fine-scale disturbances were seen as a second filter, selecting for local divergence in trait values.

At this time, Grime also elucidated the ‘scale-precision trade-off in spacial resource foraging by plants’ (49). Research during this period focused on the fast versus slow dynamics of plant communities, the strength of ecosystem processes and how these relate to functional identity (composition) of component species and intraspecific variation in traits (reflecting genetic diversity). This work was conducted with a range of collaborators, both within the University of Sheffield and abroad (50–61).

In 2012, Grime and Pierce (62) would extend these ideas of individual/genetic diversity and trait convergence/divergence to formulate the twin filter model. This explained trait convergence and divergence as responding to two filters: ‘The traits discriminated against by a “primary CSD-equilibrium filter” are those fundamental to the acquisition, retention and allocation of matter and energy utilized by primary metabolism, and are interdependent traits subject to the three-way trade-off (i.e. decline in one function is associated with gain in another). Subsequently, ‘proximal filter traits are those that affect survival but which are not integral to the CSR strategy and often reflect intermittent threats to survival acting during particular phases of development or qualitative differences in how and when functions are performed rather than performance per se’ (62).

In this period Grime and Pierce developed the idea that resource economics and size trait variation are principal axes of functional trait variability across all major clades of organisms (62), leading to the extension of CSR theory beyond plants, in the form of their universal adaptive strategy theory (UAST). Crucially, much of the evidence, including direct comparisons between plant CSR theory and life history variation in various animal and microbial groups, had previously been published and remarked upon by experts of each
particular group, with taxa spanning the entire gamut of life on Earth from archaea to mammals. UAST would put natural selection and the selfish gene (Dawkins 1976) at the heart of a universal three-way trade-off in resource investment:

> a universal three-way trade-off constrains adaptive strategies throughout the tree of life, with extreme strategies facilitating the survival of genes via: (C), the survival of the individual using traits that maximize resource acquisition and resource control in consistently productive niches, (S), individual survival via maintenance of metabolic performance in variable and unproductive niches, or (R), rapid gene propagation via rapid completion of the life cycle and regeneration in niches where events are frequently lethal to the individual.

Indeed, a global spectrum of form and function delimited by fast-to-slow life histories and body size variation has since been confirmed empirically for mammals and birds (Cooke et al. 2019), mirroring the plant global spectrum (Díaz et al. 2016).

During the 2010s, research focused on genetic diversity and intraspecific functional trait diversity (63), long-term observations of wild vegetation in the context of N deposition and grazing regimes (64), and the ideas that longer growing seasons in a changing climate favour competitors (65), and that plant functional identity determines soil microbial community composition and plant drought responses (66). Throughout Grime’s career up until this point, ecologists had only sporadically adopted CSR theory, especially as a practical tool. Indeed, even though his method (40) recognized the fundamental importance of leaf economics and plant size traits, a number of methodological drawbacks remained unresolved. For example, while many key vegetation formations are dominated by woody species, notably gymnosperm trees, the method was applicable only to herbaceous angiosperms. It also classified all plants taller than 1 m in a single height category.

A more broadly applicable CSR method arrived following confirmation that economics and size trait variation represent the principal functional space for European vascular plants (Cerabolini et al. 2010; Pierce et al. 2012, 2013), paving the way to a globally-calibrated CSR tool applicable to woody and herbaceous vascular plants worldwide (67). Grime was a co-author on this work; thus, the path from Grime’s original ‘hard’ CSR classification method based on comparative experiments with the South Yorkshire flora (13) to a ‘soft’ method applicable to wild plants globally (67) coalesced as a result of more than four decades of work and collaborative involvement.

**Legacy**

At the time of his death, Phil Grime’s research accomplishments were among the most widely appreciated of any scientist who ever worked in the field of plant ecology or vegetation science. Although many of his well-known contemporaries did not agree with key aspects of his work, perhaps no scientist had a greater impact on the direction that the field of plant ecology took between 1980 and 2000. This stems from Grime’s extensive practical experience and visionary conceptual work (occurring largely in the 1970s) and from external cultural forces that compelled ecologists to increasingly consider the global ramifications of their work, most notably concerns over biodiversity loss and climate change (during the early and late 1980s, respectively).

Grime’s ideas link convergent plant traits to environmental factors, and the survival strategies of organisms to ecosystem properties such as biomass accumulation and
productivity. His legacy continues to be apparent in the inclusion of vegetation functioning in Earth systems models, which increasingly guide society’s response to climate change. Grime’s ideas provoked debate, and yet remain our most powerful explanation of how communities of organisms arise from the natural selection pressures acting on single species. By effectively extending the theory of evolution by means of natural selection to the formation of multi-species assemblages, Grime managed to ground ecology’s central questions in biology’s greatest idea.

Honours and awards

1991 Foreign Member, the Royal Netherlands Academy of Arts and Sciences (Domain of Natural Sciences and Engineering)
1998 The Marsh Award for Ecology (British Ecological Society)
1998 Honorary Member, the Ecological Society of America
1998 Fellow, the Royal Society
1998 Honorary Doctorate, Radboud University, Nijmegen, The Netherlands
1998 Honorary Member, the British Ecological Society
2011 Inaugural recipient of the Alexander von Humboldt Award of the International Association for Vegetation Science

Acknowledgements

We thank numerous colleagues whose memories and insights regarding Phil helped us, either directly or indirectly, to paint a picture of Phil as a person and as a researcher (in alphabetical order): Andrew Askew, Rosemary Booth, Bruno E. L. Cerabolini, Roberta M. Ceriani, Mick J. Crawley, Peter Grubb, John G. Hodgson, Rod Hunt, Ken Thompson, David Wardle, Mark Westoby and, in particular, Phil’s wife and colleague, Sarah Grime, née Buckland.

The frontispiece portrait photograph was taken by Prudence Cuming Associates and is © The Royal Society.

Author profiles

Simon Pierce

Simon Pierce is an associate professor of applied and environmental botany at the University of Milan, Italy. His research interests involve plant physiological ecology, functional traits and the reproductive ecology and conservation of rare plant species. During his career, he has lived in the Republic of Panama, working at the Smithsonian Tropical Research Institute (for the University of Cambridge, UK), and has worked across the Republic of Tanzania studying cereal crop responses to parasitic plants (for the University of Sheffield, UK).
Jason Fridley is professor of biology at Syracuse University, New York, USA, with research interests that include the application of plant strategy theory, particularly in the contexts of global change and species invasions. For a decade he and Phil Grime co-directed the Buxton Climate Change Impacts Laboratory at Harpur Hill, Derbyshire, UK.

References to other authors

Adler, P. B. et al. 2011 Productivity is a poor predictor of plant species richness. *Science* **333**, 1750–1753.

Bílá, K., Moretti, M., de Bello, F., Dias, A. T. C., Pezzatti, G. B., Van Oosten, A. R. & Berg, M. P. 2014 Disentangling community functional components in a litter-macrodetritivore model system reveals the predominance of the mass ratio hypothesis. *Ecol. Evol.* **4**, 408–416. (doi:10.1002/ece3.941)

Cerabolini, B. E. L., Brusa, G., Ceriani, R. M., De Andreis, R., Luzzaro, A. & Pierce, S. 2010 Can CSR classification be generally applied outside Britain? *Plant Ecol.* **210**, 253–261. (doi:10.1007/s11258-010-9753-6)

Cerabolini, B. E. L., Pierce, S., Verginella, A., Brusa, G., Ceriani, R. M. & Armiraglio, S. 2016 Why are many anthropogenic agroecosystems particularly species-rich? *Plant Biosys.* **150**, 550–557.

Connell, J. H. 1978 Diversity in tropical rain forests and coral reefs. *Science* **199**, 1302–1310. (doi:10.1126/science.199.4335.1302)

Cooke, R. S. C., Eigenbrod, F. & Bates, A. E. 2019 Projected losses of global mammal and bird ecological strategies. *Nature Comm.* **10**, 2279. (doi:10.1038/s41467-019-10284-z)

Dawkins, R. 1976 *The selfish gene*. Oxford, UK: Oxford University Press.

Díaz, S. et al. 2016 The global spectrum of plant form and function. *Nature* **529**, 167–171. (doi:10.1038/nature16489)

Fraser, L. H. et al. 2015 Worldwide evidence of a unimodal relationship between productivity and plant species richness. *Science* **349**, 302–305. (doi:10.1126/science.aab3916)

Grace, J. B. 2001 The roles of community biomass and species pools in the regulation of plant diversity. *Oikos* **92**, 193–207. (doi:10.1034/j.1600-0706.2001.920201.x)

Grace, J. B., Adler, P. B., Harpole, W. S., Borer, E. T. & Seabloom E. W. 2014 Causal networks clarify productivity—richness interrelations, bivariate plots do not. *Funct. Ecol.* **28**, 787–798. (doi:10.1111/1365-2435.12269)

Grubb, P. J. 1977 The maintenance of species richness in plant communities: the importance of the regeneration niche. *Biol. Rev.* **52**, 107–145. (doi:10.1111/j.1469-185x.1977.tb01347.x)

Guo, W.-Y. et al. 2018 The role of adaptive strategies in plant naturalization. *Ecol. Lett.* **21**, 1380–1389. (doi:10.1111/ele.13104)

Guo, W.-Y. et al. 2019 Domestic gardens play a dominant role in selecting alien species with adaptive strategies that facilitate naturalization. *Glob. Ecol. Biogeogr.* **28**, 628–639. (doi:10.1111/geb.12882)

Hanks, P., Coates, R. & McClure P. 2016 *The Oxford dictionary of family names in Britain and Ireland*. Oxford, UK: Oxford University Press.

Harper, J. L. 1977 *Population biology of plants*. London, UK: Academic Press.

Jochum, M. et al. 2020 The results of biodiversity–ecosystem functioning experiments are realistic. *Nat. Ecol. Evol.* **4**, 1485–1494. (doi:10.1038/s41559-020-1280-9)

MacArthur, R. H. 1968 The theory of the niche. In *Population biology and evolution* (ed. R. C. Lewontin), pp. 159–176. Syracuse, NY: Syracuse University Press.
MacArthur, R. H. & Wilson, E. O. 1967 *The island theory of biogeography*. Princeton, NJ: Princeton University Press.

Odum, E. P. 1963 *Ecology*. New York, NY: Holt, Rinehart and Winston.

Pierce, S. 2014 Implications for biodiversity conservation of the lack of consensus regarding the humped-back model of species richness and biomass conservation. *Funct. Ecol.* 28, 253–257. (doi:10.1111/1365-2435.12147)

Pierce, S. & Cerabolini, B. E. L. 2018 *Plant economics and size trait spectra are both explained by one theory*. Milan, Italy: Plant Press. See https://www.researchgate.net/publication/326069336_Plant_economics_and_size_trait_spectra_are_both_explained_by_one_theory.

Pierce, S., Brusa, G., Sartori, M. & Cerabolini, B. E. L. 2012 Combined use of leaf size and economics traits allows direct comparison of hydrophyte and terrestrial herbaceous adaptive strategies. *Ann. Bot.* 109, 1047–1053. (doi:10.1093/aob/mcs021)

Pierce, S., Brusa, G., Vagge, I. & Cerabolini, B. E. L. 2013 Allocating CSR plant functional types: the use of leaf economics and size traits to classify woody and herbaceous vascular plants. *Funct. Ecol.* 27, 1002–1010. (doi:10.1111/1365-2435.12095)

Reich, P. B. 2014 The world-wide ‘fast–slow’ plant economics spectrum: a traits manifesto. *J. Ecol.* 102, 275–301. (doi:10.1111/1365-2745.12211)

Smith, M. D. *et al.* 2019 Mass ratio effects underlie ecosystem responses to environmental change. *J. Ecol.* 108, 855–864. (doi:10.1111/1365-2745.13330)

Sonkoly, J., Kelemen, A., Valkó, O., Deák, B., Kiss, R., Tóth, K., Miglécz, T., Tóthmérész, B. & Török, P. 2019 Both mass ratio effects and community diversity drive biomass production in a grassland experiment. *Sci. Rep.* 9, 1848. (doi:10.1038/s41598-018-37190-6)

Tardif, A., Shipley, B., Bloor, J. M. G. & Soussana, J.-F. 2014 Can the biomass-ratio hypothesis predict mixed-species litter decomposition along a climatic gradient? *Ann. Bot.* 113, 843–850. (doi:10.1093/aob/mct304)

Tilman, D. 1988 *Plant strategies and the dynamics and function of plant communities*. Princeton, NJ: Princeton University Press.

Westoby, M. 1998 A leaf-height-seed (LHS) plant ecology strategy scheme. *Plant Soil* 199, 213–227. (doi:10.1007/A1004327224729)

Wright, I. J. *et al.* 2004 The worldwide leaf economics spectrum. *Nature* 428, 821–827. (doi:10.1038/nature02403)

**BIBLIOGRAPHY**

The following publications are those referred to directly in the text. A full bibliography is available as electronic supplementary material at https://doi.org/10.6084/m9.figshare.c.5596159.

1. 1961 Measurement of leaf colour. *Nature* 191, 614–615. (doi:10.1038/191614b0)
2. 1963 An ecological investigation at a junction between two plant communities in Coombsdale on the Derbyshire limestone. *J. Ecol.* 51, 391–402. (doi:10.2307/2257692)
3. Factors determining the occurrence of calcifuge species on shallow soils over calcareous substrata. *J. Ecol.* 51, 375–390. (doi:10.2307/2257691)
4. 1965 (With D. W. Jeffrey) Seedling establishment in vertical gradients of sunlight. *J. Ecol.* 53, 621–642. (doi:10.2307/2257624)
5. Comparative experiments as a key to the ecology of flowering plants. *Ecology* 46, 513–515. (doi:10.2307/1934882)
6. Shade tolerance in flowering plants. *Nature* 208, 161–163. (doi:10.1038/208161a0)
7. 1968 (With S. F. MacPherson-Stewart & R. S. Dearman) An investigation of leaf palatability using the snail *Cepaea nemoralis* L. *J. Ecol.* 56, 405–420. (doi:10.2307/2258241)
8. 1969 (With G. M. Blythe) An investigation of the relationships between snails and vegetation at the Winnats Pass. *J. Ecol.* 57, 45–66. (doi:10.2307/2258207)
9. 1971 (With P. S. Lloyd & I. H. Rorison) The grassland vegetation of the Sheffield region. *J. Ecol.* 59, 863–886. (doi:10.2307/2258145)
10. 1973 Competitive exclusion in herbaceous vegetation. *Nature* 242, 344–347. (doi:10.1038/242344a0)
(11) Control of species density in herbaceous vegetation. *J. Envir. Man.* 1, 151–167.
(12) Competition and diversity in herbaceous vegetation (reply). *Nature* 244, 311. (doi:10.1038/244311a0)
(13) 1974 Vegetation classification by reference to strategies. *Nature* 250, 26–31. (doi:10.1038/250026a0)
(14) 1975 (With R. Hunt) Relative growth-rate: its range and adaptive significance in a local flora. *J. Ecol.* 63, 393–422. (doi:10.2307/2258728)
(15) 1977 Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *Am. Nat.* 111, 1169–1194. (doi:10.1086/283244)
(16) 1979 *Plant strategies and vegetation processes.* Chichester, UK: John Wiley & Sons.
(17) 1979 (With K. Thompson) Seasonal variation in the seed banks of herbaceous species in ten contrasting habitats. *J. Ecol.* 67, 893–921. (doi:10.2307/2259220)
(18) 1981 (With G. Mason, A. V. Curtis, J. Rodman & S. R. Band) A comparative study of germination characteristics in a local flora. *J. Ecol.* 69, 1017–1059. (doi:10.2307/2259651)
(19) 1982 (With M. A. Mowforth) Variation in genome size: an ecological interpretation. *Nature* 299, 151–153. (doi:10.1038/299151a0)
(20) 1986 (With J. C. Crick & J. E. Rincon) The ecological significance of plasticity. *Symp. Soc. Exp. Biol.* 40, 5–29.
(21) 1987 (With J. C. Crick) Morphological plasticity and mineral nutrient capture in two herbaceous species of contrasted ecology. *New Phytol.* 107, 403–414. (doi:11.111/j.1469-8137.1987.tb00192.x)
(22) (With J. M. L. Mackey, S. H. Hillier & D. J. Read) Floristic diversity in a model system using experimental microcosms. *Nature* 328, 420–422. (doi:10.1038/328420a0)
(23) 1988 (With J. G. Hodgson & R. Hunt) *Comparative plant ecology: a functional approach to common British species.* London, UK: Unwin Hyman.
(24) 1989 (With B. D. Campbell) A new method of exposing developing root systems to controlled patchiness in mineral nutrient supply. *Ann. Bot.* 63, 395–400. (doi:10.1093/oxfordjournals.aob.a087758)
(25) (With B. D. Campbell) A comparative study of plant responsiveness to the duration of episodes of mineral nutrient enrichment. *New Phytol.* 112, 261–267. (doi:11.111/j.1469-8137.1989.tb02382.x)
(26) (With M. A. Mowforth) Intra-population variation in nuclear DNA amount, cell size and growth rate in *Poa annua* L. *Funct. Ecol.* 3, 289–295. (doi:10.2307/2389368)
(27) 1991 (With B. D. Campbell & J. M. L. Mackey) A trade-off between scale and precision in resource foraging. *Oecologia* 87, 532–538. (doi:10.1007/BF00320417)
(28) (With B. D. Campbell) Growth rate, habitat productivity and plant strategy as predictors of stress response. In *Response of plants to multiple stresses.* (ed. H. A. Mooney, W. E. Winner & E. J. Pell), pp. 143–159. London, UK: Academic Press.
(29) (With B. D. Campbell, J. M. L. Mackey & J. C. Crick) Root plasticity, nitrogen capture and competitive ability. In *Plant root growth: an ecological perspective* (ed. D. Atkinson), pp. 381–397. Oxford, UK: Blackwell Scientific Publications.
(30) 1992 (With B. D. Campbell & J. M. L. Mackey) Shoot thrust and its role in plant competition. *J. Ecol.* 80, 633–641. (doi:10.2307/2260855)
(31) (With B. C. Campbell) An experimental test of plant strategy theory. *Ecology* 73, 15–29. (doi:10.2307/1938717)
(32) 1993 (With R. J. Reader, A. Jalili, R. E. Spence & N. Matthews) A comparative study of plasticity in seedling rooting depth in drying soil. *J. Ecol.* 81, 543–550. (doi:10.2307/2261532)
(33) (With G. A. Hendry) *Methods in comparative plant ecology: a laboratory manual.* Sheffield, UK: Springer Science & Business Media.
(34) (With S. Díaz, J. Harris & E. McPherson) Evidence of a feedback mechanism limiting plant response to elevated carbon dioxide. *Nature* 364, 616–617. (doi:10.1038/364616a0)
(35) 1995 (With C. W. MacGillivray) Testing predictions of the resistance and resilience of vegetation subjected to extreme events. *Funct. Ecol.* 9, 640–649. (doi:10.2307/2390156)
(36) 1996 (With J. H. C. Cornelissen, K. Thompson & J. G. Hodgson) Evidence of a causal connection between anti-herbivore defence and the decomposition rate of leaves. *Oikos* 77, 489–494. (doi:10.2307/3545938)
John Philip Grime

(37) 1997  (With R. Hunt, S. Díaz, G. M. Spring, J. H. C. Cornelissen & R. L. Colasanti) Effects of elevated carbon dioxide on British native grassland species and communities. *Abstr. Bot.* **21**, 275–288.

(38)  (With others) Integrated screening validates primary axes of specialisation in plants. *Oikos* **79**, 259–281. (doi:10.2307/3546011)

(39)  Benefits of plant diversity to ecosystems: immediate, filter and founder effects. *J. Ecol.* **86**, 902–910. (doi:10.1046/j.1365-2745.1998.00306.x)

(40)  (With J. G. Hodgson, P. J. Wilson, R. Hunt & K. Thompson) Allocating C-S-R plant functional types: a soft approach to a hard problem. *Oikos* **85**, 282–294. (doi:10.2307/3546494)

(41) 2000  (With V. K. Brown, K. Thompson, G. J. Masters, S. H. Hillier, I. P. Clarke, A. P. Askew, D. Corker & J. P. Kielty) The response of two contrasting limestone grasslands to simulated climate change. *Science* **289**, 762–765. (doi:10.1126/science.289.5480.762)

(42)  (With M. A. Davis & K. Thompson) Fluctuating resources in plant communities: a general theory of invisibility. *J. Ecol.* **88**, 528–534. (doi:10.1046/j.1365-2745.2000.00473.x)

(43)  (With K. Thompson, J. G. Hodgson & M. J. W. Burke) Plant traits and temporal scale: evidence from a 5-year invasion experiment using native species. *J. Ecol.* **89**, 1054–1060. (doi:10.1046/j.0022-0477.2001.00627.x)

(44)  (With S. M. Buckland, K. Thompson & J. G. Hodgson) Grassland invasions: effects of manipulations of climate and management. *J. Appl. Ecol.* **38**, 301–309. (doi:10.1046/j.1365-2664.2001.00603.x)

(45) 2001  *Plant strategies, vegetation process and ecosystem properties*, 2nd edn. Chichester, UK: John Wiley & Sons.

(46) 2002  (With J. M. L. Mackey) The role of plasticity in resource capture by plants. *Evol. Ecol.* **16**, 299–307. (doi:10.1023/A:1019640816376)

(47) 2004  (With others) The plant traits that drive ecosystems: evidence from three continents. *J. Veg. Sci.* **15**, 295–304. (doi:10.1111/j.1654-1103.2004.tb02266.x)

(48) 2006  Trait convergence and trait divergence in herbaceous plant communities: mechanisms and consequences. *J. Veg. Sci.* **17**, 255–260. (doi:10.1111/j.1654-1103.2006.tb02444.x)

(49) 2007  The scale–precision trade-off in spacial resource foraging by plants: restoring perspective. *Ann. Bot.* **99**, 1017–1021. (doi:10.1093/aob/mcm026)

(50)  (With J. D. Fridley & M. Bilton) Genetic identity of interspecific neighbours mediates plant responses to competition and environmental variation in a species-rich grassland. *J. Ecol.* **95**, 908–915. (doi:10.1111/j.1365-2745.2007.01256.x)

(51)  (With R. Whitlock, R. Booth & T. Burke) The role of genotypic diversity in determining grassland community structure under constant environmental conditions. *J. Ecol.* **95**, 895–907. (doi:10.1111/j.1365-2745.2007.01275.x)

(52) 2008  (With J. D. Fridley, A. P. Askew, K. Thompson, J. G. Hodgson & C. R. Bennett) Long-term resistance to simulated climate change in an infertile grassland. *Proc. Natl Acad. Sci. USA* **105**, 10 028–10 032. (doi:10.1073/pnas.0711567105)

(53)  (With D. Johnson & G. K. Phoenix) Plant community composition, not diversity, regulates soil respiration in grasslands. *Biol. Lett.* **4**, 345–348. (doi:10.1098/rsbl.2008.0121)

(54)  (With G. K. Phoenix, D. Johnson & R. E. Booth) Sustaining ecosystem services in ancient limestone grassland: importance of major component plants and community composition. *J. Ecol.* **96**, 894–902. (doi:10.1111/j.1365-2745.2008.01403.x)

(55) 2009  (With J. H. Markham & S. Buckland) Reciprocal interactions between plants and soil in an upland grassland. *Ecol. Res.* **24**, 93–98. (doi:10.1007/s11284-008-0485-1)

(56) 2010  (With M. C. Bilton, R. Whitlock, G. Marion & R. J. Pakeman) Intraspecific trait variation in grassland plant species reveals fine-scale strategy trade-offs and size differentiation that underpins performance in ecological communities. *Botany* **88**, 939–952. (doi:10.1139/B10-065)

(57)  (With J. D. Fridley) Community and ecosystem effects of intraspecific genetic diversity in grassland microcosms of varying species diversity. *Ecology* **91**, 2272–2283. (doi:10.1890/09-2140.1)

(58)  (With R. A. J. Whitlock & T. Burke) Genetic variation in plant morphology contributes to the species-level structure of grassland communities. *Ecology* **91**, 1344–1354. (doi:10.1890/08-2098.1)
| Year | Authors | Title and Details |
|------|---------|------------------|
| 2011 | (With J. D. Fridley, A. P. Askew, B. Moser & C. J. Stevens) | Soil heterogeneity buffers community response to climate change in species-rich grassland. *Glob. Change Biol.* **17**, 2002–2011. (doi:10.1111/j.1365-2486.20) |
| 2011 | (With R. Whitlock, M. C. Bilton & T. Burke) | Fine-scale community and genetic structure are tightly linked in species-rich grasslands. *Phil. Trans. R. Soc. B*** **366**, 1346–1357. (doi:10.1098/rstb.2010.0329) |
| 2011 | (With B. Moser, J. D. Fridley & A. P. Askew) | Simulated migration in a long-term climate change experiment: invasions impeded by dispersal limitation, not biotic resistance. *J. Ecol.* **99**, 1229–1236. (doi:10.1111/j.1365-2745.2011.01841.x) |
| 2012 | (With S. Pierce) | *The evolutionary strategies that shape ecosystems*. Chichester, UK: Wiley-Blackwell. |
| 2014 | (With C. H. Ravenscroft & J. D. Fridley) | Intraspecific functional differentiation suggests local adaptation to long-term climate change in a calcareous grassland. *J. Ecol.* **102**, 65–73. (doi:10.1111/1365-2745.12168) |
| 2016 | (With C. J. Stevens, T. Ceulemans, J. G. Hodgson, S. Jarvis & S. M. Smart) | Drivers of vegetation change in grasslands of the Sheffield region, northern England, between 1965 and 2012/13. *Appl. Veg. Sci.* **19**, 187–195. (doi:10.1111/avsc.12206) |
| 2017 | (With J. D. Fridley, J. S. Lynn & A. P. Askew) | Longer growing seasons shift grassland vegetation towards more-productive species. *Nat. Clim. Change* **6**, 865–868. (doi:10.1038/nclimate3032) |
| 2017 | (With E. J. Sayer, A. E. Oliver, J. D. Fridley, A. P. Askew & R. T. E. Mills) | Links between soil microbial communities and plant traits in a species-rich grassland under long-term climate change. *Ecol. Evol.* **7**, 855–862. (doi:10.1002/eece.32700) |
| 2017 | (With others) | A global method for calculating plant CSR ecological strategies applied across biomes world-wide. *Funct. Ecol.* **31**, 444–457. (doi:10.1111/1365-2435.12722) |