



Plasticity, stability, and yield: The origins of Anthony David Bradshaw's model of adaptive phenotypic plasticity



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ABSTRACT

Plant ecologist Anthony David Bradshaw's account of the evolution of adaptive phenotypic plasticity remains central to contemporary research aimed at understanding how organisms persist in heterogeneous environments. Bradshaw suggested that changes in particular traits in response to specific environmental factors could be under direct genetic control, and that natural selection could therefore act directly to shape those responses: plasticity was not "noise" obscuring a genetic signal, but could be specific and refined just as any other adaptive phenotypic trait. In this paper, I document the contexts and development of Bradshaw's investigation of phenotypic plasticity in plants, including a series of unreported experiments in the late 1950s and early 1960s. Contrary to the mythology that later emerged around Bradshaw's ideas, Bradshaw was engaged in a serious and sustained empirical research program concerning plasticity in the 1950s and 1960s that went far beyond a single review paper. Moreover, that work was not isolated, but was surrounded by an already rich theoretical discourse and a substantial body of empirical research concerning the evolution of developmental plasticity and stability. Bradshaw recast the problem of how to understand (and control) plasticity and stability within an epistemic framework focused on genetic differences and natural selection.

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1. Introduction

In an influential 1965 review in the journal *Advances in Genetics*, plant ecologist Anthony David Bradshaw (1926–2008) (Fig. 1) suggested that changes in particular traits of individual organisms in response to specific environmental factors could be under direct genetic control, and that natural selection could therefore act directly to shape those responses.

The many different sorts of evidence show unequivocally that the ability of plants to be modified by the environment is genetically determined. ... This control is not general to the whole genotype, but is specific for individual characters, and usually specific for individual environmental influences. ... Since the degree of plasticity of a character is under genetic

control, it must follow that it can be influenced by natural selection. (Bradshaw, 1965)

Thus the idea of "adaptive" phenotypic plasticity—according to Bradshaw, plasticity in a trait was not merely environmentally induced "noise" obscuring a core genetic signal, but was potentially specific and refined in the same way as any other adaptive trait.

Although the specifics of its interpretation have changed, Bradshaw's 1965 account remains a core premise of contemporary models of adaptive phenotypic plasticity in evolutionary ecology. It sat at the heart of a rapidly-expanding and diverse research literature during the 1980s, as evolutionary ecologists proposed new models for the evolution of plasticity in a wide range of organisms.¹ The proponents of those models asked questions like, "How and

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¹ Highly influential works from this period include (among others): Schlichting (1986), Scheiner and Goodnight (1984), Stearns and Koella (1986), Via & Lande (1985), and West-Eberhard (1989).

when is phenotypic plasticity adaptive?”, “What is its genetic basis?”, “How might it evolve?”, and “How might plasticity impact the direction and dynamics of evolutionary change?”² Those questions continue to drive research at the interface of ecology and evolutionary biology. Efforts to predict and manage the consequences of shifting global and regional climates depend on understanding how organisms respond to changes in their environments. Many scientists are now attempting to integrate the diverse theories and models of adaptive phenotypic plasticity into predictive models of population distributions (Chevin, Lande, & Mace, 2010; Hoffman & Sgrò, 2011; Reed, Schindler, & Waples, 2011).

Bradshaw was certainly not the first to call attention to the evolutionary implications of phenotypic plasticity. German limnologist Richard Woltereck intended his experiments on morphological plasticity in *Daphnia* around 1905, leading to the idea of the “norm of reaction” (now frequently used to characterize plastic responses), to lend support to Darwinian gradualism (Sarkar, 1999; Peirson, 2012a, 2012b). American geneticist Sewall Wright wrote in 1931 that “individual adaptability is, in fact, distinctly a factor of evolutionary poise,” and “perhaps the chief object of selection” (Wright, 1931, p. 147). In the 1940s, Russian geneticist Theodosius Dobzhansky argued that the evolutionary process leading to higher cognitive function in humans likely involved selection for plasticity in brain development (Dobzhansky & Montagu, 1947). Some Russian biologists did develop theoretical accounts of adaptive phenotypic plasticity in the 1930s and 1940s, but focused mostly on how phenotypic plasticity could alter evolutionary processes, rather than interrogating plasticity in specific traits as products of natural selection (Blacher, 1982; Gause, 1947; Kirpichnikov, 1947; Sarkar & Fuller, 2003; Schmalhausen, 1949).

The centrality of Bradshaw’s ideas to more recent work on adaptive phenotypic plasticity, however, makes understanding the contexts and development of his work in the 1950s and 1960s an important starting-place for contextualizing and analyzing the scientific theories, practices, and discourses that have shaped contemporary models of plasticity.

Along with the surge of interest in adaptive phenotypic plasticity during the 1980s came a new mythology about plasticity research. One example can be found in Schlichting (1986), who wrote that,

Until 1980, theoretical work on plasticity was limited; and empirical research ... was largely unfocused. The reasons for such neglect are puzzling, especially considering the clarity of Bradshaw’s [1965] review. Surely part of the problem was the growing fascination with the detection and measurement of ‘genetic’ variation, of which plasticity must have seemed the antithesis. Another problem was that environmentally induced variability in an experiment is typically avoided at all costs. Experimental complexity and the problem of measuring plastic responses also retarded progress. Thus, only recently has phenotypic plasticity become a major focus of experimental and theoretical studies. (Schlichting, 1986, p. 669)

Two elements of that mythology stand out in relation to Bradshaw’s work. The first is the impression that, despite occasional insights (especially Bradshaw’s), there was little in the way of serious and sustained theoretical or empirical research concerning adaptive phenotypic plasticity prior to the 1980s. The second is the idea that the significance of Bradshaw’s model lay in its rejection of a kind of gene-centric myopism—focusing on genetic differences—and its

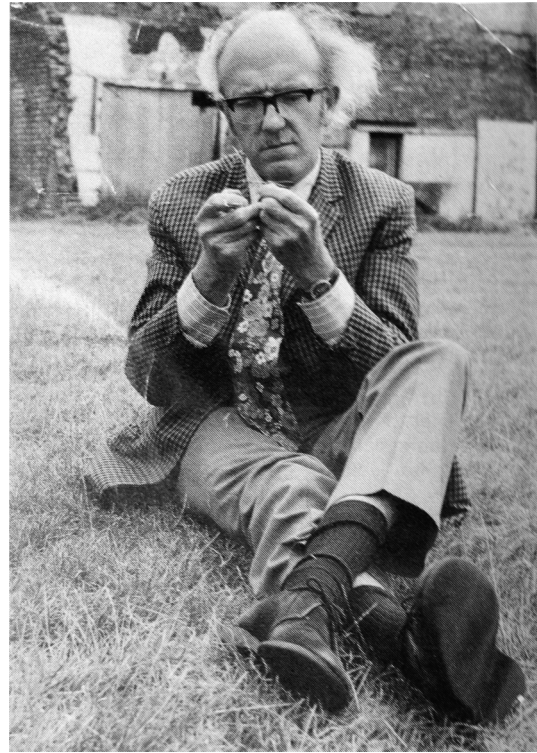


Fig. 1. Anthony David Bradshaw (1926–2008). Photograph from press clippings in Bradshaw archive, dated 1972. Bradshaw is shown inspecting a tiller while sitting in grass in an urban setting, presumably in Liverpool. By courtesy of the University of Liverpool Library. [D1041/5/1/2/33/2](#).

contribution to a “renaissance of the phenotype” (Scharloo, 1989) that emphasized the complex interplay of gene systems and environmental variation.

The main objective of this paper is to enrich our understanding of the context and development of what has become a highly influential understanding of adaptive phenotypic plasticity. I so doing, I hope to dispel some of the mythology described above as it applies to Bradshaw. My central claims are threefold: First, Bradshaw’s work on plasticity consisted of a serious and sustained empirical research program in the 1950s and 1960s that went far beyond a single review paper. Second, Bradshaw’s investigation was not isolated, but was surrounded by an already rich theoretical discourse and a substantial body of empirical research concerning the evolution of developmental plasticity and stability. Third, Bradshaw’s model of plasticity should be seen as a reformulation of that extant discourse—encompassing problems in developmental genetics, population genetics, and plant breeding—within an epistemic framework focused on genetic differences and natural selection. In other words, what made Bradshaw’s approach to plasticity different was that he operationalized a concept about the internal relations of whole organisms within an investigative tradition focused on specific adaptive traits and specific environmental factors.

In Section 2, I provide an overview of Bradshaw’s training in the agro-ecological tradition of genecology, and his ideas about intra-specific evolution in plants. In Section 3, I describe some of Bradshaw’s early ideas about phenotypic plasticity, his exchanges with population geneticist John M. Thoday, and his earliest experiments concerning plasticity in *Agrostis tenuis* (browntop, a.k.a. colonial bent grass). In Section 4, I focus on Bradshaw’s experiments with barley in 1963 and 1964 at the University of California, Davis, where

² Nicoglou (2015) addresses the broader history of concepts of plasticity in the life sciences.

he spent a sabbatical year working with population geneticist Robert Wayne Allard (1919–2003). It was during that collaboration that Bradshaw's ideas about plasticity crystallized. In Section 5, I briefly summarize the content and direction of Bradshaw's research on plasticity following the Davis sabbatical.

2. The genecological approach

Bradshaw began his training as a genecologist at the Welsh Plant Breeding Station (WPBS), in Aberystwyth, in 1948. He continued his dissertation research after taking a position in 1950 as Assistant Lecturer in the Department of Agricultural Botany at the University College of North Wales, in Bangor, and eventually completed his dissertation in 1959. In this section, I introduce genecology as an agricultural research tradition in Britain, and provide an overview of Bradshaw's early investigations of infraspecific evolution in plant populations. By the late 1950s, Bradshaw advocated a model of evolution in plant populations in which strong natural selection and attenuated gene flow produced a “graded patchwork” of local adaptation on very short time-scales. Bradshaw's genecological training and his ideas about local evolution provided the epistemic backdrop for his account of adaptive phenotypic plasticity in the 1960s.

Genecology, also known as “experimental taxonomy” or (later) “biosystematics,” emerged in the first decades of the 20th century as a heterogeneous and interdisciplinary mix of biogeography, cytology, genetics, and field botany (Hagen, 1984, 1986; Kleinman, 2009). In the 1910s and 1920s, botanists in Europe (Turesson, 1922a, 1922b), Russia (Sinskaja, 1931), the United States (Clements, 1908, 1929; Clements & Hall, 1919), and Britain (Gregor, 1931, 1938; Gregor & Sansome, 1927; Stapledon, 1913, 1928; Summerhayes & Turrill, 1939) advocated an experimental approach to the study of genetic variation within plant species. Some genecological research was framed as a more holistic approach to addressing taxonomic questions at or below the level of the species, in contrast to reliance on morphological studies of museum or herbarium collections (Hagen, 1984, 1986). A great deal of genecological research, however, had a far more practical orientation: understanding the patterns and causes of genetic variation among plant populations, and leveraging those differences to improve agricultural production.

The linkage between genecology and agriculture in Britain has deep roots. The WPBS was established in 1919 by Reginald George Stapledon (1882–1960) with funding from steel and shipping magnate Lord Milford, and later from the Ministry of Agriculture and the Empire Marketing Board (Ellis, 1972; Moore-Colyer, 1982; Palladino, 2002). Prior to and during the first world war, an abundance of cheap feed for stock shifted land-use priorities away from maintaining grazable pasture-land and toward crop production (Moore-Colyer, 1982). As the war drew to a close, however, the long-term problem of providing sustainable sources of protein for a growing British population raised concerns about food security: the continued ability to import cheap feed was not guaranteed, raising the question of how to re-establish productive pastures in Britain (Moore-Colyer, 1982). Stapledon was vocal about the importance of converting “derelict” upland areas to rotational “ley” farming, and of developing varieties of grasses and other herbage plants that could maintain high productivity on exposed and infertile hill-tops. Demonstration projects,³ grassland surveys,⁴ and an escalating

rhetoric of war-time food security during the 1930s galvanized an argument for the ‘ploughing-up’ of British hill-sides.

The cornerstone of Stapledon's paradigm for plant breeding at the WPBS, based on his research on *Dactylis glomerata* (cock's-foot grass) in the 1910s (Stapledon, 1913, 1928), was sourcing material from local populations that were adapted to prevailing conditions of soil, climate, and grazing. Stapledon and Thomas James Jenkin (1885–1965)⁵ argued that improvements in the long-term productivity of pastures required “making the habitat as suitable as possible to the desirable indigenous species,” and by “establishing local supplies of ... indigenous seed” (Stapledon & Jenkin, 1916, p.62).

Stapledon's ideas about locally-adapted populations ran parallel to Swedish botanist Göte Turesson's (1892–1970) account of intraspecific varieties, or “ecotypes,” and Stapledon readily adopted Turesson's terminology (Stapledon, 1928). Turesson described ecotypes as “the genotypical response of an ecospecies to a particular habitat,” produced by natural selection (Turesson, 1922a). By “genotypical response,” Turesson meant that selective pressures exerted by particular habitats would act to filter standing genetic variation within a species, producing hereditarily distinct habitat-specific ecotypes. According to Turesson, the genecologist's task was to detect and describe patterns of ecotypic differentiation using experimental methods designed to suppress phenotypic plasticity (Turesson, 1922a, 1922b, 1923, 1925).

The genecological approach involved two principle experimental methods. The “common garden” technique involved collecting individual plants (either as seed, or as vegetative cuttings) from contrasting habitats, and growing them under uniform conditions. Common garden experiments minimized phenotypic differences due to environmental variation, so that any remaining differences among samples could be attributed to heredity. A similar “reciprocal transplant” method was developed by Frederic E. Clements and Harvey M. Hall at the Carnegie Institution of Washington in the 1910s, and was popularized by Jens Clausen, David Keck, and William Heisey in the 1930s and 1940s (Hagen, 1982; Smocovitis, 1988). Those experiments involved collecting plants from contrasting environments, and growing them at each of a series of stations spread from the Stanford University campus (100 feet above sea level) to a site known as “Timberline” (around 10,000 feet), beyond the ridge of the Sierra Nevada mountain range. Ecotypes that were indistinguishable in one environment would often exhibit dramatic differences when grown in a contrasting environment, due to phenotypic plasticity.

As concerns about long-term food security in Britain mounted prior to and during the second world war, genecologists continued to hunt for ecotypes that could improve the grazing potential of marginal, derelict, and upland pastures (Moore-Colyer, 1982). Genecologists sampled populations of forage grasses, clovers, and other herbage plants throughout Britain and western Europe, and tested those plants in carefully controlled experimental plots in order to find hereditary differences that could be further developed through breeding (e.g. Beddows, 1949).

When Bradshaw arrived at the WPBS in 1948, the application of genecological methods to agricultural improvement remained a dominant part of the station's research agenda. Bradshaw recalled that, “the heritage of George Stapledon was never far away” (D1041/13/2/9). The genecological approach had uptake not only at the WPBS, but also by James Wylie Gregor (1900–1980) at the

³ E.g. the Cahn Hill Improvement Scheme, a privately-funded large-scale farm trial that focused on grasses, clovers, and rapeseed.

⁴ E.g. William Davies' recent country-wide pastureland survey, commissioned by the Ministry of Agriculture in 1938.

⁵ Jenkin was an Honours student in botany at UCW, who would become Stapledon's long-time research partner and eventual director of the WPBS (Moore-Colyer, 1982).

Scottish Plant Breeding Station (SPBS), near Edinburgh, starting in the 1920s (Gregor & Sansome, 1927). Gregor was among Bradshaw's most influential mentors during the early stages of his career (D1041/13/2/9).⁶

Bradshaw's dissertation research at the WPBS focused on the genecology of *A. tenuis* (colonial bentgrass) and *Anthoxanthum odoratum* (sweet vernal grass). Both species had potential for use on acidic soils and exposed upland grazings (Beddows, 1956; Davies, 1952, 1953; Jones, 1956).⁷ Bradshaw conducted a broad genecological survey in western Wales and southern England, using both common garden and reciprocal transplant methods. Bradshaw spent much of the 1950s building a research program around populations of heavy-metal tolerant *Agrostis* that he found during his initial survey (first reported in Bradshaw, 1952). Bradshaw hypothesized that particular populations of *Agrostis* were specially adapted to specific heavy metals, and that those adaptations were the result of powerful and ongoing natural selection at the edges of abandoned mineworks. That hypothesis prompted a multi-pronged research program involving further genecological trials, physiological experiments, field studies of seed and pollen dispersal, and (in the 1960s) computer simulations (Aston & Bradshaw, 1966; Bradshaw, 1963, 1966; Bradshaw, Chadwick, Jowett, & Snaydon, 1964; Bradshaw, Mcneilly, & Gregory, 1964; Bradshaw, Lodge, Jowett, & Chadwick, 1958, 1960a, 1960b; Bradshaw & Snaydon, 1959; Gregory & Bradshaw, 1965; Jain & Bradshaw, 1966).

Genecologists at the WPBS and SPBS differed from other genecologists, both in Britain and abroad, in the way that they conceptualized ecotypes. As early as the 1940s, there was growing disagreement about what counted as evidence for distinct ecotypes, and about the evolutionary and taxonomic relationships between ecotypes and other intra- and intraspecific units (e.g. see Bennett, 1964). Although Gregor had previously advocated a genecological systematics in parallel to traditional taxonomy (Gregor, 1931; Gregor, Davey, & Lang, 1936), by the 1940s he and his collaborators had moved away from attempts diagnose ecotypes as distinct, coherent, and namable entities. Instead, they focused on detecting and explaining ecotypic differentiation in *individual characters* as adaptations to *specific environmental factors*. SPBS staffer Frederick Earnshaw summarized this approach in a session on experimental taxonomy at the 7th International Botanical Congress in Stockholm, Sweden, in 1950:

Gregor has emphasized that each population must be influenced by a complex of environmental factors, each capable of independent variation. He therefore considers it will be preferable to trace eco-clinal variation in response to particular ecological gradients, rather than to attempt to name local populations as distinct ecotypes. (Earnshaw, 1950)

The rejection of discrete, objectively-delimitable ecotypes entailed a strongly operational view of the ecotype concept. When Gregor, Bradshaw, and their colleagues talked about “ecotypes,” “clines,” or “demes,” they referred to patterns that they observed and

stabilized using genecological methods, and *not* to natural kinds or entities that existed independently of those observations (Bradshaw, 1962).⁸

That emphasis on linking variation in specific traits to variation in specific environmental factors was a crucial component of Bradshaw's epistemic framework. Like many of his peers, Bradshaw recognized that there were complex developmental linkages among traits, and that those linkages could impact evolutionary processes. But when it came to making claims about ecotypic differentiation, the kind of evidence that mattered was strong geo-spatial correlations between specific phenotypic traits and specific environmental factors. For example, Bradshaw found that differences in survivorship in samples of *A. odoratum* during a very severe drought in 1949 were closely correlated with mean annual rainfall at the sites where they were collected (Fig. 2).

Bradshaw's epistemic commitments, described above, were tied to a model of infraspecific phenotypic evolution in which the spatial distribution of a species, the “pattern of the environment,” and the availability of genetic variation played dominant roles. Over the course of the 1950s Bradshaw was increasingly vocal in asserting that, even in wind-pollinated outbreeding plants like *Agrostis*, gene flow was often sufficiently attenuated and natural selection sufficiently strong to cause differentiation over distances of 100, 50, or even 15 m.⁹ “As a result,” Bradshaw wrote, “population differentiation could occur in relation to very local variations in environment. The data¹⁰ show exactly this” (Bradshaw, 1959a, 1959b, p.223).

By the end of the 1950s, Bradshaw saw plant populations as a “graded patchwork” of morphological and physiological adaptations to extremely local environments (Bradshaw, 1959a, 1959b, 1960).

It is the environment, even its local variations, which determines the pattern of the differentiation [in plant populations]. So where there are sharp changes in environment, e.g. from the foot to the top of Pen Dinas, there are sharp correlated changes in the populations.¹¹ Where there are gradual changes in environment, e.g. from the foot of Pen Dinas to the summit of Plynlymon, the population changes are equally gradual.¹² Where in such gradients there are sudden local variations, e.g. Goginan

⁸ This shift in emphasis, and a growing body of evidence from the field, suggested that evolution could occur rapidly and locally enough to be observed “as it occurred,” and not merely in retrospect.

⁹ Bradshaw (1952) reports differentiation over 100 yards, and in Bradshaw (1959a, 1959b) that number drops to 50 m. McNeilly and Bradshaw (1968) report differentiation over a distance of 15.5 m. Bradshaw's ideas about micro-geographic adaptation in plants, and its consequences for interpreting and classifying so-called ‘ecotypic differences,’ ran counter to the views of prominent genecologists and other evolutionary biologists in the United States, including the notorious and influential ‘Carnegie trio’ of Jens Clausen, William Hiesey, and David Keck at the Carnegie Institute of Washington in Stanford, California (Clausen, Keck, & Hiesey, 1939, 1940, 1947, 1948). On a visit to the Welsh Plant Breeding Station, Keck dismissed Bradshaw's findings as “accidents” (D1041/13/2/9). After Bradshaw published the results of his genecological survey in the late 1950s, Clausen wrote to Bradshaw that “As far as I can see, the area that has been sampled is climatically so uniform that no climatic ecotypes should be expected to exist ... It may come as a surprise to you, but I have a suspicion that the major part of the island of Great Britain probably belongs to one climatic zone.” (D1041/5/1/1/17).

¹⁰ Bradshaw refers to his genecological survey of *Agrostis tenuis*.

¹¹ Pen Dinas is a hill to the south of Aberystwyth. The top of the hill is exposed to strong sea winds from St. George's Channel, whereas the pasture at the foot of the hill is very effectively sheltered by the surrounding topography. Bradshaw found that *Agrostis* at the top of the hill have evolved to have a ‘dwarf’ stature and low yield, spreading primarily through protected subterranean stolons. *Agrostis* at the foot of the hill were taller in stature, with higher yield.

¹² Plynlymon is the highest hill in Wales, at 2468 feet. The gradient mentioned here is the transition from low to high altitude, accompanied by a shift from arable *Agrostis-Festuca* and *Lolium-Agrostis* pastures to the *Nardus*-dominated exposed upland grazings.

⁶ The link between genecology and agricultural research had significant consequences for international agricultural policy, as described by Pistorius (1997). Gregor, and his students and collaborators, played a significant role in translating genecological methods and theory into international policy, in part via their involvement with the United Nations Food and Agriculture Organization.

⁷ Research on *Agrostis* for breeding purposes started in the early 1920s (NLW E25/6), and showed up again in the 1940s (NLW E37/13–14; NLW C5/1). Arthur Rhys Beddows, head of the grass breeding department at the Welsh Plant Breeding Station, hailed Bradshaw's genecological research as a contribution to the grass breeding program. “We have in addition two new strains, one of bent grass (*Agrostis tenuis*) and the other of sweet vernal grass (*Anthoxanthum odoratum*), both of which may be more useful in the less fertile marginal areas” (Beddows, 1956, p.13).

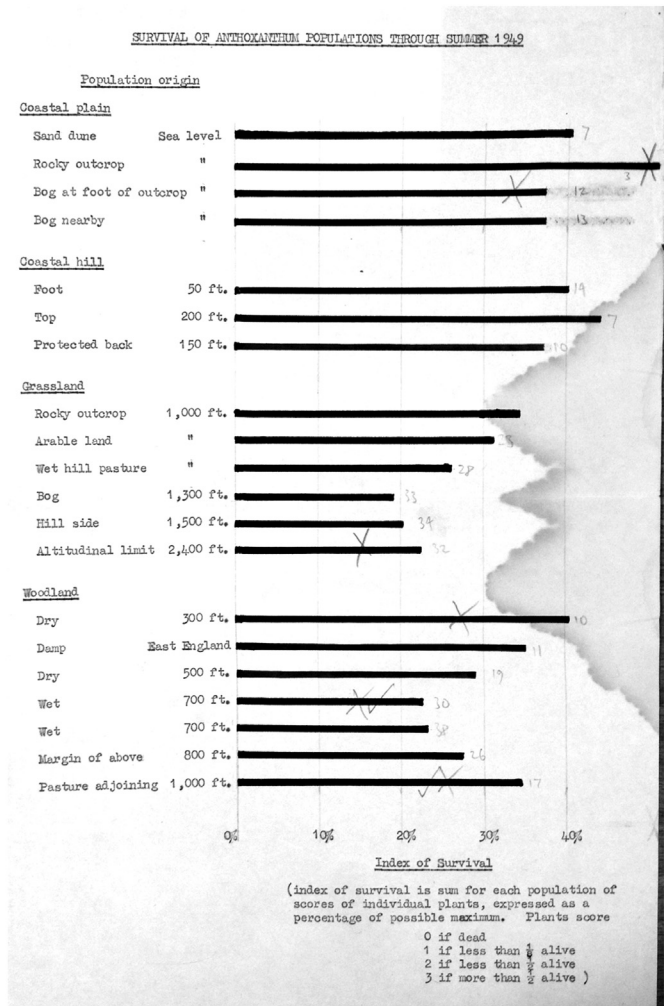
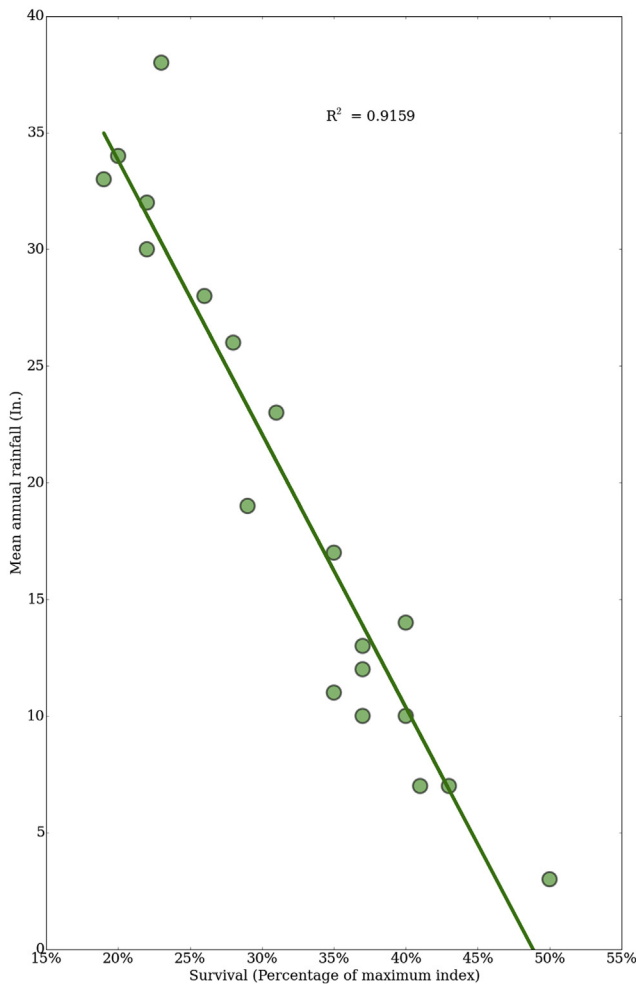


Fig. 2. Survivorship in samples of *Anthoxanthum odoratum* during a very severe drought in 1949 was correlated with the mean annual rainfall at the sites where they were collected. Bradshaw's unpublished figure is shown at right (D1041/2/8/1). By courtesy of the University of Liverpool Library. Data replotted at left.

mine, there are sudden population changes.¹³ (Bradshaw, 1959a, 1959b, p.224)

Following Gregor, Bradshaw dismissed attempts to classify plant populations as distinct ecotypes as “subjective,” and considered any system of infraspecific taxonomic classification to be “a source of confusion” (Bradshaw, 1959a, 1959b, p. 225). Bradshaw saw natural selection as the foremost explanation for patterns of differentiation in plants, writing that, “All explanations ... must be considered but in most cases it is unnecessary to postulate the effects of anything other than natural selection” (Bradshaw, 1959a, 1959b, p.225).

Bradshaw also saw local adaptive evolution as a potentially rapid process. When he began his research in 1948, Bradshaw thought that even six thousand years was insufficient for plant populations to become adapted to changes in their environments (D1041/1/11/87). But by the 1960s Bradshaw's understanding of the speed of adaptive evolution had dramatically changed. “We are brought up to think that the time scale of evolution is millennia,” he

wrote; “This may be true for the history of life but it is not true for the immediate process of evolution within species.” (Gregory & Bradshaw, 1965). In a presentation to the British Ecological Society in 1968, Bradshaw asserted that “even twenty five years grossly over estimates the time needed” for the evolution of particular phenotypic traits (D1041/1/11). Bradshaw's change of mind is representative of a broader shift in thinking by ecologists about the temporal and spatial scales of evolutionary change during this period that merits further investigation (Collins, 1986).

3. Early experiments: phenotypic flexibility in *Agrostis*

“There seem to be so many facets of [phenotypic plasticity] that it is difficult to know exactly what terms to use and almost where to begin.” (Letter from Bradshaw to Ken Lewis, Oxford Botany School, March, 1961; D1041/4/3/21)

In the last section, I introduced the main epistemic context for Bradshaw's early research, a particular flavor of genecology practiced at the Welsh and Scottish Plant Breeding Stations. In this section I describe Bradshaw's early ideas about adaptive phenotypic plasticity, and a series of unpublished experiments that explored those ideas. Bradshaw's earliest notes and correspondence on this topic place his ideas in the context of a broader discourse surrounding the relationship between heterozygosity

¹³ Bradshaw found a population of heavy-metal tolerant *Agrostis* growing on a contaminated tip at Goginan mine in the early 1950s. The *Agrostis* surrounding the mine was non-tolerant, despite being almost directly adjacent to the tolerant plants.

and developmental stability, and highlight some of the tensions that motivated his work on plasticity in the 1960s.

3.1. A nagging observation

By the mid-1950s, Bradshaw was wrestling with a nagging observation. In many cases, the differences that he found between *Agrostis* populations in his carefully-controlled common garden experiments were less distinct than what he had observed in the field (D1041/13/2/9). If, for example, plants from one population grew taller and more densely than another population in the common garden, then that difference tended to be far more pronounced—perhaps twice or three times so—in the field. Bradshaw inferred that (phenotypic) responses to the environment during development were very important component of (genetic) adaptation to specific environments.

In the fall of 1957, Bradshaw began to articulate his ideas about plasticity. On 23 November, Bradshaw floated those ideas in a presentation to the Genetical Society of Great Britain at the University College, London. Bradshaw noted that some closely related species, and perhaps even populations within a single species, differ in their “phenotypic flexibility” (Bradshaw, 1958a, 1958b). Certain species of *Potamogeton* (pondweed), for example, develop floating leaves just at the water’s surface, while others do not (D1041/4/3/29). Likewise, the leaves of *Ranunculus* subgenus *Batrachium* (the water buttercup, or water crowfoot) develop markedly different forms depending on whether the plant is submerged, and that response differs greatly among species within the subgenus (D1041/4/3/28). Bradshaw argued that, “phenotypic flexibility must ... be a character with an ordinary genetic basis,” and that “its occurrence in species and in populations will be under the control of the normal processes of natural selection” (Bradshaw, 1958a, 1958b).

During the ensuing discussion, Bradshaw’s presentation drew a rude¹⁴ rebuff from geneticist John Marion Thoday (1916–2008) (D1041/4/3/27/8). In a paper at the Society for Experimental Biology’s symposium on Evolution in 1952, Thoday discussed phenotypic flexibility as part of a larger theoretical account of fitness and “evolutionary progress” (Thoday, 1953), and Bradshaw’s conceptualization of flexibility seemed dissonant. The confrontation led to an exchange of letters a few weeks later, in which Thoday and Bradshaw staked out their positions more clearly.

Thoday agreed with Bradshaw about the adaptive significance of phenotypic flexibility. But whereas Bradshaw defined flexibility as “the ability of a genotype to vary its expression in different environments,” (D1041/4/3/27/8) Thoday defined phenotypic flexibility as the capability of an organism “of adapting itself to varying external conditions so that ... it maintains its characteristics” (Thoday, 1953, p. 99; emphasis added). Thoday thought that Bradshaw’s emphasis on morphological differences entailed too narrow a conception of the phenotype, which ought also to include biochemical and physiological characteristics. Bradshaw, on the other hand, thought that Thoday’s account was inappropriate for plants. Bradshaw wrote to Thoday,

The confusion stems, as far as I can see, from the difference between the animal and the plant approach. I can understand how your concept fits animals well, since a phenotype which

can exist in different environments without change could well be said to be flexible. But in plants the position is rather different. Many are able to exist in several different environments only as a result of considerable phenotypic changes. This is where the use of the term phenotypic flexibility gets a bit difficult. (D1041/4/3/27/8)

In response, Thoday suggested that Bradshaw adopt taxonomist William Bertram Turrill’s (1890–1961) concept of “plasticity:” the kind of measurable environmentally-induced phenotypic variation that the genecologists’ common-garden cultivation experiments were designed to minimize.

Bradshaw agreed, noting that, “I will have to make it quite clear that there are two sorts [of plasticity], that which is adaptive and that which is not” (D1041/4/3/27/8).

Bradshaw thus faced the problem of discriminating between adaptive and non-adaptive plasticity. He wrote to Thoday,

I want to go on from your deliberations in S.E.B. Symposium 7 and consider the actual types of habitats in which phenotypic flexibility is likely to be important, and the plants with high plasticity which substantiate this. (D1041/4/3/27/8)

The crux of Bradshaw’s struggle with Thoday’s account of phenotypic flexibility at that time, however, was that it gave little guidance about what kinds of phenotypic changes were adaptive and which were not. Thoday conceded that,

When it is approached from the end of observation we are in difficulties because it is clear that observable variation of phenotype with variation of environment may be evidence for adaptive changes, but may equally well be evidence that the particular genotype we are studying has no phenotypic flexibility and gets pushed around in undesirable ways by the environmental conditions. (D1041/4/3/27/6)

For a genecologist interested in the adaptive relationship between individual characters and specific environmental factors, the lack of a clear empirical criterion in Thoday’s conceptualization of phenotypic flexibility was a grave deficiency indeed.

3.2. Bradshaw’s first experiments

Bradshaw was not deterred by Thoday’s reaction to his presentation at the Genetical Society, and mapped out a series of eight experiments to be carried out in the summers of 1958 and 1959. Those experiments would examine differences in plasticity among populations of *A. tenuis* and *Agrostis stolonifera*, and among regional varieties of *Polypogon*, *D. glomerata*, *Sonchus oleraceus* (sow thistle), and *Hypericum perforatum* (St. John’s wort), in response to soil moisture, fertility, and grazing.

Bradshaw approached the problem of discriminating between adaptive and non-adaptive plasticity as a genecological one. In his research notes, Bradshaw wrote:

The normal pattern of evolution is such that characters are only developed to any marked extent in those situations where they are adaptive. In situations where they are neutral they are lost slowly or very slowly; where they are nonadaptive they are usually lost quickly unless other factors are operating. Bearing this in mind it should be possible to indicate situations in which plasticity is distinctly advantageous and discover examples to substantiate this.

Just as a strong correlation between a particular environmental factor and hereditary variation in a trait would count as evidence for adaptive (ecotypic) differentiation, so to would a correlation between environment and a plastic response.

¹⁴ Bradshaw characterized Thoday’s comments as rude (D1041/4/3/27/8), although the frankness of their exchange may have been due in part to an underlying friendship. Their correspondence shows that they were already on a first-name basis. This would not be surprising since Thoday’s father, David Thoday (1883–1964), occupied the chair of Botany at UCNW Bangor until 1949, and Bradshaw and the Thodays surely had many social and professional ties in common.

Bradshaw carried out his first experiments on phenotypic plasticity in *Agrostis* in the spring and summer of 1958, focusing on responses to both soil moisture and fertility.¹⁵ He collected tillers (side-shoots) of *Agrostis* from five sites among the thirty-three in his original genecological survey (Fig. 3):

1. PL3: *A. tenuis* from the exposed, infertile top of Plynlimon, near Bangor. Shorter plants with a dense growth habit and lower yield, relying almost entirely on subterranean rhizomes (rather than exposed stolons) to spread.
2. RS1: *A. tenuis* from a more fertile “damp oakwood on acid clay” (Bradshaw, 1959a, 1959b, p. 214) at Ruislip, northwest of London. Taller plants with more lateral growth and higher yield, spreading almost entirely by stolon.
3. OX5: *A. tenuis* from a heavily grazed lowland meadow near Oxford, preferring “drier areas poor in bases” (Bradshaw, 1958b, p.81). A taller plant with less lateral growth, and lower yield.
4. OX3: *A. stolonifera* from the same site as OX5, preferring wetter areas. Shorter than OX5, but with much higher yield and more lateral stoloniferous growth.
5. OX4: Apparent hybrids of OX5 and OX3, that “combine the ability to spread of *A. stolonifera* with the high density of tillers of *A. tenuis*” (Bradshaw, 1958b, p. 77). Bradshaw found these hybrids interesting because they occurred under conditions intermediate to those preferred by their parents, and exhibited intermediate phenotypes.¹⁶

Bradshaw chose those populations (1) to represent widely contrasting habitats (e.g. RS1 vs PL3), and (2) to explore the idea that the presence of OX4 hybrids was explained by the availability of conditions intermediate to those preferred by *A. tenuis* and *A. stolonifera*.

Bradshaw planted tillers three-to-a-pot in a corner of the greenhouse, and arranged them into six replicates of four treatments: low fertility dry, low fertility wet, high fertility dry, and high fertility wet. After the plants established themselves in their pots, he cut them back to 1/2" above the soil surface, and began watering the plants in the wet and dry treatments discriminately. Four weeks later he supplemented the high-fertility pots with John Innes “L” Feed.¹⁷ Seven weeks after the fertilizer treatment he cut the plants back again, and measured four traits for each plant: dry weight, stolon length, overall above-ground plant length, and number of tillers. For each trait, he used an analysis of variance (ANOVA) to test for differences between populations in their response to soil moisture and fertility (D1041/4/3/23/4).

The experiment yielded dramatic differences between populations in their response to varying soil moisture and fertility, except in dry weight. Bradshaw repeated the whole procedure twice, and some of the results from the second harvest are shown in Figs. 4 & 5. The four populations of *Agrostis* varied in their response to soil moisture in stolon length, overall plant length, and number of tillers. The differences among populations in response to soil

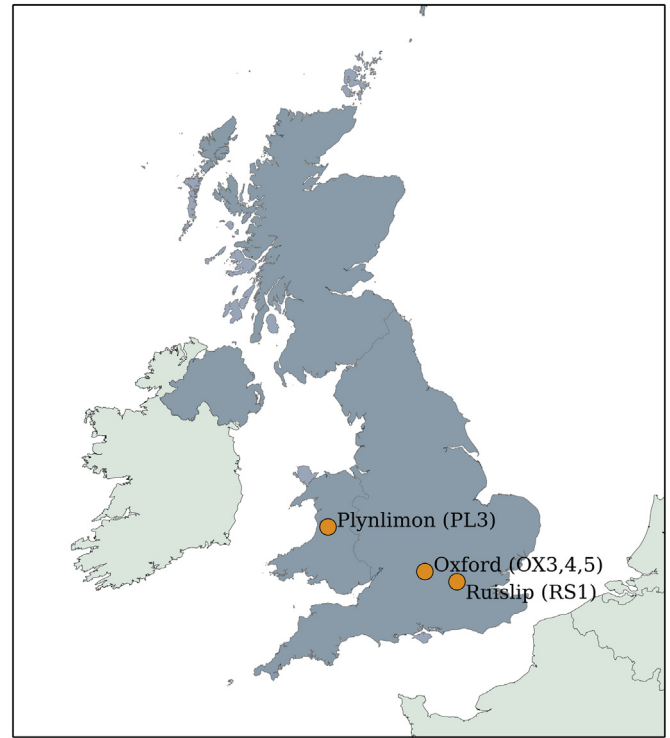


Fig. 3. Collection sites for Bradshaw's experiments on phenotypic plasticity in *Agrostis* in 1958 and 1959.

fertility were somewhat less dramatic, with differences only in plant length and number of tillers.

Bradshaw conducted a set of follow-up experiments in the summer of 1959. This time he focused only on response to soil moisture, and excluded the hybrid population from Oxford (OX4). This allowed him to increase both the number of replicates and the number of plants per replicate, and to repeat the experiment in both outdoor garden plots (planting in May, harvesting in July) and in boxed beds in the greenhouse (planting in July, harvesting in October). The results were consistent with those from the 1958 experiment (Fig. 6).

Although Bradshaw's work on plasticity tapered somewhat after the summer of 1959, he remained “rather stuck on the subject” (D1041/4/3/21). In the autumn of 1960 he wrote to the director of the Institute of Plant Systematics and Genetics at the Royal Agricultural College in Uppsala, asking for samples of two varieties of *Polygonum amphibium* (water knotweed) that Turesson had shown him a decade prior: one of which was highly plastic, and the other of which was not (D1041/4/3/20).¹⁸ It does not appear that he ever received that material, despite repeated requests. But those attempts are evidence of a sustained effort to approach the phenomenon of plasticity experimentally and comparatively.

4. The barley experiment at Davis

Meanwhile, many changes were afoot at Bangor, some of which conspired to reorient Bradshaw's research on plasticity and pave

¹⁵ Bradshaw's notes indicate that he carried out a third experiment, with *Polygonum monspeliensis*, in 1959. But no data from that experiment remain among his papers.

¹⁶ Bradshaw had found other such hybrids at ecologically similar sites around southern England. In his discussion of the *A. tenuis* × *A. stolonifera* hybrids, Bradshaw referred to Edgar Anderson's concept of “hybridization of the habitat,” in which environments intermediate to those preferred by two closely related species provide opportunities for the emergence and establishment of hybrids.

¹⁷ 18 parts N, 6 parts P₂O₅, and 6 parts K₂O.

¹⁸ Knotweed is known for its two distinct environmentally-induced growth forms—terrestrial and aquatic—that differ greatly in leaf shape and overall growth habit. In 1950 Bradshaw had attended the Botanical Congress in Stockholm and, while on a tour of the botanical garden at Uppsala, Göte Turesson showed Bradshaw two varieties: one which responded to environmental conditions, and one which did not.

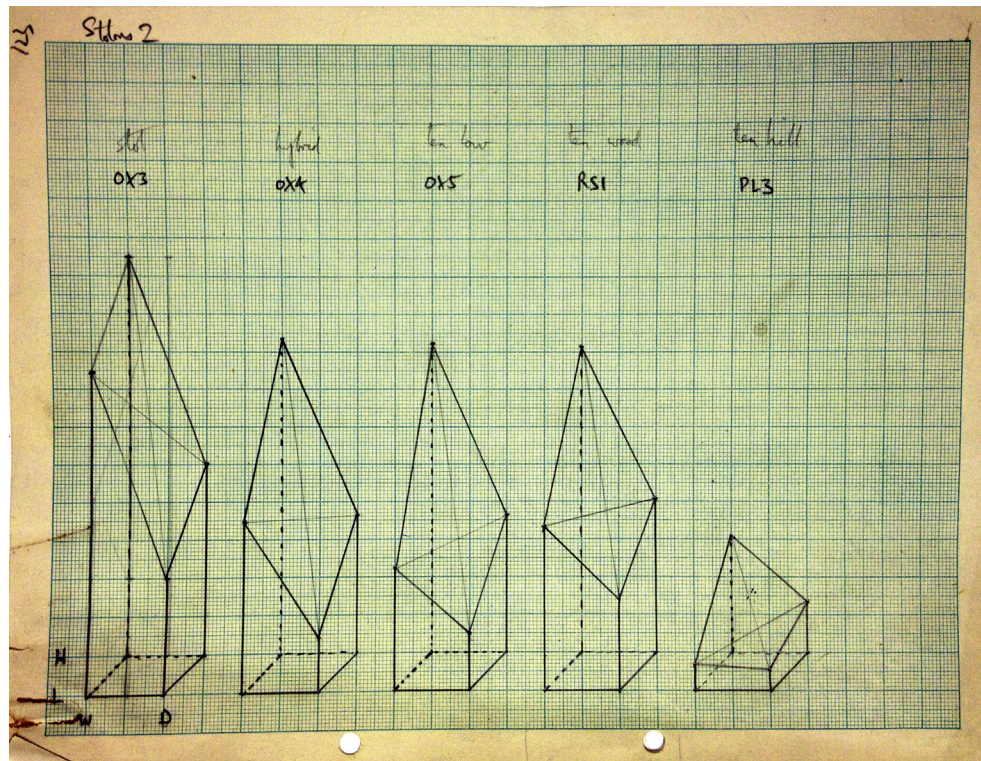


Fig. 4. Hand-drawn figure by Bradshaw depicting population differences in stolon length in response to soil moisture and fertility. By courtesy of the University of Liverpool Library. D1041/4/3/23.

the way for a collaboration with population geneticist Robert W. Allard at Davis. After a two-year search, Oxford-trained ecologist John Lander Harper replaced R. Alun Roberts as Professor of Agricultural Botany at Bangor.¹⁹ Before coming to Bangor, Harper spent a year at the University of California, Davis, working with the chair of the newly-established Department of Genetics, George Ledyard Stebbins (1906–2000). Between the buzz surrounding Bradshaw's research group on mineral nutrition and heavy metal tolerance, and Harper's own burgeoning acclaim and connections to botanists in the United States, Bangor was becoming a "mecca" for plant ecologists.

Harper's connection to Davis botanists likely helped to pave the way for Bradshaw's collaboration with Allard in 1963 and 1964. While at Davis, Harper advised Allard on an experiment concerning the stability and yield of genetically diverse strains of lima bean (Allard, 1961). In 1961, Stebbins visited Harper at Bangor. Bradshaw was drafting a manuscript about the conceptual issues surrounding phenotypic plasticity (D1041/4/3/21), and discussed his ideas with Stebbins (D1041/4/3/19). Soon, a plan was hatched for Bradshaw to visit Davis and work with Allard on the problem of the genetic and adaptive basis of plasticity and stability.

Finally, in 1963, Bradshaw secured a research fellowship from the Leverhulme Trust to fund the long-awaited trip to Davis. That autumn, after moving himself, his wife, and his two

daughters "across the pond," Bradshaw began an extensive experiment concerning phenotypic plasticity in barley. Prior to his departure, Bradshaw coordinated with Roger Whitehouse at the Plant Breeding Institute, in Cambridge, to establish a set of parallel experiments at Bangor in his absence. Those experiments would involve a few varieties of barley and of two species of oat: bred varieties of *Avena sativa*, the modern cultivated cereal, and the wild oat *Avena strigosa*. Bradshaw also tasked a new PhD student, Muhammed Akram Khan (an aspiring plant breeder from Pakistan), with studying plastic responses to density in flax.

Bradshaw's experiment at Davis sat at the intersection of multiple scientific and agro-economic contexts that were crucial for his 1965 account of adaptive phenotypic plasticity. Unfortunately, Bradshaw never published the results of that experiment, and only a small fragment of the data remains in his archive. Some indications of the results can be found in subsequent correspondence and grant applications. Yet ultimately it is the *design* of Bradshaw's experiment, rather than its results, that provide the most telling indications of the driving questions and contexts for his account of adaptive plasticity.

The barley experiment was relatively simple, albeit large. In mid-November, 1963, Bradshaw selected twelve varieties of barley (*Hordeum vulgare*), seven of which were well-adapted to the Mediterranean climate of north-central California (Table 1). Of the adapted varieties, four were reputed to produce more stable yields across a range of environmental conditions. Over the course of three days, starting on a Thursday in December, Bradshaw planted 1700 seeds of each variety in plots of equal area at three spacings: 12", 6", and 4" apart. Four months later, on a Saturday in April, the barley started to come to head. Over the next few weeks Bradshaw measured ten quantitative characters on each plant (Table 2). Bradshaw's statistical model focused on varietal differences in both

¹⁹ Bradshaw had applied for the post in 1958, with support from Roberts, tropical ecologist Paul Richards, and Herbert Baker. The search committee was unusually vague in their official reports to the College Council during this process, so it is unclear who else applied for the post. Perhaps Bradshaw's aspiration toward a full Professorship was premature: after all, Bradshaw had yet to actually acquire his PhD, despite a portfolio of almost twenty research publications. Harper accepted the position prior to his sabbatical in 1959.

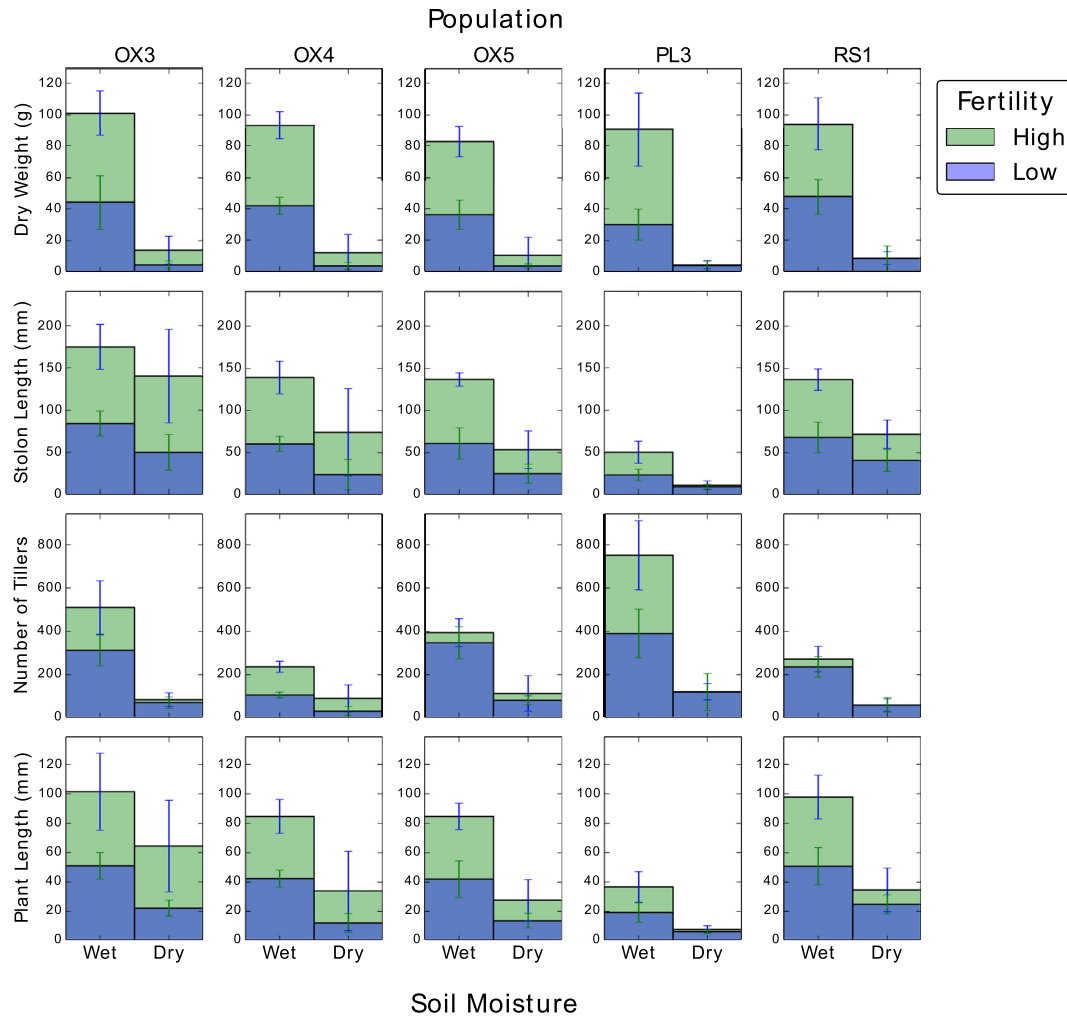


Fig. 5. Differences in response to soil moisture and fertility among plants collected from five populations of *Agrostis* spp. Data for the experiment ending 22 August, 1958, as recorded in Bradshaw's notebooks.

the mean and variance among *treatments*, among *individual* plants, and *within* individual plants.

There are three notable contrasts between Bradshaw's experiment at Davis and his earlier experiments at Bangor. First, he switched from the rampantly outbreeding bentgrasses to barley, which was largely self-fertilizing. Second, instead of testing responses to fertility and moisture, he focused on responses to planting density. Third, rather than simply comparing means among treatments and populations as he had done in the 1950s, Bradshaw compared both means and variance, and at three different levels: the response of varieties to contrasting densities, variation in response among individuals within those varieties, and (for some traits) variation in response within individual plants (Table 2). Each of those shifts is significant for understanding Bradshaw's ideas about plasticity.

4.1. The material: barley

The impetus to use a self-fertilizing cereal like barley, rather than the outbreeding bentgrasses on which Bradshaw had focused for over a decade, likely came from Allard.

Robert Wayne Allard (1919–2003) was born into a farming family in the San Fernando Valley, California. As a child, he was inspired by UC Berkeley plant breeder W. W. Mackie. He studied agriculture at the University of California at Davis, starting in 1937,

where he was influenced by the prolific cereal breeder Coit Alfred Suneson (1903–1976). As a PhD student at the University of Wisconsin, Madison, Allard was influenced by theoretical population geneticist Sewall Wright. In 1946, Allard returned to Davis as an assistant professor of agronomy, and as an assistant geneticist in the Agricultural Experiment Station where he was responsible for bean breeding (Clegg, 2006).

Allard's research on lima beans and barley in the 1950s and 1960s challenged Stebbins' model of evolution in self-fertilizing plants. Stebbins' model of evolution in inbreeders predicted that natural populations of self-fertilizing plants should be composed of reproductively isolated homozygotic lines. Occasional interbreeding between those lines would, according to Stebbins' model, produce new heterozygotic variants that would undergo selection and form new inbred lines (Stebbins, 1950). But Allard demonstrated, both theoretically and empirically, that even low levels of outbreeding (2–5%) were enough to maintain both a high level of genetic variation and a high level of heterozygosity (Allard & Jain, 1962; Allard & Workman, 1963; Jain & Allard, 1960; Workman & Allard, 1964). Allard's work opened up the range of possible approaches to breeding crops like oats, beans, and barley.

Allard advocated a "bulk population" approach to plant breeding that, he contended, was better suited to changing environmental conditions and agricultural practices, such as the increasingly intense use of fertilizers. Because breeders focused on isolating a

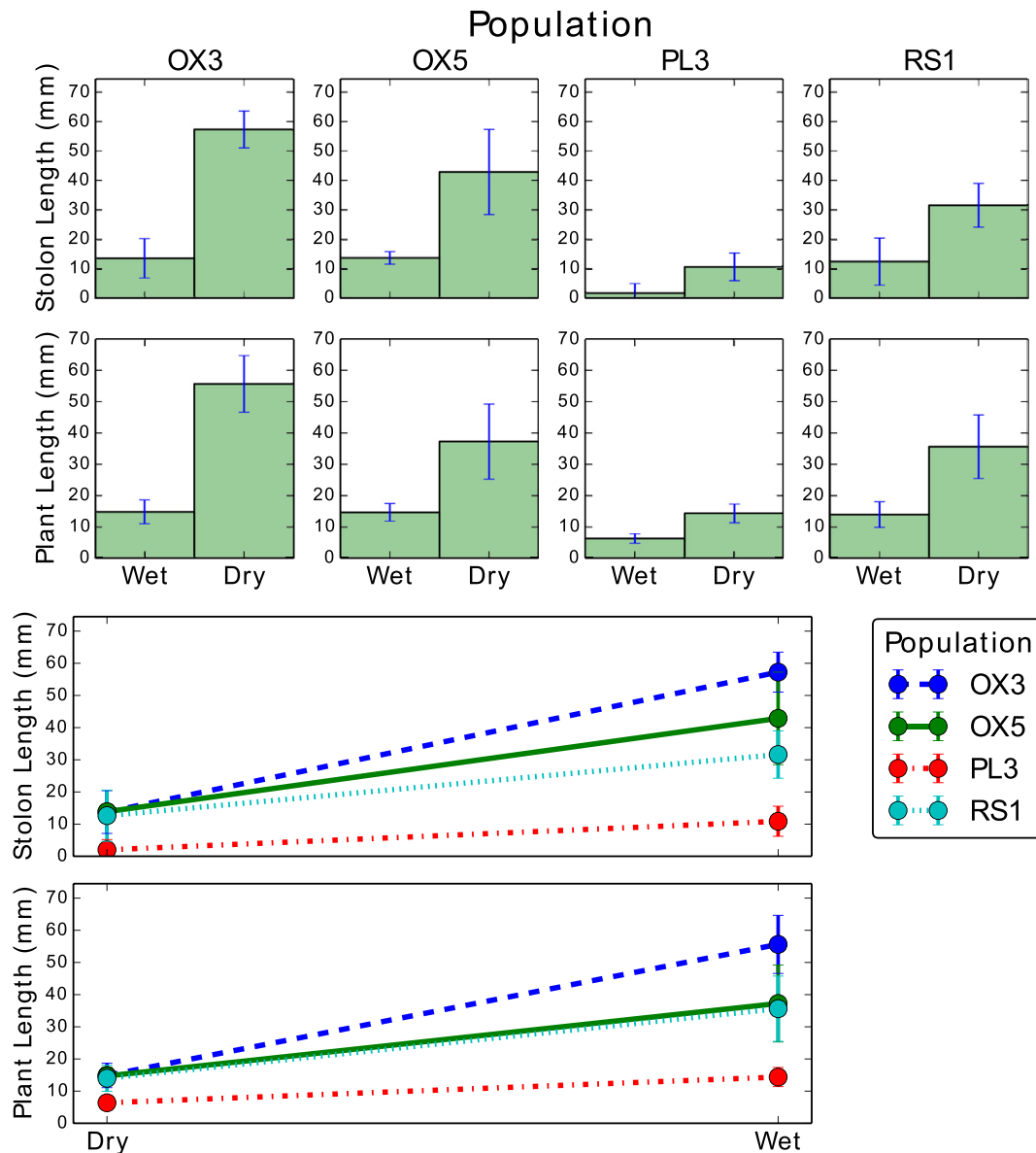


Fig. 6. Differences in response to soil moisture among plants collected from four populations of *Agrostis tenuis*. Tillers sampled from each population were planted on 13 May, 1959, in spaced plots outdoors. Data from Bradshaw's notebooks.

small number of “high value” genotypes, Allard argued, the resulting strains were left with too little genetic variation to respond to further selection (natural or otherwise) (Allard, 1961). Allard thought that instead of focusing on refining intensively-selected strains of barley and their potential hybrids, breeders should maintain highly diverse “composite cross” populations, crossing-in material from many different genetic backgrounds. Consequently, Allard was very interested in sourcing and conserving genetic variation from the wild progenitors of cultivated crops.²⁰

Under Stebbins' model, in which self-fertilizers were thought to partition themselves into reproductively isolated homogenous lines, the “bulk population” approach would have been a waste of

time. But if even low levels of outcrossing could maintain significant admixture, as Allard had shown, his approach would have multiple advantages. First, it would allow a much greater number of new combinations of genes to come together over time, and form complex interaction systems that would produce new, potentially valuable phenotypes. Second, it would permit a continued response to selection in the long run, due either to changing environments or to new breeding objectives. Third, it would lead to more stable yields in the face of environmental fluctuations.

4.2. The independent variable: density

Whereas Bradshaw's early experiments focused on responses to soil moisture and fertility, his barley experiment focused on responses to planting density.

One source of Bradshaw's interest in density was Harper's work on the effects of planting density on yield. Harper's broader

²⁰ Like many of Bradshaw's colleagues, Allard was a member of a small community of agro-ecologists who participated in the United Nations Food and Agriculture Organization's technical conferences on plant genetic resource conservation in the 1960s.

Table 1

Twelve varieties of barley in Bradshaw's experiment at Davis, 1963–1964.

	Adapted	Unadapted	Stable	Unstable
Arivat	✓		✓	
Atlas	✓		✓	
Club Mariout	✓		✓	
California Mariout	✓		✓	
Vaughn	✓			✓
Rojo	✓			✓
Trebi		✓	✓	
Trall		✓		?
Firlbecks III (2 row)		✓		?
Abyss Irregular		(✓)		?
Abyss, 6 row: CI 1227		(✓)		
Abyss, 2 row: CI 2376		(✓)		

Transcribed from Bradshaw's notebooks (D1041/2/15).

research program during this period focused on the effects of plant interactions on the composition of plant communities (Harper & Chancellor, 1959; Harper, Clatworth, McNaughton, & Sagar, 1961; McNaughton & Harper, 1960; Sagar & Harper, 1961). Harper found that, in both wheat and oats, yield was often highest at intermediate densities, driven by changes in seed output and growth habit at the level of individual plants (Harper, 1960; Harper & Gajic, 1961). In other words, population density and reproductive output were regulated in part by phenotypic plasticity.

The relationship between planting density and yield had clear consequences not only in the field, but also for genecological research at the WPBS. WPBS genecologists had long conducted common-garden experiments and varietal field-trials using a spaced-plot design, in which individual plants were grown at very low density. But Alec Lazenby, in the Grass Breeding Department, was finding that high-performing strains of forage grasses in the spaced-plot trials often fared quite poorly under higher-density broadcast seeding in pastureland. In experiments with genetically identical clones of *Lolium perenne*, Lazenby found that the response to density could vary widely among individual genotypes (Lazenby & Rogers, 1962a, 1962b, 1964, 1965a, 1965b).

Bradshaw saw density as a “cheap” environmental variable (in the sense that it could be manipulated easily), but one with considerable agro-economic significance. Bradshaw wrote that, “Since crop-density is not always precisely controlled, response to unavoidable fluctuations in density is of economic importance” (Bradshaw, 1964, p.122). From about 1960 to 1963, Bradshaw's student Mazoor Ahmed Khan studied varietal differences in linseed and flax, including their responses to density (Khan, 1963). That project set the stage for later experimental studies by Bradshaw and his students.

Table 2

Phenotypic characters measured in Bradshaw's experiment at Davis, 1963–1964.

	Within plant	Between plant	Between treatments
Components of yield			
Initial tillers		✓	✓
Fertile tillers		✓	✓
Seed number/tiller	✓	✓	✓
Seed size	✓	✓	✓
Total seed number		✓	✓
Total seed weight		✓	✓
Other correlated characters			
Internode length	✓	✓	✓
Leaf length	✓	✓	✓
Height of tillers	✓	✓	✓
Ear emergence	✓	✓	✓

Transcribed from Bradshaw's notebooks (D1041/2/15).

4.3. The dependent variables: stability and plasticity

Bradshaw's original conceptualization of phenotypic plasticity was squarely genecological: if local populations are adapted to the particular habitats in which they are found, and if the ability to respond to fluctuations in environment via alterations of phenotype is a component of that adaptation, then the salient empirical problem was to demonstrate that populations differ hereditarily in the nature or magnitude of their phenotypic response to environmental differences. Yet Bradshaw's experiment at Davis went beyond comparing changes in varietal means to contrasting environments. His experiment was designed to characterize differences not only in means, but also in variances, *among treatments*, among *individual* plants, and *within* individual plants. This shift represented an attempt to bridge two distinct investigative contexts: one surrounding the developmental-genetic causes of phenotypic stability, in which the concept of phenotypic plasticity was entrenched at the time, and the genecological approach in which Bradshaw was trained.

One of Allard's arguments for the composite-cross approach to plant breeding was that the resulting strains would produce more stable yields. Allard thought that the mechanisms underlying stability were twofold. First, at the population level, different genotypes would respond to environmental changes in different ways, so that negative and positive changes in yield would balance each other out on average. Whereas genotype–environment interaction would be a source of instability in a homogeneous variety, in a genetically diverse population it would promote overall stability. Second, high genetic diversity would mean higher levels of heterozygosity. Allard thought that high heterozygosity provided more numerous opportunities for “balanced gene complexes” to emerge, producing individual plants with much greater phenotypic stability (Allard, 1961).

Allard's thinking about stability tracked a broader debate among population geneticists at that time. An open question among population geneticists in the 1940s was how populations could persist in the face of environmental change. Allard shared the view of Theodosius Dobzhansky (1900–1975) and others that high levels of standing genetic variation in natural populations facilitated adaptive evolutionary responses to environmental fluctuations (Dobzhansky & Levene, 1955). But this raised the question of how such high levels of genetic variation—or “balanced polymorphism”—were maintained in the first place since, all else being equal, natural selection alone could only reduce variation.

Dobzhansky's collaborator Isadore Michael Lerner (1910–1977) proposed an account of “genetic homeostasis” in 1954 that connected population-level responses to environmental change to developmental-genetic mechanisms in individual organisms (Hall, 2005; Lerner, 1954). According to Lerner, genetic variation was maintained by the tendency for heterozygous individuals to have greater fitness than their homozygous counterparts, a phenomenon called “heterosis.”²¹ To explain heterosis, Lerner suggested that heterozygous individuals are more developmentally stable

²¹ So-called “hybrid vigor” had indeed been documented even in the 19th century, and was elaborated by geneticists George H. Shull and Edward M. East in the 1900s and 1910s (Paul, 1994). In the 1930s, mathematician R. A. Fisher had identified heterozygote advantage, “heterosis” (as Shull and East called it), or “overdominance” as a source of equilibrium in population genetic models: the inflated fitness of heterozygotes prevented any one allele at a given locus from going to fixation. The extent to which heterozygote advantage occurred in nature became a central point of contention in the infamous “classical/balance controversy” between Dobzhansky and H. J. Muller (1890–1967) during the 1950s and 1960s (Beatty, 2014).

(Lerner, 1954). That is, they are able to develop normally under a broader range of environmental conditions than their homozygous counterparts. On short time-scales, environmental fluctuations favor more stable, heterozygous individuals, which maintains the genetic variation needed for population-level adaptation to fluctuations on longer time-scales. The centrality of heterosis to Lerner's and other accounts led to a great deal of research and debate about the mechanisms linking heterozygosity to developmental stability, which Thoday called "phenotypic flexibility."

For Thoday, Bradshaw, and others involved in this field the concept of developmental stability was linked to the notion of developmental buffering, or "canalisation," proposed by embryologist Conrad Hal Waddington (1905–1926). According to Waddington, the phenotypic stability of wild varieties was the result of "epigenetic" systems that tracked development along well-constrained pathways, counteracting the destabilizing effects of environmental fluctuations (Waddington, 1957). Waddington thought that canalisation helped to explain "how the genotypes of evolving organisms can respond to the environment in a more coordinated fashion" (Waddington, 1942).

Disagreement among geneticists about the relationship between heterozygosity and stability revolved around two main issues.

The first issue was what it meant for organismal development to be stable or unstable, and thus what developmental-genetic mechanisms might explain it in principle. Some researchers, including Forbes W. Robertson and E. C. R. Reeve at the Institute of Animal Genetics in Edinburgh, thought that the stability of heterozygotes was a result of having a greater number of available developmental pathways (Robertson & Reeve, 1952). Similarly, Lerner speculated that heterozygotes were more stable than homozygotes because, at many loci, they possessed two alleles rather than one, permitting a wider range of biochemical interactions under different environmental conditions (Lerner, 1954).

On the other hand, Kenneth Mather (1911–1990) at the Agricultural Research Council's Unit of Biometrical Genetics at Birmingham, thought that the instability of homozygotes was caused by a disruption of complex gene combinations (present in heterozygotes) that had been tested and honed by natural selection (Mather, 1950). Dobzhansky shared that view (Dobzhansky & Wallace, 1953). Mather and geneticist John L. Jinks (1929–1987) reported that hybrids among inbred lines of *Nicotiana rustica* showed no less variability than their more homozygous parents, although levels of variability were highly heritable (Jinks & Mather, 1955). Contra Lerner, this suggested that it was not heterozygosity *per se* that was responsible for stability, but rather the coming together of particular combinations of alleles. Given a paucity of direct evidence about the mechanisms connecting specific genes to specific patterns of phenotypic variation, however, there was a great deal of latitude for theorizing and semantic squabbles (Lewontin, 1957).

The second problem was how to measure organismal stability. Thoday thought that intra-organismal symmetry—such as in the number of bristles on the abdomen of individual *Drosophila*, or in their wing morphology—was a corollary of developmental stability, and could therefore be used as a metric (Tebb & Thoday, 1954; Thoday, 1955, 1958). In contrast to Thoday, Dobzhansky's student Richard Lewontin argued that if stability were conceptualized as an adaptation, the only defensible operational measure of stability was fitness itself: the genotype with the highest average fitness across a range of environments should be considered the most stable (Lewontin, 1957).

Allard's ideas about the link between heterozygosity and stability stemmed in part from his collaboration with Jinks and Mather. Allard worked with Jinks and Mather on the quantitative genetics of *Nicotiana* while on sabbatical at the University of Birmingham in 1954 and 1955 (Allard, 1956).

Although Thoday, Lewontin, and others looked for individual traits or quantities that could serve as measures of stability, following Waddington they tended to see stability as a feature of the organism as a whole. Lewontin (1957), for example, referred to the importance of a "harmonious balance" within the organism. In his correspondence with Bradshaw, Thoday emphasized that organisms might adjust many different physiological and morphological traits to achieve survival to reproduction under adverse conditions. Those researchers looked inward, to the structural relations and complex interactions of developmental-genetic and physiological mechanisms to explain the link between heterozygosity and stability.

Because Bradshaw saw Thoday's conception of plasticity as a starting-point for his own work forced him to reconcile a discourse about internal mechanisms underlying whole-organism stability with a genecological epistemic framework focused on adaptive relationships between specific traits and specific environmental factors. In March, 1961, he confided to Ken Lewis at the Oxford Botany School that, "There seem to be so many facets of [the subject of plasticity] that it is difficult to know exactly what terms to use and almost where to begin" (D1041/4/3/21).

Bradshaw and Allard's shared interest in stability explains Bradshaw's choice of barley varieties. He sought a contrast between those well-adapted to the prevailing climate and those that were not, and between stable and unstable varieties (Table 1). The comparison between the "Vaughn" and "Atlas" varieties was particularly compelling. One of Allard's regular correspondents, crop geneticist Keith Warren Finlay in Australia, reported that those two varieties differed radically in their degree of stability: whereas Atlas gave more consistent yields from year to year, Vaughn was highly erratic. On the other hand, Vaughn was by far the superior producer under optimal conditions. Bradshaw thought that breeding for high yield might have caused a breakdown in stability, which would explain Finlay's observation.

Bradshaw's experimental design was one attempt to draw the concept of phenotypic plasticity from within the debate about stability into a genecological epistemic framework. Differences in varietal means between treatments would indicate differences in plastic response, while variance among individuals would indicate degree of stability. By analyzing variation among and within individual plants, Bradshaw could tease apart population-level stability from individual-level developmental stability. By scrutinizing correlations among responses to planting density in various traits, he could demonstrate not only that stability and plasticity varied among populations, but that plasticity or stability in a trait could vary *independently* of other traits.

Bradshaw was not alone in his attempt to reframe the concepts of plasticity and stability as genecological concepts. In the spring of 1964, Bradshaw gave a seminar about metal tolerance at the University of Oregon, where he was hosted by botanist Stanton A. Cook (b. 1929) and his wife, Joan. Cook, son of physiologist and anthropologist Sherburne F. Cook (1896–1974), studied under Lincoln Constance and Herbert Baker at the University of California, Berkeley. Cook's dissertation research focused on variation and local adaptation in *Eschscholzia californica* in California and Oregon in the late 1950s (Cook, 1960). Like Bradshaw, Cook found that adaptive differentiation could occur on very small spatial scales (Cook, 1960). After moving to the University of Oregon in 1960, Cook turned his attention to the relationship between local adaptation and

developmental flexibility in the water buttercup *Ranunculus flammula* (Cook, 2013a).²² Cook wrote a grant proposal to the National Science Foundation, awarded in 1962, in which he proposed to study adaptive differentiation in heterophylly in *Ranunculus* at various spatial scales in western Oregon (D1041/4/3/8). In addition to addressing the relationship between population-level and developmental flexibility, Cook asked whether adaptive plastic responses were linked to heterozygosity (D1041/4/3/8).

Oddly, Cook and Bradshaw did not discuss their ideas about plasticity during Bradshaw's visit in 1964 (Cook, 2013b) and so, when Bradshaw sent Cook a draft of his review on the topic later that year, Cook expressed his surprise that their "thoughts ha[d] been running along the same tracks in parallel" (D1041/4/3/9). Between 1963 and 1967 Cook and his graduate student, Michael P. Johnson, found that populations of *R. flammula* could evolve divergent plastic responses to environmental variation over distances as short as four meters, and that plasticity in different traits could evolve independently (Cook & Johnson, 1968). Bradshaw drew on Cook's grant proposal, and the extensive comments that Cook made about his draft manuscript, in developing the final version of his 1965 review (D1041/4/3/9).²³

The results of Bradshaw's experiment at Davis were never published. Bradshaw's notes and correspondence, however, indicate that the results were strongly suggestive that the plasticity and stability of some traits could vary independently. In a grant proposal to the Agricultural Research Council in 1964 (described below), he wrote that,

I believe that plasticity is under genetic control and that it is a property of individual characters. It seems likely that we will find that, as an outcome of natural selection, some characters, such as leaf area and tiller number, are allowed to vary, while other characters such as seed and flower size are held extremely constant. (D1041/4/3/2, p.3).

That statement became a crucial premise of Bradshaw's 1965 review which, after many years of planning, he drafted on the trans-Atlantic voyage back to Bangor in mid-1964.

5. An empirical research program

Bradshaw's work on phenotypic plasticity was as much an empirical project as it was theoretical. His experimental work on plasticity started in the late 1950s, many years prior to his famous 1965 review. It was not until his experiment at Davis in the early 1960s that Bradshaw felt confident to bring his long-anticipated review paper to light, and to make a serious attempt to secure funding for further empirical research on plasticity. At that time, Bradshaw thought that his work on mineral nutrition in grasses was coming to a close, and that experimental studies of plasticity represented the next major direction for his research (D1041/4/3/2, p.4).

While still at Davis in 1964, Bradshaw drafted a proposal to the Agricultural Research Council for an investigation of phenotypic plasticity in crop plants and their wild progenitors. Bradshaw's proposal revolved around four questions:

Given a variable environment:

I) Can different populations of a species differ in their ability to cope with such variation in environment?

II) How is this ability manifested in different characters? Are certain characters held constant and others allowed to vary, or is the whole organisation of the individual involved?

III) What is the contribution of different characters? Is the same end point of adaptation achieved in different ways by different genotypes?

IV) If populations of a species do differ in their ability to adjust to variation in environment, what is the genetic basis of such differences? (D1041/4/3/2, p.2)

The project outlined in that proposal was to build on work by Bradshaw's student Mazoor Ahmed Khan on response to density in linseed and flax, this time focusing on both wild and cultivated varieties of sunflower (*Helianthus annuus*), soft brome grass (*Bromus mollis*), domesticated barley (*Hordeum sativum*), and wild barley (*Hordeum spontaneum*). The grant would also fund M. Akram Khan's ongoing doctoral research on response to density in *Linum* (Khan, 1967). Bradshaw justified the project with reference to its agricultural consequences. In his proposal to the ARC, Bradshaw wrote that, "In agricultural crop varieties, where the genetic composition is held constant artificially, adaptation to the varying conditions of one year and another can only be met by plasticity," but that "we do not know a great deal about the subject despite its immediate relevance to agricultural practice." (D1041/4/3/2, p.1).

Although there is no evidence to suggest that the ARC funded Bradshaw's project, much of the proposed work was ultimately carried out. At least three of Bradshaw's graduate students, Muhammed Akram Khan, Muhammed Iqbal Khan, and Peter Kyle, conducted experimental studies of plasticity and canalisation in flax, linseed, sunflowers, and tobacco (Khan, 1967a, 1967b; Kyle, 1966; D1041/4/15). That they were carried out even in the absence of external funding suggests that Bradshaw was committed to serious and sustained experimental studies of plasticity.

Bradshaw's work on plasticity attenuated sharply after 1968. There are a variety of plausible reasons for this, including a change in the funding landscape that brought Bradshaw's work on heavy-metal tolerant plants back to the foreground. In 1966, over one hundred forty people (mostly children) in the mining town of Aberfan in South Wales were crushed by material from a colliery waste tip that was destabilized by heavy rains (Couto, 1989). The Aberfan disaster created a strong political imperative to reclaim old industrial waste and mining sites around Britain (Goodman, 1974; House of Commons, 1967) amplified by passage of the Mines and Quarries (Tips) Act of 1969. Bradshaw was soon approached by representatives of the copper industry, and found it much easier to find funding for restoration-related research (Jowett, pers. comm.). Those events coincided with an offer from the University of Liverpool to assume the Holbrook Gaskell Chair of Botany, which Bradshaw accepted in 1968. Bradshaw's willingness to move away from his work on plasticity may also have stemmed from difficulties in analyzing his data and publishing the results of his students' research.²⁴ All of those factors likely conspired to shift Bradshaw's attention to what would later be called "restoration ecology" (see Sarkar, 2011).

²² Cook visited Turesson at Uppsala en route to the 11th International Congress of Genetics at the Hague in 1963, and saw some of the same populations of *Ranunculus* that Bradshaw had seen in 1950.

²³ Cook's contributions to Bradshaw's 1965 review includes Bradshaw's opening passage, a 1914 quote from Hans Nilsson-Ehle. Cook had translated the quote and included it in his own 1961 NSF grant proposal.

²⁴ Some reviewers did not respond well to submissions based on his students' projects. The problems noted by reviewers, as well as delays in analyzing the data from his experiment at Davis, appear to have stemmed from difficulties in performing and interpreting appropriate statistical analyses. Some of the work from this period was ultimately published in the late 1970s after substantial revision, as Khan & Bradshaw (1976) and Khan, Antonovics, & Bradshaw (1976). Other manuscripts, such as one concerning canalisation of seed size in *Helianthus* based on M. Iqbal Khan's research, were never published (D1041/4/15).

6. Discussion

Bradshaw work on plasticity was not unprecedented. Moreover, his account of plasticity was not at all a shift from a gene-centric epistemology to one concerned with the interaction of heredity, developmental processes, and environmental context. In fact, such an interaction-oriented perspective was already alive and well when Bradshaw joined the fray. Bradshaw's model should be understood instead as a response to an ongoing discourse about plasticity, stability, and yield. Indeed, it can be seen as a reformulation of a structural, inward-facing, whole-organism conception of phenotypic plasticity into a functional, outward-facing one.

The collaboration between Bradshaw and Allard at Davis in the early 1960s, which catalyzed Bradshaw's influential 1965 review, represented the confluence of two extant lines of investigation: the agro-ecological tradition of British genecology, on one hand, and a lively discourse among population biologists about the evolutionary and developmental-genetic relationships between heterozygosity, phenotypic stability, and developmental canalization on the other. Bradshaw re-cast questions about developmental stability within the epistemic framework of British genecology: he appealed to specific external selective pressures on specific traits, rather than the internal structural organization of whole organisms, to explain differences in stability and plasticity among populations of organisms.

The importance of a genecological epistemic framework for Bradshaw's ideas about plasticity is reflected in his assessment of [Finlay and Wilkinson's \(1963\)](#) method for evaluating the relative stability of crop varieties, described by [Baranski \(2015\)](#):

In this respect the regression technique for the analysis of phenotypic response, introduced by [Finlay and Wilkinson \(1963\)](#), where the environment is measured by the mean growth of all the different genotypes being assessed, has almost been too successful, because it has allowed us to escape from measuring the specific attributes of the environment which are causing phenotypic change. ([D1041/4/15/1/5](#))

Bradshaw's approach to adaptive phenotypic plasticity was an attempt to operationalize it as an investigable phenomenon within a research framework that was focused on adaptation by natural selection in natural populations. Bradshaw thus directed attention away from internal mechanisms and toward the external relations action of natural selection in molding and fine-tuning phenotypes. In the genecological framework this meant attending to specific environmental factors, something that the Finlay-Wilkinson method obscured.

Understanding the theoretical context for Bradshaw's ideas about plasticity sheds some light on what Bradshaw meant when he said that plasticity in specific characters could be under "direct genetic control." In his 1965 review, he wrote:

It can be argued that the plasticity of a character is related to the general pattern of its development, and apart from this, that plasticity is a general property of the whole genotype. A review of the evidence suggests that neither of the conclusions is tenable. Plasticity of a character appears to be (a) specific for that character, (b) specific in relation to particular environmental influences, (c) specific in direction, (d) under genetic control not necessarily related to heterozygosity, and (e) able to be radically altered by selection. ([Bradshaw, 1965](#), p. 149)

The meaning and epistemic implications of "direct genetic control" became a flash-point for controversy in the 1980s and 1990s. In particular, population ecologists Sara Via and Samuel Scheiner disagreed loudly about the existence (even possibility) of so-called

"plasticity genes" that operate independently of those responsible for controlling mean trait values in populations ([Nicoglou, 2015](#)). Bradshaw was not making claims about plasticity genes, *per se*, but was mainly focused on replacing the whole-organism conception of plasticity and stability with one that could be investigated in a genecological framework. In the same vein, he resisted [Stebbins' \(1950\)](#) claim that, in [Bradshaw's \(1965\)](#) words,

...characters formed by long periods of meristematic activity (such as over-all size, leaf number, etc.) will be more subject to environmental influences and are likely to be more plastic than characters formed rapidly (such as reproductive structures) or than characters whose pattern is impressed on primordia at an early stage of development (such as bud scales, leaves, etc.). ([Bradshaw, 1965](#), p. 117).

Bradshaw did not completely reject Stebbins' views on plasticity, but did seek to emphasize situations in which plasticity was not so tightly restricted by developmental constraints.

In attending to the practices and richness of discourse surrounding adaptive plasticity in the mid-20th century, this paper contributes to an expanded historiographical framework for evolutionary biology that both enriches and transcends the Modern Synthesis narrative. Work by [Provine \(1971\)](#), [Bowler \(1983\)](#), [Smocovitis \(1996\)](#) and others (e.g. see papers in [Mayr & Provine, 1980](#); [Greene, 1986](#)) have thoroughly documented the efforts of some influential biologists in the 1930s and 1940s to establish a discipline of evolutionary biology that was centered on population studies and undergirded by theoretical population genetics. Subsequent work has emphasized the complex relationships between the Synthesis project and the diverse evolutionary research traditions that spanned that period (e.g. see chapters in [Cain & Ruse, 2009](#)). Bradshaw's model of adaptive plasticity was shaped by his attempt to operationalize theories of developmental organization within a particular set of research practices. In Bradshaw's case, we can see the significance of the genecological research tradition for what became a highly influential contribution to evolutionary theory in the decades following the Synthesis period. Further work is needed not only to understand subsequent models of adaptive plasticity, but also to fully assess the impact of the genecological research tradition on the development of 20th-century evolutionary theory.

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