

# *Population variation in root grafting and a hypothesis*

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Root grafting between conspecific individuals of forest trees is well documented and it is apparent from the literature that some species are more prone to graft than others. I report here evidence of ecotypic variation in root grafting of blackgum (*Nyssa sylvatica* Marsh.) seedlings which suggests a hypothesis for the adaptive significance of root grafting.

Blackgum is a hardwood tree distributed throughout the eastern United States. In the southern part of its range it exhibits a tremendous ecological amplitude; occurring along a gradient from the mountains, where it occurs only on well drained upland sites, to the Piedmont where in addition to upland sites it is also common in periodically flooded floodplains, to the Coastal Plain

Tab. 1. Number of 1 yr old *Nyssa sylvatica* seedlings from three different habitats with and without root grafts;  $\chi^2 = 20.78$ ,  $P < 0.005$  that root grafting is independently distributed across populations. Each habitat was represented by 10–20 different seed sources from two different populations and seedlings were grown 2 per pot under drained conditions in a greenhouse. Under these conditions there was no significant difference between populations in below-ground biomass.

	Upland	Floodplain	Swamp
Root grafted	2	4	18
Non root grafted	115	180	144

where it is often found in permanently flooded swamps, as well as floodplains and upland sites (Keeley 1979).

As part of a study on ecotypic variation in upland, floodplain and swamp populations, a significant difference in root grafting capability was observed (Tab. 1). These grafts were the result of anatomical connections between the root systems of adjacent plants. Since these plants were grown from seed in a common garden environment, it is apparent that seed source has a significant effect on root grafting capability.

The ecological significance of a greater propensity to graft by swamp seedlings, however is not obvious. Root grafts are generally appreciated for their potential role in transporting water, minerals, and photosynthates between grafted individuals. In reference to *Pinus strobus* L., Bormann (1966) summarized inter-tree translocation relationships between grafted trees as follows: 1) if both trees are co-dominant there is no exchange of food, water or minerals, 2) when one tree is dominant and the other suppressed, the dominant tree supplies photosynthates to the root system of the suppressed tree but receives no compensation, and 3) if one member of the graft is a living stump it will extract minor quantities of photosynthates from its dominant partner and in turn will provide minor quantities of water and minerals to the dominant partner.

Although Bormann's findings are of practical importance in silviculture, there is little to suggest that inter-tree translocation is of adaptive value; not only in swamp populations of *Nyssa sylvatica* but in trees in general. Specifically, in reference to the relationships cited above, case no. 1 should be selectively neutral with respect to selection for grafting ability. In case no. 2, grafts would be of value to suppressed trees but it is doubtful whether this would be of any evolutionary consequence since suppressed trees are frequently sterile (Fowells 1965) and short-lived (Bormann 1966). There may even be selection against grafting in this instance since suppressed trees would be more susceptible to diseases which would be transferred via grafts to the dominant partner (Graham and Bormann 1966).

For root grafting to be selected, the dominant member of a root grafted pair must gain an advantage since these are the individuals which will monopolize the

future gene pool. From Bormann's (1966) discussion, the only instance in which dominants gain from root grafts is when grafted to a living stump. It is certainly questionable whether or not this is sufficient to select for root grafting ability given that 1) the dominant receives only minor quantities of water and minerals, 2) repeated attempts have failed to demonstrate that this has any effect on the growth of the dominant, and 3) living stumps are relatively rare in undisturbed forest.

Assuming root grafts have some selective value to the inclusive fitness, an alternative explanation for evolution and maintenance of root grafting lies in their potential for providing support and stability as a consequence of being anchored to other root systems. This hypothesis would predict root grafts to be of selective advantage to dominants regardless of the status of the tree to which it is grafted. A prediction particularly pertinent to the present discussion is that root grafting would be of selective value in waterlogged soils because 1) root: shoot ratios are usually much lower in swamp plants than in upland plants (Keeley 1979), 2) deep tap roots are limited by anaerobic conditions in the deeper soil layers (Boggie 1972), and 3) wet soils provide less friction. In a swamp environment root grafts would enhance anchorage by producing a "snowshow effect" and dispersing the tree's compressive force over a greater surface area (Coutts 1983). This root architecture would decrease the change of blowdowns and reduce trunk settling and associated root damages as described by Smith (1972) for buttresses. In fact the high frequency of buttressing in swamp trees emphasizes the selective value attached to structures which increase support in flooded soils. Rigg and Harrar (1931) and Brown (1978) describe several other traits of tree roots in waterlogged soils that would be architecturally adaptive; viz, lateral roots 2–3 times longer than in upland grown individuals, growth in a looping fashion, and roots deeply rectangular in cross-section rather than round.

The greater frequency of root grafting in swamp populations of *Nyssa sylvatica* (Tab. 1) is consistent with the above prediction. Other work is also supportive of this prediction. Rigg and Harrar (1931) found root grafts in several tree species to be much more common in a bog than in an adjacent upland area. Bormann and Graham (1959) noted a high degree of grafting among six trees of *Pinus strobus* growing in a bog. On a broader scale, lowland tropical forests, which have many swamp-like characteristics, e.g., high soil moisture, shallow rooting, buttressing (Smith 1972), long horizontal roots (Longman and Jenik 1974), and low

Tab. 2. Lifeform distribution of species known to root graft. Gleaned from literature cited in text.

Trees	Vines	Shrubs	Herbs
192	3	7	0

root:shoot ratios (Odum 1971, Klinge et al. 1975), have many species that graft with high frequency (Beddie 1941), and are considered by La Rue (1952) to have a greater prevalence of root grafting than temperate forests.

The general case for selection of root grafting propensity should be those situations where increased support is required, e.g., environments subjected to high winds (as noted for *Pinus radiata* D. Don. by Pryor 1937), heavy crown accumulations of ice and snow, sandy soils, etc. Thus, root grafting would be of adaptive value in many environments, becoming less common in areas where support is adequate. In this light, the relative paucity of root grafts in many semi-arid land communities, even ones of very high density, such as chaparral (Saunier and Wagle 1961, Kummerow et al. 1977, Hoffman and Kummerow 1978) is to be expected.

An important deduction from this hypothesis is that the frequency of root grafting should vary with the life form. Trees should require much greater support than shrubs, and herbs the least. To test this prediction all of the root grafting literature available directly or indirectly through reviews were tallied. The results shown in Tab. 2 are striking; not only are root grafts largely restricted to trees but they are unknown in herbs.

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