Balanced parts for the ideal whole

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Key words: Ideal plant architecture, Food-nutritional security, Climate change

Abstract

Crop domestication and breeding considerably increased productivity over centuries, but simultaneously involved unconscious selection against 'selfish plant behavior'. Paradoxically, modern-day crop breeding largely enhances individual plant-fitness. As agriculture relies on community performance, embracing an "Agroecological Genetics and Genomics" viewpoint might maximize communal yield by matching crop genotypes to target environments.

Enhancing yield potential has always been the cornerstone of crop improvement. In a changing climate its relevance for ensuring food-nutritional security is now higher than ever before. Over the years, timely technological developments [1] enabled functional characterization and rapid deployment of key genes in crop breeding. Despite these advances, developing ideal plant architecture based on target environment(s) and management practices is still largely unexplored. In fact, although proposed more than half a century ago, the ideotype concept (for favorable environment) that defined key attributes of a "communal plant" for a balanced performance, both as an individual and also in an optimized community, has still neither been comprehensively tested nor realized [2]. One primary bottleneck hindering further progress may be the presence of trade-offs between major yield component traits. For instance, grain number and thousand grain weight are negatively related in wheat cultivars [3], as are increased panicle branching and reduced tillering in rice [4]. These scenarios clearly indicate that efforts to solely improve a single trait often risk compromising other traits and negating the desired selection effect. The consideration that agricultural production functions as a form of ecological engineering, i.e. the manipulation of populations, communities and agroecosystems to satisfy fundamental human requirements, may therefore help in this context [5]. Why? Because agricultural issues are mostly related to populations, communities and ecosystems. For example, crop yield per unit area is one of the most important quantity measures to determine productivity. This parameter is almost always attributed to the performance of a genetically homogeneous population in the field. For this reason, selection in crop breeding programs should rely largely on field performance under population or group selection, e.g. plot yield. But what are the decisive plant characters that make one population perform better than another? Often the determinant is the presence or absence of 'selfish' plant behavior [6].

'Selfish' behavior relates to plant traits that promise to confer an advantage when grown in natural habitats, increasing fitness; whereas the absence of 'selfishness' in a high-density population increases the overall community performance by cooperative use of available resources. Interestingly, and counterintuitively, the loss of 'selfishness' in crop plants is often associated with reduced individual plant fitness, as seen for example in the selection of the tough rachis, or semi-dwarf wheat and rice crops during the Green-Revolution [5, 6]. So, selection can reap benefits by improving productivity while unconsciously reducing individual plant fitness. Perhaps, that's why the advantages breeding could achieve through selection for yield based on single plant (e.g. from F_2 families) has plateaued over time. Hence, it is very clear that the agricultural plot as a selection environment behaves quite differently from habitats under natural selection [1]; many native 'selfish' plant traits are therefore sub-optimal or even disadvantageous in a community context. In the past, however, selection of less fit individuals improved genetic adaptation to this human-customized environment [5, 6]. In a similar way as humans have domesticated wolves (*Canis lupus*) to a highly diverse range of dog breeds from cooperative companions and helpers to cuddly wimps, one might assume that domesticated plants have undergone similar drastic changes. In contrast, however, the overwhelming majority of today's staple crops do not look fundamentally different from their wild ancestors, implicating that selection was most likely not strong enough or incorrectly placed [5], or perhaps most plant species are more resilient to radical changes **(Box 1)**.

Crop selection since the Green Revolution has been rather tedious and time-consuming, with slow yield progress and frequent tradeoffs with other relevant traits, such as resistances, quality and nutritional value. In future, recent technological advances might accelerate selection of reduced individual fitness but high field yield. But, what to select for, or against? In this context, one may have to consider two classes of 'selfish characters' that can be roughly defined as

exterior or interior. Exterior characters, already well described by C. M. Donald [2] for high-planting densities as well as well-fed growth conditions, reduce plant-plant competition while more efficiently utilizing common resources such as nutrients and light. They relate predominantly to plant architectural traits, such as a less neighbor-invasive root system, sturdy and short culm, low-tillering, erect leaves and a highly-fertile inflorescence. Although exterior characters are inherently measurable, surprisingly little research has been undertaken to create such 'idealized' genotypes for thorough hypothesis testing. Interior characters, on the other hand, are considerably less obvious features of crop plants and hence far less amenable to track, e.g. water and nutrient uptake and translocation efficiency, source-sink and growth allometric relationships, root-to-shoot or organ-to-organ signaling, or radiation use efficiency in a canopy context. All of these interior characters are genetically highly complex (quantitative) and have not been resolved in any crop or model plant to date, mainly because this kind of trait behaves like a mechanistic or genetic 'black box'. Recombining exterior and interior characters in a balanced way while selecting under relevant agroecological growth conditions may be the key to high-yielding crop communities.

Despite grand progress in recent decades, specifically through basic insights from model plants, we are still only scratching the surface of what repertoire of complex performance and response traits might be considered essential or desirable in crop plants. Nevertheless, first cautious attempts in model plants have demonstrated that 'selfish' plant behavior indeed has a genetic basis [7]. Pursuing this in crop plants will require field-phenotyping and selection under relevant conditions in a community context. Thus, connecting genetic principles with ecological and evolutionary concepts, by treating agricultural production as an ecosystem or adopting an ecological engineering approach, may open the way towards a more holistic view of "agroecological genetics and genomics" of crop plant populations for enhancing yield.

To this end, multi-omics systems analyses (genome, transcriptome, proteome, metabolome, epigenome, microbiome etc.) of diverse germplasm across critical developmental stages and large-scale phenotyping for both exterior and interior traits in relevant agroecological contexts can possibly empower research at crop community resolution **(Figure 1)**. Trait-responsive network hubs, associated genes and favorable haplotypes might support computational design of adapted, customized crop genomes [8] and assist in tailoring multiple traits. The significance of using adapted haplotypes to increase yield was reported in wheat [9] and rice [10], among others. In principle, genome engineering by multiplexed gene/haplotype editing or synthetic biology routes [1] might facilitate more rapid development of ideal crop plants in future. Another promising strategy is establishment of trait-specific donor panels harboring adapted genomic signatures **(Figure 1)**. A 'First-Generation Ideal Plant Type' (iGen-IPT) could then be developed by combining superior trait-specific near isogenic lines (NILs) through genomics-based breeding [11]. Multi-omics analyses of these iGen-IPTs could redefine molecular networks and regulators, gene-gene interactions, background effects, high-resolution computational genome and thus an improved iiGen-IPT. Similarly, such recurrent systems analyses might result in better-adapted 'next-generation Ideal Plant Types' (nxIPTs) for optimized community performance. It is important to emphasize that these nxIPTs are not universally applicable, but must vary with target-environment and management practices. However, initial investigations of germplasm in 'hotspots' representing existing environmental diversity could support rapid and effective generation of multi-omics datasets for simulating customized crop genomes suiting any target-environment, including predicted future climate scenarios; as exemplified from CGIAR's "Global Rice Array" initiative (see: http://ricecrp.org/wp-content/uploads/2017/03/Flagship-project-4.pdf).

Finally, establishment of a large multi-disciplinary "**I**nternational **C**rop **I**deotype **C**onsortium (IC^2)" (see: http://ic2.ipk-gatersleben.de) comprising experts from various domains including ecology, plant biology, genetics and breeding, systems and synthetic biology, genome engineering, crop modelling, remote sensing, etc., may trigger a much-needed breakthrough in the research arena of ideal crop plant architecture. IC^2 is designed to overcome existing yield barriers while narrowing the gap between potential and actual yield in a community setup. Such human-customized plant communities where caring and sharing is favored over competing may not only provide more resource-efficient, high-yielding, biofortified crop plants; it simultaneously may herald the prospect of more sustainable solutions to future agricultural production systems in a changing climate.

Box 1: Can lessons from dog breeding help in customizing crops?

About two centuries of breeding dogs (domesticated from wolves 15,000-10,000 years ago) resulted in over 250 diverse breeds customized with distinct morphology and behavior to suit various human needs [12]. Besides few exceptions such as teosinte vs maize, most staple food crops (domesticated >15,000 years ago) do not exhibit such drastic transformations compared to their wild relatives (**Figure I**). Perhaps in those cases, selection was not strong enough or incorrectly placed. Or, in contrast to animals, plants might be highly developmentally canalized because they are sessile individuals which evolved to cope with erratic, local environments. This may be why plants expanded their genomes with more genes and evolutionarily invented polyploidization as a consequence of natural selection. Moreover, in large crop plant genomes favorable alleles are often tightly linked to sub-optimal or deleterious alleles in the less recombining genomic regions [1], again favoring the plant's genomic resilience towards change. Precise gene editing or de novo synthesis might address some of these hurdles. Anyhow, the dog example exemplifies how powerful genetic approaches can work by molding

an organism's genetic make-up to human-customized environments. Similarly, strong group selection in crop plants under genuine agroecological growth conditions may provide useful genotypes with lowered 'selfishness'.

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Figure legends

Figure 1. Agroecological genetics and genomics for ideal crop plant community

Agriculture, being a function of community performance requires silencing of 'selfish plant behavior'. Therefore, largely practiced single-plant selection becomes less relevant and it is more expedient to avoid or minimize 'selfish' plant behavior through group selection in crop breeding. In this context, embracing an "Agroecological Genetics and Genomics" viewpoint, combining genetic principles with evolution and ecology, might pave the way to unravel key molecular factors that regulate not only well-studied "exterior" traits but also elusive "interior" plant architectural traits at community resolution. Multi-disciplinary research efforts are urgently required in this direction to silence 'selfish' traits and maximize communal yield by matching crop genotypes to target environments and management practices. One size doesn't fit all; for instance, (i.) in water scarce ecosystem drought responsive genes should also be deployed, (ii.) like-wise for biotic stress resistance, (iii.) appropriate intercropping to tackle soil nutrient deficiency, (iv.) biofortification to address malnutrition etc. Note: Superscript indicate reference number. This figure was created partly by using BioRender (https://biorender.com/).

Figure I (in Box 1). Can lessons from dog breeding help in customizing crops?

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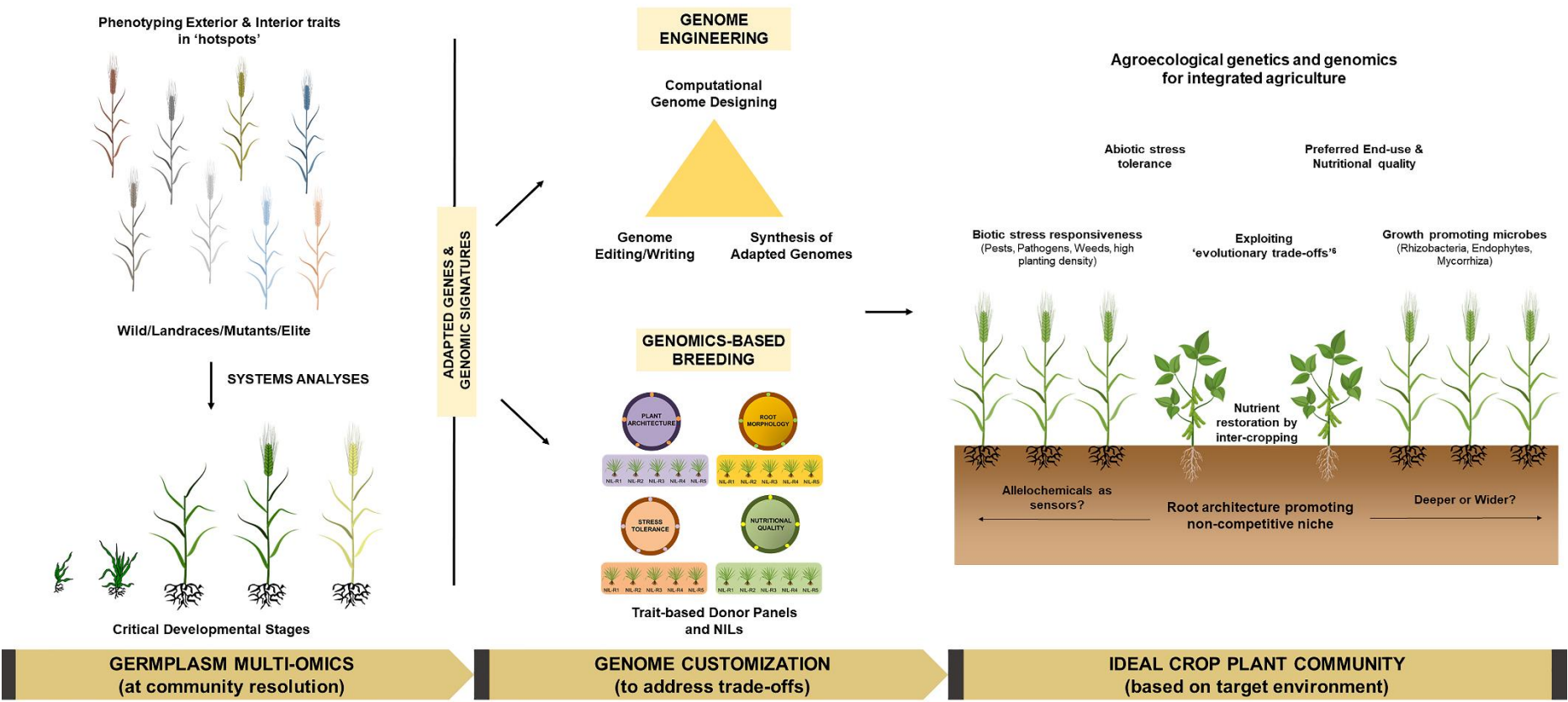
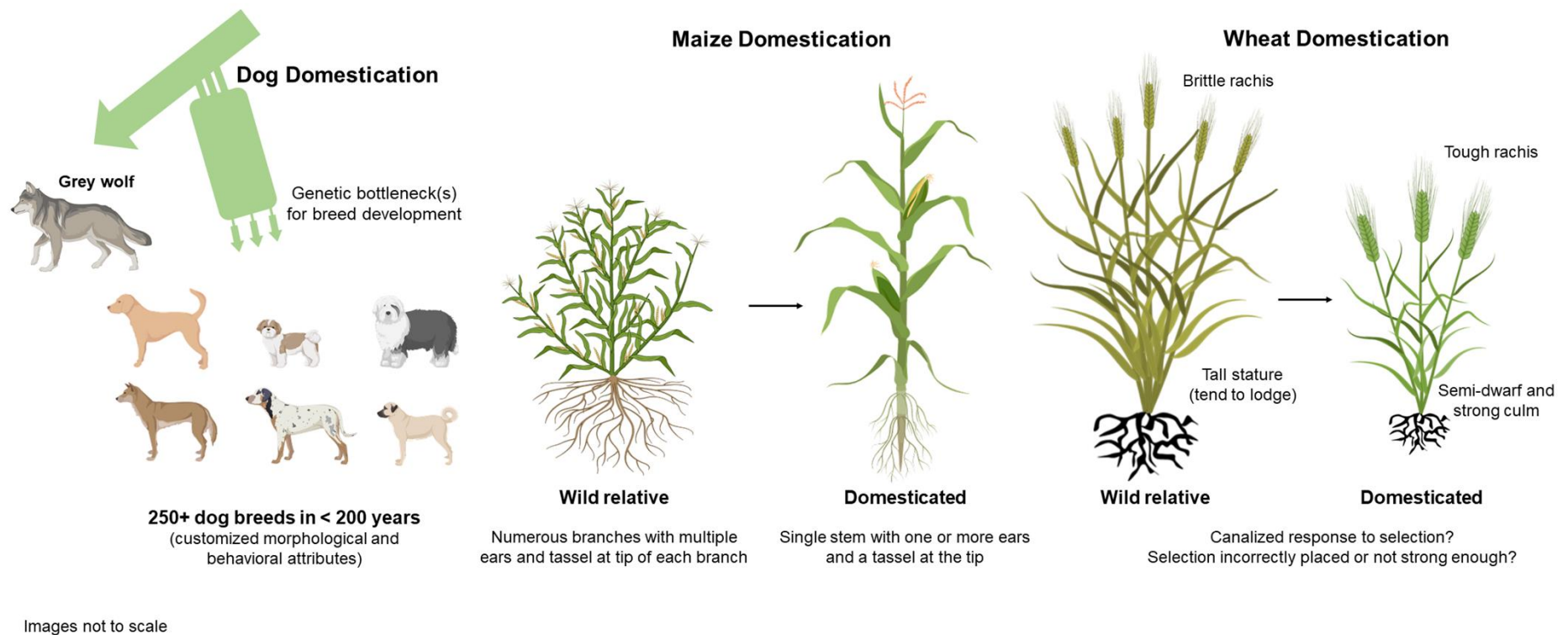**Figure 1. Agroecological genetics and genomics for ideal crop plant community**

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