Restriction of cytosolic sucrose hydrolysis profoundly alters development, metabolism and gene expression in Arabidopsis roots

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Supplementary Data

Tables S1-S4
Figures S1-S6

Tables S5-S11 are in a separate Excel spreadsheet
Table S1. Primers used in this study.

| AGI Number | Primers |
|------------|---------|
| **q-PCR primers:** | |
| CINV1 AT1G35580 | F AAATCCGCGTCTTCACCGAGACTG R AAGCTACCTTCCGAGCTTACCG |
| CINV2 AT4G09510 | F TGGCGAGTGGTTACCGGTTTGGT R TCAGCGTCACGGCAATCTG |
| SWEET3 AT5G53190 | F GGTCTTTCCGGAACAATCAATGGG R CAACAGAGAGTCCGTTTTG |
| SWEET11 AT3G48740 | F TTGCGCTGTTTCTATCTCCTGTC R ACTGAAGAGCGCACAACATAG |
| SWEET12 AT5G23660 | F CTTCTTTCTTTGCTGATGGG R CAAGAGCTTCACCGTTACCT |
| GRF1 AT2G22840 | F TCGGGGGAGTACTAAACAGCAC R TTGCAAGACGGGCTGTTAGAG |
| GRF4 AT3G52910 | F ATCAACACCTTCTTTGCTATTGGG R TGCCGTCAGTCTTACCTC |
| GRF6 AT2G06200 | F CTCCCCACTTTCTCCACAGTTTG R TCTACATCTTGGCTTACCT |
| TPPH AT4G39770 | F GAGACTAGCCGGCTTTTCTTACAGATG R ACGTTGGAAGACTCCAAAC |
| SUC2 AT1G22710 | F TAGCCATTGTCGTCCTAAGAGG R ACCACGAGTAGGGATTCGATG |
| NCED5 AT1G30100 | F ACGCGGTCTCGGAACATAGGAAGG R TCACAGAAGGTGGGCTGGAAAC |
| PCNA AT1G07370 | F CGGTAAGCAGGGAACCGTAAAC R TCACAAATTCCCTCCGGGCA |
| PIN4 AT2G01420 | F ACAAGCGGGCAACAGAACTACG R GCGTGAATCTACCAACCAAC |
| RPL5 AT2G07725 | F AACAGGAGGATAGGAGGAGGTACG R TTGGCGTGGATTGGAG |
| EXP-A AT2G03090 | F GCATTGTGCAGTAAAAGCGTGTTG R CTTCTCAACGGGACCCCTTTC |
| ATGLR2 AT2G24710 | F TGGGTCGAGTGATTGGGAGACTC R TCCAAAACGGCATCATAATCC |
| WOX5 AT3G11260 | F TTTGAAGACTCCAACTCCAAGG R GCCGTAATCTACCAACCAAC |
| WOX4 AT1G46480 | F ACGACCACTTGCTGTTCCTTAATCCG R CTCCGTCTTTCCACCAACGAGAGG |
| Gene  | Accession | Forward | Reverse |
|-------|-----------|---------|---------|
| PIN5  | AT5G16530 | ATGGCCATCGGCTCTATTGTCCCAG | AGCAGCCTGAATGATGGCTACG |
| FAF1  | AT4G02810 | TGGCCAAGCTTACACATCTCTTCCCAG | AGAAACTCATCCACCCACGTAC |
| FAF4  | AT3G06020 | TAATGATGAGCCACAGACCTCTCCAG | TCTGACACAGCCATTGCTTCGG |
| SMP1  | AT1G65660 | AGAGGCTGCCCTTGATCTGATG | TTCAACCTTTTGGGCTCTCTTTC |
| SMP2  | AT4G37120 | CTCAAGTCTGATGGCTACG | AGAAACTCCATCCACCCACGTC |
| RGF1  | AT5G60810 | TGGCCAAGCTTACCAACATCTTCCAG | AGCATGCTTTGGCAATTTTGG |
| ANT   | AT4G37750 | TAATGATGAGGCTGCCCTTGATG | TCTGACACAGCCATTGCTTCGG |
| LOG2  | AT2G35990 | AGAGGCTGCCCTTGATCTGATG | TTCAACCTTTTGGGCTCTCTTTC |
| MAP65 | AT1G14690 | TGGCCAAGCTTACCAACATCTTCCAG | AGCATGCTTTGGCAATTTTGG |
| KAN3  | AT4G17695 | TAATGATGAGGCTGCCCTTGATG | TCTGACACAGCCATTGCTTCGG |
| BEL1  | AT5G41410 | TAATGATGAGGCTGCCCTTGATG | TCTGACACAGCCATTGCTTCGG |
| HB32  | AT1G14687 | TAATGATGAGGCTGCCCTTGATG | TCTGACACAGCCATTGCTTCGG |
| HB53  | AT5G66700 | TAATGATGAGGCTGCCCTTGATG | TCTGACACAGCCATTGCTTCGG |
| NEK5  | AT3G20860 | TAATGATGAGGCTGCCCTTGATG | TCTGACACAGCCATTGCTTCGG |
| NEK6  | AT3G44200 | TAATGATGAGGCTGCCCTTGATG | TCTGACACAGCCATTGCTTCGG |
| MATE  | AT2G04070 | TAATGATGAGGCTGCCCTTGATG | TCTGACACAGCCATTGCTTCGG |
| CPK22 | AT4G04710 | TAATGATGAGGCTGCCCTTGATG | TCTGACACAGCCATTGCTTCGG |
| BGLU28| AT2G44460 | TAATGATGAGGCTGCCCTTGATG | TCTGACACAGCCATTGCTTCGG |
| DOT2  | AT5G16780 | TAATGATGAGGCTGCCCTTGATG | TCTGACACAGCCATTGCTTCGG |
| SUS6  | AT1G73370 | TAATGATGAGGCTGCCCTTGATG | TCTGACACAGCCATTGCTTCGG |
| HSP70 | AT3G12580 | TAATGATGAGGCTGCCCTTGATG | TCTGACACAGCCATTGCTTCGG |
| Gene   | Accession | Forward Sequence                                                                 | Reverse Sequence                                                                 |
|--------|-----------|----------------------------------------------------------------------------------|----------------------------------------------------------------------------------|
| NAC071 | AT4G17980 | F AAGTTGCTTCTGAGTGCTTTCCC                                                        | R AAATCCACAGTGTTGGTTGTTGCC                                                       |
| INVD   | AT1G22650 | F GCTGCATGCATAAAGACGGG                                                           | R GATTTCCTGCTACTGCTCCG                                                           |
| INVH   | AT3G05820 | F GGTCTTACACAAATGGTGTCGTC                                                       | R GAGCCCTCTCCTCGGAAGGT                                                          |
| INVC   | AT3G06500 | F CCAACTCTCTCTCTGGGACTTCA                                                      | R GGCCACTCATCTCTCTTTCCAGG                                                        |
| INVB   | AT4G34860 | F AATGGGAGGATCGTGAGGTCG                                                          | R CCTTATGAAAGCTAGGCTCTG                                                         |
| INVA   | AT1G56560 | F TGCGGAAAGCCAGAGCTGTAACG                                                        | R GGCAGAGACTGCTTTCCAATG                                                          |
| INVE   | AT5G22510 | F CAACCTCTGTATGCTGACGTCG                                                         | R CGTACTGTCGCGCCATTTCG                                                         |
| CWINV1 | AT3G13790 | F GTTGGTGCTCATGTGCTGACC                                                          | R TGGAGGATAGTGTTGCTGAGG                                                          |
| CWINV6 | AT5G11920 | F GTTATTCGTCGCGGTAACGG                                                         | R AGGATGCTCCATGCGGAAAGGA                                                      |
| VINV2  | AT1G12240 | F GAAGCATTCGCAAGGTTGG                                                           | R CGTAAACCGTCGCAATCAAGA                                                          |
| VINV1  | AT1G62660 | F GAAGGATTGCGACAGGTTGG                                                          | R GTAACGGTCGCGATCAAGG                                                          |
| 18S    | AT2G01010 | F GGTACGTGCTACTCGGATAACC                                                         | R TCTCCGGGAATCGAAACCTA                                                          |
| SUS1   | AT5G20830 | F TACCGACTTCGCCACCTTGC                                                          | R TCAGCAGCTCCTCACCAGT                                                          |
| SUS2   | AT5G49190 | F TGACTTTGCTCACTCCCAACG                                                          | R CCTGGCTGGATGATGATGGGTG                                                          |
| SUS3   | AT4G02280 | F CGAGGCTTTTGGACTTACGG                                                         | R TCGATGTGGAAACCGAGAG                                                          |
| SUS4   | AT3G43190 | F GCTATGACCTGTTGGTTACCAG                                                        | R CAGCTGCCCTTGTGACCATG                                                          |
| SUS5   | AT5G37180 | F GGTTCACATTGACCCAGG                                                           | R GCGTTGATGCCCTTACCTCAG                                                          |
| SUS6   | AT1G73370 | F AGAAGGCTTTGCTTGCACTG                                                         | R TCCCTGCTAGTTGTTGCTCAG                                                          |

**Cloning primers:**

AT1G35580g-attB1

GGGGACAAAGTTTTGTACAAAAAAGCAGGCTAT
GTAGTATGATGCAAGATTGACGAATC
AT1G35580-g-attB2  GGGGACCACTTTGTACAAGAAAGCTGGGTC
AT4G09510-g-attB1  GGGGACAAAGTTTGTACAAAAAAGCAGGCTAT
AT4G09510-attB2  GGGGACCACTTTGTACAAGAAAGCTGGGTC
AT4G34860-attB1  GGGGACAAAGTTTGTACAAAAAAGCAGGCTAT
AT4G34860-attB2  GGGGACCACTTTGTACAAGAAAGCTGGGTC
AT1G22650-attB1  GGGGACAAAGTTTGTACAAAAAAGCAGGCTAT
AT1G22650-attB2  GGGGACCACTTTGTACAAGAAAGCTGGGTC
AT1G72000-attB1  GGGGACAAAGTTTGTACAAAAAAGCAGGCTAT
AT1G72000-attB2  GGGGACCACTTTGTACAAGAAAGCTGGGTC

Genotyping primers:
SALK_095807_LP (At1g35580)  TATTGAATTTGAGTGGAGGC
SALK_095807_LP (At1g35580)  TGTAGACTGGCATAAGACAG
SAIL_518_D02_LP (At4g09510)  ACCTTCTCCATTTTTGTTTTAATG
SAIL_518_D02_RP (At4g09510)  ACCAGACTAAACAGCTTTACCAGTCC
SALK_131881_LP (At1g72000)  ACGTGGATCTTGTGTTTGTC
SALK_131881_RP (At1g72000)  TTTTGCATCGAACTTTGGAC
WiscDsLox466C11_LP (At1g22650)  TTTTTTCATCCTCCTTGTGGAAG
WiscDsLox466C11_RP (At1g22650)  CTTTTGGATCTAAGGCGTG
SALK_097137_LP (At4g34860)  GCCTCACCACCATAGGATG
SALK_097137_RP (At4g34860)  CGTTCGCTCTCTCTCTCTCG
Table S2. Transcript levels for cytosolic invertases in roots\(^a\)

| Tissue                                      | CINV1 At1g35580 | CINV2 At4g09510 | INVB At4g34860 | INVD At1g22650 | INVF At1g72000 |
|---------------------------------------------|-----------------|-----------------|----------------|----------------|----------------|
| longitudinal zone 1 \(^b\)                 | 544 ± 0 \(^c\)  | 41 ± 2          | 84 ± 17        | 10 ± 1         | 10 ± 7         |
| longitudinal zone 2                         | 753 ± 40        | 37 ± 2          | 158 ± 5        | 12 ± 4         | 5 ± 0          |
| longitudinal zone 3                         | 581 ± 22        | 43 ± 0          | 122 ± 16       | 32 ± 3         | 6 ± 2          |
| longitudinal zone 4                         | 507 ± 31        | 37 ± 6          | 86 ± 4         | 18 ± 2         | 8 ± 3          |
| epidermis and lateral root cap              | 525 ± 63        | 46 ± 5          | 84 ± 3         | 7 ± 4          | 7 ± 2          |
| columella root cap                          | 924 ± 16        | 41 ± 9          | 113 ± 17       | 25 ± 2         | 8 ± 7          |
| cortex                                      | 1015 ± 129      | 52 ± 4          | 221 ± 9        | 15 ± 1         | 3 ± 1          |
| endodermis and quiescent center             | 627 ± 144       | 52 ± 9          | 102 ± 9        | 76 ± 11        | 2 ± 0          |
| stele                                       | 629 ± 53        | 72 ± 2          | 163 ± 32       | 18 ± 14        | 9 ± 2          |
| protophloem                                 | 367 ± 112       | 41 ± 6          | 97 ± 9         | 4 ± 2          | 4 ± 3          |
| whole root                                  | 864 ± 75        | 28 ± 4          | 92 ± 1         | 13 ± 3         | 1 ± 0          |

\(^a\)Data are from [www.bar.utoronto.ca](http://www.bar.utoronto.ca), extracted from Dinneny et al. (2008). Seedlings were grown for five days on 1x Murashige and Skoog salt mixture, 1% agar, 1% sucrose. Cell type or section-specific data were generated by fluorescence-activated cell sorting or sectioning of roots, followed by RNA extraction and microarray analysis.

\(^b\)Longitudinal zone 1 (~150 µm) is from the root tip to the point at which shape changes from conical to cylindrical. Zone 2 (~200 µm) is from the top of zone 1 to the top of the meristematic zone. Zone 3 (~200-300 µm) is from the top of zone 2 to the region where root hairs emerge. Zone 4 (1 mm) is the region above zone 3.

\(^c\)Values are GCOS expression signal, and are means ± SD of measurements on two or three biological replicates.
Table S3. Leaf area and stomatal density in wild-type and mutant shoots.

|                        | Wild-type | cinv1 | cinv2 |
|------------------------|-----------|-------|-------|
| Leaf area\(^a\,b\) (mm\(^2\)) | 339 ± 41  | 153 ± 34 |
| Stomata adaxial\(^a\,c\) (number mm\(^-2\)) | 86 ± 1   | 110 ± 1 |
| Stomatal abaxial\(^a\,c\) (number mm\(^-2\)) | 125 ± 2  | 144 ± 2 |

\(^a\)Leaf area and stomatal density were measured on fully-expanded leaf 6 of 35-day-old plants.
\(^b\)For leaf area, values are from measurements on eight plants ± SD. Wild-type and mutant values are statistically significantly different (Student’s T-test, P<0.0001).
\(^c\)For stomatal density, values are means ± SD of measurements on fully-expanded leaf 6 of eight plants per genotype. For each leaf, stomata were counted on ten images, each of 0.138 mm\(^2\) of leaf surface. Wild-type and mutant values are statistically significantly different for both adaxial and abaxial surfaces (Student’s T-test, P<0.01).
Table S4. Metabolite contents of wild-type and mutant shoots.

Plants were grown for 35 days on compost in 12-h photoperiods with a light intensity of 160 μmol quanta m$^{-2}$ s$^{-1}$.

|                     | Wild-type | cinv1  | cinv2  |
|---------------------|-----------|--------|--------|
| **Shoots end of day** |           |        |        |
| Glucose μmol g$^{-1}$ FW | 0.75 ± 0.14 | 2.59 ± 0.59***b |        |
| Fructose μmol g$^{-1}$ FW | 0.30 ± 0.05 | 0.80 ± 0.13*** |        |
| Sucrose μmol g$^{-1}$ FW | 2.02 ± 0.20 | 3.34 ± 0.19*** |        |
| Starch μmol g$^{-1}$ FW | 68.0 ± 5.2 | 90 ± 5.4* |        |
| **Shoots end of night** |           |        |        |
| Glucose μmol g$^{-1}$ FW | 0.17 ± 0.11 | 0.27 ± 0.18 |        |
| Fructose μmol g$^{-1}$ FW | 0.09 ± 0.12 | 0.10 ± 0.03 |        |
| Sucrose μmol g$^{-1}$ FW | 0.88 ± 0.20 | 2.34 ± 0.41** |        |
| Starch μmol g$^{-1}$ FW | 4.3 ± 0.4 | 39.6 ± 7.5* |        |
|                  | 0.031 ± 0.004 | 0.161 ± 0.022*** |
|------------------|---------------|-----------------|
| Trehalose 6P     | 0.031 ± 0.004 | 0.161 ± 0.022*** |
| Glucose 6P       | 78 ± 9        | 65 ± 17         |
| Glucose 1P       | 28.6 ± 5.5    | 26.8 ± 6.2      |
| Fructose 6P      | 18.1 ± 2.4    | 16.6 ± 3.8      |
| 3-PGA            | 38 ± 9        | 53 ± 24         |
| PEP              | 7.4 ± 1.9     | 8.5 ± 8.7       |
| Pyruvate         | 33 ± 2        | 38 ± 8          |
Figure S1

A

Log2 fold difference

CINV1  CINV2  A/N InvD  A/N InvB  SUS1  SUS2  SUS3  SUS4  SUS5  SUS6

B

cinv1  cinv2  wild-type

C

Dimension 1

-1.0  -0.5  0.0  0.5  1.0

Dimension 2

-1.0  -0.5  0.0  0.5  0.75  1.0

D

Grown without glucose

Grown with glucose
**Fig. S1.** Transcript levels for sucrose metabolizing enzymes in *cinv1 cinv2* roots, and validation of RNA-seq data. (A) Levels of transcripts of cytosolic INV and SUS in 14-day-old seedlings, measured by q-PCR. Values are expressed as log2 fold difference in transcript abundance in *cinv1 cinv2* relative to wild-type. Values are means of measurements on three independent biological replicates ± SD. There is essentially no difference between 14-day-old mutant and wild-type roots with respect to transcript levels for *SUS1*, *SUS2*, *SUS5* and *SUS6*, and only a modest elevation (≤1.6-fold) of transcripts for *SUS1*, *SUS4*, *A/N-InvB* and *A/N-InvD*. For four-day-old plants RNA-seq data (Supplementary Table S5) show that transcript levels for *SUS2*, *SUS4*, *A/N-InvB* and *A/N-InvD*, a vacuolar INV and two mitochondrial neutral INV were slightly reduced and transcript levels of *cwINV1* and of the phloem-specific protein *SUS6* were higher in mutant than in wild-type roots; (B) Photographs of four-day-old mutant and wild-type seedlings grown without glucose. All images are at the same magnification; (C) Multi-dimensional scaling plot visualizing the distance between the libraries in the RNA-seq experiment, based on the 500 tags with the largest variation between the four treatments. The distance between each pair of libraries is equivalent to the square root of the common dispersion between these two libraries. Libraries were from roots of four-day-old seedlings. Green symbols, wild-type grown without glucose; blue symbols, wild-type grown with 55 mM glucose; black symbols, *cinv1 cinv2* grown without glucose; red symbols, *cinv1 cinv2* grown with 55 mM glucose. For each genotype/treatment, the three points represent the three independent biological replicates (see Materials and Methods); (D) Validation of RNA-seq analysis. For 38 selected transcripts representing a wide range of different cellular functions (loci given in Supplementary Table S1 below), the graphs show log2 fold differences in transcript abundance in *cinv1 cinv2* relative to wild-type from qPCR measurements (blue diamonds) and RNA-seq (red squares: see Supplementary Table S5). For qPCR, values are means of measurements on three independent biological replicates. In all cases SD was less than 10% of the mean.
Fig. S2. Original, uncropped micrographs from which the composite Fig. 1D was assembled.
Figure S3

A

| Cytosol                      | Chloroplast                  | Mitochondria                |
|------------------------------|------------------------------|-----------------------------|
| At1g35580 (CINV1, A/N-InvG)  | At5g22510 (A/N-InvE)         | At1g56560 (A/N-InvA)        |
| At4g09510 (CINV2, A/N-InvI)  |                              | At3g05820 (A/N-InvH)        |
| At4g34860 (A/N-InvB)         |                              | At3g06500 (A/N-InvC)        |
| At1g22650 (A/N-InvD)         |                              |                             |
| At1g72000 (A/N-InvF)         |                              |                             |

B

C

| M | InvD-GFP | InvF-GFP | InvB-GFP | CINV2-GFP | GFP alone | At1g22650 (InvD) | At1g72000 (InvF) |
|---|-----------|-----------|-----------|------------|-----------|------------------|------------------|
|   | GFP alone | No infiltration |

D

| Col-0 WT | cinv1 cinv2 | At4g34860 | At1g72000 | At1g22650 |

E

| Wild-type | cinv1 cinv2 |

F

| Palisade wild-type | Palisade cinv1 cinv2 | Epidermis wild-type | Epidermis cinv1 cinv2 |

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100 μm
Fig. S3. Characterization of Arabidopsis neutral INV. (A) Cellular location of the neutral INVs, deduced from (B) and (for At1g35580, At5g25510, At1g56560, At3g05820 and At3g06500) from Vargas et al. (2008); Xiang et al. (2011); Martín et al. (2013); Battaglia et al. (2017); (B) Expression in Nicotiana benthamiana of INV-GFP translational fusions for isoforms without confirmed locations. Translational GFP fusions for 4 isoforms were transiently expressed. After 3 days, GFP fusion proteins were detected by immunoblotting SDS-PAGE gels of extracts of infiltrated regions with a commercial antiserum raised against GFP. Each lane contains extract from a single leaf, all lanes represent the same fresh weight of leaf. Lane M is molecular markers (kDa). Arrow indicates fusion proteins. Predicted masses (kDa) are: InvD-GFP 91; InvF-GFP 87; InvB-GFP 95; CINV2-GFP 94. Right lanes are transient expression of GFP alone, and an uninfiltrated region. (C) Confocal microscopy of intact leaves expressing the Inv-GFP fusion proteins shown in (B). Note that fluorescence is only in the cytosol. Control panels (left), a leaf expressing 35S::GFP (fluorescence in the cytosol and nucleus), and an uninfiltrated leaf. Images are all the same magnification, bar is 50 μm. (D) Seedling growth on vertical plates of wild-type and cinv1 cinv2 mutants, and T-DNA insertion mutants for InvB, InvD and InvF; (E) Wild-type and cinv1 cinv2 plants grown in soil for 35 days, 12-h photoperiods, light intensity 160 μmol quanta m⁻² s⁻¹; (F) Abaxial epidermis and palisade mesophyll cross-sections of mature leaf 6. Bars are 100 μm.

Battaglia ME, Martin MV, Lechner L, Martinez-Noël GMA, Salerno GL. 2017. The riddle of mitochondrial alkaline/neutral invertases: A novel Arabidopsis isoform mainly present in reproductive tissues and involved in root ROS production. PLoS ONE 12:e0185286

Martín ML, Lechner L, Zabaleta EJ, Salerno GL. 2013. A mitochondrial alkaline/neutral invertase isoform (A/N-InvC) functions in developmental energy-demanding processes in Arabidopsis. Planta 237, 813-822.

Vargas WA, Pontis HG, Salerno GL. 2008. New insights on sucrose metabolism: evidence for an active A/N-Inv in chloroplasts uncovers a novel component of the intracellular carbon trafficking. Planta 227, 795-807.

Xiang L, Le Roy K, Bolouri-Moghaddam MR, Vanhaeke M, Lammens W, Rolland F, Van den Ende W. 2011. Exploring the neutral invertase–oxidative stress defence connection in Arabidopsis thaliana. Journal of Experimental Botany 62, 3849-3862.
Figure S4

A 7-day-old roots
Wild-type  cinv1 cinv2

14-day-old roots
Wild-type  cinv1 cinv2
No NAA

0.05 µM NAA

0.2 µM NAA

1.0 µM NAA

B
Wild-type  cinv1 cinv2

1.0 µM NAA
Fig. S4. Effects of auxin on cinv1 cinv2 root elongation and developmental abnormalities. (A) Appearance of wild-type and cinv1 cinv2 seedlings grown on vertical agar plates for 7 or 14 days in the presence of different concentrations of 1-naphthaleneacetic acid (NAA); (B) Differentiation status of columella cells in 4-day-old wild-type and cinv1 cinv2 seedlings grown on 1 μM NAA. Roots were stained with propidium iodide. Arrows indicate columella stem cells.
Fig. S5. Functional characterisation of genes differentially expressed in mutant and wild-type roots (DEGs) into GO-slim Biological Processes. (A) Roots of four-day old seedlings grown without 55 mM glucose; (B) Roots of four-day old seedlings grown with 55 mM glucose. Orange bars are numbers of genes in each category with higher transcript levels in mutant than in wild-type roots. Blue bars are numbers of genes in each category with lower transcript levels in mutant than in wild-type roots. Red arrows indicate some categories in which more genes are up-regulated than down-regulated in the mutant; blue arrows indicate some categories in which more genes are down-regulated than up-regulated in the mutant.
Fig. S6. MAPMAN visualization of genes differentially expressed in mutant and wild-type roots whether or not glucose was supplied. (A) Metabolism-related genes; (B) Genes involved in regulation. Blue and red boxes represent genes with reduced and elevated expression respectively, in cinv1 cinv2 relative to wild-type roots.