Theor Appl Genet
DOI 10.1007/s00122-016-2772-5

OPINION PAPER

Bandwagons I, too, have known

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Received: 28 March 2016 / Accepted: 12 August 2016

Abstract
Key message **Bandwagons come in waves. A plant breeder, just like a surfer, needs to carefully choose which waves to be on.**
Abstract A bandwagon is an idea, activity, or cause that becomes increasingly fashionable as more and more people adopt it. In a 1991 article entitled *Bandwagons I Have Known*, Professor N. W. Simmonds described several bandwagons that he encountered in his career, beginning with induced polyploidy and mutation breeding and ending with the then-new field of biotechnology. This article reviews and speculates about post-1990 bandwagons in plant improvement, including transgenic cultivars, quantitative trait locus (QTL) mapping, association mapping, genomewide (or genomic) selection, phenomics, enviro-typing, and genome editing. The life cycle of a bandwagon includes an excitement phase of hype and funding; a realization phase when the initial hype is either tempered or the initial expectations are found to have been too low; and a reality phase when the useful aspects of a bandwagon become part of mainstream thinking and practice, or when an unsuccessful bandwagon is largely abandoned. During the realization phase, a new bandwagon that draws our attention and gives us renewed optimism typically arises. The most popular bandwagons, such as QTL mapping, are those for which the needed experimental resources are accessible, the required technical knowledge and skills can be easily learned, and the outputs can almost always be reported. The favorite bandwagon of any plant breeder has, in one way or another, resulted from Mendel's seminal discoveries 150 years ago. Our community of plant breeders needs to be continually diligent in welcoming new bandwagons, but also in hopping off from those that do not prove useful.

Introduction

This special issue of *Theoretical and Applied Genetics* commemorates the 150th anniversary of Gregor Johann Mendel's article *Versuche über Pflanzenhybriden* (*Experiments in Plant Hybridization*). Mendel's 1866 report demonstrated the basic laws of inheritance that are the foundations of today's plant breeding methods. Some scientific discoveries remain a trickle for a while: it took 34 years for Mendel's work to be rediscovered by Hugo de Vries, Carl Correns, and Erich von Tschermak, and much has been written about the nature of such rediscovery (Stomps 1954; Platt 1959; Zirkle 1964; Brannigan et al. 1981; Monaghan and Corcos 1986; Corcos and Monaghan 1990; Moore 2001). In contrast, other scientific advances become a bandwagon that gains immediate attention. For example, George Harrison Shull's 1909 proposal of hybrid maize (*Zea mays* L.) gained rapid attention from his peers and quickly became a bandwagon that many investigators hopped onto (Shull 1952).

A bandwagon, such as that of hybrid maize, becomes no longer regarded as a bandwagon if and when it eventually

Communicated by H. Bürstmayr and J. Vollmann.

Electronic supplementary material The online version of this article (doi:10.1007/s00122-016-2772-5) contains supplementary material, which is available to authorized users.

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Published online: 28 September 2016

proves valuable. A useful bandwagon becomes part of the mainstream thinking and practice, the bandwagon label is shed, and people eventually forget that the erstwhile bandwagon was once considered a bandwagon. To illustrate, Shull's inbred-hybrid proposal for maize cultivars in 1909 was first met with skepticism, because the initial parental inbreds were too weak to produce sufficient amounts of hybrid seeds for planting. Shull himself and his contemporary Edward M. East were not fully convinced at first that hybrid maize cultivars would be practical (Crabb 1947). Hybrid maize became feasible only after East's student, Donald F. Jones, proposed in 1918 that breeders hybridize two single crosses to form a double-cross cultivar. By 1943, double-cross cultivars were grown on nearly 100 % of the Iowa maize hectarage and nearly 90 % of the U.S. Corn Belt hectarage (Hallauer and Miranda 1981). By the 1960s, maize parental inbreds had become sufficiently improved to the extent that producing single-cross cultivars became feasible. So to us who are living more than a century after Shull's 1909 proposal, hybrid maize was never a bandwagon because we have always known hybrid cultivars as the norm. During the course of hybrid cultivars transitioning from a novelty to the norm, principles and procedures that maize breeders have learned (e.g., early-generation testing, heterosis, combining ability, cytoplasmic male sterility, etc.) have become integrated into our plant breeding knowledge base.

Other plant breeding bandwagons, however, have not been as successful as hybrid maize. Professor Norman W. Simmonds (1922–2002) was a respected plant breeder from the UK who devoted much of his career to the breeding and genetics of banana (*Musa* sp.), sugarcane (*Saccharum* sp.), and potato (*Solanum tuberosum*). In a 1991 article entitled *Bandwagons I Have Known*, Professor Simmonds railed against six bandwagons that, in his opinion, had far outlived their usefulness—except to those who were unwilling to hop off the bandwagon. Professor Simmonds had a reputation of challenging the status quo and his article, which was published in the December 1991 issue of the *Tropical Agriculture Association Newsletter*, was particularly colorful. An excerpt from the first paragraph of the article speaks for itself:

> "… if the bandwagon is a good one (allied to competent publicity), it becomes a gravy-train; a seat on it nearly guarantees funds, grants and other goodies such as easy (and not too roughly refereed) publication, attendance at conferences and so on. Bandwagons, while they roll at all, roll smoothly and admit of no uneasy instabilities such as cause boats to rock. Boat-rockers, dissenters, sceptics, the most useful people in science (but the least popular with bureaucrats), have no place on bandwagons unless, very occasionally, they invent new ones, whereupon they usually have the good sense to get off, but quick. […] I guess that some working scientists, especially those that actually live on bandwagons, wouldn't like to admit that they even exist, still less that they represent a lamentable waste of resources. They'd prefer to call them 'the Frontiers of Science' or some such."

It has been 25 years since Professor Simmonds wrote his *Bandwagons* article, and new bandwagons have arisen in plant breeding since 1991. I myself have been on a few bandwagons, and in fact I have helped push them. The benefit of hindsight, which Professor Simmonds did not have but that we now enjoy, has shown that many of his assertions about the bandwagon that he called Biotechnology were wrong. My goal is to take a retrospective look at the bandwagons that Professor Simmonds mentioned, share my perspectives on bandwagons that we as plant breeders have encountered in the last quarter century, and describe the life cycle of bandwagons in general.

Simmonds: bandwagons until 1991

Professor Simmonds's first bandwagon, *induced polyploidy*, was popular in the late 1930s and 1940s. This bandwagon grew out of the discovery that colchicine disrupts meiosis and doubles the number of chromosomes, the latter leading to larger plant parts. However, Professor Simmonds noted that "vegetative gigas characters, it appeared, had more to do with moisture content than dry matter production; large tetraploid grains of normally diploid cereals (rice, sorghum, barley) turned out to be a consequence of infertility and bad seed setting." While the promise of induced polyploidy as a direct means to produce new cultivars was unfulfilled, colchicine later become a valuable tool for quickly developing homozygous lines through doubled haploids. In particular, colchicine is widely used when the rate of spontaneous chromosome doubling among haploids is low, e.g., after anther culture in rapeseed (*Brassica napus*), after chromosome elimination in barley (*Hordeum vulgare*) × *H. bulbosum* crosses, or after crossing maize plants with a haploid inducer.

Induced mutations were described by Professor Simmonds as a "useless, even baneful, activity" that has "generated mountains of mostly disreputable literature, some trivial ornamental mutants and nothing of practical consequence" particularly because "Plant breeders already have plenty of mutants; the difficult trick is to use them efficiently." As with induced polyploidy, the initial promise of induced mutations in plant breeding has largely been unfulfilled. Yet, mutation breeding remains widely used today in a category of species that Professor Simmonds

mentioned: ornamental plants. For example, induced mutations are routinely used today in chrysanthemum to create useful variation for flower color, shape, and size (Broertjes 1966; Zhenhua and Shouhe 1995). Visual impact is a main breeding objective in ornamental flowers, and the immediate attractiveness of new flower colors or morphologies, coupled with the vegetative mode of propagation in many ornamental species, makes mutation breeding a valuable breeding method in such species.

Professor Simmonds was careful to distinguish between *crop physiology* as a science and adjunct to crop husbandry, versus the use of physiological traits as selection criteria in plant improvement. He cited unfulfilled expectations of using nitrate reductase activity to predict yield (it did not), selection for harvest index to improve crop productivity, and breeding for an ideal plant type (i.e., ideotype). Professor Simmonds cited an example of a colleague who briefly considered but did not hop onto the ideotype bandwagon: "Back in the 1960s Donald McColl sought a sugar cane ideotype […;] he concluded that there were several routes to good sugar accumulation but no one ideotype, no quick selection fixes. Neat job, end of project, end of story. Sugar cane breeders want tonnes of sugar not an ethereal vision of a Platonic Ideal." The consensus among plant breeders today is that it is usually more efficient to select for the primary trait itself, rather than to select for multiple secondary traits that are components of or associated with the primary trait.

The fourth and fifth bandwagons that Professor Simmonds mentioned are less well known. In Professor Simmonds's view, *The Protein Gap* was a nutrition myth epitomized by the development of high-lysine maize. Professor Simmonds argued that The Protein Gap is better solved by a more-balanced diet than by plant breeding. He said that "The protagonists generally failed to note that cereals and legumes complemented each other and that vegetative proteins (such as those in potatoes, brassicas, spinaches) were nutritionally excellent." Professor Simmonds accepted that *Farming Systems Research* could, in theory, facilitate a better understanding of the value of agricultural research to small-scale farmers in the tropics. However, Professor Simmonds opined that "the subject in general blew up into a sociological balloon and, nowadays, no research enterprise is complete without a gaggle of sociologists telling each other and everyone else what to do."

Biotechnology was Professor Simmonds's "biggest and best (or worst, depending on viewpoint)" bandwagon. He lumped into biotechnology the following three areas that we consider separately nowadays: (1) embryo, meristem, and tissue culture; (2) molecular markers; and (3) transgenics. Professor Simmonds asserted that in vitro operations will be only "marginally useful in plant breeding, though they certainly have a place in propagation." He did not say much about molecular markers, but had much to say about transgenics:

> "Plant breeding is not so simple but agribusiness is big business and seed supply is a major component of it which is why the chemical corporations have been buying into plant breeding for the past 10–15 years. Perhaps they even believe their own hype to the effect that molecularology is about to transform that dim, old fashioned plant breeding into Modern Science […] But a revolution is not in prospect and for the simple reason that those clever chemists either don't know or conveniently ignore: plant breeding is a statistical process that nearly always involves several–many genes of small effect (economic characters are 'polygenic') while molecularology can only cope with one gene at a time (and that at great expense). Quantitative genetics is just too difficult for chemists. Biotechnology may be really useful sometime well into the next century but I'd want to see the crucial 10,000 hectare test passed before I'd agree that it were any use at all; I'd require 10,000 hectares of an excellent cultivar, freely chosen by farmers and uniquely constructed by molecular tricks."

In hindsight, Professor Simmonds was correct in saying that, so far, the transgenic approach has not been able to handle polygenic traits. However, he grossly underestimated the utility and value of cultivars that carried single transgenes.

Transgenic cultivars

Scientists have come a long way from the discovery of DNA as the genetic material by Avery, MacLeod, and McCarty in 1944, to developing *Flavr Savr* tomato as the first transgenic cultivar, which was first marketed 50 years later in 1994. My first encounter with transgenic crops was in the mid-1990s, while I was a maize research scientist with Limagrain Genetics in Champaign, Illinois. I recall our research station receiving a shipment of Monsanto seed stocks with the Bt gene, which imparted resistance to lepidopteran insect pests, notably the European corn borer [*Ostrinia nubilalis* (Hübner)]. The different maize seed stocks, many of which were named after Old Testament prophets, represented different transgenic events that we were to test through crosses with our private inbreds. We later received word from Monsanto that we should focus our efforts on only a few of the transgenic events, including an event named 'Ezra' which later became known worldwide as MON810 (Horner et al. 2003). The availability of 'Ezra'/MON810 brought an immediate halt to a small research project I was leading on introgressing QTL alleles

for European corn borer resistance from the donor inbred B52 to our most elite private inbreds.

The percentage of the U.S. maize hectarage with transgenic cultivars grew from 4 % in 1996 to 93 % in 2014 (James 2014). Worldwide, 18 million farmers in 28 countries planted more than 181 million hectares of transgenic crops in 2014. The worldwide area planted to transgenic crops increased 100-fold between 1996 and 2012. The main transgenic crops that have been produced are alfalfa (*Medicago sativa*), canola (*Brassica napus*), cotton (*Gossypium hirsutum*), eggplant (*Solanum melongena*), maize, papaya (*Carica papaya*), poplar (*Populus* sp.), soybean [*Glycine max* (L.) Merrill], squash (*Cucurbita pepo*), sugarbeet (*Beta vulgaris*), sweet pepper (*Capsicum annuum*), and tomato (*Solanum lycopersicum*). Countries with the most area planted to transgenic crops in 2014 were the U.S., Brazil, Argentina, India, and Canada (James 2014). On the other hand, the adoption of transgenic cultivars has been low in Europe (except for Spain, Portugal, Czech Republic, Romania, and Slovakia) and Africa (except for South Africa, Bukina Faso, and Sudan).

Since 2006, the area planted to transgenic crops each year (James 2007) has exceeded Professor Simmond's 10,000-hectare test by more than 10,000-fold. The adoption of transgenic crops in many countries remains limited due to the issues of public acceptance, safety concerns, and government regulation. The transgenic cultivars to date have been largely limited to insect resistance, herbicide tolerance, and disease resistance due to a single transgene or several stacked transgenes in a handful of major species. More recently, the transgenic approach has been used to develop drought-tolerant maize, low-lignin alfalfa, low-acrylamide (a potential carcinogen) potato, and non-browning apple (*Malus* × *domestica*). Like Professor Simmonds, I was initially skeptical in the 1990s of the impact of single transgenes: while European corn borer has been a nuisance in maize, my impression was that it was not a major problem, and it seemed to me that the problem became important only when the cure (in the form of the Bt gene) came along. Overall, the acceptance of transgenic technology in many countries indicates that it is a scientifically mature technology that will continue to be an important tool in plant improvement in areas where genetically modified cultivars are grown.

Molecular markers and QTL mapping

Whereas the transgenic approach has focused on crop improvement via one or a few transgenes, *linkage mapping of QTL* has opened the possibility of crop improvement via multiple markers associated with quantitative traits such as crop yield, quality, and adaptation. Since the 1980s, different molecular marker systems have been developed, including restriction fragment length polymorphisms (RFLP), randomly amplified polymorphic DNA (RAPD), amplified fragment length polymorphisms (AFLP), simple sequence repeats (SSR), and single nucleotide polymorphisms (SNP). Maize has a linkage map of roughly 1750 cM and early QTL mapping studies in maize utilized about 70–120 RFLP markers (Reiter et al. 1991; Beavis et al. 1991; Edwards et al. 1992; Stuber et al. 1992; Veldboom and Lee 1994). High-throughput SNP genotyping technology has since dramatically increased the number of molecular markers used in QTL discovery. In the 2010s, for example, maize QTL have been detected with 56,110 SNP markers on the Maize SNP50 BeadChip (Illumina, Inc.) (Weng et al. 2011; Wang et al. 2012; Schaefer and Bernardo 2013).

The availability of abundant RFLP markers beginning in the mid-1980s led to much optimism among many breeders and geneticists, e.g., "the advent of RFLPs, by greatly increasing the total number of polymorphic markers available to the agricultural community, may signal the advent of a new and promising era for the understanding and improvement of quantitative economic traits" (Beckman and Soller 1986; emphasis mine). The hype and excitement about QTL mapping are evidenced by the sheer numbers of mapping studies that have been conducted and QTL that has been reported. In 2008, I estimated that more than 10,000 QTL had been reported in more than 1200 studies involving 12 major plant species (Bernardo 2008). These numbers are undoubtedly higher in 2016. As of October 2014, the Genomics Database for Rosaceae (https://www.rosaceae.org/) reported 2255 marker-trait associations for 376 traits in 16 species, including apple, peach (*Prunus persica*), cherry (*Prunus* sp.), and strawberry (*Fragaria* × *ananassa*). As of March 2016, the GrainGenes database (http://wheat.pw.usda.gov/GG3/) reported a total of 1498 QTL in the *Triticeae* and in oat (*Avena sativa* L.).

Unfortunately, the optimism from the 1980s about an increased understanding and improvement of quantitative traits via QTL mapping is largely unrealized. The thousands of QTL reported in the literature did little to increase our knowledge of the actual genes underlying quantitative traits such as yield, because the information gleaned from QTL mapping was primarily statistical (in the form of marker-trait associations) rather than biological. For different reasons, including low statistical power for QTL detection, QTL × environment interaction, QTL × genetic background interaction, and different QTL segregating in different crosses, it quickly became clear that "It is easy to find a QTL, but much more difficult to find the same QTL twice." (RC Shoemaker, personal communication, ca. 1995). The following quote from Bernardo (2008) remains true today: "the vast majority of the favorable alleles at

these identified QTL reside in journals on library shelves rather than in cultivars that have been improved through the introgression or selection of these favorable QTL alleles."

On the other hand, there have been some notable success stories of utilizing QTL in cultivar development. These include the *Fhb1* QTL for Fusarium head blight resistance in wheat (*Triticum aestivum*) (Anderson et al. 2008), the *Sub1* QTL for submergence tolerance in rice (*Oryza sativa*) (Septiningsih et al. 2009), and major QTL for soybean resistance to cyst nematode (*Heterodera glycines* Ichinohe) (Concibido et al. 2004). In each of these cases, the marker-trait associations represented major QTL, not necessarily because their r^2 values exceeded a certain threshold, but because each favorable QTL allele had an effect that was large enough and consistent enough to be valuable in wheat, rice, and soybean breeding programs.

In hindsight, we as breeders became too greedy in expecting too much from the QTL mapping bandwagon. We have since learned that QTL mapping is most useful for traits, such as wheat Fusarium head blight resistance or soybean cyst nematode resistance, which might have one or a few underlying major QTL (Bernardo 2008). When a trait has major QTL, the power to detect the major QTL is high and the major QTL alleles can be easily introgressed by standard breeding procedures because the major QTL are few. The few major QTL alleles can be viewed as LEGO® building blocks that can be assembled together, via a design approach, in an improved cultivar. However, if the trait is controlled by many QTL, they will tend to have smaller effects and the power to detect them becomes low (Lande and Thompson 1990; Beavis 1994). In addition, even if a breeder somehow successfully detects a large number of minor QTL controlling a trait, the favorable alleles at many QTL cannot be efficiently bred into an improved cultivar. Suppose a trait is controlled by the joint effects of 30 unlinked QTL. If all 30 QTL are segregating in a cross, the frequency of a recombinant inbred with the favorable allele at all 30 QTL would be $(0.5)^{30} = 1$ in 1.07 billion. In other words, the favorable alleles at multiple minor QTL can no longer be viewed as LEGO® building blocks. Our initial optimism about QTL mapping has therefore been tempered by the realization of when a find-and-introgress approach for QTL works and when it does not.

Association mapping

When the excitement about QTL mapping was beginning to wane in the mid-2000s, *association mapping* emerged as a new approach for finding marker-trait associations. Association mapping has two advantages over linkage mapping of QTL in biparental crosses. First, association mapping does not entail the time, effort, and cost of creating a mapping population (e.g., recombinant inbreds) from a cross. Marker-trait associations are instead detected in a germplasm collection, which can easily be assembled. Second, the QTL can potentially be mapped at a much higher resolution. In a biparental cross, the limited number of crossover events leads to large segments of chromosomes or even entire chromosomes being passed intact from parents to offspring (Smith et al. 2008). This phenomenon allows the detection of QTL even with a moderate marker spacing. In contrast, the germplasm used in association mapping may have been subjected to multiple historical recombinations. This leads to a finer mosaic of chromosomal segments, thus leading to a potentially higher mapping resolution.

Many plant breeders and geneticists turned their attention to association mapping beginning in the mid-2000s. I, too, joined the association mapping bandwagon: colleagues and I detected maize QTL in mapping panels of up to 22,774 single crosses (Parisseaux and Bernardo 2004) and with up to 28,626 SNP markers (Schaefer and Bernardo 2013), and I proposed a 'G model' approach for association mapping (Bernardo 2013). Association mapping in plants initially tended to emphasize candidate genes (Yan et al. 2010). However, as SNP genotyping became cheaper, genomewide association studies became more common.

Unfortunately, association mapping in plants has so far failed to identify a single major QTL allele that has been found useful in cultivar development, at least in public breeding programs. The *Fhb1* and *Sub1* alleles were identified by linkage mapping and have been subsequently deployed widely in wheat and in rice. In contrast—and I may well be wrong—there has not been a single QTL that was previously unknown (i.e., not a candidate gene), was then discovered through genomewide association mapping, and has since been introgressed widely into elite germplasm.

The main reason for this failure is that association mapping detects variants that are common in a germplasm collection, but it has a low power for detecting variants that are rare. Plant breeders, on the other hand, are typically interested in discovering rare variation. Suppose a breeder aims to find major QTL alleles for resistance to Ug99 wheat stem rust (*Puccinia graminis* f. sp. *tritici*). Phenotyping of a wheat germplasm collection identifies 498 susceptible lines and only two resistant lines. Association mapping of the entire 500-line collection will fail to identify QTL alleles for Ug99 stem rust resistance, because the number of individuals that carry the resistance alleles is too low. The situation would be markedly different if the breeder is attempting to find marker-trait associations for dough quality in wheat. In this scenario, alleles that affect dough quality would include known glutenin genes, which tend to be common in wheat and can be identified—or, more

realistically, validated—by association mapping (Zheng et al. 2009).

On the other hand, a breeder can cross a Ug99-resistant line with a susceptible line to form a population for linkage mapping. Doing so will lead to allele frequencies of 50 %. The Ug99 resistance alleles will therefore no longer be rare in the mapping population, and the power to detect QTL becomes much higher than in association mapping. Candidate gene or genomewide association mapping remains useful as a genetics tool. But if the goal is to discover major QTL alleles that are currently rare, plant breeders should avoid association mapping.

Genomewide selection

Genomewide selection (or genomic selection; Meuwissen et al. 2001) became a bandwagon in plant breeding in the late 2000s. Unlike QTL linkage mapping or association mapping, genomewide selection does not attempt to identify molecular markers with statistically significant effects for a given trait. Instead, genomewide selection uses hundreds or thousands of SNP markers along with prior phenotypic data to predict the performance of new candidates for quantitative traits. Genomewide selection is therefore not a design approach that attempts to create a cultivar that has a specific combination of marker alleles. It is a purely predictive approach that uses cheap and abundant markers to identify the best candidates in a population. Genomewide selection has emerged as a valuable method for improving complex traits that are controlled by many QTL with small effects.

The first (simulation) study of genomewide selection in plants was published in 2007 (Bernardo and Yu 2007). Multiple studies that focused on prediction accuracy for quantitative traits in different species soon followed (Lorenzana and Bernardo 2009; Albrecht et al. 2011; Asoro et al. 2011; Heffner et al. 2011; Guo et al. 2012; Schulz-Streeck et al. 2012). Analytical results indicated that the prediction accuracy is expected to increase as the marker density increases; as the product of heritability (h^2) and size of the training population (N) increases; and when fewer QTL control the trait (Daetwyler et al. 2008; Lian et al. 2014). A low h^2 can be compensated by the use of a large N. It is noteworthy that Nh^2 determines both the power to detect a QTL (Lande and Thompson 1990) and the accuracy of genomewide selection.

Prediction accuracies for 969 maize crosses have shown that just as the accuracy of phenotypic selection (as measured by the square root of h^2) varies, the accuracy of genomewide selection (denoted by r_{MG}) likewise varies (Lian et al. 2014). While the estimated accuracy of phenotypic selection was always positive, the estimated accuracy of genomewide selection was sometimes negative. Nevertheless, the mean accuracy of genomewide selection across the 969 maize crosses was positive for grain yield and for each of six other traits. Therefore, just like phenotypic selection, genomewide selection should work reasonably well on average when it is applied routinely, particularly in those stages of a breeding program or in breeding situations in which phenotypic selection is nonexistent or ineffective.

Designing a training population and assessing the prediction accuracy has become routine in plants to the extent that the methodology has been explored even for domesticating a new crop such as intermediate wheatgrass [*Thinopyrum intermedium* (Host)] (Zhang et al. 2016). In the same way that there have been many studies to map QTL, there have also been many studies to assess the accuracy of genomewide selection in plants. However, in the same way that there have been far fewer studies that have actually utilized the identified QTL to develop improved cultivars, there also have been only a few published studies that have actually implemented genomewide selection in plants to develop improved germplasm. These few studies include those by Massman et al. (2013), Asoro et al. (2013), Combs and Bernardo (2013), Beyene et al. (2015), and Rutkoski et al. (2015). Private sources, on the other hand, have confirmed that major seed companies routinely implement genomewide selection in maize and in soybean.

In the public sector, the barley breeding program at the University of Minnesota represents an excellent example of how genomewide selection has been routinely used in cultivar development. Since 2010, Minnesota barley breeder Kevin P. Smith has regularly obtained genomewide predictions mainly for Fusarium head blight resistance, but also for yield, winter hardiness, and malting quality. Doing so has reduced the time and effort needed in phenotyping, with a side effect of increasing the morale of the barley breeding team. Breeders find genomewide selection convenient because, unlike QTL mapping, it does not require model selection: all markers are used in the prediction process. However, its routine application requires a cost-effective and efficient means for genotyping; software for handling, quality control, and joint analysis of marker and phenotypic data; and a streamlined work flow for using genomewide predictions within the overall breeding process and timeline. How widely genomewide selection becomes routinely implemented in public breeding programs remains to be seen.

Newer bandwagons related to P = G + E

A basic concept in genetics is summarized by P = G + E, which is shorthand for the phenotypic value being the sum of genetic and environmental effects. The bandwagons

described so far deal with the G component, and but there also has been much interest in the P and E components. *Phenomics* refers to the use of advanced methods for obtaining phenotypic data. Phenomics exploits developments in robotics, precision agriculture, remote sensing, and image analysis, and it allows real-time measurement of traits related to plant health, morphology, architecture, and composition (Furbank and Tester 2011). Indoor phenomics facilities allow detailed and rapid phenotyping of individual plants under controlled conditions. Drones have been used to phenotype plants in the field. Tractor-like phenotyping equipment with different cameras and sensors can take plant measurements at close range (White et al. 2012).

Phenomics will undoubtedly continue to be valuable in investigations of plant biology. It is less clear how the sheer amounts of data generated with phenomics can impact breeding decisions. To illustrate, breeders often record data only during certain times of the life cycle of a plant. Plant height in cereals, for example, is recorded only once after flowering. Lodging is recorded only once before harvest. Grain moisture is recorded only at harvest. Suppose phenomics allows the daily recording of plant height from sowing until flowering, and of lodging and grain moisture from flowering until harvest. How such a mass of data can be used in selection remains unclear.

In particular, a breeder needs to process (often intuitively) all available trait information into a binary, yes/no decision on which candidates to keep and which candidates to discard. A breeder may already struggle in weighing how much emphasis to give to each of 5–10 traits, and it is unclear how daily or weekly phenotypic data can contribute to better selection decisions, particularly when a main trait, such as yield, is most meaningful only at harvest. Phenomics might be most useful if it allows phenotyping for traits that are currently very difficult or expensive to collect. Root traits are a prime example, and it would be of much interest to see if phenomics technologies can be developed to quickly and cheaply measure root traits in the field.

Envirotyping refers to the characterization of environments for different nongenetic factors that affect plant growth and development (Cooper et al. 2014; Xu 2016). Examples of environmental factors include precipitation, temperature, light, wind, soil properties, and biota. In quantitative genetics, the mean performance of lines, hybrids, or clones grown in an environment has been traditionally used to measure the value of that environment. Characterizing an environment according to different physical and biotic variables would be more biologically meaningful.

Genotype × environment interaction has made cultivar development more complicated, but has also contributed to a breeder's job security. Envirotyping may lead to a better characterization of not only genotype × environment interaction, but also of QTL × environment interaction. A better characterization of how experimental cultivars respond to different environmental variables shall lead to a better understanding of plant response to environments, as well as a better placement of cultivars on different farms. Such site-specific characterization and prediction of plant performance will likely be coupled with phenomics, crop growth modeling, and genomewide prediction (Cooper et al. 2014; Xu 2016).

While envirotyping can allow breeders and crop physiologists to better predict how cultivars perform in specific environments, such predictive power cannot be fully realized because we remain unable to fully predict what a future environment will look like. Climate change is leading to long-term trends in climatic variables, and some environmental variables, such as soil type, fertility, and cultural management practices, remain fairly constant from year to year on the same farm. A maize or soybean grower, however, is not necessarily interested in crop performance under a certain set of environmental variables that were encountered in his or her farm last year. Instead, the grower needs to choose which cultivars to grow on his or her farm next year, but the grower does not know if it will be warm or cold or wet or dry or average the next year. Envirotyping can therefore give only partial predictions of which cultivars would perform the best in a future location-year combination. Overall, envirotyping is still in its infancy as a plant breeding bandwagon, and we as a community await results on the breadth and depth by which envirotyping can enhance cultivar development.

Genome editing focuses of the G component of $P = G + E$, and it represents an infinitely more precise form of mutation breeding. Genome editing allows changes in targeted DNA sequences, with the edits involving the deletion, substitution, or addition of one or more bases. Different genome-editing technologies have been developed, and the CRISPR/Cas system has emerged as a method of choice become of its efficiency, low cost, and ease of use (Xiong et al. 2015).

Mutation breeding in the 1940s and 1950s did not require any prior information on gene identity and function, and it led to random mutations. When chemical or physical mutagens are used, a useful induced mutation for one trait may be accompanied by undesirable mutations for other traits, and the useful mutant allele oftentimes needs to be bred into a clean genetic background. In contrast, genome editing requires prior information on gene identity and function and leads only to targeted mutations. In practice, however, the plant regeneration process after genome editing may lead to unwanted somaclonal variation in the target cultivar. Genome editing may be particularly valuable in plant species for which backcrossing (to introgress favorable alleles) is impractical due to a long generation interval or infeasible due to a heterozygous recurrent parent.

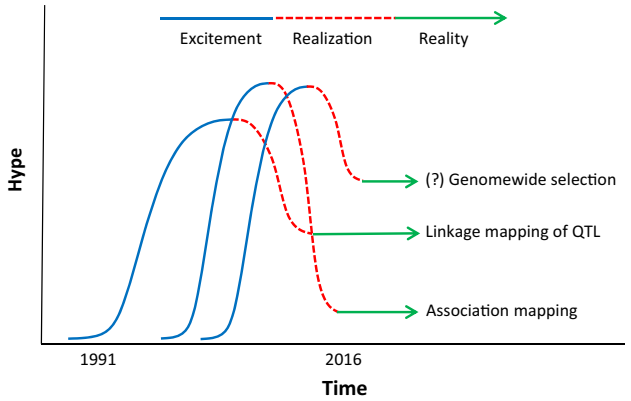

Fig. 1 Life cycle of a bandwagon, with QTL mapping, association mapping, and genomewide selection as examples. The reality level for association mapping is low, because the approach typically lacks power for detecting rare variants, which are what plant breeders most often seek. The (?) before genomewide selection indicates that the eventual level of usefulness of the procedure is still being discovered

I speculate that genome editing will be most useful in the same situations where linkage mapping of QTL is most useful: for traits that may have major QTL or major genes. For such traits, such as disease resistance or flowering date, changes in the known underlying genes can be directly made via genome editing. These changes will involve loss-of-function mutations or gain-of-function mutations equivalent to naturally occurring mutations with known effects, or novel mutations that need to be characterized via phenotypic screening.

The many genes affecting a trait such as yield in elite germplasm remain largely unknown even after whole genomes have been sequenced. Even if many or all the loci affecting yield become known, the exact per-locus edits needed to optimize yield will be unknown. The variants from genome editing for a quantitative trait will then need to be subjected to phenotypic testing, in the same way that any new variation created by hybridization is subjected to phenotypic testing. An imperfect heritability limits the ability to identify the best lines or hybrids or clones, as well as the ability to precisely estimate the effects of QTL alleles with minor effects. Likewise, an imperfect heritability will limit the ability to identify the best variants from genome editing for a polygenic trait.

Life cycle of a bandwagon and of a scientist

A bandwagon typically goes through three phases: excitement, realization, and reality (Fig. 1). The excitement phase is a period of much hype, attention, funding, and participation. Next, the realization phase occurs when research results increasingly show what the bandwagon can and cannot do. Most often, the initial hype is tempered but sometimes, as in the case of hybrid maize, the initial expectations are found to have been too low. Finally, the reality phase sets in when a successful bandwagon becomes part of mainstream practice and what has been learned from the bandwagon becomes integrated with our knowledge base—or when an unsuccessful bandwagon is largely abandoned.

The Gartner, Inc. organization described bandwagons as going through a 'Hype Cycle' that has five stages (http://www.gartner.com/technology/research/methodologies/hype-cycle.jsp). The first two stages ('Technology Trigger' and 'Peak of Inflated Expectations') correspond to the hype phase in Fig. 1; the third and fourth stages ('Trough of Disillusionment' and 'Slope of Enlightenment') correspond to the realization phase in Fig. 1; and the fifth stage ('Plateau of Productivity') corresponds to the reality phase in Fig. 1. What often happens is that during the realization phase of a current bandwagon, a new bandwagon that draws our attention and gives us renewed optimism arises. As previously mentioned, association mapping emerged as a new approach for finding marker-trait associations when the excitement about QTL mapping was beginning to wane in the mid-2000s (Fig. 1). Other current or emerging bandwagons not discussed in this article include crop adaptation to climate change, microbiome and plant–microbe interactions, epigenetics, and increasing or altering meiotic recombination.

The popularity of a bandwagon depends not only on its level of hype, but also on how easy it is to join the bandwagon. Many are apt to join a bandwagon if the needed experimental resources are accessible, the required technical knowledge and skills can be easily learned, and the outputs can almost always be reported. The QTL mapping bandwagon is a prime example of an easy-to-hop-on bandwagon, because it satisfied all the aforementioned criteria. As I wrote in an earlier article (Bernardo 2008), "if a breeder can develop a mapping population of N = 100–150 progenies derived from an F_2 or backcross population between two inbreds, obtain reasonably good phenotypic data for the traits of interest, and genotype the population with markers spaced about 10–15 cM apart, then an analysis of the phenotypic and marker data with an appropriate statistical method as implemented in a user-friendly software package will almost always lead to the identification of at least a few markers associated with each trait of interest." Other advances, such as metabolomics, never achieved bandwagon status in plant breeding. This was likely due to the high level of technical knowledge and skills, as well as equipment and infrastructure, needed for metabolomics investigations.

Because plant breeding is rooted in the science of genetics, the favorite bandwagon of any plant breeder is in some way an offshoot of Mendel's seminal discoveries 150 years

ago. The life cycle of a scientist consists of up to four stages: (1) contributing dependently; (2) contributing independently; (3) contributing through others; and (4) contributing strategically (Thompson et al. 1986). A plant breeder contributes dependently when, as a student or apprentice, he or she helps develop germplasm or helps discover new knowledge as part of a breeding team. A plant breeder contributes independently when he or she begins leading a cultivar development program or academic research program. A plant breeder contributes through others when he or she gains seniority and begins to supervise the work of others on a team, including those of graduate students. Lastly, a plant breeder contributes strategically when he or she assumes leadership responsibilities at or near the top of a breeding or research organization.

Mendel as a scientist progressed only up to the second of the four stages described above, but his work had a lasting impact. Today's plant breeders will encounter bandwagons throughout their careers. Bandwagons, as shown in Fig. 1, come in waves. Just as a surfer needs to choose a good wave, breeders need to pick which waves to be on. Graduate students need to be equipped so that they can critically evaluate the bandwagons they will encounter; breeders and professors need to determine which bandwagons to join, which old ones to abandon, and which new ones to start; and breeders in leadership positions need to discern which bandwagons their organizations should build up, watch, or avoid. Our community of plant breeders needs to be continually diligent in welcoming new bandwagons, but also in hopping off from those that do not prove useful.

Author contribution statement RB did all of the work for this article.

Acknowledgments I thank Mark Cooper (DuPont Pioneer) for encouraging me to write this article and for suggesting the title; John Snape (John Innes Centre) and Brenda Bautista Perez (CIMMYT) for sending me a copy of the Simmonds *Bandwagons* article when I could not find my old copy; and Paul Harding of the Tropical Agriculture Association for permission to include the Simmonds article as electronic supplementary material.

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