Foraging decisions by plants — Making a case for plant ethology

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The deer stand still with the grass in their mouth falling down;
The peacocks have abandoned dancing;
and shedding their grey leaves, the creepers appear to be shedding tears!

(In *Abhijnansakuntala* by Kalidasa; Act IV;
Priyamvada explaining the sorrow of nature while Sakuntala was leaving to her husband's house)

It is said that, Charles Darwin was prompted to refute Carl von Linneaus' claim that plants are incapable of exhibiting movements like animals do[1]. Demonstrating that every tendril and tip of the radicle have their own power of independent movement, he stated that plants 'acquire and display (*this*) power only when it is of some advantage to them'[2]. Unfortunately, Darwin's wisdom does not seem to have been inherited by biologists in general; even today, for most biologists, plants are incapable of behaviours such as movement, communication, aggression and sensitive responses exhibited by animals.

But in a recent report, Colleen Kelly[3] of the Oxford University, demonstrated the dramatic ways in which plants also exhibit choice over food patches as actively as animals do. Her experiment illustrates that plants exhibit behaviours similar to that by certain insect predators while searching for their prey.

For instance, coccinellid beetles searching for aphids exhibit an interesting behaviour[4-6]. On encountering a prey, they increase their sinusoidal movement and thus spend more search time and effort in and around the area of the encountered prey. If the beetle does not encounter the prey over a long search period, it then reduces the sinuosity of its search path and diverts its search efforts to other areas through relatively straight paths. Aphids are known to occur in randomly distributed clumps and hence encountering one prey increases the probability of encountering others in the same area. Thus, coccinellid beetles spend more effort in areas that are likely to reward them high and less in areas with less or no reward. In other words, they appear to make decisions regarding how long to search and/or stay in a patch.

Can plants take such active decisions? The experiment by Kelly[3] clearly demonstrates such ability of a parasitic plant, Cuscuta. She offered to the growing tips of Cuscuta, branches of the host plant, hawthorn, grown in varying nitrogen levels. Clearly, host plants grown in high nitrogen levels would be quantitatively more rewarding to Cuscuta than those grown in low nitrogen levels. She found that within three daylight hours, the tips of Cuscuta preferred to grow and stay along the host stems that were more rewarding (with high nitrogen level) and rejected and moved away from the less rewarding stems. The extent to which the stems were accepted was in proportion to their reward levels. In other words, her experiment clearly demonstrated that Cuscuta is as capable as coccinellids in making decisions while foraging and accepted or rejected the patches in accordance to the rewards from them.

In another experiment, Kelly[7] directly measured the foraging effort of Cuscuta, in terms of the extent of coiling around the stem of six host species. She found that the extent of coiling (hence foraging effort) was proportional to the returns from the different hosts in terms of the biomass per unit length of the coil, survivorship and fecundity of the parasite. Thus, similar to the coccinellid beetles, the growing tip of Cuscuta appears to invest greater foraging effort in patches that pay them high rewards and less in patches that pay low rewards.

Though such studies demonstrating the dramatic behaviour in plants are very few, it is not unlikely that they offer many more surprises if we begin examining them as systems also capable of active behaviour. Unfortunately, it was tacitly assumed and acknowledged for long that only animals are capable of active behaviour because it was only these (and not plants) that were considered capable of walking, flying and swimming and accepting or rejecting food at will.

In fact rarely in the history of biology, have there been serious attempts to treat plants as organisms capable of exhibiting behaviours as actively as animals. Though it is immediately not possible to trace the roots of such attitude, it is not unlikely that it has emerged from our tendency to regard only those that are visibly 'moving' or 'gyrating' as active life and others not. It is perhaps because of this attitude, that the recent propositions that plants can actively exhibit rivalry, mate choice, aggression, conflicts and co-operation[8-17], have frequently met with hostile response. For instance, in response to one of our such propositions on parent–offspring conflict in plants[18], Wiens *et al.*[19] replied, '*These highly anthropomorphic, sociobiological hypotheses are best not applied to plants*'.

As early as 3 BC, Theophrastus is said to have stated that leaves orient themselves actively to the sun to harvest the light energy[1]. Charles Darwin[20] in his book *Power of Movement in Plants* states, 'it is hardly an exaggeration to say that the tip of the radicle (and the stem) thus endowed, and having the power of directing the movement of the adjoining parts, acts like the brain of one of the lower animals, the brain being seated within the anterior end of the body, receiving impressions from the sense organs and directing the several movements'. Darwin[2] also demonstrated that stem apices of climbing plants that are not in contact with host, exhibited sweeping movements. It was suggested that these movements could be considered as search strategies by the climbers to latch on to their hosts.

A strong evidence suggesting that plants also exhibit search strategies as efficiently as animals has been offered by Sutherland and Stillman[21] in a stoloniferous plant system. These plants send out prostrate stems (stolons) which after a length, branch out at a definite angle. Simulating the growth of such plants in an artificial habitat with randomly assigned good and poor patches they found that in 'good' patch the optimal strategy of these plants shall be to produce short internodes and branch more frequently. They found that of the 14 reports examined, 13 supported these predictions.

Work by Drew and Ashley[22] showed similar behaviour of plant roots searching for nutrients in soils with patchy nutrient supply. Roots were found to branch more intensely in good but rarely in poor patches. This behaviour is similar to the enhanced branching of ant trails in food rich compared to poor habitats[23]. These studies establish clearly that concepts of foraging theory[24,25] may be applied equally effectively to both animals and plants.

Unlike animals, however, plants cannot frequently revise their decisions. For example, an ant searching in a less productive patch or path can abandon it, retrace its search path and explore fresh areas. In plants, because search efforts involve expending on permanent structural features in the form of roots and shoots, retracing paths would be highly constrained and, if possible, would incur considerable energy. Further, because of the relative permanence of these materials, even preliminary paths, tend to become traditive. In other words, historical contingents (errors) may significantly influence the foraging network in plants. One way to minimize such errors is to be more stringent in their decision making and to be more sensitive to the quality of the patches. In this respect, plants could be expected to have evolved with more fine-tuned strategies of responding and decision making than animals—a view that may sound ironical in the context of the generally held notion that plants are passive and lack features that could be termed behavioural.

It is probably contextual to recall the confession by a sole animal physiologist, who initially cast his vote against the publication of J. C. Bose's work on 'Irritability of Plants' by the Royal Society. Realizing his mistake, he came up to Bose and confided, '*I could not believe that such things were possible (in plants) and thought that your oriental imagination had led you astray*'[26]. After all, this oriental imagination was eventually found to be true. It is probably appropriate that the dogma, about the inability of plants to behave, be broken by the oriental biologists as their life and culture is based more deeply in a past that had acknowledged the life of plants and animals with equal respect.

In the tradition of Bose, we wish that biologists begin treating plants worthy of behavioural studies and also wish that the term 'Ethology' encompasses both plants and animals.

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