Structural evidence for electromagnetic resonance in plant morphogenesis

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A B S T R A C T
How a homogeneous collective of cells consistently and precisely establishes long-range tissue patterns remains a question of active research. This work explores the hypothesis of plant organs as resonators for electromagnetic radiation. Long-range structural patterns in the developing ovaries and male flower buds of cucurbit plants (zucchini, acorn, and butternut squash), in addition to mature cucurbit fruits (acorn, butternut, and zucchini squash; watermelon, and cucumber), were investigated. A finite element analysis (FEA) model was used to determine resonant EM modes for models with similar geometric and electrical parameters to those of developing organs. Main features of the developing ovaries (i.e. shape of placental lines, ovum location, definition of distinct tissue regions), male flower buds (i.e. early pollen tube features), and mature fruits (i.e. septa placement, seed location, endocarp and mesocarp) showed distinct correlations with electric and magnetic field components of electromagnetic resonant modes. On account of shared pattern signatures in developing organs and the EM resonant modes supported by a modelled structure with similar geometric and electrical properties to those of cucurbit organs, experimental investigations are warranted. The concept of a developing organ as an EM dielectric resonator may extend to a variety of morphogenetic phenomena in a number of living systems.

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1. Introduction

From the conventional view of modern biology, nearly every single aspect of development is seen as the consequence of molecular signals produced by, and often capable of further influencing, genetic expression. From this perspective, developmental phenomena are assumed to ultimately be co-ordinated by molecular signals (morphogens/hormones) produced by selective activation of certain genes in certain cells at certain times in the developmental process. For instance, in plant development various aspects of melon fruit formation, from the sexual expression of flowers to fruit ripening, are the consequence of tissue exposure to genetically regulated ethylene (Papadopoulou et al., 2005). Similarly, coloured stripes on the outside of some squash are the result of differential expression of gene-regulated pigments in the rind (Paris, 2008). In plants, the five major hormone groups are the auxins, cytokinins, gibberellins, abscisic acid, and ethylene, all of which are regulated by genes and evoke a variety of different physiological responses in target tissues from initiation of primordia, organ development, maturation, and senescence (Gaspar et al., 2003; Ozga and Reinecke, 2003).

It is well established that molecular signals play essential roles in development. However, in both plant and animal development there remains little understanding of how these substances can be synthesized, transported, and act at the specific locations and times necessary to bring about intricate and even mathematically precise biological patterns from a homogeneous primordium (Belousov, 2008; Ozga and Reinecke, 2003). In plant development, intricate and even mathematically precise structures are evident in leaf vascular networks (Pietak, 2009), the arrangements of leaves or branches on a stem (Jean, 1996), and as is explored here, in the arrangement of tissue in a developing ovary or flower bud. While the form of these structures remains undoubtedly influenced by molecular signals resulting from genetic expression, the mechanisms behind long-range pattern emergence from a homogeneous primordium remain an unsolved problem (Lander, 2007).

Various systems-focused answers have been proposed to account for the manifestation of long-range spatial organization in plant and animal development, and in reality a variety of different mechanisms may be simultaneously involved. Mechanisms for generating chemical patterns via differential diffusion of morphogenic chemicals, their inhibitors, and their interaction with genetic expression have been put forth (Koch and Meinhardt, 1994; Meinhardt, 1996). Other studies suggest cellular collectives can respond to mechanical stress fields generated in a growing embryo (Belousov, 2008). A radically alternative perspective sees a developing organ as a dynamic system self-trapping electromagnetic energy in a stable spatial pattern capable of informing phenomena such as cell polarization, orientation, genetic expression, and differentiation state. In other words, a trapped electromagnetic field
serves as a fundamental symmetry-breaking mechanism informing early morphogenetic events and processes.

Electromagnetism (EM) refers to the phenomenon of oscillating, coupled electric and magnetic fields which can propagate as a wave with amplitude, frequency, and wavelength. The frequency of the EM wave is related to its energy and instils it with different properties and interactions with materials. Lower frequency EM waves are used for radio broadcasts (~10^9 Hz), intermediate-range frequencies heat food in the microwave (~10^10 Hz), higher frequencies represent visual light (~10^12 Hz), and the highest correspond to ionizing radiation such as X- and gamma-rays (~10^19 Hz).

The prospect of endogenous EM production by biological systems, in a range from 10^11 to 10^12 Hz, was first developed by physicist Herbert Fröhlich in 1968 (Fröhlich, 1968a,b, 1975). More recently, quantum field theory (QFT) has been used to further elucidate the possibility of endogenous radiation in biological systems (Del Giudice et al., 1985, 2010; Preparata, 1995). Recent explorations using normal mode analysis of simulated microtubule structures have determined microtubules to be a likely source of endogenous EM up to several hundred gigahertz (Cifra et al., 2011b; Deriu et al., 2010). Microtubule vibrations may be stimulated by hydrolysis of GTP, motor protein–microtubule interactions, and energy efflux from mitochondria (Cifra et al., 2011b).

In addition, a number of experiments have directly detected non-thermal radiation in radio (Cifra et al., 2008; Pokorny et al., 2001), microwave (Gebbie and Miller, 1997), and visible-UV (Popp and Yan, 2002; Yan et al., 2005) frequencies from various organisms. Other experiments have shown cells and organisms respond in various distinct ways to externally applied non-ionizing radiation at powers low enough to avoid heating the tissue (Cifra et al., 2011a; Levin, 2003, 2009). In plants, applied low-power EM radiation in the range of 10^8–10^9 Hz results in changes to gene expression, aberrant meristem formation, altered patterns of cellular growth, and enhanced growth of the organism (Racicu and Mlclaus, 2007; Roux et al., 2008; Tafforeau et al., 2003; Tkalec et al., 2009). In a variety of plants, static electric fields have also been detected, and observed to be correlated to growth events and daily rhythms (Burr, 1942, 1945; Burr and Sippott, 1944; Leach, 1987). To the author’s knowledge, plant emissions of, or responses to, EM radiation in the range of 200–1000 GHz have not yet been explored.

On account of their physical make-up, developing plant organs may act as dielectric resonators, trapping EM energy in a spatial pattern. A dielectric is a material with molecules that become polarized (assume an electric charge separation) when the material is placed in an applied electric (static) or EM (time varying) field. This means the dielectric can support an internal electric field due to the creation of electric dipoles, and can thereby store energy as a capacitance. A dielectric resonator describes a dielectric that has trapped an EM wave in a characteristic spatial pattern (Staelin et al., 1994a; Wang and Zaki, 2007). This happens as when an EM wave travelling within a stronger dielectric medium hits an interface with a material of lower dielectric strength, some reflection of the incident EM wave occurs at the interface (Staelin et al., 1994b). Within the stronger dielectric’s interior, the incident and reflected waves interfere with one another. Depending on the geometry of the dielectric material and wavelength of the EM wave in the dielectric, certain patterns of radiation appear due to the superposition of incident and reflected waves off of internal boundaries. These highly characteristic spatial patterns are called the resonant modes of the dielectric structure, and occur only at specific frequencies of EM radiation. The resonant modes are quasi-standing wave patterns alternating in time between purely electric and purely magnetic field components (Wang and Zaki, 2007). If exposed to an electromagnetic source comprised of many frequencies the dielectric resonator acts as a filter, selecting only resonant frequencies from the broadband signal (Wang and Zaki, 2007).

| Non-ideal dielectric resonators lose energy with time. Electromagnetic energy may be lost due to leaking of fields from incomplete reflection off of internal boundaries. The lower the mismatch between the dielectric constant of the strong dielectric material and the dielectric constant of its surroundings, the lower the internal reflection, and the more leakage occurs due to EM field transmission across the boundary. Electromagnetic energy is also dissipated in lossy dielectrics due to conversion of EM energy into heat with delocalization and flow of charge carriers within the resonator. The quality factor (Q-factor) is the ratio of energy stored to the energy dissipated per oscillatory cycle. The Q-factor indicates how well the material will resonate. In general, Q-factors less than 0.5 will not support resonances and Q-factors greater than 0.5 will. The higher the Q-factor the longer a resonance will be supported after an initial energy input.

On account of its water content in the range of 85–96 wt%, a developing plant organ such as a zucchini ovary (Fig. 1A) is a relatively symmetric, cylindrically shaped organ expected to be a rather strong dielectric with an εr of approximately 40 at a frequency of 20 GHz (Nelson and Trabelsi, 2005; Sipahioglu and Barringer, 2003). Likewise, the acorn squash ovary and immature fruit have high water contents and an ellipsoidal geometry (Fig. 1B). Similarly, the developing early flower bud also has an ellipsoidal geometry (not shown). As a developing plant organ is surrounded by weakly dielectric air (εr = 1), any radiation produced within the organ, at frequencies high enough to generate wavelengths smaller than the organ diameter, would reflect from the internal air–tissue interface, leading to the formation of an EM resonant mode characteristic of a similarly shaped (ellipsoidal or cylindrical) dielectric. Of course, a strong dielectric loss is also expected for EM radiation in watery tissue for the applicable frequency range of 10^8–10^12 Hz (Gabriel and Lau, 1996; Liebe et al., 1991). These loss characteristics must be accounted for in any model assessing the feasibility of the hypothesis of plants as EM resonators.

As a well-defined geometric structure existing distinguished from the remaining flower anatomy from an early developmental stage, the cucurbit ovary is a particularly straightforward case for considering EM mode formation in plant development. Changes in the ovary cross-section from the primordial (embryonic) stage through to maturity are outlined in Fig. 2. The cucurbit ovary primordium appears as a distinguished structure from the flower (i.e. the petals, stigma, and style) early in development when flower
primordia measure approximately 0.3 mm in length (Pereira, 1968). The ovary continues to develop below the remaining flower structures as an inferior ovary, and if pollinated, develops directly into the mature fruit. When the ovary primordium first appears, and until reaching a cross-sectional radius of approximately 0.6 mm, there is no discernable pattern within the cellular collective (Fig. 2A). However, shortly after this stage (i.e. cross-sectional radius ~0.7 mm) the symmetry of the collective is broken with the appearance of three axes with spiral-like structures of opposing curl existing at the periphery (Fig. 2B). As the ovary primordium continues to develop, these structures become more pronounced while conserving their initial form (Fig. 2C). The spiral-axes become lines of placental tissue, while the geometric centre of the spirals becomes the site of ova formation. The ova go on to become the seeds of the mature fruit. Remarkably, the essential nature of the original pattern found in the ovary primordium appears to remain conserved in the set fruit, which is approximately 200 times larger than the primordium from which it arose (Fig. 2D).

While EM resonances may exist at any developmental stage, this work focuses on the dimensions of the form at the time of the first symmetry-breaking (i.e. cucurbit ovary primordia dimensions on the order of ~0.5 mm radius). In development, cells proceed along various pathways of differentiation to become more and more specialized. The main role of an EM resonance is thus hypothesized to create positional information for undifferentiated cells to respond to, in order to create spatial patterns of different tissue types. Once differentiated, cells may no longer respond to EM fields in the same way.

In this work the resonant frequencies and spatial patterns of EM-modes forming on dielectric structures with similar geometries, dimensions, dielectric permittivities, and dielectric loss tangents to developing plant ovaries and flower buds were estimated using a finite element analysis (FEA) model. Electromagnetic finite element analysis is a preeminent numerical method for finding appropriate solutions to full-wave Maxwell’s equations on a three-dimensional geometry and material of interest (Jin, 2002). The resulting FEA-modelled EM resonant mode patterns were comprehensively compared to tissue patterns in developing ovaries, male flower buds, and a variety of mature fruits. The Q-factors of EM modes forming on models with similar permittivity and loss characteristics to those of watery tissue were used as a gauge of the physical feasibility of EM resonance in developing plant organs.

2. Theory

In order to effectively model plant tissue in FEA, realistic values for the passive electrical properties (dielectric permittivity and loss) were required over a large frequency range from 1 to 1000 GHz.

In the time-dependent case of an applied EM field, the relative electric permittivity becomes a complex number, \( \varepsilon_r \), with real component \( \varepsilon_r' \) reflecting the energy storage due to electrical polarization, and imaginary component \( \varepsilon_r'' \) reflecting the energy loss due to movement of polarizable charges in phase with the electric field (\( j^2 = -1 \)):

\[
\varepsilon_r = \varepsilon_r' + j\varepsilon_r''
\]  

Under time-varying applied fields of frequency \( v \), the sample's capacitance (\( C \)) and conductivity (\( \sigma \)) are measured to define the parameters \( \varepsilon_r' \) and \( \varepsilon_r'' \) where (Pethig and Kell, 1987):

\[
\varepsilon_r'(v) \propto \frac{C(v)}{\varepsilon_0}
\]  

and

\[
\varepsilon_r''(v) = \frac{\sigma(v)}{2\pi v\varepsilon_0}
\]

The loss characteristics of a dielectric are typically expressed in terms of the dielectric loss tangent, \( \tan \delta \):

\[
\tan \delta = \frac{\varepsilon_r''}{\varepsilon_r'}
\]

In the frequency range above 1 GHz, the passive electrical properties of biological tissues are proportional to their water content. For instance, tissues such as the vitreous humour, which contain a very high water content of 95%, have dielectric permittivities and loss characteristics almost identical to those of water (Fig. 3A and B), whereas cartilage, with a lower water content of 75%, shows similar, but non-identical dielectric permittivity and loss characteristics (Fig. 3A and B). The permittivity and loss values in Fig. 3A and B were obtained from parametric models of the frequency–response of tissues (Gabriel and Lau, 1996). Similarly, plants with high water contents (85–95%) have electrical properties converging towards those of water with increasing water content of the tissue (Nelson and Trabelsi, 2005).

While the passive electrical properties of water have been well characterized over a wide frequency range (Jiang and Wu, 2004; Liebe et al., 1991), those of plant and animal tissues have only been characterized up to ~100 GHz. As this present investigation required the electrical properties of plant tissue in a range from 1 to 1000 GHz, it has been assumed that, on account of the high water content of plant materials considered in this work, their electrical properties from 1 to 1000 GHz will be similar to those of water.

The dielectric permittivity and loss tangent of water over the range from 1 to 1000 GHz used in FEA modelling are shown in Fig. 3C and D. The electrical properties of water from 1 to 350 GHz were obtained from a parametric model (Meissner and Wentz, 2004), whereas values from 350 to 1000 GHz were obtained from actual measurements of water at 19°C (Liebe et al., 1991).
3. Materials and Methods

3.1. Plant Samples and Microscopy

This study considered cross-sectional patterns in ovary primordia with cross-sectional radii ranging from ~0.5 to 1 mm from acorn squash (Cucurbita pepo), butternut squash (Cucurbita moschata), and zucchini (C. pepo); the early development of acorn squash male flower primordia with cross-sectional radius from 0.5 to 0.7 mm; and the set fruits of cucurbit-family plants acorn squash, butternut squash, zucchini, watermelon (Citrullus lanatus), and cucumber (Cucumis sativus).

Acorn, butternut, and zucchini squash plants were grown in an experimental garden (Kingston, Ontario, Canada). A total of ten ovary primordia from five different plants of each of the three squash types were selected at various stages of early development. In addition, a total of 10 male flower primordia were selected from five acorn squash plants for microscopic inspection. Thin sections were carefully cut from fresh samples with a tissue blade. Sections were stained with methylene blue, and were investigated by light microscopy (Amscope T490-B, USA) at 80× and 200× magnification.

Tissue patterns in set fruits were also investigated. Sections were taken from the set fruit (cross-sectional radii ranging from 20 to 200 mm) from acorn squash, butternut squash, cucumber, watermelon, and zucchini fruits. Five samples of each fruit were cut into cross and longitudinal sections and photographed using a digital camera.

3.2. Finite Element Analysis Modelling

A finite element analysis (FEA) model was used to identify the forms and resonant frequencies of EM resonant modes on dielectric structures intended to simulate developing plant organs (ovaries and flower buds). The eigenmode solver of Ansoft HFSS 13.0 software (Ansys, USA) was utilized in all simulations.

As all organs considered in this study assumed either a cylindrical or ellipsoidal geometry (Fig. 1), the FEA model considered dielectrics shaped as cylinders ($r = 0.5$ mm, $h = 0.5$ mm), and ellipsoids ($r_1 = 0.5$ mm, $r_2 = 0.625$ mm). The dimensions used in the model approximated those of cucurbit ovaries when patterning was first observed to arise (as shown in Fig. 2), and in correspondence with the observations of Pereira (1968). The number of tetrahedral mesh elements increased dramatically with increasing EM frequency, with a minimum of 9000 elements in the cylinder and a minimum of 10,000 elements in the ellipsoid. Typical models utilized 35,000 tetrahedral mesh elements. A maximum of 55,000 mesh elements was used for highest frequencies.

The FEA model first considered dielectrics without loss (conductivity of 0). Values of resonant frequencies change with dielectric permittivity, and the dielectric permittivity of water varies with frequency. To deal with this issue, modes were calculated for a range of dielectric permittivities from $\varepsilon_r = 3.5$–100. The frequencies of the resulting modes were considered alongside the frequency-dependent permittivity of water (Fig. 3C). In the FEA model, the permittivity of the modelled dielectric was incrementally adjusted until it was consistent with the permittivity of water in the range...
of the resonant mode frequencies calculated. Using this manual iterative procedure, a final value of $\varepsilon_r = 5$ was found to be approximately consistent with the permittivity of water in the range of relevant mode frequencies produced for the model dimensions considered. Thus, $\varepsilon_r = 5$ was used in all reported modelling results.

Dielectric loss was then introduced to the models in the form of a conductivity $\sigma$ or representative of a loss tangent via Eqs. (3) and (4). The Q-factors of modes as a function of loss tangent were evaluated at the frequency of the mode for a range of loss values below and exceeding those of water (as shown in Fig. 3D).

### 3.3. Definition of Mode Pattern Series on Dielectric Cylinders and Ellipsoids

Three different EM mode pattern series, all of them common to both cylindrical and ellipsoidal geometries, were found to be of relevance to ovary, bud, and fruit structural patterns (Fig. 4).

In the most basic pattern series, the cross-sectional view of the electric field features pairs of electric field spirals appearing sequentially as the mode frequency increases (Fig. 4 top row). This basic pattern series is referred to here as the electric spiral (ES) series, with the mode number indicated as a number after the pattern series name. The electric field of the first four ES modes in cross-section is shown in Fig. 4. The three-dimensional characteristics of the electric field of the ES3 mode are shown in Fig. 5. The magnetic field (not shown) is strongest at the centre of the electric field spirals and is oriented in the longitudinal plane, perpendicular to electric field direction.

Other pattern series of significance were electric spiral modes contained within one or more radial wavelengths reducing the ES pattern to a smaller zone closer to the centre. These pattern series are here referred to as the contained electric spiral (CES) series and the double contained electric spiral (DCES) series, with cross-sectional electric fields shown in Fig. 4 middle and bottom rows, respectively. In all modes, the magnetic field (not shown) is strongest at the centre of the electric field spirals and is oriented in the longitudinal plane.

All modes in the ES, CES, and DCES pattern series are three-dimensional constructs consisting of electric and magnetic field components, and repeating the cross-sectional pattern continuously along the mid-section of the longitudinal direction. This can be seen in the three-dimensional electric field patterns of the ES3 mode forming on a dielectric ellipsoid (Fig. 5A) and a cylinder (Fig. 5C). The conserved cross-sectional patterns of the electric field of the ES3 mode on an ellipsoid and cylinder are shown in Fig. 5B and D, respectively.

### 3.4. Schematics

While different plant species may respond to the hypothetical EM radiation in different ways, in all organs examined a consistent algorithm involving key features of the mode pattern was apparent. A schematic representing this consistent algorithm was prepared for each relevant mode by using computer drawing software (Photoshop CS4, Adobe, USA) to trace over the FEA-derived electric field pattern and superimposed magnetic flux pattern of the mode using the following rules.

<table>
<thead>
<tr>
<th>Electric Spiral Series (ES)</th>
<th>Mode 1</th>
<th>Mode 2</th>
<th>Mode 3</th>
<th>Mode 4</th>
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<tbody>
<tr>
<td>Contained Electric Spiral Series (CES)</td>
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<tr>
<td>Double Contained Electric Spiral Series (DCES)</td>
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![Fig. 4. Cross-sectional electric field patterns of three EM resonant mode series characteristic of dielectric cylinders and ellipsoids. Top row shows the electric field of the first four modes of the electric spiral (ES) series. Middle and bottom rows show the electric field of the first four modes of the contained electric spiral series (CES) and the double contained electric spiral series (DCES), respectively. Field strengths are represented in colour code with red (black) showing highest and dark blue (white) the lowest field strength. Magnetic fields (not shown) are strongest at the centre of electric field spirals and are oriented perpendicular to the cross-sectional plane. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of the article.)](image)
Firstly, in all organs evaluated, axes consisting of a significant tissue structure (i.e. septa, placental lines) distinctly related to the electric field component of the mode pattern were observed. These axes of the modelled electric fields are labelled axis 'a' in schematics of Figs. 6–8. Alternate axes in relation to the electric field patterns are labelled axis 'b' in schematics of Figs. 6–8.

Secondly, the location of highest magnetic flux density was labelled zone 'c' in the schematics of Figs. 6–8.

Thirdly, different circumferential zones of the EM mode pattern were labelled zones 'c' and 'd' in the schematics of Figs. 6–8.

Finally, secondary magnetic flux density nodes were labelled 'd' in the schematics of Figs. 6–8.

3.5. Image Analysis

Images obtained from plant investigations and FEA models of EM resonant modes fields were quantified using a consistent set of geometric measurements relating to the location of main pattern features (outlined in Fig. 9). The main features in ovary/fruit/flower cross-sections were hypothesized to correspond to the main pattern features of the electric and magnetic field cross sections of EM resonant modes.

Image measurements were performed in ImageJ 1.43u (NIST, USA), selecting features manually and using built-in commands to fit circular zones and measure areas and angles. Measurements of EM resonant mode features were made on an image with the electric field represented by a vector field and the magnetic flux as a superimposed gradient (as shown in Fig. 9). Point markers were used to identify the central location of ova/seeds or the central location of magnetic flux density maxima (red dots in Fig. 9A and B), and to define the circular boundaries and axes shown in Fig. 9. Note that all area regions defined were normalized to the total area of the circular mesocarp region or the mode exterior (the perimeter marked as region 4 in Fig. 9).

The cross-sectional tissue patterns in ovaries/set fruit of acorn, butternut, and zucchini squash shared visible similarities, and therefore these three varieties were all hypothesized to correspond to the CES3 mode pattern. For the CES3 mode, the \( q = 13 \) pattern parameters were defined as:

1. **Main axes angles**: The five angles between the main axes of the spiral pattern, where main axes were defined as the placental line or the midway-point between two ova in plants (see Fig. 9). Angles were measured progressively from a common start position to retain their independence as variables.

2. **Flux axes angles**: The five angles between the flux axes, which are defined as lines passing through the central region and the ova of plants or flux maxima marker or modes. Angles were
Fig. 6. Striking parallels exist between the tissue patterns of a developing cucurbit ovary (panel A) and the electric field (panel B) and magnetic flux (panel C) of the CES3 electromagnetic resonant mode forming on an ellipsoidal or cylindrical dielectric. Note that all patterns shown are cross-sections of 3D geometries. Placental lines (p) form in response to highest electric field (panels A and B). Ovum development (O) begins at the six regions of highest magnetic flux (panels A and C). A circumferential region corresponding to the mesocarp (M) and separate from the endocarp (E) exists in the ovary and electric field pattern of the CES3 mode (panels A and B). The exocarp (X) appeared unrelated to mode features. A schematic illustrating the combined effects of the electric and magnetic fields as a systematic tissue response is shown in panel D. Black scale-bar in panel A shows 250 μm. Field strengths are represented in colour code with red (black) showing highest and dark blue (white) the lowest field strength. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of the article.)

<table>
<thead>
<tr>
<th>Development</th>
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<th>Magnetic Flux</th>
<th>Schematic</th>
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<td>![Electric Field Image]</td>
<td>![Magnetic Flux Image]</td>
<td>![Schematic Image]</td>
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<tr>
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<td>![Electric Field Image]</td>
<td>![Magnetic Flux Image]</td>
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Fig. 7. Additional patterns in cucurbit ovaries (top row) and male flower bud development (bottom row). First column shows plant cross-sections, second column shows electric field component of mode in cross-section, third column shows the magnetic flux of mode in cross section, and final column shows schematics based on hypothetical systematic tissue response to mode patterns. In one cucurbit ovary a pattern corresponding to the CES4 mode was discovered (top row). The male flower bud pollen tube (p) development is consistent with an ES15 mode (bottom row). Scale-bar in top row image shows 100 μm, while scale bar in bottom row image shows 250 μm. Field strengths are represented in colour code with red (black) showing highest and dark blue (white) the lowest field strength. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of the article.)
<table>
<thead>
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<tr>
<td>Squash</td>
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<tr>
<td>Cucumber</td>
<td><img src="image7" alt="Electric Field" /></td>
<td><img src="image8" alt="Magnetic Flux" /></td>
<td><img src="image9" alt="Schematic" /></td>
</tr>
</tbody>
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**Fig. 8.** Comparisons between cross-sectional tissue patterns in mature cucurbit-family fruits and cross-sectional EM mode structure. In order from top to bottom, the first column shows cross-sections of watermelon, zucchini squash, and cucumber. Second column shows electric field maps of the compared EM mode pattern in cross-section. Third column shows magnetic flux density in cross-section. Fourth column shows schematic representation of apparent fruit response to hypothetical EM radiation patterns with $P_{fit}$ listed. The colour legend used for electric field and magnetic flux diagrams indicates highest fields in red (black) and lowest fields in dark blue (white). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of the article.)

**Fig. 9.** A definition of axes, regions, and angles used to parameterize and compare images from plant cross-sections and EM resonant modes from FEA. Panel A shows the main features for the superposition of electric (vector field) and magnetic (density gradient) fields of the CES3 mode shown in cross-section. Panel B shows the main features for the butternut squash ovary primordium in cross-section (radius ~ 0.7 mm). (For interpretation of the references to color in the text, the reader is referred to the web version of the article.)

measured progressively from a common start position to retain their independence as variables.

3. **Inner region ratio:** The normalized area of an inner circular region defined by three dark-stained nodes in developing ovaries or the central region of the EM mode. The perimeter of the boundary is marked as region 1 in **Fig. 9.** This parameter was included for consistency with mode patterns with a large central region such as ES15.
4. Flux region ratio: The normalized area of a circular region with a boundary passing through the centre of ova or flux maxima with perimeter marked as region 2 in Fig. 9.

5. Contained region ratio: The normalized area of a circular region with a boundary corresponding to the division between the endocarp and mesocarp in plant ovaries or the exterior of the spiral pattern in the mode, marked as region 3 in Fig. 9.

Similar parameter sets were defined for other mode and tissue patterns studied (ES3, ES15, DCES3).

The parameter set obtained from image analysis allowed comparisons to be made between patterns forming in cucurbit ovaries for different species/varieties (butternut squash, acorn squash, and zucchini squash) and developmental stages (primordia and set fruit). Measurements were made for cross-sectional images of three replicates from each variety (butternut squash, acorn squash, and zucchini squash) at two developmental stages (early: cross-sectional radius 0.6–1.2 mm; and late: cross-sectional radius 20–40 mm). The resulting parameter sets were compared in SPSS 17.0 software (IBM, USA). Independent samples t-tests were used to assess differences between early and late stages of plant pattern for each parameter in the set within each variety group, with p < 0.05 taken to be indicative of a significant difference in a parameter.

When no statistically significant differences were found between any parameter in early or late developmental stages of any of the three varieties, one-way analysis of variance (ANOVA) tests with Bonferroni post hoc comparisons were used on each parameter to detect differences between species, with p < 0.05 taken to be significant.

Image analysis also allowed for an assessment of the similarity between patterns forming in plant samples and the electromagnetic fields of EM resonant modes. A probability of fit (Pfit) was obtained for a plant tissue image to a particular resonant mode using the Chi² test of independence. Here, the set of q EM mode parameters (indexed as j) were taken to be the expected values (Ej), and the plant tissue features were taken to be the observed values (Oj) with the Chi² statistic (χ²) calculated as:

$$\chi^2 = \sum_{j=1}^{q} \frac{(O_j - E_j)^2}{E_j}$$

A Pfit value was obtained by consulting the χ² distribution with q – 1 degrees of freedom. The χ² model was tested by introducing quantified variation to the ideal parameters, demonstrating that a Pfit value of 83% represents a 20% variation between the observed and expected parameter set.

Comparisons were made between parameter sets representing the averages of three biological samples (N = 3) in butternut acorn, acorn squash, and zucchini ovary primordia and mature fruits with features of the CES3 mode. The Pfit was also used to assess image similarities in cross-sections of mature cucurbit-family fruits watermelon (N = 3) and cucumber (N = 3) with comparisons to ES3 and DCES3 mode features, respectively. Cross-sections of male acorn squash flower primordia (N = 3) were compared with the pattern of ES15. The similarities between an acorn squash bud with four main axes and the CES4 mode were also assessed by calculating a Pfit value (N = 1).

4. Results

4.1. Cucurbit Ovary Pattern Study

Patterns were found to be highly conserved amongst the three different squash varieties and at different developmental stages within each variety. No statistically significant differences in any of the 13 parameters (key image feature measurements) were found between the primordial patterns of a cucurbit variety and their respective patterns as set fruit (all p > 0.05 in independent t-tests). Comparing parameters for the three different varieties using ANOVA, only the flux angles 1 and 3 of zucchini showed significant differences with the acorn and butternut squash samples. All samples, with the effect becoming more pronounced in zucchini plants, showed an alternating pattern indicating opposing ova were attracted towards one another (this is evident in the inner middle, and outer circular regions were highly conserved (p > 0.05) in all three varieties.

These similarities between the patterns of different cucurbit varieties indicate the existence of a similar shared physiological mechanism. The similarities between primordial and mature stage patterns indicate that the tissue pattern remains invariant after the early symmetry-breaking process in the ovary primordium. The average parameter values and standard error of the mean of butternut or acorn squash and zucchini in comparison to the “ideal” values obtained from the CES3 mode are summarized in Table 1.

4.2. Parallels Between Developing Organs and EM Mode Patterns

Striking parallels (Pfit = 98.7–99.99%) were observed between tissue patterns of a developing cucurbit ovary (Fig. 6A) and the electric field (Fig. 6B) and magnetic flux (Fig. 6C) of a CES3 resonant mode forming on a dielectric cylinder or ellipsoid. Placental lines (p) appeared in regions coincident with the highest electric field strength of the CES3 mode (compare Fig. 6A and B). Ovum development (O) was coincident with the six regions of highest magnetic flux of the CES3 mode (compare Fig. 6A and C). A circumferential region corresponding to the primordial mesocarp (M) and separate from the developing endocarp (E) was found to exist in both the cucurbit ovary and electric field pattern of the CES3 mode (Fig. 6A and B). A schematic illustrating the proposed combined effects of the electric field and magnetic flux as a tissue response is shown in Fig. 6D. Cucurbit ovaries from acorn, butternut, and zucchini squash plants all showed a similar pattern to that shown in Fig. 6A. The observed features of cucurbit ovaries were also consistent with the three-dimensional characteristics of the CES3 mode.
with consistent tissue patterning observed in the longitudinal sections.

The details of pattern formation in cucurbit ovaries, and their correspondence to the CES3 mode electric field pattern, are shown in Fig. 10. There is a distinct correspondence between the whole CES3 mode (Fig. 10C) and the full view of cucurbit cross sections at early (panel A) and intermediate (panel B) stages of development. The patterns contain a highly symmetric triple axis consisting of placental lines forming at the centre of ovaries at early (Fig. 10D) and intermediate (Fig. 10E) stages of development, which correspond to the central view of the CES3 mode (Fig. 10F). Cells at early (Fig. 10G) and intermediate stages (Fig. 10H) are oriented in similar curl patterns to the back-to-back electric field spirals of the CES3 mode (Fig. 10I). Similarly, both early (Fig. 10J) and intermediate (Fig. 10K) stage ovary primordia feature regions where cells are oriented into curl patterns corresponding to the facing electric field spirals of the CES3 mode (Fig. 10L).

As the ovary matured, the pattern remained conserved but assumed a multicellular character (Fig. 10B, E, H, K).

In one of the 10 acorn squash ovaries inspected, a pattern based on a 4-fold symmetry was found with features in direct correspondence to a CES4 mode with $P_{fit} = 99.99\%$ (Fig. 7, top row). Tissue was observed to be developing in a manner consistent with that found in the more common 3-fold symmetry ovaries paralleling the ES3 mode. Cells in developing placental lines were clearly aligned with the electric field direction to form 4 sets of back-to-back spirals intersecting at a cross at the centre (Fig. 7, top row). Similarly, ovum formation was beginning at the 8 sites of highest magnetic flux at the centre of each electric field spiral (Fig. 7, top row).

The earliest development observed in male flowers of acorn squash concerned the formation of pollen tubes ‘p’ at the periphery of the developing flower bud (Fig. 7, bottom row). Similar to the developing ovary, patterns were observed in early stage buds with cross-sectional radii of approximately 0.5 mm. The pattern of pollen tube development was consistent with the features of an ES15 mode ($P_{fit} = 99.2\%$). Fifteen sets of back-to-back spiral-like septa formed close to the perimeter of the ellipsoidal bud, and pollen formation was coincident with the 30 sites of maximum magnetic flux density (Fig. 7, bottom row). The proportions of developing pollen tube length in relation to cross-sectional diameter are consistent in the male bud and the electric field spirals of the ES15 mode (Fig. 7, bottom row). Notably, in all 10 male flower buds observed, 15 sets of developing pollen tubes (30 in total) were consistently observed.
4.3. Patterns in Mature Fruits

In the *cucurbitacea* plant family, fruits arise directly from the ovary without merging with the remaining female flower anatomy, and are therefore likely to show a correspondence between first symmetry breaking in the ovary and the set fruit.

In the squashes (acorn, butternut, and zucchini), cucumber, and watermelon, tissue fibres corresponding to placental line remnants were observed aligned with the 'o' axis of electric field, while seed formation was coincident with the site of highest magnetic flux at the centre of electric field spirals in zone 'c' (Fig. 8).

Watermelon showed minimal distance between the endocarp and the rind, which is consistent with the geometry of an ES3 mode with $P_{\text{fit}} = 81.4\%$ (Fig. 8). The squashes acorn, butternut, and zucchini all shared a similar pattern featuring a distinct rim of mesocarp tissue surrounding a section of endocarp, with dimensions coinciding with those of a CES3 mode and $P_{\text{fit}}$ of 96.7, 99.99, and 88.6%, respectively (Fig. 8). The cucumber showed the largest region of endocarp to mesocarp, as well as variable-density tissue surrounding the endocarp, all of which correspond to features of a DCES3 mode with $P_{\text{fit}} = 99.8\%$ (Fig. 8).

The features of all fruits examined were consistent with the three-dimensional characteristics of the EM modes. In general, all EM modes consisted of a cross-sectional pattern featuring an arrangement of electric field spirals which were repeated consistently through the midsection of the longitudinal dimension.

4.4. Resonant Mode Frequency and Feasibility in Plant Primordia

The resonant frequency of modes in each of the four pattern series (i.e. the ES, CES, DCES, and TCES) were calculated for a model with a similar radius ($r = 0.5$ mm) to that observed at the onset of patterning in squash ovaries (see Fig. 2A). A dielectric permittivity of $\varepsilon'_r = 5$ was used in all models as it is consistent with the actual permittivity of water in the range of the calculated mode frequencies (Fig. 3C). Using these parameters, the frequency range for EM
modes of relevance to developing ovaries (i.e. ES1, ES3, CES3, CES10, DCES3, TCESS) was found to span from 150 to 1000 GHz (Fig. 11A). The Q-factor of these modes was found to increase consistently with the mode's resonant frequency (Fig. 11B) indicating higher-order modes resonate more effectively than lower-order modes.

Dielectric loss was introduced to the models and computations were repeated for the ES3 mode with progressively increasing dielectric loss tangents. While the Q-factor of the ES3 mode dropped precipitously with increasing loss, it remained well above the physical cut-off limit for resonance (Q>0.5) even for loss values exceeding those of water in the frequency range of the mode (Fig. 11C).

5. Discussion

It is well established that molecular signals play essential roles in development. However, there remains little understanding of how these substances can be synthesized, transported, and act at the specific locations and times necessary to bring about intricate and even mathematically precise biological patterns emerging spontaneously from a homogeneous primordium. The radically alternative perspective presented herein sees a developing organ as a dynamic system self-trapping EM energy in a stable spatial pattern hypothesized to inform phenomena such as cell orientation, directions of preferred growth, genetic expression, and differentiation state. Notably, the hypothesis of tissue as a dielectric resonator was previously developed for plant leaves (Pietak, 2011), and a similar concept applicable to single cells was introduced independently by Popp et al. (2005) and explored by Cifra (2010).

The results show the three-dimensional tissue structure of cucurbit ovaries, male flower buds, and cucurbit fruits show remarkable similarities with three-dimensional EM resonant mode patterns calculated using a FEA model of a dielectric with similar electrical and geometric properties to the developing plant organs. Main organ features such as placental lines and septa follow electric field spirals and form in relation to high electric field strength. Other features, such as ova/seeds and pollen tubes appear in locations correlated with areas of high magnetic field. Ultimately, the concept of EM resonant modes helps account for early spontaneous emergence of patterns from an initially homogeneous collective of cells. Electromagnetic resonance also helps to explain how highly conserved patterns can be created in different organs on the same plant, different plants, and plants of different species.

The high water content of plant tissue yields a relatively high permittivity, but also a high loss characteristic. The feasibility of this hypothesis of plants as dielectric resonators rests in part on the capacity for lossy tissue to support EM modes. Finite element analysis modelling demonstrated EM modes could be supported in the lossy organ if the mode is generated within an early developmental structure of comparable dimensions to the penetration depth of the resonant EM radiation. Even with loss characteristics exceeding those expected for water at 150–1000 GHz, the Q-factor of resonant modes remained above 0.5, demonstrating the physical capacity for resonant modes in plant tissue.

Observations of cucurbit ovary primordia indicate that once the symmetry has been broken early in development, a relatively consistent pattern remains through to organ maturation and even the set fruit, with no statistically significant changes detected in individual pattern parameters between the primordia and set fruit stages. Therefore, it is suggested that the EM resonant mode acts only during a sensitive early stage of the organ where it instigates an initial symmetry-breaking. Subsequent changes in tissue character would be mediated purely by molecular-genetic mechanisms.

In this study, cell orientation was observed aligned with hypothetical electric field direction, and different kinds of tissue differentiation were correlated to respective areas of high electric or magnetic fields. There are several ways that the electric and magnetic field components of an EM resonant mode may influence cellular behaviour in a developing primordium, including: (i) direct effects of electric and magnetic fields on cell behaviour, (ii) electrothoretic movement of charged ions, and (iii) dielectrophoretic movement/aggregation of neutral molecular and macromolecular components in response to electric field gradients.

The activity of electric fields in developing and regenerating biological systems has been particularly well documented (Levin, 2003, 2009). The application of physiologically relevant electric fields (≈50 mV/mm) can change the orientation of cells to lay parallel or perpendicular to field lines, induce migration of cells towards the positive or negative poles of the field (galvanotaxis), and can influence the direction of preferred growth in relation to field polarity (Hinkle et al., 1981; Levin, 2009; Zhao et al., 1999). Weak electric fields and intercellular ion flow have also been observed to influence embryonic and stem cell differentiation states (Garrattalla et al., 1985; Harrington and Becker, 1973; Levin, 2003, 2009). Biological voltage gradients and ion flow have also been associated with control of cell proliferation and controlled apoptosis (Levin, 2009). Weak magnetic fields have been observed to induce changes in ion flux through cell membranes and altered cell growth characteristics (Blackman et al., 1994; Lednev, 1991).

Electrical signals may be converted into second-messenger biochemical signal cascades through mechanisms such as (Levin, 2009; McCaig et al., 2005): (i) electric field modulation of voltage-sensitive ion channels, (ii) modulation of voltage-sensitive small molecule transporters, (iii) the spatial redistribution of electrically charged receptors on the surface of the cell, (iv) direction-specific electroendosmosis of morphogenic substances through the biological system, (v) signalling through electrically induced changes in membrane protein shape, and (vi) effects of field on genetic expression via affects on ion transporters in the nuclear membrane.

Dielectrophoresis describes force exerted on a dielectric particle when it is in the vicinity of a non-uniform static or time-varying electric field (Pohl, 1978). The force depends on the dielectric properties of the particle relative to those of the background medium. For biological systems in the frequency range of 1–1000 GHz, the permittivity of water exceeds that of proteins, lipids, and biopolymers. Thus, biomolecular and macromolecular substances would be expected to migrate towards areas of lowest electric field. Dielectrophoresis may therefore alter the three-dimensional distribution of morphogenetic substances in relation to a static or dynamic electric field, leading to changes in cell differentiation state and other features such as proliferation rates.

The specific mode selected by a plant organ may result from a convergence of multiple constraining factors. As mentioned above, it is hypothesized that the primordium is only sensitive to EM radiation for a window of time early in development. The dimensions and permittivity of the developing plant organ at the time it is sensitive to EM radiation define the minimum frequency that can create a resonance in the system. Generally in resonant systems, the primary excitation is the fundamental mode of lowest frequency. However, higher frequency modes are more physically feasible considering (i) that modelling indicated Q-factors of resonant modes decreased with increasing mode frequency, (ii) that the loss characteristics of water increase at frequencies decreasing from 1000 GHz leading to further decreases in lower mode Q-factors, and (iii) that the mode Q-factors are close to the threshold physical minimum of 0.5. Therefore, modes appearing in the plant organ may be the lowest mode that can be physically supported given these three existing constraints.

It is important to note that the EM source does not need to be coherent to excite a resonance in a dielectric. A dielectric resonator can be excited by an incoherent multi-frequency radiation signal.
In this scenario, the resonator will select only its resonant frequencies from the broadband signal. For this reason, dielectric resonance principles are used to create frequency filters for EM signals (Wang and Zaki, 2007). The EM resonant mode may be excited by incoherent radiation produced endogenously. In addition, incoherent black-body radiation of thermal origin may be capable of stimulating resonance in small (a radius of 0.5 mm or less) biological structures. In the frequency range above 100 GHz and at a temperature of 20 °C, the power of black-body radiation is significant and increases dramatically with increasing frequency. Moreover, water is a high emissivity substance. The suitability of various potential excitation sources for EM resonance in plant tissue will be the subject of future work.

To date and the best of the author's knowledge, little to no experimental reports have measured the effects of EM radiation in the range of 200–1000 GHz on plant tissue, nor have any attempted to measure endogenous EM radiation in this range from plant tissue. This is likely the case as there have been no reasons to investigate EM radiation in the context of plant tissue in this range. In light of the evidence presented herein, experiments to detect or influence the proposed developmental EM mechanism are warranted.

6. Conclusions

Tissue patterns in developing cucurbit ovaries, male flower buds, and mature fruits were found to show significant correlations with electromagnetic modes forming on similarly shaped dielectrics.

On account of the unique properties and characteristics of electromagnetic phenomenon, it is not possible to obtain identical patterns to those of an electromagnetic resonator from other wave phenomena such as reaction-diffusion of molecules or mechanical stress distributions. Nor are the patterns formed by an electromagnetic resonator of an arbitrary or ubiquitous nature. Therefore, the very strong correspondence between electromagnetic resonant mode patterns of dielectric structures and biological patterns in cucurbit ovaries/fruits, including the positioning of main biological features such as septa, placental lines, and ovum/seed, supports the existence of endogenous EM radiation.

Ultimately, the concept of EM resonant modes explains how pattern formation can emerge spontaneously from a previously homogeneous collective of cells, and how highly conserved patterns can be organized in different organs on the same plant, different plants, and plants of different species.

Experimental investigations to detect or disturb EM radiation in these plants are warranted. The proven existence of endogenous EM radiation would revolutionize the biological sciences by introducing a radically new mechanism underlying morphogenesis.

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