

C1–MOLECULAR CELL BIOLOGY

Organised by J. Bryant for the Cell Biology Section

C1.1–The early mammalian embryo: a model for epithelial differentiation and environmental programming

Tom P. Fleming, Biological Sciences, University of Southampton, UK

During the first four days of mammalian development, a blastocyst is generated comprising an outer polarised epithelium (trophoblast; progenitor of placental lineages) and an inner cell mass (ICM; fetal progenitor). The trophoblast creates the blastocoel cavity by vectorial transport to control the microenvironment of the ICM and provide a reservoir of nutrients, energy substrates and other factors to support ICM future development. Trophoblast differentiation in mice occurs in a step-wise manner from the 8-cell stage when cell polarity and E-cadherin mediated adhesion initiate, and is complete by 32-cell stage (24 hrs later) when blastocoel cavitation begins. We have examined mechanisms of epithelial differentiation in this model, in particular maturation of multi-protein tight junctions required for sealing of the trophoblast layer and cavitation. Key steps have been identified for the timing of transcription of specific components, post-translational modifications, and membrane assembly of junctional proteins regulated by specific PCK isoforms. In addition, cell contact patterns and asymmetric divisions coordinate segregation of trophoblast and ICM lineages. Human embryos cultured in vitro display specific abnormalities in the epithelial differentiation programme which may contribute to loss of viability. Environmental conditions experienced by embryos (eg, maternal diet, in vitro culture) can affect not only blastocyst morphogenesis but also longer-term developmental potential including aspects of postnatal physiology.

C1.2–The *Deinococcus radiodurans* microarray: changes in gene expression following exposure to ionizing radiation and desiccation

J.R. Battista, A.M. Earl, H.A. Howell and S.N. Peterson
Baton Rouge, LA and Rockville, MD

Abstract not supplied

C1.3–Role of reactive oxygen species and antioxidants in root-hair development in *Arabidopsis thaliana*

M.A. Jones, M.J. Raymond, N. Smirnov, Biological Sciences, University of Exeter, UK

Root-hair cells are an ideal system for studying polar growth in plant cells. These cells, which are important for water and nutrient uptake, grow by depositing new membrane and cell wall material at their tips. *Arabidopsis* has a family of genes encoding homologues of the catalytic subunit of the mammalian NADPH oxidase complex. These reactive oxygen species (ROS)-producing proteins appear to have roles in plant defence against pathogen attack, programmed cell death, and, surprisingly, the development of root hairs. Mutations in one member of this gene family (*RHD2/AtrbohC*) result in very short hairs that burst at their tips. We have found that tip-bursting can be induced in wild-type plants by treating root hairs with antioxidants. We present data exploring the potential relationships between reactive oxygen species and antioxidants in growing root hairs using a combination of molecular cell biology, genetics and biochemistry.

C1.4–Using the human lamin B receptor targeted to the plant nuclear envelope to study membrane traffic in mitosis

S.L. Irons, M.H.M. Debela, D.E. Evans and F. Brandizzi, Research School of Biological and Molecular Science, Oxford Brookes University

The nuclear envelope (NE) is one of the least characterised cell membrane structures in plants. Our research concentrated on the development of fluorescent protein markers that specifically highlight the nuclear envelope in living cells. The human lamin B receptor (LBR) is known to be targeted to the NE in mammals and yeast. When the first 238 amino acids of the LBR, fused to the green fluorescent protein (GFP) were expressed in tobacco plants, fluorescence accumulated solely at the NE of leaf epidermal cells. This localisation was confirmed by electron microscopy studies. The LBR chimera is therefore an effective marker for plant NE in vivo and it is the first available fluorescent marker to be targeted exclusively to the plant NE. It provides a novel opportunity to investigate the dynamics of this

membrane system in vivo. In the talk, we will present data on its traffic and targeting during the cell cycle in tobacco BY-2 cells stably expressing it. We will also present data obtained using multiply-expressing cell lines to compare its traffic with that of probes directed to other endomembranes, microtubules and chromatin. Use of photobleaching to determine the dynamics of the protein will also be described.

C1.5–Xyloglucan endotransglucosylase/hydrolase action during plant development

K. Vissenberg and J-P. Verbelen, Department of Biology, University of Antwerp, Belgium

Xyloglucan, the most abundant hemicellulose in dicotyledons, can form hydrogen bonds with cellulose microfibrils and is therefore proposed to tether adjacent microfibrils. Together with cellulose it is believed to form the load-bearing component in the cell wall. For expansion to occur, cellulose microfibrils need to move apart and/or past another after modifications of the interconnecting xyloglucans. Xyloglucan endotransglucosylase/hydrolase (XTH), an enzyme that cuts and rejoins xyloglucan chains, was proposed to be a candidate for these modifications.

With a specific fluorescent technique the transglucosylase (XET) action of XTH was mainly detected in elongating cells [1] and during the initiation and outgrowth of root hairs in *Arabidopsis* [2]. A study in roots of different families of vascular land plants revealed that XET action could be detected in the root elongation zone from very primitive plants, such as *Selaginella*, through to the most complex angiosperms [3]. Thus the emergence of XTH action preceded the evolutionary divergence of the vascular plants and is generally associated with cell elongation.

The first results on the expression analysis (in collaboration with Dr. Nishitani, Tohoku University, Japan) of some members of the 33 different XTH genes of *Arabidopsis* [4] will be presented.

[1] K. Vissenberg, I.M. Martinez-Vilchez, J-P. Verbelen, J.C. Miller, S.C. Fry, (2000) *Plant Cell* 12, 1129–1137.

[2] K. Vissenberg, S.C. Fry, J-P. Verbelen, (2001) *Plant Physiol.* 127, 1125–1135

[3] K. Vissenberg, V. Van Sandt, S.C. Fry, J-P. Verbelen, (2003) *J. Exp. Bot.* 54, 335–344.

[4] R. Yokoyama, K. Nishitani, (2001) *Plant Cell Physiol.* 42, 1025–1033.

C1.6–Identification of components of cyclin-dependent kinase (CDK) complexes from *Arabidopsis thaliana*

K.A. Wilson, X.L. Yu, P. Dupree and J.A.H. Murray, University of Cambridge

In plants, as in other eukaryotes, cell cycle progression is controlled by cyclin-dependent kinases (CDKs) which are activated by binding of their regulatory cyclin subunits. To identify the components of *Arabidopsis* CDK complexes, CDKs and associated proteins were isolated by affinity chromatography. Either anti-Arath-CDKA;1 antibodies or the *Saccharomyces cerevisiae* suc1 (a component of CDK complexes which binds to CDKs with high affinity) were used to purify CDK complexes from cell extracts prepared from exponentially growing *A. thaliana* liquid cell suspension cultures. Proteins were separated by SDS-PAGE and identified by LC-ESI-Q-TOF-mass spectrometry of tryptic peptides, followed by searches of on-line databases using the MASCOT search engine.

CDKA;1, CDKB1;1, CDKB2;1 and CDKB2;2 were detected in the suc1 isolates and, as expected, the anti-Arath-CDKA;1 antibodies bound only CDKA;1. Cyclins cycD2 and cycD3 were detected in Western blots of both isolates. CycD4;1 and CDK-subunit 1 (CKS1), the *Arabidopsis* homologue of suc1, were detected in the antibody isolate by mass spectrometry. Proteins involved in many aspects of cellular function including cytoskeletal elements (alpha- and beta-tubulins and actins), translational machinery (40S ribosomal components, translation initiation factor eIF4a, elongation factor EF1a, splicing factors and RNA helicases), a putative endoplasmic reticulum ATPase, GTP-binding proteins and S-adenosyl-methionine synthetase co purified with the CDKs. Many of these proteins contain consensus CDK phosphorylation sites and may therefore represent CDK substrates.

C1.7–Exchange of genetic material by use of *Festulolium* introgressions to improve forage quality

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In ruminants, rapid proteolysis of ingested plant protein results in significant (up to 35%) loss of nitrogen as ammonia pollution of farmland. Decreasing the rate of ruminal proteolysis would increase efficiency of protein digestion and bring environmental benefits. It has

recently been shown that plant proteases can contribute to degradation of plant protein in the rumen. Proteolytic rates in *Festuca* and *Lolium* followed an exponential decline under rumen-like conditions. However, in vitro rates of plant-mediated protein degradation vary significantly between these grass species. We aim to combine the slow protein degradation trait found in *Festuca glaucescens* with the high leaf protein content trait of *Lolium multiflorum* by introgressing the appropriate genes from *F. glaucescens* into *L. multiflorum*.

A *Festulolium* backcross family was produced by introgressing *F. glaucescens* with an artificial tetraploid of *L. multiflorum*. The F₁ hybrid was then backcrossed with a diploid *L. multiflorum*. Of the resultant backcross, genotypes 40% had inherited the slow protein degradation trait. The genes introgressed from *F. glaucescens* relating to the differences in proteolytic rate will be physically and genetically mapped. Genetic markers common to these plants will be identified by amplified fragment-length polymorphisms and used in conjunction with genomic in situ hybridisation to screen future backcross generations. Repeated production of backcross plants (BC_n × *L. multiflorum*) combined with biochemical and genetic analysis will allow the small region of interest (<10 cM) from the *Festuca* genome to be identified. The possibility that this may not be a single locus trait will be discussed.

C1.8—Effects of pH and weak acid preservatives on spore germination and mycelial growth by *Aspergillus niger*

A. Plumridge, A.J. Watson, K.C. Lowe, M. Stratford¹ and D.B. Archer, Life & Environmental Sciences, University of Nottingham, UK and ¹Unilever Research, Bedford, UK

The filamentous fungus, *Aspergillus niger* is an established food spoilage organism. Weak acid preservatives, such as sorbic or benzoic acid, together with the acidulant, acetic acid, are used to protect food against microbial spoilage. Unfortunately, some fungi, including *A. niger*, are extremely tolerant to weak acids. Thus, the effects have been studied of pH alone, and in combination with sorbic, benzoic or acetic acid, on spore germination and mycelial growth in *A. niger*. At pH 2.0, spore germination by *A. niger* was significantly ($P < 0.05$) inhibited, compared to that at pH 4.0, 6.0 or 7.6, which all showed similar growth. The minimum inhibitory concentration (MIC) of weak acid needed to completely inhibit spore germination varied according to experimental conditions. For example, at pH 4.0, the MIC of sorbic and benzoic acid were 4.5 and 5.5 mM, respectively, whereas that of acetic acid was 70 mM. At pH 6.0, the MIC of sorbic and benzoic acid were both

greater than at pH 4.0, 27 mM and >60 mM, respectively. Inhibition of mycelial growth, after transfer to media containing sorbic acid, at pH 4.0 or 6.0, revealed that this acid also suppressed growth of vegetative cells. These results show that weak acids have growth-inhibitory effects on *A. niger* that are both concentration- and pH-dependent.

C1.9—Gene Expression in the Floral Organs of *Arabidopsis thaliana*

Carole Fay, John Bryant and Steve Hughes, Biological Sciences, University of Exeter, UK

We are working with an *A. thaliana* line transformed with an enhancer trap insertion which contains the gene encoding Green Fluorescent Protein (GFP). Previous analysis in our laboratory has shown that the insertion is in a gene encoding a kinesin-like protein which contains the motor domain motif and that the gene is up-regulated in the floral abscission zone. In our current work we have now shown that expression of the GFP is apparent in the abscission zone from a very early stage in bud development right up to the time when the floral organs abscise. In young buds, GFP expression also occurs in the walls of the epidermal cells of sepals, whilst in 3-day-old seedlings expression is apparent at or near the base of the cotyledons. Exogenous application of the signalling molecule, salicylic acid causes enhanced expression in sepals, stems and leaves. The level of expression does not appear to be influenced by irradiance, temperature, variation in external carbon source or the application of osmoticum.

Thanks to Dr Jim Haselhof for providing the insertion line

C1.10—Role of reactive oxygen species and antioxidants in root-hair development in *Arabidopsis thaliana*

M.A. Jones, M.J. Raymond, N. Smirnov, Biological Sciences, University of Exeter, UK

Root-hair cells are an ideal system for studying polar growth in plant cells. These cells, which are important for water and nutrient uptake, grow by depositing new membrane and cell wall material at their tips. *Arabidopsis* has a family of genes encoding homologues of the catalytic subunit of the mammalian NADPH oxidase complex. These reactive oxygen species (ROS)-producing proteins appear to have roles in plant defence against pathogen attack, programmed cell death, and, surprisingly, the development of root hairs. Mutations in one member of this gene family (*RHD2/AtrbohC*) result in

very short hairs that burst at their tips. We have found that tip-bursting can be induced in wild-type plants by treating root hairs with antioxidants. We present data exploring the potential relationships between reactive oxygen species and antioxidants in growing root hairs using a combination of molecular cell biology, genetics and biochemistry.

C1.11—Calvin Cycle Enzymes in the Nucleus

J.A. Bryant, J.A. Littlechild, Biological Sciences, University of Exeter, UK; L.E. Anderson, A.A. Carol, Biological Sciences, University of Illinois-Chicago, USA

Immuno-localisation experiments with isozyme-specific antibodies indicate that the cytosolic forms of glyceraldehyde-3-phosphate dehydrogenase, P-glycerate kinase and aldolase are located in the nucleus, as well as in the cytosol, in pea (*Pisum sativum*) leaves. The chloroplastic forms of aldolase and P-glycerate kinase and the B subunit of the NADP-linked glyceraldehyde-3-P dehydrogenase are also present in the nucleus. Subunit A of the dehydrogenase appears to be restricted to the chloroplast.

How these proteins are recognised and imported into the nucleus is not known. Only the cytosolic form of P-glycerate kinase has an obvious nuclear localisation signal (NLS). Transport of the other isozymes into (and out of) the nucleus as subunits may be non-specific or they may be carried as part of a complex with a protein that possesses an NLS. However, the apparent incorporation of the chloroplastic glyceraldehyde-3-P dehydrogenase B subunit, but not the A subunit, suggests that some difference between the very similar subunits is responsible for discrimination in uptake into the nucleus. The nuclear proteins recognised by the anti-chloroplastic P-glycerate kinase antibody and the anti-chloroplastic aldolase antibody appear to be the same length as the mature chloroplast isozymes, which suggests that the chloroplast transit peptides have been removed.

Apparently these enzymes are 'moonlighting' as nuclear enzymes, with secondary functions not directly related to their respective roles in glycolysis and in photosynthetic CO₂ fixation. The ability to sense redox-changes may account for the localisation of the B subunit of the NADP-linked glyceraldehyde-3-P dehydrogenase, which contains the regulatory redox-sensitive cysteines, in the pea leaf nucleus. Both the chloroplastic and cytosolic P-glycerate kinase function as primer-recognition proteins for pea shoot DNA polymerase- α . All of these enzymes are known to bind DNA. It seems possible that they sense metabolite levels and couple DNA replication and gene expression in the nucleus to carbon metabolism in the cytosol and in the chloroplast.

C1.12—Probing plant nuclear envelope dynamics using GFP-constructs

M.H-M. Debela, S.L. Irons, F. Brandizzi and D.E. Evans

Research School of Biological and Molecular Science, Oxford Brookes University

The scarce availability of markers limits the study of the traffic and transport of nuclear envelope (NE) proteins in plant cells. In this project, we have sought to develop a number of fluorescent protein markers targeted to the NE in tobacco suspension cells and plants. To do this, we identified proteins that are likely to be exclusively, predominantly or partially NE located and created GFP chimaeras. These include ECA1 (an SR/ER type Ca ATPase, obtained from J. Pittman and L. Williams, Southampton University), calmodulin (donated by A. Galichet, Swiss Federal Institute of Technology, Zurich) and MAF1 (MFP1 associated factor 1 protein 1, from I. Meier, Dupont Central Research and Development, Wilmington).

In the poster we will describe the design of the constructs and the location of the GFP-chimeras by transient expression in tobacco leaves observed by confocal microscopy. In addition we will present a strategy to explore plant NE targeting sequences by using the human lamin B receptor mutated in a putative chromatin binding region.

C1.13—Characterization of genes involved in root hair development

P.A. Hemsley, A.C. Kemp and C.S. Grierson, Biological Sciences, University of Bristol

TIP1 is involved in cellular growth of Arabidopsis. Mutations in TIP1 lead to an overall reduction in plant size due to reduced cell growth¹. The mutant phenotype is especially pronounced in the root hairs and pollen tubes of mutant plants, with root hairs of *tip1* being shorter and wider than wild type plants and frequently branching at the base^{1,2}. Root hairs of *tip1* seedlings have also been observed showing an exaggerated response to their immediate environment. The TIP1 locus has been mapped to the top of chromosome 5. Two mutant alleles of TIP1 are available and both are being used in complementation studies to identify TIP1. The *tip1* mutation has been complemented by biolistic transformation³ with several overlapping BACs and sub-clones and four predicted ORFs have been identified. We are trying to identify the TIP1 ORF by a) biolistic complementation testing with genomic fragments and cDNAs. b) Sequencing of the region in the two mutants corresponding to the smallest complementing wild type genomic clone and c) examining a range of T-DNA insertion lines in candidate ORFs for the *tip1* phenotype.

References: 1. New Phytol. 138: 49–58 2. Plant Physiol. 103: 979–985 3. Plant J. 27: 367–71.

C1.14—Newly characterized tomato haemoglobins

A-H. Quélo and J-P. Verbelen, Biology, University of Antwerpen; L. Kiger and M. Marden, Inserm U473, Paris; S. Dewilde, E. Geuens and L. Moens, Biochemistry, University of Antwerp

Symbiotic haemoglobins were the first haemoglobins discovered and studied in the plant kingdom. Their role is to facilitate oxygen diffusion to the nitrogen-fixing symbionts in legume nodules where they are exclusively found (Appleby, 1992). A second group, the non-symbiotic haemoglobins, was found more recently in both dicot and monocot plants. The phylogenetic analysis of all currently known non-symbiotic haemoglobin genes showed the existence of only one class of haemoglobin in monocots, whereas two distinct classes of haemoglobin genes were detected in the dicots (Hunt, 2001). In tomato (*Lycopersicon esculentum*) plants also, two haemoglobin genes, *LycGLB1* and *LycGLB2*, were found. We detected *LycGLB1*, a 456bp gene, in a cDNA bank and we expressed the corresponding 18kD protein in *E. coli* (BL21(DE3)pLysS) using the Pet3a expression vector. After purification on cation-exchange column and on a Sephacryl S200 column the ligand binding properties of this tomato haemoglobin were studied. With a $K_{on}O_2$ of $31 \mu M^{-1}.s^{-1}$ and a $K_{off}O_2$ of $0.5 s^{-1}$ *LycGLB1* appeared to have very high affinity for oxygen. The moderate association constant and the extremely low dissociation constant that characterise *LycGLB1* are a common feature for non-symbiotic haemoglobins as shown for *Arabidopsis*, rice and barley haemoglobins in other studies.

Recent investigations have also demonstrated the existence of a third family of plant haemoglobins called truncated haemoglobins because of their shorter amino acid sequence. This family of small oxygen-binding haem proteins was up to now mostly encountered in bacteria and protozoa. Tomato plants also appear to express this third haemoglobin.

C1.15—Characterization of *Arabidopsis* PLC1 T-DNA tagged mutant with impaired NaCl tolerance

T.E. Lasheen, A.R. Bahrami, D.J. Gilmour, J.E. Gray, Molecular Biology and Biotechnology, University of Sheffield

Phospholipase C is believed to be responsible for the release of Ins(1,4,5)P3 from the membrane which in turn causes the release of calcium from internal stores

in response to extracellular stimuli. To investigate the role of *Arabidopsis* AtPLC1, enhancer trap *Arabidopsis* lines were screened with PLC gene-specific primers followed by hybridization with a gene-specific probe. An individual with a single T-DNA insertion in the first exon of *AtPLC1* was identified. This insertion resulted in a deletion of 29 bp including the start codon (ATG), and an addition of 290 bp at the right border site of insertion. RT-PCR with PLC primers spanning the insertion failed to amplify any wild-type transcript. However primers downstream of the insertion amplified a band of the expected size suggesting that another ATG is utilized. Homozygous mutant plants tended to have reduced growth rate, delayed flowering and wider mature leaves. Mutant seedlings showed hypersensitivity to NaCl treatment and seed germination was more sensitive to ABA treatment. GUS activity, which should reflect the expression of the PLC gene in the mutant plants, was detected in the inflorescence, shoot, leaf and root (adjacent to the lateral root initiation meristem) under unstressed conditions. GUS activity was not detected in the root of flowering plants. Under NaCl, ABA and cold stresses the intensity of the GUS staining was increased. Expression of GUS in the root apex was detected only following ABA treatment. These results support a role for AtPLC1 in NaCl and ABA signal transduction pathways.

C1.16—A New Method of Genome-wide Identification of Differences Between Closely Related Species in Integrations of Mobile Elements: Application to Recent Human Evolutionary History

A. Buzdin, S. Ustyugova, K. Khodosevich, I. Mamedov, Y. Lebedev and E. Sverdlov. Shemyakin-Ovchinnikov Institute of Bioorganic Chemistry, Moscow, Russia.

We have developed a method of targeted genomic difference analysis (TGDA) for genome wide detection of interspersed repeats integration sites differences between closely related genomes. The method includes a whole-genome amplification of the flanks adjacent to target interspersed repetitive elements in both genomic DNAs under comparison, and subtractive hybridization (SH) of the selected amplicons. The potential of TGDA was demonstrated by the detection of differences in the integration sites of human endogenous retroviruses K (HERV-K) and L1 retrotransposons between the human and chimpanzee genomes. A total of 60 new human-specific retroelement integrations were found. Based on sequences of human-specific HERV-K LTRs we created a consensus sequences for two evolutionary young groups of human-specific LTRs (HS-a and HS-b), presented in human genome by about 150 copies; these

results suggest simultaneous activity of two HERV-K master genes in the hominid lineage. We also mapped 15 human-specific HERV-K LTRs in introns of known human genes. TGDA application to detection of human-specific L1s allowed us to find in human DNA for the first time a new family of retrotranscripts generated in the genome by fusion of two well known components of the genome – U6 snRNA genes and L1 retrotransposons. This new family of U6-L1 hybrid pseudogenes is presented in the human genome by at least 56 members. In this report we provide strong evidence that integrations of such fusions in the genome took place until recently, one of such insertions was found to be polymorphic in humans. Our experimental results evidence in favor of a new mechanism for the chimera formation, which involves the L1 enzymatic machinery and probably a switch of templates during L1 mRNA reverse transcription.

C1.17–Plastid morphology in tomato: a model for studying stromule function

M.T. Waters and K. Pyke, School of Biosciences, University of Nottingham, UK

Plastids are a family of cellular organelles that perform several essential functions in plant cells. Studies into plastid biochemistry, morphology and division processes are fundamental to understanding plant development, and so the visualisation of plastids is a powerful tool in unravelling their behaviour. Plastid-targeted green fluorescent protein (GFP) has permitted the visualisation of non-pigmented plastids and has revealed the complex morphology of plastids: most notably the presence of dynamic, tubular extensions of the plastid envelope termed stromules (Kohler et al. 1997). During the development of tomato fruit, plastids in the pericarp cells undergo major biochemical changes. As chlorophyll degrades and carotenoids accumulate, plastid morphology also changes dramatically (Howells and Pyke, 2002). Chromoplasts in ripe fruit exhibit vast, extended stromules which frequently interlink individual plastids.

In contrast, plastids in unripe fruit are largely separate, although their morphology depends on their starch and chlorophyll content. Using a variety of approaches this work aims to detail the changes in plastid morphology that occur during fruit ripening, and to improve our understanding of stromule biology in general. Tomato fruit represents a good model system due to the well-defined plastid differentiation during fruit development. Fruit ripening mutants are being used to assess the effect of aberrant plastid development on stromule formation. Dual labelling studies with fluorescent proteins will assess the spatial relationship of stromules with mitochondria and the cytoskeleton.

C1.18–*suffulta*: a group of plastid division mutants in tomato

Daniel Forth, Kevin Pyke, School of Biosciences, University of Nottingham, UK; David Leader, Syngenta, UK

Tomato fruit colouration is a result of the accumulation of carotenoid pigments in plastids known as chromoplasts. An understanding of plastid division is crucial to attempts to manipulate agronomic traits influenced by plastid size and number. Screening of the alleles of the tomato mutant, *suffulta*, led us to discover that this group of mutants show abnormal plastid division. These mutants demonstrate a dramatically reduced rate of plastid division in leaf and stem tissues but chromoplast division is not affected to the same extent. This indicates that regulation of chromoplast division is partially independent of the genetic factors regulating division in leaf and stem tissues. The greatest reduction in plastid division is in the *su* and *su-3* mutants, which also have pale stems and slow plant growth. Plastid division in *su-2* is affected less severely than *su* or *su-3* but does not show any inhibition of plant growth. Despite the dramatic plastid phenotypes of these plants, they grow more vigorously than tomato plants with abnormal plastid division generated by the over-expression of the plastid division protein, FtsZ.