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CONTROL OF GROWTH EFFICIENCY IN YOUNG PLANTATION LOBLOLLY PINE AND SWEETGUM THROUGH IRRIGATION AND FERTIGATION ENHANCEMENT OF LEAF CARBON GAIN

L. J. Samuelson

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Work Performed Under Contract No. DE-FC07-97ID13528

For
U.S. Department of Energy
Assistant Secretary for
Environmental Management
Washington, DC

By
Auburn University
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DISCLAIMER

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Control of Growth Efficiency in Young Plantation Loblolly Pine and Sweetgum through Irrigation and Fertigation Enhancement of Leaf Carbon Gain

Final Report for DE-FC07-97ID13528

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BACKGROUND

In the southeastern United States, volume production in managed pine and hardwood stands is below maximum because of limitations in nutrient and water availability, and consequent reductions in leaf photosynthetic efficiency, leaf area, and/or aboveground carbon allocation. Large gains in productivity in response to resource augmentation have lead to testing of irrigation and fertigation, cultural practices that may maximize wood and fiber production on resource limited sites. International Paper initiated such a test in 1995 to examine the productive potential of sweetgum (*Liquidambar styraciflua*) and loblolly pine (*Pinus taeda*).

As trees and stands age, growth efficiency (aboveground biomass increment / leaf area or weight) usually declines when light, water and nutrient availability become limiting, and growth efficiency may decline as soon as three years after plantation establishment. After two years of intensive culture, sweetgum and loblolly pine stands receiving fertigation exhibited self-shading and carried 5 times and double, respectively, the leaf area of control stands. Because fertilization has been found to improve growth efficiency at high leaf area indices, we hypothesized that trees supplemented with fertigation will show no decline in growth efficiency because of improved leaf photosynthetic efficiency. We proposed that irrigation and fertigation would increase stomatal and mesophyll conductance, light use efficiency, and stomatal conductance at high vapor pressure deficit. Information gained by this study will improve basic understanding of tree physiological mechanisms that control forest productivity.

The overall objective of this study was to improve our understanding of mechanisms controlling tree growth and refine silvicultural practices aimed at maximizing wood and fiber production through resource management. More specific objectives were:

1. To determine if growth efficiency of loblolly pine and sweetgum can be maintained or improved by fertigation, and whether increased leaf carbon gain is the mechanism controlling growth efficiency response to fertigation.

2. To elucidate the specific physiological mechanisms that respond to resource amendment and improve leaf carbon gain.

3. To improve basic understanding of tree physiological mechanisms that control forest productivity.

GENERAL EXPERIMENTAL APPROACH

Leaf carbon gain and growth efficiency were examined in 3-year-old loblolly pine and sweetgum subjected to (i) weed control only, (ii) weed control + irrigation, (iii) weed control + irrigation with a liquid fertilizer (fertigation), and (iv) weed control + fertigation + pest control (pine only) since plantation establishment. Irrigation and fertigation were supplied via a drip irrigation system. In 1997, daily additions were applied over several hours by block from March through November at a monthly rate from May-September of 45,000-75,000 l plot $^{-1}$. In 1998, plots were irrigated for 6 hours a day from January through October at a monthly rate from of 51,000-75,000 l plot $^{-1}$. The fertigation treatment consisted of weed control and drip irrigation (described above) with a fertilizer solution of NH_4NO_3 and urea (135 kg N ha^{-1} yr^{-1} in 1997, 112 N kg ha^{-1} yr^{-1} in 1998), H_3PO_4 (33 kg P ha^{-1} yr^{-1} in 1997, 28 kg P ha^{-1} yr^{-1} in 1998) and K_2O (130 kg K ha^{-1} yr^{-1} in 1997, 90 kg K ha^{-1} yr^{-1} in 1998). Treatment plots (0.2 ha) are arranged in a randomized complete block design with three replicates.

Key leaf physiological processes in the upper canopy were examined two times a growing season over the third (1997) and fourth (1998) growing seasons. Photosynthetic response to intercellular CO_2 concentration and photosynthetically active radiation, with other leaf environmental conditions held constant, was measured in fully-developed, current year foliage. These response curves were used to determine the influence of intensive culture on the following fundamental leaf physiological processes: quantum yield or light use efficiency, light saturated net photosynthesis (A_{max}), dark respiration (R_d) and carboxylation efficiency. Quantum yield, A_{max}, and R_d in lower canopy leaves were measured twice during the second measurement season in irrigation and fertigation treatments to determine if fertilization improved light use efficiency in shade leaves.

In addition to response curve analyses, *in situ* (at ambient temperature and vapor pressure deficit) light-saturated rates of net photosynthesis (P_{net}) and stomatal conductance (g_s) in sun leaves of six trees on each plot were monitored 3 to 4 times a growing season to increase the sample size and further test the influence of intensive culture on leaf physiological function.

Stem growth was monitored each growing season. Trees (2/plot) were harvested at the end of each growing season and the increment in aboveground woody biomass and leaf mass was used to calculate growth efficiency and examine biomass accumulation in foliar, branch and stem tissues.

Repeated measures analysis with block and treatment as main effects was used to determine if measurement date by treatment interactions were significant ($P<0.10$) for leaf physiological variables measured repeatedly within a growing season. Treatment effects on variables that were not repeatedly measured were tested using a randomized complete block design (n=3). Duncan's Multiple Range Test was used to separate treatment means. Treatment effects on allometric relationships were tested using dummy variable analysis.

PROPOSAL DEVIATIONS:

1. Photosynthetic and stomatal response to temperature was not measured because of the difficulty in lowering the cuvette temperature at high ambient temperatures (40°C).
2. Stomatal response to vapor pressure deficit (VPD) was measured under controlled cuvette conditions only once because of the difficulty in maintaining a low VPD at high ambient temperatures. Alternatively, we examined stomatal response to VPD using the *in situ* data.
3. Response curves were measured two rather than three times a season because the grant was awarded late the first year and bad weather the second season.
4. Only upper branches were measured the first measurement year to avoid the confounding influence of light on treatment comparisons. The lower canopy in control treatments was open and fully exposed to light whereas the lower canopy in fertigation treatments was partially shaded. During the second measurement season, photosynthetic light use efficiency in the lower canopy was compared between irrigated and fertigated treatments, because of similar shading.
5. CO_2 and light response curves were measured on one tree per plot the first year and two trees per plot the second year.
6. The number of tree replicates per plot for *in situ* (at ambient temperature and VPD) measures of leaf photosynthesis was increased from three to six both years.
7. Tree canopy structure measures using biomass by strata (upper, middle and lower crown) were dropped, because branches greatly deviated from their initial position on the bole.
8. Winter measures of *in situ* leaf photosynthesis of loblolly pine were added to the 1998/1999-measurement year.

RESULTS

Foliar Nutrition

In loblolly pine, a two-way interaction between measurement date and treatment in 1997 indicated that between date variation in foliar P concentration differed with treatment (Table 2). Fertigation increased leaf N concentration in sweetgum in 1997, and in 1998, foliar N concentration of sweetgum was decreased by irrigation (Table 2, Figure 1). During both growing seasons, P and K concentrations in sweetgum leaves were unaffected by treatment. No influence of intensive culture on loblolly pine foliar N or K concentration was observed either year, but in 1997 foliar P concentration was decreased by fertigation, most likely because of a dilution effect in response to increased leaf area (Figure 1). Despite large gains in growth in response to intensive management (see below), individual leaf nutrition was not significantly improved. However, whole plant nutrient uptake was increased as a result of greater crown mass in response to intensive culture.

Water Relations

Repeated measures analyses indicated a significant interaction between date of measurement and treatment for predawn leaf water potential in loblolly pine during the 1998 growing season and the 1998/1999 winter (Table 1). Predawn leaf water potential of loblolly pine was increased by irrigation in June, July and August of 1998, and in December of 1998 water potential was highest in the fertigation treatments (Figure 2). Lower leaf water potential of loblolly pine in 1998 indicated greater water stress in control trees relative to 1997. In contrast to loblolly pine, irrigation did not increase predawn leaf water potential of sweetgum either growing season (Table 2 and Figure 2).

Leaf Physiology

Intensive culture had no significant influence on quantum yield and R_d of either species in 1997 and 1998 (Tables 1 and 2, Figure 2). Carboxylation efficiency was unaffected by treatment in sweetgum both seasons, but in loblolly pine carboxylation efficiency was increased by fertigation plus pest control in 1997 and by irrigation in 1998 (Figure 3). In 1998, A_{max} was higher in response to fertigation relative to the irrigation in sweetgum, and increased by irrigation in loblolly pine. Maintenance of A_{max} and carboxylation efficiency in loblolly pine during severe drought in 1998 contributed towards greater growth in response to irrigation. In contrast, A_{max} of sweetgum was lower in irrigation treatment compared to fertigation treatment in 1998, most likely due to nutrient depletion in response to irrigation.

No significant influence of fertigation relative to irrigation on leaf quantum yield or A_{max} of lower canopy leaves was observed in sweetgum or loblolly pine in 1998 (data not shown). Thus, the addition of fertilizer did not increase light use efficiency in shade leaves.

Two-way interactions between date of measurement in 1997 and treatment indicated that *in situ* P_{net} was increased by irrigation in September, g_s was highest in response to fertigation plus pest control in July, and g_s was increased by irrigation in September (Table 1 and Figure 4). During the 1998 growing season, a treatment main effect revealed that g_s and P_{net} of loblolly pine were higher in the irrigation and fertigation treatments compared to the control and fertigation plus pest control treatments. In December 1998 and January 1999, P_{net} was lower in response to fertigation plus pest control relative to the other treatments. In both species, leaf physiological rates were lower in 1998 relative to cooler and wetter 1997 growing season.

No influence of intensive culture on *in situ* P_{net} and g_s of sweetgum was observed in 1997 (Table 2 and Figure 5). In 1998, a two-way interaction between date and treatment indicated that P_{net} of sweetgum was lower in the irrigation than control treatment in August, and P_{net} was highest in the control treatment relative to the irrigation and fertigation treatments in September (Figure 3).

Stomatal response to vapor pressure deficit (VPD) was significant for all treatments in sweetgum both growing seasons and VPD explained from 56 to 90% of the variation in g_s (Figure 6). Stomatal response to VPD differed among treatments during the hotter 1998 season. The slope of g_s response to VPD was lower (more negative) in the control versus irrigation and fertigation treatments. Therefore, sweetgum trees growing with intensive culture were less sensitive to VPD than control trees. In contrast, during both growing seasons, VPD was significant in explaining variation in loblolly pine g_s only in control treatments (Figure 7).

Growth

In loblolly pine, height both years and diameter at breast height (dbh) in 1998 were greatest in response to fertigation with pest control (Figure 8). Height and dbh at the end of the 1998 season were increased from 5 m and 9 cm, respectively, in the control treatment to 7 m and 13 cm, respectively, in response to fertigation with pest control. Relative to the control, woody (stem + branch) cumulative net primary productivity of loblolly pine was increased from 11.9 to 30.6 Mg ha^{-1} in response to treatment with fertigation plus pest control for four years (Figure 9). After four years of treatment, projected LAI of loblolly pine was approximately 6 in stands receiving fertigation plus pest control (Figure 10). Intensive management induced changes in stem allocation of loblolly pine. Allometric analysis indicated that stem allocation was greater in the irrigation versus fertigation treatment (data not shown). No other changes in loblolly pine allocation were observed.

For sweetgum, irrigation and fertigation successively increased height and dbh both years (Figure 8). At the end of the fourth growing season, sweetgum height and dbh were increased from approximately 4 m and 4.5 cm, respectively, in the control treatment to 6 m and 11 cm, respectively, in response to fertigation treatment. Relative to the control, woody (stem + branch) net primary productivity of sweetgum was increased from 3.3 to 19.5 Mg ha^{-1} in response to fertigation for four years (Figure 9). After four years of treatment, LAI was approximately 6 in the fertigation treatment and similar to loblolly pine receiving the most intensive treatment (Figure 10). Relative to the control treatment, sweetgum treated with fertigation allocated more dry mass to stem and less to branch (data not shown).

Despite large increases in LAI in response to the most intensive management, no reduction in growth efficiency of either species was observed in response to the most intensive culture (Figure 10). No significant main effects of year or treatment by year interactive effects on growth efficiency were detected for sweetgum. In loblolly pine, growth efficiency in all treatments was higher in 1998 than in 1997.

CONCLUSIONS

Objectives of this study were to (1) determine if growth efficiency of loblolly pine and sweetgum can be maintained or improved by fertigation, and whether increased leaf carbon gain is the mechanism controlling growth efficiency response to fertigation, (2) elucidate the specific physiological mechanisms that respond to resource amendment and improve leaf carbon gain, and (3) improve basic understanding of tree physiological mechanisms that control forest productivity. After four years of intensive management, nutrient and water augmentation resulted in a more than 3-fold increase in woody net primary productivity in both species. Growth efficiency of both species was maintained by the most intensive culture despite large increases in total height, LAI, aboveground biomass, crown closure and self-shading. Trees supplemented with fertigation and fertigation plus pest control exhibited the largest increase in growth and biomass. The addition of pest control to prevent tip moth damage increased leaf area and growth of loblolly pine.

Greater growth in response to the most intensive culture was facilitated by gains in leaf mass and whole tree carbon gain rather than large increases in key leaf physiological processes that may improve leaf carbon gain. Although irrigation improved leaf photosynthesis in loblolly pine and stomatal response to VPD in sweetgum in 1998, fertigation increased only A_{max} in sweetgum during one season. In fact, lower P_{net} and g_s were observed in loblolly pine in response to fertigation plus pest control. Because the fertigation plus pest control treatment carried more leaf area, it is possible that lower rates were a result of a down regulation of individual leaf water loss to regulate whole tree water loss. Because individual leaf carbon gain was not significantly influenced by the most intensive culture, our hypothesis that increased leaf carbon gain in response to the most intensive culture will maintain growth efficiency was unsupported. Maintenance of growth efficiency may have been accomplished by shifts in carbon allocation from below to aboveground structures. However, this hypothesis requires testing.

Table 1. Observed probability values for main and interaction effects of date of measurement within a growing season and intensive management treatment observed for foliar N, P, and K concentrations, carboxylation efficiency (CE), quantum yield (QY), maximum net photosynthesis (A_{max}), dark respiration (R_d), *in situ* net photosynthesis (P_{net}) and stomatal conductance (g_s), and predawn leaf water potential (WP) of loblolly pine.

Year	Variable	Date	Date x treatment	Treatment
Jul-Sep 1997	N	0.003	0.286	0.272
	P	0.121	0.047	0.002
	K	0.040	0.202	0.693
	CE	0.204	0.559	0.079
	QY	0.024	0.417	0.513
	A_{max}	0.091	0.926	0.245
	R_d	0.337	0.901	0.489
	P_{net}	<0.001	0.040	0.030
	g_s	<0.001	0.003	0.061
	WP	0.066	0.154	0.322
Jun-Sep 1998	N	0.012	0.115	0.001
	P	0.030	0.181	0.444
	K	0.009	0.194	0.716
	CE	0.002	0.026	0.666
	QY	0.649	0.932	0.430
	A_{max}	0.581	0.752	0.022
	R_d	0.303	0.816	0.836
	P_{net}	0.005	0.366	0.051
	g_s	0.028	0.524	0.018
	WP	<0.001	0.052	0.003
Dec 98-Jan 1999	P_{net}	0.226	0.568	0.028
	g_s	<0.001	0.191	0.160
	WP	0.066	0.007	0.004

Table 2. Observed probability values for main and interaction effects of date of measurement within a growing season and intensive management treatment observed for foliar N, P, and K concentrations, carboxylation efficiency (CE), quantum yield (QY), maximum net photosynthesis (A_{max}), dark respiration (R_d), *in situ* net photosynthesis (P_{net}) and stomatal conductance (g_s), and predawn leaf water potential (WP) of sweetgum.

Year	Variable	Date	Date x treatment	Treatment
Jul-Sep 1997	N	0.018	0.497	<0.001
	P	0.026	0.639	0.116
	K	0.400	0.420	0.289
	CE	0.064	0.924	0.836
	QY	0.060	0.534	0.717
	A_{max}	0.425	0.491	0.592
	R_d	0.098	0.821	0.445
	P_{net}	0.007	0.620	0.226
	g_s	0.189	0.890	0.264
	WP	0.054	0.982	0.128
Jun-Sep 1998	N	0.012	0.115	0.001
	P	0.030	0.181	0.444
	K	0.009	0.194	0.716
	CE	0.064	0.924	0.836
	QY	0.130	0.593	0.634
	A_{max}	0.016	0.277	0.061
	R_d	0.011	0.047	0.902
	P_{net}	0.016	0.055	0.054
	g_s	0.019	0.380	0.664
	WP	0.582	0.175	0.771

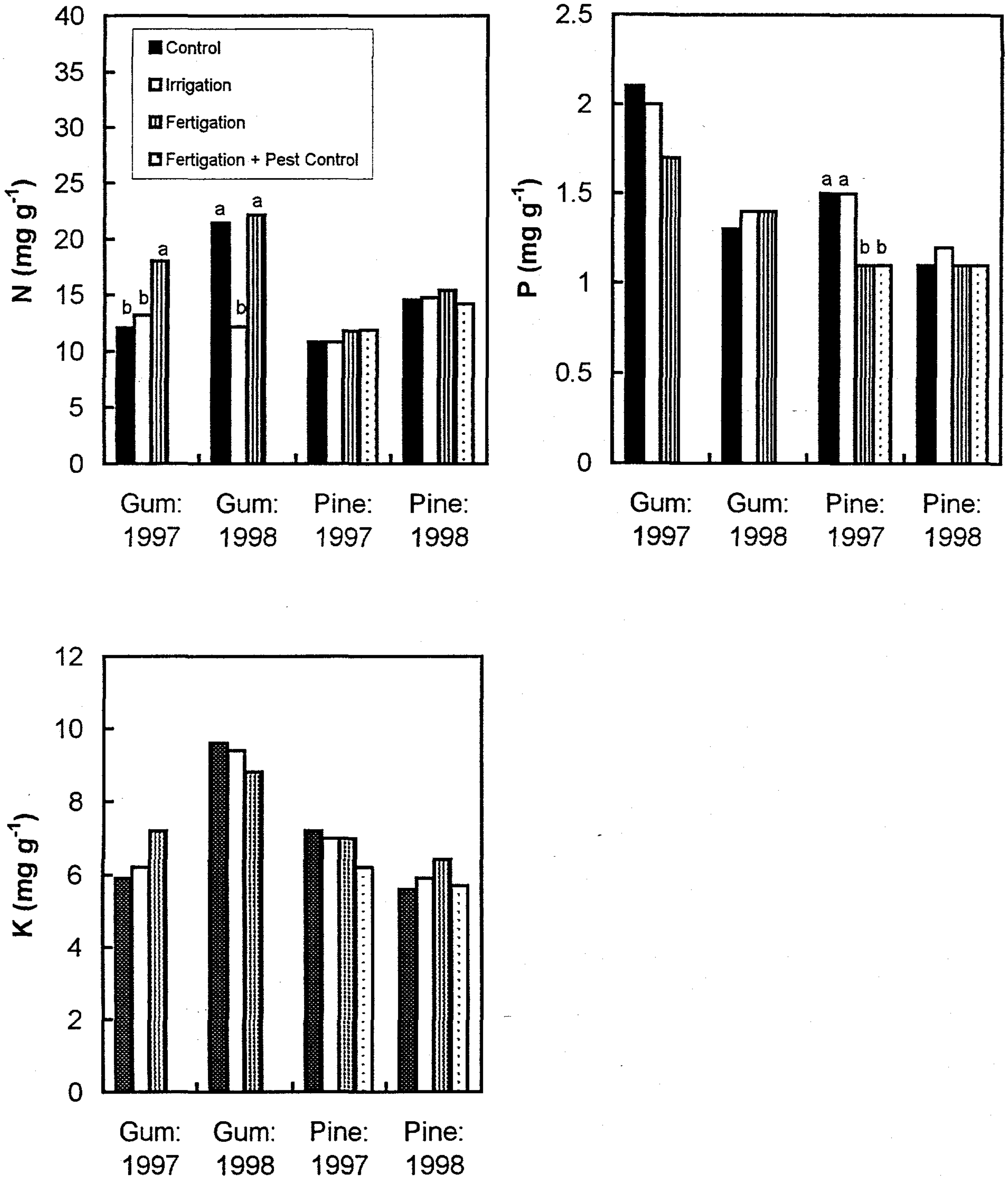


Figure 1. Influence of intensive management on foliar N, P and K concentrations in sweetgum and loblolly pine during the 1997 and 1998 growing seasons.

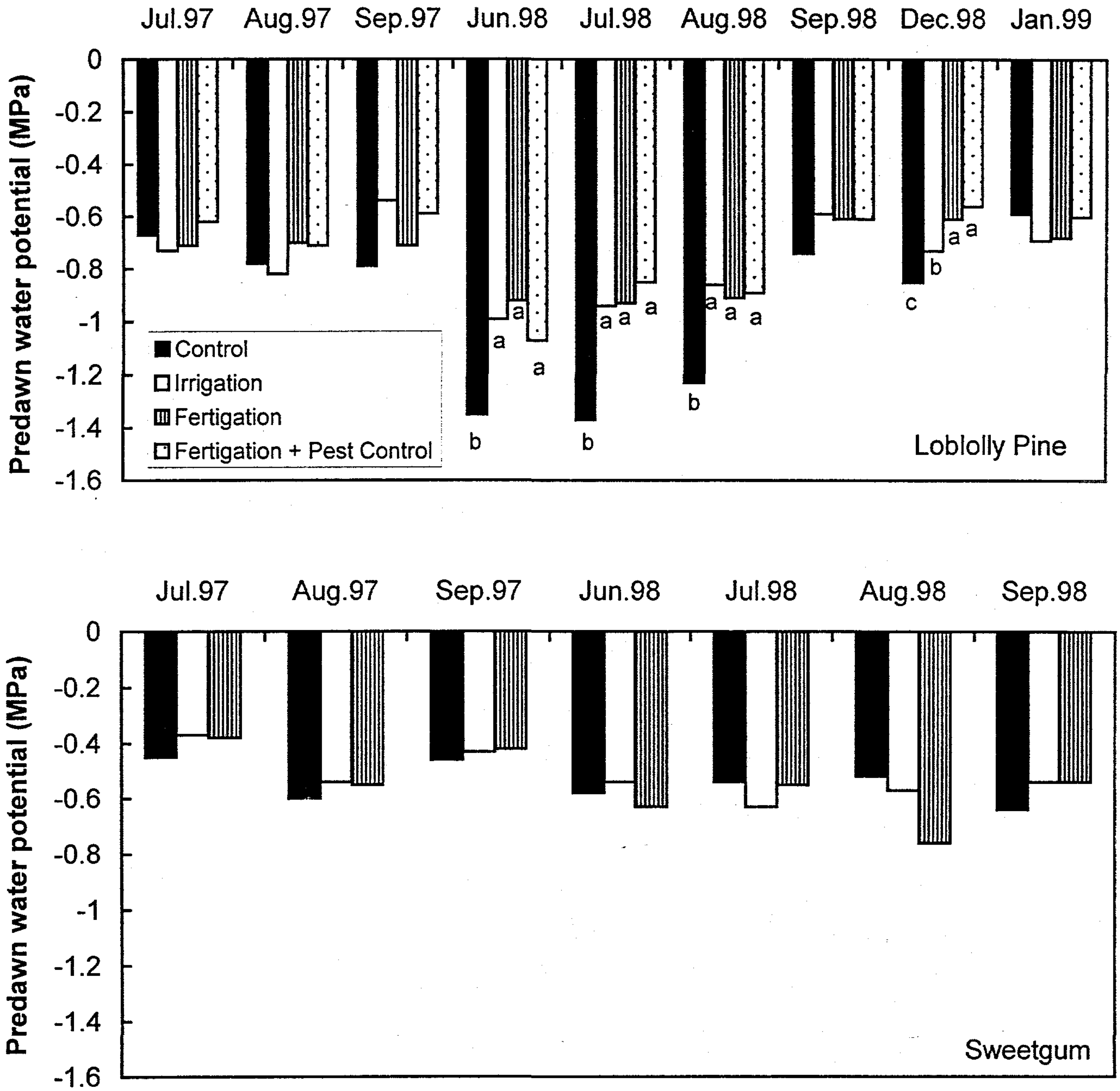


Figure 2. Influence of intensive management on predawn water potential in sweetgum and loblolly pine.

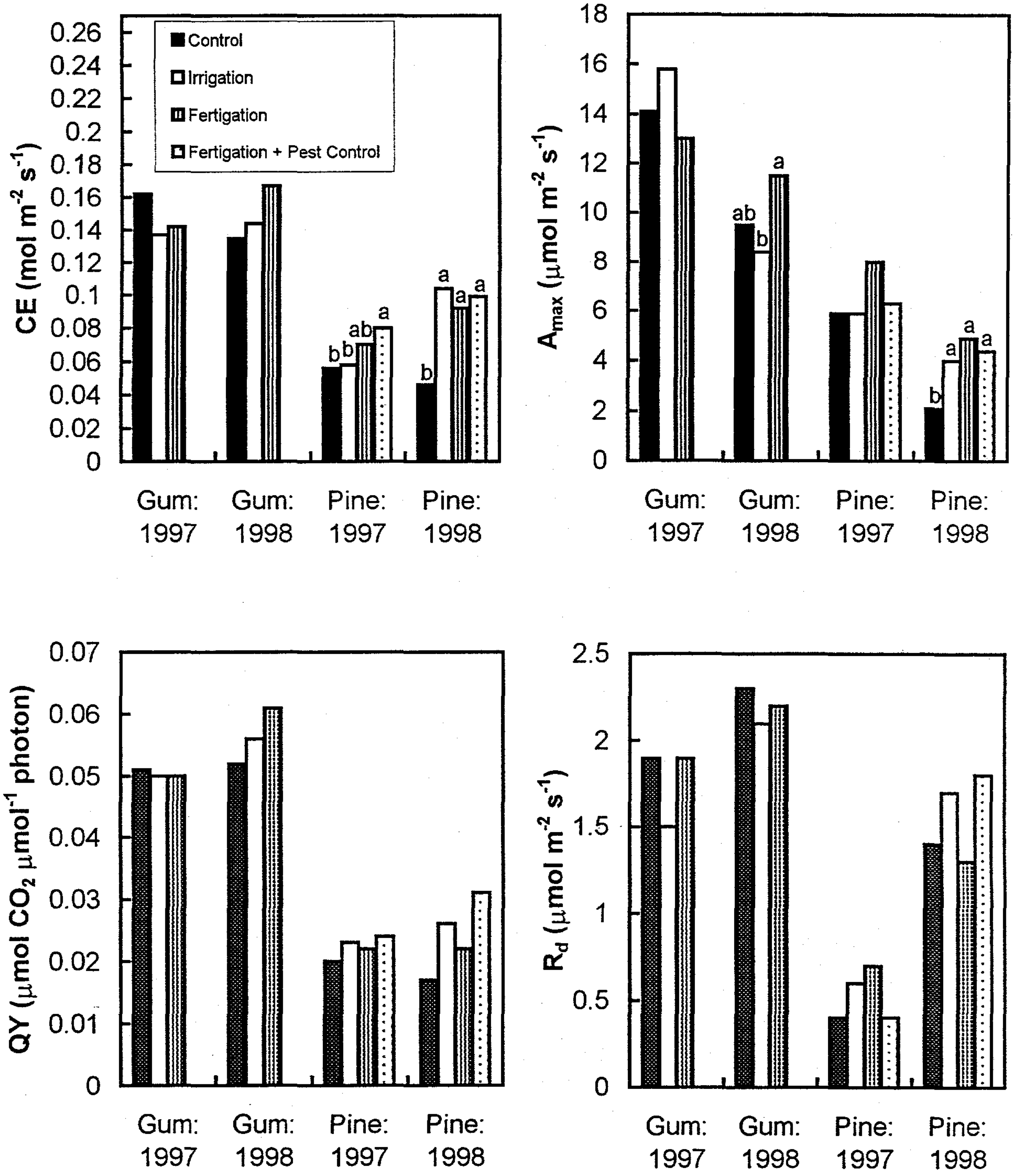


Figure 3. Influence of intensive management on leaf carboxylation efficiency (CE), maximum photosynthesis (A_{max}), quantum yield (QY), and dark respiration (R_d) in sweetgum and loblolly pine during the 1997 and 1998 growing seasons.

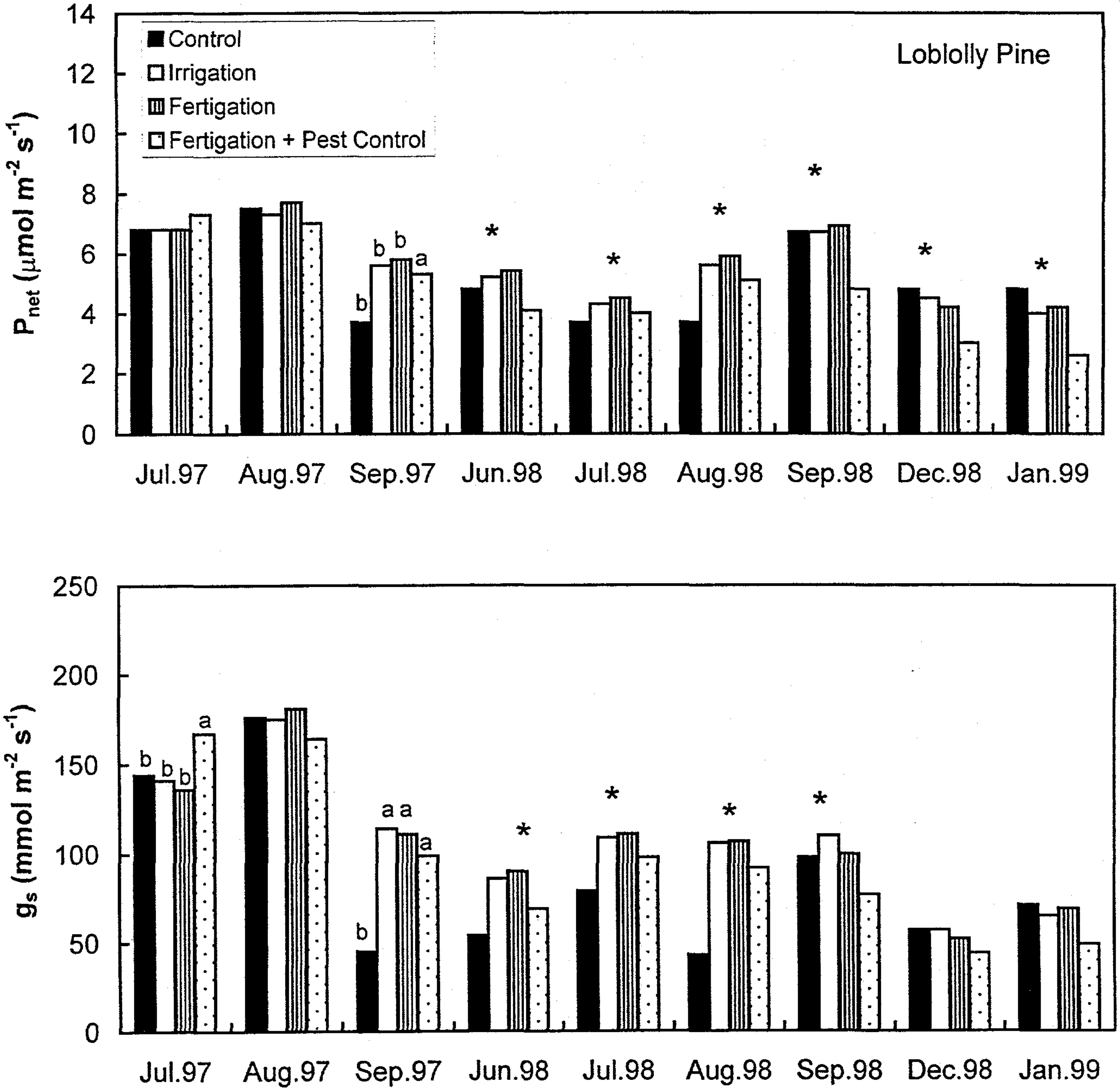


Figure 4. Influence of intensive management on *in situ* net photosynthesis (P_{net}) and stomatal conductance (g_s) in loblolly pine.

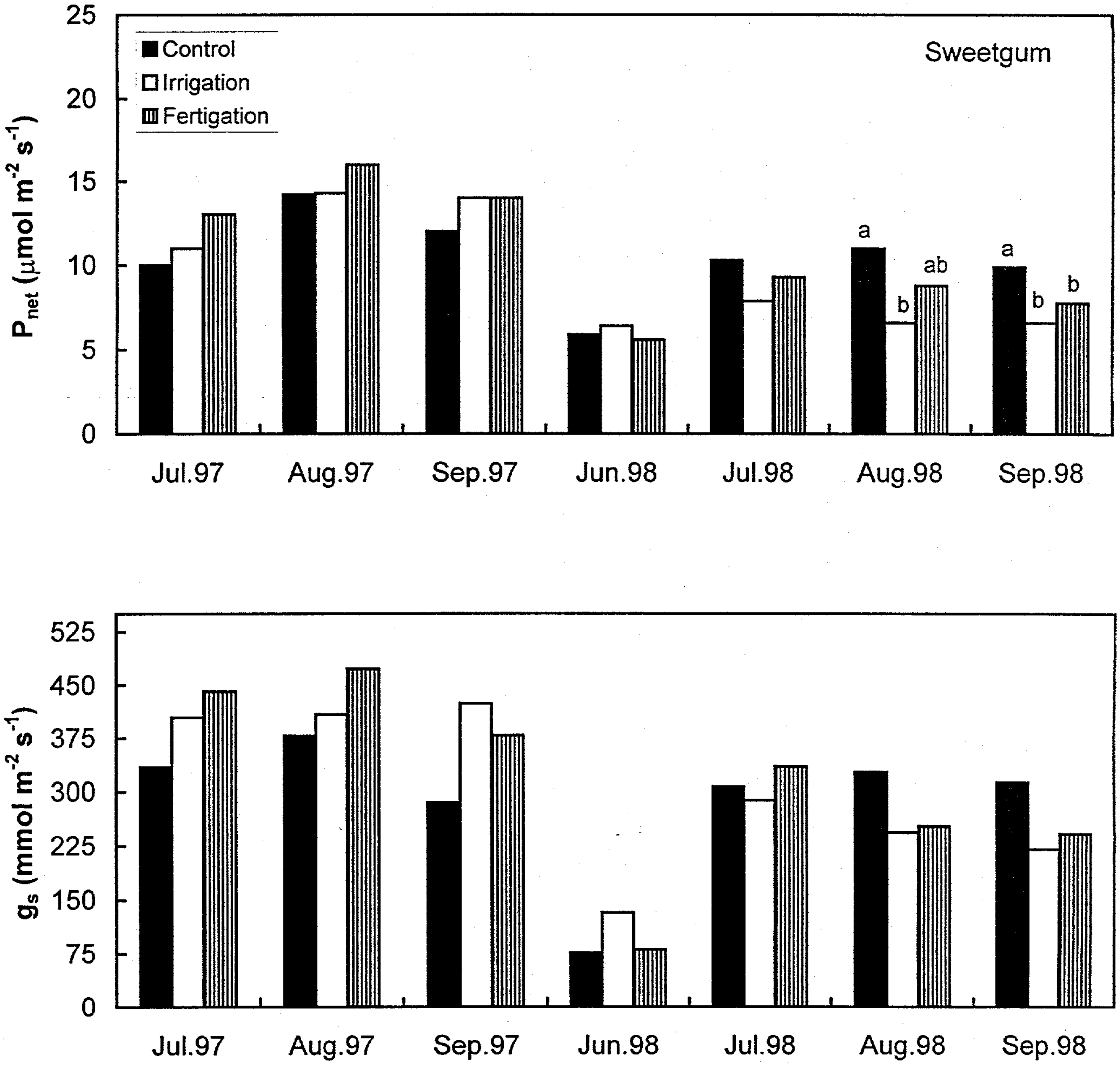


Figure 5. Influence of intensive management on *in situ* net photosynthesis (P_{net}) and stomatal conductance (g_s) in sweetgum.

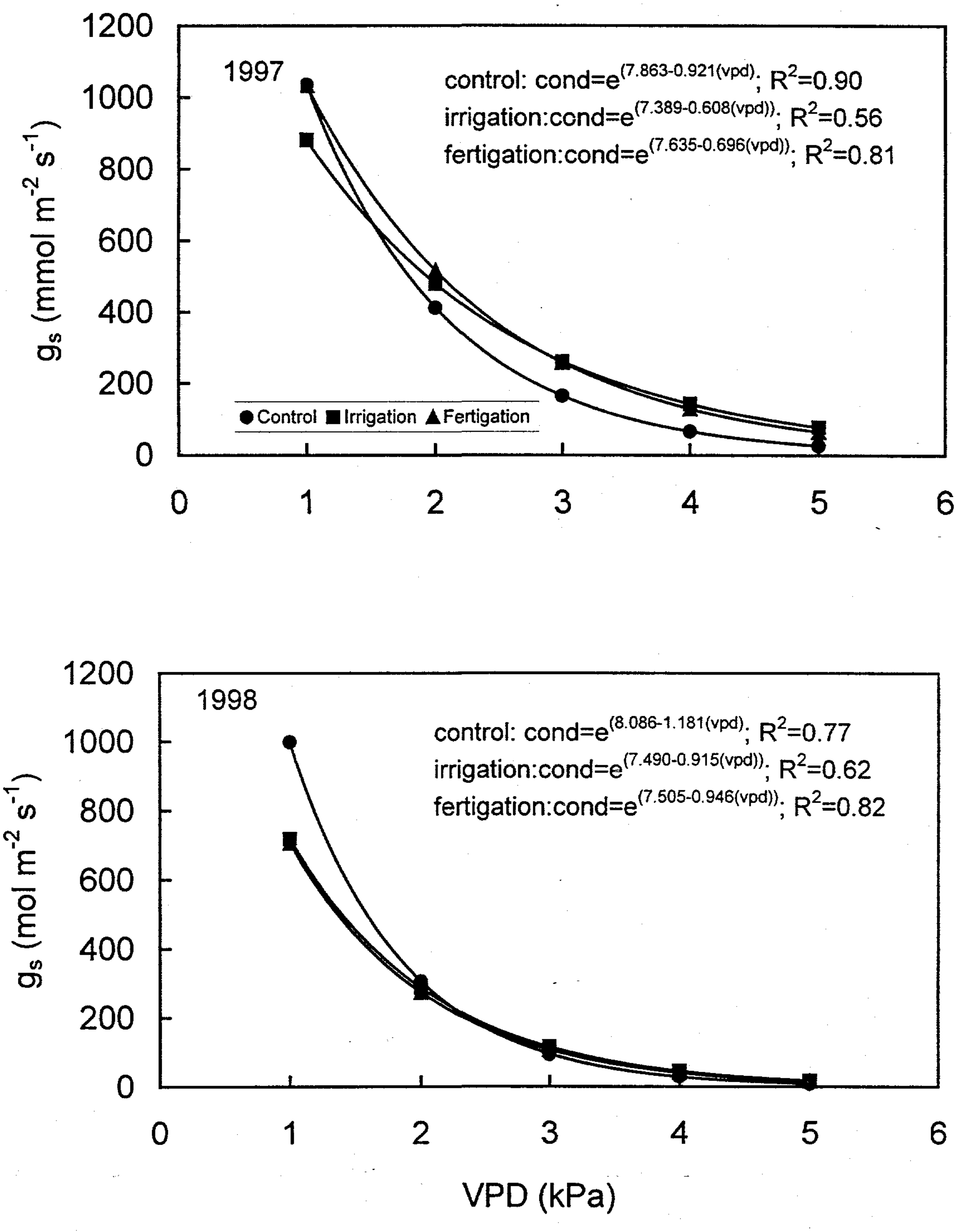


Figure 6. Influence of intensive management on stomatal conductance (g_s) response to vapor pressure deficit (VPD) from leaf to air in sweetgum.

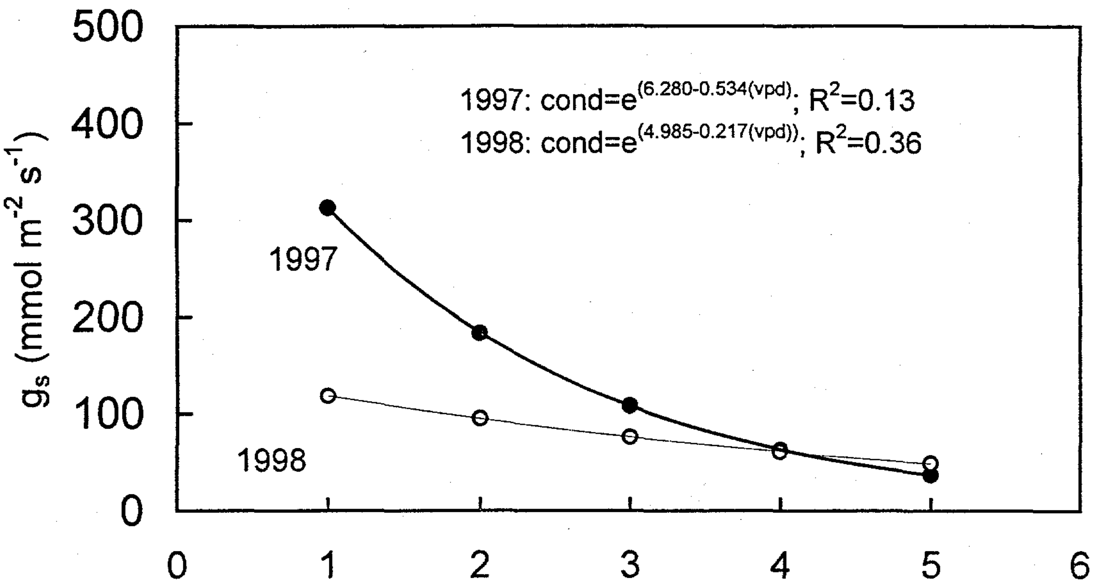
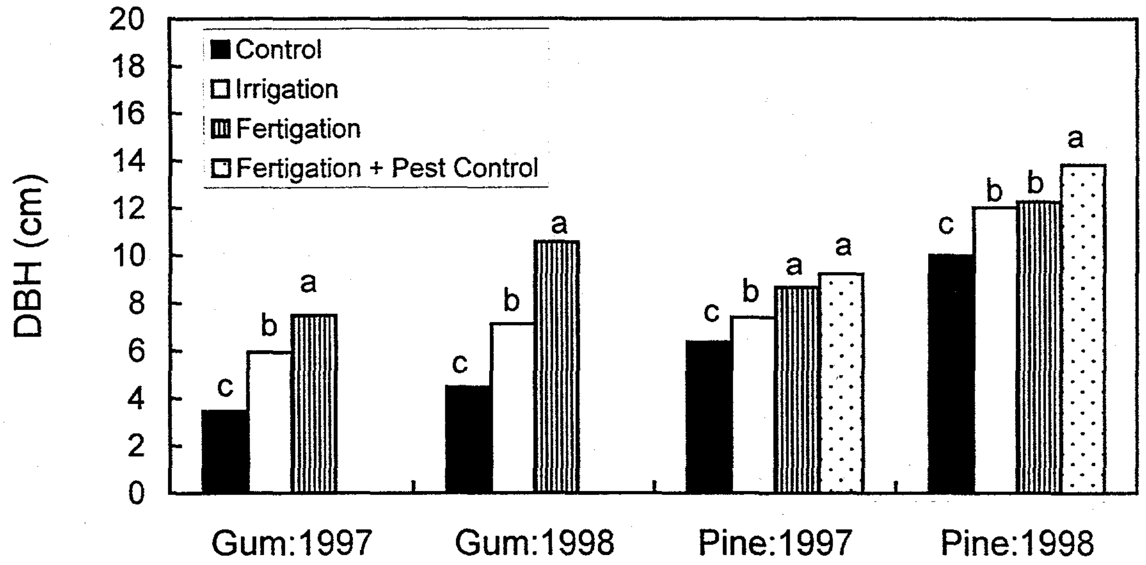


Figure 7. Stomatal conductance (g_s) response to vapor pressure deficit in control treatment loblolly pine.



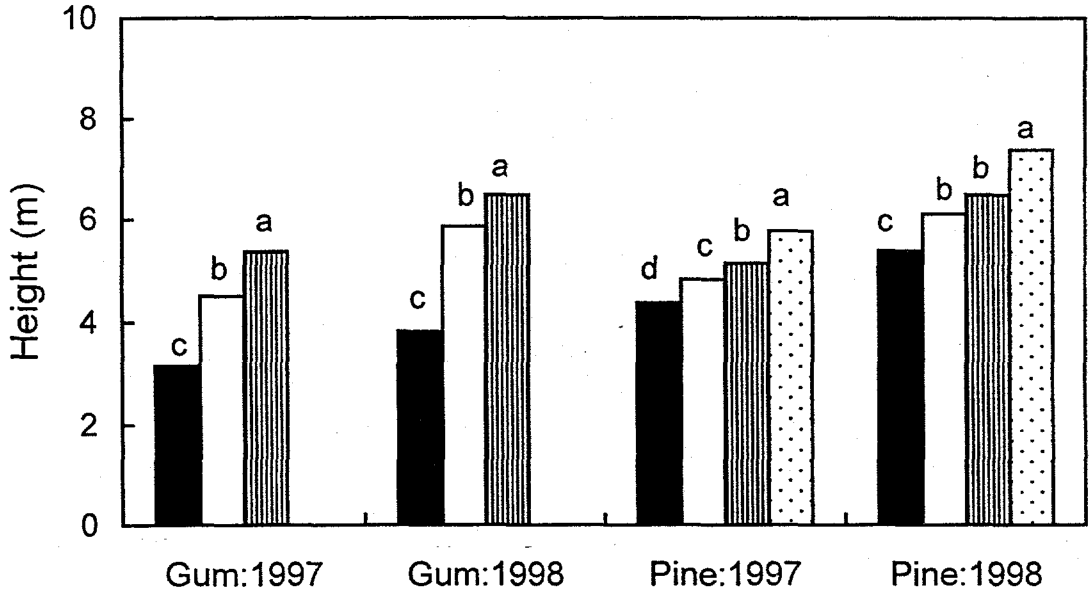


Figure 8. Influence of intensive management on height and diameter at breast height (DBH) in sweetgum and loblolly pine during the 1997 and 1998 growing seasons.

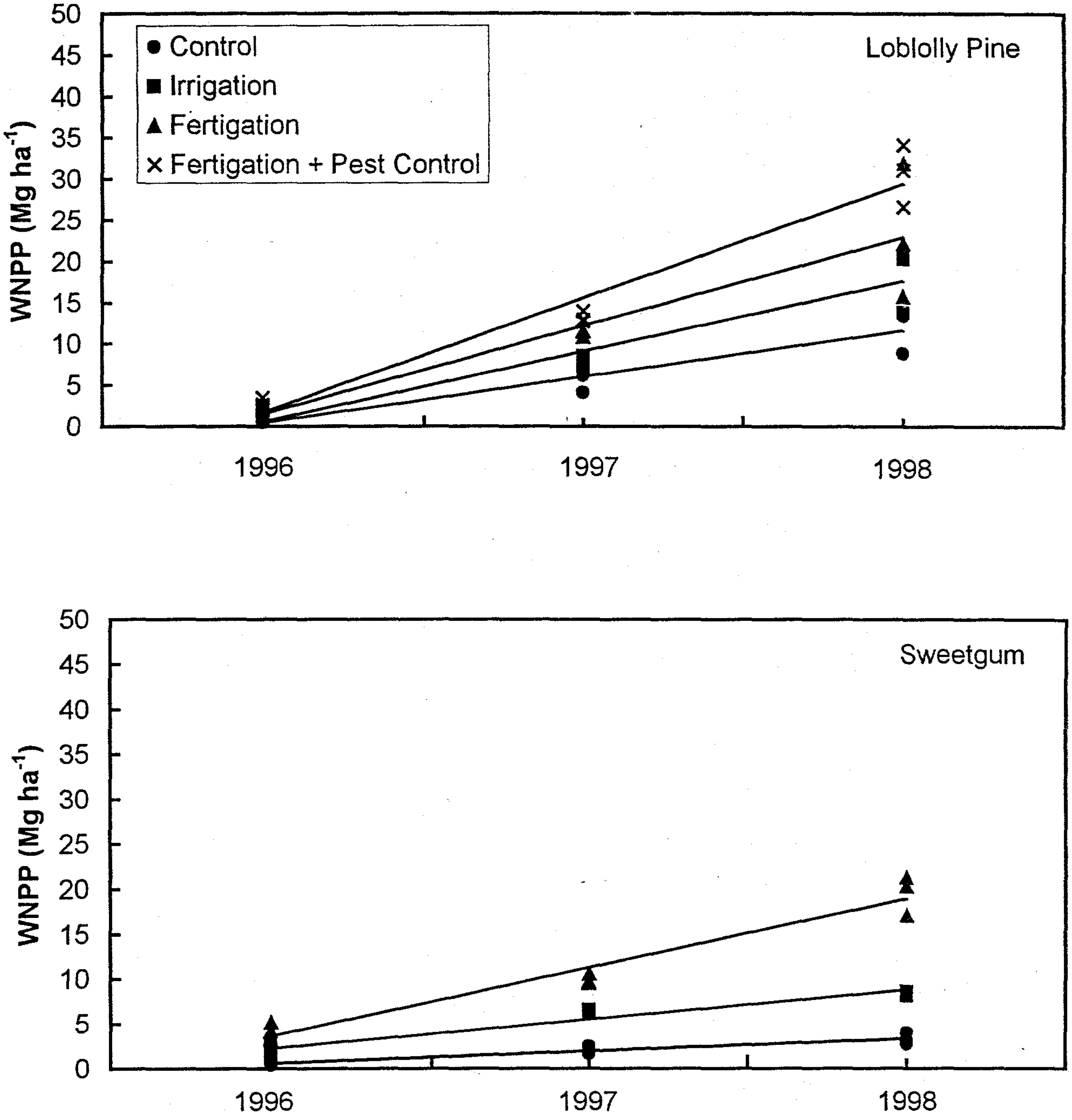


Figure 9. Influence of intensive management on cumulative woody (stem + branch) net primary productivity (WNPP) of sweetgum and loblolly pine.

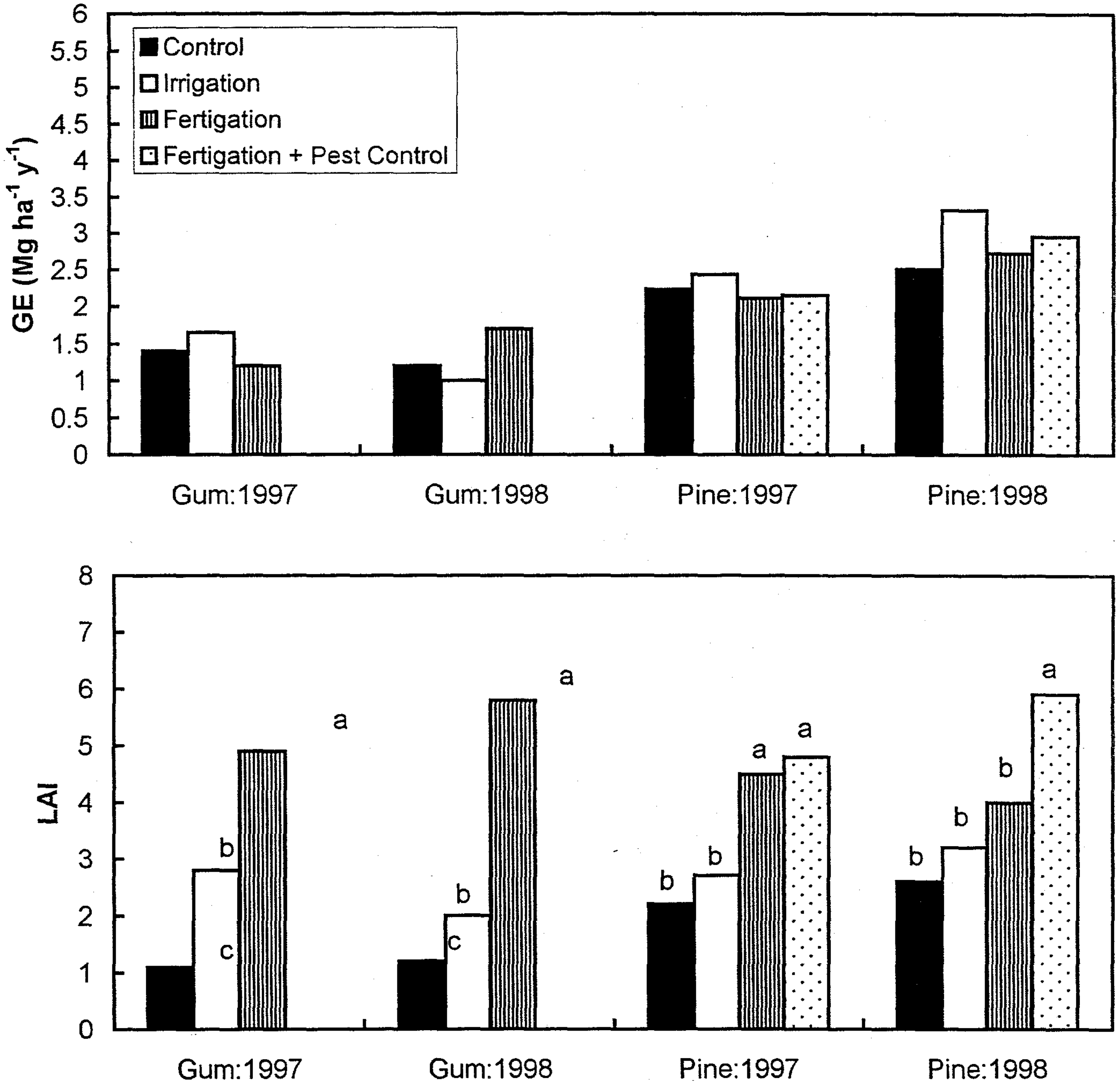


Figure 10. Influence of intensive management on growth efficiency (GE) and leaf area index (LAI) of sweetgum and loblolly pine during the 1997 and 1998 growing seasons.