INFLUENCE OF LIGHT AND MOISTURE ON LONGLEAF PINE SEEDLING GROWTH IN SELECTION SILVICULTURE

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ABSTRACT

Selection silviculture has become increasingly common for longleaf pine management, yet questions remain regarding residual canopy effects on seedling survival and growth. To determine what levels of residual overstory promote adequate seedling recruitment, 600 containerized longleaf pine seedlings were planted on two sites during the 2007-2008 dormant season. To differentiate overstory from understory influences, half of the seedlings were randomly selected for understory removal (with herbicide). Canopy gap fraction was determined using hemispherical photography and average soil moisture was determined from four time domain reflectometer (TDR) measurements during the 2008 and 2009 growing seasons. Seedling groundline diameter (GLD) was measured at planting and in August, 2008 and 2009. First-year results showed weakly positive relationships between soil moisture and seedling growth, whereas generally negative but statistically non-significant relationships existed between gap fraction and seedling growth. Second-year results showed few significant relationships, but generally positive trends between gap fraction and GLD growth. No general trend was present between soil moisture and GLD growth. Data collected during this study support previous research suggesting that initial longleaf pine survival and growth are limited by moisture availability, but following establishment, light becomes the primary driver of longleaf pine seedling growth.

INTRODUCTION

Longleaf pine (*Pinus palustris* Mill.) forests and woodlands of the Southeastern Coastal Plain have declined by more than 98 percent from their previous 28-36 million hectares (Means and Grow 1985, Noss 1988, 1989, Goetz 1998, Ware and others 1993, Mitchell and others 2000). Interest in restoring and managing longleaf pine ecosystems has steadily increased during the past four decades and especially in recent years (Brockway and others 2005), with restoration a high conservation priority (Kirkman and others 2004). 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.

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 silvicultural 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. Specific research has addressed the use of selection silviculture in longleaf pine forests and has found that both group selection and single-tree selection are practicable (Mitchell and others 2006). Still, selection silviculture represents a trade-off, because a spatially and temporally continuous overstory suppresses seedling growth by outcompeting seedlings for available growing space.

Previous studies have addressed competitive effects of residual overstory on longleaf pine seedlings on various sites and site types. These studies investigated growth of planted and natural seedlings in natural and artificial canopy gaps as well as underneath the forest matrix. Brockway and Outcalt (1998) found that natural-seedling aggregations in the center of canopy gaps on a xeric sandhill site were largely a result of competition for moisture and other soil resources. Therefore, they suggested that gap-based regeneration techniques should be included in uneven-aged management systems. Similarly, studies on mesic sites also have shown that growing season soil moisture availability can limit radial growth of artificial and natural reproduction (Rodriguez-Trejo and others 2003, Pederson and others 2008).

Contrary to studies from xeric sites, some experiments on mesic sites have shown that competition for light may be a more limiting factor in longleaf pine seedling growth and eventual recruitment than competition for moisture and nutrients. For example, studies from southwest Georgia have shown seedling growth to decrease as overstory stocking

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increases (Palik and others 1997, McGuire and others 2001, Pecot and others 2007). Furthermore, the overstory has been shown to actually facilitate seedling survival over the short term in some instances (Pecot and others 2007). Management recommendations resulting from these studies have focused on localized disturbances, particularly single-tree selection, since that approach allows for precise regulation of overstory density and thus understory light availability. Given these mixed results, site appears to be an important factor in the competitive relationships affecting longleaf pine seedling growth and recruitment, and as a result the appropriate selection systems may differ with site.

Prior studies have all examined only one site type per study. Additionally, methodologies have varied among studies and site types. To address those gaps in the literature, the objective of this study was to determine what levels of overstory retention in selection silviculture best promote longleaf pine seedling growth and recruitment by examining growth of longleaf pine seedlings planted within mature longleaf pine stands on both a subxeric and a mesic site.

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 and others 2005) and experience a warm, subtropical climate with a mean annual temperature of 19 °C. Annual rainfall at Blackwater averages 1650 mm, with 45 percent occurring between June and September; Ichauway receives mean annual rainfall of 1320 mm evenly distributed throughout the year. Troup loamy sand was the primary soil series at Blackwater, whereas the Ichauway site was located on Wagram soils. Both sites contain 75-95 year old second-growth longleaf pines in the overstory and species-rich native groundcover dominated by wiregrass (*Aristida beyrichiana* Trin. & Rupr.). Management activities at both sites have included prescribed burning targeted on one to three year return intervals and periodic timber harvests. During this study, the Ichauway site was burned by prescription in March of 2008.

EXPERIMENTAL DESIGN AND SAMPLING

Six hundred containerized longleaf pine seedlings were planted at Blackwater in December, 2007, and at Ichauway in February, 2008. Seedlings were grown at Meeks Tree Farm in Kite, Georgia, in 108 mL containers at a density of 530 seedlings m^{-2}. To standardize planting date, 120 additional seedlings were planted at Blackwater the week following the planting at Ichauway. Seedlings at both sites were planted in twelve arrays of 50 seedlings, with arrays arbitrarily located to provide an adequate range of canopy densities resulting from different uneven-aged silvicultural systems. Seedlings in each array were arranged in 5 rows of 10 trees on a 5-by-5 meter grid. The second planting at Blackwater was arranged as a sixth row of seedlings at each existing seedling array and was treated and sampled identically thereafter. 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 percent glyphosate) following the label instructions (5 percent 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. At Ichauway, fuels were raked away from seedlings prior to the prescribed fire to protect them from open flames.

All measurements were conducted at each seedling. Canopy gap fraction was determined from hemispherical photographs taken 1.4 m above the ground between May and August (so the canopy had reached its maximum cover) when the solar disk was completely obscured. Obscured-disk conditions result in canopy gap fraction estimates falling on an approximately 1:1 line with actual percent photosynthetic photon flux density in longleaf pine forests (Battaglia and others 2003). Volumetric soil moisture content for the top 30 cm of soil at each seedling was recorded four times each growing season using time domain reflectometry (TDR). Seedling groundline diameter (GLD) was measured at time of planting and again in August, 2008 and 2009. GLD growth was calculated as the difference between August diameter measurements and initial seedling diameters.

Because the herbicide treatment was applied to randomly-selected seedlings within each seedling array and all measurements were repeated at each seedling, 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 Inc. 2004). 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 both 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.

RESULTS AND DISCUSSION

CANOPY GAP FRACTION

Mean gap fraction was 0.497 at Blackwater and was significantly larger than the mean gap fraction of 0.402 at Ichauway (two-tailed t-test for unequal variance: t= 23.65, p< 0.0001). Figure 1 shows histograms of gap fraction at Blackwater and Ichauway. These histograms document horizontal canopy structure and show that light is more available in the understory on the subxeric site. In contrast, the mesic site has a less-open canopy, resulting in less available understory light. Previous studies have shown that more xeric sites do not necessarily have higher mean canopy gap fraction (Brockway and Outcalt 1998, Sheffield and others 2003). Still, more xeric sites characterized by low soil fertility and common moisture stress tend to support more-open canopies (Myers 1990). Thus, site quality likely is one factor affecting the forest structure at these sites, but is not the only factor.

SURVIVAL

Survivorship figures for 2008 and 2009 are presented in Figure 2. Following one growing season (2008), survivorship was over 90 percent at Blackwater but was less than 80 percent at Ichauway. Survivorship among remaining seedlings during the 2009 growing season was above 90 percent for Ichauway; for Blackwater, survivorship was 76 percent for control seedlings and 84 percent for understory removal. Total survivorship (Figure 2) represents the number of surviving seedlings in 2009 as a percent of the original number of seedlings planted and was similar between the two sites even with the differing annual patterns. At Blackwater, 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 (Figure 2). Seedling survival in this study was not substantially different from figures reported for old-field, cutover, and intact forest sites, which have ranged from 70 to greater than 90 percent (Palik and others 1997, South and others 2005, Jackson and others 2010). Furthermore, previous studies at Ichauway have documented similar survival rates for containerized seedlings (McGuire and others 2001, Pecot and others 2007).

SEEDLING GROUNDLINE DIAMETER

To maintain valid comparisons, results reported below are those for Ichauway and the second Blackwater planting, which have comparable planting dates. Mean initial seedling GLD for each treatment at both sites was significantly greater than the 6.35 mm minimum suggested by Barnett and others (2002) and Dumroese and others (2009) (one-tailed t-tests: t= 18.39 (Blackwater); t= 35.82 (Ichauway); p< 0.0001). At Ichauway, 3 seedlings were smaller than the recommended 4.75 mm "cull" threshold. There were no significant differences in initial seedling diameters, and means for both treatments at both sites were greater than 8 mm. Although seedling diameter is not the only factor in seedling quality, it is most important because, with proper seedling handling and planting, it is strongly correlated with seedling survival and growth after outplanting (South and others 2005, Jackson and others 2007).

After two growing seasons, two-way ANOVA showed that control seedlings at Ichauway grew significantly less than all Blackwater seedlings (F= 6.86, p= 0.0002), but no growth difference existed between Ichauway understory removal seedlings nor any Blackwater seedlings (Figure 3). Examining growth differences by year showed that Blackwater seedlings grew less during the second growing season than in the first, whereas Ichauway seedlings showed increased growth during the second year (Figure 4). In the 2009 growing season, understory removal at Ichauway resulted in mean seedling growth significantly greater than both treatments at Blackwater, whereas no statistically significant growth differences were present between control seedlings at Ichauway and all Blackwater seedlings in 2009 (Figure 4). It is also interesting to note that, even though the Ichauway site is classified as a mesic site, survival and growth were not necessarily greater for this site. As is intuitive, this result shows that weather conditions in the first few years after planting may be more important for survival and growth than rankings of broad site classifications.

First-year seedling survival and growth at Ichauway was negatively affected by prescribed fires during the spring of 2008, shortly after planting. Even though seedlings were protected from the flaming front, most seedlings lost all foliage due to scorch from radiant heat. Jack and others (2010) examined natural-seedling mortality resulting from prescribed fires and found similar survival rates ("low litter" treatment is comparable to what seedlings in the present study experienced). They also point out that mortality was concentrated in the smallest seedlings (<0.2 m tall), in which all seedlings in this study would be classified.

It is worth noting that mean two-year seedling growth measured in this study was minimal compared to some seedlings planted in even-aged systems, yet was not aberrant for underplanted seedlings. For instance, Jackson and others (2010) report seedling diameter growth of up to 10 mm per year in old-field conditions. In contrast, Gagnon and others (2003) planted seedlings in artificial canopy gaps during a multi-year drought and found seedling diameter growth between 1-4 mm per year for the first two growing seasons post-planting. Thus, although weather conditions (especially rainfall) and planting sites do affect seedling growth responses after planting, the suppressive effects of mature overstory trees are clear.

Seedling growth at Ichauway was negatively affected by the forest understory, whereas effects were negligible at Blackwater. Not only did understory removal result in a greater increase in seedling survival at Ichauway, but it also led to significantly greater seedling diameter growth. In contrast, understory removal did not significantly affect seedling growth at Blackwater. These results point to potentially more vigorous understory competition on the mesic site and possibly more growth suppression because of that competition.

GROWTH MODELS

First-year (2008) results did not suggest the existence of clear controls of longleaf pine seedling growth. While a negative trend between seedling growth and gap fraction existed in each case except for that of control seedlings at Blackwater (Table 1), gap fraction was a significant predictor only for control seedlings at Ichauway ($t= -2.61$, $p= 0.01$). In contrast, a positive relationship existed between mean percent soil moisture and seedling growth for all seedlings during the first growing season. This trend was significant for each group except understory removal seedlings at Blackwater. 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. The only significant relationships existed at Ichauway, where there was a highly significant positive relationship between seedling growth and gap fraction for both control ($t= 3.16$, $p= 0.002$) and understory removal ($t= 5.30$, $p< 0.0001$) seedlings. At Blackwater there were positive but non-significant trends between seedling growth and gap fraction for seedlings of both treatments. While soil moisture was no longer a significant predictor at either site, the trend was generally positive. Still, all relationships remained weak, with the largest coefficient of determination only 0.13 (Table 1).

Results of the present study support those of prior research showing that high light exposure is initially a negative factor for longleaf pine seedlings, but that over time increased light availability can result in greater seedling growth (Palik and others 1997, McGuire and others 2001, Gagnon and others 2003, Pecot and others 2007). In effect, relative increases in overstory shade may have been a benefit to seedlings in this study until the seedlings developed root systems capable of procuring dependable soil moisture. At that point, increased light levels tended to positively affect growth. Even though soil moisture was less important to seedling growth during the second growing season of this study, it was possibly due to greater and more regular rainfall. As a result, seedlings may have been less limited by soil moisture, thus reducing the identification of soil moisture-effects on seedling growth.

MANAGEMENT IMPLICATIONS

Results of this study document both positive and negative effects of a mature forest canopy on longleaf pine seedlings. While residual overstory trees typically suppress seedling growth relative to that on clearcut sites, an intact forest overstory appears to provide seedlings some shelter from extreme moisture stress and benefits seedling growth in the short term. As a result, preliminary results from this study give more short-term examples of the effectiveness of multi-aged stand management. The importance of the observed reduction in early seedling growth in multi-aged stands will depend on objectives and may be acceptable for ecological rather than production-oriented management objectives. However, results also show the negative impacts that prescribed fire can have on seedling survival and growth and document the importance of using precise burn prescriptions to achieve specific objectives.

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Table 1—Regression models for seedling GLD growth after the first two growing seasons

	Model	R-square	Pr > F
	2008		
Blackwater			
Understory Removal[1]	y = 1.36 - 0.25GF + 0.04Moisture	0.02	0.53
Control	y = 0.35 + 0.85GF + 0.12Moisture	0.08	0.07
Ichauway			
Understory Removal	y = 0.65 - 2.06GF + 0.07Moisture	0.08	<0.0001
Control	y = 0.45 - 0.76GF + 0.05Moisture	0.03	0.014
	2009		
Blackwater			
Understory Removal	y = 1.45 + 2.81GF - 0.01Moisture	0.03	0.49
Control[2]	y = 1.31 + 3.39GF - 0.02Moisture	0.06	0.25
Ichauway			
Understory Removal[1]	y = -2.25 + 9.87GF + 0.08Moisture	0.13	<0.0001
Control[1]	y = -0.36 + 4.62GF + 0.06Moisture	0.05	0.016

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

[2]Transformed with square-root function

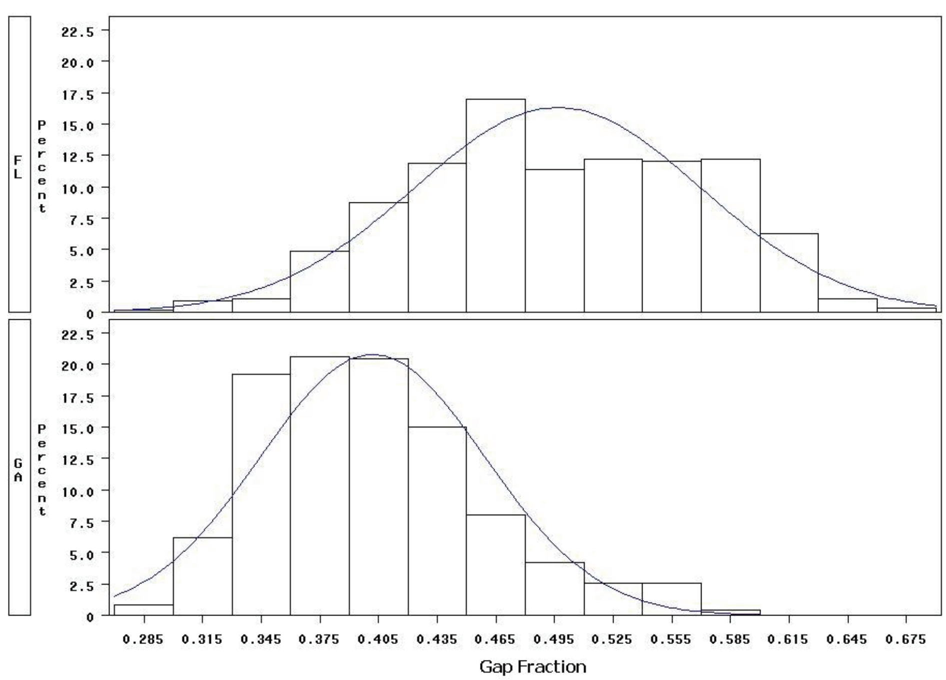

Figure 1—Histogram of gap fraction by site showing Blackwater (top) and Ichauway (bottom). The difference in means is statistically significant.

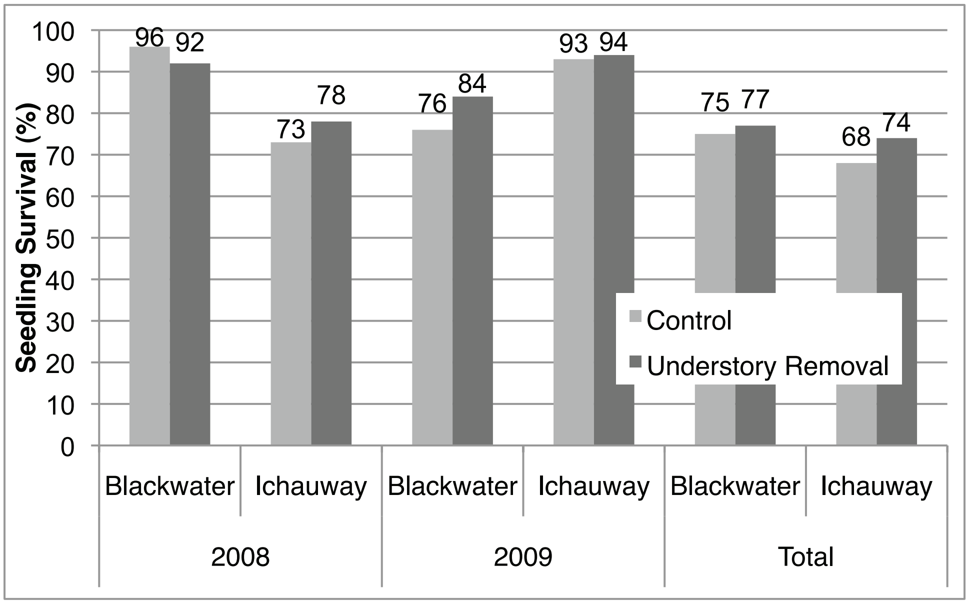

Figure 2—Percent seedling survival by site and year. Figures for 2009 represent percent survival among 2008 survivors. "Total" represents percent survival of original planted seedlings.

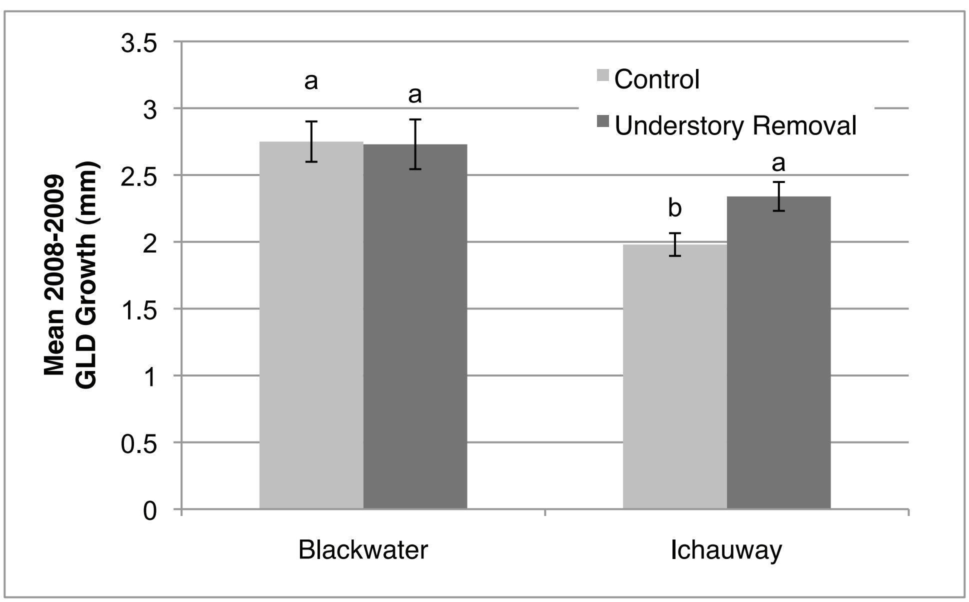

Figure 3—Mean 2008-2009 seedling GLD growth for seedlings planted in February, 2008. Bars with different letters indicate statistical significance.

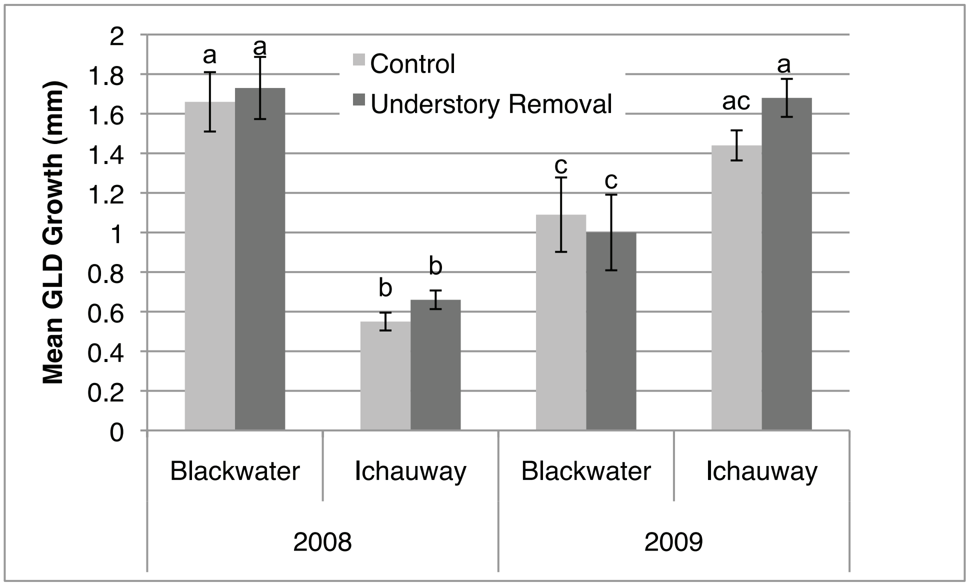

Figure 4—Mean seedling GLD growth by year. Bars with different letters indicate statistical significance.