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carbanions in the substrates as electron donors (12), a mechanism that is not likely in the case of a polysaccharide substrate. If the oxidation step was to happen first, this would imply that CBP21 catalyzes cofactor-independent oxygenation of a saturated carbon, which is unprecedented and perhaps not very likely. On the other hand, such a mechanism could yield an intermediate product (for example, an ester bond) that may be more prone to hydrolysis than the original glycosidic bond. Alternatively, the hydrolytic step could occur first, which would imply that CBP21 is capable of hydrolyzing glycosidic bonds in a crystalline environment using a hitherto unknown mechanism. Such a hydrolytic step would require some degree of substrate distortion (13, 14), which seems challenging in a crystalline packing. However, in favor of this mechanism, the subsequent oxidation of the resulting sugar aldehyde ("reducing end") is more straightforward than oxidation of a saturated carbon. Clearly, further experiments are needed to unravel mechanistic details of the remarkable reaction catalyzed by CBP21.

CBP21 introduces chain breaks in what probably are the most inaccessible and rigid parts of crystalline polysaccharides, and its mode of action differs fundamentally from the mode of action of glycoside hydrolases. Glycoside hydrolases are designed to host a single "soluble" polysaccharide chain in their catalytic clefts, and their affinity and proximity to the crystalline substrate tend to be mediated by nonhydrolytic binding domains. In contrast, CBP21 binds to the flat, solid, well-ordered surface of crystalline material and catalyzes chain breaks by a mechanism that results in oxidation of one of the new chain ends. The chain break will result in disruption of crystalline packing and increased substrate accessibility, an effect that may be enhanced by the oxidation of the new chain end that disrupts the normal chair conformation of the sugar ring and introduces a charge.

The enzyme activity demonstrated in this study is difficult to identify because products have low solubility and potentially a high tendency to remain attached to the crystalline material. Based on the structural homology and other similarities discussed above, we propose that GH61 proteins may have the same activity as CBP21, but the even lower product solubilities and higher crystalline packing of cellulose compared with chitin (15) make direct detection of this activity very challenging. However, a first glimpse of the potential of GH61 proteins for cellulose conversion has been presented recently (7). The dependency of these enzymes on the presence of molecular oxygen and reductants provides guidelines for process design.

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Areawide Suppression of European Corn Borer with Bt Maize Reaps Savings to Non-Bt Maize Growers

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Transgenic maize engineered to express insecticidal proteins from the bacterium Bacillus thuringiensis (Bt) has become widely adopted in U.S. agriculture. In 2009, Bt maize was planted on more than 22.2 million hectares, constituting 63% of the U.S. crop. Using statistical analysis of per capita growth rate estimates, we found that areawide suppression of the primary pest Ostrinia nubilalis (European corn borer) is associated with Bt maize use. Cumulative benefits over 14 years are an estimated $3.2 billion for maize growers in Illinois, Minnesota, and Wisconsin, with more than $2.4 billion of this total accruing to non-Bt maize growers. Comparable estimates for Iowa and Nebraska are $3.6 billion in total, with $1.9 billion for non-Bt maize growers. These results affirm theoretical predictions of pest population suppression and highlight economic incentives for growers to maintain non-Bt maize refugia for sustainable insect resistance management.

During the past decade, adoption of transgenic crop technology increased worldwide to reach 134 million ha of transgenic crops planted in 25 countries during 2009 (1). In the United States, maize has been the most abundant transgenic crop planted to resist insect pests, with hybrids engineered to express insecticidal proteins isolated from the bacterium Bacillus thuringiensis [i.e., Bt maize (1, 2)]. Historically, the most widespread insect pest throughout the U.S. Corn Belt has been the European corn borer,

Ostrinia nubilalis (Hübner). The pest was accidentally introduced in the eastern United States in 1917 and subsequently spread with devastating results; losses are estimated at $1 billion per year (3). Given the broad host range of O. nubilalis, the potential for Bt maize to suppress populations regionally was unclear. Furthermore, the economic impacts of such suppression had not been considered.

In 2009, plantings of Bt maize (with traits specific to preventing damage by lepidopteran pests) reached 22.2 million ha, and for the first time exceeded 63% of the total area planted with maize in the United States (4). Most of the Bt maize is distributed throughout the Midwestern U.S. Corn Belt (4) (Fig. 1). Although "stacked" Bt events (maize varieties expressing multiple Bt toxins) directed at preventing herbivory from multiple insect pests are available (1, 4), nearly all Bt maize hybrids sold in the United States express toxins that control O. nubilalis (2, 4, 5). Because of Bt maize's high efficacy (6), there is concern that insects will evolve resistance to Bt

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toxins (5, 7, 8). To delay evolution of resistance, the U.S. Environmental Protection Agency (EPA) mandated that a minimum 20 to 50% of total on-farm maize be planted as non-Bt maize within 0.8 km of Bt fields as a structured refuge for susceptible O. nubilalis. Use of non-Bt maize refugia is an important element of long-term insect resistance management (9).

Some maize producers have been skeptical of allowing O. nubilalis damage in non-Bt maize refugia (10, 11). However, modeling (7, 12) provided a theoretical rationale for how local suppression of O. nubilalis could occur. Suppression was supported by the hypothesis that preferential moth oviposition in early-planted Bt maize fields (7) would reduce larval damage in nearby late-planted non-Bt maize. More generally, for Bt and non-Bt maize fields with similar planting dates, O. nubilalis females are not able to distinguish between Bt and non-Bt maize for oviposition (13). Thus, with high larval mortality, Bt maize fields become an effective "dead-end" trap crop for O. nubilalis originating elsewhere (14). Although the models were theoretically appealing, it was not possible during early Bt maize commercialization to verify the magnitude of pest population suppression. Adult O. nubilalis are known to readily disperse among farms at distances of at least 800 m throughout their lifetime (15). Also, although maize is a major host, this pest colonizes >200 host plants including green beans, potato, and numerous weed species common to the Midwest region (3).

Surveys of O. nubilalis populations have extended from the initial documented invasion of the pest into the midwestern United States in the 1940s through the commercial adoption of Bt maize during the period 1996 to 2009. Surveys have included statewide annual fall surveys (16) for diapausing larvae in Minnesota, Illinois, and Wisconsin, and less extensive summer trapping for adult moths with light traps (17, 18) in Illinois, Minnesota, Nebraska, and Iowa. These states have experienced a range of Bt maize adoption since 1996, including high levels in Minnesota, Nebraska, and Iowa, moderate levels in Illinois, and low levels in Wisconsin (Figs. 1 and 2) (18).
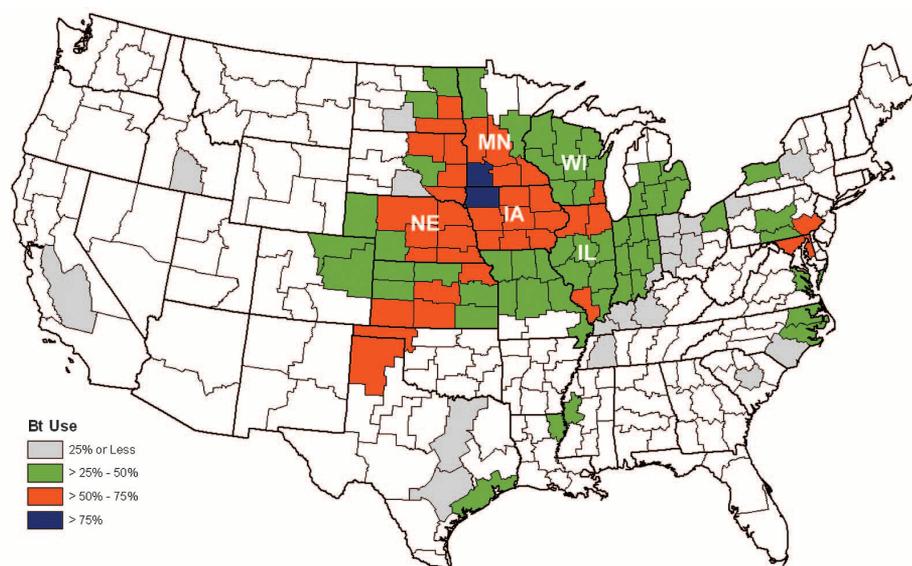
Historically, larval surveys have indicated that O. nubilalis populations have been episodic, characterized by ~6- to 8-year periodicity indicative of density-dependent population growth (7, 12). Much of the population cycling has been attributed to the pathogen Nosema pyrausta (12, 19). However, since commercialization of Bt maize, some periodicity has persisted (Fig. 2), but larval populations have declined relative to the pre-Bt era, particularly since 2002. These trends are evident in measures of larval abundance in non-Bt refuge fields alone, as well as in landscape-level means, for Bt- and non-Bt fields combined. Similar declines were found in measures of adult moth populations at eight locations in Minnesota, Illinois, Iowa, and Nebraska (18) (fig. S1).

To analyze the effects of Bt maize adoption on O. nubilalis populations, we estimated annual per capita growth rates (20) from fall larval surveys in non-Bt fields and analyzed them in relation to concurrent proportions of maize planted with Bt maize. Estimation also included antecedent larval densities in non-Bt fields, because O. nubilalis larval mortality increases with larval density (7, 12) and population growth more generally de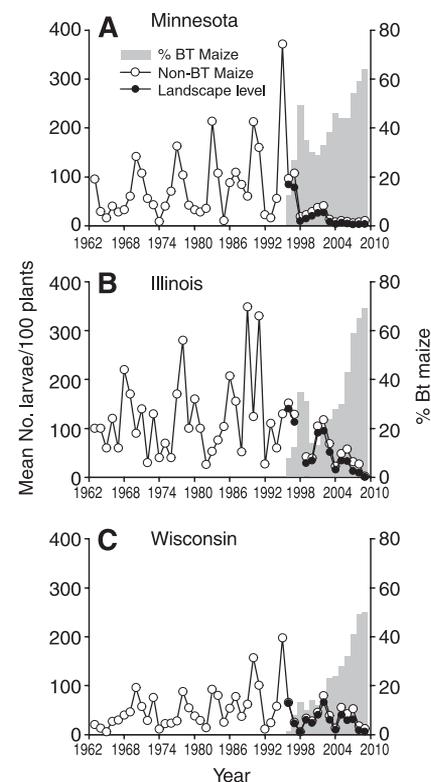pends inversely on density (21). Analysis used least-squares regression of growth rates in natural logarithm scale with three main effects: a state indicator variable to capture historical differences in mean densities among the three states, the natural logarithm of the antecedent larval density, and the proportion of Bt maize. Relative support for different models was evaluated with multimodel inference, with support weights based on the Bayesian information criterion, which balances reductions in residual sums of squares with numbers of parameters estimated (18, 22).

Relative support was greatest (82%) for the hypothesis that per capita growth rates differed among the three states, were inversely related to larval density, and were also inversely related to level of Bt maize adoption in each state (Table 1 and Fig. 3). The model with greatest support accounted for 38% of the variation in growth rates in non-Bt fields over all states and years combined. Models with just one or two of the three main effects and with interactions among the main effects had weak support (18) (table S2).

We used the fitted regression models to estimate mean densities for populations before and after adoption of Bt maize in each state (Table 1). Before Bt maize was adopted, the density in Minnesota was 59 larvae per 100 plants; from 1996 onward, when

Fig. 2. Statewide average numbers of O. nubilalis larvae per 100 plants over the period 1963 to 2009 in (**A**) Minnesota, (**B**) Illinois, and (**C**) Wisconsin. Minnesota data were adjusted to landscape means (Bt and non-Bt maize fields) for comparisons with Illinois and Wisconsin landscape means, based on proportion of non-Bt corn hectares (18). Illinois and Wisconsin landscape means were adjusted for non-Bt maize hectares planted in each state (18).

Fig. 1. Spatial distribution of maize containing one or more Bt traits for O. nubilalis control in 2006 in the United States. Bt maize data are from USDA crop reporting districts reporting >40,470 ha of maize, including the five states represented in this analysis (IL, Illinois; MN, Minnesota; WI, Wisconsin; IA, Iowa; NE, Nebraska). Areas in white had negligible maize hectares. Data are based on addresses of customer or retail outlet seed sales accounts, which may not accurately indicate cropping districts in which seed was ultimately planted. [©2008 Agricultural Biotechnology Stewardship Technical Committee]

Table 1. Regression statistics and estimated mean densities of *O. nubilalis* larvae per 100 plants before adoption of Bt maize in three midwestern states, and in non-Bt fields for 14 years (1996 to 2009) after adoption of Bt maize. Coefficients for the regression model for per capita growth rate, $r = \ln(N_t/N_{t-1})$, are b_0 for intercept, b_1 for regressor $D = \ln(N_{t-1})$, and b_2 for regressor $PBt = $ Bt maize proportion of crop.

Analysis*	State	n	R^2	Model coefficients			Pre-Bt density†		Avg. PBt	Bt-era density	
				b_0 (±SE)	b_1 (±SE)	b_2 (±SE)	Mean	CI		Mean	CI
By state	Minnesota	46	0.35	2.75 (0.56)	−0.67 (0.13)	−2.20 (0.67)	59	40–88	0.40	16	9–29
	Illinois	64	0.44	4.35 (0.64)	−0.93 (0.14)	−2.98 (0.60)	105	87–128	0.32	38	26–56
	Wisconsin	67	0.37	2.82 (0.45)	−0.76 (0.12)	−1.10 (0.76)	40	31–51	0.23	29	19–44
Combined	Minnesota	—	—	3.07 (0.15)	—	—	57	44–75	0.40	18	11–27
	Illinois	177	0.38	3.51 (0.35)	−0.76 (0.07)	−2.23 (0.37)	103	80–131	0.32	40	28–57
	Wisconsin	—	—	2.85 (0.14)	—	—	43	32–58	0.23	22	15–31

*Model fit to data from individual states separately, $r = b_0 + b_1D + b_2PBt$, or to the three states combined, but with differences among states reflected by state-specific intercepts. †Mean densities of larvae were estimated by setting $r = 0$ and solving for $N^* = \exp[-(b_0 + b_2PBt)/b_1]$ (see Fig. 3). Mean for pre-Bt era used $PBt = 0$; Bt era used 14-year average PBt. Confidence intervals (95% CIs) were estimated with the delta method (*18*) in log scale and then back-transformed to arithmetic scale.
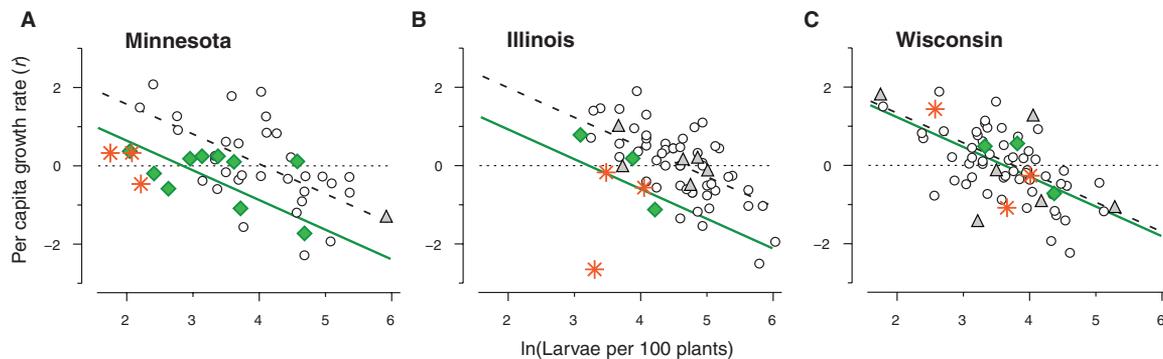
Fig. 3. Effects of Bt maize adoption on relation between larval density and annual per capita growth rates of *O. nubilalis* larval populations in non-Bt maize in three U.S. states: (**A**) Minnesota, (**B**) Illinois, (**C**) Wisconsin. Symbols indicate level of Bt maize adoption: open circles, pre-Bt years; gray triangles, 1 to 25%; green diamonds, 26 to 50%; orange asterisks, >51%. Bold dashed black line is least-squares fit for main-effects model, states combined, with $PBt = 0$; green line is same with PBt equal to respective statewide 14-year average (Table 1). Intersections between dotted lines at $r = 0$ and bold dashed lines indicate estimated mean density before adoption of Bt maize, and intersections with green solid lines show extent to which density declined with adoption of Bt maize in each state (Table 1).

the proportion of maize planted to Bt averaged 0.40 (i.e., 40% adoption), mean density declined by ~73% to ~16 larvae per 100 plants. In Illinois and Wisconsin, where respective average Bt adoption levels were 32% and 23%, mean densities were reduced by ~64% and ~27%, respectively. Similar reductions in estimated mean densities were observed when data from all three states were analyzed together (Table 1) and when landscape-level means from Bt fields and non-Bt fields were analyzed (*18*) (table S3 and fig. S2). Although many factors are known to affect *O. nubilalis* population dynamics, including weather and natural enemies (*3, 12, 16, 19*), these results indicate that reductions in *O. nubilalis* were associated with commercialization of Bt maize.

Of the five states analyzed, Iowa, Illinois, Nebraska, and Minnesota are the top four maize-producing states in the United States, with yields in 2009 valued at $27.1 billion (*18*) (tables S1 and S4). Combining analysis of the larval and moth data with annual USDA data for maize yield, price, and planted area, we estimated the annual benefits from 1996 to 2009 for both Bt- and non-Bt maize growers in each state (*18*). Direct benefits for Bt maize growers were calculated as the value of the yield gain for Bt maize relative to non-Bt maize, minus the additional cost for Bt maize seed (*18*) (tables S4 and S5). Suppression benefits for non-Bt maize growers

were calculated as the value of avoided yield losses under the assumption that the *O. nubilalis* populations in each state would have remained at their respective historical averages if Bt maize had not been commercialized. What actual *O. nubilalis* populations would have actually been without commercialization of Bt maize cannot be determined. However, midwestern farmers expected continual problems, as 67% of midwestern farmers reported in 1997 that *O. nubilalis* was a consistent problem in their fields (*10*). Mean yield losses for our analysis were calculated on the basis of *O. nubilalis* population densities and estimated models of larval stalk tunneling and associated yield loss (*23, 24*). Calculations used observed statewide survey densities for Illinois, Minnesota, and Wisconsin. For Iowa and Nebraska, observed average larval densities collected at research plots at locations around the state were used when available (1997, 2000, 2001, and 2002); otherwise, larval densities were estimated from historical averages at a few locations and the observed proportional larval decline in Minnesota, a state with Bt maize adoption rates similar to Iowa and Nebraska (*18*) (Fig. 1, table S1, and supplemental documentation file). Given the different nature of these larval data, loss estimates for Iowa and Nebraska are reported separately.

On the basis of these calculations, we estimate that cumulative benefits for both Bt and non-Bt

maize growers during the past 14 years were almost $6.9 billion in the five-state region (18.7 million ha in 2009)—more than $3.2 billion in Illinois, Minnesota, and Wisconsin, and $3.6 billion in Iowa and Nebraska (Fig. 4). Of this $6.9 billion total, cumulative suppression benefits to non-Bt maize growers resulting from *O. nubilalis* population suppression in non-Bt maize exceeded $4.3 billion—more than $2.4 billion in Illinois, Minnesota, and Wisconsin, and $1.9 billion in Iowa and Nebraska—or about 63% of the total benefits. Direct benefits for Bt maize growers (Fig. 4, A and B) were reduced because of the additional cost for Bt seed over the 14 growing seasons, which we estimate to have a cumulative value of almost $1.7 billion, whereas non-Bt maize experienced lower *O. nubilalis* damage as a result of areawide suppression at no additional cost.

In Illinois, Minnesota, and Wisconsin, suppression benefits for non-Bt maize growers (Fig. 4C) were initially larger (albeit dominated by Illinois and Minnesota) but more quickly exceeded the direct benefits for Bt maize, because population suppression occurred more rapidly than in Iowa and Nebraska (Fig. 4D). In Iowa and Nebraska, total grower benefits were larger because initial long-term population densities were greater. From 2007 onward, cumulative benefits for non-Bt maize growers exceeded benefits for Bt maize growers because suppression had become more effective.
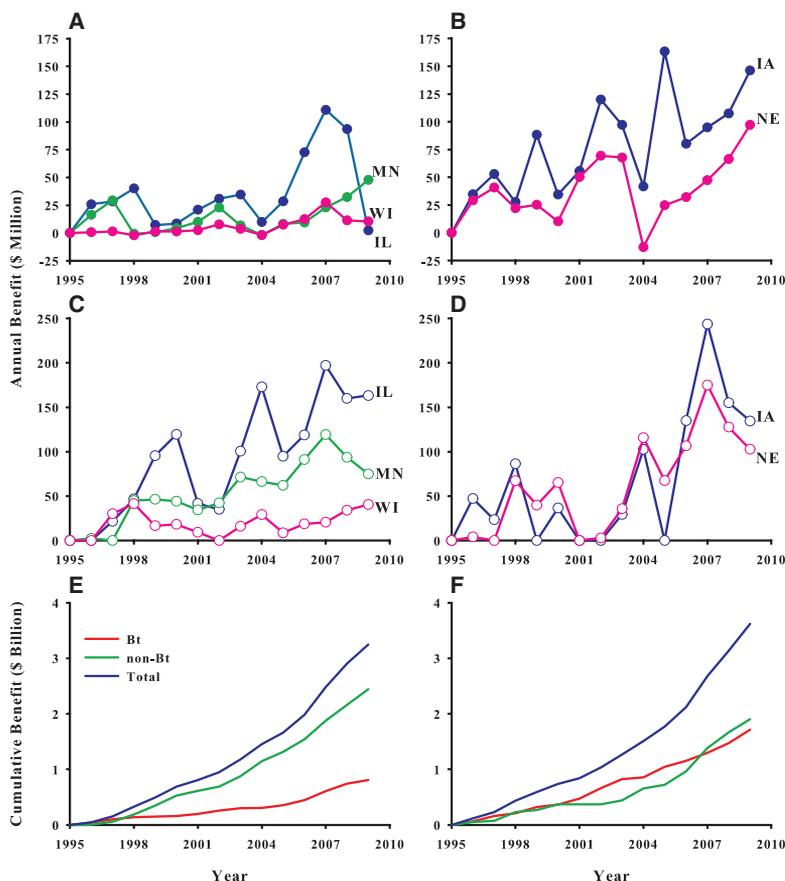
Fig. 4. (**A** and **B**) Annual benefits for Bt maize hectares, by state. (**C** and **D**) Annual pest suppression benefits for non-Bt hectares, by state. (**E** and **F**) Cumulative benefits across states. Benefits are expressed in 2009 dollars.

These benefit estimates do not incorporate effects of price changes and shifts in planted area that would have resulted without commercialization of Bt maize. Nevertheless, the calculations serve to indicate the potential magnitude of maize supply increase, and its market value resulting from area-wide suppression of *O. nubilalis* in these five states.

Regional reductions in the pink bollworm (*Pectinophora gossypiella*), which is fairly specialized to cotton (near-monophagous), have been reported from the use of Bt cotton in the United States (*25*). Also, areawide suppression of the polyphagous lepidopteran pest *Helicoverpa armigera* by Bt cotton in China has been reported (*26*). Reductions in *O. nubilalis* populations related to Bt maize have also been reported in other parts of the United States (*27*). We show here that pest suppression is directly associated with the use of transgenic maize. In addition, our findings indicate that economic benefits accrue not only to farmers planting Bt maize, but also to those planting non-Bt maize as a result of areawide pest suppression, and that these suppression benefits can equal or exceed the benefits to Bt maize growers.

These results highlight the need to account for economic benefits of pest suppression for non-Bt maize, as well as for direct economic benefits of Bt maize (*28*). Moreover, as *O. nubilalis* is highly poly-phagous, the observed regional population declines suggest that traditional and organic farmers growing other crops might also benefit (*29*). Sustained economic and environmental benefits of this technology, however, will depend on continued stewardship by producers to maintain non-Bt maize refugia (*5, 7–10*) to minimize the risk of evolution of Bt resistance in crop pest species, and also on the dynamics of Bt resistance evolution at low pest densities and for variable pest phenotypes (*30, 31*).

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