Evolutionary tradeoffs as opportunities to improve yield potential

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ABSTRACT

Photosynthetic efficiency and stress tolerance are examples of traits that had been improved by natural selection for millions of years prior to domestication of crops. Further improving such traits often requires accepting tradeoffs that would have reduced fitness of the crop's ancestors where they evolved. For example, improvements in yield potential have mostly come from reversing past selection for individual-plant competitiveness that conflicted with plant-community efficiency, or from tradeoffs between adaptation to past versus present conditions. A brief review of cold- and drought-tolerance did not find evidence of tradeoff-free improvements in crops, relative to wild ancestors. Identifying evolutionary tradeoffs that impose minimal agronomic tradeoffs can point the way to further improvements in yield potential and other community-level traits, perhaps including weed suppression. Crop genotypes that benefit subsequent crops merit more attention. Radical innovations never tested by natural selection may have considerable potential, but both tradeoffs and synergies will often be hard to predict.

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1. Introduction

Charles Darwin was very impressed by the accomplishments of plant breeders. He argued, however, that natural selection has achieved results "immeasurably superior to man's feeble efforts" because it has operated over much longer time periods (Darwin, 1859). Plant breeders have often accelerated the evolution of adaptation to new conditions, including resistance to pests and pathogens to which a crop has only recently been exposed. But for traits that consistently enhance individual-plant fitness across environments – efficient enzymes, for example – what opportunities remain for further improvement?

Prior to domestication, natural selection had already tested many more alleles for stress tolerance and efficient use of solar radiation, nutrients, and water than plant breeders ever will. I have therefore hypothesized that improving such traits through plant breeding has required and usually will require either radically different phenotypes (never tested by past natural selection) or accepting tradeoffs rejected by past natural selection (Denison et al., 2003; Denison, 2012).

Examples of tradeoffs include those based on conservation of matter, such as the tradeoff between seed size and seed number or allocation to shoot versus root. Tradeoffs may sometimes be obscured by differences among individual plants in total resource supply (Spaeth and Sinclair, 1984; Roff and Fairbairn, 2007). Also, the fitness costs of chemical defenses in the absence of pests can be much greater than predicted from their metabolic costs (Kakes, 1989; Agrawal and Karban, 1999). Some tradeoffs not directly linked to conservation of matter include those between resistance to rust versus Victoria blight in oats (Wolpert et al., 2002), photosynthesis rate versus leaf lifespan (Reich et al., 2003), and salt tolerance versus desirable fragrance in rice (Fitzgerald et al., 2010). Known tradeoffs may be outnumbered by tradeoffs that have not yet been discovered.

Based on the evolutionary-tradeoffs hypothesis, I expressed doubt (Denison, 2012) that any benefits from increased expression of a transcription factor involved in drought tolerance (Nelson et al., 2007) will prove to be tradeoff-free. My assertion was based on the assumption that there must be at least several single-base mutations that affect the expression of that (or any given) gene. With 10 million plants per km^2 and a mutation rate of 10^{-8} per base per generation (Koch et al., 2000), each single-base mutation that increases the expression of a given gene would arise about once per generation per 10 km^2. Given these repeated opportunities for natural selection to increase expression of the "drought-tolerance" transcription factor, I concluded that higher expression levels must have arisen repeatedly in the past. The evolutionary persistence of lower expression levels therefore suggests that mutants with higher expression levels paid a fitness cost.

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Any yield benefits from increased gene expression would therefore depend on a negative relationship between fitness in past environments and agronomic performance today. Such negative relationships can certainly exist, as discussed below, but they cannot simply be assumed. Similar arguments would apply to any phenotypic change that could be achieved by increasing or decreasing expression of an existing gene (even one that regulates many other genes), whether this is achieved through traditional breeding or biotechnology.

Fortunately for plant breeders, traits key to whole-crop yield today often differ from those that enhanced individual-plant fitness in past environments. Past evolutionary tradeoffs will not necessarily cause agronomic tradeoffs today. This creates opportunities for improvements through either traditional breeding or biotechnology.

For example, we can accelerate crop adaptation to current or future agricultural environments, sacrificing adaptation to environments that may no longer exist. Consider the tradeoff between rubisco's reaction rate and its CO_2-specificity, which reduces wasteful photorespiration (Tcherkez et al., 2006). As atmospheric CO_2 increases, CO_2-specificity becomes less important, whereas greater rubisco activity would increase water-use efficiency and perhaps nitrogen-use efficiency. When conditions change, natural selection lags behind: our crops are better adapted to past CO_2 concentrations than to future ones (Zhu et al., 2004).

Tradeoffs between individual-plant fitness and the collective performance of crop communities may be even more important than tradeoffs between adaptation to past versus present conditions. As de Wit (1978) noted, "there is nothing in the process of evolution that has any aspect of community behaviour as a goal." This aspect of the evolutionary-tradeoffs hypothesis is consistent with Donald's (1968) proposed tradeoff between "competitive ability of cultivars... and their capacity for yield in pure culture", Loomis's (1993) claim that "natural selection has already found efficient solutions to traits such as photosynthesis that lend *individuals* success in competition", a focus on "attributes that increase total crop yield but reduce plants' individual fitness" (Weiner et al., 2010), and the assertion by Sadras et al. (2013) that "natural selection favours, whereas selection for yield in crops reduces, the competitiveness of individual plants."

The evolutionary-tradeoffs hypothesis does not assume that natural selection always finds the best-possible solutions. If a hypothetically superior phenotype requires simultaneous modification of several genes, it may not have arisen often enough, even over millennia, to ensure displacement of inferior phenotypes via natural selection. Multistep improvement is common, however, as explored in detail for antibiotic resistance (Poelwijk et al., 2007). Complex adaptations like C4 photosynthesis or hosting nitrogen-fixing symbionts have arisen repeatedly, although their evolvability may depend on preconditions that are not found in all crops. For example, evolution of C4 photosynthesis in grasses was apparently limited to lineages that already had relatively close spacing of bundle-sheath cells (Christin et al., 2013). Similarly, modeling has suggested that lineages with an uncharacterized "precursor state" were one-hundred times likely to evolve nitrogen-fixing symbiosis (Werner et al., 2014).

When biotechnology introduces changes more radical than those that often occur in nature – more radical than C4 photosynthesis, say – tradeoff-free improvements are conceivable, though far from inevitable. For example, transformation with five bacterial genes moved some photorespiratory CO_2 release from mitochondria to chloroplasts, enhancing net photosynthesis in a way that has not evolved naturally in plants (Kebeish et al., 2007).

2. Natural versus human selection for abiotic stress tolerance

Before considering opportunities linked to the evolutionary-tradeoffs hypothesis, we should consider evidence that might disprove it (Kinraide and Denison, 2003). For example, what can we conclude from the expansion of crops beyond the geographic range of their wild ancestors?

If successful growth of a crop in colder climates is due to tradeoff-free improvements in cold tolerance, relative to its wild ancestors, that could potentially disprove the evolutionary-tradeoffs hypothesis. This disproof would depend on the assumption that the wild ancestor was under frequent selection for cold tolerance, at least at the colder edges of its range. Furthermore, the evolutionary-tradeoffs hypothesis could survive if greater cold tolerance came with tradeoffs.

There is apparently little evidence for recent improvement in cold tolerance of wheat, where cultivars released before 1915 are still among the most cold-tolerant (Limin and Fowler, 1991) or barley, where landraces, old cultivars, and new cultivars tend to have similar cold tolerance (Gabor et al., 2013).

Cold tolerance in maize may seem more promising as a possible example of plant breeders improving a trait that already had a long history of improvement by natural selection. After all, maize can survive and reproduce (with human assistance) far beyond the northern boundary of teosinte, its wild ancestor. Growth of human-tended crops in colder environments may not always depend on improved cold tolerance. Breeding for early maturity may minimize cold exposure even in colder climates, although earlier maturity will usually decrease yield potential. The spread of wild species into colder environments has not always depended on freezing tolerance per se; dropping leaves or overwintering as seeds are additional options (Zanne et al., 2014). Still, if natural selection is so powerful, why did not teosinte populations at the northern edge of its range evolve enough cold tolerance to spread northward?

Gene flow from the interior of a species' range may swamp natural selection for abiotic stress at range boundaries, limiting adaptation (Kirkpatrick and Barton, 1997), although gene flow among areas exposed to similar abiotic stress can enhance adaptation by countering inbreeding (Sexton et al., 2011). Given the extremely dry conditions in northern Mexico and the southern US, however, it is not clear that evolution at the northern range limit of teosinte was driven mainly by cold.

The strongest selection for cold tolerance may be found in high-altitude populations of teosinte. *Zea mays* ssp. *mexicana*, in particular, survives and reproduces at altitudes from 1600 to 2700 m, where average minimum temperature is below 4 °C (Hufford et al., 2012). High-altitude tropical maize landraces are apparently more cold-tolerant than those grown much farther north, including a "frost tolerant" population from Nebraska (Hardacre and Eagles, 1980; Hardacre et al., 1990).

The superior cold tolerance of high-altitude maize in Mexico is apparently due to "incorporation of adaptive mexicana [teosinte] alleles into maize", including alleles for cold-adaptation via anthocyanin and insulating hairs, whereas there is little evidence of beneficial gene flow from maize to teosinte (Hufford et al., 2013). Similarly, Doebley (1984) found little gene flow from maize to teosinte populations "at least in respect to those characters that affect the survival of teosinte in the wild."

In rice, too, beneficial gene flow may be predominantly from wild species to crops. The flooding-tolerant *SUB1A* gene now being transferred among rice varieties is also thought to have originated in wild relatives (Pucciariello and Perata, 2013), although gene flow from domesticated to wild rice also occurs. *SUB1A* flooding tolerance comes from reducing elongation when submerged, which conserves resources for growth after flooding subsides