Lehr- und Forschungszentrum für Landwirtschaft
Raumberg-Gumpenstein

61. Tagung der Vereinigung der Pflanzenzüchter und Saatgutkaufleute Österreichs 2010, 5 - 7
ISBN: 978-3-902559-53-1

How to increase yield and quality of wheat?

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Abstract

Wheat, one of the three major food crops, has been tremendously neglected in breeding research at least in comparison to maize. This must change immediately at a strong pace. It is intolerable that breeding targets defined already decades ago have to be reactivated just now, when gains in genetic yield potential have to become twice higher to secure global food resources. Alarmingly, yield increases in major production areas seem to have flattened off instead during the last decades. But genetic gains may be hidden by climatic or socioeconomic changes. From the 1960s to the late 1980s intensive research has been carried out in many parts of the world on the physiology of wheat development and the physiology of all processes determining final grain growth and yield. This research, however, was never efficiently translated into breeding action. As growth rates of potential yield have declined globally mostly below 1% per year, some old propositions for breeding targets have been taken up again. Yield progress is still associated closely with an increased number of grains per area on a global level. The critical phase for grain number is just before flowering and there exists underutilized photosynthetic capacity during grain filling, suggesting unnecessary floret abortion. Recent progress seems to be related to increased photosynthesis before and around anthesis, although no direct measurements were carried out. But accurate and easy methods for phenotyping are still missing to implement radiation use efficiency directly in breeding. Although marker assisted selection is gaining in pace, it is still most used just for the selection of simple traits. Can annual increase of potential yield be boosted again from 1% to more than 2.5%, needed to master the future, by implementing old and new strategies? There is no choice, it must be done!

Keywords

Genetic gain, *Triticum aestivum*, wheat breeding, yield progress

Our mission: Doubling the yield potential of all crops within four decades!

Mankind needs tremendous increases in the yield potential for all three major food crops, wheat, rice and maize as these cover more than half of all arable land in a time when we are faced with the task to double production within 40 years.

We have experienced a century of yield increase in wheat, based on breeding Mendelian laws, though at different paces in world regions. In the aftermath of the so called food crisis of 2007 several reviews by leading wheat experts have appeared. Therefore, here no new screening of the multitude of research based wheat publication will be attempted. Instead the recent reviews from 2009 to 2011 will be scrutinized for an appraisal of the present situation, of what has been realized from former proposals in the 'golden age' of wheat physiology, and of what is proposed for the near and distant future.

Are genetic gains flattening off?

Some recent reviews deal with the actual situation of yield increase in wheat by breeding. They all bear the disturbing message that these increases have flattened off in the last two decades. What are the indicators for a missing increase in wheat yield potential? According to PELTONEN-SAINO et al. (2009) there might be several genetic reasons, the two major ones exploitation of physiological traits like the harvest index (HI) and the increase in grain number per area. It had been a certain frustration for crop physiologists in the 1960s to realize that the shoot biomass potential had remained unchanged over 100 years, just the distribution between vegetative and generative mass had gone up in favor of the grains up and above 0.5 with a concomitant shortening of the culm (c.f. STAMP and HERZOG 1984). That this is close to physiological maximum for a healthy vigorous plant seems to be realized now worldwide. A second reason believed by PELTONEN-SAINO et al. (2009) is an already maximum increase of grain number per area. This trait has been regarded by crop physiologists and plant breeders since several decades as the new driving force for potential yield increase, and it still is (EVANS 1998, REYNOLDS et al. 2010). Further non-genetic reasons can be regarded as distortions, e.g. wheat has replaced more adapted cereals in less favorable production areas or arable areas were extended to less suitable land (PELTONEN-SAINO et al. 2009). Furthermore, it is difficult to separate the yield levels attained in certain regions from hot and dry spell as well as devastating short spell events like storm, hail and severe frost without previous hardening, as they are believed to be the companions of climatic change. Fully manmade or demanded by society, the socioeconomic policies especially in Europe demand a reduction in management tools for cereal production, with an impact almost impossible to disentangle from interacting forces mentioned above. Herein PELTONEN-SAINO et al. (2009) are fully corroborated by BRISSON et al. (2010) in their France based study, who

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claim that besides agronomic changes related to policy and economy since 2000, heat stress during grain filling and drought during stem elongation have confounded the visibility of a genetic progress, which according to them has not yet stopped in their region.

Just recently GRAYBOSCH and PETERSON (2010) published a similar story that there have been little genetic gains in the USA since two decades. Their chosen region for an analysis, the Midwest is subject to a continental climate with a much lower realizable yield ceiling then the aforementioned European regions. Therefore, the exact time phase coincidence must not be based on causal facts though this cannot be excluded. Anyhow, their publication was called by CSSA News somewhat dramatically an 'A wake-up call'. The authors agreed with the European experts that breeders must look for new avenues to open up a seeming bottleneck for the increase of yield potential, though the use of synthetic hexaploids makes just sense with a clear breeding goal in mind and stay-greens for stress adaptation is already in the limelight of CIMMYT breeders (REYNOLDS et al. 2010).

What messages have come down to us from the 'golden age' of crop physiology?

From the 1960s to the late 1980s intensive research has been carried out in many parts of the world on the physiology of wheat (and barley) development and the physiology of all processes determining final grain growth and yield. A review that never achieved much notice was published by STAMP and HERZOG (1984) on the driving forces for the growth and development of the wheat grain. Based on their own results and supported by a wide array of available literature then they made the following statements: (i) sink and source are balanced by maximum numbers of grains shortly before and of endosperm cells shortly after flowering; (ii) this contrasts the low assimilate needs of young grains at that early stage; (iii) water, light and nitrogen impact number and potential size of grains just a week before and after flowering; (iv) but moderate losses of source have little impact when two weeks have passed since flowering.

In 1998 the probably most important wheat physiologist of his time, Lloyd T. Evans, published his famous book '*Feeding the ten billions - plants and population growth*' (EVANS 1998). There he made similar statements, providing major insights in an intelligent context, i.e. that the shape of the plant is less important than a high number of grains per area set synchronously; that the single leaf photosynthesis is lower in modern than in wild genotypes but that the green leaf area duration immensely increased, in direction of stay-green. Retrospectively, it almost seems tragic that these insights in wheat physiology were achieved by sophisticated laborious methods that were never successfully translated into breeding action. Maybe the time gap to molecular driven breeding strategies was just too long.

How about the situation today?

Tony Fischer and Greg Edmeades, the two well-known former experts for scientifically based wheat and maize breeding from CIMMYT, delivered one of the most comprehensive studies on the situation of cereal yield potentials on a global level, inspired by their common engagement for global food security (FISCHER and EDMEADES 2010). In this analysis they made a clear discrimination and definition of the potential yield (PY), to be achieved with the best variety and management in the absence of manageable abiotic and biotic stresses, and the farm yield (FY), the actual production per area in a country or region. Although this concept is not really new, by following strictly these definitions they provided a good basis to judge on the PY for a region and the realized FY, regarding their difference, the yield gap, as an indicator for the agricultural technology applied. According to them, the economic optimum seems to be at about 80% of the PY, a level attained just in some countries like the UK. Of course, these processes are interlinked, without an adaptation of agricultural technology, breeding progress cannot be translated, and a PY increase is essential for progress in FY. At the moment PY growth rates have declined globally mostly below 1% per year. This is alarming and corroborates the studies on flattening off in breeding progress cited above as yields must be doubled until 2050, demanding a linear progress 2.5 times the current rates (FISCHER and EDMEADES 2010). They contradict PELTONEN-SAINIO et al. (2009) insofar, that yield progress is still associated closely with an increased number of grains per area on a global level. Similar conclusions are drawn by REYNOLDS et al. (2010) from actual CIMMYT experiences, confirming that the critical phase for grain number is just before flowering and there exists underutilized photosynthetic capacity during grain filling, suggesting unnecessary floret abortion. This was already known almost three decades ago - see above the 'golden age' of wheat physiology - it sheds light on a comparative neglect of this self-pollinating crop despite its immense present and future role for global food security. The authors plead for a holistic plant view, as some resources will still be needed for deeper roots, improved root anchorage and stem strength to support increased grain numbers per area.

FISCHER and EDMEADES (2010) conclude from present data that recent progress in wheat yield is related to increased photosynthesis before and around anthesis, although no direct measurements were carried out. Retrospectively this is motivating for all researchers who tried in vain to increase wheat yield potential by increased photosynthesis in bygone decades. High yielding varieties seemingly are able to achieve greater crop growth rate and radiation use efficiency (RUE) in the period leading up to flowering, a critical phase for grain set and grain growth potential as outlined above. These views are shared by REYNOLDS et al. (2010) who see here a new avenue for breeding progress especially under situations of high temperature and drought, i.e. when photorespiration is high. Global change in the shape of CO_2 enrichment will increase, of course, RUE continuously, this will have to be discriminated from genetic gains. Unluckily, one thing has not changed: due to missing accurate and easy methods for phenotyping it is still difficult to implement RUE directly in breeding.

Plant physiologists have resumed their interest in photosynthesis and wheat yield after some decades (ZHU et al. 2010), albeit targeting with their analyses possibilities that will not be translated into field-proven varieties in the near future. They draw from recent evidence that inefficient energy transduction from light interception to carbohydrate synthesis limits yield. Optimized single steps in the chain might double the yield potential of our major crops. But this requires fundamental changes in the photosynthetic system that can only be achieved by advanced molecular devices in the long-term. Of course it is promising that the genome of Chinese Spring is known since 2009. But according to personal views of Matthew Reynolds from CIMMYT it will take further five years to have it fully sequenced, only then the breeders work can start. In other words, a real impact will be seen not before at least two more decades have passed. Therefore, investment in conventional breeding and agronomic research must go on strong in parallel. According to GUPTA et al. (2010) marker assisted selection (MAS) in wheat is gaining in pace. At the moment the most promising solution may be provided by simple traits. Although it is not the focus here, yield consistency demands the genetically most effective low energy protection of plants against pest and diseases, the rapidly improved understanding of the mode of action for major resistance genes, their known sequences paving the way for a targeted gene mining of genetic resources up to now untapped. This may ease the work of breeders in this important domain. At the moment the most efficient use of MAS lies in backcrossing and F2 enrichment. An important statement by GUPTA et al. (2010) can just be underlined: Breeders must be involved in defining targets and key germplasm for efficient MAS!

How about yield and quality

The composition of storage proteins is well known to be complex in wheat, they are encoded by about 100 genes for HMW and LMW glutenins, as well as gliadins (GOBAA 2007). These proteins mainly accumulate during linear grain growth. Unluckily, the gene expression can be modified by the environment, seemingly reacting mostly to N availability. But no causal relationship is known yet between high quality and low yield at the physiological level. Therefore, it is a challenge to allocate functions to single gliadins and glutenins, to understand the expression strength of their underlying genes, and much more tricky, their interactions and exchangeabilities. Maybe this will allow wheat breeders in the future to judge more accurately the costs of a high protein quality and quantity in the grain (GOBAA et al. 2008).

Outlook

Wheat - one of the major global food crops - has been tremendously neglected in breeding research at least in comparison to maize. This must change immediately at a strong pace as it is scarcely tolerable that breeding targets defined decades ago are just now reactivated, when gains in genetic yield potential have to become twice higher to secure global food resources in forty years from now. A shift in harvest index bolstered wheat yield increases throughout most of the last century, a way gone now. What remains from former breeding targets is a grain set optimization and a linked higher single grain potential as options to boost yield. But finally an increase in RUE seems feasible; an increase in sink needs more than ever to be balanced by a high and long photosynthesis around and after anthesis. Hopefully present bottlenecks in this fundamental chain can be opened up by molecular approaches in the more distant future. Already now MAS offers hope for a more efficient and eventually more durable protection against pests and diseases, providing free capacity for physiological yield increase. Furthermore, genes coding quality storage proteins are becoming amenable for MAS. Their composition must be at optimum to buffer nitrogen dilution at high yield.

But this quality complex has been maybe too deeply fixed in our western minds. If wheat will keep its strong place in global agriculture, why not attempt to improve the protein content of hexaploid wheat to much higher level as existing for example in *Triticum dicoccoides* in combination with a much better biological protein value. This would allow converting photosynthetic capacity into more product value per area without changing the weight levels to be borne by a culm: An advantage to all monogastrics, including humans who deny eating toast bread.

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