# INFLUENCE OF COMPETITION ON LONGLEAF PINE SEEDLING RECRUITMENT IN SELECTION SILVICULTURE

By

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*A drive through the virgin long-leaf pine forest will long be remembered. The stately trunks rise forty to sixty feet and then spread out their dense foliage, which joins above like the arches of a cathedral. There is little or no undergrowth, and the view fades into a maze of column-like trunks.*

(Emerson, 1919).

# Abstract

The longleaf pine (*Pinus palustris* Mill.) ecosystem's decline has resulted in the loss of 97 percent of the 24-36 million hectares it covered prior to European settlement, but interest in longleaf pine restoration and management has increased in recent decades. This project sought to determine what levels of residual overstory in selection silviculture promote adequate longleaf pine seedling recruitment. Six hundred containerized longleaf pine seedlings were planted on two sites, one subxeric and one mesic, in the 2007-2008 dormant season. Half of the seedlings at each site were randomly selected for understory removal (with herbicide) in order to differentiate overstory influences from those of the understory. Canopy gap fraction above each seedling was determined using hemispherical photography, and average soil moisture was determined from four time domain reflectometer (TDR) measurements at each seedling during the 2008 and 2009 growing seasons. Seedling groundline diameter (GLD) was measured at time of planting and in August, 2008 and 2009. First year results indicated that mean moisture was not significantly different between herbicide and control treatments at either site. Regression analyses showed weakly positive relationships between moisture and seedling growth for both treatments at both sites, whereas a generally negative but non-significant relationship existed between gap fraction and seedling growth. Second year results showed a similar absence of a treatment effect on soil moisture at both sites. Total 2008-2009 mean seedling growth and soil moisture were significantly greater at the subxeric site than at the mesic site. Regression analyses showed few significant relationships, but generally positive trends existed between gap fraction and seedling GLD growth. In contrast, no general trend was present between mean soil moisture and GLD growth. Root excavations from a subsample of seedlings showed that root growth was not extensive, in that estimated mean taproot depth was shallower than 90 cm. Furthermore, no relationship existed between GLD and root depth.

Due to confounding factors, hypothesis testing could not be conducted, and results represent circumstantial evidence only. However, results document the severity of longleaf pine's growing environment on both mesic and subxeric sites and suggest that seedlings frequently experienced moisture stress during years slightly below average and above average for total rainfall. Although immature, data collected in this study support that of other research suggesting that early longleaf pine growth and survival is increased by moisture availability, but that with time light becomes the primary driver of longleaf pine seedling recruitment.

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# List of Abbreviations

| | |
|---|---|
| BA | Basal area |
| dbh | Diameter at breast height (1.4 m) |
| GLD | Groundline diameter |
| GLI | Gap light index |
| NPP | Net primary productivity |
| PAR | Photosynthetically active radiation |
| PDSI | Palmer Drought Severity Index |
| PWP | Permanent wilting point |
| RBI | Root-bound index |
| RCD | Root collar diameter |
| SEZ | Seedling exclusionary zone |
| TDR | Time domain reflectometry |

# CHAPTER I

# INTRODUCTION

Interest in restoring and managing longleaf pine (*Pinus palustris* Mill.) ecosystems has steadily increased during the past four decades and especially in recent years (Brockway et al., 2005a), with restoration a high conservation priority (Kirkman et al., 2004). In fact, the longleaf pine forests and woodlands of the Southeastern Coastal Plain have been described as “critically endangered” because of their more than 98 percent decline from their previous 28-36 million hectares (Means and Grow, 1985; Noss, 1988, 1989; Goetz, 1998; Ware et al., 1993; Mitchell et al., 2000). Concern has also been expressed due to recent statistics showing that most remaining longleaf stands are aging without replacement (Brockway and Outcalt, 2000), meaning that many mature longleaf pine stands lack the younger age classes necessary to replace mortality in the near-term.

Noting this dramatic decline in longleaf acreage and unsustainable demographics of remnant longleaf pine stands, Noss (1989) and Gilliam and Platt (2006) call for silviculture that mimics natural processes rather than the often more artificial and intensive methods employed by modern industrial silviculture. They further state that good ecosystem management of the remaining sites with longleaf pine and native groundcover is at least as important as restoration on disturbed sites. More specifically, Kirkman and Mitchell (2006) and Brockway and others (2005b) assert that the longleaf pine ecosystems’ long-term sustainability and recovery depend on managing for structural features that promote fire and permit natural regeneration of overstory species that leads to normal stand replacement dynamics.

Longleaf pine savanna ecosystems lend themselves to simultaneous management for timber and biodiversity better than any other forest ecosystem in the United States (Freeman and Jose, 2009). Thus, one potential tool that could fulfill the aforementioned restoration and conservation goals for longleaf pine is uneven-aged management, which can allow for managing timber and biodiversity together. While scientists have previously stated that longleaf pine is not suited to selection silviculture (e.g., Wahlenberg, 1946, p. 255), more recent information suggests that, when carefully applied, uneven-aged systems provide a workable solution to the range of objectives that are common in longleaf pine management. For example, Noel and others (1998) examined stand structure in old-growth and second-growth longleaf pine forests and suggested that many of the second-growth stands [most of which are the coincidental result of "cut-and-run" logging that removed all merchantable stems (Boyer and Peterson, 1983)] may be well-suited to selection silviculture.

Anecdotal evidence supports the conclusion that selection silviculture can be applied successfully in longleaf pine ecosystems. The Stoddard-Neel approach, a form of single-tree selection which prioritizes conservation values, has been applied to longleaf pine forests in southern Georgia and northern Florida for decades (Jack et al., 2006b; McIntyre et al., 2008). Specific research has addressed the use of selection silviculture in longleaf pine forests as well, and it has found that both group selection and single-tree selection are practicable (Mitchell et al., 2006). Although various studies (e.g. Palik et al., 1997; Battaglia et al., 2003; Palik et al., 2003; Pecot et al., 2007) have addressed the mechanisms of longleaf pine seedling recruitment that are integral to successful selection silviculture, applied research has yet to demonstrate and quantify longleaf pine seedling recruitment in stands managed with selection, or how selection can be applied to shorten the length of time between seedling establishment and recruitment.

Several previous studies have examined seedling recruitment in naturally-occurring gaps and underneath both dispersed and aggregated overstory retention in stands managed by selection systems (Palik et al., 1997; Brockway and Outcalt, 1998; McGuire et al., 2001; Palik et al., 2003;

Pecot et al., 2007). These studies present two different hypotheses with respect to the influence of the forest canopy on longleaf pine seedling recruitment. Light and moisture are considered to be the primary limiting factors for seedling growth, respectively. Still under debate is which of these factors is ultimately limiting. This, in turn, affects how stands can be best managed to increase seedling growth underneath an unevevn-aged structure. Specifically, the importance of gaps to successful stand-wide regeneration is unclear. Gaps provide early-successional conditions, so they often benefit longleaf pine seedling establishment which may accelerate recruitment (Palik et al., 2003). However, silviculture that relies on gaps is not necessarily ideal due to both ecological and operational concerns (Guldin, 1996; Mitchell et al., 2006; Pecot et al., 2007). Single-tree selection is an alternative to gap-based approaches. It does not rely on area control, but still may create openings in the canopy when two or more adjacent trees are selected for removal. In effect, it provides the flexibility needed to satisfy the varied and seemingly contradictory requirements of longleaf pine silviculture.

Longleaf pine seedlings are subject to competition from the understory as well as the overstory. It is recognized that less competition allows seedlings to grow faster and eventually be recruited into the stand more readily. However, the relative effects of both an intact understory and a mature overstory on longleaf pine seedlings are less understood. Further complicating the competitive dynamic, the reduction of overstory competition through silvicultural manipulations often releases the forest understory. This, in turn, exerts further competition toward grass-stage longleaf pine seedlings (Pecot et al., 2007). Thus, the continua of competition for aboveground and belowground resources between structural layers within the forest need to be better investigated by scientific experiments.

While understanding competitive relationships is integral to developing selection systems, those relationships are unlikely to be steadfast in all situations. Site is one important variable that has yet to be investigated by a single study. The above studies (i.e. Palik et al., 1997; Brockway and Outcalt, 1998; McGuire et al., 2001; Pecot et al., 2007) all examined only one site each, which is a potential cause of their differing results. Because site quality often varies locally and certainly varies across the region, effects of differing site conditions must be addressed in order to adequately address seedling recruitment issues.

The importance of basic research is clear because it lays the foundation for other applied research, the results of which can be directly utilized by practitioners. Recent studies (Palik et al., 1997; Pecot et al., 2007) as well as many prior studies of longleaf pine seedling competition (Pessin, 1938, 1939a) have tended to be fundamentally-oriented, leaving practitioners with substantial need for applied research. The applied orientation of this research study affords an opportunity to both synthesize and build upon previous basic research and also provide information that can be directly implemented in both the management of existing longleaf pine forests as well as ongoing and future restoration efforts.

In response to the call for uneven-aged management of longleaf pine and to address the significant need for applied research that examines multiple sites, the objective of this study is to determine how selection silviculture can best be applied to longleaf pine ecosystems. Specifically, it asks what residual stand densities of dispersed overstory retention create conditions best suited to longleaf pine seedling recruitment by investigating the impacts of light and moisture as influenced by site.

# CHAPTER II

# LITERATURE REVIEW

## Overview of Longleaf Pine Stand Dynamics

The early accounts of longleaf pine forests allow for conflicting interpretations of stand structure prior to extensive European settlement. Some descriptions suggest stands were dominated largely by one cohort, but others lead to the conclusion that stands were multi-aged at a localized scale (see Bartram, 1791 [1996]; Schwarz, 1907; Penfound and Watkins, 1937; Wahlenberg, 1946). Additionally, the scientific literature offers differing accounts of “natural” stand dynamics. While some scientists have concluded that longleaf pine stand dynamics were driven by large disturbances and were patchy even-aged stands (Wahlenberg, 1946; Meldahl, 2002), other research presents evidence that longleaf pine grew primarily in uneven-aged stands (Platt et al., 1988; Pederson et al., 2008).

It is difficult to determine exactly what was present in the pre-European settlement forest, and conjecture about the original forests necessarily must come from relict old-growth stands or stands in the latter stages of stand development. Pederson and others (2008) examined 70-90 year old second-growth stands at Ichauway in southwest Georgia and found that recruitment had occurred in gaps smaller than 1.3 hectares. This information supports the early descriptions of longleaf pine forests as uneven-aged. Similarly, data collected at the Wade Tract—an old-growth stand in southern Georgia typically used as a reference site—also demonstrate uneven-aged stand structure (Platt et al., 1988). Nevertheless, it is unlikely that an amalgam of ecosystems spanning

36 million hectares exhibited only one path of succession or age structure. Rather, the longleaf pine ecosystems that extend across physiographic regions from the Cumberland Plateau in Alabama to the peninsula of Florida and on the Coastal Plain from southern Virginia to east Texas are driven by different ecological processes on different sites. For example, data presented by Schwarz (1907), although limited, document even-aged stand structure in Alabama, Mississippi, and Louisiana.

Because of a lack of long-term data, establishing the normal disturbance regime in longleaf pine forests has been difficult. However, studies have shown that the most common disturbances are small-scale ones that tend to affect individual trees or small groups of larger trees (Palik and Pederson, 1996; Outcalt, 2008). Larger-scale disturbances affect larger areas. They may develop quickly, but they occur less frequently. Although lightning is usually a small-scale disturbance, it can form openings as large as 0.2 ha (Palik and Pederson, 1996) and tends to enlarge such gaps over time (Outcalt, 2008). Still, mortality rates are usually not high, and entire stand replacement has been estimated to take between 263-292 years (Palik and Pederson, 1996). Thus, management should acknowledge this disturbance regime and employ a long-term perspective in stand management, particularly in regeneration.

Longleaf pine “succession” [regeneration] has been a concern for more than a century. Schwarz (1907) identified a need for studying tolerance, fires and the effects of different groundcovers on “natural rotation of [longleaf] forests”. However, Schwarz focused only on above-ground resources, suggesting that light was the most important limiting resource (p. 11), while not mentioning moisture availability. Because he considered light as the limiting resource, Schwarz suggested that regular recruitment was unnecessary because cohorts could not be recruited successfully without canopy mortality or disturbance (pp. 20-23). It is interesting that over 100 years later a clear pattern of what controls the successful recruitment of longleaf pine in uneven-aged stands has not yet been established.

## Longleaf Pine Biology

Longleaf pine has been described as a very intolerant pioneer species (Baker, 1949; Boyer, 1993b; Hardin et al., 2001, p. 144), but unlike most pioneer species, it is typically a poor (irregular) seed producer (Landers et al., 1995; Boyer, 1998), and has large seeds that do not remain viable for a long time. Good seed crops are estimated to occur once every 5-7 years (Hardin et al., 2001, p. 144) or sometimes only once every 8 to 10 years (Maki, 1952). Bumper seed crops are not common (Boyer, 1987), although cone production varies year-to-year and place-to-place (Boyer, 1993b). However, region-wide data show that the frequency of cone crops adequate for regeneration has increased in recent years (Pederson et al., 2000; Brockway et al., 2006). Largely due to seed predation, few seeds become established seedlings (Boyer, 1964a), so bumper crops make successful regeneration more likely.

Longleaf pine's large seeds typically do not disperse over long distances. Along forest edges and in younger stands, seeds rarely adequately disperse farther than 30 m from the source tree (Boyer, 1958, 1963b). However, in old-growth stands, peak seed dispersal can occur at distances between 35-60 m from the parent tree, with few seeds landing within 10 m of the parent and as much as 15 percent of seeds dispersing farther than 75 m (Grace et al., 2004). This suggests that seed dispersal may not necessarily be a problem, as dispersal distance can be affected by existing stand structure and management techniques.

Unlike most southern pines, under good conditions longleaf pine seedlings germinate within one (Boyer, 1990) and five (Hardin et al., 2001, p. 144) weeks. Longleaf seedlings produce virtually no above-ground stems; this stemless condition is called the "grass stage" and is a time during which the seedling's growth is concentrated in the root system. Seedlings remain in the grass stage until they have developed a root collar of about 2 to 2.5 cm in diameter (Pessin, 1939a; Wahlenberg, 1946; Haywood, 2000), after which they begin height growth, a process referred to as "bolting." The grass stage can last from 1 to more than 20 years, but 3 to 6 years is typical (Hardin et al., 2001, p. 144). Factors causing seedlings to languish in the grass stage include repeated defoliation from severe brown-spot needle blight infections (caused by *Mycosphaerella dearnesii* M.E. Barr) (Pessin, 1944) and lack of prescribed fires (Wakeley and Muntz, 1947; Phelps et al. 1978). A prolonged grass stage can be a compounding problem: the longer seedlings stay in the grass stage, the more susceptible they become to brown-spot (Johnson and Gjerstad, 2006). Other potential pathogens that could lengthen the grass stage include insect infestations such as pine webworm (*Pococera robustella* Zeller) (Mayfield, 2007). Seedlings that survive the grass stage and "bolt" (begin rapid height growth) are considered established once they reach 1 meter in height (Wahlenberg, 1946).

## Competition and Longleaf Pine Seedlings

### *Overview*

Longleaf pine's greatest mortality occurs in its period of "dwarfness" (Ashe, 1895, cited by Pessin, 1944). So, reducing the length of the grass stage should diminish seedling mortality and allow for improved regeneration success. As early as 1909, Chapman noted the lack of seedlings adjacent to mature trees, even in areas with sufficient light. He suggested that this was the result of root competition (Brown, 1964, p. 4). Again, in a 1940 paper, Chapman and Bulchis suggested that longleaf reproduction could not thrive within about 10 meters of mature trees. Smith (1955) found that longleaf pine seedlings can persist for 5 to 6 years underneath an overstory of pine and oak without suffering serious mortality, but that the presence of an overstory negatively affects seedlings' release rate. After 9 years, the same seedlings showed greater growth with increased distance from large trees, of which large oaks were more suppressive than pines (Smith, 1961). Expanding on Chapman's work, Walker and Davis (1956) suggest that competition between seedlings and residual trees decreases with distance from the mature tree, but that the influence may extend as far as 15 meters from the tree—well beyond the width of the crown. Similarly, Platt and Rathbun's (1993) model predicted that the zone of influence of subadult and adult trees on seedlings extended—although weakly—beyond distances of 30 meters.

The results of Chapman (1909), Chapman and Bulchis (1940), and Walker and Davis (1956) were further supported by Grace and Platt (1995b), who found that on the Wade Tract, an old-growth stand on a high-quality site, large (>30 cm dbh) longleaf pines negatively affected the growth and survival of naturally established one-year-old seedlings up to 15 and 18 meters away, respectively. They further found that small neighbors do compete with new seedlings, but only at very close distances. In a related study, Grace and Platt (1995a) support those findings, suggesting that the density of adult trees may have a long-term effect on longleaf pine demography that begins early in the species' life cycle. The work of Platt and Rathbun (1993) also shows that smaller trees, especially those in the smallest size classes, exhibit depressed growth and survival due to competition with mature trees. So, both stand structure and density can have important effects on seedling growth and establishment.

Seedling suppression has been observed on multiple site- types and in stands of various ages. For example, Brockway and Outcalt (1998), studying a 71 year-old second-growth stand on xeric sandhills, described the existence of a "seedling exclusionary zone" (SEZ), 12 – 16 meters wide around the edge of canopy gaps, in which competition from mature trees resulted in significantly reduced densities of grass-stage seedlings and impaired seedling development (i.e., fewer "bolted" seedlings). Grace and Platt (1995b), working in an older stand on a higher quality mesic site at the Wade Tract, also documented a zone of heightened competition of similar width, but higher densities of grass-stage seedlings indicated greater abundance from lower mortality. In a poorly drained flatwoods savanna in North Carolina, Avery and others (2004) reported that competitive influences were reduced at distances beyond 6 meters from the gap edge. It therefore seems clear that any more-established stems in competition with longleaf seedlings will retard, if not prohibit, their recruitment. Furthermore, the above studies indicate that the competitive zone of reduced seedling growth may become narrower as moisture availability increases.

While the forest overstory has been the primary subject of study in longleaf pine seedling suppression, the importance of the understory also has been investigated. Common understory species include clonal oaks as well as grasses and other shrubs. Thus, the understory is often composed of both shallow-rooted and deeply rooted species with expansive and highly competitive fibrous root systems. The importance of this source of competition is suggested by Rodriguez-Trejo and others (2003), Pecot and others (2007), and Knapp and others (2008), who recognize that new seedlings lack extensive root systems and can be adversely affected by such competition, resulting in both reduced growth and increased mortality. The understory's ability to reduce light availability has also been documented (Knapp et al., 2008). Thus, Pessin's (1944) conclusion about the importance of light competition within the understory is logical.

As Brockway and Outcalt (1998) indicated, fire also can affect seedling location. While longleaf pine seedlings can often survive prolonged overstory competition when protected from fire (Smith, 1961; Boyer, 1963), increased fire intensity can reduce seedling survival among the often smaller seedlings under longleaf canopies (Boyer, 1974). However, Boyer (1974) documented highest seedling mortality (62%) under 7 $m^2\ ha^{-1}$, a residual overstory density that is recommended for the shelterwood regeneration method, which is supposed to be less suppressive on reproduction. Thus, variable seedling mortality suggests that seedlings clustered in canopy gaps are only those that survive the competitive pressures for above-ground and belowground resources and are not killed or sufficiently stunted by fire or pathogens.

There is strong evidence that longleaf pine seedlings are negatively affected, both directly and indirectly, by competition from overstory and understory plants. While the proportional importance of differing factors may vary by site type, it is generally accepted that lack of vigorous longleaf pine seedlings underneath or adjacent to mature trees is the result of competition for light, moisture and nutrients. Therefore, competition for these resources is a central factor in of seedling survival and release.

### *Light*

Because competition is such an important factor in seedling growth and recruitment, competition control was an early research topic. Pessin (1944) examined seedling height growth (release) in plots in which herbaceous vegetation was denuded with hoes, spaded, or burned, versus a control. He found that after 4 years, height growth on denuded plots was 11 times greater than the control and that more than two-thirds had exited the grass stage, or “bolted.” In contrast, nearly 95% of seedlings in all other treatments were still in the grass stage. This implies that longleaf pine seedlings are exposed to heavy competition from groundcover as well as the overstory. Yet, Pessin (1944) suggested that his observed increase in height growth of longleaf pine seedlings in denuded plots resulted from reduced light competition from grasses and associated groundcover rather than a lack of root competition. Watered seedlings did not show any significant difference in height growth. It therefore appears that longleaf pine seedlings compete for light on two levels.

The competitiveness of the forest understory has been documented recently as well. Carraway (2001) conducted a study similar to Pessin’s (1944), but controlled grasses with selective herbicide. She found that 3-year-old grass stage natural reproduction in herbicided plots increased in biomass by 479% during its fourth year. Other results from Carraway’s (2001) research indicate that grasses, not shrubs and forbs, are more competitive with longleaf seedlings. However, Carraway (2001) did not address either light or soil moisture availability. Knapp and others (2008) found that light was positively related to planted seedling diameter in the second growing season, and that the understory’s growth reduced the light available to seedlings by 3 percent, thus demonstrating the importance of shrub-layer competition.

Separating various competitive influences addresses an important knowledge gap in seedling competition. Pecot and others' (2007) trenching study found that the overstory facilitated longleaf pine seedling survival, but that seedling growth decreased both with increasing overstory stocking and in gaps with intact understory. In canopy gaps, they found the understory was able to outcompete longleaf pine seedlings by filling the associated root gaps. Thus, they conclude that in such cases light is the determining factor in longleaf pine seedling growth. Yet, Pecot and others (2007) also suggest that advance hardwood reproduction in gaps preempts soil resources from longleaf pine seedlings. These findings support earlier work by Muntz (1951), who found higher longleaf pine seedling survival underneath oak crowns than in gaps, but also pointed out that hardwood sprouts could cause reduced pine survival in gaps.

Similar to Pessin's (1944) results, Palik and others (1997) found that gap soil moisture was not affected by overstory basal area, nor did it impact the seedling response within that gap, the latter of which was supported by Gagnon and others' (2003) results. Palik and others (1997) suggested that seedling biomass increases were dependent on light and nitrogen availability rather than soil moisture. However, since Palik and others' 1997 study found that as little as 6 $m^2$ $ha^{-1}$ can reduce above-ground and belowground seedling biomass by 50%, light must not be the single limiting factor—logically, a basal area of 6 $m^2$ $ha^{-1}$ should provide seedlings with plenty of light (Battaglia et al., 2003).

### *Soil Moisture*

Studies have observed that both radial growth of established longleaf pines (Pederson et al., 2008) and survival among recently planted longleaf pine seedlings (Rodriguez-Trejo et al., 2003) can be limited by growing season soil moisture availability. Experiments also have shown that water is often an important factor in seedling growth. In a greenhouse study, Jose and others (2003) found that light and nitrogen availability played an important role in seedling growth, especially when soil water was not limiting. Since their seedlings were potted and thus not subject to competition, Jose and others' (2003) results support the conclusions of Walker and Davis (1956) that seedling growth can depend on moisture and nutrient availability.

Competition for soil moisture often comes from different sources. Brockway and Outcalt (1998) state that, while seedling mortality is indirectly influenced by a mature overstory through needle deposition and the resulting increase in fire intensity, the canopy trees also directly compete with seedlings for limited site resources, especially moisture and nutrients. They demonstrate that, although variable, canopy cover in a mature longleaf pine woodland averaged only 57% and that light was evenly distributed on the forest floor across canopy gaps. Thus, they showed that light was not influencing the clustering of longleaf seedlings in the center of gaps. This supports their conclusion that regeneration success is actually controlled by the presence and size of the root gap. Jose and others (2003) conclude that in water-limited systems [such as that examined by Brockway and Outcalt (1998)] increasing light and nutrients may not increase seedling growth, thus further supporting Brockway and Outcalt's (1998) findings.

Nelson and others (1985) examined the use of herbicides to reduce herbaceous competition and found that removing competing weeds reduced the duration of the grass stage by approximately one year. In contrast to Pessin (1944), they suggested that their observed increase in seedling growth on plots receiving herbaceous weed control was due to decreased competition for moisture. Still, competition dynamics likely vary from place to place. Pecot and others (2007) showed that plant-plant interactions between adult pines and pine seedlings were not likely to be driven by competition for water. Also, results from a flatwoods site in North Carolina show that higher soil moisture reduced seedling diameter after two growing seasons (Knapp et al., 2008).

Light and soil moisture availability may cause differing competitive interactions. A study by Jones and others (2003) found that root competition dropped to near zero at about 65 percent gap fraction – approximately the level at which Palik and others (1997) noticed substantial seedling responses to increases in light availability. This seems to suggest that both above-ground and below ground factors may be important in the growth rate of longleaf seedlings depending on the edaphic conditions. It is clear that there is no single variable controlling these dynamics. Rather, complex interactions among many variables ranging from light and other site resources to management practices (e.g. fire) and competition all variably affect seedling survival and growth. Gilliam and Platt (1999) support this conclusion by demonstrating the underlying importance of site, particularly soil texture and moisture/fertility on stand structure and species composition. They suggest that their results support those of Glitzenstein and others (1995), who concluded that population dynamics depended more on habitat type than on fire history.

Maintaining volume growth and adequate recruitment thus is dependent on the rate at which seedlings bolt from the grass stage and begin their period of rapid growth. As mentioned above, the presence of any residual mature trees tend to prolong the grass stage. So, it is clear that longleaf pine seedlings are negatively affected both directly and indirectly by competition from both the overstory and understory. However, if adequate vegetation control (including burning) is applied, height growth can occur as early as the second year post-planting (third year overall) (Barnett, 1992). While in each case varying factors are at play, it is generally accepted that lack of vigorous longleaf pine seedlings underneath or adjacent to mature trees is the result of competition for moisture, nutrients, and light. Thus, the varying degree of such competition is important in seedling survival and release, and stand manipulations to affect competitive relationships among seedlings, the understory, mid-story, and overstory layers can provide growing space sufficient for adequate longleaf pine seedling recruitment.

## Even-Aged Management Systems

### *History*

Known for its infrequent cone crops, poor seed dispersal, intolerance to competition, and slow juvenile growth, longleaf pine is considered a species that can be difficult for land managers to regenerate naturally (Gemmer et al., 1940; Wakeley, 1954; Boyer, 1964b; Croker, 1979; Boyer and Peterson, 1983). Following initial logging, some early longleaf pine forests were abandoned because the concept of sustainable forest management had not yet reached the United States and the notion of sustained timber flow were not even considered (Earley, 2004, p. 175). Later loggers considered reforestation to be too impractical because of the perceived problems with longleaf pine regeneration (Croker, 1979). Since then, decades of research have gone into examining the masting requirements of longleaf pine as well as the requirements of seedlings for both successful survival and establishment. Largely because of its characterization as "intolerant," the first management systems for longleaf pine used even-aged silviculture, which manages single-cohort stands after complete removal of the overstory.

### *Overview*

Even-aged silviculture manages single-cohort stands, meaning that seedlings are not subject to competition from older, more established trees, and therefore their time as sub-merchantable stems is minimized. Clearcutting followed by artificial regeneration can be utilized in longleaf pine management, but such an approach is more typically used for restoring sites currently lacking longleaf pine rather than for maintaining existing stands of longleaf pine. The substantial up-front expenses associated with site preparation and tree planting most often make natural regeneration of longleaf pine a more feasible management option (Brockway et al., 2006). Furthermore, clearcutting results in a dramatic alteration of forest structure that significantly impairs values related to the quality of wildlife habitat and aesthetics (Brockway and Lewis, 2003; McIntyre et al., 2008). Alternatively, there are two other even-aged management systems using natural regeneration methods that can be applied to longleaf pine: the seed-tree and the shelterwood.

*Seed-Tree*. The seed-tree method removes most of the mature overstory while leaving a selected few dominant, mature stems fairly evenly scattered across a site to provide seed for establishing a new cohort and thus regenerating the stand (Smith, 1997, p. 302). A prerequisite for successful use of the seed-tree method is that residual seed trees be distributed so that the entire site is within acceptable seed dispersal distance (Guldin, 2004). A particular benefit of the seed tree system is that it allows for seed trees to be selected by phenotype, which may indicate good genetic material (Brockway et al., 2006).

Even though the accepted wisdom dating from the early twentieth century suggested use of the seed-tree method (leaving between 7 and 25 cone-producing trees per hectare) for longleaf pine management (e.g. Schwarz, 1907, p. 114), regeneration failures were common (Wahlenberg, 1946). Because of cone crop variability and the limited dispersal distance for large seeds (Boyer, 1958, 1963b), the seed-tree regeneration method often did not adequately distribute seeds across the sites. Also, by reducing residual basal area to as low as 2.3 to 3.5 $m^2$ $ha^{-1}$, seed-tree harvests also tend to release hardwood competition and make prescribed fire more difficult to apply because of reduced needle fall and the resulting lack of fine fuels sufficient to carry a fire (Brockway et al., 2006). Thus, retaining more canopy may be required for restoration goals (Kirkman et al., 2007). Furthermore, reducing stocking to such low levels results in a loss of site productivity (Croker, 1954) and significant changes in ecosystem structure and function (Brockway et al., 2006). By the 1960s, the seed-tree regeneration method had proven inadequate for longleaf pine, and its regeneration failures, together with longleaf pine's infrequent seed crops and slow initial growth, had prejudiced many foresters and landowners against the species (Croker, 1969; 1987). However, at about this same time, the shelterwood system (another even-aged regeneration method) was proving to be more effective for regenerating longleaf pine (Croker, 1979; Boyer 1993a).

*Shelterwood*. The shelterwood method is similar to the seed-tree method, but it leaves more mature trees behind to regenerate the stand and provide shelter (i.e., more conducive microclimate) for reproduction; a key distinction to the shelterwood method compared to the seed-tree method is that it favorably alters the stand-wide microenvironment for seedlings (Smith et al., 1997, p. 302). Like the seed-tree method, the shelterwood method typically uses 2-3 harvests (Boyer, 1979), but it is more flexible because modification of the amount and spatial distribution of the residual overwood allows for creation of an optimal microenvironment for seedling development (Brockway et al., 2006). Additionally, the larger number of residual stems per acre makes the shelterwood system more ecologically sound and aesthetically pleasing (Brockway et al., 2006).

Early on, it was suggested that the shelterwood method would stimulate cone production without reducing the site's overall growth increment as much as the seed-tree method (Croker, 1954). Research showed that a shelterwood cut to 7-9 $m^2$ $ha^{-1}$ kept the site in production and limited hardwood encroachment during the period of regeneration (Boyer, 1975, 1979a; Boyer and Peterson, 1983). The greater overstory density also achieved better seed dispersal. Seedling establishment and survival is also often higher (McGuire et al., 2001; Pecot et al., 2007), and brown-spot infections less common (Phelps et al., 1978) under the higher residual stand densities provided by the shelterwood method.

With shelterwood harvests, tree mortality is a concern, but mortality of the residual overwood should not exceed that of any longleaf pine stand on a per-unit area basis: Boyer (1979b) found that annual mortality in shelterwood stands in a two-year, region-wide study averaged less than 1 percent, including mortality resulting from Hurricane Camille. While such data suggest that mortality of seed-bearing trees is unlikely to prevent successful regeneration, leaving so few stems per acre does leave some exposure to stochastic events that could cause localized regeneration failures. But, by leaving more residual stems, the shelterwood method has a lower potential for regeneration failures resulting from overwood mortality than does the seed tree method.

The shelterwood method as applied by Boyer (1993a) did not leave enough residual trees to fully occupy the available growing space, meaning that the total site productivity was not fully utilized during the regeneration phase. However, use of the irregular shelterwood, a two-aged system, can help the process of stand development and diminish the likelihood of creating unoccupied growing space through time. Smith and others (1997, p. 357) point out that the residual trees in an irregular shelterwood stand can actually benefit the forest by inducing heterogeneity of height into the densely aggregated new cohorts/advance reproduction and thereby imposing dominance on certain stems, which prevents overstocking. In the same manner, intraspecific and interspecific competition among longleaf pine seedlings can benefit the overall recruitment process by allowing for the early dominance of individual seedlings which prevents stand stagnation in areas of high seedling densities (Boyer and Peterson, 1983; Brockway et al. 2006).

The shelterwood method has thus proven to be effective for natural regeneration, but it is intended (especially in its uniform version) as an even-aged management tool, meaning that once the new cohort of trees is established, the overwood is removed, leaving an even-aged stand behind. So, when carefully implemented, the seed-tree and shelterwood methods can be used to produce conditions similar to those resulting from natural medium- scale to large-scale disturbances (Sharitz et al., 1992). However, using even-aged methods such as shelterwood interrupts the forest ecosystem both spatially and temporally, meaning that the goods and services provided by that ecosystem are also interrupted. The ideal solution to the periodicity of even-aged systems may be uneven-aged management because it can generate goods and services more continuously as a result of its greater inherent stability over a shorter temporal scales and a smaller spatial scales.

## Uneven-Aged Management Systems

### *History*

The use of selection silviculture to manage longleaf pine is not a new idea. Chapman (1909) described a “two-cutting” system (similar to irregular shelterwood) which would allow for logging operations that were prolonged, potentially indefinitely. While this article does not mention “selection,” it does describe a partial cutting method similar to uneven-aged silviculture employing a 20 year cutting cycle. Of particular interest is Chapman’s description of proper marking, which clearly identifies his method as selection (improvement cutting) rather than a selective cut (high-grading). Another example of forward-thinking in longleaf pine management appears in Barrett (1929), who examined growth increases in previously unmerchantable stems that had been left when the virgin forest was cut over. He pointed to the possibility of leaving residual stems for both natural regeneration and additional volume growth. This seems to be one of the earliest mentions of the value of managing stands under a continuous mature tree cover.

Not everyone agreed that uneven-aged management would work in longleaf pine ecosystems. Not long after Chapman (1909) and Barrett (1929) suggested alternatives to even-aged silviculture, other scientists suggested that selection systems were impractical for longleaf pine due to the tree’s intolerance and the need for stand-wide regeneration (Wahlenberg, 1946, p. 255; Croker, 1969; Croker and Boyer 1975). Many attempts at uneven-aged silviculture in longleaf pine forests have been deemed failures after the desired reproduction was not successfully established (Guldin, 2006). This same difficulty is pointed out by Sharitz and others (1992), who warn that continued uneven-aged management may result in a reduction in numbers of valuable shade-intolerant species (such as longleaf pine), but who also suggest that combining even-aged and uneven-aged systems can be used to simulate the disturbances which were integral in stimulating the evolution of the longleaf pine ecosystems.

However, after successfully implementing volume regulation, area control, and structural control for 10 years, Farrar and Boyer (1991) state that longleaf pine is suitable for uneven-aged management on a wide variety of sites. Other research has allowed selection to become increasingly popular in longleaf pine silviculture since an uneven-aged structure readily develops due to the variable suppression influence of the overstory (Boyer, 1993a).

*Overview*

Selection silviculture is especially adaptable to individual forest ecosystems for attaining a range of natural resources management goals. With uneven-aged management there is no rotation age (Meyer, 1952), but the cutting cycle is typically uniform. However, with longleaf pine the cutting cycle can be modified to coincide with cone crops so that a new cohort of reproduction is secured. Thus, properly implemented selection silviculture may be the ideal management tool in response to Boyer (1999), who states that the primary management goal for conservation and restoration of longleaf pine ecosystems should be the use of silviculture that can sustain those ecosystems in perpetuity. Additionally, properly applied selection silviculture allows for continuous stand-wide regeneration, meaning that the periodic dips in growth increment with even-aged management observed by Boyer (1993a) are less likely to occur. Croker (1979) stated that the best hope for longleaf pine's future lay in landowners with multiple-use goals. Because it allows for the maintenance of a continuous mature canopy across the property, uneven-aged management often appeals to landowners with multiple management goals (Palik et al., 2003; Van Lear et al. 2005). In selection silviculture a portion of any given cohort is typically maintained on the site at all times, and this provides the stakeholder with a variety of benefits including aesthetics, steady timber revenues, natural plant communities, and wildlife and endangered species habitat. Because longleaf pine ecosystems are able to produce such a variety of benefits, there is an obvious synergy between selection silviculture and longleaf pine management.

Uneven-aged management systems are dependent on maintaining a desired structure, or diameter distribution. Boyer (1993a) monitored both the seed-tree and shelterwood methods for their effectiveness at establishing new cohorts of longleaf pine. He found that, while maintaining even as few as 9 to 15 residual trees per hectare (1.6 to 2.3 $m^2$/ ha BA) can reduce volume ingrowth by over one-half, it does serve to transform (or maintain) the structure of the stand into the reverse-J curve characteristic of sustainable uneven-aged stands. Thus, an irregular shelterwood harvest would be an appropriate method for converting even-aged stands to stands with uneven-aged structure. However, a single-tree or group selection method more closely mimics frequent natural mortality (e.g., lightning) (Outcalt, 2008) and allows for varying the scale of disturbance similar to natural stand dynamics (Palik and Pederson, 1996). Mimicking natural disturbance helps to build or maintain the complex old-growth structure described by Schwarz (1907), Platt and others (1988), Noel and others (1998), and Varner and others (2003): juveniles highly aggregated in even-aged cohorts within a loose matrix of large/old trees of varying ages present across the forest.

*Group Selection*. Group selection is often recommended and applied as an uneven-aged management system for intolerant species (Guldin, 2006). Because residual mature trees can strongly inhibit longleaf pine seedling growth and eventual recruitment, causing the surviving seedlings to cluster in canopy gaps (Brockway and Outcalt, 1998; McGuire et al. 2001), group selection is well suited to longleaf pine ecosystems. With group selection, the stand matrix is typically thinned in order to promote stand health and maintain acceptable stocking levels, and then groups are located either in areas with existing advance reproduction or in areas of unsuitable stocking (either too high or too low) (Guldin, 2006).

While early recommendations for naturally regenerating longleaf pine used dispersed retention, meaning that the residual trees were more or less evenly distributed across the stand (e.g. Croker, 1954; Croker and Boyer, 1975), more recent research (Palik et al., 2002, 2003; Pecot et al., 2007) has documented the positive effects of aggregated retention rather than the more traditional dispersed retention. These studies were individual parts of a group of studies including the work of Battaglia and others (2002, 2003) which examined the role of overstory structure on the longleaf pine regeneration process. These studies used three retention treatments: single-tree selection, small-group (0.1 ha gap) selection, and large-group (0.2 ha gap) selection (along with a control) and showed that using aggregated retention (i.e. group selection) can lead to increased longleaf pine seedling growth in those gaps. For example, after aggregating the residual trees and thus concentrating harvesting into 0.2 hectare gaps, Palik and others (2003) found significantly larger biomass increments in seedlings associated with increasingly aggregated retention plots (meaning increasingly larger gap size). In effect, dispersed retention (i.e., single-tree selection) did not provide as favorable growing conditions as did aggregated retention (i.e. large group selection). Yet, dispersed retention can benefit longleaf pine seedlings by limiting the growth of understory hardwood species (Pecot et al., 2007).

Reduced competition and increased seedling growth in natural and silviculturally-created gaps has been documented repeatedly (Palik et al., 1997; Brockway and Outcalt, 1998). Brockway and others (2005a, 2006) and Gagnon and others (2003) seem to agree that gap-based approaches, or group selection, are more appropriate for regenerating longleaf pine and releasing advance reproduction. However, Gagnon and others (2004) found that while seedling numbers and root collar diameters (RCD) were significantly higher in gaps, gap size did not affect the stocking or density of seedlings during the short term. Yet, this may not be true in every case. According to Boyer (1958, 1963b), longleaf pine seeds are rarely dispersed farther than 30 m from forest edges. Thus, gaps larger than 0.28 hectares might not be adequately stocked with sufficient numbers of seedlings.

Longleaf pine forms naturally gappy forests (McGuire et al., 2001), and the formation of natural gaps in longleaf pine ecosystems has been investigated. Palik and Pederson (1996) found lightning to be the most frequent disturbance agent in a longleaf pine forest in southwestern Georgia. Similarly, in central Florida, lightning mortality created gaps suitable for longleaf pine seedling establishment and recruitment on a regular and fairly rapid basis (Outcalt, 2008). Outcalt's (2008) results therefore indicate that gap-based regeneration methods may be integral to successful longleaf pine regeneration and recruitment because of the prevalence of lightning-created gaps within the larger forest matrix. Outcalt's (2008) data suggest the (at least historical) importance of gaps in regenerating natural longleaf pine forests prior to modern silvicultural manipulations. Apparently, lightning is a source of mortality not only for individual trees and groups of trees, but is even more likely to strike trees adjacent to gaps, serving to enlarge the gaps and further remove competition from seedlings within those gaps. Such a process gradually gives additional growing space to seedlings as they recruit into larger size classes.

However, the necessity of silviculturally-created gaps for capturing and releasing reproduction is still debated. Jack and others (2006a) present data that suggest the existence of a horizontal asymptote for growth of planted seedlings at approximately 15 meters from the gap edge, indicating that longleaf pine seedling development is not inhibited beyond this point on a mesic site. Brockway and Outcalt (1998) similarly noted that the greatest number of bolting seedlings occurred at 16 meters or more from the gap edge, but significantly lower densities of suppressed seedlings (172 to 3017 seedlings per hectare) were present in a SEZ within 12 to 15 meters of the gap edge on a xeric sandhills site. Brockway and Outcalt (1998) examined natural seedlings that had survived many cycles of fire and drought, but did not document seedling age. So it is difficult to know how comparable their results are to those of the young seedlings studied by Jack and others (2006a). But, the results of Jack and others (2006a) suggest that the larger gap sizes of 0.2 ha recommended by Palik and others (2002) and 0.1 to 0.8 ha by Brockway and others (2006) may not be required for securing adequate reproduction. Rather, smaller gaps created through single-tree selection may be sufficient.

For conservation management, a varied approach is likely the most appropriate. A Louisiana study showed that higher light levels due to canopy gaps benefited monocarpic, short-lived herbaceous species rather than overall species diversity (Platt et al., 2006). Thus, Platt and others (2006) suggest that a larger number of evenly-distributed small gaps (<0.1 ha) benefits understory groundcover diversity more than large-gap approaches. In addition to supporting understory diversity concerns, difficulties with implementing prescribed fire, wildlife habitat considerations, and other landowner objectives might make aggregated retention a less appropriate harvesting method. In that case, it is still important to better understand the dynamics of seedling growth in stands with dispersed retention or smaller gap sizes resulting from selection systems.

It can be difficult to effectively implement area-control methods such as group selection when practicing selection silviculture. Roach (1974) analyzes the utility of group selection as an uneven-aged management system. He states that group selection is not a complete silvicultural system, as silvicultural systems require the tending of the entire stand with every stand entry. Rather, group selection is in truth only a regeneration method, and it effectively creates small, even-aged stands within the forest. Therefore, the tendency is for the stand to convert to small, even-aged patches which eventually must be treated separately. Further, area-control methods imposed on forest systems are thus not necessarily robust to the underlying ecology within which they are designed to work (Guldin, 1996).

Area-control can be problematic from a logistical as well as an ecological standpoint. Roach (1974) says that group selection has been grafted into selection cutting as a regeneration method for less tolerant species (such as longleaf pine), but that true uneven-aged and even-aged regulatory systems will not hybridize. Depending on group selection as a tool in selection silviculture will ultimately result in large fluctuations in yields at some point in the future. However, if sustained timber yields are not a priority (which can often be the case for today's landowners), group selection can be used successfully to maintain the forest (Roach, 1974).

*Single-Tree Selection*. Single-tree selection imitates the smallest scale of disturbance, such as lightning or disease, which typically kills only one or two mature trees (Guldin, 2006). As with group selection, trees of all size-classes are individually selected for removal more-or-less uniformly based on their condition and location in order to generate the desired stand structure and stocking and to promote the growth and vigor of the remaining trees (Johnson et al., 2002). However, unlike the group selection method, deliberate gaps are not created for the purposes of regenerating the stand (Johnson et al., 2002). Although single-tree selection has historically been assumed effective only with tolerant species, it has been shown to work for intolerant species on poor sites (Smith et al., 1997, p. 384; Johnson et al., 2002). Longleaf pine ecosystems are a prime example of the poor-site, intolerant species described by Troup (1952, p. 113) that are more open and have little resemblance to selection forests composed of shade-tolerant species. The Stoddard-Neel approach is an adaptation of single-tree selection specifically for longleaf pine that has been practiced for over 60 years on quail hunting plantations in Georgia and Florida (Jack et al., 2006b; McIntyre et al., 2008).

Since selection silviculture leaves residual mature trees [which are known to drastically inhibit the ingrowth of new cohorts (Smith, 1955; Boyer, 1963; Walker and Davis, 1956; Platt et al., 1988)] distributed across the stand, seedling growth and recruitment is typically slower. Yet, over time many seedlings will survive and start height growth even near large pines (Smith, 1961). According to Palik and others (2002), any selection system for longleaf pine must create gaps of at least 0.14 hectares for regeneration to take place, but they cite McGuire (1999) who indicates that this can sometimes be accomplished by removing only one or two trees because of the naturally low-density canopies in longleaf pine forests. Therefore, securing longleaf pine reproduction in stands managed with single-tree selection should not be problematic.

The problem, then, is how to effectively manage an uneven-aged longleaf pine stand and still maintain regular ingrowth from natural regeneration. Wahlenberg (1946) stated that it would be impossible to use the selection system in longleaf pine forests because the selection system is designed to produce all-aged stands, and that longleaf pine (due to its intolerance) could not reproduce itself under such conditions. However, Wahlenberg may have been unaware that a viable and sustainable selection system may best be maintained with the episodic regeneration of a small number of regularly spaced age classes (Loewenstein et al., 2000; Loewenstein, 2005).

## Research Needs

As a result of misconceptions about longleaf pine's intolerance, requirements for regeneration, and difficulties recruiting new cohorts under a mature overstory (see Wahlenberg, 1946; Boyer, 1993a; Palik et al., 1997), little is known about the long-term consequences of alternatives to the traditional even-aged management paradigm for longleaf pine or the adaptability of those alternatives to varying site conditions (Boyer, 1998, 1999). Although the suitability of the group selection method (i.e., aggregated retention) has been recently recognized and increasingly recommended (Farrar 1996; Palik et al. 1997, 2002, 2003; Brockway and Outcalt 1998; Brockway et al., 2005a, 2005c), the single-tree selection method (i.e., dispersed retention) may be more appropriate for conservation management, especially when considering the potential problems of implementing prescribed fires in stands treated with group selection (Pecot et al. 2007). Thus, applied research is needed to build upon earlier basic research.

The current body of research concerning longleaf pine seedling establishment and release is somewhat limited and contradictory. The negative effects of the residual overstory on seedling growth within the uniform shelterwood method (complete overwood removal) and irregular shelterwood method (retaining the residual trees indefinitely) have been demonstrated (Brockway et al. 2006). Similar inhibitory competition dynamics have also been described for selection methods, but research concerning the factors causing reduced seedling growth and survival offers conflicting results. Brockway and Outcalt (1998) suggest that competition for soil resources (i.e., water and nutrients) is an important factor in seedling establishment and survival (along with long-term exposure to periodic cycles of fire and drought) and that light did not appear to be a limiting factor. Conversely, McGuire and others (2001) found that light was the variable most strongly correlated with seedling growth. Pessin (1944), Palik and others (1997), and Pecot and others (2007) all offer evidence that light, not moisture availability, is the variable more responsible for affecting seedling growth. However, substantially different methods were employed in each of these studies, with Brockway and Outcalt studying naturally-regenerated seedlings in a xeric sandhills ecosystem and McGuire, Palik, and Pecot studying planted seedlings on more mesic sites.

The influence of different forest site-types (i.e., ambient environments) should not be overlooked. Midstory density, leaf area, and hardwood species composition are known to vary substantially along the soil moisture gradient from mesic to xeric sites (Hiers et al., 2007). Thus, the limiting factors and drivers of stand dynamics can logically be expected to vary across the range of sites, differentially affecting competition and seedling recruitment. Implementing a study that employs a uniform methodology along such a soil moisture gradient in order to examine the effects of overstory, midstory, and understory variation should provide land managers with valuable information that can be directly applied in forest management.

### *Importance of Selection Silviculture*

As Lhotka and Loewenstein (2008) point out, models that link stand structure with seedling growth are essential for successful implementation of true selection silviculture by field foresters. Brockway and others (2005a) describe a need for information about the structures and processes affecting longleaf pine regeneration, specifically mentioning canopy-gap and root-gap dynamics in conjunction with the influences of light, nutrients, moisture, and fuels on seedling survival and growth. Additionally, they suggest that there is a need for further research in silvicultural methods for effective regeneration in uneven-aged, two-aged and even-aged stands, as well as the use of such methods to mimic patterns of natural disturbances.

Palik and others (2002) describe the use of natural disturbance as a guide for uneven-aged silviculture. Under this model, varying methods can be used to mimic various natural disturbances, from single-tree selection, which mimics lightning mortality, to group selection, which is more similar to larger-scale disturbances. However, the authors point out that patterning silviculture after natural disturbances is challenging due to the inherent complexity of natural disturbance regimes and suggest that there is probably no one model that is appropriate for managing the entire ecosystem for multiple goals. This applied research study aims to examine one such model which will be applicable to multi-resource management that provides ecological services and timber-related products.

## Objectives

The objective of this study was to determine the range of residual overstory densities in selection silviculture that best promotes adequate longleaf pine seedling recruitment. Canopy gap fraction and soil moisture availability were examined to ascertain their effects on near-term seedling growth and eventual recruitment. The following null hypotheses were investigated:

In mature longleaf pine forests managed with selection silviculture, longleaf pine seedling survival and growth were not significantly affected by

(1) canopy gap fraction on a mesic site,
(2) soil moisture availability on a mesic site,
(3) canopy gap fraction on a subxeric site, or
(4) soil moisture availability on a subxeric site.

Analyses determined whether each hypothesis could be falsified, in which case, the null hypothesis was rejected and the corresponding alternative hypothesis was accepted as factual (within the design and statistical limits of the methods).

# CHAPTER III

# RESEARCH METHODS

## Study Sites

This project was installed on two study sites: the Blackwater River State Forest (30.8°N, 86.8°W) in Santa Rosa County, Florida, (hereafter: “Blackwater”) and The Joseph W. Jones Ecological Research Center at Ichauway (31° N, 84° W) in Baker County, Georgia (hereafter: “Ichauway”). Blackwater is a subxeric sandhill site, whereas Ichauway is considered a richer, more mesic site. Both sites lie in the Middle Coastal Plain physiographic province (Craul et al., 2005) and in Bailey’s (1995) Humid Temperate Domain, Subtropical Division, Outer Coastal Plain Mixed Province. According to Bailey (1995), such sites are characterized by high humidity and the lack of cold winters; rainfall is well distributed throughout the year. This area has the highest precipitation in the Eastern Deciduous Forest Biome (except for specific high-elevation areas in the southern Appalachians), but rainfall often occurs in heavy downpours, leading to proportionally higher runoff (Bailey, 1995). Furthermore, this region experiences the most rain-free days and the highest evaporation rates in the East (USGS, 1970). Soils are principally derived from Coastal Plain sediments ranging from heavy clays to gravel, with sand predominating (Bailey, 1995), often leading to low capacity for water storage. Thus, upland plants in this region may suffer moisture stress more frequently or for longer duration than in most other eastern forests (Ware et al., 1993). Uplands areas are typically covered by subclimax pine forests (savannas) with understories of grasses and sedges, but are interspersed with un-drained or poorly drained pocosins that can allow evergreen shrubs to predominate (Bailey, 1995).

*Blackwater River State Forest*. The Blackwater site (E 2/3, Section 23, T4N, R26W, Santa Rosa County, FL) is located in the Southern Pine Hills region of northwest Florida, which is part of the Alabama Area longleaf pine site zone (Craul et al., 2005). As described by Myers (1990), sandhills are dry, infertile ecosystems typified by open overstories of longleaf pine and groundcovers composed of perennial grasses and forbs interspersed with deciduous clonal oaks. Topography on the Blackwater study site is characterized as gently sloping to sloping (Weeks et al., 1980), with elevations between 60-75 m. Climate is warm, humid-temperate with long, warm, humid summers and short, mild winters. Average annual temperature is 19 °C, and rainfall averages 1650 mm per year, of which 45% occurs between June and September, although unusual amounts can occur any month. July and September are the wettest months, whereas October is the driest (Weeks et al., 1980). The growing season averages 300 days (U.S. Department of Commerce, 1964, 1972, cited by Weeks et al., 1980). The primary soil phase on the study site is Troup loamy sand (0-5% slopes)—loamy, silicious thermic Grossarenic Paleudults, but also present are Orangeburg sandy loam (2-5% slopes)—fine-loamy, siliceous, thermic Typic Paleudults; Lucy loamy sand (0-5% slopes)—loamy, siliceous, thermic Arenic Paleudults; and Dothan fine sandy loam (2-5% slopes)—siliceous, thermic Plinthic Paleudults (Weeks et al., 1980). Water tables in these soils are typically 6 feet and deeper with the exception of the Dothan phase, whose water table is usually shallower than 6 feet (Weeks et al., 1980).

The overstory on the Blackwater study site is predominately longleaf pine that developed from natural seeding after the original forest was cutover in the 1920s. The oldest pines are approximately 80 years old, and most mature pines on the site are at least 60 years old. Various oak species including southern red oak (*Quercus falcata* Michx.), turkey oak (*Q. laevis* Walt.), and sand post oak (*Q. margaretta* Ashe) are present in the midstory and overstory. The understory is largely composed of wiregrass (*Aristida* spp.) and associated species, but woody plants including sassafras (*Sassafras albidum* Nutt.), persimmon (*Diospyros virginiana* L.), blueberry (*Vaccinium* spp.), and various clonal oaks (*Quercus* spp.) are also common. The stand received improvement cuts in the winter of 1981 and spring of 1991. A tree salvage operation after Hurricane Ivan followed in the winter of 2005, and the harvests for the experimental treatments for a larger study (single-tree selection, irregular shelterwood, group selection, and uncut control) took place in the fall of 2006. Records show that prescribed fire has been used on a 2 to 3 year return interval since 1970 and was most recently applied in May of 2003 (R. Jones, Florida DOF, pers. comm.).

*Joseph W. Jones Ecological Research Center at Ichauway*. The Ichauway site (LD 12, LL 27, 28, Baker County, GA) lies in the Dougherty Plain of southwest Georgia and in the Georgia Area longleaf pine site zone (Craul et al., 2005). Topography at Ichauway is gentle (typically 1-5% slope) (Pecot et al., 2005); elevation at the study site is between 40-50 meters. Climate is subtropical, with long, hot summers and fairly short, cool winters (Stoner, 1986). Average annual temperature is 19 °C; mean annual rainfall is 1320 mm and is evenly distributed throughout the year. July is on average the wettest month, whereas October is the driest month (Stoner, 1986). The growing season for most crops lasts from April through September (Stoner, 1986). Soils at the study site are in the Wagram series (0-5% slopes)—loamy, siliceous, thermic Arenic Paleudults (Stoner 1986). Wagram soils may include small areas of Norfolk, Lucy, Orangeburg, and Troup series (Stoner, 1986; Battaglia et al., 2002); available water capacity is low. Ichauway is a characteristic naturally established, single-cohort second-growth longleaf pine forest 70-95 years in age (Palik et al., 2003; Pecot et al., 2007). Since its establishment, the stand had been subject to little harvesting other than the occasional salvage of trees killed by lightning or windthrow prior to the 1990s (Palik and Pederson, 1996).

The overstory at Ichauway is largely composed of longleaf pine with occasional southern red oak and sand post oak (Palik and Pederson, 1996). The understory is dominated by wiregrass, but has many other grasses, forbs, and woody (notably *Quercus* spp.) species present (Kirkman et al., 2001). In late fall, 1997, the overstory was harvested using four methods: an uncut control in addition to single-tree selection, small gap (0.1 ha), and large gap (0.2 ha) harvesting (Battaglia et al., 2003). Trees were harvested with a feller-buncher and removed with a grapple skidder. Limbs were severed before stems were removed to minimize understory disturbance (Jones et al., 2003; Palik et al., 2003). The most recent harvesting occurred in December, 2005, when the entire stand was thinned using the Stoddard-Neel approach (see McIntyre et al., 2008). The stand has been maintained with prescribed fire on a 1-3 year interval for over 60 years (Battaglia et al., 2002), and prescribed fire was implemented during this study in March and April, 2008, and January, 2009.

The main factor distinguishing the climate between the Georgia and Alabama site zones is that the Alabama zone is wetter, averaging 150 to 350 mm of extra precipitation per year (Craul et al., 2005). Soils at Blackwater and Ichauway are Ultisols, suborder Udults. Myers (1990) states that true sandhills are present on Entisols, which lack any profile development, and describes clayhills as the community located on Ultisols, which are characterized by clayey subsoils overlain by sand or clayey sand, often deeper than 1 meter. Thus, Blackwater is more accurately classified as subxeric. However, the vegetation present at the Blackwater site is indicative of the more xeric sandhill ecosystems in places and of richer clayhills in others. Myers (1990) describes the difference in terms of water availability—in clayhills, water is more available in the subsoil. Although there are minimal soil series differences between Blackwater and Ichauway, topographic and soil phase differences are enough to make Blackwater the more xeric site, even though it typically experiences more annual rainfall.

## Experimental Design

Six hundred containerized longleaf pine seedlings from Smurfit-Stone Corporation's Rock Creek Nursery in Brewton, Alabama, were hand-planted at Blackwater in December, 2007. At Ichauway, six hundred containerized longleaf pine seedlings from Meeks' Farms and Nursery, Inc., in Kite, Georgia, were planted in February, 2008. Seedlings from both nurseries were grown in 108 mL containers at a density of 530 seedlings $m^{-2}$. As a check, 120 seedlings (ten per seedling array) from the Meeks' nursery were then planted at Blackwater in February, 2008.

Seedlings at both sites were planted in twelve arrays of 50 seedlings, with arrays arbitrarily located to adequately provide a range of canopy densities resulting from different uneven-aged harvesting regimes. Seedlings in each array were arranged in 5 rows of 10 trees on a 5-by-5 meter grid. To separate the competitive influences of the forest canopy and the understory, half of the seedlings in each array were randomly selected for complete understory removal and treated with RazorPro herbicide (41% glyphosate) following the label instructions (5% solution; spray to wet) in May, 2008. The treatment extended to a 0.5 meter radius from the seedling and was re-treated or weeded by hand as necessary to insure complete elimination of understory competition.

### Measurements

*Canopy Gap Fraction*. Canopy gap fraction was determined using hemispherical photography.  Gap fraction is defined as the proportion of visible sky within a given sky sector defined by a range of zenith and azimuth angles; a gap fraction of zero indicates completely blocked sky, whereas a gap fraction of one means the sky is completely visible in that sector (Delta-T Devices, Ltd., 1999). Battaglia and others (2003) showed that in a longleaf pine forest hemispherical photographs fell nearly on a 1:1 line with actual percent photosynthetic photon flux density (PPFD). Therefore, canopy gap fraction is a useful measure of light availability to seedlings.

Hemispherical photography is an effective way to sample canopy structure and light environment (Rich, 1990). Hemispherical canopy photographs were taken for every seedling between May and August, 2008, at times when the solar disk was entirely obscured: prior to sunrise, after sunset, or during completely overcast conditions. Photographs were taken 1.4 meters above each seedling using a Nikon Coolpix 5700 (5 megapixel) camera and FC-E9 fisheye lens converter (183 degree view angle). Each photograph was taken using standard camera settings provided by Frazer and others (2001) and Lhotka and Loewenstein (2006): image quality—1:4 compression JPEG format; saturation—black and white; image size—full (2560 x 1920 pixels). Prior to taking each photograph, the camera was leveled and then oriented toward magnetic north using a compass. These photographs were used to quantify canopy closure (gap fraction) using Hemiview version 2.1 software (Delta-T Devices, Cambridge, UK). Individual threshold values indicating “sky” versus “canopy” were determined manually for each photograph according to Hemiview’s user manual (Delta-T Devices, Ltd., 1999); to minimize variance in this process, one operator completed all analyses.

*Soil Moisture*. Volumetric soil water content at each seedling was determined on four occasions during the 2008 and 2009 growing seasons (May-August) using a MoisturePoint 917 time domain reflectometry (TDR) device (Environmental Sensors, Inc., Sidney, BC, Canada) with a 30 cm “single-diode rugged” probe. Stated accuracy for this device is plus or minus 3 percent. For the 2009 growing season, two HOBO data loggers (Onset Computer Corp., Bourne, MA) equipped with S-SMA-M003 or S-SMA-M005 soil moisture sensors (accuracy: ± 4%) at 30 cm, 60 cm, and 90 cm depths were installed at each site. One data logger at each study site was located in a canopy gap and was equipped with an S-RGB-M002 rainfall sensor (accuracy: ±1%) in addition to the soil moisture sensors.

*Groundline Diameter*. Seedling groundline diameter (GLD) was measured at time of planting and again in August, 2008 and August, 2009. GLD growth was calculated as the difference between August diameter measurements and initial seedling diameters.

*Root Depth*. Seedling rooting depth was sampled for a subset of seedlings in August, 2009. The diameter distribution of Blackwater B and Ichauway seedlings were divided into thirds (small, medium, large) in which six seedlings were randomly selected for excavation (n=18 seedlings/planting group). Rooting depth for Blackwater A seedlings was sampled in the same manner, but subdivisions were established into thirds separately due to a different diameter distribution. Roots were excavated until they broke or to a maximum depth of 90 cm, and taproot diameter was recorded at 10 cm depth increments.

### Statistical Analyses

All measurements were taken at each seedling location. Because the herbicide treatment was applied to randomly-selected seedlings within each seedling array, it was possible to conduct statistical analyses with the seedling as the experimental unit. Statistical analyses were conducted using SAS version 9.1 software (SAS Institute, Cary, NC). For all tests, statistical significance was determined at $\alpha = 0.05$.

Mean growing season soil moisture for each seedling was calculated as the average of the four 30 cm depth TDR samples taken in 2008 and 2009. Mean seedling GLD growth was analyzed between sites, treatments, and years with factorial ANOVA F-tests; significant differences were separated with Tukey's Honestly Significant Difference (HSD) test. Square-root transformations were applied as necessary to meet the assumptions of ANOVA. Regression analyses were used to relate canopy gap fraction, mean soil moisture, and seedling diameter growth.

A regression approach to ANOVA was used to test for differences in rooting depth among planting group and site. Because few taproots were entirely excavated, a root taper equation with root depth/diameter data was developed to predict extrapolated rooting depth individually for each seedling. Average root diameter at the deepest-excavated point among unbroken taproots was 1.23 mm, so the root taper equation was used to predict taproot depth at a diameter of 1.0 mm.

# CHAPTER IV

# RESULTS

## Gap Fraction

Mean gap fraction was 0.497 at Blackwater and was significantly larger than the mean gap fraction of 0.402 at Ichauway (Figure 1) (two-tailed t-test for unequal variance: $t= 23.65$, $p< 0.0001$). Figure 2 shows histograms of gap fraction at Blackwater and Ichauway.

## Initial Groundline Diameter

Mean seedling GLD at time of planting was 9.32 (± 0.059 mm) for Blackwater A and 8.71 (± 0.059 mm) at Ichauway; mean initial GLD for Blackwater B seedlings was 8.63 (± 0.133 mm). Initial seedling GLD was significantly larger for Rock Creek Nursery seedlings (Blackwater A) than for Meeks Tree Farm seedlings (Ichauway, Blackwater B) (two-tailed t-test for unequal variances: $t= 7.49$, $p< 0.0001$). Mean initial seedling GLD for each group of seedlings (Blackwater A, B, Ichauway) was significantly greater ($\alpha = 0.05$) than the 6.35 mm minimum suggested by Barnett and others (2002) and repeated by Dumroese and others (2009) (one-tailed t-tests: $t= 50.20$, 18.39, and 35.82, respectively; $p< 0.0001$). At Blackwater A, 1 seedling was smaller than the recommended 4.75 mm minimum (Barnett et al. 2002, Dumroese et al. 2009). At Ichauway, 3 seedlings were smaller than 4.75 mm. All Blackwater B seedlings exceeded the suggested minimum.

Three-by-two factorial ANOVA showed that both herbicide and control seedlings in Blackwater A were significantly larger than seedlings in all other planting groups except for

Blackwater B control (F=11.76, $p < 0.0001$). There were no significant differences in initial diameters among the treatments for Meeks seedlings (Figure 3).

### Survival

Survivorship figures for 2008 and 2009 are presented in Figure 4. Following one growing season (2008), survivorship was over 90 percent at Blackwater A and B but was less than 80 percent at Ichauway. Survivorship among remaining seedlings during the 2009 growing season was above 90 percent for both Blackwater A and Ichauway; for Blackwater B, survivorship was 76 percent for control seedlings and 84 percent for understory removal. For Blackwater A, survivorship was higher among control seedlings both years; among Blackwater B seedlings, survivorship was initially higher among seedlings with understory removal, but the pattern was reversed after the 2009 growing season. At Ichauway, survivorship was lower among control seedlings in both growing seasons. Blackwater A seedlings showed mean total survival 24 percent greater than Blackwater B and Ichauway seedlings (Figure 4).

### Soil Moisture

TDR measurements showed that mean 30 cm growing season soil moisture was significantly higher at Blackwater in both 2008 and 2009 (two-way ANOVA: F= 63.36, $p < 0.0001$) (Table 1; Figure 5), even though mean number of days since previous recorded rainfall was higher at Blackwater in 2008. However, data from HOBO soil moisture sensors point to the variability of soil moisture at Blackwater (Table 2). Understory removal (with herbicide) resulted in higher soil moisture only at Blackwater in 2008. Two-year average growing season soil moisture was between 10-11 percent at Blackwater and 8-9 percent at Ichauway, representing a significant difference (two-way ANOVA: F= 61.39, $p < 0.0001$) (Figure 6).

Data recorded by the HOBO weather stations in 2009 show that soil moisture is extremely ephemeral both within and between days (Figures 7-10). Despite Blackwater's characterization as the more xeric site, soil moisture data from both sources show that it typically had higher soil moisture content, but also had the potential for severe drought (Table 2).

### Weather Data

Annual rainfall data were collected from the Ichauway main weather station (also publicly available at www.georgiaweather.net) and from the Blackwater Forestry Center in Munson, FL. Total rainfall for Ichauway during 2008 was 1313 mm, making it an average year for precipitation. In contrast, Blackwater received 1940 mm, making it an above-average year. Table 3 gives adjusted rainfall totals for 2008 which include the final week of December, 2007, when Blackwater A seedlings were planted. Blackwater B and Ichauway seedlings received less rainfall in 2008 than the annual total due to their February planting dates.

### Seedling GLD Growth

Mean 2008 seedling GLD growth approached 3 mm for Blackwater A seedlings but was barely 0.5 mm for Ichauway seedlings, representing a significant difference ($F= 566.43$, $p< 0.0001$) (Figure 11). However, mean 2009 GLD growth did not differ between site or treatment for Blackwater A and Ichauway ($F= 0.64$, $p= 0.53$).

Figure 12 shows mean 2008-2009 seedling GLD growth among Blackwater A and B seedlings. Blackwater B seedlings grew significantly less than Blackwater A ($F= 31.37$, $p< 0.0001$). This shows the confounding factors of nursery and planting date to be significant, and thus the direct comparison between Blackwater A and Ichauway is not valid.

Mean 2008-2009 GLD growth is presented in Figure 13. Mean seedling GLD growth for Blackwater A seedlings was 4.39 (± 0.1 mm) for both understory removal and control seedlings, which was significantly higher than Blackwater B and Ichauway seedlings ($F= 108.43$, $p< 0.0001$). Significant differences were not present between understory removal and control treatments at either site. However, mean GLD growth for control seedlings at Ichauway was significantly less than all Blackwater B seedlings (p= 0.01; p= 0.03) (Figure 13). Due to the statistically significant confounding factors of nursery and planting date, the best comparison possible is between Blackwater B and Ichauway seedlings because it eliminates nursery and effective planting date as confounding factors. Two-way ANOVA showed that control seedlings at Ichauway grew significantly less than all Blackwater B seedlings (F= 6.86, p= 0.0002), but no growth difference existed between Ichauway understory removal seedlings nor any Blackwater B seedlings (Figure 14).

Examining growth differences between Blackwater B and Ichauway seedlings by year showed that Blackwater B seedlings grew less during the second growing season than in the first, whereas Ichauway seedlings showed increased growth during the second year (Figure 15). In the 2009 growing season, understory removal at Ichauway resulted in mean seedling growth significantly greater than both treatments at Blackwater B, whereas no statistically significant growth differences were present between control seedlings at Ichauway and all Blackwater B seedlings in 2009.

### Root Depth

Mean sampled root depth by site and seedling diameter class is presented in Table 4.Three-by-three ANOVA showed that root depth did not differ between GLD class or site (F= 1.54, p= 0.17). Regression approach to ANOVA also showed a lack of significance between seedling GLD and root depth for each planting group except for the smallest seedlings at Ichauway (Table 5). Due to lack of normality, the square-root transformation was applied to data for Ichauway seedlings. Regression analyses pooling all seedlings by planting group (Blackwater A, B, Ichauway) showed significant non-linear relationships between root depth and root diameter for all seedlings at Blackwater and Ichauway (Figures 16-18).

Because many roots broke during excavation, root diameter/depth data were used to develop a taper equation for predicting actual root depth. Likelihood ratio tests were used to determine if seedlings from each planting group (Blackwater A, B, Ichauway) needed to be fit separately. Results showed that Meeks seedlings could be fit to the same model (F= 1.86, p= 0.16) and then that all seedlings could be fit to the same model (F= 0.24, p= 0.78).

Data were fit with PROC NLIN to the model

$$y = e^{(4.7422x)},$$

where

$$y = \frac{L}{LL}$$

$$x = \frac{(D - d)}{(GLD - d)}$$

and

L = root length to d
d = root diameter at L
LL = Root length at end of measurements
D = root diameter at LL
GLD = root collar diameter at length 0.

Thus, the ratio of predicted root depth (length L) to measured root depth can be calculated for a root by setting a minimum root diameter at length L. For the purposes of this analysis, root depth was predicted to a minimum root diameter of 1.0 mm (d= 1). Data from seedlings whose taproot did not extend beyond the container plug (n= 5) were excluded from the analysis.

Results from the taper equation showed the largest predicted rooting depth was 91.25 cm (Table 4). Analysis of variance showed that significant differences in predicted taproot depth between GLD class and planting group were not present (F= 2.10, p=0.058; Table 4). Regression approach to ANOVA showed that the only significant relationship between GLD and predicted rooting depth existed with smallest seedlings (GLD 8.67-12.75 mm) at Blackwater A (F= 6.96, p= 0.046; Table 5).

## Regression Analyses

First-year results did not suggest the existence of clear controls of longleaf pine seedling growth (see Appendix B). While a negative trend between seedling growth and gap fraction existed in each case except for that of understory removal seedlings at Blackwater B (Appendix B.7), the relationship was significant only for control seedlings at Ichauway (t= -2.61, p= 0.0096) (Appendix B.9). A positive relationship existed between mean percent soil moisture and seedling growth for all seedlings except understory removal seedlings of Blackwater B (Appendix B.7). In each case, relationships were weak: coefficients of determination were all below 0.1.

Regression analyses after the 2009 growing season gave similarly unclear results (Table 6; Figures 19-31). The only significant relationships existed at Ichauway, where there was a highly significant positive relationship between seedling growth and gap fraction for control (t= 3.16, p= 0.002) and understory removal seedlings (t= 5.30, p< 0.0001). Although not significant, there were positive trends between seedling growth and gap fraction for control and understory removal seedlings for both Blackwater A and B. While soil moisture was not a significant predictor, the trend was generally positive. All relationships remained weak, with the largest coefficient of determination only 0.12.

Table 1. Mean number of days since recorded rainfall at Ichauway and Munson (Blackwater) weather stations and mean percent (standard error) volumetric soil moisture recorded with MP 917 TDR device. Different letters indicate statistical significance.

| | | Days Since Rainfall | Understory Removal | Control |
|---|---|---|---|---|
| | | | Percent Soil Moisture | |
| 2008 | Blackwater | 5 | 12.6 (0.24)$^{a}$ | 11.62 (0.22)$^{b}$ |
| | Ichauway | 2 | 9.93 (0.115)$^{c}$ | 9.43 (0.15)$^{cd}$ |
| 2009 | Blackwater | 3 | 9.35 (0.2)$^{cd}$ | 9.14 (0.175)$^{d}$ |
| | Ichauway | 3 | 7.09 (0.119)$^{e}$ | 6.78 (0.151)$^{e}$ |

Table 2. Mean percent (standard deviation) soil moisture by site from HOBO weather stations and seedling-based TDR (MP 917) sampled during May-August 2009.

| Device | Soil Depth | Blackwater-Gap | Blackwater | Ichauway-Gap | Ichauway |
|---|---|---|---|---|---|
| HOBO | 30 cm | 2 (2.7) | 9 (2.2) | 7 (2.9) | 6 (2.9) |
| HOBO | 60 cm | 0 (1.9) | 9 (1.7) | 7 (1.9) | 7 (2.1) |
| HOBO | 90 cm | 3 (2.0) | 11 (2.2) | 6 (1.1) | 6 (1.6) |
| | | Blackwater | | Ichauway | |
| MP 917 | 30 cm | 9.2 (3.1) | | 7 (1.7) | |

Table 3. 2008-2009 rainfall totals for Ichauway and Blackwater study sites. Totals in parentheses for 2008 represent amount of rainfall Blackwater B and Ichauway seedlings actually received due to later planting.

| | Rainfall (mm) | |
|---|---|---|
| | Ichauway | Blackwater |
| 2008[a] | 1399 (1182) | 1983 (1624) |
| 2009[b] | 1063 | 1872 |

[a] Dec. 26, 2007-Dec. 31, 2008

[b] Jan. 1, 2009-Aug. 23, 2009

Table 4. Mean (standard error) seedling root depth by planting group and GLD class. Differences were not significant.

| | | GLD Class (mm) | | |
|---|---|---|---|---|
| | | 8.67-12.75 | 12.76-14.49 | 14.50-20.39 |
| Blackwater A | Sampled | 47.35 (8.39) | 54.29 (11.38) | 43.63 (10.11) |
| | Predicted | 51.95 (9.03) | 60.18 (12.30) | 56.26 (9.19) |
| | | | GLD Class (mm) | |
| | | 7.39-9.75 | 9.76-11.50 | 11.51-21.66 |
| Blackwater B | Sampled | 35.24 (8.61) | 29.32 (4.30) | 29.21 (7.35) |
| | Predicted | 28.09 (7.30) | 32.77 (2.90) | 35.56 (6.45) |
| Ichauway | Sampled | 27.09 (5.91) | 28.36 (4.36) | 33.97 (6.02) |
| | Predicted | 35.57 (6.92) | 36.23 (4.21) | 31.13(10.16) |

Table 5. Results from regression approach to ANOVA for seedling root depth by GLD.

| Site | D-class | F Value | Pr > F | F Value | Pr > F |
|---|---|---|---|---|---|
| | | Sampled Depth | | Predicted Depth | |
| Blackwater A | Small | 7.79 | 0.038 | 6.96 | 0.046 |
| | Medium | 0.03 | 0.88 | 0.04 | 0.85 |
| | Large | 0.98 | 0.38 | 0.01 | 0.92 |
| Blackwater B | Small | 0 | 0.97 | 0.15 | 0.72 |
| | Medium | 0.8 | 0.42 | 0.07 | 0.81 |
| | Large | 3.6 | 0.13 | 4.04 | 0.11 |
| Ichauway | Small | 0.03 | 0.88 | 0.53 | 0.51 |
| | Medium | 0.01 | 0.94 | 1.09 | 0.36 |
| | Large | 2.3 | 0.2 | 2.27 | 0.23 |

Table 6. Summary of regressions for two-year seedling GLD growth with gap fraction and mean growing season soil moisture as predictors.

|  | DF | Sum of Squares | F Value/ t Value | Pr > F | R-square |
|---|---|---|---|---|---|
| Blackwater A |  |  |  |  |  |
| Understory Removal[1] | 262 | 40.6 | 2.29 | 0.1 | 0.017 |
| Control | 281 | 714.52 | 1.72 | 0.18 | 0.012 |
| Blackwater B |  |  |  |  |  |
| Understory Removal | 45 | 71.8 | 0.72 | 0.49 | 0.032 |
| Control[1] | 51 | 5.31 | 1.39 | 0.25 | 0.054 |
| Ichauway |  |  |  |  |  |
| Understory Removal[2] | 219 | 33.86 | 13.07 | <0.0001 | 0.108 |
| Gap Fraction | 1 |  | 4.93 | <0.0001 |  |
| Mean Moisture | 1 |  | 1.5 | 0.13 |  |
| Control[2] | 204 | 23.81 | 4.21 | 0.016 | 0.04 |
| Gap Fraction | 1 |  | 2.73 | 0.007 |  |
| Mean Moisture | 1 |  | 1.15 | 0.25 |  |

[1] Transformed with square-root function

[2] Transformed with square root(1+y) function

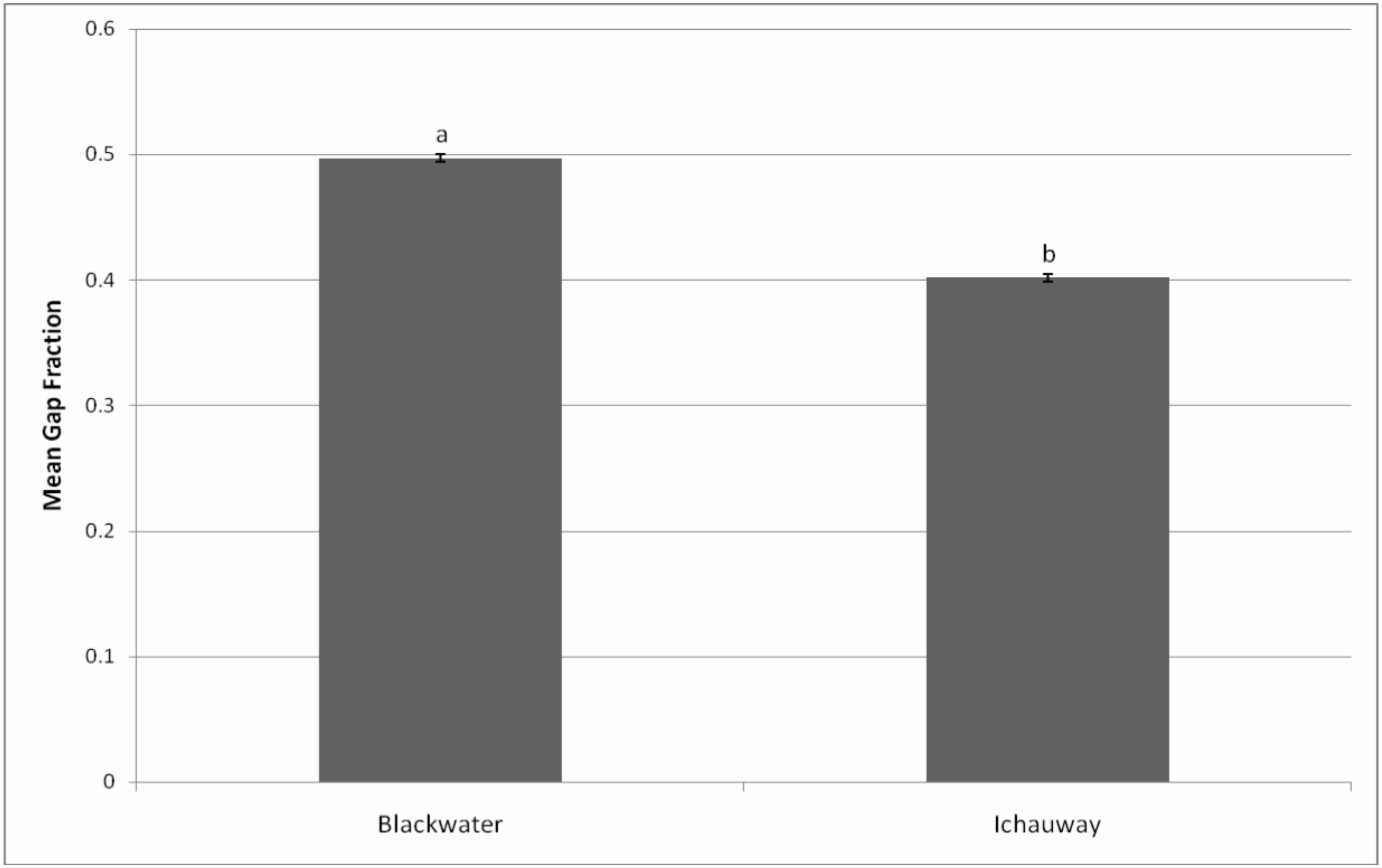


Figure 1. Mean gap fraction by site. Different letters indicate statistical significance.

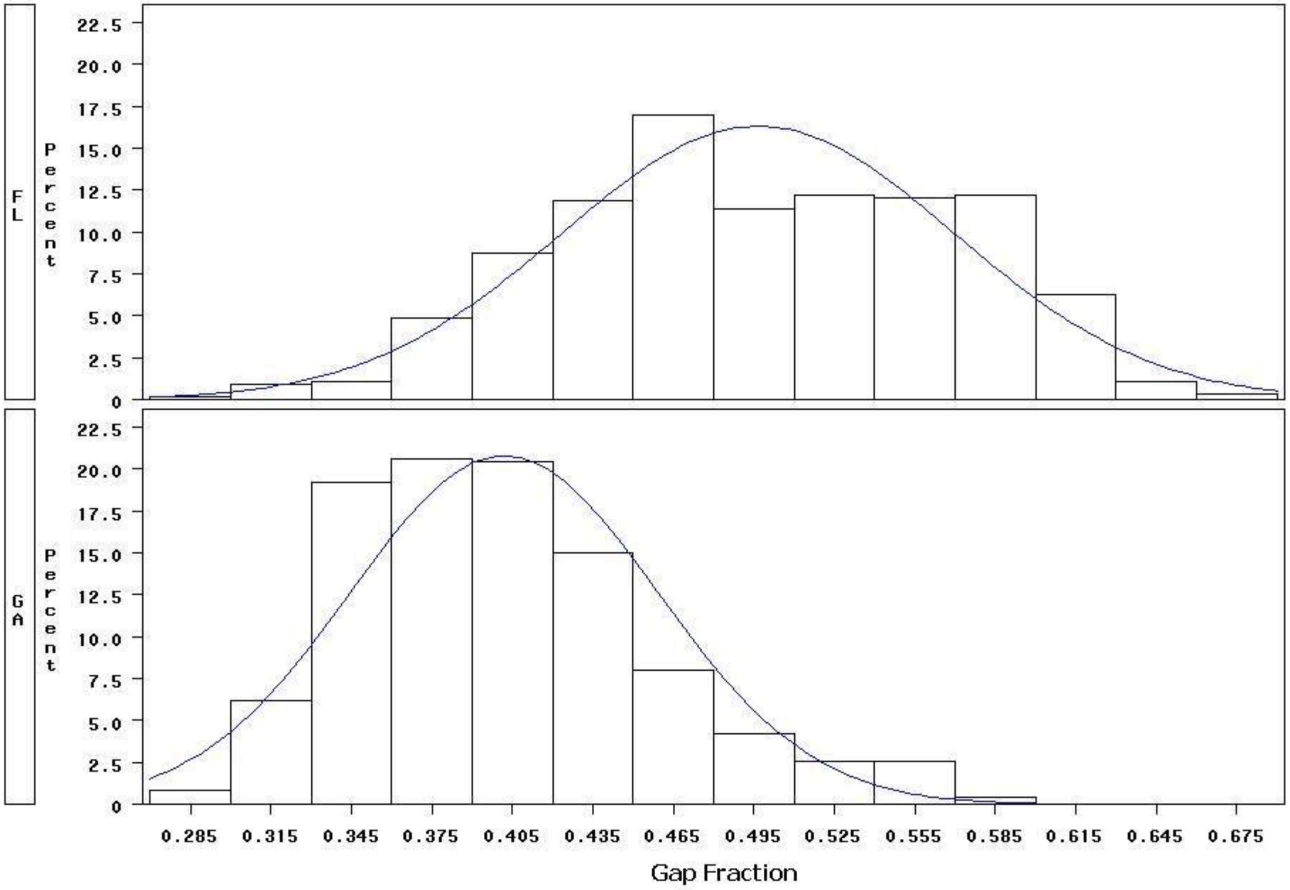


Figure 2. Histogram of gap fraction by site showing Blackwater (top) and Ichauway (bottom).

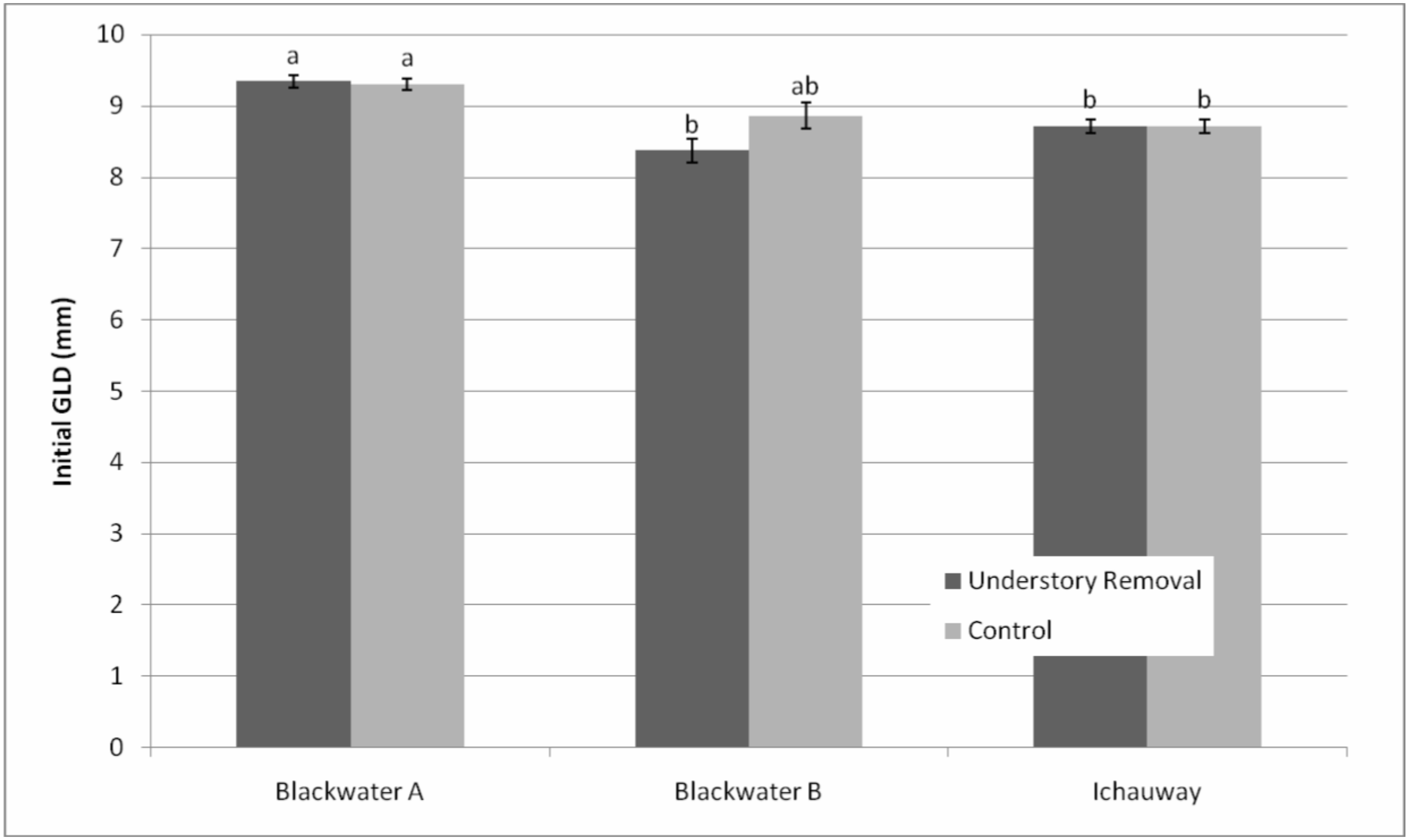


Figure 3. Mean seedling groundline diameter (GLD) at time of planting. Bars with different letters indicate statistical significance.

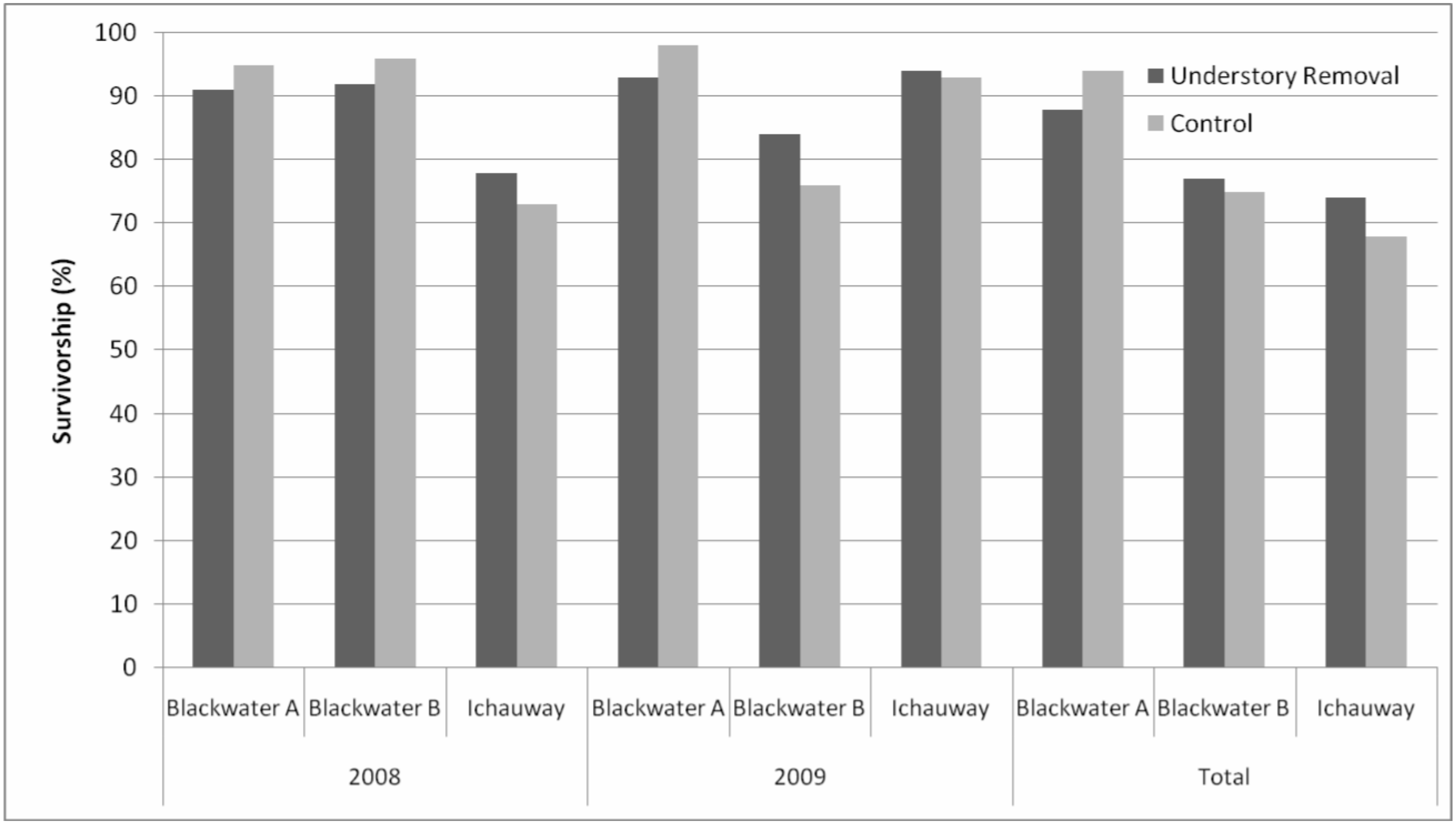


Figure 4. Percent seedling survival by site and year. Figures for 2009 represent percent survival among 2008 survivors.

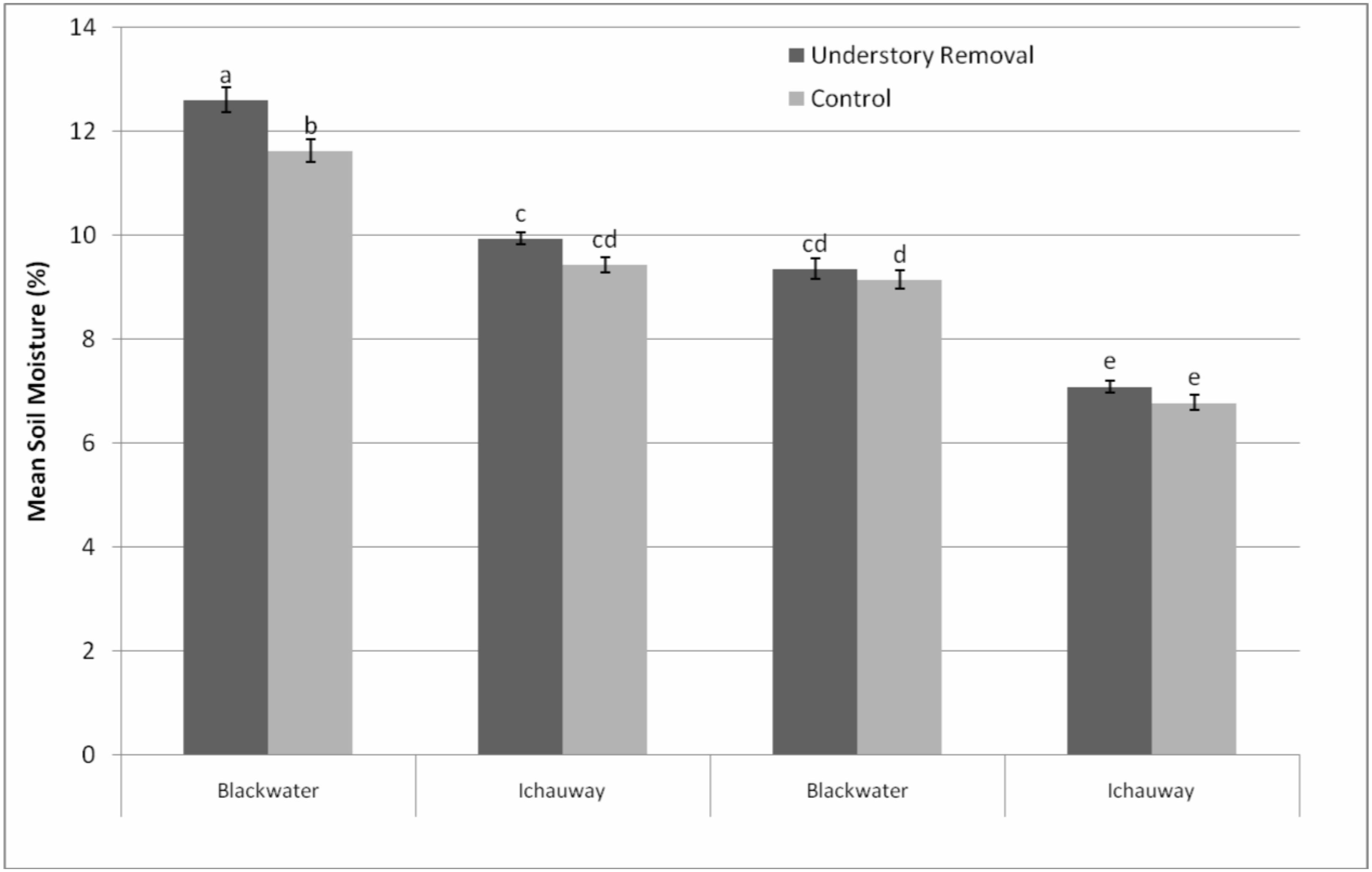


Figure 5. Mean 30 cm soil moisture by site and year. Bars with differing letters indicate statistical significance.

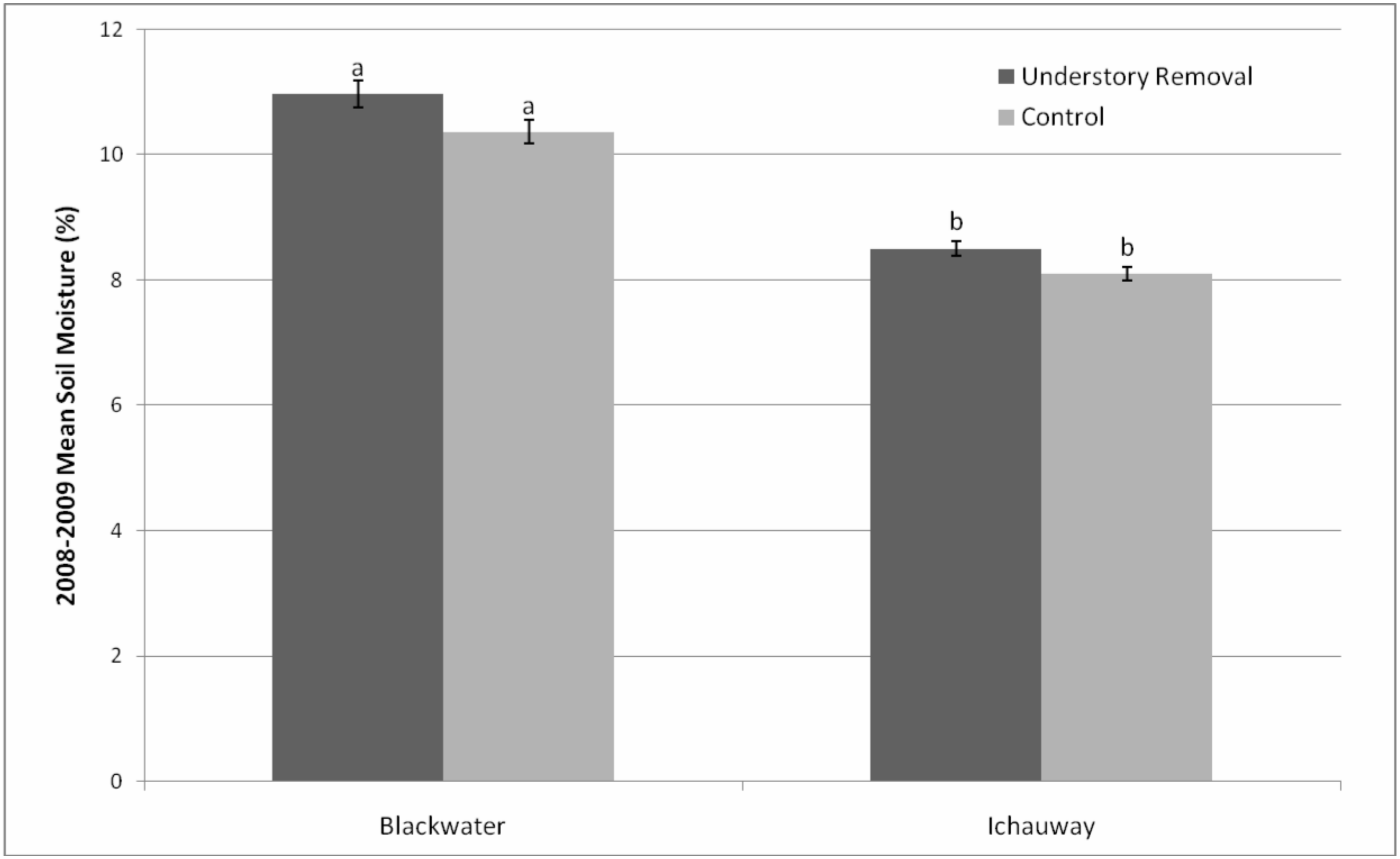


Figure 6. Mean 2008-2009 growing season soil moisture by site. Bars with different letters indicate statistical significanc

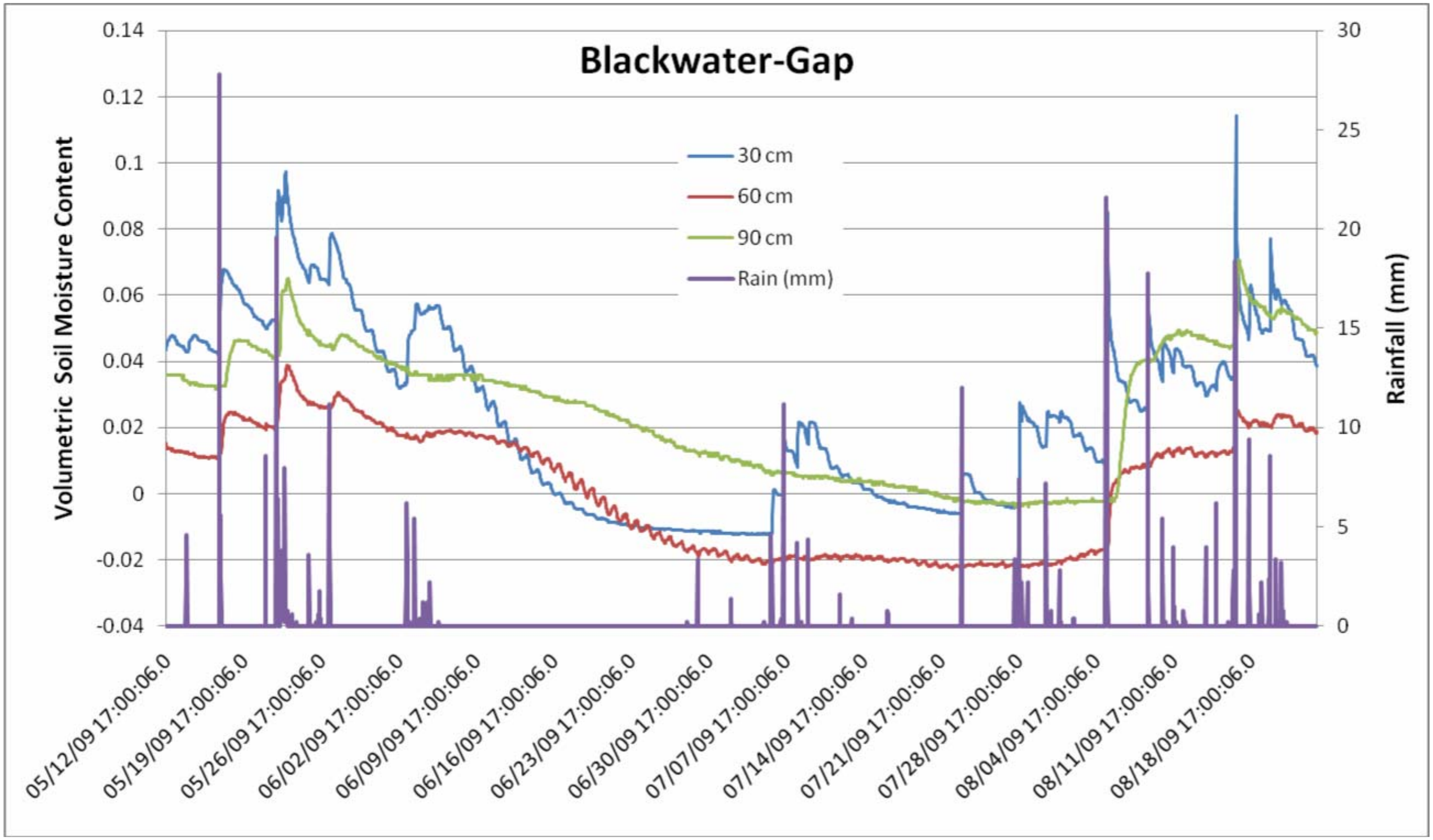


Figure 7. Volumetric soil water content and rainfall data from HOBO weather station located in a canopy gap at Blackwater during 2009 growing season.

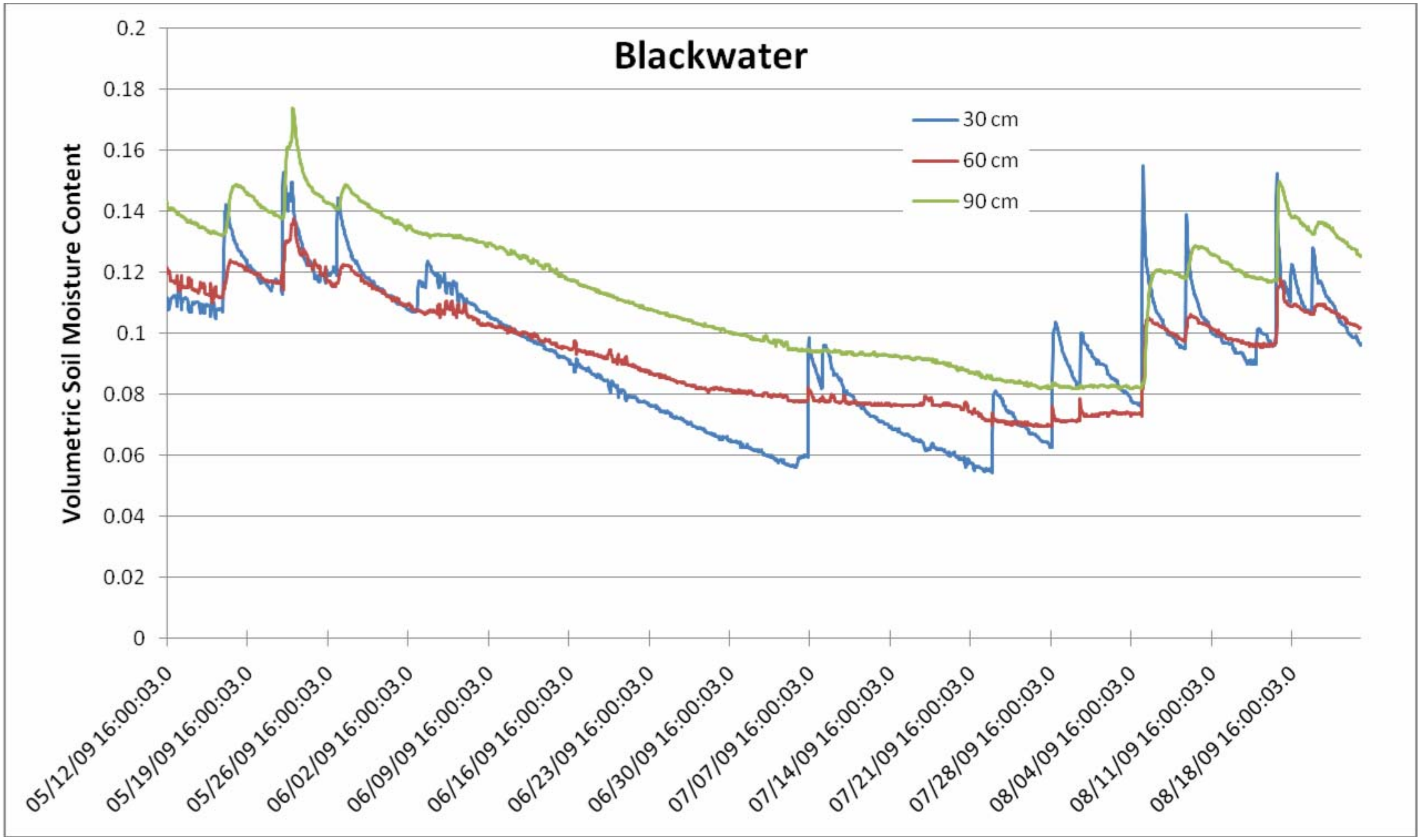


Figure 8. Volumetric soil water content from HOBO weather station located under intact canopy at Blackwater during 2009 growing season.

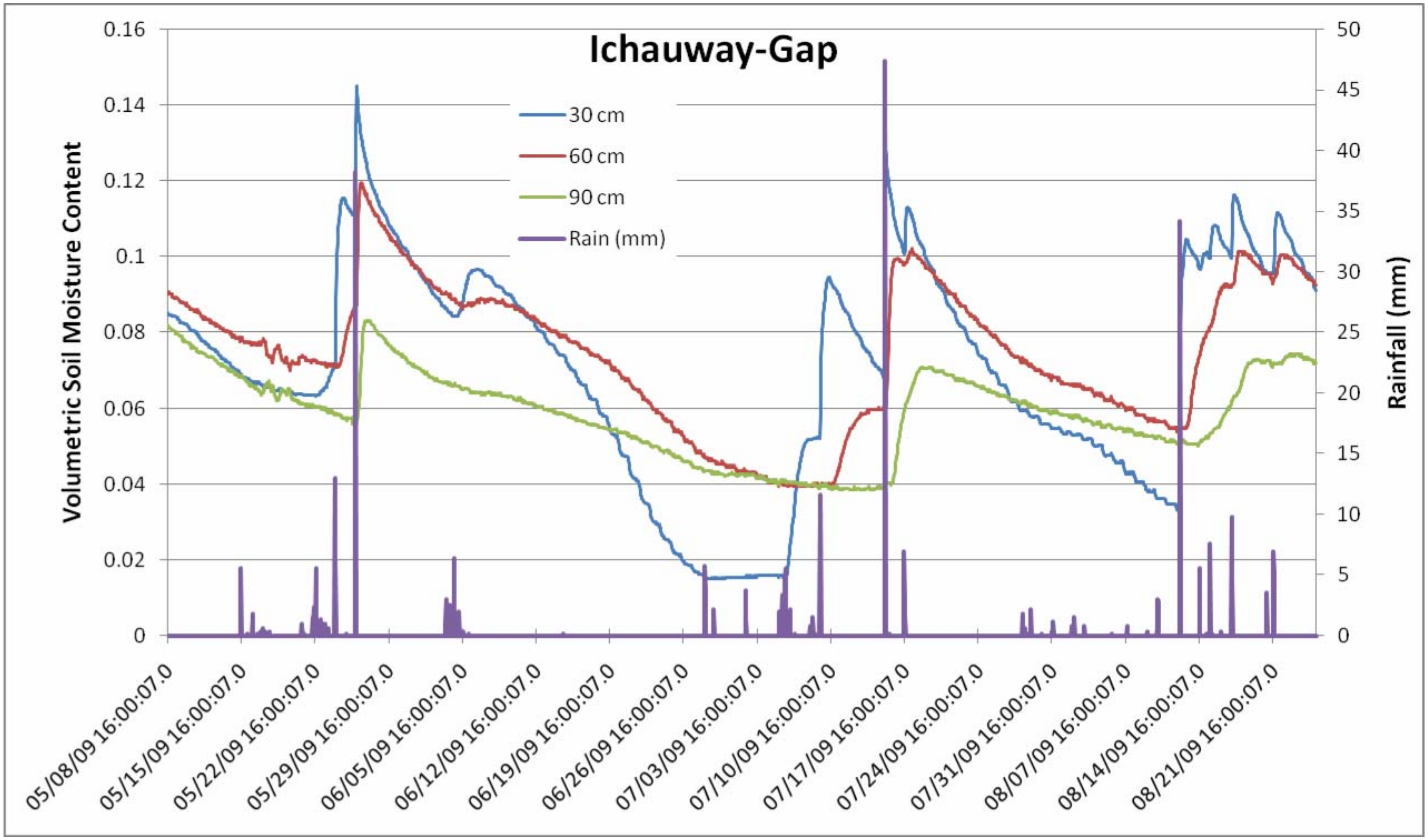


Figure 9. Volumetric soil water content and rainfall data from HOBO weather station located in a canopy gap at Ichauway during 2009 growing season.

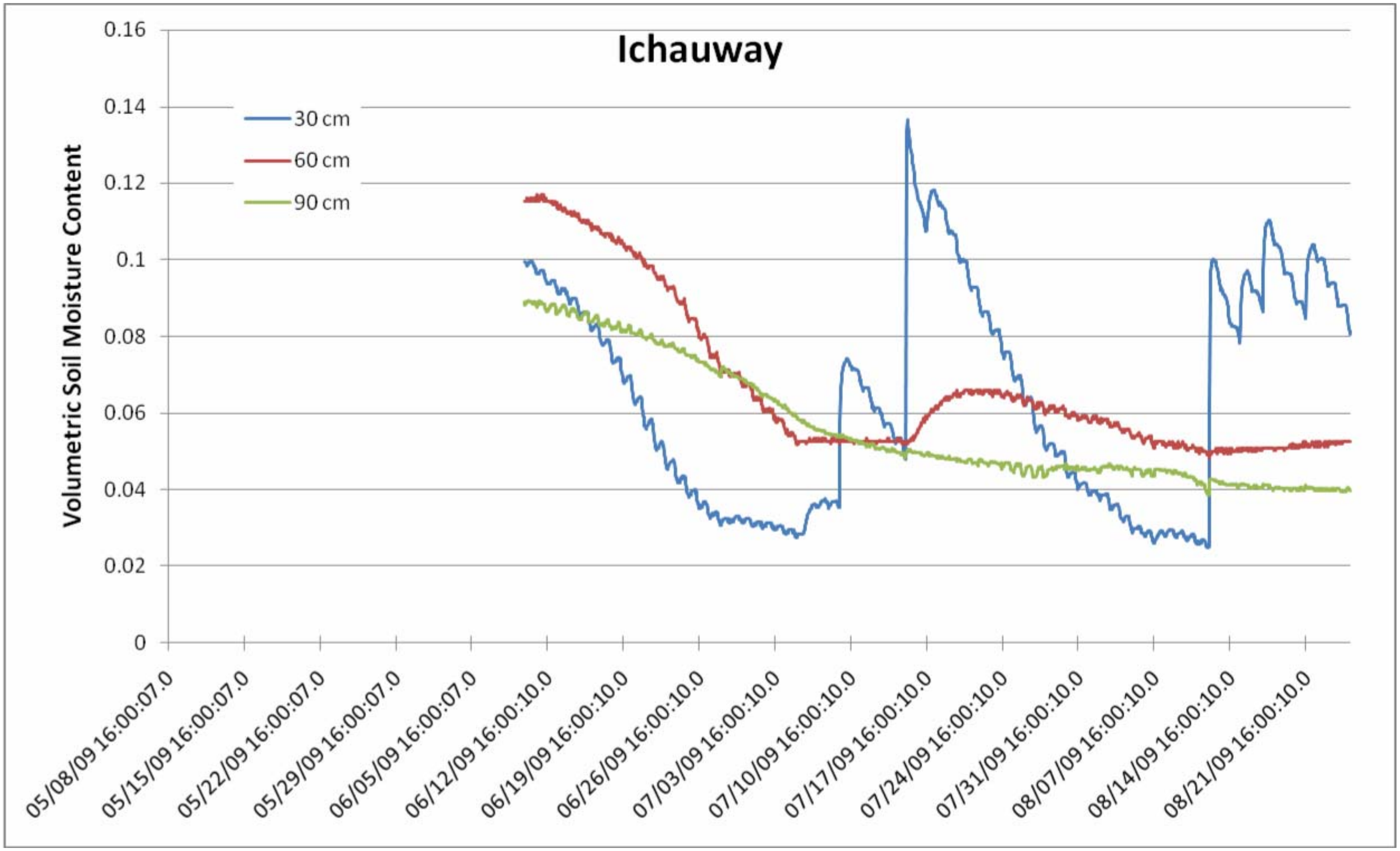


Figure 10. Volumetric soil water content from HOBO weather station located under intact canopy at Ichauway during 2009 growing season. Data points begin June 10.

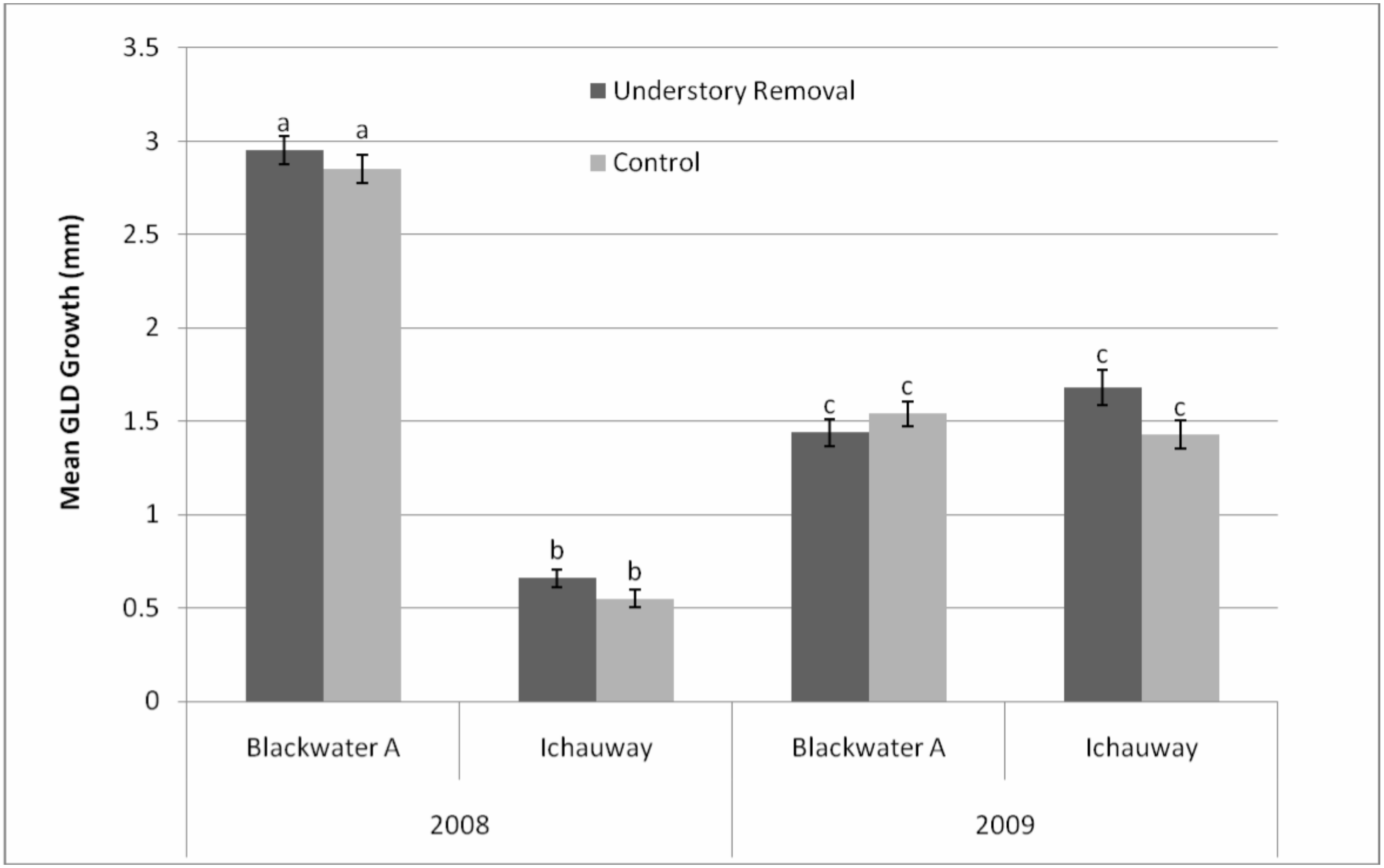


Figure 11. Mean seedling GLD growth for 2008 and 2009 growing seasons. Bars with different letters indicate statistical significance.

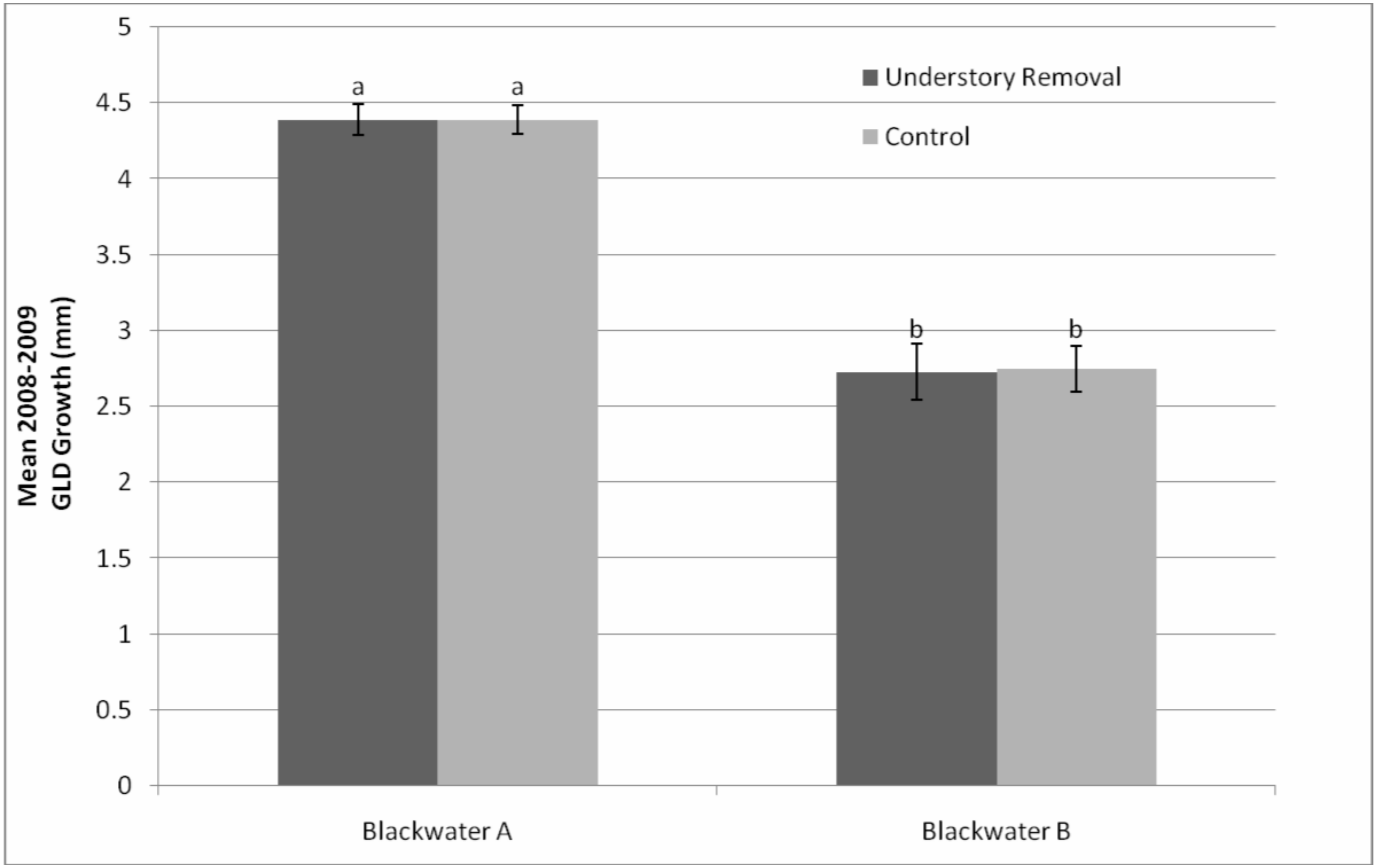


Figure 12. Comparison between Blackwater A (Rock Creek Nursery) and Blackwater B (Meeks Nursery) seedlings. Bars with different letters indicate statistical significance.

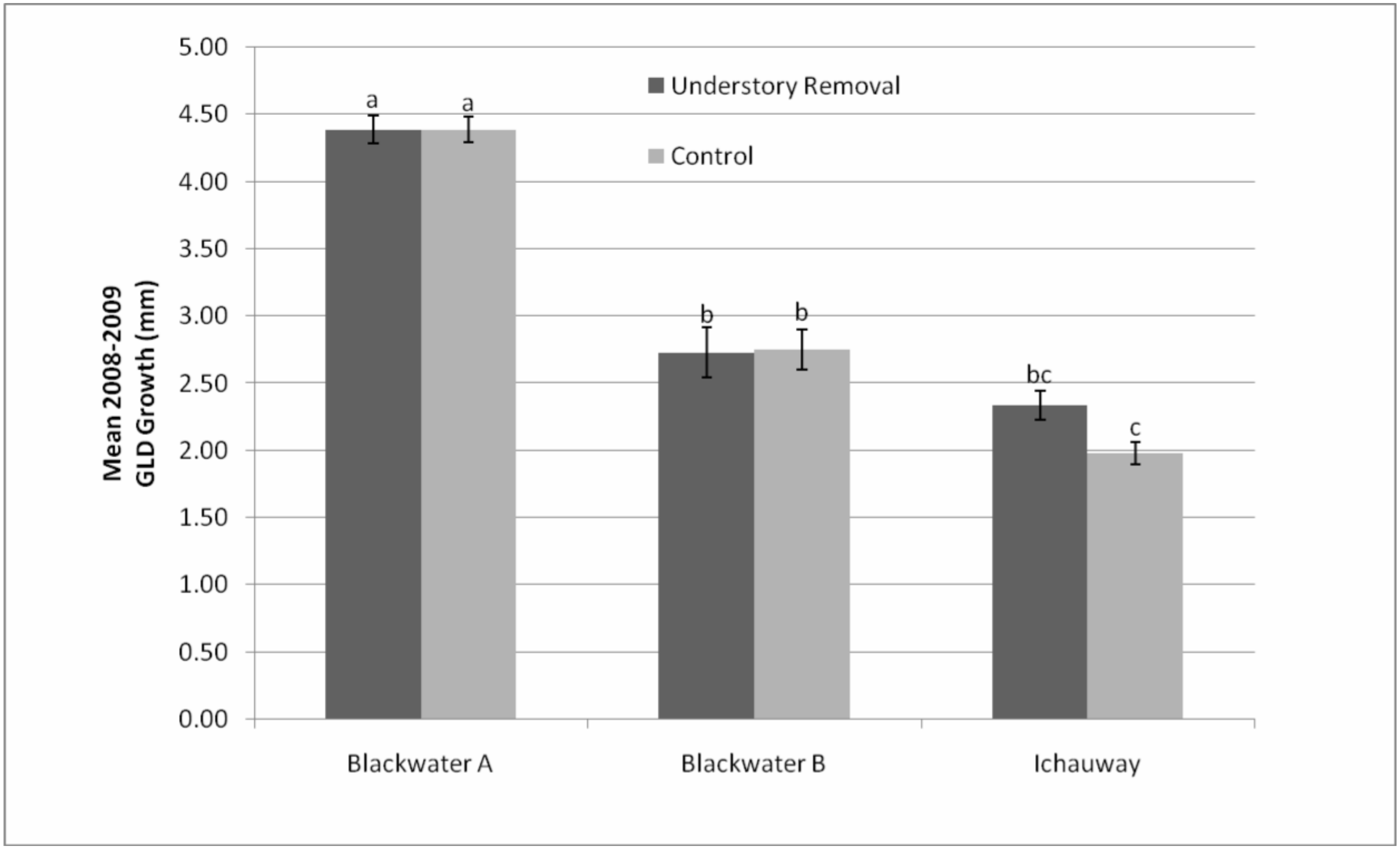


Figure 13. Mean 2-year seedling growth by site. Bars with different letters indicate statistical significance.

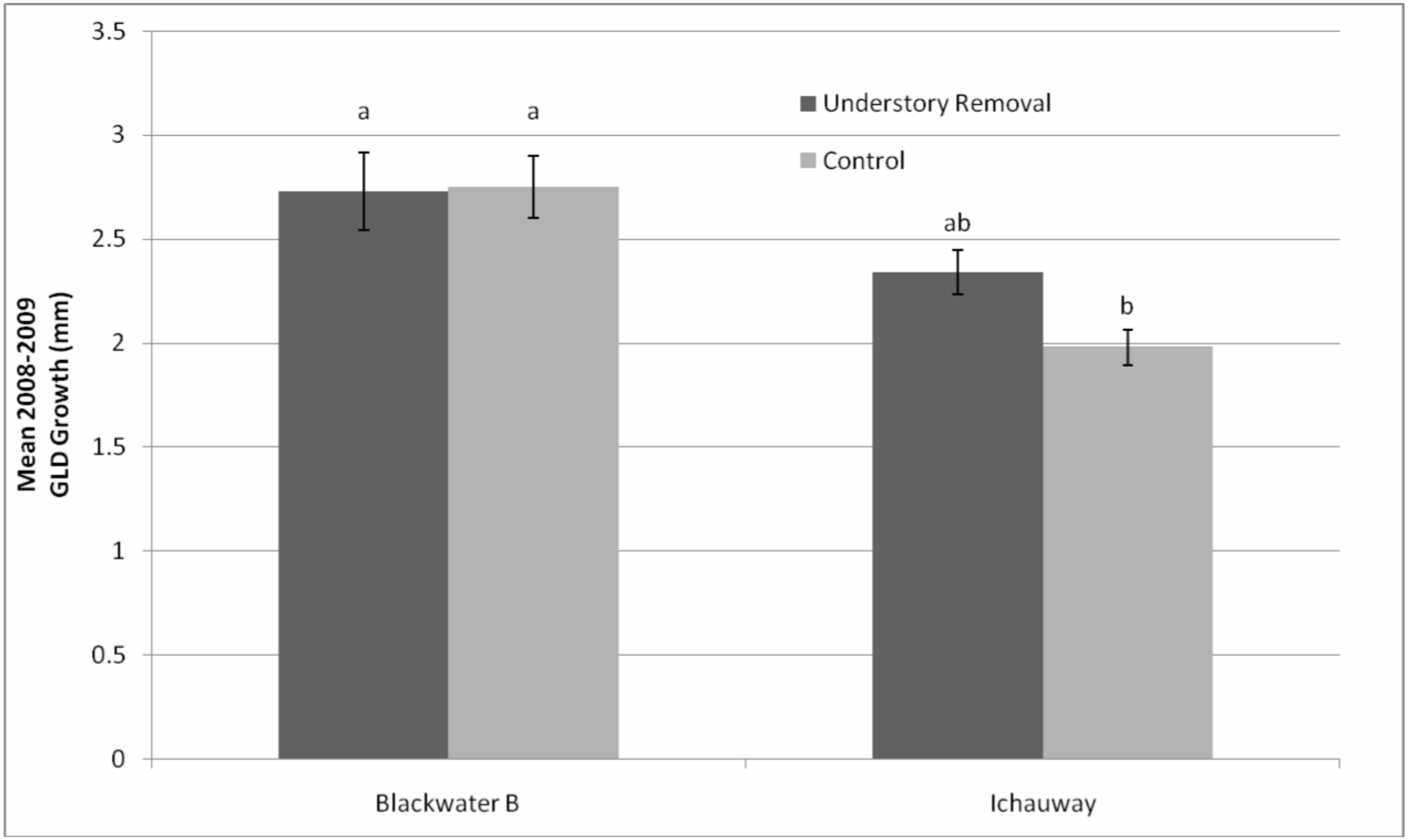


Figure 14. Mean 2008-2009 seedling GLD growth for Meeks seedlings (Blackwater B and Ichauway) planted in February, 2008. Bars with different letters indicate statistical significance.

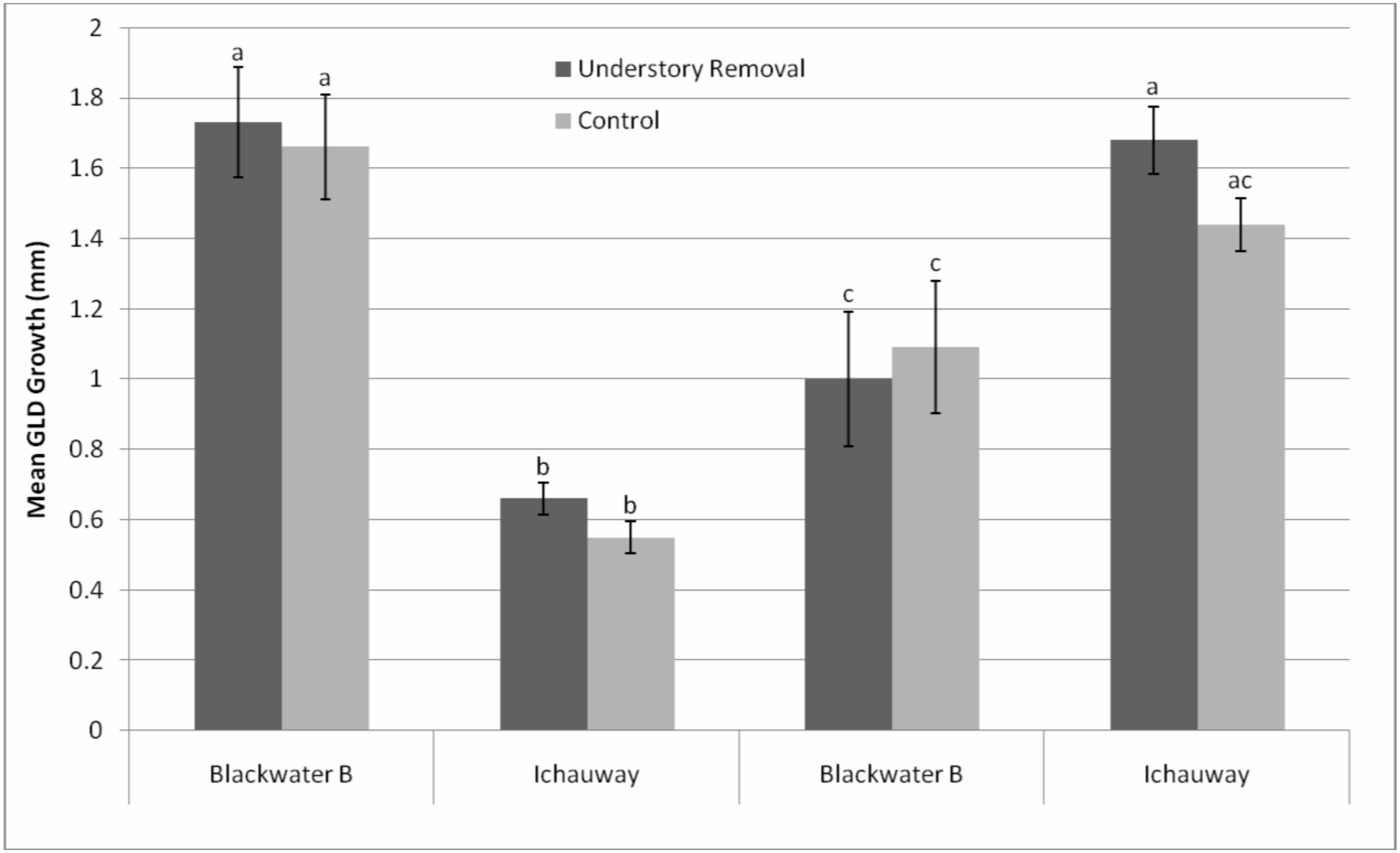


Figure 15. Mean GLD growth by year for Meeks Seedlings (Blackwater B and Ichauway).

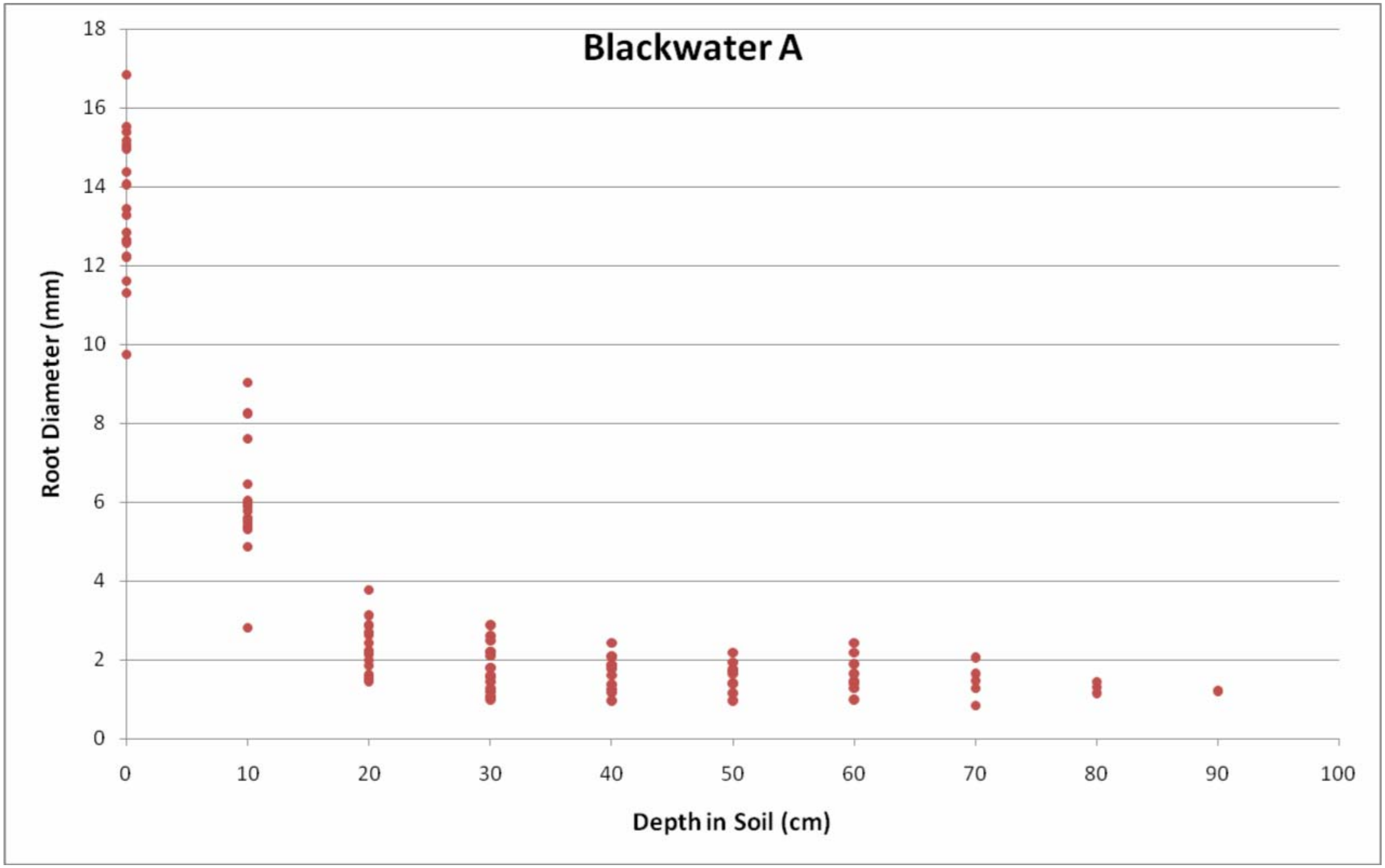


Figure 16. Root diameter by depth for subsample (n= 18) of Blackwater A seedlings.

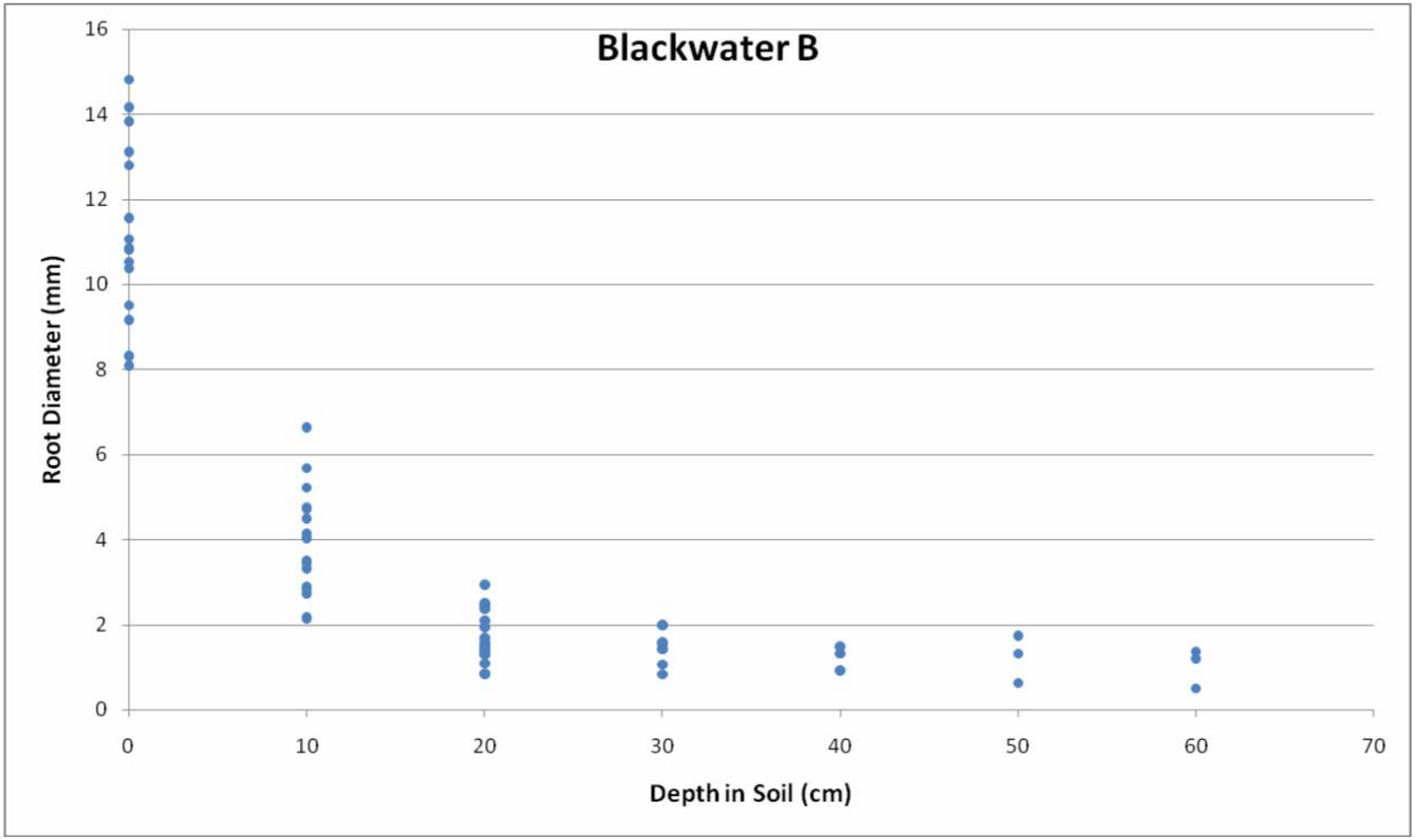


Figure 17. Root diameter by depth for subsample (n= 18) of Blackwater B seedlings.

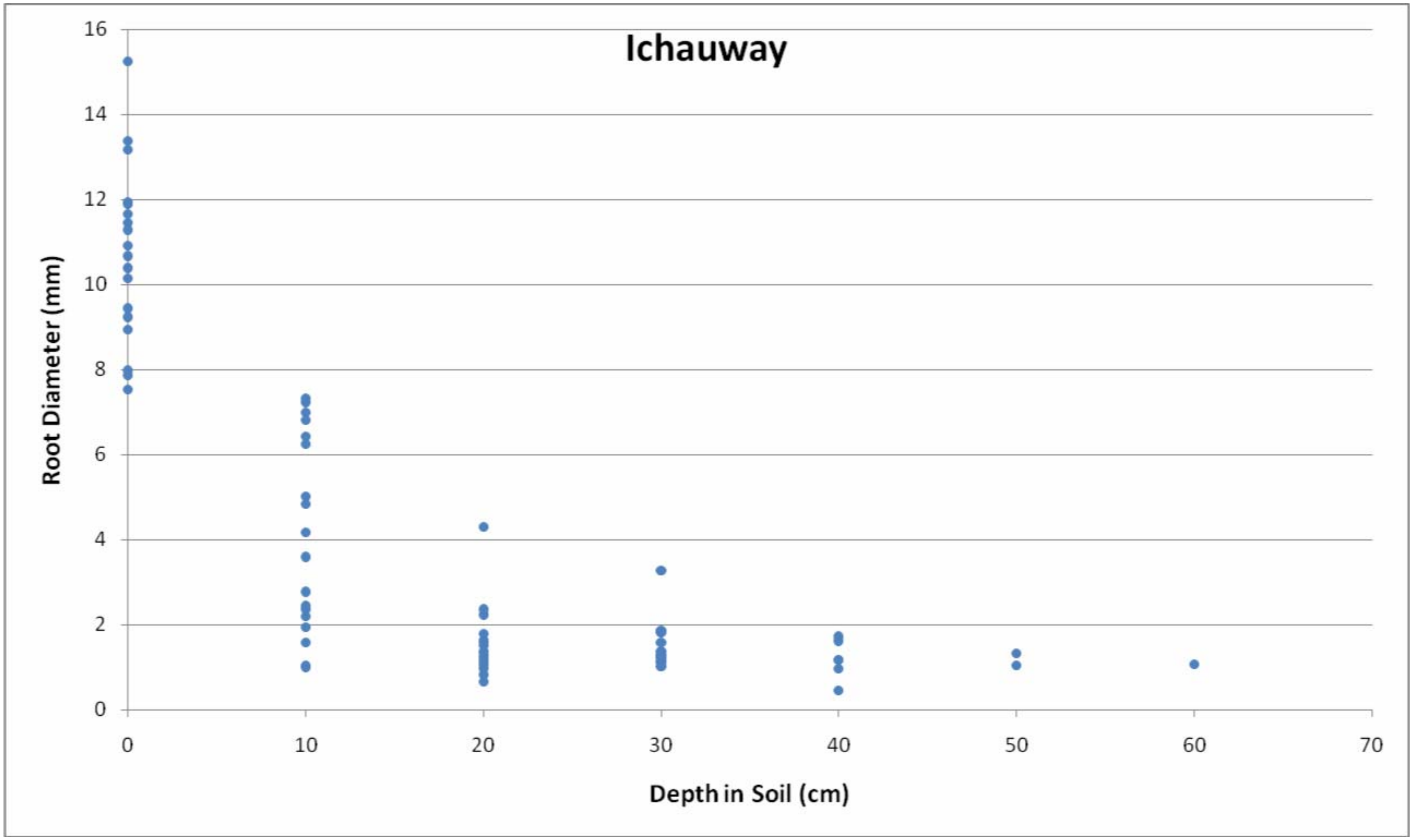
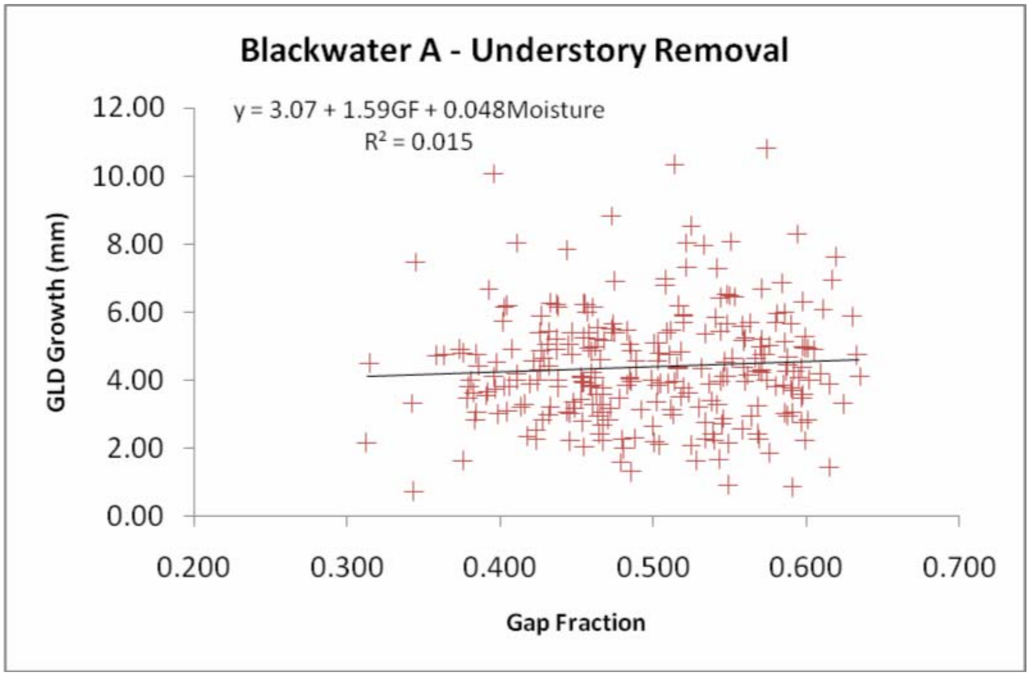


Figure 18. Root diameter by depth for subsample (n= 18) of Ichauway seedlings.



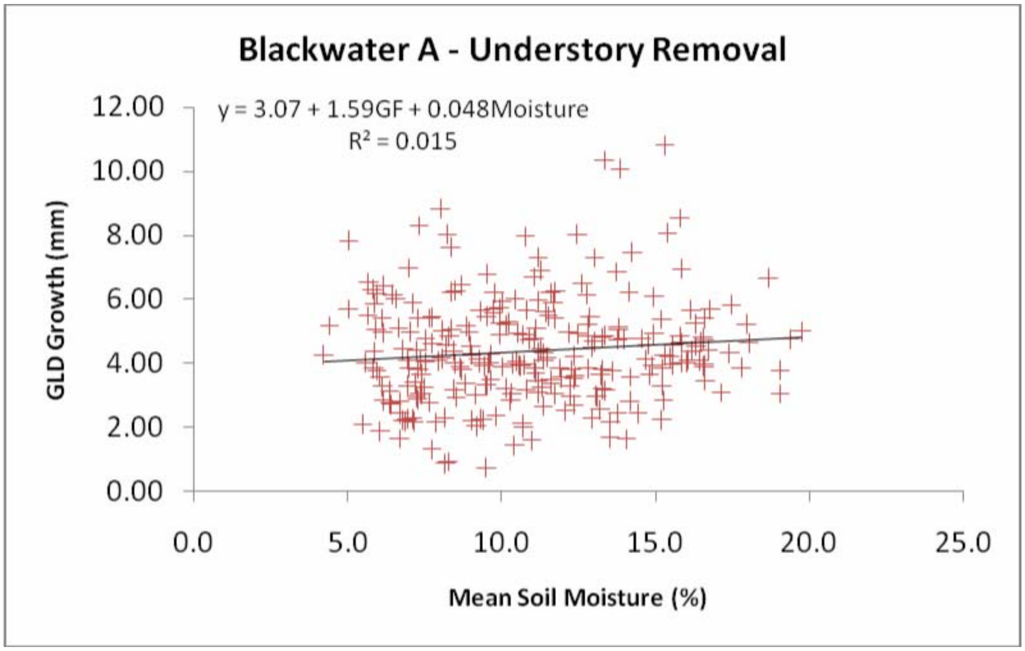
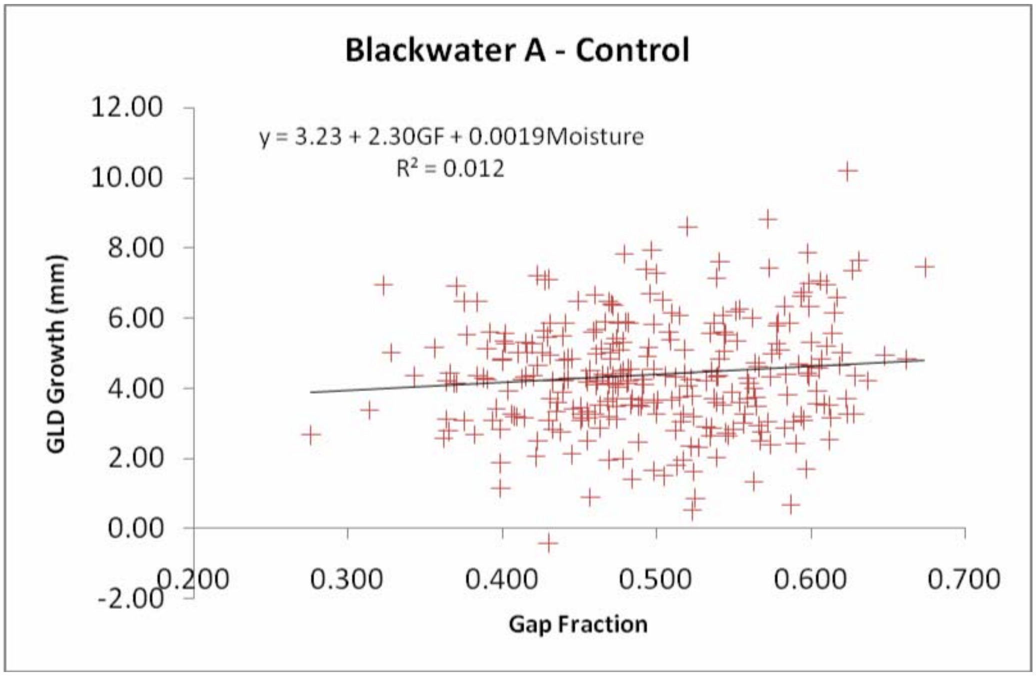


Figure 19. Multiple linear regression for Blackwater A understory removal seedling GLD growth with gap fraction and soil moisture as predictors.



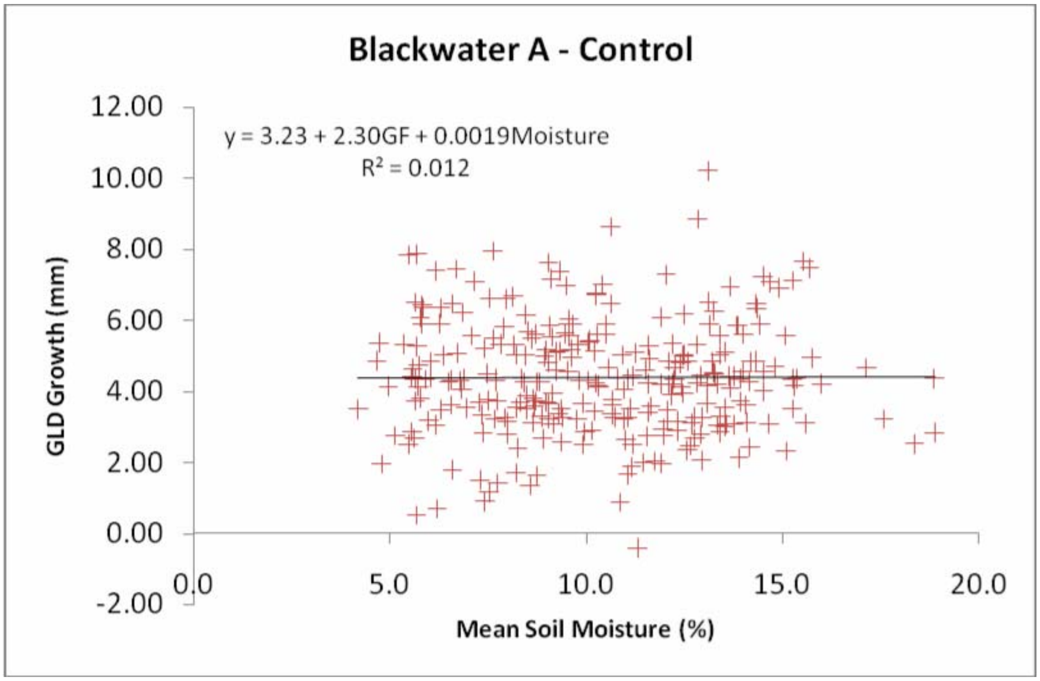
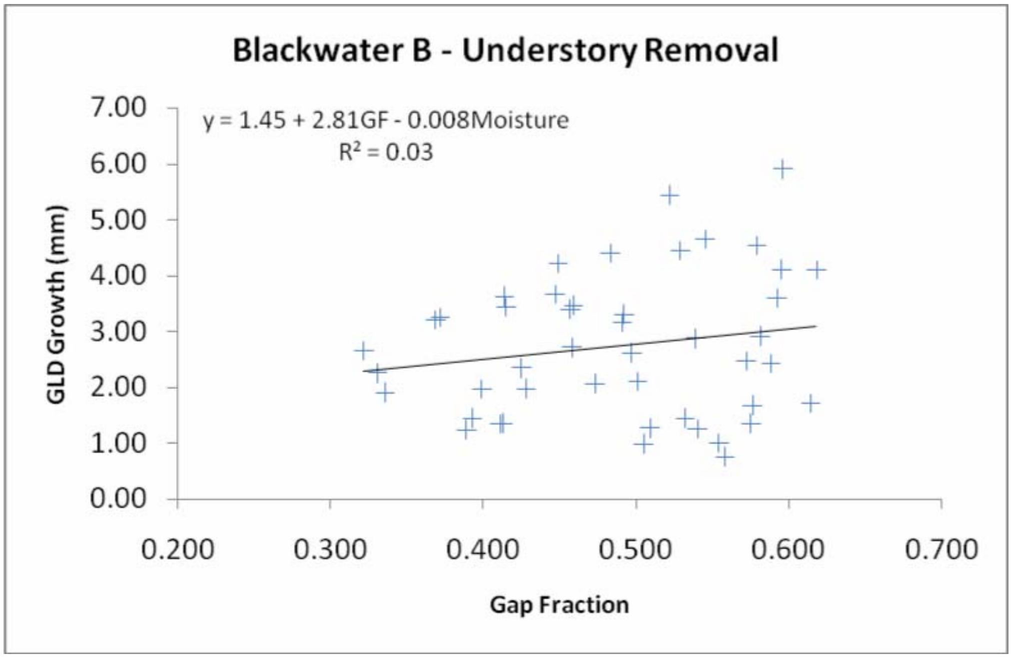


Figure 20. Multiple linear regression for Blackwater A control seedling GLD growth with gap fraction and soil moisture as predictors.



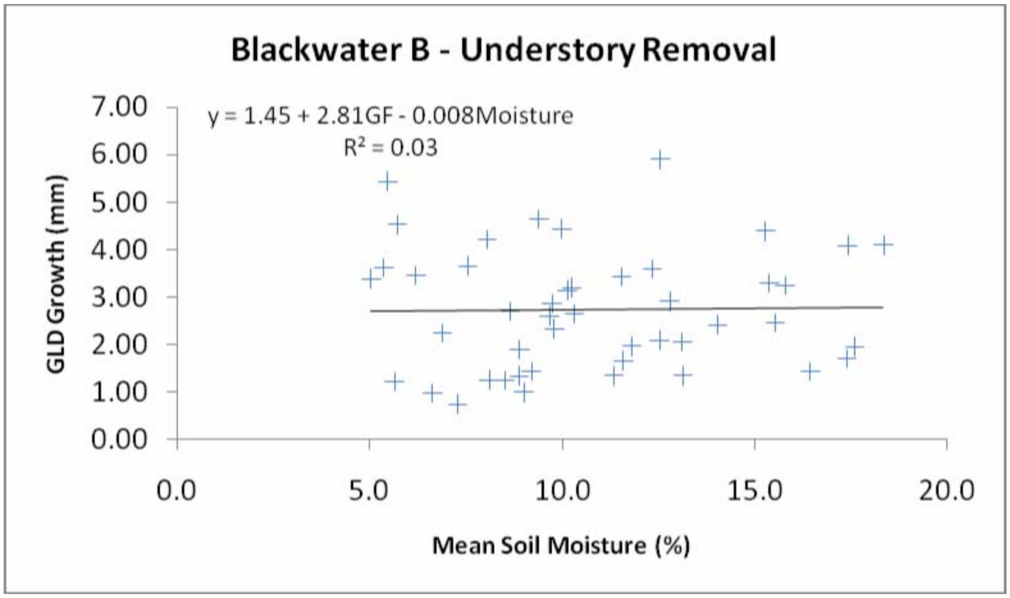
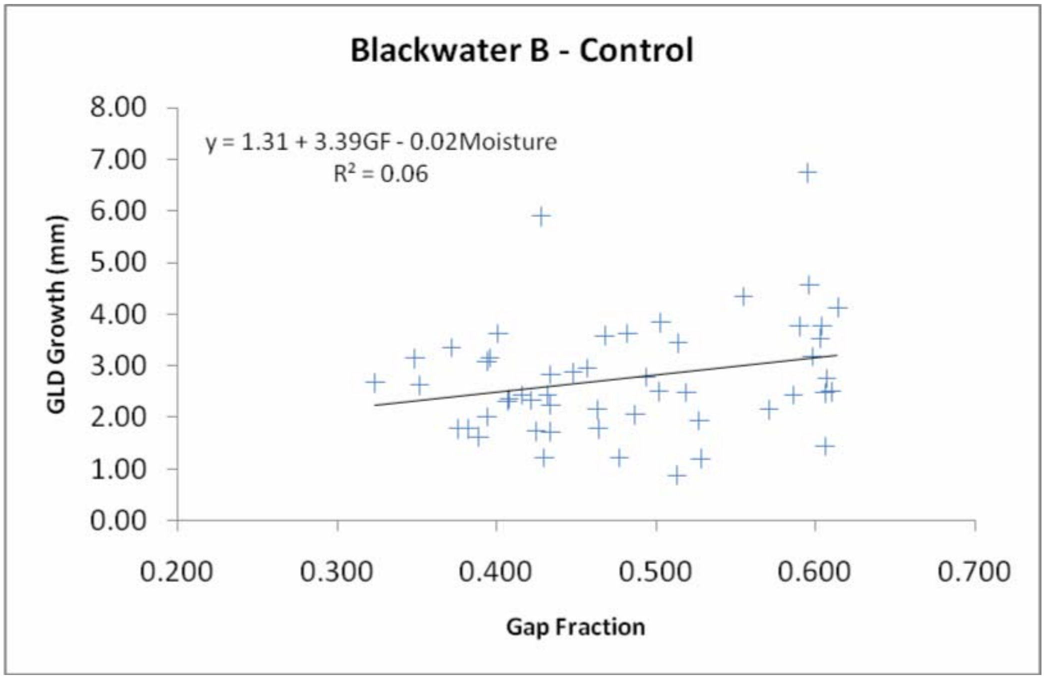


Figure 21. Multiple linear regression for Blackwater B understory removal seedling GLD growth with gap fraction and soil moisture as predictors.



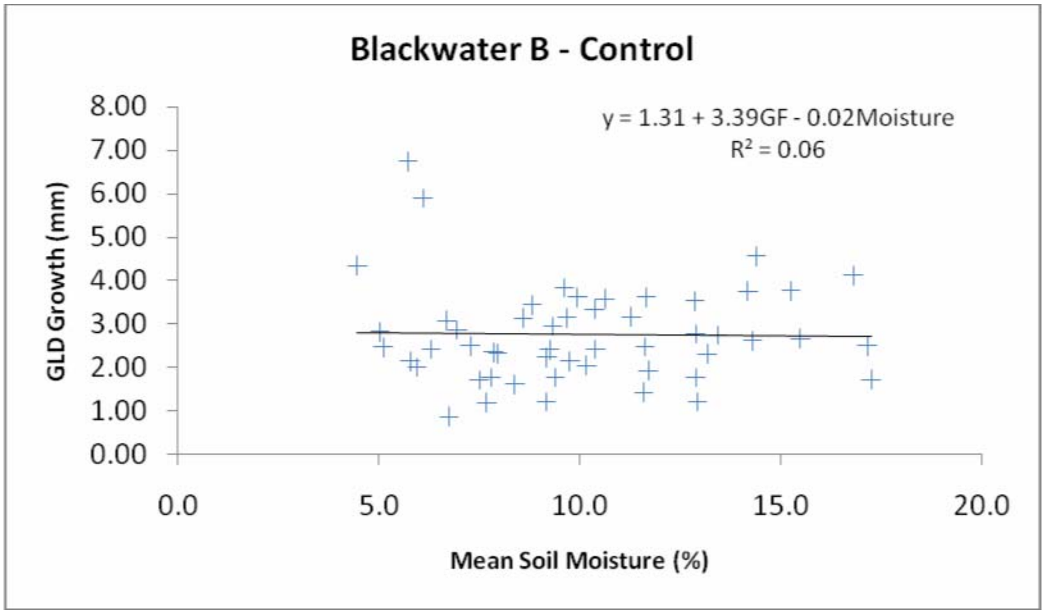
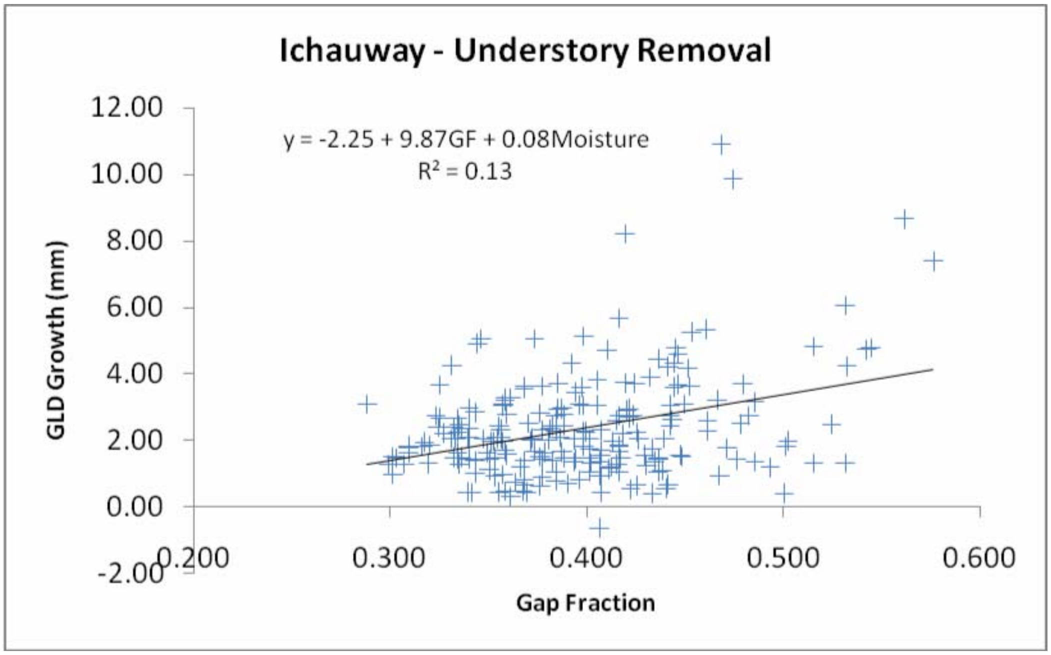


Figure 22. Multiple linear regression for Blackwater B control seedling GLD growth with gap fraction and soil moisture as predictors: growth by soil moisture.



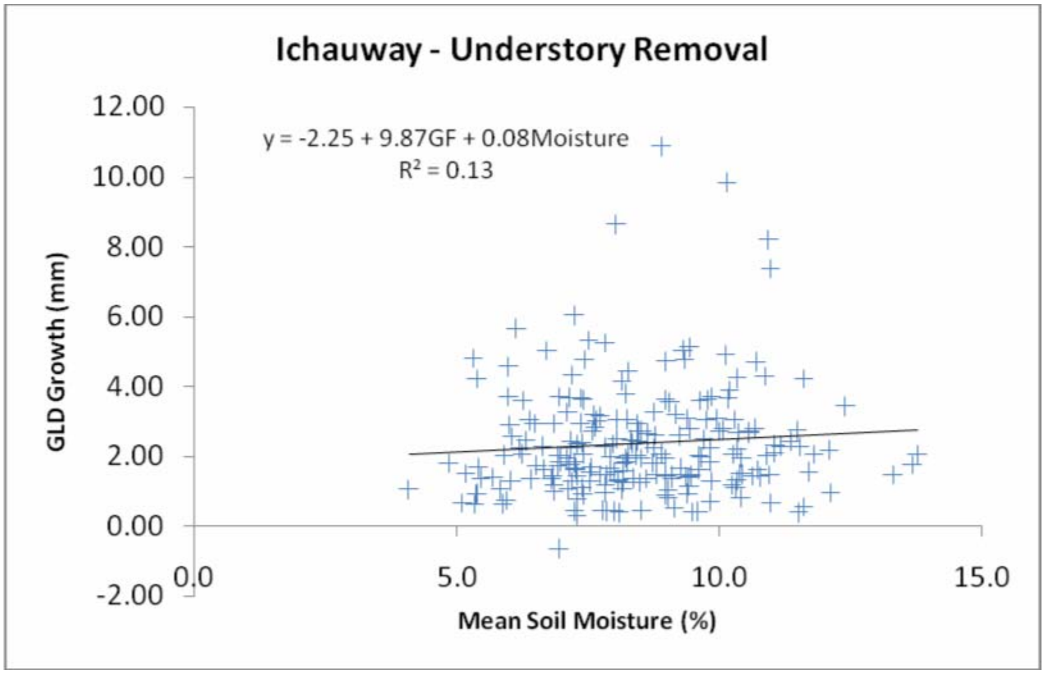
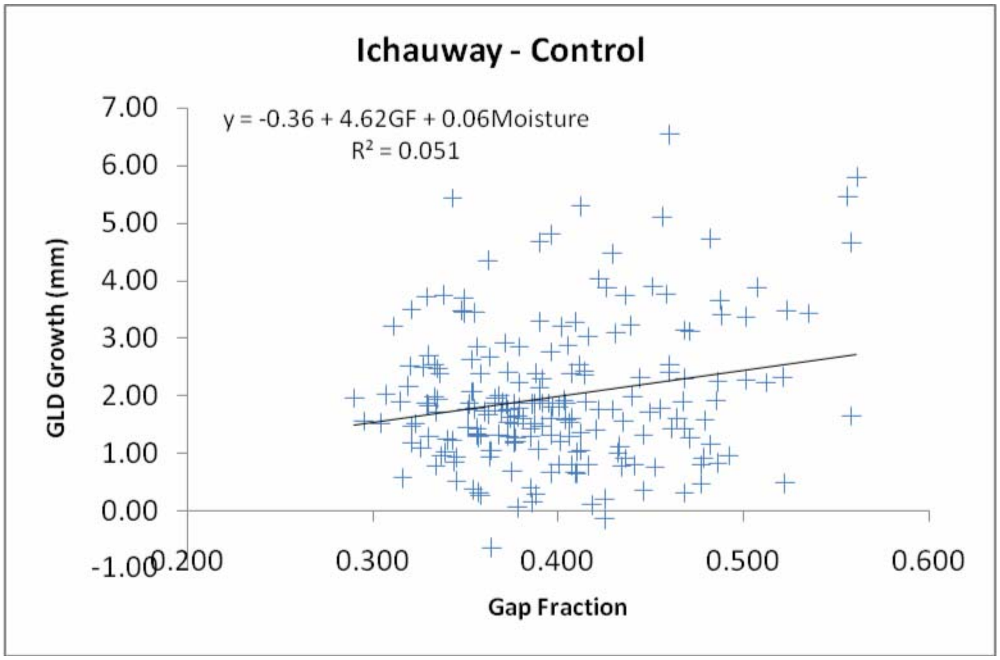


Figure 23. Multiple linear regression for Ichauway understory removal seedling GLD growth with gap fraction and soil moisture as predictors: growth by soil moisture.



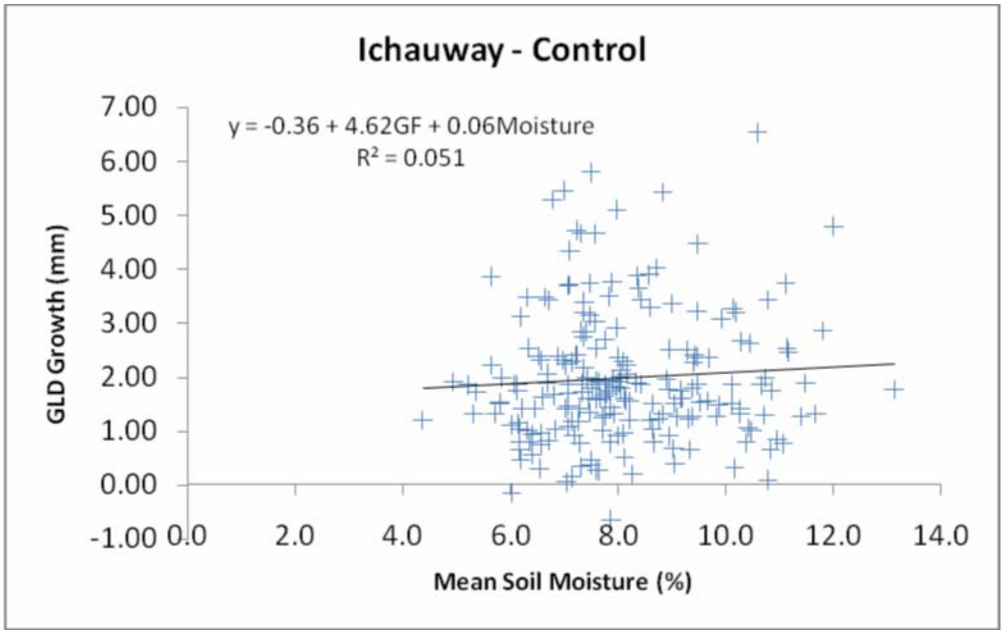


Figure 24. Multiple linear regression for Ichauway control seedling GLD growth with gap fraction and soil moisture as predictors: growth by soil moisture.

# CHAPTER V

# DISCUSSION

## Canopy Gap Fraction

Distributions of canopy gap fraction for both Blackwater and Ichauway are typical for second-growth longleaf pine forests. Additionally, they support prior descriptions of longleaf pine site types. Blackwater, which is more characteristic of xeric sites, has a more open canopy typical of lower site classes resulting from less fertile soils and common moisture stress. Such sites were referred to as “wet deserts” by Brockway and Outcalt (1998). In contrast, Ichauway, a mesic site typically less subject to prolonged moisture stress, supports a denser canopy.

Other studies (Palik et al., 1997; Brockway and Outcalt, 1998, McGuire et al., 2001, Pecot et al., 2007) have examined longleaf pine seedling growth under canopy gradients on one site only, meaning that their results are not directly comparable to different site types. However, canopy conditions may not be the primary driver of seedling competition. Brockway and Outcalt’s (1998) study documented 57 percent canopy cover on a xeric site, which is comparable to the 60 percent mean canopy cover (0.402 gap fraction) measured at Ichauway in this study. Another study at Ichauway documented canopy gap fraction at 0.61 for a xeric site and 0.60 for a mesic site (Sheffield et al., 2003). So, overstory density does not necessarily differ with site conditions.

Gap light index (GLI) specifies the percentage of incident photosynthetically active radiation (PAR) transmitted through a canopy gap to any particular point in the understory over the course of a growing season (Canham, 1988). In effect, GLI shows a gap’s contribution to the light regime at any given point in the understory, measured as a percent of PAR received at an open site (Canham, 1988). Using Battaglia and others' (2002) regression of GLI by gap fraction, estimated mean gap fraction among uncut forest matrix at Ichauway was 0.417, supporting the estimate from this study and further suggesting that overstory conditions on xeric and mesic sites do not necessarily vary. Still, stand structure tends to be more open on xeric sites than on sites with higher soil moisture content (Mitchell et al., 1999a; Sheffield et al., 2003).

### Seedling Survival

Seedling survival in this study was similar to reports from other studies. Survivorship at Blackwater was similar to that reported by Jackson (2006), who found 87 percent survival after one year for seedlings planted in open field conditions in Louisiana. Second-year survival of 70-80 percent was reported by Ramsey and others (2003) for seedlings planted in old-field conditions in Santa Rosa County, FL. On a cutover site in nearby Escambia County, AL, South and others (2005) found 85 percent survival after two years. Similarly, survival of 90-97 percent was observed by Palik and others (1997) among seedlings planted under overstory gradients at Ichauway. For underplanted seedlings, degree of overstory stocking does not necessarily affect survival (Kirkman et al., 2007).

The lower survival experienced at Ichauway in this study was not anomalous. Although substantially lower than at Blackwater, seedling survival at Ichauway was similar to the 67-73 percent reported by Pecot and others (2007), who also studied underplanted seedlings at Ichauway during drought conditions. McGuire and others (2001) observed survival between 50-70 percent after one growing season on another mesic site. However, such low survival should not be unexpected. Stoner (1986) warns that, due to low available water capacity, longleaf pine seedling mortality on soils at the Ichauway site may approach 25-50 percent even if properly planted in good conditions. Similarly, the soils at Blackwater can cause 0-50 percent mortality

(Weeks et al., 1980). According to Wakeley (1954 p. 5), mortality is likely to continue as height growth is unduly delayed.

Several possibilities exist to explain the higher survival exhibited by Blackwater A seedlings. Although data do not exist to specifically test the cause of mortality differences, the timing of planting is likely to be an important factor. Seedling survival depends on the root system's ability to quickly expand and begin taking up water and nutrients (Lantz et al., 1989, South et al., 2005), and earlier planting tends to allow seedlings to develop better root systems, making the seedlings more drought tolerant and more able to tolerate competition (Franklin, 2008). Thus, planting in cool, damp conditions is a benefit to root growth and survival. While all seedlings in this study were planted during the dormant season, Blackwater A seedlings were planted six weeks earlier than Ichauway seedlings and nearly eight weeks earlier than Blackwater B seedlings. This additional time during the dormant season would presumably provide an advantage by allowing seedlings to grow better root systems and thus show better survival.

Seedling quality, measured specifically as seedling diameter, is perhaps equally if not more important to seedling survival. The current interim nursery guidelines for containerized longleaf pine seedlings (Dumroese et al., 2009) recommend larger-diameter seedlings because they tend to exit the grass stage earlier, but also because research has documented that smaller seedlings tend to show poorer survival. South and others (2005) found a parabolic relationship between containerized seedling diameter and survival: survival was poorer among smaller-diameter seedlings, but overly large seedlings also had low survival due to a high root bound index ("RBI," South and Mitchell, 2006), which is calculated by dividing a containerized seedling's root collar diameter (RCD) by the container's diameter.

A third important factor which could explain lower first-year survival at Ichauway is fire, whose potentially negative effects on seedling survival (especially among smaller seedlings) have been documented by Boyer (1974). The 2008 prescribed fires at Ichauway affected some seedlings in March and affected the rest in early April. March prescribed fires have been shown especially harmful to seedling growth and survival over time (Grelen, 1975; Haywood et al., 2001; Haywood, 2009). While seedling arrays were protected so that no seedlings were consumed by fire, many seedlings were scorched by radiant heat and completely shed their needles. Most seedlings survived to produce new foliage, but many had fewer fascicles after the first growing season than at time of planting. Furthermore, a mid-summer drought seemed to precipitate mortality among already-stressed seedlings. Varner and others (2007) found that crown scorch during spring fires can cause mortality up to two years later for overstory pines, so the same could be true for seedlings.

Survival between the first and second growing seasons shows a different pattern. While Blackwawter A continued to show high survival, Blackwater B seedlings showed substantially lower survival during the second year. In contrast, during the second year Ichauway seedlings showed survival comparable to that of Blackwater A. This could further support the importance of planting high-quality seedlings to insure good seedling survival. Blackwater A seedlings had the highest initial GLD and showed the highest survival. In contrast, Blackwater B and Ichauway seedlings were significantly smaller at time of planting and showed noticeably lower survival. It is probable that the prescribed fire at Ichauway killed the smaller, less fit seedlings Boyer (1974). For Blackwater B, the weakest seedlings thus may have survived the first growing season only to reach comparable mortality figures during the second year. Still, it is worth noting that Blackwater B's smaller sample size makes the survival figures not fully comparable.

## Soil Moisture

Soil moisture figures recorded during this study period are comparable to those found in other studies at Ichauway. Mulligan and others (2002) sampled 15 cm soil moisture on a monthly basis and reported means between 5-14 percent. Wilson and others (2002) calculated mean annual 10 cm gravimetric soil moisture content to be a significantly drier 4.4 percent for xeric sites compared to 9 percent for intermediate (mesic) sites. Another study on a xeric location (Addington et al., 2004) found 0-90 cm volumetric soil moisture content ranged from only 2-8 percent. However, soil moisture during this study was lower than the 12 percent mean soil moisture for 0-30 cm and 16 percent for 0-90 cm depths reported by Pecot and others (2007).

Other sites in the region have shown similar or higher, but more variable, soil moisture. Substantially broader ranges of 7-21 percent was reported for 0-30 cm and 26-34 percent for 30-60 cm depth on a cutover site in Covington County, Alabama (Bales, 1999), approximately 50 km north of the Blackwater site. Similar growing season soil moisture ranges have been reported for heavier soils in the Upper Coastal Plain of Alabama for 0-14 cm depths (5-19 %) (Mitchell et al., 1993), 0-20 cm depths [4-16 % (by weight)] (Zutter et al., 1986) and for 0-30 cm depths (5-25 %) (Mitchell et al., 1999b). This indicates that soil moisture data measured during 2008 and 2009 for this study are not atypical for the region. These studies also suggest that summertime soil moisture may not be substantially less than winter soil moisture. As Bruce (1951) showed, these examples also point to the importance to mean soil moisture of soil properties and topography, both of which can cause extreme variation in soil moisture both locally and regionally. They furthermore demonstrate the importance of identifying soil moisture availability in order to understand competitive dynamics of a given site.

Hourly soil moisture data from this study show the same trends as Mitchell and others (1993, 1999b), in which soil moisture in deeper soil horizons fluctuates less, yet displays similar overall trends. However, in this study mean 60 and 90 cm soil moistures were not consistently higher than mean 30 cm soil moisture (Table 2). While this may seem counterintuitive, data from a xeric site at Ichauway showed 90 cm average soil moisture to be 29 percent lower than average 30 cm soil moisture (5% vs. 7%) (Sheffield et al., 2003). Unlike the biweekly data presented by Mitchell et al. (1993, 1999b), hourly soil moisture data collected in this study documented diurnal fluctuations in soil moisture content at 30, 60, and 90 cm depths. Also of note is that the 30 cm soil horizon remained at the permanent wilting point (PWP) identified by Heyward (1939) and

Scheer and Woods (1959) of 1.4-2.1 percent soil moisture for one week or more on multiple occasions during the 2009 growing season. Since 2009 experienced greater overall rainfall and fewer periods of drought, it can be assumed that during 2008 soils spent more time at PWP.

Soil moisture data collected during the 2008 and 2009 growing seasons showed that mean soil moisture was higher at Blackwater in both years, which is contrary to the inherent assumption that Blackwater was the more xeric site. However, the different fire intervals between Ichauway (1 year) and Blackwater (5-6 years) may have been a factor. A study by Heyward (1939) suggested that dense, tangled growth of grasses resulting from seven years without burning helped conserve soil moisture. Research has long accepted that Ichauway is generally a mesic longleaf pine site (e.g., Mitchell et al., 1999a; Pecot et al., 2007), so it appears that [as Heyward (1939) suggested] during this study site quality was not strictly a function of soil moisture. However, of note is the high geographic variability of soil moisture at Blackwater shown in the HOBO data—whereas data from a canopy gap show extremely dry soils even at 90 cm, data from another point show soil moistures nearly twice as high (Figures 7 and 8). In contrast, both HOBO sensors at Ichauway showed similar results, implying that soil moisture there may not be as variable.

That 30 cm TDR sampling showed soil moisture to be higher at both Blackwater and Ichauway during 2008 (when both sites received less rainfall) suggests that the sampling regime was inadequate to accurately represent the soil moisture dynamic at each site. Surface soil moisture was highly dependent on the amount of time since the most recent rain event (Figures 7 and 9). Thus, in order to get a truly unbiased sample at both sites it would be useful to sample at a set number of days after rain events so that the chance occurrence of rainfall during sampling periods would not artificially inflate soil moisture estimates.

Weather data can be used to more clearly understand soil moisture availability during this study. Rainfall data in Table 4 include rain resulting from Tropical Storm Fay on August 22-24, 2008, thus obscuring what was in fact a drier growing season and year. Ichauway received 330 mm due to Fay, whereas Blackwater received 150 mm. Furthermore, since Ichauway seedlings were planted in February, they missed 217 mm of rainfall that occurred in January and early February, leaving them with only 1182 mm in 2008; Blackwater B seedlings missed 316 mm from the 2008 calendar year, leaving them with a total of 1624 mm (Table 4). If Fay's precipitation is excluded for analytical purposes, Ichauway experienced a more severe drought year, but Blackwater's total was still above the long-term average. Rainfall totals were substantially higher for 2009: rainfall totals through August 23, 2009, approached total rainfall for 2008 at both sites.

## Root Depth

The lack significant differences in mean seedling root depth between sites and nurseries means that neither Blackwater A, nor Blackwater B, nor Ichauway seedlings were able to access soil moisture from deeper horizons. Also, the absence of relationships between GLD and measured and predicted root depth suggests that seedling growth differences were not due to different root depths nor presumed access to deeper soil moisture. Moreover, even 90 cm depth soil horizons did not show noticeably more soil moisture than the shallower horizons. Thus, all seedlings are presumed without access to dependable moisture, which is a probable explanation for the overall lack of major growth differences among seedlings.

## Seedling GLD Growth

Due to the confounding of nursery and planting date, seedling growth data are limited in their use for cross-site comparison, and hypothesis testing is not valid. However, considerable circumstantial evidence does exist to help explain the results gathered in this project.

### *Effect of Seedling Quality*

Even though comparison between Blackwater A and Ichauway seedlings is confounded by nursery and planting date, there are noteworthy relationships present. During the first growing season Blackwater A seedlings grew approximately five times more than those at Ichauway (Figure 11), but mean GLD at Ichauway following the first growing season was not statistically different from the initial GLD of Blackwater A seedlings. In effect, it took one growing season for Ichauway seedlings to "catch up" to Blackwater A seedlings. While it may be coincidence, during the second growing season post-planting (2009), there were no significant differences among Blackwater A or Ichauway seedling growth (Figure 11). Trees grow as a function of size (Perry, 1985), so lack of significant growth differences during the 2009 growing season suggests the possible existence of a GLD threshold around 9 mm above which seedlings are equally equipped to respond to their environment (show similar growth curves), absent external factors.

Effects of initial seedling size (seedling quality) have been studied for loblolly and slash pines. Long-term data summarized by Wakeley (1969) showed that larger seedlings consistently showed better survival and growth, even after 30 years. Britt and others (1991) found that initial seedling size affected aboveground biomass through the sixth year, regardless of the degree of weed competition, yet growth differences were declining with time. Similarly, South and others (1985) found that seedling grade significantly affected survival and growth in both the short term and also the long term.

Fewer such studies exist for longleaf pine, but with proper handling and planting, larger bare-root (White, 1981) and containerized (South et al., 2005; Jackson et al., 2007; Dumroese et al., 2009) seedlings generally show higher survival rates and more rapid growth. An apparent exception to this rule is for the largest containerized seedlings: South and Mitchell (2006) showed a convex survival curve with an inflexion point at 27% RBI, meaning that seedlings with RCDs greater than 27 percent of the container's diameter showed lower survival after outplanting. Thus, it is possible that some, if not all, of the growth differences observed could be attributed to the initial differences in seedling GLD. Continuing to collect data from this study in future years would provide useful information about the long-term effects of seedling quality and later planting dates on longleaf pine seedling growth.

### *Effect of Understory Competition*

Understory competition is especially damaging to pine seedlings on xeric sites (Hebb, 1957) but also appears to be significant on mesic sites. Comparison between Blackwater B and Ichauway seedling growth removes nursery and planting date as confounding factors and points to the importance of understory competition on higher-quality sites. Even though soil moisture was more abundant at Blackwater during both growing seasons, data suggest that release from understory competition is more beneficial at Ichauway than at Blackwater. Even though there was no treatment effect on soil moisture at either site, after two growing seasons control seedlings at Ichauway had grown significantly less than Blackwater B seedlings. There was no treatment effect on growth at Ichauway, but the absence of a growth difference between of understory removal seedlings at Ichauway and both treatments at Blackwater B shows that understory competition was an important negative influence at Ichauway—without understory competition, Ichauway seedlings were able to equal the growth of Blackwater seedlings.

The negative impact of mesic-site understory competition can be further illustrated by examining 2009 data alone (Figure 15). During the second growing season, control seedlings (subject to understory competition) at Ichauway did not show growth significantly different than Blackwater B seedlings. In contrast, understory removal appears to have allowed seedlings at Ichauway fully to take advantage of the higher site quality, since they grew significantly more than seedlings of both treatments at Blackwater, the lower-quality site. Studies have documented that aboveground net primary productivity (NPP) of longleaf pine-wiregrass ecosystems increases with soil moisture (e.g., Mitchell et al., 1999; Kirkman et al., 2001; Ford et al., 2008). So, it is logical to assume that the competitive interactions are also stronger on sites with increasingly higher soil moisture availability. Kirkman and others (2001) found xeric sites to contain only 30 percent of total understory species, whereas “intermediate” (mesic) sites contained 55 percent of the total number of species. Clearly, mesic sites (such as Ichauway) can support higher productivity and more intense competition.

The only significant treatment effect on soil moisture occurred at Blackwater in 2008, where soil moisture was higher with understory removal. Findings from other studies suggest that any increases in soil moisture due to competition control are likely to be offset by increased soil temperatures (Mulligan et al., 2002). Such a lack of treatment effects on soil moisture at both sites suggests that understory competition may not affect long-term moisture availability to longleaf pine seedlings. This partially supports the suggestion by Pessin (1944) that the advantage to longleaf pine seedlings from competition control was due to higher light availability rather than to reduced root competition. More recent research has also documented the importance of understory light competition, yet has done so on sites where moisture was not a limiting factor. Knapp and others (2008) found that percent understory cover was negatively related to seedling diameter for seedlings two years post-planting on a poorly drained site. Conversely, they found a positive relationship between percent full sunlight and seedling diameter. So, relative abundance of light and moisture seem to be at least as important as overall quantity.

Examining mean annual seedling growth (Figure 15) provides an important perspective to fully understand two-year mean GLD growth. Whereas during the first growing season Blackwater B seedlings nearly tripled the growth of Ichauway seedlings, during the second growing season understory removal seedlings at Ichauway grew significantly more than Blackwater B seedlings, a pattern that was expected given Ichauway’s higher site classification. Furthermore, no significant difference was present between Blackwater B seedling growth in 2008 and Ichauway seedling growth in 2009. This trend points to the confounding effect caused by the 2008 prescribed fire at Ichauway which badly scorched seedlings.

### *Effect of Fire*

Because longleaf pine seedlings are not susceptible to fire after reaching 7-10 mm GLD (Wahlenberg, 1946), most Ichauway seedlings were not immediately killed by the prescribed fire. However, it is probable that 2008 Ichauway seedling GLD growth was substantially reduced due to their need to spend reserves producing new needles following the spring fires. Boyer (1987) found significant growth reductions in 24 year-old longleaf pines after seven years of biennial prescribed fires. Studies in slash pine (Johansen, 1975) and loblolly pine (Cain, 1985) have linked growth losses to crown scorch. Assuming that complete scorch and defoliation of a seedling is equivalent to crown scorch in larger trees, it is not extraordinary that Ichauway seedlings showed higher mortality and significantly less growth during the first growing season, but rather it is notable that they exceeded Blackwater B seedlings in the second growing season.

Fire has been documented to increase longleaf pine survival and height growth over the long term. Bruce (1951) found that prescribed fires significantly increased height growth and predicted the response resulted from reduced vegetative competition and brown-spot infection. Similarly, Bruce and Bickford (1950) found increased survival and height growth among seedlings burned up to twice between ages 1 and 6. Ichauway seedlings in this study were burned prior to their first growing season post-planting, and the stand was burned again a year later, prior to the second growing season. As a result, brown-spot disease was virtually absent from Ichauway seedlings, whereas infection was common among Blackwater seedlings. Although no seedlings bolted during this study, according to Bruce and Bickford (1950) and Bruce (1951), with time the lack of prescribed fires and brown-spot infections at Blackwater could cause a decreased bolting rate.

### *Effect of Soil Moisture*

Despite the high, regular rainfall that occurs annually in the longleaf pine region, soil moisture is probably the most important factor influencing forest growth (Heyward, 1939). Not only do high temperatures and intense solar radiation result in high evapotranspiration rates, but sandy soils and vigorous understory vegetation also combine to make available soil moisture scarce (Heyward, 1939; Hebb, 1957). Not surprisingly, research has shown significant positive correlations between percent soil moisture and seedling height growth (Bruce, 1951). Such correlations support hypotheses of water-limited growth in longleaf pine ecosystems.

That observed mean growing season soil moisture was higher at Blackwater was contrary to expectations but not necessarily aberrant. Nevertheless, hourly soil moisture data indicate that Blackwater often had lower soil moisture than Ichauway. With its unexpectedly higher soil moisture, Blackwater seedlings outgrew those at Ichauway during the study period. This difference seems to suggest that site quality is not solely dependent on moisture availability and that early seedling growth largely is. However, it is important to note that statistical significance does not necessarily indicate differences of ecological significance.

Site quality is certainly an important factor in growth, but it may not be an ultimate limitation. Mature longleaf pine trees are capable of altering their physiology to best exploit resources on drier sites. In fact, physiological adjustments can allow xeric-site longleaf pines to maintain stomatal conductance similar to that of mesic-site pines (Addington et al., 2006). But, xeric-site nutrient cycling may be different enough to cause proportionally longer drought stress, thus reducing the growth capacity of xeric-site longleaf pines relative to those on mesic sites (Addington et al., 2006). Sheffield and others (2003) point out that it is an extrapolation to extend information from mature trees to seedlings because characteristics of pine phenology differ with developmental stage. However, it is still possible that seedlings would react similarly to the same environmental conditions.

After the first growing season (2008), regression showed that mean soil moisture was a positive and often significant predictor for seedling growth, meaning that higher soil moisture resulted in greater seedling growth. This relationship is expected because of increases in aboveground NPP along soil moisture gradients ranging from xeric to mesic and hydric sites

(Mitchell et al., 1999a; Kirkman et al., 2001; Ford et al., 2008). However, after the second growing season (2009), the only significant regressions existed at Ichauway, and mean soil moisture no longer significantly affected seedling growth. The first-year results are consistent with results in the literature (e.g., McGuire et al., 2001; Knapp et al., 2008), but the lack of relationships between soil moisture and growth during the second growing season was unexpected. It is possible, though, that more abundant and evenly-distributed rainfall in 2009 diluted soil moisture's effect on growth.

Dendrochronological research has shown that current-year spring and summer rainfall is strongly correlated to longleaf pine growth (Meldahl et al., 1999; Henderson and Grissino-Mayer, 2009) and that even October rainfall can affect latewood formation (Meldahl et al., 1999). However, as weather data from 2008 show, frequency of rainfall may be as important as total rainfall—while only one major storm event (e.g., Tropical Storm Fay) can replenish annual rainfall deficits, large rainfall events do not provide a sustained or dependable source of soil moisture, particularly in sandy soils. On xeric sites, the combination of high percolation and evapotranspiration rates results in soil moisture deficiency being the norm (Hebb, 1957). For instance, a study on north Florida sandhills showed that surface soils (8-23 cm depth) were at or below PWP after only 14 summertime rainless days (Scheer and Woods, 1959). Although water-holding capacity can be as high as 40 percent, soil moisture capacity is normally only 10-11 percent in the top 10 cm (Heyward, 1939).

Scheer and Woods's (1959) data suggest that soils in this study were often experiencing extreme drought. During this study, there were 12 periods of 10 days or longer without rainfall at Ichauway, of which 7 were in the April-September growing season. At Blackwater there were 11 such periods, of which 6 were in the growing season. Although the soils examined by Scheer and Woods (1959) were poorer and more xeric than those in the present study, combining current data to theirs suggests that it is also safe to assume summertime moisture limitation during extended rainless periods on the subxeric and mesic sites investigated by this study.

Extended rainless periods could be one cause of seedling mortality in this study, as Knapp and others (2008) found an inverse relationship between soil moisture and mortality during the first growing season post-planting. To better account for the temporal aspect of rainfall, some studies (e.g. Meldahl et al., 1999; Foster and Brooks, 2001) have used the Palmer Drought Severity Index (PDSI) as an indicator of soil moisture availability. Recording PDSI and incorporating it into the analysis for the present study would have added another useful dimension to soil moisture data.

In this study, rainfall was less evenly distributed during the first growing season, likely repeatedly putting seedlings under moisture stress. Although trends following the first growing season showed positive relationships between soil moisture and seedling GLD growth, gap fraction and seedling growth were generally negatively related. This suggests that increased light may actually be detrimental to seedlings under moisture stress. In mature longleaf pine trees, decreases in hydraulic conductivity between the soil and needles results in lower stomatal conductance (Addington et al., 2004) and presumably reduced growth. Therefore, periods of drought can have substantial effects on tree growth that persist longer than those droughts (Addington et al., 2004). Moisture stress is likely to cause similar physiological effects in seedlings, too, only results could be more striking.

Pessin (1939a) predicted that soil moisture was unlikely to be the limiting variable in longleaf pine seedling growth because of the high annual rainfall across the species' range and suggested that understory competition limited longleaf pine seedling growth by preempting soil nutrients. Since regression analyses in this study showed generally positive but non-significant relationships between soil moisture and seedling growth, Pessin (1939a) may have been correct that moisture is important, but not limiting. Still, it is worth noting that there are numerous different longleaf pine ecosystems and that each may be governed by different factors depending on site type, topography, and climate, among others. Thus, even though light may have been the primary driver in Pessin's (1944) work, studies have documented increasing NPP with moisture availability (Ford et al., 2008) and even moisture-limitation of productivity (Mitchell et al., 1999). In contrast, Knapp and others (2008) studied a poorly drained site in North Carolina and found an inverse relationship between growth of planted seedlings and soil moisture, suggesting that overabundant soil moisture can limit productivity. So, it would be unrealistic to define one model for the controls of longleaf pine seedling growth.

### *Effect of Light*

A general trend in the literature shows that increased light exposure is initially a negative factor for longleaf seedlings, but that as seedlings grow and develop root systems, increased light can increase seedling growth (see Palik et al., 1997; McGuire et al., 2001; Pecot et al., 2007). This dynamic can be explained with findings by Addington and others (2004) that show the importance of maintaining the hydraulic conductance of the soil-to-leaf pathway for carbon gain. If roots are not sufficiently moist, leaf water potential drops, vapor pressure deficit rises, and stomatal conductance tends to be reduced (Addington et al., 2004). Thus, there is a physical reason for the observed reduced seedling growth with increased light exposure. The same trend seems to be forming in the current study, although the data are too immature to show significance.

Regression analyses showed that gap fraction (and thus light availability) is becoming a significant factor in seedling growth over time. Whereas during the first growing season gap fraction was generally a negative and non-significant predictor, after the second growing season gap fraction was generally a positive (but non-significant) predictor. The trend for light to become more positively related with seedling growth over time seen in this study has been observed previously. A review by Kirkman and Mitchell (2006) shows unpublished data that document an increasingly positive relationship between gap fraction and seedling biomass over time. While they saw no relationship between gap fraction and biomass after one growing season, an increasing curvilinear relationship had developed after three years. After five years, however, the relationship was not as strong, suggesting that seedlings with lower gap fractions were catching up. Thus, it is possible that with time the same relationship will develop at Ichauway in this study, too.

Gap fraction estimates for Blackwater and Ichauway suggest a substantial difference in light availability between the two sites. According to the highly linear relationship between gap fraction and GLI observed by Battaglia and others (2002), mean GLI for Blackwater can be estimated at approximately 58 percent, compared to an estimated mean GLI of 48 percent at Ichauway. Thus, light availability may be over 20 percent higher at Blackwater than at Ichauway. While Brockway and Outcalt (1998) found that PAR was evenly distributed across canopy gaps, more recent research by Battaglia and others (2003) documented light transmittance by a more powerful method and showed it to be significantly affected by canopy density. Measures of average canopy cover in the stands studied by Palik and others (1997) and Brockway and Outcalt (1998) were not drastically different, thus suggesting that actual transmittance values should be equally similar. Therefore, light availability may not have been responsible for different conclusions by Palik and others (1997) and Brockway and Outcalt (1998).

The conclusions of Palik and others (1997) and Brockway and Outcalt (1998) are thus more similar than they initially appear. Whereas recruitment at the mesic site studied by Palik and others (1997) was driven by light, it is still possible that presumably similar (if not greater, due to latitude) light availability at Brockway and Outcalt's (1998) xeric site was less important to seedling recruitment than were underground resources. The different conclusions reached by Palik and others (1997) and Brockway and Outcalt (1998) from studies in fairly similar overstory conditions suggest that it is probable that the 20 percent difference in light availability between sites in this study could alter the competition dynamics and thus provide an explanation for differing recruitment patterns on different quality sites.

Comparing studies from mesic sites (e.g., Battaglia et al., 2002; Palik et al., 2007) to those of xeric sites (e.g., Brockway and Outcalt, 1998) underscore the complexity of longleaf pine ecosystems and the difficulty of isolating the factors that control seedling recruitment. The xeric "wet desert" studied by Brockway and Outcalt (1998) apparently supported a canopy of similar density to Ichauway, yet it is still presumed that light was the controlling variable at Ichauway (Palik et al., 2007), while underground resources ultimately limited seedling recruitment on the xeric site (Brockway and Outcalt, 1998). Results from the present study show the same trend. Although relationships were not strong, a developing trend suggests that seedling growth at Ichauway, the mesic site, is more significantly affected by light availability. At Blackwater, the subxeric site, a trend could not be generalized. But, the lack of significant or noticeably positive trends with light may show that light availability is not as important at Blackwater as at Ichauway.

# CHAPTER VI

# SUMMARY AND CONCLUSIONS

## Project Summary

Because of the marked decrease in the extent of longleaf pine ecosystems, management of the remaining longleaf pine ecosystems and restoration of degraded ones is currently a priority on both public and many private lands. These conservation goals for longleaf pine ecosystems mean that multiple-use management is often employed. Uneven-aged silviculture, because it maintains continuous forest cover, is thus a valuable tool for managing longleaf pine stands. However, the effects of stand structure—especially residual canopy density—on longleaf pine recruitment patterns are not fully understood. The success of uneven-aged systems depends on recruitment of new cohorts into the canopy, so understanding competitive dynamics between understory and overstory vegetation and longleaf pine seedlings is vital for maintaining ingrowth sufficient to sustain longleaf pine stands.

The goal of this project was to expand the current understanding of longleaf pine seedling recruitment dynamics through the perspective of applied research. Previous studies have examined the same topic through basic research and have documented specific interactions between the forest overstory and understory in longleaf pine ecosystems, thus leaving a foundation for research that shows how specific stand manipulations can be used to achieve desired seedling stocking, establishment, and recruitment. To collect information about the effects of residual longleaf pine overstory on seedling survival and growth, this project modeled two-year growth of longleaf pine seedlings planted under mature, second-growth longleaf pine stands that are currently managed with selection silviculture. Because longleaf pine ecosystems exist on a variety of site-types and previous studies have examined only one site in any single study, a substantial gap existed in the literature. To address that gap, this project examined growth patterns on a subxeric site and also on a mesic site, making it one of the first such studies.

This study was designed to investigate competitive relationships of longleaf pine seedlings within mature longleaf pine forests. Competition aboveground and belowground was investigated by sampling the canopy gap fraction and average growing season soil moisture for every seedling. Understory removal was used to separate the influences of the forest overstory from those of the forest understory. Seedling growth was measured after one and two growing seasons to document the effect of overstory density and soil moisture on seedling growth.

Confounding factors including different seedling sources and fire invalidate the use of hypothesis testing with these data, but supporting evidence is offered. First-year results showed that increased soil moisture tended to result in increased seedling growth, whereas increased canopy gap fraction resulted in generally reduced seedling growth. These results are consistent with those of previously published studies. Second-year results showed no relationship between average growing season soil moisture and seedling growth, but generally positive trends between gap fraction and seedling growth. The implication from these findings is that early seedling growth depends on access to soil moisture and benefits from overstory shading. The data suggest that over time, presumably as the seedlings develop more substantial root systems, soil moisture becomes less important and growth is benefited by increased light exposure.

## Management Implications

This study documented the complexity of competitive influences on longleaf pine reproduction, but showed a developing trend that supports previously published findings. Data summarized by Kirkman and Mitchell (2006) exhibit the importance of various sources of competition to longleaf pine seedlings, including aboveground and belowground influences of the forest overstory and understory. Whether the ultimately limiting factor is light or moisture, it is important that only some seedlings survive the negative pressures of moisture stress, prescribed fire, and light competition. Brockway and Outcalt (1998) recognized the importance of natural selection to seedling recruitment in that seedling recruitment takes place as individual seedlings survive competitive pressures.

Studies by Palik and others (1997), Brockway and Outcalt (1998), and Pecot and others (2007) all support the importance of using selection harvests to create stands with a range of overstory densities that allows seedlings in openings to rapidly begin height growth yet still “stores” some reproduction underneath denser canopies that later can be thinned as needed to release seedlings. Still, using continuous-cover management represents a trade-off that results in slower timber production (Boyer, 1993a; Brockway et al., 2005c). Results of the present study, however, show that residual overstory may increase short-term seedling growth, which suggests that carefully implemented selection silviculture may benefit long-term timber production.

## Future Research

Because of confounding factors, this study did not provide data directly applicable to longleaf pine management, and many potential avenues of applied research remain. Models for longleaf pine seedling growth in the literature should not be applied to all longleaf pine ecosystems. Yet, the current study showed that similar trends were developing on a subxeric and a mesic site. A logical starting point for future research would be investigating recruitment of naturally-regenerated seedlings in stands of known productivity. Such research could effectively address the effects of site-type while avoiding the artificial effects of studying planted seedlings.

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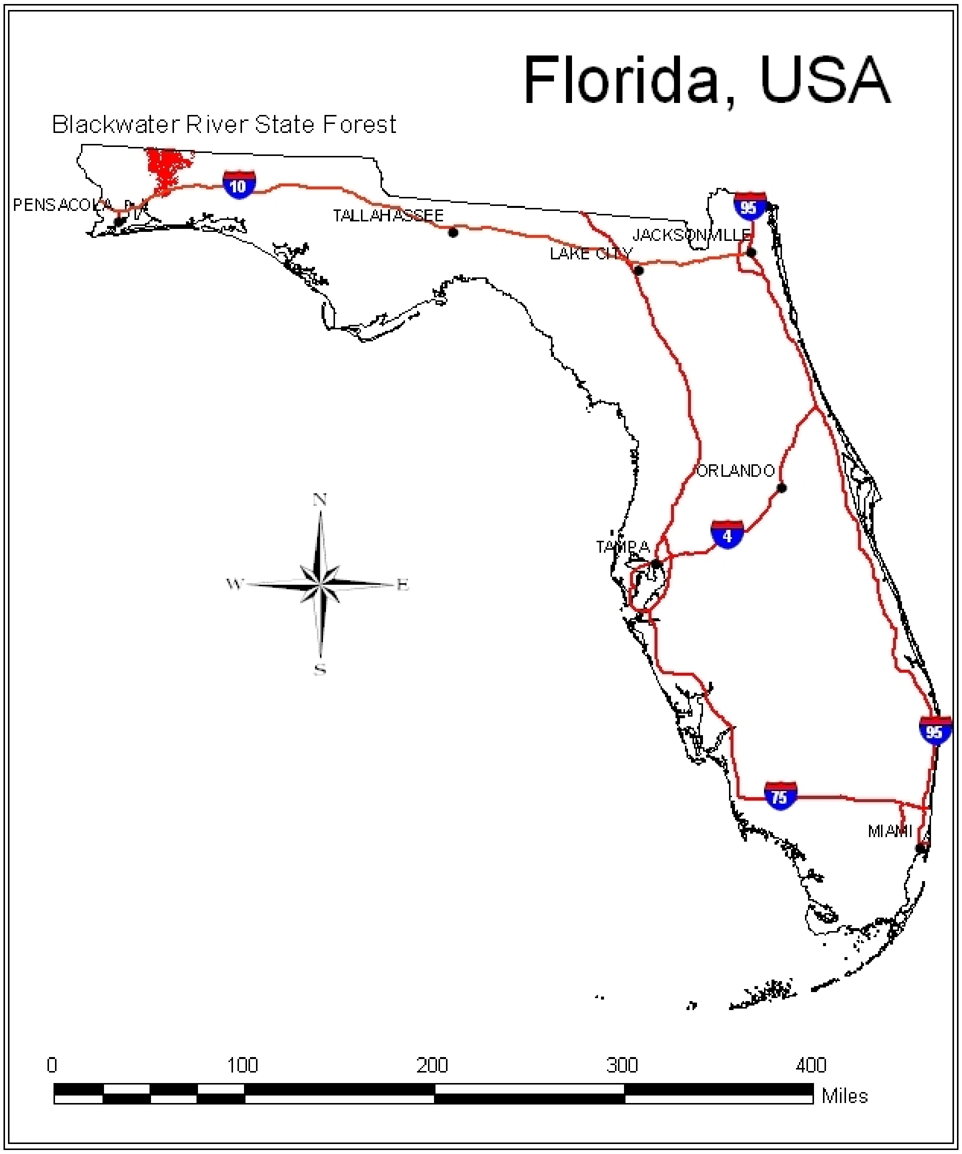
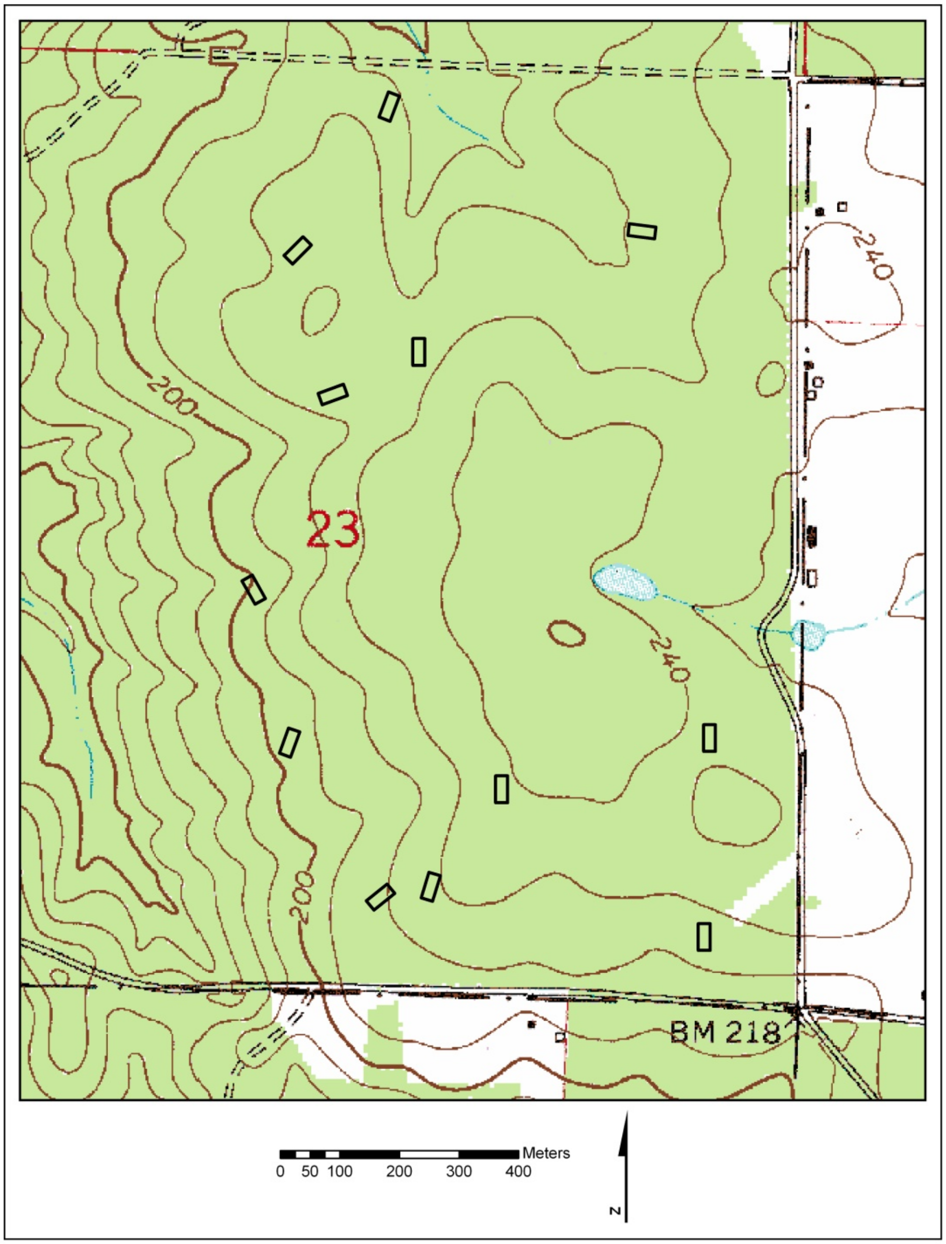
# APPENDICES

# APPENDIX A

# STUDY LOCATION MAPS

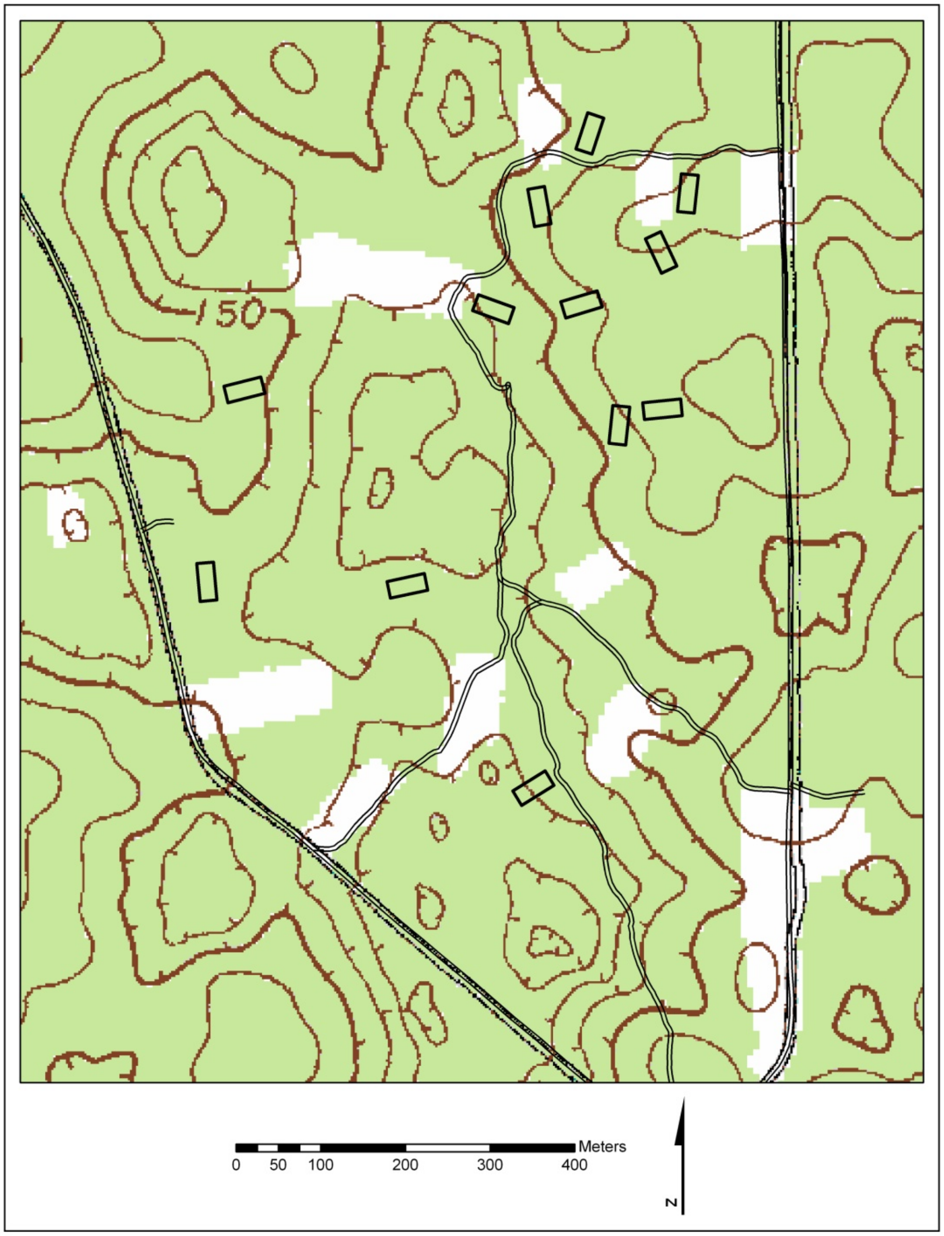


Appendix A.1. Generalized location map of Blackwater study site.



Appendix A.2. Map of seedling arrays at Blackwater study site, 0.5 miles south of FL 4 on Old Martin and Charlie Foster Roads.

Appendix A.3. Generalized location map of Ichauway study site.



Appendix A.4. Map of seedling arrays at Ichauway study site in the Conservation Demonstration Area

# APPENDIX B

## SUMMARY STATISTICS FOR CANOPY GAP FRACTION AT BLACKWATER AND ICHAUWAY STUDY SITES

Appendix B.1. Summary statistics for canopy gap fraction at Blackwater and Ichauway.

| | n | Minimum | Maximum | Mean | Standard Deviation |
|---|---|---|---|---|---|
| Blackwater | 573 | 0.276 | 0.674 | 0.497 | 0.073 |
| Ichauway | 500 | 0.288 | 0.577 | 0.402 | 0.058 |

# APPENDIX C

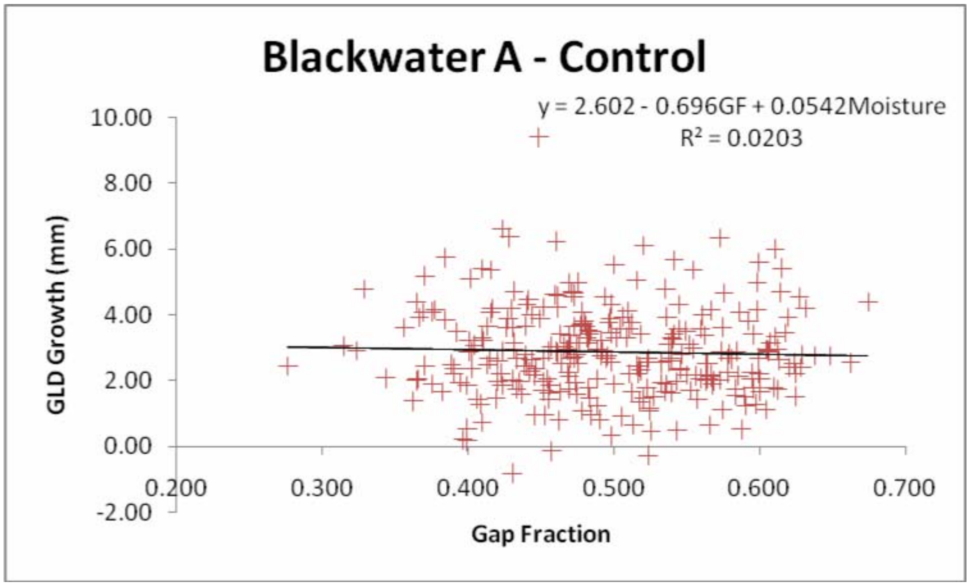
# REGRESSION MODELS FOR LONGLEAF PINE SEEDLING GROWTH AFTER ONE GROWING SEASON

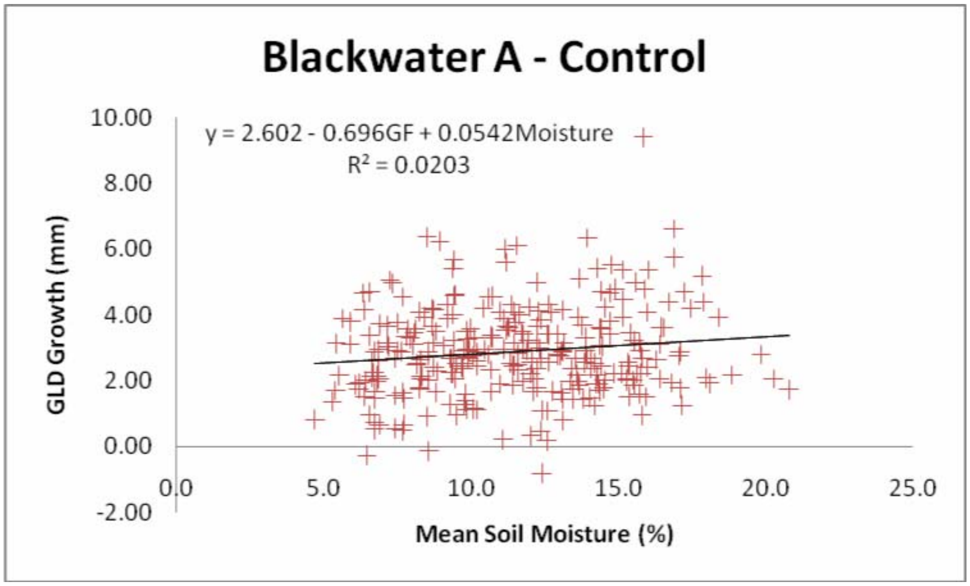
Appendix C.1. First-year multiple linear regression model for square-root transformed Blackwater A control seedlings.

| Analysis of Variance | | | | | |
|---|---|---|---|---|---|
| Source | DF | Sum of Squares | Mean Square | F Value | Pr > F |
| Model | 2 | 0.69 | 0.34 | 2.83 | 0.06 |
| Error | 287 | 34.77 | 0.12 | | |
| Corrected Total | 289 | 35.45 | | | |

| | | | |
|---|---|---|---|
| Root MSE | 0.35 | R-Square | 0.019 |
| Dependent Mean | 1.94 | Adj R-Sq | 0.125 |
| Coeff Var | 17.96 | | |

| Variable | DF | Parameter Estimate | Standard Error | t Value | Pr > \|t\| |
|---|---|---|---|---|---|
| Intercept | 1 | 1.84 | 0.152 | 12.09 | <0.0001 |
| Gap Fraction | 1 | -0.12 | 0.27 | -0.44 | 0.66 |
| Mean Moisture | 1 | 0.014 | 0.006 | 2.34 | 0.02 |





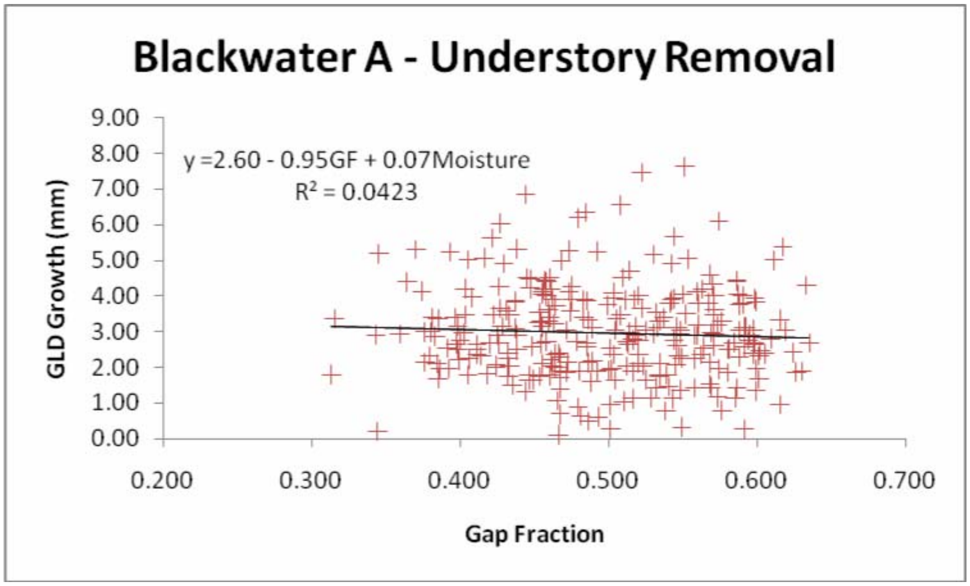
Appendix C.2. First-year multiple linear regression for Blackwater A control seedlings.

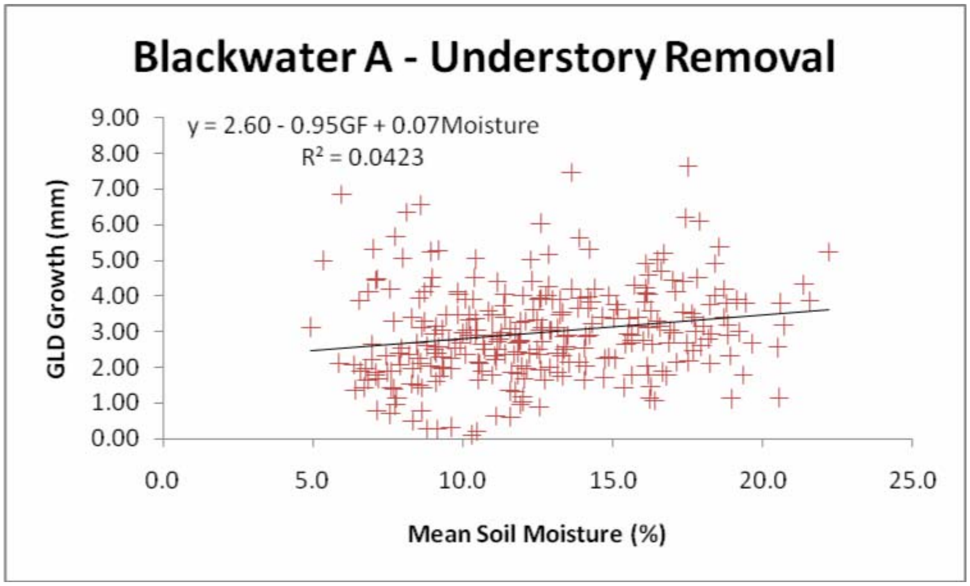
Appendix C.3. First-year multiple linear regression model for square-root transformed Blackwater A understory removal seedlings.

| Analysis of Variance | | | | | |
|---|---|---|---|---|---|
| Source | DF | Sum of Squares | Mean Square | F Value | Pr > F |
| Model | 2 | 2.27 | 1.13 | 7.53 | 0.0007 |
| Error | 280 | 42.2 | 0.15 | | |
| Corrected Total | 282 | 44.47 | | | |

| | | | |
|---|---|---|---|
| Root MSE | 0.39 | R-Square | 0.051 |
| Dependent Mean | 1.68 | Adj R-Sq | 0.044 |
| Coeff Var | 23.12 | | |

| Variable | DF | Parameter Estimate | Standard Error | t Value | Pr > \|t\| |
|---|---|---|---|---|---|
| Intercept | 1 | 1.53 | 0.18 | 8.51 | <0.0001 |
| Gap Fraction | 1 | -0.28 | 0.325 | -0.88 | 0.382 |
| Mean Moisture | 1 | 0.02 | 0.006 | 3.78 | 0.0002 |





Appendix C.4. First-year multiple linear regression for Blackwater A understory removal seedlings.

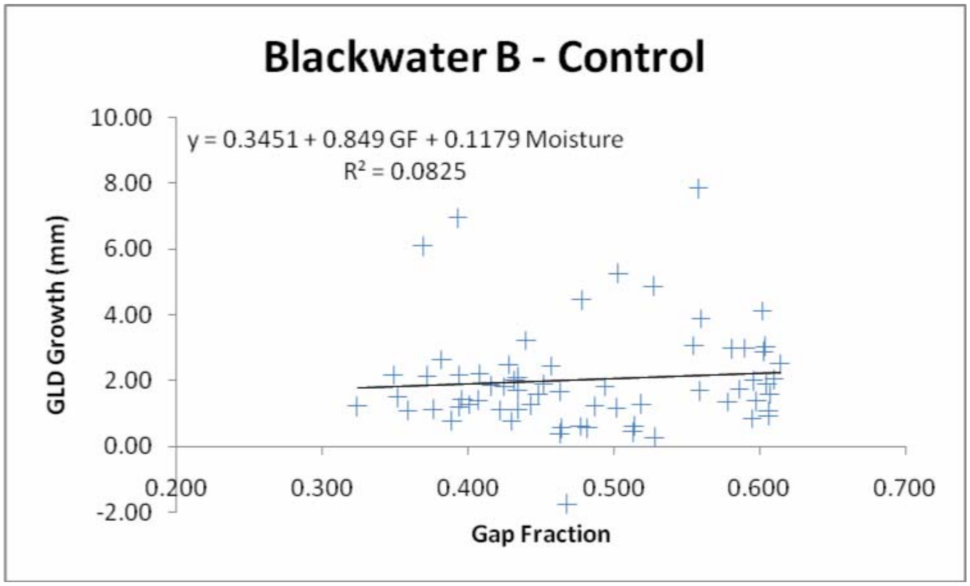
Appendix C.5. First-year multiple linear regression for Blackwater B control seedlings. Normality was assumed under the Central Limit Theorem.

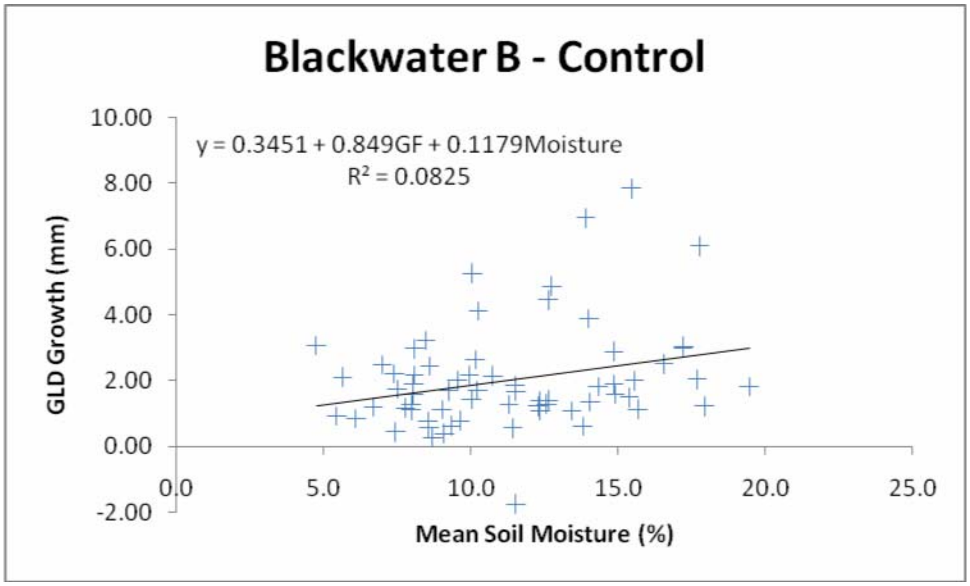
Analysis of Variance

| Source | DF | Sum of Squares | Mean Square | F Value | Pr > F |
|---|---|---|---|---|---|
| Model | 2 | 12.18 | 6.09 | 2.79 | 0.07 |
| Error | 62 | 135.37 | 2.18 | | |
| Corrected Total | 64 | 147.55 | | | |

| | | | |
|---|---|---|---|
| Root MSE | 1.48 | R-Square | 0.083 |
| Dependent Mean | 2.08 | Adj R-Sq | 0.053 |
| Coeff Var | 70.97 | | |

| Variable | DF | Parameter Estimate | Standard Error | t Value | Pr > \|t\| |
|---|---|---|---|---|---|
| Intercept | 1 | 0.35 | 1.158 | 0.3 | 0.77 |
| Gap Fraction | 1 | 0.85 | 2.189 | 0.39 | 0.7 |
| Mean Moisture | 1 | 0.12 | 0.052 | 2.26 | 0.027 |





Appendix C.6. First-year multiple linear regression for Blackwater B control seedlings.

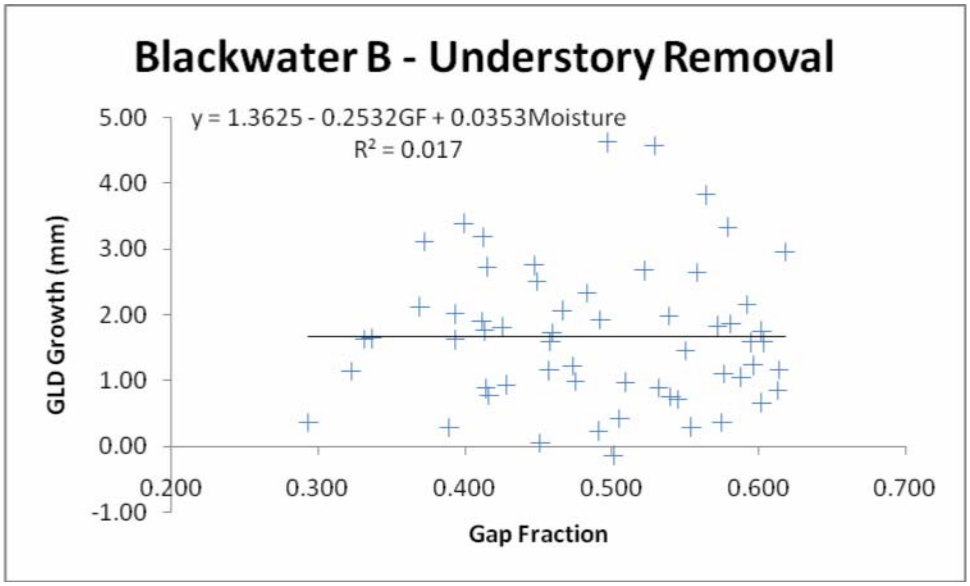
Appendix C.7. First-year multiple linear regression model for square-root(1+y)-transformed Blackwater B understory removal seedlings.

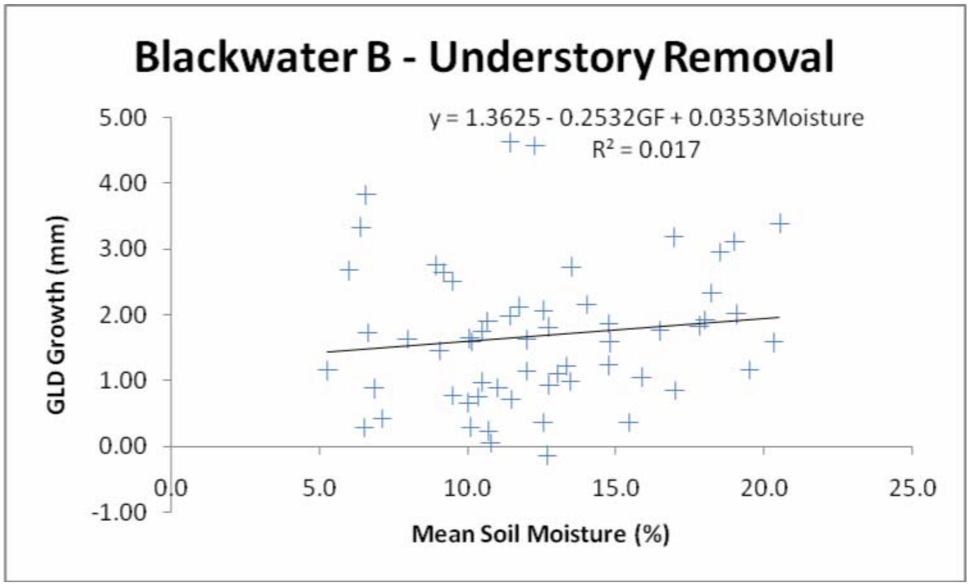
Analysis of Variance

| Source | DF | Sum of Squares | Mean Square | F Value | Pr > F |
|---|---|---|---|---|---|
| Model | 2 | 0.13 | 0.07 | 0.64 | 0.53 |
| Error | 56 | 5.85 | 0.1 | | |
| Corrected Total | 58 | 5.98 | | | |

| | | | |
|---|---|---|---|
| Root MSE | 0.32 | R-Square | 0.022 |
| Dependent Mean | 1.6 | Adj R-Sq | -0.013 |
| Coeff Var | 20.15 | | |

| Variable | DF | Parameter Estimate | Standard Error | t Value | Pr > \|t\| |
|---|---|---|---|---|---|
| Intercept | 1 | 1.5 | 0.264 | 5.68 | <0.0001 |
| Gap Fraction | 1 | -0.097 | 0.05 | -0.19 | 0.85 |
| Mean Moisture | 1 | 0.012 | 0.011 | 1.13 | 0.26 |





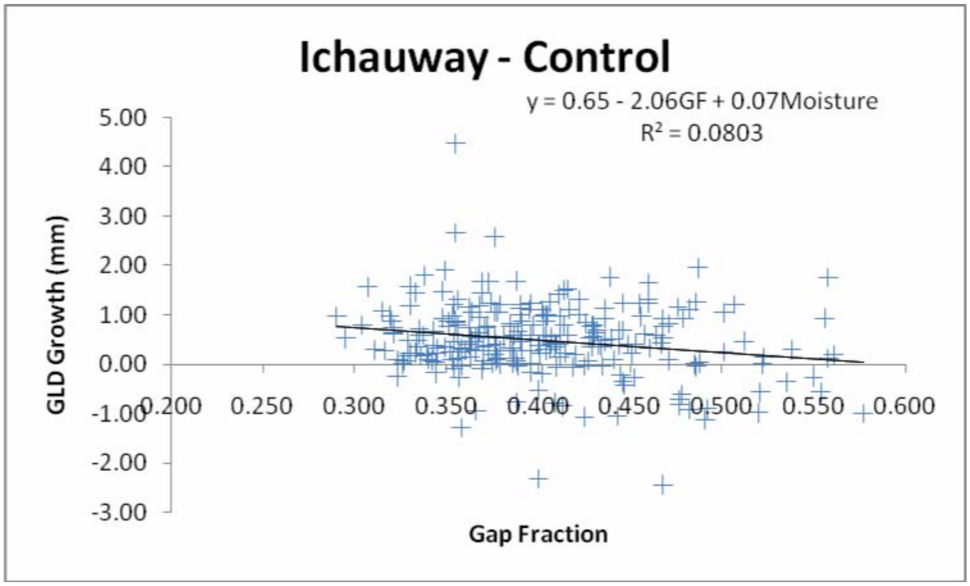
Appendix C.8. First-year multiple linear regression for Blackwater B understory removal seedlings.

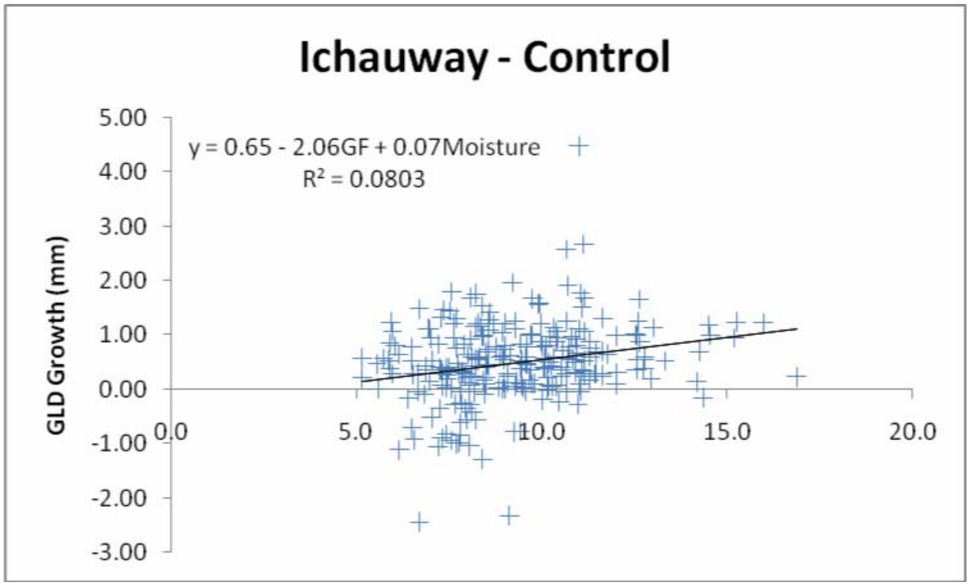
Appendix C.9. First-year multiple linear regression model for Ichauway control seedlings. Normality was assumed under the Central Limit Theorem.

| Analysis of Variance | | | | | |
|---|---|---|---|---|---|
| Source | DF | Sum of Squares | Mean Square | F Value | Pr > F |
| Model | 2 | 10.75 | 5.38 | 10.69 | <0.0001 |
| Error | 245 | 123.16 | 0.5 | | |
| Corrected Total | 247 | 133.91 | | | |

| | | | |
|---|---|---|---|
| Root MSE | 0.71 | R-Square | 0.08 |
| Dependent Mean | 0.49 | Adj R-Sq | 0.073 |
| Coeff Var | 144.36 | | |

| Variable | DF | Parameter Estimate | Standard Error | t Value | Pr > \|t\| |
|---|---|---|---|---|---|
| Intercept | 1 | 0.65 | 0.407 | 1.6 | 0.11 |
| Gap Fraction | 1 | -2.06 | 0.79 | -2.61 | 0.01 |
| Mean Moisture | 1 | 0.07 | 0.022 | 3.31 | 0.001 |





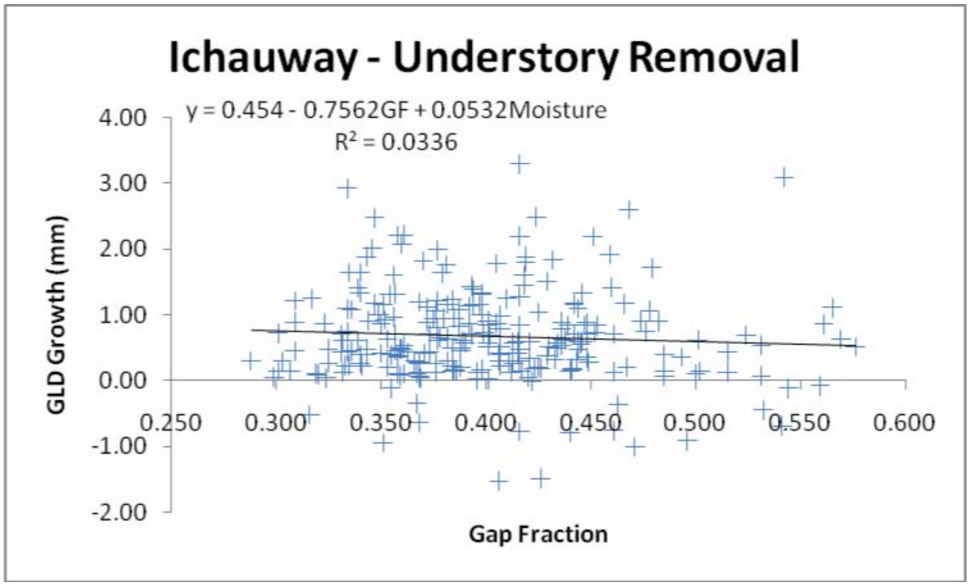
Appendix C.10. First-year multiple linear regression for Ichauway control seedlings.

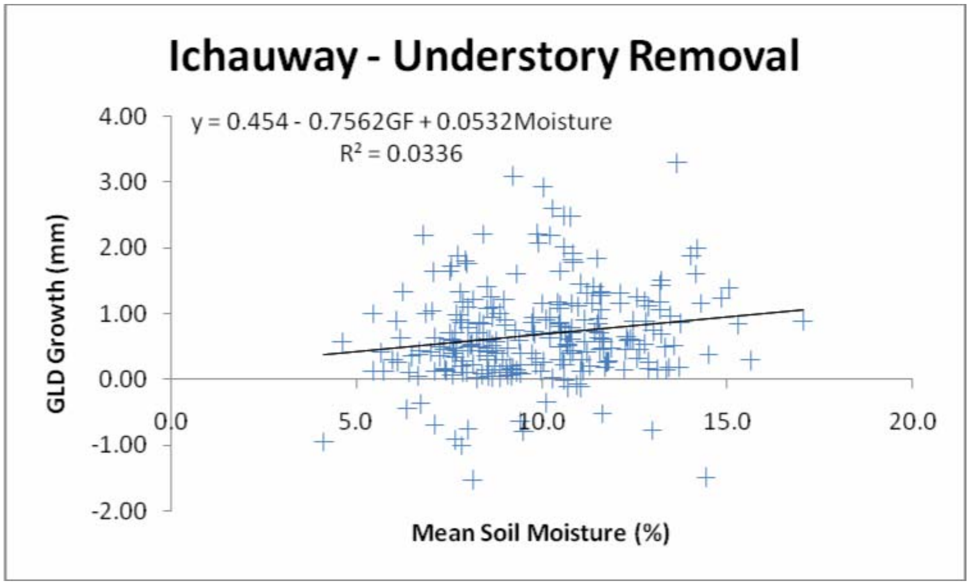
Appendix C.11. First year multiple linear regression model for Ichauway understory removal seedlings. Normality was assumed under the Central Limit Theorem.

| Analysis of Variance | | | | | |
|---|---|---|---|---|---|
| Source | DF | Sum of Squares | Mean Square | F Value | Pr > F |
| Model | 2 | 4.24 | 2.12 | 4.33 | 0.014 |
| Error | 249 | 121.73 | 0.49 | | |
| Corrected Total | 251 | 125.97 | | | |

| | | | |
|---|---|---|---|
| Root MSE | 0.7 | R-Square | 0.034 |
| Dependent Mean | 0.68 | Adj R-Sq | 0.026 |
| Coeff Var | 103.43 | | |

| Variable | DF | Parameter Estimate | Standard Error | t Value | Pr > \|t\| |
|---|---|---|---|---|---|
| Intercept | 1 | 0.45 | 0.368 | 1.23 | 0.22 |
| Gap Fraction | 1 | -0.76 | 0.769 | -0.98 | 0.33 |
| Mean Moisture | 1 | 0.05 | 0.019 | 2.76 | 0.006 |





Appendix C.12. First-year multiple linear regression for Ichauway understory removal seedlings.

# APPENDIX D

# REGRESSION MODELS FOR LONGLEAF PINE SEEDLING GROWTH AFTER TWO GROWING SEASONS

Appendix D.1. Multiple linear regression model for Blackwater A control seedlings.

| Analysis of Variance | | | | | |
|---|---|---|---|---|---|
| Source | DF | Sum of Squares | Mean Square | F Value | Pr > F |
| Model | 2 | 8.68 | 4.34 | 1.72 | 0.18 |
| Error | 279 | 705.84 | 2.53 | | |
| Corrected Total | 281 | 714.52 | | | |

| | | | |
|---|---|---|---|
| Root MSE | 1.59 | R-Square | 0.0121 |
| Dependent Mean | 4.39 | Adj R-Sq | 0.0051 |
| Coeff Var | 36.21 | | |

| Variable | DF | Parameter Estimate | Standard Error | t Value | Pr > \|t\| |
|---|---|---|---|---|---|
| Intercept | 1 | 3.23 | 0.7 | 4.59 | <0.0001 |
| Gap Fraction | 1 | 2.3 | 1.24 | 1.85 | 0.065 |
| Mean Moisture | 1 | 0.002 | 0.03 | 0.06 | 0.95 |

Appendix D.2. Multiple linear regression model for square-root-transformed Blackwater A understory removal seedlings.

Analysis of Variance

| Source | DF | Sum of Squares | Mean Square | F Value | Pr > F |
|---|---|---|---|---|---|
| Model | 2 | 0.7 | 0.35 | 2.29 | 0.1 |
| Error | 260 | 39.9 | 0.15 | | |
| Corrected Total | 262 | 40.6 | | | |

| | | | |
|---|---|---|---|
| Root MSE | 0.39 | R-Square | 0.0173 |
| Dependent Mean | 2.06 | Adj R-Sq | 0.0097 |
| Coeff Var | 19.03 | | |

| Variable | DF | Parameter Estimate | Standard Error | t Value | Pr > \|t\| |
|---|---|---|---|---|---|
| Intercept | 1 | 1.74 | 0.187 | 9.3 | <0.0001 |
| Gap Fraction | 1 | 0.36 | 0.338 | 1.03 | 0.29 |
| Mean Moisture | 1 | 0.013 | 0.007 | 1.87 | 0.063 |

Appendix D.3. Multiple linear regression model for square-root-transformed Blackwater B control seedlings.

| Analysis of Variance | | | | | |
|---|---|---|---|---|---|
| Source | DF | Sum of Squares | Mean Square | F Value | Pr > F |
| Model | 2 | 0.29 | 0.14 | 1.39 | 0.25 |
| Error | 49 | 5.03 | 0.1 | | |
| Corrected Total | 51 | 5.31 | | | |

| | | | |
|---|---|---|---|
| Root MSE | 0.32 | R-Square | 0.054 |
| Dependent Mean | 1.63 | Adj R-Sq | 0.015 |
| Coeff Var | 19.66 | | |

| Variable | DF | Parameter Estimate | Standard Error | t Value | Pr > \|t\| |
|---|---|---|---|---|---|
| Intercept | 1 | 1.22 | 0.297 | 4.37 | <0.0001 |
| Gap Fraction | 1 | 0.89 | 0.535 | 1.67 | 0.1 |
| Mean Moisture | 1 | -0.002 | 0.014 | -0.14 | 0.89 |

Appendix D.4. Multiple linear regression model for Blackwater B understory removal seedlings.

| Analysis of Variance | | | | | |
|---|---|---|---|---|---|
| Source | DF | Sum of Squares | Mean Square | F Value | Pr > F |
| Model | 2 | 2.31 | 1.16 | 0.72 | 0.49 |
| Error | 43 | 69.49 | 1.62 | | |
| Corrected Total | 45 | 71.8 | | | |

| | | | |
|---|---|---|---|
| Root MSE | 1.27 | R-Square | 0.032 |
| Dependent Mean | 2.73 | Adj R-Sq | -0.013 |
| Coeff Var | 46.5 | | |

| Variable | DF | Parameter Estimate | Standard Error | t Value | Pr > \|t\| |
|---|---|---|---|---|---|
| Intercept | 1 | 1.45 | 1.178 | 1.23 | 0.23 |
| Gap Fraction | 1 | 2.81 | 2.363 | 1.19 | 0.24 |
| Mean Moisture | 1 | -0.008 | 0.053 | -0.16 | 0.88 |

Appendix D.5. Multiple linear regression model for Ichauway control seedlings transformed with square-root(1+y).

| Analysis of Variance | | | | | |
|---|---|---|---|---|---|
| Source | DF | Sum of Squares | Mean Square | F Value | Pr > F |
| Model | 2 | 0.95 | 0.48 | 4.21 | 0.016 |
| Error | 202 | 22.86 | 0.11 | | |
| Corrected Total | 204 | 23.81 | | | |

| | | | |
|---|---|---|---|
| Root MSE | 0.34 | R-Square | 0.04 |
| Dependent Mean | 1.69 | Adj R-Sq | 0.03 |
| Coeff Var | 19.87 | | |

| Variable | DF | Parameter Estimate | Standard Error | t Value | Pr > \|t\| |
|---|---|---|---|---|---|
| Intercept | 1 | 1.1 | 0.213 | 5.18 | <0.0001 |
| Gap Fraction | 1 | 1.13 | 0.415 | 2.73 | 0.007 |
| Mean Moisture | 1 | 0.017 | 0.149 | 1.15 | 0.25 |

Appendix D.6. Multiple linear regression model for Ichauway understory removal seedlings transformed with square-root(1+y).

| Analysis of Variance | | | | | |
|---|---|---|---|---|---|
| Source | DF | Sum of Squares | Mean Square | F Value | Pr > F |
| Model | 2 | 3.64 | 1.82 | 13.07 | <0.0001 |
| Error | 217 | 30.22 | 0.14 | | |
| Corrected Total | 219 | 33.86 | | | |

| | | | |
|---|---|---|---|
| Root MSE | 0.37 | R-Square | 0.108 |
| Dependent Mean | 1.79 | Adj R-Sq | 0.099 |
| Coeff Var | 20.84 | | |

| Variable | DF | Parameter Estimate | Standard Error | t Value | Pr > \|t\| |
|---|---|---|---|---|---|
| Intercept | 1 | 0.72 | 0.221 | 3.26 | 0.001 |
| Gap Fraction | 1 | 2.24 | 0.454 | 4.93 | <0.0001 |
| Mean Moisture | 1 | 0.02 | 0.014 | 1.5 | 0.134 |

# APPENDIX E

## SAMPLE CALCULATION OF PREDICTED ROOTING DEPTH USING ROOT TAPER EQUATION

The following is a sample calculation of predicted rooting depth using the taper equation developed using root diameter/depth data collected from root excavations in each planting group. Data from an example seedling are given in Table E.1.

Table E.1. Root excavation data from seedling 981. Lengths are in cm; diameters are in mm.

| Group | Seedling | RCD | d | L | D | LL |
|---|---|---|---|---|---|---|
| Blackwater | 981 | 12.65 | 5.59 | 10 | 1.19 | 84.46 |
| Blackwater | 981 | 12.65 | 2.42 | 20 | 1.19 | 84.46 |
| Blackwater | 981 | 12.65 | 2.2 | 30 | 1.19 | 84.46 |
| Blackwater | 981 | 12.65 | 1.87 | 40 | 1.19 | 84.46 |
| Blackwater | 981 | 12.65 | 1.64 | 50 | 1.19 | 84.46 |
| Blackwater | 981 | 12.65 | 1.64 | 60 | 1.19 | 84.46 |
| Blackwater | 981 | 12.65 | 1.64 | 70 | 1.19 | 84.46 |
| Blackwater | 981 | 12.65 | 1.43 | 80 | 1.19 | 84.46 |

L = root length to d
d = root diameter at L
LL = Root length at end of measurements
D = root diameter at LL
RCD = root collar diameter at length 0

Results of applying the root taper equation

$$y = e^{(4.7422x)},$$

where

$$y = \frac{L}{LL}$$

$$x = \frac{(D - d)}{(RCD - d)}$$

are given in Table E.2.

Table E.2. Results from root taper equation giving ratio of L:LL and predicted rooting depth in cm at root diameter of 1 mm.

| Group | Seedling | y = L/LL | x = $\frac{(D-d)}{(RCD-d)}$ | x (d=1.0) | y (d=1.0) | Predicted Length (cm) |
|---|---|---|---|---|---|---|
| Blackwater | 981 | 0.1184 | -0.62323 | 0.016309 | 1.08041 | 91.25143 |
| Blackwater | 981 | 0.2368 | -0.12023 | 0.016309 | 1.08041 | 91.25143 |
| Blackwater | 981 | 0.3552 | -0.09665 | 0.016309 | 1.08041 | 91.25143 |
| Blackwater | 981 | 0.4736 | -0.06308 | 0.016309 | 1.08041 | 91.25143 |
| Blackwater | 981 | 0.592 | -0.04087 | 0.016309 | 1.08041 | 91.25143 |
| Blackwater | 981 | 0.7104 | -0.04087 | 0.016309 | 1.08041 | 91.25143 |
| Blackwater | 981 | 0.8288 | -0.04087 | 0.016309 | 1.08041 | 91.25143 |
| Blackwater | 981 | 0.9472 | -0.02139 | 0.016309 | 1.08041 | 91.25143 |