

Patterns of sap-foraging on willows (*Salix spp.*) by a keystone species: the Red-naped
Sapsucker (*Sphyrapicus nuchalis*)

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Abstract

The Red-naped Sapsucker (*Sphyrapicus nuchalis*) is a keystone species in montane/subalpine ecosystems of the Rocky Mountains of Colorado. By excavating nest cavities in aspen trees and sap wells in willow shrubs, sapsuckers indirectly provide nest holes and food, respectively, to many other species. The objective of my project was to determine which characteristics of willow shrubs were most important to sapsuckers in their choice of stems to drill for sap. The most important factors revealed in my study were the frequency of past sap well excavation. The probability of a stem being excavated for sap wells decreased as the frequency of past foraging increased, as measured by the proportion of stems that were dead (sap well excavation kills the willow stem) and/or had old sap well scars. Presumably willow shrubs with a higher frequency of past sap well excavation were less healthy and thus less optimal for new sap drilling, possibly due to decreased sap flow potential. The negative relationship between the frequency of past sap feeding and new sap well excavation may have ecological and evolutionary implications; these include the possibility that sap-foraging occurs in a way that allows willow shrubs to recover, thus maximizing their long-term sap-producing potential, and the possibility that sapsucker feeding patterns reflect coevolution of defenses against sap-feeding by the willows and counter-adaptations by the sapsuckers.

Keywords

Red-naped sapsucker, double keystone species, willows, sap-feeding, willow selection, foraging patterns.

Introduction

Plants and animals have coexisted for millions of years. In that time they have been forced to adapt to changing ecosystems, new climates and each other. There are dynamic relationships between plants and animals that exist within an ecosystem, and it is these relationships that drive coevolution of species within a community. Coevolution is considered a significant force in the adaptations of interacting species in a common ecosystem. In order for coevolution to occur, the adaptations of one species must pressure one or more additional species to counter-adapt to a new situation (Bercerra 2003). In the case of plant-herbivore interactions the act of feeding on a plant can induce the development of defense mechanisms that increase resistance to herbivory. Consequentially, the increased resistance to herbivory developed by the plant can lead to an adaptive change in the physiology or behavior of the herbivore that reduces the effect of the plant's defenses (Baldwin and Preston 1999). Evidence of this phenomenon can be seen by investigating patterns of interaction between organisms sharing a particular ecological relationship (Ehrlich and Raven 1964, Benson et al. 1975). Investigations of coevolution have become increasingly important to biologists and conservationists as it has become more apparent how quickly the changing relationships between species can affect a community (Thompson 2001).

Coevolution between a keystone species and the organisms that species relies on for survival, such as insects and plants that act as important food sources, may have a large impact on an ecosystem. As a keystone species in the subalpine/montane region of the Colorado Rockies, the Red-naped Sapsucker (*Sphyrapicus nuchalis*) holds a fundamental position in its community. The nesting and feeding habits of the Red-naped Sapsucker provide resources to many species in its environment. This species of

woodpecker excavates new nests every breeding season by hollowing out cavities in aspen trees infected with the aspen heartrot fungus, *Phellinus tremulae*. The following season Red-naped Sapsuckers excavate new nests, leaving the previous season's nests to be utilized by a number of other species of secondary cavity nesting birds (Walters et al. 2002)

One of the major sources of food for nesting Red-naped Sapsuckers is sap from trees and shrubs, including three large species of willows: *Salix drummondiana* (Piper), *S. boothii* (Andersson), and *S. brachycarpa* (Nutt.). In the upper East River Valley near the Rocky Mountain Biological Laboratory, Gothic, Colorado, Daily et al. (1993) found evidence that Red-naped Sapsuckers prefer to nest less than 100 m from willows. However, sapsuckers also commonly feed at willows more than 200 m from their nests (C. Floyd, unpublished data). Sap from willows is acquired by drilling small holes that penetrate the phloem of the willow stem (Walters et al. 2002). Sap wells not only provide food for sapsucker adults and their young, but also for several other animals such as hummingbirds, rodents and insects that rob the wells (Daily et al. 1993). The ecological importance of red-naped sapsuckers is well-documented (Dailey et al. 1993, Walters et al. 2002); however little is known of the actual relationship between the Red-naped Sapsucker and the willow plants. Although, plant-herbivore interactions are well studied and complex plant responses to herbivory have been documented, important details of these interactions are not completely understood (Baldwin and Preston 1999). Some plants respond to herbivory with systemic direct defenses that increase the plant's resistance to further herbivory, increasing or decreasing growth or changing resource allocation; this can induce a change in the behaviors or foraging patterns of the herbivore. Defensive responses by the plant can motivate an herbivore to move its foraging to a different part of a plant or to another plant altogether (Baldwin and Preston 1999). It is common to observe Red-naped Sapsuckers foraging on multiple branches of a single willow as well as multiple willows in a single willow patch, but little is known about how the sapsuckers choose which willows to forage in or how they choose individual branches on which to drill their wells. It is not well understood whether this behavior is a response by the sapsuckers to an existing defensive mechanism of the willows, or if the willows are compensating for the effects foraging, or possibly a combination of both. Many plants that suffer from herbivorous predators exhibit defensive mechanisms such as the production of secondary metabolites that act as toxins, protective anatomical features, or other deterrents that reduce the palatability of the plants (Elseth et al. 1981). It is unknown whether the willows preferred by Red-naped Sapsuckers possess such defensive mechanisms against sap well feeding; however, a coevolutionary arms race between the sapsuckers and the willow plants is possible. One explanation could be that the sapsuckers avoid individual willows that have stronger defenses and prefer willows that have weaker defenses. Another explanation could be that certain individual willow shrubs may produce more sap than other individual willow shrubs. In this case the sapsucker should show a preference for willows that would provide the most sap.

To better understand the evolutionary relationship between the Red-naped Sapsuckers and the three species of willow that act as a primary food source, it is important to observe the sapsuckers' foraging behaviors and identify patterns that may signify particular preferences for willows of certain physiological conditions. It is also important to reveal physiological effects on willows as a result of past sap foraging that

may influence the likelihood of future foraging. This study investigated the sap-foraging patterns of Red-naped Sapsuckers in willows in the upper East River Valley, near Gothic, CO. The objective was to reveal any foraging patterns and preferences by the sapsuckers by measuring feeding patterns on stems. We hypothesized that the probability of a sapsucker choosing a willow shrub for sap foraging is partially a function of the frequency of past sap-well excavation on the shrub and related physiological conditions, namely number of stems that were injured or killed by sap-well excavation. Studying the Red-naped Sapsucker and willow plant-herbivore interaction will lead to a better understanding of the coevolutionary responses between the species and a better understanding of the coevolution of the organisms within a community.

Methods

I conducted this study at the Rocky Mountain Biological Laboratory and surrounding areas in Gunnison, Co Colorado, USA. Sites were selected by using Google Earth to locate willow patches. Twelve sites were chosen; these were comprised of small, amorphous, non-riparian clumps that were isolated from the large willow patches that can be found in the Upper East River Valley. Each selected patch was located within 200 meters of an aspen grove infected with aspen heartrot fungus (*Phellinus tremulae*), nesting habitat for Red-naped Sapsuckers. Current Red-naped Sapsucker nests were found in the aspen groves near many of the sites and old sapsucker nests were found in the aspens at every site. Sapsuckers were seen foraging, pecking was heard and offspring were heard at most of the sites.

Individual willows were randomly selected by overlaying a numbered grid on Google Maps and using a random number generator to select 10 coordinate points at each site. The willow at or nearest the selected point was measured. If the point was equidistant from two or more willows a single willow was randomly selected by blindly spinning a compass for several turns. The closest willow in the direction the compass landed was used in the study. In a few cases the chosen coordinate was at a point where an individual willow could not be distinguished from the surrounding willows or was in a location that could not physically be reached. In these cases a willow was chosen by traveling to the nearest open area and randomly spinning the compass. The willow located nearest in the direction the compass pointed was used. For each selected willow exact coordinates were recorded. A sample of 5-10 leaves and a single flower or catkin (when present) were collected for later species identification using *Colorado Flora* by Weber and Wittmann (1996). Each willow was marked with blue flagging tape and assigned a number along with the location.

Each branch (dead and available) was counted and marked with a blue tree crayon. Branches included in the count were primary, secondary and tertiary branches greater than 5.0 millimeters in diameter. Primary branches were defined as those growing directly from the trunk of the willow, secondary branches as those growing directly from the primary branches, and tertiary branches as those growing directly from the secondary branches. The trunk is defined in this study as largest portion of the willow protruding from the ground. On some of the measured individuals the trunk was not visible above ground, and the primary branches were defined as any branch growing directly from the ground. Primary branches located > 20 cm from the trunk or cluster of primary branches forming the shrub were considered part of a separate shrub and were not included in the

count for that shrub. Additionally, the number of dead branches was recorded (separately from the number of total branches). Branches were considered dead if they were (1) heavily damaged or broken, (2) showed no leaves, flowers, catkins, (3) were rotting, or dry or brittle. Branches included in the count were considered available for foraging if they were primary, secondary, or tertiary, had a diameter no smaller than 0.5cm, and were alive.

Branches containing sap wells were classified according to the amount of damage around the sap wells (1 = the sap wells were fresh and ranged from still wet with sap to moderately dry. Exposed tissue was still light in color, the branch was healthy with no other signs of stress; 2 = the sap wells were completely dry and scar tissue was visible, the branch is healthy and flowering; 3 = the branch was beginning to show signs of stress and was less healthy but flowering some, smaller branches above wells were showing signs of stress, less healthy but flowering some, branches below sap wells are healthy and flowering; 4 = the branch was under extreme stress and was dying, some smaller branches were still flowering but most dead or dying, the branch was bending or breaking in the areas around the sap wells, the bark was beginning to peel away from sap wells; 5 = the branch was obviously dead or broken above or below sap wells, the bark was peeling or completely peeled away from sap wells, there were no living smaller branches, no leaves and no flowering; Figure 1) Each branch was recorded as being primary, secondary or tertiary. The diameter of the branch was measured at the midpoint of the set of sap wells with calipers. The midpoint is considered to be halfway between the top of the highest well up the branch and the bottom of the lowest well down the branch of a single set of wells.

All initial data collection at each site was completed on the same day it was started. A second visit was made to each site after initial data was collected from all twelve sites and after a minimum of one week from initial data collection to check for new sap wells.

To determine correlations between variables simple regression models were used. The proportion of available branches containing new sap wells per willow (dependent variable) was compared to the proportion of dead branches per willow (independent variable) to determine the likelihood a willow would acquire new sap wells. The proportion of branches with old sap wells (independent variable) was compared to the proportion of dead branches (dependent variable) to determine if there is relationship between the amount of past foraging and the amount of dead branches found on a willow present. The proportion of primary branches with old sap wells (independent variable) was compared to the proportion of dead branches (dependent variable) to determine if a relationship between the amount of past foraging on primary branches and the amount of dead branches found on a willow was present. The proportion of branches with old sap wells (independent variable) was compared to the proportion of available branches with new sap wells (dependent variable) to determine if a relationship between the amount of past foraging and the amount of future foraging was present. Data were analyzed by using JMP 9.0.2 (SAS Institute Inc. 2010)

Results

There was a significant negative correlation between the proportion of dead branches and the proportion of available branches with new sap wells ($F\text{-ratio} = 32.0086$,

$DF = 1$, $P = <0.0001$; Fig. 2). As the proportion of dead branches increased the proportion of available branches with new sap wells decreased, thus less foraging took place on willows with a higher proportion of dead branches (Fig. 2).

There was a significant positive correlation between the proportion of branches with old sap wells and the proportion of dead branches ($F\text{-ratio} = 21.5670$, $DF = 1$, $P = <0.0001$; Fig. 3). As the proportion of branches with old sap wells increases the proportion of dead branches increases (Fig. 3).

There was a significant positive correlation between the proportion of primary branches with old sap wells and the proportion of dead branches ($F\text{-ratio} = 4.5097$, $DF = 1$, $P = 0.0358$; Fig. 4). As the proportion of primary branches with old sap wells increased the proportion of dead branches increased (Fig. 4). There was no significant correlation between the proportion of secondary branches with old sap wells and the proportion of dead branches ($F\text{-ratio} = 0.0983$, $DF = 1$, $P = 0.7554$; Fig. 5). There was no significant correlation between the proportion of tertiary branches with old sap wells and the proportion of dead branches ($F\text{-ratio} = 2.8097$, $DF = 1$, $P = .0963$; Fig. 6).

There was no significant correlation between the proportion of branches with old sap wells and the proportion of available branches with new sap wells ($F\text{-ratio} = 2.7049$, $DF = 1$, $P = 0.1027$; Fig. 7).

Discussion

The purpose of this study was to investigate the foraging behaviors of the Red-naped Sapsucker to determine their foraging patterns that may suggest preferences for willow shrubs based on several variables. It was found that the amount of new foraging on willow shrubs had a significant negative correlation to the proportion of dead branches but, surprisingly, not to the amount of past foraging. It was also found that the proportion of dead branches had a significant positive correlation to past foraging on primary branches but there was no significant correlation to secondary or tertiary branches.

The results support the hypothesis that the proportion of available branches on a willow shrub that will receive new sap wells is negatively correlated to the proportion of dead branches. As the proportion of dead branches increases the proportion of available branches with new sap wells decreases, which suggests that Red-naped Sapsuckers are more likely to forage upon willow shrubs that have a lower proportion of dead branches.

A positive correlation between the proportion of branches with old sap wells and the proportion of dead branches suggests that a higher amount of sap foraging leads to a higher amount of branch death since willow branches that have been foraged on by sapsuckers typically die within one year of the sap wells being drilled (Daily et al. 2003). A higher proportion of dead branches can be an indication of a less healthy shrub which has a lower level of sap production and a less favorable food source for the sap suckers. There is a positive correlation between the proportion of primary branches with old sap wells and the proportion of dead branches; however there is no significant correlation between the proportion of secondary or tertiary branches with old sap wells and the proportion of dead branches. When a primary branch with old wells is dead the secondary and tertiary branches originating from it are also typically dead (*pers. obs.*). This could explain the relationship between the amount of primary branches that has been foraged on in the past and the amount of dead branches found on each willow. It is possible that primary branches have higher sap flow and are thus preferred to secondary and tertiary

branches by sapsuckers. An alternative is willow shrubs may have a higher number of available primary branches than secondary or tertiary branches (i.e. some shrubs may be lacking secondary or tertiary branches, secondary or tertiary branches may be too small for foraging). This pattern suggests a preference for primary branches by the sapsuckers, possibly due to access to a better sap source or to a greater availability or access to a sap source. There is no significant correlation between the proportion of total branches with old sap wells and the proportion of available branches with new sap wells however there is a trend toward negative correlation. This suggests that the number of branches foraged on in the past does not determine the number of branches that will be foraged on in the future but may decrease the likelihood of future sap foraging.

A preference for certain individual willow shrubs over others shows that the sapsuckers are utilizing particular willows as a food source and not utilizing others, suggesting variation in sap production among individual willows. These individual variations may be the result of physical or physiological adaptations, or responses by individual willows to foraging that causes the herbivores to move from tissues with stronger direct defenses (a willow that is able to endure a huge loss and respond with a stronger resistance to herbivory) to tissue that has weaker direct defenses (a willow that is less capable of resisting herbivory) (Baldwin and Preston 1999). It is common for plants to slow growth during periods of stress and limited resource availability. This slow growth typically favors stronger antiherbivore defenses, thus an alternative explanation for this behavior could be that the sapsuckers prefer willows with a lower proportion of dead branches due to the fact that those individual willows are healthier, faster growing and have greater sap production and higher nutritional payoff than individuals with a higher proportion of dead branches (Coley et al 1985). It is unknown whether the willow plants preferred by the Red-naped Sapsuckers follow either pattern or possess any such defense mechanisms and further studies would need to be conducted to determine if a higher proportion of dead branches increases the willow's ability to resist foraging or decreases the willow's ability to produce phloem sap. It can be speculated, however, that there is a possible coevolutionary arms race occurring between the sapsuckers and the willow plants where the foraging patterns of the sapsuckers suggest a response to the compensation by the willow shrubs.

Our results suggest that sapsuckers do show a preference for individual willows and this preference decreases with a higher amount of past sap well excavation and branch death experienced by the shrub. This negative relationship is likely due to reduced health of the shrub as a result of sap foraging and leads to reduced sap flow potential. As a result, Red-naped Sapsuckers prefer to feed from healthier willow shrubs. Further study should be conducted to determine if this negative relationship is a result of decreased sap production in the willows or a response by the sap suckers to a reduction in the amount of branches available for foraging. Understanding the relationships recognized in this study will lead to a greater understanding of this plant-herbivore interaction. As a keystone species in the Colorado Rocky Mountains, the Red-naped Sapsucker plays a vital role in the continued existence of many other species of animal and insect. By observing how the Red-naped Sapsucker interacts with other species in its community we can begin to understand if and how the sapsucker is coevolving with these species, how this coevolution is affecting an ecosystem as a whole, and we can begin to predict what might affect this ecosystem in the future.

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Figures



Figure 1. Classification of branches with sap wells.

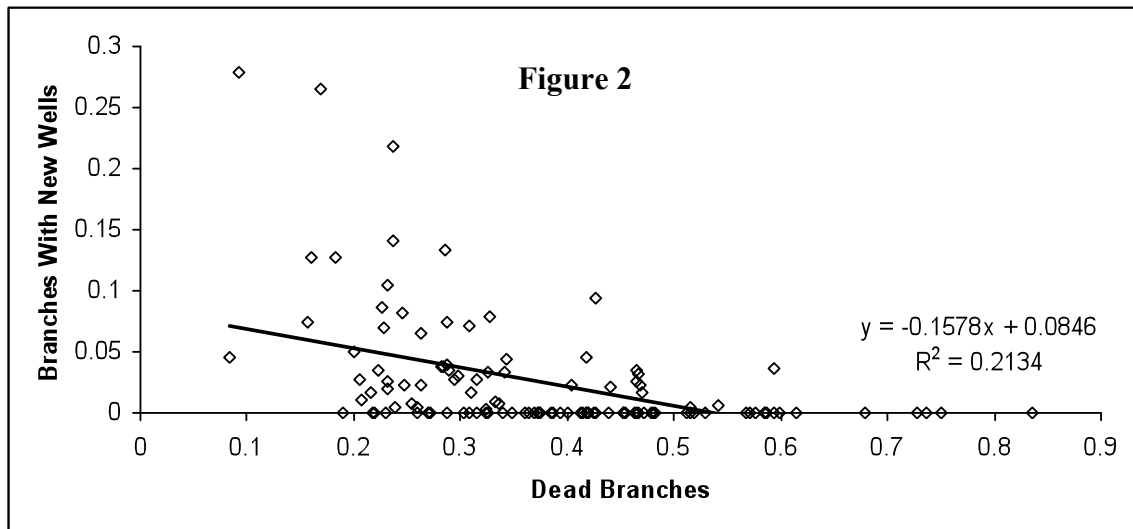


Figure 2: Incidence of new sap wells seen on available branches versus prevalence branches that were dead. Proportion of new sap wells on available branches was plotted as a function of and regressed against the proportion of branches that were dead on the same willow shrub.

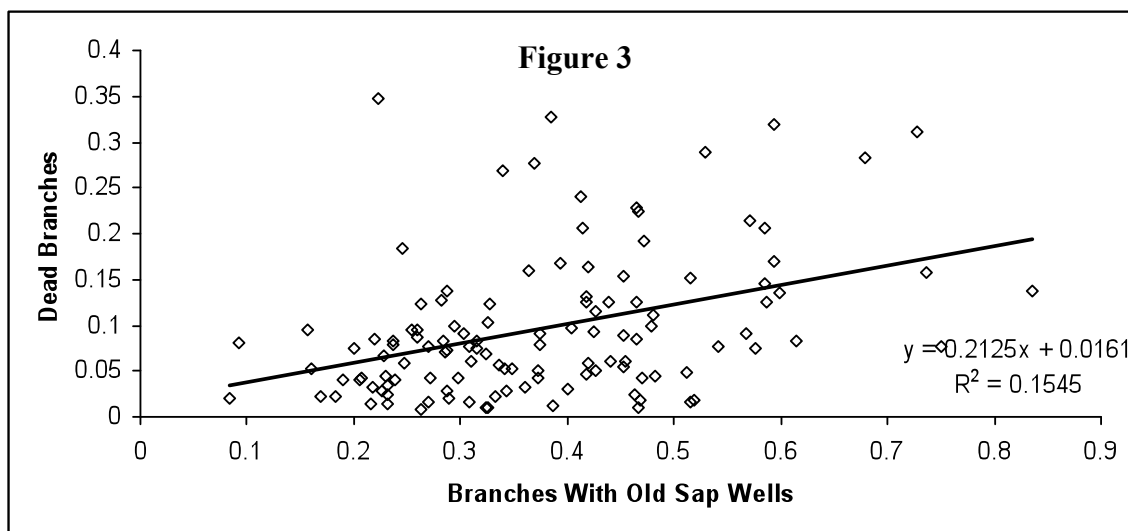


Figure 3: Prevalence of dead branches versus the incidence of old sap wells on branches. The proportion of branches that were dead was plotted as a function of and regressed against the proportion of branches with old sap wells.

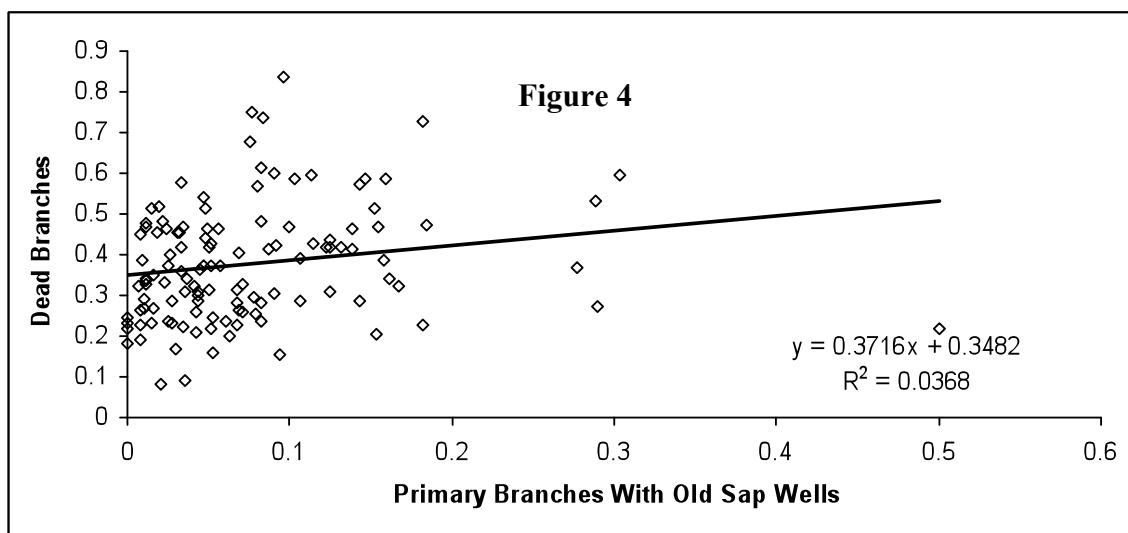


Figure 4. Prevalence of dead branches versus the incidence of old sap wells on primary branches. The proportion of branches that were dead was plotted as a function of and regressed against the proportion of primary branches with old sap wells.

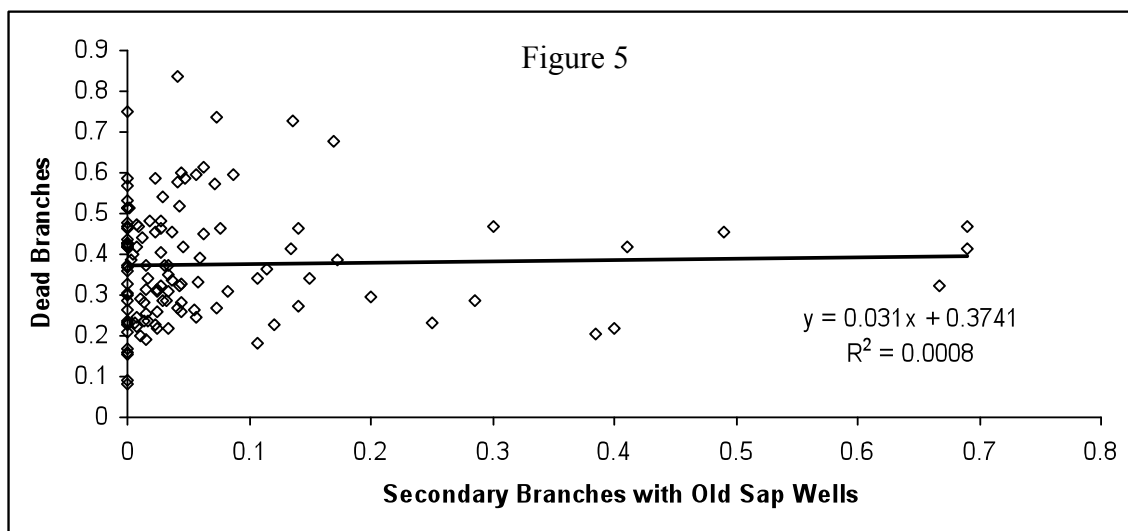


Figure 5. Prevalence of dead branches versus the incidence of old sap wells on secondary branches. The proportion of branches that were dead was plotted as a function of and regressed against the proportion of secondary branches with old sap wells.

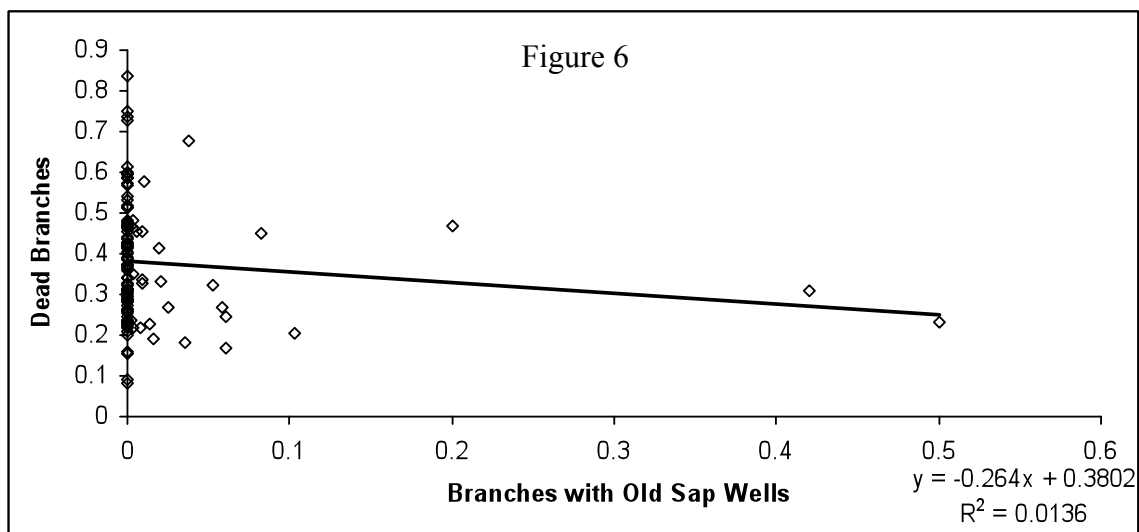


Figure 6. Prevalence of dead branches versus the incidence of old sap wells on tertiary branches. The proportion of branches that were dead was plotted as a function of and regressed against the proportion of tertiary branches with old sap wells.

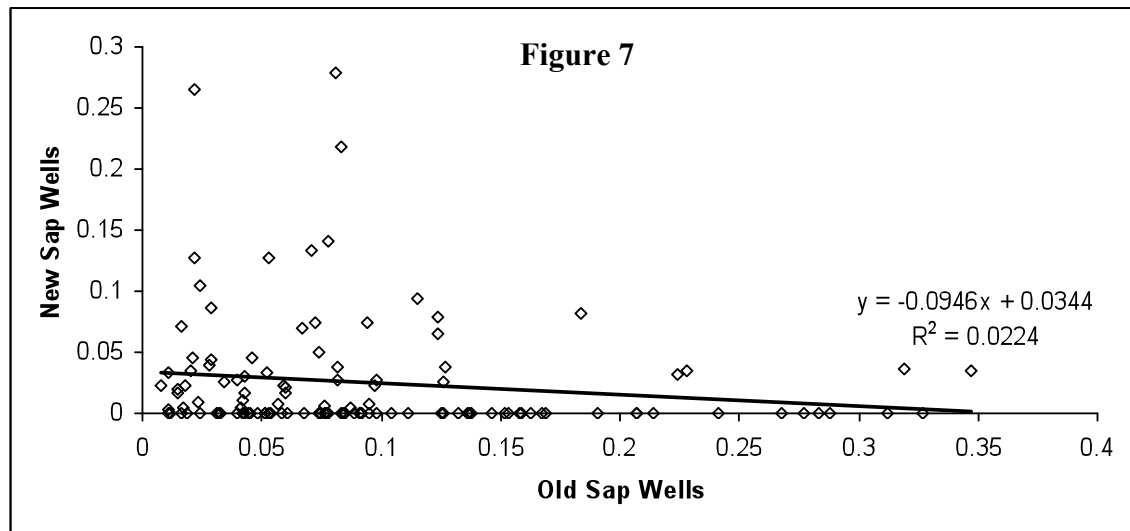


Figure 7. Incidence of new sap wells seen on available branches versus incidence of old sap wells on branches. Proportion of new sap wells on available branches was plotted as a function of and regressed against the proportion of branches with old sap wells.