5-2014

Developing a Field Indicator for Suckering Ability of Quaking Aspen

Abbey M. Hudler Oksness
Utah State University

DEVELOPING A FIELD INDICATOR FOR SUCKERING ABILITY OF QUAKING ASPEN

by

Abbey M. Hudler Oksness

A thesis submitted in partial fulfillment
of the requirements for the degree

of

MASTER OF SCIENCE

in

Forestry

Approved:

Frederick A. Baker Major Professor	James N. Long Committee Member
Helga Van Miegroet Committee Member	Mark R. McLellan Vice President for Research and Dean of the School of Graduate Studies

UTAH STATE UNIVERSITY
Logan, Utah

2014

ABSTRACT

Developing a Field Indicator for Suckering Ability of Quaking Aspen

by

Abbey M. Hudler Oksness, Master of Science

Utah State University, 2014

Major Professor: Dr. Frederick A. Baker
Department: Wildland Resources

Many quaking aspen (*Populus tremuloides*) stands throughout western North America are considered mature, overmature, or decadent, and lack root suckering to replace the overstory mortality. To mimic natural disturbance and stimulate aspen suckering, prescribed burning or harvesting is needed. It is important to identify pre-disturbance indicators so that land managers will have a way to assess potential sucker production resulting from a prescribed treatment.

In fall 2011, eight field sites were located in the Cedar Mountain study area in southern Utah, and two field sites were located on Deseret Land and Livestock land in northern Utah. At each site, two aspen stands were selected within 50 m of each other, one having a relatively low live aspen basal area and one stand having a relatively high live aspen basal area. Above- and belowground pre-disturbance site characteristics for each paired plot were measured and compared. In spring 2012, all trees within 12.2 m (40 ft) of plot center were felled to stimulate a suckering response from the root system.

Root diameter and root surface area proved to be the best predictors of sucker regeneration density after a disturbance. Sucker densities decrease with increasing root diameters, and most suckers are produced on roots less than 2.5 cm in diameter. The highest sucker densities were recorded on plots which contained abundant roots less than 2.5 cm in diameter. A simple methodology for sampling aspen roots in the field is outlined and is based on the relationship between root diameter, root surface area and sucker production. There was no relationship between total nonstructural carbohydrate (TNC) concentration in the roots (measured as starch and water soluble carbohydrates (WSC), % dry weight) and sucker density, indicating that TNC concentration cannot be used as an indicator of sucker ability of aspen after a disturbance. This study also documents the effect of herbivory on sucker height. In areas where grazing and browsing pressures were great, sucker potential was severely decreased due to the effects of repeated hedging below the browse line or complete sucker elimination. If aspen are to persist on the landscape under these circumstances, management strategies must be implemented to enhance aspen regeneration.

(90 pages)

PUBLIC ABSTRACT

Developing a Field Indicator for Suckering Ability of Quaking Aspen

Abbey M. Hudler Oksness

Quaking aspen is an ecologically valuable deciduous tree species in the high elevation environment typical across many parts of western North America. It is a clonal tree species which primarily depends on vegetative regeneration by root suckering after an aboveground disturbance, e.g., wildfire, removes the stems. A flush of suckers will be stimulated after a disturbance and the resulting regeneration relies on available resources from the undamaged root system for resprouting. Due to wildfire suppression efforts of the last century, many aspen stands are considered mature, overmature, or decadent and lack regeneration to replace the overstory mortality. In the absence of natural disturbance, direct management intervention in the form of prescribed burning or harvesting is needed to ensure the survival of aspen-dominated communities. In order to identify which aspen stands should be targeted for priority treatment, it is important to develop a pre-disturbance field indicator that can be used as a predictor of sucker ability.

The objectives of this study were to (1) examine the relationship between individual/ general root characteristics and aboveground metrics of stand deterioration, (2) examine the relationship between individual/ general root characteristics and the number and height of suckers produced after a managed disturbance, and (3) develop a simple method for sampling roots in the field. This third objective was developed to provide foresters and land managers with assistance in making decisions on aspen

regeneration capacity and also to contribute to the understanding of the future health of the stand.

This study identified two root characteristics that can be used as predictive field indicators of quaking aspen sucker ability after a disturbance. Root diameter and root surface area proved to be the best predictors of regeneration density after a disturbance. All in all, the highest sucker densities were recorded on plots which contained abundant roots measuring less than 2.5 cm in diameter, indicating that most root suckers originate from small diameter roots. My results also document no relationship between carbohydrate concentration in the roots and sucker density, indicating that carbohydrate concentration cannot be used as an indicator of sucker ability.

Excessive browsing of aspen regeneration by wild and domestic ungulates has become one of the primary topics of concern regarding overall aspen decline in western North America. My study points to the importance of aspen suckers rapidly growing above the herbivore browse line, so that a certain amount of leaf area can be maintained and root reserves do not become exhausted. If browsing is excessive, aspen suckers will repeatedly be hedged below the browse line or browsed down to the ground and completely eliminated.

ACKNOWLEDGMENTS

I want to express sincere gratitude to all of the individuals who helped me along the way and ultimately towards the completion of this project. First and foremost, thank you to my advisor, Dr. Fred Baker, who has been the guiding force behind everything that I have accomplished during my time at USU. I also want to thank my committee members, Dr. Jim Long and Dr. Helga Van Miegroet, for their advice and suggestions.

Dr. Shaun Bushman, Lisa Michaels, Kim Thorsted, and Tyler Taylor of the USDA research lab in Logan provided instrumental assistance with the carbohydrate analysis. Chad Reid and Sarah Sampson were especially important in helping me locate appropriate study sites, and make contact with available field help and with landowners. Scott Schmidt and Nicholas Jacobsen of Cedar City were great field hands to have on board for this project and I greatly appreciate the long hours they dedicated.

I am especially appreciative of all of the landowners who showed interest in this study and allowed me to access their land. Without their cooperation and understanding this project would not have been possible. Thank you to Dennis Flanigan, Dick Webster, Rick Middleton, Sharon Wright, Howard Jones, Tom Williams, Colin Rose, and Jared Cornelius of Cedar City. Thank you to Deseret Land and Livestock, especially Rick Danvir and Todd Black.

Last but not least, thank you to my husband, Jamison Oksness, who was endlessly supportive through this entire process.

Abbey M. Hudler Oksness

CONTENTS

Page

LIST OF TABLES

Table Page

LIST OF FIGURES

Figure Page

CHAPTER I

INTRODUCTION

Quaking aspen (*Populus tremuloides* Michx.) is an ecologically valuable deciduous tree species in the high elevation environment typical across many parts of western North America. Most importantly it provides watershed protection, forage and habitat for big game and livestock, and overall increases the esthetic value of the montane landscape (Collins and Urness, 1983; McCool, 2001; Desilets et al., 2007). Mortality of this species has increased over the past 15 years, most notably along the southwestern edge of continuous aspen habitat in areas such as Arizona and northern Mexico (Zegler et al., 2012). In addition, rapid increases in quaking aspen mortality have been reported across the Intermountain West (Bartos and Campbell, 1998a; Bartos, 2001; Worrall et al., 2008) and farther north into the prairie provinces of Canada (Hogg et al., 2008). This decline is relatively widespread throughout the region and has been largely attributed to multiple factors including fire suppression, extreme weather events such as severe drought and high temperatures, overbrowsing by ungulates, and natural forest succession to a conifer-dominated overstory (Schier, 1976; Kaye et al., 2005; Zegler et al., 2012).

Quaking aspen is a clonal tree species. It depends primarily on vegetative regeneration by root suckering after an aboveground disturbance, e.g., wildfire, removes the stems or ramets, altering the flow of two hormones, cytokinin and auxin (Bancroft, 1989). Instances of large-scale successful seedling establishment have been reported after stand replacing fires (Quinn and Wu, 2001). Sexual reproduction among aspen is essential for maintaining genetic diversity and variation at the population level (Mock et al., 2008). However, sexual reproduction or seeding events are relatively rare and episodic in the Intermountain West (Mitton and Grant, 1996) and should not be relied on as a means for successful reestablishment.

Many quaking aspen stands in western North America are considered mature, over-mature, or decadent, and lack root suckering to replace the overstory mortality. As these stands deteriorate, some suckering may occur from the root system (Bartos, 2001) but new suckers are often consumed year after year by wild or domestic ungulates as a preferred source of browse (Kaye et al., 2005; Jones et al., 2011). Repeated destruction of new suckers leads to regeneration failure and an overall reduction in vigor (Schier, 1976; Bartos, 2001) (Fig. A.1). In efforts to mimic natural disturbance and stimulate aspen suckering, direct management intervention in the form of prescribed burning or harvesting is needed to ensure the survival of aspen-dominated communities (Mueggler, 1989). Land managers are often uncertain whether decadent stands will regenerate after a prescribed treatment. However, we know that without implementation of regeneration strategies these stands are at risk of rapid deterioration and likely conversion to grasslands, shrublands, or a conifer-dominated overstory.

Purpose of Study

The rapid recovery of tree species capable of resprouting after disturbance is largely dependent on available resources, including carbohydrates, nutrients, and water, from the undamaged root system (Iwasa and Kubo, 1997; Zhu et al., 2012). Many factors may play an important role in aspen sucker initiation and growth. Frey et al. (2003) suggested that the variability in sucker development between sites is, “a function of root abundance and distribution within a stand following disturbance, the physiological and environmental condition of roots, and growing conditions under which the suckers establish."

Total nonstructural carbohydrates (TNC) in plant roots consist of starch plus water-soluble carbohydrates (WSC), which are made up of mono- and disaccharides, oligosaccharides, and fructans. After a disturbance, TNC reserves in the parent root system are consumed for respiratory maintenance of the surviving root system and the production and respiratory maintenance of new suckers (Wachowski et al., 2014). After initiation, suckers need energy for shoot growth until the shoot grows above the soil surface, develops leaf tissue, and begins photosynthesis (Schier, 1976).

The relationship between quaking aspen regeneration potential and TNC reserves in the roots is unclear. Root carbohydrate reserves have been used as an indicator of host vigor in several hardwood tree and shrub species (Wargo et al., 1972; Bond and Midgley, 2001), but this relationship has not been explored in aspen. This research quantified TNC root reserves and other variables associated with aspen roots, including root diameter and root surface area, and evaluated the use of these variables as indicators of host vigor and of an aspen stand's ability to produce abundant suckers following treatment. After examining these relationships, we can identify and quantify an aspen stand which could potentially be losing the ability to produce ample suckers post-treatment. Until now, this has been relatively subjective in nature. I also modified a simple method for sampling roots in the field, thereby providing foresters with a tool to assist in predicting which stands may produce suckers after treatment and which stands may not. Overall, the goal of this research project was to examine the relationship between root variables and other stand variables on sucker production after a managed treatment or disturbance, e.g. clearcutting, controlled burning.

Research Objectives and Hypotheses

This study looked at selected site-related variables including pre-disturbance stand conditions and individual root characteristics as well as general rooting characteristics, in order to assess potential sucker production resulting from a disturbance or prescribed treatment.

The objectives of this research were:

1. Examine the relationship between individual/general root characteristics and aboveground metrics of stand deterioration.

- H_0: A significant relationship exists between individual/general root characteristics (measured variables include starch and WSC concentrations (i.e. TNC concentration), root diameter, and root surface area) and aboveground metrics of stand condition (measured variables include live aspen basal area, sapwood basal area, and site index). This would indicate that a belowground component does exist in stand deterioration.
- H_a: No significant relationship between one or more of the above sampling variables.

2. Examine the relationship between individual/general root characteristics, and the number and height of suckers produced after a managed disturbance. The purpose of this second objective was to provide predictive information about the state of aspen stands

post-treatment, allowing foresters and land managers to target stands requiring priority treatment.

- H_0: A significant relationship exists between individual/general root characteristics and the number or height of suckers produced after a managed disturbance, which would indicate a difference in suckering potential between aspen stands.
- H_a: No significant relationship between one or more of the above sampling variables.

3. In the case of a significant interaction between root carbohydrate reserves and sucker production after a disturbance, a third objective will evaluate a simple, field-based assessment of root starch as a predictor of suckering ability. Root segments will be stained in the field and the stain intensity, and therefore root starch, will be categorized as high, medium, low or depleted. In the case of a significant interaction between other root variables (diameter, surface area) and sucker production, the objective will instead involve the development of a simple method for sampling roots in the field. Overall, the goal in either case is to develop an assay that will assist foresters and land managers in making decisions on aspen regeneration capacity and will also contribute to the understanding of the future health of the stand.

CHAPTER II

LITERATURE REVIEW

General Species Introduction

Quaking aspen has the largest distribution of all tree species in North America. It commonly occurs in large swaths of continuous habitat coinciding with the boreal forest region as far north as Alaska, and in highly segmented habitats on warmer and drier sites towards the southernly edge of its distribution in northern Mexico (Baker, 1925; Sargent, 1961). Throughout its range, quaking aspen shows large variation in size, form, and growth, all three of which are intimately tied to the growing environment. They can vary from a twisted dwarf shrub with a height of less than 2 m to straight stems easily reaching heights of 15.2 to 27.4 m and 30.5 to 61.0 cm in diameter. Mitton and Grant (1996) performed an experiment in Waterton Lakes National Park, Alberta, Canada, using multiple linear regression to predict growth rates of aspen as a function of elevation, slope position, age, and exposure to the wind. This study revealed that growth rate declined with increasing elevation, steepness of the slope, age of the ramet, and exposure to wind.

Quaking aspen is often the only deciduous tree species present in the high elevation environment typical throughout parts of western North America. The climate is severe over the winter months, with freezing temperatures commonly occurring for four to five consecutive months and moisture in the ground freezes (Bailey, 1998). The dominance of conifers such as pine, fir, and spruce over angiosperms is a reflection of the harsh environmental conditions that tend to favor coniferous survival and growth over that of angiosperms in general.

Quaking aspen has evolved certain physiological traits which allows for its survival with increased latitude and elevation. Primarily, it has relatively soft, moderately specialized, and diffuse-porous wood, all characteristics that allow for the species survival when temperatures drop below freezing and ice crystals form between the cells (versus within the cells, which can be lethal) (Cronquist, 1988). Due to the smaller diameter of the pores or vessels in the wood of diffuse-porous species, gas embolisms are more easily dissolved in the spring than in ring-porous species. This results in diffuse-porous species maintaining a higher number of functional vessels and subsequently ten or more functional rings. In comparison, ring-porous species are more susceptible to gas embolisms, which often render the vessels non-functional and results in only the current rings maintaining functionality (personal communication, Dr. Terry Sharik, Utah State University, Logan, UT, 2011).

Secondarily, in quaking aspen, the bark lives and carries out photosynthesis, attributes that make it unique among North American trees. The soft tan to greenish hues of the bark visually mark this important physiological trait, which is a result of the presence of chloroplasts in the phelloderm (Strain and Johnson, 1963; Foote and Schaedle, 1978). Foote and Schaedle (1978) found that carbon dioxide was assimilated by the bark tissue at different rates over the course of a year. Of the total annual carbon dioxide fixed by the stem; 27% was fixed during the months of March through May; 59% was fixed June through August; 10% was fixed September through November; and 4%

was fixed December through February. With the absence of leaves in the winter months, cortical photosynthesis contributes significantly to the carbohydrate supply of the aspen stem. However, the disadvantages of this type of bark includes susceptibility to attack by insect, disease, and low fire resistance (Strain and Johnson, 1963). Overall, it is likely that these two physiological traits (diffuse-porous wood and photosynthetic bark) of quaking aspen are responsible for the impressive geographic range and overwintering survival capabilities of the species.

Ecologically, the distribution of quaking aspen is a highly integrated and essential component of the natural environment across the Northern Hemisphere. As with many other tree species, aspen has associated species (i.e. plants, fungi, insects, birds, and mammals) that depend upon its presence for a variety of functions including protection, creation of essential habitat, and food sources. Campbell and Bartos (2001) label quaking aspen as a keystone species, primarily due to the biodiversity that aspen communities support when compared to other ecosystems and forest types in the Intermountain West. Campbell and Bartos use the following passage from Wilson (1992) to define a keystone species: “A species that affects the survival and abundance of many other species in the community in which it lives. Its removal or addition results in a relatively significant shift in the composition of the community and sometimes even in the physical structure of the enivironment.” We can see this is especially true of quaking aspen in terms of supporting wildlife habitats and providing food sources. Some examples from the literature that support aspen’s classification as a keystone species include: 1) Large mammals, such as mule and white-tailed deer, elk, moose, and mountain sheep, primarily consume the twigs and buds for browsing materials over the winter and the foliage during the summer (Martin et al., 1951); 2) Beavers use the branches for dam and lodge construction and consume the inner bark as a preferred food source, with few other trees being cut where these are present (Van Dersal, 1938); and 3) Numerous wild bird species such as grouse, quail, prairie chicken, finch, towhee, and grosbeak, get valuable nutrition from consumption of the buds and catkins, as well as essential nesting habitat (Martin et al., 1951). Overall, it is clear that sustaining aspen communities on the landscape and throughout its historical abundance would potentially fulfill multiple objectives outlined for management of biodiversity throughout the Intermountain West.

Decline of Quaking Aspen in the Intermountain West

Repeat aerial photographs and comparisons between historical and current data compilations from the Rocky Mountain Research Station's Forest Inventory and Analysis (FIA) surveys are two ways scientists can evaluate the decline of quaking aspen on the landscape over time. Zegler et al. (2012) classified aspen decline into two groups: 1) A reduction in aspen forest type driven mostly by successional processes under altered disturbance regimes, and 2) A rapid and synchronous mortality of aspen due to a complex of predisposing (e.g. site and stand conditions), inciting (e.g. episodic drought), and contributing factors (e.g. fungi or insects).

Wildfire suppression efforts made throughout the last century have clearly altered the historical disturbance regime that promotes quaking aspen in the landscape. Shepperd (1990) performed a survey of aspen stands in the central Rocky Mountains and found that there was a predominance of mature to overmature stems in the overall stand structure of many aspen dominated forests. The connection between fire suppression and stand deterioration has been proven (Gruell and Loope, 1974; Romme et al., 1995). Fire is an essential component of aspen ecology on a landscape scale and will successfully stimulate a flush of stand-replacing regeneration (Baker, 1918). However, in areas where ungulate pressure is great, repeated grazing or browsing of newly formed suckers not only exhausts carbohydrate reserves in the roots (Schier, 1976), but also reduces sucker densities (Romme et al., 1995), putting the stand at risk for future stocking and stand replacement issues.

Periods of extreme drought, high temperatures, or sudden and unexpected frost events can cause acute stress on trees and accelerate mortality. Fairweather et al. (2008) reported an accelerated rate of aspen mortality across the Coconino National Forest in northern Arizona following a frost event in June 1999, and a period of severe drought and extreme high temperatures from 2001 through 2002. They observed aspen mortality of 95% on low-elevation (<2286 m) xeric sites, 61% mortality on mid-elevation (2286-2590 m) sites, and 16% mortality on high elevation (>2590 m) more mesic sites. Worrall et al. (2008) reported similar findings on the Mancos-Dolores Ranger District in the San Juan National Forest, south western Colorado. They found rapid increases in aspen mortality where the area affected increased 58% between 2005 and 2006, confirming field observations that most of the aspen mortality occurred rapidly and recently, over a span of 3 years or less. These studies have many implications for the future of quaking aspen in the arid landscapes of the Intermountain West, and suggest mortality will rise as global climate change is expected to increase the frequency and severity of extreme weather events around the world.

In terms of natural forest succession, quaking aspen plays a very important role in the post-disturbance regime as a primary pioneer species. It is common for aspen to dominate the overstory with shade tolerant coniferous species such as subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.) as the understory species in historically burned or disturbed areas during secondary succession. Aspen provide protection and nutrients, facilitating the establishment of slower growing conifers. The conifer seedlings thrive in the moist, shaded understory, eventually stretching above the original pioneers. This change from shade to sun in coniferous growth marks the beginning of the end for the trees of the first forest stage. They will essentially become "choked out" as the denser crowns of the conifers decrease the amount of available light (Weigle and Frothingham, 1911). Scientists have identified this successional pathway as one of the major causes of the decline of aspen throughout the Intermountain West (Bartos, 2001). Implications for this forest type conversion include loss of valuable forage production and wildlife habitat (Stam et al., 2008), water depletion as conifers transpire more water than aspen (Bartos and Campbell, 1998b), and alteration of the site's soil properties (Woldeselassie, 2009; Woldeselassie et al., 2012).

Regenerating Quaking Aspen in the Intermountain West

Successful seedling establishment by sexual reproduction is considered to be relatively rare for quaking aspen in the arid and semi-arid environment common throughout the Intermountain West (Mitton and Grant, 1996). Aspen is a wind-pollinated species which bears its seeds on catkins and a mature tree is estimated to produce 1.6 million seeds yearly (Maini, 1968). Capsules on the catkins typically dehisce 4-6 weeks after fertilization, which happens to coincide with snowmelt and runoff, when sites favoring seedling establishment are most abundant (Braatne et al., 1996). The seeds are classified as microbiotic and they retain their germinative capacity for only short periods of time, ranging from a few weeks to a month under natural conditions. If germination does occur, the seedlings will usually wither and die before their roots reach water. The short period of seed viability can be attributed to a relatively thin and permeable testa (Kittredge and Gevorkiantz, 1929), making the environmental conditions of the seedbed at the time of seed dispersal the most important factor in successful seedling germination and establishment. McDonough (1979) states that "aspen produces abundant germinable seeds that have no dormancy, but have critical requirements for adequate soil water through germination and early seedling growth . . . . and a bare mineral surface is favorable for emergence". McDonough also found that normal germination occurs at temperatures from 2° C to 30° C, but declined sharply when seeds were exposed to higher or lower temperatures. With these strict seedbed requirements, it seems unlikely that land managers in the Intermountain West should rely on sexual reproduction as a means of successful establishment of quaking aspen in wildland management situations. This reiterates the importance of directly managing aspen to promote root suckering via asexual reproduction for regeneration (Romme et al., 1995).

Vegetative propagation is a form of asexual reproduction and it is one of the distinct characteristics of quaking aspen (Figs. A.3, A.4). The quaking aspen root system is lateral, tending to be rather shallow and spreading in nature (Arno and Hammerly, 1977). Root suckering is the process by which a single, individual stem sends up adventitious shoots (suckers) from its root system. They arise from meristems on the roots, usually those less than 2 cm in diameter and growing near the soil surface (Schier, 1982). Meristems are formed any time during root growth, but meristem development is initiated after an aboveground disturbance (i.e. wildfire, logging, avalanche, etc.) disrupts the flow of auxin (a growth suppressing hormone) to the roots (Schier, 1973). As auxin concentrations in the roots begin to drop, the hormonal balance that previously existed in the tree shifts to favor sucker initiation. This physiological change results in a high cytokinin (a growth promoting hormone) to auxin ratio (Schier, 1976).

Once sucker development is initiated, the amount of growth depends on stored carbohydrates in the roots. Sucker elongation may be halted when root carbohydrates become depleted (Schier, 1976). The suckering process is repeated, essentially forming one interconnected genetic individual, or clone. As a result of clonal growth, whole stands of trees may be either staminate or pistillate and show identical leaf characteristics. As a result of the separation of sexes, clones often persist solely by the spread of root suckers, showing little to no sexual reproduction (Barnes, 1969). With the relatively recent suppression of wildfires over the last century, aspen clones have been stripped of the primary disturbance which promotes asexual regeneration and stems are becoming mature. As a result, the stems and root systems of many clones throughout the Intermountain West are growing decadent and losing vigor, promoting the spread of decay fungi through the interconnected root systems (Schier and Campbell, 1980).

Is My Stand Vigorous or Decadent?

The categorization of vigorous and decadent quaking aspen stands is often visually difficult and suffers from loose usage of terminology among studies. Schier (1975) suggests the definition of a deteriorating stand is one in which sucker numbers are insufficient to replace the overstory mortality. Foresters and land managers are primarily concerned with the issue of identifying which stands are capable of producing suckers after disturbance and which are not, allowing for the allocation of forest treatments where they are needed most. This marks the importance of identifying a factor, or factors, which could indicate suckering ability of aspen after disturbance and be used as an indicator in the field pre-treatment. Schier (1982) categorized a deteriorating stand as one in which death of overmature stems had reduced stocking to a basal area of less than 10 m^2/ha; vigorous stands in the area had basal areas ranging from 25 to 50 m^2/ha, suggesting that the pre-existing stand conditions may be a good indicator of sucker ability. Site index, basal area, and sapwood basal area are easily measured, but the literature is unclear as to whether or not these factors are reliable indicators of sucker ability. Schier (1975) found that sucker regeneration in “healthy” clones (average basal area of 28.4 m^2/ha) was higher than in “deteriorating” clones (average basal area of 5.1 m^2/ha), but Shepperd et al. (2001) could not find any relationship between site characteristics or climate and regenerating and non-regenerating clones, suggesting there may be a belowground component to sucker ability.

Role of Carbohydrate Reserves and Other Root Characteristics in Regeneration

After initiation, quaking aspen suckers rely on carbohydrate reserves in the parent root system for energy for bud initiation and shoot growth. This continues until the shoot grows above the soil surface, develops foliage, and begins to photosynthesize on its own (Schier, 1976). Then, photosynthates produced in the autotrophic portions of the shoot are translocated to the root system, allowing for the development of independent root systems (Galvez et al., 2011), and essentially completing the regeneration process (Schier, 1982).

Starch is the major reserve carbohydrate in the roots of deciduous trees and it is commonly consumed during the resprouting process following an aboveground disturbance (Kays and Canham, 1991). Wargo et al. (1972) suggest that starch content in the roots may be useful as an index of tree vigor of defoliated trees, finding that starch content reflected both degree and frequency of defoliation. This indicates that starch concentration in the roots is very sensitive to stresses from the environment and could be a reliable indicator of sucker ability in quaking aspen stands after a disturbance. In a resprouting experiment involving species of oak, Zhu et al. (2012) found that early resprouting of *Quercus* shrubs is “largely determined by the initial carbohydrate pool but not by the carbohydrate concentrations in roots.” In a greenhouse study, Schier (1975) found that sucker production from root cuttings taken from healthy and deteriorating clones indicated no relationship between deterioration and sucker ability, but starch concentration was not measured. All in all, the role of starch concentration in relation to stand deterioration of aspen has not been widely investigated.

Other characteristics of the root system may also be important indicators of sucker ability. Shepperd et al. (2001) found that regenerating clones had greater numbers of roots and greater total root surface area than non-regenerating clones, suggesting there may be a connection between the number of roots, root surface area, and suckering ability. They also found that the average root diameter and volume was significantly greater in one regenerating clone than in its paired non-regenerating clone, but this was not the case in the other two pairs studied.

CHAPTER III

METHODS AND MATERIALS

Study Area

Field sites were located primarily on Cedar Mountain in Iron and Washington Counties of southern Utah, and secondarily on Deseret Land and Livestock in Rich County of north eastern Utah. In general, the majority of the Cedar Mountain study area is composed of relatively flat terrain consisting of mountain meadows interspaced within quaking aspen woodlands. Cedar Mountain is both privately and federally managed and the land has been historically grazed since the 1860's by domestic sheep and cattle (Family: *Bovidae*) (Oukrop, 2010). Wild ungulate grazing by deer and elk (Family: *Cervidae*) is unregulated and occurs for most of the year, except when ungulates move to lower elevations to escape high snow levels. The vegetation responses to the impact of long-term grazing (Bowns and Bagley, 1986) in combination with strong efforts for fire suppression has likely lead to the present state of aspen stands being dominated by over-mature stems and little or no regeneration. Quaking aspen mortality on Cedar Mountain is considered by some to fall under the coined term "sudden aspen decline" (Worrall et al., 2008) within the Intermountain West, due to the rapid and synchronous mortality across a landscape-size scale (Oukrop, 2010), although this labeling is debatable.

Site Selection and Establishment

In fall 2011, eight field sites were located in the Cedar Mountain study area in southern Utah, and two field sites were located on Deseret Land and Livestock land in northern Utah. At each site two stands were selected within 50 m of each other, one stand having a relatively low live aspen basal area and one stand having a relatively high live aspen basal area. The paired stands were selected to minimize potential site differences between pairs such as slope, aspect, soil type and depth, nutrient availability, browsing pressures, and competition from conifers. Aspen clones were not distinguished during site selection because this study intended to develop an assay that could be used in the field, where it is often difficult to distinguish between clones visually and without the aid of laboratory testing. Stands which had low live aspen basal area were also visually characterized by having large numbers of dead standing or fallen stems, abundant cankers (Fig. A.2), less foliage, and a high percentage of dead branches in the crown. Stands which had high live aspen basal areas were more densely stocked, had more foliage, fewer signs of cankers, and fewer dead branches in the crown. Two additional criteria for site selection for both stand types was the overall absence of regeneration in the understory and the absence or minimal presence of conifers.

A plot center was randomly established and marked with a flag within each stand type. The location of each plot center was recorded using a global positioning system. Condition class categories for all quaking aspen stems on each plot were recorded as live or standing dead. Aspen stems with any amount of green foliage or live cambial tissue were categorized as “live.” Mensurational data (tree age, height, and diameter at breast height (dbh) measured at 1.37 m above ground) were collected for all live aspen trees on the 0.11 hectare plots (6.1 m, 20 ft radius).

Methods and Sampling

Root Sampling, Calculations and Iodine-Staining. At the time of site selection (fall 2011) aspen roots were sampled by randomly locating and excavating four – 35x35x35 cm pits and collecting all live aspen roots measuring > 1cm in diameter at mid-point. Baker et al. (1993) used a similar technique to quantify root disease in conifers including ponderosa pine and lodgepole pine. Lazorko and Van Rees (2011) found that the majority of roots (>70%) at their boreal forest sites (consisting of *Populus tremuloides*, *Picea glauca*, *Picea mariana*, and *Larix laricina*) were distributed in the upper 30 cm of the soil profile. So, while I acknowledge that roots may be deeper than 35 cm in the soil profile, this root sampling technique will at least provide an unbiased sample of aspen roots and allow for total root surface area, average root diameter, and TNC concentration (water soluble carbohydrates plus starch) comparisons between plots.

The diameter (measured at the mid-point) and length of each root segment were recorded. For the purposes of this study, root surface area index was calculated on a root surface area to pit surface area basis. Root surface areas were calculated using the equation for the surface area of a cylinder (Surface Area = (2 x pi x radius^2) + (2 x pi x radius x length)). Pit surface area was calculated using the equation for the area of a square (Area = length of a side^2). So, root surface area index was calculated by taking the sum of the root surface areas (cm^2) for each plot and dividing by the total pit surface area excavated for each plot (four 35x35 cm pits). Average root diameter was calculated by taking the sum of the root diameters from each plot and dividing by the total number of roots excavated from each plot.

Root starch concentration was estimated in the field by staining cross-sections of whole root segments with an iodine (I_2KI) solution. The solution contained 15 g of KI and 3 g of crystalline I_2 in 1 L of distilled water. The root cross-sections were placed in a shallow dish, flooded with I_2KI solution, and allowed to sit undisturbed. After 5 minutes the stain was blotted and the sections were rinsed twice with distilled water (Wargo, 1975). Staining results were photographed within 5 minutes of rinsing to ensure that the stain intensity showed no signs of fading. Root starch concentration, as reflected by the color intensity of the stain, was rated as high, medium, low or depleted. Segments were placed on ice for further carbohydrate analysis in the laboratory.

Cutting Treatment. In order for aspen to initiate a suckering response from the root system, an aboveground disturbance must take place which removes living stems and alters the hormonal (cytokinin/auxin) balance within the tree. Felling was the chosen method for this study, so in spring 2012, all trees within 12.2 m (40 ft) of plot center were felled to stimulate a suckering response. (Note: We did not receive landowner consent to fall trees on sites 4 and 6 on Cedar Mountain, therefore, data were not collected after felling at these sites.) Because the Cedar Mountain study area is located primarily on private land and landowner consent was required, the allowable size of the felled area had to be acceptable to the landowners as well as large enough to initiate a measureable suckering response. Groot et al. (2009) found that the density of aspen regeneration was significantly affected by opening type and size. They found that the average regeneration density at year 10 was 18,600 stems per ha in a clearcut, 11,900 stems per ha in 18 m strips, 4,600 stems per ha in 9 m strips, 600 stems per ha in 18 m circular openings, and

200 stems per ha in 9 m circular openings. Tew et al. (1969) found that the greatest distance between two connected quaking aspen stems in northern Utah was 16.9 m, but the average distance was only 6 m. Therefore, the size of the circular openings chosen for this study (12.2 m radius) was large enough to reduce auxin transport to the roots and initiate a suckering response. After felling, all boles and slash were left on each plot creating a “jackstraw” effect to discourage browsing (Figs. A.5, A.6). In addition, a disk was taken from each cut tree at breast height for determination of sapwood basal area. The disks were placed in storage for 6 months and allowed to air dry. The disks were then sanded until they measured approximately 2.5-3.8 cm in thickness and subsequently rehydrated in a water bath for 24 hours to expose the sapwood.

Exclosures and Sucker Counts/Measurements. Immediately following the felling, four exclosures were erected in random locations on each of the plots to protect any resulting suckers from grazing and to allow for accurate measurement of suckering potential. Each exclosure consisted of approximately 7.6 m (25 ft) of 1.8 m (6 ft) high galvanized mesh fencing which was wrapped around metal t-posts and secured with galvanized wire. The exclosures varied slightly in shape in order to set them in between the fallen boles, but efforts were made to maintain similar dimensions. The exact dimension of each exclosure was measured so that regeneration counts could be quantified per unit area. In fall 2012 and fall 2013, aspen suckers were counted inside the exclosures (Figs. A.7, A.8). Sampling also occurred outside the exclosures at four randomly located areas within 4.6 m (approximately 15 ft) of each exclosure using a 1.42 m (4.66 ft) square pvc frame (Fig. A.9). This was done to assess the effects of herbivory on suckers that were not protected by exclosures. All sucker counts were combined for each plot and converted to a per-hectare basis for comparison. Sucker height was recorded for the tallest sucker in each sample and averaged on a per plot basis. General grazing pressure was noted for each site.

Root Sample Preparation. Root samples were analyzed at the USDA Research Lab in Logan, UT. In order to prepare the samples for extraction of TNC, all remaining soil was washed from the roots using deionized water. The samples were then dried in an oven at 68° C for 2 – 3 days and ground in a Wiley mill to 40 mesh, with a minimum sample mass of 200 mg. Samples were stored in air tight vials at room temperature in the dark.

Water Soluble Carbohydrate Extraction and Analysis. Water soluble carbohydrates (WSC) were extracted from ground root samples according to a reducing sugar assay procedure (AOAC method 999.03), further adapted by Dr. MaryBeth Hall (Research Animal Scientist, USDA – Agricultural Research Service, Madison, WI). Approximately 200 mg of ground root sample or control powder was placed in a 50 mL polypropylene screw-top conical tube with 32 mL of deionized water. Samples were briefly mixed on a vortex mixer and then incubated at 40° C for 1 hour in an orbital shaker (160 rpm). A 1.6 mL aliquot of the extract was transferred to a 2 mL microfuge tube and centrifuged at 12,000g for 10 minutes at room temperature. To keep the values within the standard curve later, 1:2 dilutions with deionized water were done by mixing 800 µL of deionized water and 400 µL of sample extract in a 2 mL microfuge tube. Fifty µL of 0.11 M sulfuric acid was placed into the acid wells and 50 µL of deionized water was placed into the water wells of a deep 96-well plate. A 100 µL aliquot of the water extracted sample was added to each well and the plate was covered with adhesive film. The plate was incubated in a 80° C water bath for 70 minutes and then allowed to cool to room temperature for approximately 10 minutes. For determination of sugars, 30 µL of sample or standard was added to 500 µL of 4-Hydroxybenzoic acid hydrazide (PAHBAH) reagent in a deep 96-well plate. The plate was covered with adhesive film and centrifuged for 30 seconds. After centrifugation, the plate was incubated in a 95° C water bath for 6 minutes and immediately placed in ice water for 5 minutes. Of this, 200 µL was pipetted into an optically clear 96-well plate and read in a SpectraMax Plus (Molecular Devices) plate reader at 410 nm within 10 minutes. Reducing sugar products were compared to a standard curve of an equimolar mixture of glucose and fructose at concentrations ranging from 0 to 275 µM.

Starch Digestion to Glucose and Analysis. Following removal of WSC, starch was determined from the remaining pellet according to a modified amyloglucosidase/α-amylase enzymatic assay procedure (from Megazyme International Total Starch Assay Procedure booklet, AOAC method 996.11/ AACC method 76.13). Approximately 50 mg of the pellet was weighed and placed in a 15 mL polypropylene screw-cap tube. In order to wet the sample and aid in tissue dispersion, 0.2 mL of aqueous ethanol (80% v/v) was added to each tube and then stirred on a vortex mixer. Thermostable α-amylase was diluted from stock solution at a ratio of 1 mL thermostable α-amylase to 30 mL 100 mM sodium acetate buffer, pH 5.0 with 5 mM calcium chloride. To begin digestion, 3 mL of α-amylase solution was added to each tube and tubes were placed in a boiling water bath for 12 minutes. To ensure complete homogeneity of the slurry and removal of lumps, the tubes were mixed at 4, 8 and 12 minutes on a vortex mixer. The tubes were then allowed to cool for 5 minutes in a cold water bath followed by the addition of 0.1 mL of amyloglucosidase solution (as supplied). Tubes were mixed on a vortex mixer to resuspend tissue, then placed in 50° C water bath and allowed to incubate for 30 minutes. Each sample was diluted to 10 mL with distilled water and then centrifuged at 3,000 rpm for 10 minutes. Glucose hydrolyzed from starch was measured enzymatically with Megazyme's GOPOD reagent (glucose oxidase/ peroxidase). A 0.1 mL aliquot of the diluted sample was transferred to the bottom of a 15 mL polypropylene screw-cap tube. Three mL of GOPOD reagent was added to each tube and the tubes were allowed to incubate in a 50° C water bath for 20 minutes. D-glucose controls consisted of 0.1 mL of D-glucose standard solution (1 mg/mL) and 3.0 mL of GOPOD reagent. Reagent blank solutions consisted of 0.1 mL of water and 3.0 mL of GOPOD reagent. The absorbance for each sample and the D-glucose control were read at 510 nm against the reagent blank.

Statistical Analysis. Plot data were categorized into two groups, labeled low BA and high BA, and analyses were performed to determine if any statistical differences existed. Data distributions were examined for each sample variable within the two groups and were identified as either normally or abnormally distributed. The paired two-sample t test was used to perform a hypothesis test and compute a confidence interval of the difference between the means, in the case of normally distributed data. Likewise, the Mann-Whitney test was used to perform a two sampled rank test of the equality of two population medians, in the case of abnormally distributed data. In order to test for any significant interactions existing between sucker counts and all other sample variables, regression analyses were used. The confidence interval for all tests was set at 95%, corresponding to a *P* value < 0.05. Adjusted R^2 was reported for all statistically significant regression analyses. This statistic includes an adjustment to R^2 which reduces the R^2 for every term added to the model, essentially safeguarding against overfitting and therefore providing the most accurate level of prediction. All statistical analyses were performed using MINITAB version 15.

CHAPTER IV

RESULTS

Above- and Belowground Plot Measurements. Aboveground measurements for the plots are given in Table 1. Live aspen basal area was measured for each of the plots and ranged from 9.2 to 59.7 m^2 ha^{-1}, with a mean of 31.5 m^2 ha^{-1}. Plots classified as “low BA” had significantly less live aspen basal areas, ranging from 9.2 to 32.1 m^2 ha^{-1} with a mean of 20.2 m^2 ha^{-1}, than plots classified as “high BA”, which had live aspen basal areas ranging from 27.5 to 59.7 m^2 ha^{-1} with a mean of 42.7 m^2 ha^{-1} (Fig. 1) ($P < 0.0001$). Sapwood basal areas ranged from 1.3 to 37.5 m^2 ha^{-1}, with a mean of 15.3 m^2 ha^{-1}. Plots classified as “low BA” had significantly lower sapwood basal areas, ranging from 1.3 to 14.6 m^2 ha^{-1} with a mean of 8.85 m^2 ha^{-1}, than plots classified as “high BA”, which had sapwood basal areas ranging from 8.7 to 37.5 m^2 ha^{-1} with a mean of 21.8 m^2 ha^{-1} (Fig. 1) ($P = 0.007$). Aspen site indices (Edminster et al., 1985) ranged from 9.7 to 17.8 m (base 80 years). There was no significant difference in site indices between “low BA” and “high BA” plots ($P = 0.059$).

All roots collected from the pits were averaged on a per plot basis and gave the following measurements: 1) Mean root starch concentrations ranged from 0.24 to 6.94 %, with an overall mean of 3.16 %; 2) Mean root WSC concentrations ranged from 9.94 to 27.26 %, with an overall mean of 17.63%; 3) Mean root diameter ranged from 1.6 to 5.7 cm, with a median of 2.5 cm; and 4) Root surface areas ranged from 416 to 3884 m^2/ha, with a mean of 1603 m^2/ha (Table 2). Plots classified as “low BA” had significantly lower root starch concentrations, ranging from 0.24 to 4.48 % with a mean of 2.17%, than plots classified as “high BA”, which had root starch concentrations ranging from 2.88 to 6.93% with a mean of 4.15% (Fig. 2) (P = 0.013). There was no significant difference in WSC (P = 0.136), root diameters (P = 0.141), and root surface areas (P = 0.097) between “low BA” and “high BA” plots.

Table 1. Description of the study plots. Aboveground measurements shown are mean values for each plot.

	Site	Plot	Stem age (*years*)	d.b.h. (*cm*)	Total height (*m*)	Basal area (*m2/ha*)	Sapwood basal area (*m2/ha*)	Site index (*m*)
Cedar Mountain	1	low BA	111	36.6	18.2	9.2	4.3	15.1
study area	1	high BA	132	40.8	23.9	45.9	37.5	17.8
	2	low BA	126	31	18.9	18.4	7.4	14.8
	2	high BA	116	27.5	18.0	45.9	16.9	14.3
	3	low BA	96	31.5	14.9	13.8	3.7	13.7
	3	high BA	131	32.8	17.7	50.5	23.0	13.2
	4	low BA	--	43.3	18.2	32.1	--	--
	4	high BA	--	37.4	19.9	32.1	--	--
	5	low BA	102	37.8	16.7	18.4	13.5	14.8
	5	high BA	113	38.9	18.2	27.5	20.1	15.0
	6	low BA	--	22.7	10.7	23.0	--	--
	6	high BA	--	24.6	10.1	45.9	--	--
	7	low BA	146	37.8	18.7	23.0	14.6	13.6
	7	high BA	117	28.6	18.4	36.7	16.6	15.9
	8	low BA	118	41.7	19.4	18.4	11.9	15.1
	8	high BA	110	39.2	19.1	41.3	21.7	15.9
Deseret	9	low BA	86	31.2	12.7	27.5	14.1	13.4
study area	9	high BA	79	29.2	15.6	59.7	30.4	15.7
	10	low BA	50	12.3	6.9	18.4	1.3	9.7
	10	high BA	70	18.4	12.4	41.3	8.7	14.9

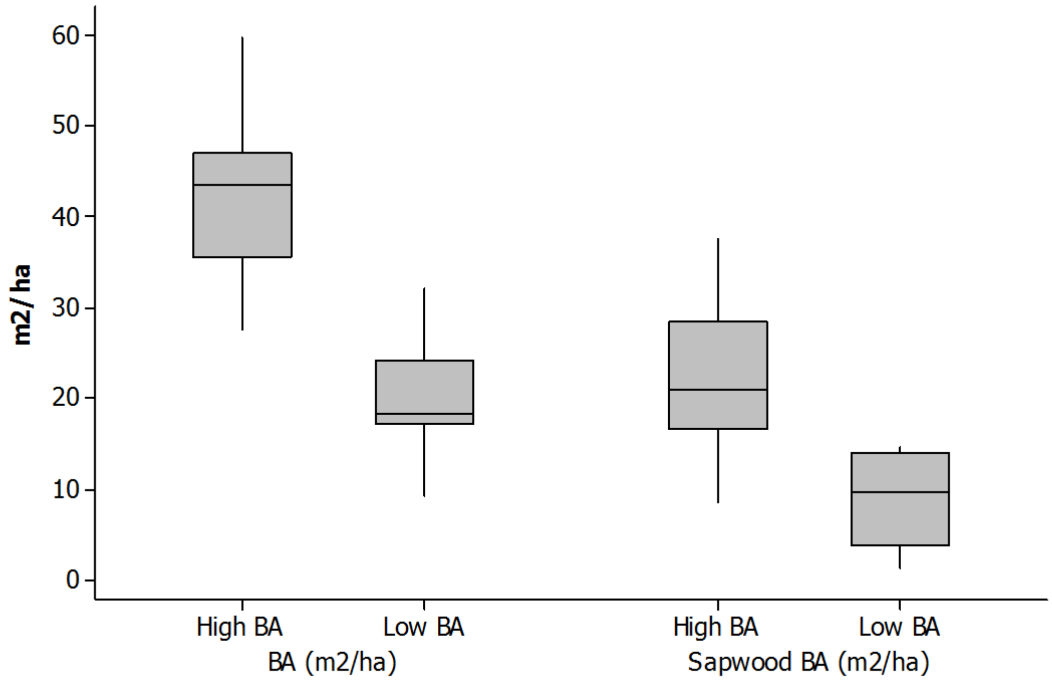

Fig. 1. Boxplot displaying significant differences in live aspen basal area (m^2/ha) and sapwood basal area (m^2/ha) between "high BA" and "low BA" plots. Data is summarized in five statistics: minimum, first quartile, median, third quartile, and maximum.

Table 2. Description of the study plots. Belowground measurements shown are mean values for each plot, except root surface area which is a summed value.

	Site	Plot	Starch concen. (%)	WSC concen. (%)	Root diameter (c*m*)	Root surface area (*m2/ha*)
Cedar Mountain	1	low BA	3.13	12.55	2.5	1086
study area	1	high BA	3.71	17.17	2.4	1737
	2	low BA	4.00	18.67	4.1	1617
	2	high BA	4.21	18.84	5.7	3884
	3	low BA	0.24	9.94	2.5	606
	3	high BA	6.94	22.25	1.8	1963
	4	low BA	0.37	17.82	2.9	1098
	4	high BA	2.97	19.57	1.9	1704
	5	low BA	2.34	21.31	3.8	713
	5	high BA	3.20	12.77	4.2	2245
	6	low BA	1.75	12.97	4.1	3213
	6	high BA	5.46	19.45	2.1	1441
	7	low BA	2.04	19.65	3.8	1502
	7	high BA	3.73	20.63	2.4	1755
	8	low BA	4.48	12.95	2.4	1384
	8	high BA	4.16	13.84	1.7	1280
Deseret	9	low BA	2.34	19.15	1.6	416
study area	9	high BA	4.29	20.24	1.9	926
	10	low BA	1.01	15.59	3.5	1208
	10	high BA	2.88	27.26	2.0	2290

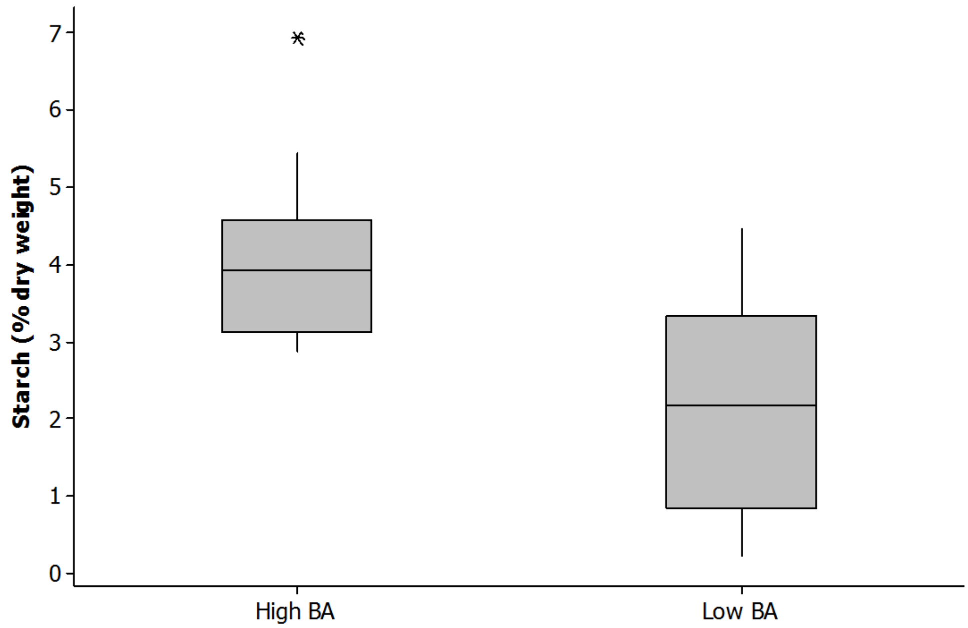

Fig. 2. Boxplot displaying significant difference in root starch concentration (% dry weight) between "high BA" and "low BA" plots. Data is summarized in five statistics: minimum, first quartile, median, third quartile, and maximum. An outlier is represented with an * symbol.

Root Characteristics vs. Aboveground Metrics of Stand Deterioration. Three significant relationships were apparent between root characteristics and aboveground stand characteristics. A regression analysis of live aspen basal area to root diameter (Fig. 3) reveals that average root diameter decreased with increasing live aspen basal area (P = 0.043) ($y = 3.416 - 0.00546 \times x - 0.000476 \times x$; R^2 (adj) = 0.240). In addition, regression analysis reveals that root starch concentration increased with increasing live aspen basal area (Fig. 4) (P = 0.029) ($y = 2.314 - 0.0271 \times x + 0.001445 \times x$; R^2 (adj) = 0.277) and, similarly, root WSC concentration increased with increasing live aspen basal area (Fig. 5) (P = 0.047) ($y = 8.669 + 0.4436 \times x - 0.004196 \times x$; R^2 (adj) = 0.232).

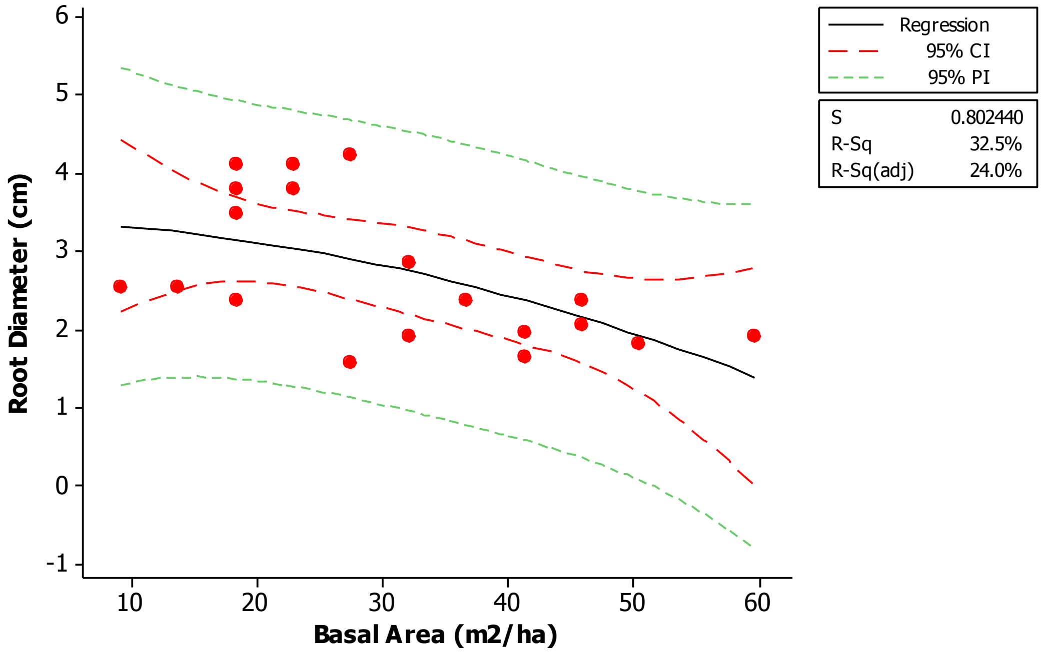

Fig. 3. Polynomial regression analysis of live aspen basal area (m^2/ha) versus average root diameter (cm). Graph displays the completed fitted line plot, with both sets of intervals including the 95% confidence interval (CI) displayed as a red dashed line and the 95% prediction interval (PI) displayed as a green dashed line. The flare out in the 95% CI lines at the ends of the plot reflect increased uncertainty in those areas.

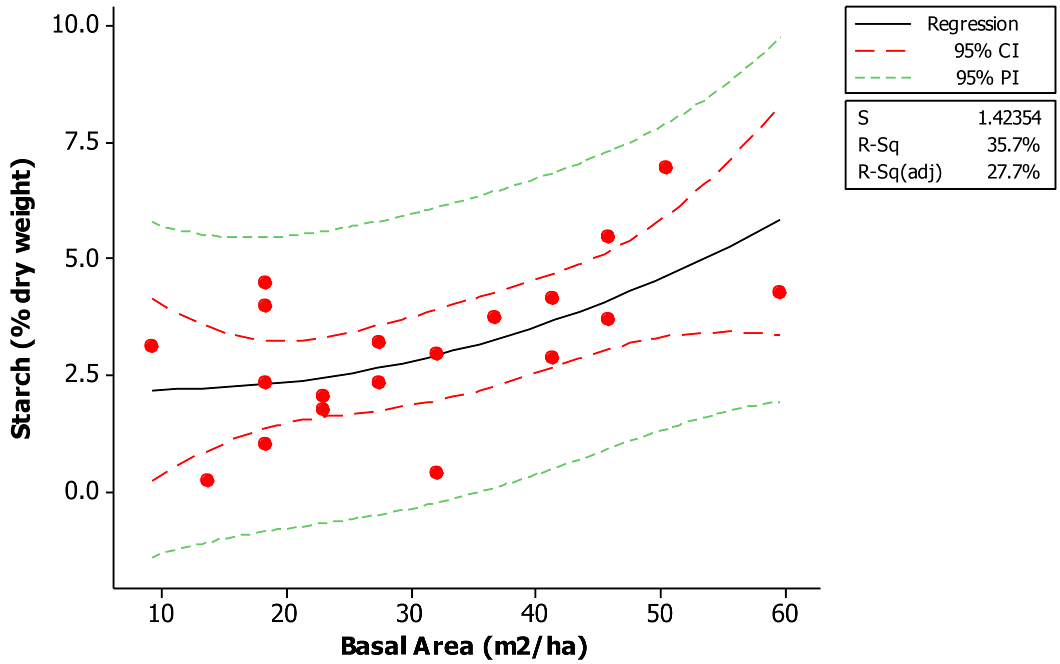

Fig. 4. Regression analysis of live aspen basal area (m^2/ha) versus root starch concentration (% dry weight).

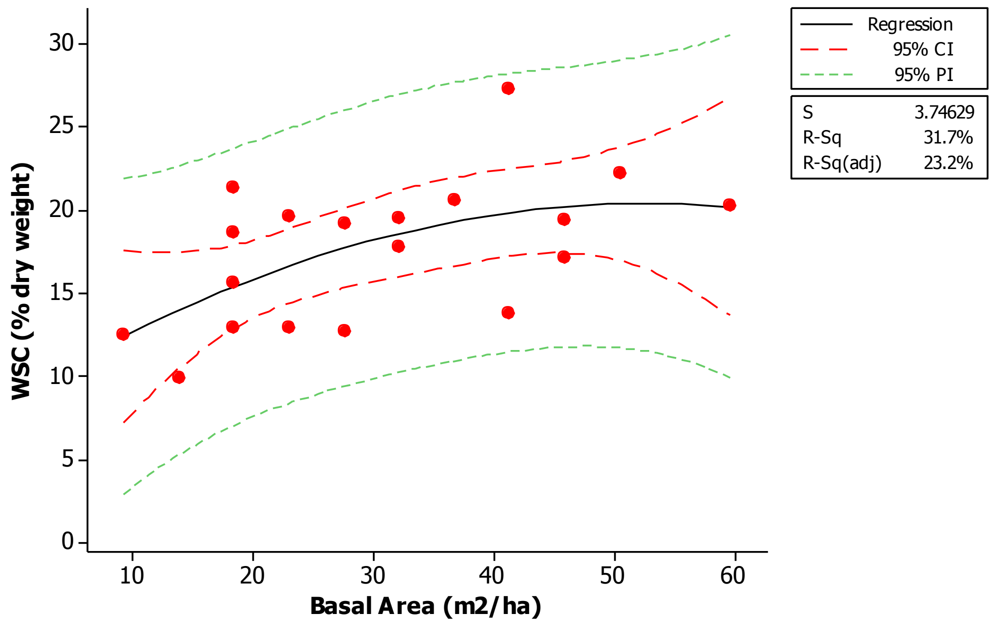

Fig. 5. Regression analysis of live aspen basal area (m^2/ha) versus root water soluble carbohydrate (WSC) concentration (% dry weight).

Density and Height of Sucker Regeneration Produced after a Managed Disturbance. Mean sucker counts measured in 2012 and 2013 from inside and outside the exclosures are given in Table 3. No significant relationships were found between sucker counts taken outside the exclosures and all other measured variables. Therefore all of the following results refer to sucker counts taken within the exclosures. Tallest sucker heights measured in 2012 and 2013 from inside and outside the exclosures are given in Table 4. There was a significant difference in sucker heights measured inside versus outside the exclosures, reflecting the effects of herbivory. These results are presented later in the '*Effects of Herbivory*' section on page 43.

Density of suckers in 2012 ranged from 1,142 to 45,354 suckers ha^{-1}, and in 2013 ranged from 1,142 to 59,800 suckers ha^{-1}. There was no significant difference in sucker density between "low BA" and "high BA" plots in 2012 (P = 0.8622) and 2013 (P = 0.375). Tallest sucker heights (measured inside the exclosures) per plot in 2012 ranged from 23 to 91 cm, and in 2013 ranged from 67 to 201 cm. There were no significant differences in tallest sucker heights between "low BA" and "high BA" plots in 2012 (P = 0.943) and 2013 (P = 0.481).

Table 3. Mean sucker counts per hectare on "low BA" and "high BA" plots, measured in 2012 and 2013. Outliers are marked with an * symbol.

			Suckers per ha, inside exclosures		Suckers per ha, outside exclosures	
			Collection year		Collection year	
	Site	Plot	2012	2013	2012	2013
Cedar Mountain	1	low BA	7515	12882	2788	4337
study area	1	high BA	16992	12461	34697	16729
	2	low BA	5543	5543	5886	3717
	2	high BA	11337	14738	12082	11772
	3	low BA	40155	28682	4337	2478
	3	high BA	21206	30135	28192	57621
	4	low BA	--	--	--	--
	4	high BA	--	--	--	--
	5	low BA	5849	32757	31290	10533
	5	high BA	1142	1142	26643	9913
	6	low BA	--	--	--	--
	6	high BA	--	--	--	--
	7	low BA	5966	5966	18898	25403
	7	high BA	4585	3439	4027	8055
	8	low BA	24742	29240	9914	5576
	8	high BA	38006	40242	3718	19827
Deseret	9	low BA	30754	59800	2788	6196
study area	9	high BA	45354	25701	20137	9913
	10	low BA	6640	11067	2478	8674
	10	high BA	82150 *	29450	20447	11152

Table 4. Tallest sucker heights (cm) measured inside and outside the exclosures, in 2012 and 2013.

			Sucker height (cm), inside exclosures		Sucker height (cm), outside exclosures	
			Collection year		Collection year	
	Site	Plot	2012	2013	2012	2013
Cedar Mountain	1	low BA	55	109	60	87
study area	1	high BA	37	101	37	61
	2	low BA	91	162	32	96
	2	high BA	66	140	37	81
	3	low BA	88	130	29	98
	3	high BA	23	85	37	35
	4	low BA	--	--	--	--
	4	high BA	--	--	--	--
	5	low BA	35	67	23	37
	5	high BA	61	67	25	13
	6	low BA	--	--	--	--
	6	high BA	--	--	--	--
	7	low BA	33	95	30	76
	7	high BA	74	201	24	98
	8	low BA	55	125	10	16
	8	high BA	60	148	38	44
Deseret	9	low BA	56	107	14	33
study area	9	high BA	81	143	34	79
	10	low BA	24	133	49	50
	10	high BA	43	136	34	94

Root Characteristics vs. Density and Height of Suckers. Two significant relationships emerged between root characteristics and the number of suckers produced on each plot after the cutting treatment. A regression analysis of root diameter to sucker count (Fig. 6) reveals that sucker counts increase with decreasing average root diameter (2012 sucker counts: P = 0.009; y = 76,088 – 30,791 × x + 3,207 × x; R^2 (adj) = 0.494); (2013 sucker counts: P = 0.014; y = 123,988 – 65,217 × x + 9,165 × x; R^2 (adj) = 0.455).

Regression analysis also indicated a significant relationship between sucker count and root surface area. In order to look at this relationship more closely, roots were grouped into four diameter classes (<2.54 cm, 2.54-3.81 cm, 3.82-5.08 cm, and >5.08 cm) (Fig. 7). Sucker counts decrease with increasing root surface area, apparently due to the presence of roots in the larger diameter classes, 3.82-5.08 cm and >5.08 cm. Plots with multiple small roots will have lower root surface area measurements than plots which have large roots; the highest sucker counts occur on plots with more roots in the smaller diameter classes, <2.54 cm and 2.54-3.81cm. Regression analysis was used to further test the relationship between root surface area in the smallest diameter class only, <2.54 cm, and the number of suckers produced on each plot after the cutting treatment (Fig. 8). Analysis showed an increase in sucker counts with increasing small root surface area (2012 data: P = 0.040; y = 3,067 + 26.76 × x; R^2 (adj) = 0.321).

Regression analysis revealed no statistically significant relationship between sucker count from 2012 and 2013 and root starch concentration (P = 0.835; P = 0.926) or WSC concentration (P = 0.508; P = 0.868). In addition, regression analysis revealed no significant relationship between sucker count and aboveground stand conditions at the time of disturbance including live aspen basal area (P = 0.168; P = 0.715), sapwood basal area (P = 0.340; P = 0.848), or site index (P = 0.62; P = 0.804). Regression analysis revealed no statistically significant relationship between tallest sucker heights from 2012 and 2013 and all other measured variables.

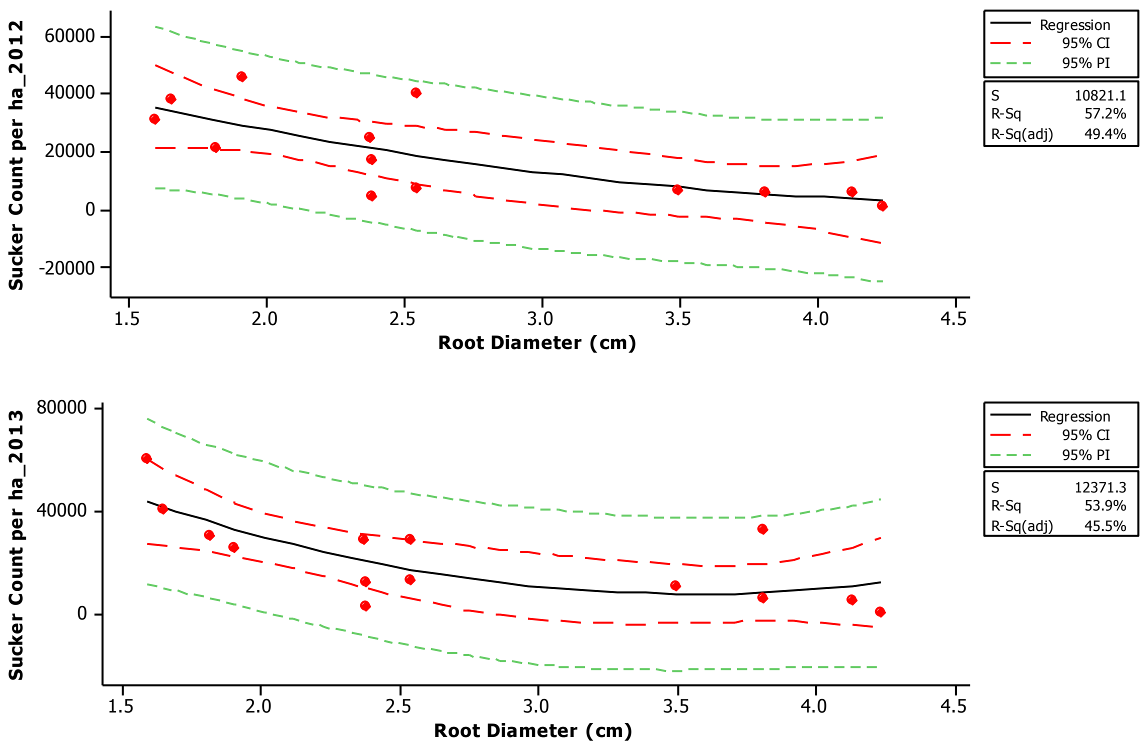

Fig. 6. Polynomial regression analysis of average root diameter (cm) versus sucker counts per hectare for 2012 and 2013.

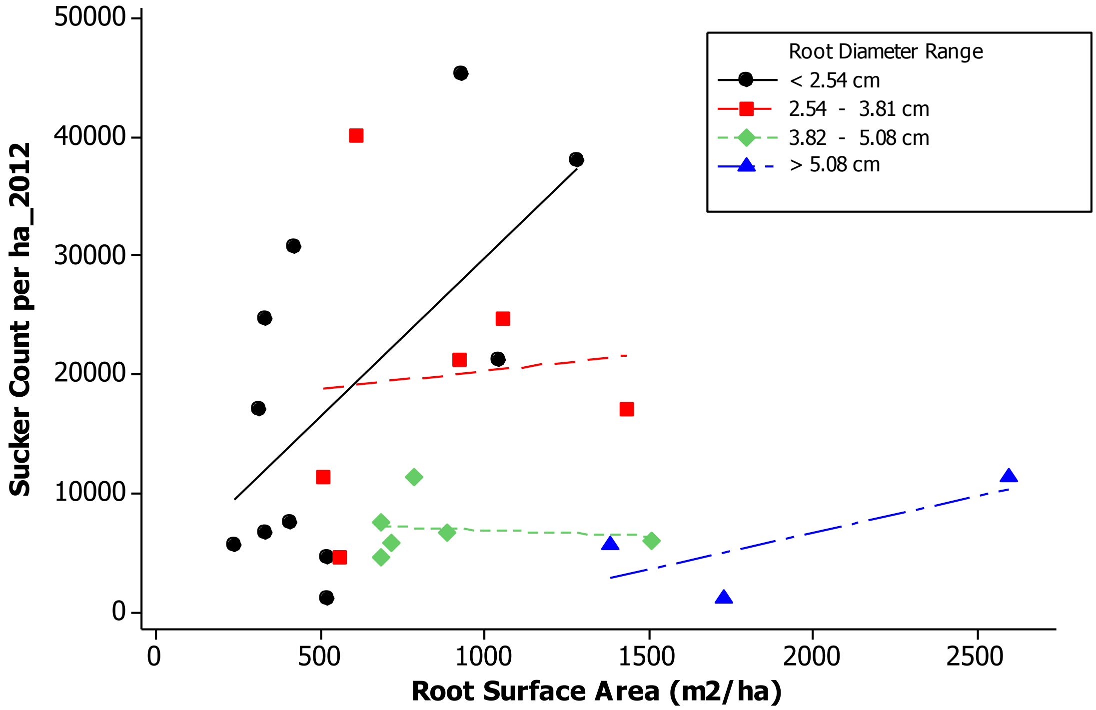

Fig. 7. Scatter plot showing root surface area (m^2/ha) versus sucker counts per hectare for 2012. Root diameters were grouped into four diameter classes (<2.54 cm, 2.54-3.81 cm, 3.82-5.08 cm, and >5.08 cm). Similar relationships exist for 2013 (not shown).

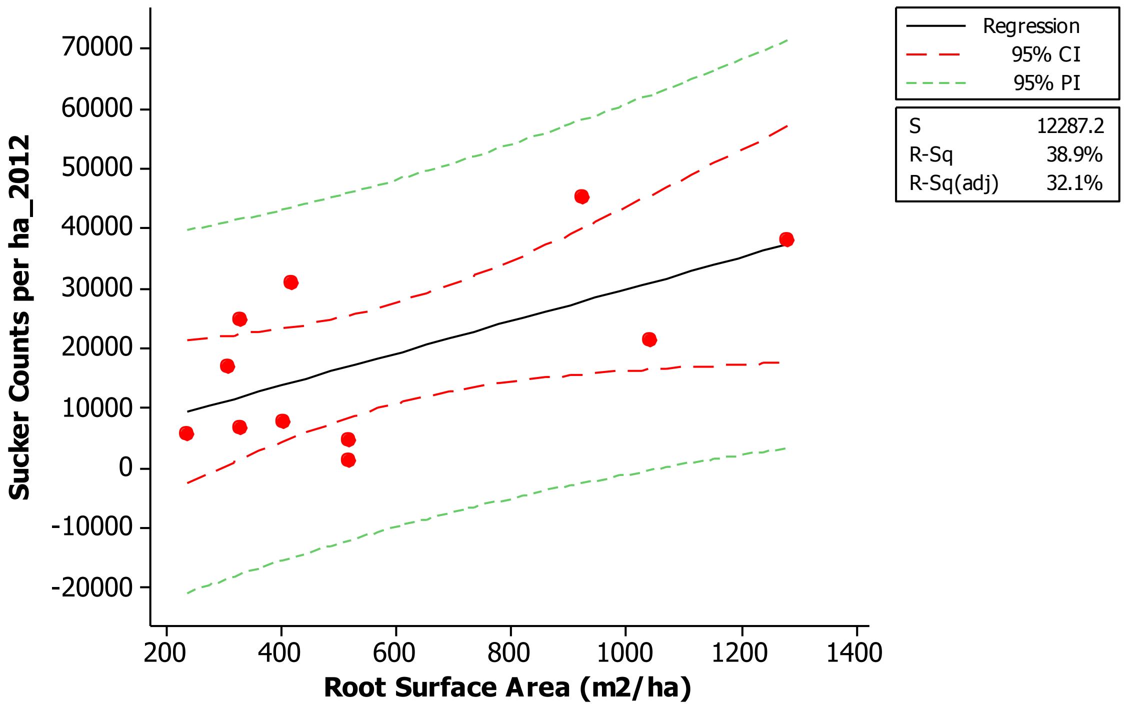

Fig 8. Regression analysis of root surface area (m^2/ha) for the <2.54 cm diameter class versus sucker counts per hectare for 2012. Similar relationships exist for 2013 data (not shown).

Effects of Herbivory. The effects of herbivory on aspen regeneration can be seen when comparing sucker heights measured within the exclosures versus outside the exclosures. Sucker heights measured outside the exclosures in 2012 were significantly shorter, ranging from 10 to 60 cm with a mean of 32.2 cm, than sucker heights measured inside the exclosures, which ranged from 23 to 91 cm with a mean of 55.1 cm (Table 4, Fig. 9) ($P = 0.001$). Similarly, sucker heights measured outside the exclosures in 2013 were significantly shorter, ranging from 13 to 98 cm with a mean of 62.4 cm, than sucker heights measured inside the exclosures, which ranged from 67 to 201 cm with a mean of 121.7 cm (Table 4, Fig. 9) ($P < 0.0001$).

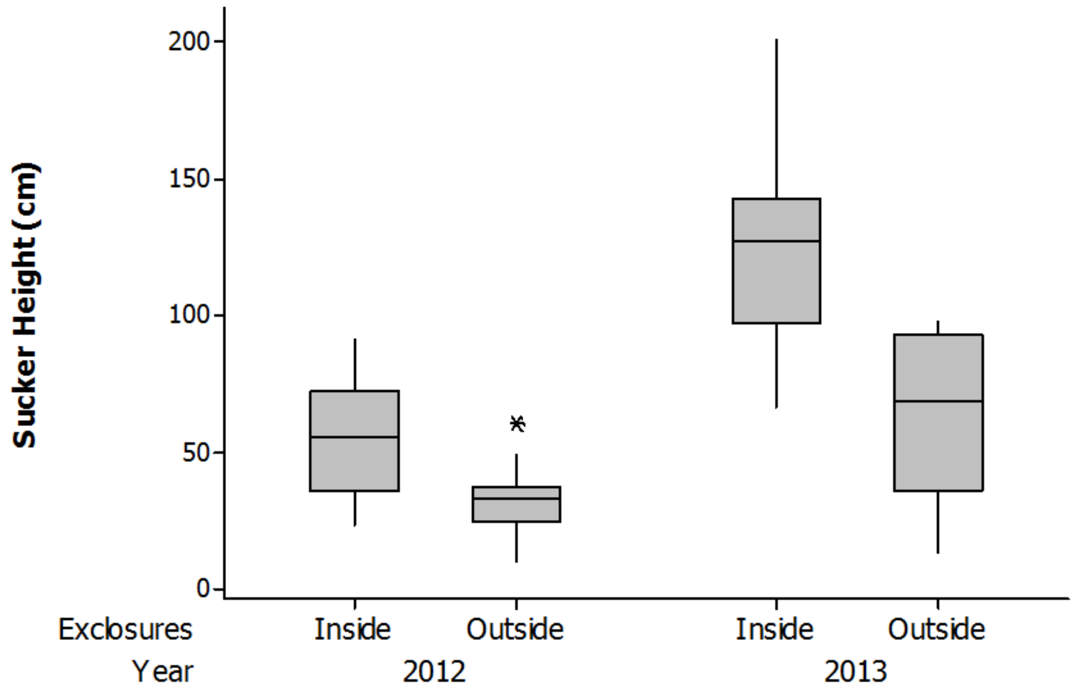

Fig. 9. Boxplot displaying the effects of herbivory on aspen regeneration height (cm), measured in 2012 and 2013. Height measurements were taken inside the exclosures where suckers were protected from browsing and outside the exclosures where browsing was unmonitored. Data is summarized in five statistics: minimum, first quartile, median, third quartile, and maximum. An outlier is represented with an * symbol.

Iodine-Staining. Root cross-sections were sorted into four categories of starch concentration (high, medium, low, and depleted) based on visual analysis of iodine-stain intensity of starch granules done in the field. The ranges that corresponded with these four categories of starch concentration, expressed as percent dry weight of tissue extracted, were chemically determined in the laboratory. The ranges were 6 to 10%, 3 to 5.99%, 1.5 to 2.99%, and 0 to 1.49% (Table 5, Figs. 10, 11, 12, 13, 14). Overall, starch concentration for individual roots ranged from 0.12 to 9.19%.

Table 5. Starch and WSC concentrations (expressed as percent dry weight of tissue extracted) of individual roots. Roots are ordered from lowest to highest starch concentration and visual categories are represented (d=depleted, l=low, m=medium, h=high, -- indicates the root sample was not visually categorized).

Root #	Starch concen. (%)	WSC concen. (%)	Visual category	Root #	Starch concen. (%)	WSC concen. (%)	Visual category
3	0.12	3.00	d	59	3.35	28.88	m
23	0.23	9.36	d	39	3.50	18.99	m
14	0.24	9.94	d	25	3.61	19.73	m
35	0.24	4.65	d	62	3.76	10.43	m
53	0.26	10.40	d	46	4.06	14.96	m
26	0.31	13.26	d	13	4.17	16.63	--
27	0.33	13.66	d	57	4.27	33.81	m
22	0.52	26.28	d	7	4.57	17.17	m
36	0.56	16.17	d	63	4.64	16.03	m
54	0.63	22.03	d	24	4.71	27.00	m
66	0.68	14.45	d	40	4.76	19.25	m
41	0.89	17.36	d	50	4.79	22.99	m
33	0.96	13.25	--	11	4.90	20.04	m
60	1.03	19.21	d	64	5.04	12.40	m
65	1.27	14.68	d	32	5.11	14.70	m
31	1.62	8.26	--	34	5.23	17.81	m
55	1.66	25.68	l	12	5.33	19.35	m
52	1.76	20.79	l	45	5.39	21.71	m
48	1.80	17.43	l	49	5.44	19.33	m
9	2.00	16.33	l	4	5.87	20.07	m
5	2.18	13.67	l	28	5.87	24.18	m
6	2.21	17.78	l	8	5.996	21.01	m
43	2.25	21.88	l	2	6.01	18.36	h
29	2.34	21.31	l	38	6.01	18.16	h
10	2.46	19.34	--	21	6.08	22.88	h
51	2.65	18.38	l	56	6.17	35.80	h
30	2.86	15.36	l	15	6.34	25.56	h
47	2.88	20.87	l	68	7.01	12.12	h
58	2.93	27.63	l	19	7.51	18.97	h
61	3.03	25.06	m	37	7.55	21.40	h
42	3.19	21.94	m	67	7.67	14.13	h
44	3.21	23.99	m	16	7.72	20.52	h
1	3.24	16.30	m	20	8.49	27.34	h
17	3.24	16.87	m	18	9.19	23.60	h

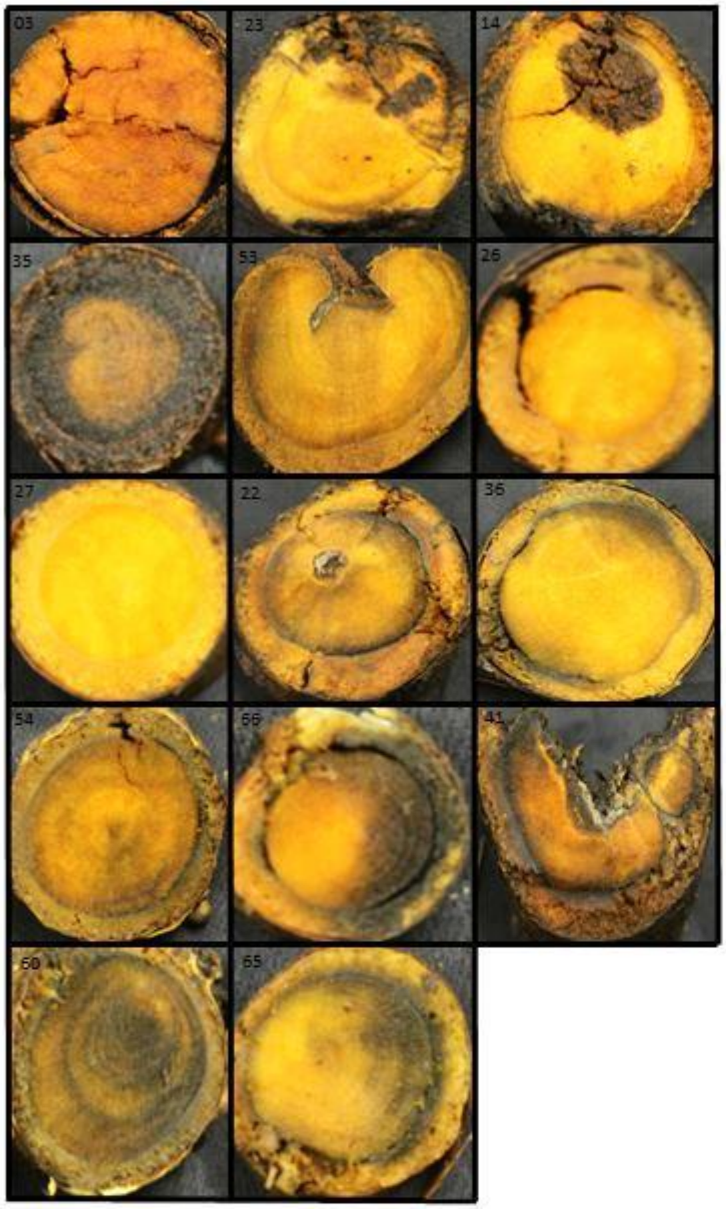

Fig. 10. Visual categorization of starch concentration, based on iodine-staining of starch granules, for depleted category.

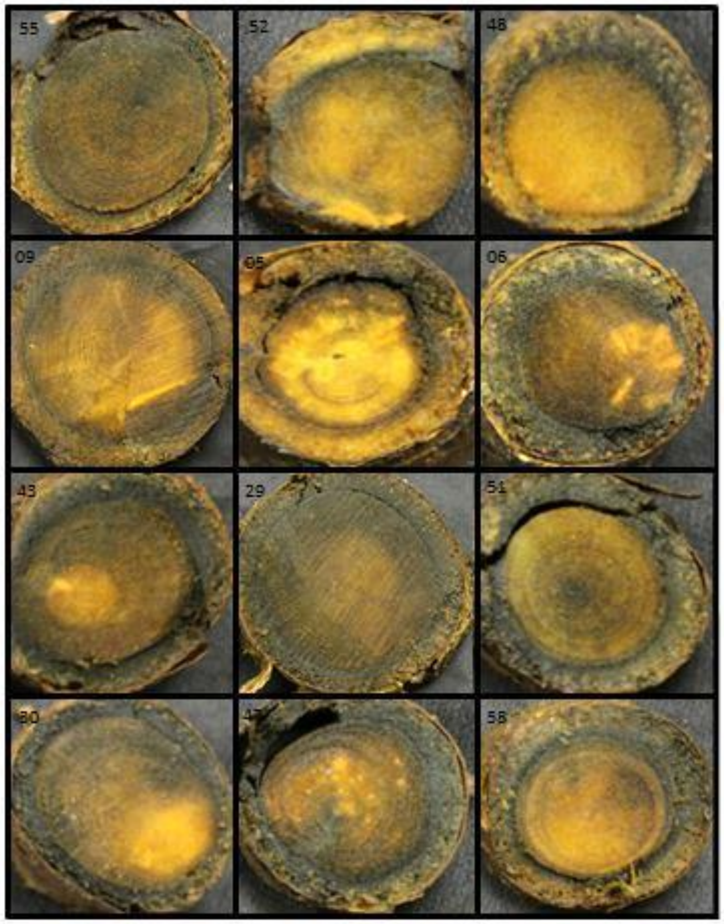

Fig. 11. Visual categorization of starch concentration, based on iodine-staining of starch granules, for low category.

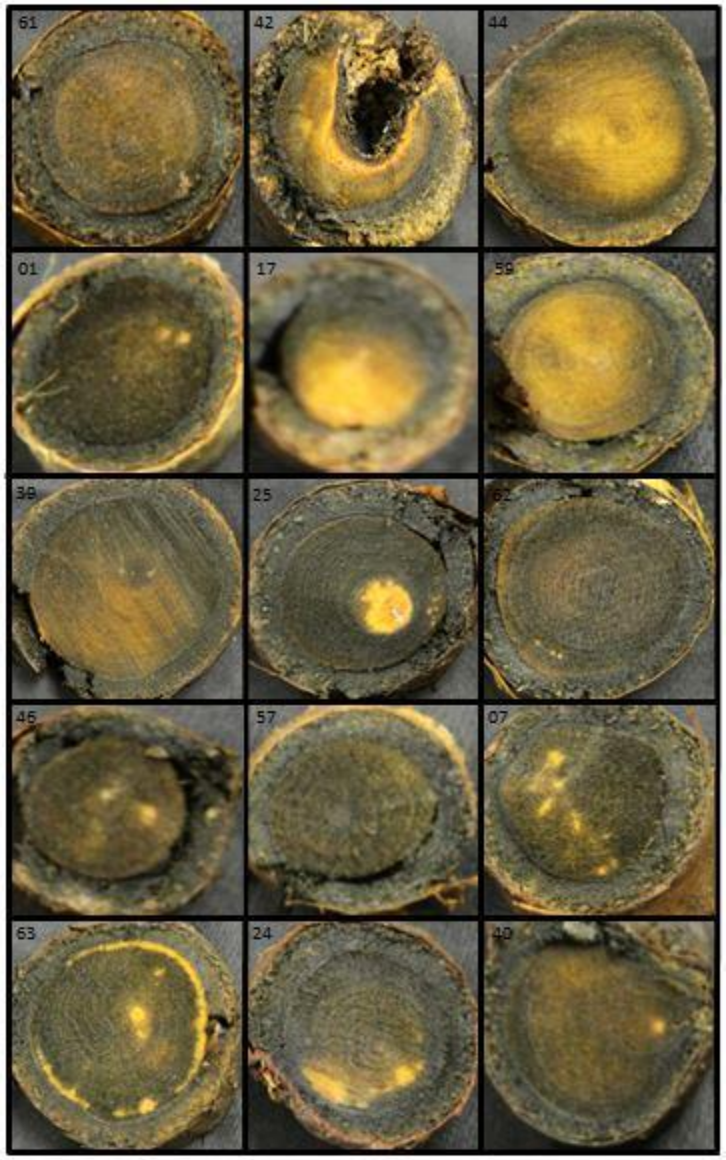

Fig. 12. Visual categorization of starch concentration, based on iodine-staining of starch granules, for medium category.

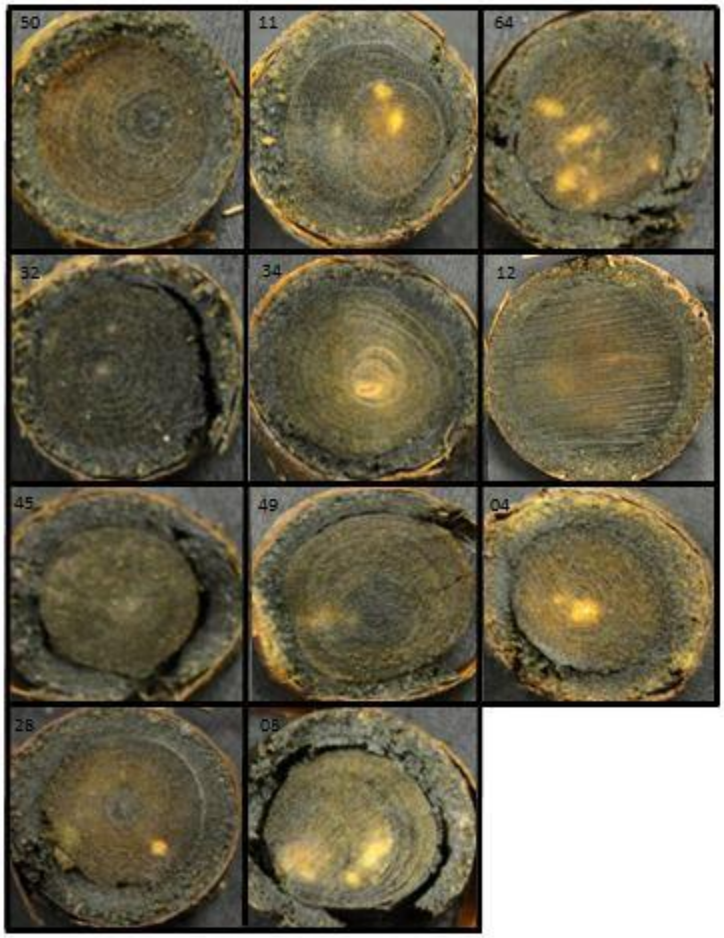

Fig. 13. Visual categorization of starch concentration, based on iodine-staining of starch granules, for medium category (cont'd.).

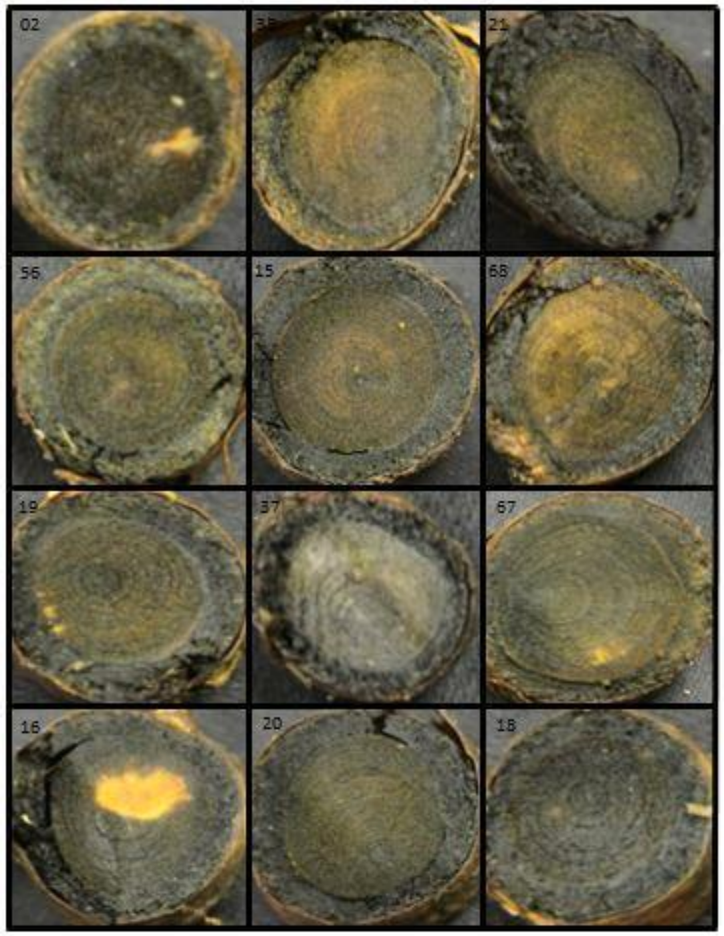

Fig. 14. Visual categorization of starch concentration, based on iodine-staining of starch granules, for high category.

CHAPTER V

DISCUSSION

My results describe the relationship between quaking aspen root characteristics and other pre-disturbance stand variables and sucker potential following a disturbance in pure stands of quaking aspen, primarily on Cedar Mountain in southern Utah and secondarily on Deseret Land and Livestock land in northern Utah.

Root Characteristics vs. Aboveground Metrics of Stand Deterioration. Live aspen basal area is related to multiple belowground variables including average root diameter, root starch concentration, and root WSC concentration. My results conclude that as live aspen basal area increases, root starch and WSC concentrations increase and average root diameter decreases. My results are consistent with a significant relationship between these root characteristics and pre-disturbance site conditions for quaking aspen across the study sites, indicating that there is a quantifiable belowground component in stand deterioration. In addition, low basal area is an indicator of deterioration and indicates fewer small roots and, thus, reduced suckering ability.

The significant relationship that exists between live aspen basal area and root starch and WSC concentrations is most likely a reflection of differences in leaf area, a relationship previously suggested by Landhausser and Lieffers (2002). Photosynthates produced in the autotrophic portions of the tree are translocated to the root system where they accumulate and are stored as carbohydrates. In the event of a disturbance which removes the aboveground trees, rapid suckering is required to renew the leaf area in order to maintain respiratory functions in the root system. The rapid suckering initially relies on reserves coming from the undamaged root system (Landhausser and Lieffers, 2002). My results support their findings, suggesting that the concentration of reserve carbohydrates stored in the root system at the time of disturbance is a reflection of aboveground leaf area and that higher leaf areas lead to the storage of higher concentrations of reserve carbohydrates.

High concentrations of reserve carbohydrates also allow a stand to retain proportionally more of its root system after a disturbance (Landhausser and Lieffers, 2002). The most likely explanation for the abundance of smaller diameter roots on plots with higher live aspen basal areas is that high leaf areas lead to high accumulations of carbohydrates in the root system, allowing for the maintenance and expansion of the parental root system through the formation of new roots, instead of strictly maintaining the parental root system, as would be the case in a stand with reduced leaf area and therefore reduced reserve carbohydrates.

There were significant differences between the live aspen basal area and aspen sapwood basal area of “low BA” and “high BA” plots. My initial visual categorization of “low BA” and “high BA” plots was primarily based on differences in live and dead aspen stems (which was quantified as live aspen basal area), in addition to other visual cues indicative of overall stand health. These included the presence of stem cankers, the presence of dead branches in the crown, and amount of foliage, all of which were noted but not quantified for the purposes of this study. Schier (1982) categorized stands as deteriorating or vigorous based upon pre-determined live aspen basal areas for clones located in the Wasatch Mountains east of Logan in northern Utah. Stands were selected in which basal areas of less than 10 m^2 ha^{-1} were considered “deteriorating” and basal areas ranging from 25 to 50 m^2 ha^{-1} were considered “vigorous.” My “low BA” and “high BA” plots had slightly different live aspen basal areas, ranging from 9.2 to 32.1 m^2 ha^{-1} for “low BA” plots and from 27.5 to 59.7 m^2 ha^{-1} for “high BA” plots. Sapwood basal areas ranged from 1.3 to 14.6 m^2 ha^{-1} for “low BA” plots and from 8.7 to 37.5 m^2 ha^{-1} for “high BA” plots. The area of overlap (live aspen basal areas from 27.5 to 32.1 m^2 ha^{-1} and sapwood basal areas from 8.7 to 14.6 m^2 ha^{-1}) between these two categories suggest a range of ambiguity and may indicate that some of the plot classifications were either incorrect or that other variables indicative of stand health should be used to determine if the stand would be considered “low BA” or “high BA”. Therefore, live aspen basal area and sapwood basal area are important aboveground indicators of stand deterioration for most stands, but may be poor indicators of stand deterioration for stands which fall within the mid-range of stand deterioration, referred to above as the “range of ambiguity,” for the purposes of this study. In order to clarify this for future studies, other variables indicative of stand health that one might measure include any of the following: 1) characterize the leaf area index for each stand type, 2) quantify stem cankers, and 3) collect and stain root samples to estimate root starch concentrations in the field. Many factors can affect basal area and basal area alone is not always an indicator of stand condition.

In addition to identifying live aspen basal area and sapwood basal area as important aboveground indicators of stand deterioration, we also identified a single belowground indicator of stand deterioration. Root starch concentrations were significantly less on “low BA” plots than on “high BA” plots, most likely a reflection of differences in leaf area, as previously discussed. Starch concentrations ranged from 0.24 to 4.48% on “low BA” plots, and from 2.88 to 6.93% on “high BA” plots. Other belowground variables such as WSC concentration, root diameter, or root surface area did not differ between “low BA” and “high BA” plots. This was somewhat unexpected due to the fact that regression analysis demonstrated moderate correlations between live aspen basal area and starch concentration (P = 0.006), WSC concentration (P = 0.016) and root diameter (P = 0.022), indicating there may be significant differences in all three of these variables between “low BA” and “high BA” plots. However, the t-test showed that only one of these variables, starch concentration, was statistically significant and therefore we could not use either WSC concentration or root diameter as potential belowground indicators of stand deterioration, even though regression analysis indicated a correlation with live aspen basal area.

Root Characteristics vs. Density and Height of Suckers. A significant relationship exists between sucker density after a disturbance and two quantifiable belowground variables: root diameter and root surface area.

The variation in root diameter and sucker density observed among plots in this study exhibited a pattern similar to that observed by Schier (1978). He found that most suckers originate from lateral roots ranging from 1 to 2.5 cm in diameter. I observed similar results in that sucker densities increased with decreasing root diameters. Sandberg (1951) and Schier (1973) both identified that the presence of newly initiated meristems and preexisting primordia are significantly important in terms of sucker production after disturbance and that more of these structures occur on younger roots. Due to the clonal growth habit of aspen, younger roots generally occur around the outer edge of the clone and produce a proportionally larger number of suckers, otherwise known as a “skirt” or “fairy ring” of regeneration. This condition type has been labeled as “stable” or “properly functioning” aspen, where a clone is successfully replacing itself with pulses of regeneration around the edges in combination with various sized stems in the interior (Bartos and Campbell, 1998a). Although a selection criteria for my plots was the absence of regeneration in the understory, my results indicate that roots in the smaller diameter class (< 2.5 cm) are an essential component for successful stand regeneration after disturbance.

In addition to root diameter, root surface area is also essential for successful stand regeneration and high sucker densities. The plots with the highest sucker densities were plots which had the highest number of roots or highest root surface area, of roots measuring less than 3.8 cm in diameter. My findings support observations made by Shepperd et al. (2001), where they found that regenerating clones had more roots and greater total root surface area than non-regenerating clones. However, they did not find significant differences in average root diameters between regenerating and non-regenerating clones overall, contrary to my findings noted previously. Their study design consisted of three paired clones while my study included eight paired plots, indicating that their sample size may not have been large enough to observe a significant relationship.

Shepperd et al. (2004) demonstrated a potential relationship between root diameter and total nonstructural carbohydrate concentrations. They found that “small roots do not appear to play a significant role in carbohydrate storage and that carbohydrates needed to reinitiate growth in the spring apparently accumulate in large aspen roots over the winter”. My study, however, found no statistically significant variation between large and small diameter roots in starch or WSC concentrations. This can most likely be attributed to differences in the month of collection. I sampled roots in the fall after leaf abscission, unlike Shepperd et al. (2004) who collected roots at four different times from August to May, with the most significant differences between root diameter and stored carbohydrates occurring in February and May.

I found no significant relationship between TNC concentration (measured as root starch and WSC concentrations) and sucker density, supporting similar observations made by Schier and Zasada (1973). It is widely accepted that bud initiation and shoot outgrowth rely on root carbohydrate reserves for energy until the shoot emerges at the soil surface (Tew, 1970; Schier and Zasada, 1973; Bowen and Pate, 1993). Once suckers emerge from the soil the leaf area is renewed rapidly and photosynthesis begins, allowing for the replenishment of root carbohydrate reserves and sustainment of the respiratory demands of the root system for maximum root retention after disturbance (Landhausser and Lieffers, 2002). Carbohydrate reserves can become severely depleted, for example, after repeated defoliation by insects or destruction by heavy grazing. In extreme cases such as these where carbohydrate reserves are exhausted, Schier and Zasada (1973) hypothesize “the absence of an effect of total non-structural carbohydrate concentration on number of suckers produced does not necessarily mean that carbohydrate reserves have no effect on the density of vegetative reproduction of aspen under natural conditions.” They propose that “because sucker growth in darkness is affected by root carbohydrate concentration, the number of suckers would be expected to be positively correlated with levels of reserve carbohydrates”. I feel this is a valid hypothesis and a possible explanation for the importance of carbohydrate reserves in the development of suckers after disturbance. Though it was beyond the scope of this study, a controlled greenhouse experiment evaluating how sucker density relates to carbohydrate reserves is the next logical step. All in all, this would allow for determination of a critical threshold for root carbohydrate reserves, below which no suckers would emerge from the soil.

There were no significant differences between the sucker densities or tallest sucker heights of “low BA” and “high BA” plots, indicating no definite relationship between sucker ability and stand deterioration. Of the paired plots measured in 2012, five produced fewer suckers on the “low BA” plots than on the “high BA” plots and one produced about the same number; two produced more suckers on the “low BA” plots than on the “high BA” plots. When tallest sucker heights were compared, I found that four paired plots had shorter suckers on the “low BA” plots than on the “high BA” plots and one pair had similar sucker heights; three had taller suckers on the “low BA” plots than on the “high BA” plots. It is important to note that these comparisons used average sucker density and height measurements on a per plot basis and have no statistical significance. A t-test could not be used in this case because of the limited sample size, i.e. sucker counts and measurements occurred in only four exclosures and so only four data points were available per plot. More exclosures would have solved this problem and so inclusion of these comparisons were only presented for the purposes of discussion. Thus, I could not fully evaluate the relationship between stand deterioration and ability to sucker or expected sucker height after a disturbance.

Effects of Herbivory. Excessive browsing of aspen regeneration by wild and domestic ungulates has become one of the primary topics of concern regarding overall aspen decline in the Intermountain West. For the purposes of this study, the effects of herbivory can best be seen when comparing sucker heights measured within the exclosures (i.e. suckers were protected from browsing pressure) versus outside the exclosures (i.e. suckers were unprotected from browsing pressure) (Figs. A.10, A.13, A.14). For measurements taken in both 2012 and 2013, suckers outside the exclosures were significantly shorter than suckers inside the exclosures. Jones et al. (2011) conducted a 2 year grazing study on Lassen National Forest in California and determined that aspen suckers had the highest nutrition when compared to aspen understory and meadow vegetation and is therefore a preferred source of browse throughout the year. In addition, they hypothesize that ungulates may be preferentially attracted to grazing or browsing in or near aspen communities due to their general proximity to attractants such as meadows and drinking water sources, and aspens “patchy” growth habit which concentrates available nutrients in relatively small areas making browsing easier. My study points to the importance of aspen suckers rapidly growing above the herbivore browse line, so that a certain amount of leaf area can be maintained and carbohydrate reserves do not become exhausted. If browsing is excessive, aspen suckers will repeatedly be hedged below the browse line or browsed down to the ground and completely eliminated (Fig. A.12). It was apparent that where stems were dense some suckers were protected by “jackstrawing” (Fig. A.11), but often there were too few trees on the small plots for this to be an effective method for discouraging browsers.

Iodine-Staining. The visual technique for estimating starch concentration, described by Wargo (1975), proved potentially useful for determining relative starch concentration in roots of quaking aspen in the field. Although I found no statistical significance between sucker count from 2012 or 2013 and root starch concentration (thereby making use of this technique in my study irrelevant), I found the visual technique for estimating starch concentration in the field to be accurate and could certainly be used in future studies involving determination of tree vigor or stress thresholds, etc.

CHAPTER VI

CONCLUSIONS

The purpose of this research project was to examine the relationship between root variables and other stand variables on quaking aspen sucker production after a managed treatment or disturbance. This study of paired plots on Cedar Mountain in southern Utah and on Deseret Land and Livestock land in northern Utah documented two root characteristics that can be used as predictive field indicators for the ability of aspen to sucker after a disturbance. In addition, my results document the relationship between an aboveground indicator of stand deterioration, i.e. live aspen basal area, and multiple root variables including diameter, starch, and WSC concentrations.

Root diameter and root surface area proved to be the best predictors of sucker regeneration density after a disturbance. I found that sucker densities decrease with increasing root diameters, and that most suckers are produced on roots less than 2.5 cm in diameter. I found that as the frequency of roots less than 2.5 cm in diameter increases on a plot (quantified in this study as increasing total root surface area), that sucker densities increase. All in all, the highest sucker densities were recorded on plots which contained abundant roots measuring less than 2.5 cm in diameter.

I found no relationship between TNC concentration in the roots (measured as starch and WSC) and sucker density, indicating that TNC concentration cannot be used as an indicator of sucker ability of aspen after a disturbance. It is however suggested that further research be conducted that aims at understanding the relationship between TNC concentration and sucker density under extreme conditions where reserves may have become exhausted over time, such as repeated defoliation from insects or heavy ungulate browsing. Under these conditions, it is very possible that exhausted TNC concentrations would not be sufficient to supply the energy needed to allow sucker growth above the soil level.

Live aspen basal area was related to multiple root variables in the following way. As live aspen basal area increases, root starch and WSC concentrations increase and average root diameter decreases. Assuming that live aspen basal area is a surrogate for leaf area, it is safe to assume these relationships are documenting the effects that leaf area has on the structure and TNC concentration of the root system. To summarize, I hypothesize that reduced leaf areas lead to decreased TNC concentration in the root system and, under these growing conditions, energy is most likely used for maintenance rather than expansion of the root system, leading to reduction in the presence of small diameter or new roots. Low basal areas equal fewer small roots and, thus, a reduction in regeneration ability.

This study also documents the effect of herbivory on sucker height. In areas where grazing and browsing pressures are great, sucker potential is severely decreased due to the effects of repeated hedging below the browse line or complete sucker elimination. If aspen are to persist on the landscape under these circumstances, management strategies must be implemented to enhance aspen regeneration. Jones et al. (2011) suggest a list of possible management strategies to include any combination of the following: 1) set stocking rates so that ungulates have access to satisfactory forage throughout the growing season, 2) provide nutritious supplements making aspen suckers less attractive, 3) implement early-growing season grazing strategies to reduce aspen sucker consumption, 4) construct exclusionary fencing to protect sensitive aspen communities, and 5) implement grazing management strategies which insure years with mid- and late-growing season rest from heavy browsing.

Due to the significant interaction between root diameter, root surface area and sucker production, the third objective outlines a simple method for sampling roots in the field. The relationships that I have documented will allow for measures of these belowground, pre-disturbance stand characteristics to be used as predictors of regeneration density after a disturbance. Ultimately, this guide will provide foresters and land managers with a tool to assist in making decisions on aspen regeneration capacity and allow for allocation of resources where it is needed most. The methodology is described below.

1.) Identify plot center within an aspen stand and mark with a flag.

2.) Randomly locate and excavate four – 35x35x35 cm pits within 6.1 m/ 20 ft from plot center.

3.) Collect all live aspen roots encountered, that measure < 2.54 cm in diameter.

4.) Record the diameter (measured at the mid-point) and length of each root segment.

5.) Calculate individual root surface areas using the equation for the surface area of a cylinder, (Surface Area = (2 x pi x radius^2) + (2 x pi x radius x length)).

6.) Calculate the total root surface area to pit surface area ratio for the plot by summing the root surface areas (cm^2) and dividing by the total pit surface area excavated (4 pits measuring 35x35 cm = 4,900 cm^2).

7.) Convert calculation from step 6 from cm^2/cm^2 to m^2/ha.

8.) Use Table 6 to get an estimate of aspen regeneration density after treatment.

Table 6. Ranges of root surface areas (m^2/ha) and the corresponding prediction interval for sucker counts that could be expected after an aboveground disturbance. Extrapolations are marked with an * symbol.

Root Surface Area (m2/ha)		Predicted Sucker Count per hectare	
Low	High	Low	High
0	300	0	41,500
301	500	0	46,500
501	700	0	51,000
701	900	0	57,000
901	1100	0	64,500
1101	1300	1,000	70,000
1301	1500	3,000	>70,000*

LITERATURE CITED

Arno, S.F., Hammerly, R.P., 1977. Northwest trees. The Mountaineers, Seattle, WA, 222 p.

Bailey, R.G., 1998. Ecoregions: The ecosystem geography of the oceans and continents. Springer-Verlag, New York, 176 p.

Baker, F.A., Durham, S., DeNitto, G., 1993. Estimating the proportion of ponderosa pine roots with *Heterobasidion annosum*. In: Proceedings 8th International Conference on Root and Butt Rots of Trees, pp. 554-559.

Baker, F.S., 1918. Aspen reproduction in relation to management. J. For. 16, 389-398.

Baker, F.S., 1925. Aspen in the Central Rocky Mountain Region. USDA Bulletin 1291, 47 p.

Bancroft, B., 1989. Response of aspen suckering to pre-harvest stem treatments: A literature review. For. Can.- Pacific Forest Centre, FRDA Report 087, 55 p.

Barnes, B.V., 1969. Natural variation and delineation of clones of *Populus tremuloides* and *P. grandidentata* in northern lower Michigan. Silvae Genetica 18, 130-142.

Bartos, D.L., 2001. Landscape dynamics of aspen and conifer forests. In: Shepperd, W.D., Binkley, D., Bartos, D.L., Stohlgren, T.J., Eskew, L.G. (Compilers), Sustaining aspen in western landscapes: Symposium proceedings; 13-15 June 2000; Grand Junction, CO. Proceedings RMRS-P-18. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, pp. 5-14.

Bartos, D.L., Campbell, R.B. Jr., 1998a. Decline of quaking aspen in the Interior West – Examples from Utah. Rangelands 20, 17-24.

Bartos, D.L., Campbell, R.B. Jr., 1998b. Water depletion and other ecosystem values forfeited when conifer forests displace aspen communities. In: Potts, D.F. (Compiler), 1998 Proceedings of AWRA Specialty Conference, Rangeland Management and Water Resources, American Water Resource Association. Proceedings TPS-98-1. Herndon, VA, 474 p.

Bond, W.J., Midgley, J.J., 2001. Ecology of sprouting in woody plants: The persistence niche. Trends Ecol. Evol. 16, 45-51.

Bowen, B.J., Pate, J.S., 1993. The significance of root starch in post-fire shoot recovery of the resprouter *Stirlingia latifolia* R. Br. (Proteaceae). Ann. of Bot. 72, 7-16.

Bowns, J.E., Bagley, C.F., 1986. Vegetation responses to long-term sheep grazing on mountain rangelands. J. Range Manage. 39, 431-434.

Braatne, J.H., Rood, S.B., Heilman, P.E., 1996. Life history, ecology and conservation of riparian cottonwoods in North America. In: Stettler, R.F., Bradshaw, H.D., Heilman, P.E., Hinckley, T.M. (Compilers), Biology of *Populus*: Implications for Management and Conservation, National Research Council, Ottawa, Canada, pp. 57-85.

Campbell, R.B., Bartos, D.L., 2001. Aspen ecosystems: objectives for sustaining biodiversity. In: Shepperd, W.D., Binkley, D., Bartos, D.L., Stohlgren, T.J., Eskew, L.G. (Compilers), Sustaining aspen in western landscapes: Symposium proceedings; 13-15 June 2000; Grand Junction, CO. Proceedings RMRS-P-18. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, pp. 299-307

Collins, W. B., Urness, P. J., 1983. Feeding behavior and habitat selection of mule deer and elk on northern Utah summer range. J. Wildlife Manage. 47, 646-663.

Cronquist, A., 1988. The evolution and classification of flowering plants, 2nd ed. New York Botanical Garden, Bronx, New York, 555 p.

Desilets, S.L.E., Nigssen, B., Ekwurzel, B., Ferre, T.P.A., 2007. Post-wildfire changes in suspended sediment rating curves: Sabino Canyon, Arizona. Hydrological Proc. 21, 1413-1423.

Edminster, C.B., Mowrer, H.T., Shepperd, W.D., 1985. Site index curves for aspen in the central Rocky Mountains. USDA Research Note RM-453.

Fairweather, M.L., Geils, B.W., Manthei, M., 2008. Aspen decline on the Coconino National Forest. In: McWilliams, M. (Compiler), Proceedings of the 55th Western International Forest Disease Work Conference, Oregon Department of Forestry, Salem, OR, pp. 53-62.

Foote, K.C., Schaedle, M., 1978. The contribution of aspen bark photosynthesis to the energy balance of the stem. For. Sci. 24, 569-573.

Frey, B.R., Lieffers, V.J., Landhausser, S.M., Comeau, P.G., Greenway, K.J., 2003. An analysis of sucker regeneration of trembling aspen. Can. J. For. Res. 33, 1169-1179.

Galvez, D.A., Landhausser, S.M., Tyree, M.T., 2011. Root carbon reserve dynamics in aspen seedlings: Does simulated drought induce reserve limitation? Tree Physiol. 31, 250-257.

Groot, A., Man, R., Wood, J., 2009. Spatial and temporal patterns of *Populus tremuloides* regeneration in small forest openings in northern Ontario. The Forestry Chronicle 85, 548-557.

Gruell, G.E., Loope, L.L., 1974. Relationships among aspen, fire, and ungulate browsing in Jackson Hole, Wyoming. National Park Service, U.S. Department of the Interior, Moose, WY. 33 p.

Hogg, E.H., Brandt, J.P., Michaelian, M., 2008. Impacts of regional drought on the productivity, dieback, and biomass of western Canadian aspen forests. Can. J. For. Res. 38, 1373-1384.

Iwasa, Y., Kubo, T., 1997. Optimal size of storage for recovery after unpredictable disturbances. Evol. Ecol. 11, 41-65.

Jones, B.E., Lile, D.F., Tate, K.W., 2011. Cattle selection for aspen and meadow vegetation: Implications for restoration. Rangeland Ecol. Manage. 64, 625-632.

Kaye, M.W., Binkley, D., Stohlgren, T.J., 2005. Effects of conifers and elk browsing on quaking aspen forest in the central Rocky Mountains, USA. Ecological Apps 15, 1284-1295.

Kays, J.S., Canham, C.D., 1991. Effects of time and frequency of cutting on hardwood root reserves and sprout growth. For. Sci. 37, 524-539.

Kittredge, J. Jr., Gevorkiantz, S.R., 1929. Forest possibilities of aspen lands in the Lake States. Technical Bulletin 60, Minnesota Agriculture Experiment Station, 84 p.

Landhausser, S.M., Lieffers, V.J., 2002. Leaf area renewal, root retention and carbohydrate reserves in a clonal tree species following above-ground disturbance. J. Ecol. 90, 658-665.

Lazorko, H., Van Rees, K.C.J., 2011. Root distributions of planted boreal mixedwood species on reclaimed saline-sodic overburden. Water, Air and Soil Pollution 223, 215-231.

Maini, J.S., 1968. Silvics and ecology of *Populus* in Canada. In: Maini, J.S., Cayford, J.H. (Compilers), Growth and utilization of poplars in Canada, Canadian Department of Forestry and Rural Development, Publication 1206, pp. 20-69.

Martin, A.C., Zim, H.S., Nelson, A.L., 1951. American wildlife and plants. McGraw-Hill Book Co., New York, 500 p.

McCool, S.F., 2001. Quaking aspen and the human experience, dimensions, issues, and challenges. In: Shepperd, W.D., Binkley, D., Bartos, D.L., Stohlgren, T.J., Eskew, L.G. (Compilers), Sustaining aspen in western landscapes: Symposium proceedings; 13-15 June 2000; Grand Junction, CO. Proceedings RMRS-P-18. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, pp. 147-162.

McDonough, W.T., 1979. Quaking aspen – seed germination and early seedling growth. USDA Research Paper INT-234, 13 p.

Mitton, B.J., Grant, M.C., 1996. Genetic variation and the natural history of quaking aspen. Bioscience 46, 25-31.

Mock, K.E., Rowe, C.A., Hooten, M.B., Dewoody, J., Hipkins, V.D., 2008. Clonal dynamics in western North American aspen (*Populus tremuloides*). Mol. Ecol. 17, 4827-4844.

Mueggler, W.F., 1989. Age distribution and reproduction of Intermountain aspen stands. Western J. App. For. 4, 41-45.

Oukrop, C.M., 2010. Assessing quaking aspen (*Populus tremuloides*) decline on Cedar Mountain in southern Utah using remote sensing and geographic information systems. Masters thesis, Utah State University, Logan, UT, 129 p.

Quinn, R.D., Wu, L., 2001. Quaking aspen reproduce from seed after wildfire in the mountains of Southeastern Arizona. In: Shepperd, W.D., Binkley, D., Bartos, D.L., Stohlgren, T.J., Eskew, L.G. (Compilers), Sustaining aspen in western landscapes: Symposium proceedings; 13-15 June 2000; Grand Junction, CO. Proceedings RMRS-P-18. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, pp. 369-376.

Romme, W.H., Turner, M.G., Wallace, L.L., Walker, J.S., 1995. Aspen, elk, and fire in northern Yellowstone National Park. Ecology 76, 2097-2106.

Sandberg, G.A., 1951. The regeneration of quaking aspen by root suckering. Masters thesis, University of Minnesota, Minneapolis, MN, 172 p.

Sargent, C.S., 1961. Manual of the trees of North America. Dover Publications Inc., New York, 910 p.

Schier, G.A., 1973. Origin and development of aspen root suckers. Can. J. For. Res. 3, 45-53.

Schier, G.A., Zasada, J.C., 1973. Role of carbohydrate reserves in the development of root suckers in *Populus tremuloides*. Can. J. For. Res. 3, 243-250.

Schier, G.A., 1975. Deterioration of aspen clones in the middle Rocky Mountains. USDA Research Paper INT-170, 14 p.

Schier, G.A., 1976. Physiological and environmental factors controlling vegetative regeneration of aspen. In: Hessel, D.L., Betters, D.R., Loring, T.J., Porter, L.D., Bennett, J.E. (Compilers), Utilization and Marketing as Tools for Aspen Management in the Rocky Mountains: Symposium Proceedings; Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, pp. 20-23.

Schier, G.A., 1978. Vegetative propagation of Rocky Mountain aspen. USDA General Technical Report INT-44, 13 p.

Schier, G.A., Campbell, R.B., 1980. Variation among healthy and deteriorating aspen clones. USDA Research Paper INT-264, 12p.

Schier, G.A., 1982. Sucker regeneration in some deteriorating Utah aspen stands: Development of independent root systems. Can. J. For. Res. 2, 1032-1035.

Shepperd, W.D., 1990. A classification of quaking aspen in the central Rocky Mountains based on growth and stand characteristics. Western J. App. For. 5, 69-75.

Shepperd, W.D., Bartos, D.L., Mata, S.A., 2001. Above- and below-ground effects of aspen clonal regeneration and succession to conifers. Can. J. For. Res. 31, 739-745.

Shepperd, W.D., Reichert, D.R., Mata, S.A., 2004. Overwinter storage of carbohydrate in aspen. Transactions of the Western Sec. of the Wildlife Soc. 40, 45-48.

Stam, B.R., Malechek, J.C., Bartos, D.L., Bowns, J.E., Godfrey, E.B., 2008. Effect of conifer encroachment into aspen stands on understory biomass. Rangeland Ecol. Manage. 61, 93-97.

Strain, B.R., Johnson, P.L., 1963. Cortical photosynthesis and growth in *Populus tremuloides*. Ecology 44, 581-584.

Tew, R.K., DeByle, N.V., Schultz, J.D., 1969. Intraclonal root connections among quaking aspen trees. Ecology 50, 920- 921.

Tew, R.K., 1970. Root carbohydrate reserves in vegetative reproduction of aspen. For. Sci. 16, 318-320.

Van Dersal, W.R., 1938. Native woody plants of the United States: their erosion control and wildlife values. USDA, Washington, DC. 362 p.

Wachowski, J., Landhausser, S.M., Lieffers, V.J., 2014. Depth of root placement, root size and carbon reserves determine reproduction success of aspen root fragments. For. Ecol. Manage. 313, 83-90.

Wargo, P.M., Parker, J., Houston, D.R., 1972. Starch content in roots of defoliated sugar maple. For. Sci. 18, 203-204.

Wargo, P.M., 1975. Estimating starch content of roots of deciduous trees – a visual technique. USDA Research Paper NE-313, 9 p.

Weigle, W.G., Frothingham, E.H., 1911. The aspens: their growth and management. USDA Bulletin 93, 35 p.

Wilson, E.O., 1992. The diversity of life. W. W. Norton and Co., New York, 424 p.

Woldeselassie, M.K., 2009. Soil organic carbon and site characteristics in aspen and evaluation of the potential effects of conifer encroachment on soil properties in northern Utah. Masters thesis, Utah State University, Logan, UT, 165 p.

Woldeselassie, M.K., Van Miegroet, H., Gruselle, M.C., Hambly, N., 2012. Storage and stability of soil organic carbon in aspen and conifer forest soils of northern Utah. Soil Sci. Soc. Amer. J. 76, 2230-2240.

Worrall, J.J., Egeland, L., Eager, T., Mask, R.A., Johnson, E.W., Kemp, P.A., Shepperd, W.D., 2008. Rapid mortality of *Populus tremuloides* in southwestern Colorado, USA. For. Ecol. Manage. 255, 686-696.

Zegler, T.J., Moore, M.M., Fairweather, M.L., Ireland, K.B., Fule, P.Z., 2012. *Populus tremuloides* mortality near the southwestern edge of its range. For. Ecol. Manage. 282, 196-207.

Zhu, W.Z., Xiang, J.S., Wang, S.G., Li, M.H., 2012. Resprouting ability and mobile carbohydrate reserves in an oak shrubland decline with increasing elevation on the eastern edge of the Qinghai-Tibet Plateau. For. Ecol. Manage. 278, 118-126.

APPENDIX

Fig. A.1. A decadent aspen stand near Site 4, Plot "low BA" on Cedar Mountain, Utah. Notice the high number of dead or fallen stems and the general lack of root suckering to replace the overstory mortality.

Fig. A.2. Sooty-bark canker caused by the fungus *Encoelia pruinosa* on the bole of aspen. This is a common canker of aspen, often killing trees within 3-10 years. The abundance of this canker in a stand was one of the visual indicators that I used to identify study plots with low live aspen basal area or "low BA" plots.

Fig. A.3. A stable aspen stand on Cedar Mountain, Utah. Notice the “skirt” of successful regeneration around the perimeter of the stand.

Fig. A.4. Close-up of regeneration from Fig. A.3.

Fig. A.5. Example of cutting treatment at Site 5, Plot "low BA" on Cedar Mountain, Utah.

Fig. A.6. Example of cutting treatment at Site 1, Plot "high BA" on Cedar Mountain, Utah.

Fig. A.7. Example of exclosure and aspen suckers produced after felling treatment at Site 2, Plot "low BA" on Cedar Mountain, Utah.

Fig. A.8. Example of exclosures and aspen suckers produced after felling treatment at Site 8, Plot "low BA" on Cedar Mountain, Utah.

Fig. A.9. Example of 1.42 m (4.66 ft) square pvc frame used to assess the effects of herbivory on aspen suckers that were not protected by exclosures.

Fig. A.10. Aspen suckers and other vegetation being protected from excessive browsing by an exclosure at Site 3, Plot "high BA" on Cedar Mountain, Utah.

Fig. A.11. Aspen suckers effectively being protected from herbivory by “jackstraw” effect after the cutting treatment.

Fig. A.12. Aspen suckers that have been browsed down to the ground, most likely resulting in complete elimination.

Fig. A.13. Clump of aspen suckers that have had their terminal shoots and the majority of foliage removed by browsing.

Fig. A.14. Clump of aspen suckers that have been protected by an exclosure for 2 years. These suckers grew rapidly with the terminal shoots and foliage remaining intact.