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The maize low-lignin mutant F2bm3 shows pleiotropic effects on photosynthetic and cell wall metabolisms in response to chilling

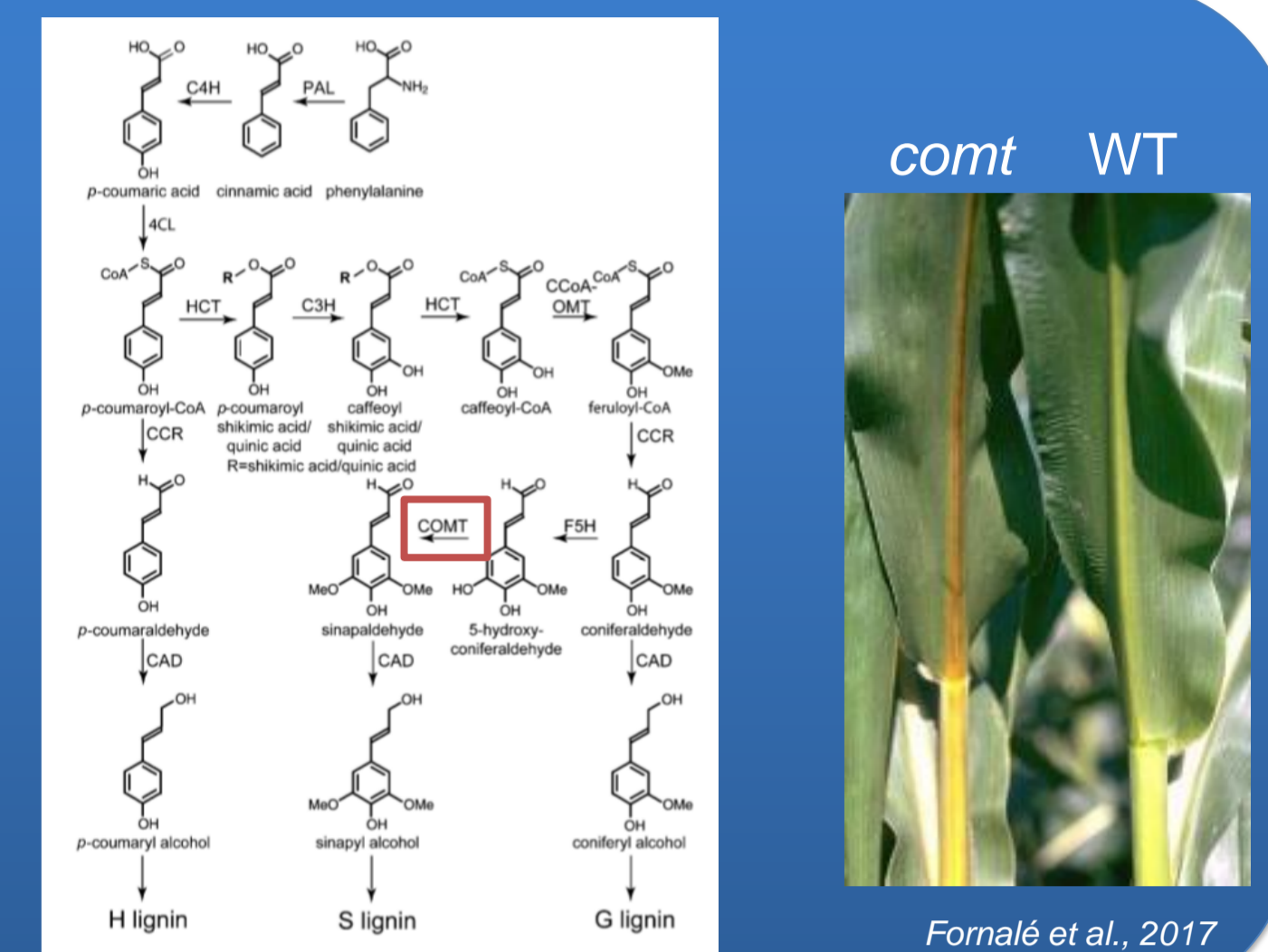
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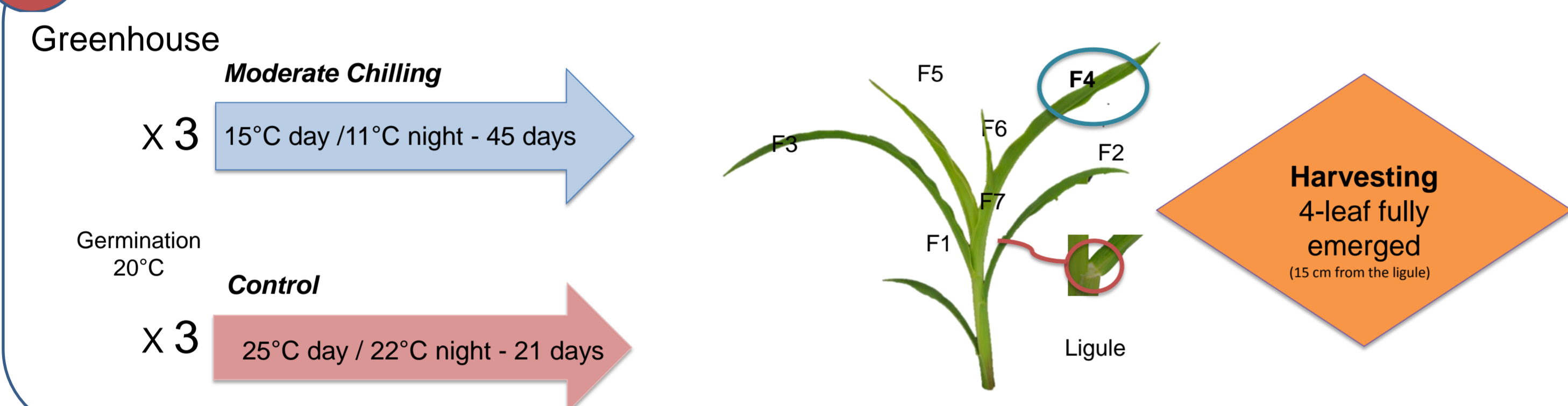
Introduction

Maize (*Zea mays* L.) is one of the major crops in the world and is highly sensitive to low temperature due to its tropical origin. Chilling may particularly affect maize during early seedling growth by altering physiological processes including photosynthesis and cell wall properties, leading to biomass reduction. Changes in photosynthetic and cell wall metabolisms were investigated during a long chilling exposure in a low-lignin maize mutant, *brown midrib3* (*bm3*), which contains a null-mutation in the gene encoding caffeic acid O-methyltransferase (*COMT*). Wild-type F2 plants and the near-isogenic F2*bm3* mutant were grown during 60 days with a day/night temperature regime of 15°C/11°C in a greenhouse. Photosynthetic pigments, cell wall sugars, lignin, cell wall bound hydroxycinnamic acids (HCA) contents were determined when the 4th leaf had fully emerged.

Does *COMT* mutation compensate or increase deleterious chilling effects on growth or development ?



1 Experimental growth conditions



4 Chlorophyll and zeaxanthin pigments are more abundant in F2bm3 than in F2 under chilling exposure

Some photosynthetic pigments content in F2 and F2bm3 leaves

Pigment	25°C/22°C		15°C/11°C		25°C/22°C		15°C/11°C	
	F2		F2		F2bm3		F2bm3	
	SD		SD		SD		SD	
Chl a (μmol.g ⁻¹ FW)	2.77 ± 0.19	b	2.47 ± 0.13	b	6.23 ± 0.12	a	5.95 ± 0.16	a
Chl b (μmol.g ⁻¹ FW)	0.78 ± 0.11	b	0.74 ± 0.12	b	0.93 ± 0.05	a	0.67 ± 0.10	b
Chl a+b (μmol.g ⁻¹ FW)	3.55 ± 0.30	b	3.21 ± 0.13	b	7.16 ± 0.14	a	6.62 ± 0.22	a
Chl a/b	3.58 ± 0.29	c	3.41 ± 0.73	c	6.72 ± 0.38	b	9.04 ± 1.19	a
Zeaxanthin (μmol.g ⁻¹ FW)	0.003 ± 0.000	c	0.015 ± 0.002	b	0.002 ± 0.001	c	0.070 ± 0.001	a
Carotenoid /Chl a+b	0.56 ± 0.05	a	0.60 ± 0.10	a	0.25 ± 0.02	b	0.24 ± 0.02	b

Data are means ±SD (n=16). Differences were statistically analyzed using Student's t-test. Different letters indicate significant differences between groups (P < 0.05).

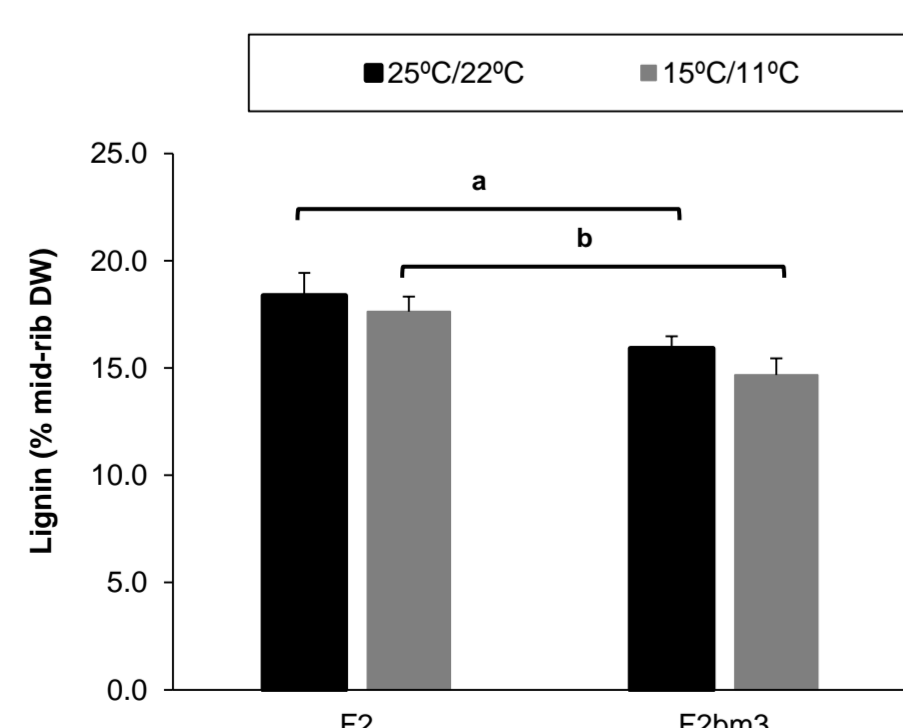
6 Chilling increases hydroxycinnamic acids in F2bm3

Cell wall hydroxycinnamates content in F2 and F2bm3 leaves

Genotype	25°C/22°C		15°C/11°C		25°C/22°C		15°C/11°C	
	F2		F2		F2bm3		F2bm3	
	SD		SD		SD		SD	
FA (Ester) (mg.g ⁻¹ DW)	0.13 ± 0.07	b	0.36 ± 0.09	a	0.24 ± 0.13	b	0.41 ± 0.05	a
FA ester /Ara	9.63 ± 5.86	a	12.89 ± 1.47	a	15.18 ± 8.53	a	14.93 ± 0.84	a
FA (Ether) (mg.g ⁻¹ DW)	0.14 ± 0.05	b	0.13 ± 0.04	b	0.18 ± 0.02	b	0.28 ± 0.08	a
TOTAL FA (mg.g ⁻¹ DW)	0.27 ± 0.12	b	0.49 ± 0.08	b	0.41 ± 0.13	b	0.70 ± 0.10	a
pCA (Ester) (mg.g ⁻¹ DW)	0.66 ± 0.09	a	0.36 ± 0.03	b	0.34 ± 0.06	b	0.40 ± 0.08	b
pCA (Ether) (mg.g ⁻¹ DW)	0.48 ± 0.06	a	0.25 ± 0.15	b	0.26 ± 0.03	b	0.23 ± 0.06	b
TOTAL pCA (mg.g ⁻¹ DW)	1.14 ± 0.11	a	0.60 ± 0.37	b	0.60 ± 0.08	b	0.63 ± 0.13	b
TOTAL FA + pCA (mg.g ⁻¹ DW)	1.43 ± 0.21	a	1.09 ± 0.45	b	1.02 ± 0.21	b	1.32 ± 0.23	a
pCA/FA	4.88 ± 2.45	a	1.18 ± 0.59	b	1.60 ± 0.65	b	0.92 ± 0.28	b

Data are means ±SD (n=16). Differences were statistically analyzed using Student's t-test. Different letters indicate significant differences between groups (P < 0.05), ferulic acid (FA), p-coumaric acid (pCA), arabinose (Ara).

7 Chilling does not change lignin content but H-residues increases while a reduction in S- and G-units is observed in F2bm3



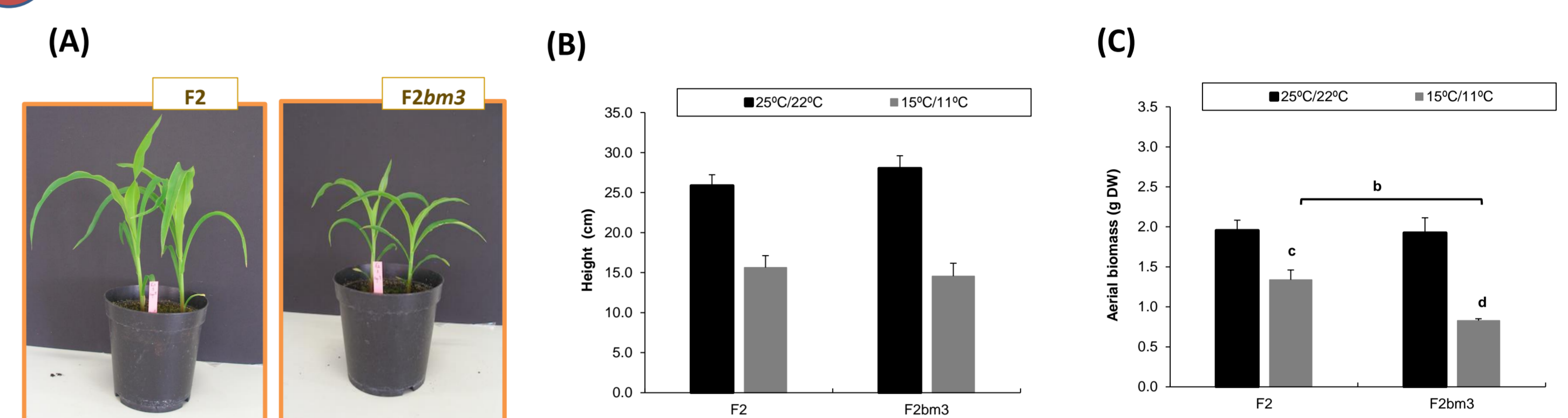
Lignin content using acetyl bromide method

Data are means ±SD (n=16). Differences were statistically analyzed using Student's t-test. Letters denote differences at P<0.05, a between F2 and F2bm3 with a day/night temperature regime of 25°C/22°C, b between F2 and F2bm3 with a day/night temperature regime of 15°C/11°C, c and d between temperatures for each genotype. Black columns represents the experiment under ambient temperature condition and grey columns under chilling exposure.

Identification of H, S and G phenylpropanoid units (%) by thioacydolytic in F2 and F2bm3 leaves.

Genotype	25°C/22°C		15°C/11°C		Genotype	25°C/22°C		15°C/11°C	
	F2		F2			F2bm3		F2bm3	
	SD		SD			SD		SD	
H	7.00 ± 0.06		2.00 ± 0.03		H	0.00 ± 0.00		14.00 ± 0.03	
G	64.00 ± 0.12		59.00 ± 0.02		G	82.00 ± 0.13		73.00 ± 0.07	
S	29.00 ± 0.06		39.00 ± 0.04		S	18.00 ± 0.13		13.00 ± 0.04	

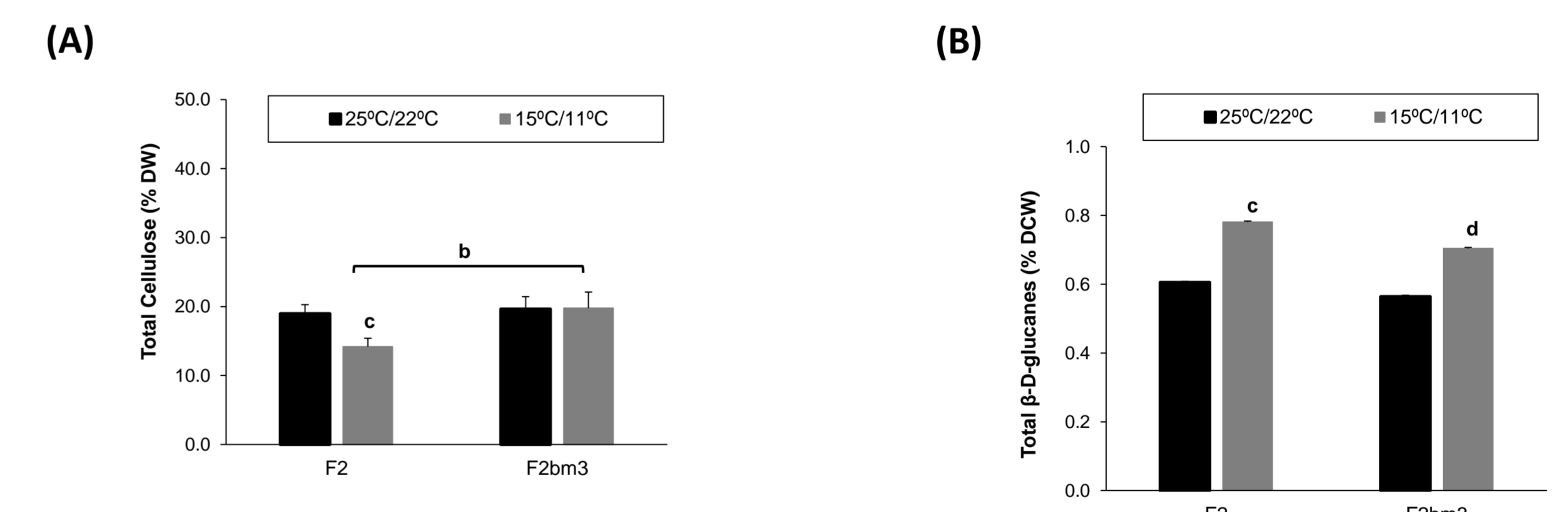
3 A long chilling treatment affects plant growth and development



Chilling effects on plant growth and biomass in the lignin maize deficient mutant F2bm3 and the normal F2 line. (A) Phenotype of F2 and F2bm3 after 45 days of chilling stress. (B) Plant height under ambient growth condition (black bar) and chilling stress (grey bar). (C) The average of aerial biomass (Dry Weight) after 45 days of chilling stress with a day/night temperature regime of 15°C/11°C.

Data are means ±SD (n=8). Differences were statistically analyzed using Student's t-test. Letters denote differences at P<0.05, a between F2 and F2bm3 at 25°C/22°C, b between F2 and F2bm3 at 15°C/11°C, c and d between temperatures for each genotype.

5 Chilling changes the cell wall sugars composition in both F2 and F2bm3 lines



(A) Cellulose and (B) (1→3),(1→4)-β-D-glucan content in F2 and F2bm3 leaves under ambient temperature (black bar) and chilling (grey bar).

Data are means ±SD (n=16). Differences were statistically analyzed using Student's t-test. Letters denote differences at P<0.05, a between F2 and F2bm3 with a day/night temperature regime of 25°C/22°C, b between F2 and F2bm3 with a day/night temperature regime of 15°C/11°C, c and d between temperatures for each genotype.

Non-cellulosic sugars content in F2 and F2bm3 leaves

Genotype	25°C/22°C		15°C/11°C		25°C/22°C		15°C/11°C	
	F2		F2		F2bm3		F2bm3	
	% mole	SD	% mole	SD	% mole	SD	% mole	SD
Polysaccharide								
Rha	0.73 ± 0.24	a	0.77 ± 0.32	a	0.71 ± 0.07	a	0.76 ± 0.43	a
Ara	14.68 ± 3.55	b	27.35 ± 4.30	a	15.77 ± 1.09	b	27.67 ± 3.78	a
Gal	2.84 ± 1.13	b	4.27 ± 1.28	a	3.15 ± 0.54	b	4.08 ± 1.02	a
Glc	12.00 ± 3.79	a	14.50 ± 2.59	a	10.94 ± 3.23	a	13.65 ± 2.50	a
GalUA	2.22 ± 0.46	a	3.07 ± 0.95	a	2.64 ± 0.47	a	2.85 ± 0.88	a
GlcUA	1.31 ± 0.20	a	1.42 ± 0.40	a	1.21 ± 0.21	a	1.39 ± 0.39	a
Xyl	66.23 ± 7.57	a	48.62 ± 7.09	b	65.57 ± 3.90	a	49.58 ± 7.18	b
Ara + Xyl	80.91 ± 4.88	a	75.97 ± 4.77	a	81.34 ± 3.71	a	77.25 ± 4.67	a
Ara / Xyl	0.23 ± 0.08	b	0.58 ± 0.17	a	0.24 ± 0.03	b	0.57 ± 0.13	a

Data are means ±SD (n=16). Differences were statistically analyzed using Student's t-test. Different letters indicate significant differences between groups (P < 0.05). Rhamnose (Rha), arabinose (Ara), galactose (Gal), glucose (Glc), galacturonic acid (GalUA), glucuronic acid (GlcUA), Xylose (Xyl).

Conclusion

- The increase in arabinose substitution on the xylan backbone and the abundance of HCA in the F2bm3 mutant could reinforce the cell wall and maintain the hydration status of the cell wall during chilling.
- The reduction in G-residues in F2bm3 may be due to a greater demand in ferulic acids as photoprotectant under chilling.
- Therefore, the F2bm3 displays photosynthesis and cell wall traits that might be useful to cope with early sowing stress.

