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Ecological Consequences of Root Grafting in Tabonuco (*Dacryodes excelsa*) Trees in the Luquillo Experimental Forest, Puerto Rico[1]

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ABSTRACT

Root grafting was commonly found in tabonuco (*Dacryodes excelsa* Vahl), a dominant tree species of tabonuco forest in the subtropical wet forest of Puerto Rico. Over 60 percent of all stems and basal area of tabonuco occurred in unions, clumps of trees interconnected by root grafts. Self and intraspecific grafting were extensive, while interspecific grafting was not common in tabonuco trees. Seedlings and saplings did not show any grafting, probably because of their size or age. Grafted trees were taller and had a smaller crown/DBH ratio. Hurricane damage was significantly higher in isolated individual tabonuco trees than those in unions. Weak relationships between diameter class, area, and size of union, and inter-tree distances and the sum of the trunk circumferences of the two nearest neighbors suggested that a noncompetitive force such as root grafting was more important than competitive forces in maintaining the unions of tabonuco, and thus the forest community. A conceptual model of the costs and gains of tabonuco in unions is presented.

Key words: community; diameter class; dominant species; hurricane damage; nearest neighbors; noncompetitive force; Puerto Rico; root grafting; tabonuco; unions.

Root grafting is the morphological interconnection of roots of the same tree or different trees of the same or different species. Natural root grafting is common in many forest tree species (Rigg & Harrar 1931; Millner 1932; Small 1932; LaRue 1934, 1952; Bormann & Graham 1959; Graham 1959; Bormann 1961, 1966; Kozlowski & Cooley 1961; Saunier & Wagle 1965; Kozlowski 1971; Stone 1974; Keeley 1988). LaRue (1952) observed the intraspecific root grafting in 34 genera of tropical trees growing in Puerto Rico and suggested that natural root grafting is more common in tropical tree species than in temperate ones.

It has been proposed that root grafting increases the anchorage, support, and stability of the trees growing in shallow soils (Graham & Bormann 1966, Kumar *et al.* 1985, Keeley 1988). Some authors have shown the communal importance of root grafting in inter-tree translocation of mineral nutrients and water (Bormann 1966, Graham & Bormann 1966). However, Loehle and Jones (1990) have suggested that root grafting does not necessarily have an adaptive significance because it is encouraged by various proximate factors such as moist, shallow soils, and genetic relatedness. They con-

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cluded that windfirmness was a plausible benefit of grafting, but it had not been actually demonstrated.

In this paper, we present our finding of root grafting and its ecological significance in a tropical tree species, tabonuco (*Dacryodes excelsa* Vahl) in the Bisley Watersheds of the Luquillo Experimental Forest (LEF), Puerto Rico. The large surface roots that run for dozens of meters over the forest floor have been reported by Odum (1970), but no attention has been given to the role of these roots in the formation of tree unions. A union is defined as a clump of tabonuco trees interconnected by root grafting (Basnet 1990). Tabonuco was not included in the list of tropical trees with grafts reported by LaRue (1952).

STUDY SITE

The LEF is located in the northeast corner of Puerto Rico and is one of the NSF Long-Term Ecological Research (LTER) sites. The Bisley Watersheds of the LEF range in elevation from 261 to 450 m and support subtropical wet forest (Holdridge 1967) with an average annual rainfall of 3300 mm (Scatena 1989). The area is a steep, highly dissected terrain with well-defined ridges, slopes, and valleys (Basnet 1990).

Large-scale disturbances such as hurricanes, tropical depressions, and storms of smaller scale are common in the area (Wadsworth & Englerth 1959, Saliva 1972, Weaver 1986). On average, at least one severe hurricane strikes the forest every 60 years (Scatena 1989). The forest locally is called tabonuco forest after the dominant tree species, tabonuco. Other major overstory tree species of the forest include *Sloanea berteriana* Choisy, *Guarea guidonia* L., *Manilkara bidentata* (A. DC.) Cher., and *Buchenavia capitata* (Vahl) Eichl. (Briscoe & Wadsworth 1970).

Tabonuco occurs primarily along ridges and slopes despite frequent high wind velocities in these areas (Wadsworth 1951, 1953; Basnet 1990, 1992). Tabonuco trees occur commonly in unions of 2–14 individuals which are interconnected by extensive self and intraspecific root grafts (Fig. 1). In the LEF, root grafting is also observed in other species such as *Sloanea berteriana* and *Guarea trichilioides,* but tabonuco is unique in extensive grafting and forming such unions.

METHODS

Excavation.—Along an altitudinal gradient within 2 adjacent watersheds, 25 tabonuco unions (1 outside the watershed boundary) were located. We excavated root systems (structural roots) of tabonuco trees of different stages (seedlings, saplings, polesize, and mature tabonuco trees) during the summers of 1988 and 1989 to examine the presence or absence, kinds (self, intraspecific or interspecific), and degree of root grafting which was measured by the number of grafts. For each individual union, frequency of root grafting, distance, and depth of lateral roots were determined by shallow excavation (<25 cm) and probing the subsurface with a thin metal rod (Basnet 1990).

Survey and mapping.—Within each union, we measured the total height of trees and diameter at breast height (DBH). Inter-tree distances within a union were measured and the area occupied by each union was defined as the area inscribed by the stems. Crown diameter was measured along two axes and averaged. Four unions were mapped in detail to show relative positions of trees within unions (Fig. 1). Abundance of tabonuco trees in unions and as individuals was assessed using twelve permanent transects each 5 m wide and 60–70 m long in the watersheds (Basnet 1990). Damage by Hurricane Hugo was assessed in nine of these transects (Basnet *et al.,* 1992).

Data analysis.—A test of dependence, *G*-test (Sokal & Rohlf 1981), was used to determine if root grafting was independent of different stages of tabonuco. A student's *t*-test was used to test the hypothesis that the crown/dbh ratios were the same in unions and individual trees. Blowdown (uprooting) of tabonuco trees (individual vs union) was compared using contingency table analysis. Correlation analysis was done to examine the relationships between diameter of trees and area of union, size of unions (number of trees in a union), and inter-tree distances, and the sum of the trunk circumferences of the pair of the nearest neighbors (Pielou 1961, 1977).

RESULTS AND DISCUSSION

Tabonuco root graft.—Over 60 percent of all stems (61.5%, SD = 37.4) and basal area (62.8%, SD = 39.2) of tabonuco in the study area occur in unions. Root grafts in tabonuco we observed were usually exposed at the soil surface and rarely occurred deeper than 10–20 cm. Grafts occur when two structural roots of the same or different sizes touch and produce an anatomical connection. A

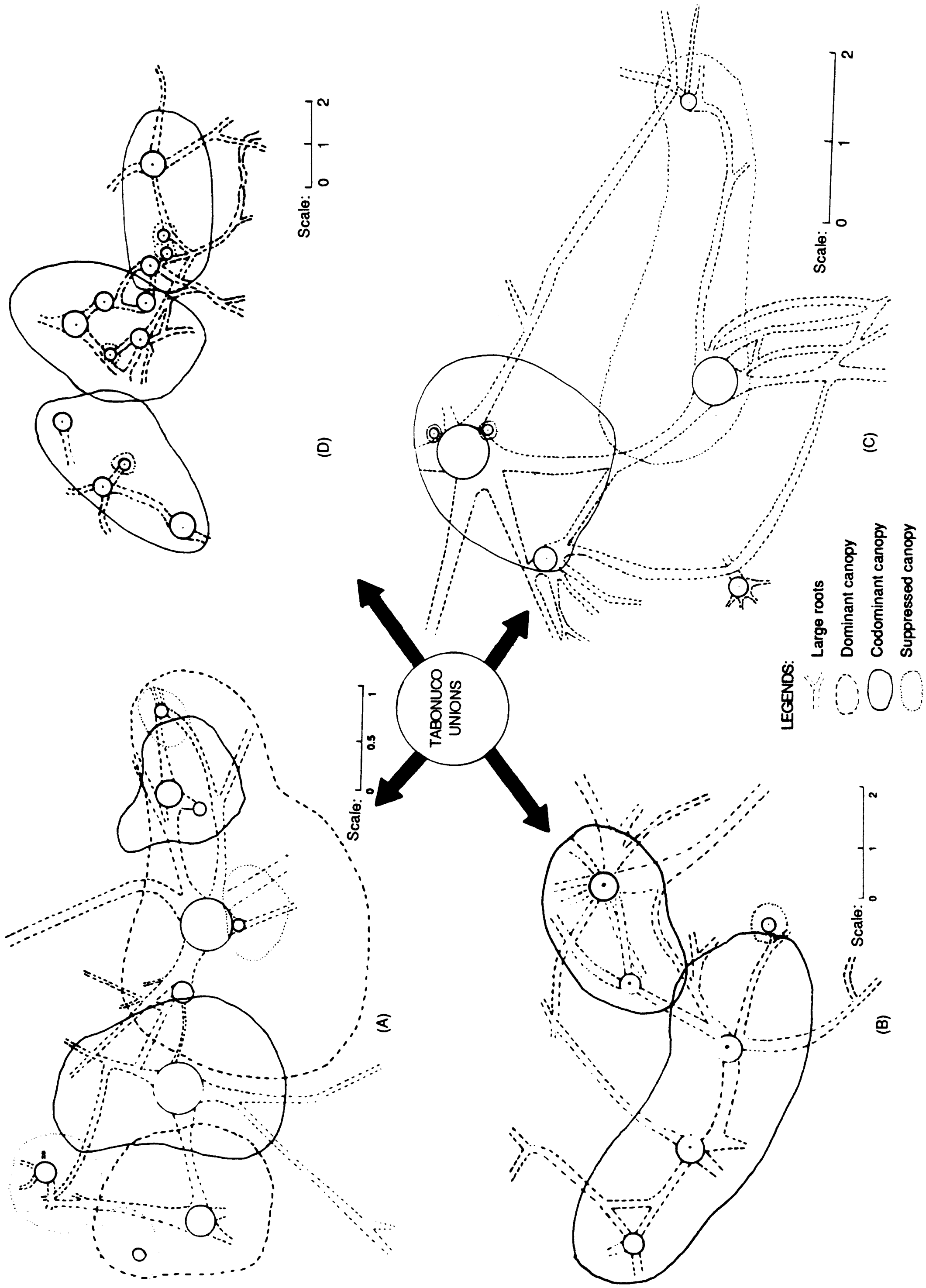
TABONUCO UNIONS
(A)
Scale: 0 0.5 1
(B)
Scale: 0 1 2
(C)
Scale: 0 1 2
(D)
Scale: 0 1 2
LEGENDS:
Large roots
Dominant canopy
Codominant canopy
Suppressed canopy

TABLE 1. *Frequency (% occurrence) of root grafts in tabonuco trees in sample transects of the Bisley Watersheds. Individuals in the different stages were selected "randomly" throughout the Bisley Watersheds 1 and 2. G-test for root grafting among the stages of the species was significant at* P < 0.05. *Values in parentheses indicate the degree of grafts (number of grafts): 1 = 1–5 grafts, 2 = 6–10 grafts, 3 = >10 grafts. Seedlings (<2.5 cm), Saplings (2.5–5 cm), Pole size (5–10 cm), and Trees (>10 cm) in diameter. Within 11 unions there were 72 trees.*

		Frequency of root grafts		
Stage	No.	Self	Intra-specific	Inter-specific
Seedlings	20	0 (0)	0 (0)	0
Saplings	5	0 (0)	0 (0)	0
Pole size	3	100 (3)	33 (1)	0
Trees (11 unions)	72	100 (3)	100 (3)	0
Unions	25	100 (3)	100 (3)	0

summary of root grafts found in tabonuco in our study area is given in Table 1.

Grafting depended upon the stages of the species (*G*-test, $P < 0.05$). Seedlings and saplings (<5 cm DBH) did not show any grafts, probably due to their small size and presumably young age. Self grafts (within the root system of a single tree) and intraspecific root grafts (between two or more trees of the same species) were extensive in tabonuco trees (Table 1). We did not find any interspecific grafts in tabonuco.

STRUCTURAL CHARACTERISTICS OF UNIONS.—Crown/DBH ratio in grafted trees was significantly smaller (Student's *t*-test, $P = 0.03$) than that in individual trees (Fig. 2). This ratio is a measure of resistance to wind and gravity, which limit tree size and shape (see McMahon 1975, King & Loucks 1978). This result suggested that the crown load supported by the stem was relatively reduced in grafted trees (Curtis 1943, Hutte 1968) and smaller crowns flex in high winds and reduce the drag force on the tree trunk (King & Loucks 1978). A comparative study of grafted and individual tabonuco trees of different

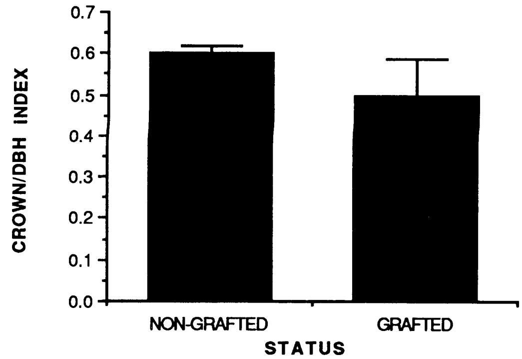

FIGURE 2. Crown/diameter index of tabonuco trees.

diameter classes, showed that grafted trees in unions were taller than individual trees (*G*-test, $P < 0.05$). This is probably because grafted trees received additional support from being anchored to other root systems (Keeley 1988) and soil moisture and/or nutrient conditions may have been better in areas where unions occurred. In a union, trees function as a unit (Bormann & Graham 1959) and have an enlarged base which can support taller objects (see Keller & Niordson 1966). There was a significantly high correlation ($P < 0.05$) between height and DBH of both grafted ($r^2 = 0.98$) and nongrafted ($r^2 = 0.91$) trees. The stability of trees largely depends upon these parameters (Putz *et al.*, 1983).

Studies have shown that roots modify architecturally for adaptive reasons, such as mechanical support or nutrient uptake (Rigg & Harrar 1931, Bormann & Graham 1959, Brown 1978, Deans & Ford 1983, Keeley 1988, Schaetzl *et al.* 1989). Shallow rooting (Smith 1972), long horizontal roots (Longman & Jenik 1974), low root-shoot ratios (Odum 1971, Klinge *et al.* 1975) and high frequency of grafts (Beddie 1941, LaRue 1952) are distinct in tropical rain forest tree species. Tabonuco root systems exhibited all of these characteristics. Sometimes their horizontal roots were 15 m or longer (Basnet 1990).

ECOLOGICAL CHARACTERISTICS OF UNIONS.—Weak linear correlations were obtained for the relationships between union area and mean diameter of trees and

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FIGURE 1. Plane table sketch of unions of tabonuco trees with their root grafting: (A, C) more than one dominants, codominants, and suppressed canopy trees and (B, D) only codominants and suppressed canopy trees in the Bisley Watersheds.

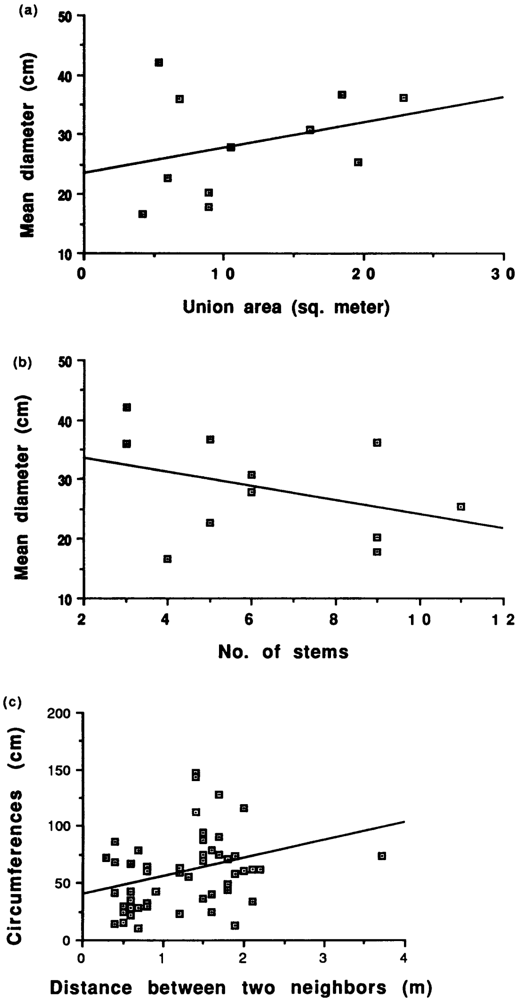

FIGURE 3. Relationships between diameter of trees in unions and (a) union area (b) number of stems and (c) inter-tree distances and the sum of trunk circumferences of the two nearest neighbors. Level of significance for the regression lines is $P < 0.05$.

number of stems and mean diameter size (Fig. 3). There was a very weak relationship between the sum of the trunk circumferences of the pair of nearest neighbors and the distance between the trees (Fig. 3). These results suggest that there was no inter-tree competition (Pielou 1961, 1977) and thus provide evidence that the unions of tabonuco are maintained by noncompetitive forces *e.g.*, root grafting (see Bormann 1966).

Root grafts are potentially advantageous in tabonuco because they can make trees more resistant to windthrow (Rigg & Harrar 1931, Pryor 1937).

TABLE 2. *Tabonuco trees damaged by Hurricane Hugo: Uprooted vs snapped vs standing for individuals vs unions. Snapped category include branch broken and stem broken trees. Chi-square test was significant at* $P < 0.005$.

Tabonuco trees	% Uprooted	% Snapped	% Standing
Individuals	40.0	40.0	20.0
Unions	0.0	40.0	60.0

Tabonuco was the most resistant species to Hurricane Hugo in the forest (Basnet 1990, Basnet *et al.*, 1992). Hurricane damage was significantly higher in individual tabonuco trees than those in unions (Table 2). Not a single tabonuco tree in unions was uprooted. During the 2 years prior to Hurricane Hugo in 1989, there were only 2 large tabonuco blowdowns (9.5% of the total blowdowns) in the area; these trees were not in unions.

Intraspecific grafts can increase the absorptive capacity and the area of coverage for nutrition by roots (Bormann 1966, Fig. 1). We found that the network of large root systems of tabonuco trees form organic benches (flat areas rich in organic matter) on the upslope side of the union (Fig. 4). These benches accumulate sediments and litter (10–20 times thicker than the average litter mat on the forest floor) and are eventually invaded by thick mats of tabonuco fine roots. The ecological advantage of these organic benches could be that they create favorable conditions for root aeration and accumulate organic matter and nutrients from the parent tree, its neighbors, and downslope flow. Presumably, such nutrient accumulations would be advantageous to the tree union because nutrients may be more concentrated in the organic bench than they are in the mineral soil; thus, faster growth rates could be supported. This is presented in a model (Fig. 4) which shows overall functions of a tabonuco union–its main components, the factors affecting its behavior, and the processes that can take place in a union.

Root grafting may also promote the dominance of tabonuco over other species because dominant trees in a union supply photosynthates to the suppressed trees (Kuntz & Riker 1956, Bormann 1966) which are quickly released for growth if a gap in the canopy occurs (Brokaw 1985, Denslow 1987). We observed "resurrection" of "dead" tabonuco trees after Hurricane Hugo battered tabonuco unions. Suppressed trees are often sterile (Fowells 1965) and short-lived (Bormann 1966, Graham &

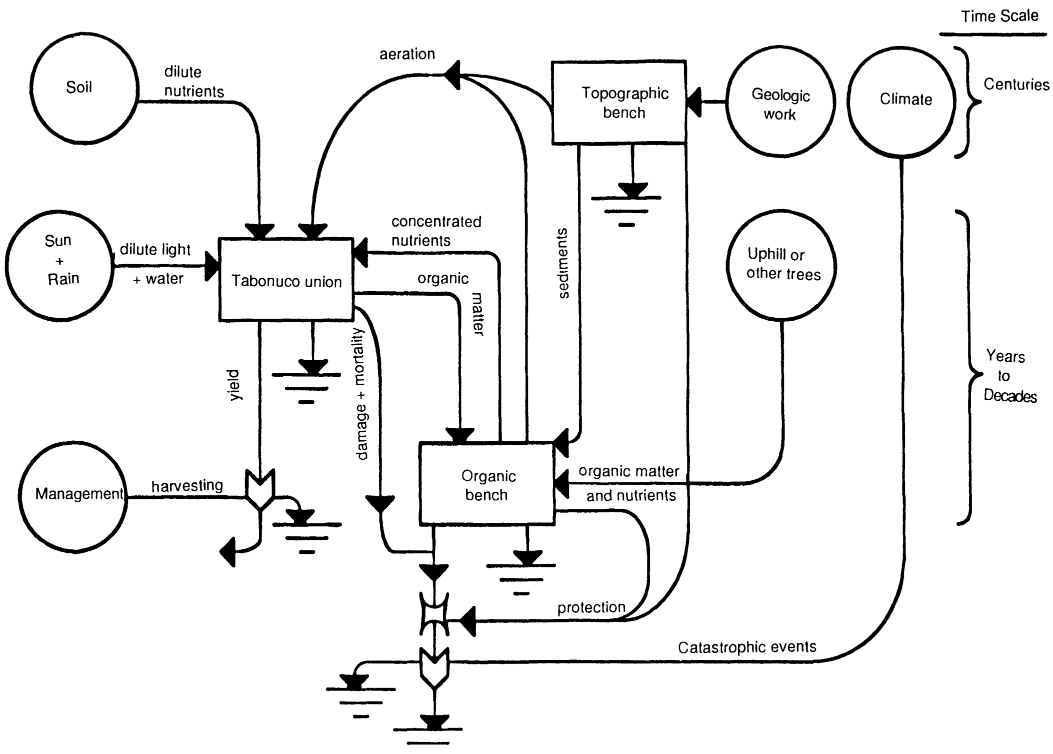

FIGURE 4. Conceptual model of the costs and benefits of tabonuco unions in the Bisley Watersheds. Organic benches formed by tabonuco unions are ecologically important in all time scales. Symbols are those of Odum (1983).

Bormann 1966). Such effects in tabonuco, however, are not pronounced because it is a shade tolerant and late successional species (Weaver 1983). In fact, more tabonuco trees (stems and basal area) occurred in unions than as individuals in the Bisley Watersheds.

CONCLUSION

There are both costs and benefits associated with tabonuco trees forming unions (Fig. 4). Considering the high levels of disturbance in this forest (Saliva 1972, Weaver 1986, Scatena 1989, Basnet *et al.*, 1992) and low shear strength of clayey soil, any increased mechanical support is important for the survival and continuity of the species. This study suggests that root grafts provide additional support and stability to tabonuco trees as they are anchored to one another by large roots (Keeley 1988, Basnet 1990, Loehle & Jones 1990).

The high frequency of root grafting in tabonuco and the interrelationships of grafted trees (Fig. 3) indicate that noncompetitive forces are more important than competitive forces in shaping the tabonuco unions and thus the community of the tabonuco forest (see Bormann 1962). Since root grafts are common in tropical trees (LaRue 1952), the importance and implications of tree unions to management and silvicultural practices in other tropical forests should be investigated.

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