Branch–branch connections in trees analogous to hyphal fusions in fungal colonies

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In the leopard tree *Caesalpinia ferrea* (Leguminosae) – a native of eastern Brazil – some of the leader branches connect to and fuse with neighbouring branches of the same tree. The bridge initials project out as pegs or protuberances and apparently extend in a coordinated manner, connecting branches up to 4 ft apart. The fusion of two branches of the same tree implies intra-plant communication involving signalling factor(s). The bridges resemble fusions between hyphae in a fungal colony. Whereas hyphal fusions are common and the process is apparently completed in <1 h, branch fusions in *C. ferrea* tree are limited and a slow process, apparently requiring several months to years to complete. Branch fusions in *C. ferrea* are in accord with Claus Mattheck's analysis that tree branches actually seek contact rather than avoid contacts.

Keywords: Branch fusions, *Caesalpinia ferrea*, fungal hyphae, tree branching, tree design, signalling.

WHILE documenting the flora of the century-old Indian Institute of Science campus[1], we observed four trees of *Caesalpinia ferrea* (Brazilian Ironwood) showing an unusual structural design. Some of the leader branches arising from the main trunk were either interconnected by H-shaped woody bridges or fused laterally (Figure 1). What is the significance of this structural design? How, and approximately at what stage of tree development are the branch–branch connections effected? Do branch–branch connections occur in other tree species also?

C. ferrea is a native of eastern Brazil. It is also known as the Leopard tree, undoubtedly because when its thin bark is shed off at places, the undetached brown pieces on smooth, whitish bole appear as spots as in a leopard body (Figure 2). The observations reported here are based on the tallest tree which has a girth of ~5.5 ft at waist height. The trunk bifurcated at ~7.5 ft from the ground level, with the bifurcations extending acropetally, and subsequently these re-branch at an angle of ≤45° degree. Rather than extending horizontally, the branches ascend and form a canopy comprising monolayered foliage. This facilitated viewing of intra-branch connections even from the ground level. In the region between ~7.5 and ~25 ft, the dichotomous branches are arranged mostly at acute angles, and show four or more interconnections between the woody branches. The interconnecting branch simulates a mechanical cross-weld (transverse graft). Fusions were not seen above 25 ft. Subsequently, branch interconnection was also encountered in a single specimen each of mature trees of *Ilex paraguanensis* (Aquifoliaceae), commonly known as Paraguay Tea, growing in the Lalbagh Botanical Garden; and in *Delonix regia* (Leguminosae, Caesalpinioideae), commonly known as Gulmohur (Figure 3) growing in the premises of a hotel in Bangalore. The essential morphogenetic questions that arose was what determines the origin of bridge primordia in a particular branch, and at what age, and what cues control their extension in a direction that would maximize their chance of encountering a partner for contact?

In the trees observed there was no evidence that the union of branches was due to their rubbing against each other leading to the formation of callus-like tissue, as suggested in 1917 by Dallimore[2]. Rather, the branch interconnections suggested some form of communication among branches within the tree not recognized previously. The sightings of interconnected branches, of pegs/

Figure 1. ***a***, Physiognomy of *C. ferrea* showing branching characteristics. The tree branch on the left is that of *D. regia*. ***b***, Anastomosing branches in the mid-tree region. The boxed area shows cross-contact and enlargement of contact area. Note absence of kink. ***c***, Fusion of three intersecting branches at the top region.

Figure 2. Initiation of fusion bridges as peg-like outgrowth from mid-portion of *C. ferrea* tree (circled). Lateral fusion of two branches (rectangle) in top-portion of tree (Figure 1 *c*).

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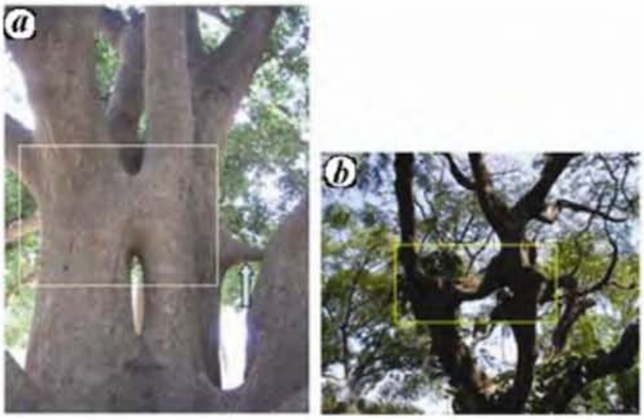

Figure 3. Sensing and fusion of lateral branches (boxed). ***a***, *I. paraguanensis*. H-shaped fusion above the branch fork. To the right of boxed area is a bridge primordium pressing against a trunk branch. ***b***, H-shaped bridge in *D. regia*.

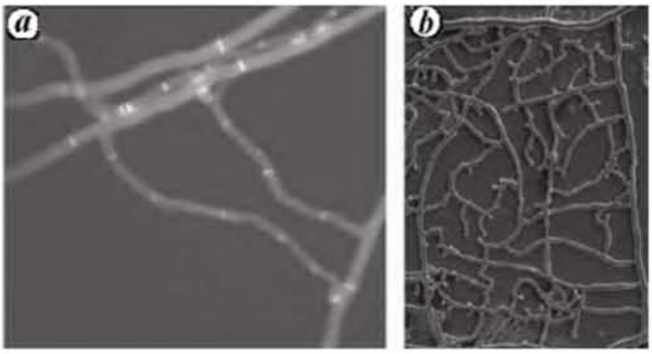

Figure 4. *Neurospora crassa*. ***a***, H-bridge between two hyphae. Photo: N. Louise Glass. ***b***, Interconnected hyphae forming mycelial network. Photo: K. Lord, C. E. Jeffree and N. D. Read.

protuberances ('bridge primordia') further suggest that branch fusion may be a result of a highly regulated process that involves the development of series of primordia at pre-determined sites on the longitudinal axis of the branch stem or another branch stem near it. Presumably, the primordia development is due to some chemical form of communication among the tree branches. Eventually, partner primordia must mutually coordinate their rate of extension and direction for the fusion of two oppositely extending branches to occur accurately, that is, free from kink. Interestingly, some of the branch primordia in *C. ferrea* were in an aborted state. Perhaps these had started extension growth in response to some environmental signal but because of some defect, they failed to make contact, ceased growth and dried. Since we did not sight stubs, this suggests that the final mechanical contact and organic fusion occurs quickly.

The formation of bridges between the branches of the same tree is a manifestation of intraplant communication. Interestingly, branch fusions by H-bridges in trees show features parallel to a fungal colony (Figure 4). This suggests a mechanistic homology in cell or organ fusion in the phylogenetically disparate plant and fungal kingdoms[3,4]. Perhaps chemical signals are involved in formation of branch primordia and their mutual contact with partner branches. However, since plants are autotrophic whereas the fungi are heterotrophic, fusions in the two systems may be effected for different reasons. The hyphal interconnections in a radially-expanding fungus colony may be important for translocation and distribution of nutrients absorbed by mycelium from the substratum, particularly at the time of spore formation for packaging into spores. An image of cytoplasmic flow in two interconnected hyphae may be viewed at wings.buffalo.edu/.../bio-sci/faculty/free.html. We have no evidence if the bridges in *C. ferrea* also serve in diverting the flow of water and nutrients as in fungal mycelium. This would require experiments involving dye injection or radioactive tracers and tracking their movement. On the other hand, fusions between strategically-placed tree branches could play a role in limiting the out-of-proportion extensions and their risk of breakage due to weight.

In *C. ferrea*, the length of the bridges (distance between fusing stems) varied from 1 to 4 ft, implying remote sensing of branch initials which start out as spaced row of initial bulges on longitudinal, opposite faces of the neighbouring stems, and the coordination of their individual extensions in determined direction for physical contact and fusion to occur. Even when rather rudimentary, the lateral outgrowth (Figure 4) from the trunk is woody, suggesting its capacity for limited extension only. From the origin of pegs/protuberances on the two facing sides of neighbouring leader branches, we presume that the sites of origin of the two bridge primordia are predetermined. However, since neither the cues responsible for initiating their formation nor the cues that activated their extension growth are known, no firm conclusion is possible. In the upper regions of the tree, the branches tended to contact the inconspicuous H-bridges.

Interestingly, in contrast to above-ground stem fusions, the underground root fusions (natural grafts) in forest trees have received considerable attention because of their role in transmission of viruses[5]. Dallimore[2] reported natural joining of branches to be fairly common in beech, oak, holly, lime, willow, yew and Scots pine. Mattheck[6] too states branch fusions in beech trees to be common. He illustrates the strangler fig (*Ficus* sp.) where the vertically-hanging aerial roots join together into a framework and fusions among them seem essential for the survival of the tree. Based on extensive observations of contact of trees with inanimate objects in nature, and among trees of the same species, Mattheck put forth his view that 'trees do not avoid mechanical contact but actually seek it'. We speculate that interconnecting branch design limits the outstretching of branches from overshooting equilibrium, which may otherwise break during swaying of canopy in gusty winds and high rainfall. The mechanical advantage of cross welds in distributing stress may be analysed by using computer-aided optimization developed at the Karlsruhe Research Centre, Germany[6].

Finally, the type of intraplant communication described has some parallel to interplant communication. Two decades ago, it was reported that plants attacked by arthropods communicated with neighbouring plants of the same species via volatile emissions, inducing changes in the secondary metabolites in receiver plants and conferring resistance to arthropods[7]. In lima beans attacked by predatory mites, volatile chemicals emitted by infested plants were shown to induce gene expression in uninfested neighbouring plants[8]. In recent years, plant–plant interaction via air-borne chemicals (for example, ethylene, methanol, isoprene, acrolein, methacrolein, monoterpenes and other substances) which are emitted temporally in defined quantity, has come to light[9,10]. Communication among plants via air-borne signalling factors has led to the 'talking trees' concept[11]. Thus, both short- (branch–branch) as well as relatively long-distance (inter-plant) communication apparently may occur in trees. However, we have no evidence for volatile factors being involved in the formation of branch bridges seen in this study.

Hopefully, this communication will provide an impetus to the little-known intra-tree branch connections and their advantage to the tree, with special focus on other plant systems where the phenomenon may be experimentally tractable, and in particular in the fungi where the filamentous hyphae communicate with genetically identical individuals by fusions. Since the lifespan of a tree is generally longer than that of a human, there is need for databases on tree biology.

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