

# Radio frequency plasma capacitor can increase rates of seeds imbibition, germination, and radicle growth

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**Abstract.** Cold atmospheric pressure plasma jets are used in agriculture for the treatment of seeds and plants but they generate reactive oxygen and nitrogen species (RONS) that can induce multiple side effects such as redox reactions, peroxidation, acidification of bio-tissue and genotoxic side effects. Here, we show that the treatment of *Phaseolus vulgaris* L. (bush bean) and *Cucurbita pepo* L. (pumpkin) seeds by a plasma ball or flat plasma panel can also accelerate seed imbibition, germination, and radicle growing rates. Generated by the plasma lamps, high frequency electromagnetic fields and photons can penetrate seed coats and modify their surface properties. Atomic force microscope data show that the plasma ball treatment induced corrugation of seed coats, produces pores and surface defects. The plasma lamp treatment of seeds caused the hydrophilisation of seed coats and decreased the apparent contact angle between a water drop and the seed surface, thereby improving the wetting properties of seeds surfaces. Magnetic resonance imaging (MRI) studies showed acceleration of water uptake in seeds exposed to a plasma lamp. Treatment using a plasma lamp had no side effects but was not as effective as treatment by a cold atmospheric pressure plasma jet. Plasma lamps can be used in agriculture for the acceleration of seed germination, increasing growth of plant seedlings, poration and corrugation of the bio-tissue surfaces without the side effects of RONS generated by plasma jets.

**Keywords:** cold atmospheric pressure plasma jet, *Cucurbita pepo* L., electroporation, germination, imbibition, *Phaseolus vulgaris* L., plasma ball, plasma lamp, radicle growth, radio frequency capacitor, seed growth.

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## Introduction

Cold atmospheric pressure plasma jet (CAPPJ) treatment is a highly efficient method of protecting seeds, plants, flowers, fruits and trees from diseases and infection, and improve crop yield (Filipov *et al.* 2007; Bormashenko *et al.* 2012, 2015; Ling *et al.* 2014, 2015; da Silva *et al.* 2017; Sivachandiran and Khacel 2017; Volkov *et al.* 2017, 2019a, 2019b). CAPPJ has effects on the speed of seed imbibition and germination, plant growth, nutrient uptake and enzymatic and ion channel activities (Zhou *et al.* 2016; Volkov *et al.* 2017, 2019a, 2019b). CAPPJ can induce gene expression and has an influence on ion transport and bio-electrochemical characteristics of plant tissue. There are a few different methods of seed treatment by CAPPJ. Treatment of seeds by cold atmospheric pressure helium- or argon-plasma jet is an effective method for acceleration of seed imbibition and germination (Volkov *et al.* 2019a) but it is a rather expensive method. Some companies in Europe produce multi-jet equipment for treatment of large amounts of seeds in agriculture. It would be interesting to use a plasma ball or its

modification, the plasma panel, as an inexpensive and affordable method for pre-sowing seed treatment.

A plasma ball (also called plasma lamp, globe, dome, sphere, plasma panel, Tesla ball) is a clear glass lamp filled with a combination of noble gases (Ar, Ne, Kr, Xe) at atmospheric pressure with an electrode in the centre of the sphere (Tesla 1894; Linardakis and Borg 2008; Campanell *et al.* 2010; Burin *et al.* 2015; Rusakova *et al.* 2017). Plasma inside the ball and seeds outside act as the plates of a radio frequency capacitor (RFC) and the glass wall is a dielectric between them (Fig. 1a).

While the plasma inside a plasma ball is surrounded by a glass wall and does not produce reactive oxygen and nitrogen species (RONS) outside the ball, the high frequency outside the plasma ball does propagate electromagnetic radiation. Radio frequency field produced by plasma balls can interfere with some electronic devices. Plasma lamps were developed by Tesla (1894) and their physical properties were investigated recently (Burin *et al.* 2015; Campanell *et al.* 2010; Rusakova *et al.* 2017; Volkov *et al.* 2019a). Commercial

plasma lamps (balls) can be used for electrostimulation of seeds and plants (Volkov *et al.* 2019a, 2019b). The effects of electrical fields on vegetation have been the subject of research since the 19th century (Solly 1846; Lemström 1904; Murr 1963; Shabala *et al.* 2003; Volkov 2006, 2012a, 2012b).

Plasma balls are safe for seed treatment but cold atmospheric pressure plasma jet can induce side effects such as RONS, peroxidation of lipids, damage of proteins and genotoxic effects of UV photons.

Both methods (CAPPJ and plasma lamp) generate strong high frequency electromagnetic fields that penetrate seeds or other biological tissues. Both emit visible light but the CAPPJ also emits UV radiation. The main difference between these two methods is the emission of RONS, ions, electrons and neutral molecules by CAPPJ. Examples of RONS produced by CAPPJ include O, O\*, O<sub>2</sub>\*, O<sub>3</sub>, N, N<sup>+</sup>, NO, NO<sub>2</sub>, N<sub>2</sub>O, NO<sub>3</sub>, N<sub>2</sub>O<sub>5</sub>, H, H<sub>2</sub>, OH, H<sub>2</sub>O, H<sub>2</sub>O<sub>2</sub>, HO<sub>2</sub>, HNO, HNO<sub>2</sub> and HNO<sub>3</sub>. The most stable compounds are HNO<sub>3</sub>, H<sub>2</sub>O<sub>2</sub>, O<sub>3</sub> and NO<sub>x</sub>. UV light from CAPPJ can disinfect seed surfaces and has antibacterial and antifungal properties; however, RONS can have side effects and produce damage of a bio-tissue (Lackmann *et al.* 2013; Randeniya and de Groot 2015).

In this paper, we have attempted to study mechanisms of seeds responses to our new method of treatment by the RFC of the plasma lamp.

## Materials and methods

### Seeds

Seeds of *Phaseolus vulgaris* L. (bush bean) cv. Dragon's Tongue were received from Catbird Seat Garden Center (Madison, Alabama, USA) and from Johnny's Selected Seeds (Winslow, Maine, USA). The mean length of the dormant seed was 1.47 cm (median, 1.50 cm; s.d., 0.12; s.e., 0.03; *n*, 20).

Seeds of *Cucurbita pepo* L. (pumpkin) cv. Cinderella were received from Bioelectrochemistry LLC (Madison, Alabama, USA). Several hundred seeds were removed from pumpkins, rinsed and dried for 7 days. The mean germination rate of imbibed *C. pepo* seeds was 96.00% (median, 100.00%; s.d., 19.69; s.e., 1.97; confidence interval (95%), 3.91; confidence interval (99%), 5.17; *n*, 100).

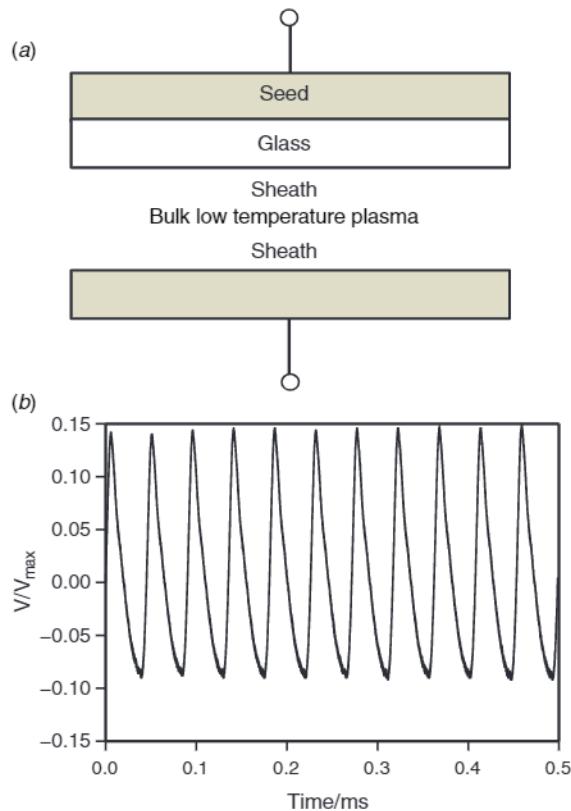
All experiments were performed on healthy seeds. The humidity in the laboratory was kept at 40– 0%. The temperature of the air was 21°C.

### Chemicals

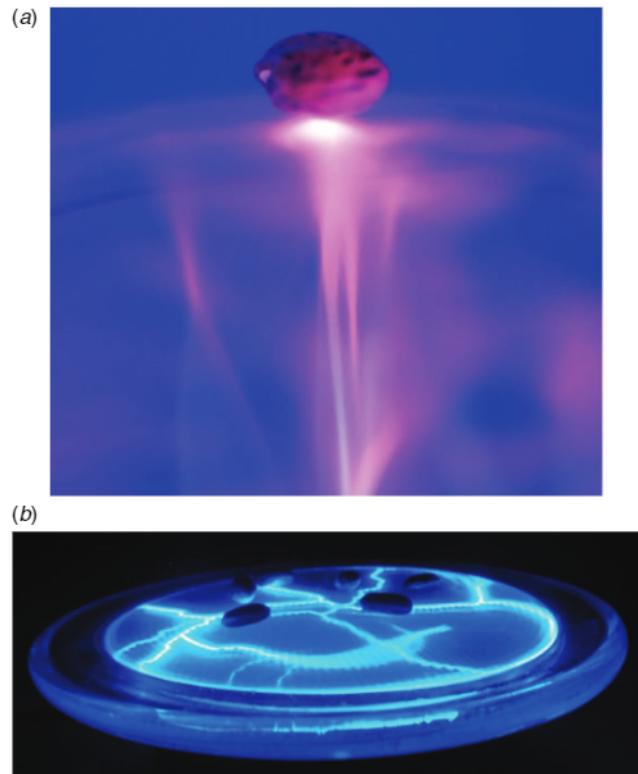
Ozone test strips (Macherey-Nagel Co.) were used to determine the ozone concentration in the air near the surface of a plasma ball and the plasma jet.

### Plasma lamps

A common commercial plasma Nebula Plasma Ball (Theefun) was used as a radio frequency capacitor (RFC) for electrostimulation of the seeds (Fig. 2a). The plasma ball is a 20.32-cm diameter clear borosilicate (Pyrex) glass sphere filled with low pressure rare gases such as neon or argon. The plasma is generated inside the ball by a high voltage AC signal from the central bulb. If a seed is placed on the outer surface of the plasma ball or near the ball, capacitive coupling can



**Fig. 1.** (a) Radio frequency plasma capacitor and (b) electrical oscillations near the surface of a plasma ball.



**Fig. 2.** Electrostimulation of seeds by (a) plasma ball and (b) flat plasma panel lamp.

energise a high voltage load up to several kV with a frequency of 21.86 kHz (Fig. 1b). The electrical signal generated by the plasma ball is not confined by the glass sphere but propagates into the ambient air as electromagnetic interference (EMI). The EMI was measured with a PR-55 high voltage probe connected to a oscilloscope (MDO3024, Tektronix). The amplitude of the electrical signal, located at 1 cm from the plasma ball, was 628 V. Detection of ozone at the surface of our plasma balls by commercial ozone test strips did not show production of ozone in the air. Visible light and UV-A radiation can penetrate through the glass surface of the plasma ball.

The surface temperature of the plasma lamps was 21°C during the duration of the study. An infrared laser thermometer was used to measure the temperature of air, seeds and plasma lamps. A common commercial plasma super bright flat panel (6'plasma plate Lumin Disk, BetterJonny) was used as RFC for electrostimulation of a large amount of seeds (Fig. 2b).

#### Atomic force microscope

The surface of seeds was analysed using the Pico-Plus atomic force microscope (AFM; Agilent Technologies) as described by Volkov *et al.* (2019a). The AFM creates a 3D representation of the sample surface by monitoring the force of interaction between the seed surface and a cantilever probe. AFM can be used to obtain topographical images of seeds in their natural state without surface damage. Seeds of *P. vulgaris* were placed on top of a microscope cover glass (22 × 22 mm) and images were topographically obtained using the contact mode of the AFM. The 3D topographic images of the *P. vulgaris* seeds were then analysed. The software Gwyddion-2.51 (<http://gwyddion.net/>, verified 28 October 2020) was used as a tool for AFM data visualisation and analysis.

#### Magnetic resonance imaging

The seeds were imaged using a 9.4T system (BioSpec, Bruker BioSpin GmbH) equipped with a surface coil as a receiver (Volkov *et al.* 2019a). Axial T2-weighted images were acquired with a T2-weighted fast spin echo sequence (rapid acquisition with relaxation enhancement). The parameters were as follows: TR, 2500 ms; TE, 36 ms; rare factor, 8; field of view, 20 × 20 mm; matrix size, 200 × 200 mm (10 slices); slice thickness, 1 mm; average of 120 signals; total acquisition time of 2 h 5 min for each state (open or closed).

#### Images

A photo camera Nikon D3x with AF-S Micro Nikkor 105 mm 1:2.8 G ED VR lens (Nikon Instruments) was used for the photography of plants.

#### Statistics

All experimental results were repeated at least 16 times using different plants. Software SigmaPlot 12 (Systat Software Inc.) was used for statistical analysis of experimental data.

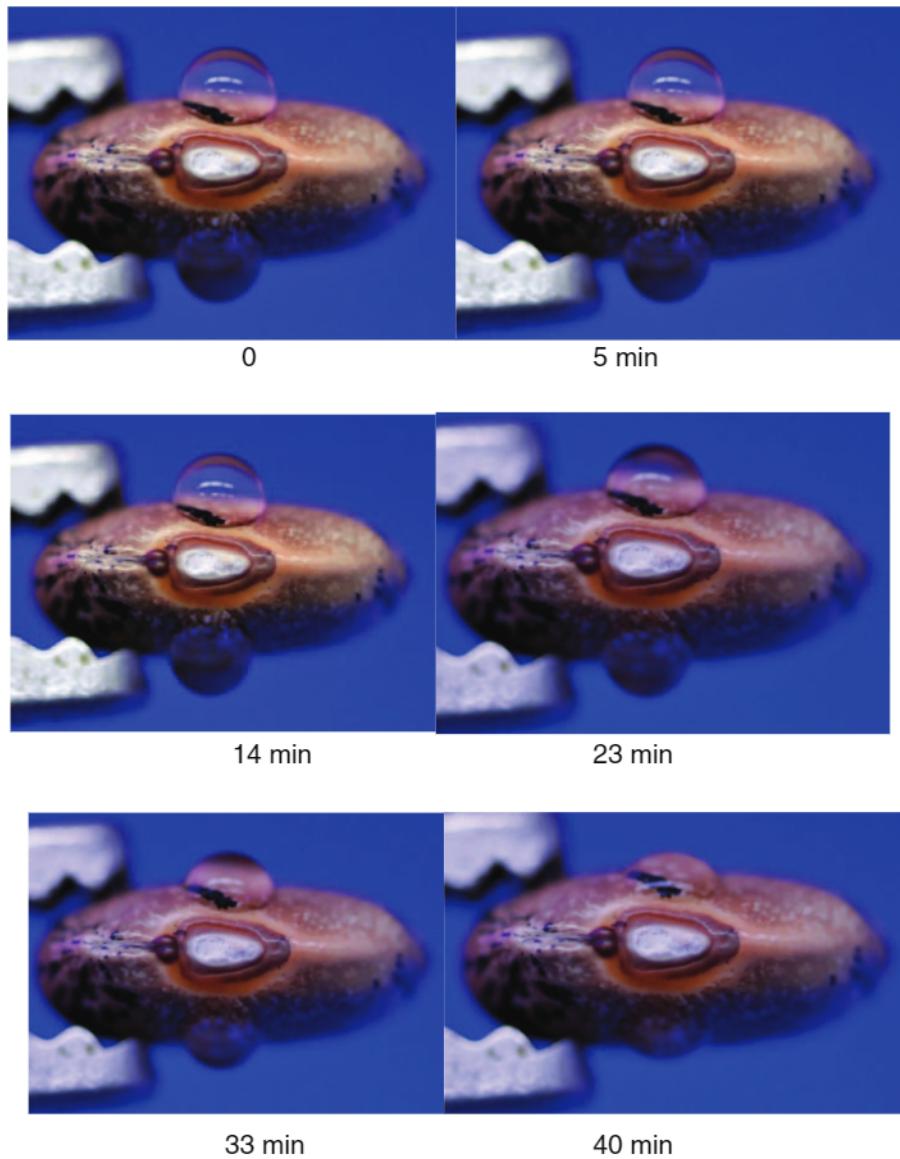
## Results

### Imbibition and germination of seeds

Treatment of dormant seeds by the plasma lamp can induce poration, corrugation and hydrophilisation of the seed's surface without direct contact between plasma and seeds. The roughness of a seed's surface can affect its wetting properties, with various roughness causing differential attraction or repulsion of water (Volkov *et al.* 1998). Such an effect can be explained by the fact that at a contact angle  $\theta < 90^\circ$  for a smooth surface, water penetrates into the cavities of the surface. This improves the wetting of a seed with a rough surface. At  $\theta > 90^\circ$ , water does not penetrate into seed cavities and this decreases the wetting of a rough surface. Roughness makes a hydrophilic surface even more hydrophilic as well as a hydrophobic surface even more hydrophobic. On real seed surfaces, which are usually rough, one must distinguish between the Young contact angle ( $\theta$ ) and the apparent contact angle ( $\theta_A$ ). In the case of a rough surface, the Young contact angle is measured between the tangent to the water-air interface and the tangent to the local seed surface. The apparent contact angle is measured between the tangent to the water-air interface and the macroscopic seed surface.

Fig. 3 shows that decreasing the  $\theta_A$  of the dormant seed coat surface and penetration of a water drop into seed without a treatment by a plasma ball is slow. Formation of hydrophilic pores in a seed coat was detected with water drop experiments (Fig. 4). Drops of pure water (placed on the top and bottom of the seed) penetrated inside dormant seeds following treatment by a RFC (Fig. 4). A water drop on the bottom of a seed does not fall down under the gravitational force because of the balance of gravitational and capillary forces. Penetration of aqueous drops through the seed coat of a dormant *P. vulgaris* seed is induced by the difference of water potentials outside and inside the seed. Formation of hydrophilic pores and surface defects in the seed coats of *P. vulgaris* seeds, induced by cold plasma jet, can facilitate water transport during imbibition and germination processes. Redox interactions of RONS, generated by plasma, with the organic compounds on the seed surface can induce formation of hydrophilic compounds and groups. Hydrophilisation of seed coats and decreasing the  $\theta_A$  of water drops on the surface of seed coat takes place during absorption of a water drop (Fig. 4).

A pulsed electric field was used to create pores in seed coats for the acceleration of water and RONS absorption by the seeds. An estimate of the size of pores or defects required to create hydrophilic surfaces sufficient to hold water droplets under a seed (Fig. 4) can be done from a phase equilibrium energy analysis. In the case where three phases meet a solid seed coat, liquid water and gaseous air, the system as a whole tends to minimise the total value of surface energy. The behaviour of such a system depends upon the ratio between the values of surface energies on all three interfaces: seed-water, seed-air and water-air. If the energy of the interaction between the molecules of water and the seed is greater than that between the water and air, the aqueous phase will tend to occupy a greater area on the surface of a seed, thereby replacing the molecules of air in the same volume. The equilibrium state, corresponding to a minimum of total surface



**Fig. 3.** Kinetics of 10  $\mu\text{L}$  water drops penetrating the seed coat of a dormant seed of *Phaseolus vulgaris* L. (bush bean) cv. Dragon's Tongue from the top and from the bottom of the seed. Seed has not been treated by plasma lamp.

energy of the system, will be achieved when the energy gain due to replacement of air by water is compensated by expended energy due to increased surface area of liquid (Ksenzhek and Volkov 1998).

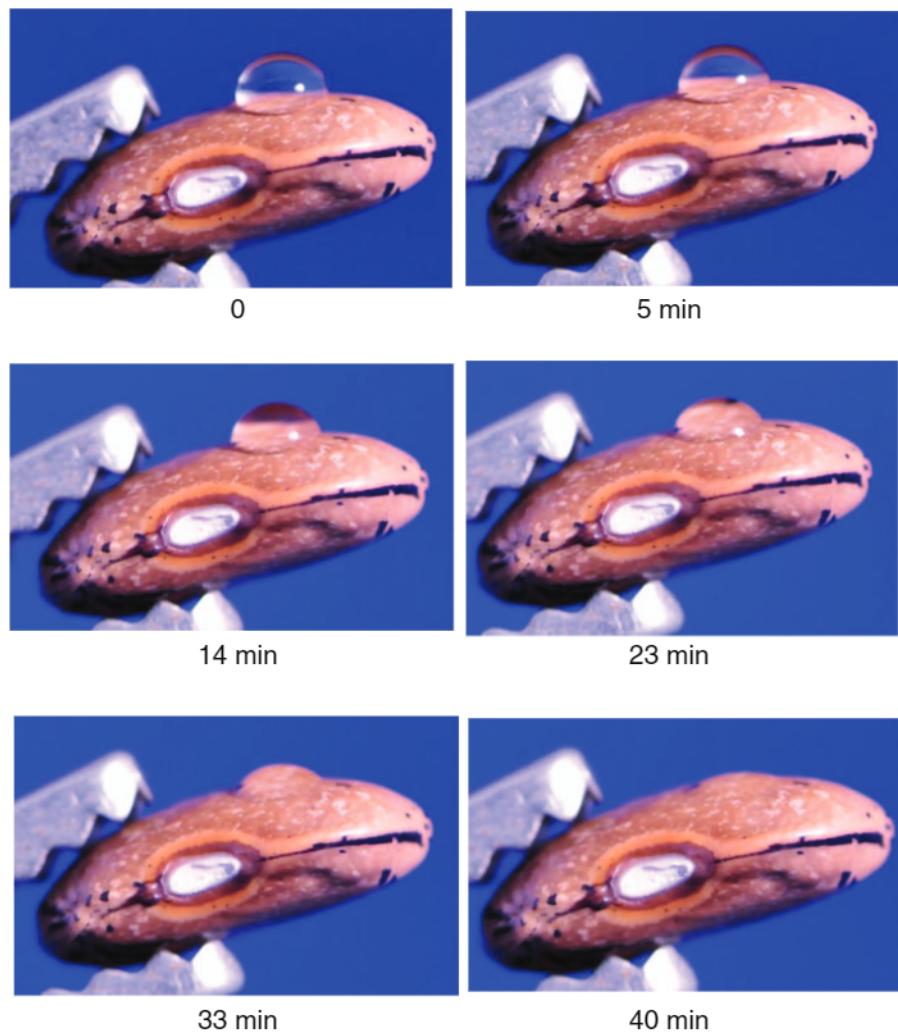
Difference in water potentials inside and outside the seed coat allows water to penetrate through the seed coat. Formation of surface defects and hydrophilic pores in seed coats will accelerate water transport, imbibition and germination of *P. vulgaris* seeds.

The treatment of seeds by plasma lamps accelerated their germination and radicle development (Figs 5, 6; Table 1). Radicle is the embryonic root that will develop into the primary root of the plant. It is usually the first part of the embryo to push its way out of the seed during

germination. Radical length increased after treatment with a plasma lamp.

#### *Atomic force microscope imaging to measure corrugation of seed coats by plasma*

AFM topographic images show changes to the seed surface of dormant seeds of *P. vulgaris* (Fig. 7) and *C. pepo* (Fig. 8) before and after plasma ball treatment. Dormant seeds have flat surfaces with some roughness of the seed cover (Figs 7, 8), while seeds treated with the plasma showed significant changes in the seed topography of both *P. vulgaris* (Fig. 7) and *C. pepo* (Fig. 8). When the seeds were placed on the surface of a plasma ball, corrugation of the seed coat became



**Fig. 4.** Kinetics of 10 µL water drops penetrating the seed coat of a dormant seed of *Phaseolus vulgaris* L. (bush bean) cv. Dragon's Tongue that has been treated by a flat plasma panel lamp for 15 min (Fig. 2).

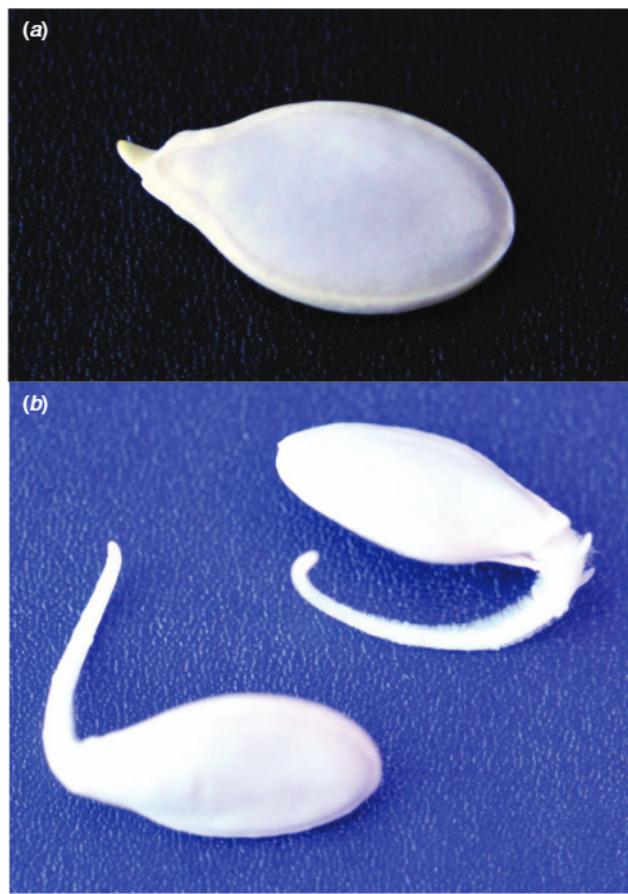
**Table 1. Radical length of seeds of *Phaseolus vulgaris* L. (bush bean) cv. Dragon's Tongue after treatment with a radio frequency plasma capacitor for 1 min. After treatment, seeds were incubated in water for 7 h**

Treatment	Radicle length, mm (n, 20 for both plant spp.)				
	Mean (cm)	Median (cm)	s.d.	s.e.	Confidence intervals (95%, 99%)
Plasma ball surface	2.70	2.50	0.52	0.12	0.24, 0.33
Flat plasma panel lamp	2.77	2.90	0.60	0.13	0.28, 0.38
Control, untreated	1.80	1.55	0.67	0.15	0.31, 0.43

visible (Figs 7, 8). The plasma ball radio frequency electromagnetic field can also lead to the formation of pores in a seed coat. As shown earlier by Volkov *et al.* 2019a, a treatment by CAPPJ on the dormant seeds created even more corrugation of the seed surface with clear spots of pore

formation indicated by the dark red and black spots in the AFM map.

AFM is a powerful tool that can measure the topography of very small surfaces with accuracy. Images of surface topography of seeds obtained by AFM is commonly



**Fig. 5.** Germination of imbibed seeds of *Cucurbita pepo* L. (pumpkin) cv. Cinderella pumpkin at 4 days after incubation in water for 7 h. (a) control, untreated seed and (b) seed treated by a flat plasma panel lamp for 15 min.

displayed as a pseudo-colour plot representing the different relative heights of the surface. However, as the colours are auto-scaled for each given image, they are not wholly useful for cross-comparison.

#### *Magnetic resonance imaging of seeds imbibition*

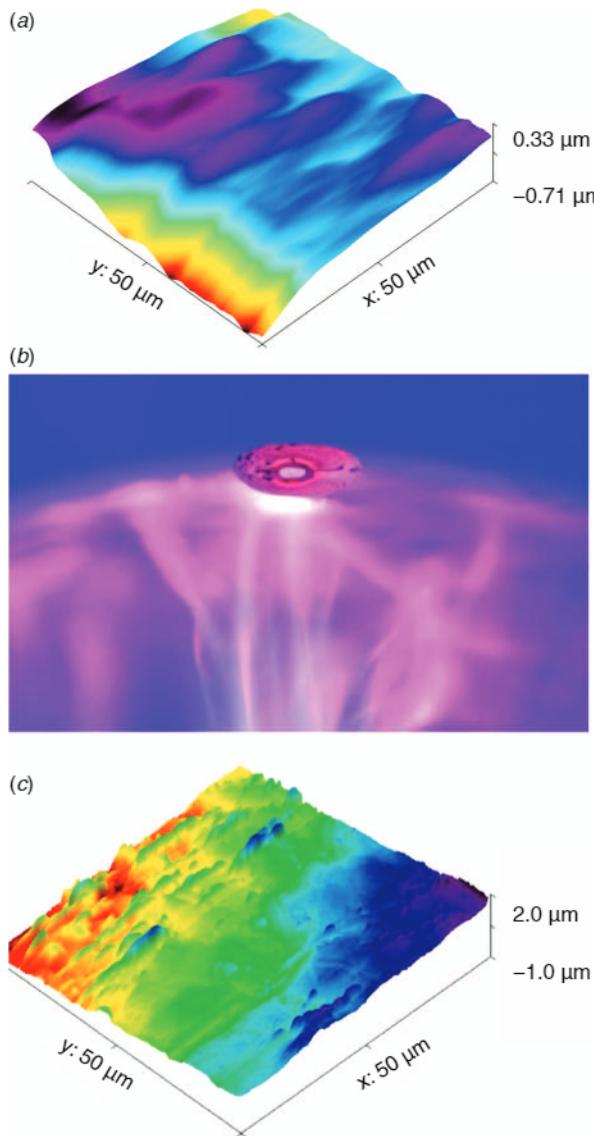
Non-invasive MRI allows us to obtain a spatial representation of the water distribution in seeds. MRI results of the *P. vulgaris* seed water content are in Fig. 9. The images show the presence of water in both dormant (Fig. 9a) and imbibed seeds (Fig. 9b, 9c). According to the literature, dormant seeds contain 5–18% moisture. Fig. 9a shows that dormant seeds have tiny inherent water content (small grey spot in the centre of the image). The imbibed seeds in Fig. 9b were not treated by cold plasma, while imbibed seeds in Fig. 9c were treated by a plasma ball for 15 min. Water content increased in the imbibed seeds treated by a plasma ball. This is likely due to plasma-induced electroporation and corrugation of seed coats that enhanced the penetration of water penetration into seeds. MRI studies show enhancement of water uptake in seeds treated with a plasma ball. Treatment of seeds by cold plasma before imbibing water clearly increased the aqueous content inside the seeds (Fig. 9).



**Fig. 6.** Germination of imbibed seeds of *Phaseolus vulgaris* L. (bush bean) cv. Dragon's Tongue 2 days after incubation in water for 7 h. Seeds were located for 1 min on the (a) plasma ball surface, (b) flat plasma panel lamp and (c) control, untreated.

#### **Discussion**

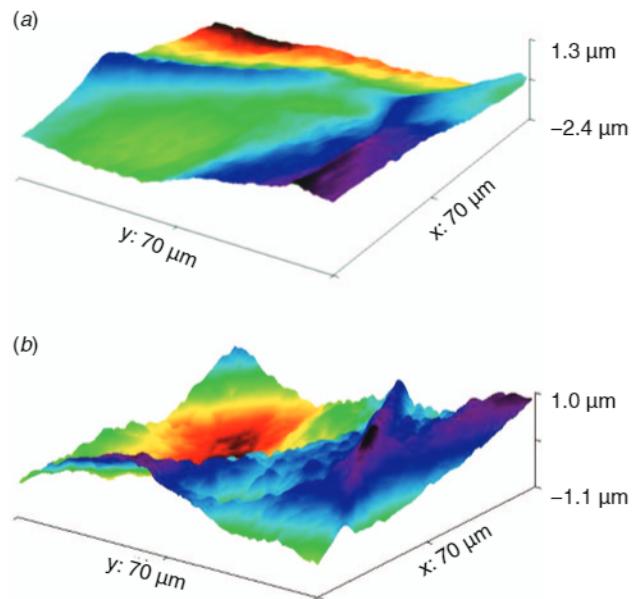
Plasma lamps induce strong radio frequency electromagnetic radiation, which may induce electroporation of seeds (Figs 4, 7, 8). The mechanism responsible for the effect of a plasma ball on the speed of seed germination and plant growth is still



**Fig. 7.** Atomic force microscope (AFM) topographic imaging of a surface of a dormant seed of *Phaseolus vulgaris* L. (bush bean) cv. Dragons Tongue (a) before treatment by plasma ball, (b) at the surface of a plasma ball and (c) after treatment by plasma ball for 15 min. The surface heights are shown on the z-axis scale and the colour plots in each image correspond to their respective height scales.

debatable. This is because seeds are an extremely complex biological object and the effect of a plasma ball on seeds can occur by modifying the surface of seeds, electroporation and strong radio-frequency electromagnetic field.

Plasma balls and flat plasma panels also accelerated the imbibition of seeds (Figs 4, 5, 6) and germination (Fig. 5, 6). Due to the significant differences between the plasma ball and plasma jet power sources and operating conditions, it was not possible to replicate the field of the plasma ball with the jet. The plasma jet is designed to specifically shield out the EMI except where the plasma actually exits. Separating the

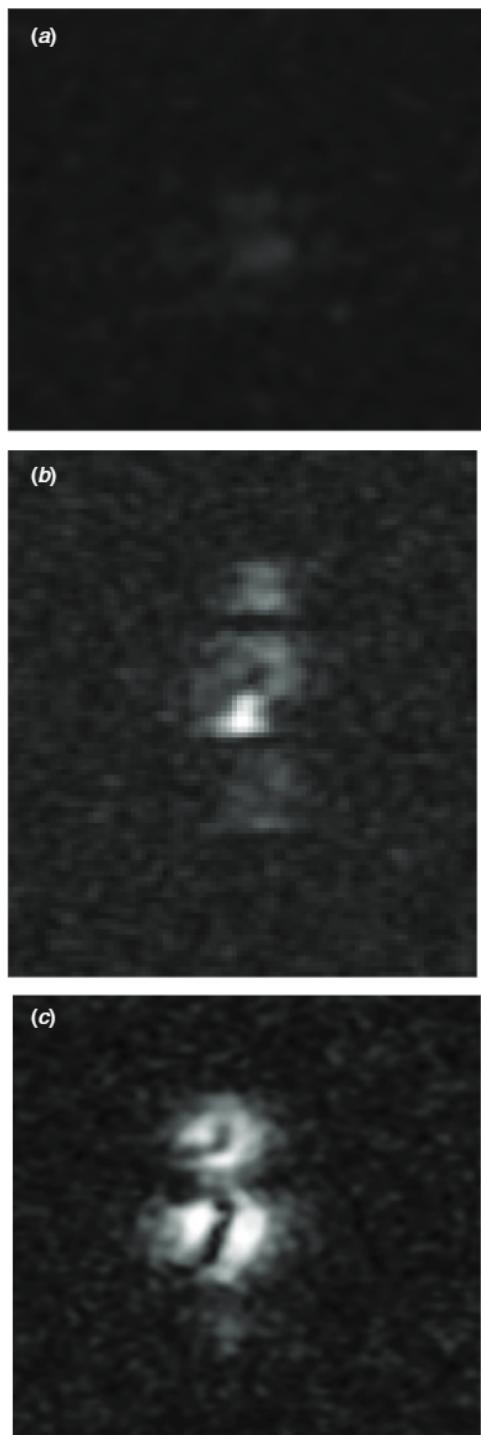


**Fig. 8.** Atomic force microscope (AFM) topographic imaging of a surface of a dormant seed of *Cucurbita pepo* L. (pumpkin) cv. Cinderella seed (a) before and (b) after treatment by plasma ball for 15 min. The surface heights are shown on the z-axis scale and the colour plots in each image correspond to their respective height scales.

electromagnetic component from the plasma jet would be difficult and cause interferences with electronics. Thus, the use of the plasma ball seemed a reasonable test to determine if the radio frequency electromagnetic field alone could have an effect. The helium plasma jet produces a strong oscillating electromagnetic field, UV-Vis and RONS while the plasma ball induced effects of the radio frequency electromagnetic field and UVA-Vis. Comparison of MRI and AFM for plasma jet (Volkov *et al.* 2017, 2019a, 2019b) and plasma lamps shows that RONS and strong high frequency oscillating electromagnetic field from plasma jet are more efficient in seed poration than the electrical field from the plasma lamp.

The initial absorption of water by seeds is primarily a physical process of hydration and osmosis. Water permeation across seed coats can occur by the partition mechanism or through pores and surface defects (Volkov *et al.* 1997, 1998, 2012). Partition transport through a thick seed coat into the seed can be extremely slow, thus the observed fast water transport across thick coats occurs through hydrophilic pores and surface defects.

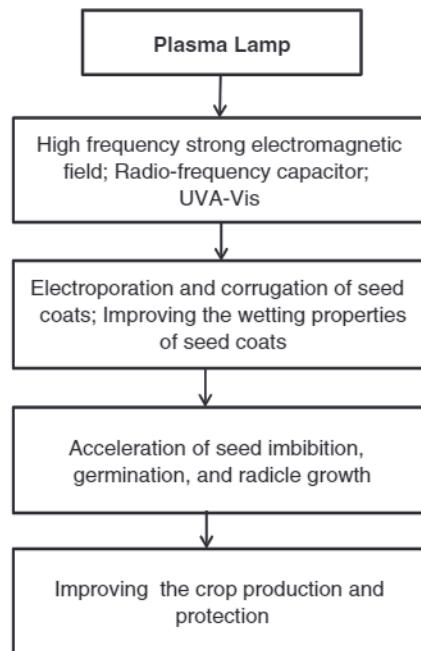
Understanding the mechanisms of CAPPJ and plasma lamp interaction with seeds and plants could promote plasma-based technology for the production of 'plasma seeds' (Filipov *et al.* 2007), better control of plant developmental, increased yield, growth rates and protection of plants from pathogens. Our work offers new insight into mechanisms that trigger water transport and absorbance, seed germination and activation of metabolism by cold plasmas. Fig. 10 presents a scheme of plasma lamps interaction with seeds.



**Fig. 9.** Magnetic resonance imaging (MRI) of dormant seed of *Phaseolus vulgaris* L. (bush bean) cv. Dragon's Tongue imbibed in water for 7 h. (a) Control, untreated, (b) after treatment by a flat plasma panel lamp and (c) after treatment with a plasma ball for 15 min. Imbibed water in the seeds appears as the white regions in the images.

## Conclusions

Our new method of electrostimulation of seeds by RFC of plasma lamps can accelerate seed imbibition (Figs 4–7) and



**Fig. 10.** Schematic diagram of interaction of a plasma lamp with seeds.

germination (Figs 6, 7). Radio frequency electromagnetic field and UVA-Vis photons generated by a plasma lamp can penetrate into seed coats and modify their surface properties (Figs 4, 8, 9). AFM data shows that a plasma ball increases corrugation of seed coats, surface defects and pores in the seed coat. These structural deformations can enhance water uptake by seeds during the imbibing process, accelerate seed germination and increase the speed of seedling growth. The plasma lamp treatments of seeds produce hydrophilisation of seed coats and decrease the  $\theta_A$  between a water drop and the seed surface, thereby improving the wetting properties of seed surfaces. MRI studies show the acceleration of water uptake in seeds treated by RFC of a plasma lamp. Corrugation and electroporation by electromagnetic fields with UV-Vis photons is more efficient than electroporation by electromagnetic field only. The treatment of seeds by an RFC can also accelerate rates of seed imbibition, germination and radicle growth. RFC of plasma lamps can be used in agriculture for acceleration of seed germination, increasing growth of plants seedlings, poration and corrugation of the bio-tissue surfaces without the side effects of reactive oxygen and nitrogen species and genotoxic processes generated by plasma jets.

## Conflicts of interest

The authors declare no conflicts of interest.

## Acknowledgements

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## References

Bormashenko E, Grynyov R, Bormashenko Y, Drori E (2012) Cold radiofrequency plasma treatment modifies wettability and germination speed of plant seeds. *Scientific Reports* **2**, 741. doi:[10.1038/srep00741](https://doi.org/10.1038/srep00741)

Bormashenko E, Shapira Y, Grynyov R, Whyman G, Bormashenko Y, Drori E (2015) Interaction of cold radiofrequency plasma with seeds of beans (*Phaseolus vulgaris*). *Journal of Experimental Botany* **66**, 4013–4021. doi:[10.1093/jxb/erv206](https://doi.org/10.1093/jxb/erv206)

Burin MJ, Simons GG, Ceja HG, Zweber SJ, Nagy A, Brunkhorst C (2015) On filament structure and propagation within a commercial plasma globe. *Physics of Plasmas* **22**, 053509. doi:[10.1063/1.4919939](https://doi.org/10.1063/1.4919939)

Campanell MD, Laird JN, Provost T, Vasquez SW, Zweber SJ (2010) Measurements of the motion of filaments in a plasma ball. *Physics of Plasmas* **17**, 053507. doi:[10.1063/1.3406546](https://doi.org/10.1063/1.3406546)

da Silva ARM, Farias ML, da Silva DLS, Vitoriano JO, Alves-Junior C (2017) Using atmospheric plasma to increase wettability, imbibition and germination of physically dormant seeds of *Mimosa caesalpiniifolia*. *Colloids and Surfaces. B, Biointerfaces* **157**, 280–285. doi:[10.1016/j.colsurfb.2017.05.063](https://doi.org/10.1016/j.colsurfb.2017.05.063)

Filipov AK, Fedorov MA, Filipov DA (2007) Method of pre-sowing treatment of plant seeds. Russian patent RU2293456C1.

Ksenzhek OS, Volkov AG (1998) 'Plant energetics.' (Academic Press: San Diego, CA, USA.)

Lackmann JW, Schneider S, Edengeiser E, Jarzina F, Brinckmann S, Steinborn E, Harenith M, Benedikt J, Bandow JE (2013) Photons and particles emitted from cold atmospheric-pressure plasma inactivate bacteria and biomolecules independently and synergistically. *Journal of the Royal Society, Interface* **10**, 20130591. doi:[10.1098/rsif.2013.0591](https://doi.org/10.1098/rsif.2013.0591)

Lemström K (1904) 'Electricity in agriculture and horticulture.' (Electrician Publications: London, UK.)

Linardakis P, Borg G (2008) Harmonic and intermodulation distortion output of a radio-frequency plasma capacitor. *IEEE Microwave and Wireless Components Letters* **18**, 164–166. doi:[10.1109/LMWC.2008.916777](https://doi.org/10.1109/LMWC.2008.916777)

Ling L, Jiafrng J, Jiangang L, Minchog S, Xin H, Hanliang S, Yuanhua D (2014) Effects of cold plasma treatment on seed germination and seedling growth of soybean. *Scientific Reports* **4**, 5859. doi:[10.1038/srep05859](https://doi.org/10.1038/srep05859)

Ling L, Jiangang L, Minchog S, Clunlei Z, Yuanhua D (2015) Cold plasma treatment enhances oilseed rape seed germination under drought stress. *Scientific Reports* **5**, 13033. doi:[10.1038/srep13033](https://doi.org/10.1038/srep13033)

Murr LE (1963) Plant growth response in a simulated electric field-environment. *Nature* **200**, 490–491. doi:[10.1038/200490b0](https://doi.org/10.1038/200490b0)

Randeniya LK, de Groot GJB (2015) Non-thermal plasma treatment of agricultural seeds for stimulation of germination, removal of surface contamination and other benefits: a review. *Plasma Processes and Polymers* **12**, 608–623. doi:[10.1002/ppap.201500042](https://doi.org/10.1002/ppap.201500042)

Rusakova A, Nosachev I, Lysenko V, Guoa Ya, Logvinov A, Kirichenko E, Varduny T, Cherednikov S, Chugueva O (2017) Impact of high strength electromagnetic fields generated by Tesla transformer on plant cell ultrastructure. *Information Processing in Agriculture* **4**, 253–258. doi:[10.1016/j.inpa.2017.05.002](https://doi.org/10.1016/j.inpa.2017.05.002)

Shabala S, Shabala L, Van Volkenburgh E (2003) Effect of calcium on root development and root ion fluxes in salinized barley seedlings. *Functional Plant Biology* **30**, 507–514. doi:[10.1071/FP03016](https://doi.org/10.1071/FP03016)

Sivachandiran L, Khacel A (2017) Enhanced seed germination and plant growth by atmospheric pressure cold air plasma: combined effect of seed and water treatment. *Royal Society of Chemistry Advances* **7**, 1822–1832. doi:[10.1039/C6RA24762H](https://doi.org/10.1039/C6RA24762H)

Solly E (1846) On the influence of electricity on vegetation. *Journal of Horticulture Society* **1**, 81–109.

Tesla N (1894) Incandescent electric light. U.S. Patent number 0.514.170.

Volkov AG. (Ed.) (2006) 'Plant electrophysiology.' (Springer: Berlin, Germany.)

Volkov AG. (Ed.) (2012a) 'Plant electrophysiology. Methods and cell electrophysiology.' (Springer: Berlin, Germany.)

Volkov AG. (Ed.) (2012b) 'Plant electrophysiology. Signaling and responses.' (Springer: Berlin, Germany.)

Volkov AG, Paula S, Deamer DW (1997) Two mechanisms of permeation of small neutral molecules and hydrated ions across phospholipid bilayers. *Bioelectrochemistry (Amsterdam, Netherlands)* **42**, 153–160.

Volkov AG, Deamer DW, Tanelian DL, Markin VS (1998) 'Liquid interfaces in chemistry and biology.' (Wiley: New York, USA.)

Volkov AG, Murphy VA, Markin VS (2012) Mechanism of passive permeation of ions and molecules through plant membranes. In 'Plant Electrophysiology – Methods and Cell Electrophysiology.' (Ed. A. G. Volkov.) pp. 323–356. (Springer: New York, USA.)

Volkov AG, Xu KG, Kolobov VI (2017) Cold plasma interactions with plants: morphing and movements of Venus flytrap and *Mimosa pudica* induced by argon plasma jet. *Bioelectrochemistry (Amsterdam, Netherlands)* **118**, 100–105. doi:[10.1016/j.bioelechem.2017.07.011](https://doi.org/10.1016/j.bioelechem.2017.07.011)

Volkov AG, Hairston JS, Patel D, Gott RP, Xu KG (2019a) Cold plasma poration and corrugation of pumpkin seed coats. *Bioelectrochemistry (Amsterdam, Netherlands)* **128**, 175–185. doi:[10.1016/j.bioelechem.2019.04.012](https://doi.org/10.1016/j.bioelechem.2019.04.012)

Volkov AG, Xu KG, Kolobov VI (2019b) Plasma generated reactive oxygen and nitrogen species can lead to closure, locking and constriction of the *Dionaea muscipula* Ellis trap. *Journal of the Royal Society Interface* **16**, 20180713. doi:[10.1098/rsif.2018.0713](https://doi.org/10.1098/rsif.2018.0713)

Zhou R, Zhou R, Zhang X, Zhuang J, Yang S, Bazaka K, Ostrikov K (2016) Effects of atmospheric-pressure N<sub>2</sub>, He, air, and O<sub>2</sub> microplasmas on mung bean seed germination and seedling growth. *Scientific Reports* **6**, 32603. doi:[10.1038/srep32603](https://doi.org/10.1038/srep32603)

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