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Neither crop genetics nor crop management can be optimised

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ABSTRACT

Natural selection does not lead to optimal solutions due to trade-offs and environmental variation, genetic and developmental constraints, and historical contingency. In this paper we propose that constraints like these also often apply to the improvement of both crop varieties and management practices, creating a dual biological and agronomic barrier for the optimisation of crops. We discuss constraints on optimisation of 1) crop ancestors, by natural selection, 2) crop traits, by artificial selection and biotechnology, and 3) crop management. We outline how trade-offs and environmental variation make single-factor optimisation (e.g. “optimum leaf angle” or “optimal fertiliser rate”) impossible. Definitions of “optimal” that recognise trade-offs and variability can help, but we argue there are major constraints on even those forms of optimality. Optimality theory may be useful to formulate null hypotheses, however, as divergence between actual traits and theoretical optima can highlight constraints that are biologically interesting and agronomically relevant. Understanding the nature and size of these constraints can help us map more likely pathways for future improvements in agriculture.

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1. Introduction

Our ability to improve agriculture is constrained by various trade-offs, which are not always recognised. For example, a recent review argued that we could achieve food security without expanding agricultural land, mainly by increasing crop yields to 95% of potential while also increasing resource-use efficiency (Foley et al., 2011). However, these two proposals conflict. Owing to the law of diminishing returns, resource-use efficiency decreases with increasing resources (Gastal et al., 2015) yet higher inputs are often necessary to reduce the gap between actual and potential yield (Connor and Mínguez, 2012; Sinclair and Ruffy, 2012). Because marginal economic costs of increasing inputs to reach 95% of yield potential would often exceed marginal economic benefits, farmers typically limit inputs and accept yields that are well below potential (Lobell et al., 2009). For example, in low-risk cropping systems such as irrigated maize in the US, the best growers operate at about 80% of potential yield (Lobell et al., 2009; van Ittersum et al., 2013; Grassini et al., 2015). Larger yield gaps are required to deal with risk in low-rainfall cropping systems (Monjardino et al., 2015). Increasing food production from existing farmland by closing yield gaps

would require increasing inputs, which conflicts with both higher resource-use efficiency and the economic goals of individual farmers.

Despite such trade-offs, optimisation of inputs (e.g. irrigation water, nitrogen) and other management practices (e.g. sowing date, crop-rotation sequences) is an important agricultural goal (Detlefsen and Jensen, 2007; Neumann et al., 2009; Deng et al., 2014). Similarly optimisation of plant and crop traits, such as DNA repair, light harvesting, photosynthesis, stomata physiology, or plant allocation of resources has often been proposed (Richard et al., 2012; Tie et al., 2014; Way et al., 2014; Ruban, 2015). A well-known example of a crop-trait trade-off is the greater yield potential, but lower competitiveness with weeds, of shorter wheat and rice (Denison, 2012).

Given such trade-offs, it is important to use some composite objective function (e.g. yield potential and competitiveness with weeds), rather than a single criterion, to define optimality. We can then use modelling and mathematical tools to design crop ideotypes for defined conditions (e.g. high-fertility, few weeds) (Donald, 1968; Messina et al., 2009; Martre et al., 2015). Similarly, we can design crop-management strategies for simultaneous optimisation of multiple objective functions (Detlefsen and Jensen, 2007; Rapidel et al., 2015). This does not mean that the real world offers optimal solutions, however, because trade-offs are not the only constraints on optimisation.

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Natural selection does not lead to optimal solutions due to trade-offs and environmental variation, various constraints, and historical contingency (Gould and Lewontin, 1979; Smith et al., 1985; Parker and Smith, 1990; Dudley and Gans, 1991; Farnsworth and Niklas, 1995; West-Eberhard, 2003; Blount et al., 2008; Piersma and van Gils, 2011; Latta et al., 2015; Miller and Greig, 2015; Wüest et al., 2015). Further, these constraints are not independent but involve critical connections, e.g. between trade-offs and environmental variation (Saeki et al., 2014; Latta et al., 2015) or between genetic and developmental constraints (West-Eberhard, 2003; Wüest et al., 2015).

In this paper, we argue that constraints similar to those on natural selection often apply to crop genetic improvement and to decision making in agriculture, hence the dual biological and agronomic barrier for the optimisation of crops and cropping systems. We will discuss constraints on optimisation of 1) crop ancestors, by natural selection, 2) crop traits, by artificial selection and biotechnology, and 3) crop management. We outline how trade-offs and environmental variation make single-factor optimisation (e.g. “optimum leaf angle” or “optimal fertiliser rate”) impossible. More-flexible definitions of “optimal” (e.g. “risk-adjusted yield potential”) can help, but we argue there are major constraints on even those forms of optimality. Optimality theory may be useful to formulate null hypotheses, however, as divergence between actual and optimal solutions can help identifying constraints that are biologically interesting and agronomically relevant.

2. Constraints to optimisation of crop ancestors by natural selection

Evolutionary trade-offs are “negative reciprocal causal relationships in net benefits between trait magnitudes” (Saeki et al., 2014). In thinking of optimal solutions, trade-offs are often but not always recognised. For example, some models emphasise the role of stomata in the regulation of gas exchange under the assumption that transpiration efficiency, i.e. the ratio of carbon fixation and transpiration, should be optimised (Cowan and Farquhar, 1977; Way et al., 2014; Brodribb et al., 2015). But, in addition to regulating gas exchange, stomata play a role in modulating canopy temperature (Burke et al., 1988; Lu et al., 1994) and preventing cavitation (Tyree and Sperry, 1989; Brodribb et al., 2015). Whereas maximising transpiration efficiency and prevention of cavitation requires some degree of stomata closure at high vapour pressure deficit, evaporative cooling requires open stomata. Empirical evidence in wheat, cotton and grapevine indicates that for some combinations of genotypes and environments, the need for evaporative cooling overrides the putative role of stomata in optimising transpiration efficiency (Lu et al., 1994; Fischer et al., 1998; Soar et al., 2009; Nautiyal et al., 2012; Rizza et al., 2012). The trade-off between transpiration efficiency and canopy cooling is thus a barrier for the optimisation of stomata behaviour (Sadras et al., 2012). Indeed, inter- and intra-specific variation in stomata responses to soil and air dryness in a range from anisohydric (allowing leaf water potential to vary) to isohydric reinforces the notion that there is no single, optimal solution (Tardieu and Simonneau, 1998; Casadebaig et al., 2008). Of interest, important physiological and behavioural traits in birds and mammals can be explained in terms of the trade-off between water economy and thermal regulation mediated by evaporative cooling (Piersma and van Gils, 2011).

A simplistic view of optimality in evolution relies on the unrealistic assumption that selective forces are temporally invariant in character and magnitude (Dudley and Gans, 1991). Yet conditions vary over every time scale, so adaptation to a given environment will not optimise long-term fitness. For domesticated species, genetic changes from deliberate human selection interact with

unintended selection imposed by agricultural environments, which are constantly changing. Analyses of kernels and charcoal samples from Upper Mesopotamia archaeological sites spanning from the onset of agriculture to the turn of the era showed that water availability for crops, inferred from carbon isotope discrimination, was two- to four-fold higher in the past than at present, with a peak between 10,000 and 8000 cal BP. Meanwhile, nitrogen isotope composition ($\delta^{15}\text{N}$) decreased over time, thus indicating declining soil fertility (Araus et al., 2014).

Four contrasting strategies have been identified for coping with environmental variation (DeWitt and Langerhans, 2004); they are: (1) specialisation, whereby a single phenotype is produced that is well adapted to a particular environment even though the specialist may experience a range of environments; (2) generalisation, whereby a “general purpose” phenotype is produced, with moderate fitness in most environments; (3) bet-hedging, whereby an organism produces either several phenotypes (e.g. among units in a modular plant) or single phenotypes probabilistically (e.g. a mixture of dormant and non-dormant seeds); (4) phenotypic plasticity, whereby environmental cues trigger production of alternative phenotypes. Modelling these four strategies under the assumption of “perfect plasticity” and a simplified range of environments returned a ratio of fitness after four generations of 1:1.6:1.5:25 (DeWitt and Langerhans, 2004). The conclusions from this type of analysis are that in the absence of constraints, plasticity is superior in variable environments.

The fact that plasticity is not unlimited, despite its theoretical advantages, suggests the existence of ubiquitous constraints on its evolution. The more likely constraints include a relatively high cost for plasticity, developmental and genetic constraints, and unreliability of environmental cues used to guide development (DeWitt and Langerhans, 2004; Pigliucci, 2005; Sadras and Slafer, 2012; Donaldson-Matasci et al., 2013). As plasticity is defined in relation to environmental cues, part of the costs are associated with the building and maintenance of the sensory system of the plant, e.g. phytochromes involved in perception of neighbouring plants mediated by changes in red: far red ratio of light. However, these sensor-construction costs may be small, relative to the risk of misinterpreting environmental cues. For example, benefits to plants from responding to current light-quality cues may depend on correctly predicting how much neighbours will grow (Novoplansky, 1991). Moreover, there is an important difference between costs of plasticity, which reduce fitness, and constraints, which set the boundaries for the expression of a phenotype, although these two aspects are difficult to separate (Pigliucci, 2005).

Trade-offs and environmental variation prevent natural selection from optimising individual physiological processes or overall adaptation. However, trade-offs alone would not necessarily prevent optimisation by some appropriate composite criterion whereby the “optimal” genotype could be defined as one whose geometric-mean fitness across a range of conditions is greater than that of any alternative genotype (Simons, 2009). For example, we could model a genotype where stomata physiology leads to an optimal balance (likely involving phenotypic plasticity or bet-hedging) among transpiration efficiency, canopy temperature, and cavitation risk. Modelling using a Pareto approach, Shoval et al. (2012) found that best-trade-off phenotypes are weighted averages of archetypes, which are “specialists” in DeWitt & Langerhans classification above. For two tasks, phenotypes fall on the line connecting the two archetypes, whereas for three tasks phenotypes fall within a triangle in phenotype space, whose vertices are the archetypes. Yet, these hypothetical optimal genotypes might never evolve due to genetic, functional and developmental constraints, and historic contingency.

Genetic constraints include the amount of additive variance, pleiotropy, maladaptive gene flow and canalization. Given enough

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