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Nitrogen and water resources commonly limit crop yield increases, not necessarily plant genetics

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Frequently, improved plant genetics is viewed as the path to increased crop yields. However, in this manuscript, we argue that yield increases most often result from a combination of improved genetics and increased availability of nitrogen and water resources. At this time, it is likely that resource availability is the main impediment to yield increase in many cropping systems. In developing regions, it appears that nitrogen availability limits crop yield. In developed regions, rainfall and water availability commonly impose a substantial constraint on further crop yield increase. Strategies are examined to enhance resource accumulation and use in cropping systems of the future.

1. Introduction

"Miracle wheat" and "miracle rice", which were developed and released in the Green Revolution of the 1960s, firmly embedded the idea that improved plant genetics was the route to increased crop yields. Today, even in the face of slowing in yield increases in many crops, the argument is often made that yield genes now need to be identified and stacked to achieve the next large jump in crop yields. However, research investment heavily favoring the genetic approach is not supported by a long-view of agricultural history.

In their review of the history of agricultural development, Sinclair and Sinclair (2010) identified several Green Revolutions. All were fundamentally dependent on providing crops with greater resources – more water and nitrogen. The Sumarians, who were the first civilization, were not coincidentally the first to cultivate crops on a large scale and bring about the first Green Revolution. Their success was based on the construction of elegant systems of canals that brought water and nutrients from the Euphrates River to their fields. Yields of barley and wheat were approximately 2 t ha^{-1}.

A second major Green Revolution occurred in the United Kingdom in the 1700s when crop rotation was introduced. The Norfolk rotation included a cycle of legume/grass pasture to feed livestock. Wheat yield across Europe at that time was commonly 0.8 t ha^{-1} and the Norfolk rotation more than doubled them to about 2 t ha^{-1}. The key to the yield increase was inclusion of the nitrogen-fixing legume that added nitrogen to the cropping system. This dramatic yield increase provided inexpensive bread to feed the expanding numbers of factory workers in the Industrial Revolution.

The modern Green Revolution, often described as a success of crop breeding, was again dependent on increasing nitrogen resources. Double-cross maize was developed in the 1920s in U.S., but the varieties initially had little commercial success. Superiority of the hybrids was eventually realized during the Dust Bowl of the 1930s when yield losses under the water-deficit conditions were less than those of the conventionally selected varieties. Average maize yield above 2 t ha^{-1} only occurred after World War II (Fig. 1). The facilities for manufacturing ammonium nitrate for munitions in World War II became available for production of nitrogen fertilizer. The rapid increases in crop yields in industrial countries in the 1950s and 1960s were closely associated with higher nitrogen fertilizer applications.

Even the yield gains of the miracle wheat and rice in the developing countries during the latter 20th Century were based on applications of fertilizer. One of the challenges with introduction of advanced cultivars was obtaining the fertilizer to allow expression of their yield potential. Borlaug (1972) stated that "*chemical fertilizer is the fuel that has powered* [*the Green Revolution's*] *forward thrust*".

It is now clear that the "wagon" of yield increase is pulled by a pair of "horses" – increased availability of nitrogen and water, and improved genetics to take advantage of greater resources. Indeed, the sustainability of cropping systems in the future will be intimately tied to the availability and efficient use of nitrogen and water. This article examines the limits of nitrogen and water availability and use, and their impact on crop yields. The conclusion

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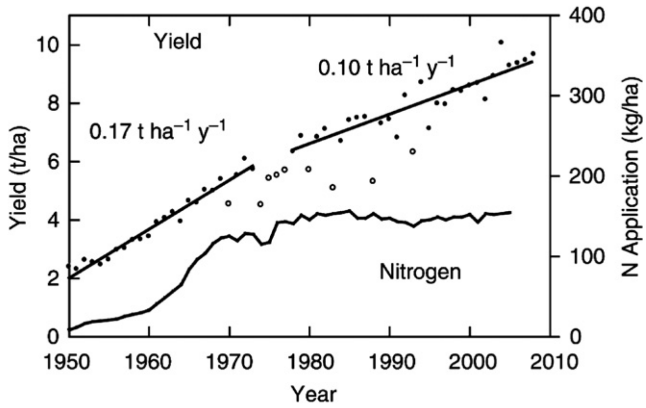

Fig. 1. U.S. national average maize yield (linear lines) and nitrogen application to maize (jagged line) since 1950. The open circles were years of low yield, mainly from water-deficits, and were not included in the linear regressions.

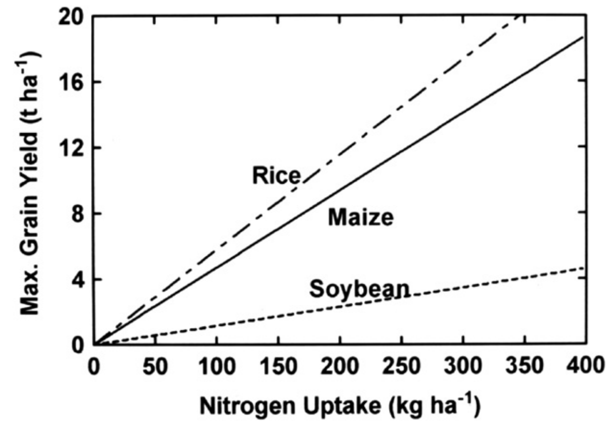

Fig. 2. Maximum grain yield calculated as a function of nitrogen uptake for rice, maize, and soybean using Eq. (1).

in both cases is that crop growth and yield are most often severely constrained by the availability of these two resources and there may well be little genetic opportunity to overcome the basic resource limitations.

2. Nitrogen

Nitrogen, as a critical component of all proteins and nucleic acids, is essential to allow development of new plant cells and crop growth. A continual stream of reduced nitrogen to meristems drives cell production and growth processes. Further, metabolic activity of existing tissues is closely related to amounts of critical proteins in cells. For example, there is a close relationship between leaf photosynthesis rates and the nitrogen content per unit leaf area within each crop species (Sinclair and Horie, 1989). Growth is slowed, sometimes severely, when a nitrogen deficiency lowers protein levels and depresses cell function.

The nitrogen requirements of crop plants extend to seed development, the plant component commonly harvested for yield. The combination of active synthetic and storage proteins in developing seeds is the basis for seed viability. And in modern agriculture, commercial demands require seed protein concentrations in a fairly narrow range in many crops. Wheat grain used for making bread and soybean seeds used as animal feed, for example, must meet protein standards or the farmer is docked severely in the marketplace. Such standards require that nitrogen must be accumulated by plants and provided in appropriate quantities to the seeds to achieve the desired protein concentrations.

The important link between plant yield and seed N can be seen in a simple model describing seed yield. Given the concentration of nitrogen in seeds (N_{seed}, g g^{-1}) and the fraction of total accumulated nitrogen in the plant that ends up in the seed (nitrogen harvest index, NHI, g g^{-1}), a simple expression of maximum crop yield (Y_{max}, g m^{-2}) based on accumulated nitrogen (N_{accum}, g m^{-2}) can be written as

$$Y_{max} = N_{accum}\mathrm{NHI}/N_{seed} \qquad (1)$$

The linear increase in Y_{max} with N_{accum} is shown in Fig. 2.

Although N_{seed} is stable in most crops due to commercial demands, this has not been the case for maize in the U.S. In the period from 1960 to 1991, the seed protein concentration decreased by 0.03% per year (Duvick, 1997). As shown in Eq. (1), the decrease in N_{seed} is predicted to result in increased yields and helps to explain the low, but continual increase in maize yields since the mid 1970s (Fig. 1).

2.1. The agronomic problem

A major challenge in increasing crop yield, therefore, is to increase N_{accum}. To meet this challenge, synchronization is required between nitrogen availability in the soil and the ability of plants to accumulate nitrogen. In modern high-yielding cropping systems, mechanized farming requires that fertilizer must often be applied at sowing or shortly thereafter. Young plants, however, do not yet have an extensive root system in the soil and their overall mass is low so they do not have the capacity to store the nitrogen. Thus, nitrogen uptake capacities are inherently low early in the growing season and substantial amounts of soil nitrogen can be lost by denitrification or leaching from the rhizosphere. Physiologically, nitrogen uptake occurs only as fast as plants can grow; that is, maximum accumulation rates are regulated by feedback control systems that balance nitrogen uptake with plant capacity to use the nitrogen (Clarkson 1986; Glass 2003). The ability of plants to store and use nitrogen increases with time as they proceed through the rapid vegetative growth phase. But often, by the time plants reach the reproductive growth stage, insufficient nitrogen is available in the root zone to meet the demand for high uptake rates.

It is sometimes erroneously assumed that plants have a poor ability to take up nitrogen from the soil during vegetative growth and that they are inefficient in using nitrogen to produce crop yield. This perception is fueled by the widely recognized inefficiency of fertilizer nitrogen use, where rarely does more than 50% of the applied nitrogen ends up in the crop. Crop plants are actually very adept at recovering nitrogen from the soil solution to meet the nitrogen requirements for growth. Nitrogen is readily taken up from the soil solution using several types of mechanisms (Glass, 2003, 2009), and absorbed nitrogen is readily assimilated into the necessary protein and nucleic acid end products (Rufty, 1997). Neither occurs if feedback restrictions are in place. Because plants are highly efficient in the use of the nitrogen they accumulate, the challenge is to allow plants to accumulate more nitrogen from the soil before it is lost.

It must also be recognized that even though plant 'demand' for nitrogen may be strong during the reproductive growth phase, physiological factors cause limitations in acquisition of soil nitrogen. The sink strength of the developing seed dominates partitioning of available carbohydrate generated in photosynthesis by the leaf canopy, and the amounts of carbohydrate transported to the root system (Wardlaw, 1990). As a result, root growth and energy reserves in the root decline during seed growth so that metabolic activity for nitrogen uptake declines. With lower nitrogen uptake into the plant and high nitrogen