

Kin recognition by roots occurs in cycads and probably in conifers

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Kin recognition by the roots of *Cycas edentata* was recently demonstrated. Our extensive literature search revealed this to be the first report of kin recognition in any spermatophyte other than angiosperms. Based on this new validation that the phenomenon occurs among phylogenetically diverse taxa, we conclude that kin recognition by roots may be an ancient phenomenon.

The ability to recognize whether neighbors are closely related or not has been shown for individual cycad plants.¹ A split-root design (“fence-sitter” design²) was used, with *Cycas edentata* seedlings serving as the focal plant. A half-sibling was grown in one pot and plants exhibiting varying degrees of relatedness were grown in the other pot. Within the context of the study, root contact with close relatives minimized root proliferation and whole plant growth, but root contact with non-relatives maximized root proliferation and whole plant growth. Phylogenetic implications were not discussed.

This is the first demonstration of kin recognition – via split root or any other design – in any plant species other than angiosperms. While hardly extensive, there have been diverse reports of kin recognition in flowering plants.^{3–8} A recent review⁹ lists six genera with kin/non-kin recognition and 12 genera with self/non-self recognition. All 18 genera were either eudicots or monocots and included the quintessential model organism *Arabidopsis thaliana*.^{10,11} Detection of kin recognition systems included split-root designs (both owner and sharer scenarios),^{2,9,12–14} ramet-pair

designs including some pots with kin and other pots with non-kin,⁵ introduction of root exudates,^{10,15} and introduction of volatiles.¹⁶

Surprisingly we could find no explicit mention of kin-recognition or self-recognition in gymnosperms, including in conifers. Extensive root grafting has been documented for conifers,^{17,18} but no effort was invested to determine if root grafting was due to random contact of roots rather than proximate roots somehow being attracted to one another. Root grafting is more extensive in natural stands (which presumably are outbred) than in cultivated stands (which presumably are inbred), while root grafting suppresses outward growth of roots.¹⁸ These observations imply that conifer root grafting is more common in strangers than in relatives, which is consistent with kin recognition and kin selection in conifers.

The recent validation of kin recognition in *Cycas edentata*¹ is interesting if one follows Peter Crane’s tree of life phylogenetic tree (<http://tolweb.org/Spermatopsida/20622>), with one massive polytomy for all extant seed plants and many extinct ones. While seed plant phylogenetic trees seem to be eternally in flux,^{19,20} there are reasons to question Crane’s tree, such as the hypothesis that Gnetales are aberrant conifers.²¹ Cycads and ginkgos are unique among extant seed plants in having enormous sperm cells with flagella; sperm cells that eventually grow much larger than the pollen/prepollen grain that carried them to the female cone (zoidigamy).^{22,23} All other extant

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seed plants (angiosperms, conifers, Gnetales) have largely unbranched pollen tubes containing small sperm cells that lack flagella (siphonogamy). This dichotomy between zoidogamy and siphonogamy may help resolve the basal seed plant polytomy. However, *Cycas edentata* shows that both zoidigamous and siphonogamous plants can have roots that recognize kin.

Validation of kin recognition in *Cycas edentata*¹ may be even more interesting if cycads are sister to all other extant seed plants. Cycads may have descended from medullosan seed ferns.^{24,25} Cycads and

medullosans share the following highly unusual characters: (1) ovule with double vasculature that is radially arranged, with integument vasculature arising from a basal vascular disc,^{24,26} (2) pollen/prepollen with alveolate sexine (the outermost layer of the grain has compartments of irregular size and shape),^{27,28} (3) presence of secondary phloem fibers,^{24,29} and (4) the more common feature of anamocytic/haplocheilic stomata (guard cells and subsidiary cells in a single stoma developed from a single initial epidermal cell).^{30,31} Details about putative relationships between Cycadales and Medullosales

do not matter so much as does the hypothesis that kin recognition by roots may be an ancient phenomena, at least as demonstrated by the phylogenetically wide occurrence of this phenomenon from angiosperms to conifers to cycads.

Disclosure of Potential Conflicts of Interest

No potential conflicts of interest were disclosed.

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