

Preface

As we enter the new millennium, plant biology is witnessing dramatic advancements in studies related to the complex behaviour of higher plants which are now beginning to reveal intelligent behaviour. Surprisingly, it is plant ecology which is leading in the revelation that plants behave as though having conscious comprehension of themselves and of their environment. Charles Darwin was the first who noted the abilities of plants to communicate with their environment and translate this information into active movements of their organs (Darwin 1880).

Plants recognize other organisms such as bacteria, fungi, other plants, insects, birds, and animals that presumably also include us, humans (Takabayashi and Dicke 1996; Paré and Tumlinson 1999; Kessler and Baldwin 2001). For instance, to accomplish their sexual reproduction, plants rely on complex interactions with insects and birds. In order to achieve this, and as Charles Darwin was one of the first to show (Darwin 1862), plants generate specially shaped sexual organs which allow insects and birds access to their flowers. Moreover, plants reward these pollinators with nectar and other compounds which are both attractive and a necessary part of the diet of these insect/bird feeders (Cozzolino and Widmer 2005). Complex interactions have been recorded between insect pheromones and plant volatile semiochemicals (Reddy and Guerrero 2004). In the case of many *Arum* spp., the insect-attracting plant volatiles with a dung-like odour are exactly those chemicals which attract insects to animal dung where they would otherwise gather and reproduce (Kite et al. 1998). These plants are thus masters of a deceptive and intelligent strategy for their own reproduction. Moreover, plants appear to possess an innate type of immunity system which closely resembles that of animals (Nürnberger et al. 2004) and, interestingly in this respect, there are also several parallels between the recognition of self and non-self in plant breeding systems and histocompatibility in animals (Nasrallah 2005). Plant roots of *Fabaceae* can recognize and 'domesticate' *Rhizobium* bacteria within nodules, and the composite bacteroids then supply the host plants with nitrogen. Less well known, perhaps, is that some plants recognize and communicate with ants (and vice versa) which protect them against herbivores, pathogens as well as competing vegetation (Brouat et al. 2001; Dejean et al. 2005). The plants, in

turn, reward the ants by secreting nectar (Heil et al. 2005) and constructing special food bodies (Solano et al. 2005). Plants actively recognize the identity of herbivores and are then able to recruit their enemies (Arimura et al. 2005). For instance, plant roots attacked by insect predators release volatiles which then attract particular species of nematodes that kill these predators (Rasman et al. 2005). In addition, by releasing volatiles into the aerial environment, plant shoots infected by pathogens inform their neighbouring plants about immanent danger and they can then increase their immunity against these pathogens (Paré and Tumlinson 1999; Reddy and Guerrero 2004). Intriguingly, the signature of released volatiles is characteristic for herbivore damage but is different from that resulting from a general wound response (Reddy and Guerrero 2004; Arimura et al. 2005). *Nicotiana attenuata* attacked by the hornworm, *Manduca sexta*, accumulates nicotine, which poisons acetylcholine receptors, and is thus toxic to those organisms which rely on neuromuscular junctions (Baldwin 2001). Interestingly in this respect, plants express neuronal acetylcholinesterase (Sagane et al. 2005) and use acetylcholine also for their neuronal-like cell-cell communication (Momonoki et al. 1998). Furthermore, during their phylogeny, plants can also switch from an autotrophic to a heterotrophic lifestyle – a feat which, in the case of parasitic or carnivorous plants, requires the active selection of suitable host/prey organisms (Albert et al. 1992).

Plants are extremely mechanosensitive. Their roots exhibit thigmotropism, which enables them to explore, with an animal-like curiosity, their environment in a continual search for water and solutes, and their shoots sometimes seek support by means of tendrils, assisted in this task by volatiles such as jasmonates. Root apices constantly monitor the numerous physical parameters of the soil and use this information in their search for better niches for survival and reproduction. In this behaviour, plant roots closely resemble fungi and, indeed, most roots enter symbiotic interactions with mycorrhizal fungi in order to increase their efficiency in obtaining critical ions such as phosphorus. In fact, roots might prove to be descendents of ancient fungi which, by entering into close association with their symbiotic photoautotrophs, have developed into heterotrophic roots – there are, after all, close resemblances between the anatomies and functions of apices of both rhizomorphs and roots (Botton and Dexheimer 1977) – while photoautotrophs have developed into the autotrophic shoots of the organisms now known as vascular plants (Atsatt 1988; Selosse and Le Tacon 1998; Heckman et al. 2001). This scenario is strongly supported by present-day pioneer colonizers such as lichens, which, just as was the case with early land plants (Yuan et al. 2005), are able to survive in even the most extreme of environmental conditions.

Literally, plants nourish the whole world. They intercept the light energy arriving on Earth from the sunbeams and transform it via energy-poor

inorganic compounds into energy-rich organic matter which then serves as the food for all heterotrophic organisms. Also, the gasoline which fuels many of Man's mechanical devices is of plant origin. Plants thus stand at the interface between a seemingly hostile and violent universe, and a fertile planet Earth teeming with life. We might postulate that if we could understand plants better, they could reveal to us something of the great mystery of life. Aristotle and his pupils were convinced that plants have complex inner life including thoughts, memories, dreams, and plans for the future. Unfortunately, our contemporary science considers plants rather as passive creatures to be exploited if discovered to be useful, and to be cleared away if not. However, their passivity – that is, their inability to change their location or to communicate via sounds – is only relative to the hyperactivity of human existence and the fleeting timescale of Man's artefacts. But the recent advances in ecology and phenomenology outlined above urge a change in this biased perception of higher plants.

We should also remember that action potentials, the very characteristic and rapidest way of neuronal communication, were discovered in plants in 1873 (Davies 2004). In those early days, the cellular basis of animal brains was not accepted and the neuronal processes in brains were just starting to be explored. Since then, a large amount of data has been accumulated on electric phenomena in plants (Meylan 1971; Davies 2004). Currently, new exciting discoveries are revealing that electrical signals modulate and control such basic physiological processes in plants as photosynthesis and phototropism (Koziolek et al. 2004; Volkov 2005). Unfortunately, the mainstream of plant biology has never completely accepted plant electrophysiology, so this field has survived in a quasi-dormant state up until now when exciting advances in plant biology are allowing the introduction of plant neurobiology as a newly emerging field of plant sciences. One foundation of this new science is the discovery that not only do plant cells express diverse neuronal molecules but that they also communicate together via plant synapses (Baluška et al. 2005).

These glimpses of the fascinating and breathtaking complexity of plants raise urgent questions which will dominate the whole field of plant biology in the next decades. In particular: Do plants have some type of neuronal system which resembles that which underlies the behaviour of animals? Conversely, if plants turn out to be 'brain-less', then the question will emerge where and how do they store and process the information which they obtain about both the abiotic and biotic environments, and how do they then use this information to optimize their future behaviour? Do plants feel (as suggested by Aristotle) and experience pain? Further: Do plants hear, and can they perceive odours? The truth is that we do not know, although their extreme sensitivity to mechanical vibrations indicates that they can perceive voices and their responses to volatile gases suggest they have a type

of olfactory response. Importantly, our lack of knowledge should not justify claims that plants do not possess these abilities and properties. In fact, their complex, rational, and surely intelligent behaviour suggests just the opposite. This is why we should be more sensitive to these issues and should commence a serious enquiry into these urgent questions, utilizing minds trained in the 'scientific method' but which can also clearly differentiate between speculation and hypothesis (Huszagh and Infante 1989).

Is it by chance that the Greek word 'neuron' refers to vegetable fibre? In fact, this happy and synchronistic coincidence might be taken to signify that the term plant neurobiology is fully justified! This book brings together all these new plant neuronal aspects and combines them with the classical plant electrophysiology. Plant neurobiology is commencing its emergence as a coherent science.

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Finally, we wish to remember with affection Jolana Albrechtová (co-author of Chap. 25) who tragically died in a car accident on the 29th of November 2005 at the age of 39 years.

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