A COMPARISON OF WATER-STRESS EFFECTS FOR TWO UNFERTILIZED, FERTILIZED, AND NODULATED ALDER SPECIES

By

EDWARD MARK LORENZI

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Thesis Approved:

Thomas C. Hennessey
Thesis Adviser

Hedeel S. Vidaver

Ronald W. McNew

Norman N. Durham
Dean of the Graduate College

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CHAPTER I

INTRODUCTION

With growing demands worldwide for forest products, many forest managers are realizing the need to increase intensive forestry practices to achieve more efficient production of wood fiber per unit area of land. Included in these practices are shorter rotation periods and improved cultural regimes. However, nutrient removal is accelerated by shorter rotations, especially in the case of total-tree harvesting (19). The maintenance of site productivity under short-rotation management will require replacement of nutrients at a greater rate than under conventional management systems.

While selected forest industries have utilized commercial fertilizers to enhance soil-plant nutrition, the production and application of these fertilizers is very expensive and time consuming. Associated problems following widespread fertilizer applications may include the addition of nitrates in forested watersheds, as well as high rates of volatilization when applied under high seasonal temperatures. In addition, the timing of application must be delayed until stand crown closure to avoid competition from understory weeds and to maintain high wood quality. Also, the effects of applied fertilizers are relatively short-term, and there is a significant time lag before application costs are returned at harvest. Finally, food production

is likely to have priority over fiber production in competition for future limited supplies of nitrogen fertilizer.

Because of these considerations associated with the use of commercial fertilizers, widespread research is being conducted to evaluate alternative methods for supplying shorter rotation forests with adequate nitrogen, the nutrient most limiting within forest soils. One promising alternative involves the use of nonleguminous dinitrogen-fixing woody plants within silvicultural systems. These "actinorhizal" trees are capable of adding a considerable quantity of organically fixed nitrogen to forest soils via the abscission of leaves high in nitrogen, and through root exudation.

The actinomycetous bacterium Frankia is a major endophyte now known to infect and produce functional, nitrogen-fixing nodules in over 160 species within 15 genera, 18 families, and 7 orders of woody dicots (5). The Alnus genus has 95 percent of the member species known to form efficient nodules. In Alnus, as well as other nonleguminous woody plants, an infecting hair, or hyphae, from the bacterium invades the root and initiates a colonization which results in a root nodule (37). It is the nodule which is the structure containing the nitrogenase enzyme that catalyzes the reaction to convert atmospheric nitrogen to the ammonium ion. Once the ammonium ion is formed and converted to amino acids it is transported into the root for transport via the xylem to various nutrient sinks located on the plant (4, 37). This process has the added advantage over most fertilizers of by-passing the energy consuming step of converting nitrate to ammonium in the nitrogen metabolism process.

Many forest managers in the Western United States have already realized the practical benefits of dinitrogen-fixing nonleguminous trees and have incorporated selected species into forest plantations (14, 15, 31, 43). However, these pioneering studies of mixed-species plantations have identified certain key physiological relationships which may limit the widespread use of nitrogen-fixing woody plants in commercial forestry operations. For example, there is a critical need for research to evaluate the impact of water-stress on the process of biological dinitrogen fixation (20, 34).

Accordingly, a cooperative project funded by the National Science Foundation is underway at Oklahoma State University to investigate the effects of water-stress in one actinorhizal system, using Alnus as a model genus. This paper is a part of that project. In this study, the effects of water-stress upon an actinorhizal system consisting of one Frankia bacterium of known xerotolerance combined with two Alnus species known to produce effective nodules and known to have contrasting xerotolerance, were monitored and analyzed. These results will provide a model for investigations into the relative contributions of host/Frankia/nodule to xerotolerance in other actinorhizal systems and, since tree-breeding is an expensive and long-term project, may save considerable effort in the development of plants suitable for the many areas commonly stressed simultaneously by water availability and nitrogen limitation.

CHAPTER II

LITERATURE REVIEW

The intent of this section is to review the literature that deals specifically with the effects of water-stress on the actinorhizal system. Extensive reviews of field studies documenting the benefits of nitrogen-fixing woody plants to various forestry operations can be found elsewhere (14, 15, 31, 43).

Currently, there are few studies dealing with the effects of water-stress on actinomycetes-nodulated plants, and little quantitative data exists. The majority of available information on this topic has been reported as inferences from either ecological studies or field studies designed to evaluate growth and yield of various actinorhizal species. McVean (30), for example, reviewing British alder populations, suggested that stomatal control of transpiration was poor in Alnus glutinosa (L.) Gaertn. Gordon (16) reported that Alnus rubra Bong. appeared to be more mesic in its site requirements than Alnus glutinosa. Other studies have dealt only with the nitrogenase activity of nodules from field grown plants under seasonal climatic stress (11, 29). While the effects of water-stress on nodulated legumes have been investigated in greater detail (40), their investigations do not provide a model for actinorhizal plants which have very different nodule morphology (44). Absence of detailed information about the effects of water-stress on actinorhizal plants has been recognized by

other researchers who have emphasized that moisture-stress tolerance is a quality considered important in Alnus selection (20, 34).

Actual water-stressing of several species, including Alnus glutinosa, was studied by Takahashi (42). He exposed seedlings to three levels of moisture-stress: (1) soil moisture levels kept at 82-93 percent of field capacity, (2) at 55-66 percent of field capacity, and (3) at 27-38 percent of field capacity. Over these regimes, Alnus glutinosa showed a reduction in dry matter production as water became more limited. However, the transpiration ratio (a measure of the efficiency of dry matter production per unit water usage) was lowest for Alnus as compared to unknown seed sources of Picea, Larix, Abies, and Betula. It was suggested that Alnus had a lower transpiration ratio due to nitrogen supplementation by the Frankia-infected root nodules. Kramer (25) also stated that field fertilization of many crops tended to decrease the transpiration ratio and increase the efficiency of water use.

The effect of water-stress, temperature, and light on photosynthesis in speckled alder (Alnus incana (L.) Moench) was studied under controlled conditions by Hari and Luukkanen (21). Results demonstrated the influence of temperature in controlling photosynthesis of plants under water-stress: after prolonged stress, higher temperatures caused a large decrease in net carbon dioxide uptake even if the plant apparently had sufficient water.

Braun (7) conducted comparative studies on Alnus glutinosa and Salix alba concerning water economy and growth of various plant organs. The results indicated that although the two species are similar ecologically, their physiological behavior differs. Salix was found

to have a much greater consumption of water for a given stem and leaf volume increment as compared to Alnus. For similar water consumption, Salix produced only two-thirds the biomass of Alnus.

In a related study, Braun (8) compared Alnus glutinosa and Salix alba regarding growth patterns, water use, and productivity of water use (liters per square meter of leaf area). Results indicated that alder consumed less water in relation to leaf mass than willow.

Finally, Bair and Hennessey (2) reported on studies to investigate the quantitative effects of controlled water-stress on three species of alder, the only actinorhizal genus for which reliable cloning methods exist. The studies compared uninoculated (but fertilized) seedlings of Alnus glutinosa, Alnus serrulata (Alt.) Willd., and Alnus maritima Muhl. ex Nutt., using stomatal resistance, leaf area, and height development as indices of drought sensitivity. Statistically significant differences were found between the three species in response to controlled water-stress, with Alnus glutinosa showing poor stomatal control and structural degeneration under severe stress. In contrast, Alnus maritima maintained the lowest values of stomatal resistance under conditions of both moderate and severe water-stress. These studies quantified for the first time variation in xerotolerance between actinorhizal species. Because of the very limited amount of work that has been conducted in this area, considerable research is needed to establish whether water-stress effects are primarily on host or nodule physiology, what role the xerotolerance of the symbiont plays, or whether the nodule protects the endosymbiont from environmental aridity. The experiments reported in this thesis were designed to partially address these questions.

CHAPTER III

MATERIALS AND METHODOLOGY

Clonal material of European Black Alder (Alnus glutinosa, clone 2-58 of unknown seed source) and Seaside Alder (Alnus maritima, parent plant collected near Tishomingo, Oklahoma) was necessary in order to reduce the amount of plant-to-plant variation (48). The cloning process began with the severing of expanding branch tips from stock trees, leaving three to four leaves on the cutting for photosynthate production during rooting. The cuttings were then dipped into an IBA solution (8000 ppm in 2 percent ETOH as described in Appendix A, Table V) for 20 seconds. A fungicide mixture of five percent Benlate in talc was then applied to the stem of the cuttings to prevent damping off in the mist chamber.

The stem of each cutting was then implanted into a perlite-vermiculite heated rooting bed under a controlled mist system in a greenhouse environment. The cuttings were exposed daily to a 10 second mist every 15 minutes for an entire 16 hour controlled photoperiod. The duration of the mist was determined to insure a constant film of water on the leaf material to minimize transpiration and thus allow more photosynthate to be available for root production. Once the cuttings established a stable, uniform root system (trials have indicated a period of four to six weeks), the cuttings underwent a weaning process to eliminate plant shock when removed from the mist

system. The weaning process involved increasing the interval time between mists by 15 minutes every other day for one week.

Those cuttings which were to be nodulated in the experiment had 0.5 ml of inoculum Frankia MP 1 (from Dr. Helen Vishniac of the Oklahoma State University Botany and Microbiology Department) dribbled onto the root systems prior to being potted in six inch pots filled with a 2:1 mixture of Jiffy-Mix and oil dry potting mediums. All other cuttings were potted directly into the soil mixture. These latter plants were then put under a shade cloth in a greenhouse where they were fertilized and watered until adequate uniform growth was achieved. The inoculated plants were also put under a shade cloth in a greenhouse, but they were watered with a half-strength, nitrogen-free Van der Crones solution and a 10-15 mg NH_4-N per liter (ammonium sulfate) solution, which has been shown to aid the nodulation process (4). Previous trials indicated (by actual excavation of root systems) that adequate nodulation could be assumed by observing an overall "greening up" of the plant leaves. A lack of deep green colored leaves by the fifth week following inoculation was a sign that the Frankia endophyte did not infect the root system and nodulation did not occur.

Once adequate nodulation was observed, all the plants to be used for the experiment were placed in a controlled environmental chamber. The plants were exposed to a controlled 16 hour photoperiod at a plant surface light intensity of 720 microEinsteins per meter squared per second, with a day/night temperature setting of 25°C/15°C. All plants were then treated with 0.10 grams of Timek per pot for spider mite control. The design within the chamber followed a randomized block

design with each block being a replication of all treatment combinations. Species, type of fertilization, and moisture regime were the three factors involved in the determination of the treatment combinations.

The species factor was at two levels: Alnus glutinosa and Alnus maritima. The type of fertilization factor was assigned within the two species at three levels: (1) unfertilized and unnodulated (-FERT), which received no fertilizer for the entire 30 day experiment as well as not having been inoculated prior to the experiment; (2) fertilized and unnodulated (+FERT), which received a one-time dose of 10 grams of Osmocoat (19-6-12) slow release fertilizer just prior to the 30 day experiment; and (3) nodulated and unfertilized (NOD), which received no fertilizer for the entire 30 day period but did exhibit a functioning nodulated root system. Within the above factors, three levels of the moisture regime factor were imposed as follows: (1) well watered controls, (2) moderately stressed, and (3) severely stressed. To determine the actual allocations of water (per plant) all 54 plants (three replications of the above 18 treatment combinations) had their pots and stems (to the first leaf) enclosed in a plastic bag to eliminate soil water evaporation, and each day for one week the amount of water necessary to maintain a well watered condition was measured. This was achieved by measuring the amount of water used by the plant each day, indicated by slowly watering (from a known amount of water) each plant until field capacity of the soil was reached and water exuded from tiny holes near the bottom of each pot. The average water volume over the seven days determined the well watered level for that particular plant. Once the experiment was begun, the numerical water

regimes for the first 10 day period were as follows: (1) well watered control plants received 100 percent of the well watered level daily, (2) moderately stressed plants received 75 percent of the well watered level daily, and (3) severely stressed plants received 50 percent of the well watered level daily. The amount of water was reduced by 1/12 of the well watered level for each of the second and third 10 day periods, except for the well watered control plants, which were well watered throughout the duration of the experiment (1).

Growth and stress related parameters were measured every other day of the experiment beginning on the second day. Height, leaf area expansion, and diffusive stomatal resistance were the parameters monitored. Height growth was measured to the nearest 0.5 cm from the root collar to the base of the smallest emerging leaf. Leaf area expansion was measured to the nearest one square centimeter using a Li-Cor model LI 3000 portable leaf area meter. The expansion was measured above a predetermined point on the stem of each plant. For analysis of the leaf area expansion data and the height growth data. The initial measurement was subtracted from each subsequent measurement to reduce plant size variability as a factor. Diffusive stomatal resistance was measured to the hundredth of a second per centimeter using a Li-Cor model LI 1600 steady state porometer. Resistance was monitored using the LPA (Leaf Plastichron Age)=4 leaf every time to insure a uniformly aged leaf throughout the experiment. Further variation was reduced by measuring the resistance at the same time of day, presumably at the peak of photosynthetic activity each measurement day (i.e., between 2:30 and 3:30 p.m.).

Dinitrogen fixation was measured prior to the initiation of the experiment (i.e., before any stress was imposed) and again at the conclusion of each 10 day period. The nitrogenase enzyme activity was measured using the acetylene reduction method (18), and was expressed as millimoles of nitrogen fixed per plant per hour.

The acetylene reduction method used required that each sampled plant and its pot be enclosed in a fresh, nonreactive plastic bag below the first branch. To insure a gas-tight seal and to allow ease of gas sampling from the bag, a glass tube was fitted with a septum and a small amount of plasticine (nonreactive) clay was fitted at the neck of the bag and fastened with a twist-tie. Acetylene gas was generated each measurement day by the addition of calcium carbonate to water, and the gas was collected in a football bladder fitted with plastic tubing and a gas-tight septum. Each plant was then exposed to 10-15 percent concentration of this acetylene (by volume) and returned to the controlled environment chamber. At the end of one hour, the bag was agitated and two samples of gas were collected from each bag using Vacutainers. Unnodulated plants, empty bags, and evacuated Vacutainers served as controls. These two samples were later analyzed using a Tracor 565 gas chromatagraph fitted with a 1/8 inch outside diameter column packed with Poropak R with the oven temperature set at 150°C, and controllers 1, 2, 3, and 4 set at temperatures of 0°C, 275°C, 275°C, and 210°C, respectively. Data were processed using a Hewlett-Packard 3390 A integrator. Values of ethylene produced were then determined using a standard curve, which was generated each sampling day by injection of known concentrations of ethylene into the gas chromatagraph. These values were checked

periodically throughout the assaying process by reinjecting the known concentrations of ethylene.

An analysis of variance was used to compare treatment effects. Analysis was performed by species, fertilizer treatment, and water-stress level. Results of the analysis producing an observed significance level of $p \leq 0.05$ at a 95 percent probability level were considered statistically significant.

CHAPTER IV

RESULTS

Diffusive Stomatal Resistance

Diffusive stomatal resistance was monitored every other day during the 30 day experiment, beginning on the second day. The readings were taken using a Li-Cor steady state porometer at the peak of photosynthetic activity. Because the watering scheme was developed utilizing three 10 day periods, the stomatal resistance data collected were analyzed using three period groupings. Using the table of means generated from the data (Appendix A, Table VI), Table I was developed using the LSD procedure (41).

The analysis of the data showed that when comparing species, the Alnus maritima (Am) seedlings maintained a significantly lower stomatal resistance than the Alnus glutinosa (Ag) seedlings in the (+) fertilization and nodulated treatments as the water-stress moved from the control level to the severe level (Table I). These findings are consistent with earlier data analyzed by Bair (1).

The comparison for nodulated versus (+) fertilization treatments (Table I) showed similar responses for both species. Nodulated plants maintained stomatal resistance measurements generally comparable to the (+) fertilized plants even under moderate and severe water-stress. In fact, for the third period of the moderately stressed plants, the

TABLE I

STATISTICAL ANALYSIS OF DIFFUSIVE STOMATAL RESISTANCE DATA

Stress:		Control			Moderate			Severe		
Period:		1	2	3	1	2	3	1	2	3
					Alnus glutinosa (Ag) vs *Alnus maritima* (Am)					
	(-) FERT	NS	NS	NS	NS	NS	NS	NS	NS	NS
TRT:	(+) FERT	NS	NS	NS	S↑	S↑	S↑	S↑	S↑	S↑
	NOD	NS	NS	NS	NS	NS	NS	S↑	S↑	S↑
					Nodulated vs (+) Fertilization					
Species:	Ag	NS	NS	NS	NS	NS	S↓	NS	NS	NS
	Am	NS	NS	NS	NS	NS	S↓	NS	NS	NS
					Nodulated vs (-) Fertilization					
Species:	Ag	NS	NS	NS	NS	S↑	S↑	NS	S↑	S↑
	Am	NS	NS	NS	NS	NS	NS	S↓	NS	S↑
					(+) Fertilization vs (-) Fertilization					
Species:	Ag	NS	NS	NS	NS	S↑	S↑	NS	S↑	S↑
	Am	NS	NS	NS	NS	NS	S↑	NS	NS	S↑

Note: NS = No significant difference between means at the α=.05 level.

S = Significant difference between means at the α=.05 level, with direction of largest treatment (or species) mean indicated by arrows.

nodulated plants had significantly lower stomatal resistance readings than the (+) fertilized plants, for both species (Table I).

The comparisons of nodulated versus (-) fertilization and (+) fertilization versus (-) fertilization produced trends similar to one another for both species (Table I). Under the control level of water-stress there were no significant differences in either of the mean comparisons for either species. However, in the moderate and severe levels of stress, the Ag (-) fertilized plants maintained lower stomatal resistance readings than either the Ag nodulated plants or the Ag (+) fertilized plants in both periods two and three of the water-stress treatments (Table I). The same relationship holds for the Am (-) fertilized plants, but their stomatal resistance readings were significantly lower only in the third period of the water-stress treatments (Table I).

Height Growth

Height measurements were taken every other day during the experiment to the nearest 0.5 centimeters. These data were analyzed by subtracting the initial height from each measurement to adjust for variation among plant heights at the beginning of the experiment. An analysis of variance was performed on these adjusted values, and regression lines were generated for each treatment (Appendix B, Figures 1-6). From the regression lines, period growth values were calculated by determining incremental growth in centimeters per period. Table II shows the period growth values by period, treatment, water-stress level, and species, and the results of analysis for comparisons between these period growth values. Significant height

TABLE II

STATISTICAL ANALYSIS OF INCREMENTAL PERIOD HEIGHT GROWTH (cm/PERIOD)

Period:		1			2			3		
		- FERT	+ FERT	NOD	- FERT	+ FERT	NOD	- FERT	+ FERT	NOD
Control	Ag	a*1.0c	b 6.8e	b 3.5d	a 1.0c	a 4.0d	b 2.8d	b 2.6c	a 4.0c	b 3.8c
	Am	a 1.8c	a 4.3d	a 1.5c	b 2.2d	a 4.4e	a 0.8c	a 1.0c	b 5.5d	a 1.2c
Moderate	Ag	a 0.2c	b 4.3e	a 2.2d	a 0.2c	a 2.5d	b 1.8d	a 0.9c	a 1.5c	a 1.1c
	Am	a 0.1c	a 2.5d	a 0.8c	a 0.1c	a 2.0d	a 0.5c	a 0.2c	a 2.0d	a 0.3c
Severe	Ag	a 0.7c	b 2.9c	a 1.6c	a 1.0c	a 1.5c	a 1.0c	a 0.4c	a 1.6c	a 0.6c
	Am	a 0.4c	a 1.5cd	a 1.5d	a 0.2c	a 1.0c	a 0.2c	a 0.4c	a 0.4c	a 1.1c

*Species comparison indicated by letters preceding values. Fertilizer treatment comparisons indicated by letters following the values. Values preceded by or followed by same letters indicates no significant height difference for that specific comparison at the $\alpha = .05$ level.

Note: Ag = Alnus glutinosa; Am = Alnus maritima; LSD = 1.40, 1.18, and 1.41 for Periods 1, 2, and 3, respectively (to be used for any comparison within specific period).

growth differences were determined using a 95 percent confidence interval which was calculated for each of three periods using the appropriate analysis of variance table.

Table II indicates that the species comparison showed several significant height differences. The majority of these differences were found within the control water-stress level. Nodulated Alnus glutinosa (Ag) control plants consistently outgrew the Alnus maritima (Am) plants. The (+) fertlizer Ag control plants initially outgrew the Am plants, but the trend shifted so that within the third period Am outgrew Ag. The (-) fertilizer control plants had no consistent trend with regard to height growth. Within the moderately stressed level, one trend appeared in the first period where the (+) fertilizer Ag plants outgrew the (+) fertilizer Am plants. However, the above trend was not consistent throughout the experiment. The Ag nodulated, moderately stressed plants outgrew the Am nodulated, moderately stressed plants in the second 10 day period, but this trend did not continue for the third 10 day period. In the severely stressed plants, the only significant height difference occurred in the first 10 day period where the (+) fertilizer Ag plants outgrew the (+) fertilizer Am plants, but again this did not continue throughout the experiment.

A primary fertilizer treatment comparison of interest was the nodulated versus the (+) fertilization treatment. Within both the control and moderate water-stress levels for period one, the (+) fertilizer plants significantly outgrew the nodulated plants for both species. This trend held for the whole experiment for the Am plants, but there was no significant height difference between Ag nodulated

plants and Ag (+) fertilizer plants in the second or third periods (Table II). Within the severe water-stress level, the nodulated and (+) fertilizer plants expressed no significant height growth difference for either species within any period.

The comparisons of (+) fertilizer plants versus (-) fertilized plants and nodulated plants versus (-) fertilized plants showed that Ag (+) fertilizer plants and Ag nodulated plants outgrew the Ag (-) fertilizer plants within the control and moderate stress levels during the first and second periods, but not the third period. The Am (+) fertilizer plants outgrew the Am (-) fertilizer plants as well as the Am nodulated plants within the control and moderate stress levels for all three periods. Table II also shows that within the severe stress level there was no significant fertilizer treatment difference within either species for any period.

Leaf Area Expansion

Leaf area expansion measurements were taken every other day during the experiment using a Li-Cor model LI 3000 portable leaf area meter. These data were analyzed by subtracting the initial leaf area (measured from a predetermined point on the stem) from each subsequent measurement. An analysis of variance was performed on these adjusted measurements and regression lines were generated for each treatment (Appendix B, Figures 7-12). From the regression lines, period growth values were calculated by determining incremental growth in square centimeters per period. Table III shows the leaf area expansion values by period, treatment, water-stress level, and species, and the results of the statistical analysis for comparisons between these

TABLE III

STATISTICAL ANALYSIS OF INCREMENTAL LEAF AREA EXPANSION DATA (cm^2/PERIOD)

Period:		1			2			3		
		- FERT	+ FERT	NOD	- FERT	+ FERT	NOD	- FERT	+ FERT	NOD
Control	Ag	a*20.6c	a 170.0d	a 55.0c	a 37.5c	a 160.0d	a 150.0d	a 60.0c	a 135.0cd	a 210.0d
	Am	a -6.9c	a 120.0d	a 75.0d	a 28.8c	a 210.0e	a 115.0d	a 28.8c	a 160.0d	a 135.0d
Moderate	Ag	a -9.4c	a 135.0d	a 0.0c	a 22.5c	a 155.0d	a 115.0d	a 9.4c	a 110.0d	a 40.0cd
	Am	a 24.4c	a 100.0d	a 10.0c	a 23.8c	a 130.0d	a 65.0cd	a-11.9c	a 95.0d	a 10.0c
Severe	Ag	b-129.3c	a 120.0d	a 55.0d	a -7.5c	a 140.0d	a 60.0c	a -7.5c	a 100.0d	a 25.0cd
	Am	a-21.3c	a 100.0d	a 30.0cd	a 15.0c	a 80.0c	a 10.0c	a -6.9c	a 60.0c	a 47.5c

*Species comparison indicated by letters preceding values. Fertilizer treatment comparisons indicated by letters following the values. Values preceded by or followed by same letters indicates no significant leaf area expansion difference for that specific comparison at the $\alpha = .05$ level.

Note: Ag = Alnus glutinosa; Am = Alnus maritima; LSD = 75.53, 76.49, and 79.34 for Periods 1, 2, and 3, respectively (to be used for any comparison within specific period).

values. Significant leaf area expansion differences were determined using a 95 percent confidence interval which was calculated for each of the three periods using the appropriate analysis of variance table.

Table III shows that for the species comparison, there were no significant leaf area expansion differences between the two species for both the control and moderately stressed plants and across all three fertilizer treatments. In the severely stressed treatment, the Am (-) fertilizer plants outperformed the Ag (-) fertilizer plants within the first period, but the difference was not significant in the other two periods.

The analysis of the fertilization treatment comparisons indicated several significant leaf area expansion differences. A primary concern was how the nodulated plants performed compared to the (+) fertilizer treatment. In the control water-stress level, the leaf area of the nodulated plants was significantly lower than the leaf area of (+) fertilizer plants for Alnus glutinosa in the first period. However, in the second and third periods, the nodulated and (+) fertilizer plants expressed no significant leaf area expansion difference. The AM (+) fertilizer control plants showed a significantly greater leaf area expansion than the Am nodulated control plants in period two, but the difference was not significant in periods one or three.

Within the moderately stressed level, the Ag plants exhibited similar trends as in the control level, resulting in the nodulated plants performing as well as the (+) fertilizer plants. The Am plants, however, showed a reversal of the trend within the moderate level compared to the control level: the Am nodulated plants exhibited less leaf area expansion in both the first and third periods, and

growth was comparable to the (+) fertilizer plants in only the second period.

Within the severely stressed level, the Ag nodulated plants showed no significant leaf area expansion difference from the Ag (+) fertilizer plants in periods one and three. The Ag (+) fertilizer plants expressed significantly higher leaf area expansion than the Ag nodulated plants in the second period. The Am nodulated plants showed no significant leaf area expansion difference compared to Am (+) fertilizer plants in all three periods.

The (+) fertilization treatment versus (-) fertilization treatment and the nodulation treatment versus (-) fertilization treatment comparisons (Table III) showed that the Ag (+) fertilization outgrew the Ag (-) fertilization within the first and second periods for the control level and within all periods for the moderate and severe levels. The Ag nodulated plants outgrew the Ag (-) fertilizer plants within the second and third periods for the control level; within the second period for the moderate level; and within the first period for the severe level. The Am (+) fertilizer plants exhibited greater leaf area expansion than Am (-) fertilizer plants within all three periods for the control and moderate levels and within the first period for the severe level. The Am nodulated plants outgrew the Am (-) fertilizer plants within all three periods for the control level but within no periods of the moderate or severe levels.

Nitrogen Fixation Capacity and Efficiency

Nitrogen fixation capacity was measured by taking acetylene reduction assays (as described earlier) prior to the initiation of any

water-stress (period = 0) and at the end of each 10 day period. The data were converted from mg/l/hr ethylene produced to mmoles N reduced per plant per hour, assuming a 3:1 ratio of C_2H_2 to N_2 reduced, based on the C_2H_2 to C_2H_4 reaction requiring two electrons and the N_2 to NH reaction requiring six electrons. An analysis of variance was performed on the converted data (Appendix A, Table VII) and a table of means and the ranking of the means using the Duncan's New Multiple Range Test (41) at the α =.05 level was generated (Table IV).

The analysis shows that for Alnus glutinosa (Ag) there were no significant period differences between nitrogen fixation capacity means, nor any significant water stress level differences between the means. The only significant period difference for Alnus maritima (Am) was for the second period of the control plants, where the value was significantly greater than for periods zero and one, but was not significantly different from period three (Table IV).

The analysis of variance indicated that there was no significant mean difference between species; however, the trend is such that over 80 percent of the Ag means were greater than the Am means. Table IV also shows that under moderate and severe water-stress, the Ag nodulated plants had greater capacity values (though not statistically significant) when compared to Am nodulated plants. Within the Ag plants there is a clear trend showing a decrease in capacity as the stress levels get more severe. However, this trend is not statistically significant. Values for the moderately and severely stressed Am plants were consistently lower than those for the control Am plants (Table IV). However, this trend is not statistically significant.

TABLE IV

STATISTICAL ANALYSIS OF NITROGEN FIXATION CAPACITY
DATA (mMOLES/PLANT/HOUR)

		Control	Moderate	Severe	Control	Moderate	Severe
		Alnus glutinosa			*Alnus maritima*		
Period:	0	a*15.90e	a 13.63e	a 11.67e	a 11.07e	a 2.49e	a 7.27e
	1	a 10.58e	a 8.75e	a 7.53e	a 10.95e	a 3.76e	a 3.77e
	2	a 15.50e	a 9.55e	a 6.66e	b 23.89f	a 2.78e	a 3.10e
	3	a 18.91e	a 7.94e	a 5.62e	ab 17.89e	a 4.17e	a 3.05e

*Period comparisons are indicated by letters (based on N = 3 observations) preceding means. Water-stress level comparisons are indicated by letters following means. Means either preceded or followed by like letters indicate no significant capacity differences based on Duncan's test at $\alpha = .05$.

Discussion and Summation

The study found that Alnus glutinosa (Ag) exhibited higher stomatal resistance than Alnus maritima (Am) in the (+) fertilization treatment under moderate stress and in the (+) fertilization and nodulated treatments under severe stress (see Table I). The (+) fertilization data agrees with the findings of Bair (1), who showed similar species differences. The reasons for this species difference could be either anatomical or physiological in origin. Siwecki and Kozlowski (39), working with Populus clones, showed that differences in diffusive stomatal resistance could be linked to variations in stomatal size, stomatal frequency, or control of the stomatal aperture. Davies et al. (13) produced evidence that stomatal length and stomatal frequency can vary dramatically among genera and between species within a genus. Therefore, one or more of these factors could vary between the Alnus species, causing a significant difference in stomatal resistance values. Physiologically, the Am plants may maintain significantly lower stomatal resistance values than Ag plants by better controlling the internal water balance, rather than by better stomatal control. For example, the Am plants may be capable of adjusting osmotically as a mechanism to tolerate water-stress. In contrast, the Ag plants apparently close stomates at the first sign of stress, as a method of avoiding the effects of water-stress.

The fact that there was no significant species difference within the control level indicates that stress conditions must be present before the clones of these Alnus species can be screened for stomatal resistance differences. This observation is different from the

findings of Kelliher (24), who found, when working with Eastern cottonwood (Populus deltoides Bartr.), that clonal differences in stomatal resistance could be detected within the control (or well-watered) water-stress level.

By examining the magnitudes of the stomatal resistance values, it is evident that as the stress level moved from the control to the severe level, the values increased progressively. This is an indication that the method of stressing the plants was successful in achieving moderate and severe levels of stress. However, no mortality was observed, even at the extreme range of the stress treatments.

Data in Table I indicate that the nodulated plants of both species exhibited statistically similar stomatal resistance measurements to the (+) fertilizer plants within all water-stress levels. However, the (-) fertilizer plants exhibited stomatal resistance values statistically similar or lower than either the nodulated or (+) fertilizer plants of both species, even when under stress. This may be explained by at least two reasons: (1) the lack of necessary nutrients, coupled with the imposed water-stress, led to the structural degeneration of leaf material in addition to chlorosis; and (2) the imposed stress levels caused initial leaf drop by the (-) fertilizer plants, leading to a situation where the amount of water initially designated to acheive moderate or severe stress levels may actually have been more than adequate to produce low stomatal resistance values.

Bair (1) found that measurements of stomatal resistance alone were not adequate selection criteria, but when combined with height growth and leaf area expansion data, a more sensitive indicator of water-stress was formulated. Table III shows that the Ag nodulated

plants exhibited significantly less leaf area expansion than the (+) fertilizer plants within period one for the control and moderate stress levels, but for the second and third periods, the two treatments expressed statistically similar growth. This could have been due to the fact that as the plant grew, more photosynthate was being transported to the nodules, enabling them to gain in efficiency. The Am nodulated plants maintained comparable growth to Am (+) fertilizer plants for the control and severe stress levels. However, the Am nodulated plants exhibited significantly less leaf area expansion than Am (+) fertilizer plants in periods one and three of the moderate stress level. The data from Table III occasionally showed that the (-) fertilizer plants of both species grew as well as the (+) fertilizer and nodulated plants. In fact, under both the moderate and severe stress levels, the (+) fertilizer and nodulated plants consistently had greater leaf area expansion than the (-) fertilizer plants. In addition, the (-) fertilizer plants often experienced a decrease in leaf area expansion under moderate and severe stress levels.

The leaf area expansion data also indicated that there were no significant species differences, regardless of treatment or level of stress. This observation agrees with the relative leaf area expansion data of (+) fertilizer plants studied by Bair (1).

The height growth data in Table II indicated that, of the 27 individual species comparisons, the Ag plants expressed significantly more height growth than the Am plants eight times, the Am plants expressed significantly more height growth than Ag plants twice, and the height growth difference between the species were not significant 17 times. The only trend observed was that 70 percent of the

findings of Kelliher (24), who found, when working with Eastern cottonwood (Populus deltoides Bartr.), that clonal differences in stomatal resistance could be detected within the control (or well-watered) water-stress level.

By examining the magnitudes of the stomatal resistance values, it is evident that as the stress level moved from the control to the severe level, the values increased progressively. This is an indication that the method of stressing the plants was successful in achieving moderate and severe levels of stress. However, no mortality was observed, even at the extreme range of the stress treatments.

Data in Table I indicate that the nodulated plants of both species exhibited statistically similar stomatal resistance measurements to the (+) fertilizer plants within all water-stress levels. However, the (-) fertilizer plants exhibited stomatal resistance values statistically similar or lower than either the nodulated or (+) fertilizer plants of both species, even when under stress. This may be explained by at least two reasons: (1) the lack of necessary nutrients, coupled with the imposed water-stress, led to the structural degeneration of leaf material in addition to chlorosis; and (2) the imposed stress levels caused initial leaf drop by the (-) fertilizer plants, leading to a situation where the amount of water initially designated to acheive moderate or severe stress levels may actually have been more than adequate to produce low stomatal resistance values.

Bair (1) found that measurements of stomatal resistance alone were not adequate selection criteria, but when combined with height growth and leaf area expansion data, a more sensitive indicator of water-stress was formulated. Table III shows that the Ag nodulated

plants exhibited significantly less leaf area expansion than the (+) fertilizer plants within period one for the control and moderate stress levels, but for the second and third periods, the two treatments expressed statistically similar growth. This could have been due to the fact that as the plant grew, more photosynthate was being transported to the nodules, enabling them to gain in efficiency. The Am nodulated plants maintained comparable growth to Am (+) fertilizer plants for the control and severe stress levels. However, the Am nodulated plants exhibited significantly less leaf area expansion than Am (+) fertilizer plants in periods one and three of the moderate stress level. The data from Table III occasionally showed that the (-) fertilizer plants of both species grew as well as the (+) fertilizer and nodulated plants. In fact, under both the moderate and severe stress levels, the (+) fertilizer and nodulated plants consistently had greater leaf area expansion than the (-) fertilizer plants. In addition, the (-) fertilizer plants often experienced a decrease in leaf area expansion under moderate and severe stress levels.

The leaf area expansion data also indicated that there were no significant species differences, regardless of treatment or level of stress. This observation agrees with the relative leaf area expansion data of (+) fertilizer plants studied by Bair (1).

The height growth data in Table II indicated that, of the 27 individual species comparisons, the Ag plants expressed significantly more height growth than the Am plants eight times, the Am plants expressed significantly more height growth than Ag plants twice, and the height growth difference between the species were not significant 17 times. The only trend observed was that 70 percent of the

significant differences occurred in the control stress level, indicating that height growth was generally comparable in the moderate and severe stress levels. The Ag nodulated plants exhibited less height growth than Ag (+) fertilizer plants within the first period of the control and moderate stress levels, but by the third period the difference in height growth between the two treatments was not significant. The Am nodulated plants exhibited less height growth than Am (+) fertilizer plants within all periods for the control and moderate stress levels. There was no significant growth difference between nodulated plants and (+) fertilizer plants within all periods for the severe stress level for both species. Thus, the act of nodulation enabled the Ag plants to perform as well as the fertilized plants regarding height growth, except when the plants were under severe water-stress. The Am plants, however, did not seem to benefit by the act of nodulation with regard to height growth.

Baseline responses of the two Alnus species to the varying water regimes can also be obtained from Tables II and III. A comparison of the height growth and leaf area expansion for the control, moderate, and severe water stress levels within a period for each species indicated that the Ag and Am (+) fertilizer plants exhibited superior height growth in the control regime compared to the moderate and severe stress regimes, but only the Am (+) fertilizer plants expressed more leaf area expansion in the control regime compared to the moderate or severe stress regimes. For the nodulated treatment, the Ag plants expressed significantly greater height growth and leaf area expansion consistently in the control regime compared to the moderate or severe stress regimes. The Am nodulated plants expressed superior

leaf area expansion in the control regime compared to the moderate or severe stress regimes, with no significant stress level in height growth. Therefore, different Alnus species react differently to progressive water stressing.

Coupling the height growth and leaf area expansion data with the stomatal resistance data suggests that the process of nodulation was of more benefit to the Ag plants compared to Am plants, as exemplified by: (1) the Ag nodulated plants maintained comparable stomatal resistance to Am nodulated plants until the severe stress level, whereas the Ag (+) fertilizer plants expressed higher stomatal resistance measurements than Am (+) fertilizer plants within the moderate and severe stress level; and (2) the Ag nodulated plants exhibited comparable height growth and leaf area expansion to Ag (+) fertilizer plants by the third period of the experiment for all stress levels, whereas Am nodulated plants exhibited less height growth and leaf area expansion than Am (+) fertilizer plants by the third period of the experiment 67 percent of the time (Tables II and III).

The nitrogen fixation capacity analysis showed no species difference regardless of level of stress (Appendix A, Table XIV). The Ag and Am nodulated plants exhibited a trend of decreasing nitrogen fixation capacity with increasing water-stress, but statistically the trend was not significant. Therefore, unstressed and severely stressed nodulated plants expressed statistically comparable values of nitrogen fixation capatiy. At the time when stress was imposed, neither the nodulated plants nor the (+) fertilizer plants experienced leaf abscission, whereas the (-) fertilizer plants expe-rienced dramatic leaf drop. A problem associated with the nodulated plants is the queston

of initial uniformity of nodulation. It could be possible to better quantify the degree of nodulation by expressing the nodule fresh weight on a leaf dry weight, leaf area, or total dry weight basis. This would not guarantee uniform nodulation but rather serve as an index of the degree of uniformity achieved.

Summary

This experiment, conducted within a controlled environment chamber, was designed to compare the effects of water-stress on two unfertilized, fertilized, and nodulated species of Alder. Care should be taken when extrapolating the results of this study to different growth chamber and field environments.

Major findings of the experiment are presented as follows:

1. The Alnus maritima (Am) plants generally exhibited lower stomatal resistance values than Alnus glutinosa (Ag) plants when stress was imposed. This may have been due to variation in stomatal frequency, stomatal size, leaf thickness, or the ability to osmotically adjust.

2. The nodulated plants of both species exhibited statistically similar stomatal resistance values to (+) fertilizer plants for all stress levels.

3. The magnitude of the stomatal resistance values increased for both species as the degree of stress increased. This agrees with the results of Bair (1) and confirms the validity of the method of stressing used in this study.

4. The (-) fertilizer plants of both species had statistically similar or lower stomatal resistance values than the (+) fertilizer

plants or the nodulated plants of both species for all the stress levels. However, this could be explained by structural leaf degeneration and initial leaf abscission due to stress shock, resulting in a possible masking of the true effect of the stress upon the (-) fertilizer plants.

5. In order to detect species differences for the two Alnus clones studied utilizing stomatal resistance as a screening tool, it was necessary to impose progressive water-stressing (i.e., species differences were not evident under well-watered conditions).

6. The leaf area expansion data showed that there was no species difference for any stress level within any fertilization treatment. This is consistent with the findings of Bair (1).

7. The nitrogen fixation capacity of the nodulated plants showed a trend of decreasing capacity as stress became more severe. However, this trend was not statistically significant. Likewise, species differences in nitrogen fixation capacity were not significant at any stress level. It is possible that values of nitrogen fixation efficiency by water stress level would show species differences.

The following are modifications which, in retrospect, could be made concerning the methodology of this experiment:

1. An index needs to be devised to better estimate the degree of nodulation of the plants entering the experiment. Nodule fresh weight per leaf area or leaf dry weight could be used by destructively sampling a portion of the nodulated plants prior to allocation in the experiment.

2. Height and leaf area expansion need not be measured as often as in this experiment. Measurements taken at the beginning and end of each period would suffice to supply data for analysis.

3. A better understanding of the sensitivity of stomatal control could be achieved by measuring the stomatal resistance every day of the experiment.

4. To quantify the effects of fertilization, the nitrogen content of both the (+) fertilizer and the nodulated plants should be assayed at the conclusion of further experiments using the Kjeldhal analysis.

5. It would be interesting to correlate the stress data collected here with actual water potential data. Therefore, monitoring the water potential of both the plant and soil should be included in any future studies.

It is anticipated that future studies utilizing the findings of this experiment, when coupled with the results of xerotolerance testing of various Frankia strains, will allow a more complete analysis of water-stress effects in the Alnus genus.

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APPENDIXES

APPENDIX A

TABLES

TABLE V

IBA ROOTING HORMONE SOLUTION
(8000 ppm, 2% ETOH)

Materials

IBA powder (Sigma I1875)
2N NaOH
2N HCl
100% ETOH
Distilled Water

Directions

1. Mix 0.8g IBA in 4 ml of 2N NaOH. Stir.
2. Add 2 ml of 100% ETOH. IBA should be in solution.
3. Dilute to 92 ml by slowly adding distilled water.
4. Slowly adjust pH to ca. 6.3 with 2N HCl.
5. If IBA precipitates, back titrate with 2N NaOH until precipitate disappears. Then, very slowly, readjust pH to ca. 6.3 with 2N HCl.
5. Make final dilution to 100 ml with distilled water.

Note: Keep refrigerated and protected from light to prevent oxidation of hormone. Use immediately. This formula has a very short shelf life.

TABLE VI

DIFFUSIVE STOMATAL RESISTANCE MEANS (s/cm)

Period:		1	2	3			1	2	3
		Alnus glutinosa (control)					*Alnus maritima* (control)		
	- FERT	0.98	0.75	0.55		- FERT	10.43	3.54	2.30
TRT:	+ FERT	2.78	1.11	2.00	TRT:	+ FERT	4.22	1.08	1.55
	NOD	1.11	0.88	0.51		NOD	1.68	2.85	1.56
		Alnus glutinosa (moderate)					*Alnus maritima* (moderate)		
	- FERT	2.34	4.84	1.27		- FERT	4.41	5.35	5.84
TRT:	+ FERT	18.31	34.18	47.93	TRT:	+ FERT	4.54	16.36	34.35
	NOD	9.18	23.09	28.80		NOD	6.42	12.57	10.88
		Alnus glutinosa (severe)					*Alnus maritima* (severe)		
	- FERT	20.51	3.25	6.09		- FERT	20.62	17.00	6.39
TRT:	+ FERT	24.73	41.19	39.69	TRT:	+ FERT	13.01	22.59	24.28
	NOD	17.67	31.39	44.68		NOD	4.43	23.61	24.44

TABLE VII

NITROGEN FIXATION CAPACITY AND EFFICIENCY, BY SPECIES AND WATER-STRESS LEVEL

Species	Water Stress	0***	1	2	3	Final Fresh Nodule Weight (g)	Period 3 Efficiency****
Ag*	C**	14.48	14.07	18.46	17.87	3.18	5.62
Ag	M	13.75	9.33	11.96	9.28	6.21	1.49
Ag	S	16.16	6.72	7.87	4.38	3.57	1.23
Am	C	9.36	12.73	22.70	19.20	3.19	6.02
Am	M	0.04	3.87	0.03	2.70	0.45	6.00
Am	S	9.14	6.30	4.30	2.98	2.41	1.24
Ag	C	17.81	12.54	1.24	14.86	2.49	5.97
Ag	M	11.02	6.62	9.48	7.56	4.87	1.55
Ag	S	9.79	3.61	4.50	5.08	1.70	2.99
Am	C	19.14	14.92	37.53	20.88	3.04	6.86
Am	M	3.33	6.00	5.01	4.86	0.64	7.59
Am	S	4.56	2.48	0.10	1.10	1.11	0.99
Ag	C	15.40	5.14	26.78	24.00	6.10	3.93
Ag	M	16.11	10.30	7.22	6.98	5.32	1.31
Ag	S	9.07	12.26	7.62	7.40	3.40	2.18
Am	C	4.70	5.21	11.43	13.59	2.86	4.75
Am	M	4.11	1.42	3.30	4.96	1.52	3.26
Am	S	8.12	2.52	4.90	5.06	1.99	2.54

*Ag = Alnus glutinosa; Am = Alnus maritima; **C = Control, M = Moderate, S = Severe; ***Nitrogen fixing capacity (mmN_2/plant/hr), by periods 0, 1, 2, 3; ****Nitrogen fixing efficiency (mmN_2/gm f.w. nodule/hr).

TABLE VIII

STATISTICAL ANALYSIS FOR ADJUSTED LEAF AREA EXPANSION WITHIN PERIOD 1

SOURCE	DF	SUM OF SQUARES	MEAN SQUARE	F VALUE	PR > F	R-SQUARE	C.V.
MODEL	68	15339293.02685229	225577.83863018	191.13	0.0001	0.984771	16.4721
ERROR	201	237221.52499956	1180.20659204		ROOT MSE		DIFFLA MEAN
CORRECTED TOTAL	269	15576514.55185185			34.35413501		208.55925926

SOURCE	DF	TYPE I SS	F VALUE	PR > F
BLOCK	2	290565 69629630	123.10	0.0001
S	1	32956.62592593	27.92	0.0001
F	2	7600307.47407407	3219 91	0.0001
S*F	2	199589 91851852	84.56	0.0001
W	1	2868526 27222222	2430 53	0.0001
W*W	1	31023.42407407	26.29	0.0001
W*S	1	177158 93888889	150.11	0.0001
W*F	2	124048.74444444	52.55	0.0001
W*S*F	2	270796 94444444	114.72	0.0001
W*W*F	2	56215 07037038	23.82	0.0001
S*F*WTRT*BLOCK	37	3363901.44259264	77.03	0 0001
D1	1	169708 01666667	143.80	0.0001
D1*S	1	2352 09074074	1.99	0.1596
D1*F	2	71465 47777778	30.28	0 0001
D1*S*F	2	75 89259259	0 03	0.9684
W*D1	1	47219 80277779	40.01	0 0001
W*D1*S	1	868 00277778	0 74	0.3921
W*D1*F	2	7993.67222224	3.39	0.0358
W*D1*S*F	2	6291 27222221	2.67	0.0720
W*W*D1	1	11040 00833342	9.35	0.0025
W*W*D1*F	2	7188.23888919	3.05	0.0498

2xS.E. = 75.53

TESTS OF HYPOTHESES USING THE TYPE I MS FOR S*F*WTRT*BLOCK AS AN ERROR TERM

SOURCE	DF	TYPE I SS	F VALUE	PR > F
S	1	32956.62592593	0.36	0 5508
F	2	7600307 47407407	41.80	0.0001
S*F	2	199589 91851852	1.10	0.3443
W	1	2868526 27222222	31.55	0.0001
W*W	1	31023 42407407	0 34	0 5627
W*S	1	177158 93888889	1.95	0 1711
W*F	2	124048.74444444	0 68	0 5117
W*S*F	2	270796 94444444	1.49	0.2387
W*W*F	2	56215 07037038	0.31	0.7359

TABLE IX

STATISTICAL ANALYSIS FOR ADJUSTED LEAF AREA EXPANSION WITHIN PERIOD 2

SOURCE	DF	SUM OF SQUARES	MEAN SQUARE	F VALUE	PR > F	R-SQUARE	C.V.
MODEL	68	6293670.20185188	92553.97355665	84.36	0.0001	0.966147	27 8667
ERROR	201	220525.72777775	1097.14292427		ROOT MSE		DIFFLA MEAN
CORRECTED TOTAL	269	6514195.92962963			33.12314786		118.86296296

SOURCE	DF	TYPE I SS	F VALUE	PR > F
BLOCK	2	146886.49629630	66.94	0.0001
S	1	675 29259259	0.62	0.4336
F	2	3360994 49629630	1531.70	0 0001
S*F	2	123772.80740741	56.41	0.0001
W	1	781310.45000000	712.13	0.0001
W*W	1	118 53518519	0.11	0.7427
W*S	1	116994 00555556	106.64	0.0001
W*F	2	5083 23333333	2.32	0.1012
W*S*F	2	42969.21111111	19.58	0.0001
W*W*F	2	23041 18148148	10 50	0 0001
S*F*WTRT*BLOCK	37	1291106 62037040	31.81	0 0001
D1	1	262020 41666667	238.82	0.0001
D1*S	1	4340 66851852	3.96	0.0481
D1*F	2	94318 74444445	42.98	0.0001
D1*S*F	2	5145 60370370	2 35	0 0985
W*D1	1	23944 71111112	21 82	0.0001
W*D1*S	1	864 90000000	0 79	0.3757
W*D1*F	2	5406 00555557	2.46	0.0877
W*D1*S*F	2	4545.14999999	2.07	0.1287
W*W*D1	1	43 20000000	0.04	0.8429
W*W*D1*F	2	88.47222221	0.04	0.9605

2xS.E. = 76.49

TESTS OF HYPOTHESES USING THE TYPE I MS FOR S*F*WTRT*BLOCK AS AN ERROR TERM

SOURCE	DF	TYPE I SS	F VALUE	PR > F
S	1	675 29259259	0.02	0.8901
F	2	3360994.49629630	48.16	0.0001
S*F	2	123772.80740741	1.77	0.1839
W	1	781310 45000000	22.39	0.0001
W*W	1	118.53518519	0 00	0 9538
W*S	1	116994 00555556	3.35	0 0752
W*F	2	5083.23333333	0 07	0 9299
W*S*F	2	12969.21111111	0.62	0 5457
W*W*F	2	23041 18148118	0.33	0 7209

TABLE X

STATISTICAL ANALYSIS FOR ADJUSTED LEAF AREA EXPANSION WITHIN PERIOD 3

SOURCE	DF	SUM OF SQUARES	MEAN SQUARE	F VALUE	PR > F	R-SQUARE	C.V.
MODEL	68	1463284.19120376	21518.88516476	21.82	0.0001	0.909845	88.6997
ERROR	147	144993.95694439	986.35344860		ROOT MSE		DIFFLA MEAN
CORRECTED TOTAL	215	1608278.14814815			31.40626448		35.40740741

SOURCE	DF	TYPE I SS	F VALUE	PR > F
BLOCK	2	24290.25925926	12.31	0.0001
S	1	13035.57407407	13.22	0.0004
F	2	463212.78703704	234.81	0.0001
S*F	2	19843.39814815	10.06	0.0001
W	1	91960.56250000	93.23	0.0001
W*W	1	852.89120370	0.86	0.3540
W*S	1	61959.50694444	62.82	0.0001
W*F	2	21217.79166667	10.76	0.0001
W*S*F	2	19690.68055556	9.98	0.0001
W*W*F	2	21540.86574074	10.92	0.0001
S*F*WTRT*BLOCK	37	499922.83101852	13.70	0.0001
D1	1	78984.90370370	80.08	0.0001
D1*S	1	28.03333333	0.03	0.8664
D1*F	2	111473.00851852	56.51	0.0001
D1*S*F	2	4692.20555556	2.38	0.0962
W*D1	1	11178.56805556	11.33	0.0010
W*D1*S	1	2980.86805555	3.02	0.0842
W*D1*F	2	2097.25277778	1.06	0.3480
W*D1*S*F	2	5678.28611112	2.88	0.0594
W*W*D1	1	285.28935185	0.29	0.5915
W*W*D1*F	2	8358.56759264	4.24	0.0163

2xS.E. = 79.34

TESTS OF HYPOTHESES USING THE TYPE I MS FOR S*F*WTRT*BLOCK AS AN ERROR TERM

SOURCE	DF	TYPE I SS	F VALUE	PR > F
S	1	13035.57407407	0.96 NS	0.3324
F	2	463212.78703704	17.14 S	0.0001
S*F	2	19843.39814815	0.73 NS	0.4867
W	1	91960.56250000	6.81 S	0.0130
W*W	1	852.89120370	0.06	0.8030
W*S	1	61959.50694444	4.59	0.0389
W*F	2	21217.79166667	0.79	0.4635
W*S*F	2	19690.68055556	0.73	0.4893
W*W*F	2	21540.86574074	0.80	0.4582

TABLE XI

STATISTICAL ANALYSIS FOR ADJUSTED HEIGHT GROWTH WITHIN PERIOD 1

SOURCE	DF	SUM OF SQUARES	MEAN SQUARE	F VALUE	PR > F	R-SQUARE	C.V.
MODEL	68	798.04722222	11.73598856	31.90	0.0001	0.936538	29.7075
ERROR	147	54.07777778	0.36787604		ROOT MSE		DIFFHT MEAN
CORRECTED TOTAL	215	852.12500000			0.60652786		2.04166667

SOURCE	DF	TYPE I SS	F VALUE	PR > F
BLOCK	2	3.17361111	4.31	0.0151
S	1	21.40740741	58.19	0.0001
F	2	319.79861111	434.66	0.0001
S*F	2	13.34953704	18.14	0.0001
W	1	35.00694444	95.16	0.0001
W*W	1	0.75000000	2.04	0.1555
W*S	1	0.06250000	0.17	0.6808
W*F	2	12.76388889	17.35	0.0001
W*S*F	2	0.87500000	1.19	0.3074
W*W*F	2	37.09722222	50.42	0.0001
S*F*WTRT*BLOCK	37	114.59027778	8.42	0.0001
D1	1	142.28148148	386.76	0.0001
D1*S	1	8.35648148	22.72	0.0001
D1*F	2	53.63101852	72.99	0.0001
D1*S*F	2	4.49490741	6.11	0.0028
W*D1	1	17.11250000	46.52	0.0001
W*D1*S	1	0.73472222	2.00	0.1597
W*D1*F	2	7.70833333	10.48	0.0001
W*D1*S*F	2	1.94444444	2.64	0.0745
W*W*D1	1	2.53518519	6.89	0.0096
W*W*D1*F	2	0.37314815	0.51	0.6032

2xS.E. = 1.40

TESTS OF HYPOTHESES USING THE TYPE I MS FOR S*F*WTRT*BLOCK AS AN ERROR TERM

SOURCE	DF	TYPE I SS	F VALUE	PR > F
S	1	21.40740741	6.91	0.0124
F	2	319.79861111	51.63	0.0001
S*F	2	13.34953704	2.16	0.1302
W	1	35.00694444	11.30	0.0018
W*W	1	0.75000000	0.24	0.6256
W*S	1	0.06250000	0.02	0.8878
W*F	2	12.76388889	2.06	0.1417
W*S*F	2	0.87500000	0.14	0.8687
W*W*F	2	37.09722222	5.99	0.0056

TABLE XII

STATISTICAL ANALYSIS FOR ADJUSTED HEIGHT GROWTH WITHIN PERIOD 2

SOURCE	DF	SUM OF SQUARES	MEAN SQUARE	F VALUE	PR > F	R-SQUARE	C.V.
MODEL	68	7250.34166667	106.62267157	405.45	0.0001	0.992762	8.1399
ERROR	201	52.85833333	0.26297678		ROOT MSE		DIFFHT MEAN
CORRECTED TOTAL	269	7303.20000000			0.51281202		6.30000000

SOURCE	DF	TYPE I SS	F VALUE	PR > F
BLOCK	2	123.01666667	233.89	0.0001
S	1	326.70000000	1242.31	0.0001
F	2	3343.47222222	6356.97	0.0001
S*F	2	94.83888889	180 32	0.0001
W	1	1347.53472222	5124 16	0.0001
W*W	1	36 03750000	137.04	0.0001
W*S	1	2.81250000	10.69	0.0013
W*F	2	594 83611111	1130.97	0 0001
W*S*F	2	63.95833333	121 60	0.0001
W*W*F	2	43 95277778	83 57	0 0001
S*F*WTRT*BLOCK	37	1121 81027778	115 30	0 0001
D1	1	78 58518519	298.83	0.0001
D1*S	1	1.35000000	5 13	0.0245
D1*F	2	16 25092593	30 90	0 0001
D1*S*F	2	3.50833333	6 67	0 0016
W*D1	1	29 46944444	112 06	0 0001
W*D1*S	1	0 90000000	3 42	0 0658
W*D1*F	2	6.57222222	12 50	0 0001
W*D1*S*F	2	7.80000000	14 83	0 0001
W*W*D1	1	6 84814815	26.04	0.0001
W*W*D1*F	2	0.05740741	0.11	0 8966

2xS.E. = 1.18

TESTS OF HYPOTHESES USING THE TYPE I MS FOR S*F*WTRT*BLOCK AS AN ERROR TERM

SOURCE	DF	TYPE I SS	F VALUE	PR > F
S	1	326.70000000	10.78	0 0023
F	2	3343.47222222	55.14	0.0001
S*F	2	94.83888889	1.56	0.2228
W	1	1347.53472222	44.44	0.0001
W*W	1	36 03750000	1 19	0.2827
W*S	1	2.81250000	0 09	0.7624
W*F	2	594 83611111	9 81	0.0004
W*S*F	2	63.95833333	1.05	0.3585
W*W*F	2	43.95277778	0.72	0.4912

TABLE XIII

STATISTICAL ANALYSIS FOR ADJUSTED HEIGHT GROWTH WITHIN PERIOD 3

SOURCE	DF	SUM OF SQUARES	MEAN SQUARE	F VALUE	PR > F	R-SQUARE	C.V.
MODEL	68	3344.50115741	49.18384055	132.31	0.0001	0.978148	13.1800
ERROR	201	74.71736111	0.37172816		ROOT MSE		DIFFHT MEAN
CORRECTED TOTAL	269	3419.21851852			0.60969514		4.62592593

SOURCE	DF	TYPE I SS	F VALUE	PR > F
BLOCK	2	46.09629630	62.00	0.0001
S	1	187.50000000	504.40	0.0001
F	2	1738 19074074	2337 99	0.0001
S*F	2	76 33888889	102.68	0.0001
W	1	443.36805556	1192 72	0.0001
W*W	1	1.61157407	4.34	0.0386
W*S	1	3.33472222	8.97	0.0031
W*F	2	196.05277778	263.70	0.0001
W*S*F	2	0 85277778	1.15	0.3196
W*W*F	2	39 67870370	53.37	0.0001
S*F*WTRT*BLOCK	37	488.79398148	35 54	0.0001
D1	1	72 23379630	194.32	0 0001
D1*S	1	2 74490741	7.38	0.0072
D1*F	2	24.12314815	32.45	0.0001
D1*S*F	2	2 75648148	3 71	0 0262
W*D1	1	12 65625000	34.05	0.0001
W*D1*S	1	0 03402778	0 09	0 7625
W*D1*F	2	5.51250000	7.41	0.0008
W*D1*S*F	2	1 52638889	2.05	0.1310
W*W*D1	1	0.51134259	1.38	0.2422
W*W*D1*F	2	0 58379630	0.79	0.4574

2xS.E. = 1.41

TESTS OF HYPOTHESES USING THE TYPE I MS FOR S*F*WTRT*BLOCK AS AN ERROR TERM

SOURCE	DF	TYPE I SS	F VALUE	PR > F
S	1	187 50000000	14.19	0.0006
F	2	1738.19074074	65.79	0.0001
S*F	2	76.33888889	2.89	0.0682
W	1	443 36805556	33.56	0.0001
W*W	1	1.61157407	0 12	0 7289
W*S	1	3 33472222	0 25	0 6183
W*F	2	196.05277778	7 42	0.0020
W*S*F	2	0.85277778	0.03	0.9683
W*W*F	2	39 67870370	1 50	0.2360

TABLE XIV

STATISTICAL ANALYSIS FOR NITROGEN FIXATION CAPACITY

SOURCE	DF	SUM OF SQUARES	MEAN SQUARE	F VALUE	PR > F	R-SQUARE	C.V.
MODEL	35	2915.07494801	83.28785567	5.23	0.0001	0.835592	42.3060
ERROR	36	573.55845000	15.93217917		ROOT MSE		M2FIX MEAN
CORRECTED TOTAL	71	3488.63339801			3.99151339		9.43666111

SOURCE	DF	ANOVA SS	F VALUE	PR > F
REP	2	4.76213611	0.27	0.7612
SPECIES	1	180.97531250	11.36	0.0018
WATER	2	1366.49701944	42.85	0.0001
SPECIES*WATER	2	165.41732500	5.19	0.0104
REP*SPECIES*WATER	10	577.90708056	3.63	0.0021
PERIOD	3	90.44843750	1.90	0.1483
SPECIES*PERIOD	3	90.44911528	1.90	0.1483
WATER*PERIOD	6	337.52325833	3.53	0.0075
SPECIES*WATER*PERIOD	6	98.09440389	1.03	0.4243

TESTS OF HYPOTHESES USING THE ANOVA MS FOR REP*SPECIES*WATER AS AN ERROR TERM

SOURCE	DF	ANOVA SS	F VALUE	PR > F
SPECIES	1	180.97531250	3.13	0.1072
WATER	2	1366.49701944	11.81	0.0023
SPECIES*WATER	2	165.41732500	1.43	0.2841

APPENDIX B

FIGURES

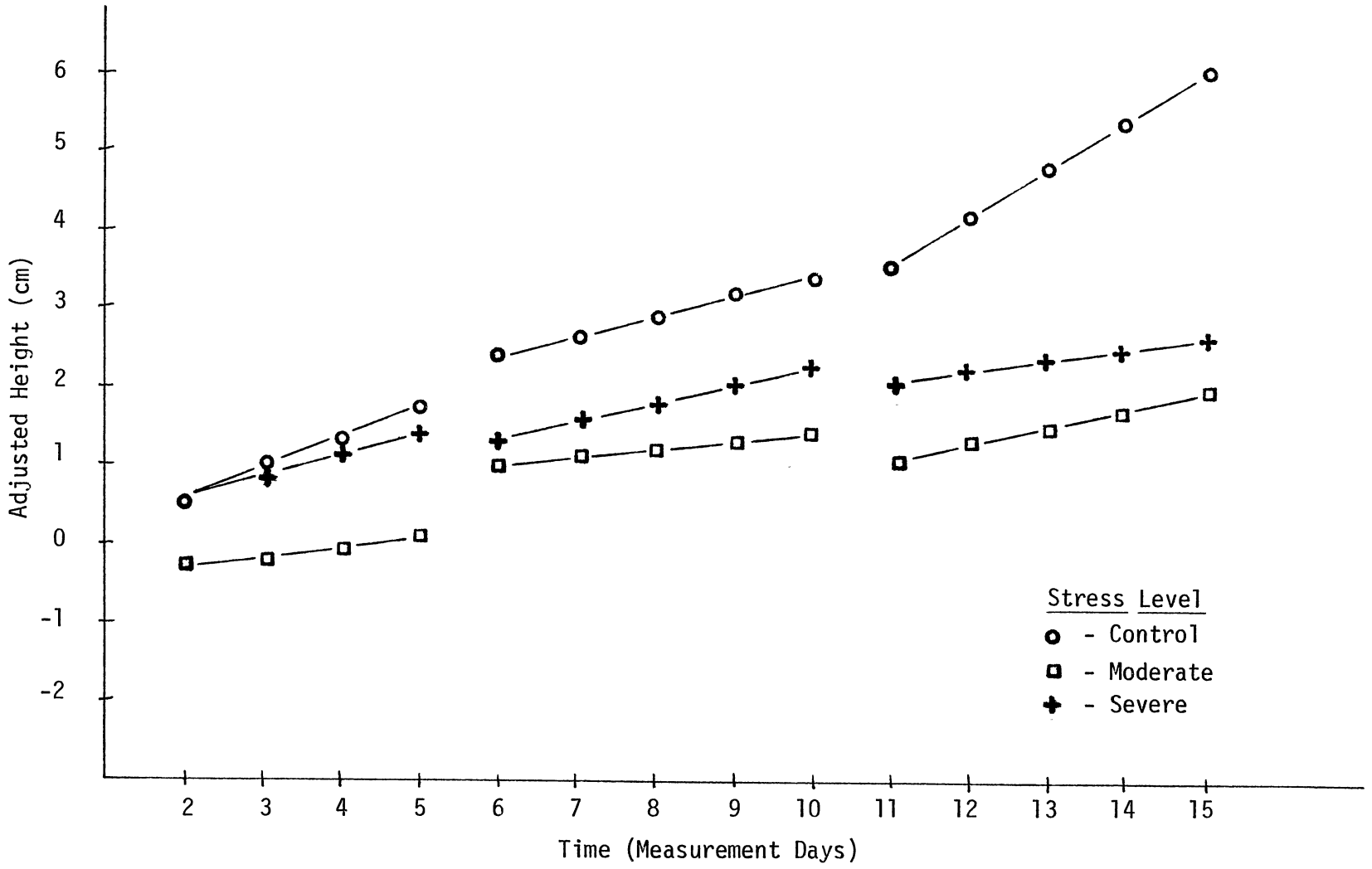

Figure 1. Height Growth Regression Lines for Alnus glutinosa (- FERT)

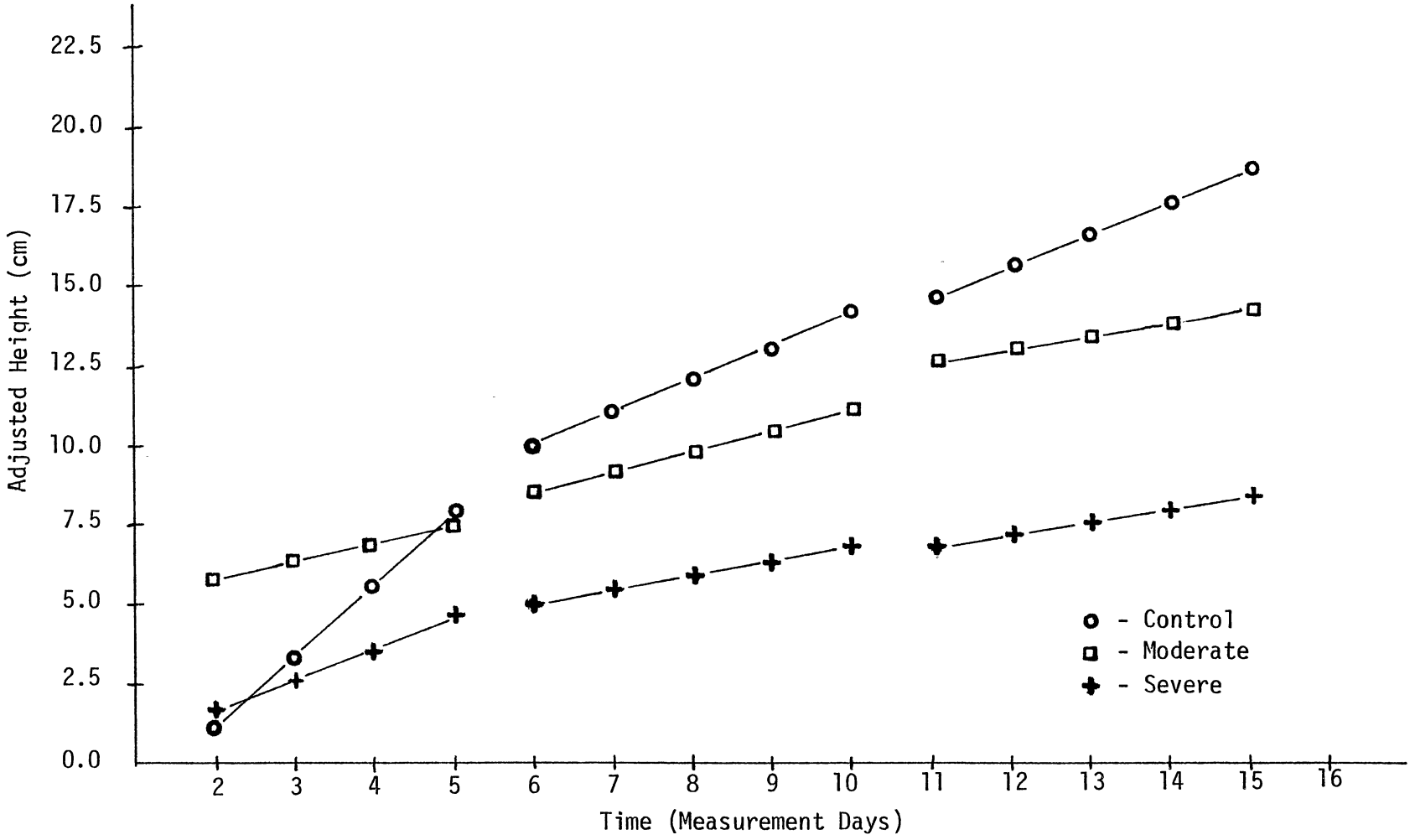

Figure 2. Height Growth Regression Lines for Alnus glutinosa (+ FERT)

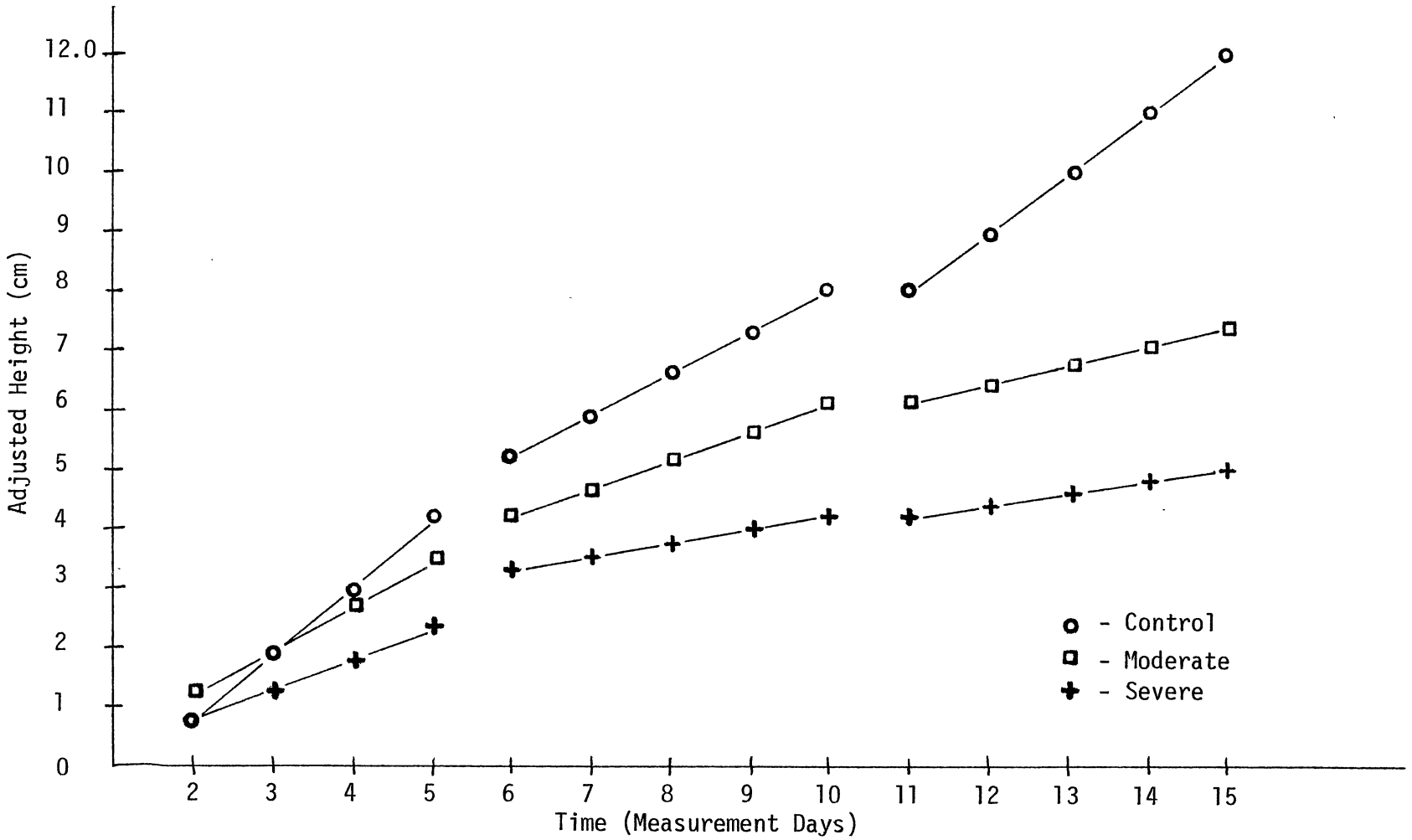

Figure 3. Height Growth Regression Lines for Alnus glutinosa (NOD)

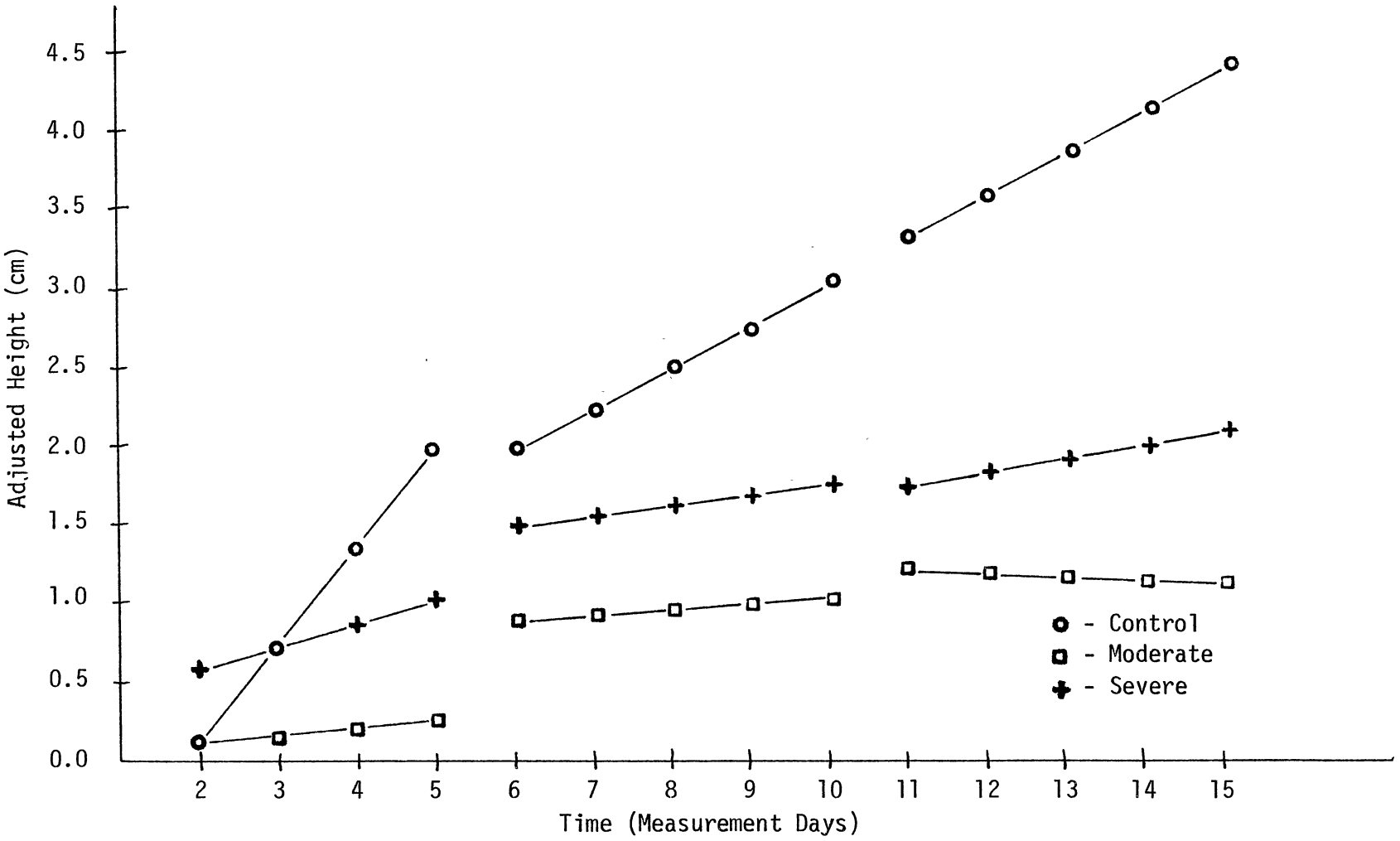

Figure 4. Height Growth Regression Lines for Alnus maritima (- FERT)

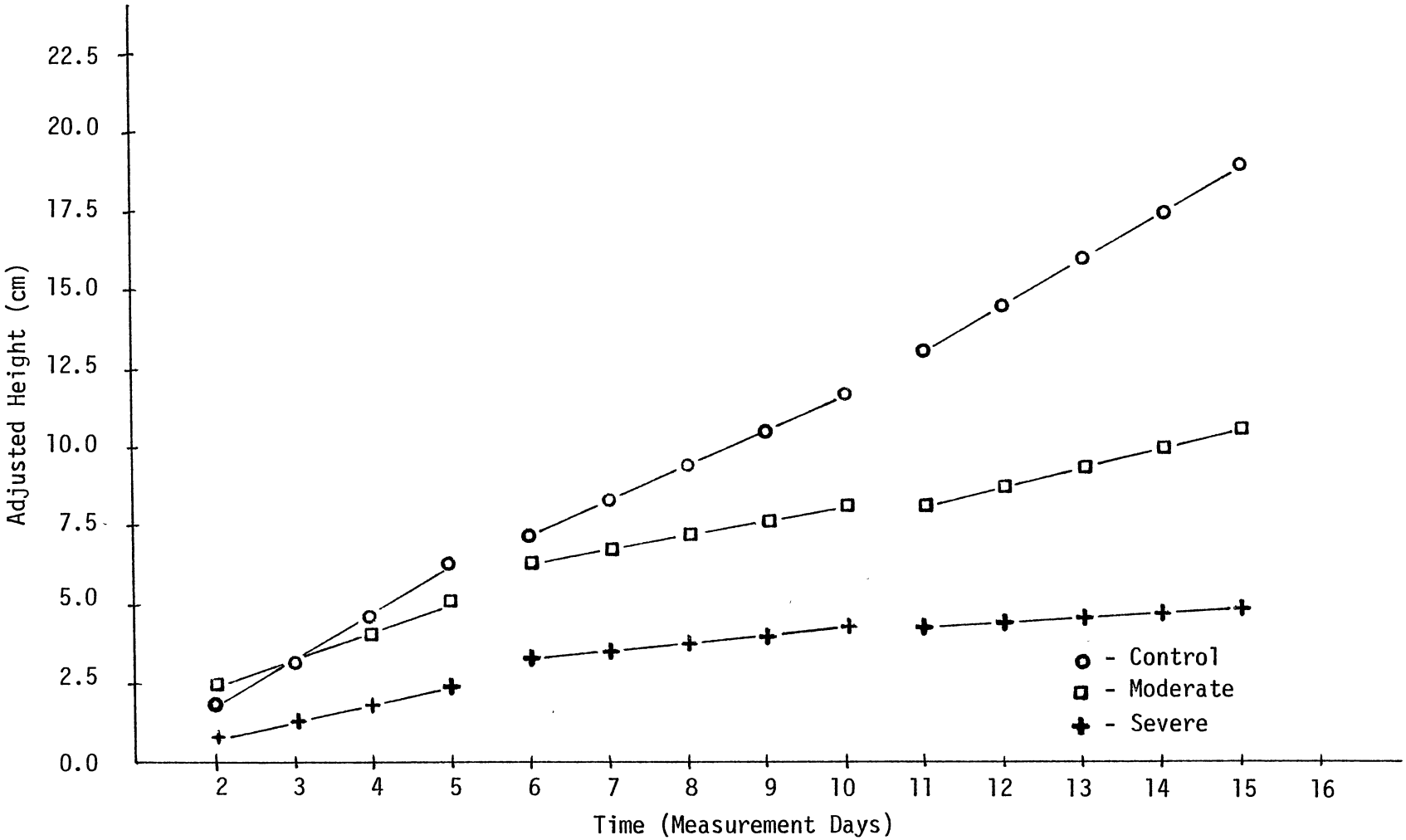

Figure 5. Height Growth Regression Lines for Alnus maritima (+ FERT)

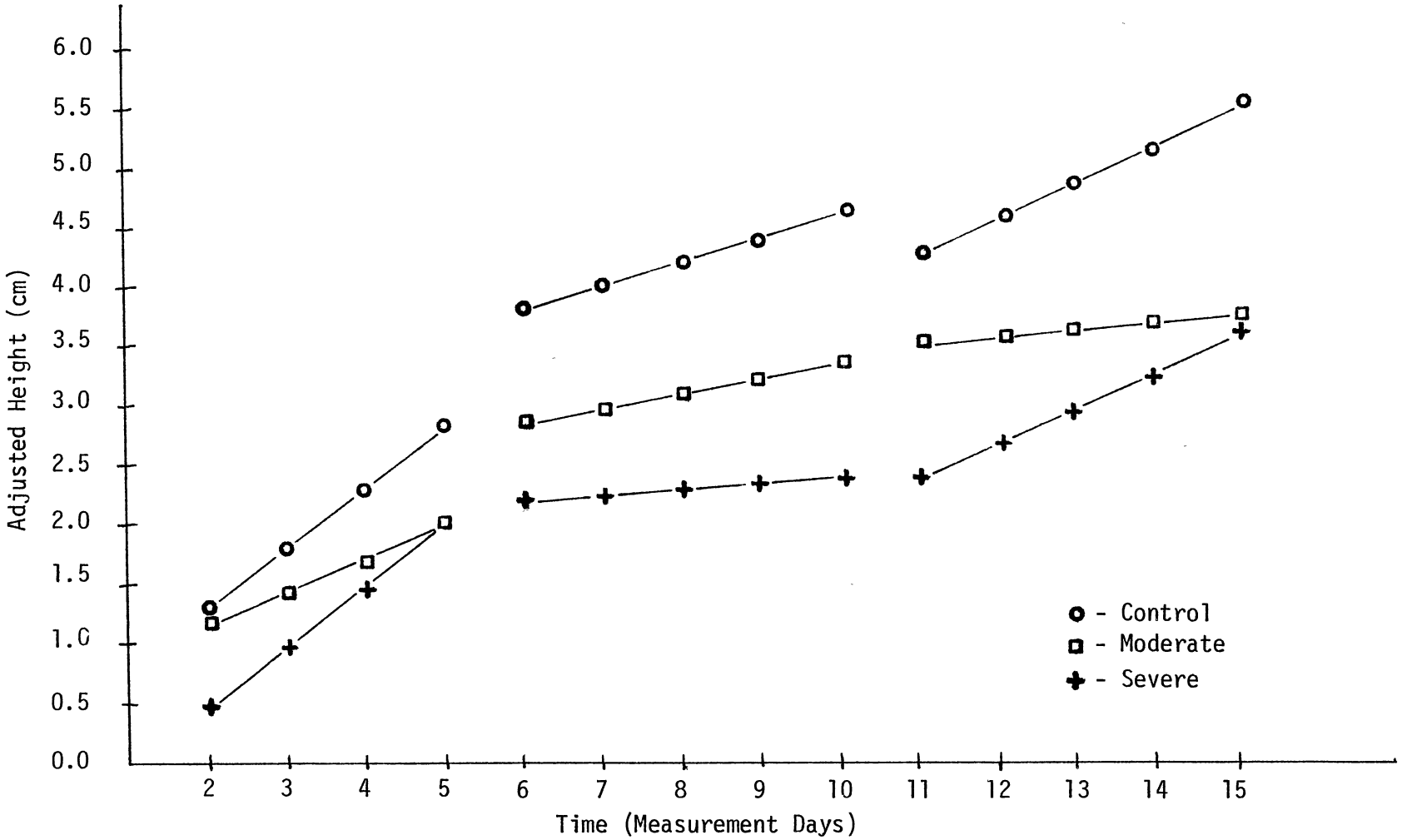

Figure 6. Height Growth Regression Lines for Alnus maritima (NOD)

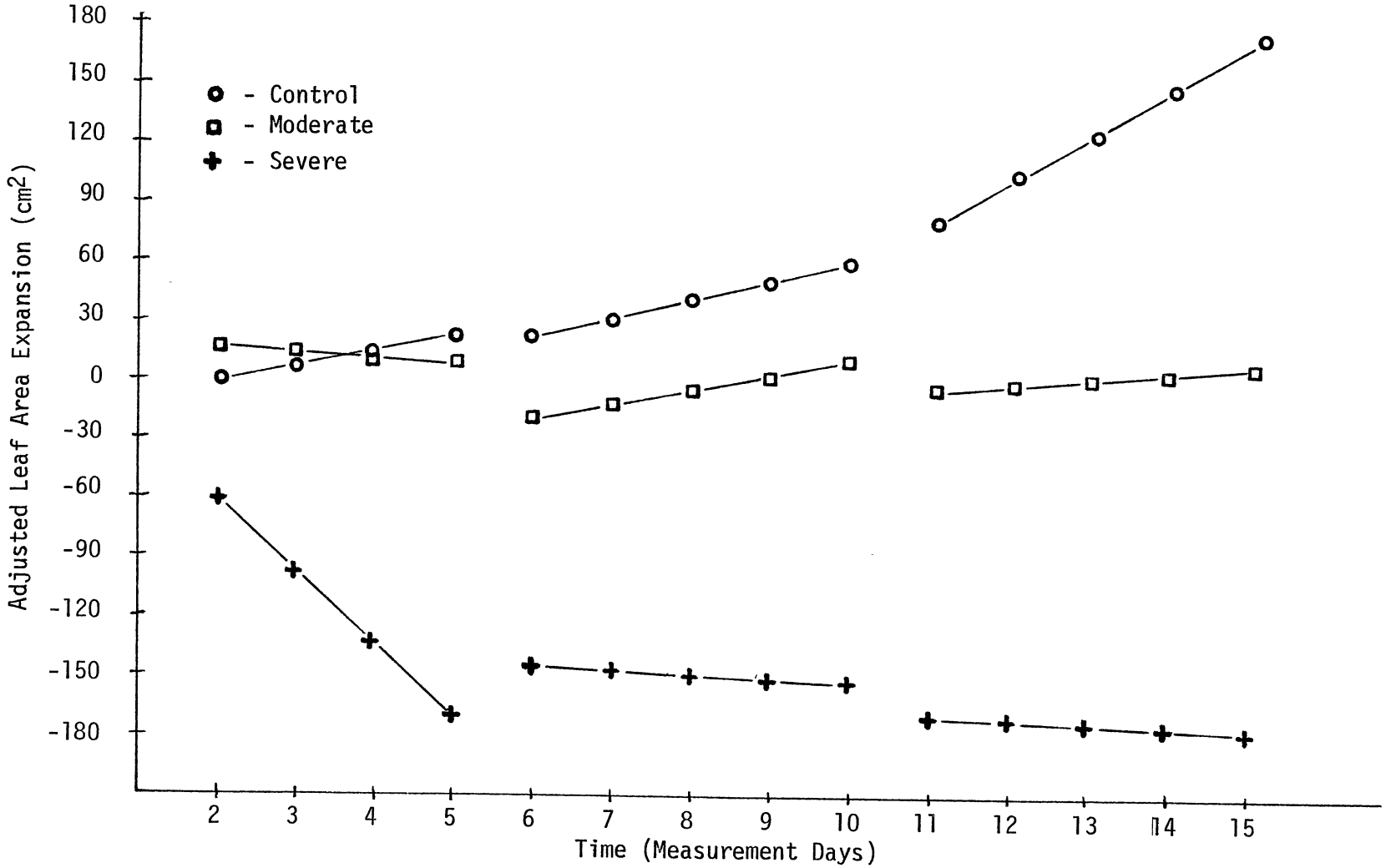

Figure 7. Leaf Area Expansion Regression Lines for Alnus glutinosa (- FERT)

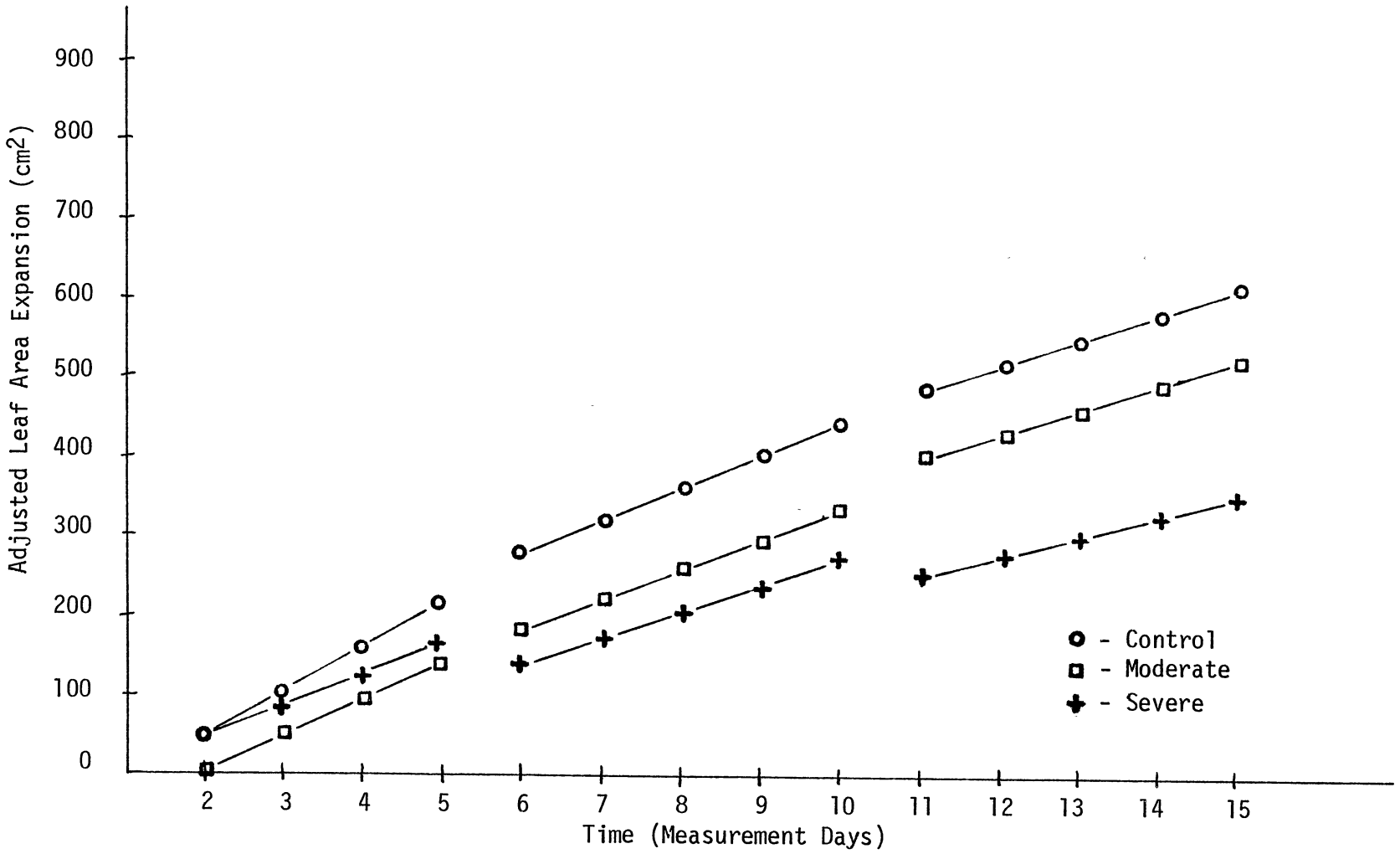

Figure 8. Leaf Area Expansion Regression Lines for Alnus glutinosa (+ FERT)

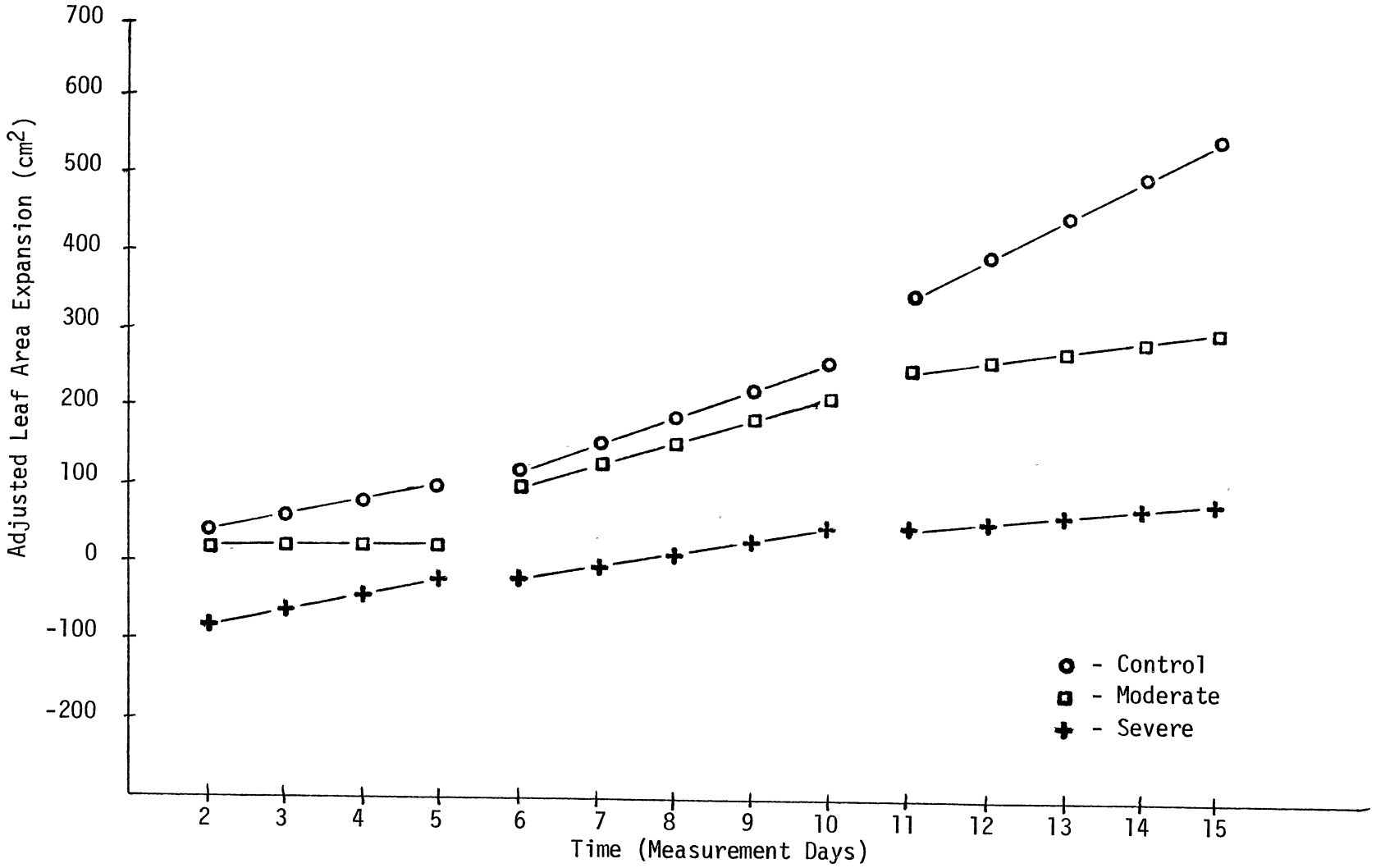

Figure 9. Leaf Area Expansion Regression Lines for Alnus glutinosa (NOD)

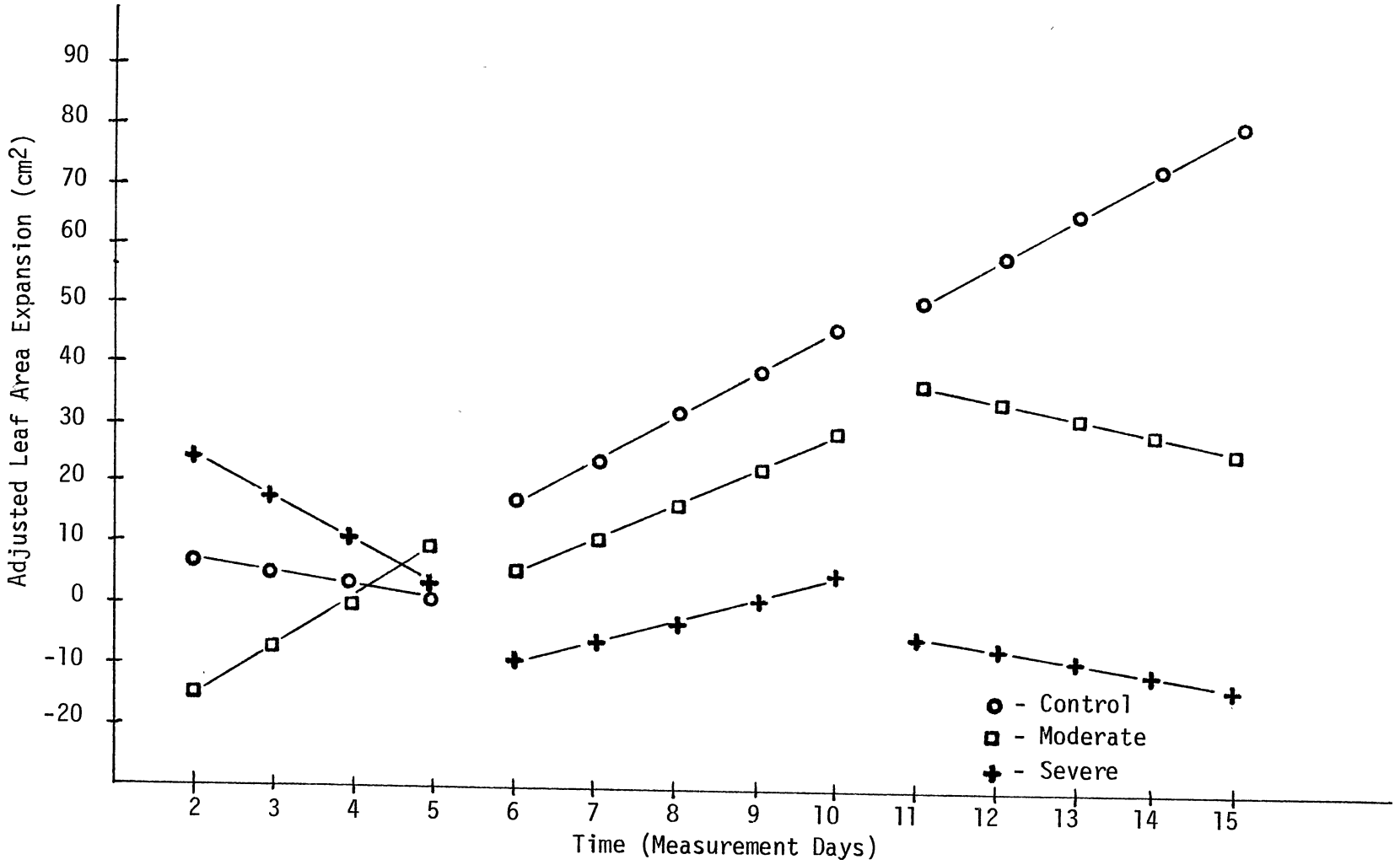

Figure 10. Leaf Area Expansion Regression Lines for Alnus maritima (- FERT)

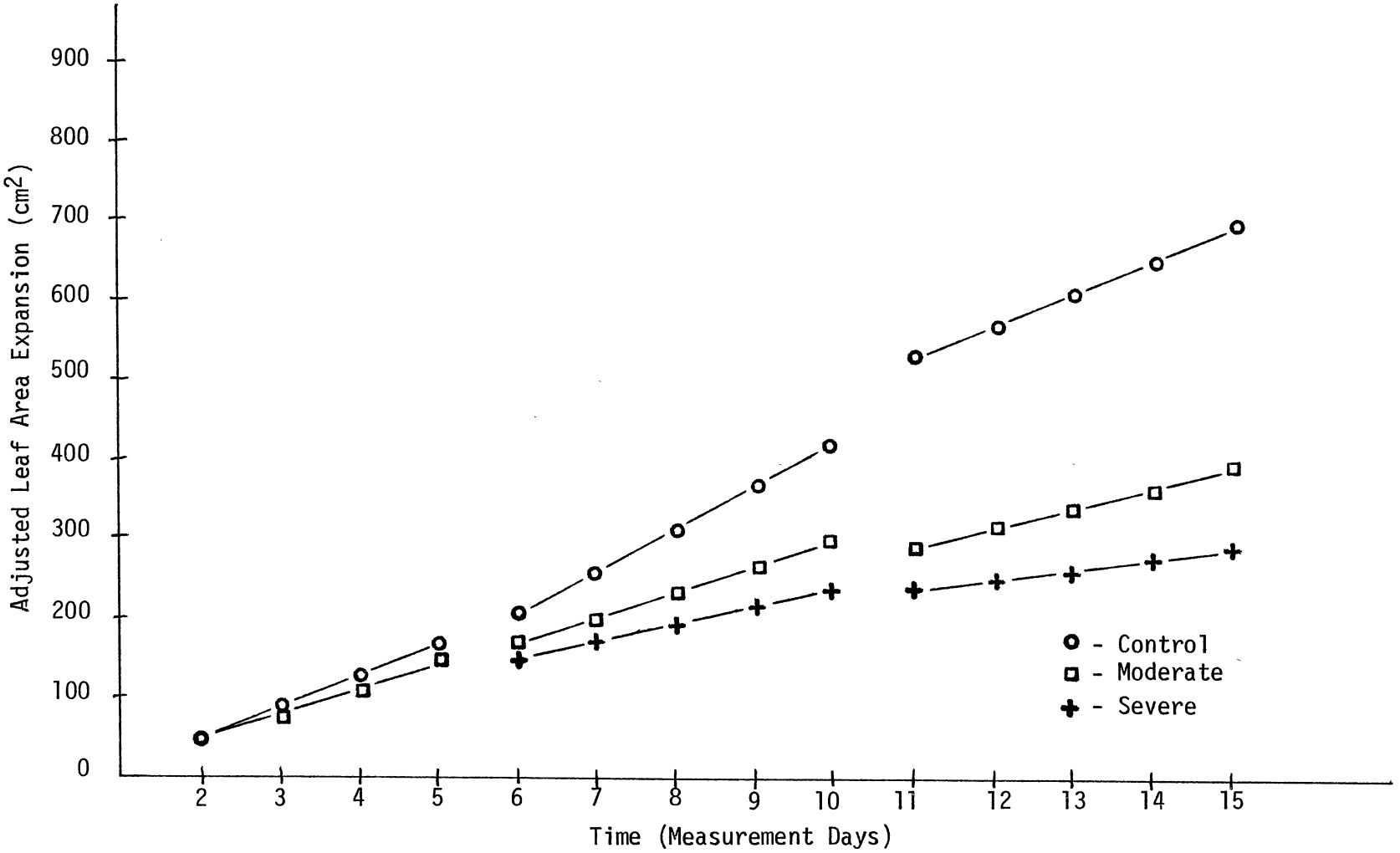

Figure 11. Leaf Area Expansion Regression Lines for Alnus maritima (+ FERT)

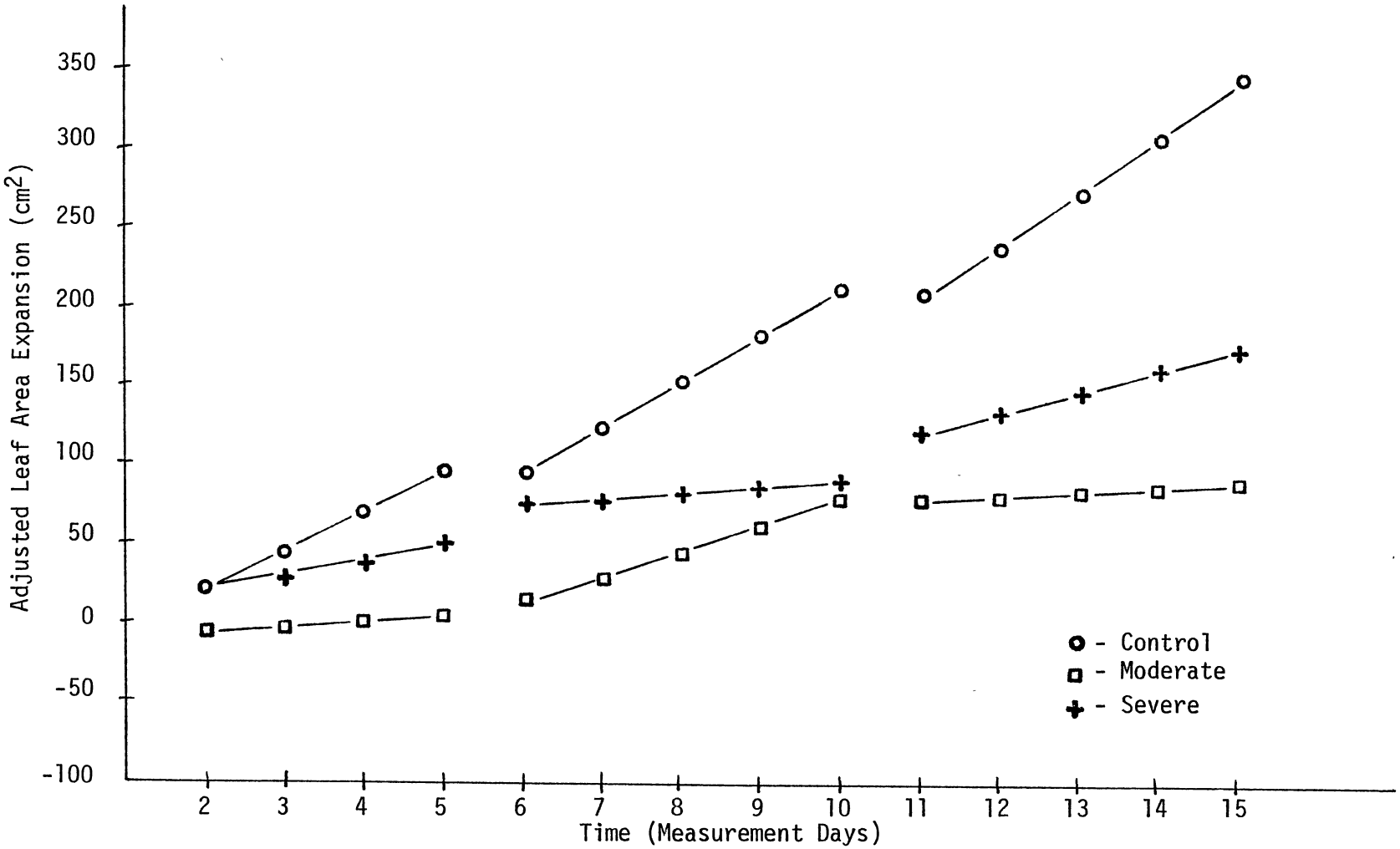

Figure 12. Leaf Area Expansion Regression Lines for Alnus maritima (NOD)

VITA 2

Edward Mark Lorenzi

Candidate for the Degree of

Master of Science

Thesis: A COMPARISON OF WATER-STRESS EFFECTS FOR TWO UNFERTILIZED, FERTILIZED, AND NODULATED ALDER SPECIES

Major Field: Forest Resources

Biographical:

Personal Data: Born in Belle Vernon, Pennsylvania, December 10, 1958, the son of Edward J. and Norma L. Lorenzi. Married to Gloria G. Pritt in 1981.

Education: Graduated from Eisenhower High School, Lawton, Oklahoma, in May, 1977; attended Cameron University, Lawton, Oklahoma, 1977-78; received Bachelor of Science degree in Agriculture (major in Forestry) from Oklahoma State University in 1981; completed requirements for Master of Science degree at Oklahoma State University in May, 1984.