Fertilization and Irrigation Effect on Botryosphaeriaceae Canker Development in Intensively Managed Sweetgum (*Liquidambar styraciflua*)

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Abstract

The influence of irrigation and fertilization on the response of sweetgum (*Liquidambar styraciflua* L.) to branch inoculation by species in the Botryosphaeriaceae family, *Botryosphaeria dothidea* (Moug.:Fr.) Ces. & De Not and *Lasiodiplodia theobromae* (Pat.) Griffon & Maubl., was tested over summer and winter seasons for 2 years. Sweetgum planted in South Carolina received irrigation, fertilization, fertilization + irrigation, or no amendments April to September each year. Both Botryosphaeriaceae inoculants caused larger cankers compared with the water agar control with the exception of one winter season, in which *L. theobromae* canker development was insignificant. The irrigation and fertilization amendments, on an individual level, did not directly affect canker development of these Botryosphaeriaceae pathogens on sweetgum; however, an interaction did occur between the amendments and season. By the summer of 2004, plots with the amendments had larger trees than plots with no amendments, leading to more crown closure. The resulting shading of inoculated branches in these plots likely contributed to larger cankers.

Introduction

Sweetgum (*Liquidambar styraciflua* L.) is commercially planted in the midcoastal plains of the Southeastern United States, from Virginia to north Florida and east Texas (Kline and Coleman 2010). A common bottomland hardwood, sweetgum grows well on a variety of sites and has relatively few pest problems (Kormanik 1990). Because of these factors and its excellent hardwood quality, the forest industry considers sweetgum to be an excellent candidate for commercial and bioenergy production (Kline and Coleman 2010).

Although sweetgum is a relatively vigorous tree with few pathogen problems, widespread damage to seedlings from stem cankers and dieback associated with species in the Botryosphaeriaceae family have occurred in nurseries and outplantings in the Southeastern United States (Carey et al. 2004, Cashion 1981, Filer and Randall 1978, Garren 1956, Neely 1968). Unfortunately, considerable past confusion regarding species taxonomy in the Botryosphaeriaceae family means the species identification from past studies must be interpreted with caution (Slippers and Wingfield 2007). Fungi isolated from cankers on sweetgum were previously identified as *Diplodia theobromae* (Pat.) Now. (Garren 1956), *Botryosphaeria ribis* Grossenbacher & Dugar, and/or *B. dothidea* (Moug.:Fr.) Ces. & De Not (Carey et al. 2004, Cashion 1981, Filer and Randall 1978, Neely 1968). *D. theobromae*, identified in 1956 by Garren as associated with sweetgum dieback, would likely be identified today as *Lasiodiplodia theobromae* (Pat.) Griffon & Maubl. (Alves et al. 2008, Goos et al. 1961). The more recent use of DNA-based molecular techniques has proven that *B. ribis* and *B. dothidea* are separate species (Smith and Stanosz 2001). The identification of *B. ribis* as the cause of cankers on sweetgum in older studies is likely accurate given that the anamorph of *B. ribis* is morphologically different than *B. dothidea*, and the authors clearly did not accept earlier attempts to synonymize these species (Slippers et al. 2004, Smith and Stanosz 2001).

In the late 1990s, Botryosphaeria canker occurred on sweetgum seedlings with extensive dieback in nurseries and outplantings near Summerville, SC (Carey et al. 2004). Isolates of *B. dothidea* from sweetgum seedlings in a Summerville, SC nursery (Collector: K. Britton) were included in the molecular and morphological differentiation of *B. dothidea* (Smith and Stanosz 2001). In 2002, predominately *B. dothidea*, and occasionally *Lasiodiplodia theobromae* (Pat.) Griffon & Maubl., were isolated from cankers on dying sweetgum seedlings at an outplanting in Olar, SC (Britton 2002). Cankers and dieback caused by *B. dothidea* and *L. theobromae* are some of the most commonly reported disease problems of woody plant species worldwide (Jurc et al. 2006, Sinclair and Lyon 2005, Slippers et al. 2004, Slippers and Wingfield 2007, Smith et al. 1996, Taylor et al. 2005). *B. dothidea* and L. theobromae are ubiquitous fungi and typically operate as endophytes and opportunistic pathogens of weakened trees (Sinclair and Lyon 2005, Slippers and Wingfield 2007). Stress factors that increase susceptibility of tree hosts to these, and other species in Botryosphaeriaceae, include other pathogens (Maloney et al. 2004), drought, freezes, defoliation (Crist and Schoeneweiss 1975, Wene and Schoeneweiss 1980), competition, and physical damage (Slippers and Wingfield 2007). Of these stress factors, drought is the most cited factor associated with Botryosphaeriaceae disease expression (Desprez-Loustau et al. 2006, Slippers and Wingfield 2007). Many studies have shown drought stress increases host susceptibility of various tree species to both *B. dothidea* (Crist and Schoeneweiss 1975, Ma et al. 2001, McPartland and Schoeneweiss 1984, Pusey 1989) and *L. theobromae* (Lewis and Van Arsdel 1978, Mullen et al. 1991).

Studies on the effects of nutrients on disease development by species in the Botryosphaeriaceae family are limited. One study utilizing young sweetgum, by Garren (1956), found a low-nutrient environment predisposed seedlings to leader dieback after inoculation with *L. theobromae* (=*D. theobromae*). In another study, a boron deficit was related to an increase in *B. ribes* in eucalyptus (*Eucalyptus citriodora* Hook.; Silveira et al. 1998). Increasing tree vigor by reducing nutrient and drought deficits may reduce the effects of Botryosphaeriaceae-related diseases (Brown and Britton 1986). In contrast, high levels of fertilizer and foliar nitrogen have been associated with increased disease development by *Diplodia pinea* (Desm.) Kickx. (Blodgett et al. 2005, Stanosz et al. 2004) and *B. dothidea* (Wilber and Williamson 2008). No studies have reported on the impact of standard fertilization on canker development from Botryosphaeriaceae fungi in sweetgum plantations.

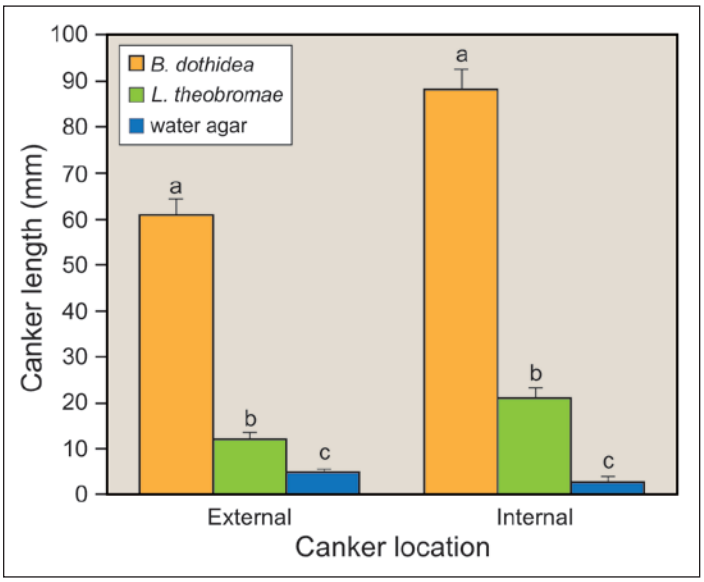

Figure 1. Mean branch canker lengths from *Botryosphaeria dothidea*, *Lasiodiplodia theobromae*, or water agar control inoculations on intensively managed sweetgum (*Liquidambar styraciflua* L.) from November 2002 to 2004. Means of canker length (exterior or interior) sharing a letter are not significantly different at a = 0.05 (Tukey-Kramer test).

Figure 2. Example of cankers on sweetgum (*Liquidambar styraciflua* L.) 6 months after inoculation with (a) *Botryosphaeria dothidea* and (b) *Lasiodiplodia theobromae*. (Photo by Michelle Cram, April 2003).

The primary objective of this study was to measure the response of young sweetgum saplings to inoculation by Botryosphaeriaceae species, *B. dothidea* and *L. theobromae*, under different irrigation and fertilizer amendments used in intensively managed forest plantations. The study also compared winter and summer inoculation to test for potential seasonal effects.

Materials and Methods

Study Site

The study was conducted at the U.S. Department of Energy's Savannah River Site, a National Environmental Research Park near Aiken, SC (33° 23' N, 81° 40' W). A detailed description of the plant material, silvicultural treatments, and experimental design can be found in Coleman et al. (2004) and Coyle et al. (2008). Prior to logging in 1999, vegetation included 14-year-old, pulp-quality loblolly pine (*Pinus taeda* L.) and 38-year-old pole-timber quality longleaf pine (*Pinus palustris* Miller), with an oak (*Quercus* sp.) understory. Following logging, all soil and debris were homogenized to a depth of 30 cm (11.8 in). Temperature and rainfall were recorded continuously during the study period by a weather station (Campbell Scientific, Inc., Logan, UT) installed in a cleared area 50 m (164 ft) west of the site. Total rainfall was 467, 829, 231, and 715 mm (18.4, 32.6, 9.1, and 28.2 in), respectively, for the winter 2002, summer 2003, winter 2003, and summer 2004 seasons. Average air temperatures for the corresponding time periods were 8.7, 21.1, 9.3, and 22.1 °C (47.7, 70.0, 48.7, and 71.8 °F).

Silvicultural Treatments

In spring 2000, open pollinated 1-0 sweetgum seedlings (Westvaco Inc., Summerville, SC) were planted in a randomized complete block design on 0.22-ha (0.54-ac) plots containing 14 rows of 21 trees (294 trees total) planted at 2.5 by 3.0 m (8.2 by 9.8 ft) spacing. Silvicultural amendment treatments were replicated in three blocks and consisted of control, fertilization, irrigation, and fertilization + irrigation. Irrigated treatments received 5.0 mm (0.2 in) water d^{-1} via an automated drip irrigation system. Liquid fertilizer was applied in 26 weekly applications, from the first of April through the end of September each year, via the drip irrigation system to fertilizer and fertilizer + irrigation treatments at 40, 40, 80, 80, and 120 kg N ha^{-1} yr^{-1} (36, 36, 71, 71, and 107 lb N ac^{-1} yr^{-1}) in 2000, 2001, 2002, 2003, and 2004, respectively. The increase of fertilizer corresponded with the increasing nutritional demand of growing trees. All plots except controls received 5.0 mm (0.2 in) water wk^{-1}, which was required to flush the drip irrigation lines. Weed control was applied equally to all plots and included an oxyflourfen (Goal® 2XL, Rohm and Haas Co., Philadelphia, PA) application prior to bud break, and glyphosate (Roundup® Pro, Monsanto Corp., St. Louis, MO) applications as needed throughout the growing season. All pesticides were applied according to label directions.

Inoculation Treatments

Botryosphaeriaceae cultures were obtained from infected sweetgum on a plantation in Olar, SC (33° 17' N, 81° 15' W) in 2002 and stored on silica gel at 20 °C (68 °F). *B. dothidea* was identified by comparing the isolate with type culture *B. dothidea* 97-23 (Smith and Stanosz 2001). The *L. theobromae* isolate, originally identified as its telemorph *Botryosphaeria rhodina* (Cooke) Arx, was verified by internal transcribed spacer sequence with the assistance of Thomas Harrington (Iowa State University, Ames, IA).

The study was conducted over four seasons: the winters of 2002 and 2003 (November to April) and the summers of 2003 and 2004 (April to November). Different subplots of trees within treatment plots were used each season. Inoculum was prepared in the laboratory by placing *B. dothidea* and *L. theobromae* isolates on fresh potato broth dextrose agar with 1 percent lactic acid. For each season, 10 sweetgum trees per silviculture treatment (4) and block (3) were systematically selected for inoculation. Each tree received all three inoculum treatments: *B. dothidea*, *L. theobromae*, and water agar control. Inoculum treatments were randomly applied on the right, center, or left branches of the south side of each tree within 1.0 to 2.0 m (3.3 to 6.6 ft) of the ground. Branches were inoculated by removing a small (3.0 to 5.0 mm [0.1 to 0.2 in] diameter) short side shoot with a sterile razor and placing a 5.0 mm (0.2 in) plug of inoculum or water agar flush on the cut branch surface. The wound was then wrapped with Parafilm®. During the study, 480 sweetgum trees were inoculated.

Measurements

For each season, branches were clipped 26 weeks after inoculation from the inoculation point to approximately 20 to 30 cm (8 to 12 in) above the treatment area, placed in plastic bags at 4.0 °C (39.2 °F), and transported to the U.S. Department of Agriculture (USDA), Forest Service Laboratory in Athens, GA. External and internal canker length was measured on all branch samples within 48 hours. Necrotic or dead tissue that developed from the inoculation was measured along the length of the branch for the external canker. The branches were then cut in half lengthwise with a flame-sterilized knife, and any internal necrotic tissue that developed from the inoculation was measured along the length of the branch for the internal canker.

Data Analysis

Canker length data were log(x + 1) transformed prior to analysis to improve normality and homogeneity of variance. Transformed data were analyzed using PROC MIXED on a split-split plot design of three inoculations by four silvicultural treatments by four seasons with replication by block (3) and estimation based on the residual (restricted) maximum likelihood method (SAS Version 8.01, SAS Institute, Inc., Cary, NC). We examined the main effects of fertilization, irrigation, season, and inoculum, and their interactions using the adjusted Tukey-Kramer test for multiple comparisons in which the experiment-wise error rate was 0.05.

Results

Season and Botryosphaeriaceae inoculum treatments interacted significantly to affect canker length (table 1). Overall, the *B. dothidea* isolate produced greater external and internal canker length than the *L. theobromae* isolate. Both species produced significantly longer cankers (figures 1 and 2) than the water agar controls with the exception of winter 2003, when the *L. theobromae* canker lengths did not differ from the water agar control (table 2). Canker lengths were greater in summer 2004 than all other seasons, but canker lengths in both winters were roughly equivalent (table 2).

Fertilization, irrigation, and the fertilization + irrigation treatments individually did not affect external and internal canker development, nor was there any interaction between inoculum and the amendments (table 1 and figure 3). Similarly, we found no fertilization by season interactions on canker lengths. An interaction between irrigation and season for external canker formation occurred (table 1). In summer 2004, the mean external cankers were larger (P = 0.0457) on irrigated trees (50.6 mm [2.0 in]) compared with those that were not irrigated (27.7 mm [1.1 in]). The internal canker length was affected by an interaction

Table 1. Effects of silvicultural amendment, season, Botryosphaeriaceae inoculum, and their interactions on external and internal canker lengths in intensively managed sweetgum. Significant statistical effects are in bold type.

Canker type	Effect[1]	df[2]	F	*P*-value
External	F	1, 6	0.00	0.9708
	I	1, 6	1.39	0.2826
	FI	1, 6	0.03	0.8698
	S	3, 24	23.44	**<0.0001**
	F × S	3, 24	2.17	0.1180
	I × S	3, 24	4.44	**0.0128**
	FI × S	3, 24	2.32	0.1003
	IN	2, 64	347.40	**<0.0001**
	F × IN	2, 64	0.66	0.5216
	I × IN	2, 64	0.38	0.6851
	FI × IN	2, 64	1.60	0.2104
	S × IN	6, 64	7.32	**<0.0001**
	F × S × IN	6, 64	1.67	0.1437
	I × S × IN	6, 64	0.39	0.8807
	FI × S × IN	6, 64	0.42	0.8603
Internal	F	1, 8	0.39	0.5478
	I	1, 8	0.53	0.4868
	FI	1, 8	0.09	0.7665
	S	3, 88	27.72	**<0.0001**
	F × S	3, 88	0.16	0.9249
	I × S	3, 88	0.99	0.4016
	FI × S	3, 88	3.09	**0.0311**
	IN	2, 88	347.48	**<0.0001**
	F × IN	2, 88	1.05	0.3528
	I × IN	2, 88	0.29	0.7464
	FI × IN	2, 88	0.20	0.8210
	S × IN	6, 88	20.23	**<0.0001**
	F × S × IN	6, 88	1.22	0.3048
	I × S × IN	6, 88	1.44	0.2070
	FI × S × IN	6, 88	0.73	0.6301

[1]F=fertilization; I=irrigation; FI=fertilization + irrigation; S=season; IN=inoculum.
[2]df= degrees of freedom

Table 2. Mean (±SE) external and internal canker length on intensively managed sweetgum over four seasons in South Carolina.*

Season**	Treatment	External stem canker length (mm) (±SE)	Internal stem canker length (mm) (±SE)
Winter 2002	*B. dothidea*	70.6 (± 6.4)a	65.3 (± 7.0)a
	L. theobromae	12.3 (± 0.8)b	19.6 (± 2.3)b
	Water agar control	3.9 (± 0.5)c	0.5 (± 0.2)c
Summer 2003	*B. dothidea*	29.8 (± 3.2)a	72.4 (± 7.5)a
	L. theobromae	5.3 (± 0.3)b	5.0 (± 1.3)b
	Water agar control	2.8 (± 0.2)c	0.9 (± 0.1)c
Winter 2003	*B. dothidea*	54.7 (± 7.9)a	62.8 (± 8.8)a
	L. theobromae	7.7 (± 0.3)b	3.6 (± 0.5)b
	Water agar control	7.6 (± 1.7)b	4.7 (± 1.7)b
Summer 2004	*B. dothidea*	88.6 (± 8.4)a	152.0 (± 9.2)a
	L. theobromae	23.4 (± 4.8)b	57.0 (± 6.7)b
	Water agar control	5.5 (± 0.5)c	6.1 (± 3.3)c

SE = standard error.
* Means by season that share a letter are not significantly different at $\alpha = 0.05$ (Turkey-Kramer test).
** Winter timeframes were from November to April; summer timeframes were from April to November.

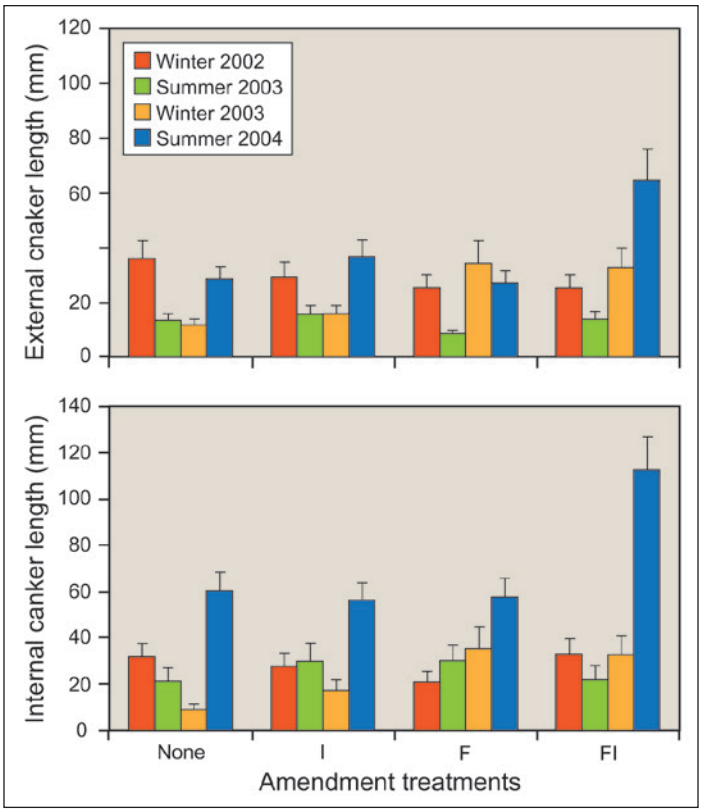

Figure 3. Mean external and internal canker lengths on sweetgum *(Liquidambar styraciflua* L.) by silvicultural amendment (I = irrigation, F = fertilization) and season of inoculation.

between fertilization, irrigation, and season (table 1), but the Tukey-Kramer test for multiple comparisons was unable to separate out individual significant interactions. Internal canker length was similar among treatments within a season, with the exception of the 2004 summer season when lengths were significantly longer, especially for those in the fertilization + irrigation silvicultural treatment (figure 3).

Discussion

The Botryosphaeriaceae isolates used in this study were found to be pathogenic on sweetgum and able to produce cankers regardless of silvicultural amendments or season of inoculation. Previous Botryosphaeriaceae inoculation tests on sweetgum seedlings and saplings have predominately used *B. ribis* Grossenb. & Duggar (Filer and Randall 1978, Neely 1968, Toole 1963). A coppice test using sweetgum seedlings infected with *B. dothidea* led to natural infection of subsequent coppice sprouts 6 months later but no canker symptoms (Cashion 1981). It is likely that *L. theobromae* was the species utilized by Garren (1956) that was found to cause dieback under certain conditions, including when grown in a low-mineral medium. The only other test of *Botryosphaeria* on sweetgum was an unidentified isolate that had no effect on seedlings (Carey et al. 2004). Our inoculations of sweetgum indicate that *B. dothidea* and *L. theobromae* are capable of causing areas of necrotic tissue in sweetgum within 6 months of inoculation. This result is not surprising given that inoculation studies with these Botryosphaeriaceae species also cause cankers on many other tree species (Brown and Hendrix 1981, Chen et al. 2014, Lewis and Van Arsdel 1978, Michailides 1991, Mullen et al. 1991, Peterson 1976, Pusey et al. 1986, Úrbez-Torres et al. 2013). The dieback of sweetgum seedlings in the Olar, SC plantation, where the *B. dothidea* and *L. theobromae* isolates were originally obtained, was likely affected by the presence of these Botryosphaeriaceae species. The report that most of the cankers on dying seedlings at the Olar plantation were associated with *B. dothidea* is likely due to the greater pathogenicity of *B. dothidea* compared with *L. theobromae*, as indicated by our inoculation trials.

Both *B. dothidea* and *L. theobromae* are able to operate as endophytes and latent pathogens affecting a broad range of hosts and geographic areas (Marsberg et al. 2017, Mohali et al. 2005). Although

many inoculation studies with these species show that cankers can be induced without the host under stress, the size and number of Botryosphaeriaceae cankers is known to increase with stress conditions (Crist and Schoeneweiss 1975, Lewis and Van Arsdel 1978, Mullen et al. 1991, Pusey 1989). The irrigation and fertilizer applied during this study was designed to meet tree nutritional and moisture needs, with a goal of maximizing tree growth each year (Coleman et al. 2004). Rainfall records at the study site from 2002 to 2004 indicated that both summer and winter seasons received approximately the same amount of rainfall and were not classified as drought conditions according to the Palmer drought index (Palmer 1965). Overall, the addition of irrigation under nondrought conditions either had no effect, or a minimal effect, on sweetgum response to inoculation by Botryosphaeriaceae. Also, no stress factor was related to a nutrition deficit or excessive nitrogen that would lead to increased cankers. The optimization of nutrient and moisture had no direct positive or negative affect on canker size; however, some amendment-by-season interactions led to an increased canker length.

Interactions between amendment and season were associated with increased canker lengths that developed in the summer of 2004. During the final inoculum test period, the sweetgum trees were approaching 4 years in age and ranged from 5.2 to 6.7 m (17.0 to 22.0 ft) in height (Coyle et al. 2008). Young sweetgum trees have a conical growth shape and lower branches on the trees were beginning to touch adjacent trees in the planting. This additional shading may be the cause of the increase in canker lengths found during the summer 2004 season, especially in the internal cankers, compared with the previous seasons (figure 3). The fertilization + irrigation treatment had visibly more crown closure (figure 4), with the greater diameter, height, and aboveground biomass after the 2003 growth season (Coyle et al. 2008). This result, coupled with no clear differences in canker development during 2002 to 2003 in the fertilization + irrigation treatment, indicates that

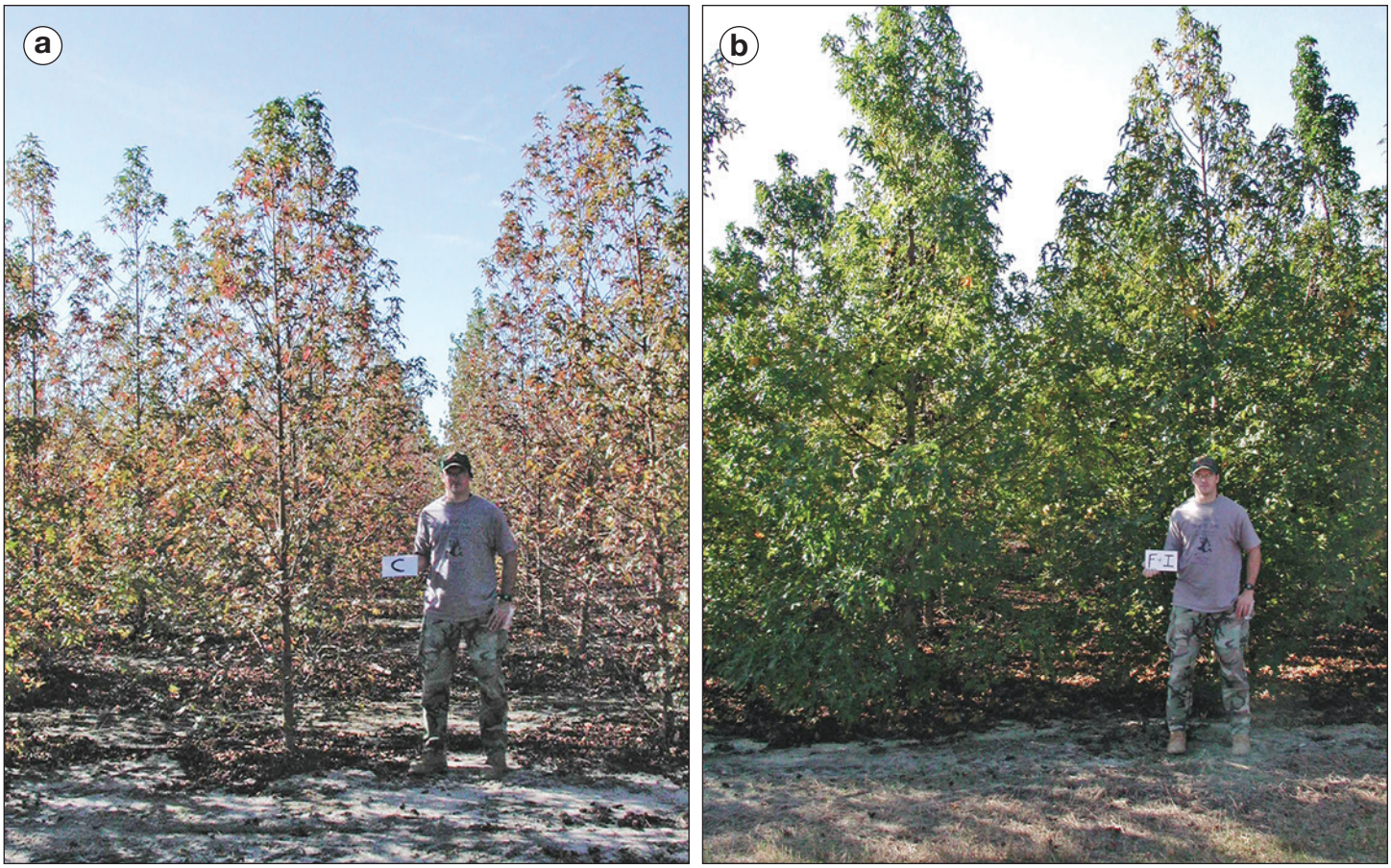

Figure 4. Photos of sweetgum (*Liquidambar styraciflua* L.) plots (a) without amendments and (b) with fertilization + irrigation amendments. (Photos by Michelle Cram, November 2003).

crown closure and shading of inoculated branches in 2004 may have affected canker development. The competition for light of the inoculated branches in the lower canopy is a stress factor that would allow for these pathogens to expand faster (Slippers and Wingfield 2007).

Internal canker length from the *B. dothidea* inoculation tended to exceed external canker length. These results are similar to Brown and Hendrix (1981), in which *B. dothidea* growth was rapid once established in the xylem vessels of apple stems. Brown and Hendrix (1981) also found no differences in *B. dothidea* growth between 15 and 35 °C. This ability of *B. dothidea* to grow under this wide range of temperatures would allow for internal canker growth to continue throughout the winter in the Southern United States. The slowed growth of the exterior canker may be in part due to proliferation of parenchyma cells, which can separate the healthy tissue from the infected tissue (Brown and Hendrix 1981).

Our study indicates that Botryosphaeriaceae species *B. dothidea* and *L. theobromae* are pathogenic on sweetgum and could contribute to dieback of sweetgum seedlings. Results also suggest that these pathogens could accelerate self-pruning of lower canopy branches. The lack of a direct effect by irrigation or fertilization treatments on the canker development is likely due to the lack of a stress-inducing drought period or a nutrient deficiency on our study site. Under normal growing conditions, the application of silvicultural amendments to optimize tree growth does not appear to directly influence Botryosphaeriaceae canker development. To determine if drought or a nutrient deficiency would have an effect on canker development in sweetgum with these Botryosphaeriaceae species would require controlled tests with these stress factors.

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