# Swarms, swarming and entanglements of fungal hyphae and of plant roots

Peter W. Barlow[1,*] and Joachim Fisahn[2]

[1]School of Biological Sciences; University of Bristol; Bristol, UK; [2]Max Planck Institute of Molecular Plant Physiology; Potsdam, Germany

There has been recent interest in the possibility that plant roots can show oriented collective motion, or swarming behavior. We examine the evidence supportive of root swarming and we also present new observations on this topic. Seven criteria are proposed for the definition of a swarm, whose application can help identify putative swarming behavior in plants. Examples where these criteria are fulfilled, at many levels of organization, are presented in relation to plant roots and root systems, as well as to the root-like mycelial cords (rhizomorphs) of fungi. The ideas of both an "active" swarming, directed by a signal which imposes a common vector on swarm element aggregation, and a "passive" swarming, where aggregation results from external constraint, are introduced. Active swarming is a pattern of cooperative behavior peculiar to the sporophyte generation of vascular plants and is the antithesis of the competitive behavior shown by the gametophyte generation of such plants, where passive swarming may be found. Fungal mycelial cords could serve as a model example of swarming in a multi-cellular, non-animal system.

## Introduction

Recent exploration of the oriented "collective motion" inherent to inanimate physical and chemical systems during phase transitions,[1,2] where the rule is that "a given particle ... assumes the average direction of motion of the particles in its neighborhood,"[1] has led to the question of whether similar types of collective motion can be found in animate, biological systems.[3,4] Examples of the coordinated collective motion of animals include the swarming of insects, the flocking of birds and the schooling of fish. Bacteria also show such swarming. Although the inanimate and animate systems differ in scale and in mode of operation, the similarity of behavior displayed by the elements (particles) in the respective swarming systems suggest the operation of some general principle underlying collective motion, wherever it might be recognized. Against this theoretical and experimental background, it is not surprising that attention should have been given to the question of whether plants or plant parts also display features of collective motion, or "plant swarming".[5] In this regard, the putative "swarming" behavior of plant roots might be a pertinent example.[6] Furthermore, the possibility has been raised of the operation of a "swarm intelligence",[5,7] or "group cognition",[8] by means of which roots, through their oriented collective motion (via directional growth), optimize interaction with their environment.

Whereas swarming in non-animal systems, e.g., the aggregation and collective movement of bacterial cells,[9-11] and perhaps of diatoms also, where it manifests as a temporary agglutination of cells,[12,13] is quite well accepted, the idea of swarming in relation to higher plants is new. However, this idea need not be surprising since one out of several functions of a swarm is to serve as a collective unit of nutrient foraging,[14] a process which necessitates an economy of movement toward or through a potentially more favorable nutritious environment. Plants, being built according to a modular, or metameric, body-plan,[15-17] besides having an inherently plastic morphology—a plasticity evoked by differential responses to the environment—are ideally equipped to utilize their properties of modularity and plasticity to produce organ swarms when the need arises.[18,19]

In addition to its general relevance to the hypothesis of there being similar principles of collective motion in both animate and inanimate particle systems, the proposal that plant roots, specifically, could show swarming behavior has a number of other probable intellectual origins. The first is that interest in the topic of swarming in plants has arisen, as is often the case, in emulation of the more advanced state of research into the collective behavior of animal organisms.[20] Second, the last decade has seen the development of sophisticated observational and mathematical techniques for the analysis of animal swarming in terms of topology, motion and mutual positioning of the elements within the swarm.[4,20-22] And these methods have recently been applied

to the collective motion of algal unicells in order to establish whether they, too, show swarming.[23] A third strand of interest has resulted from an exploration of cognitive processes, not only as they apply to both individuals and groups throughout the realm of biology,[24,25] but also in relation to higher plants, in particular.[26,27] This interest in cognition has been coupled with a project to find commonalities in both the organization and, importantly, the behavior, of plant and animal organisms,[28,29] even though the last common ancestor of plants and animals is believed to have been unicellular and pre-dated by about 1 billion years (1Ga) the first multicellular organisms, which originated not less than about 0.6 Ga before the present.[30] Relevant to this last-mentioned strand of research are the questions which flow from the self-evident observation that roots occupy a variety of environments from which they have to acquire the major part of the water and minerals necessary for plant life on land. Thus, in addition to being dependent upon both plastic, anatomical modifications and tropic growth responses to deal, in the short-term, with subtle variations in their environment, it may be asked whether there are long-term behaviors and strategies employing putative cognitive faculties by which individual roots and root systems cope with these variations. In this regard, it may be that spatio-temporal modulation of root and root-system growth involves processes such as memory and the prioritisation of alternative modes of response to multiple stimuli.[31,32] Moreover, collective motion in general, and root swarming in particular, may be examples of an evolutionarily conserved behavioral strategy which operates within the sphere of ecological interactions[31] and which relates to the way in which members of a given species interact with the prevailing edaphic environment. A further possibility is that collective swarming behavior could assist long-distance dispersal of species,[32] changing that process from a stochastic event[33] to one shaped by evolutionary-developmental processes. Fungal rhizomorphs, which we shall discuss briefly, may be notable examples of this possibility since they are among the most physically extensive and long-lived of organs.[34]

While some caution is necessary in using, in the context of plant biology, terms which have originated in animal behavior (especially bearing in mind the distinctive origins of animals and plants, mentioned above), objection is unlikely to be raised to the application, in a general way, of the terms "swarm" (noun) and "swarming" (verb, present participle) to certain defined features of collective plant root growth and root system development. Nevertheless, before exploring more precisely what the concept of the "swarm" could mean in relation to plant root biology (or indeed to any other plant part), consideration should be given to the criteria by which a swarm is defined. Without such definition, the term "swarm" might simply be used as a simile, or figure of speech, drawing attention to any cluster of moving elements. However, the very recognition of this possibility leads to the profound question of what feature might distinguish a "biological swarm" from a "figurative swarm". We take it that, in a biological context, the term "swarm" pertains to a certain type of organization of elements (or "particles", in the terminology of Vicsek and Zafeiris[4]), which has been reached by means of an objectively recognizable behavioral process, "swarming",

involving self-propelled, coordinated movement in response to some critical change within the environment. By contrast, when the term "swarm" is used figuratively, the elements of the "figurative swarm" are brought to a state of aggregation in accordance with spatial and geometric constraints imposed upon them from without, by their surroundings, and not as a result of volitional, self-directed movement. Thus, biological swarms may be qualified either as "active", or as "passive": self-generated motion is here the critical feature that differentiates the two types of swarm.

## Swarm Criteria

The criteria we propose for active swarms and swarming are as follows: 1) A swarm consists of elements—mainly organisms in the case of animals, and mainly organs in the case of plants; 2) The swarm elements belong to the same species: they are conspecific; 3) The elements are mobile—due either to their intrinsic mobility (animals) or to their growth movements (plants); 4) Owing to this mobility, elements can, under circumstances which often relate to perception of environmental cues, aggregate (i.e., show collective motion), and thereby give rise to a swarm; 5) During swarming, although the mobile elements may initially be drawn together from different directions, they eventually come to adopt similar directions and velocities of movement; 6) The swarm aggregate has a distinct morphology and pattern of behavior, which represents a new state of organization; 7) Swarms are often temporary and disperse into their elements, or they may even die, after exploiting an environmental opportunity.

Evidently, the operations mentioned at points 4 to 7 above, come into effect when particular cognitive or physiological thresholds are overcome. Furthermore, in relation to criterion 6, the most complex expression of swarming, as displayed by animals, is where a self-propelled mobile element interacts with its neighbors in such a way that not only is its direction of motion changed, but so also is that of the swarm of which the element is a part. The converse also holds: if a swarm changes direction then the direction of each individual element will probably also change so that they remain accommodated within the swarm.

There may, therefore, be two tiers of active swarm behavior. The first and most complex is where there is a mutuality of interaction between the swarm and its elements, where the vector of an element can influence the vector of the swarm, but still be accommodated within it. The second is where the movements of the elements and of the swarm are oriented in the same direction. In each case, however, there is a probability of randomness associated with the direction of element motion. When this probability is zero, the swarm persists. When the probability is moderately high and there is no self-correcting mechanism to correct deviant directional motion, elements will sometimes leave the swarm. But if randomness of motion increases, the swarm will then break down into its elements; the swarm then seems to represent a meta-stable state. Plant organs, with their fewer degrees of freedom of movement, may conform to the second tier of swarm behavior and either have no randomness of motion, or, if they do, have an efficient self-correcting mechanism.

## Swarm Features

We take a biologically active swarm to be comprised of a number of similar individual elements ε. These may correspond to cells, organs, organisms, where the latter may also be represented by unicells. Under certain circumstances, the elements can aggregate and form a coherent collective unit, the swarm, ε*. Aggregation (i.e., "swarming") can be qualified according to whether this event is initiated by an active sensing and/or signaling process which leads to an attraction between elements and their subsequent coalescence fostered by their own inherent mobility, or from random collisions between elements following which the elements remain aggregated, the number of elements within the swarm being augmented by further collisions. Accordingly, there should be a certain number of elements, με, and a certain threshold of element density, $\rho\varepsilon_{crit}$, above which a swarm, now with element density ρε*, can be said to have formed (i.e., ρε* > $\rho\varepsilon_{crit}$); below the critical density, swarming would not be recognized (i.e., ρε < $\rho\varepsilon_{crit}$ ≤ ρε*). In the case of the flocking of birds, e.g., starlings, swarm density, in its three-dimensional aspect, may typically be in the order of ρε* ≈1000 individuals per m[3,35] whereas in the case of roots, in their one- or two-dimensional aspect, the threshold, in terms of the distance between root tips, can be in the order of $\rho\varepsilon_{crit}$ ≈ 10 tips per 100 μm linear length.

Although the elements of the swarm often retain both their individuality and their characteristic properties, the collective unit, by virtue of its aggregated nature, acquires its own structure and properties. Swarming should therefore be seen as a process which permits an entity residing at one level, or state, of organization, η, to become an element within a new swarm state η*. This occurs when the density threshold $\rho\varepsilon_{crit}$ is exceeded. Thus, it is axiomatic that the establishment of a swarm involves alteration, or state change, to the usual pattern of movement of the individual elements and a reconfiguration of their spatial relationships as, according to Vicsek's rule,[1] each element contributes to the average direction of motion of the aggregate. In addition to the mentioned morphological (state) transition which accompanies swarm formation, when entities at level (state) η become elements that foreshadow the emergence of state η*, there is also a transition from a relatively low degree of internal order to one of higher degree. In this context, "order" is related to not only the spacing relationships but also the sensing capabilities and possible communicative relationships inherent to the two states. These alternative states, η and η*, have consequences for efficiency with respect to some function such as resource capture or survival strategy, perhaps in consequence of the spacing of the elements or their density (ρε, ρε*). If the sensing abilities or communicative relationships are weak, and if autonomous (random) movements occur with high probability and are not corrected, the state η* is then recognized as being meta-stable.

By now it should be possible to see how swarming of plants (individual entities of level or state η) or plant parts (organ entities of level or state η-1) could be recognized. For example, in the context of roots and root systems, aggregates in excess of the critical element density $\rho\varepsilon_{crit}$, and the adoption, by the elements, of a new morphological state as a supra-organ η*-1, could be indicative of a swarm. However, to take a simple example where swarming is precluded, the typical longitudinal, "herring-bone" spacing pattern of lateral roots as they emerge in sequence from a main axis would probably not be regarded as swarming behavior because the critical element density is not exceeded. It is evident that the value of a critical density $\rho\varepsilon_{crit}$ is set somewhat arbitrarily. Nevertheless, as we shall see, the sudden burst of emergence of densely clustered lateral roots upon supporting root axes of plants within the family Proteaceae in response to a particular stimulus from their immediate environment might well be recognized as a swarming activity. Here, the usual (default) root-element density ρε is increased to ρε* of the cluster-root (swarming) state and, moreover, the density $\rho\varepsilon_{crit}$ is as great as it can be, given the anatomical origin of these roots.

As mentioned, a swarm is considered to be meta-stable, dispersing into its constituent elements after an indeterminate length of time, as is the case for animal and insect swarms. However, in some of the cases of plant root swarms to be described—here the roots stop growing or become lignified, for example—the root swarm cannot disperse because of the rigidity and immobility of mature tissue. This swarm state η* may maintain its physiological function for as long as the swarming elements remain alive, dispersing only after their death and decay. This particular distinction between animal and plant swarms in terms of their eventual dispersion points to the contrasting manner in which animal and plant swarms come into being: animal swarms are comprised of organisms which are independent, autonomous units (where μ entities of state η collectively enter state η*) which are able to sense each other, thereby maintaining the coherence of state η* until random motions force swarm breakdown, whereas the plant swarms considered here are comprised of inter-dependent parts of the whole organism, the parts having less freedom to dissociate.

Because time and space are related, and because movement is inherent to the concept of the biological swarm, comparisons between swarms of animals and those of plant roots need to take account of the different timescales over which animals and plants operate. Animal movements commonly occur with velocities of kilometres per hour, whereas plant root movements (which are often the most rapid of all plant growth movements) are in the range of tens of micrometres per hour. Moreover, animal bodies move much more freely in space in contrast to vegetative plant bodies which are to many intents and purposes sedentary, and re-locate themselves, or re-position their parts, relatively slowly (e.g., refs. 36 and 37). Any movement in relation to active plant organ swarming occurs in the context of growth rather than of free movement, as is the case in animal swarming. (Wind dispersal of, for example, the familiar propagules of Compositae, composed of achene and pappus, would result in a figurative, "passive" swarm since their movement is not directly generated by the plant part, and any collective motion of the propagule elements is a matter of chance.) Moreover, the scope of plant growth movements is constrained owing to growth occurring mainly at the apices of plant organs; the basal, more mature portions of organs,
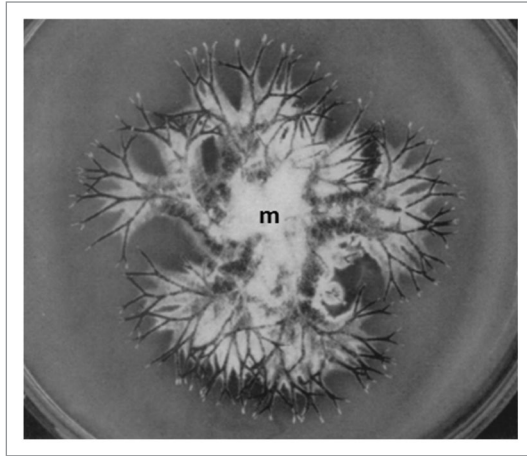
**Figure 1**. Mycelial cords of *Armillaria mellea* with dichotomous branching emerge from the hyphae (m) which grow out from the initial explant. Modifed from Figure 1 in ref. 45.
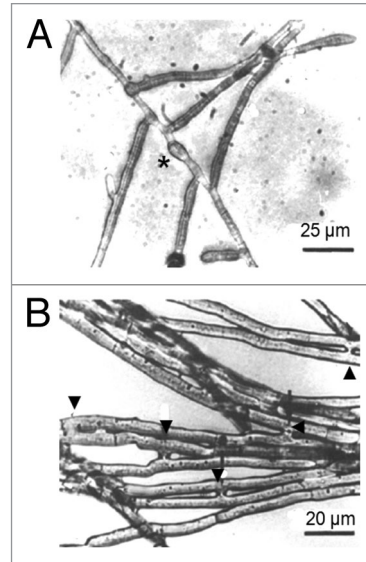


**Figure 2**. Stages of mycelial cord development in *Sphaerostilbe repens*, 20–40 h after inoculation. (**A**) 20 hours. Hyphae grow and branch from the single spore (*) used as inoculum. (**B**) 40 hours. Hyphae behind the margin of the hyphal colony show numerous anastomoses between adjacent filaments (arrowheads), helping them line up as a mycelial cord. Modified from Figures 2 and 4 in ref. 47.

**Table 1. Examples of swarming and its outcome in fungi and plants**

| 1. Element (state η-1) | 2. Condition for State transition (η-1 → η*-1) | 3. Type of element aggregation | 4. Resulting aggregate (Swarm) | 5. Emergent form (state η*-1) | 6. Example | 7. Reference |
|---|---|---|---|---|---|---|
| A. Fungal mycelia hyphae | Hyphal adhesions | Mutual anastomoses; Polarized elongation | Fungal mycelial cord | Supra-cellular, syncytial organ | Armillaria mellea (Basidiomycete); Sphaerostilbe repens (Ascomycete) | 45 and 47 |
| B. Primary and secondary roots | Susception of chemical or electrical field; Adhesion of dermatogens | Mutual appression | Root entanglement | Root association | Arabidopsis thaliana; Zea mays | 6 and 58 |
| C. Roots of root system (Multi-order laterals) | Reproductive death of apical meristem | Reoriented vector of root elongation | Sympodial root system | Root clusters | Platanus hybrida | 68 |
| D. Roots of root system (Multi-order laterals) | Internal phosphorus depletion | Clustered lateral root primordia | Root clusters | Root clusters | Hakea spp; Lupinus albus | 75 |
| E. Shoot-borne (adventitious) roots | Environment of leaf bases; Ortho-gravitropism | Appression to supporting stem | Root-stem | Supra-organ pseudostem | Vellozia spp; Xanthorrhoea spp | 83 and 84 |
| F. Roots of root system (Multi-order laterals) | Adhesion of root barks | Anastomosis (Grafting of cambium layer) | Anastomized root system | Supra-root system | Dacryodes excelsa; Nyssa sylvatica | 89 and 91 |

Rows **A–F** list details of swarm development. Column **1** indicates the elements and states of development (see text) proposed as participating in swarming. Columns **2** and **3** indicate the conditions for the transition to swarming to occur. Columns **4** and **5** indicate the resulting form or state of the swarm and its role in fungal and plant life.
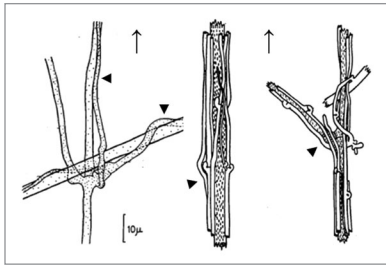
**Figure 3**. Intertwining hyphal branches at an early stage of mycelial cord formation in *Merulius* (*Serpula*) *lacrymans*. Elongation growth is in the direction arrowed. Cord progression is acropetal, though a few hyphae extend basipetally. In the two right-hand panels, slender branching hyphae wind around a wider main hypha (arrowhead) and form a thin mycelial cord. Scale bar = 10μm applies to each panel. Modified from ref. 49, with permission from OUP. Figure is not included in copyright agreement, for reuse permission, please contact journals.permissions@oup.com.
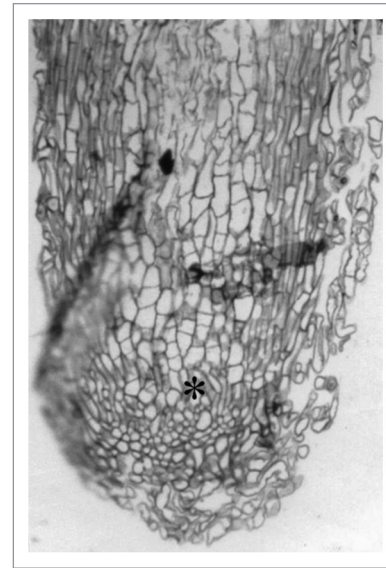


**Figure 4**. Median longitudinal semi-thin section through the tip of a mycelial cord of *Armillaria mellea*. Note the distinction between the inner portion of the cord, with inter-hyphal spaces, and the outer portion, with a more compact structure. A possible "meristematic" zone (*), with short cells, occupies the tip.

which are non-growing and, hence, immobile, may in some cases limit the degrees of freedom of movement of the growing apical portion.

At a higher level of organization, the boundaries of plant species move with time. In this respect, it is well to consider whether the term "hybrid swarm", as used by population biologists,[38] is a figure of speech or, as seems more likely, denotes a "real" active, though slow-moving, swarm of hybrid plants. The introgression and physical movement of the hybrids (assisted by active processes of pollination, seed dispersal and selective advantage) into a parent population occurs over many plant generations, operating within slow timescales, such as apply to geophysical changes.[39] If assisted by fast-growing vegetative runners, say, as in the case of the bramble, *Rubus ulmifolia*, the mobility of a hybrid swarm could be considerably enhanced.

The plant roots, and also the fungal hyphae and mycelial cords, which we shall consider with respect to swarming, grow outwards, or acropetally, from their site of origin owing to asymmetric, unidirectional organ growth, all files growing away from their immobile, more mature basal regions. This acropetal progression toward swarming of organs contrasts with the basipetal production of cell files within roots or hyphae where all files are descended from cells located at the respective acropetally growing apices. These files of cells, with symmetrical bidirectional growth, could, in conformity with the criteria above, also be considered as basipetal swarms of cells [or quasi-swarms, since the cell files are neither free-moving (active swarm) nor totally constrained (passive swarm)] enclosed within the dermis of an organ.

## Fungal Hyphal and Plant Root Swarms

We now consider examples of the elements and processes by which certain fungal and plant swarms are developed, and the nature of the emergent forms produced by swarming elements. **Table 1** lists these examples and also briefly summarizes: 1) the individual elements (in the case of plants and fungi, these are organs at state η-1); 2) the critical condition or process by which transition from the elemental state to swarming comes about, when the critical element density, $\rho\epsilon_{crit}$, is exceeded; 3) the form of the swarm that emerges from this transition, i.e., the supra-organ of state η*-1.

### Fungal mycelial cords

The initiation and resulting forms of mycelial cords provide an introduction to swarm development in fungi. We use the term "mycelial cord" to cover three types of mycelial aggregate: mycelial cords, mycelial strands and rhizomorphs, all of which have been described in the literature,[40,41] and all of which have close developmental relationships.[42] Mycelial-cord formation is favored by the presence of localized sources of nutrients and modulated by long-distance transport of stimuli from other regions of the mycelium,[43] as well as by specific nutritional conditions present in the substrate or growth medium.[44] Snider[45] documented the formation of mycelial cords in laboratory cultures of the basidiomycete, *Armillaria mellea*.

Each inoculum developed initially as a cluster of individual hyphae from which thick mycelial cords subsequently emerged (**Fig. 1**). The cords outgrew the remaining mycelial hyphae, probably because cord growth was more polarized and unidirectional than was the growth of the hyphae in the original cluster, which tended to ramify in many directions. With further growth, the cords bifurcated. At later stages, individual hyphae (as well as secondary cords) emerged from the primary cord, as though the basic swarm structure of the mycelial cord was meta-stable and becoming dispersed. Snider could not establish the means by which the cords originated within the mycelial cluster, but he supposed this to be the result of lateral appression of hyphae. Valder[46] believed that the hyphae collided at random. However, some factor other than mere contact might be necessary for the appression of hyphae: for example, attraction between hyphae
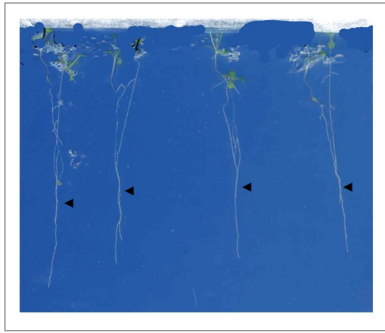
**Figure 5.** Growth of seedlings of *Arabidopsis thaliana* on a vertical agar plate. Primary roots of four pairs of seedlings make contact (arrowheads). Lateral roots also contact and aggregate with the primary roots.

mediated by electro- or chemo-tropism may be at work. Following on from this early observation of Snider,[45] the initial stages of cord development were studied in cultures of the ascomycete, *Sphaerostilbe repe*.[47] Prior to cord formation, hyphae became appressed longitudinally, and this association was consolidated by anastomoses between hyphae (**Fig. 2**). Hyphae subsequently became intertwined as cord development proceeded.[48]

Observations by Butler[49] on *Serpula* (formerly *Merulius*) *lacrymans*, and more recently by Schweiger et al.,[50] using confocal microscopy to view the developing mycelial cords of *Paxillus involutus* (both the mentioned species are basidiomycetes), have demonstrated a similar pattern of interweaving hyphae. In Serpula, this occurred between hyphae of different branching order, all branches tracing back to a common hyphal axis (**Fig. 3**). Hyphal interweaving, as well as hyphal appression, seem to establish the mycelial cords in these species, and may be a general feature of cord development.

With regard to the emergent properties of the developing mycelial cord, in comparison to the elemental hyphae, not only is there a faster extension of the nutrient-capturing cord apparatus, and thus a faster rate of foraging and nutrient acquisition, but there is also concomitant internal differentiation within the cord, which may facilitate its more rapid growth. For example, the so-called "tracheode",[51] at the interior of the cord, is an assemblage of loosely packed hyphae which permits the transport of air toward the growing tip. More solid tissues are developed toward the outside of the cord as a sheath-like protective cortex and a superficial, melanized dermis. There is also differentiation at the tip of the mycelial cord (**Fig. 4**). In *A. mellea*, for example, the tip of the rhizomorph contains packets of small cells that resemble those of a root apical meristem.[52] However, the presence of such a discrete meristem is disputed.[42] It is noteworthy that not only do the swarming cellular aggregates of the bacterium, *Bacillus subtilis*, show bifurcation patterns similar to *A. mellea* rhizomorphs, but that these patterns can also be simulated (by computer modeling procedures) with differential chemotactic cues as one of the variables.[53] Furthermore, swarming aggregates of *B. subtilis* are characterized by clusters of small, meristem-like cells enclosed within a fluid membrane at the growing tip of the swarm.[53]
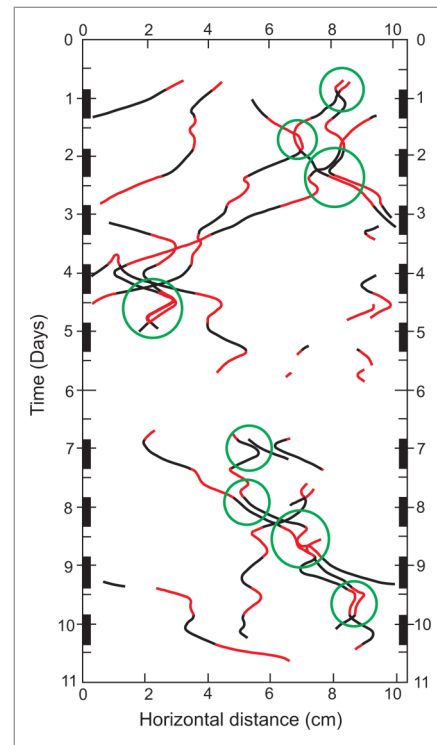


**Figure 6.** Trajectories of six roots of *A. thaliana*, such as those shown in **Figure 4**, recorded by time-lapse infra-red photography, during eleven days of growth on a vertical agar plate. The position of the root tip was recorded at half-hourly intervals. Red and dark lines are the root trajectories during the light and dark periods, respectively: L D 12: 12 h. The dark period is indicated by black bars on the horizontal time-axis. Encircled areas indicate periods of root-root contact/entanglement and joint growth. Breaks in the trajectories were due to technical reasons.

Fungal mycelial cords, in their fulfilment of the criteria by which a swarm can be defined, seem to have the potentialities to become model systems for experimental studies of swarming. We now ask whether these criteria are satisfied by the next example, plant primary roots, to which swarming properties have been attributed?[6] Then we discuss the putative swarming of branch roots.

**Plant primary roots**

Evidence from *Zea* roots

Soon after germination, vertical, or near-vertical primary roots of *Zea mays*, grown either in soil or in laboratory conditions on filter paper, usually extend downwards as a consequence of their graviperception (i.e., the roots are positively orthogravitropic). However, there are circumstances which modify the orthogravitropic response and the roots achieve a angles other than vertical. Such a situation was shown for 4-d-old maize roots in Figure 1D of Ciszak et al.[6] The consistent non-vertical orientations adopted by the numerous roots used in the experiment of these authors, and where many of the roots turned in the same direction, was taken as an indication of root swarming. The authors argued that, if the phenomenon was one of swarming, it would be placed on a firmer basis if the roots consistently and

coherently re-oriented their growth from vertical to some other angle, either to the left or right of vertical. In the mentioned figure (**Fig. 1D** of Ciszak et al.[6]), most roots were shown growing to the right. The authors supposed that the roots had "chosen" this right-ward direction in preference to the alternative left-ward direction, or to growing downwards (the presumed default orientation). If, as the authors say, the growth conditions precluded localized stimuli, then the possibility exists that the putative root swarming event came about because a stimulus emanating from one or a few randomly rightwards-moving roots induced neighboring roots to reorient likewise and "swarm" toward the right-hand side of the growth chamber. However, in experiments of this kind, the orientation of the grain is important because, in addition to a gravisensor located in the root tip, there is another gravisensor in the embryonic tissue (aleurone) which, if an embryo is displaced away from vertical, can affect the subsequent orientation of the emerging radical.[54,55] In Figure 1D of Ciszak et al.,[6] the grains do not all share a similar upright orientation, which would favor orthogravitropic root growth, and this may have led to irregular orientations of the roots. Furthermore, the roots were growing upon a surface inclined at 75° to the horizontal. The single root shown growing in Supplementary Video S2 of Ciszak et al.,[6] performs looping, thigmotropic movements as a result of intermittent contact between the root tip and the support surface (see refs. 56 and 57); such movements may account for some of the deviations from vertical of the many roots shown in Figure 1D and Supplementary Video S1 of Ciszak et al.[6]

A statistical analysis of the root growth data was summarized in Figure 4 of Ciszak et al.[6] The distribution of root growth velocity vectors was used to reveal bias toward either right-ward or left-ward growth. The velocities of left-wards and right-wards growing roots would be expected to show similar distributions. In the experimental material, although the two classes of root (left- and rightwards growing) did have similar velocity distributions, there was a greater proportion of rightwards growing roots. Directional bias was estimated as a difference R between the maximal frequencies of the velocity distributions of the left- and rightwards growing roots. Taking values of R = +0.0175 and R = −0.0175 as the boundary values associated with simulated root growth rates and random directional growth, and which could serve as a control against which any significant growth reorientation could be judged, the results of K = 10 experiments indicated that 5 out of the 10 sets of maize roots had velocity vectors biased to right-ward growth, whereas only 1 set out of
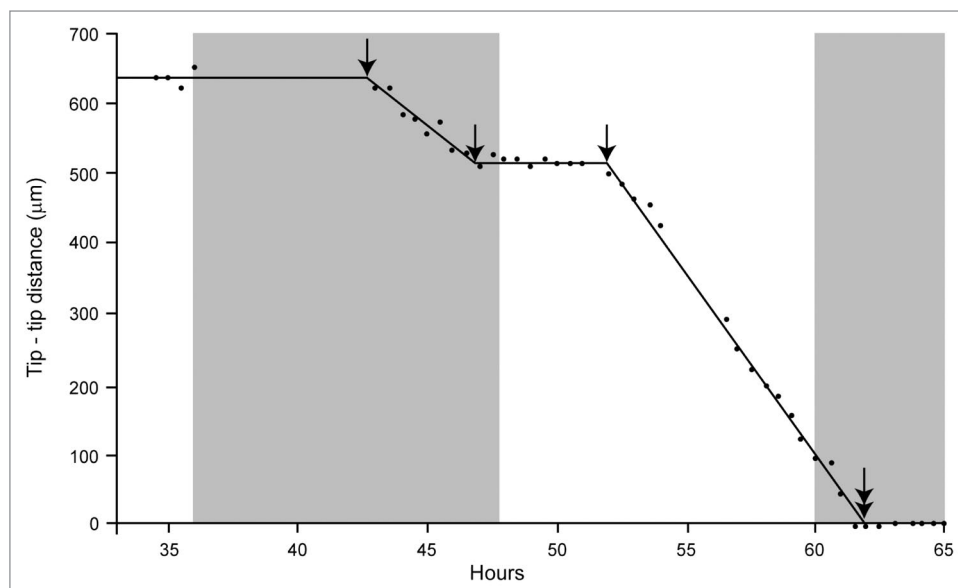


**Figure 7.** Estimates of the shortest distance (μm) between a pair of root tips (of left-hand and right-hand roots) during the course of root growth shown in **Supplementary Video S1.** Major reorientations of growth direction are indicated (single arrows) at 42.5, 44, and 51 h. The two root tips made contact at 62.5 h (double arrow). Time, in hours, is from the commencement of video recording.

10 was biased to left-ward growth; 4 sets out of the 10 were within the random category, where R = ± 0.0175. The bias to the right (5 right: 1 left) might indicate some influence upon root growth orientation from within the environment of the growth chamber itself, as though the roots were attracted toward one or other side of the chamber. In addition, it is possible that the root orientations are indicative of an "escape reaction"[57] in response to the light flashes necessary to photograph the roots. Interestingly, the "control" boundary values (R < ± 0.0175) themselves seem biased to the right: the R values of K = 10 simulations using a random growth orientation model do not average at the expected R = 0, but shows a positive R value because of a few relatively large +R values.

### Evidence from *Arabidopsis* roots

Evidence gathered from roots of *Arabidopsis thaliana* by J Fisahn[58] has given support for an attraction between roots and, hence for the possibility of active swarming. Pairs of plantlets placed 8 mm apart, and with the centers of each pair spaced approx 35 mm from each other, were placed on a vertical nutrient-agar surface. Primary roots of each pair were attracted to each other (**Fig. 5**). Also, lateral roots of one of the pair of primary roots often appeared to associate with the primary root of the other member of the pair. It might be argued that the surface tension between the moisture films on both agar and root, and between paired roots, played a role in this root-root association, and that, as a consequence, one root cannot pass readily over or under another root should the two meet. However, plots of the positions of *A. thaliana* root apices as they grew over the agar surface showed that not only did roots cross over each other but that pairs of roots also formed temporary associations (**Fig. 6**): roots
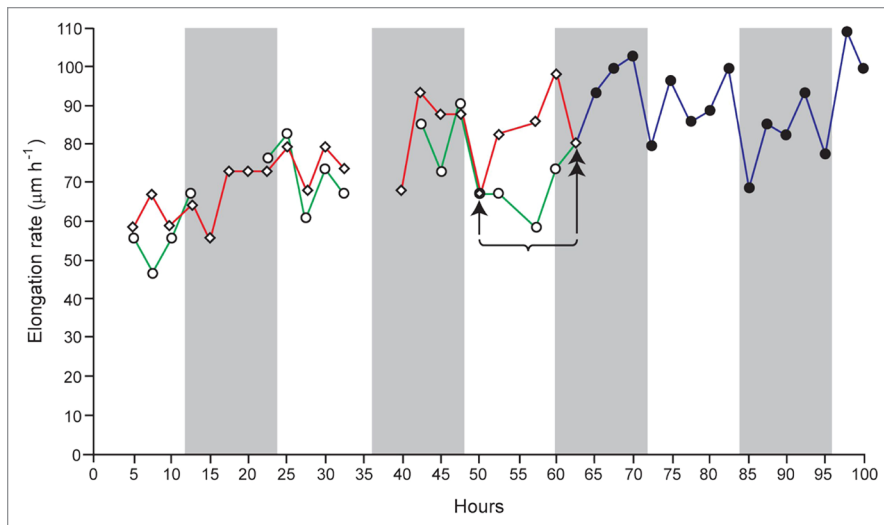
**Figure 8.** Rates of root elongation (µm h⁻¹) of the left-hand (green line) and right-hand (red line) roots of the pair of roots shown in **Supplementary Video S1**, estimated at 2.5 h intervals. The rates were approximately similar for the two roots, but there were noticeable differences (bracketed region) when the two root tips began to move towards each other (at 50–62.5 h, single and double arrows). Thereafter, the two roots grew together (blue line) at the same rate. Time, in hours, is from the commencement of video recording.

approached (or were attracted to) one another, made contact, grew together and then diverged. Contact and pairing occurred during the dark period of a daily L D 16: 8 h light/dark cycle. A video film (**Supplementary Video S1**) in the Supplementary Material shows details of the apparent attraction between a pair of roots and their subsequent course of growth. An analysis of the trajectory of the two roots (**Figs. 7 and 8**) shows the time course of the attractive movement. As the two root tips approached each other, one tip increased its elongation rate while the other tip slowed down (**Fig. 8**), as if to facilitate the meeting of the two tips. Thereafter, the two roots grew vertically at similar rates, as though they were one root.

Both Ciszak et al.[6] and Fisahn[58] found that their respective roots of *Zea* and *Arabidopsis* grew alongside each other for short periods of time (**Fig. 6**). If this type of growth pattern could be demonstrated to occur not by chance but as the result of information passing from one root to another, which subsequently led to a growth movement indicative of attraction or repulsion (**Fig. 8**), then there would be a case for saying that roots show active "swarming". Interestingly, in another set of observations, roots of *A. thaliana*,[58] which were initially growing vertically downwards, reoriented to arrive at similar, non-vertical orientations and then reoriented again toward the vertical. That some of the reoriented axes remained parallel to each other during these two periods of growth, even though separated by a few millimeters, suggests some form of communication between roots across the surface of the vertical agar plate.

In the same way that the *A. thaliana* roots seemed to form meta-stable associations (entanglements), as suggested by the growth trajectories in **Figure 6**, temporary associations were found between roots of barley (*Hordeum vulgare*) and other species growing within a rhizotron.[60] Root-to-root interactions,

often thought of as being mediated by root exudates,[61] have implications for the possible communication not only between roots within a root system but also between root systems of different species.[62-65] Intimate, physical root-root associations, or entanglements, should be added to the list of possible communicative systems operating within the rhizosphere, although how and what these root-root contact-associations may communicate is not known. It is likely, however, that presently unknown signaling methods between roots remain to be discovered,[66] and that some of these might require close root-root associations.

Apart from the mentioned observations using a rhizotron system,[60] associations of primary roots, growing in soil under field conditions or in any other medium, have not, to our knowledge, been reported. In any case, roots in soil, besides their movements due to nutations, would be expected to make small deviations in growth direction due to contact with soil particles.[67] These random growth movements may negate any tendency toward coherent, or coordinated, directional growth. From a teleological point of view, the function of orthogravitropic primary roots is to grow downwards within the soil and to serve as a platform from which plagiotropic secondary lateral roots extend, and from which root systems subsequently develop. Aggregation, or swarming, of primary roots belonging to different plants of the same species would, on the one hand, appear to frustrate the efficient foraging for nutrients since members of the root "swarm" would compete with each other. On the other hand, a temporary association of roots might be sufficient to reorient the growth of root No. 2, say, toward a source of nutrients which had already been perceived and responded to by root No. 1.

**Sympodial and other types of branching within root systems**
An example of an oriented, swarm-like growth of root tips is exhibited by the lateral roots of the tree, *Platanus hybrida* (**Fig. 9**). In their analysis of root systems of 30 trees of *P. hybrida*, Atger and Edelin[68] consistently found sympodial root branching, with lateral roots of orders above and including the fourth-order showing determinate growth and their apices dying after a relatively short period of growth. The death of each apex activated the next branch-order of laterals whose primordia were already present on the supporting axes. This temporal pattern of branching—outgrowth of branches after a waiting period— is known as prolepsis.[16,69] The newly activated, proleptic roots always oriented their growth in an acropetal direction, following the orientation previously held by the aborted apex. This rule was followed by the newly formed roots regardless of whether the supporting root axes were growing vertically or horizontally. Whether there is communication between roots which encourages their similar orientation is not known. The appearance of this sympodial system gives the impression that the root tips of the
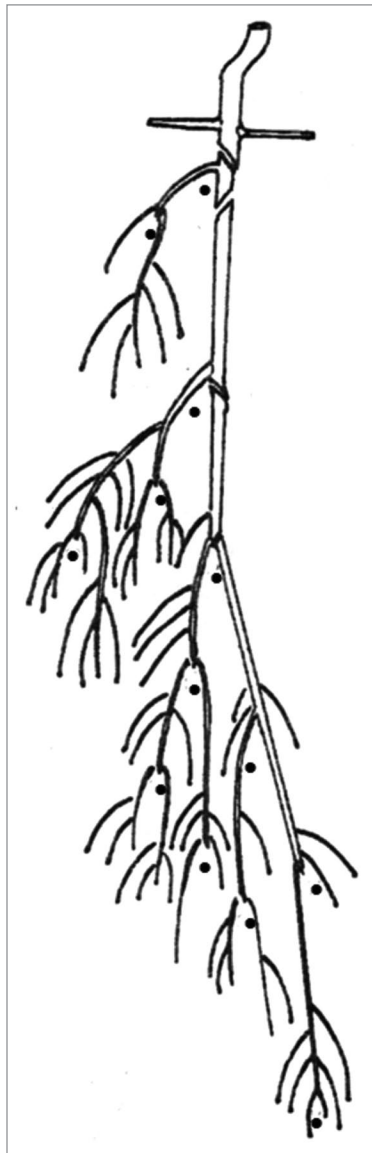
**Figure 9**. Acropetally-progressing, lateral roots of *Platanus hybrida*. The symodial branching system, having the appearance of a swarm, was accompanied by the death of the principal apex (filled circle) of each order of branching, from whose axis the laterals roots emerged. The root tips were oriented vertically downwards. Modified from Figure 2 in ref. 68.



**Figure 10**. Stages of root cluster development in two species of *Hakea*. (**A**) Root clusters regularly spaced along two root axes of *H. petiolaris*. (**B**) Sequence of development of a root cluster of *H. prostrata* on the days indicated. On days 1–2 the roots emerged; on day 20 the clusters were senescing. Scale bars = 20 mm in (**A**) and = 10 mm in (**B**). Photographs kindly provided by Dr MW Shane.

different orders of laterals always swarm toward unexplored territories of soil. This feature was especially marked in the higher-order branch roots, which were both thinner and more crowded together on their parent axes. Additional observations indicated that the symodial pattern of root branching is not uncommon in trees,[70] and details similar to those of *A. hybrida* were described for root systems of the tropical tree species, *Cecropia obtusa* and *Laetia procera*.[70]

A symodial, acropetally oriented system of root branching and growth accompanied by proleptic root production seems an efficient way of filling-in, at a later date, the voids in the three-dimensional volumes of soil residing between older portions of already established root axes.[70] Lyford and Wilson[71]
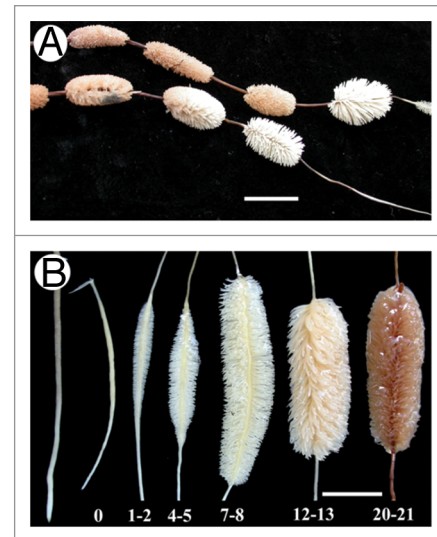
described similar dense, in-filling clusters of determinate 3rd- or higher-order lateral roots of the red maple tree, *Acer rubrum*, growing in Harvard Forest. Here, the lengths and diameters of the root tips growing within the upper soil horizon, close to the base of mature trees, were 1–10 mm and 0.2–0.3 mm, respectively. These "root fans", as they were called, not only forage for nutrients and water but also help bind together the layer of leaf litter of which the forest soil surface is comprised. The root-tip density, $\rho\epsilon$, of laterals of the lower-order, woody root axes was 0.3–1.0 per cm of root length, whereas $\rho\epsilon^*$ of the swarming, higher-order root fans was 10 times greater. Moreover, in samples of soil cut from the forest floor, Lyford[72] recorded over 1100 root tips per $cm^3$ of soil, the individual root tips being even smaller than those recorded earlier,[71] being about 0.1–0.2 mm diameter and not easily seen with the naked eye. This enormously dense population of root tips might be considered a swarm, though one made up of microscopic sub-swarms of roots of different branch order oriented at right-angles to each other. Thus, swarms of high-order branch root apices provide a physiological system whose topology maximizes the collecting of nutrients and solutes from the soil and its superficial leaf-litter layer. Moreover, as pointed out in relation to the two-dimensional branching pattern of fungal mycelia,[73] when fractal dimensions (FD) are estimated, these have FD values of approx 1.8. This value suggests that dense branching patterns, such as the high-order tree-root laterals described by Lyford,[72] are a compromise between explorative and exploitative growth strategies. Fractal dimensions may be a further way of describing the swarm properties of branched elements.

Interestingly, in the tropical tree species already mentioned,[70] the symodial branching habit of the roots was repeated in the pattern of branches within the leafy canopy of the shoot
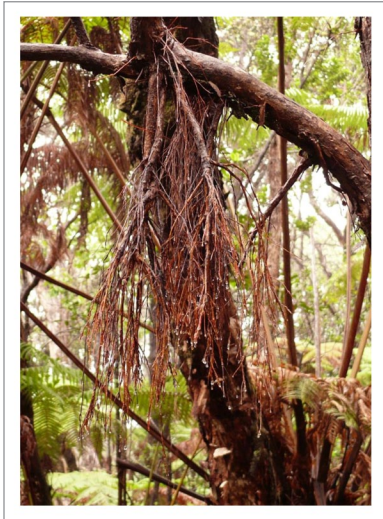
**Figure 11.** Clusters ("swarms") of aerial roots hanging from branches of the rata tree, *Meterosideros polymorpha*. Note water droplets at the tips of the roots. Photograph kindly provided by Dr JG Dubrovsky.

system.[74] However, as Lyford[72] pointed out, the axes of the canopy intermingle to a much lesser extent than do the axes of the tree's root system. The roots occupy a much more variable environment (soil) than does the canopy (air); the respective fractal dimensions may indicate the optimum branching system in foraging either for solutes or for light.

### Cluster roots

A characteristic root branching, as well as a spectacular example of collective motion coinciding with a state transition, is displayed by cluster roots (formerly termed "Proteoid" roots due to their prevalence in root systems of plants belonging to the family Proteaceae). A list of species showing cluster roots in the Proteaceae and other families was published by Shane and Lambers.[75] These types of roots (**Fig. 10**) are important in the context of root swarming, even though, initially, the swarming elements are the cells of the supporting root's pericycle and endodermis from which, having perceived a suitable stimulus (i.e., a stimulus by which the transition from monoaxial root growth to multiaxial growth takes place), the primordia of the future cluster roots are formed. During their proliferative period, prior to emergence from the parent root, the primordial precursor cells swarm basipetally (see Introduction). Later, following the simultaneous emergence of the new rootlets from the parent root (see **Supplementary Video S2**), the roots swarm acropetally as a cluster.

The spacing between the cluster-root primordia is minimal, with few if any cells remaining uninvolved in primordium formation, either in the circumferential or the longitudinal planes of the initiating pericycle tissue.[76,77] The density $\rho\epsilon^*$ of cluster roots of Proteaceae is of the order of 100–200 roots per 1 cm segment of supporting root axis, whereas in the Fabaceae, including *Lupinus albus,* it is about 10 roots per cm of axis. In each case, the default density $\rho\epsilon$ is < 1 root per cm of axis. Therefore, 1–10 roots per cm length of axis is the critical density $\rho\epsilon_{crit}$ above which a cluster root swarm is recognized.

A more detailed examination of the clusters shows that the roots emerge in longitudinal rows (6 rows in *H. prostrata*) defined by the axial course of the protoxylem elements within the root, opposite which the cluster root primordia form.[76] The siting of the strands and primordia, as well as the rectilinear elongation of the new roots, determines the centrifugal emergence of the cluster roots and the globular appearance of the developing cluster. Given the ontogeny of lateral root primordia,[69] there may be as few as 16 cells ( = $\rho\epsilon_{crit}$ at the cellular level) between the centers of the cellular groups along each row from which cluster-root primordia form.

Often, but not always, the clusters form in acropetal sequence along their supporting root axis (**Fig. 10A**). Explanation for the spacing between each discrete globular cluster is lacking, but may relate to the extent and rate of mineral foraging by the apex. Hence, a new cluster, or root swarm, is initiated when the tip of the supporting root enters a zone that is free from the influence of the last-formed cluster, basal to that tip—a quasi-apical-dominance effect. The determinant of cluster size is also unknown, but obviously relates to the number of sites that can be recruited to cluster primordium formation upon receipt of the rhizogenic stimulus.

The transition from pericycle cellular elements to a cluster-root swarm is triggered by a low level of phosphorus or iron within and around the parent supporting root,[75,77,78] perhaps resulting from an alteration of internal hormonal correlations which regulate mitotic cell cycle activity. Sometimes, first-order cluster roots branch to give second order cluster roots. In each case, growth of the roots is determinate, ceasing when they are typically < 3–4 cm long. The root tips then commence to solubilize phosphate and iron salts in the surrounding soil. The respective ions are then imported by the cluster roots during the final, ion-importing phase of their short life. In experimental studies on cluster root development and physiology, two species, *Grevillea robusta* (Proteaceae) and *Lupinus albus* (Leguminosae), have tended to serve as model systems.[79]

Low phosphorus regimes are able to re-program plant root architecture in a number of species, thus allowing the genetic controls of this reprogramming to be studied.[80] However, local applications of nitrate ($NO_3^-$) as well as other ions ($NH_4^+$, $PO_4^-$) to portions of the primary root axes of barley (*Hordeum vulgare*) can also stimulate correspondingly local productions of lateral roots.[81] These swarming responses appear to be the result of alteration to resource allocation within the primary root axes in response to differential (high/low) ion distribution in the soil surrounding the axes. Whether the cellular elements from which the root clusters arise are pre-formed and exist as dormant primordia until evoked by the environment (i.e., they are proleptic primordia), or whether the primordia are developed de novo within barren, pre-existing portions of root axes (i.e., the roots are adventive[16,69]) is not known.

Two contrasting examples of clusters of shoot-borne roots should be mentioned here: those of *Ficus pumila* and of *Metrosideros* spp. In the first example, the roots are short (1 mm) and determinate, developing at the nodes of juvenile stems of *F. pumila*.[82] About 30–50 roots appear nearly simultaneously, over

a 4-d period, along a distance of approx 8 mm of stem, thus giving a $\rho\epsilon^*$ value of 4–6 roots per mm length. The roots splay outwards, developing as an adhesive pad, which glues the stem the stem to any underlying solid surface, and even to other stems. However, if a cluster contacts the soil, then the roots branch, lose their determinate state and develop as part of the terrestrial root system. The same pattern of short-root development is also found along shoots of a number of species, including English Ivy, *Hedera helix*. The probable stimuli for root cluster formation and oriented growth include contact with a surface (thigmomorphogenesis), hydrotropism and skototropism. In the second example, of *Metrosideros*, "broom" root clusters (**Fig. 11**) form extensive aggregates, or swarms, which efficiently attract moisture from mists, in the form of water droplets collecting on the root tips. They can also form root-stems that clasp and strangle an adopted host tree.[83] However, in this case, it may be that the term "swarm" is being used figuratively; the criteria for active swarming may not have been completely satisfied, since neither the stimulus for cluster formation nor the sequence of their formation seems to be known. This cautions that swarm terminology might be harder to apply at higher levels of plant organization, where the defining criteria of growth movement, orientation and growth stimulus are less readily identified. "Entanglements" may, in some cases, be a more appropriate term for these associations, especially where the roots make contact with each other.

### Other shoot-borne roots

Plants depend upon their underground roots for anchorage within the soil, but some rely also upon above-ground roots to support their shoots. Members of two families, Velloziaceae and Xanthorrhoeaceae, produce roots from predetermined sites on the stems, which grow downwards within the mantle of decaying leaf bases that encircle the stem (**Fig. 12**), and thence into the soil. These aerial roots thereby become a major support for the stem.[84,85] And as they grow, they capture both water and nutrients which have collected as moisture and as dust particles, respectively, amidst the fibers of the leaf bases.

However, shoot-borne roots are sometimes plagiogravitropic and extend horizontally, bending downwards later under their own weight. In the species of the two families mentioned above, it may be that, on the one hand, the leaf sheaths bring about an alteration of the default horizontal condition of the shoot-borne roots and physically enforce collective vertical root growth. If so, this change of the growth direction serves as the critical condition that enables formation of an "active" root swarm with an increased $\rho\epsilon$—the number of root tips per unit area of stem perimeter. On the other hand, the constraint of the leaf bases may force the roots to assume only the appearance of a swarm, in which case the aggregate would be classed as a "passive" swarm.

In other species of *Ficus* the consolidation of natural root-root grafts, or fusions, transforms the vertically hanging swarm
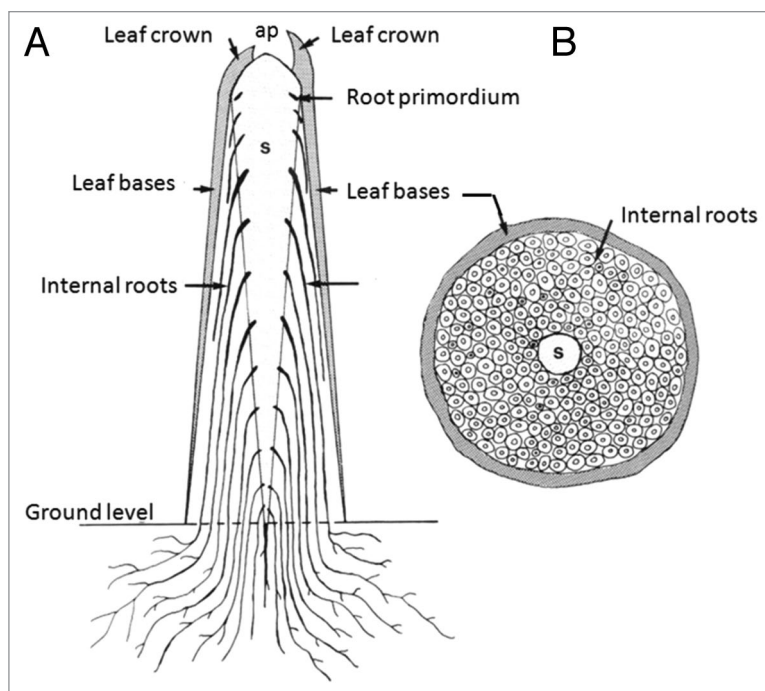


**Figure 12**. (**A**) Shoot-borne internal roots of *Vellozia* sp. growing towards the ground, through the leaf bases which ensheath the principal stem. (**B**) Cross section through the base of a stem, showing the formation of the aggregated root-stem. ap, shoot apex; s, stem. Adapted from and redrawn from figures in ref. 84.

of roots into an entangled root-stem supra-organ.[86] Root fusions occur between these aerial roots (these fusions may be temporary, the root elements entangling, fusing, and then moving apart, see **Fig. 13A**), as well as between vertical and horizontal roots (**Fig. 13B**). The fusions trace to the propensity of the soft bark of the fig tree's aerial roots to become abraded when the growing axes make close contact and, subsequently, to form graft unions.[87]

The functional significance of the new, supra-organ of fused shoot-borne roots is evident from the observation that, in the case of the strangling fig, *F. religiosa*, the original support stem eventually dies and disintegrates. Thereafter, this pseudo-stem structure is the sole support for both the trunk and canopy of the fig tree.[88] This additional support function is a consequence of the active swarming property of the aerial roots.

Support of the stem solely by aerial roots is a feature found also in some species of tropical palms, e.g., *Iriartea exorrhiza*. Here, however, support is given not by a root-stem, but by numerous independent (not fused), gracefully arching aerial stilt roots, which arise just above where the natural disintegration of the base of the stem commences. The roots then enter the ground.[86]

### Anastomosed root systems

The roots mentioned in the preceding section were all aerial roots, and aggregations with or without fusions took place mostly in the vertical plane, as the roots grew downwards toward the soil. Root-root fusions also occur underground within certain forest environments. Here, the direction of root growth may not be of particular importance—though generally it is acropetal, away from the supporting axis—so long as there is some form of
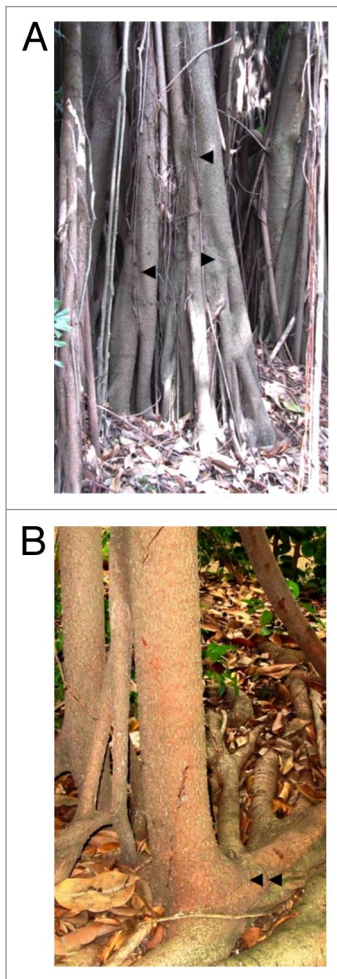
**Figure 13.** (**A**) Fusions of downward-growing aerial roots (single arrowheads) of a wild fig tree (*Ficus* sp.) and (**B**) fusion between a vertical and a horizontal root (double arrowhead). All fusions contribute to the formation of a root-stem supra-organ.

Thus, the swarming (grafting) effect was limited to members of the same species and relied on physical contact between their elements, this contact being brought about by both axial and radial (thickening) growth of the roots. In view of what was said above in relation to root-root attraction (or swarming) in *Arabidopsis* and *Zea*, it is not impossible that similar attractions occur during root system development, thus preparing the way for future conspecific root anastomosis.

Intra-specific root grafts between neighboring tabonuco trees were shown to confer stability on the forest system.[89] Following hurricane damage to the Experimental Forest in 1989, 40% of individual tabonuco trees which showed no root grafting were found to be uprooted, 40% had snapped trunks, and only 20% remained standing and intact. By contrast, among the tabonuco trees that had root graft unions, no trees were uprooted, and 60% of them remained standing and intact.

Root grafting appears to have adaptive value, especially to trees.[90] A survey of root grafting in 200 different woody species,[91] using published literature, indicated that it was much more frequently expressed by tree species than was the case for shrub species. It was found that the propensity for root grafting was a heritable property, positively selected in accordance with the environment.[91] For example, young trees of *Nyssa sylvatica* (blackgum) raised from seeds of trees growing in swampy, low-lying locations in the eastern United States had a higher frequency of grafting (11%) than did trees originating from seeds of blackgum growing in well drained, upland locations (2%) of the same geographical area.

### Swarms and inter-specific interactions

Although supra-root associations are usually intra-specific, inter-specific associations feature at a higher level of developmental organization, they need not necessarily involve roots, but do seem to involve a loose type of swarming. For example, seeds which have fallen to the ground from inflorescences of the epiphyte, *Monstera gigantea*, germinate simultaneously. The young seedlings "swarm" toward, and then ascend, the trunk of the tree that will be their adopted host. The stimulus for the directional, collective growth movement of the seedlings is triggered by low light intensity. The skototropic seedlings grow toward the dark trunk of the prospective host and away from the penumbra of the host canopy.[92]

The inter-specific association of epiphyte and host/support plant may be benign, but not always so (e.g., the strangling fig, mentioned earlier). More aggressive are parasitic associations, good examples of which are those between dodder (*Cuscuta* spp) plantlets and their hosts.[93] At the cellular level, the multiple connections between the dodder parasite and host are made via a number of prehaustoria, which are modified shoot-borne roots.[86] Once penetration of the host has taken place, each prehaustorium disperses into a number of fine strands called "hyphae".[94] This behavior is reminiscent of the meta-stability of the fungal cords discussed earlier, where initially there is a collectively mobile hyphal aggregate (analogous to the prehaustorium in the dodder example) which subsequently disperses into individual hyphae.

cooperation between the entangled or aggregated, anastomosed elements. From this point of view, underground root systems with fused (aggregated) root elements can be regarded as active swarms, or entanglements. Here, however, the swarm/entangled elements become irreversibly bound together owing to collective fusion events spread over time. The swarm is stable until its structure dies and its elements disintegrate.

In one example, about 100 root systems of the tree, *Dacryodes excelsa* (tabonuco), growing within the Luquillo Experimental Forest in Puerto Rico, were excavated during 1988–89 and the frequencies of root axis fusions (grafts) estimated and the origins of the roots involved identified.[89] At depths not more than 10–20 cm, over 60% of all trees within study areas of about 300 m$^2$ showed graft unions not only between the roots of a tree's own root system (self-grafts) but also between roots that traced to different trees (intra-specific grafts) (**Fig. 14**). Although at least four other species of tree were growing within the test site, two of which showed intra-specific grafts, no inter-specific root grafts involving the tabonuco trees were found.

## Discussion

The idea that swarms and swarming might be a property of plant roots[6] necessitates a careful examination of the properties of swarms, as commonly perceived in relation to animals and insects. An assessment can then be made of whether or not analogous properties are demonstrated by members of the fungal and plant kingdoms. Of broader interest is whether the rather wide gap commonly perceived to exist between animals and plants on account of their respective phylogenies,[30] and which some have sought to bridge by a consideration of traits such as sensory and communicative abilities,[28,29] can be further narrowed by considering their respective swarming behaviors.[5]

Animals and plants are often faced with similar challenges and life-threatening hazards, requiring interpretation of the attendant signals and cues before a suitable response can be initiated. It would be surprising, therefore, if each class of organism, having inherited a common metabolic toolbox in the service of development, behavior and evolution,[95,96] as well as a general set of movement responses, had not enfolded these movements into their respective behavioral repertoires. Biological swarming, recognized as the shared movement of aggregated organismic units, or elements, might be one of the processes which plants and animals have in common to deal with certain types of environmental perturbations and opportunities. Because swarming is a communal activity expressed at a high level of developmental organization, it may have arisen relatively late in animal and plant phylogenies and display features of convergent evolution[97] in order to promote the well-being and survival of both individual organisms and the functional, or societal, group of which the individuals are a part.

We introduced a set of criteria by which swarming phenomena could be ascribed to plants. These criteria should not be considered as being purpose-built for plants alone, but to be generally acceptable and able to subsume the more evidently purpose-built criteria proposed in relation to swarming of bacteria[10] and fish,[98] for example. And should swarming be recognized within the "natural history" of plants, then the question arises of the level, or levels, of developmental organization at which the swarm and swarming is manifested. Whereas entire terrestrial plants are relatively immobile, their organs show mobility because it is here that the growing points of the plant are located. Moreover, this activity can potentially be collective if roots, say, can co-orient their movements. From this perspective, examination of plant swarming seems not to be a trivial pursuit, but one which leads to deeper questions concerning the possibility of collective responses of plants and their organs to their environment. Not only are pathways leading from signal or stimulus perception to growth movements, which might also be coherent and cooperative movements, opened for investigation, but possible species-specific characteristics come into question also, not least because swarming is largely a conspecific activity which excludes individuals who are not of the same species. Hence, the means by which individuals recognize others, conspecific or otherwise, need to be uncovered (see refs. 62–65 for a discussion of this topic of self/non-self recognition in relation to plant roots).
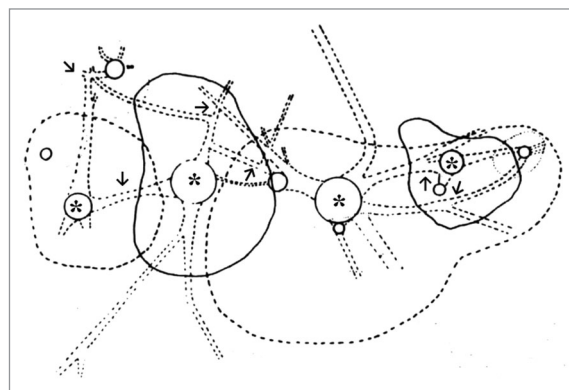


**Figure 14**. Plan of anastomosing root systems of *Dacryodes excelsa*, revealed after removal of the surface soil. Roots (dashed outlines) radiate from a number of stem bases (circles and asterisk). Sites of possible root fusions are indicated by arrows. Edges of the canopies of the individual trees are marked by solid and broken lines. Modified from Figure 1A in ref 89.

The criteria for swarming seem to have been satisfied at the levels of plant organization in which roots are the mobile elements (**Table 1**). The criteria also apply in relation to fungal hyphae and the establishment of mycelial cords. It is worth remarking that mycelial cords (rhizomorphs) are widespread in soil, and not easy to distinguish from thin plant roots.[51] They also comprise some of the longest-lived and longest-reaching structure in the biosphere,[34] thus attesting to the advantages of cooperative swarm behavior.

As we have argued, some form of plant swarming can be recognized at levels encompassing roots and root systems. These units are components of the vegetative sporophyte generation. By contrast, swarming—at least, active swarming—does not seem to be a feature of the sexual gametophyte generations of angiosperms and gymnosperms, where the male gametophyte is the only mobile component, notably with respect to the growth of pollen tubes. Although one might encounter a phrase such as "a swarm of pollen tubes" (ref. 99, p 123), as it is used here "swarm" is likely to be a figure of speech (simile) rather than describing a particular behavioral state of the male gametophyte. It is the passive aspect of pollen tube aggregation which is being referred to: a state in which the tubes are bunched together within the confines of the transmitting tissue of a style. However, one should be cautious of denying the effect that such constraint might have on pollen tube growth, or that pollen tubes do not interact as they grow. For example, the relative motility of animal cells in vitro is affected by the topological constraints of their substrate.[100] The collective, "active" and cooperative aspect of swarming of male gametophytic elements would seem to be antithetical to one of the principles of evolution and reproduction, which is competition and selection of the fittest gamete (see refs. 101 and 102) for a discussion of male gametophyte competition), and should not allow unfit elements to be carried along within a "Trojan Horse" of an "active" pollen-tube swarm. If any cooperative behavior does take place in the gametophyte generation, it would perhaps be most advantageously expressed in the inter-sexual attraction between the pollen tubes of the male and the synergids of the

female gametophyte,[103,104] during the final stages of pollen tube growth within the style.

It could be held that pollen grains exist as a "swarm" before any gamete competition comes into play, notably in the grain-collectives of pollinia and massulae of orchids, these "swarms" being advantageous for the transportation of pollen to receptive female carpels. But these, too, are likely to be passive swarms since they do not rely on any self-propelled mobility, the pollen elements being bound together by viscin threads, an aggregating factor produced by the sporophytic anther tissue. A further aspect of pollen pseudo-swarm aggregation might relate to—again without the participation of any movement or innate mobility—the packing patterns of the grains within anthers: patterns which favor the assemblage of large-scale, passive pollen pseudo-swarms could result from the high-order polyhedral forms of pollens found in certain species (e.g., *Stellaria* spp).[105,106]

Nor is active swarming a feature of the male gametes (spermatocytes) of bryophytes and pteridophytes. In fact, the converse—passive swarming—seems to be the case, for when bryophyte spermatocytes are released into water from an antheridium they are embedded in a lipid matrix. The lipid then disperses and decreases the surface tension, thereby enabling the rapid dispersal of the previously clustered gametes.[107,108] It is the surface-tension-driven dispersal, rather than active, long-distance swimming by means of flagellae, that is the major contributor to fertilization in bryophytes.[109,110] Nevertheless, it might be argued that this dispersion of antherozoids is in line with the meta-stable state of a swarm—even of a passive swarm.

A collective swimming velocity and polarity has been reported for the flagellated unicellular green alga, *Chlamydomonas rheinhardtii*, features which might be taken to indicate swarming behavior.[23] In these particular observations, it was the experimental imposition of both phototaxis and a critical cell density that led to a phase transition, which then favored the putative swarming behavior. However, these observations on artificially dense suspensions of Chlamydomonas seem to indicate that the swarming which we have designated as "passive" (due to the physical confinement of cells) could become "active" in special circumstances: in this case, when photoperception was linked with the innate motility of the photoresponsive organism.

There is no compelling reason to believe that swarming depends upon the participation of "intelligence" or "consciousness" (see "Introduction"), in the generally accepted senses of these words. However, one can understand how consciousness has become linked with swarming, given that the genetic relatedness or otherwise of the swarming elements is a consideration: that is, whether or not the elements of a swarm have conspecific identity. Another aspect especially relevant to plant swarming is whether neighboring organs can sense—cognize—each other's state and thereby develop a collective growth movement in which elements interact and affect each other's motion. The swarming of hyphae and of plant roots—and also of insects[14]—are adequately understood as phenomena issuing from innate and deterministic movements of growth, and that these movements can be set in motion by purely by physical determinants. Stigmergy, the response of one mobile organism (or organ, in the case of roots, or cell, in some other cases) to the trace left behind in the environment by another organism (or organ or cell),[111] may be a further swarm-modulating factor, as it is for bacteria[112] and for mixed cultures of human fibroblasts and carcinoma cells,[113] and which may perhaps play a role in the apparent attraction of one growing root toward another (**Fig. 8**; **Supplementary Video S1**).

Because the processes of active swarming reveal similarities throughout many biological systems, it may be that swarming is a fundamental property of organisms arrived at by an evolutionary convergence. Active swarming may also indicate a propensity for cooperation between mobile organismic elements that is ultimately of benefit to the species and its gene pool.

### Disclosure of Potential Conflicts of Interest

No potential conflicts of interest were disclosed.

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### Supplementary Material

Supplementary material may be found here: www.landesbioscience.com/journals/cib/article/25299

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