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

B.R. Erick Peirson*

School of Life Sciences, Arizona State University, PO Box 873301, Tempe, AZ 85287-3301, USA

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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

* Tel.: +1 (360) 531 4474.
E-mail address: erick.peirson@asu.edu.

[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).

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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

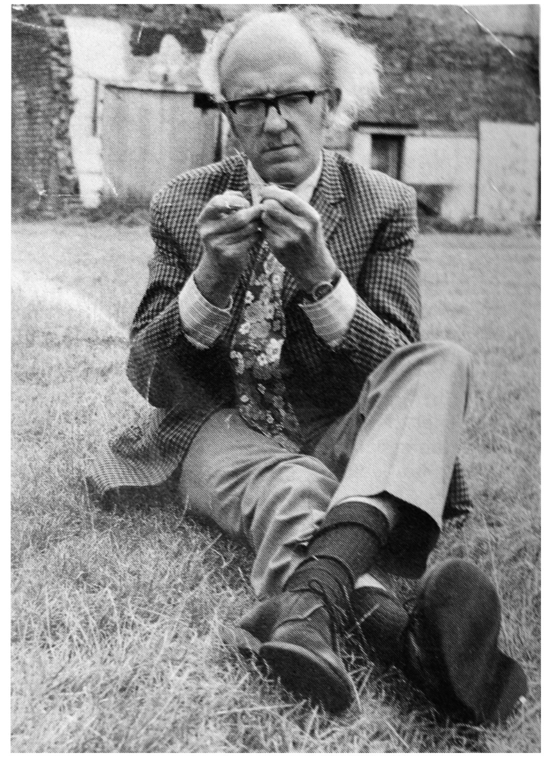

Fig. 1. Anthony David Bradshaw (1926–2008). Photograph from press clippings in Bradshaw archive, dated 1972. Bradshaw is shown inspecting a tiller while sitting in grass in an urban setting, presumably in Liverpool. By courtesy of the University of Liverpool Library. D1041/5/1/2/33/2.

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 intraspecific 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.