DP-MS-88-241

ADAPTIVE SIGNIFICANCE OF ROOT GRAFTING IN TREES

by

C. Loehle[1] and R. Jones[2]

1 E. I. du Pont de Nemours and Company
Savannah River Laboratory
Aiken, SC 29808-0001

2 E. I. du Pont de Nemours and Company
Savannah River Ecology Laboratory
Aiken, SC 29802

DISCLAIMER

Portions of this document may be illegible in electronic image products. Images are produced from the best available original document.

DP-MS-88-241

ADAPTIVE SIGNIFICANCE OF ROOT GRAFTING IN TREES

by

C. Loehle[1] and R. Jones[2]

1 E. I. du Pont de Nemours and Company
Savannah River Laboratory
Aiken, SC 29808-0001

2 E. I. du Pont de Nemours and Company
Savannah River Ecology Laboratory
Aiken, SC 29802

Abstract

Root grafting has long been observed in forest trees but the adaptive significance of this trait has not been fully explained. Various authors have proposed that root grafting between trees contributes to mechanical support by linking adjacent root systems.[1] Keeley proposes that this trait would be of greatest advantage in swamps where soils provide poor mechanical support. He provides as evidence a greenhouse study of *Nyssa sylvatica* Marsh in which seedlings of swamp provenance formed between-individual root grafts more frequently than upland provenance seedlings. In agreement with this within-species study, Keeley observed that arid zone species rarely exhibit grafts. He also demonstrated that vines graft less commonly than trees, and herbs never do.[2] Since the need for mechanical support coincides with this trend, these data seem to support his model. In this paper, we explore the mechanisms and ecological significance of root

* The information contained in this article was developed during the course of work under Contract No. DE-AC09-76SR00001.

grafting, leading to predictions of root grafting incidence. Some observations support and some contradict the mechanical support hypothesis.

Introduction

The hypothesis that grafting increases mechanical support has some theoretical but no direct empirical evidence to support it. Grafting could be important in one component of windfirmness, the tensile strength of roots and soil on the upwind side of the tree. This theory has been researched by different authors.[3] Coutts described how root grafting within a tree root system could increase windfirmness on the upwind side by effectively increasing branchiness, which acts to increase soil/root contact, and therefore anchoring the tree.[4] Grafting between trees could provide even more support by extending the length of root over which force is being exerted and by increasing branchiness which gives additional anchoring. Detailed study of these benefits could follow the methods of other researchers.[5] If trees respond to wind by increasing grafting, then this would be an adaptive response. Swaying of trees that are inadequately anchored causes abrasions between adjacent roots which could encourage subsequent graft formation as a healing response in a coincidental fashion in just those trees requiring increased support. It has been argued, however, that such abrasions will interfere with graft formation if the roots continue to be moved by the wind.[6] No data exists to reconcile outcomes.

Discussion

The evolution of grafting for windfirmness as a cooperative behavior raises questions of mutualism and group selection. According to Franklin and Forman, windfirmness is a trait in which group "cooperation" is logically possible, because if weaker individuals are blown down and the stand is opened up, the damage tends to spread and other trees become more susceptible to windthrow.[7] Neighbors remain neighbors until one dies, which makes mutualism more likely. However, there is a conflict between competition and cooperation thus coevolution should not be predicted. While there is thus some plausibility to the windfirmness argument for root grafting, it does not represent a complete explanation for the phenomenon.

A first alternative hypothesis is that there is no overt significance to root-grafting trends. That is, in some cases root grafts or their lack may be determined by factors other than selective advantage. For example, even though grafts might be advantageous, morphological or physiological constraints could limit their occurrence. Conversely, grafts may not be advantageous, in which case their occurrence is only a serendipitous side effect of other factors. It is important to note that grafting is a trait not without costs. Inter-tree grafts have been shown by different authors to be a major transmission route for pathogens and may thus present a significant mortality risk.[8] Other researchers have found that a net flow of metabolites from dominant trees to subordinate trees may exist.[9]

The physiological and morphological mechanisms of root grafting are not entirely understood. According to Graham and Bormann, the origin of grafts usually involves the development of a pressure point in the zone of contact between two woody roots growing in girth.[10] The pressure point results in bark atrophy and, eventually, the fusion of the vascular cambia of the two roots. According to Kozlowski, roots growing over stones are enforced together and tend to graft more.[11] Sutton and Keeley observed that 1 to 3 years grafts occur in seedlings as young as 1 to 3 years old.[12] However, the incidence of grafting is apparently correlated with the density of thick woody roots. Thus, writers agree that stands with high densities of large roots (e.g., older stands with high tree densities and shallow rooting) tend to have a higher incidence of grafting than do stands with lower large root density.[13] This suggests proximity as a partial, non-evolutionary explanation for root grafting incident trends.

When in contact, roots do not always form grafts. Grafting is related to wound healing and immune responses. It is necessary for an organism to recognize self from non-self when wounded or invaded by pathogens. We would thus expect between-species grafts to be very rare. In fact, this is so. Horticultural grafting between species requires special manipulations and usually only related species can be grafted. A family such as the *Rosaceae* in which between-species grafts are observed is notable in its uniqueness to several authors.[14] Between-individual chemical differences are not as great as between-species differences but could still be a barrier. Evidence that this is so is that same-tree grafts are far more common than between-tree grafts. The implication is that generally a greater degree of genetic similarity should lead to greater grafting between trees. There is some direct evidence for this. Red pine (*Pinus resinosa*) is notable in the extent of grafting. Dosen and Iyer wrote that most stumps may survive thinning treatments[15] and is also remarkably genetically uniform. Other species are notable for root sprouts or suckers (e.g., aspen, birch, beech, and sassafras). In stands of such species clumps of trees may be genetically identical, and thus grafting between trees is essentially the same as grafting within a tree and may not signify any adaptive benefit. Isolated or relict stands may also be suspected of being genetically homogeneous. Even in typical stands, parthenocarpy or limited send dispersal may mean that adjacent trees are fairly closely related. In stands with low genetic diversity, selection for grafting to promote windfirmness becomes more likely and approaches kin-selection rather than group-selection.

Root placement provides another line of argument against the significance of grafting or lack thereof. On dry sites, lower total tree biomass results in a lower density of roots. Dry site trees tend to be deep rooted, which distributes roots over a greater volume of soil. These two factors reduce the frequency with which roots contact each other and thus reduce grafting incidence Thus Keeley's observation that arid zone species exhibit little grafting may be unrelated to the potential advantages of grafting for windfirmness.[16] In fact, dry site trees are typically exposed to far more wind because of exposure. The situation in which the most roots are in contact with each other is when they tend to or are forced to grow in a thin layer near the surface. In fact, the combination of moist sites (high root mass) and shallow rooting produces the most dramatic incidence of root self-grafting (e.g., yellow birch, beech, and hemlock growing on moist hillsides or thin soils).

Coincidentally, shallow rooting conditions also provide selective pressure for windfirmness. Even in drier habitats, trees growing in shallow soil over rocks will exhibit abundant self-grafting as several authors have noted.[17]

For trees that engage in chemical warfare, lack of grafting may be unrelated to windfirmness or other potential benefits. Black walnut, for example as noted by Fowells, produces chemical compounds that prevent their own seedlings from surviving under the parent tree.[18] They generally tend to grow as isolated trees rather than in pure stands. As another example, Reinartz and Popp found that root systems of adjacent clones of northern prickly ash (*Xanthoxylem Americanum*) never came in contact, evidently because of chemical inhibitors diffused through the soil.[19] In species such as these, no root grafting between individual trees is likely because roots do not have a chance to contact each other. Note that prediction of failure to graft are difficult to test with existing literature because what has often been recorded is frequent grafting. Lack of grafts is difficult to distinguish from lack of data. An exception is sweetgum. P. Kormanik of the USDA Forrest Service, Athens, Georgia, excavated root systems of a number of adult trees and over 5000 saplings planted at close spacing. He never observed grafting between trees during this time.[20] Sweetgum is notable among hardwoods for its production of resinous aromatic sap, which could conceivably act as a chemical inhibitor to grafting or root contact.

Keeping in mind all of the above constraints, there is an alternative adaptive hypothesis to mechanical support. We propose that there could be a strong selective advantage for seedlings to graft onto roots of the parent tree. The fact that seedlings in nurseries form grafts supports the possibility of this hypothesis. For many species, survivorship of seedlings as advanced regeneration is key to long-term persistence. Some studies have shown that in clonal plants survivorship of seedlings is very low in closed forest, whereas vegetative propagules have much better survival due to support from the parent.[21] A seedling that could graft onto the parent rootstock would have the survivorship advantage of clonal reproduction but the genetic advantage of sexual reproduction. On average, the seedling will be only one-half related to the parent, so graft acceptance must be somewhat indiscriminate for such grafts to occur. If so, then grafts with other non-related individuals will also be more likely, though only as a side-effect and not as a trait selected for per se. In population with limited dispersal, trees breed with adjacent related trees, giving sibling-parent relatedness >1/2. In environments where species are shallow-rooted, the seedling and parent tree will be more likely to root in the same zone with consequent greater likelihood of grafting. Grafting would be particularly advantageous in unstable muck habitats as a form of support, which might explain Keeley's results.[22] Huenneke and Sharitz showed that seedlings in riverine swamps were rarely found away from firm support and attributed this to effects of moving water during flooding.[23] Grafting onto existing roots could help stabilize seedlings and increase their survival. The benefit of seedling grafts accrues to both adult and seedling with minor costs to the adult tree (mainly from grafts by unrelated seedlings), so overall this hypothesized selective advantage for grafting is plausible. No data currently exists to test this hypothesis.

A final proposed adaptive explanation is that grafting may represent reciprocal parasitism. It is distinguished from mutualism because only one tree benefits at any given time, and the loser may not benefit during the entire relationship. For grafted trees of equal dominance status, neither tree benefits in terms of energy, water, or nutrients as noted by one author.[24] When one tree is subordinate, it parasitizes the dominant tree, receiving assimilates and perhaps growth hormones. For suppressed trees the assimilates obtained may be sufficient to prolong survival by several years. The dominant receives nothing. If the subordinate dies, the dominant may capture part of its root system. Dosen and Iyer indicated that remaining trees receive a growth advantage from captured root systems, though there is some disagreement on this.[25] At the time when grafts are forming, either tree may turn out to be the parasite. How natural selection will operate under these unusual circumstances is open to question.

What predictions does the above framework allow a researcher to make concerning lack of grafting in herbaceous species? Mechanical support is not a problem for herbaceous species which are not subject to windthrow due to their stem flexibility and stature. Thus any mechanical advantage due to either within-plant or between-plant grafting does not apply to herbaceous plants. Potential advantages due to seedling grafts onto the parent root stock are not likely because most herbaceous plants are short-lived, with little overlap between generations. Considering longer lived herbaceous plants such as bunch grasses, most of their roots are short-lived (less than a year), so there is no time for grafts to occur. In addition, there is little or no secondary thickening of the roots which is necessary for true grafting. Thus lack of grafting in herbaceous plants is not surprising given the lack of selective pressure for grafting, but may also be due to the short lives of individual roots. Vines and low woody plants of course represent intermediate cases and should show some grafting, as documented by Keeley.[26] Smaller size and shorter life spans lead to less grafting in vines and shrubs (since dbh and root diameter in trees have been shown to be predictive of grafting incidence). It is not clear, however, that vines and shrubs have ever really been studied for frequency of grafting. Trees have been studied largely for foresters. Botanists have been less interested in grafting. Thus lack of grafting in vines and shrubs could be partially an artifact of lack of data.

Conclusion

There are multiple potential costs and benefits to root grafting as well as significant determination by coincidental factors such as root morphology, root density, soil moisture, chemical inhibition, and genetic relatedness. The disadvantages due to grafting (metabolite parasitism by subordinates and pathogen transmission) suggest that grafting between individual trees would not be genetically selected for unless it were advantageous. Windfirmness and grafting of seedlings onto adult roots are proposed as two plausible selective advantages of grafting. Further work is required to untangle the complex mechanisms of grafting.

References

1. F. H. Bormann, 1966, "The Structure, Function, and Ecological Significance of Root Grafts in *Pinus Strobus*," L. Ecol. Monogr., 36:1-26.
   H. Kumar, D. Kulkarni, and R. A. Srimathi, 1985, "Natural Grafts in Sandal," Indian J. For., 8:153-154.

2. J. E. Keeley, 1988, "Population Variation in Root Grafting and a Hypothesis," Oikos, 52:364-366.

3. M. P. Coutts, 1983, "Root Architecture and Tree Stability," Plant and Soil, 71:171-188.
   S. D. Warren, H. L. Black, D. A. Eastmond, and W. H. Whaley, 1988, "Structural Function of Buttresses of *Tachigalia versicolor*," Ecology, 69:532-536.

4. Coutts, pp. 171-188.

5. Coutts, pp. 171-188.
   T. A. McMahon, and R. E. Kronauer, 1976, "Tree Structures: Deducing the Principle of Mechanical Design," J. Theor. Biol., 59:443-466.
   Warren, Black, Eastmond, and Whaley, pp. 532-536.

6. T. T. Kozlowski, 1988, personal communication.

7. J. F. Franklin, R. T. T. Forman, 1987, "Creating Landscape Patterns by Forest Cutting: Ecological Consequences and Principles," Landscape Ecology, 1:5-18.

8. P. F. Hessburg, and E. M. Hansen, 1986, "Mechanisms of Intertree Transmission of *Ceratocystis wageneri* in Young Douglas-fir," Can. J. For. Res. 16:1250-1254.

9. B. F. Graham, and F. H. Bormann, 1966, "Natural Root Grafts," Bot. Rev., 32:255-292.
T. T. Kozlowski, 1971, "Growth and Development of Trees II: Cambial Growth, Root Growth, and Reproductive Growth," Academic Press, NY.
P. J. Kramer, and T. T. Kozlowski, 1960, "Physiology of Trees," McGraw-Hill, NY.

10. Graham, and Bormann, pp. 255-292.

11. T. T. Kozlowski, 1971, "Growth and Development of Trees II: Cambial Growth, Root Growth, and Reproductive Growth," Academic Press, NY, p. 256.

12. Keeley, pp. 364-366.
R. F. Sutton, 1969, "Form and Development of Conifer Root Systems," Commonwealth Agricultural Bureau, Tech. Report No. 7, Oxford, England, p. 131.

13. Graham, and Bormann, 1966, "Natural Root Grafts," Bot. Rev. 32:255-292.
K. M. Reynolds, and W. J. Bloomberg, 1982, "Estimating Probability of Intertree Root Contact in Second-Growth Douglas-fir," Can. J. for. Res. 12:493-498.

14. Kozlowski, personal communication.

15. R. C. Dosen, and J. G. Iyer, 1979, "Effect of Grafted Roots of Stumps on the Growth of a Thinned Red Pine Plantation," Tree Planters Notes, 30:19-21.

16. Keeley, pp. 364-366.

17. R. E. Saunier, and R. F. Wagle, 1965, "Root Grafting in *Quercus turbinella* Greene," Ecology, 46:249-250.
A. R. Tiedemann, W. P. Clary, and R. J. Barbour, 1987, "Underground Systems of Gambel Oak (*Quercus gambelii*) in Central Utah," Amer. J. Bot., 74:1065-1071.

18. H. A. Fowells, 1965, "Silvics of Forest Trees of the United States," USDA For. Serv. Agr. Handbook, 271.

19. J. A. Reinartz, and J. W. Popp, 1987, "Structure of Clones of Northern Prickly Ash (Xanthoxylum Americanum)," Amer. J. Bot., 74:415-428.

20. P. Kormanik, personal communication.

21. R. E. Cook, 1983, "Clonal Plant Populations," American Science, 71:244-253.
C. Loehle, 1987, "Partitioning of Reproductive Effort in Clonal Plants: a Benefit-Cost Model," Oikos, 49:199-208.

22. Keeley, pp. 364-366.

23. L. F. Huenneke, and R. R. Sharitz, 1986, "Microsite Abundance and the Distribution of Woody seedlings in a South Carolina Cypress-Tupelo Swamp," Am. Midl. Nat., 115:328-335.

24. Bormann, pp. 1-26.

25. Dosen, and Iyer, pp. 19-21.

26. Keeley, pp. 364-366.