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Review Article

Visualizing the dynamics of plant energy organelles

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Plant organelles predominantly rely on the actin cytoskeleton and the myosin motors for long-distance trafficking, while using microtubules and the kinesin motors mostly for short-range movement. The distribution and motility of organelles in the plant cell are fundamentally important to robust plant growth and defense. Chloroplasts, mitochondria, and peroxisomes are essential organelles in plants that function independently and coordinately during energy metabolism and other key metabolic processes. In response to developmental and environmental stimuli, these energy organelles modulate their metabolism, morphology, abundance, distribution and motility in the cell to meet the need of the plant. Consistent with their metabolic links in processes like photorespiration and fatty acid mobilization is the frequently observed inter-organellar physical interaction, sometimes through organelle membranous protrusions. The development of various organelle-specific fluorescent protein tags has allowed the simultaneous visualization of organelle movement in living plant cells by confocal microscopy. These energy organelles display an array of morphology and movement patterns and redistribute within the cell in response to changes such as varying light conditions, temperature fluctuations, ROS-inducible treatments, and during pollen tube development and immune response, independently or in association with one another. Although there are more reports on the mechanism of chloroplast movement than that of peroxisomes and mitochondria, our knowledge of how and why these three energy organelles move and distribute in the plant cell is still scarce at the functional and mechanistic level. It is critical to identify factors that control organelle motility coupled with plant growth, development, and stress response.

Introduction

Plant cells are often envisioned as the classic textbook cartoon: static organelles spaced indiscriminately in the cytoplasm within the confines of rigid cell walls. However, organelles are highly dynamic, as their quantities fluctuate via biogenesis, fission, fusion, and degradation and their morphologies shift among a variety of sizes and shapes. Organelles traverse the cell by cytoplasmic streaming and organelle-specific, targeted motility along the cytoskeleton, driven by molecular motors that travel along the tracks of the cytoskeletal filaments.

Eukaryotic cells employ the cytoskeletal motors of kinesins, dyneins, and myosins that hydrolyze ATP to propel organelle transport directionally along polarized microtubule and actin tracks, whose orientation dictates the direction of travel. Active motor-mediated movement can trigger other modes of transportation, including cytoplasmic streaming and 'hitchhiking', in which organelles are transported indirectly by associating with cargoes already being carried by motors [1].

In animal cells, the microtubule-based cytoskeleton, along with kinesin and dynein motors, are predominantly responsible for vesicle and organelle trafficking [2–4]. In contrast, actin filaments comprise the major intracellular highway system in plants for long-range organelle trafficking, driven primarily by the class XI myosin proteins [5–9]. Plant microtubules and their associated motors, kinesins, mainly direct short-range organelle movement, pauses, and orientation in coordination with the actin cytoskeleton [10–14]. Additionally, the endoplasmic reticulum (ER) is intricately involved in

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motor-assisted organelle motility. For example, the ER is associated with the dynamic cytoskeletal network through tethering and anchoring mechanisms, most especially at ER-plasma membrane contact sites [6,15]. Furthermore, proximity and interactions among organelles correlate with fluctuations in ER morphology, which suggests that the ER mediates the positioning and movements of organelles, including chloroplasts, mitochondria and peroxisomes [16,17].

A number of studies testing organelle motility in *Arabidopsis* myosin mutants and myosin localization in plant cells indicate functional redundancy in the Myosin XI protein family and targeting of the same myosin motor to multiple types of organelles [5,18–22]. The apparent promiscuity in the interactions between myosin motors and organelles beckons for regulatory mechanisms of organelle movement that is possibly governed by organelle-specific receptors/adaptors, which recruit designated Myosin XI motors [23].

These molecular motors and their associated cytoskeleton facilitate the movement and dynamics of the nucleus and endomembrane system, including ER, Golgi, and vesicles, which have been expertly reported in several recent papers [24–27]. In this review, we focus on the motility of plant energy organelles — chloroplasts, mitochondria, and peroxisomes — which work independently as well as in concert during energy metabolism. These organelles modulate not only their metabolism and morphology but also their distribution and motility in accordance with developmental stages and environmental conditions. Here, we introduce the collaborative nature of these three energy organelles in photosynthetic organisms and methods used to study their motilities and discuss the factors that trigger and modulate their movement and distribution. We apologize to researchers whose publications cannot be cited due to space limitation.

Organelle functions

Chloroplasts, enclosed by double envelopes and containing their own genome, house the photosynthetic machinery that performs light capture and carbon assimilation, along with many other vital cellular functions beyond direct energy production, such as the biosynthesis of lipids, phytohormones and other key molecules [28–31]. Mitochondria are double-membraned, DNA-containing organelles whose primary role is cellular respiration while also performing plant-specific functions such as malate oxidation and photorespiration [32]. Peroxisomes are single-membraned and DNA-less organelles involved in fatty acid degradation and detoxification of reactive oxygen species, along with plant-specific functions such as phytohormone production and photorespiration [33–35].

Several of the above-mentioned processes require the collaboration of chloroplasts, mitochondria, and/or peroxisomes [36–38]. Namely, the photorespiratory pathway requires these three organelles to recover misassimilated carbon produced due to the oxygenase activity of the photosynthetic enzyme Rubisco, protecting the plant cell from toxic byproducts [39,40]. Besides being essential to the survival of organisms performing oxygenic photosynthesis in ambient air, photorespiration also has a demonstrated role in immunity [41]. In addition, during the metabolism of fatty acids, triacylglycerol stored in oil bodies can be degraded in peroxisomes via β-oxidation, after which the glyoxylate cycle, also housed in peroxisomes, produces metabolites that are exported to mitochondria for the tricarboxylic acid (TCA) cycle to ultimately release the stored energy [33,42]. Moreover, lipid transfer can occur directly between chloroplasts and mitochondria during phosphate starvation [43]. As a final example, jasmonate (JA) biosynthesis requires chloroplasts to produce the precursor 12-oxo-phytodienoic acid (OPDA), which is then imported into the peroxisome to be converted to JA via β-oxidation [33,44,45].

Consistent with their metabolic connections, these organelles are often observed to be in close physical proximity. Mitochondrial associations with chloroplasts increase under high light in the diatom *Phaedactylum*, as well as during mixotrophy (compared with phototrophy) in the alga *Nannochloropsis* [46]. In *Arabidopsis*, the proximity area between these organelles expands in light compared with dark [47]. Chloroplast-peroxisome-mitochondrion complexes are formed more frequently in light than in dark, and light-induced triple organelle interaction is suggested to be regulated by photosynthesis and facilitated by ER-chloroplast nexuses [47–49]. ER reorganization is also proposed to contribute to the formation of tubular protrusions from chloroplasts, peroxisomes, and mitochondria, termed stromules, peroxules, and matrixules, respectively [50]. During high light irradiation, small mitochondria cluster around peroxules [49]. While proximity among all three energy organelles increases in mesophyll in light [47,48] and stromule formation is more frequent in light-treated epidermal pavement cells (Figure 1A), similar numbers of mitochondria and peroxisomes interact with both the chloroplast body and stromules in these pavement cells [51]. These organelle protrusions very likely provide a platform for inter-organellar interaction and metabolite exchange among the organelles.

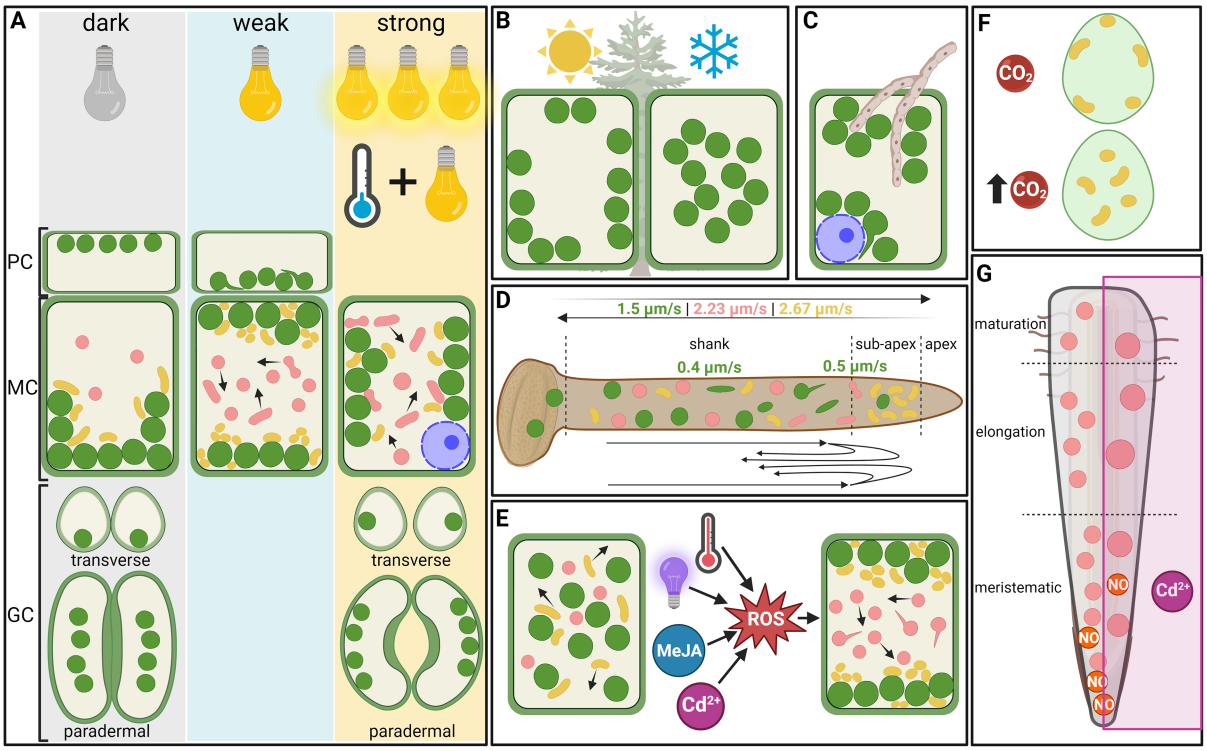

Figure 1. Examples of energy organelle dynamics in photosynthetic organisms during environmental and developmental changes.

Changes in the distribution and movement of chloroplasts/plastids (green), mitochondria (yellow), and peroxisomes (pink) are shown. (**A**) Chloroplasts and mitochondria exhibit photorelocation and cold positioning in *Arabidopsis* and tobacco pavement cells (PC), mesophyll cells (MC), and guard cells (GC). Peroxisome proliferation and motility increase in light. Light-induced morphological changes include mitochondrial aggregation, peroxisome elongation, and chloroplast stromule formation. (**B**) Seasonal rearrangement of chloroplasts occurs in conifer species. (**C**) Chloroplasts redistribute during pathogen infection and immune response in *Arabidopsis* and tobacco leaves. (**D**) The three energy organelles are differentially distributed and vary their motility during pollen tube development in flowering plants. (**E**) Dynamics of the three energy organelles shift in response to reactive oxygen species (ROS) in *Arabidopsis* leaves. Mitochondria slow and aggregate while peroxisomes speed up and form peroxules. (**F**) Mitochondria slow down, redistribute under fluctuating carbon dioxide (CO_2) levels in Chlamydomonas. (**G**) Peroxisomes are more concentrated in the meristematic zone in root tips and their morphology is altered in response to cadmium (Cd^{2+}) toxins in roots. Arrows in (**A**), (**D**) and (**E**) represent general motility patterns. MeJA, methyl jasmonate; NO, nitric oxide. The nucleus (blue) is only depicted when its interaction with energy organelles is involved. Created with BioRender.com.

Methods for organelle and cytoskeletal visualization

Chloroplasts, due to their superiorly large size and chlorophyll autofluorescence, can be readily visualized through light and fluorescence microscopy [52].

In early studies, detections of peroxisomes and mitochondria were largely dependent on organelle-specific enzymes or distinct properties of their membranes. For example, using fluorescence microscopy, plant peroxisomes were detected by immunofluorescence using antibodies against catalase [53] while mitochondria were probed by dyes like rhodamine 123 that binds to P-glycoproteins [54,55]. Due to disadvantages associated with rhodamine 123 like challenges of sample washes and photostability, it has largely been replaced by synthetic hydrophobic dyes commonly known as MitoTrackers, which bind to mitochondrial membranes and can be conjugated with different fluorophores [56] to track mitochondria in living plant cells [57].

Lately, fluorescent protein (FP) tags introduced by recombinant DNA techniques have been widely adopted to monitor the dynamic behavior of peroxisomes and mitochondria, when either stable transformation or

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transient expression is applicable in the host cells. Besides the founding green fluorescent protein (GFP), numerous FPs may be chosen nowadays for their features of color, brightness, quantum yield, maturation property, pKa, and lifetime, which are frequently updated by the research community (https://www.fpbase.org/). When covalently attached to proteins that are unique to the respective organelle at either the organelle membranes or lumens after translation, these FPs faithfully report the intracellular positions of the organelles by fluorescence microscopy. Moreover, organelle and cytoskeletal FP marker collections have expanded beyond model plants and are now optimized for uses in crop plants like maize [58], rice [59,60], and barley [61]. Several excellent articles have summarized typical examples [62–64].

To label peroxisomes, a 3-amino acid canonical peroxisomal targeting signal 1 (PTS1) sequence, such as Ser-Lys-Leu (SKL) or Ser-Arg-Leu (SRL), is usually translationally conjugated to the C-terminus of an FP [63,65]. Peroxisomes can also be illuminated using the fusion of the N-terminus of a peroxisome matrix protein containing the PTS2 nonapeptide, such as that from the 3-ketoacyl-CoA thiolase or the glyoxysomal malate dehydrogenase, and the FP [66]. When an FP-PTS1 or PTS2-FP fusion protein is expressed under constitutively active promoters like the viral 35S promoter, it is in high abundance so that peroxisomes are brightly labeled for convenient observation by confocal microscopy.

Similarly, mitochondria can be labeled by attaching their targeting sequence at the N-terminus of FPs. A widely used targeting sequence in plants is a 29-amino acid peptide derived from the yeast cytochrome *c* oxidase IV (COX4) [63]. Mitochondrial-specific proteins like the γ-subunit of F1-ATPase serve the purpose equally well in plant cells [64]. Although they require transcription and translation in host cells, such FP-based probes are often favored over lipophilic dyes because of their organelle specificity.

The motility as well as polarized distribution of plant organelles including peroxisomes and mitochondria is dependent primarily on actin microfilaments and employs the myosin motors [18,53]. Live-cell imaging of actin filaments has evolved from the application of the fluorescent dye-conjugated fungal toxin of phalloidin to FP-tagged polypeptides of various actin-binding proteins [67,68]. Earlier adoption of the actin-binding protein talin often resulted in the formation of thick actin bundles [68]. As a replacement, ABD2, an actin-binding domain of the *Arabidopsis* fimbrin 1 protein, or the 17-amino acid Lifeact peptide derived from the yeast actin-binding protein Abp140 [69], is often used these days, both of which can significantly reduce the bundling and aggregation of actin microfilaments.

The ever-growing diversity of FPs and highly sophisticated microscopes with exceptional resolution enable synchronous visualization of multi-organellar and cytoskeletal topology in living cells. For example, peroxisomes, mitochondria, and actin labeled with multicolored FP-fusion biomarkers as described above, along with autofluorescent chloroplasts, can be monitored simultaneously in living tobacco epidermal cells (Figure 2). This concurrent visualization enables direct comparisons of organelles in the context of one another. Moreover, intricate visualization techniques have vast potential to further illuminate organelle dynamics and motility by rapid capture of organelles in action (Supplementary Movie 1).

FP-tagged probes are also used to detect the dynamic microtubule network in plant cells. The microtubule-binding domain (MBD) derived from the mammalian microtubule-associated protein 4 (MAP4) decorates cortical microtubules in fava bean epidermal cells upon transient expression [70]. This GFP-MBD renders superior brightness, possibly resulted from induced microtubule bundling. Alternatively, an MBD derived from the atypical casein kinase CKL6 has also been used to mark microtubules in living plant cells [71]. To minimize the potential impact of ectopically expressing an MBD in plant cells, one wishes to fuse FP with tubulins so that microtubules are labeled when the FP-tubulin fusion is incorporated into polymerized microtubules, which often requires stable transformation as demonstrated first by a GFP-α-tubulin in *Arabidopsis* [72]. The β-tubulin isoform *TUB6* was later chosen because of its minimal toxicity after ectopic expression [73]. Stable expression of TUB6 under its native promoter in *Arabidopsis* results in neglectable disturbance to the dynamic remodeling of microtubule arrays and plant growth [74].

Progressively advanced, specific, and tunable visualization techniques equip researchers to uncover the nuances of energy organelle dynamics and expand our current knowledge of chloroplastic/plastidial, mitochondrial, and peroxisomal distribution and motility.

Chloroplasts

As light-harvesting apparatus, chloroplasts optimize photon capture by shifting their positions in the cell, a process termed photorelocation [75–78] (Figure 1A). In the dark, chloroplasts are distributed along the bottom

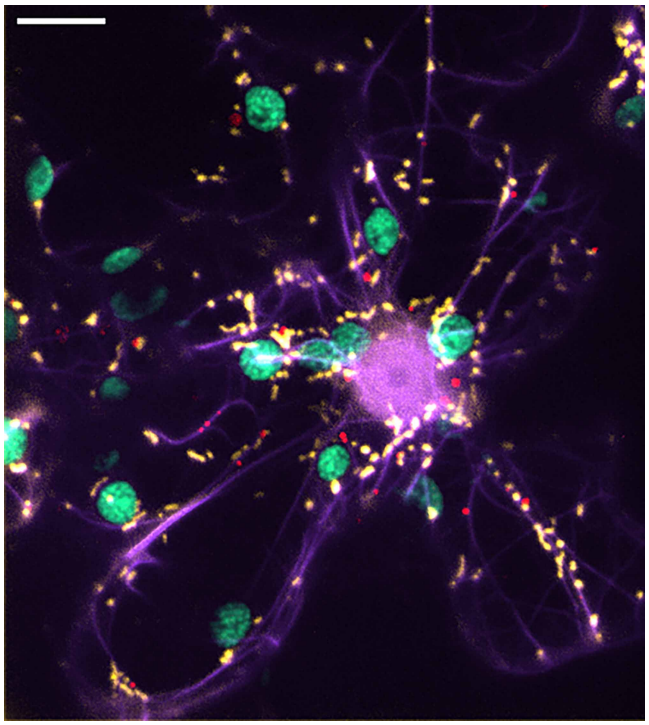

Figure 2. Simultaneous visualization of plant energy organelles and actin in tobacco cells.
Chloroplasts (chlorophyll autofluorescence, green), mitochondria (COXIV^{29aa}-eYFP, yellow), peroxisomes (mScarlet-I-SRL, red), and actin (Lifeact-eGFP, purple) in *Nicotiana tabacum* were imaged using a 3i spinning disk confocal microscope with excitation wavelengths 640 nm, 515 nm, 561 nm, and 488 nm, respectively. The emission capture range for each fluorophore is as follows: 672–712 nm for chlorophyll, 528.5–555.5 nm for eYFP, 580.5–653.5 nm for mScarlet-I, and 510–540 nm for eGFP. Scale bar represents 10 μm.

of mesophyll cells and the top of pavement cells [51,79]. However, in shaded or low-light environments, chloroplasts accumulate across the peri-clinal cortex to increase light absorbance and energy capture, and pavement cell chloroplasts relocate to the bottom of the cell nearer to mesophyll chloroplasts. Conversely, when light intensity exceeds the plant's photosynthetic capacity, chloroplasts reduce photodamage by employing an avoidance mechanism in which they stack along the anti-clinal walls of the cell [51,80] (Figure 1A). During blue-light avoidance, nuclei move concordantly with chloroplasts by hitchhiking as passengers of chloroplasts to protect DNA from UV damage [81,82] (Figure 1A). While photorelocation is predominantly described in mesophyll cells where photosynthesis is most active, evidence suggests that chloroplasts are repositioned in an actin-dependent manner in guard cells in the epidermis as well. Shifts in light modulate stomatal aperture, which is also regulated by phytohormones produced in the chloroplast. Chloroplasts in tobacco guard cells redistribute from the inner peri-clinal walls to the dorsal walls at the center of guard cells during white light-induced stomatal opening (Figure 1A), a process proposed to be mediated by stochastic dynamics of actin filaments [83,84].

Because light availability fluctuates, chloroplasts must readily initiate photorelocation routinely. Blue-light receptors (phototropins) trigger the reorganization of specialized chloroplast actin filaments (cp-actin) via actin-bundling proteins, while Chloroplast Unusual Positioning Protein 1 (CHUP1) mediates interactions among chloroplasts, cp-actin, and the plasma membrane [77,79,85–87]. Although some data suggests the involvement of myosin proteins in chloroplast photorelocation [88], the process predominantly depends on actin reorganization itself in which cp-actin aggregates at the leading edge of chloroplasts to direct movement towards anti- or peri-clinal cell walls [83,87,89].

Critical to the cold acclimation of photosynthesis, the chloroplast avoidance response can be triggered by weaker light intensities at low temperatures in *Arabidopsis* (Figure 1A), suggesting the modulation of photoprotective mechanisms upon the onset of dark when temperatures drop [90,91]. Since cold positioning was first

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described in ferns [92], researchers have further elaborated on the links between photorelocation and cold acclimation in bryophytes [90,91] and flowering plants [90]. Phototropins act as thermosensors via blue-light regulated autophosphorylation [95] and subcellular re-localization [96–98], modulating the actin-dependent repositioning of chloroplasts as unfused aggregates in response to cold [99–101]. Seasonal rearrangement of chloroplasts was also observed in the mesophyll of two conifer species, in which chloroplasts move from the periphery along the cell wall in the summer to a more internal location in the cell in the winter (Figure 1B), a process that involves the vacuole and cytoplasmic strands [102].

Chloroplasts cluster around the nucleus during innate immune response. Oppositional movement of nuclei and chloroplasts is proposed to contribute to the formation of stromules enriched in proximity to the nucleus (Figure 1C), possibly to facilitate the exchange of defense signals [103–107]. Independent of nuclear movement, chloroplasts accumulate at the pathogen interface (Figure 1C) during *Phytophthora infestans* infection in *Nicotiana benthamiana* [108]. They even employ some components of the photorelocation mechanism for motility in *Arabidopsis* epidermal cells during fungal infections [109,110]. Immunity-related repositioning observed in tobacco is directed by the coordinated efforts of actin, microtubules, and stromules [103], all of which have dynamic roles in chloroplast motility and environmental stress response [111].

During pollen tube elongation, plastids exhibit differential motility patterns that are loosely correlated with a variety of plastid morphologies, where spherical plastids correspond with less streaming and elongated plastids and stromules with higher rates of streaming. Specifically, plastids move long-distances from pole-to-pole at high velocities (~1.5 μm/s), with slower motions (~0.4 μm/s) and arrests predominating in the middle region of the tube, and short vibrations or fluctuations at the tip end of the shank with a velocity of ~0.5 μm/s [112,113] (Figure 1D).

Mitochondria

Early characterizations of mitochondrial dynamics describe the organelle behavior and morphology as highly heterogeneous [114], which is further emphasized by the mitochondrial diversity recently observed across microalgae [46], indicating its multipotent functions in photosynthetic organisms. Mitochondria traverse plant cells along actin filaments in a variety of patterns, including short oscillations, bidirectional long-range movement, and turnaround motions facilitated by circular actin bundles [115,116]. Their morphology and motility are influenced by development, cell-type, proximity to other organelles, and environmental conditions, as described below.

The fundamental regulation of mitochondrial movement is likely combinatorial and collaborative, involving actin and myosins for various speeds and patterns of motion as well as microtubules and likely kinesins for positioning [116,117]. This translocation and positioning infrastructure enables the mitochondria to meet the energy demands of the cell. For example, lily mitochondria are concentrated at the sub-apex of the pollen tube (Figure 1D), where energy is required for elongation [14,118,119]. The pollen tube exhibits a characteristic reverse fountain-like pattern of cytoplasmic streaming in which organelles, including mitochondria, move through the shank towards the apex (~2.67 μm/s) but then reverse course (Figure 1D) as the actin structure shifts from long filaments to shorter parallel bundles referred to as the actin fringe [118,120,121]. This fast forward movement followed by slowing down in the sub-apical region is attributed to actin/myosins and microtubules/kinesins, respectively [122]. In fact, specific motors Kinesin-like Protein 1 [123] and Myosin XI-C2 are associated with mitochondria, and Myosin XI-C2 contributes to mitochondrial as well as peroxisomal and Golgi movement in *Arabidopsis* pollen tubes [124].

ROS accumulation acts as a trigger for mitochondrial redistribution during heat stress-, UV- and methyl jasmonate (MeJA)-induced programmed cell death, in which mitochondria aggregate in clusters, shift from elongated morphology to more swollen and spherical shapes, and decrease their overall motility [125–127] (Figure 1E). These morphological changes are believed to be pivotal early steps in the progression of programmed cell death.

The trend towards more spherical, shorter, or simplified shapes for mitochondria is also evident in the transition from dark to light in *Arabidopsis* mesophyll cells [47] (Figure 1A). Light conditions also influence mitochondrial distribution and mobility. In *Arabidopsis* mesophyll cells, weak and strong blue light illuminations cause differential localization of mitochondria compared with mesophyll cells in the dark, mirroring chloroplast accumulation and avoidance [128] (Figure 1A). Mitochondrial long-range motility is dependent on actin, whereas they become more static in the proximity of chloroplasts, adopting slower, actin-independent wiggling-

type motions [129]. In the green alga *Chlamydomonas*, mitochondria are closely associated with the plasma membrane in ambient CO_2 and more uniformly distributed throughout the cytoplasm under high CO_2 [130] (Figure 1F). These mitochondrial movements may facilitate necessary associations among chloroplasts, mitochondria, as well as peroxisomes during processes requiring their collaboration, such as photorespiration that is modulated by light and CO_2 levels [131].

Peroxisomes

Despite having a simple structure, peroxisomes are highly dynamic in size, number, morphology, and biochemistry [33]. For instance, light increases peroxisome abundance in dark-grown *Arabidopsis* seedlings (Figure 1A) through a phytochrome A-mediated signaling pathway involving the transcription factors Homolog (HYH) and (Forkheaded-Associated Domain 3) FHA3 and the peroxisome elongation factor Peroxin 11b (PEX11b) [132–134]. In addition, peroxisomes in *Arabidopsis* mesophyll are significantly larger in light compared with the dark, and as their volume increases, they become less spherical [47] (Figure 1A). Moreover, chloroplast-associated peroxisomes are more elliptical (Figure 1A), increasing surface area available for interorganellar interaction. This notion is further supported by stronger adhesion between these organelles in red/blue light, although these changes are not regulated by the red and blue light receptors phytochromes and phototropins [48]. In *Arabidopsis* root tips, peroxisomes are more intensely concentrated in the elongation and meristematic zones compared with the maturation zone, which is correlated with the finding that nitric oxide (NO), which exists in the peroxisome, distributes mostly in the primary and lateral root apices [135] (Figure 1G). Interestingly, cadmium (Cd^{2+})-imposed ROS increases peroxisome proliferation in *Arabidopsis* leaves and induces peroxule formation [136,137] (Figure 1E), while Cd^{2+} decreases the number of peroxisomes in primary roots and increases peroxisome size (Figure 1G), suggesting increased organelle fusion [135].

Peroxisomes display various patterns of movement: vibrations or oscillations in place, short-range travel, and traversing longer distances [7]. While myosin drives fast and long-range movement [18,138,139], oscillatory patterns of peroxisome motion correlate with ER dynamics in *Arabidopsis* seedling epidermal cells, suggesting a possible concomitant regulation of ER-peroxisome motility [140]. Moreover, individual peroxisomes switch directions, speeds, and motions all within the same cell type and timeframe in *Arabidopsis* epidermal cells [7]. As such, peroxisomes are not simply passive passengers but rather are subject to yet undiscovered biological triggers that govern their movements.

Developmental stage and tissue type is suggested to have an impact on peroxisome motility. Brownian-type vibrations have been ascribed to peroxisomes in leaves, with slower velocities in younger leaves, whereas more rapid peroxisomal movement is described in *Arabidopsis* roots, trichomes, mature leaves, and pollen tubes [19,121,138,139,141]. However, these velocities are highly variable: <0.2 μm/s in seedling epidermis [141], ~2.23 μm/s in pollen tubes [121], up to 7 μm/s in seedling mesophyll [49], indicating that careful consideration regarding age, tissue, and cell type must be taken when evaluating peroxisome movements. Moreover, environmental factors likely influence peroxisomal motion. For example, significantly more peroxisomes are mobile in light compared with dark in *Arabidopsis* mesophyll cells (Figure 1A). Organelle mobility is maintained by actin filaments as peroxisome-chloroplast interactions increase, while peroxisome-chloroplast tethering is an actin-independent process involving peroxule formation [48,142]. Motility quickens during Cd^{2+}-induced oxidative stress, which is hypothesized to be regulated by increased peroxisomal levels of ROS and may involve calcium signaling [141] (Figure 1E). While overall motility increases 1–3 days following Cd^{2+} treatment, peroxisomes were previously reported to pause during peroxule formation within 15 min of exposure to Cd^{2+}, followed by an increase in proliferation [136,141]. These data suggest peroxisomes may dwell when undergoing morphological changes or intra/inter-organelle contact, and the number and size of peroxisomes may affect their motility.

Perspectives

- Chloroplasts, mitochondria, and peroxisomes are essential organelles functioning independently as well as coordinately during plant energy metabolism and other key processes. The motility and distribution of these energy organelles are fundamentally important for plant physiology and defense.

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- Besides morphing between shapes, dividing and fusing, these energy organelles move throughout the cell and interact with one another and with other cell compartments to accomplish their roles efficiently. Most of what we know till now about their motility and distribution in photosynthetic organisms addresses general patterns and velocity changes in response to developmental and environmental cues, whereas the underlying mechanisms are largely unknown.

- Many questions remain to be addressed in future research. For example, how are the molecular motors recruited to the organelles selectively? Which signaling pathways trigger the various modes of organelle positioning, movement, and physical interaction? What functional role does organelle motility play in plant physiology and health? How do these organelles coordinate their physical interaction and movement along the cytoskeletal tracks while performing collaborative metabolic functions?

Competing Interests
The authors declare that there are no competing interests associated with the manuscript.

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Author Contributions
A.M.K., B.L. and J.H. co-wrote the manuscript. A.M.K. generated the figures.

Abbreviations
CHUP1, Chloroplast Unusual Positioning Protein 1; COX4, cytochrome c oxidase IV; ER, endoplasmic reticulum; FP, fluorescent protein; GFP, green fluorescent protein; JA, jasmonate; MBD, microtubule-binding domain; MeJA, methyl jasmonate; NO, nitric oxide; PTS1, peroxisomal targeting signal 1; ROS, reactive oxygen species; SKL, Ser-Lys-Leu; SRL, Ser-Arg-Leu.

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