ANATOMY OF ELMS INJECTED TO CONTROL DUTCH ELM DISEASE

by Alex L. Shigo, Richard Campana, Fay Hyland, and Janet Anderson

Abstract. American elm trees that had widely separated vessels, compartmentalized discolored wood associated with injection wounds to small volumes. Discolored wood associated with the injection wounds was confined to tissues present at the time of wounding. The relationship of anatomical features to the degree of compartmentalization of discolored wood and to the resistance of elms to Dutch elm disease is discussed. All injection methods inflict a wound in the xylem. This paper gives some information on the compartmentalization of wound-altered tissues associated with injection wounds made for the prevention of Dutch elm disease in American elm, *Ulmus americana* L.

Results of recent research suggest that the degree of compartmentalization — strong or weak — is under genetic control (Shigo et al. 1977). It may not be so much the intrinsic capacity to compartmentalize that is under genetic control, as it is the anatomical features and biochemical systems of the tree. The degree of compartmentalization would then be an indirect result of the inheritance of certain anatomical features and biochemical systems. Eckstein et al. (1979) showed that vessel features were strongly related to the degree of compartmentalization. It is of great interest to note that several investigators (Elgersma 1967, 1969, 1970; McNabb et al. 1970; Sinclair et al. 1975) showed that vessel features were also strongly related to the degree of resistance to Dutch elm disease.

Vessels are a weak link in the defense system of deciduous angiosperms because they must remain open to maintain the liquid transport essential for life. The open vessels provide easy access for microorganisms to enter the tree after injury. After injury and infection, vessels must be plugged rapidly in some way or the tree is doomed. The type of vessel system in a tree and the response of the tree to plug the vessels is critical for survival.

There are two major parts to the compartmentalization process: (1) Walling off injured and infected xylem to the smallest possible volume within xylem present at the time of wounding; (2) walling off xylem present at the time of wounding from xylem that forms subsequently.

Materials and Methods

Over 500 stained thin sections were made from selected samples of elms injected in various ways and with various chemicals. These sections came from the elms described by Shigo and Campana (1977). Some trees were large mature elms from diverse sites in the Northeast, while others were small, young elms injected at one period as part of other experiments at the USDA, ARS Laboratories in Delaware, Ohio. Thin sections were cut from strong and weak compartmentalizers (Figures 1, 2).

Figure 1. Strong compartmentalization; the discolored wood associated with the four injection wounds did not spread laterally (arrows).

Results

From a cross-sectional view, there were three basic patterns of discolored wood associated with the injection wounds; Type A, strong compartmentalization, small columns (vertical areas of tissue), no lateral spread; Type B, medium compartmentalization, large columns, some lateral spread; and Type C, weak compartmentalization, very large columns, and rapid lateral spread (Figure 3). Most of the elms were Types B and C.

Figure 2. Weak comaprtmentalization; the discolored wood associated with the four injection wounds spread laterally to almost completely fill the diameter of the tree at the time of wounding.

The anatomy of Type C was represented by an abundance of vessel groups in late wood tissues, all closely aligned (Figure 4). Type A had a more typical ring-porous structure with large single vessels abundant early in the growth ring and smaller vessels throughout the ring (Figure 5). Type B tissues were intermediate to Types A and C.

The discolored wood associated with the injection wounds had dark deposits in the ray parenchyma and the vessels had an abundance of tyloses (Figure 6). The parenchyma cells were dead in the discolored wood.

After the injection wound was inflicted, the living cambium began to form a new protective tissue called the barrier zone. The zone had fewer vessels and bulging ray parenchyma (Figure 7). The zone also had an abundance of parenchyma cells that had died soon after they were formed. The cells were then filled with dark deposits (Figure 8).

Discussion

Elms resistant to Dutch elm disease have vessels that are in widely separated groups, while susceptible elms have vessels that are closely

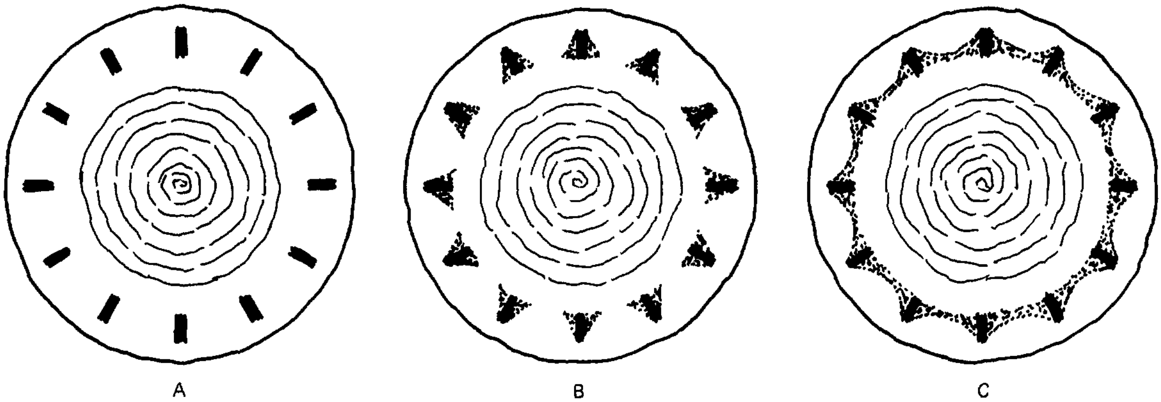

Figure 3. Three basic patterns of discolored wood associated with injection wounds; Type A, strong compartmentalization, Type B, moderate compartmentalization, Type C, weak compartmentalization.

grouped (Elgersma 1967, 1969, 1970); McNabb et al. 1970; MacHardy 1978; Sinclair et al. 1975). The closely grouped vessels would facilitate lateral movement of a fungus. Lateral spread of a pathogen is the most serious threat to the life of any particular infected stem, and to the life of a tree. A tree could withstand a great amount of vertical infection and still remain alive, but circumferential spread can kill quickly.

Eckstein et al. (1979) showed that trees which were strong compartmentalizers had widely spread groups of vessels, while weak compartmentalizers had very closely grouped vessels. There was great lateral spread of discolored wood in the trees that were weak compartmentalizers.

Results from our study agree with those of Eckstein et al. (1979) in that Type A elms had widely spaced vessel groups made up of more solitary vessels, while Type C elms had closely grouped vessels.

The results suggest that elms resistant to Dutch elm disease are also strong compartmentalizers. The trees may be resistant because they have an anatomy that can quickly respond to injury and infection by compartmentalizing. This may help to explain some of the variation in response to injections. The trees that have the best response to the chemicals may be both strong compartmentalizers and resistant trees.

If this is so, and if further experiments continue to show that compartmentalization is under genetic control, then resistant elms could be selected on the basis of their response to wounding. Methods for doing this have been developed (Shigo 1979).

Barrier zones are anatomical and biochemical zones that separate infections within wood present at the time of wounding from wood that forms subsequently (Moore 1978; Mulhern et al. 1979). Barrier zones formed after the elm trees were injected. The barrier zone confined the discolored wood associated with the injections to the tissues present at the time of wounding. This is very beneficial, especially when injection

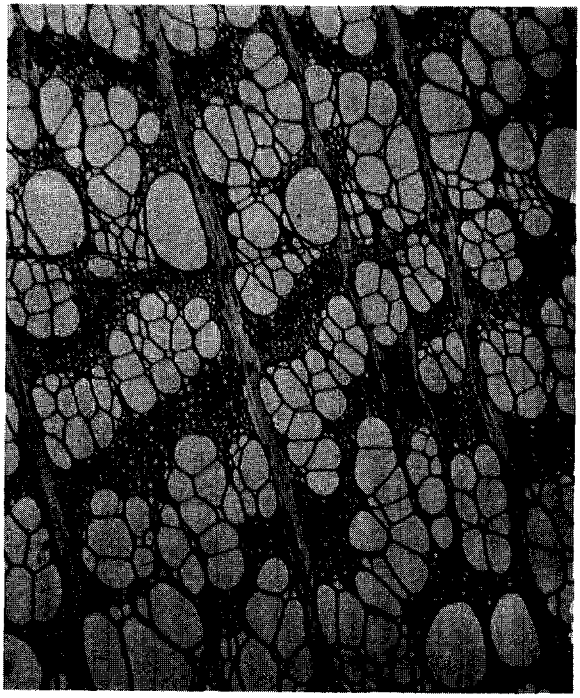

Figure 4. Anatomy of Type C American elm; cross section showing thin sheets of ray parenchyma and abundance of closely aligned groups of vessels.

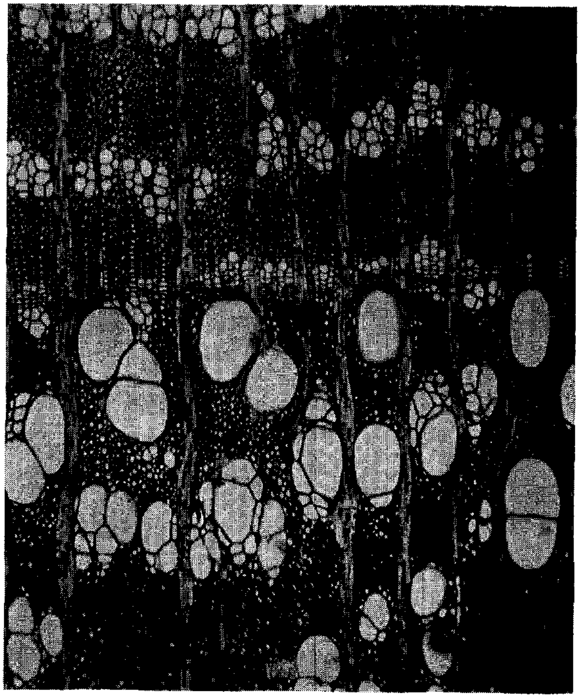

Figure 5. Anatomy of Type A xylem in American elm; cross section showing thick sheets of ray parenchyma and large solitary vessels.

wounds are widely spread on the trunk and the injections are not repeated annually. If injections are repeated annually, the most recent barrier zone will be within the current growth ring. When the zones coalesce circumferentially, all that will remain in the tree at the position of the injection will be a portion of the current growth ring. The situation can be even more serious because the barrier zone is primarily a protective tissue and not a conducting tissue (Mulhern et al. 1979; Moore 1978). This means that when the barrier zones coalesce circumferentially, there will be little conducting tissue remaining in the current growth ring. How soon after repeated annual injections this occurs will depend on whether the tree is a Type A or Type C. It could occur as soon as 3 years in a Type C tree that receives annual injections. Although it is not likely that this would kill the tree, it could greatly weaken one.

A type A tree might withstand the coalescence of the barrier zones for 6 to 8 years, but eventually coalescence occurs. Until less injurious injection methods are developed, great care must be taken with annual injections (Campana 1977; Shigo and Campana 1977). Where possible, annual injections should be avoided. This would allow the tree to develop new growth rings free of discolored wood. The risk here is infection from Dutch elm disease during the years that the tree is not injected.

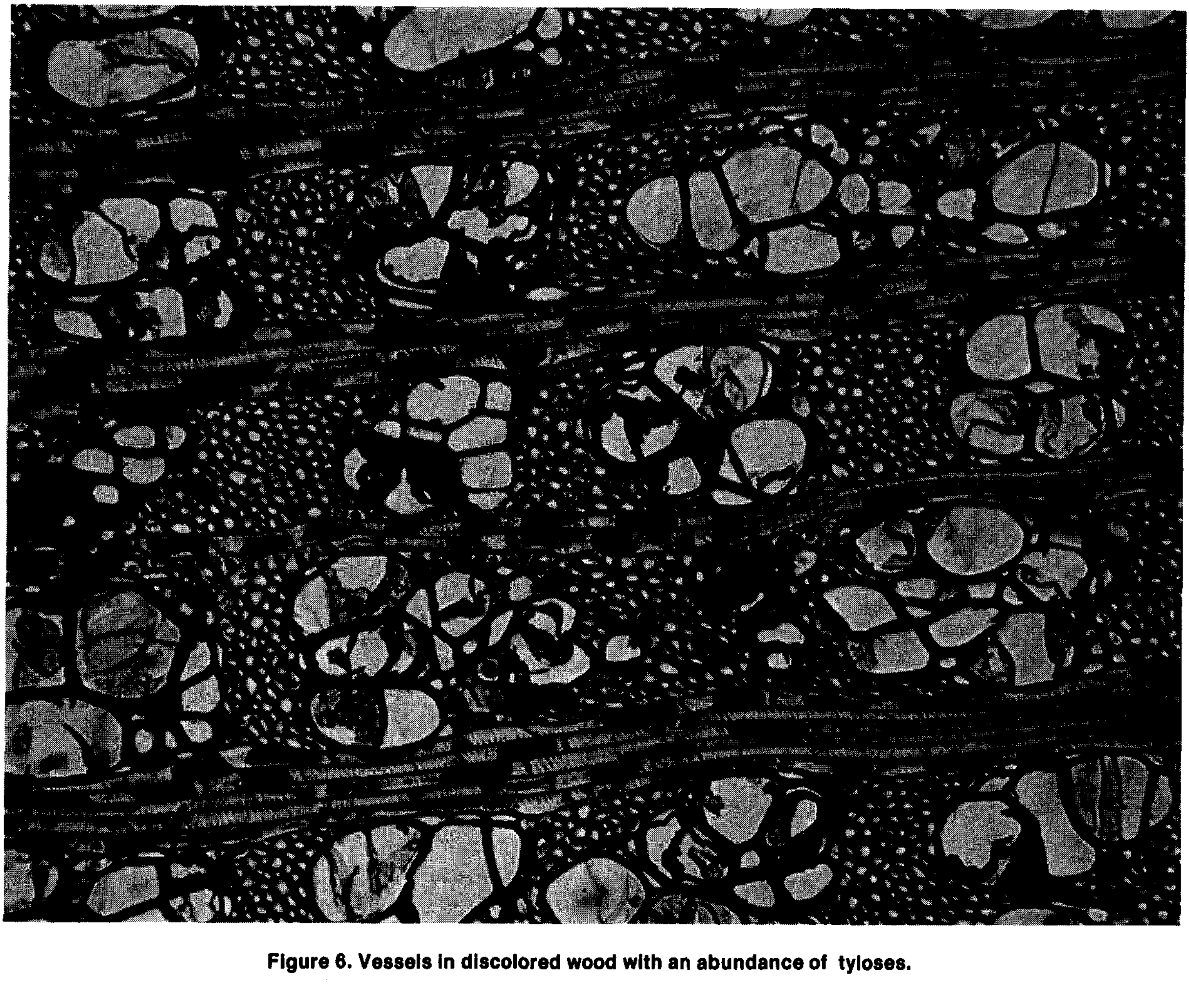

Figure 6. Vessels in discolored wood with an abundance of tyloses.