

PLANT SCIENCE

Soybean photosynthesis and crop yield are improved by accelerating recovery from photoprotection

Amanda P. De Souza¹, Steven J. Burgess^{1,2}, Lynn Doran¹, Jeffrey Hansen¹, Lusya Manukyan¹, Nina Maryn³, Dhananjay Gotarkar², Lauriebeth Leonelli^{1,4}, Krishna K. Niyogi^{3,5}, Stephen P. Long^{1,6*}

Crop leaves in full sunlight dissipate damaging excess absorbed light energy as heat. This protective dissipation continues after the leaf transitions to shade, reducing crop photosynthesis. A bioengineered acceleration of this adjustment increased photosynthetic efficiency and biomass in tobacco in the field. But could that also translate to increased yield in a food crop? Here we bioengineered the same change into soybean. In replicated field trials, photosynthetic efficiency in fluctuating light was higher and seed yield in five independent transformation events increased by up to 33%. Despite increased seed quantity, seed protein and oil content were unaltered. This validates increasing photosynthetic efficiency as a much needed strategy toward sustainably increasing crop yield in support of future global food security.

The number of people affected by food insufficiency continues to grow (1). Projections clearly show that food supply is not increasing fast enough to guarantee food security. As a result, it is expected that more than 840 million people worldwide will be undernourished by 2030. Providing seed that can achieve higher yield per unit land area is an effective way to reduce this food shortage, provide food security to the poorest, and avoid yet more land being brought into production. Improving photosynthesis has been suggested as a major opportunity to gain the needed jump in yield potential (2).

Plants dissipate potentially damaging excess absorbed light energy in full sunlight by inducing a mechanism termed nonphotochem-

ical quenching (NPQ) (3). This process is essential in avoiding the formation of reactive oxygen species that would damage the photosynthetic apparatus (4). However, NPQ mechanisms are slow to relax following the frequent sun-shade transitions that occur within crop canopies. This results in a substantial loss of photochemical energy (i.e., between 7.5 and 30%) that could otherwise be used for photosynthesis (5, 6). For soybean crop canopies, this slow NPQ relaxation upon sun-shade transitions was calculated to cost >11% of daily carbon assimilation (7).

NPQ combines several different mechanisms that vary in relaxation kinetics during sun-shade transitions (8, 9). Energy-dependent quenching (qE) is the major and most rapidly

induced component, initiated within seconds up to a few minutes upon transfer of leaves to high light (3, 10). The induction of qE during exposure to high light requires acidification of the thylakoid lumen to activate violaxanthin de-epoxidase (VDE), which converts violaxanthin to zeaxanthin via the intermediate antheraxanthin in the VAZ xanthophyll cycle (11). When the leaf transitions back to low light, the reverse reaction converts zeaxanthin back to violaxanthin on a much slower time scale via the activity of zeaxanthin epoxidase (ZEP) (12). Photosystem II (PSII) subunit S (PsbS) is also implicated in qE modulation of NPQ (13), causing PSII-associated antennae to undergo a conformational change. Zeaxanthin accumulation is also responsible for a more slowly induced and relaxing NPQ component that is independent from both PsbS and lumen acidification. This component, termed zeaxanthin-dependent quenching (qZ), is where zeaxanthin binds to light-harvesting complex proteins and is induced during the first ~ 8 to 10 min of high light (3).

¹Carl R Woese Institute for Genomic Biology, University of Illinois at Urbana-Champaign, Urbana, IL, USA. ²Department of Plant Biology, Morrill Hall, University of Illinois at Urbana-Champaign, Urbana, IL, USA. ³Howard Hughes Medical Institute, Department of Plant and Microbial Biology, University of California, Berkeley, CA, USA. ⁴Department of Agricultural and Biological Engineering, University of Illinois at Urbana-Champaign, Urbana, IL, USA. ⁵Molecular Biophysics and Integrated Bioimaging Division, Lawrence Berkeley National Laboratory, Berkeley, CA, USA. ⁶Lancaster Environment Centre, Lancaster University, Lancaster, UK. *Corresponding author. Email: slong@illinois.edu

Fig. 1. Protein expression, yield, and seed composition in engineered soybeans. (A) Representative immunoblots comparing the protein abundance of wild-type (WT) and eight independent transgenic soybean lines expressing *AtVDE*, *AtPsbS*, and *AtZEP* (VPZ) grown in the field at Urbana, IL, USA. Band corresponding to *AtPsbS* is the lower band; 30 µg of total soluble protein was loaded per well; Coomassie Blue-stained gel (CB) is presented to show uniformity of loading. Immunoblots of all biological replicates are shown in figs. S1 and S2 for 2020, and in figs. S3 to S9 for 2021. (B) Seed yield in tonnes per hectare (t. ha⁻¹) obtained at final harvest in 2020. (C) Protein, oil, fiber, and ash content in percentage of dry mass of seeds in 2020. Given the high similarity between biological replicates, statistical differences were obtained, even though most were <1% different from WT. These statistical differences are for protein between WT and ND-18-56, YZ-19-8A, and ND-18-44; for oil between WT and ND-18-56, YZ-26-1C, and ND-17-20; for fiber between WT and ND-18-56 and ND-17-20; and for ash, between WT and ND-18-56. Given the small magnitude of difference, these are very unlikely to have any physiological meaning. Bars and values are the mean (±1 SE). Asterisks indicate significant differences between WT and VPZ transgenic line (**P < 0.05, *P < 0.1; n = 15 experimental blocks).

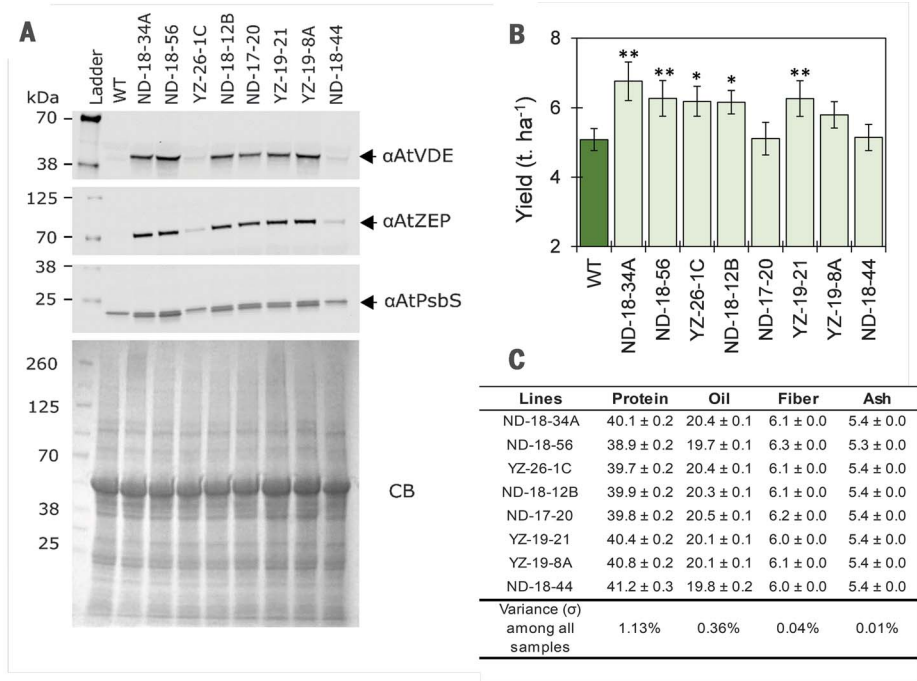
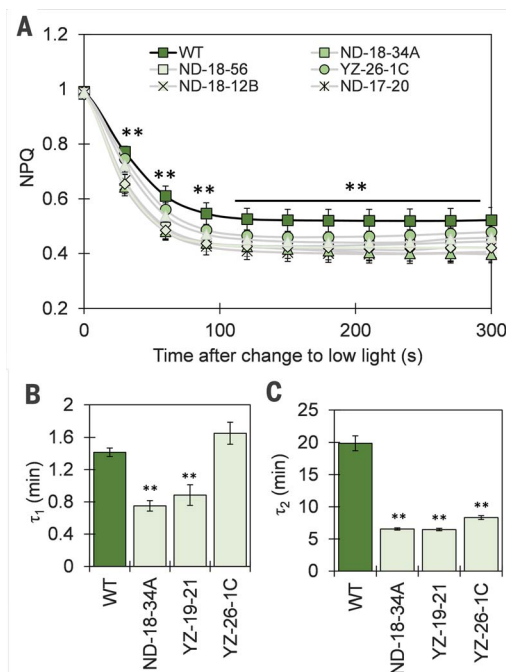


Fig. 2. Relaxation of NPQ on high- to low-light transitions.

(A) Relaxation of NPQ in the last of five cycles of 4 min under high light ($2000 \mu\text{mol m}^{-2} \text{s}^{-1}$ PFD) followed by 3 min under low light ($200 \mu\text{mol m}^{-2} \text{s}^{-1}$ PFD) in wild-type (WT) and independent transgenic soybean lines expressing *AtVDE*, *AtPsbS*, and *AtZEP* (*VPZ*) grown in the field at Urbana, IL, USA in 2020. NPQ throughout the five cycles is shown in fig. S12. Values were normalized to NPQ in high light to allow easier comparison among lines; points shown are means (± 1 SE) for each time point ($n = 8$ biological replicates). (B) Mean (± 1 SE) of the time constants (τ) of the fast (τ_1) and (C) medium (τ_2) relaxing components of NPQ in field-grown plants in 2021. Time constants were obtained by fitting a double exponential curve (8) to the time course of NPQ relaxation ($n = 16$ biological replicates). Semi-log plot of the NPQ values used for these calculations is shown in fig. S13. Asterisks indicate significant difference ($**P < 0.05$) between WT and transgenic lines.



Up-regulation of *VDE*, *PsbS*, and *ZEP* (*VPZ*) in tobacco significantly accelerated the violaxanthin xanthophyll cycle (VAZ), leading to faster induction and relaxation of NPQ. This increased the efficiency of CO_2 assimilation and electron transport through PSII in fluctuating light conditions, without altering photosynthetic efficiency at steady state. In replicated field trials, shoot biomass production was increased 14 to 21% across three independent transgenic events (14). However, a study in transgenic *Arabidopsis thaliana* (*At*) containing the *VPZ* expression cassette failed to show increased biomass accumulation. This observed discrepancy was suggested to be due to negative effects of faster relaxation on photoprotection, or the result of feedback controls related to lack of sink strength (15). Others have claimed that increases in biomass in *VPZ* tobacco can be due to reasons other than photosynthesis such as changes in hormone levels (16) or suggested that sink limitations will prevent any realization of increased seed yield in food crops (17–19). To test whether a yield increase could be achieved in a major agronomical crop, we introduced the *VPZ* construct into soybean [Glycine max (Gm)]. In terms of total global production, soybean is the fourth most important grain crop and the most important single source of vegetable protein.

Results

Engineered acceleration of NPQ relaxation increases soybean yield

During the summers of 2020 and 2021, field experiments were performed in Urbana, IL, USA to test the impact of the *VPZ* construct

on photosynthesis, growth, and seed yield in independent transgenic lines of T_4 and T_5 homozygote progeny of soybean (cv. Maverick). Maverick is an elite soybean genotype that is resistant to stress conditions and has been used as a proof of concept of different transgenes (20–22) because of its amenability to genetic transformation.

AtVDE, *AtPsbS*, and *AtZEP* protein and mRNA were detected in all transgenic lines in both years and at different stages of plant development (Fig. 1A, figs. S1 to S9, and table S1). The *PsbS* antibody detected both native *GmPsbS* and the transgenic *AtPsbS* proteins. The *AtPsbS* protein was observed as a lower band just below 23 kDa on a Western blot, which was absent in wild-type (WT) samples (Fig. 1A and figs. S1 to S9). Transgene expression was variable with the lowest abundance observed in YZ-26-1C and ND-18-44 lines in both protein and RNA levels (Fig. 1A and table S1). As might be expected, the ratio of increases in each of the three proteins appears more important than the total increase (fig. S10). For instance, YZ-26-1C had low overall increases and showed a 21.7% yield increase, whereas ND-17-20 had high amounts of protein without a significant increase in yield (Fig. 1, A and B). This is consistent with the mathematical simulations that show that the ratio of expression of *VDE*, *ZEP*, and *PsbS* is more important in achieving altered NPQ kinetics than is absolute abundance (fig. S10).

In 2020, the overexpression of *VPZ* transgenes led to a significantly higher seed yield (Fig. 1B). Of eight independent transgenic lines, five showed a significant increase in seed

yield, and none showed a lower yield. The yield increase averaged across these five transgenic lines was 24.5% compared to the WT with the largest difference being observed for the line ND-18-34A (+33%). Higher yields were due to a higher seed number per plant (fig. S11A). Except for the line YZ-19-21 that showed greater seed mass, seeds from transgenic lines were overall smaller than WT (fig. S11B). The same trend was observed during 2021 on number and size of seeds (fig. S12, A and B), although those differences did not translate into a significantly higher seed yield at the end of the 2021 season (fig. S12C). Increased seed production in 2020 was achieved with less than 1.3% change in protein and oil content, and most other components of seed quality (Fig. 1C and table S2). Similar results were obtained for seeds produced in 2021 (tables S2 and S3).

Did the overexpression of *AtVDE*, *AtPsbS*, and *AtZEP* (i.e., *VPZ* genes) lead to a faster NPQ relaxation and higher photosynthetic efficiency in soybean? As observed in tobacco (14), the overexpression of these three transgenes in soybean accelerated the relaxation of NPQ during sun-to-shade transitions (Fig. 2), resulting in increased photosynthetic efficiency under fluctuating light (Fig. 3). The difference in NPQ relaxation was assessed by comparing the normalized NPQ values at different time points or the time constant of NPQ components after the transition from high to low light. In both years, NPQ relaxation was faster in all transgenic lines (Fig. 2). Between 90 and 300 s after the sun-shade transition, reduction in NPQ across transgenic lines during 2020 was 11 to 23% greater than in WT (Fig. 2A). Similarly, in 2021, the fast (τ_1) and medium (τ_2) relaxing time constants for NPQ relaxation were 37 to 67% smaller in the transgenic lines than in WT; i.e., relaxed more rapidly (Fig. 2, B and C, and fig. S13).

Although all transgenic lines showed faster NPQ relaxation rates, the amplitude of NPQ varied between lines. For instance, ND-18-34A and YZ-19-21 had significantly higher NPQ under high light, whereas YZ-26-1C had NPQ values similar to those of the WT under the same conditions (fig. S14). The increased NPQ levels under high light did not confer any benefit to the plants, because the photoprotection index (23) did not differ throughout the day between any of the *VPZ* lines and WT (fig. S15).

Effects of the engineered change beyond yield

The overexpression of *VPZ* genes in soybean led to an overall reduction in levels of violaxanthin in ND-18-34A and YZ-19-21 with a concomitant increase in zeaxanthin in the periods of high light exposure (i.e., 2 p.m.) (figs. S16, A and C, and S17). Levels of antheraxanthin in all transgenic lines did not change relative to WT (fig. S16B). Differences

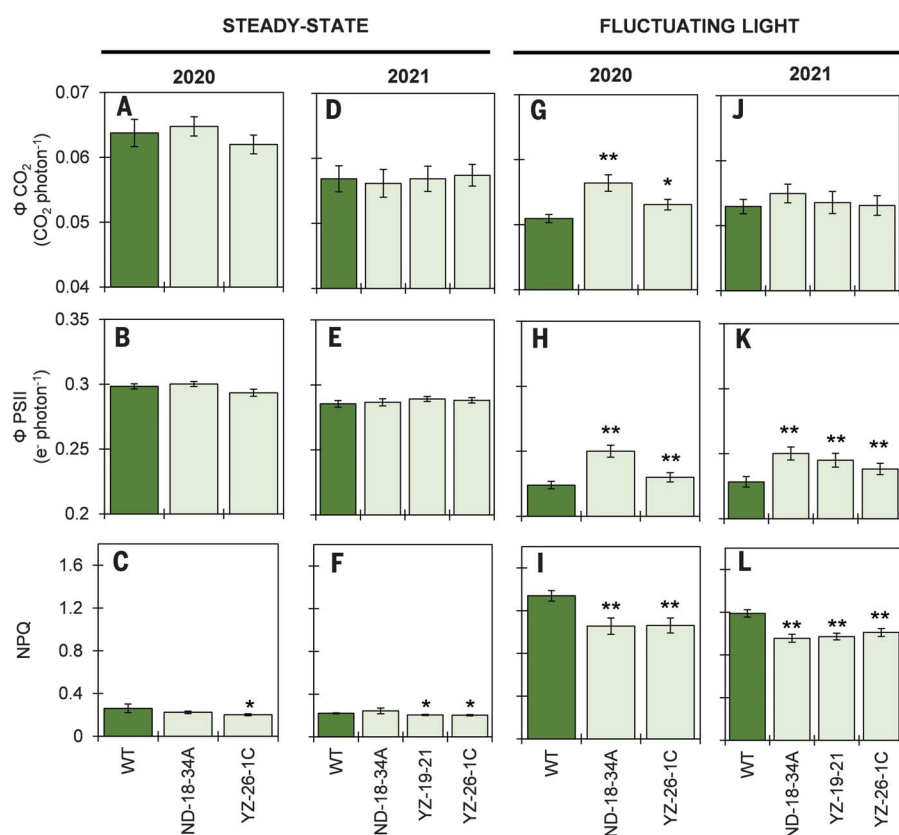


Fig. 3. Photosynthetic efficiency in steady-state and fluctuating light. (A and D) Quantum efficiency of CO_2 assimilation (ΦCO_2) under steady-state light. (B and E) Quantum efficiency of linear electron transport (ΦPSII) under steady-state light. (C and F) Average NPQ corresponding to A – B and D – E, respectively. Panels (G to L) are, respectively, the equivalent measures under fluctuating light. Data are for wild-type (WT) and soybean lines expressing AtVDE, AtPsbS, and AtZEP (VPZ) grown in the field at Urbana, IL, USA during 2020 and 2021. Bars are the mean (± 1 SE) for measurements made during vegetative and seed-filling stages ($n = 16$ biological replicates). Asterisks indicate significant differences between WT and VPZ transgenic lines (** $P < 0.05$; * $P < 0.1$). The separate values for each developmental stage are listed in table S4.

in zeaxanthin accumulation altered the de-epoxidation state (DES) in the VPZ lines. Whereas YZ-26-1C had a lower DES throughout the day, ND-18-34A and YZ-19-21 showed an increase in DES at mid-day in relation to the WT, but a faster decrease in DES in the late afternoon (fig. S16D). In both soybean and tobacco, VPZ expression was associated with faster epoxidation of zeaxanthin, faster τ_1 and τ_2 recovery, and less residual NPQ after transition from excess light to limiting light. Apparently, unlike tobacco, soybean has a second xanthophyll cycle, the lutein epoxide cycle (LxL cycle), which converts lutein epoxide into lutein during exposure to high light. The LxL cycle is catalyzed by the same enzymes as the VAZ cycle (24) and similarly contributes to the photoprotection mechanism, but is typically present only in trace amounts in those plant species examined (24–26). Here, overexpression of VPZ genes increased lutein epoxide levels relative to WT with a concomitant decrease of lutein and an average reduction of

5% in DES related to the lutein epoxide cycle (LxL DES; fig.S18). Introduction of the LxL cycle in *Arabidopsis* generated plants that had increased photosynthetic efficiency over the WT (27). Thus, activation of the LxL cycle in the VPZ soybean could potentially contribute to the phenotypes observed in the VPZ transgenic lines. However, epoxidation of lutein is significantly slower than that of zeaxanthin (28, 29) and would not explain the observed faster relaxation of NPQ.

Changes in photosynthetic efficiency were evaluated through the response of photosynthesis to different light levels under steady-state and fluctuating light conditions (Fig. 3). At steady state, there were no differences between transgenic lines and WT in quantum efficiencies of CO_2 assimilation (ΦCO_2) or of linear electron transport (ΦPSII) in 2020 (Fig. 3, A and B) and 2021 (Fig. 3, D and E). Under fluctuating light, ΦCO_2 was significantly increased by 1 to 10% relative to WT across the two years (Fig. 3, G and J). In parallel, ΦPSII

in fluctuating light was increased 2.5 to 11.5% (Fig. 3, H and K). These increases were consistent with those observed previously in tobacco (14). Consistent with the increase in ΦCO_2 and ΦPSII under fluctuating light, NPQ values in these fluctuating light conditions averaged 21% lower in 2020 (Fig. 3I) and 17% lower in 2021 (Fig. 3L) relative to WT. Increased photosynthetic efficiency did not alter plant growth, plant development, or stem biomass (figs. S19 to S21). Carbon and nitrogen ratio (C/N) and phosphorus levels in leaves during vegetative and reproductive stages or in seeds were not different between WT and transgenic lines (fig. S22), suggesting that the increase in photosynthetic efficiency did not alter nutrient contents per unit mass.

Weather may affect the yield response

So, how did the faster NPQ relaxation and increased photosynthetic efficiency promoted by the overexpression of VPZ genes lead to a higher seed production in 2020? Accelerating the rates of NPQ relaxation can only benefit productivity when there are fluctuations in light (Fig. 3) (14). Thus, it is expected that VPZ plants exposed to a larger number of sun-to-shade transitions during their growth will have an advantage over plants exposed to a lower number of those transitions. As evidenced by our 2020 field season findings, the VPZ lines significantly outperformed WT while yield gains were lacking in 2021. Strong interannual variation in seed production has been observed in other transgenic yield traits (30), so what may explain the difference between years in our study? First, in 2021, a severe storm just before the critical stage of seed filling lodged the crop, causing upper leaves to lie on lower leaves in the canopy, leading many to be permanently shaded and so, lacking the sunflecking that would have occurred in an upright canopy. Second, sun-shade transitions caused by intermittent cloud cover and of the duration in which photosynthesis would benefit from the bioengineered increase in NPQ relaxation were 20% fewer in 2021 compared to 2020 (fig. S23).

The number of pods produced by VPZ plants shows further evidence that the leaves of the middle canopy are important for the observed increase in yield in VPZ soybean. The number of pods in soybean is determined during the period from beginning of flowering to the beginning of seed filling (31) and shows a linear and positive correlation with canopy photosynthesis (32, 33). At harvest in 2021, transgenic plants had on average 13% more pods than WT (fig. S24F), indicating that prior to the lodging, VPZ soybeans were on track for a higher seed yield than WT plants in terms of pod numbers. However, at harvest, the number of pods with four seeds, typically the highest number, was lower in the transgenic lines compared to WT, whereas the number of

0-seed and 2-seed pods was higher (fig. S24, A, C, and E). Although the number of seeds per pod in soybean has high heritability (34), reduced number of seeds per pod and increased abortion occur when photosynthate availability becomes limiting (35, 36).

In conclusion, the overexpression of *AtVDE*, *AtPsbS*, and *AtZEP* in soybean promoted acceleration of NPQ relaxation with a concomitant improvement in photosynthetic efficiency under fluctuating light over 2 years in field trials. By accelerating NPQ relaxation, an average seed yield increase of 24.5% across five independent events was observed in 2020. This is equivalent to the average biomass increase achieved previously for tobacco plants. This demonstrates that under field conditions, direct bioengineering of increased photosynthetic efficiency leads to increased yield in replicated plots in a major food and feed crop. Further, in line with agronomic practice, no nitrogen fertilizer was added to the soybean crop. Yet, more seed was produced without any reduction in protein, nitrogen, and oil content, showing this as a means to the sustainable increases in yield urgently needed to help ensure future food security.

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SUPPLEMENTARY MATERIALS

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Material and Methods

Figs. S1 to S26

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Soybean photosynthesis and crop yield are improved by accelerating recovery from photoprotection

Amanda P. De SouzaSteven J. BurgessLynn DoranJeffrey HansenLusya ManukyanNina MarynDhananjay GotarkarLauriebeth LeonelliKrishna K. NiyogiStephen P. Long

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More soybeans by light management

Plants protect themselves from too much sun by dissipating excess light energy. Unfortunately, the switch from dissipating light energy to using light energy for photosynthesis is not as nimble as the clouds moving across the sky. De Souza *et al.* applied a bioengineered solution that speeds up accommodation by nonphotochemical quenching in soybeans, a widely cultivated and essential crop. In field trials, seed yield increased in some cases up to 33%. —PJH

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