

1 **COULD PLANTS BE SENTIENT?**

2

3

4 **Paco Calvo^{1,2}, Vaidurya Sahi³ and Anthony Trewavas⁴.**

5

6

7 **(1). EIDYN Research Centre and Institute of Molecular Plant Sciences, University of Edinburgh,**
8 **Edinburgh EH9 3JH.**

9 **(2) Minimal Intelligence Lab, Universidad de Murcia, Spain**

10 paco.calvo@ed.ac.uk

11 **(3). Molecular Cell Biology, Karlsruhe Institute of Technology, Kaiserstrasse 2 76131 Karlsruhe,**
12 **Germany**

13 vaidurya.sahi@kit.edu

14 **(4). Institute of Molecular Plant Science, Mayfield Road, University of Edinburgh, Edinburgh EH9**
15 **3JH.**

16 trewavas@ed.ac.uk

17 **Keywords.**

18 **Sentience. Action potentials. Mental states. Nervous network. Phloem.**

19

20

21 **Abstract.**

22 Feelings in humans are mental states representing groups of physiological functions that usually
23 have defined behavioural objectives or purpose. Feelings are thought to be coordinated in the brain
24 stem of animals and are evolutionarily ancient. One function of the brain is to prioritise between
25 competing mental states, and thus groups of physiological functions and in turn behaviour. Anger,
26 fear or pain call for immediate action whereas hunger, or thirst, signify longer term needs and a
27 requirement for search. Plants use groups of coordinated physiological activities to deal with defined
28 environmental situations but currently have no known mental state to prioritise any order of
29 response. Plants do have a nervous system based on phloem which is highly cross linked. Its
30 potential for forming a mental state is unknown but it could be used to distinguish between
31 different and even contradictory signals and thus determine a priority of response. The vascular
32 nervous system stretches throughout the whole plant providing the potential for assessment in all
33 parts and commensurate with its self-organising, phenotypically plastic behaviour.

34

35 INTRODUCTION.

36 Sentience is commonly regarded as the capacity to feel subjectively and is used to distinguish
37 feelings from reason or logic. Feelings are mental experiences of body states. But they are subjective
38 making it difficult to know if the internal experience is even identical between different human
39 individuals. Whether animals are sentient is a question that gives rise to huge controversy (Boyle,
40 2009). Could plants be sentient? Even if the evidence was encouraging, it would always remain
41 unanswerable.

42 Sentience is generally considered limited to organisms that have a nervous system and a centralised
43 brain. For organisms without these supposed requirements, the notion of sentience has been
44 rejected out of hand. Plants are placed in this category (Grinde, 2013. Animal Ethics Inc.
45 www.animal-ethics.org/beings-conscious). The reasons for rejection are four fold

46 (1). The supposed absence of a mechanism for transmission of information similar to the animal
47 nervous system. This article shows that plants do have such a mechanism, something known a
48 century ago.

49 (2). Plants don't have brains the supposed seat of feelings. Again there is reason to doubt this claim
50 as will be described later.

51 (3). Plants are simple. They don't move and thus don't need a nervous system. A recent attempt to
52 compare the complexity of large angiosperms with large animals using discrete complexity criteria
53 failed to distinguish the two (Trewavas, 2014). Long range communication within any plant is
54 essential to balanced development, growth and survival.

55 (4). The capacity to feel arose in evolutionary terms solely from its usefulness in motivating animals;
56 it doesn't make sense for plants that can't run away from a threat or forage for a food they enjoy.
57 On the contrary threats to plant life are very common and are counteracted. Aspects of the
58 behaviour of some like parasitic plants are clearly motivated and they forage sensibly (Trewavas,
59 2017).

60 This article deals with these reasons for rejection and points to errors in knowledge which are not
61 uncommon amongst many animal scientists and even some who research plants (Chamovitz, 2012).

62 **Perceptual bias generates erroneous understanding of plant behaviour.**

63 Subjective, anthropomorphic attitudes are commonly used to judge plant behaviour but the bias
64 often goes unrecognised. Behaviour is classed as the specific response to one or a group of stimuli.
65 In animals it is easy to characterise because it usually results in visible movement. Absence of visible
66 movement leads to common assessments that plants lack behaviour altogether with, of course, a
67 few exceptions like *Dionaea*, (Venus fly trap) or the sensitive plant (*Mimosa pudica*). However our
68 ability to see movement is constrained within discrete limits (Trewavas, 2014). The perceptual bias
69 involved can be illustrated by asking instead what is the commonest form of biological behaviour.

70 Amongst virtually all angiosperm plants, behaviour can be characterised as either molecular changes
71 in composition, or reversible movements of leaves, tendrils, stomatal cells for example, or the more
72 easily seen but slower phenotypic plasticity. It is not difficult to see the plasticity of shoots when

73 looking at the branching patterns of two deciduous trees of the same species and age and noting,
74 when present, how the positions and characteristics of branching reflects close-by neighbours. Light
75 is the source of energy for virtually all plants (some 5000 species of parasitic plants being exceptions)
76 and is fought for when neighbours are sufficiently close to compete. Equally complex competitive
77 behaviour is exhibited by the root system something rarely seen except under exceptional
78 experimental conditions. Long range communication is essential to ensure reasonable balance
79 between shoot (trunk) and root. Time lapse photography of the shoot has fortunately started to
80 change perspectives on plant behaviour and there are many examples on youtube. The phenotype is
81 a history of the environmental conditions it has experienced.

82 99% or more of eucaryotic life on this planet is however plant, not animal as indicated by the ratio of
83 oxygen to carbon dioxide. Thus the commonest form of behaviour is not movement we see but that
84 expressed by plants. Phenotypic plasticity certainly occurs in animals and humans too. Weight lifters
85 and all those obsessed with the manipulation of the body beautiful are cases in point. Again note
86 that these changes which, in wild circumstances, would reflect on fitness, are only detectable after
87 weeks to months; similar to plant plasticity.

88 **These differences in behaviour probably started with the first eukaryotic cells.**

89 Animals and plants separated in evolutionary terms at probably the single cell stage. The
90 fundamental difference lies in the means to acquire necessary energy for survival. Movement was
91 nearly always essential for primordial animal cells to find food. Predator-prey relationships amongst
92 animals, almost certainly accelerated the familiar characteristics of elaborate sensory systems
93 coupled with a highly evolved musculature. Finally these were coupled together by a fast
94 communication nervous channel, that increased the probability of the predator to capture prey or
95 for the prey to escape being eaten.

96 The primordial plant cell on the other hand, acquired a blue green algal symbiont and became
97 photosynthetic. Photosynthetic products are often osmotically active. To prevent these
98 photosynthetic cells from exploding, it was necessary to concomitantly evolve a relatively rigid wall,
99 a severe impediment to movement. Coupled with the ubiquity of light around the earth,
100 evolutionary pressure to move quickly and easily was never an evolutionary imperative.

101 **Plant behaviour is complex not simple.**

102 Plants and animals are entirely different eukaryotic solutions to the problems of survival. But there
103 are marked differences in perception. Roving animals in search of prey need only make a cursory
104 search of any environment. Even insect herbivores need only detect green vegetation for feeding.

105 Being largely confined to the place in which they germinate and grow, higher plants distinguish the
106 features of their environment with much greater discrimination. The resources necessary for life,
107 minerals, water, light, are effective plant food. But they are patchily distributed around the plant
108 body and are fought over competitively not only to acquire them but to acquire them first and deny
109 them to others. Fine discrimination leads to better exploitation but an exploitation that requires
110 growth and the internal resources from either root or shoot to enable plasticity in growth. In those
111 plants that have been investigated there is competition for these internal resources too. Decisions
112 have therefore to be made out of a range of possibilities; those plants that can make them more

113 quickly, with lower cost are more likely to accumulate more food , produce more seeds and siblings
114 and thus are fitter (Trewavas, 2014; 2016). Nature red in tooth and claw might describe the animal
115 world but in the plant world it is green, overgrowth and phenotypic plasticity.

116 **Threats to survival of the individual plant.**

117 Herbivory, other physical damage by for example wind or trampling, disease, light or shade, drought,
118 flooding, cold and hot temperature extremes all initiate dramatic phenotypic responses including
119 resistance unless overwhelmed. Less stressful episodes of cold, heat, water loss or mechanical stress
120 by wind, are learnt so that further episodes are dealt with more robustly, more quickly and with
121 greatly improved resistance to the threat. Herbivory and disease prime the plant. After the first
122 episode of insect damage, any subsequent attacks again are responded to more rapidly and greatly
123 enhanced in size. Priming is clearly a learning mechanism and the induced memory lasts for years
124 and in some plants survives reproduction (Frost et al., 2008; Zimmermann et al., 2016). Basically it is
125 behaviour profiting from experience, a common definition of intelligence (Trewavas, 2017). Changes
126 in chromatin structure are its likely basis (Ali et al., 2013). Recognition of the species of attacking
127 caterpillar is gained through recognition of the precise chemical composition of salivary juice. In turn
128 the attacked plant emits complex signatures, mixtures of volatile chemicals that are recognised by
129 parasitoids of the specific caterpillar, a kind of burglar alarm with associated police response (Diezel
130 et al., 2009). Further attacks lead to a much quicker and greatly elevated resistance response.
131 Priming can last years and even in some cases survives reproduction.

132 Similar problems beset the root. Soil strength, stones, compaction, all require morphological change
133 and phenotypic adaptation; disease and nematode damage require a plethora of responses.
134 Interactions with various fungal species can lead to beneficial symbiosis ranging all the way down to
135 parasitism or disease. Roots from adjacent competitive neighbours are sensed and lead to
136 proliferation to deny resources to the neighbour as well as the benefits of acquiring the soil
137 resources first. A variety of soil chemicals are sensed and acted upon. Each signal constructs a
138 different phenotype with a unique underlying molecular base. Mechanisms that transduce many of
139 these environmental signals are known (Trewavas, 2014). Errors in behavioural responses are
140 recognised and corrected (Trewavas, 2017). There is nothing simple here.

141 Differing groups of signals appear at different times and can be contradictory. A key question then is
142 how plants place weight upon any of the signals perceived and how they prioritise them in terms of
143 response. That is one of the questions this article attempts to raise.

144 Growing wild plants self-organise; each stage of development acts as a platform for the next.
145 Development itself is thus a learning process and the unpredictable environment acts as the context
146 in which learning takes place. Higher plant organisation can be described as analogous to a republic
147 in contrast to the monarchical animal. However the organisation of a republic is still coherent but
148 permits a much greater level of distributed and local control than is present in a monarchical or
149 dictatorial system. These two great kingdoms reflect different facets of organisation that in turn
150 reflect the different evolutionary decisions made when both were single cells as to the means for
151 acquiring energy. Animal development is constrained within relatively rigid boundaries; that is the
152 price paid for the lifestyle that necessitates movement.

153

154 **THE NATURE OF FEELINGS IN ANIMALS.**

155 Sentience is generally held to describe the presence of emotions and feelings in human beings as
156 contrasted with logic and reason. Whilst humans can put words to internal experiences such as
157 hunger, pain, fear, anger, well-being or the more nuanced feelings of compassion, gratitude, even
158 sexual love these are, and recognisably, entirely subjective even to the human individual (Damasio
159 and Carvalho, 2013). Their presence in ourselves however has given rise to an enormous discussion
160 and literature arguing for equivalent feelings in other animals (Boyle, 2003). The best that can be
161 suggested, usually in discussion of pain, is a kind of insurance; we should avoid certain actions with
162 animals, in case it is indeed equivalent in intensity and damage to that in human beings.

163 Charles Darwin (1872) in his book on animal emotions extensively summarised previous studies and
164 combined them with his own considerable observations most notably on zoo primates. He also
165 included cats, dogs, horses etc., in his discussion. By observing behaviours which he could interpret
166 as analogous to those in humans, he considered that emotions were present. Anthropocentric
167 attitudes again complicate the issue of assessing primate behaviour, experience and emotion. Two
168 well-known primates, Washoe and Koko, chimpanzee and gorilla respectively and others, were
169 taught sign language and acquired some 300-1000 words after several years of training (Gardener et
170 al., 1989; Patterson and Linden 1981). Intellectually these primates were rated as equivalent to a 2-
171 3 year old human child. But how well would a 2-3 year old human child survive in the wild
172 circumstances familiar to chimps and gorillas which they manage with alacrity? Chimps recognise in
173 a few seconds their social position when placed in a new tribe, a behaviour crucial to their survival.
174 What emotion is involved there? Is it well-being, fear, or a simple survival mechanism performed
175 without any emotional content?

176 There is more to intellect than learning signs for language and trying to identify apparent emotions.
177 Human language is complex and in its complexity maybe unique, but judgements made on language
178 alone are entirely flawed. In their true wild context these animals are surely highly intelligent and
179 their survival depends upon it.

180 Strong drivers of feelings are the nociceptors. These transmit information to the brain on tissue
181 damage and the detection of noxious or potentially noxious circumstances eliciting the sensation of
182 pain. Whether a nervous system is essential for sensing and response to damage can be queried.
183 Jennings (1926) discusses sentience, experience and cognition in the context of single-celled animals.
184 When *Amoeba*, *Stentor* or *Paramecium* perceive localised, damaging circumstances they move in the
185 opposite direction and into what, we judge to be, a more equitable environment or one in which
186 threat is diminished. Is this behaviour he asked, consistent with what would be expected if the single
187 cell experienced the equivalent of pain in noxious circumstances? He concluded that it would, but
188 added the obvious proviso that it could never be known if pain was involved. Are then nervous
189 systems really a prerequisite for feelings? Or are they merely an elaboration of sensory experience,
190 feelings experienced even by the simplest of organisms?

191 As to the actual human experience of pain, it is difficult to assess how well we distinguish actual pain
192 from our perception that it must be painful. There are certainly a range of sensitivities between
193 different humans from highly sensitive to effectively null experience of pain itself. There are, as well,
194 good anecdotal examples of men who lost limbs in battle with seemingly little painful effect because

195 they continued to fight. Animals do react when injured in a way that we would interpret as painful to
196 us. But can we ever know their actual experience?

197 **Human feelings have an evolutionary benefit.**

198 Feelings in humans like all other human characteristics are present because they served a role in
199 natural selection and subsequent evolution. They represent a mental state which is connected to
200 groups of physiological and metabolic activities focussed on required individual behaviours (Damasio
201 and Carvalho 2013). Perhaps the most familiar to the reader is that of flight or fight, which can vary
202 enormously in intensity between human individuals. The threat signal generates a mental state
203 involved in energising the familiar group of physiological responses; increased cardiac and
204 respiratory activity, elevated blood flow rates, blood sugar, dilated pupil and increased secretions of
205 adrenalin and cortisol amongst others. By providing the necessary assessment of a potential or
206 potentially threatening future, the brain constructs priorities between competing problems.
207 Amongst a plethora of potential behaviours, which one needs attention first.

208 Behaviours in animals as in plants are a way of maintaining as far as possible what might be termed
209 a state of life cycle well-being. It enables the individual to continue the path to reproduction with
210 least interruption and culminating in satisfactory reproduction. It is not clear that well-being is a
211 definable mental state in humans. But well-being circumstances may be easier to characterise for
212 many crop plants. Good, well-drained soil with nutriment and water readily available, no wind, an
213 optimal temperature, freedom from disease and herbivory and an abundance of pollinators.
214 Reproductive abundance is the consequence, a commonly-used proxy in the wild for fitness. But
215 these crop plants have been selected from the enormous range of genotypes in the wild and bred to
216 respond well to these circumstances.

217 Feelings are thought to originate in the brain stem first and thus their evolution is probably ancient
218 (Damasio and Carvalho, 2013). What came first was the grouping of physiological responses
219 together in response to defined environmental perturbations; only later it is thought were these
220 coordinated by nervous activity. The incorporation of mental states helped provide the organism
221 with a potential guide to adaptive behaviours including intelligent learning and memory. Gardner
222 (1983) in his creative approach to intelligence, incorporates both emotional and social intelligence as
223 critical aspects of this behaviour. An arguable case can be made for single cells expressing many of
224 the fight or flight biochemical responses in response to a damaging environment.

225 **Groups of plant physiological and phenotypic changes are induced by specific signals.**

226 There is organisational similarity in the way that both animals and plants respond to external signals.
227 Perception leads to assessment and in turn a sensible response. In higher animals, perception
228 involves detection in one or more sensory systems and is communicated to assessment areas in the
229 brain via nervous connections or hormones. Responses are initiated through activating specific
230 muscles and coincident usually with new hormone release. Furthermore the organism monitors
231 whether the response is sufficient leading to further action if it isn't. The immune system, which
232 both learns and remembers, may be the exception in not directly using nervous communication but
233 its behaviour is generally integrated with the whole organism.

234 Perception in plants is located in groups of cells, whole tissue or tissues. There are subsequent
235 downstream effects that often involve long distance communication to other tissues or organs.
236 Chemical communication is common and complex, involving small and large RNAs, proteins,
237 peptides, oligosaccharides and a large range of smaller chemicals some of which are designated as
238 hormones although these usually lack the discrete site of synthesis in a gland or tissue familiar with
239 mammalian endocrinology (Trewavas, 2014). Even minerals and water can be employed to
240 communicate internal information. Finally there is electrical communication which follows on this
241 section of the article.

242 At some stage the nature of the perceived signals are assessed and subsequent downstream
243 changes initiated leading for example redirection of leaf position, closure of leaf stomata, or tendril
244 curling taking some 10-15 minutes. Phenotypic changes obviously take much longer and probably
245 use a variety of feedback mechanisms to optimise the appearance and growth of the new structure.
246 There is evidence that predictions are commonly made of potential futures and included in the
247 eventual responses. One feature of plant response currently lacking is the identity of signals that
248 indicates to remote tissues and organs that information has been received and acted upon.

249 **The cellular basis of feelings and behaviour.**

250 Sentience and consciousness have a recognisable cellular basis in humans and other animals. They
251 involve synapses, action potentials, membrane potentials and behavioural synchronisation of a
252 number of neurones (Cook, 2006). The cellular origin of feelings in animals does commence with
253 induced changes in single cells. The route of nervous transmission from sensory system to brain
254 involves two kinds of nerve cell; those that are myelinated and those that are not. Myelin insulates
255 the nerve cell quite effectively from outside interference. The non-myelinated route is thought to be
256 the kind used in the origin of feelings and most of their transmission. Quite clearly such cells are
257 open to environmental influences and it is considered that the membrane potential of any of these
258 is a better indicator of the likely conveyance of information than the action potential itself (Damasio
259 and Carvalho, 2013). Membrane potentials and action potentials figure strongly in plants too.

260 **THE 'NERVOUS' SYSTEM IN PLANTS.**

261 One of the primary objections indicated earlier to the possibility for plant sentience was the
262 apparent absence of a nervous system. It is certainly true that the familiar anatomical animal
263 neurone has no equivalent in plants. That was recognised in the 19th century and was also stated by
264 Charles Darwin (1880). He did draw analogies with the behaviour of the root tip (more likely the cap
265 (Trewavas, 2016) and the brain of one of the lower animals. However the lack of obvious neurones
266 does not preclude a functional, excitable but unrecognised, equivalent, capable of electrical
267 transmission which most certainly is present.

268 J.C Bose, was an Indian scientist, a physicist who worked initially with Rayleigh and was the first to
269 use semiconductor junctions to detect radio signals. He continued research on returning to India in
270 the late 19th century but changed direction and confined himself to investigating the
271 electrophysiology of plant behaviour early in the 20th century. His physical expertise enabled him to
272 construct many pieces of extremely elegant electrical equipment, well before others. He could for
273 example, monitor electrical activity and latent periods of responses within 0.005 seconds. The
274 majority of his studies from this period on, are to be found in some six papers published in the

275 Proceedings of the Royal Society (to which society he was also subsequently elected in 1920) and
276 one in the Journal of the Linnean Society. There is a further paper in the Royal Society archives which
277 was unpublished, apparently due to objections from Burdon-Sanderson who claimed (wrongly) that
278 only plants with visible movement used action potentials; Bose showed that many others did too.
279 Most of the research material is to be found summarised in two large books, “Plant Response as a
280 Means of Physiological Investigation” (1906) and “Comparative Electrophysiology” (1907). The latter
281 compares plant and animal nervous systems. Additional material is to found in nigh on a dozen
282 books in total. His output was certainly prodigious.

283 Four years after retirement in 1926, Bose published “The Nervous Mechanism of Plants”. This book
284 describes about one hundred experiments most of whose results are illustrated and contains some
285 additional material not found in the two primary texts. It is not possible to detail all the experiments
286 that Bose performed and instead we have relied on quotations as summary from Bose, (1926).

287 “The most important fact established in plant response was the nervous character of the impulse
288 transmitted to a distance”. “The conduction of excitation in the plant is fundamentally the same as
289 that of the nerve of the animal”. “The response of the isolated plant nerve is indistinguishable from
290 that of the animal nerve, through a long series of parallel variations of condition” (all page viii). “ In
291 *Mimosa* the velocity of nervous impulse is 400mm/second”. “My recent discovery of the
292 transformation of the afferent or sensory into an efferent or motor impulse in the reflex arc of
293 *Mimosa* , will materially advance our knowledge of the nervous impulse in general” (page ix).

294 “It has been identified that **excitation is conducted by the phloem of the vascular bundle** and that
295 conduction can be modified experimentally, in the same way as in the animal nerve” (page 215).

296 Bose established that there was an excitable system in many if not all plants and that it used action
297 potentials. That demonstration, made over 100 years ago, rebuts claims that plants have no
298 ‘nervous’ system, claims that failed to recognise there might be a functional equivalent. But it is the
299 phloem, part of the vascular system, that is conducting electricity over long distances in plants. The
300 phloem has therefore dual functions; transport of organic materials (sugars, amino acids, proteins,
301 peptides, RNA’s of varying size, hormones) as well as conducting electrical impulses and action
302 potentials.

303 To clarify the distinction with animal neurology, the term phytoneurology and classing individual
304 phloem cells as phytoneurons can be used, when conduction is through excitable phloem cells.

305 Numerous modern investigations (e.g. Volkov and Ramatunga, 2006; Fromm and Lautner, 2007;
306 Zimmermann et al., 2016; Pickard, 1973 and references therein) have confirmed the validity of these
307 early claims of electrical communication by Bose. Vascular bundles (phloem, cambium and xylem)
308 stretch from the top to the bottom of the individual plant and there is therefore the potential for
309 very long distance communication in large plants and at considerable speeds (Galle et al., 2015;
310 Fromm and Lautner, 2007; Fromm and Bauer, 1994; Yan et al, 2009; Zimmerman et al. 2016). Action
311 potentials in plants can move from 0.5 to 20 cm/sec and the distance covered may be helped by the
312 recently described system potentials (Zimmerman et al., 2016). In addition to action potentials,
313 variation potentials have also been characterized. They are at least 20 fold slower in transmission
314 and may last up to 30 minutes influencing surrounding cell behaviour during this time period.
315 Variation potentials are also dose dependent and more localised near to the site of stimulation.

316 These two phytoneurological signals (action and variation potentials) rapidly separate from each
317 other following signal initiation. Specific information is thus conveyed by the separation of distance
318 between these two phytoneurological signals as well as amplitude, duration and profile which
319 appear also to be signal specific.

320 Voltage-gated and mechanosensitive channels are used in the phloem. Instead of initiation by
321 sodium channels in nerves, phytoneurons use chloride efflux throughout specific chloride channels
322 followed by activation of calcium and potassium channels. Plasmodesmata transmit the excitable
323 state and variation potentials to other cells. These phytoneurological signals can be transferred over
324 at least half a metre in young trees and damage or cold shock to one leaf is experienced by other
325 leaves remote from the signal. (Oyarce and Gurovich, 2010; Gurovich and Hermosilla 2009; Lautner
326 et al., 2005)

327 Action potentials are also accompanied by a cytosolic-free Ca^{2+} wave thus providing excellent cellular
328 interpretation of the information (Choi et al., 2016). Hundreds of downstream proteins (including
329 many sequence-separable calmodulins) in plants are Ca^{2+} sensitive and able to interpret the
330 perceived signal.

331 **What plant signals induce phytoneurological events and what responses result?**

332 The signals initiating action potentials have been tabulated on several occasions. Numerous aspects
333 of behaviour and development are consequently altered (Fromm and Lautner, 2009; Galle et al.,
334 2015; Pickard, 1973; Trebacz, 1989; Yan et al., 2009). The signals involved are herbivory,
335 (caterpillars, beetles on shoot and nematodes on roots), light-dark changes, temperature variations
336 (cold shock, heat shock), mechanical stimulation, (bending usually resulting from wind impact and
337 inducing stress and strain in cells including and activating mechanosensitive channels in phloem),
338 reductions in mineral uptake, application of saline conditions to roots, watering droughted plants,
339 application of pollen to the stigma, leaf and fruit removal. The consequential changes involve
340 alterations in gene expression, reductions of photosynthesis and increased respiration. Others
341 include a lower rate of phloem translocation, reductions in turgor pressure and stem growth, closure
342 of stomata, induction of hormone synthesis (notably ethylene, abscisic acid, jasmonic acid) and
343 increased nectar secretion. Most of these signals can be classed as indicators or are clearly
344 associated with stressful and potentially damaging conditions.

345 One critical signal generating action potentials is herbivory. Leaves and stems are damaged and
346 eaten with a high degree of probability by invertebrate and vertebrate herbivores. Below ground,
347 nematodes can create root damage opening up the tissues to fungal infection. As a result of the
348 action potentials generated and variation potentials in cells adjacent to the excitable phloem,
349 defence mechanisms are initiated. One of the commonest reactions is the synthesis and circulation
350 of natural pesticides like caffeine or nicotine, but usually specific to the species. There are an
351 estimated 100,000 natural pesticides reflecting 200 million years of evolutionary arms race between
352 angiosperms and insect pests. Additional responses include wall hardening, the production of gums
353 or attraction of parasitoids as indicated earlier. The herbivore-induced action potential is the first
354 step that leads to a complex set of specific resistance mechanisms that engender memories of
355 differing length.

356 **THE NERVOUS SYSTEM OF PLANTS CONSISTS OF COMPLEX NETWORKS OF EXCITABLE TISSUES**
357 **CARRYING ELECTRICAL SIGNALS. IS THIS A BRAIN-LIKE ACTIVITY?**

358 **The need for assessment.**

359 Animals are unitary organisms. Rapid movement to find food or avoid being eaten places strong
360 constraints on the phenotype that develops. Assessment is commonly limited to the brain. Memory
361 is accessed and compared to present circumstances activating muscles when needed to initiate
362 movement. Later hormone secretion helps coordinate a whole organism response.

363 The self-organising plant permits a greater level of distributed control as reflected in plasticity of the
364 phenotype but decisions have to be made after assessment of the prevailing circumstances as well
365 as the requirement to generate the optimal response (Trewavas, 2014). In changing the phenotype
366 resources have to be redirected. This is accomplished by proliferation of new vascular tissue by the
367 cambium to provide these resources to potentially productive branches, by blocking off some
368 vascular elements to those less productive and blocking them entirely to those that provide nothing.
369 Herbivore damage is in part responsible for the need for assessment and specific alteration of
370 phenotypic structure. The cambium itself may be the recipient of the required information from the
371 excitable phloem and the site of assessment here whose need is as important in plants as it is in
372 animals. Without it the phenotype would simply become random and chaotic.

373 “No form of ganglion however has ever been observed in plants but it is not impossible that the
374 physiological facts may one day receive histological verification” (Bose (1926). page 218). Although
375 Bose recognised the absence of an anatomical animal ganglion in plants, that is, a recognisable
376 conglomerate of nerve cells clustered together, we consider there is one piece of evidence, initially
377 collected by Bose, which may suggest a kind of functional equivalent. It is shown in figure 1 which is
378 taken from figure 54 of Bose (1926). The figure shows one layer of the vascular tissue in *Papaya*.
379 Again quotation reveals Bose assessments. “How reticulated they (vascular bundles) may often be
380 even in the trunk of a tree is shown in the photograph of the distribution of vascular bundles in the
381 main stem of *Papaya* (figure 54). This network of which only a small portion is seen in the
382 photograph girdles the stem throughout its whole length and in this particular case, there were as
383 many as twenty such layers one within the other” (Bose, (1926), page 121). Figure 1 shows the
384 vascular system of this mature plant to consist of numerous vertical vascular elements cross-linked
385 extremely frequently by numerous irregularly-distributed horizontal and tangential connections. A
386 complex network of excitable phloem cells is clearly present.



387

388 **Figure 1. Distribution of vascular tissue in a single stem layer of *Papaya*.** There are 20 such
389 layers one inside the other. The bundles are connected through enormous numbers of

390 anastomoses and tangential connections to form a complex excitable structure. “The existence of
391 a system of nerves enables the plant to act as a single organised whole” a requirement perhaps
392 for selection on fitness. Figure and quote taken from figure 54, Bose (1926).

393

394 **Leaf excitable phloem networks.**

395 The connection with individual leaves is also made by Bose. “The expanded lamina of the leaf in
396 which bundles are spread out in fine ramifications is not merely a specialised structure for the
397 stimulus of light but also a catchment basin for the stimulus of light which is gathered into larger and
398 larger nerve trunks for transmission to the interior of the plant”. And of course other signals too.

399 There are at least four orders of vein (xylem and phloem) in many angiosperm leaves based on
400 diameter (Sack and Scoffoni, 2013). This hierarchical leaf vein system of angiosperms results in the
401 smallest (finest) veins having a total greater than 80% of the vein length and producing a highly and
402 finely reticulated mesh. There is certainly some degree of irregularity in the fine branching and
403 spatial position.

404 Leaves generate action potentials in response to cold treatments and mechanical damage from
405 caterpillars and no doubt light and hydraulic signals (Fromm and Bauer, 1994; Zimmermann et al.,
406 2016). Leaves of many species maintain an internal temperature of $21.4 \pm 2.2^{\circ}$ C throughout the
407 growing season when the external environment varied from $6-30^{\circ}$ C, (Helliker and Richter, 2008). A
408 variety of mechanisms (movement into or out of direct sunlight, stomatal aperture, chloroplast
409 movement, hair numbers and reflective /non reflective wax and local leaf number) are used to
410 either warm or cool the leaf keeping the temperature at this homeostat optimum (Trewavas, 2014).
411 Some of these changes take just a few minutes others, a few days. Given the vascular network in the
412 leaf, an action potential generated in part of the leaf would travel throughout. Cells adjacent to the
413 phloem would either experience an action potential themselves or longer lived variation potentials.
414 However an action potential generated in one leaf on a Poplar stem passed into the excitable stem
415 phloem and initiated action potentials further down on leaves remote from the source leaf and on
416 the alternate (acropetal) side (Lautner et al., 2005). The phloem network obviously permits
417 transverse signalling. Bearing in mind the huge numbers of leaves on trees particularly in season, the
418 potential for detailed monitoring of the above ground environment must be enormous. Necessary
419 information on herbivory is likely to be experienced by the whole plant and resistance mechanisms
420 initiated.

421 **The stem phloem forms an equally complex network.**

422 In very young plants, phloem anastomoses (cross links), up to 7000/stem internode in number, have
423 been reported (e.g. Aloni and Sachs, 1973; Aloni and Barnett, 1996). Computer-assisted tomography
424 has been used to identify a complex network of xylem vessels (Brodersen et al., 2011). However
425 xylem does not differentiate in the absence of phloem although the converse is not true (Roberts et
426 al., 1988. Page 47). So the observed vessel network probably indicates the phloem network too.

427 In more mature stems and with appearance of additional secondary and supernumery cambia and
428 other features of secondary growth, plant vascular architecture becomes extremely complex.
429 Tangential connections and anastomoses between numerous bundles become very frequent as do

430 radial connections between different stem layers (Carlquist, 1975; Dobbins, 1971; Horak, 1981;
431 Wheat, 1977; Zamski, 1979). These anastomoses do not occur simultaneously in the xylem and
432 phloem and they do construct a “complex netlike structure” already observed in some related 20
433 families of plants and with further research no doubt most others, confirming Bose observations.
434 The complexity of the excitable phloem network is nothing like the simple structures of vascular
435 tissue presented in text books which are usually limited to seedlings. Woody tissues are penetrated
436 by the phloem and starch deposited which is then mobilised on a seasonal basis.

437 The majority of dicotyledonous angiosperm species are trees. Very complex networks of phloem can
438 be expected to be present. The assessment capabilities of these excitable phytoneurological
439 networks remain currently unknown but as indicated earlier they should be capable of both local
440 control and control throughout the whole plant since the vascular tissue is present from top of the
441 trunk to the thousands of roots. The key question now: is this network and its behaviour sufficiently
442 complex to be analogous to a mental state?

443 **Potential behaviour of this complex electrical network?**

444 Networks of all kinds possess emergent properties; properties that originate from the connections
445 between the constituents and nervous systems are one of these (Trewavas, 2007). Even very simple
446 networks of some five interconnected nerve cells exhibit a capability for memory, error correction,
447 time sequence retention and a natural capacity for solving optimisation problems (McCulloch and
448 Pitts, 1943; Hopfield, 1982; Hopfield and Tank, 1986). Learning in nervous systems consists of the
449 construction of either new channels of communication (connections) or altering connection strength
450 between pre-existing neurones (Bray 1990).

451 Bose (1926) investigated the behaviour of whole vascular tissues which he isolated. He reported that
452 continued stimulation of the phloem phytoneurone increased the size of electrical transmission from
453 the same signal and demonstrated a similar property for the frog nerve. Such capabilities suggest a
454 potential for learning in plants through modification of the phytoneurological connection strength.
455 In this network increased or decreased connection could result from changing the numbers of
456 anastomoses. However testing this potential in the complex mature plant vascular system will not be
457 easy.

458 Zimmermann et al., (2016) report that there are discrepancies between different publications as to
459 variations of voltage kinetics and magnitudes of action potentials. The information is summarised in
460 a table in their report. While they make some suggestions by way of explanation, there is no
461 recognition that the electrical system is highly branched, that the response is likely holistic and that
462 branching would be variable between individual plants and along single vascular strands (Aloni and
463 Sachs, 1973). While complex branching of the phloem might not explain all such variations it seems
464 to us that it will be a major variable. Measurements need to be conducted with that realisation in
465 mind. Alternatively since the phloem is the primary conductive tissue, electrodes should always be
466 placed into this tissue to try and ensure better uniformity.

467 **Is this excitable electrical system primed for response and in constant operation?**

468 Both shoots and roots maintain a bioelectric field around themselves (Lund, 1947; McAulay and
469 Scott, 1954; Scott and Martin, 1962). The field has a distinct polarity with different regions

470 exhibiting different potential differences (e.g shoot and root tip more negative than base). These
471 measurements were made on growing organs. The bioelectric fields are in a sense holistic, reflecting
472 the contribution of thousands of cells at any one time. However shoots and roots grow from their
473 respective apices which contain the regions of cell division and growth. The bioelectric field for
474 individual cells must then be dynamic as cells disappear from the zone of division and then
475 subsequently enlarge thus changing their position and their electrical contribution.

476 However one of the most important observations is that both root and shoot bioelectric fields
477 oscillate by some 30mV in size and with frequencies from 4-15 minutes in roots and 10 to 50
478 minutes in shoots (Lund, 1947; MacAulay and Scott 1954). Oscillations are usually driven by forms of
479 negative feedback and in this case issuing from the fluctuations of ion flux into and out of cells. A
480 system that oscillates however is primed for response, ready to respond rapidly upon receipt of
481 signals. Measurement of internal electrical potential in tall trees indicate the same pattern of
482 oscillation, or pulsations as Bose (1923) describes them. He was able to demonstrate that these
483 oscillations occur in the endodermis, a group of cells that surrounds the excitable phloem. Later
484 work demonstrated that the endodermis in shoot stems contains the statoliths, the necessary
485 agents detecting gravitational signals (Psaras, 2004; Morita et al., 2002). These observations
486 indicate the electrical system is maintained in an active state and the oscillations keep it in a state of
487 ready alert.

488 Mechanical, gravitational, electrical signals, temperature and light alter the characteristics of the
489 bioelectric field in the shoot of young plants. When oriented horizontally, the tip/base separation of
490 voltage is now replaced by the equivalent voltage separation across from the upper to the lower
491 stem tissue. The changes in bioelectric field are detectable within one minute. They precede changes
492 in hormone synthesis whose effects on growth are only detectable some 20-30 minutes later
493 (Schrank, 1944; 1945). Recent measurements confirm that electrical changes precede those of
494 growth and may be responsible for them (e.g. Weisenseel and Meyer, 1997; Monshausen et al.,
495 2011).

496 The root bioelectric field is sensitive to inhibition of growth, temperature osmotic effects and light
497 again. Oscillations in bioelectric field are mimicked by oscillations in ion uptake (Shabala, 2003). The
498 uptake of ions by the root is controlled by the shoot and when dark changes to light an electrical
499 signal provides the necessary information opening up channels and ion movement through the root
500 (Shabala et al., 2007).

501 **PRIORITISING WHICH SIGNAL TO RESPOND TO.**

502 Mental states in animals are thought to be able to prioritise the importance of different signals. Wild
503 plants are subject to huge variations in environmental information from outside and a complex of
504 signals internally. Some of these signals can, when used singly, elicit effective contradictory
505 responses when in combination with some others. Some form of prioritisation of any tissue or organ
506 as to which to respond to first, would then seem essential. From what has been described above
507 some suggestions are now possible.

508 The set of conditions that initiate action potentials can be loosely grouped as potentially
509 threatening; mechanical damage including predation and physical disruption, cold or heat shock.
510 Physical disruption from bending results from wind signals and those of frictional touch. Changes in

511 tension and compression in all the cells of the tissue can be considerable. The impacts of both wind
512 and touch induce immediate cytosolic Ca^{2+} transients indicative of action potentials (Knight et al.,
513 1993). Bending and flexing in gusty wind can seriously damage leaves and young branches and many
514 plants respond with thickening and increased lignification to reduce movement. We anticipate that
515 excessive movements of leaves will cause extreme flexure in the attaching petiole and the leaf blade
516 and that should generate action potentials along with those generated in the flexing stem or trunk.

517 However in humans these damaging and temperature treatments are those that deliver pain
518 through nociceptors. By so doing they indicate a priority in both attention and response. The action
519 potentials that are generated in plants will, we suggest, provide a priority to the response against
520 other potential signals. Perhaps the most interesting is how these action potentials are assessed and
521 here the phloem network may be the key. Nothing is known of the behaviour of the phloem
522 anastomoses; will these have any kind of synaptic function? Detailed anatomical and functional
523 analysis of these anastomoses has yet to be performed. Current literature shows almost no
524 awareness of their presence.

525 The potential for modification of transmission has been referred to earlier which is suggestive at
526 present but no more than that. Networks particularly ones as clearly complex as these should have
527 some potential for assessment, and if not in the phloem itself, then in the cells that surround them
528 and that also experience the specific electrical changes. Signalling in these can induce a variety of
529 molecular changes of differing length and these memories should be accessible through long term
530 modifications in protein expression, particularly chromatin modification.

531 One other induced action potential that involves the light dark transition may have critical functions
532 in the assessment of shade. The impact is one of reduced nutrition or energy capture unless
533 behaviour is induced to counterbalance. Shade avoidance is a defined syndrome in young plants that
534 attempts to increase shoot growth rates with lower branching rates at the expense of roots and
535 whose function is to overgrow the competition. A daily assessment at the light/dark transition may
536 be the means of making that assessment although in large woody angiosperms likely complex.

537 Signals that do not induce action potentials seem at present to be most notably those of gravity. In
538 green stems, the statoliths enabling gravitropic responses are located in the endodermis, a group of
539 cells surrounding the excitable phloem (Psaras, 2004; Morita et al., 2002). But if green plants grown
540 in pots are inverted over a light source the gravity response is overridden. Phytochrome A, a light
541 sensitive pigment is found at highest concentrations in these endodermal cells too (Hisada et al.,
542 2000). In this case the prioritisation might simply be brute force in the responsive cells with stronger
543 promoters for light reactions against those for gravitropism responses. Alternatively in the root cap
544 which normally contain cells with statoliths, placement of other signals at right angles to gravity
545 leads to loss of the statoliths (Massa and Gilroy, 2003; Eapen et al., 2005). In this case priority is
546 gained by elimination of alternative sensing.

547 If a plant is subject to shade situations and to a mild deprivation of water, which response would be
548 priority? The shade avoidance syndrome normally leads to enhancement of stem growth at the
549 expense of the root. Water deprivation is normally claimed to lead to reductions in shoot growth,
550 enhancement of root growth and if necessary loss of leaves. Would the stem grow faster or
551 resources instead be given to enhance root exploration for water? Would the phytoneurological
552 network indicated above resolve such situations and thus provide a way in which the individual plant

553 can assess the environmental situation and determine which physiological group is pre-eminent?
554 These questions need better resolution if understanding of the behaviour of wild plants and trees is
555 to be gained.

556 **CONCLUSION.**

557 The reticulated excitable phloem system described above offers a potential for assessment of signals
558 and perhaps their prioritisation. The phytoneurological system is present throughout any growing
559 plant and thus should be capable of dealing with local signals as well as those that require a more
560 integrated response. Both local and long distance changes are characteristic of higher plants. Bose
561 (1926) suggests that it provides for the construction of an integrated whole organism. The vascular
562 network is some kind of complex interactive system and once stimulated has the potential for
563 assessment through possible feedbacks and alterations of connection strength. Whether it should be
564 regarded as a functional equivalent to a fairly primitive brain cannot be determined until its
565 properties are more clearly defined by research. But a feature of most plants is phenotypic plasticity
566 and any kind of phytoneurological system has to accommodate that too. As in other organisms it is
567 no doubt the mixture of chemical and nervous connections that is used for communication
568 throughout the organism.

569 This article commenced by pointing out that lack of obvious movement in plants has led to a
570 downgrading of any kind of nervous control altogether and this needs rebalancing. The article here
571 raises important issues that have been neglected and that require suitable answers not least from
572 electrophysiologists of all kinds. With recognition that this nervous system might act holistically,
573 some issues that have dogged this area of research might be better understood.

574

575 **Acknowledgments**

576 This research was supported by Spanish Ministry of Education, Culture and Sport through a “Stays of
577 professors and senior researchers in foreign centres” fellowship to P.C.

578

579 **References**

580 Ali, M., Sugimoto, K., Ramadan, A. and Arimura, G. Memory of plant communications for priming
581 anti-herbivore responses. *Science Reports* (2013). 3, 1872.

582 Aloni, R and Barnett, J.R. (1996). The development of phloem anastomoses between vascular
583 bundles and their role in xylem regeneration after wounding in *Cucurbita* and *Dahlia*. *Planta* 198,
584 595-603.

585

586 Aloni, R and Sachs, T. (1973). The three-dimensional structure of primary phloem systems. *Planta*
587 113, 345-353.

588

589 Animal Ethics Inc. What beings are not conscious. www.animal-ethics.org/beings-conscious/

590 Bose, J.C. (1923). *Physiology of the ascent of sap*. London, Longmans, Green and Co. Ltd

- 591 Bose, J.C. (1926). The nervous mechanism of plants. London, Longmans, Green and Co, Ltd.
- 592 Boyle, E. (2009). Neuroscience and Animal Sentience. www.animalsentience.com
- 593 Bray, D. (1990). Intracellular signalling as a parallel distributed process. Journal of Theoretical
594 Biology 143; 215-231.
- 595
- 596 Brodersen, C.R., Lee, E.F., Choat, B., Jansen, S., Phillips, R.J., Shackel, K.A., McElrone, A.J. and
597 Matthews, M.A. (2011). Automated analysis of three dimensional networks using high resolution
598 computed tomography. New Phytologist 191; 1168-1179.
- 599
- 600 Carlquist, S. (1975). Wood anatomy of Ongraceae with notes on alternative modes of photosynthate
601 movement in dicotyledon woods. Annals of the Missouri Botanical Garden 62; 386-424.
- 602
- 603 Chamovitz, D (2012). What a plant knows. Oxford, One World Publications.
- 604
- 605 Choi, W-G., Hilleary, R., Swanson, S.J., Kim, S-U., Gilroy, S. (2016). Rapid long-distance electrical and
606 calcium signalling in plants. Annual Review of Plant Biology 67; 287-307.
- 607
- 608 Cook, N.D. (2006). The neuron level phenomena underlying cognition and consciousness: synaptic
609 activity and the action potential. Neuroscience 153; 556-570.
- 610
- 611 Damasio, A. and Carvalho, G.B. (2103). The Nature of Feelings: evolutionary and neurobiological
612 origins. Nature Reviews Neuroscience. 14; 143-152.
- 613
- 614 Darwin, C. (1872). The expression of the emotions in man and animals. London, John Murray.
- 615
- 616 Darwin, C. (1880). The power of movement in plants. London, John Murray
- 617 Diezel C, Von Dahl CC, Gaquerel E, Baldwin IT. Different Lepidopteran elicitors account for Cross-Talk
618 in herbivory-induced phytohormone signaling. (2009). Plant Physiology, 150; 1576–1586
- 619 Dobbins, D.R. (1971). Studies on the anomalous cambial activity in *Doxanthia unguiscati*
620 (Bignoniaceae). II. A case of differential production of secondary tissues. American Journal of
621 Botany 58; 697-705.
- 622 Eapen, D., Barroso, M.L., Ponce, G., Campos, M.E. and Cassab, G.I. (2005). Hydrotropism: root
623 responses to water. Trends in Plant Science 10; 1360-1365.
- 624 Favre, P. and Agosti, R.D. (2007). Voltage dependent action potential in *Arabidopsis thaliana*.
625 Physiologia Plantarum 131; 263-272.
- 626 Fromm J. and Bauer T. (1994). Action potentials in maize sieve tubes change phloem translocation.
627 Journal of Experimental Botany 45,463-469.
- 628
- 629 Fromm, J. and Lautner, S. (2007). Electrical signals and their physiological significance in plants.
630 Plant Cell and Environment 30; 249-257.

- 631 Frost, C.J., Mescher, M.C., Carlson, J.E. and de Moraes, C.M. (2008). Plant defence priming against
632 herbivores: getting ready for a different battle. *Plant Physiology* 146; 818-824.
- 633 Galle, A., Lautner, S., Flexas, J., and Fromm, J. (2015). Environmental stimuli and physiological
634 responses: the current view on electrical signalling. *Environmental and Experimental Botany* 114; 15-
635 21.
- 636
- 637 Gardner, H. (1983). *Frames of Mind*. New York, Basic Books, Inc.
- 638
- 639 Gardner, R.A., Gardner, B.T., and Van Cantfort, T.E. (1989), *Teaching Sign Language to Chimpanzees*,
640 Albany: SUNY Press.
- 641
- 642 Griffin, D.R. (1976). *The Question of Animal Awareness*. New York, Rockefeller UP.
- 643
- 644 Grinde, B. (2013). The evolutionary rationale for consciousness. *Biological Theory* 7, 227-236.
- 645
- 646 Gurovich, L.A. and Hermosilla, P. (2009). Electric signalling in fruit trees in response to water
647 applications and light darkness conditions. *Journal of Plant Physiology* 66; 290-300.
- 648
- 649 Helliker, B.R. and Richter, S.L. (2008). Sub-tropical to boreal convergence of tree leaf temperature.
650 *Nature* 454, 511-514.
- 651
- 652 Hisada, A., Hanzawa, H., Weller, J.L., Nagatari, A., Reid, J.B. and Furuya, M. (2000). Light-induced
653 nuclear translocation of endogenous pea phytochrome A visualised by immunocytochemical
procedures. *Plant Cell*, 12; 1063-1078.
- 654 Hopfield, J.J. (1982). Neural networks and physical systems with emergent, collective, computational
655 properties. *Proceedings of the National Academy of Sciences, USA* 79; 2554-2558.
- 656 Hopfield, J.J. and Tank, D.W. (1986). Computing with neural circuits: a model. *Science*, 233; 625-633.
- 657 Horak, K. (1981). The three dimensional vascular structure in *Stegnosperma*. *Botanical Gazette* 142,
658 545-549.
- 659
- 660 Jennings, H.S. (1926). *Behaviour of the Lower organisms*. New York, Columbia UP.
- 661
- 662 Knight, M.R., Read, N.D., Campbell, A.K. and Trewavas, A.J. (1993). Imaging calcium dynamics in
663 living cells using semi-synthetic recombinant aequorins. *Journal of Cell Biology* 121; 83-90.
- 664 Lautner, S., Grams, T.E.E., Matyssek, R., Fromm, J. (2005). Characteristics of electrical signals in
665 poplar and responses in photosynthesis. *Plant Physiology* 138; 2200-2209.
- 666 Lund, E.J. (1947). *Bioelectric fields and Plant Growth*. Austin, University of Texas Press.
- 667 MacAulay, A.L. and Scott, B.I.H. (1954). A new approach to the study of electric fields produced by
668 growing roots. *Nature* 174; 924-925.
- 669 Massa, G. and Gilroy, S. (2003). Touch modulates gravity sensing to regulate the growth of primary
670 roots of *Arabidopsis thaliana*. *Plant Journal* 33, 435-445.

- 671 McCulloch, W.S. and Pitts, W. (1943). A logical calculus of the ideas immanent in nervous activity.
672 Bulletin of Mathematical Biophysics 5; 115-133.
- 673 Mikesell, J.E. (1979). Anomalous secondary thickening in *Phytolacca americana* L. (Phytolaccaeae).
674 American Journal of Botany 66; 997-1005.
- 675 Morita, M.T., Kato, T., Nagafusa, K., Saito, C., Ueda, T., Nakano, A. and Tasaka, M. (2002).
676 Involvement of the vacuoles of the endodermis in the early process of shoot gravitropism in
677 *Arabidopsis*. Plant Cell 14; 47-56.
- 678 Oyarce, P. and Gurovich, L. (2010). Electrical signals in avocado trees. Responses to light and water
679 availability conditions, Plant Signalling and Behaviour 5; 34-41.
680
- 681 Patterson, F.G. and Linden E. (1981), *The education of Koko*, New York: Holt, Rinehart and Winston
- 682 Psaras, G.K. (2004). Direct microscopic demonstration of the statolith sedimentation in endodermal
683 cells of leaf petioles after gravistimulation; evidence for the crucial role of action filaments. Phytion
684 44:191-201.
- 685 Roberts, L., Gahan, P.B. and Aloni, R. (1988). Vascular differentiation and plant growth regulators.
686 Berlin, Springer.
- 687 Sack, L., and Scoffoni, C (2013). Leaf venation; structure, function, development, evolution, ecology
688 and application in the past present and future. New Phytologist 198, 983-1000.
- 689 Schrank, A.R. (1944). Relation between electrical and curvature responses in the *Avena* coleoptile to
690 mechanical stimuli. Plant Physiology 19; 198-211.
- 691 Schrank, A.R. (1945). Changes in electrical polarity in the *Avena* coleoptile as an antecedent to
692 hormone action in geotropic response. Plant Physiology 20; 133-136.
- 693 Scott B.J.H, Martin, D.W. (1962) Bioelectric fields of bean roots and their relation to salt
694 accumulation. Australian Journal of Biological Science 15; 83-100.
- 695 Shabala, S. (2003). Physiological implications of ultradian oscillations in plant roots. Plant and Soil
696 255; 217-226.
- 697 Shabala, S., Pang, J., Zhou, M., Shabal, L., Cuin, T.A., Nick, P., Wegner, L.H. (2007). Electrical
698 signalling and cytokinins mediate effects of light and root cutting on ion uptake in intact plants.
699 Plant Cell and Environment, 32; 194-207.
- 700 Trebacz, K. (1989). Light triggered action potential in plants. Acta Societatis Botanicorum Poloniae
701 58; 141-156.
- 702 Trewavas, A.J. (2007). A brief history of systems biology. Plant Cell; 18, 2420-2430.
703
- 704 Trewavas, A.J. (2014). Plant Behaviour and Intelligence. Oxford UP.
705
- 706 Trewavas, A.J. (2016). Intelligence, cognition and language of green plants. Frontiers in Psychology 7;
707 588.

- 708 Trewavas, A.J. (2017). The foundations of plant intelligence. *Journal of the Royal Society interface*.
709 (in press).
- 710 Volkov, A. and Ranatunga, D.R.A. (2006). Plants as Environmental Biosensors. *Plant Signaling and*
711 *Behaviour*. 1; 105-115.
- 712 Weisenseel, M.H., Becker, H.F. and Ehlgötz, J.G. (1992). Growth, gravity and endogenous ion currents
713 of Cress roots (*Lepidium sativum*). *Plant Physiology* 100; 16-25.
- 714 Wheat, D (1977). Successive cambia in the stem of *Phytolacca dioica*. *American Journal of Botany*
715 64; 1209-1217.
- 716
- 717 Yan X., Wang, Z., Huang, L., Wang, C., Hou, R., Xu, Z., and Qiao, X. (2009). Research progress on
718 electrical signals in higher plants. *Progress in Natural Science* (2009). 19; 531-541.
- 719
- 720 Zamski, E. (1979). The mode of secondary growth and the three dimensional structure of the
721 phloem in *Avicennia*. *Botanical Gazette* 140; 67-76.
- 722
- 723 Zimmermann, M.R., Mithöfer, A., Will, T., Felle, H.H. and Furch, A.C.U. (2016). Herbivore-triggered
724 electrophysiological reactions: candidates for systemic signals in higher plants and the challenge of
725 their identification. *Plant Physiology* 170; 2407-2419.