



university of
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biology

Extending crop growing season to improve yield



**Bachelor thesis Ecology and Evolution
 Plant Ecophysiology**

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 Date: July 2012

Abstract

In order to keep up with growing demands on food worldwide, different ways in which crop yields can be improved need to be investigated. Genetic yield potential depends in part on the total incident solar radiation, which is related to the length of the growing season. This paper aims to give a preliminary assessment of the potential for increasing crop yields by extending the growing season, in the light of expected climatic changes, with the focus on the situation in the cool temperate climate of north-west Europe. In this region the growing season is mainly limited by low temperatures. There is evidence, however, that many crops do not make use of their full potential growing season. In order to extend the growing season, cold tolerance will need to be dealt with. But one of the effects of climate change seems to be a lengthening of the growing season because of higher air temperatures. This would facilitate earlier planting of crops, although this will require the use of longer season cultivars to counteract the expected yield decline in cereal crops due to an increased speed of development. So in order to prolong the growing season, more cold-tolerant and longer season cultivars are needed. The use of landraces and wild relatives may be promising sources for new genetic variation, which could be used to breed new varieties with the desired traits. Marker-assisted (recurrent) selection and genome-wide selection are relatively new technologies available for breeding, which can help in selecting for the desired phenotypes. And a modeling approach, finally, in which genetic mapping is combined with ecophysiological models shows promise for gaining better understanding of the genotype-phenotype relationships and could allow selection of the best genotype for a specific set of environmental conditions.

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Introduction

Global food security is increasingly becoming an issue as the human population keeps growing and more and more agricultural land is lost to urbanization and soil degradation (Zhu, Long & Ort, 2010). Crops are the main sources of food production, comprising about 80% of human food, with a total of 50% of food production coming from cereals (Langridge & Fleury, 2011). Over the past 50 years there has been an enormous increase in crop production, amounting to an increase of about 140%, while the area used for agriculture only increased by 11% (Langridge & Fleury, 2011). Per year, global food production has been increasing by about 32 million metric tons (**Fig. 1**), but in order to meet the growing demands for food security, which is reflected by the Declaration of the World Summit on Food Security target to increase global food supply by 70% before 2050, the yearly increase in food production will have to rise to 44 million metric tons per year, for 40 years (Tester & Langridge, 2010). In fact, contrary to this, there is evidence that the yields increase has been slowing down over the past decade (Zhu et al., 2010). Three main factors contributing to the increases in the past were the use of new varieties thanks to developments in breeding technology, an expansion of the use of irrigation, and the use of fertilizers. Increasing the use of irrigation will further enhance problems with water availability in many parts of the world and the use of fertilizers has already caused large-scale problems with eutrophication, So continuing with these trends in irrigation and fertilizer use are not sustainable options. The major solutions for future increases in yields will have to be found in genetic improvements of crops (Langridge & Fleury, 2011; Zhu et al., 2010).

Different factors affect the yield that a crop will produce, and understanding these can give some insight into the possible improvements that can be made. When a crop is grown under optimal management conditions, free of biotic and abiotic stresses, it can produce a theoretical maximal yield that is only dependent on the genetic make-up: the genetic yield potential. Monteith (1977) introduced a formula for the genetic yield potential, in which the dry matter production has a linear relationship with the total amount of light intercepted during the growing season and the efficiency with which the energy from the light is converted to chemical energy. An adaptation of Monteith's formula by Zhu, Long and Ort (2010) gives the theoretical maximum harvestable yield of a crop (in MJ g⁻¹) raised under ideal circumstances:

$$Y = 0.487 \cdot S_t \cdot \varepsilon_i \cdot \varepsilon_c \cdot \varepsilon_p \quad (1)$$

Here S_t (GJ m⁻²) represents the total incident solar radiation during the growing season. In order to take only photosynthetically active radiation (light with a wavelength between 400-700 nm) into account, this variable is multiplied by the correction factor 0.487. Most of the radiation at other wavelengths is transmitted without being used for photosynthesis. Next, ε_i represents the light interception efficiency. This is a measure of how much light is actually intercepted by the leaves, and this depends on leaf absorbance and the size, density and longevity of the canopy. Conversion efficiency, ε_c , is the total gross photosynthesis of the whole plant, minus losses to respiration. And ε_p , finally, is the partitioning efficiency. This term, also known as the harvest index, is the proportion of the total achieved biomass that ends up in the harvestable part of the crop.

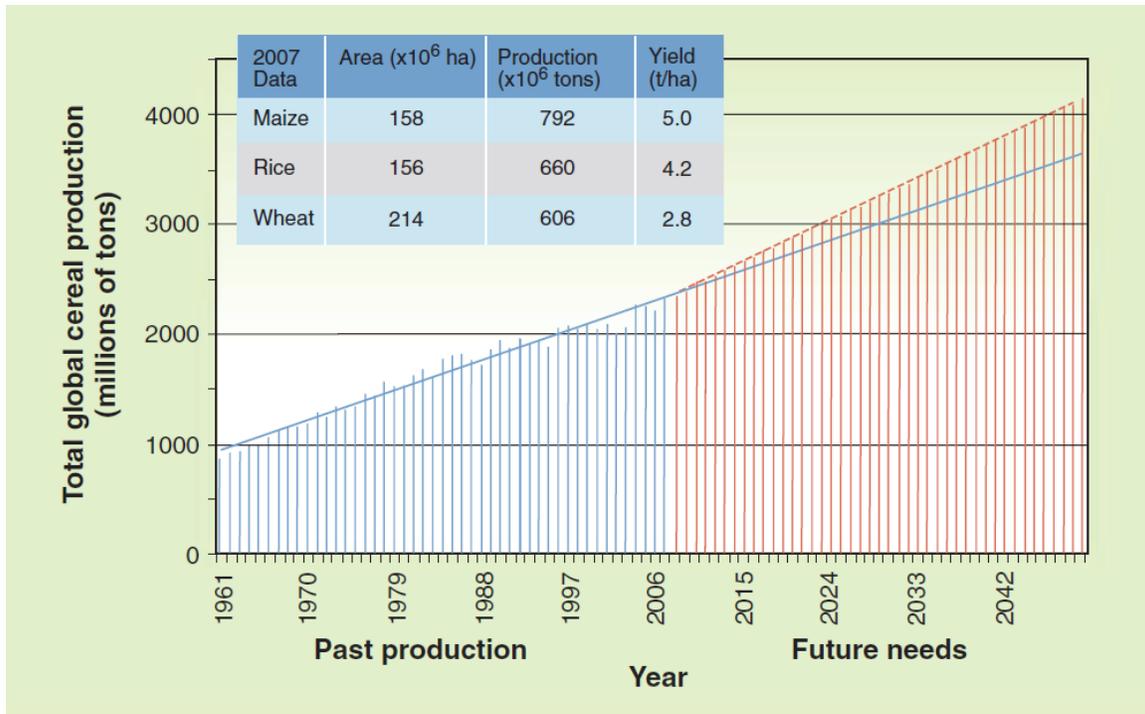


Figure 1.

Between 1961 and 2007 global cereal production has risen from 877 million tons to 2351 million metric tons (blue line). This was an increase of 32 million metric tons per year. But in order to meet the predicted demands production will need to increase to over 4000 million metric tons by 2050 (red line). This would require the rate of yield increase to rise to 44 million metric tons per year, an increase of 37%. In the inset table data from 2007 is shown for the three most important cereals. (Image adapted from Tester and Langridge 2010).

The increases in yield potential over the past 50 years are mainly due to increases in ε_p and ε_i . Dwarfing and an increase in the number of seeds produced per plant are the main contributions to an increased ε_p , and the increases in ε_i can be attributed to the development of cultivars with larger leaves and a decreased timespan between germination and ground coverage. Dwarfing has also helped to improve ε_i by making the plants sturdier, which lessens the losses to flattening of the crop after hail or rainfall (Zhu et al., 2010).

Due to such improvements, the main grain crops show little potential for further increases in ε_i as there will always be some radiation lost to interception in the time between germination and canopy closure, and the leaves of unstressed crops typically intercept about 90% of photosynthetically active radiation (Zhu et al., 2010). For ε_p values up to 60% have been found in several major crops. The potential for further increase is probably not very high, since in order to form the organs which are harvested, enough leaves need to be formed in order to produce a closed canopy (Monteith, 1977), and it is impossible to convert 100% of plant biomass to the harvestable parts (Zhu et al., 2010). This leaves only S_i and ε_c for future improvements (Zhu et al., 2010). A fair amount of attention is being given to ε_c , and improving photosynthetic efficiency is seen as a promising strategy to improve yield potential (Parry et al., 2010; Zhu et al., 2010). No such comprehensive investigations were found concerning the potential for increasing

S_t . There are indications that S_t can be improved by increasing the growing season (Zhu et al., 2010), which is defined as “the period between bud burst and leaf fall”(Linderholm, 2006, p. 1). The length of this period is expected to increase because of global warming, although this may not be the case in all regions (Linderholm, 2006). This paper aims to give a preliminary assessment of the potential for increasing crop yield by extending the growing season, in the light of expected climatic changes, with the focus on the situation in the cool temperate climate of north-west Europe.

Limitations to the growing season

When modern cultivars are grown under good conditions (optimized spacing, no diseases or pests etc.), their ε_i is typically around 90%. This means that during the growing season most of the available photosynthetically active radiation is intercepted (Zhu et al., 2010). However, most crops do not fully utilize their potential growing season, suggesting that the yield potential may be increased by increasing S_t . This could be achieved by lengthening the growing season (Zhu et al., 2010).

The potential growing season is defined as the period during which the temperature and availability of water allow the plant to grow (Zhu et al., 2010). In the temperate zone frost and low non-freezing temperatures are important limitations for the production of cereal crops, while in other regions drought can be limiting, especially during summertime (Li et al., 2011; Louarn, Chenu, Fournier, Andrieu & Giauffret, 2008; Oleson et al., 2011).

The effect of cool temperatures on crop yield has been well studied in maize (*Zea mays*) (Beale, Bint & Long, 1996; Louarn et al., 2008). In general, C4 plants are not very well adapted to temperate climates. As the main C4 crop that is grown in northern Europe, maize is subjected to suboptimal temperatures during part of the growing season. This is especially the case in early spring. Many effects of cold on plant growth and photosynthesis have been reported, including decreased leaf expansion rates and reduced rates of carbon assimilation due to changes in the stomatal opening, chloroplast structure and pigment composition (Beale et al., 1996; Lee, Staebler & Tollenaar, 2002; Louarn et al., 2008). In maize the effects of low temperatures are reflected in the changes in photosynthetic efficiency of mature leaves as well as in newly formed leaves (Beale et al., 1996). In case of mature leaves, exposure to a high light intensity at low temperatures (under 15°C) can lead to photo-inhibition of photosystem II. This results in reduced quantum efficiency (Beale et al., 1996). When the exposure to low temperatures takes place during leaf development, this can lead to deficiencies in the photosynthetic apparatus, with a reduction of the light-saturated rates of carbon dioxide uptake as a result (Beale et al., 1996). A decrease in photosynthetic capacity will have negative consequences for canopy development (Beale et al., 1996) because it will cause the growth to be slower. This is supported by a study by Louarn *et al.* from 2008. Here they used a modeling approach to determine the relative contribution of light interception (cumulated photosynthetically active radiation intercepted, PAR_c) and radiation use efficiency (RUE). As a basis for this model they used Monteith's formula, describing a linear relationship between the biomass production (dry weight, DW) and PAR_c .

$$DW = RUE \times PAR_c \quad (2)$$

Note that formula (1) describes the harvestable yield, by adding the term ε_p to calculate only the biomass that is partitioned to the harvestable parts of the crop, while formula (2) gives the total plant biomass. The term PAR_c is the equivalent of $0.487 \cdot S_i \cdot \varepsilon_i$ and RUE is the same as ε_c . In formula (2) RUE is defined as the slope of the relationship between DW and PAR_c . Such a linear relationship was found for a wide range of crops, at least throughout the period of vegetative growth, and in a field experiment with barley, sugar beet, potatoes and apples a surprisingly similar slope was found amounting to an efficiency of about 2,4% (Louarn et al., 2008; Monteith, 1977). Any deviation from this relationship should indicate some limiting factor (Louarn et al., 2008). Using this as a basis for their model, Louarn *et al* found that the loss of biomass after a cold event could mainly be attributed to a reduction of RUE. First of all they found that after a cold event during early leaf development, light interception was greatly reduced. This was caused by a reduction of the leaf area of all the leaves that would develop after the event. In this case the lasting reduction in canopy size has a cumulative effect on PAR_c , outweighing the effect on RUE, which is only a temporary reduction of the conversion efficiency of radiation energy to biomass. Despite this lasting effect, Louarn *et al.* argue that RUE plays a bigger part in reducing crop yields during cold events. Any cold events that occur after the initial leaf development only marginally affect PAR_c , but the decreased RUE will have a larger impact, because it will affect a much larger leaf area than in the case of an early cold event. This is especially the case when there are several cold events or when they occur late in the season, after flowering (Louarn et al., 2008). Another effect that is seen in maize is an increase in the root/shoot dry matter ratio with a decrease in temperature. This may also lead to a reduction in biomass because at lower temperatures less biomass is partitioned to the leaves, causing a reduction in leaf area and thus lowering PAR_c (Lee et al., 2002). In short, cold stress may cause a reduction in crop yield by lowering the photosynthetic efficiency, ε_c , itself, but it can also lead to a reduction of ε_i by reducing canopy development, especially during early cold events, which may occur more frequently when crops are sown early.

So it appears that low temperatures limit the growing season, because planting a crop too early will have negative effects on the growth and productivity. But there are indications that the potential growing season is longer than what is currently put to use by most crops (Zhu et al., 2010). This can be seen in the comparison of the biomass production of maize with that of *Miscanthus x giganteus*. This is a C4 grass that is unusually tolerant to the low temperatures of the cooler temperate climate (Beale et al., 1996; Zhu et al., 2010). In a study performed in the Midwest of the USA, one of the most productive areas in the world for maize, *M. x giganteus* produced 60% more biomass than maize did. The explanation for this is that, although the two species had a very similar ε_c , *M. x giganteus* was much faster in producing a closed canopy and better at maintaining it, achieving an ε_i of > 0.9 four weeks earlier, and lasting another four weeks longer than the maize did. This longer use of the growing season added about 60% to the cumulative intercepted radiation (Zhu et al., 2010). So it should be possible to make use of more of the growing season by sowing earlier, but only if cold tolerance can be addressed.

The effects of climate change on growing season and yield

In order to thoroughly understand the limitations of the growing season and the potential for extended use of it, the effects of climate change needs to be understood. Oleson and Bindi (2002) reviewed research on the effects of climate change and assessed the expected effects on agricultural productivity in Europe. Among the expected climatic changes are an increase in temperature, increased atmospheric [CO₂] and higher incident of drought and extreme weather conditions. The increased levels of CO₂ will lead to increased plant productivity and efficiency of water, radiation and nitrogen use (Oleson & Bindi, 2002). In general, the increase in air temperature, combined with the expected changes in rainfall patterns, will most likely lead to changes in the agro-climatic zones in Central Europe (Trnka et al., 2011). The expected impact on agriculture differs per region. A modeling study by Trnka *et al.* (2011), in which they discuss a software package that has been developed to help assess climate related stress factors in agricultural crop production, predicts that there will be a shift in the productivity of crop areas. By 2020 the areas that are currently the most productive are expected to become warmer and dryer, and areas at a higher latitude and elevation will become more suitable for agriculture because of an increase in air temperature (Trnka et al., 2011).

This prediction is consistent with the findings of Oleson and Bindi, who reported on the impact of climate change in the different regions of Europe. In northern and western parts of Europe the effects are expected to be mostly positive. The temperature rise is expected to cause an increase in suitable crop land towards more northern regions. These shifts in the agro-climatic zones will make different crops available for cultivation in a particular region. The suitable ranges for all cereals and many other crops is expected to expand northward, allowing cooler season crops like faba bean and oil seed to be cultivated more freely in the Nordic regions, while warmer season crops like soybean and sunflower will also become available farther north than is presently the case (Oleson & Bindi, 2002). This increase in suitable land, combined with the use of new varieties and different crop species more suited to the increased temperatures, as well as higher plant productivity, will allow a continuation of the current trend of intensification of agriculture in these northern regions (Oleson & Bindi, 2002). In southern parts of Europe, negative effects are expected to be more influential than positive. The frequency of drought and extreme weather is expected to increase, leading to reduced and more variable yields and loss of agricultural land that is suitable for traditional crops (Oleson & Bindi, 2002). This will also further the trend by which agriculture in the Mediterranean and southeastern regions of Europe is extensified, while at the same time, agriculture is becoming more intensive in the northwestern regions (Oleson & Bindi, 2002). But the positive effects that are expected for the northern parts of Europe might only be temporary, as the dry conditions expected for central and southern Europe might expand further northward as quickly as 2050, leaving the north to deal with the same problems as the south will face in the near future (Trnka et al., 2011).

Several studies have reported on the expected lengthening of the growing season as a result of climate change (Linderholm, 2006; Oleson et al., 2011; Trnka et al., 2011). In the Northern Atlantic region, for example, a prolongation of the growing season is expected for winter wheat, spring barley and maize, among others, although for some

crops the opposite effect is expected, which will be discussed further down (Oleson et al., 2011; Oleson & Bindi, 2002). Just as the positive effects mentioned in the previous paragraph, this lengthening is especially expected to occur at higher latitudes (Linderholm, 2006; Oleson & Bindi, 2002). It is apparent that this lengthening is already in progress. Data from phenological, satellite and climatological studies indicate that a 10-20 day increase in the growing season has already taken place during the past decades. This increase is mostly due to an earlier start of the growing season (Linderholm, 2006).

This climate related change in crop yield is expected to vary depending on different factors. On the one hand the expected change is different for the different regions. The crop yield at northern latitudes is expected to increase while the impact on crop yields is supposed to be mostly negative in the warmer regions of Europe, around the Mediterranean, the south-western Balkans and southern European Russia (Oleson et al., 2011). Besides a shortening of the growing season because of water deficiency, a decrease in the yield is to be expected in these areas due to faster development of the plants, giving them less time to build up dry matter (Linderholm, 2006). On the other hand, the expected effects on the length of the growing season and the yield depend on the type of crop. Higher temperatures during the growing season appear to have a different effect on determinate crops than on indeterminate ones. Determinate crops have a fixed end to their development, after which they need to be harvested, while indeterminate crops will keep on producing until they are either harvested or freeze. For determinate crops (including cereals, oilseed and pulses) the time to maturity depends mainly on day length and temperature (Oleson & Bindi, 2002). Every day in which the temperature is high enough for a plant to grow will add to the number of growing-degree days (GDDs) that a plant has accumulated, in proportion to how warm it has been during that day. The stages of development are often regulated by the GDDs. Since an increase in the air temperature will speed up growth and development because of a faster accumulation of GDD, the growing season of determinate crops is expected to shorten. This will decrease crop yields if no changes are made in the cultivars used (Oleson & Bindi, 2002; Peiris et al., 1996). Even though the growing season of determinate crops is expected to decrease, the photosynthetic rate will increase because of the higher air temperatures. But the expected net result is still a reduction in yield (Peiris et al., 1996). For indeterminate crops (such as root crops), on the other hand, the growing season will probably lengthen because of the reverse effect: because of the increased temperature these crops will grow at a faster rate, and will continue to do so until they are harvested. This means that if the harvest date stays the same, they will be able to accumulate more biomass (Oleson & Bindi, 2002; Peiris et al., 1996).

In order to maintain current levels of yield and minimize the problems that climate change poses, it will be necessary to adapt farming strategies to these changing circumstances. Adaptation strategies may include: *i*) the use of different crop species and cultivars that will do better under the changed circumstances; *ii*) sowing earlier in the season; *iii*) the use of fertilizers, irrigation and drainage to deal with changes in soil nutrient turnover and changes in precipitation patterns; and *iv*) changing land use and farming systems (Bindi & Oleson, 2011). Some of these strategies use the opportunities given by climate change in order to increase yields. A lengthening of the potential growing season combined with higher temperatures is expected to increase crop potential at high latitudes, while earlier planting may allow crops to mature before the onset of the

dry season in more southern regions, making optimal use of winter precipitation, and it might even make multiple cropping possible in some areas (Linderholm, 2006, Oleson et al., 2011). By sowing earlier, farmers in cool temperate regions can make use of the early start of the growing season as the number of suitable sowing days increases (Trnka et al., 2011). In areas where sufficient water is available throughout the season and the risk of heat stress is low, making use of long season cultivars for early spring sowing will help to increase the length of the growing season (Oleson & Bindi, 2002). Using longer season cultivars will counteract the expected yield loss resulting from the increased rate of development and help to maximize yields (Oleson & Bindi, 2002).

These changes in cultivation timing have already been observed to some extent in different regions of Europe, especially in the cooler climatic zones and to a lesser extent in the Mediterranean (Oleson et al., 2011). The observed changes in cropping schemes do not seem to include shifting to different crop species, as most farmers seem to be introducing new cultivars of crops that are presently used that are more suitable for the changing environment, rather than changing to entirely new crop species (Oleson et al., 2011).

Approaches for realizing a longer growing season

Earlier planting and use of long season cultivars

The first and most obvious approach for achieving a more efficient use of the growing season is to sow or plant the crops earlier in the season (Lee et al., 2002; Louarn et al., 2008; Schittenhelm, 2001). Especially along the northern borders of the area of cultivation, this would allow a more efficient use of available resources (Louarn et al., 2008), resulting in an increased yield. A problem that needs to be faced, however, is that earlier planting will expose the crops to more days at suboptimal temperatures (Lee et al., 2002), although climate change may be working against this effect by raising average air temperatures. Maize, for instance, is very sensitive to cold, and earlier planting to increase yield causes the plants to spend a larger part of their early development at suboptimal temperatures (Lee et al., 2002). Cold stress, is an important limiting factor for cereal crops in the temperate zone, especially in the case of frost (Li et al., 2011). In an experiment by Schittenhelm (2001), the potential for increasing yield by sowing earlier in the spring was assessed in root chicory. For several different cultivars, several sowing dates between mid-March and early May were evaluated. The reasoning for this was that earlier sowing would allow earlier crop establishment, increasing the interception of solar radiation, resulting in a higher yield potential (Schittenhelm, 2001). In most cultivars early sowing led to losses in yield due to low crop emergence and high incidence of bolting. But at least one cultivar was found for which this bolting did not pose as much of a problem, leading to the conclusion that increasing chicory root yield potential by early sowing was mainly limited by poor crop establishment caused by suboptimal temperatures (Schittenhelm, 2001).

Crop yields can be affected by both the planting date and the number of growing degree days (GDD) required by the crop (Sacks & Kucharik, 2011). In order to determine how much of the recent increase in crop yield could be explained by these factors, Sacks and Kucharik (2011) analyzed 25 years of maize and soybean data from the US

department of Agriculture. On average planting dates for maize moved forward by about 10 days between 1981 and 2005 and soybean planting dates had moved about 12 days. This coincided with a lengthening of the growing period. From planting to maturity, the growing period for maize had increased by about 12 days in the studied time period. This lengthening of the growing period could be partly explained by a lengthening of the vegetative growth period, because the lower temperatures early on in the season lead to a slower accumulation of GDD, but it was also found that there had been a 14% increase in the total number of GDD needed for maize to reach maturity. This was found to indicate the use of longer season cultivars, allowing the crop to take more time to accumulate biomass before maturity. The observed change in planting dates had allowed the use of longer season cultivars, thus contributing significantly to the yield increase over the past 25 years (Sacks & Kucharik, 2011). Other species also have potential for increased productivity by using longer season cultivars. A study of several wheat cultivars with different durations till maturity grown in the central wheat belt of Western Australia showed that long season cultivars could be sown before mid-May, without loss in productivity. This would allow a shift in the growing season from May into late April (Anderson, Heinrich & Abbotts, 1996).

Another possibility for lengthening the growing season is the use of lower-latitude cultivars at higher latitudes. This effect is promoted by Parrish and Fike (2005) for the biofuel crop Switchgrass, because the growth rate is dependent on temperature, but the time to maturity is dependent on photoperiod. As a result, using lower-latitude cultivars at higher latitudes will allow the plants to accumulate more biomass before maturation. But just as in the other species discussed, prolonging the growing season will mean that cold tolerance could become a problem (Parrish & Fike, 2005). A note concerning the relevance of this finding is that since Switchgrass has only been cultivated for a very short period of time (about 50 years), the varieties are all still closely adapted to their local circumstances (Parrish & Fike, 2005). But owing to their long history of cultivation and the subsequent loss of genetic diversity (Jones et al., 2011) this local adaptation is likely not as strong in modern cultivars. So it is debatable whether the effects found for using lower-latitude cultivars of Switchgrass might also be present in cereal crops. But because this effect depends on a certain level of adaptation to local day-lengths, using landraces and wild relatives for breeding purposes might provide a solution to this problem.

Breeding and biotechnology

Traditionally, plant breeding focuses on phenotype selection. This works well for genes that have a major effect on the phenotype, but the situation is more complicated when the desired trait is not monogenic. For phenotypes that are the result of an additive or interactive effect of many genes, or where the genetic base is not well understood, large populations are used and selection is aimed at shifting the mean of the population response towards the desired trait in the hope of combining the responsible alleles at multiple loci into one line. For species undergoing extensive selective breeding, like the cereals, this process requires the evaluation of millions of lines each year. The use of molecular markers, providing information about the genetic position of important loci, has allowed this process to be speeded up (Langridge & Fleury, 2011).

In order to improve a crop's performance under certain circumstances, genetic variation is necessary. The rate at which new varieties are created can be increased by either increasing the amount or range of variation that can be selected, or by speeding up the selection process for desired traits (Langridge & Fleury, 2011). Some sources for genetic variation and technologies that are increasingly becoming available for breeding will be discussed in the following sections.

Sources of genetic variation

There are number of different sources that can be tapped in the search for new genetic material for breeding programs. Especially the use of wild relatives seems to be a promising strategy for crop improvement (Feuillet, Langridge & Waugh, 2008; Flood, Harbinson & Aarts, 2011; Jones et al., 2011). At the level of photosynthesis, there is a lot to be gained by exploring these resources. Efforts for direct selection on photosynthesis were abandoned early on because studies on the effects of improved photosynthesis on yield showed no strong relationship between the two. But it has been argued that this lack of a relationship between level of photosynthesis and yield had to do with faulty measurement methods in which the photosynthesis was measured under conditions that were in no way representative of field conditions. As a result, there is potential for improvement in this area (Flood et al., 2011). Evidence points to the existence of variation in photosynthesis-related traits in both crop and wild species. A greater understanding of the genetic regulation of these traits can provide a basis for the improvement of our crops (Flood et al., 2011). But also looking at utilization of the potential growing season, there is evidence that searching for genetic variation in related species could be a promising strategy. As mentioned earlier, the biofuel grass *Miscanthus x giganteus* uses much more of the potential growing season than its relative *Zea mays* does, making it a potential source for genetic variation (Beale et al., 1996; Zhu et al., 2010). If the processes underlying the cold tolerance and early canopy closure can be understood and the responsible genes identified, this could mean a great improvement in maize yields in cool temperate climates.

The use of closer relatives as a source of genetic variation is also likely to be a promising strategy for other cereal species. Because of their agricultural importance, the crop species of the Triticae tribe (barley, wheat, rye) have been bred intensively over the past century, greatly improving productivity and quality. A problematic side effect of this, however, is that it has caused a decline in the available genetic diversity within the elite germplasm. A promising solution for this problem is to tap into the genetic reservoir of landraces, local cultivars and related (wild) species (Feuillet et al., 2008). Studying the evolutionary background of crop species can be of help in this, as it may lead to identification of new sources for breeding (Jones et al., 2011). Before the onset of modern cultivation in the last century, barley, for example, had thousands of different landraces throughout Europe, that were often adapted to local circumstances. Many of these landraces have since died out, but there are still seed collections available of thousands of varieties from different parts of Europe (Jones et al., 2011). To make the best use of these sources of genetic material, it is necessary to not only understand the phenotypic characteristics and the adaptation to local circumstances, but also the evolutionary background. By tracing different genetic backgrounds that are the linked to

the same desirable trait this kind of understanding could provide alternative ways to introduce a desired characteristic (Jones et al., 2011).

In their discussion of the use of genetic material from wild relatives for crop improvement, Feuillet, Langridge and Waugh (2008) named introgression as a barrier for introducing new traits. Especially the issues with linkage drag remained to be solved (Feuillet et al., 2008). As will be discussed in the next section, the availability of new technologies like marker-assisted recurrent selection (MARS) and genome-wide selection (GWS) might remove some of these obstacles, greatly improving the chances for using wild relatives for breeding (Langridge & Fleury, 2011; Tester & Langridge, 2010). By reproducing the hybridization event between durum wheat (*Triticum turgidum ssp. durum*) and *Aegilops Tauschii*, a wild species, that originally led to the creation of the modern bread wheat (*Triticum aestivum*), the creation of synthetic wheats has also allowed new genetic material to be added to breeding programs (Feuillet et al., 2008). Although the available genetic variation in cultivated wheat and barley is still quite limited, it seems likely that this situation will change rapidly over the coming decades, as the problems faced in breeding programs are solved by the new technologies that are becoming available.

Moving beyond the variation that is available for breeding using traditional and more advanced breeding techniques, there is still a world of genetic material with unimagined possibilities. GM technology would allow the creation of new variation, that cannot be found in natural or deliberately mutated populations. The use of these technologies is restricted by political issues, but in the long run it is likely that this will be a big source of novel traits, not just by providing new genes, but also by allowing the discovery and use of new and more efficient regulatory sequences (Tester & Langridge, 2010). One partial solution for the political problems connected to GM technology is the introduction of so-called cis-genic techniques. These deal with within-species transfers of targeted genes, which should have a less negative effect on consumer opinion (Tester & Langridge, 2010).

Some promising new technologies

Over recent years there have been many changes in breeding methods, leading to an increase in the rate of crop improvement. But despite many new technologies becoming available, many of these are not yet widely used. These new technologies include using sophisticated genetics to aid selection, use of computer technologies to aid in design, tracking and management of field trials and the use of biometric methods to help understand the interactions between genotypes, environment and management (Tester & Langridge, 2010). In this section a number of methods employing the use of genetics to aid selection will be discussed.

Marker-assisted selection (MAS) is a current method that is based on the use of DNA markers for finding desirable alleles that can be used for breeding. This method is broadly used for tracking simple monogenic traits (Langridge & Fleury, 2011). Single-gene introgression is then used to transfer the desired region into the parent genome. In order to do this, the genome with the target gene is repeatedly backcrossed into a line with all the background traits, into which the gene is meant to be inserted (Langridge & Fleury, 2011). MAS has a number of advantages over phenotype-based selection.

Especially when the desired traits are recessive or would require difficult or expensive phenotyping, MAS performs better than phenotype-based selection (Langridge & Fleury, 2011, Tester & Langridge, 2010). MAS can also be used to reduce linkage drag, meaning that the use of markers can help to make sure that only the target gene enters the new line, without incorporating large flanking regions from the same chromosome during the process (Langridge & Fleury, 2011). Finally, MAS is the only way to achieve pyramiding of genes (Langridge & Fleury, 2011; Tester & Langridge, 2010). Pyramiding allows several genes to be combined into a new genotype. The result is a so-called ideotype, which is a mosaic of desired pieces of genetic material from each of the parents. This approach is especially attractive for (partial) traits that are carried by many different genes, such as disease resistance. Based on phenotype alone, it may be impossible to distinguish plants carrying different resistance genes. So the only way to create an ideotype with several of these resistance genes, which would then give the plant a more robust or more complete resistance to the disease, is by using MAS (Langridge & Fleury, 2011).

An important thing to take into consideration is that the markers need to be good predictors of the phenotypes they are supposed to indicate. Especially for complex traits, like tolerance to stress caused by climate change, the components of this trait need to be analyzed and the regions in the DNA coding for these traits need to be found, rather than just looking at the overall level of tolerance in the plant. In order to do this, high-throughput phenotyping will be necessary (Tester & Langridge, 2010). Phenomics will allow screening different populations for desired traits and a more thorough understanding of the relationship between a phenotype and molecular markers, facilitating introgression of the right combination of tolerance genes into new commercial varieties (Tester & Langridge, 2010).

Using MAS for pyramiding becomes increasingly complex, expensive and even unreliable when a large number of target loci need to be combined into one genotype (Langridge & Fleury, 2011). A way to deal with this is to use recurrent selection to increase the frequency of desired alleles in the population before forming the inbred lines. Marker-assisted recurrent selection (MARS) is a relatively new method that can be used for this (Langridge & Fleury, 2011, Tester & Langridge, 2010). MARS is a method in which specific markers are used for fingerprinting of the progeny, in order to determine the genotypic value. Based on this genotypic value, individuals are selected for the next round of crossings. Repeating this cycle a number of times will allow accumulation of favorable alleles (Langridge & Fleury, 2011; Tester & Langridge, 2010). Although yield improvements have been achieved using this method, the results of different assays that have been performed were not consistent (Langridge & Fleury, 2011). A disadvantage of this approach is that it works best with genes or quantitative trait loci that have a large phenotypic effect (Langridge & Fleury, 2011; Tester & Langridge, 2010).

A method that can be used to overcome the problems of working with multiple loci that each only has a small genetic effect is genome-wide selection (GWS) (Tester & Langridge, 2010). This is a form of marker screening, for which it is not necessary to have information about the relationship between the traits and markers. In this approach, populations are extensively genotyped first and, based on the phenotypes, an estimation is made of the breeding value of each marker. After this has been done, it is only necessary to genotype an individual plant in order to determine the “genomic estimated breeding

value”, which is calculated by summing the breeding values of individual markers. In this way, a segregating population can be screened for individuals with the right phenotypic performance, greatly facilitating selection for multiple loci of small genetic effect (Langridge & Fleury, 2011; Tester & Langridge, 2010).

An important limitation in the use of markers is a lack of sufficient markers for some species. But the new sequencing platforms have made it possible to screen species for single-nucleotide polymorphisms on a large scale, allowing the discovery of new markers for species where not many were known before (Tester & Langridge, 2010). Combined with the selection methods that make use of markers, this could provide a basis for great progress in the fields of crop breeding and genetics (Tester & Langridge, 2010).

Another challenge in the process of gene discovery that needs to be faced is the identification of the actual gene or regulatory sequence that is involved in the phenotype (Langridge & Fleury, 2011). Positional cloning is informative, but does not indisputably link a sequence to the target phenotype. Using omics technology can help to identify a gene and to understand the way in which the phenotype comes to be. So assessing RNA, protein and metabolite levels can provide support for positional cloning (Langridge & Fleury, 2011).

Modeling genotype-phenotype relationships

When analyzing the relationship between genotype and phenotype, geneticists often forget to take into account how large the impact is of factors relating to the environment (competition, density, morphology etc) (Yin & Struik, 2010). As a result gene-environment interactions often play only a minor role in statistical models, although it is known that crop yields based on performances of small numbers of plants grown under testing conditions do not give an accurate prediction of yields under field conditions, in which competition and other such factors can play a limiting role (Yin & Struik, 2010). To understand a complex phenotype such as crop yield, it is essential to understand both the effects of multiple interacting genes and of environmental conditions.

Crop models are useful tools for yield predictions and general agricultural purposes (Louarn et al., 2008, Yin & Struik, 2010), but they are often too simplistic to help understand genotype-phenotype relationships. To counteract this, a more ‘bottom-up’ approach is being developed in systems biology (Yin & Struik, 2010). One goal of systems biology is to integrate information from multiple levels of organization in mathematical models. Such information includes genome, transcriptome, proteome and metabolome data (Yin & Struik, 2010). Yin and Struik had previously worked on incorporating physiological parameters at the single-organ level into a model, and managed to show that this could result in realistic predictions about crop performance under changing field conditions (Yin & Struik, 2010).

Such ecophysiological models give some information about gene-environment interactions, but the differences due to the genetic background often enter these models in the form of ‘genetic coefficients’ that do not take the complexities of the genetic basis into account. Genetic mapping, on the other hand, in which the quantitative trait loci (QTLs) connected to a trait are identified, can give information about the relationship between genotype and phenotype, but it can only offer limited predictions about trait

phenotypes in different environmental conditions. Yin and Struik (2010) have proposed an integration of the two, making use of omics data, in order to allow analysis of complex yield traits and determine the effects of the QTLs of components of these traits over time at the crop level and under different environmental conditions. First attempts at 'QTL-based ecophysiological modeling' have been made, and the results achieved *in silico*, at least, are promising. This kind of approach would make it possible to predict crop yields for different genetic make-ups and in different environments, greatly improving the potential of marker-assisted breeding (Yin & Struik, 2010).

Summary and conclusions

In the cool temperate climate of north-west Europe, the length of the growing season, which determines S_i , is mainly limited by low temperatures. These low temperatures negatively affect the plant by frost damage or by cold stress, which results in a temporary impairment of ε_c and in a reduction of ε_i . Ideally crops will be planted at a time of year in which the yield losses due to cold are minimized, both at the start and the end of the season. There is evidence, however, that the potential growing season for some crops is longer than what is actually used. So it might be possible to extend the growing season and plant crops earlier in the year, but cold tolerance will need to be dealt with. The effects of climate change may already be leading to an extension of the growing season, at least in the more northern regions where higher temperatures are expected to increase crop productivity. This may allow earlier sowing, because the risk of cold damage in the spring will decrease. But on the other hand, the temperature rise will likely speed up the development of cereal crops, leading to decreased yields unless longer season cultivars are used. In other parts of Europe droughts and extreme weather are expected to become more prevalent, and there the growing season will be increasingly limited by water shortage.

In order to make use of a longer growing season and also do so under the rising temperatures of the coming decades, crops will need to become more cold tolerant and take more time to reach maturity. A possible approach for finding longer season cultivars is to plant locally adapted cultivars from lower latitudes, although the level of local adaptation might not be high enough in highly cultivated crops species for this approach to be successful. This problem might be solved by using landraces or wild relatives as a source of genetic material, as these are more locally adapted and provide a much wider range of genetic variation. If the political issues can be solved, GM technologies could provide access to a much larger range of novel traits. But this will probably remain a distant possibility for a fair number of years. As new breeding technologies are being developed, however, the possibilities for improving specific traits are steadily increasing. Marker-assisted selection is allowing difficult-to-phenotype traits to be selected for and helping to reduce linkage drag. The development of marker-assisted recurrent selection expands on this principle, enabling pyramiding of multiple target loci into one line. And genome-wide selection is a useful technique when the genetic basis of a trait is not well understood or when there are many genes involved that each contribute only a small amount to the desired trait. Finally, by integrating genetic mapping and omics information into ecophysiological crop models, the relationship between genotype and phenotype can be studied under different environmental conditions. This could greatly improve selection strategies.

In short, there are some promising options for improving crop yield by extending the growing season. But it might be worthwhile to investigate whether this would be the best approach when improving world-wide food security is our purpose. With the threats of climate change haunting our foreseeable future, and to some extent already taking their toll in the present, it might be that our attention should rather be focused on making our crops more resistant to drought and salinity, which are conditions that are expected to have a major impact on crops in large parts of the world.

Acknowledgments

I would like to express my gratitude towards Kashmiri Stec for proofreading, and to Theo Elzenga for his supervision.

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