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The effect of breeding on allometry and phenotypic plasticity in four varieties of oat (*Avena sativa* L.)

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Abstract

New directions in crop improvement via alteration of plant responsiveness to variation in growth conditions are being actively debated. It appears, however, that little is known about the impact of previous breeding on the phenotypic plasticity of plants, which results from correlated responses to selection on high yield. We used four oat (*Avena sativa*) varieties, originating from 1930, 1952, 1980 and 1999, to examine the effects of long-term breeding on the patterns of autecological phenotypic responses to variation in light and nutrient supply. The modern variety showed the least plasticity in stem elongation in response to variation in light conditions. As a by-product of decreased sensitivity to light availability, the modern oat variety appeared to be more susceptible to low light levels compared to other varieties. The patterns of plastic response in leaf area and root biomass were similar in all varieties. Changes in allocation to panicles in response to resource variation were completely attributable to passive plasticity, i.e. the proportion of biomass invested into reproduction varied as a function of total plant size. Interestingly, variation in specific leaf mass, the trait considered to be important in adaptive shade-avoidance responses, was only partially attributable to ontogenetic plasticity (environmentally induced adjustments of ontogeny). Our results support the idea that it can be more advantageous in the breeding of crop plants to select for a fixed pattern of allocation to different tissues, dependent on developmental stage, than to select for the ability to adjust the whole ontogeny to particular environmental conditions. Uniform high-nutrient conditions and completely predictable changes in light environment during ontogeny are common for crop plants, and are known to enhance genetic differentiation, not plasticity. Obviously, it is not possible to lose ontogenetic plasticity, as such, entirely: plants will have to adjust their development in response to stressful conditions if the allocational pattern of underdeveloped plants is not consistent with optimal foraging behaviour. On the other hand, the similar patterns of plastic responses in the studied varieties imply that further development of more plastic varieties can be precluded by homogenizing selection on optimal reaction norm (greater plasticity can be associated with excessively high costs and can outweigh possible advantages).

Keywords: *Avena sativa*; Allometry; Breeding; Light availability; Nutrient availability; Phenotypic plasticity

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1. Introduction

The effects of long-term agricultural breeding on plant species allometry, plasticity and autecology have not been investigated extensively. Consequently, there is little information available about how, and in which direction, plant traits, other than those under direct selection, have evolved through breeding time. Similarly, it would be valuable to know the overall effect of unidirectional breeding on plant ontogeny, and an understanding of the mechanisms behind the high yield potentials of modern crops could have important implications for further plant breeding.

The phenotype changes through ontogeny and environment exert a strong influence on plant growth and development. The specific pattern of interactions between a given genotype and environmental conditions (norm of reaction) has evolved in response to numerous selection pressures and constraints. Little is known about how plants' responsiveness to a given environmental signal is affected by other environmental factors, and how the alterations of the mechanisms controlling individual plant plasticity influence the functioning and productivity of the plant community as a whole (Schmitt et al., 1986, 1995; Ballaré and Scopel, 1997; Ballaré et al., 1997; Ballaré and Casal, 2000; Callaway et al., 2003).

Phenotypic variation may be a consequence of variation in growth rate, developmental trajectory or programmed phenotypic change during ontogeny. Wright and McConnaughay (2002) suggested that it is important to distinguish ''ontogenetic plasticity'' from ''passive plasticity'' if we are to obtain a more complete understanding of plants' ability to respond to different environments and of the nature of the plastic response observed. Plants grown in different environments are considered to exhibit ontogenetic plasticity if environmental change induces variation in the ontogenetic trajectory of a trait (also called adaptive plasticity and true plasticity—Sultan, 1995 and McConnaughay and Coleman, 1999, respectively). Passive plasticity—phenotypic change in a predictable way as a function of plant growth or development, is also referred to as ontogenetic drift (Evans, 1972), apparent plasticity (McConnaughay and Coleman, 1999), and inevitable plasticity (Sultan, 1995). In order to distinguish between passive and ontogenetic plasticity, one should compare plants through the entire course of growth (ontogenetic trajectory) or as a function of plant size (allometric trajectory).

Observation of plasticity in a phenotypic trait does not necessarily indicate adaptation (Weiner, 1988). Many empirical studies of putatively adaptive phenotypic plasticity rely strongly on the plausibility that a plastic response is adaptive, rather than on definitive tests of the hypothesis of adaptation (see e.g., Bonser and Aarssen, 1994; Winn, 1996; Sultan and Bazzaz, 1993). Explicit tests of fitness consequences of plasticity have rarely been performed (Schmitt et al., 1995; Dudley and Schmitt, 1996; Schmitt, 1997; Winn, 1999; Dorn et al., 2000; Weinig, 2000a).

Plasticity is favoured if an environmental factor varies at the same scale as the response unit (e.g., leaf, whole plant), if there are costs to inappropriate, specialized phenotypes, when environmental variation is highly but not completely predictable, and the plant is able to track or anticipate changes in the environment closely enough (Bradshaw, 1965; Van Tienderen, 1991; Weinig, 2000b; Alpert and Simms, 2002; Givnish, 2002). A number of constraints on the evolution of phenotypic plasticity have been suggested, including deficient sensory capabilities, lag-time between environmental and phenotypic change, lack of genetic variability, maintenance of the genetic and cellular machinery necessary for plastic response, and integrated response caused by strong genetic correlations between a suite of traits across and within environments (Van Tienderen, 1991; Schmitt, 1997; DeWitt et al., 1998; Van Kleunen et al., 2000; Pigliucci, 2001; Diggle, 2002).

Despite the strong selection for high yield in monocultures, some modern crops seem to retain the agronomically undesirable patterns of response to stress that characterized their uncultivated ancestors. The petiole and stem elongation response to crowding might reduce assimilate availability for agriculturally more productive activities, such as root, grain, or fruit growth, and might increase crop susceptibility to lodging. If this is correct, rendering a plant insensitive to neighbour presence should payoff in terms of reduced wasteful allocation (Smith, 1992). However, plastic responses to light availability also have a number of desirable effects on whole-canopy growth and crop yield. These effects involve a more efficient arrangement of canopy leaf area with respect to the