THE DETECTION AND NATURE OF FUNCTIONAL UNDERGROUND CONNECTIONS BETWEEN MEMBERS OF CERTAIN WOODY SPECIES OF THE OKLAHOMA CROSS TIMBERS

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Submitted to the Faculty of the Graduate College
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in partial fulfillment of the requirements
for the Degree of
DOCTOR OF PHILOSOPHY
May, 1971

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ACKNOWLEDGMENTS

I would like to thank Dr. Jerry J. Crockett, the major adviser for this study, for his patience, advice, and encouragement.

The motivation and suggestions provided by the other committee members, Drs. Basler, Thomas, Todd, and Wilhm, are also appreciated.

Special acknowledgments are due Dr. B. F. Graham of Grinnell College for his help with the literature and to Velda Davis for her valuable aid in manuscript preparation.

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CHAPTER I

INTRODUCTION

Malcolm (1966) listed ten functional relationships that might exist between living organisms. Three of these relationships had not previously been named. He postulated that the lesser interactions have been neglected by ecologists' preoccupation with competition, predation, and parasitism.

Interspecific interactions are usually discussed and exemplified, but analogous intraspecific relationships are known to exist. Intraspecific competition is often considered to be the most severe competition in nature due to the similarity of requirements of members of the same species, although Billings (1964) noted the severity of competition between similar life forms which might not be genetically related. Even this modification would support the original thesis because the members of the same species have the most similar life form.

Traditionally, competition studies have dominated interaction analyses in forest ecosystems. Kozlowski (1949) reviewed the long history of the study of competition for light and soil moisture among forest trees. These studies have resulted in many basic concepts dealing with tolerance and succession and have also resulted in more profitable forestry practices such as the proper spacing of plantation trees.

As long as trees are considered to be discrete, biological units it is difficult to visualize other than competetive or other negative interactions. In recent years, however, studies have shown that many trees are not, in fact, anatomically and physiologically isolated from each other. Trees appearing to be isolated individuals may be connected underground by functional root or stem structures. These studies may be grouped according to the type of connection involved: (1) those dealing with intraclonal connections resulting from root sprouting (Debyle, 1964), (2) those concerning intraclonal connections of a rhizomatous nature (Duncan, 1935), and (3) those in which the connection results from the natural grafting of roots (Bormann and Graham, 1959). Natural grafts are classified into three types. Self grafts are those occurring in a single tree. Intraspecific grafts are between members of the same species and interspecific grafts are those between members of different species.

Intraclonal connections of both types are related in that they result from vegetative reproduction and the "members" of the group are genetically identical. Natural root grafts might involve trees that are genetically different.

Two other phenomena have been shown to offer the possibility of a less direct exchange of materials between trees. Slankis, Runeckles, and Krotkov (1964) have shown that trees actively liberate metabolites from their root systems that might influence other trees. Woods and Brock (1964) and Reid and Woods (1969) provide evidence that mycorrhizal fungi can offer channels for the transfer of materials from tree to tree. They sum up all of these possibilities by considering the root mass of a forest ecosystem as a single, functional unit.

The existence of these direct and indirect connections, if functional, make the concept of the "individual" forest tree to be as uncertain as it has been in other vegetation (Whittaker, 1965; Grieg-Smith, 1966). The existence also strengthens the suspicion that mutualistic or other cooperative interactions might be involved in forest trees.

Much work must be done on these positive interactions and on the connections involved in different species and areas. This is important, not only for the ecological implications, but also because underground connections have been shown to be involved in problems such as disease transmission (Kuntz and Riker, 1950) and in herbicide "backflash" (Cook and Welch, 1957).

No detailed study of underground connections has been undertaken in the woody species of the Oklahoma Cross Timbers. The present study has attempted to provide some basic information by exploring detection techniques for locating direct, functional, underground connections and to investigate the nature of these structures in this geographical area. Postoak (*Quercus stellata* Wang.)[1] and blackjack oak (*Q. marilandica* Muenchh.) have been investigated most rigorously in the present study because they are the major dominants of the region (Rice and Penfound, 1959). Other woody species have received less consideration in the present study.

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[1] Botanical nomenclature of local species will follow that of Waterfall, 1966.

CHAPTER II

REVIEW OF THE LITERATURE

Forest tree root studies present massive sampling problems as attested to by work done with the root systems of fruit trees. Weaver (1932) describes one of these studies in which the soil penetrated by the roots was removed in 50 cm cubes. Sixty tons of material were excavated in the case of each 10 year old apple tree.

The earliest references to root grafting deal with the aboveground observation that some stumps continue to live, heal, and add tissue for many years. Theophrastus wrote of this situation in his "Enquiry into Plants" (Hort, 1916). He observed that silver fir, when cut or broken, often continued to grow a black, hard callus on the stump. It is not clear who first linked this stump occlusion with the grafting of the roots of a stump to those of a living tree. Weaver, in 1871, attributed stump occlusion, in certain species, to the facility with which their branches and roots become grafted and allow procurement of nourishment from a neighboring tree (Graham, 1966).

Some controversy developed in explaining stump growth. Sorauer (1919) conceded that, in many cases, the stumps were grafted to a donor but when the stumps were remote from a donor, they were living on stored food at first and then on chlorophyll that developed in the cortex of the callus.

Dallimore (1917) reviewed the situation and revealed a letter he had received from C. C. Pemberton, who could find no case of a living stump that was not grafted. Pemberton (1920) published a detailed study in which he again reported that all of the living stumps he excavated proved to be root grafted. He noted one group of nine living stumps that were found to be grafted to a tree 50 feet away. Pemberton also reported many dead stumps whose root systems were alive for years because of grafts.

Page (1927) added some of the conifers of the Northeastern United States to the list of species known to form living stumps. On two thinned sites he found 58 per cent and 54 per cent of the stumps alive after one year and 36 per cent and 34 per cent alive two years after cutting. The average annual ring thickness was one-seventh the average of all previous annual growth rings.

Lanner (1961) states that only in lightly cut stands will the number of living stumps indicate the amount of root-grafting in the stand. He concludes, "There will always be more root-grafting in a stand than the numbers of living stumps indicate."

Bormann (1961) showed that non-grafted stumps (Pinus strobus L.) could survive only one growing season after cutting. He attributed this to a lack of auxin-induced cambial activity, even though food was present. He observed from 3 per cent to 44 per cent living stumps in partially cut stands.

Lanner (1961) reported a Douglas fir living stump that persisted about a century while Newins (1916) observed a stump of the same species that had survived 200 years after cutting.

Occluded stumps seem to be much more common in conifers than in other species; however, a few reference to the phenomenon in

Angiosperms exist. Acer saccharinum L. was reported to occlude by LaRue (1934) and some of the birches were noted by Laitkari (1935). The only reference to oaks was seen in abstract and concerned Quercus pubescens Willd. (Romashkin, 1956).

Many other discoveries of root grafts have taken place in exposed areas such as gullies and in the grubbing out of old roots or in an easily excavated substratum like sphagnum. Rigg and Harrar (1931) found grafting in seven tree species in bog areas near Seattle. LaRue (1934) examined 3000 grubbed out white pine stumps that had been used for fences. He recognized self grafts in all of them, with intraspecific grafts still visible in a few. He also found intraspecific grafts in a cut made by a meandering stream. Ulmus americana, Tilia americana, Betula lutea, and Acer saccharinum were seen to produce great numbers of grafts.

Beddie (1941) added 30 species of New Zealand trees to the list of known root-grafters. He also suspected six other species, but noted the difficulty in being able to differentiate between well developed grafts and root suckers. Adams (1940) working in Australia, on an area where roots were grubbed for housebuilding, recorded the frequency and shallowness of most grafts. He found no grafts below 2.5 feet. LaRue (1952), exploring road cuts and washes in Puerto Rico, found 34 genera belonging to 18 different families that grafted. He concluded that root-grafting may be more common in tropical trees than in those of temperate regions.

Exploring prospect holes, gullies, and road cuts in Arizona, Saunier and Wagle (1965) found self and intraspecific grafts in Quercus turbinella Greene. They considered this to be a significant report because it has been rare to find grafting among the widely spaced woody plants of arid and semiarid regions.

Many reports of root-grafting have resulted from the use of various tracers. Baldwin (1938) injected dye into beech trees and found other beeches within a radius of 50 feet to also be dyed. In recent years injected dyes, radioisotopes, and silvicides have been preferred methods of graft location (Fraser and Mawson, 1953; True et al., 1955; Graham, 1960; Woods and Brock, 1964; Miller and Woods, 1965). Fischer et al., (1960) used an antibiotic as a tracer in spruce trees.

Other reports of root grafting have resulted from deliberate excavations. Examples are those of Weaver's (1932) work with bur oak and Kozlowski and Cooley's (1961) use of a washing technique with 11 species in Wisconsin. Stout (1956) also used a hydraulic system in his root mapping of a group of deciduous trees in the Black Rock Forest.

Graham and Bormann (1966) surveyed the literature and found more than 150 woody species that had been reported to root graft. They believe that other species certainly graft and that the phenomenon may be almost universal. In Graham and Bormann's (1966) review was a 1958 report of interspecific grafts between postoak and _Carya_ sp. The presence of interspecific grafts between _Quercus marylandica_ and _Q. velutina_ had been noted at the Central States Forest Experiment Station (1958). The more common intraspecific and self grafts had not been reported in postoak or blackjack oak at the time the review was written. Functional interspecific grafts have rarely been reported.

One view on the cause of root grafting held that wind sway or other movement of the trees might wear away the bark of touching roots and allow contact of meristematic regions (Rigg and Harrar, 1931; Small, 1932; Cook and Welch, 1957). LaRue (1934) took the position that this abrasion was unnecessary, particularly since Millner (1932) had shown that *Hedera helix* stems could graft with no abrasion. LaRue held that the soil is so resistant to the diameter growth of the roots that as the roots grow in contact with each other, they are subjected to tremendous fusion pressures. This seems to be the more common view today. A bark pocket, within the developing graft, is often left at the contact point showing that the bark does not have to be worn away (Newins, 1916; Saunier and Wagle, 1965). Graham and Bormann (1966) suspected that the abrasion might do more to disrupt the delicate, forming, vascular unions than to aid in their formation. Yli-vakkuri (1953) found that the union occurs, not at the contact point but from callus ridges that form next to the point. Bormann (1966) showed the roots responded to pressure by forming a "doughnut" shaped ring of new tissue around the pressure point.

Beddie (1941) classified the forms of grafts, but the system worked out by Graham (1959) seems to be more complete:

> 1) 'Intersections', wherein the grafted roots cross at angles approaching the perpendicular. Such grafts may occur between roots of approximately the same size, or between roots of quite different sizes. If of two sizes, the smaller root may be tangential to the larger, or it may pierce it diametrically. 2) 'Longitudinal grafts' result when roots lying parallel and contiguous to one another become fused. The actual grafted region in longitudinal grafts may vary from a point contact to a meter or more in extent. The roots involved may be oriented in the same direction or in opposite directions. 3) 'Web-grafts', duck-foot-like anastomoses of roots, result from their confinement by such edaphic factors as stony soil, shallow soil overlying bedrock, hardpan or heavy clay, or a high water table. 4) The 'bridge-root' typically connects two roots but extends beyond neither. The two roots thus connected by the bridge may arise from the same tree, or from different trees.

Graham suggested that the "bridge-root" graft resulted from polarity changes which caused the extremities of the bridge root to be subject to decay and subsequent disappearance.

Other types of underground tree connections may be due to the various methods of natural vegetative reproduction. These methods are reviewed by Smith (1962) in a work on the practice of coppicing. He distinguishes among stump sprouts, root sprouts, and layering. Stump sprouts are the most common and arise from dormant buds that usually lie in the root collars (Busgen and Munch, 1929; Woods and Cassady, 1961). These dormant buds may be at higher levels and, when activated, result in epicormic branches that do not have a high survival record. In their usual form, stump sprouts would not give rise to connected trees that would appear as isolated "individuals". Nevertheless, the possibility for underground connection exists. A kind of "layering" by low coppice shoots, rooting under the leaf litter, was noted in the hornbeam (Busgen and Munch, 1929).

Root suckers are sprouts that arise on the surface or in the outer layers of roots. These suckers usually arise from adventitious buds (Busgen and Munch, 1929), although Brown and Kormonic (1967) have reported finding suppressed buds in the periderm of the lateral roots of _Liquidambar_ _styraciflua_. When released, these buds develop into shoots. Brown and Kormonic hypothesize their presence in other woody, root sprouting species. Root suckers have a high survival rate due to the lack of butt rot and the fact that they are more evenly spaced than stump sprouts (Smith, 1962).

The clone in plant life is discussed by Stout (1929). He introduced the terms, ortet, for the original seedling and ramet, for the members of the clone. He concluded that the botanical status of the entire group of plants in a clone is that of the individual plant from which the clone was derived. He was speaking of the taxonomic status of the clone but Debyle (1964) expands this idea to the physiology and ecology, if the underground connection remains functional. He believes that clones would be functioning as single tree units, and the individual stems would be analogous to branches.

Much of the research on sprouting has been related to the forester's use of the process in coppicing timber species. Many factors are involved in sprouting. It can be the result of sudden death of the tree by fire or cutting or may result from injury or physiological disorder (Smith, 1962). The age of the tissue (Neinstaedt et al., 1958) and time of year (Stoeckler and Macon, 1956) are important as are the hormonal relations in apical dominance (Farmer, 1962). Woods and Cassidy (1961) have shown that even sudden light changes or increased bark temperatures may interrupt the downward movement of auxins sufficiently to stimulate the growth of dormant buds.

Many, if not most, species of trees are capable of sprouting in some manner but Busgen and Munch (1929) believe that the tendency is less in conifers than in broad-leaved trees.

There is an extensive literature concerning the aspens, in which root sprouting is the main mode of regeneration. Many workers (Brown, 1935; Buell and Buell, 1959; Farmer, 1962; Zahner and Crawford, 1963; Debyle, 1964; Barnes, 1966) have studied their biology and some have noted that the connecting roots might remain functional.

Two sources of much information about the shrubbier organisms that are found in the Oklahoma Cross Timbers are those of Weaver (1919) and Duncan (1935). Weaver writes of the role of "rhizomes" in the spread of

Symphoricarpos and *Rhus* into the prairies. Duncan notes the great lateral spread of the root systems of *Rhus copallina* L., *Symphoricarpus orbiculatis* Moench, and *Smilax rotundifolia* L. He also discussed how their efficient, vegetative reproduction aids in their establishment of an intermediate position in the slow change from prairie to deciduous forest. He refers to all of the shrubs as "rhizomatous" species. Gilbert (1966) also refers to the horizontal, reproductive roots of *Rhus* as rhizomes but presents no anatomical or morphological evidence for this choice of terms.

Sprouting in the oaks has been extensively studied but there seems to be confusion as to whether they will sprout in some manner that will leave underground connection. Several sources note the prevalence of conventional, collar sprouts in the oaks (McIntyre, 1936; Roth and Hepting, 1943; Liming and Johnston, 1944). Woods and Cassidy (1961) have shown how effectively unwanted oaks can sprout and reclaim an area after bulldozing or other clearing treatment.

Oak root sprouting that might leave functional connection is probably rare. Busgen and Munch (1929), Baker (1934), and Cheyney (1942) all report little oak reproduction from root sprouts. On the other hand, Dwyer and Santelmann (1964), working with postoak and blackjack oak in Payne County, reported little or no reproduction from acorns but noted that the many young oaks present were the sprouts from the roots of older trees. Mignery (1965) hints at some type of horizontal sprouting by reporting that the postoak spreads rapidly into grasslands after fires are controlled. He believed that much of the spread was of sprout origin.

Ecological and silvicultural consequences of underground connection have been proposed. Rigg and Harrar (1931) and Pryor (1937) believed that self grafting would give resistance to windthrow. There seems to be no reason to believe that intraspecific grafts would not also aid in this resistance. Wendelken (1955) proposed the encouragement of intraspecific grafting as offering promise for preventing windthrow in the shallow, gravel plains of New Zealand.

Non-competitive relationships were proposed because various materials had been shown to be passed through intraspecific grafts (Bormann, 1962). In riparian situations, trees in moister sites might be able to transfer water to their graft-partners in dryer soils. Kuntz and Riker (1956) observed that the predominant movement of their tracer was from dominant oaks to smaller oaks perhaps aiding in their survival. Bormann (1966) completed an extensive investigation in white pine and concluded that water and minerals moved across the grafts only with great difficulty due to the necessary cross grain movement in the xylem. Phloem transport of organic substances was found to occur readily; therefore, food and growth regulators could move to influence grafted trees. Rahteenko (1958) found transference of mineral nutrients in _Quercus_, _Acer_, _Tilia_, _Fraxinus_, and other genera. Perhaps the graft, wood anatomy differs enough among the various tree types for both of these observations to be accurate. Bormann (1966) used his extensive data plus that of others in summarizing the noncompetitive relationships in white pine as follows:

> a) both trees dominant: a relationship with balanced exchange of food between trees; b) one tree dominant, the other suppressed: in the late stages, this relationship is analogous to hemiparasitism between species. Food moves from the dominant tree to the smaller tree, but the dominant tree is not compensated for its investment of energy; c) one tree dominant, the other a living stump: a type of neutralistic relationship with the dominant investing minor amounts

of food in the stump and getting minor amounts of water and minerals in return.

Page (1927) reasoned that intraspecific grafting could greatly increase the growth of surviving trees after thinning by suddenly increasing their absorbing area and supply of stored food. Beskaravainyi (1956a and 1956b) seems to have data to support this idea. Bormann (1966), however, found no significant difference between the growth of grafted and non-grafted trees.

Some of the literature concerning the spread of infection through root connections is reviewed by Graham and Bormann (1966). Many forest pathogens are believed to be transferred in this manner. Of particular interest in the Cross Timbers is the pathogen, Ceratocystis fagacearum (Bretz) Hunt which causes oak wilt. Root grafts were first suggested to be involved in the passage of this disease by Henry et al. (1944). Many workers have data that lends credence to this view (Kuntz and Riker, 1950 and 1956; Boyce, 1957 and 1960). Other researchers feel that the incidence of oak root-grafting is too low to account for much disease spread (Jones and Partridge, 1961) or that the fungus might not move through the grafts into healthy trees (U.S.F.S. Southeastern Forest Experiment Station, 1958).

"Backflash" of silvicides was first named by Cook and Welch (1957) but referred to a phenomenon that had been previously observed. Poisonous substances were shown to pass through underground connections from treated trees to unsuspected recipients by Kuntz and Riker (1950) and Boyce (1957). "Backflash" has occurred in thinning or clearing operations and in chemically peeling the bark from standing trees. The first report of an organic herbicide "backflashing" was in the use of 2,4,5-T in sweetgum stands of New Jersey (Fenton, 1965).

Debyle (1964) postulated that clonal connections should have ecological implications that are similar to those reported for root grafts. He noted one major difference. A root-grafted stand moves toward a dependence on the connections whereas a clonal stand starts dependent on the connection and, as the suckers develop their own root systems, becomes less dependent. If the underground connections remain functional, a mature clonal stand should be analogous to the heavily grafted forests that have been reported.

CHAPTER III

DESCRIPTION OF THE STUDY AREA

The historical concept and naming of the Cross Timbers is discussed by Dyksterhuis (1948). Foreman (1947) has also collected data about the area from the early accounts of army officers and other explorers. Braun (1950) describes the region as an oak-hickory savannah stretching through Oklahoma from the Red River into southern Kansas and coinciding with the "Sandstone Hills" and "Chautaqua Hills" where the underlying rock is sandstone. She states that, in the south, the savannah is continuous with the Ouachita oak-hickory forest but is separated from the Ozark flora in the north by a broad *Andropogon* prairie. Weaver and Clements (1938) portray the region as part of the deciduous forest formation being, "Two large bodies of xeric species of oak occurring in Texas and Oklahoma, where they are known as Cross-Timbers and constitute relicts of a former much wider extension of this formation."

Ecologists have differed in their interpretation of the nature of the climax in the Cross Timbers. Bruner (1931) interpreted the area as postclimax and wrote, "it is essentially a transition community between forest and prairie but its' extent and character are controlled by the sandy texture of the soil." Weaver and Clements (1938) also described the area as a postclimax in a prairie climate. Dyksterhuis (1948) agreed with Weaver and Clements that the Cross Timbers should be regarded as oak savannah with the grasses as the climax dominants. He noted, however, that the present day vegetation is more oak woodland than savannah and interpreted the current Cross Timbers as a disclimax due to grazing and fire. Rice and Penfound (1959) found that the upland forests of Oklahoma form a vegetational continuum from the xeric west to the more mesic east. They, nevertheless, found it desirable to divide the oak-hickory forest association into five faciations. The Cross Timbers is included in the more xeric groups: oak-hickory savannah and oak savannah. Since the stands they measured were reproducing satisfactorily, they suggested that the two savannahs be designated as climax communities.

Parts of the Cross Timbers in Payne, Noble, Lincoln, Pottawatomie, Pawnee, and Creek counties were visited in the pilot project, but most of the present study was made in the Lake Carl Blackwell land use area owned by Oklahoma State University. The primary site lies in the S.E. ¼ of Section 16 - T.19N - R1E of Payne County. This typical Cross Timber stand was readily accessible and University officials granted permission to cut trees and excavate.

The forest stand chosen was located and mapped from a large scale aerial photograph. It is about 9 ha in area and is a typical "finger-like" projection of the Cross Timbers so often seen in the region. It slopes slightly to the east. It is joined on the west by prairie and on the east by a ravine vegetated by more mesic species (*Ulmus* spp. and *Celtis* spp.) than the postoak blackjack oak forest.

Dwyer and Santelman (1964) reported that the area had never been cleared but that some trees were cut and used by homesteaders. Moderate winter grazing has been practiced since 1936.

Three workers had measured the upland forests in Payne County and all showed the dominance of postoak and blackjack oak. Rice and Penfound (1959) reported the Central Oklahoma upland forests to average 181 trees and 207 saplings per acre and to have a total basal area of 48.6 ft^2 per acre. Basal areas in their stands were typically between 30 and 60 ft^2 per acre. Payne County was among those with the higher readings with a basal area of 56.4 ft^2 per acre. Dwyer and Santelman (1964), comparing two soil types in Payne County, found a total basal area of 73.2 ft^2 per acre on the Stephenville type and 53.3 ft^2 per acre on the Darnell soil. Parker (1967), sampling the two soils together, found a total basal area of 59.6 ft^2 per acre and a total density of 314.2 trees per acre on his more level stands. The stand chosen for the present study was measured using the method of Rice and Penfound (1955) and showed a basal area of 2.43 m^2 per ha (62.5 ft^2 per acre) and a density of 118.7 trees per ha (293 per acre). The stand was judged to be fairly typical of the richer Cross Timber vegetation.

An overlay and soil description was obtained (Soil Conservation Service, U. S. Department of Agriculture) and three soil series were found to underlie the stand. In most of the area two of these soils are complexed and are usually considered together.[1] These are the Stephenville and Darnell fine sandy loams. They are described as occurring on 1-8% slopes and are shallow to deep sloping soils that develop under a cover of oak forest. Sandstone outcrops are common in the more sloping areas. Drainage is moderate to rapid from the surface and internally. This complex is highly susceptible to erosion when cleared. The other soil, under only two small parts of the stand, is the Vernon clay loam.

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[1] Personal communication, Beryl G. Baggett; U.S.D.A. Soil Conservation Service; Stillwater, Oklahoma.

Slopes are 5-12% and it is a shallow to very shallow, steep, clayey soil that is highly susceptible to water erosion.

The closest complete climatological data for the stand is that of the Stillwater station which is about seven miles east (Climatological Summary - U. S. Department of Commerce, 1968). The summary and monthly records show a temperate, continental climate with pronounced seasonal variations in temperature and precipitation. The mean yearly temperature is 60.6 F with January the lowest month at 37.2 F and July the highest at 81.8 F. Extreme temperatures from -15 F to 113 F have been recorded. Annual precipitation has ranged from 16.68 inches to 61.87 inches with a mean of 32.17 inches. Eleven per cent of the annual precipitation falls in winter, 29% in spring, 35% in summer, and 25% in fall. The usual frost free season in the county is from 205 to 211 days.

CHAPTER IV

METHODS

Exploration

During the summer and fall of 1966 a series of explorations were conducted to determine the types of underground connections that might exist in the Cross Timber species. County section line road cuts, in many cases, have not been stabilized and are subject to erosion. Approximately 130 miles of these roads were examined in western Payne County, grafts noted, and photographed. Many of these grafts were collected and dissected to determine if they were functional. "Functional" specified those situations when vascular continuity could be shown by dissection or when tracer movement occurred from stem to stem. Nonfunctional root unions are referred to as "apparent" grafts.

Several small gullied areas in Payne and Noble Counties and an extensive area in Lincoln County were walked out and connections were noted and collected. Lake, pond, and road construction also offered an opportunity to observe underground tree parts. Two pond construction sites in the Oklahoma State University land use area were visited during the clearing and land moving operations. Access road construction in the Keystone Lake area of Creek and Pawnee Counties was also visited. The basin of the Broken Bow reservoir was being cleared in the late summer and fall of 1966, and in a large area, trees were completely bulldozed out and removed. Permission was obtained from the Tulsa

District, U. S. Army Engineers to enter and observe the operation. This area is not in the Cross Timbers but the oak-pine formation of the area shares many species with the more xeric Oklahoma forests.

Reproduction

It is possible that underground, clonal connections exist in addition to intraspecific root grafts. Oak reproduction was analyzed during May, 1967 to determine the existence and extent of underground vegetative reproduction. The arms-length rectangle of Rice and Penfound (1955) was used to provide rectangular quadrats. Randomization was carried out by drawing from a table of random numbers (Steele and Torrie, 1960) and locating the 40 random points on a numbered grid over the map. Sampling was without replacement. Rectangles from these points were oriented east and west to cross the gradient from prairie to mesic ravine as recommended by Bormann (1955).

In order to improve the precision of the arms-length rectangle in sampling small reproduction (less than 2.5 cm d.b.h.), a modification was developed (Figure 1). A light, folding, wood sweep was constructed. A 1.8 m horizontal bar was found to be practical in moving through the, sometimes, dense reproducing vegetation. This sweep was moved down a distance of 22.1 m along a pinned steel tape; thus covering 0.004 ha (0.01 acre). Each postoak or blackjack "seedling" was recorded and a small pick was used to remove enough soil to reveal if the unit was, in fact, a seedling or was of sprout origin.

Figure 1. Measuring the Reproduction

Detection of Underground Connections With Tracers

The inherent limitation of observation in excavations and eroded areas has led workers to develop a variety of tracer techniques to discover underground tree connections. Graham (1959) developed a stump collar technique that eliminated transpirational pull into the donor tree and exposed all of the vascular tissue to the tracer solution. True et al., working with oaks in West Virginia, had previously developed and used an almost identical method. The concept devised by these two researchers was used in the present study. The writer was usually working alone and many trial and error efforts were made before successful modifications could be worked out that would allow one person to complete the process quickly. Most of the changes were in materials used but one procedure had to be added. Heart rot was frequently encountered in the blackjack oak stumps and a sealing process was developed. Figures 2 through 7 show the main steps in the construction of the stump reservoirs.

The donor tree was felled with a chain saw. The resulting stump top was then leveled by checking it with a hand level and resawing (Figure 2).

Figure 2. Leveling the Donor Stump

The bark was smoothed near the top of the stump for about 10 to 15 cm below the stump surface. A sharp drawknife was found to be best for this task. Small imperfections were quickly removed with a wood rasp.

The smoothed bark surface was coated with a waterproof, adhesive substance. Asphalt roofing cement, rope and canned caulking compounds, and below-grade linoleum cement were tried as adhesives. Butyl-rubber roof mastic was found to be superior, primarily because it would adhere to the moist surfaces of the freshly cut oak stumps.

Figure 3. Smoothing the Bark

Figure 4. Applying the Adhesive

The collar was made of a strong, waterproof, sisal reinforced paper. The type used in the present study is sold under the name "Sisalcraft". A roll of this material was pre-measured and cut so as to extend about 20 to 30 cm above the stump surface and about 10 cm below that surface. The length of the paper was the circumference of the stump plus a 10 cm overlap. The paper was stapled onto the mastic bed and pulled tight around the stump to form a cylinder. A vertical strip of mastic was applied between the overlap.

Figure 5. Attaching the Collar

All joints in the collar were oversealed with mastic and strips of paper. A 5 cm wide band of rubber was stapled at one end, stretched around the base, and fixed by stapling at the other end. The tension of the rubber effectively seated the collar into the cement bed and maintained this condition. A pre-measured cylinder of hardware cloth was fitted inside the paper collar to assure rigidity. A centimeter rule was attached to a nail driven into the stump surface. Tracer solution was added to a 10 cm level above the stump surface. A light, polyethylene film covering was used to prevent evaporation and entry of precipitation or other foreign materials.

Figure 6. Collar Sealed and Reinforced

The blackjack oak heart rot proved to be a difficult problem. Many solutions to the problem were investigated, even to plugging the rotted areas with a quick setting hydraulic concrete. A procedure was developed that stopped the leakage from the rotted stumps. The rotted region was tamped and chiseled down about 8 to 10 cm below the stump surface. Wood chips were hammered into the bottom of the depression to form a solid base for a plug of butyl-rubber cement. More wood chips were forced down on the plug to cause the cement to penetrate thoroughly. The hole was then filled with cement to make a level, sealed surface.

Figure 7. Completed Reservoir

The collar construction was tested and if all components were premeasured and cut, it was possible for one man to complete the procedure in less than 15 minutes. It is doubtful that the xylem water columns were interrupted that long. In many cases, an exudation occurred at the stump surface after cutting and continued for a short time. These collars were constructed between an hour before and an hour after dawn.

Tracer levels were maintained and recorded each hour during the first day and at longer intervals as tracer use declined. After the sixth day, the collar was removed and a 3 to 4 cm thick cross section of the stump surface was removed. Annual growth rings were counted and total surface area and sapwood transmitting area were determined for the donor stumps. This was accomplished by tracing the areas on a clear film and measuring these tracings with a compensating polar planimeter (Table IV, Appendix A). Total tracer volume used, and the volumed used per square centimeter of transmitting sapwood could then be computed.

The stump collar procedure was used to introduce tracer into post-oak, blackjack oak, and _Celtis_ spp. Smaller trees and shrubs could not be treated in this manner. A rubber collar and siphon arrangement was tried on topped _Prunus_ _angustifolia_ Marsh. The most successful tracer introduction method in _Rhus_ _copallina_ L., _R_. _glabra_ L. and _Symphoricarpus_ _orbiculatus_ Moench proved to be the immersion of the excavated, horizontal roots or rhizomes in a tracer solution.

Figure 8. Tracer Introduction in Sumac

Silvicides, radioisotopes, and dyes have been used as tracers by investigators. All seem to be effective in locating underground connections. Dyes were used in the present study because of their low cost, safety, and visual advantage. Eosin B, acid fuchsin and malachite green were tried during the pilot study. A 0.15% aqueous solution of acid fuchsin was found to perform satisfactorily. It moved quickly from donor to recipient and was visible and long lasting in the foliage and stained wood. No damage to the recipient was noted at the time of the staining or up to a year later. When diluted to 0.15%, the cost of the tracer solution was about 13 cents per liter. Measured containers of water and dry stain were dispersed throughout the study area. This assured a fresh dye supply, when needed, without carrying from donor to donor the large quantities found necessary to keep the reservoirs at the desired level.

Selection of the Experimental Plots

The dye tracer technique was used in a population defined as postoak and blackjack oak trees with at least one neighbor, of the same species, no less than 1 m and no more than 4 m distant. The 1 m distance ruled out companion collar sprouts and the 4 m limit, obviously, enhanced the likelihood of finding connections. A series of compass lines were walked through the stand and "groups" that met the criteria were tagged and numbered. These groups were sufficiently isolated from each other to rule out inter-group movement of tracer. Eighty-six such groups of trees were identified. Thirty of the groups were chosen, using a random number table (Steele and Torrie, 1960). Seventeen were predominantly postoak and 13 were blackjack oak.

Figure 9. Typical Postoak "Group"

A donor tree was chosen in each group. Usually this was a central tree but free fall of the tree had to be considered. A circular area around this donor was considered to be the experimental plot. All of the neighboring trees in the plot were measured (d.b.h., distance from donor, azimuth) and the data recorded (Table III, Appendix A). The plots were photographed and mapped with each possible recipient labeled alphabetically starting with zero degrees azimuth. Each postoak unit was denoted as Qst 1 to Qst 19 and each blackjack oak as Qma 1 to Qma 17. The reason for the number discrepancy is that some of the groups had been dyed in 1966, prior to the random drawing. Two of the postoak groups and four blackjack groups did not appear in the drawing.

Identification of Recipients and Excavating

After applying the tracer, recipients were easily identified. The foliage was stained a definite red (Figure 10). Fraser (1958) had noticed that radioactive tracers accumulate around insect holes in the leaves of yellow birch. Graham (1959) found concentrations of dye in the veins, tips of marginal serrations, and surrounding necrotic tissue and insect injuries in aspen and white birch leaves. The writer found this same concentrating effect in both postoak and blackjack oak. The dye not only concentrated in these regions but moved to these regions first. Examination of the leaves with a hand lens could detect the dye some time before it was generally visible from a distance. Several of these early detected leaves were tagged and timed for later distance measurement to get velocity data for dye movement through underground connections.

Figure 10. Dyed Leaves of a Recipient

After the tracer application had been completed, the excavation phase was started. The first operation was to dig out around the base of each recipient to locate the functioning root or underground stem. A hatchet or knife cut flap easily identified these heavily stained structures. The major excavations were then carried out by following the recipient structures back to the donor.

Hydraulic excavation methods could not be used in the present study because of the large quantities of water required and the necessary 20% grade (Stout, 1956). Miller and Woods (1965) and Weir (1966) developed a compressed air soil removal technique. This process and supplementary hand digging was used for the major excavations.

An 85 p.s.i. Chicago Pneumatic compressor was used as an air source. One hundred feet of three-fourths inch pressure hose was attached to either of two types of tools. A straight tool was made from a five foot length of pipe fitted with a regulating valve. The end of the pipe was flattened and ground to produce a sharp, chisel-like edge. This tool was used for the basic "digging". The curved tool was used to blow the loosened soil up and out of the excavations.

After the excavations were completed, the connections were labeled, measured, mapped, and photographed. Some of the structures were removed for further study.

Figure 11. Air Compressor and Tools

CHAPTER V

FINDINGS AND DISCUSSION

Exploration of Eroded Areas and Excavations

Excavation project exploration produced little data. Modern earth moving machinery operates at high speeds and exposed root systems are soon distorted and confused. Many self-grafts were seen but there existed few cases in which one could verify that suspected intraspecific grafts were not also self-grafts. These visits were discontinued because of danger and the lack of opportunity for cautious observation.

Exploring eroded areas proved to offer a better opportunity to observe underground plant parts. Self-grafts were commonly observed with far fewer sightings of intraspecific grafts. Perhaps root systems that are highly anastomosed give enough protection to the soil to partially prevent erosion.

Exploration was judged to be useful in a qualitative sense. One could determine if members of a certain species form grafts or clonal connections and material could be collected for morphological and anatomical study. It is difficult to visualize how the observations could be quantified in meaningful terms.

On the following pages are some of the photographs taken of observed underground connecting structures.

Figure 12. A Postoak System With Many Functional Self and Intraspecific Grafts (Three trees were involved in the network.)

Figure 13. A Postoak System in Which a 1.5 m Horizontal Root Functionally Grafted to the Tap Root of Another Postoak

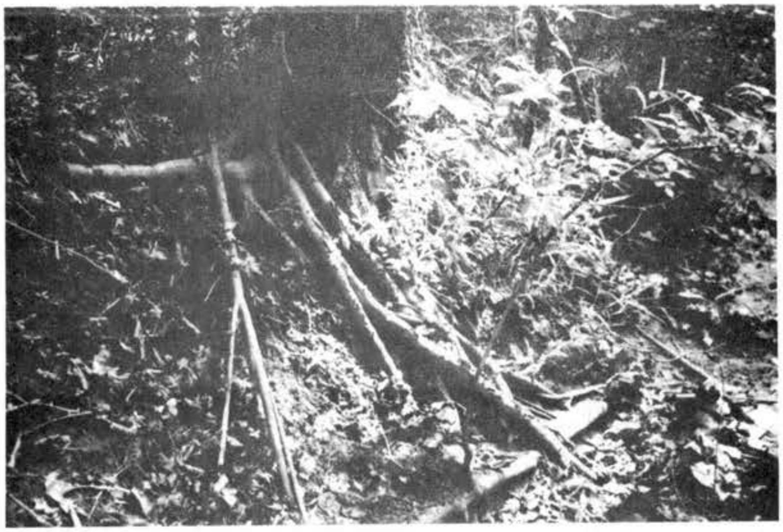

Figure 14. An Exposed Celtis spp. System That Appeared to Consist of One Large Stem With a Clonal Stem Arising From a Long Horizontal Root (A middle tree, that appeared to be of independent origin, is functionally grafted to the horizontal.)

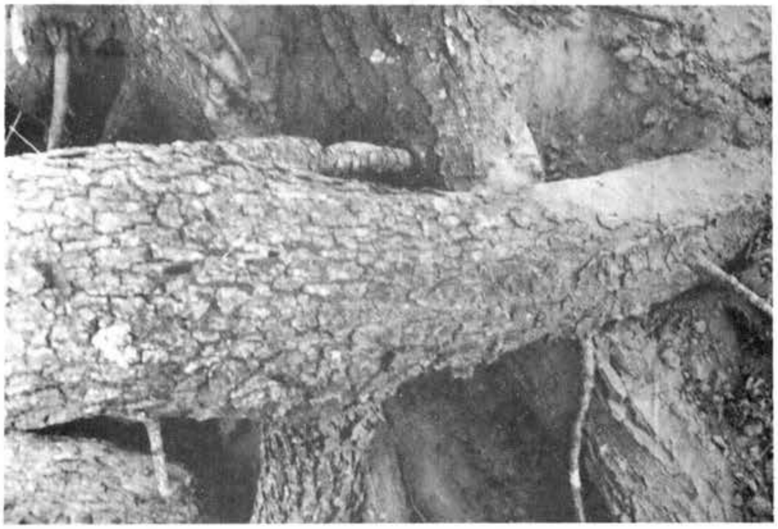

Figure 15. An Apparent Interspecific Graft Between Postoak and Blackjack Oak

As noted in the literature review, functional interspecific grafts have been reported by a few workers. In all phases of this work, only two cases of suspected interspecific grafting were seen. Both of these grafts were between postoak and blackjack oak trees and both were "apparent" only. Dissection showed them to be nonfunctional because degraded bark still separated their respective vascular tissues. Figure 15 shows the more unusual of the two. A small root of the postoak may be seen penetrating directly into the larger root of the blackjack oak. The penetration proved to be only about 3 cm and ended with the bark separation intact.

The following list summarizes the functional grafts seen during the exploration phase of this study: Postoak - self and intraspecific, blackjack oak - self and intraspecific, _Celtis_ spp. - self and intraspecific, _Ulmus_ _americana_ L. - self and intraspecific, _Carya_ _illinoensis_ (Wang.) K. Koch - self and intraspecific, _Juglans_ _nigra_ L. - self and intraspecific, _Quercus_ _Shumardii_ Buckl. - self only. No literature reference to intraspecific grafting in postoak and blackjack oak was found. No root graft reference was found for _Celtis_ spp., pecan, black walnut, or Shumard oak.

Analysis of Reproduction

Pilot observations of the oak reproduction were rather conflicting. Both of the dominant oaks formed typical, upright, stump or collar sprouts but in the postoak much of the reproduction was from a horizontal, underground structure. This gave rise to a pattern of vegetative reproduction that resembled root suckering. In the absence of definite knowledge of the nature of this structure, it was decided to temporarily classify it as a "horizontal" sprout. The upright sprout was classed as a "collar" sprout and the third class was the seedling. Using the methods described in Chapter IV, the measurements and classifications were completed and the results are summarized in the following table.

TABLE I

REPRODUCTION IN THE PRIMARY STUDY STAND

Species	Seedlings No./ha	Collar Sprouts No./ha	Horizontal Sprouts No./ha	Per Cent Total Sprouts
Postoak	292	969	3044	93.2
Blackjack oak	267	2034	0	88.4

These data are comparable to those of Liming and Johnston (1944) for the Missouri Ozarks. They found 90.9% sprout reproduction in postoak and 88.7% in blackjack oak. Their average total reproduction was 1765 per acre (4361 per ha) for postoak and 1761 per acre (4351 per ha) for blackjack oak compared to 4305 per ha and 2301 per ha, respectively, in the present study. The Missouri stands were much more diverse than the Cross Timbers with hickories, white oak, black oak, and shortleaf pine in addition to the postoak-blackjack oak dominants. Arend and Julander (1948) found average reproduction in postoak-blackjack oak stands in the Arkansas Ozarks to be 3000 trees per acre (7413 per ha).

They give no data on the relative numbers of seedlings and sprouts but they state the following:

> The reason for the prevailing dominance of these species on such sites where the tops of the young trees are repeatedly killed by fire is the prolific sprouting ability of black-jack and post oak in comparison to the other forest species.

McIntyre (1936) showed that 75% of the oak forests of Pennsylvania had originated from sprout groups.

In the summer of 1968, the stand was revisited. No quantitative study was done at that time but far more seedlings were observed than in the previous year. If this is a valid observation, perhaps it can be explained by climatic differences, insect infestations or a cyclic seed production phenomenon.

Whether the "horizontal" postoak sprouts were stems or roots proved to be difficult to determine. Underground stems become more rootlike in their secondary growth. Esau (1965) stated, "Roots and stems can be made to produce tissues resembling those of the opposite organ by reversing their environmental conditions."

Figure 16 shows one of these sprouts after a few years of secondary growth. The sprouts originate at the collar as do the upright sprouts but these then grow horizontally just under the soil surface for a distance and then surface as an aboveground, leafy stem. The longest sprout of this type that was located measured about 2.5 m in length. More commonly, they were from 1 to 1.5 m long. This is a sufficient distance from the parent stem for the reproduction to appear as separate seedlings or root sprouts.

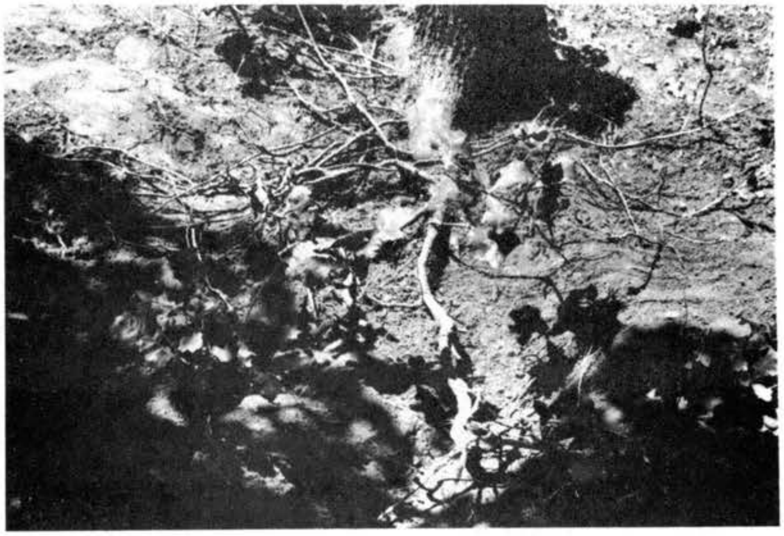

Figure 16. An Excavated, "Horizontal" Postoak Sprout

The Southern Forest Experiment Station staff found no references to the horizontal sprouting habit of postoak.[1] Personal communications with Arnold L. Mignery[2] and Dr. Paul T. Koshi[3], both of whom had worked with postoak, also failed to reveal any information on this subject. Dr. Koshi did suggest that the morphological features alone should be sufficient to determine the nature of the structures.

When horizontal sprouts were found with their growing tips still in the primary growth state, it became clear that they were stems. Figure 17 shows one of these young sprouts. Scale leaves and, thus, nodes and

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[1] Personal communication. R. L. Scheer, Assistant Director, U.S.D.A. Southern Forest Experiment Station, New Orleans, Louisiana. 1968.

[2] Personal communication. Arnold L. Mignery, Project Leader, U.S.D.A. Southern Forest Experiment Station, New Orleans, Louisiana. 1968.

[3] Personal communication. Paul T. Koshi, Research Soil Scientist, U.S.D.A. Agricultural Research Service, Big Spring Field Station, Big Spring, Texas. 1968.

internodes can be seen in the youngest portions of the sprouts that are still penetrating just beneath the soil surface. Sectioning of the sprouts reveals pith. None of these features should be found on or in the roots of a "higher" plant (Esau, 1965).

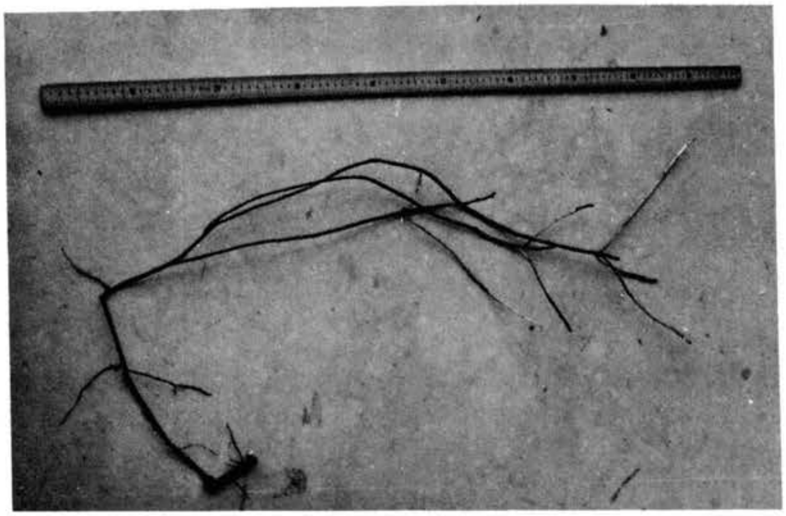

Figure 17. A Young, Excavated Postoak "Horizontal" Sprout

These horizontal sprouts are, apparently, rhizomes or are structures left as a result of a process similar to the low layering described by Busgen and Munch (1929) as occurring in the hornbeam. After the stem moves above ground, the underground portion forms roots of its' own but retains a functional connection with the parent stem. It has often been observed that sprouts act like rejuvenated tissue and root much better than other parts of the mature tree (Neinstaedt et al., 1958).

Root suckers are less likely to develop butt rot than stump sprouts and are not confined to the stump vicinity but may be spaced more evenly around the parent tree (Smith, 1962). This results in better spacing and better growth form. The postoak horizontal sprouts may give results that are similar to this phenomenon. This may be one of the reasons that the postoaks are usually more evenly spaced and have better form than the blackjack oaks which were not found to have the horizontal sprout habit.

Movement of Tracers

Several parameters were monitored during the dye intake phase of this study: The number of recipients in which dye appeared and the time elapsed before the first appearance in a recipient, hourly volume intakes during the first day, day-night intakes for five 24-hour periods. All times reported are adjusted to central standard time.

Graham (1960) found that the downward movement of dyes in white pine stumps was in the entire sapwood area with none moving in the heartwood. He reasoned that rates should be expressed as dye volume per square centimeter of sapwood per unit of time in order to make more comparable the data from stumps of different size. Upon sectioning donor stumps of postoak and blackjack oak, the same sapwood transfer was noted and Graham's reasoning was used in the present study.

Ten of the postoak donors proved to be strongly connected to other trees over 2.5 cm d.b.h. Three more of the postoaks were only connected to horizontal sprouts but the number of these sprouts, with their leafy, transpiring portions, were able to significantly affect the dye intake. These three donors were classified as weakly connected. Four of the postoaks did not show any tracer transfer to a neighbor and were considered, by the criteria of this study, to be completely isolated. The 10 strongly connected units were involved with 27 recipient trees. In one case, Qst 2, six recipients were united with a single donor but more commonly from one to four recipients were involved (Table II). The distances from donor to recipient ranged from 1 m to 3.9 m with a mean distance of 1.76 m.

Only three of the 13 blackjack oaks tested were found to be connected. In their case, each donor was connected to a single recipient. The distances ranged from 1.02 m to 4.32 m with a mean distance of 2.14 m.

Graham (1960) and others have observed that one could introduce tracers into a tree, record the recipients, then introduce the tracers into one of the recipients and find new trees involved in the connected system. This was attempted in the pilot project for the present study. One postoak donor was found connected to two recipients. When one of the recipients was used as a donor, two additional trees were involved. No attempt was made to continue this progression operation but one can hypothesize large numbers of trees being included in a united system. The complications introduced by this situation make probability statements more difficult to make. If, however, one merely subjects the donor to a connect-nonconnect decision, binomial procedures can furnish a statement about the probability of a donor being connected to a recipient (Goldstein, 1964). In the case of the postoaks, the probability of connection and its' 95% confidence interval was 0.59 ± 0.23. The probability and confidence interval for blackjack oak was 0.23 ± 0.21. In considering these statements, one should remember the bias introduced by the 1 to 4 m nearest neighbor criterion for each donor.

Other workers have attempted to measure the amount of root-grafting that occurs in the oaks. A U. S. Forest Service note (S.E.F.E.S., 1957) from Tennessee and North Carolina reports that about 15% of the red and white oaks were grafted. Boyce (1957), working in the Appalachians, also reported the grafting incidence to be about 15%. Jones and Partridge (1961) found 16% of the black oaks and 20% of the white oaks to be grafted in Missouri. They concluded that for the oak forests, as a whole, about 17% of the trees are root-grafted. Forty per cent of the oaks tested in the present study were found to be connected to other trees by functional sprout or graft unions. The most obvious explanations for this high per cent of connection are the near neighbor requirement in choosing the donor trees and the presence of the postoak horizontal sprout. A less obvious explanation is that the horizontal sprout habit found in the postoaks might leave groups of trees that can graft with less tissue incompatibility. It is probable that large groups of trees exist with identical genotypes.

The first day hourly dye intake readings were made because of the necessity to refill the reservoirs periodically in order to maintain a fairly uniform hydrostatic pressure on the stump surface. Another reason was to check the hypothesis that these readings might reflect the transpirational status of any recipient. Any stomatal changes in a recipient should cause tension changes in the vessel water columns and should be reflected in increased or decreased dye intake. Graham (1960) showed that temperature and humidity affected the intake readings.

Figures 18 and 19 (data in Table V, Appendix B) show the hourly fluctuations in dye intake during the first day. The strong and weakly

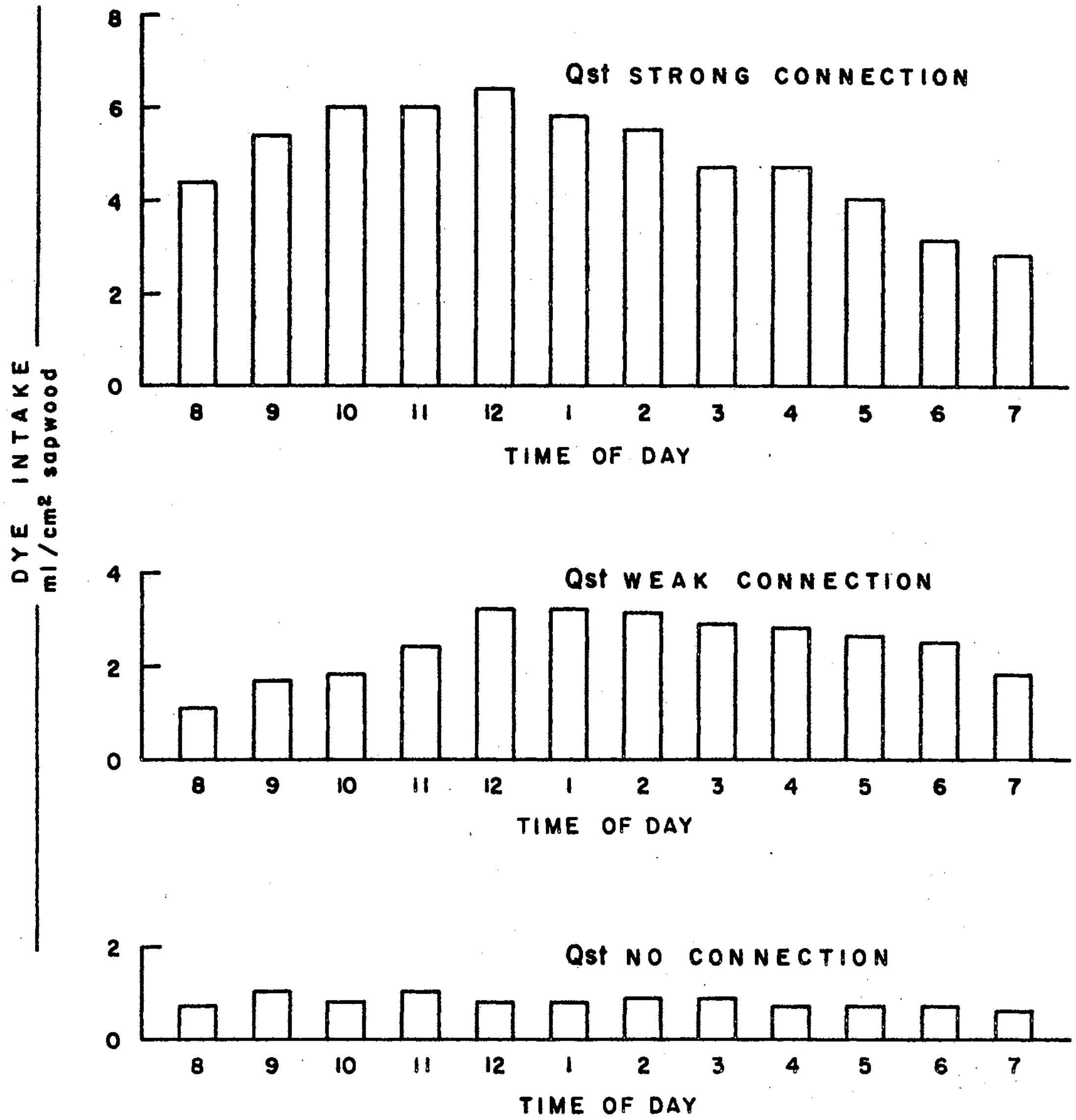

Figure 18. Average First Day, Hourly, Dye Intake Rates in Postoak

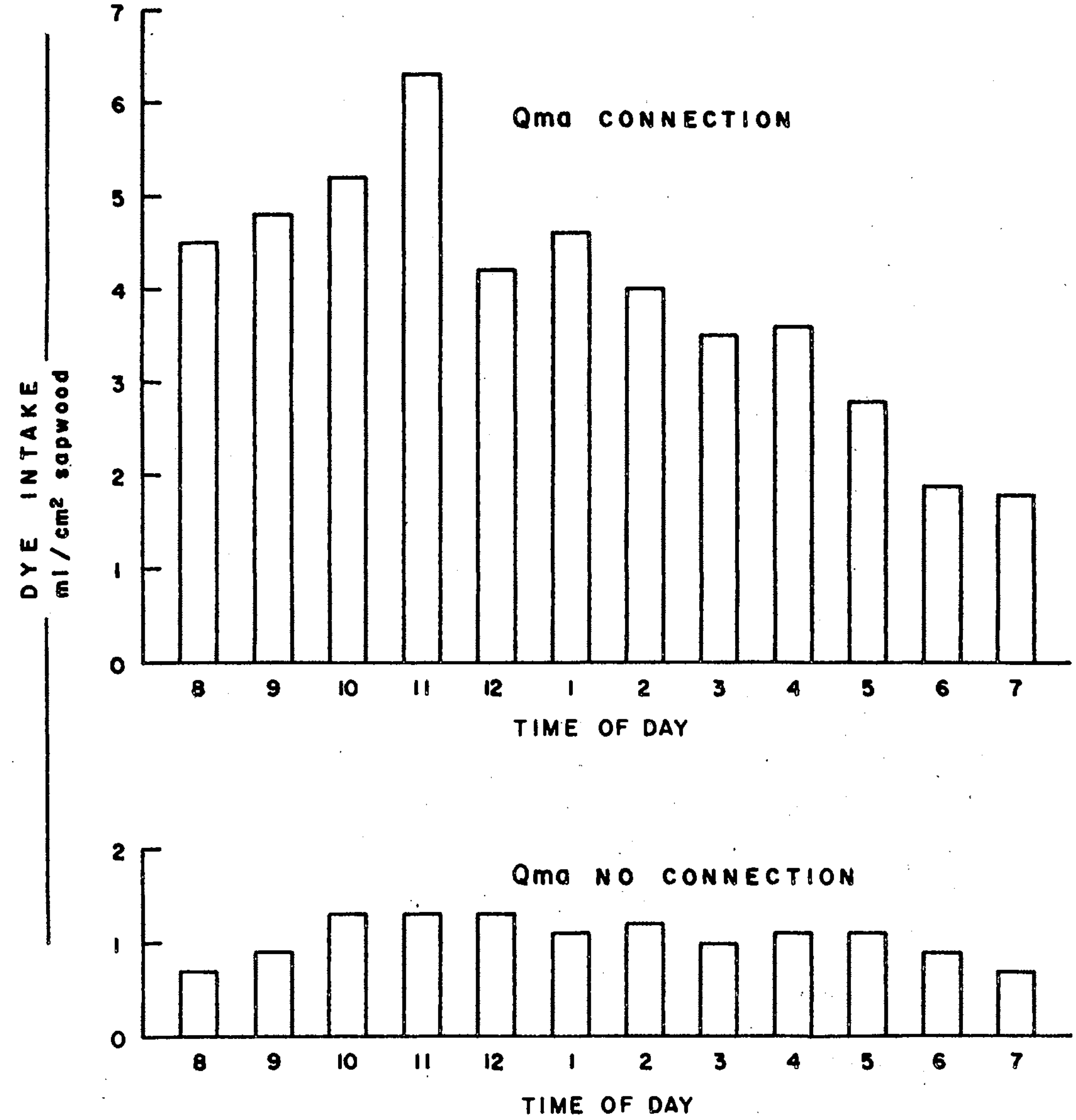

Figure 19. Average First Day, Hourly, Dye Intake Rates in Blackjack Oak

connected postoaks and the connected blackjack oaks show a definite increase until midday and a decline thereafter. The non-connected stumps absorbed the dye solution at a more steady rate and with a slight increase at midday.

During the pilot project, it was thought that midday stomate closure might be indirectly observed using this procedure. Midday closure seems to be a common phenomenon (Kozlowski, 1964). Temperature, carbon dioxide level, and temporary water stress are all suggested as interacting in the process. The water stress is important as shown by the fact that Kramer (1959) found the closure occurring earlier each day during drought periods. No evidence for the influence of midday closure is shown in the hourly readings of the present study. Blackjack oaks that were connected did show an 11:00 A.M. decline but recovered by noon. Most studies of the closure show the recovery to occur much later in the afternoon. Kramer's discovery might explain the negative results. The tracer technique used offers a maximum amount of water to the vessels and stomates. This may prevent any water stress in the tissues that would affect the recipients transpiration and, thus, prevent the typical midday closure.

In Graham's (1960) work, no statistically significant differences were shown between day and night intakes of 10 white pine stumps. Although seven of the stumps were root-grafted to 13 receptors, in seven of the 10 time periods recorded, the night intakes exceeded those for the days. Figures 20 and 21 (data in Table VII, Appendix B) show the day-night intake information gathered during the present study. The connected oaks, of both species, show much more pronounced day-night variations than did Graham's pine trees. There seems to be a rather

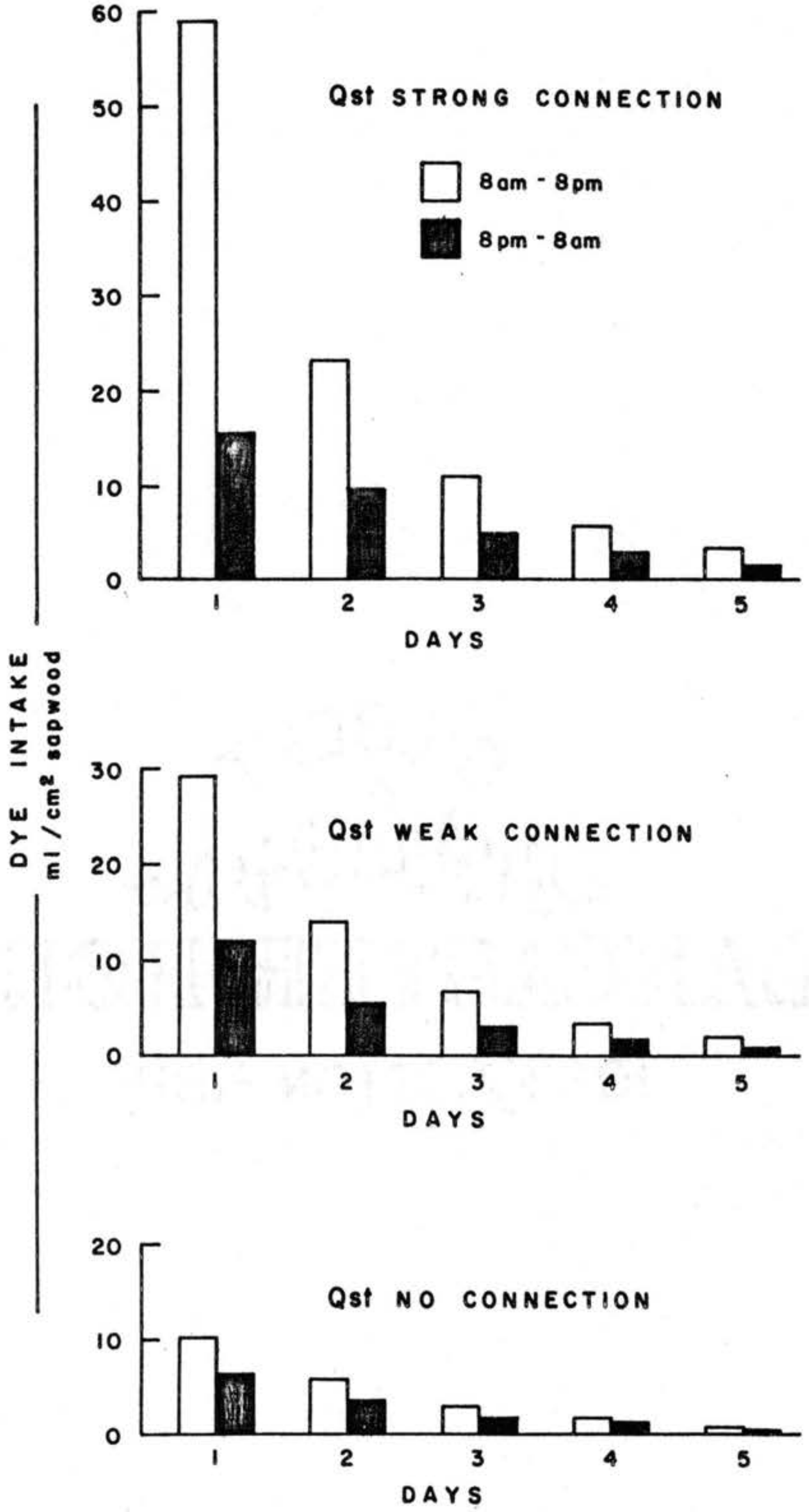

Figure 20. Average Day-Night Dye Intake Rates in Postoak

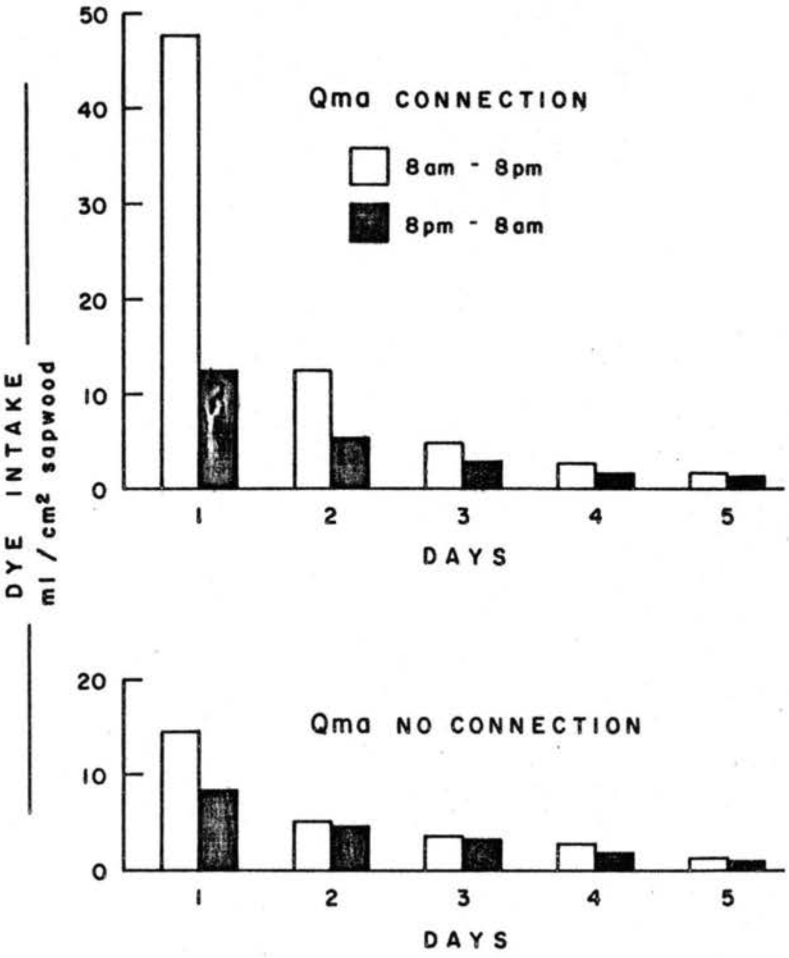

Figure 21. Average Day-Night Dye Intake Rates in Blackjack Oak

constant decline in dye intakes from day to day (Figures 22 and 23) and, thus, a decision was made to perform t tests on the total day means compared to the total night means rather than comparing each day and night mean. The day means for postoak strong and weak connected and blackjack oak connected were found to be statistically different from their corresponding night means at $P = 0.05$. The non-connected trees, both postoak and blackjack oak showed no statistically significant night-day differences at $P = 0.05$. Perhaps the lack of agreement with Graham's findings is due to tension differences in the non-porous pine xylem. This might cause a lag effect in the pines. It is well documented that sap velocity is much less in the conifers than in some hardwoods, particularly the ring-porous oaks (Kramer and Kozlowski, 1960).

Rumbold (1920) noticed the initial surge and subsequent slowing of materials being injected into chestnut trees. Fraser and Mawson (1953) found the same situation in their radioisotope introductions into yellow birch. True et al., (1955) working with oak trees and using essentially the same technique used in the present study stated: "The uptake of water by stump tops was greatest during the first 24 hours. After this time considerably less water was taken up." Figure 22 (data in Table IX, Appendix B) shows this decline in both postoak and blackjack oak whether the donor stump was connected to a recipient or not. This decline is logarithmic in nature for the first five days. In the pilot study, the intake was found to level off after five days and almost cease. Fraser and Mawson (1953) postulated that the reduction resulted from lowered tensions due to the solution intake. This would only explain a lessening of the amount taken in but not the almost complete cessation. An

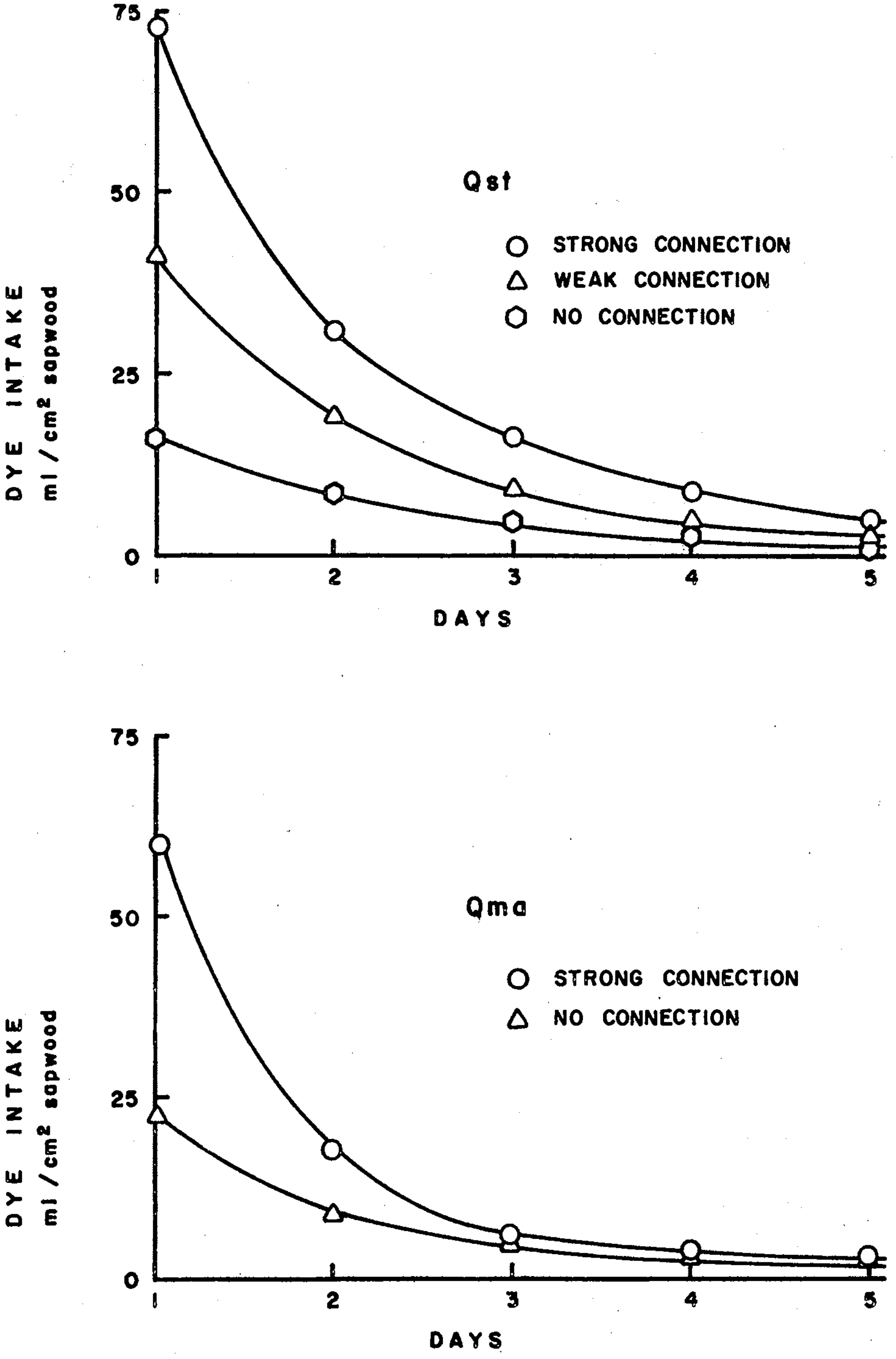

Figure 22. Average Twenty-four Hour Dye Intake Rates in Postoak and Blackjack Oak

explanation based on changes at the dye-stump interface is tempting but must be rejected because the phenomenon occurs even with plain water (True et al., 1955). The trauma of cutting could result in tylosing of the vessels but no evidence of this was gathered.

True et al. (1955) noticed the great increase in dye intake if companion sprouts or root-grafts were present. He hypothesized that prolongation of intake into a stump would be sufficient, in itself, to indicate underground connection to a transpiring recipient. In the present study, the differences in the quantities of tracer taken in by the connected and non-connected stumps was more impressive than the prolongation of intake. The 24-hour dye intake means of the two types of connected postoaks were tested against the same means of the isolated postoaks, using t tests. All of the daily means of the strongly connected and non-connected postoaks showed a statistically significant difference at $P = 0.01$. All weakly connected postoak means were different from the non-connected means only at $P = 0.1$. When connected and non-connected blackjack oaks were tested, the first two daily means were significantly different at $P = 0.001$. The other three daily means showed no statistically significant difference even at $P = 0.1$. One could conclude from these tests that large amounts of liquid taken in during the first two days would be indicative of functional connection to a transpiring recipient.

Since True et al. (1955) was working with oaks, it was felt that a comparison of the absolute amounts of tracer used (Table VIII, Appendix B) would be interesting. He found that an isolated 5.7 inch d.b.h. stump absorbed about two liters of azosulfamide dye in five days. The closest isolated tree to this size, in the prest study, was Qst 5. This tree was

16 cm (6.3 inches) d.b.h. and absorbed 3.9 liters in five days. True found one 6-inch stump with two recipients that absorbed 15 liters in five days. The closest comparisons the writer could make were Qst 12 which was 12 cm (4.7 inches) d.b.h. and had two recipients and Qst 15 at 18 cm (7.1 inches) d.b.h. and two recipients. Qst 12 absorbed 12 liters in five days while Qst 15 took in 24 liters during the same period. Comparisons are probably of little value until more of the interacting factors are taken into consideration such as, 1) stump sapwood area, 2) the number and size of transmitting structures, 3) the compatibility of the grafted tissues, 4) the area of the sapwood in which the dye is moving up the recipient, 5) the area of the transpiring leaves, and 6) climatic conditions during the intakes.

Tracer Velocity

The time necessary for the aqueous acid fuchsin to move from a donor through an underground connection and to be noticeable in a recipient was measured in seven of the postoaks. As explained in Chapter IV, the early evidence of dye reception was around injured areas and at the leaf margins. The dilute dye must have arrived at these points some time before it was noticeable with a hand lens; therefore, all computed velocities must be considered to be lower than the actual rate of sap flow.

The velocities computed ranged from 1.1 m/hr in Qst 2-A to 3.0 m/hr in Qst 7-E. The mean velocity and its 95% confidence interval was 2.7 m/hr ± 0.28 m/hr.

After excavating, it was found that six of the seven recipients were receiving dye through horizontal sprout connections while one had received dye through a root-graft. The graft connection was in Qst 4-A and the velocity, 2.3 m/hr, is within the 95% confidence interval.

Kramer and Kozlowski (1960) review some stem xylem water velocities and report rates from less than 0.5 m/hr in conifers to rates of 60 m/hr in some oaks. Kuntz and Riker (1955), using a radioisotope, found velocities of from 27.5 m/hr to 60 m/hr in _Quercus macrocarpa_. The great differences between the reported velocities in oak tree trunks and the velocities found in the present study might be due to differences in technique or might reflect the tortuous pathway the xylem stream has to follow through the donor's collar zone, into and through the underground connection and up through the recipient's collar to the trunk. Root velocity might be lower than stem velocity. Another factor, in the case of root grafts, might be Graham's (1960) postulation that somewhat incompatible tissues might affect translocation.

More work, using various detection techniques, needs to be done. The acid fuchsin tracer may be unsuitable for velocity determinations. Vite (1959) found that aqueous acid fuchsin moved in ponderosa pine at 0.35 m/hr while acid fuchsin plus alcohol moved almost twice as fast at 0.6 m/hr.

Dye Pattern in the Receptors

When the dye tracer moves into a receptor tree, the usual pattern is for only some of the limbs to be stained while others do not appear to change (Figure 10). During the pilot project, it was found that all recipient limbs that were going to be stained were colored during the first 24 hours. Tracer was applied up to 10 days with no new stained limbs being detected. This observation held up during the study proper although the tracers were only applied for five days. Miller and Woods (1965) found this uneven distribution persisted in loblolly pine for three weeks.

The observation that injected materials move upward in the trunks in narrow streaks (Kozlowski and Winget, 1963) may account for not all limbs being dyed. The dye entering from a single root or sprout is analogous to one of these injections in that it also moves up in a single band or streak (Figure 23). As would be expected in the ring porous oaks, the movement is only in the outer one or two annual growth rings. Limbs that have vascular connection with the streak receive the dye while others do not. The spiraling of the grain has been reported often (Kuntz and Riker, 1955; Kozlowski, 1961). Kozlowski and Winget (1963) reported the paths in northern pin oak, white oak, and bur oak to all be vertical or spiral, turning either to the left or right. Only four of the postoak recipients in the present study were sectioned or blazed but all spiraled upward to the right. This would help to explain the observation that limbs on different sides of the trees at higher levels were dyed.

The persistent lack of greater dye spread is probably related to a lack of lateral transport in the stem. Lateral transport systems must exist for the movement of sap around horizontal saw cuts to occur (Greenidge, 1955; Postlethwait, 1958). Whether or not these systems function under natural conditions is another problem. Biddulph (1959), Rinne and Langston (1960), and Caldwell (1961) have supported a direct, polar mineral pathway from roots to the foliage above. Baker and Milburn (1965) present evidence that the water tensions developed by foliar evaporation cause water movement to follow the path of least resistance. If these polar tensions are relaxed for any reason, lateral tensions can induce lateral movement of both solutes and solvent. Molotokov (1956) showed that tangential sap movement between wood cells also varied with the time of year and the sap condition. Apparently, little lateral movement would be expected unless lateral gradients were induced.

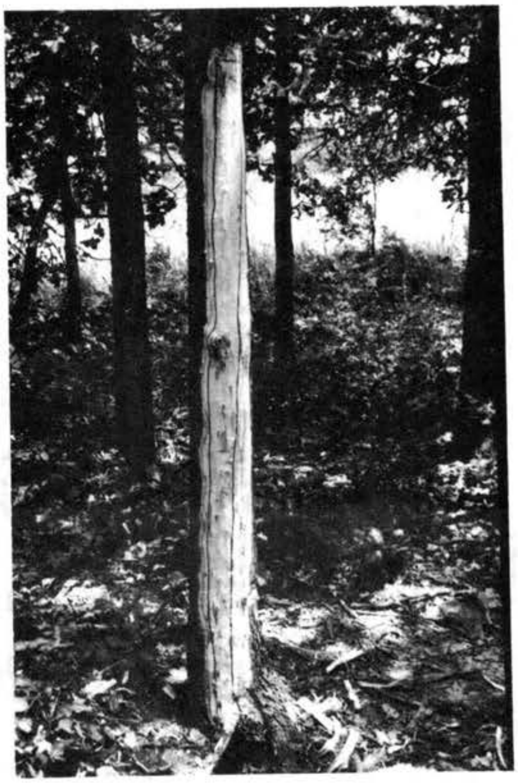

Figure 23. The Path of Dye Rise in a Postoak Recipient (The band is outlined with ink.)

Evaluation of the Air Excavation Technique

One of the objectives of this study was to evaluate the use of compressed air as an excavation tool. The air stream was most valuable for removing the leaf litter and the A horizon of the soil, but it was also capable of heavier digging and soil removal. In dry, sandy soil the air stream was sufficient to completely excavate the underground plant parts. Some of the soils encountered were clayey and the air had to be supplemented with hand digging. On these sites, the air was used to blow loosened soil from the excavation and to clean the exposed root or sprout systems. Isolated sandstones were frequently present and the air stream was useful to cut around and loosen the stones so that they could be removed.

Figure 24. The Air Excavation Tools in Use

Eighty-five pounds of air pressure was sufficient and under some conditions, better results were achieved by reducing this with the valve on the pipe tools. The high pressure stream did not damage the smaller rootlets.

Analysis of the Excavated Connections

As reported earlier, 10 postoak donor stumps were found to be transmitting dye tracer to recipients that were larger than "seedling" size and were referred to as those with strong connection. The three postoak stumps that were connected only to small, leafy sprouts were not further excavated. Three of the blackjack oak stumps showed recipient dye intake and required excavation. Table II shows the numbers and types of connections revealed by the soil removal.

The connections discovered are probably not the only unions existing between the trees. Graham (1960) and Miller and Woods (1965) encountered situations when their tracers did not move through existing grafts. One example of a non-transmitting connection was noted in the present study (in Qst 15). More probably existed but only areas around roots and stems that showed tracer tranfer were excavated.

Figure 25 shows a photograph and a semi-scale representation of plot Qst 12. Angles and distances are scaled but stump and root diameters are not. The photograph was taken facing the south while the drawing has north at the top of the page. Dyes moved from the donor, through a graft to B and then through a long, horizontal root, close under the donor to graft to another recipient some distance away.

TABLE II

UNDERGROUND CONNECTIONS REVEALED BY EXCAVATION

Plot No.	Connected Recipients	Type of Connection	Surface Distance to Donor in cm	Distance Dye Moved Collar to Collar in cm
Qst 2	A	S	100	113
	B	G	244	260
	D	G to Recip. E	165	31
	E	S to Recip. F	165	37
	F	S	122	110
	M	G	229	240
Qst 4	A	G	135	174
	D	G	191	384
	G	S	102	122
	H	S	185	223
Qst 6	A	S	157	188
	C	S	122	241
	D	S	152	213
	F	S	107	210
Qst 7	A	2G-in series	234	305
	D	NL*	175	?
	E	S	178	198
Qst 8	B	NL**	135	?
	D	NL	180	?
	E	NL	180	?
Qst 10	D	G	102	119
Qst 12	A	G to Recip. B	390	524
	B	G	142	186
Qst 14	B	S	211	247
Qst 15	A	S	211	247
	B	S	229	223
		G - parallel		180
Qst 19	F	G and	193	281
		G - parallel		195
Qma 3	C	G	432	519

TABLE II (Continued)

Plot No.	Connected Recipients	Type of Connection	Surface Distance to Donor in cm	Distance Dye Moved Collar to Collar in cm
Qma 9	A	C	109	112
Qma 16	A	G and G - parallel	102	103 112

*Dye moving from donor and into the recipient via a sprout, interrupted by a large sandstone boulder. Tentative conclusion: Horizontal sprout.

**Many large sandstone boulders were just beneath the surface. Dye was entering the donor via several small roots. Tentative conclusion: All root-grafts.

G - Root graft.

S - Horizontal sprout.

C - Collar series.

NL - Not located.

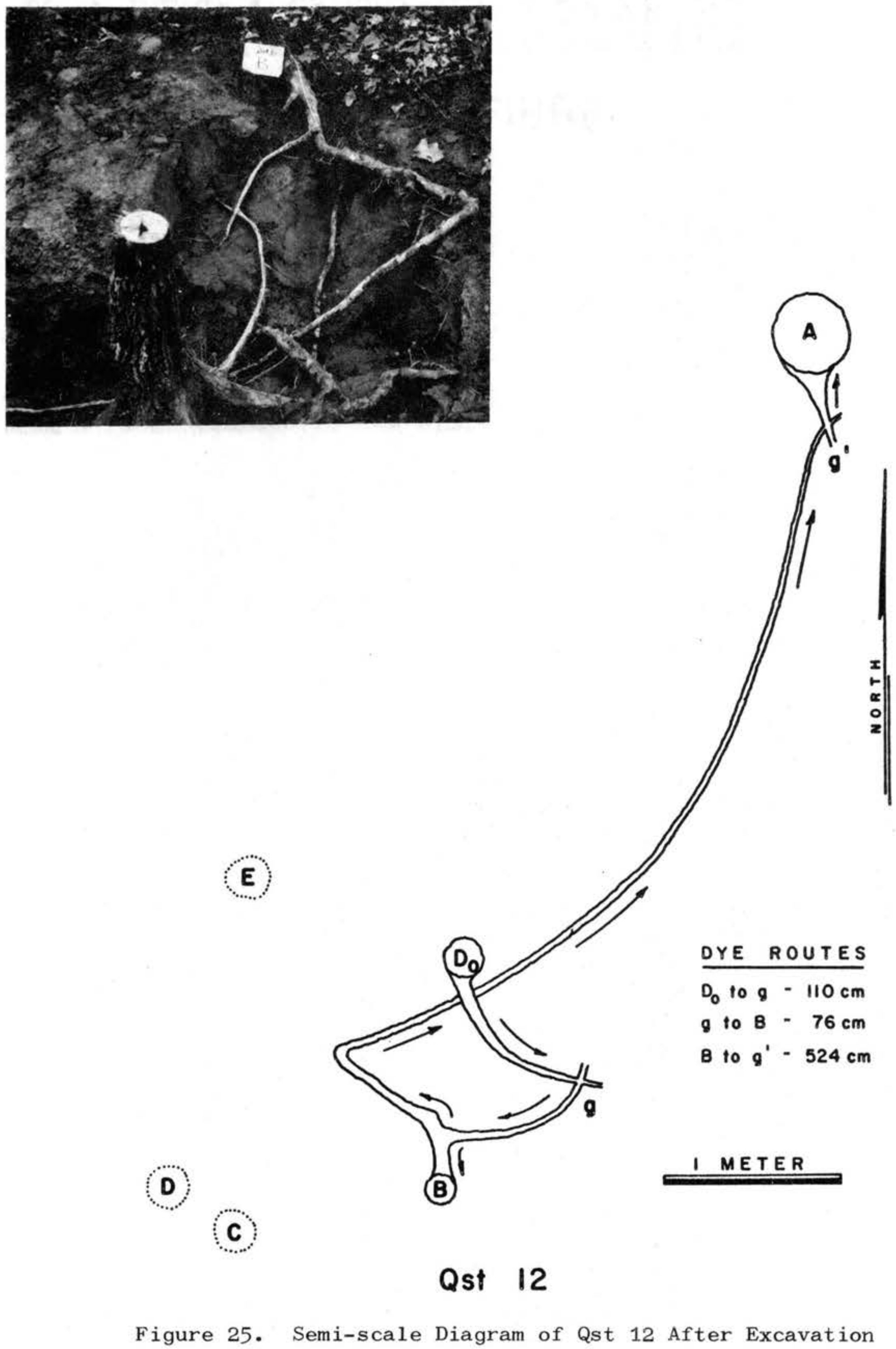

Figure 25. Semi-scale Diagram of Qst 12 After Excavation

The next four figures show the results of some of the other postoak excavations.

Figure 26. Excavated Sprout Connection in Qst 14

Qst 14 had a single recipient connected to the donor stump. This is the typical, mature horizontal sprout connection. Beddie (1941) noted the difficulty in distinguishing older grafts from clonal connections. In the present study, all suspected horizontal sprouts were examined carefully for graft evidence. Near the upper center of Figure 26 can be seen evidence of an older stem that has decayed back to below the ground level. Other plots also showed evidence of former stems. Qst 7 had a large, burned stump between the donor and recipient. Qst 6 showed evidence of three old, decayed stems. The coppicing practices in Europe still continue on centuries old root systems (Smith, 1962).

Perhaps fire and other trunk killing influences have led to the same situation in the Cross Timbers. The largest sprout connected donor-recipient pair encountered in the present study was in Qst 6. The donor proved to be 43 years old and the recipient was 41 years in age. There is no reason to believe that these sprout connections could not be much older than the stems.

Part of Qst 2, which included six recipients, is shown in Figure 27. Three sprouts and three grafts were involved in the system. Four stems were directly connected to the donor and two were connected via sprout then root-graft to one of the recipients.

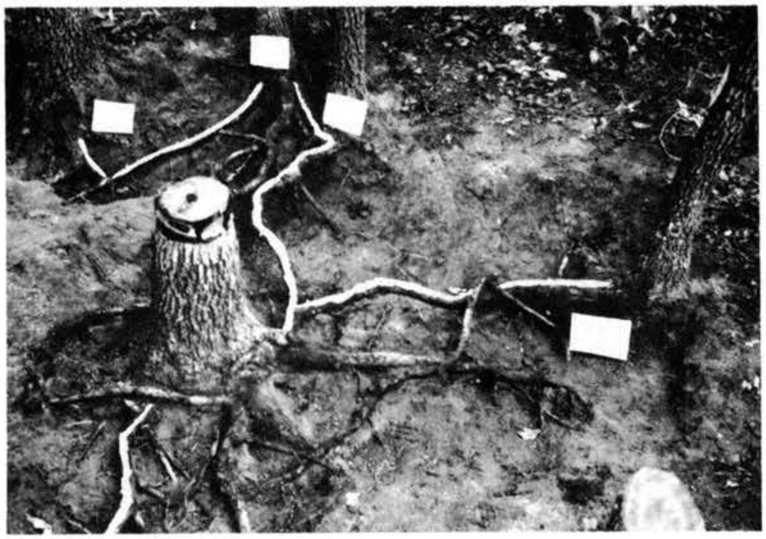

Figure 27. Part of Qst 2 (Dye transmitting structures are painted white.)

Qst 15 is shown in Figure 28 and consisted of the donor and two recipients connected in a complex manner. The recipient at upper right had two dye routes from the lower left donor. A sprout route is above and a graft route is at the lower center of the figure. Note that the root that plunges downward is grafted to two of the horizontal structures. Evidence of an old stump exists near the center of the system.

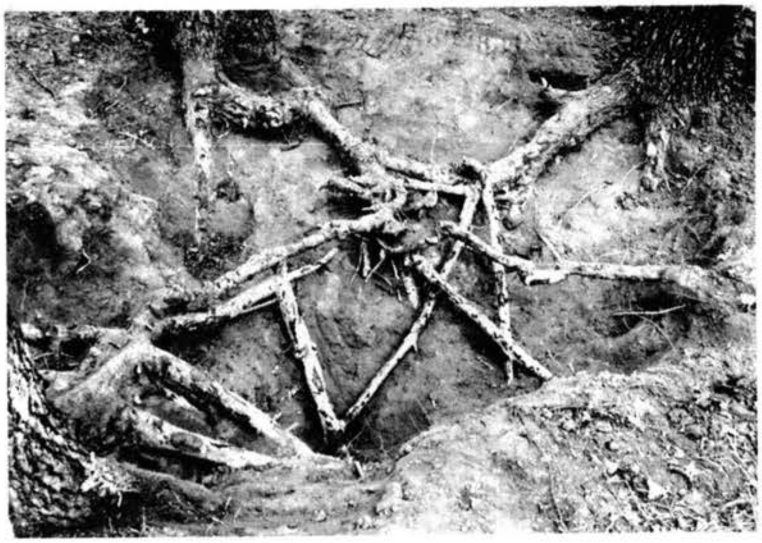

Figure 28. Donor and Two Recipients in Qst 15

Figure 29 shows the single graft found in Qst 10. The dye moved down the donor root from top right, then back up the vertical branch to the horizontal root and exited to the recipient at top left. It appears that the vertical, recipient root has been captured by the donor root because it is much smaller and in a partial state of decay above the graft. This might be due to the polarity changes described by Graham (1959).

Figure 29. Root Graft in Qst 10

The smallest diameter but longest grafted roots occurred in Qma 3. Figure 30 shows the donor root entering the picture at lower left. It is longitudinally grafted to the recipient root near the center of the meter stick. The total distance traversed by the dye, from collar to collar, was 5.19 m.

Qma 9, with an unusual type of underground connection, is shown in Figure 31. The donor at left proved to be a collar sprout of an old, buried, partially decayed stump. This collar was next to another similar structure from which the adjacent recipient, apparently, grew. Two root grafts can also be seen. Most of the collar tissue and the grafts were infused with dye.

Figure 30. Root Graft in Qma 3
(Roots are
painted.)

Figure 31. Two Collars and Grafts Connecting
the Donor and Recipient in Qma 9

Observations of Other Phenomena

In the ravine on the northeast side of the primary study site was a group of even age, well spaced hackberry or sugarberry trees (*Celtis* spp.). One of these trees was chosen as a donor and aqeous acid fuchsin introduced using a collar reservoir. At the end of the first day, three receptors were noted. The excavation of this area was extremely difficult because of the dense, heavy mass of roots and sprouts. Hydraulic excavation would have to be used in a moist site such as this in order to expose the root systems in an undamaged condition. Both horizontal roots and root grafts were found to be functioning in the transmission of the tracer. It appears that root sprouting might occur in this genus. Krajicek (1965) states only, "Hackberry can be propagated by cuttings and by layering. Sprouts develop from stumps of small trees but rarely from those of large trees." The dye was very visible in the almost white wood of both stem and root.

Plum (*Prunus angustifolia* Marsh.) was the only species tested that did not show any movement of the tracer to a recipient. The dye was introduced into this species with a tight rubber collar and siphon arrangement. Whether the failure to find functional connections was due to faulty technique or to the lack of these connections is not known.

Both *Rhus copallina* L. and *R. glabra* L. were investigated by introducing tracer directly into what was assumed to be a horizontal root. Other workers have termed the structure a rhizome (Weaver, 1919; Duncan, 1935; Gilbert, 1966). No precise anatomical study was carried out in the present work but the horizontal structures seen are more rootlike in nature. They have a well developed stele that is surrounded by an easily sloughed cortex and have no pith. The deeper, vertical roots resemble the horizontal structures in the traits mentioned.

The movement of dye was slow through the horizontal structures. Two days were required for the dye to reach its maximum dispersion. The intakes were left in place for seven days but no further penetration took place. A great deal of a milky, sticky exudate seeps out of the cortex. This substance could seal off the conducting channels and prevent intake after a time.

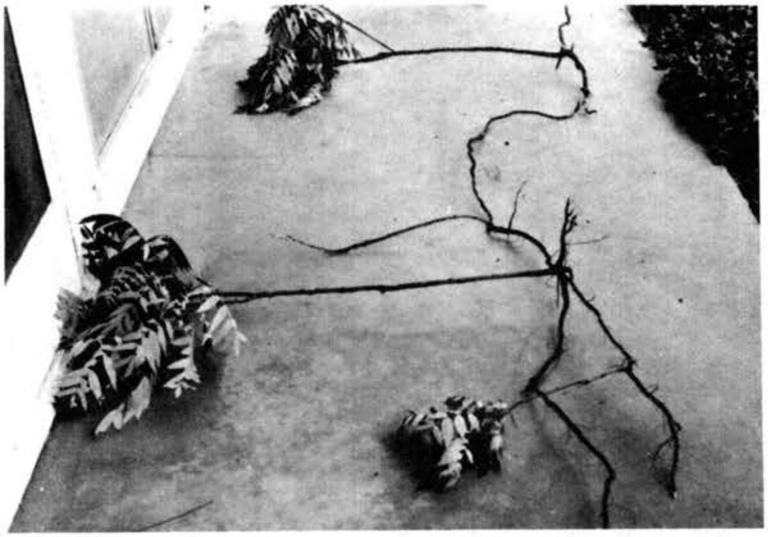

Figure 32. Root Connections in Smooth Sumac

Figure 32 shows the longest sumac system located after 10 trials. All of the living sumac stems had been dyed by the process. The intake root exits the photograph at the lower right of the photograph. The dye moved up to the large stem and back along another horizontal to the small stem. It continued on from the first large stem to below a dead stem. It did not rise in this stem but continued on to another large stem. The total distance traversed was 3.18 m.

An interesting situation exists in Symphoricarpus orbiculatus Moench. Duncan (1935), while studying old fields in Indiana, noticed that this species spreads only by aboveground runners. Earlier Weaver and Kramer (1932) had observed both the aboveground runners and underground rhizomes involved in vegetative reproduction in Nebraska. Duncan hypothesized that the difference in propagation was due to the rhizome being a more effective mechanism in the more xeric Nebraska. The plants of this species that were examined, in the Cross Timbers, had both runners and rhizomes. The rhizomes seemed to be more common.

Ten Symphoricarpus rhizomes were excavated and immersed in aqueous acid fuchsin. All showed dye transfer to two or three recipient stems. The horizontals have a pith and appear to show nodes and internodes. Rhizome and runner or stolon seems to be their true identity.

The last observation made concerned herbicide "backflash" in postoak and blackjack oak. In late July of 1967, four postoaks and four blackjack oaks with near neighbors were chosen. These trees were frill girdled and the frills were filled with a water soluble solution of 2,4,5-T and 2,4-D (Smith, 1962).

The test trees showed signs of heavy damage at one and two weeks. No "backflash" was noticeable at that time. The sites were checked again in June of 1968. After almost a year, all of the frilled blackjack oak trees were dead above the collar but they were sprouting from the collar zone. It is not known if the sprouts survived. Leonard (1957) reports that basal sprouting is common after herbicide treatment but that these sprouts sometimes die after a year. No damage occurred to nearby trees.

After almost a year, all of the frilled postoak trees were dead. One tree had no dead or damaged neighbors, one had a single dead neighbor, and the other two each had three trees close by that showed dead limbs and leaves in several places on the trunks. The herbicide seemed to have "backflashed" in the same pattern that was produced when the dyes stained only certain limbs and leaves of the recipients. It is not known if these unevenly damaged trees continued to live.

CHAPTER VI

SUMMARY

Forest trees might be connected underground by channels that can function in the transmission of both organic and inorganic materials. The present study was undertaken to investigate this phenomenon in the Oklahoma Cross Timbers.

In order to observe underground plant parts, several excavation sites and eroded areas were studied. The eroded areas furnished much more information than did the excavations. Functional self and intraspecific grafts were seen in postoak, blackjack oak, American elm, pecan, black walnut, and Celtis spp. Self grafts only were seen in Shumard oak.

The oak reproduction was analyzed and found to be predominantly of sprout origin. Postoak was found to propagate by a horizontal underground sprout that may be a rhizome or a horizontal stem left as a result of a low layering process. These structures were found to be common and capable of transmitting dye tracer for at least 41 years.

A stump dye tracer intake procedure was adapted that detected connected systems of trees and marked the underground structures that had functioned in the transfer of dye. Ten of 17 postoaks were found to be united with a total of 27 postoak recipients that were larger than 2.5 cm d.b.h. Three postoaks were united to small, transpiring postoak sprouts. Four postoaks were independent as far as dye transfer was concerned. Three of 13 blackjack oaks were connected to three other trees of the same species.

Midday closure of recipient stomates was not reflected in the dye intake data. Day-night intake differences of trees with recipients were statistically significantly different at $P = 0.05$. Non-connected trees showed no statistically significant night-day difference at $P = 0.05$. Stump intake of dye showed a logarithmic 24 hour decline over five days. When 24 hour dye intake readings for connected trees were tested against those for non-connected, the strongly connected postoaks were statistically significantly different at $P = 0.01$; blackjack oaks, for the first two days, were different at $P = 0.001$ but the last three days showed no significant statistical difference even at $P = 0.1$.

Dye velocity was computed for seven postoak receptions. The mean velocity and its 95% confidence interval was 2.7 ± 0.69 m/hr.

Receptor dye patterns were in streaks or narrow bands spiraling up to the right. Little or no lateral movement of the tracer was noticed and this probably accounts for the staining of only certain limbs.

An air excavation technique was tested and found to be useful especially for the A soil horizon and for dry, light soils. Using this and hand digging, 10 strongly connected postoaks were found to be transmitting dye through 13 horizontal sprouts and 13 root grafts. The three connected blackjack oak systems involved three grafts and one collar series between the donors and recipients. The maximum distance between donor and recipient was 3.9 m in a postoak and 4.32 m in a blackjack oak.

Dye movement through underground connections was also observed in *Celtis* spp., smooth and winged sumac, and buckbrush.

Herbicide "backflash" was observed in postoak with either death or uneven damage to the recipient trees.

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APPENDIX A

EXPERIMENTAL PLOT DESCRIPTIONS

TABLE III

EXPERIMENTAL PLOT DESCRIPTIONS

Plot No.	Member	Azimuth Degrees	dbh cm	Distance From Donor cm	Plot No.	Member	Azimuth Degrees	dbh cm	Distance From Donor cm	Plot No.	Member	Azimuth Degrees	dbh cm	Distance From Donor cm
Qst 2	Do		18		Qst 6	Do		20			C	70	16	376
	A	5	10	100		A	30	18	157		D	135	18	328
	B	30	17	244		B	70	11	160		E	160	10	213
	C	73	17	203		C	120	S*	122					
	D	129	15	165		D	155	19	152	Qst 12	Do		12	
	E	152	9	165		E	200	S*	262		A	30	31	390
	F	173	10	122		F	220	S*	107		B	195	S*	142
	G	185	22	231							C	220	17	216
	H	239	9	130	Qst 8	Do		16			D	230	17	249
	I	279	15	170		A	60	18	240		E	290	11	231
	J	290	15	130		B	105	16	135					
	K	325	11	218		C	120	14	230	Qst 13	Do		17	
	L	345	16	183		D	195	17	180		A	190	29	168
	M	350	15	229		E	270	15	180		B	300	25	368
Qst 4	Do		10		Qst 9	Do		14		Qst 14	Do		12	
	A	5	10	135		A	60	9	307		A	90	16	163
	B	75	14	201		B	220	S*	140		B	120	15	137
	C	195	11	229		C	300	9	257					
	D	205	15	191						Qst 15	Do		18	
	E	215	8	221	Qst 10	Do		20			A	40	20	211
	F	230	8	132		A	0	27	328		B	70	18	229
	G	265	S*	102		B	100	19	216					
	H	270	15	185		C	185	19	203	Qst 16	Do		12	
						D	220	8	102		A	25	18	213
Qst 5	Do		16			E	280	15	320		B	150	13	404
	A	50	15	102							C	285	21	300
	B	110	15	231	Qst 11	Do		12			D	305	9	114
	C	265	13	257		A	35	13	198					
	D	315	14	160		B	60	9	236					

TABLE III (Continued)

Plot No.	Member	Azimuth Degrees	dbh cm	Distance From Donor cm
Qst 17	Do		18	
	A	80	24	488
	B	175	23	213
	C	335	14	384
Qst 18	Do		10	
	A	120	37	196
	B	150	S	320
	C	270	26	427
Qst 19	Do		17	
	A	60	15	437
	B	195	18	213
	C	205	18	251
	D	210	9	292
	E	235	24	259
	F	285	22	193
	G	300	12	274
	H	325	16	318
Qma 3	Do		22	
	A	30	21	132
	B	220	27	284
	C	255	S*	432
	D	310	21	188
Qma 4	Do		22	
	A	30	14	140
	B	170	S*	145
	C	275	S*	323
Qma 6	Do		16	
	A	45	9	282
	B	200	S*	183
	C	255	S*	152
Qma 8	Do		23	
	A	0	16	427
	B	40	14	305
	C	80	S*	274
	D	270	15	203
Qma 9	Do		18	
	A	10	23	109
	B	210	25	135
Qma 10	Do		16	
	A	195	14	206
	B	250	20	152
Qma 11	Do		16	
	A	115	20	254
	B	235	14	249
	C	330	15	384
Qma 12	Do		16	
	A	10	23	274
	B	270	25	427
Qma 13	Do		20	
	A	240	9	226
	B	320	9	109
	C	330	8	330
Qma 14	Do		22	
	A	140	S*	244
	B	240	32	305
Qma 15	Do		14	
	A	185	13	254
	B	320	S*	287
Qma 16	Do		18	
	A	20	16	102
	B	145	19	132
	C	150	18	226
	D	166	10	216
	E	182	20	201
Qma 17	Do		29	
	A	25	25	318

*S = Sapling

TABLE IV

DONOR DESCRIPTIONS

Plot No	Diameter cm	Stump Area cm^2	Sapwood Area cm^2	Age Years	Plot No	Diameter cm	Stump Area cm^2	Sapwood Area cm^2	Age Years
Qst 2	18	206	129	49	Qst 18	10	54	43	44
Qst 4	10	73	64	31	Qst 19	17	199	110	61
Qst 5	16	184	117	42	Qma 3	22	351	196	47
Qst 6	20	167	128	43	Qma 4	22	326	168	55
Qst 7	18	188	119	53	Qma 6	16	194	101	36
Qst 8	16	163	128	41	Qma 8	23	346	219	50
Qst 9	14	155	141	29	Qma 9	18	219	120	51
Qst 10	20	266	145	67	Qma 10	16	190	97	41
Qst 11	12	84	72	40	Qma 11	16	152	87	48
Qst 12	12	80	53	36	Qma 12	16	164	117	45
Qst 13	17	242	100	47	Qma 13	20	199	112	61
Qst 14	12	105	72	35	Qma 14	22	293	190	51
Qst 15	18	261	116	49	Qma 15	14	176	117	40
Qst 16	12	71	59	49	Qma 16	18	184	93	52
Qst 17	18	224	110	58	Qma 17	29	485	187	71

APPENDIX B

DYE INTAKE RATES

TABLE V

FIRST DAY, HOURLY DYE INTAKE RATES IN MILLILITERS PER SQUARE CENTIMETER OF SAPWOOD

Plot No.	Time of Day											
	8	9	10	11	12	1	2	3	4	5	6	7
<u>Postoak - Strong Connection</u>												
Qst 2	4.4	4.8	4.8	5.1	5.6	5.0	4.5	3.5	3.5	3.4	3.4	2.1
Qst 4	6.7	9.5	9.6	9.8	6.3	6.3	5.4	5.0	4.6	3.2	2.3	1.1
Qst 6	5.9	7.8	4.6	3.3	4.6	3.9	3.7	3.1	2.9	1.6	1.4	1.3
Qst 7	5.6	9.5	5.6	4.8	8.1	8.4	8.3	8.4	8.3	6.4	5.4	3.2
Qst 8	2.6	2.6	4.6	4.5	5.2	4.0	3.6	3.1	3.2	3.1	3.1	2.4
Qst 10	1.8	2.2	2.4	2.8	3.3	1.8	1.8	1.8	1.8	1.8	1.8	1.8
Qst 12	6.1	4.6	8.5	9.1	12.2	9.3	12.2	11.4	11.1	10.2	5.0	4.7
Qst 14	6.1	7.2	9.0	9.2	6.4	4.5	5.5	4.7	4.5	3.2	3.1	2.9
Qst 15	4.9	5.4	9.7	9.5	9.9	11.5	9.0	4.5	6.5	6.8	4.9	4.5
Qst 19	0.4	1.3	1.5	2.9	3.3	3.3	2.0	1.5	1.5	1.1	0.9	0.7
Means	4.4	5.4	6.0	6.0	6.4	5.8	5.5	4.7	4.7	4.0	3.1	2.4
<u>Postoak - Weak Connection</u>												
Qst 9	1.0	1.0	1.3	2.3	3.2	3.8	3.5	2.3	2.2	2.1	1.6	1.2
Qst 16	1.3	2.0	1.7	2.4	3.1	2.9	3.1	3.9	3.6	3.5	3.5	2.2
Qst 17	1.0	2.3	2.5	2.5	3.3	3.1	2.7	2.7	2.7	2.3	2.5	2.0
Means	1.1	1.7	1.8	2.4	3.2	3.2	3.1	2.9	2.8	2.6	2.5	1.8
<u>Postoak - No Connection</u>												
Qst 5	0.6	0.8	0.8	1.4	0.8	0.9	0.9	0.9	0.8	1.1	0.8	0.6
Qst 11	0.7	0.6	0.6	0.6	0.6	0.5	0.6	0.6	0.5	0.5	0.6	0.5
Qst 13	1.0	1.5	1.2	1.2	1.2	1.2	1.2	1.5	1.2	0.7	1.0	0.7
Qst 18	0.8	1.1	0.9	0.9	0.8	0.9	1.0	0.8	0.5	0.5	0.4	0.5
Means	0.7	1.0	0.8	1.0	0.8	0.8	0.9	0.9	0.7	0.7	0.7	0.6

TABLE V (Continued)

Plot No.	Time of Day											
	8	9	10	11	12	1	2	3	4	5	6	7
Blackjack Oak - Connection												
Qma 3	2.5	3.2	3.9	5.4	3.8	5.0	4.3	3.6	3.9	3.2	2.2	2.2
Qma 9	4.6	4.6	4.9	6.4	4.6	5.1	4.9	3.7	4.4	2.7	2.2	2.0
Qma 16	6.5	6.7	6.9	7.1	4.3	3.9	3.0	3.2	2.6	2.6	1.4	1.2
Means	4.5	4.8	5.2	6.3	4.2	4.6	4.0	3.5	3.6	2.8	1.9	1.8
Blackjack Oak - No Connection												
Qma 4	0.0	2.0	2.0	3.0	0.4	0.2	1.2	1.0	1.2	1.0	1.0	0.8
Qma 6	0.4	1.0	1.0	1.7	2.1	2.3	2.1	1.0	1.7	1.5	1.3	1.1
Qma 8	0.8	0.8	0.8	1.3	1.6	2.2	1.9	1.9	1.7	1.7	1.6	1.4
Qma 10	0.4	0.6	0.6	0.2	0.0	0.4	0.8	0.6	0.6	0.6	0.6	0.4
Qma 11	0.5	0.5	0.7	0.5	0.7	0.5	0.5	0.7	0.5	0.5	0.3	0.5
Qma 12	0.7	1.0	1.4	1.4	1.7	1.4	1.1	1.1	1.3	1.0	1.1	0.8
Qma 13	1.8	0.0	1.4	0.9	1.6	1.2	1.4	1.1	1.6	1.4	0.9	0.9
Qma 14	1.5	1.5	1.5	1.5	0.8	0.8	0.6	0.8	0.6	0.8	0.6	0.3
Qma 15	0.8	1.5	1.7	2.1	2.3	2.1	1.8	1.5	1.5	1.2	1.4	1.2
Qma 16	0.0	0.5	2.1	0.5	0.5	0.8	1.0	0.5	0.5	0.5	0.5	0.5
Means	0.7	0.9	1.3	1.3	1.3	1.1	1.2	1.0	1.1	1.1	0.9	0.7

TABLE VI

FIRST DAY, HOURLY DYE INTAKE RATES IN CENTILITERS

Plot	Time of Day											
No.	8	9	10	11	12	1	2	3	4	5	6	7
Qst 2	62	62	62	66	72	64	58	58	45	45	43	27
Qst 4	43	60	61	63	40	40	34	32	29	20	15	7
Qst 5	7	9	9	17	9	11	11	11	9	13	9	7
Qst 6	75	100	59	42	59	50	47	40	37	20	18	17
Qst 7	66	113	66	57	96	100	98	100	98	75	64	38
Qst 8	33	33	59	57	67	51	46	39	41	39	39	31
Qst 9	16	16	19	33	45	54	50	33	31	30	23	17
Qst 10	27	32	35	40	48	27	27	26	26	27	26	26
Qst 11	5	4	4	4	4	3	4	4	3	3	4	3
Qst 12	32	24	45	48	64	49	64	60	58	54	26	25
Qst 13	10	15	12	12	12	12	12	15	12	7	10	7
Qst 14	44	51	65	66	46	33	40	34	33	23	22	21
Qst 15	57	63	112	110	115	133	104	52	76	78	57	52
Qst 16	8	12	10	14	19	17	19	23	21	21	21	13
Qst 17	11	25	27	27	36	34	29	29	29	25	27	22
Qst 18	3	5	4	4	3	4	4	3	2	2	2	2
Qst 19	4	14	16	32	36	36	22	16	16	12	10	8
Qma 3	49	63	77	105	74	98	84	70	77	63	42	42
Qma 4	0	33	33	49	7	3	20	16	20	16	16	13
Qma 6	4	10	10	17	21	23	21	10	17	16	14	12
Qma 8	17	17	17	28	35	49	42	42	38	38	35	31
Qma 9	55	55	59	77	55	61	59	44	53	33	26	24
Qma 10	4	6	6	2	0	4	8	6	6	6	6	4
Qma 11	5	5	6	5	6	5	5	6	5	5	3	5
Qma 12	8	12	16	16	20	17	13	13	15	12	13	10
Qma 13	20	0	16	10	18	14	16	12	18	16	10	10
Qma 14	29	29	29	29	15	15	12	15	12	15	12	6
Qma 15	9	18	20	25	27	25	21	18	18	14	16	14
Qma 16	61	63	64	66	41	37	28	30	24	24	13	11
Qma 17	0	10	39	10	10	15	19	10	10	10	10	10

TABLE VII

DAY-NIGHT DYE INTAKE RATES IN MILLILITERS PER SQUARE CENTIMETER OF SAPWOOD

Plot	Time Period									
	d = 8 a.m.-8 p.m.					n = 8 p.m.-8 a.m.				
No.	1d	1n	2d	2n	3d	3n	4d	4n	5d	5n
Postoak - Strong Connection										
Qst 2	48.4	13.5	19.5	5.0	6.9	2.9	5.3	2.6	3.4	1.6
Qst 4	69.6	9.2	18.1	3.5	3.0	0.7	0.8	0.2	0.6	0.3
Qst 6	44.1	7.6	10.5	4.4	5.9	1.9	2.6	1.3	1.6	0.9
Qst 7	81.8	28.6	38.4	13.5	16.9	9.21	12.5	6.5	8.3	3.6
Qst 8	44.7	13.1	20.0	7.9	10.3	4.3	7.8	2.6	3.6	2.3
Qst 10	25.2	11.3	12.4	3.8	5.5	1.6	3.8	1.5	1.3	0.7
Qst 12	104.4	22.7	25.1	20.8	16.0	10.2	8.0	5.6	4.3	3.5
Qst 14	64.7	27.5	33.4	17.7	18.5	7.1	7.3	4.1	5.4	2.2
Qst 15	87.1	15.1	42.1	16.1	20.3	8.3	8.8	4.5	5.0	1.8
Qst 19	20.1	0.8	9.8	5.3	5.6	3.1	3.1	0.9	1.1	0.4
Means*	59.0	15.6	22.9	9.7	10.8	4.9	5.9	2.9	3.4	1.7
Postoak - Weak Connection										
Qst 9	25.8	4.9	6.2	1.5	3.3	1.3	1.5	1.0	1.1	0.4
Qst 16	33.2	14.7	17.8	7.6	8.5	4.1	4.7	3.3	3.3	1.1
Qst 17	29.2	16.4	18.0	8.0	8.0	3.5	4.0	1.4	1.8	0.8
Means*	29.3	12.0	14.0	5.7	6.6	2.9	3.4	1.8	2.0	0.7
Postoak - No Connection										
Qst 5	10.0	3.3	7.0	2.8	4.2	1.4	2.3	0.9	1.3	0.8
Qst 11	6.6	5.9	2.6	2.6	1.8	2.4	2.1	1.9	0.6	0.3
Qst 13	14.8	10.2	8.7	4.9	2.9	2.4	1.7	1.2	0.5	0.2
Qst 18	9.0	6.1	5.3	3.7	3.5	1.8	1.5	0.9	0.4	0.3
Means**	10.1	6.3	5.9	3.5	3.0	1.9	1.9	1.2	0.6	0.4
Blackjack Oak - Connection										
Qma 3	41.8	17.9	11.7	6.5	4.5	3.4	2.5	1.8	1.6	1.4
Qma 9	52.0	11.0	16.1	6.8	6.6	4.0	4.2	2.3	3.3	2.2

TABLE VII (Continued)

Plot	Time Period									
	d = 8 a.m.-8 p.m.					n = 8 p.m.-8 a.m.				
No.	1d	1n	2d	2n	3d	3n	4d	4n	5d	5n
Qma 16	49.3	8.5	9.5	3.4	3.5	1.2	1.8	1.0	1.0	0.6
Means*	47.7	12.4	12.4	5.5	4.8	2.8	2.8	1.7	1.9	1.3
Blackjack Oak - No Connection										
Qma 4	13.4	0.8	6.0	5.2	5.2	4.3	3.7	2.1	1.9	1.9
Qma 6	33.3	15.1	6.5	5.7	4.0	3.8	3.4	2.1	1.0	1.1
Qma 8	17.2	9.9	6.0	4.9	4.9	4.7	4.1	3.8	1.9	1.6
Qma 10	5.7	5.3	4.9	4.7	2.3	2.2	1.0	1.0	0.8	0.8
Qma 11	7.3	7.0	5.4	4.9	4.2	3.9	2.6	2.6	1.4	1.2
Qma 12	14.0	8.9	5.1	4.4	3.2	3.1	2.7	2.1	1.8	1.0
Qma 13	14.3	8.7	4.5	4.5	3.9	3.6	2.9	2.3	1.2	0.7
Qma 14	11.8	6.3	3.4	3.9	3.1	3.4	3.4	0.8	0.8	0.8
Qma 15	19.1	9.8	5.7	4.8	4.4	2.7	1.8	1.8	1.5	0.8
Qma 17	8.1	4.7	4.4	3.1	3.4	2.6	1.8	1.3	1.3	0.8
Means**	14.4	8.3	5.1	4.6	3.8	3.4	2.7	1.9	1.3	1.0

*Total day means different from the total night means at the 5% level of confidence.

**Total day means not different from the total night means at the 5% level of confidence.

TABLE VIII

DAY-NIGHT DYE INTAKE RATES IN CENTILITERS

	Time Period									
Plot	d = 8 a.m.-8 p.m.					n = 8 p.m.-8 a.m.				
No.	1d	1n	2d	2n	3d	3n	4d	4n	5d	5n
Qst 2	622	173	251	64	89	37	68	33	43	21
Qst 4	445	59	116	23	19	4	5	2	4	2
Qst 5	118	39	81	33	50	17	28	11	15	9
Qst 6	563	97	134	57	75	25	33	17	20	12
Qst 7	970	339	456	160	200	109	149	77	98	43
Qst 8	574	168	257	101	132	56	100	33	46	29
Qst 9	365	70	87	22	47	19	22	14	16	6
Qst 10	367	165	181	56	80	24	56	21	19	11
Qst 11	48	43	18	18	13	18	15	13	4	3
Qst 12	549	119	132	110	84	54	42	30	22	18
Qst 13	147	102	87	48	29	24	17	12	5	2
Qst 14	467	198	241	128	133	51	53	29	39	16
Qst 15	1010	175	489	185	235	97	102	52	57	21
Qst 16	197	87	106	45	51	24	28	20	20	7
Qst 17	320	179	197	87	87	38	43	16	20	9
Qst 18	39	26	23	16	15	8	7	4	2	1
Qst 19	221	86	107	58	62	34	34	10	12	4
Qma 3	818	351	228	126	88	67	49	35	32	28
Qma 4	225	130	101	88	88	72	62	36	33	33
Qma 6	337	153	66	58	41	39	35	21	10	12
Qma 8	377	218	132	107	107	104	90	83	42	35
Qma 9	625	132	193	81	79	48	51	35	40	26
Qma 10	55	51	48	46	23	21	10	10	8	8
Qma 11	64	61	47	43	67	33	23	23	12	11
Qma 12	164	104	59	51	38	36	31	25	21	12
Qma 13	159	98	50	50	44	40	32	26	14	8
Qma 14	225	120	64	73	59	64	64	15	15	15
Qma 15	223	114	67	46	51	47	32	21	18	9

TABLE VIII (Continued)

Plot No.	Time Period d = 8 a.m.-8 p.m. n = 8 p.m.-8 a.m. 1d	1n	2d	2n	3d	3n	4d	4n	5d	5n
Qma 16	460	79	88	31	33	11	17	9	9	6
Qma 17	150	87	83	58	63	49	34	24	24	15

TABLE IX

TWENTY-FOUR HOUR TOTAL DYE INTAKE RATES IN MILLILITERS PER SQUARE CENTIMETER OF SAPWOOD

Plot No.	Twenty-Four Hour Period 1	2	3	4	5
Postoak - Strong Connection					
Qst 2	61.9	24.5	9.8	7.9	5.0
Qst 4	79.1	21.6	3.7	1.0	0.9
Qst 6	51.7	14.9	7.8	3.9	2.5
Qst 7	110.4	51.9	26.1	19.0	11.9
Qst 8	57.8	27.9	14.6	10.3	5.9
Qst 10	36.5	16.2	7.1	5.3	2.0
Qst 12	127.1	45.9	26.2	13.5	7.8
Qst 14	92.2	51.2	25.6	11.4	7.5
Qst 15	102.2	58.1	28.6	13.3	6.8
Qst 19	27.8	15.1	8.7	3.9	1.5
Means	74.6**	32.7**	15.8**	8.9**	5.1**
Postoak - Weak Connection					
Qst 9	30.7	7.7	4.6	2.5	1.5
Qst 16	47.9	25.4	12.5	8.0	4.4
Qst 17	45.6	26.0	11.5	5.3	2.6
Means	41.4**	19.7*	9.5*	5.2*	2.8*
Postoak - No Connection					
Qst 5	13.5	9.7	5.6	3.2	2.1
Qst 11	12.5	5.2	4.2	4.0	0.9
Qst 13	25.0	13.6	5.3	2.9	0.7
Qst 18	15.1	9.0	5.3	2.4	0.7
Means	16.4	9.3	5.1	3.1	1.1
Blackjack Oak - Connected					
Qma 3	59.7	18.2	7.9	4.3	3.0
Qma 9	63.0	22.9	10.6	6.5	5.5

TABLE IX (Continued)

Plot No.	Twenty-Four Hour Period 1	2	3	4	5
Qma 16	57.8	12.9	4.7	2.8	1.6
Means	60.1***	17.9***	7.7	4.5	3.3
Blackjack Oak - No Connection					
Qma 4	21.2	11.2	7.1	5.8	3.8
Qma 6	48.4	12.2	7.8	5.5	2.1
Qma 8	27.1	10.9	6.6	7.9	3.5
Qma 10	11.0	9.6	4.5	2.0	1.6
Qma 11	14.3	10.3	8.1	5.2	2.6
Qma 12	22.9	9.5	6.3	4.8	2.8
Qma 13	23.0	9.0	7.5	5.2	1.9
Qma 14	18.1	7.3	6.5	4.2	1.6
Qma 15	28.9	10.5	8.5	4.5	2.3
Qma 17	12.8	7.5	6.0	3.1	2.1
Means	22.7	9.7	6.8	4.8	2.4

*Different from corresponding no connection mean at the 10% level of confidence.

**Different from corresponding no connection mean at the 1% level of confidence.

***Different from corresponding no connection mean at the 0.1% level of confidence.

VITA

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