Overcompensation Can Be an Ideal Breeding Target

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Abstract: The phenomenon of overcompensation has been reported in various plant species although it has been treated by some as isolated incidents with only limited values. Reviewing reports on the extensive studies of defoliation in maize showed that different genotypes respond differently to defoliation, varying from phenomenal increase to significant loss in grain yield. The different responses of maize in kernel yield among genotypes to defoliation are confirmed in our experiments conducted in both China and Australia. Defoliated plants are likely to use less water during vegetative growth and that they also have better ability to extract water from the soil. We also found that defoliation dramatically delayed plant senescence under dry conditions, facilitating the production of high quality silage by widening the harvest window. As overcompensation occurs only in some genotypes, we believe that exploiting defoliation as a management practice directly for crop production can be risky. However, the fact that significant yield increase following defoliation does occur and that large genetic variation does exist meet the requirements for a successful breeding program. The detection of sizable quantitative trait locus (QTL) in the model plant species provides further evidence indicating the feasibility of exploiting this phenomenon through breeding. The stunning magnitudes of desirable responses reported in the literature suggest that overcompensation could become the most valuable breeding target in at least some species and its impact on crop production could be huge even if only a proportion of the reported variations could be captured.

Keywords: overcompensation; crop production; defoliation; maize; plant senescence

1. Introduction

Food security is a serious and pressing contemporary issue. With the increase in both the population and the per capita income, global demand for agricultural crops is increasing rapidly. It is estimated that, compared to that of 2005, 60% more food will be required by 2050 to meet human nutrition needs [1]. As the potential of arable land expansion is limited, most of the increase may have to come from methods that provide new ways to increase yield per unit area [2]. Maize, also known as corn, is the largest grain crop in the world. The estimated production of maize in 2020 was 1.06 million tons (https://www.worldcornproduction.com, accessed on 21 August 2019). The massive quantity of this crop species produced worldwide means that even a small percentile change in yield could be substantial in regard to global food security.

Similar to the situations in many other crop species, the trends for increased yield per hectare have dramatically slowed in maize as incremental increases through improved agronomic management and genetic improvement approach their optima. To reach projected demands within the next thirty years, a breakthrough similar in impact to the ‘Green Revolution’ is required. Based on the extensive reports of defoliation in maize as a case study, we argue that the phenomenon that damaged plants may produce significantly more biomass or kernel yield compared with undamaged ones, termed as overcompensation,
may offer huge potentials to dramatically enhance productivities of at least some plant species.

2. The Overcompensation Controversy: Does Defoliation Result in Dependable Yield Increase?

Evidence for overcompensation has been reported in numerous plant species including *Ipomopsis arizonica* [3], *Gentianella campestris*, *G. amarelle* [4,5], *Arabidopsis thaliana* [6–9], *Solanum tuberosum* or potato [10,11], and *Erysimum strictum* [12]. Some of the responses are fascinating. For example, Paige and colleagues showed that when mule deer and elk removed 95% or more of the aboveground biomass of the monocarpic biennial scarlet gilia, *Ipomopsis aggregata*, the plants produced 4.1 times as many flowering stalks, 2.8 times as many flowers, and 3.1 times as many fruits per plant as the ungrazed control [12–16]. In studying aphid resistance in radish (*Raphanus sativus* L.), Agrawal (1998) and Agrawal et al. (1999) [17,18] reported that induction of resistance against aphids early in the season significantly increased the index of lifetime female fitness by over 60% compared with controls. Poveda et al. (2010) [10] reported that field-grown potato plants attacked by low numbers of potato moth larvae produce a 2.5-fold higher marketable potato yield than undamaged plants. Like those reported in maize, these authors also noted large genotypic variations in the level of overcompensation and the influence of biotic and abiotic factors on compensatory responses. Trials under field conditions found that plants with compensation doubled the mean productivity of a potato farm in relation to those undamaged plants, which convinced the authors that overcompensation can be incorporated into management practices in crop production [19].

However, overcompensation has been marked by controversies. Firstly, the phenomenon was not detected in some follow-up studies in apparently comparable situations [20]. Secondly, the phenomenon contradicts what we think we know about photosynthesis and the optimal resource allocation models that determining yield potential [17,21]. Naturally, we can question the phenomenon of overcompensation when it conflicts with what we think we know of. At the same time, there is no reason why we cannot question whether some of the accepted theories are in fact flawed. Here we utilize results from studies of defoliation in maize as a case to highlight what we feel are the limiting factors in reaching a consensus position on the value of exploiting overcompensation in crop production. We also argue that all key elements required for a successful breeding program exist for exploiting the phenomenon of overcompensation in crop production.

3. Yield Response to Defoliation Varies Greatly among Genotypes

Genotypes responding differently to defoliation have been reported in all studies where two or more genotypes were used. Echarte et al. (2006) [22] found that the impact of defoliation on kernel weight was more severe on newer hybrids in comparison to those older ones. Significant differences between genotypes with different maturity were reported. Hanway (1969) [23] reported that defoliation caused greater grain yield losses for early maturing genotypes in comparison to that of the late maturing ones. Interestingly, Hicks and Crookston (1976) [24] found that defoliation dramatically boosted kernel yield of a short-season hybrid while slightly reduced the yield of a full-season genotype.

Huge differences in response to defoliation between genotypes have been reported in numerous other studies [22,25,26]. However, differences in maturity among genotypes used in most of these studies were unknown. Further, defoliation for each of these studies was carried out at a single developmental stage measured by leaf numbers. It is known that different genotypes produce different numbers of leaves, that leaf numbers for a given genotype change between environments and that genotypes with higher leaf numbers take longer to mature [27]. In other words, two genotypes with the same number of leaves may differ in their physiological stages of development. We thus suggest measuring the physiological growth stage (Ps) when defoliation is conducted by dividing the leaf number with the total number of anticipated leaves a genotype would produce in a given environment. For example, the ‘droopy’ method has been widely used to measure
development stages in previous studies [22, 24, 26]. Beginning with the short first leaf (D1), this method counts the number of leaves that are at least 40% exposed from the whorl. Ps at D7 for a genotype with 14 leaves is equivalent to D9 for a genotype with 18 leaves (PsD7/14 = PsD9/18 = PsV0.50). Using such a measurement should make results from genotypes belonging to different maturity groups more comparable.

Results from our own experiments showed huge variation in the effects of defoliation on kernel yield (Table 1) (unpublished). The effects do not only vary between hybrids but also seem to be strongly associated with the levels of drought severity. The large genotypic variations in response to defoliation make it more difficult to adopt the practice directly in maize production. However, similarly to any other characteristic, genotypic variations are the foundation for breeding. With the availability of such large differences in genetic variation, all is required for a successful breeding program is to identify the conditions when a few genotypes give a positive response. One of the unique features of a breeding program is that positive responses from all genotypes and under all circumstances are not required. The detection of sizable QTL responsive for overcompensation in the model plant species Arabidopsis thaliana [8] provides further evidence suggesting that targeting this phenomenon in breeding should be feasible.

### Table 1. Changes in kernel yields following defoliation in maize.

| Year | Location | Hybrid  | Control Yield (kg/ha) | Defoliated Yield (kg/ha) | Yield Change (%) | p Value |
|------|----------|---------|-----------------------|--------------------------|------------------|---------|
| 2016 | Langfang (China) | Jinrui88 | 2441.3 | 3930.0 | 61.0% | p < 0.05 |
|      |          | Cangyu76 | 7222.5 | 8756.3 | 21.2% | p < 0.05 |
|      |          | Wuke2   | 10,796.3 | 11,010.0 | 2.0% | p > 0.05 |
|      |          | Yufeng303 | 12,853.3 | 12,115.0 | −5.7% | p < 0.05 |
|      |          | Shiyu9  | 4507.5 | 4125.0 | −9.3% | p < 0.05 |
|      |          | Xianyu335 | 9967.5 | 8343.0 | −16.3% | p < 0.05 |
|      |          | Jufeng558 | 9761.3 | 7646.3 | −21.7% | p < 0.05 |
|      |          | PAC727IT | 5125.2 | 5510.8 | 7.5% | p < 0.05 |
|      |          | PAC606IT | 5853.4 | 5874.2 | 0.4% | p > 0.05 |
|      |          | Jinsai29 | 6784.5 | 7701.0 | 13.5% | p < 0.05 |
| 2017 | Gatton (Australia) | PAC727IT | 5125.2 | 5510.8 | 7.5% | p < 0.05 |
|      | Tangshan (China) | Jinsai29 | 6784.5 | 7701.0 | 13.5% | p < 0.05 |
|      |          | Huanong887 | 10,692.7 | 11,596.0 | 8.4% | p < 0.05 |
|      |          | Jinghai5 | 6829.5 | 5667.0 | −20.5% | p < 0.05 |
|      |          | Zhendan958 | 7959.5 | 6344.0 | −25.5% | p < 0.05 |

All three trials were irrigated immediately following sowing. The trial conducted at Langfang (latitude 39.410° N; longitude 116.818° E) was then run as rain-fed without further irrigation and severe drought symptom (leaf rolling) was observed. The trial conducted at Tangshan (latitude 39.631° N; longitude 118.180° E) was well irrigated and apparent symptom of drought stress was not observed. The trial conducted at Gatton (latitude 27.533° S; longitude 152.339° E) was well irrigated until tasselling, and symptom of drought stress was observed about ten days after the irrigation had been stopped.

4. Genotype, Environment, as Well as Method and Timing of Defoliation, Are All Critical for Positive Maize Yield Response

The first reports on maize defoliation appeared more than a century ago and they were conducted with the aims of investigating damages from hail [28, 29], pathogens, or insects [30]. Artificial defoliation was employed to understand the expected grain yield loss following the removal of a given percentage of the leaf area at different stages of plant development [31]. As anticipated, defoliation often leads to yield loss, and the impacts depend on both the proportion of leaves removed and timing (developmental stages) when defoliation was carried out. Results from most studies show that mild defoliation (removing 25% or less of the leaves) has little impact on grain yield irrespective of when (developmental stages of plants) it is conducted [31–34]. Removing some 33% of the leaves decreased grain yield by about 13%, again with no significant differences regarding the growth stages [35]. However, plants at different growth stages respond very differently to more severe defoliation. Results from the majority of studies showed that the relationship between the timing of defoliation and yield response exhibits a bell-shaped distribution: yield losses from defoliation on young [36] and old plants [30–32, 36] are
often minimal. Defoliation conducted around tasselling has the most severe impacts on grain yield \([23,30,32,33,37-39]\). Further, the impacts of defoliation on grain yield also differ with different methods of leaf removal. This was illustrated by the results from Hanway (1969) \([23]\) who found different responses between removing (a) alternate pairs of leaves (every other two leaves), (b) all leaves from one side of each plant, (c) 1/2 of each leaf (lengthwise), (d) all leaves above the uppermost ear, (e) all leaves below the uppermost ear, and (f) terminal 1/2 of each leaf.

However, significant increases in grain yield following defoliation have also been reported from several of these early defoliation studies. Cloninger et al. (1974) \([40]\) assessed 28 hybrids and conducted partial defoliations at D4, D6, and D8. Increases in grain yields were obtained from 5 of the 28 hybrids defoliated at D4, and one at D6. By cutting the ‘stalk’ of the plant below the collar of the second leaf and removing the first leaf blade by hand pulling at D5 on a short-season corn hybrid (Trojan TXS85), Hicks and Crookston (1976) \([24]\) found a significant increase in grain yield, varied between 30% and 80% with an average of 48% over 3 consecutive years. The authors noticed that the defoliated plants quickly developed new leaf tissue and little difference in total leaf or stalk tissue between the defoliated and control plants remains by tasselling. These researchers then further tested the responses of 12 different hybrids. Defoliation resulted in a significant yield increase for seven of these hybrids, showed no effect on four while reduced the yield of one genotype. Yield changes from these varieties were huge, varying from -14% to +37% \([25]\). Hicks et al. (1977) \([26]\) speculated that defoliation at the time of reproductive initiation had to induce drastic change in source-sink relations, thus stimulating embryonic ear growth. However, a similar study conducted at a similar time in Illinois found that defoliation at early seedling stage resulted in an 11% yield reduction \([22]\).

It is interesting to note that, like those obtained in other regions \([26]\), the best responses to defoliation were all obtained by cutting plants below the collar of the second leaf around D5. Defoliation carried out earlier or later is more likely to lead to yield decrease (Figure 1) \([41]\). However, as discussed below, leaf numbers cannot be used to reliably identify physiological stages of plant development. Using leaf numbers to determine the time of defoliation can thus be one of the reasons contributing to the different responses among different genotypes.

![Figure 1](image_url)

**Figure 1.** Response to defoliation conducted at different stages of plant development measured by leaf numbers. Results were obtained from three hybrids (V1 = Heyu187; V2 = Yuhe988; and V3 = Chengyu13) defoliated at four time points (from D4 to D7 leaves). Data used for this figure were reported by Pang et al. 2016 \([41]\).
5. Positive Yield Responses to Defoliation Typically Occur in Drought Stress Environment

Based on defoliation trials conducted in a total of 11 years, Crookston and Hicks (1988) [42] concluded that significant yield increase occurred only in seasons when crop yields were dramatically reduced by drought. By assessing two maize inbreds and their single cross hybrid, Vasilas and Seif (1985) [43] showed that grain yield increase under drought was associated with decreasing transpiration or delaying flowering. Shanahan and Nielson (1987) [44] found that treating maize plants with growth regulators resulted in a significant reduction in early-season plant growth and evapotranspiration, leading to soil-water conservation which benefits plant development under drought. Similar conclusions were reached by Crookston and Hicks (1988) [42] who believed that defoliation can be a profitable management practice for maize crop grown in areas where drought routinely occurs or where seasonal soil-water shortage is predictable during grain filling. However, the practice has little or even a negative impact on yield in environments where soil water is not limiting plant growth [22,43,45].

The likelihood that water availability can be an important factor affecting the impact of defoliation on grain yield is clear. Reduced symptom severity from drought stress in defoliated plants has been repeatedly observed. We notice that there are at least two different mechanisms leading to better performance of defoliated plants. One of these is that defoliated plants must reduce water usage during vegetative growth. This can be seen from that the first row of non-defoliated plants grows much better than others (Figure 2A). The other possible mechanism is that defoliated plants seem to have improved ability to get water from the soil. This can be illustrated by the trial we conducted in Australia. The trial was well-irrigated before tasselling (thus root systems must be well-developed) and severe symptoms of drought stress appeared much faster in the non-defoliated plants when the irrigation had been stopped (Figure 2B).

With the change in farming practices from irrigated to mainly rain-fed crops, impacts of defoliation on grain yield also changed in northern China. During the times when irrigation was widely used for maize production, positive responses to defoliation were rare [46,47]. In addition to water availability, timing and methods of defoliation may also contribute to the negative responses. However, situations have changed in recent years. Significant grain yield increase in maize following defoliation has been repeatedly reported in northern China [41,48–53] (Table 2) and some farmers there have incorporated the practice in production (Figure 3).

Negative or neutral effects of defoliation on grain yield occurred mainly in summer-sown crops or in situations where drought was not a factor seriously limiting crop production [54]. Crookston and Hicks (1988) [44] also found strong correlations between levels of yield change following defoliation and end-of-season soil moisture. However, soil-water conservation may not be the only reason for the yield increase following defoliation. Compared with the non-defoliated controls, defoliated maize plants also showed reduced symptoms of water deficiency even if they were well-watered until tasselling (Figure 2B).
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**Figure 2.** Defoliation improves drought tolerance. Defoliation was carried out by cutting all tissues above the first leaf at D5. The symptom of drought stress (leaf rolling) was clear in the non-defoliated control plants. (A) The photo was taken from a trial conducted in northern China. It is of note that, of the non-defoliated control, the row next to the defoliated ones had the best performance. This indicates that the defoliated plants must have used less water. (courtesy of Mr Baojian Su); (B) The photo was taken from a trial conducted in Queensland, Australia. The trial was well irrigated (about 40 mm per week) until tasselling. The symptom of water stress appeared in the non-defoliated plants soon after the stopping of irrigation, indicating that defoliation may also improve the capacity of roots in extracting water from the environment. Also note that, different from the non-defoliated controls, few of the defoliated plants grew vegetative tillers (or suckers) which produce very small or no ears.
Table 2. Changes in grain yield of maize following defoliation at D5 in Northern China.

| Year | Location (Latitude/Longitude) | Genotype | Yield (kg/ha) | Difference | Reference |
|------|--------------------------------|----------|--------------|------------|-----------|
|      |                                |          | Non-Defoliation | Defoliation |           |
| 2014 | Langfang, Hebei (39.520° N/116.680° E) | Chengyu13 | 7731.8 | 8499.3 | 9.9% | [52] |
|      |                                | Yuhe988  | 7419.3 | 8954.0 | 20.7% |
|      |                                | Heyu187  | 7299.9 | 9495.0 | 30.1% |
| 2016 | Tongliao, Neimenggu (43.517° N/121.967° E) | Chunyu968 | 11,444.3 | 13,350.8 | 16.7% | [53] |
|      | Langfang, Hebei (39.520° N/116.680° E) | Nongda372 | 6982.5 | 7638.8 | 9.4% | [51] |
|      | Linfen, Shanxi (36.359° N/111.558° E) | Huaneng887 | 7130.3 | 9582.8 | 34.4% |
| 2016 | Yichun, Heilongjiang (47.727° N/128.841° E) | Demeiya1 | 7740.0 | 9075.0 | 17.2% | [50] |
|      | Harbin, Heilongjiang (45.803° N/126.535° E) | Nongyu7 | 4887.0 | 5467.5 | 11.9% |
|      | Qiqihar, Heilongjiang (47.354° N/123.918° E) | Jida935 | 4434.0 | 4990.5 | 12.6% |
| 2017 | Taoyuan, Hunan (28.902° N/111.488° E) | Qiyu7 | 9704.0 | 9975.0 | 2.8% | [48] |
| 2016 | Langfang, Hebei (39.520° N/116.680° E) | Heyu187 | 7290.0 | 9500.0 | 30.3% | [51] |
| 2017 | Fengcheng, Liaoning (40.452° N/124.066° E) | Liangyu99 | 10,139.2 | 11,336.5 | 11.8% | [53] |
|      | Jili, Jilin (43.501° N/126.330° E) | Xianyu335 | 11,512.6 | 12,990.9 | 12.8% | [52] |

Figure 3. The practice of defoliation has been adopted by some farmers in maize production in northern China (courtesy of Mr Baojian Su).

6. Changes in Plant Morphology and Yield Components in Maize Crops Responded Positively to Defoliation

Measurements on yield components following defoliation were not taken in many studies from which significant yield increase was reported following defoliation. It was noticed that defoliation at D5 delayed tasselling by 2–8 days but the difference became...
Defoliation dramatically delayed plant senescence under dry conditions. The photo was taken from a trial conducted in Queensland, Australia. The trial was irrigated weekly with about 40 mm of water until tasselling. It was noted that the color of cobs on the defoliated plants indicated that they reached physiological maturity while the plants were still green.

7. Conclusions

The phenomenon of overcompensation is fascinating especially considering what we think we know about photosynthesis and resource allocation in plant development. As it occurs only in some genotypes under certain conditions, overcompensation has been treated as isolated incidents with limited values for practical adoption. As that may be, we know that overcompensation does in fact occur, and genotypic variations in compensatory responses do exist, and as such converting such ‘isolated incidents’ into reliable approaches for production should be possible through breeding. In fact, the magnitude of some of the reported compensatory responses is phenomenal in comparison to the variations we routinely come across for various characteristics targeted in breeding programs. The phenomenal responses of plants to different types of damage also indicate that overcompensation can become the most valuable target in breeding programs and its contribution to crop production can be huge even if we can only capture a proportion of the stunning variations reported in various species. To realize the full potential of overcompensation, however, we must work out what conditions are required for it to occur and understand the mechanisms underpinning different genotypic responses to foliar damage. We believe that considered application of defoliation in conjunction with
strategies for targeted improvement of this trait through breeding could offer the potential of another agricultural revolution required to meet crop yield targets by 2050.

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