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Genetic Variation in Two Contrasting Habitats of Eastern Cottonwood: Responses to Different Water Status and Nitrogen Levels

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Eko Bhakti Hardiyanto

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Ph.D degree in Forest Genetics

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GENETIC VARIATION IN TWO CONTRASTING HABITATS OF EASTERN COTTONWOOD: RESPONSES TO DIFFERENT WATER STATUS AND NITROGEN LEVELS

By

Eko Bhakti Hardiyanto

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ABSTRACT

GENETIC VARIATION IN TWO CONTRASTING HABITATS
OF EASTERN COTTONWOOD:
RESPONSES TO DIFFERENT WATER STATUS AND NITROGEN LEVELS

By

Eko Bhakti Hardiyanto

Selection for clones of eastern cottonwood (Populus deltoides Bartr.) that grow well on marginal lands is very important for plantation establishment. The objective of the study was to assess the genetic variation of trees from two contrasting habitats of eastern cottonwood in their response to water stress and nitrogen fertilization.

Four clones from a sand dune (dry site) and another four clones from a floodplain (wet site) were used to establish field plot and greenhouse studies. Both studies used a split-split plot arranged in a randomized complete block design. Three different water regimes were applied: severe, moderate, and no-water stress. More severe water stress treatments were applied in the greenhouse study. Nitrogen levels used in the field plot study were 0, 200, and 400 kg N/ha/yr, while those in the greenhouse were 0, 2.25, and 4.50 gr N per plant.

The following measurements were made for the field plot study: height, diameter, leaf area, specific leaf

weight, leaf water potential, stomatal conductance, transpiration, and photosynthesis. Similar measurements were taken for the greenhouse study with the following additional measurements: shoot biomass, root biomass, and root-shoot ratio.

Water stress reduced all characteristics, except photosynthesis in the field plot study. Nitrogen fertilization had no significant effects on any characteristics. The effects of water status were independent of nitrogen level in all characteristics. Clones between sites (habitats) differed significantly only for height and diameter. No interactions involving clones with other treatments were detectable. Clones from the wet site grew faster than those from the dry site. For height and diameter the contribution of clones between sites to the total variation was large.

In the greenhouse study, the effects of water status usually depended upon nitrogen level. The effect of nitrogen was more profound under well-watered conditions. Under well-watered conditions, nitrogen fertilization resulted in increased height, diameter, shoot biomass, leaf area, specific leaf weight, stomatal conductance, and transpiration, but decreased root biomass and root-shoot ratio. Leaf water potential and photosynthesis were not affected significantly by nitrogen fertilization.

For height, diameter, and shoot biomass, clones between sites differed significantly under well-water

conditions. For other characteristics, the site of origin of clones was not significantly different. Except for height, diameter, and shoot biomass, interactions involving clones between sites and water status were of little importance. None of the interaction involving clones between sites and nitrogen level was significant. The contribution of clones between sites to the total variation was small. However, clones from the wet site were more plastic to changes in water status.

Results of these studies suggested that clones from the dry site did not grow better than those from the wet site under water stress. Selection for clones as source material for plantation establishment or breeding programs for marginal lands needs to be undertaken cautiously.

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Finally, I wish to express my gratitude to my parents for their support and encouragement throughout my academic career.

To my parents and grandmother

and

to the memory of my mother (1933-1963)

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

INTRODUCTION

Eastern cottonwood (Populus deltoides Bartr.) is one of the largest and most widespread tree species in the eastern United States. Due to its rapid growth rate and ease of vegetative propagation, this species has become commercially important, particularly in the southern United States along the Mississippi River Valley. Eastern cottonwood provides an excellent material for pulp, sawlogs and veneer (Drew and Bazzaz, 1978). Eastern cottonwood is also an excellent species for genetic improvement work since intra- and interspecific hybridization can be done relatively easily (Dickmann and Stuart, 1983).

In the North Central Region of the United States, eastern cottonwood and hybrid poplars perform well under conventional and short rotation intensive culture (SRIC). With improved varieties and cultural methods, eastern cottonwood could be planted more extensively in Michigan and elsewhere in this region (Kelly et al., 1978).

Although eastern cottonwood can grow in a wide variety of site conditions, it achieves optimal growth on rich bottomland soil. In the future, however, it seems that sites designated for forest plantations will be on more marginal sites due to the use of forest land for other purposes. Furthermore, the forested acreage is shrinking due to conversion to agriculture. Consequently, eastern

cottonwood will be grown on sites that are less than optimal for this species. On such sites the availability of water and nutrients may be critical for plantation establishment.

Selection for genotypes of eastern cottonwood that perform well under water and nutrient- poor conditions is a logical measure. Effective selection for plant characteristics can be achieved only if genetic variation exists.

With these factors in mind, the objectives of this study were to:

1. determine if there is genetic variation between cottonwood populations found in two contrasting habitats, namely sand dune and floodplain populations for growth and physiological characteristics;
2. estimate the magnitude of genotype-environment interaction and genotype stability of these populations;
3. observe the effect of water deficit and nitrogen fertilization upon growth and physiological characteristics of these two contrasting populations of eastern cottonwood.

LITERATURE REVIEW

Genetic Variation in Eastern Cottonwood

Eastern cottonwood occurs naturally in most of the eastern half of the United States and southern Canada. It is usually associated with bottomland, alluvial, and riparian areas. Fertile, well-drained, fine sandy-loams are the most satisfactory site, but eastern cottonwood will grow almost anywhere and is relatively resistant to drought (Dickmann and Stuart, 1983).

Since eastern cottonwood grows in a wide range of environments, the existence of natural genetic variation is expected. Provenance studies are the first step for assessing genetic variation in tree breeding programs. Mohn and Pauley (1969) reported from a provenance study in Minnesota that high growth rate of eastern cottonwood was associated with southern latitude, but seedlings from the more southern latitude had poor survival in Minnesota due to winter injury. A somewhat similar result was reported by Ying and Bagley (1976) from a provenance study in Nebraska representing a major part of the natural range of eastern cottonwood. Variation of growth, morphological, and phenological characteristics followed a clinal pattern from north and west to south and east.

Genetic variation at stand and family levels has also been reported in eastern cottonwood. Farmer and Wilcox

(1966) progeny tested open-pollinated cottonwood families and measured variation in a number of traits at the end of the second growing season. Variation among families for height, diameter, specific gravity, and fiber length was significant. Farmer (1970 a) conducted a similar study and found that variation among families was also significant for various characteristics such as height, diameter, specific gravity, and incidence of leaf rust.

Nelson and Tauer (1987) reported from an open-pollinated progeny test that differences among stands were significant for height, diameter, incidence of leaf rust, and number of branches at two years of age. Differences among family within stands were also significant for those characteristics.

Several studies have been carried out to document clonal variation in eastern cottonwood. Farmer and Wilcox (1968), for example, reported that clonal variation in the test population was great for several characteristics such as height, diameter, volume, specific gravity, fiber length, and leaf rust. This indicates that improvement through clonal selection is possible.

Randall (1973) collected clones from different populations in western Kentucky, western-central Mississippi, north-eastern Texas, southern Arkansas, and east-central Illinois. The clones were then planted in Illinois. Data were collected when the trees were one, two, three, and five years of age. The clones from the

southern populations had larger diameter and faster height growth rate than those from local populations at all ages. There were also differences among clones within populations for the traits measured.

Randall and Cooper (1973) reported in a test study that clones differed significantly for height, diameter, and specific gravity at five years of age.

Genetic variation in physiological characteristics has also been studied in eastern cottonwood. For example, Kelliher and Tauer (1980) compared stomatal resistance between clones collected from a dry site and from a wet site in northern Oklahoma after subjecting them to different water regimes. The result indicated that the dry-site plants had lower stomatal resistance values than the wet-site plants, even under well-watered conditions.

Genotype-Environment (GE) Interactions in Eastern Cottonwood

A number of studies have indicated that eastern cottonwood genotypes vary in their response to environmental differences. Randall and Mohn (1969) found substantial clone-site interactions for height and diameter at ages one to four among 79 clones grown on two sites. Mohn and Randall (1973) obtained a similar result from a different study for height, diameter, and number of first year branches at three years old. Clone-site interactions seemed to be more important than clone-planting year interactions.

Bridgewater (1972) selected clones from natural stands and tested them at two locations in Oklahoma. Significant clone-site interactions for growth rate and yield were observed. Only three clones performed well at both locations.

Randall (1973) collected clones from several localities (Kentucky, Mississippi, Texas, Arkansas and Illinois) and planted them in Illinois. He found that there were significant interactions for clone-site, clone within population-site, and population-site.

Randall and Cooper (1973) reported that GE component of variance was large. Among 32 cottonwood clones tested at three locations, the GE component of variance for height growth was as large as the genotype component at one year of age. At later ages, it was approximately half as large as the genotype component.

In a recent study, Nelson and Tauer (1987) progeny tested 159 open-pollinated families representing 40 natural stands. At two years of age, significant stand-location interactions were detected for height, leaf rust, and number of branches, while family-location interactions were significant for date of leaf fall only.

Differential responses of cottonwood genotypes upon application of different water regimes and fertilizer levels have also been reported. Curlin (1967) found strong clone-fertilizer interactions for height, diameter, and volume, but not for specific gravity at two years old in the field.

Broadfoot and Farmer (1969) applied two different water regimes on 30 clones of cottonwood. Significant clone-moisture interactions were not detected. On the other hand, Farmer (1970 b) reported in a similar study that clone-moisture interactions were significant for growth, shoot-root ratio, and wood properties, although the interaction component of variance for these characteristics was relatively small.

In tree breeding programs, genotypes that have high productivity and perform well across different environmental conditions are desirable (Shelbourne, 1972; Zobel and Talbert, 1984). Genotypes that show little GE interaction have high stability or low plasticity.

There are many ways to assess GE interaction and genotype stability. The earliest approach involves analysis of variance (Spraque and Federer, 1951; Plasteid and Peterson, 1959; Comstock and Moll, 1963). Another approach for analyzing GE interaction is joint linear regression. This method was popularized by Finlay and Wilkinson (1963) and used among others by Freeman and Perkins (1971), Eberhart and Russell (1966) and Tai (1971).

Multivariate methods have also been employed to analyze GE interaction and genotype stability in recent years. These methods include cluster analysis and principal component analysis. Cluster analysis was used, among others, by Abou-El-Fittouh et al. (1969), Mungomery et al. (1974), Lin and Thompson (1975), Lin (1982) and Gadhery et al. (1982), while

principal component analysis was used, among others, by Kempton (1984), Wescott (1987), Crossa (1988) and Crossa et al. (1988).

There is no best method for analyzing GE interaction. Every method has its advantages and disadvantages. This matter has been discussed quite extensively in many scientific journals (Freeman and Perkins, 1971; Wescott, 1986, 1987).

FIELD PLOT STUDY

Experiment One

MATERIALS AND METHODS

Establishment

Eight clones were used in this study. Four dry-site clones were collected from sand dunes at the Saugatuck State Park, while another four clones, representing a wet site, were collected from the floodplain of Kalamazoo River about 10 to 15 kilometers from the sand dunes. These two habitats are located at the township of Laketown, Allegan County, Michigan (Figure 2). These clones were collected in March, 1987.

The plants were grown from hardwood cuttings, 1 - 2 cm in diameter, 20 cm in length and having at least two buds. Cuttings were soaked in tap water for 72 hours and then dipped in 4 ppm Indole-3- Butyric Acid (IBA) diluted in a 1 : 1 ratio of distilled water and 75 % alcohol. Cuttings were then grown in paper pots (7.61 cm diameter, 27.94 cm high) using media containing a 3 : 2 ratio of peat moss and vermiculite. Plants were grown in a greenhouse under ambient light conditions and given supplemental fluorescent lighting to maintain a 16 hour photoperiod. Temperatures were ± 27 ^{o} C during the day to ± 18 ^{o} C during the night. The plants were transferred to a shadehouse for two weeks before outplanting. The experiment was established on May

Figure 1. The location of clone collection (circles)

27 - 29, 1987 at the Tree Research Center, Department of Forestry, Michigan State University, East Lansing, Michigan.

The experiment used a split-split plot arranged in a completely randomized block design. Water regimes were the main plot and nitrogen levels were the subplot, while clones were used as the sub-subplot. Each experimental unit was represented by two ramets. The spacing was 1.5 x 1.5 m.

The following water treatments were applied:

1. no water stress (NWS): soil water potential was kept at -0.01 MPa or less;
2. moderate water stress (MWS): soil water potential was brought back to -0.01 MPA whenever it reached -0.03 MPa;
3. severe water stress (SWS): no water supply except natural rainfall.

The main plots were separated from one another by a plastic barrier 0.5 m deep in the soil. For the water treatment, microsprinklers were installed 30 cm from the plants. Every plant had two microsprinklers.

There were also three nitrogen levels used:

1. no nitrogen application (N1);
2. 200 kg N per hectare per year equivalent (N2);
3. 400 kg N per hectare per year equivalent(N3).

The nitrogen treatments were applied using ammonium nitrate (NH_4NO_3) in the months of June, July, August and September.

The experiment was kept free from weeds throughout the year by spraying with glyphosate a week before and about a month after planting.

Data Collection and Analyses

Soil was analyzed and a soil moisture retention curve was developed using a pressure plate apparatus according to the method developed by Richard (1965). Rainfall data were also collected from the weather station at the Tree Research Center.

Height and diameter growth were measured at planting time. At the end of the first growing season, height and root-collar diameter data were collected. No physiological characteristics were measured.

The data were analyzed using analysis of covariance with the following model:

$$Y_{ijkl} = \mu + R_i + W_j + RW_{ij} + N_k + NW_{jk} + RNK_{ijk} + C_l + WC_{jl} + NC_{kl} + WNC_{jkl} + b(X_{ijkl} - \bar{X}) + \epsilon_{ijkl}$$

where

Y_{ijkl} = height or diameter in replication i, water status j, nitrogen level k and clone l;

μ = grand mean;

R_i = the effect of the i^{th} replicate;

W_j = the effect of the j^{th} water status;

RW_{ij} = the experimental error for the main plot;

N_k = the effect of the k^{th} nitrogen level;

NW_{jk} = the effect of interaction between the j^{th}

water status and k^{th} nitrogen level;

RNK_{ijk}= the experimental error for the sub-plot;

C_l = the effect of the l^{th} clone;

WC_{jl} = the effect of interaction between the j^{th} water status and l^{th} clone;

NC_{kl} = the effect of interaction between the k^{th} nitrogen level and l^{th} clone;

WNC_{jkl}= the effect of interaction between the j^{th} water status, k^{th} nitrogen level and l^{th} clone;

b = regression coefficient between Y and X;

X_{ijkl} = initial height or diameter in the replication i water status j, nitrogen level k and clone l;

$\bar{X}$ = the mean value of X;

ϵ_{ijkl} = the experimental error for the sub-sub- plot.

Analysis of covariance was used because of heterogeneity of the initial height and diameter. In the model, water status and nitrogen level were considered as fixed effects, while clone and site (population) were considered as random effects. Clones were nested within sites. Plot means were used as data entries.

To ascertain the amount of genetic variation that can be attributed to clones between sites, clones within sites, and second and third order interactions involving clones, components of variance were calculated from the expected mean squares (Table 1).

Table 1. Expected mean square estimation used to calculate variance component

Source of variation	Mean Square	Expected Mean Square
Clones		
Between sites	MSBS	$\sigma^2E + rwn\sigma^2WS + rwnc\sigma^2BS$
Within sites	MSWS	$\sigma^2E + rwn\sigma^2WS$
W x C	MSWC	$\sigma^2E + rn\sigma^2WC$
N x C	MSNC	$\sigma^2E + rw\sigma^2NC$
W x N x C	MSWNC	$\sigma^2E + r\sigma^2WNC$
Error	MSE	σ^2E

W, N and C are water status, nitrogen level and clones, respectively.
r,w,n and c are the number of replicate, water status, nitrogen level and clones within sites, respectively.

RESULTS

Soil Analysis and Rainfall

The physical and chemical properties of the soil in the field experiment are shown in Table 2. A soil moisture retention curve and the amount of rainfall occurring during the study are presented in Figure 2 and Table 3, respectively.

Height

A test of homogeneity of variance indicated that the variance among clones across two sites was homogeneous. The measurement data in height growth after one growing season were then analyzed using analysis of covariance as shown in Table 4.

Differences between water status in height growth were significant. The adjusted mean height growths were 181, 183, and 153 cm for NWS, MWS, and SWS, respectively. The Duncan's multiple range test in Figure 3 indicated that the adjusted mean height growth between NWS and MWS was not significantly different. SWS had a significant effect in reducing height growth.

Although differences between nitrogen levels in height were statistically not significant, nitrogen application did tend to increase the height growth. The adjusted mean heights due to nitrogen application were 167, 174, and 177 cm for N1, N2, and N3, respectively. Significant

Table 2. Physical and chemical properties of soil in the field plot study

Texture (%)*			Concentrations (ppm)						pH
Sand	Silt	Clay	N	P	K	Ca	Mg	Na	
67.8	18.7	13.4	555.8	281.4	36.1	315.3	71.0	20.2	6.5

* sandy loam

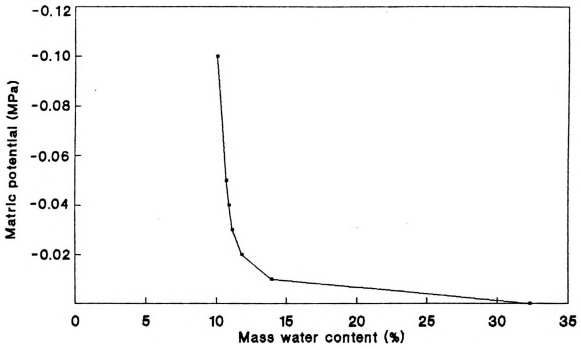

Figure 2. Moisture retention curves for soil in the field plot study.

Table 3. Rainfall and temperatures in experiment one of the field plot study

Date	Amount of rainfall (inches)					
	May	June	July	Aug.	Sept.	Oct.
1	-	-	0.01	0.02	-	0.15
2	-	-	-	0.07	0.15	0.10
3	0.18	0.44	-	-	-	-
4	-	-	-	0.25	-	-
5	-	-	-	-	-	-
6	-	0.24	0.15	-	-	0.08
7	-	0.21	-	-	-	0.02
8	-	-	-	-	0.09	-
9	0.05	0.10	-	0.56	0.24	-
10	-	-	1.00	0.04	-	-
11	-	-	0.29	-	1.20	-
12	0.33	0.28	-	-	-	-
13	-	-	-	-	0.23	-
14	-	-	0.03	-	-	-
15	-	-	-	0.30	0.48	-
16	-	-	0.11	-	-	-
17	-	-	-	0.40	0.13	0.10
18	-	-	-	-	0.12	0.08
19	0.11	-	-	0.10	-	-
20	0.18	-	-	-	-	0.52
21	0.40	-	0.03	-	0.15	0.13
22	-	1.14	-	1.99	0.24	0.07
23	-	-	-	-	-	0.30
24	-	-	-	-	-	0.13
25	-	-	0.54	-	-	0.21
26	-	-	0.35	-	-	
27	-	-	-	1.41	-	0.36
28	-	-	-	0.12	-	
29	-	-	-	0.07	0.58	0.04
30	-	0.16	-	-	0.14	
31	0.22	-	-	0.21	-	
Total	1.47	2.57	2.51	5.52	3.75	2.30
Normal*)	2.57	3.50	2.78	3.04	2.54	2.13
	Average temperature (^{o}C)					
Max.	23	28	28	26	23	11.5
Min.	9.5	18	17.5	15	11	1.5

*)Source: United States, Dept. of Commerce.

Table 4. Analysis of covariance for height in experiment one of the field plot study

Source of variation	DF	Sum of cross product X,X	Sum of cross product X,Y	Sum of cross product Y,Y	Y adjusted for X DF	Y adjusted for X SSD	Y adjusted for X MSD	F value
Replicates	2	190.861	2105.961	28023.017				
Water status (W)	2	101.778	- 277.664	37979.575				
Error (a)	4	39.611	155.664	4275.620	3	3648.046	1216.015	
W + Error	6	140.389	- 122.000	42255.195	5	42149.175		
W adjusted					2	38501.129	19250.565	15.83 *
Nitrogen levels (N)	2	9.083	- 188.233	3938.325				
W x N	4	69.055	535.039	12050.092				
Error (b)	12	87.695	25.027	12451.916	11	12444.774	1131.343	
N + Error	14	96.778	- 163.206	16390.241	13	16115.001		
W + Error	16	156.750	560.066	24502.008	15	22500.898		
N adjusted					2	3670.227	1835.113	1.62 ns
W x N adjusted					4	10056.124	2514.031	2.11 ns
Clones (C)	7	960.773	7808.396	87917.237				
Between sites	1	525.782	6129.970	71467.765				
Within sites	6	434.991	1678.426	16449.472				
W x C	14	308.296	255.923	5153.166				
N x C	14	35.213	200.159	4530.305				
W x N x C	28	282.427	96.813	12240.167				
Error (c)	126	1674.166	308.015	94256.750	125	94166.821	753.335	
C + Error	133	2634.939	8196.411	182173.990	132	156677.71		
B.S.+ Error	127	2199.948	6517.985	165724.520	126	146413.100		
W.S + Error	134	2109.157	2066.985	110706.220	133	108680.560		
WxC + Error	140	2062.462	643.933	99409.916	139	99208.867		
NxC + Error	140	1709.379	508.174	98787.055	139	98584.672		
WxNxC+Error	154	1956.593	296.972	106496.920	153	106451.85		
C adjusted					7	22383.530	3197.504	4.24 *
Between sites adjusted					1	52246.279	52246.279	21.60 **
Within sites adjusted					6	14513.739	2418.957	3.21 **
WxC adjusted					14	5042.046	360.146	0.48 ns
NxC adjusted					14	4417.851	315.561	0.42 ns
WxNxC adjusted					28	12285.020	438.750	0.58 ns

CO-(a)= 19.19 %, CO-(b)= 18.45 %, CO-(c)= 15.06 %.
PE (a)= 37.92 %, PE (b)= 87.45 %, PE (c)= 91.78 %.
X, Y = height measured at the planting time and the end of growing season, respectively.
*, ** = significant at the 5 % and 1 % levels, respectively; ns= not significant.

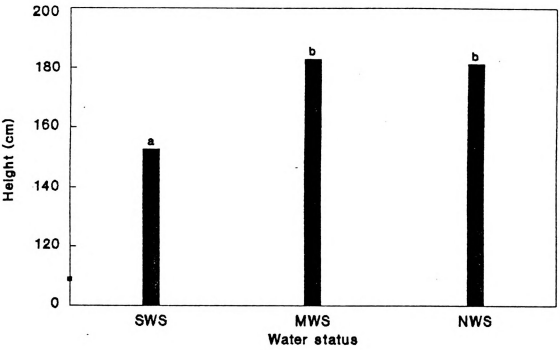

Figure 3. The effect of water status on height after one growing season in experiment one of the field plot study. Any means with the same letter are not significantly different by Duncan's multiple range test at the 5 % level. SWS= severe water stress; MWS= moderate water stress; NWS= no water stress.

interactions between water and nitrogen treatments were not detected, indicating that the effect of the water stress treatments on height growth was independent of the rates of nitrogen.

Differences among clones between sites, as well as differences among clones within sites were significant. The adjusted mean height growths were 155, and 190 cm for the dry site and the wet site, respectively. None of the two-way or three-way interactions involving water status, nitrogen levels and clones were significant, indicating that each factor acted independently in affecting height growth.

Diameter

As with height growth, a test of homogeneity of variance showed that the variance among clones across the two sites was homogeneous. The result of analysis of covariance is presented in Table 5.

Water treatment had a significant effect on diameter after one growing season. The adjusted mean diameters were 24, 21, and 19 mm for NWS, MWS, and SWS, respectively. As can be seen in Figure 4, the adjusted mean diameter at NWS was significantly different from that of MWS and SWS, indicating that both MWS and SWS reduced diameter growth.

As with height growth, nitrogen application did not have a statistically significant effect upon diameter growth. The adjusted mean diameters as affected by nitrogen application were 20, 22, and 21 mm for N1, N2, and N3,

Table 5. Analysis of covariance for diameter in experiment one of the field plot study

Source of Variation	Df	Sum of Cross Product XX	XY	YY	Df	Y adjusted for X SSQ	MSQ	F value
Peplicates	2	17.2315	42.1876	247.6321				
Water status (W)	2	6.6273	-31.2812	1027.2990				
Error (a)	4	1.6157	- 7.6702	107.2772	3	70.8645	23.6215	
W + Error	6	8.2430	-38.8514	1134.5762	3	951.4595		
W adjusted					2	880.5950	440.2975	18.64 **
Nitrogen levels (N)	2	0.3773	0.5000	67.4460				
W x N	4	0.6991	4.5903	71.2359				
Error (b)	12	8.1736	-19.3960	197.7779	11	151.8791	13.8072	
N + Error	14	8.5509	-18.8960	265.2239	13	223.4670		
WxN + Error	16	8.8727	-14.5903	269.0138	15	245.0215		
N adjusted					2	72.7147	36.3574	2.63 ns
WxN adjusted					4	94.2692	23.5673	1.71 ns
Clone (C)	7	22.8472	62.3542	384.8508				
Between site	1	14.0047	65.3126	304.5939				
Within sites	6	8.8425	- 2.9584	80.2569				
W x C	14	9.4097	-14.5375	87.8118				
N x C	14	2.5486	0.2222	74.9442				
W x N x C	28	10.9061	30.1292	155.5492				
Error (c)	126	45.6459	69.0334	1226.3131	125	1121.9092	8.8725	
C + Error	133	68.4931	131.3876	1611.1639	132	1359.1203		
B.S. + Error	127	59.6506	134.3460	1530.9070	126	1228.3309		
W.S. + Error	132	54.4084	66.0750	1306.5700	131	1226.4446		
WxC + Error	140	55.0556	59.4959	1314.1249	139	1249.8306		
NxC +Error	140	48.1945	69.2556	1301.2573	139	1201.7369		
WxNxC +Error	154	56.6320	99.1626	1381.8623	153	1208.2286		
C adjusted					7	237.2191	33.8884	3.82 *
Between sites adjusted					1	106.4217	106.4217	6.11 *
Within sites adjusted					6	104.5354	17.4226	1.94 ns
WxC adjusted					14	127.9214	9.1372	1.02 ns
NxC adjusted					14	79.8877	5.7020	0.64 ns
WxNxC adjusted					28	86.3194	3.0828	0.34 ns

CV(a) = 23.01 %, CV(b) = 16.87 %, CV(c) = 14.10 %.
PE(a) = 31.21 %, PE(a) = 116.68 %, CV(c) = 101.54 % .
X, Y= diameter measured at the planting time and the end of growing season, respectively.
*, ** = significant at the 5 and 1 % levels, respectively; ns = not significant.

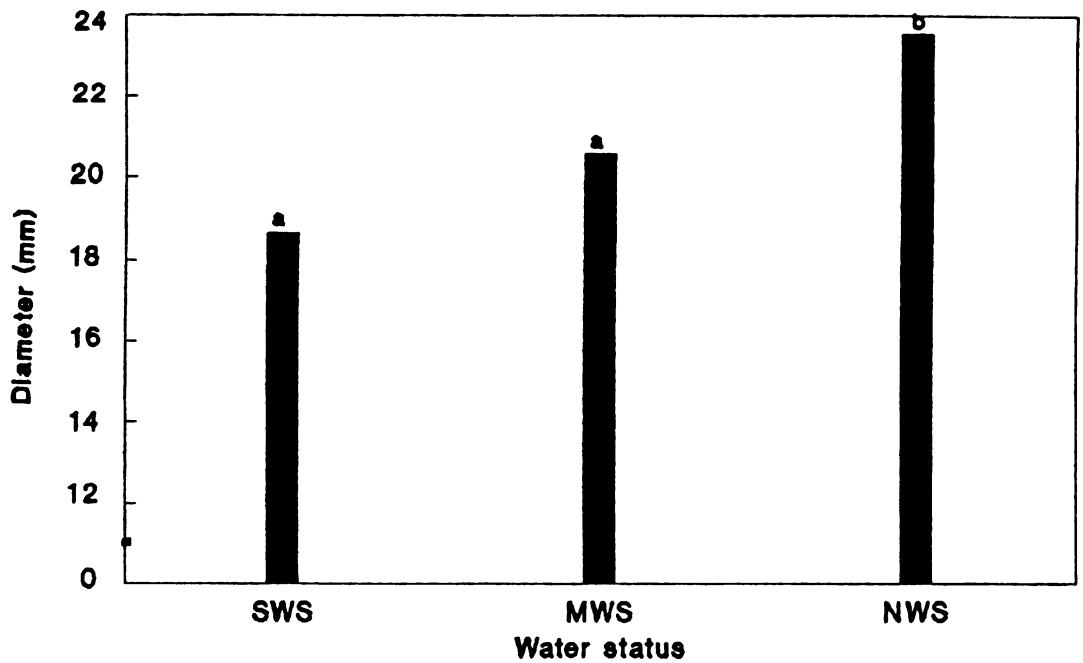

Figure 4. The effect of water status on diameter after one growing season in experiment one of the field plot study. Any means with the same letter are not significantly different by Duncan's multiple range test at the 5 % level. SWS= severe water stress; MWS= moderate water stress; NWS= no water stress.

respectively. Interaction between water and nitrogen treatments was also negligible.

There were significant differences among clones between sites, as well as among clones within sites. The adjusted mean diameter for clones originated from the dry site was 20 mm, while the adjusted mean for clones from the wet site was 22 mm.

As with height growth, no significant effect for two-way or three-way interactions involving clones, water status and nitrogen levels was detected.

Variance Component Estimation

The estimation of variance components for height and diameter growth is presented in Table 6. Of the total genetic variation (clones), clones between sites were the major source of variation for both height and diameter. The contribution of clones between sites to the total variation was higher for height growth.

Table 6. Variance component estimates for height and diameter in experiment one of the field plot study

Source of variation	Component estimates (%)	
	Height	Diameter
Clones		
Between sites	36.2	8.2
Within sites	4.8	3.2
W x C	0	0.3
N x C	0	0
W x N x C	0	0
Error	59.0	88.4

Experiment Two

MATERIALS AND METHODS

Establishment

The plantation of experiment one was coppiced to about 20 cm above ground in March, 1988. The stumps were allowed to sprout the following spring, and thinned to one vigorous sprout per stump. This material was the basis of experiment two.

In this experiment water and nitrogen treatments were similar to those applied in experiment one. Soil moisture sensors (Soiltest, Inc.) were installed in every SWS treatment in addition to tensiometers, to record soil water potential below - 0.08 MPa. In May, 1988 glyphosate herbicide was sprayed onto the experiment for weed control.

Data Collection and Analyses

On July 29 - 31, 1988 a number of physiological traits were measured. Stomatal conductance, photosynthetic and transpiration rates were measured using an ADC open system infrared gas analyzer. The measurement was taken on the youngest fully-expanded leaf of each tree. A leaf of the tallest tree within plot was used for the physiological measurements. A preliminary study indicated that the results of measurement conducted at the youngest fully-expanded leaf were strongly correlated with those taken from whole crown (an average of several measurements taken at several height positions). For example, the coefficients of correlation

between the youngest fully-expanded leaf and the whole crown were 0.8 and 0.79 for stomatal conductance and photosynthetic rate, respectively. These correlations were significant at the 1 % level based on 24 samples which were taken 5 days before the actual measurement.

Stomatal conductance, photosynthesis and transpiration were measured from 10.00 am to 2.30 pm. To reduce error due to measurement time, each block was measured at approximately the same time. At the time of measurement photosynthetically active radiation (PAR) was above 2000 μmol $m^{-1}s^{-1}$.

Leaf water potential was determined on the same leaf as other physiological traits soon after the measurements were finished using a PMS pressure chamber (PMS Instrument Co., Corvallis, Oregon) The leaf was then taken to the laboratory for specific leaf weight (leaf area/leaf dry weight) determination.

At the end of the growing season, height and root collar-diameter were measured. Additional rainfall and daily temperature data were collected from the weather station nearby.

The data were analyzed using analysis of variance. The variables and assumptions regarding the variables were similar to those used in experiment one. Plot means were used as data entries.

RESULTS

Rainfall and Temperature

The data of rainfall and temperatures during the experiment are presented in Table 7. During the first three months of the experiment, the rainfall was considerably below normal, resulting in a severe drought. Then, from August onward the average amount of rain fell.

Height

Water status had a highly significant effect upon height after one growing season (Table 8). The mean heights as affected by water status were 280, 324, and 332 cm for severe water stress (SWS), moderate water stress (MWS) and no water stress (NWS), respectively (Figure 5). Water stress reduced height growth 15.5 % and 2.5 % for SWS and MWS, respectively.

Nitrogen level as well as interaction between water status and nitrogen level had no statistically detectable effect on height growth. Nevertheless, nitrogen fertilization enhanced height growth. The mean heights as influenced by nitrogen rate were 306, 316, and 314 cm for no nitrogen (N1), 200 kg/ha/yr (N2), and 400 kg/ha/yr (N3), respectively.

There were highly significant differences among clones between sites as well as among clones within sites. However, no second or third order interactions involving

Table 7. Rainfall and temperatures recorded in experiment two of the field plot study

Date	Rainfall (inches)					
	May	June	July	August	Sept.	Oct.
1	-	-	-	-	-	-
2	-	0.14	-	-	-	0.75
3	-	0.02	-	-	0.30	-
4	-	-	-	-	-	-
5	-	-	-	-	0.20	0.11
6	-	-	-	0.80	-	-
7	-	-	-	-	-	-
8	-	-	-	-	-	-
9	0.04	0.04	-	0.03	-	0.49
10	0.21	-	-	0.06	-	0.05
11	-	-	0.05	-	-	-
12	-	-	-	-	-	0.04
13	-	-	-	0.10	0.46	-
14	-	-	-	-	-	-
15	-	-	-	0.59	-	-
16	0.31	-	-	-	-	0.06
17	0.04	-	1.43	0.10	-	0.50
18	-	-	-	1.50	-	0.83
19	-	-	0.20	0.14	0.29	0.13
20	-	-	-	-	1.16	-
21	-	-	-	-	0.11	0.04
22	-	-	-	-	-	-
23	-	-	-	0.64	1.70	-
24	-	-	-	0.10	-	0.53
25	-	-	0.33	-	-	0.25
26	-	-	0.04	-	-	-
27	-	-	-	-	-	-
28	-	-	-	-	-	0.04
29	-	0.06	-	-	-	-
30	-	-	-	-	-	-
31	-	-	-	-	-	-
Total	0.60	0.26	2.34	4.08	4.22	3.82
Normal*)	2.57	3.50	2.78	3.04	2.54	2.13
	Average temperature (^{o}C)					
Max.	22.5	29	31	29	22.5	12
Min.	7.5	12	16	17	10	2.5

*) Source: Unites States, Dept. of Commerce.

Table 8. Analysis of variance for height in experiment two of the field plot study

Source of Variation	Df.	Mean Square	F value
Replicates	2	--------	
Water status(W)	2	55091.040	22.20 **
Error (a)	4	2481.629	
Nitrogen levels (N)	2	2084.145	1.14 ns
W x N	4	1415.079	0.77 ns
Error (b)	12	1833.238	
Clones (C)	7	21829.570	28.73 **
Between sites	1	102643.100	12.28 *
Within sites	6	8360.650	11.02 **
W x C	14	460.932	0.61 ns
N x C	14	594.789	0.78 ns
W x N x C	28	594.663	0.78 ns
Error (c)	126	759.936	

CV(a)= 15.96 %; CV(b)= 13.72 %; CV(c)= 8.83 %.
*,**=significant at the 5 and 1 % levels, respectively.
ns= not significant.

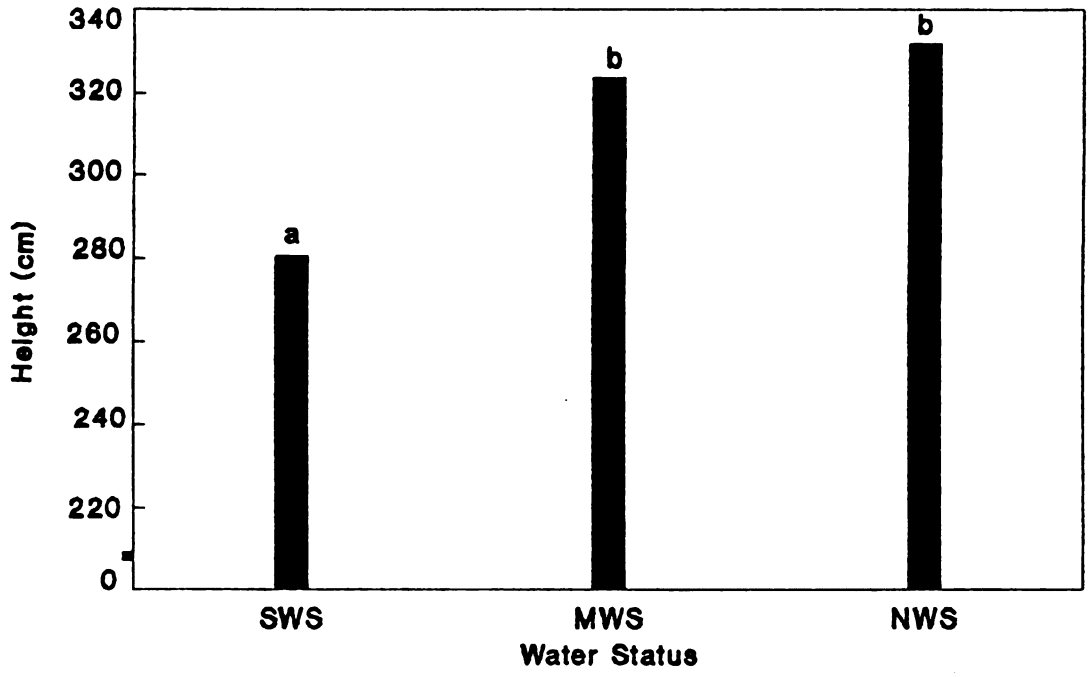

Figure 5. The effect of water status on height after one growing season in experiment two of the field plot study. Any means with the same letter are not significantly different by Duncan's multiple range test at the 5% level. SWS= severe water stress; MWS= moderate water stress; NWS= no water stress.

water status, nitrogen level and clone were detected. This indicates that the site where clones were collected had an independent effect of water status and nitrogen rates on height growth. Plants originated from the dry site grew more slowly than those from the wet site regardless of water status and nitrogen levels. The average height growth across all treatments for plants from the dry site was 290 cm, whereas the corresponding figure for plants from the wet site was 334 cm. Clones from the wet site grew 13 % faster in height than those from the dry site.

Diameter

As with height, water status influenced diameter growth significantly after one growing season (Table 9). The mean diameters were 27, 33, and 36 mm for SWS, MWS, and NWS, respectively, and all three differed significantly (Figure 6). Water deficit reduced diameter growth by 26 % and 8 % for SWS and MWS, respectively.

Nitrogen level had a minor effect on diameter growth. The interaction between water status and nitrogen rate was also negligible.

Differences among clones between sites as well as among clones within sites were highly significant. As with height, no interaction involving water status, nitrogen levels and clones was statistically significant. The average diameter of clones from the dry site was always smaller than that of the wet site clones, irrespective of water status

Table 9. Analysis of variance for diameter season in experiment two of the field plot study

Source of Variation	Df.	Mean Square	F value
Replicates	2	-------	
Water status (W)	2	1679.832	60.38 **
Error (a)	4	27.822	
Nitrogen levels(N)	2	57.469	0.78 ns
W x N	4	84.660	1.15 ns
Error (b)	12	73.622	
Clones (C)	7	322.629	14.32 **
Between sites	1	1410.002	9.97 *
Within sites	6	141.399	6.28 **
W x C	14	3.523	0.16 ns
N x C	14	16.096	0.71 ns
W x N x C	28	12.568	0.56 ns
Error (c)	126	22.523	

CV(a)= 16.40 %; CV(b)= 26.68 %; CV(c)= 14.76 %.
*,**=significant at the 5 and 1 % levels, respectively.
ns = not significant.

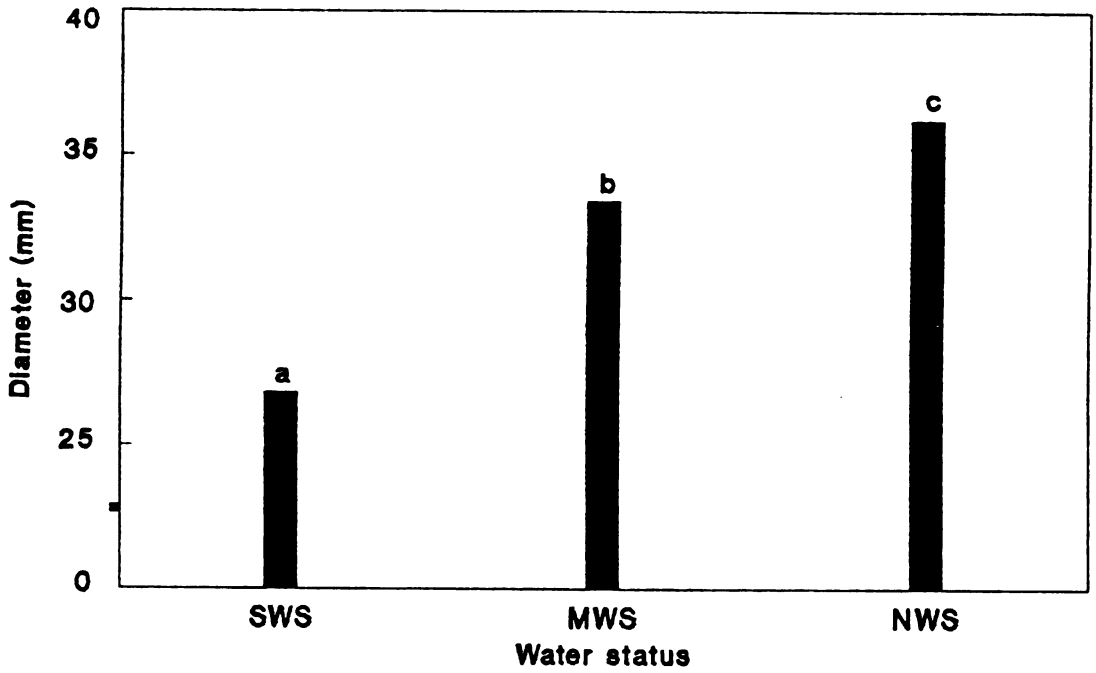

Figure 6. The effect of water status on diameter after one growing season in experiment two of the field plot study. Any means with the same letter are not significantly different by Duncan's multiple range test at the 5 % level. SWS= severe water stress; MWS= moderate water stress; NWS= no water stress.

or nitrogen level. The mean diameters were 30 and 35 mm for clones from the dry site and clones from the wet site, respectively. Clones from the wet site grew 15 % faster in diameter than clones from the dry site.

Leaf area

Water status was the only variable that showed a significant effect upon leaf area (Table 10), and all three water status treatments differed significantly (Figure 7). All interaction effects were negligible.

Even though there were no significant differences among the nitrogen treatments, nitrogen application tended to increase leaf area. The mean leaf areas as affected by nitrogen level were 134, 138, and 140 cm^2 for N1, N2, and N3, respectively.

Clones between sites did not differ significantly, despite the fact that clones from the wet site had greater leaf area than those from the dry site. The mean leaf areas due to site were 113 and 161 cm^2 for clones from the dry site and wet site, respectively.

Specific Leaf Weight

Water regimes influenced specific leaf weight (SLW) significantly (Table 11). Water deficit appeared to increase SLW. The mean SLWs were 8.9, 8.2, and 7.7 for SWS, MWS, and NWS, respectively (Figure 8). All three water status treatments differed significantly in SLW.

Table 10. Analysis of variance for leaf area in experiment two of the field plot study

Source of variation	Df.	Mean square	F value
Replicates	2	-------	
Water status (W)	2	7533.884	21.54 **
Error (a)	4	349.766	
Nitrogen levels (N)	2	756.479	1.23 ns
W x N	4	49.097	0.08 ns
Error (b)	12	697.746	
Clones (C)	7	56476.310	75.84 **
Between sites	1	122136.600	2.68 ns
Within sites	6	45532.933	61.14 **
W x C	14	1067.196	1.43 ns
N x C	14	1261.636	1.69 ns
W x N x C	28	745.227	1.00 ns
Error (c)	126	744.672	

CV(a)= 13.63 %; CV(b)= 18.05 %; CV(c)= 19.89 %.
** = significant at the 1 % level.
ns = not significant.

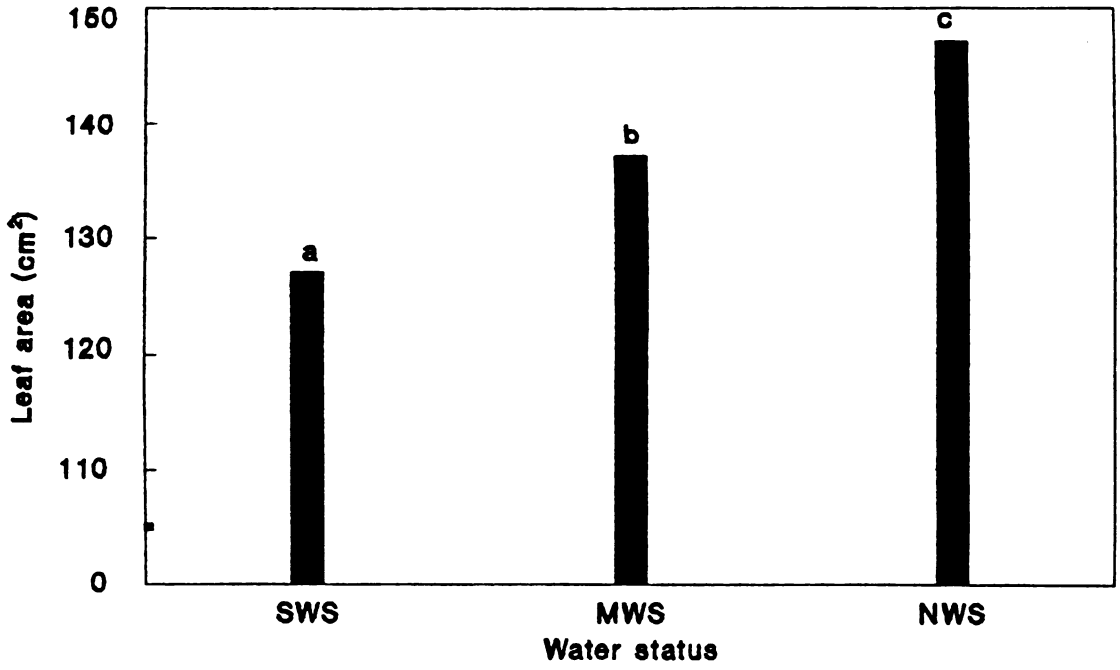

Figure 7. The effect of water status on leaf area at the end of July, 1988 in experiment two of the field plot study. Any means with the same letter are not significantly different by Duncan's multiple range test at the 5 % level. SWS= severe water stress; MWS= moderate water stress; NWS= no water stress.

Table 11 . Analysis of variance for SLW in experiment two of the field plot study

Source of variation	Df.	Mean square	F value
Replicates	2	--------	
Water status (W)	2	23.7125	29.60 **
Error (a)	4	0.8012	
Nitrogen levels (N)	2	2.5127	1.16 ns
W x N	4	0.4983	0.23 ns
Error (b)	12	2.1617	
Clones (C)	7	4.0800	6.63 **
Between sites	1	0.7609	0.16 ns
Within sites	6	4.6332	7.53 **
W x C	14	0.3640	0.59 ns
N x C	14	1.0315	1.68 ns
W x N x C	18	0.5719	0.93 ns
Error (c)	126	0.6149	

CV(a)= 10.85 %; CV(b)= 17.30 %; CV(c)= 9.50 %.
** = significant at the 1 % level.
ns = not significant.

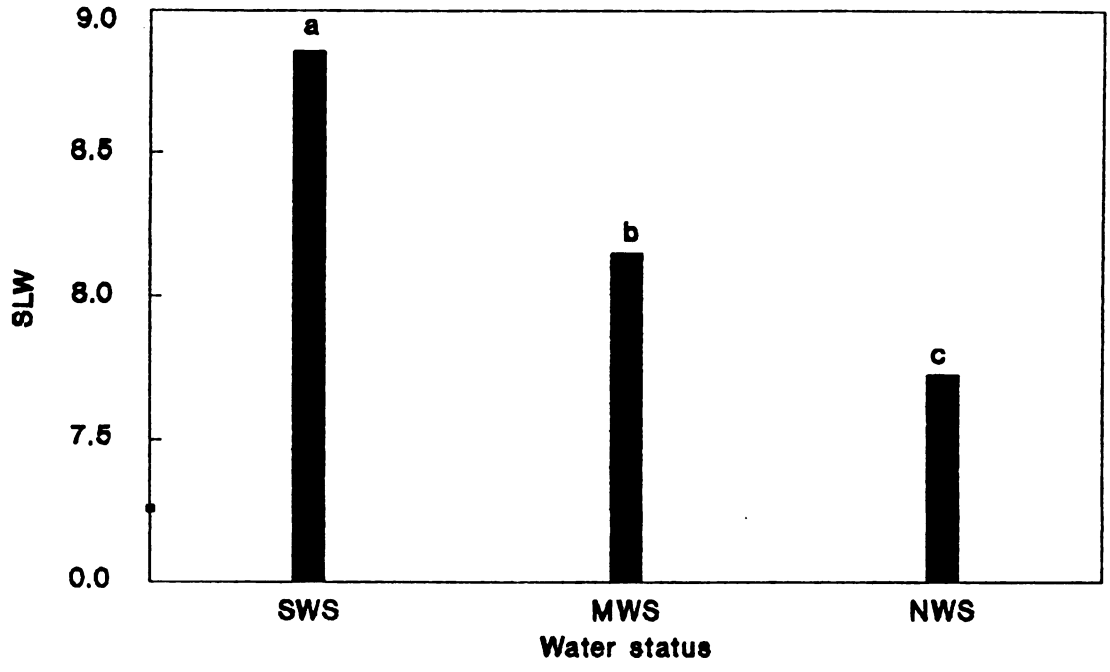

Figure 8. The effect of water status on SLW at the end of July, 1988 in experiment two of the field plot study. Any means with the same letter are not significantly different by Duncan's multiple range test at 5 %. SWS= severe water stress; MWS= moderate water stress; NWS= no water stress.

The effects of nitrogen levels and clones between sites on SLW were not significant. None of the interaction effects were statistically significant. There were, however, large differences among clones within sites that were statistically significant.

Leaf Water Potential

Soil water status affected leaf water potential significantly (Table 12). As the water deficit increased in the soil, leaf water potential decreased. The mean leaf water potentials were -1.06, -1.01, and -1.01 MPa for SWS, MWS, and NWS, respectively. Only the SWS treatment was significantly different from the other water regimes for leaf water potential (Figure 9).

Nitrogen treatments did not have a significant effect upon leaf water potential. Differences among clones between sites, as well as all interaction effects, were not significant. Clones within sites, on the other hand, differed significantly.

Stomatal Conductance

Among the many variables involved in the analysis, only water status had a significant effect on stomatal conductance (Table 13). No interaction terms were significant.

The mean stomatal conductances, as affected by water status, were 0.46, 0.61, and 0.72 mol $m^{-2}s^{-1}$ for SWS, MWS, and NWS, respectively. SWS, MWS and NWS treatments were

Table 12. Analysis of variance for leaf water potential in experiment two of the field plot study

Source of variation	Df.	Mean square	F value
Replicates	2	-------	
Water status (W)	2	6.1817	7.29 *
Error (a)	4	0.8484	
Nitrogen levels (N)	2	3.4456	2.23 ns
W x N	4	0.9682	0.63 ns
Error (b)	12	1.5464	
Clones (C)	7	3.3953	5.39 **
Between sites	1	4.5938	1.44 ns
Within sites	6	3.1956	5.08 *
W x C	14	0.4211	0.67 ns
N x C	14	1.0144	1.61 ns
W x N x C	28	0.6659	1.06 ns
Error (c)	126	0.6296	

CV(a)= 8.95 %; CV(b)= 12.09 %; CV(c)= 7.71 %
*,**=significant at the 5 and 1 % levels, respectively.
ns = not significant.

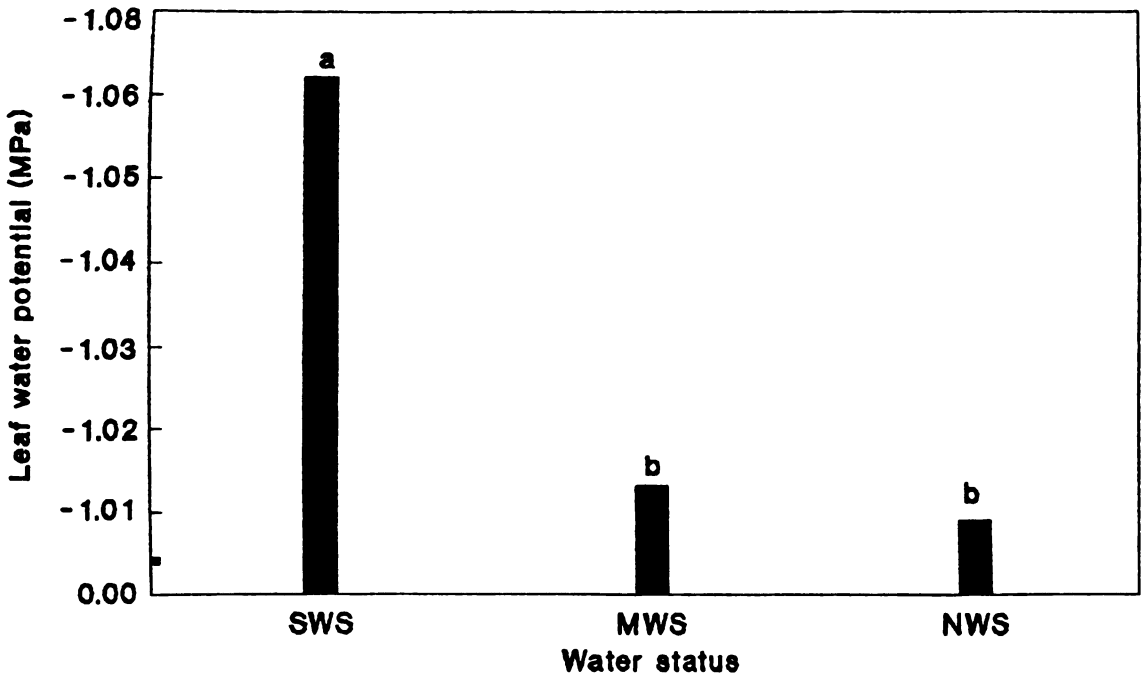

Figure 9. The effect of water status on leaf water potential at the end of July, 1988 in experiment two of the field plot study. Any means with the same letter are not significantly different by Duncan's multiple range test at the 5 % level. SWS= severe water stress; MWS= moderate water stress; NWS= no water stress.

Table 13. Analysis of variance for stomatal conductance in experiment two of the field plot study

Source of Variation	Df.	Mean Square	F value
Replicates	2	--------	
Water status (W)	2	1.2101	37.12 **
Error (a)	4	0.0326	
Nitrogen level (N)	2	0.0061	1.22 ns
W x N	4	0.0127	2.54 ns
Error (b)	12	0.0050	
Clones (C)	7	0.0008	0.07 ns
Between sites	1	0.0006	0.06 ns
Within sites	6	0.0095	0.82 ns
W x C	14	0.0099	0.85 ns
N x C	14	0.0125	0.89 ns
W x N x C	28	0.0452	1.25 ns
Error (c)	126	0.0116	

CV(a)= 30.29 %; CV(b)= 11.86 %; CV(c)= 18.07 %.
**= significant at the 1 % level.
ns= not significant.

significantly different from one another in stomatal conductance (Figure 10). SWS and MWS reduced stomatal conductance about 57 % and 18 %, respectively.

Transpiration

As with stomatal conductance, only water status had a significant effect upon transpiration. None of the other main effects or interaction terms were statistically significant (Table 14). The average transpiration rates were 9.5, 10.5, and 10.3 mol $m^{-2}s^{-1}$ for the SWS, MWS, and NWS treatments, respectively.

The SWS treatment reduced transpiration rate significantly (Figure 11). The MWS and NWS, treatments, however, did not differ significantly in transpiration rate.

Photosynthesis

Unlike stomatal conductance and transpiration, no main factors had a significant effect on the photosynthetic rate (Table 15), although water deficit tended to lessen photosynthesis. The mean photosynthetic rates, as affected by water status were 15.9, 17.9, and 17.3 μmol $CO_2m^{-2}s^{-1}$ for the SWS, MWS, and NWS treatments, respectively.

Correlations Between Characteristics

A correlation analysis was carried out on the physiological characteristics measured in the experiment (Table 16). Most of the correlation coefficients were low.

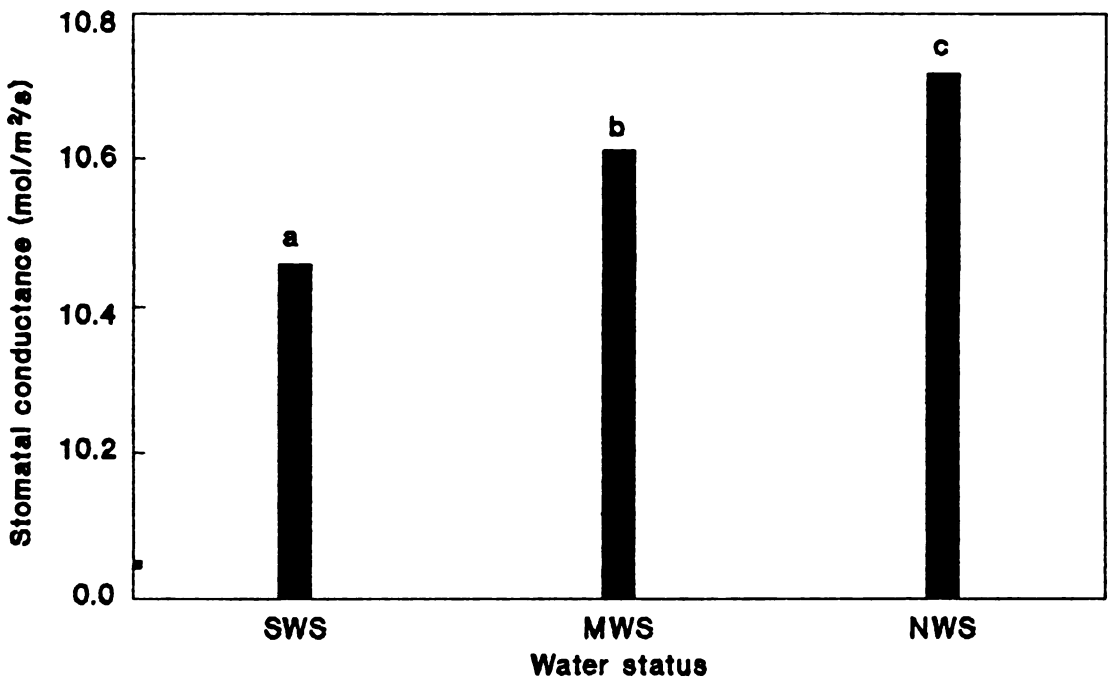

Figure 10. The effect of water status on stomatal conductance at the end of July, 1988 in experiment two of the field plot study. Any means with the same letter are not significantly different by Duncan's multiple range test at the 5 % level. SWS= severe water stress; MWS= moderate water stress; NWS= no water stress.

Table 14. Analysis of variance for transpiration rate in experiment two of the field plot study

Source of variation	Df.	Mean square	F value
Replicates	2	---------	
Water status (W)	2	18.0080	9.48 *
Error (a)	4	1.9001	
Nitrogen level (N)	2	3.4548	3.59 ns
W x N	4	1.3952	1.45 ns
Error (b)	12	0.9631	
Clones (C)	7	0.3245	0.39 ns
Between sites	1	0.0937	2.43 ns
Within sites	6	0.0385	0.05 ns
W x C	14	0.9715	0.39 ns
N x C	14	0.6255	0.76 ns
W x N x C	28	0.7660	0.93 ns
Error (c)	126	0.8249	

CV(a)= 13.68 %; CV(b)= 9.74 %; CV(c)= 9.01 %
* = significant at the 5 % level.
ns = not significant.

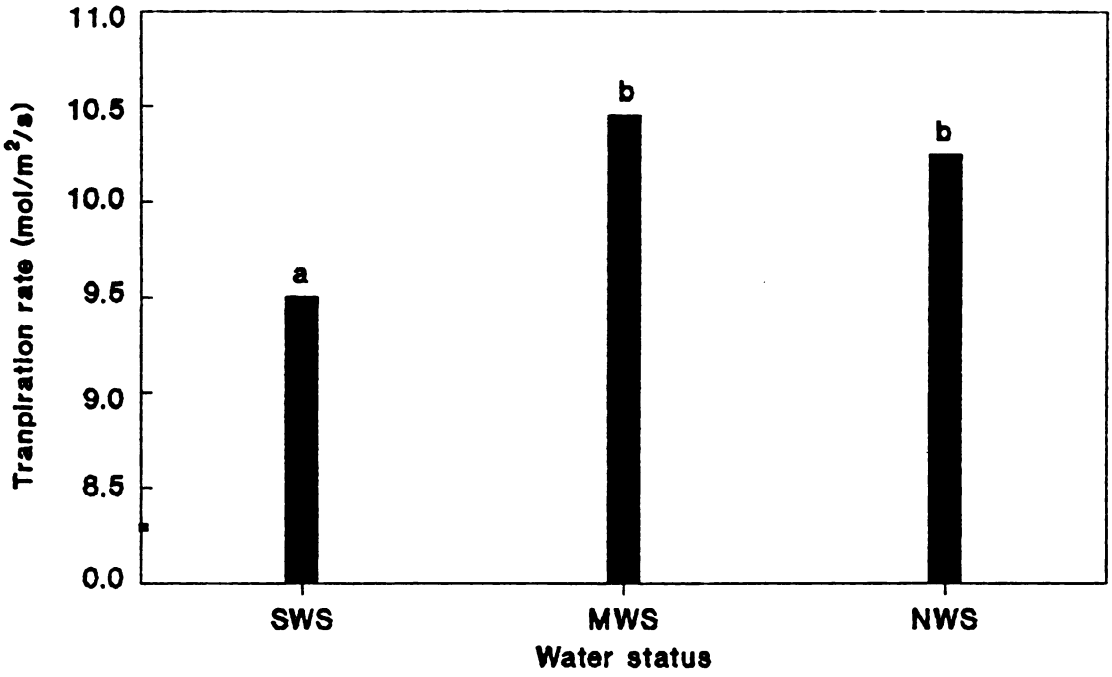

Figure 11. The effect of water status on transpiration rate at the end of July, 1988 in experiment two of the field plot study. Any means with same letter are not significantly different by Duncan's multiple range test at the 5 % level. SWS= severe water stress; MWS= moderate water stress; NWS= no water stress.

Table 15. Analysis of variance for photosynthetic rate in experiment two of the field plot study

Source of variation	Df.	Mean square	F value
Replicates	2	--------	
Water status (W)	2	72.9058	1.70 ns
Error (a)	4	42.9984	
Nitrogen levels (N)	2	22.1677	1.67 ns
W x N	4	17.2935	1.30 ns
Error (b)	12	13.2593	
Clones (C)	7	2.1968	2.42 ns
Between sites	1	1.6119	0.70 ns
Within sites	6	2.2943	0.45 ns
W x C	14	9.0633	1.76 ns
N x C	14	6.3590	1.23 ns
W x N x C	28	6.6598	1.29 ns
Error	126	5.1496	

CV(a)= 38.54 %; CV(b)= 21.40 %; CV(c)= 13.34 %.
ns = not significant.

Table 16. Correlations between the physiological characteristics measured in experiment two of the field plot study

	Leaf Water Potential	Stomat. Cond.	Transp. Rate	Photosyn. Rate
Leaf Water potential		-0.15*	-0.07^{ns}	-0.15*
Stomatal conductance			0.53**	0.45**
Transpiration rate				0.23**

*,**=significant at the 5 and 1 % levels, respectively.
ns = not significant.

However, there are several points worth mentioning. Leaf water potential was negatively correlated with stomatal conductance, transpiration, and photosynthetic rates. In this regard the coefficients of correlation were -0.15, -0.07, and -0.15 for stomatal conductance, transpiration, and photosynthetic rates, respectively. Only the correlation between leaf water potential and transpiration rate was not significant. Stomatal conductance was positively correlated with transpiration and photosynthetic rates.

Variance Component Estimation

The amount of variation for the characteristics measured that can be attributed to clones between sites, clones within sites, interaction involving clones, as well as residual error was estimated using components of variance (Table 17).

The contribution of clones between sites to the total variation was quite large for characteristics such as height and diameter. The amount of variation that accounted for by clones between sites were 46 and 30 % for height and diameter, respectively. The contribution of clones within sites to the total variation was relatively small for height and diameter.

For leaf area, clones within sites were the major source of variation (52 %), but the variation that was attributable to the clones between sites was relatively large (22 %).

Table 17. Variance component estimation in experiment two of the field plot study

Characteristics	Component of variance (% of total)					
	σ^2_{BS}	σ^2_{WS}	σ^2_{WC}	σ^2_{NC}	σ^2_{WNC}	σ^2_{E}
Height	45.6	14.7	0	0	0	39.7
Diameter	30.4	11.4	0	0	0	58.2
Leaf area	22.1	51.7	1.1	1.8	0.	23.2
SLW	0	2.2	0	6.9	0	90.9
Leaf water potential	1.5	10.7	0	4.8	12.3	70.8
Stomatal conductance	0.1	0	0	0.5	6.9	92.5
Transpiration rate	0	0	1.9	0	0	98.1
Photosynthetic rate	0	0	7.2	2.1	8.0	82.7

Unlike the growth parameters, the major source of variation for SLW and physiological characteristics was residual variance. Both clones between sites and clones within sites made little or no contribution to the total variation.

GREENHOUSE STUDY

MATERIALS AND METHODS

Establishment

As mentioned in the field plot study, the plants in experiment one were coppiced in March, 1988. The shoots removed were used to establish a greenhouse study. These plant materials were kept in cold storage until further use.

Hardwood cuttings (25 cm in length, 1 - 2 cm in diameter and having at least two buds) were soaked in tap water for 72 hours. The cuttings were then planted in polyethylene containers containing a 2 : 1 ratio of sand and sandy-loam soil. The containers were 15.2 cm in diameter and 61 cm in height. The spacings were 35 and 25 cm between and within plots, respectively. Temperatures varied from ± 36.5 ^{o}C during the day to ± 17 ^{o}C during the night. Plants were grown under ambient light condition. The experiment was established on April 17, 1988 in a greenhouse of the Tree Research Center, Department of Forestry, Michigan State University.

Treatment combinations and design of the experiment were similar to those of the field plot study. However, in the greenhouse study the plants were subjected to more severe water stress treatments. The following water treatments were applied:

1. severe water stress (SWS): plants were watered when soil water potential reached -0.2 MPa;
2. moderate water stress (MWS): plants were watered when soil water potential reached -0.1 MPa and
3. no water stress (NWS): plants were kept at soil water potential -0.001 MPa or less.

Soil water potentials at the NWS treatment were monitored using tensiometers, while those at the SWS and MWS treatments were monitored with soil moisture sensors (Soiltest, Inc.).

For nitrogen fertilization the following rates were used:

1. no nitrogen fertilizer (N1);
2. 2.25 gr N equivalent per plant (N2) and
3. 4.50 gr N equivalent per plant (N3).

Water treatment and nitrogen fertilization were applied 1.5 months after planting. Ammonium nitrate (NH_4NO_3) was used as the nitrogen source.

Data Collection and Analyses

In August, 1988 stomatal conductance, transpiration, and photosynthetic rates were measured on the youngest fully-expanded leaf using an ADC open system infrared gas analyzer. PARs were above 1000 μmol $m^{-1}s^{-1}$ when the measurements were carried out. Correlations between values for the youngest fully-expanded leaf and measurements taken over the whole plant (an average of several measurements

taken at several height positions) were high. For example, the coefficient of correlation for stomatal conductance was 0.97, while that for photosynthetic rate was 0.79. These correlations were significant at the 1 % level. The correlation analyses were based on 24 samples taken 9 days before the actual measurement.

Leaf area and specific leaf weight (SLW) were determined on the leaf where stomatal conductance, transpiration, and photosynthetic rates were measured. Leaf water potential was measured using a PMS pressure chamber (PMS Instrument Co., Corvallis, Oregon) at several height positions. The reading was then determined as an average of these measurements.

Height and root-collar diameter measurements were made at the end of the experiment (2.5 months after the water treatments and nitrogen fertilization were started). The shoots were harvested and dried in an oven. The roots were extracted by soaking in tap water and then dried in an oven. The dried shoot and root were then taken to the laboratory for weighting.

Data were analyzed using analyses of variance with the model and assumptions being similar to those of the field plot study. Water status and nitrogen level were considered as fixed effects, while clone and site (population) were considered as random effects. Clones were nested within sites. Plot means were used as data entries.

The contribution of population to the total variation was estimated based upon variance component estimations. Stability or plasticity of the populations to changes in water status were examined by the method of Eberhart and Russell (1966). The parameters are defined with the following model:

$$Y_{ij} = \mu_i + \beta_i I_j + \delta_{ij}$$

where Y_{ij} is the population mean of the i^{th} population at the j^{th} water status (i=1,2 ...v, j= 1, 2 ... n);

μ_i is the mean of the i^{th} population over all environments;

β_i is the deviation from regression coefficient that measures the response of the i^{th} population to varying water status;

δ_{ij} is the deviation from regression of the i^{th} population at the j^{th} water status and

I_j is the environmental index obtained as the mean of all populations at the j^{th} water status minus the grand mean.

The first stability parameter is

$$b = \Sigma_j Y_{ij} I / \Sigma_j I^2_j$$

and the second stability parameter is

$$Sd^2_i = [\Sigma_j \delta^2_{ij}/n-2] - Se^2/r$$

where Se^2/r is the estimate of pooled error and

$$\Sigma_j \delta^2_{ij} = [\Sigma_j Y^2_{ij} - Y^2_{i}./n] - [\Sigma_j Y_{ij} I_j]2/\Sigma_j I^2_j$$

This method defines a stable population or lack of plasticity as one with a regression slope (b) of unity and a small residual mean square (Sd^2i). A population exhibiting a high b value is defined as a population that is more responsive to an environment of high productivity, while a low b value is associated with a population that does not respond to favorable environments.

RESULTS

The physical and chemical properties of the soil media used in the greenhouse study are given in Table 18, while the soil moisture retention curve is presented in Figure 12. Average temperatures recorded during the study are shown in Table 19.

Height

There were significant differences in height between water status treatments after 2.5 months (Table 20). There were also significant height growth differences between nitrogen levels. The analysis of variance showed highly significant linear and quadratic effects on height for nitrogen fertilization.

The effect of nitrogen, however, was dependent upon water status, since the interaction between water status and nitrogen levels was highly significant. Both linear and quadratic responses of this interaction were significant. The nature of this interaction effect can be seen further in Figure 13. The added nitrogen dramatically increased height growth if the plants were not under water stress. Nitrogen fertilization had little effect, or even tended to decrease height growth, when the plants were subjected to water stress.

Table 18. Physical and chemical properties of soil media in the greenhouse study

Texture (%)*			Concentration (ppm)						pH
Sand	Silt	Clay	N	P	K	Ca	Mg	Na	
90.3	4.4	5.4	354.8	177.1	36.7	450	48.3	20.4	7.5

* sand

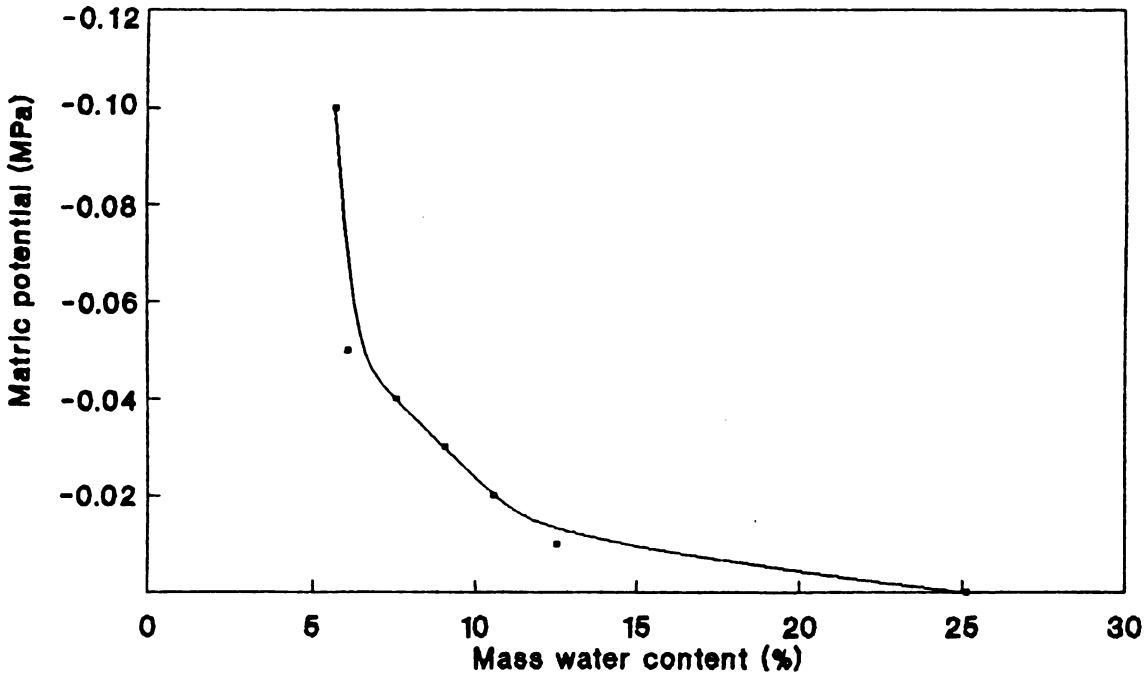

Figure 12. Soil moisture retention curve for soil media of the greenhouse study.

Table 19. Average temperatures in the greenhouse study

	Average temperature (^{o}C)			
	May	June	July	August
Maximum	36.0	36.5	36.5	35.5
Minimum	17.0	18.0	20.0	20.0

Table 20. Analysis of variance for height in the greenhouse study

Source of variation	Df.	Mean square	F value
Replicates	2	--------	
Water status (W)	2	101151.300	731.99 **
Error (a)	4	138.187	
Nitrogen levels (N)	2	11650.140	24.16 **
Linear	1	16673.266	34.58 **
Quadratic	1	6627.004	13.75 **
W x N	4	11594.170	24.05 **
Linear	2	19156.083	39.73 **
Quadratic	2	4032.257	8.36 **
Error (b)	12	482.119	
Clones (C)	7	2230.928	21.45 **
Between sites	1	5033.921	2.85 ns
Within sites	6	1763.763	16.97 **
W x C	14	308.246	2.97 **
N x C	14	128.019	1.23 ns
W x N x C	28	114.723	1.10 ns
Error (c)	126	103.945	

CV(a)= 16.87 %; CV(b)= 31.52 %; CV(c)= 14.63 %.
** = significant at the 1 % level.
ns = not significant.

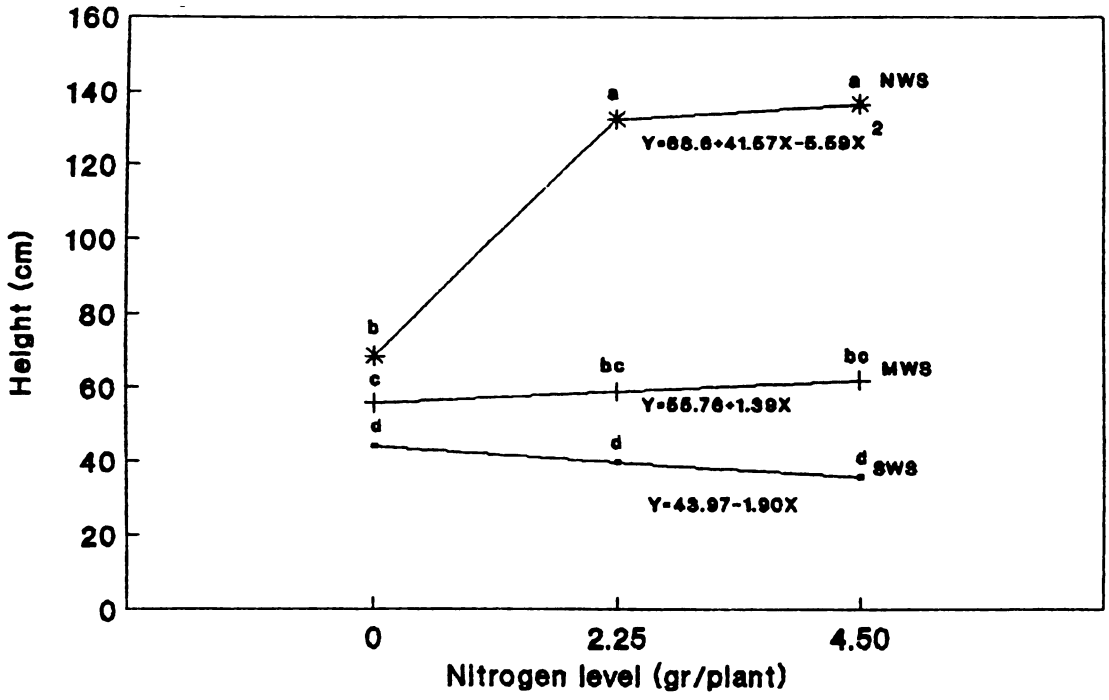

Figure 13. The effect of water status on height after 2.5 months, as affected by nitrogen levels in the greenhouse study. Any means with the same letter are not significantly different by Duncan's multiple range test at the 5 % level. SWS= severe water stress; MWS= moderate water stress; NWS= no water stress.

The effect of site origin of clones upon height growth varied according to water status. This effect was significant only when the plants were not under water stress (Figure 14). The nature of the interaction was apparently not a difference in the direction, but rather a difference in the response magnitude. Plants from the dry site grew more slowly than those from the wet site under well-watered conditions.

Diameter

The nature of responses for diameter after 2.5 months was similar to that of height (Table 21). The interaction between water status and nitrogen levels was highly significant, indicating that the effect of water status varied with the rate of nitrogen applied. Both linear and quadratic effects of the interaction were significant (Figure 15).

As with height growth, nitrogen fertilization showed little impact on diameter growth when plants were under water deficit. In fact, the added nitrogen had a negative effect in the SWS treatment. Nitrogen increased diameter growth dramatically in the NWS treatment, but an increase of nitrogen rate above 2.25 gr produced little additional response.

The growth of clones collected from different sites varied according to water status, which was shown by a significant interaction effect between water status and

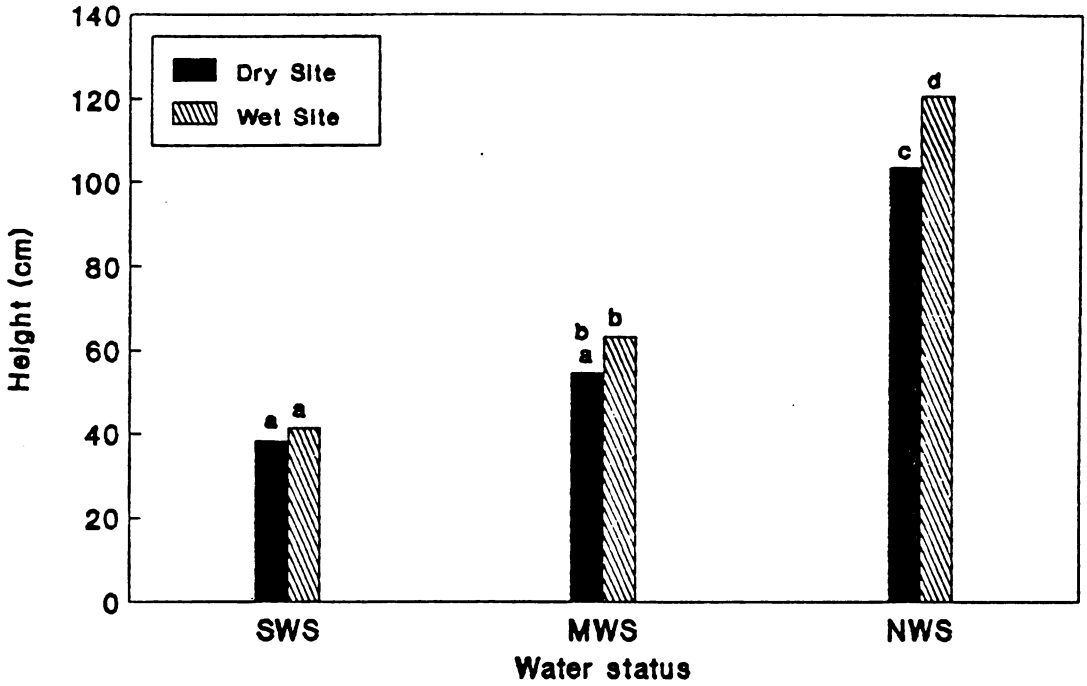

Figure 14. The effect of site origin of clones on height after 2.5 months, as affected by water status in the greenhouse study. Any means with the same letter are not significantly different by Duncan's multiple range test at the 5 % level. SWS= severe water stress; MWS= moderate water stress; NWS= no water stress.

Table 21. Analysis of variance for diameter in the greenhouse study

Source of variation	Df.	Means square	F value
Replicates	2	---------	
Water status (W)	2	193.8419	405.03 **
Error (a)	4	0.4786	
Nitrogen levels (N)	2	16.6126	11.59 **
Linear	1	17.6680	12.33 **
Quadratic	1	15.5572	10.86 **
W x N	4	17.3625	12.12 **
Linear	2	29.1562	20.35 **
Quadratic	2	5.5688	3.89 *
Error (b)	12	1.4329	
Clones (C)	7	5.6829	18.47 **
Between sites	1	7.4370	1.38 ns
Within sites	6	5.3905	17.52 **
W x C	14	0.6753	2.19 *
N x C	14	0.4089	1.33 ns
W x N x C	28	0.4869	1.58 ns
Error (c)	126	0.3077	

CV(a)= 10.02 %; CV(b)= 17.34 %; CV(c)= 8.03 %.
*,**=significant at the 5 and 1 % levels, respectively.
ns= not significant.

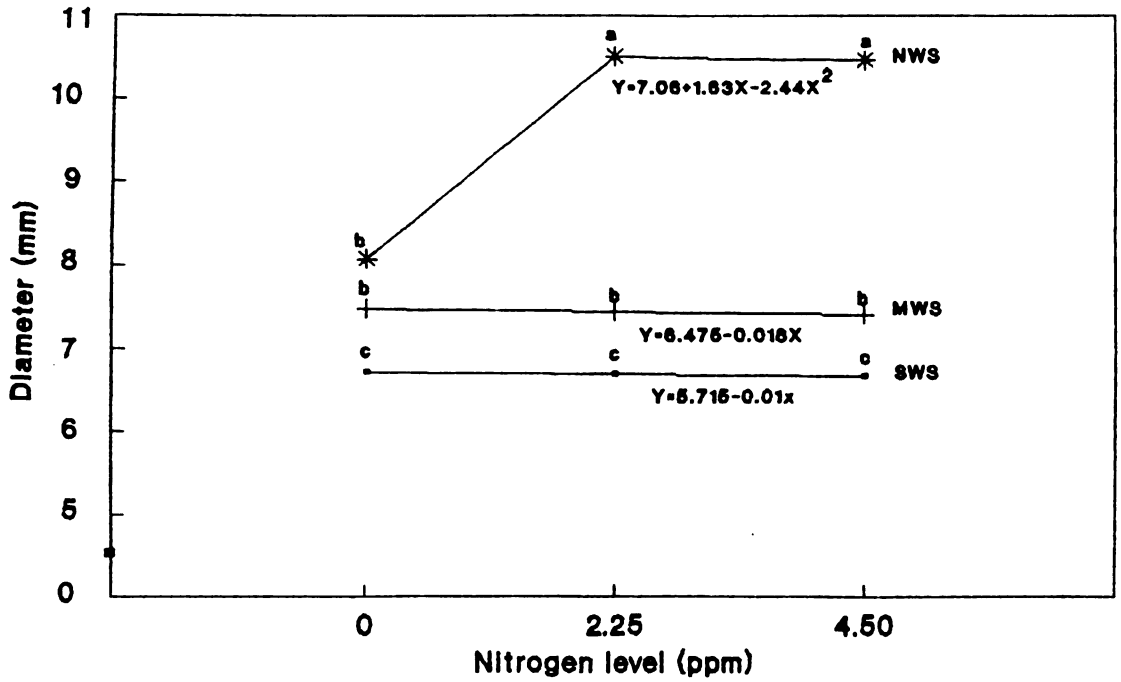

Figure 15. The effect of water status on diameter after 2.5 months, as affected by nitrogen levels in the greenhouse study. Any means with the same letter are not significantly different by Duncan'multiple range test at the 5 % level. SWS= severe water stress; MWS= moderate water stress; NWS= no water stress.

clones (Figure 16). Again, the nature of the interaction among clones between sites and among water regimes was in magnitude of response instead of direction of response. Clones from the dry site had smaller diameter than those from the wet site in all three water status treatments. Only those in the NWS treatment were significantly different.

Leaf Area

The analysis of variance for leaf area was conducted on transformed data due to the heterogeneity of variance among the water treatments. Natural log-transformations were employed, since the standard deviations of the treatments were more or less proportional to their means.

The effect of water status on leaf area was dependent upon the rate of nitrogen applied, since the interaction between water status and nitrogen was highly significant (Table 22). Both linear and quadratic responses of this interaction were highly significant. To further elucidate the joint effect of water status and nitrogen level, an additional analysis was carried out (Figure 17).

As with height and diameter, nitrogen fertilization had a significant effect under the condition where plants were not lacking water (NWS). Leaf area was reduced significantly when nitrogen was not added in the NWS treatment. Increasing the nitrogen level to more than 2.25 gr had little effect on increasing leaf area. By contrast,

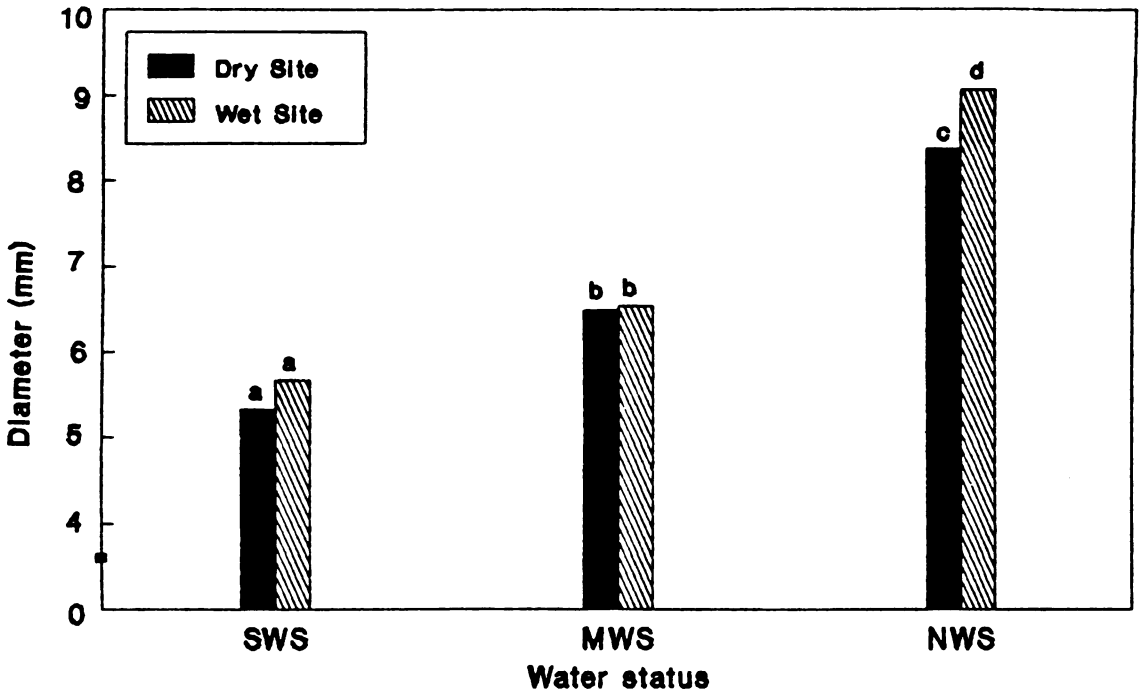

Figure 16. The effect of site origin of clones on diameter after 2.5 months, as affected by water status in the greenhouse study. Any means with the same letter are not significantly different by Duncan's multiple range test at the 5 % level. SWS= severe water stress; MWS= moderate water stress; NWS= no water stress.

Table 22. Analysis of variance for leaf area in the greenhouse study

Source of variation	Df.	Mean square	F value
Replicates	2	--------	
Water status (W)	2	8.8019	20.57 **
Error (a)	4	0.4279	
Nitrogen levels (N)	2	9.8364	49.88 **
Linear	1	14.6564	74.32 **
Quadratic	1	5.6951	28.88 **
W x N	4	5.0879	25.80 **
Linear	2	8.0856	41.00 **
Quadratic	2	2.0902	10.60 **
Error (b)	12	0.1972	
Clones (C)	7	0.5000	9.63 **
Between sites	1	0.4606	0.91 ns
Within sites	6	0.5066	9.77 **
W x C	14	5.7450	1.11 ns
N x C	14	0.0639	1.23 ns
W x N x C	28	0.0798	1.53 ns
Error (c)	126	0.0519	

CV(a)= 15.01 %; CV(b)= 10.19 %; CV(c)= 5.22 %.
** = significant at the 5 % level.
ns = not significant.

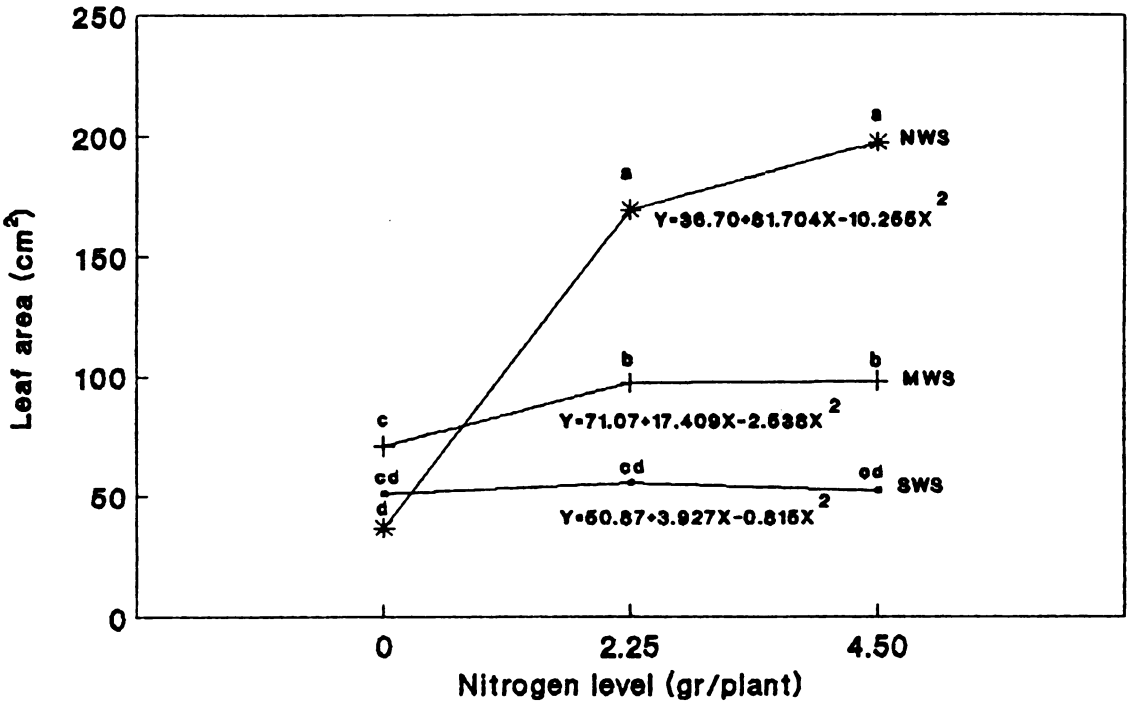

Figure 17. The effect of water status on leaf area after 2.5 months, as affected by nitrogen levels in the greenhouse study. Any means with the same letter are not significantly different by Duncan's multiple range test at the 5 % level. SWS= severe water stress; MWS= moderate water stress; NWS= no water stress.

adding nitrogen above 2.25 gr tended to reduce leaf area when the plants were under water stress.

Differences among clones between sites in leaf area were not significant, but clones within sites differed significantly. No interaction involving clones was detected, indicating that the response of clones was independent of water status and nitrogen levels. Despite the fact that differences among clones between sites were not significant, clones from the dry site had smaller leaf areas than those from the wet site. The weighted mean leaf areas were 74.7 and 81.9 cm^2 for clones from the dry and wet sites, respectively.

Specific Leaf Weight

Water status had no significant effect on leaf specific weight (SLW) (Table 23). The effect of nitrogen, on the other hand, was highly significant and its effects varied according to water status. The interaction effect between water status and nitrogen level was primarily due to the linear component. The added nitrogen reduced SLW in a dramatic fashion in the NWS treatment (Figure 18). In every water status, the addition of nitrogen at levels greater than 2.25 gr tended to reduce SLW.

As with leaf area, differences among clones between sites were not significant. Clones within sites, however, differed significantly. The effect of the second order interaction was also significant. Analysis of the

Table 23. Analysis of variance for SLW in the greenhouse study

Source of variation	Df.	Mean square	F value
Replicates	2	-------	
Water status (W)	2	4.8380	1.90 ns
Error (a)	4	2.5524	
Nitrogen levels(N)	2	12.7808	6.99 **
Linear	1	25.1004	13.72 **
Quadratic	1	0.4612	0.25 ns
W x N	4	2.3770	8.28 **
Linear	2	24.3272	13.30 **
Quadratic	2	5.9680	3.26 ns
Error (b)	12	1.8295	
Clones (C)	7	4.1550	6.01 **
Between sites	1	3.8346	0.91 ns
Within sites	6	4.2084	6.08 *
W x C	14	1.0459	1.51 ns
N x C	14	1.1841	1.71 ns
W x N x C	28	1.2671	1.83 **
Error (c)	126	0.6918	

CV(a)= 24.12 % CV(b)= 20.42 %; CV(c)= 12.55 %.
*,**=significant at the 5 and 1 % levels, respectively.
ns = not significant.

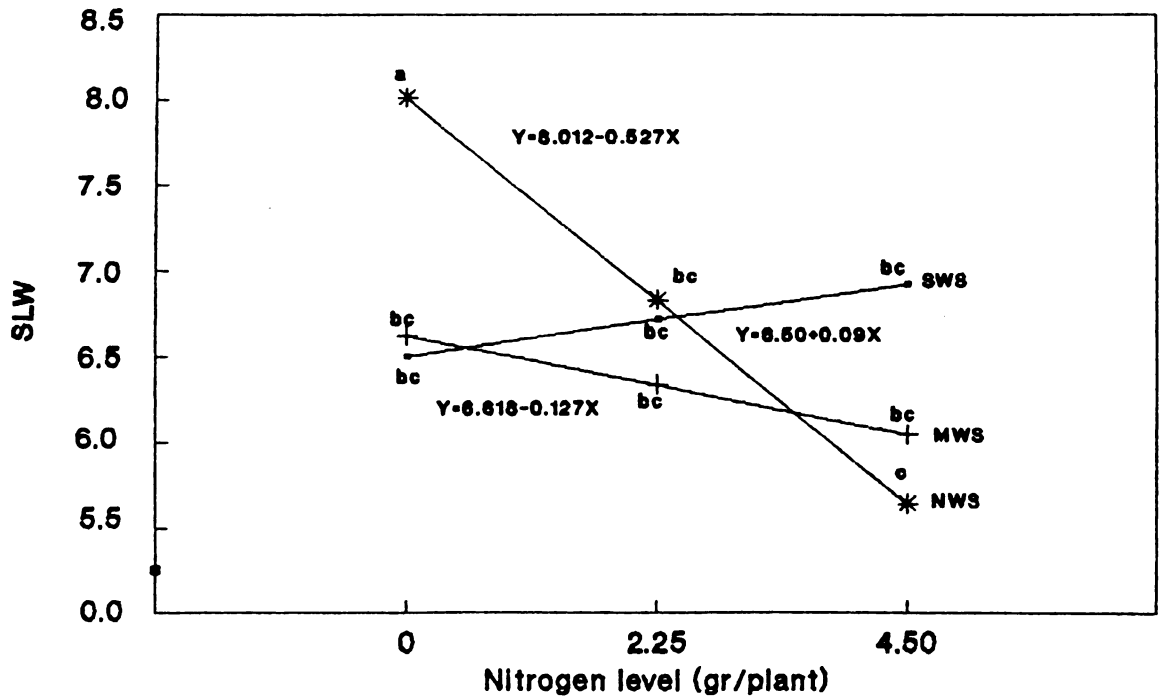

Figure 18. The effect of water status on SLW after 2.5 months, as affected by nitrogen levels in the greenhouse study. Any means with the same letter are not significantly different by Duncan's multiple range test at the 5 % level. SWS= severe water stress; MWS= moderate water stress; NWS= no water stress.

interaction involving site origin of clones and other treatments revealed no significant effect.

Shoot Biomass

Data transformations were conducted prior to performing the analysis of variance for shoot biomass. Log transformation was used, since the standard deviations of the water treatment were proportional to their means. The effects of water stress and nitrogen treatments were highly significant for shoot biomass after 2.5 months (Table 24). The interaction between water status and nitrogen level was also significant. The interaction effect was primarily linear. (Figure 19). Again, the added nitrogen fertilizer had its greatest effect when the trees were not under water stress. The addition of nitrogen fertilizer at levels greater than 2.25 gr resulted in little increase in shoot biomass in NWS. Conversely, when the plants were under water stress, nitrogen fertilization had a minor or negative impact on shoot biomass.

As with the previous characteristics, shoot biomass of clones between sites did not differ significantly. Clones within sites, however, showed significant differences. The interaction between site origin of clones and water status was also significant (Figure 20).

Differences in shoot biomass between clones from the dry site and wet site were apparent only when plants were not under water deficit. Under water stress conditions (SWS

Table 24. Analysis of variance for shoot biomass in the greenhouse study

Source of variation	Df.	Mean square	F value
Replicates	2	--------	
Water status (W)	2	45.2280	436.77 **
Error (a)	4	0.1036	
Nitrogen levels (N)	2	2.8553	8.85 **
Linear	1	1.6394	5.08 *
Quadratic	1	4.0707	12.61 **
W x N	2	3.2431	10.05 **
Linear	1	5.8900	18.25 **
Quadratic	1	0.5959	1.85 ns
Error (b)	12	0.4220	
Clones (C)	7	1.4769	12.37 **
Between sites	1	3.2593	2.76 ns
Within sites	6	1.1797	9.88 **
W x C	14	0.2890	2.42 **
N x C	14	0.1471	1.23 ns
W x N x C	28	0.1083	0.91 ns
Error (c)	126	0.1194	

CV(a)= 13.25 %; CV(b)= 23.39 %; CV(c)= 14.23 %.
*,**=significant at the 5 and 1 % levels, respectively.
ns = not significant.

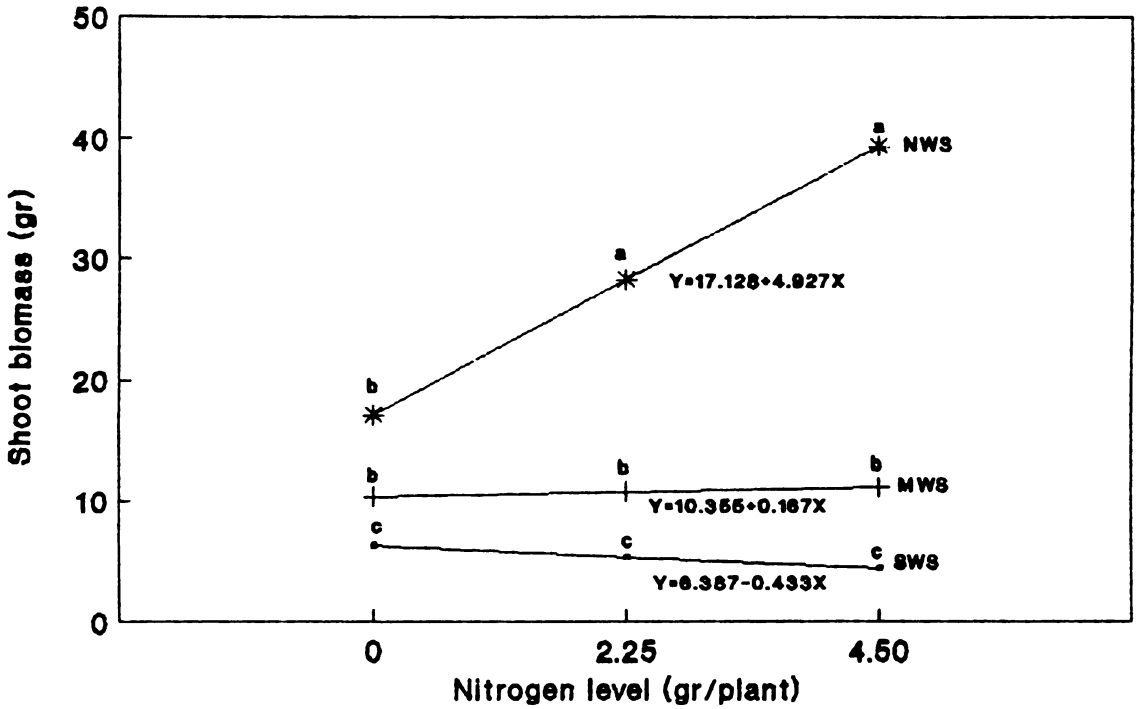

Figure 19. The effect of water status on shoot biomass after 2.5 months, as affected by nitrogen levels in the greenhouse study. Any means with the same letter are not significantly different by Duncan's multiple range test at the 5 % level. SWS= severe water stress; MWS= moderate water stress; NWS= no water stress.

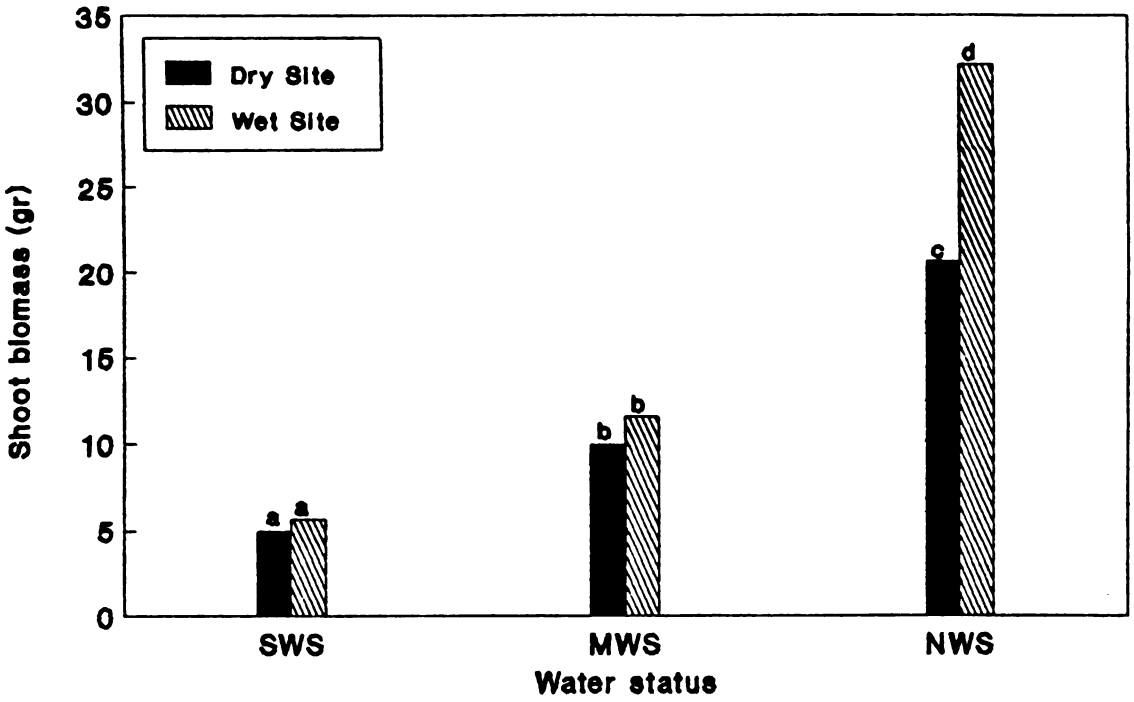

Figure 20. The effect of site origin of clones on shoot biomass after 2.5 months, as affected by water status in the greenhouse study. Any means with the same letter are not significantly different by Duncan's multiple range test at the 5 % level. SWS= severe water stress; MWS= moderate water stress; NWS= no water stress.

and MWS) these differences were negligible even though clones from the dry site had lower shoot biomass than those from the wet site.

Root Biomass

Log transformations were also employed for root biomass prior to performing an analysis of variance. Water status treatments had a highly significant effect upon root biomass (Table 25). The effect of water status on root biomass was independent of the rates of nitrogen applied. Figure 21 shows that all three water regimes differed from one another significantly in root biomass. The weighted mean root biomass after 2.5 months as affected by the water stress treatment were 2.2, 3.5, and 6.4 gr for SWS, MWS, and NWS, respectively.

Nitrogen fertilization also had a significant impact on root biomass, but unlike shoot biomass the interaction between water status and nitrogen rates was of little significance. Nitrogen application appeared to reduce root biomass. The major effect of nitrogen on root biomass was linear (Figure 22). The effect of nitrogen was also independent of clones.

There were no significant differences among clones between sites, but clones within sites differed significantly. The effect of clones seemed to vary according to water status. However, the interaction involving water status and site origin of clones is of

Table 25. Analysis of variance for root biomass in the greenhouse study

Source of variation	Df.	Mean square	F value
Replicates	2	--------	
Water status (W)	2	19.9920	36.98 **
Error (a)	4	0.5406	
Nitrogen levels (N)	2	1.2051	9.58 **
Linear	1	1.8732	14.90 **
Quadratic	1	0.5370	4.27 ns
W x N	4	0.0822	0.70 ns
Error (b)	12	0.1311	
Clones (C)	7	0.9566	13.65 **
Between sites	1	1.0895	1.17 ns
Within sites	6	0.9344	13.33 **
W x C	14	0.2456	3.50 **
N x C	14	0.0861	1.23 ns
W x N x C	28	0.0864	1.23 ns
Error (c)	126	0.0701	

CV(a)= 56.58 %; CV(b)= 27.28 %; CV(c)= 20.37 %.
** = significant at the 1 % level.
ns = not significant.

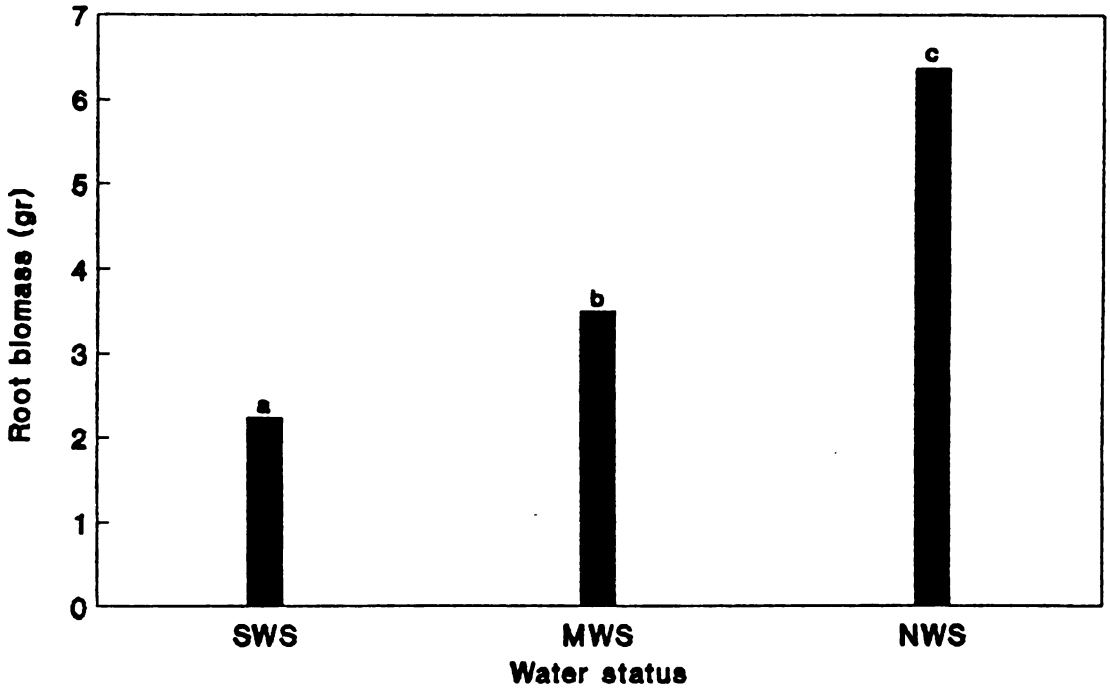

Figure 21. The effect of water status on root biomass after 2.5 months in the greenhouse study. Any means with the same letter are not significantly different by Duncan's multiple range test at the 5 % level. SWS= severe water stress; MWS= moderate water stress; NWS= no water stress.

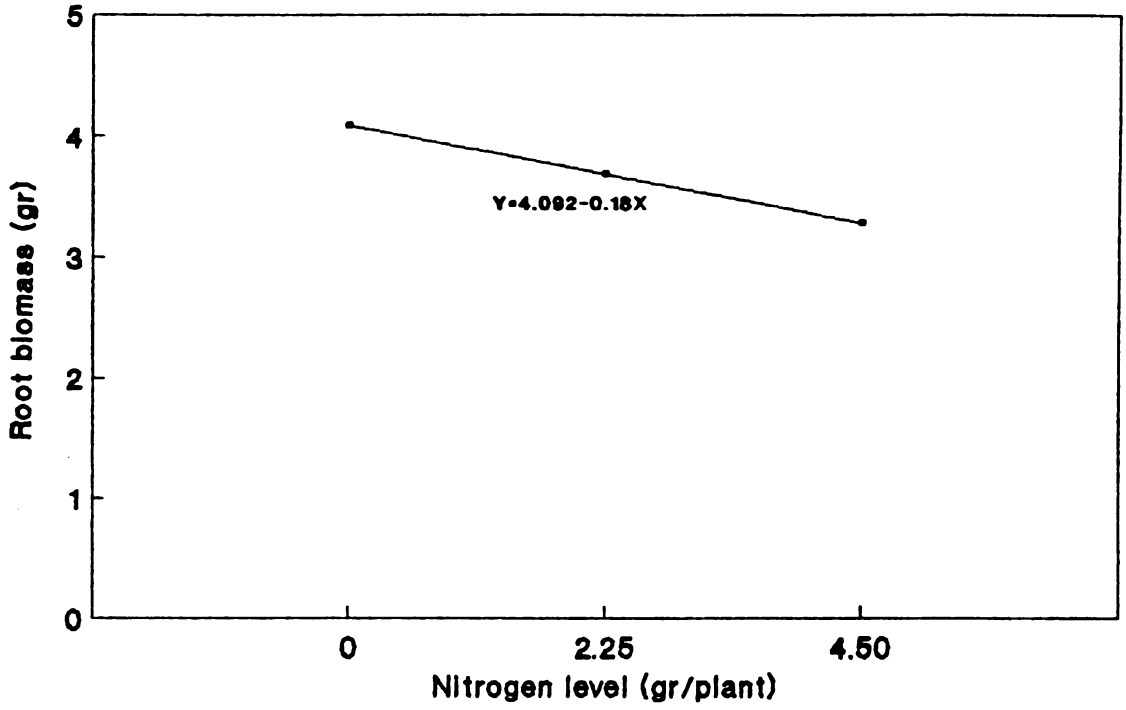

Figure 22. The effect of nitrogen levels on root biomass after 2.5 months in the greenhouse study.

interest, even though it was not significant. Clones from the dry site and clones from the wet sites did not differ significantly under the different levels of water stress.

Root-Shoot Ratio

As with shoot and root biomass, log transformations were needed prior to performing the analysis of variance on data for root-shoot ratio, due to the heterogeneity of variance. Water regimes and nitrogen levels had highly significant effects on root-shoot ratios after 2.5 months (Table 26). In addition, the effect of water status was dependent upon nitrogen levels. Both linear and quadratic responses of interaction were significant. Figure 23 shows that water status had a great impact upon root-shoot ratios. Plants under water deficit tended to have greater root-shoot ratios than those under well-watered conditions. Under all three water status treatments, the root-shoot ratio decreased when the rate of nitrogen was increased. However, a more dramatic effect was observed in the NWS treatment, where the additional nitrogen resulted in a significant reduction in the root-shoot ratio.

The average response of the clones was not significantly different between the two sites, but the performance of clones within sites differed significantly. The first order and second order interactions involving clones with other treatments were highly significant. Analyses of the interaction involving site origin of clones

Table 26. Analysis of variance for root-shoot ratio in the greenhouse study

Source of variation	Df.	Mean square	F value
Replicates	2	--------	
Water status (W)	2	3.7676	21.72 **
Error (a)	4	0.1735	
Nitrogen levels (N)	2	3.5334	32.59 **
Linear	1	6.7664	62.42 **
Quadratic	1	0.3005	2.77 ns
W x N	4	1.2534	11.56 **
Linear	2	1.9946	18.40 **
Quadratic	1	0.5122	4.72 *
Error (b)	12	0.1084	
Clones (C)	7	0.1084	6.64 **
Between sites	1	0.8981	1.92 ns
Within sites	6	0.4667	5.86 *
W x C	14	0.2215	2.78 **
N x C	14	0.0512	0.69 **
W x N x C	28	0.1322	1.65 *
Error (c)	126	0.0796	

CV(a)= 11.87 %; CV(b)=9.39; CV(c)= 8.04 %.
*,**=significant at the 5 and 1 % levels, respectively.
ns= not significant.

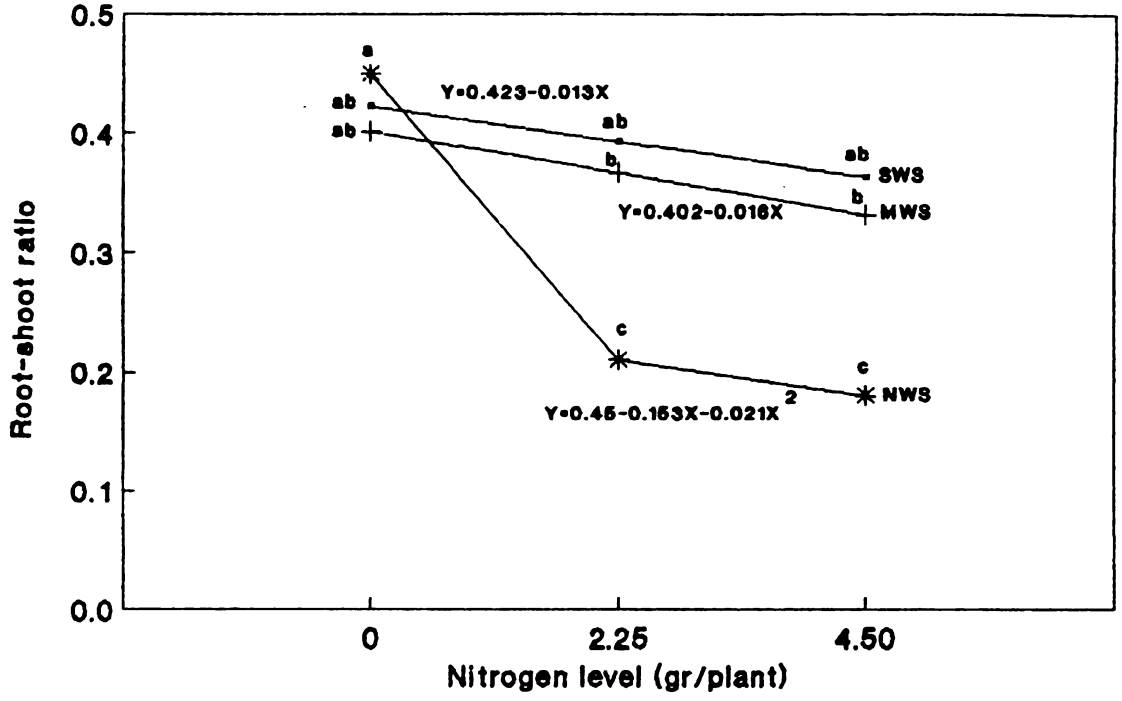

Figure 23. The effect of water status on root-shoot ratio after 2.5 months, as affected by nitrogen levels in the greenhouse study. Any means with the same letter are not significantly different by Duncan's multiple range test at the 5 % level. SWS= severe water stress; MWS= moderate water stress; NWS= no water stress.

and other treatments showed no significant effect. Although the root-shoot ratio of clones between sites was not significantly different, clones from the dry site tended to have higher root-shoot ratios in every water status than those from the wet site.

Leaf Water Potential

The differences in leaf water potential between water status were highly significant (Table 27). Nitrogen rates, on the other hand, had a negligible effect. The interaction effect between water status and nitrogen levels was also very small. The leaf water potentials in all three water status treatments were significantly different (Figure 24). Water stress caused the leaf water potential to be more negative.

There were no significant differences among clones between sites for leaf water potential. Clones within sites, however, differed significantly in leaf water potential. The interaction between water status and clones was also significant. Again, the interaction involving site origin of clones and water status was analyzed further. Its result indicated that the interaction was not significant in this regard. Nonetheless, the leaf water potential for clones from the dry site tended to be higher than those from the wet site.

Table 27. Analysis of variance for leaf water potential in the greenhouse study

Source of variation	Df.	Mean square	F value
Replicates	2	--------	
Water status (W)	2	1157.6860	78.14 **
Error (a)	4	14.8154	
Nitrogen levels (N)	2	3.6213	1.25 ns
W x N	4	7.0364	2.44 ns
Error (b)	12	2.8789	
Clones (C)	7	16.9418	9.69 **
Between sites	1	44.6901	3.67 ns
Within sites	6	12.1702	7.05 **
W x C	14	5.7876	3.31 **
N x C	14	1.8302	1.05 ns
W x N x C	28	2.0747	1.19 ns
Error (c)	126	1.7480	

CV(a)= 30.50 %; CV(b)= 13.45 %; CV(c)= 10.48 %.
** = significant at the 1 % level.
ns = not significant.

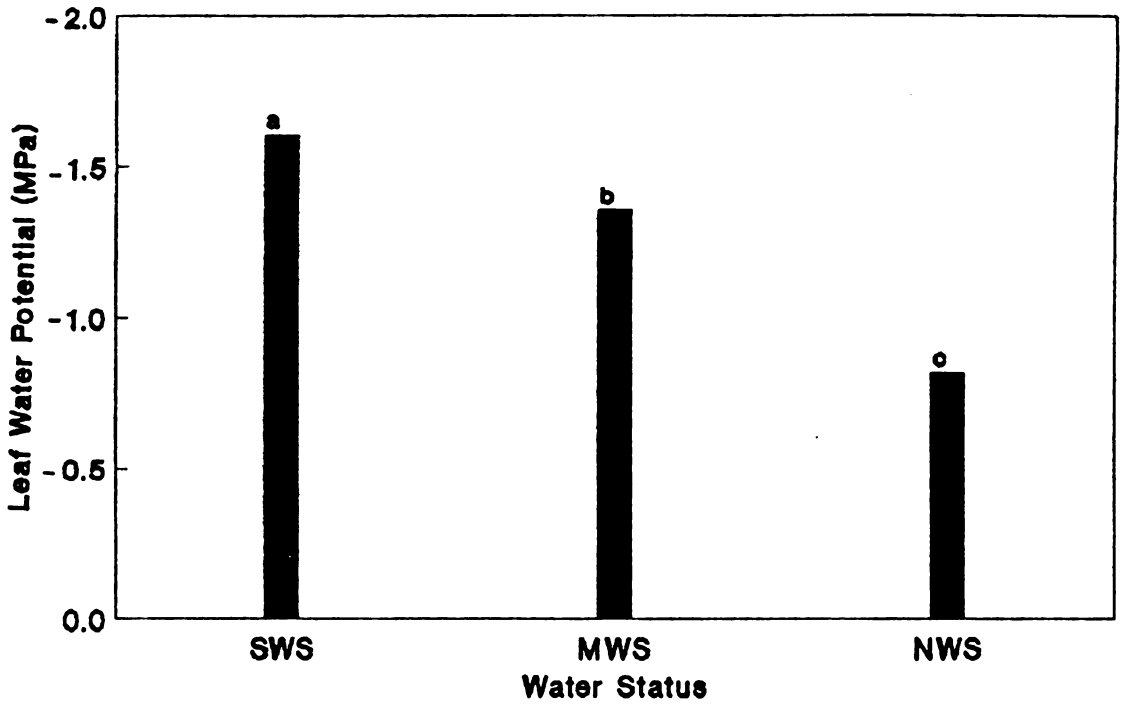

Figure 24. The effect of water status on leaf water potential after 2.5 months in the greenhouse study. Any means with the same letter are not significantly different by Duncan's multiple range test at the 5 % level. SWS= severe water stress; MWS= moderate water stress; NWS= no water stress.

Stomatal Conductance

Because of the heterogeneity of variance, log transformations for stomatal conductance data were required before conducting an analysis of variance. Log transformation was used. There were highly significant differences in stomatal conductance between the water stress treatments, as well as between nitrogen levels (Table 28). However, the effects of water status and nitrogen levels on stomatal conductance was inter-dependent. The interaction effect was primarily linear (Figure 25). Added nitrogen had little influence upon stomatal conductance when plants were under water stress. In contrast, nitrogen increased stomatal conductance under well-watered conditions.

Neither the clones between sites nor clones within sites terms contributed significantly to the observed variance in stomatal conductance. However, plants from the dry site had a slightly higher stomatal conductance than those from the wet site. The weighted mean stomatal conductances for plants from the dry site and wet site were 0.21 and 0.20 mol $m^{-2}s^{-1}$, respectively. No interaction involving clones was detected.

Transpiration

The analysis of variance for transpiration rate was carried out on log-transformed data. The analysis of variance in Table 29 shows that water status and nitrogen levels influenced transpiration rate significantly. However,

Table 28. Analysis of variance for stomatal conductance in the greenhouse study

Source of variation	Df.	Mean square	F value
Replicates	2	---------	
Water status (W)	2	64.8919	109.82 **
Error (a)	4	0.5910	
Nitrogen levels (N)	2	0.7236	5.80 **
Linear	1	1.3843	11.10 **
Quadratic	1	0.0629	0.50 ns
W x N	4	0.4073	3.27 *
Linear	1	0.6316	5.06 *
Quadratic	1	0.1831	1.47 ns
Error (b)	12	0.1247	
Clones (C)	7	0.2240	1.50 ns
Between sites	1	0.1017	0.68 ns
Within sites	6	0.2444	1.64 ns
W x C	14	0.1957	1.31 ns
N x C	14	0.1591	1.07 ns
W x N x C	28	0.1463	0.98 ns
Error (c)	126	0.1489	

CV(a)= 25.59 %; CV(b)= 11.76 %; CV(c)= 12.85 %.
*,**=significant at the 5 and 1 % levels, respectively.
ns = not significant.

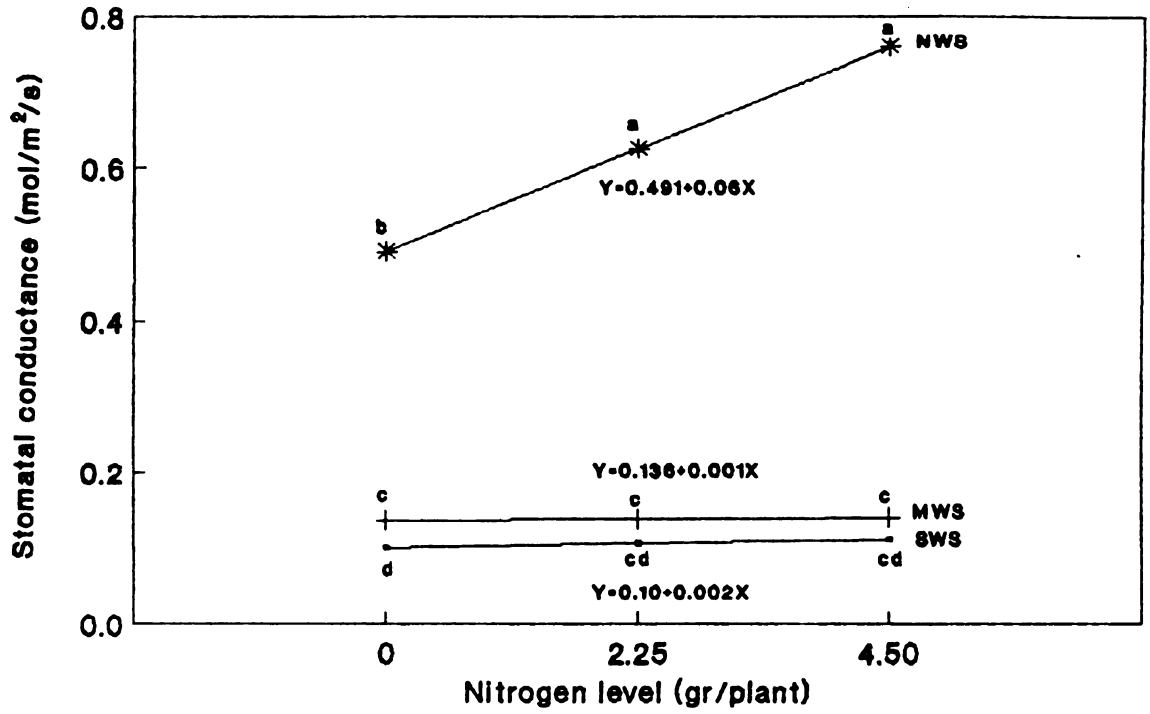

Figure 25. The effect of water status on stomatal conductance after 2.5 months, as affected by nitrogen levels in the greenhouse study. Any means with the same letter are not significantly different by Duncan's multiple range test at the 5 % level. SWS= severe water stress; MWS= moderate water stress; NWS= no water stress.

Table 29. Analysis of variance for transpiration rate in the greenhouse study

Source of variation	Df.	Mean square	F value
Replicates	2	--------	
Water status (W)	2	16.4883	139.73 **
Error (a)	4	0.1180	
Nitrogen levels (N)	2	0.0864	4.67 *
Linear	1	0.1436	7.76 *
Quadratic	1	0.0292	1.58 ns
W x N	4	0.0793	4.29 *
Linear	2	0.1041	5.63 *
Quadratic	2	0.0546	2.95 ns
Error (b)	12	0.0185	
Clones (C)	7	0.0020	0.05 ns
Between sites	1	0.0501	1.28 ns
Within sites	6	0.1412	3.61 ns
W x C	14	0.0236	0.60 ns
N x C	14	0.0127	0.32 ns
W x N x C	28	0.0148	0.38 ns
Error (c)	126	0.0391	

CV(a)= 20.56 %; CV(b)= 8.22 %; CV(c)= 11.83 %.
*,**=significant at the 5 and 1 % levels, respectively.
ns = not significant.

the effect of water status was not independent of the effect of nitrogen. This interaction was mainly due to the linear component, since the quadratic response was not significant. Figure 26 indicates that nitrogen levels did not have a great impact upon transpiration rate when the plants were under water deficit. The addition of nitrogen, on the other hand, resulted in increased transpiration rates when plants were well-watered.

As with stomatal conductance, no significant effect on transpiration was observed among clones between sites, nor among clones within sites. The interaction involving clones was also of little importance.

Photosynthesis

The photosynthetic rate data were also log-transformed due to the heterogeneity of variance. Among the many factors involved in the analysis, apparently only water status influenced photosynthetic rate significantly (Table 30).

All water status treatments differed significantly from one another (Figure 27), with the SWS treatment showing no net photosynthesis and the MWS treatment showing negligible rates.

Correlations Between Characteristics

A correlation analysis between physiological traits was conducted (Table 31). All the characteristics analyzed were strongly intercorrelated. Leaf water potential was

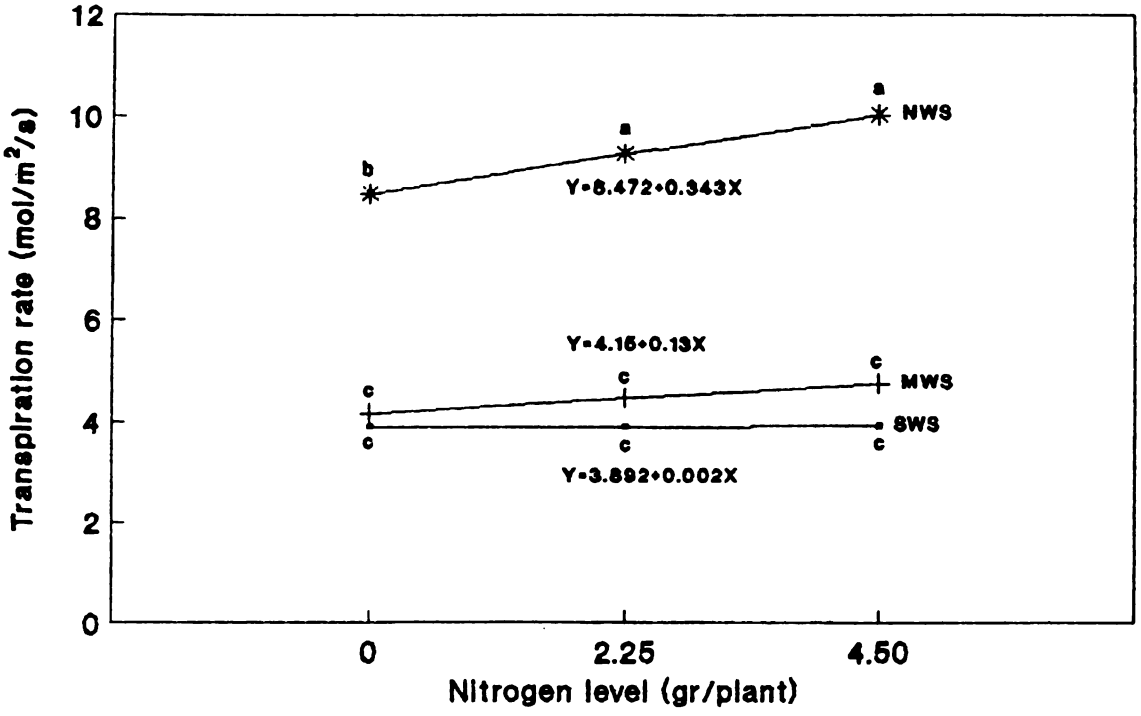

Figure 26. The effect of water status on transpiration rate after 2.5 months, as affected by nitrogen levels in the greenhouse study. Any means with the same letter are not significantly different by Duncan's multiple range test at the 5 % level. SWS= severe water stress; MWS= moderate water stress; NWS= no water stress.

Table 30. Analysis of variance for photosynthetic rate in the greenhouse study

Source of variation	Df.	Mean square	F value
Replicates	2	--------	
Water status (W)	2	628.5542	58.32 **
Error (a)	4	10.7782	
Nitrogen levels (N)	2	6.7379	2.41 ns
W x N	4	4.7412	2.80 ns
Error (b)	12	2.7980	
Clones (C)	7	3.8863	0.60 ns
Between sites	1	0.3057	0.05 ns
Within sites	6	4.4830	0.69 ns
W x C	14	8.1016	1.25 ns
N x C	14	6.6128	1.02 ns
W x N x C	28	7.2619	1.12 ns
Error (C)	126	6.4789	

CV(a)= 39.72 %; CV(b)= 20.25 %; CV(c)= 30.80 %.
** = significant at the 1 % level.
ns = not significant.

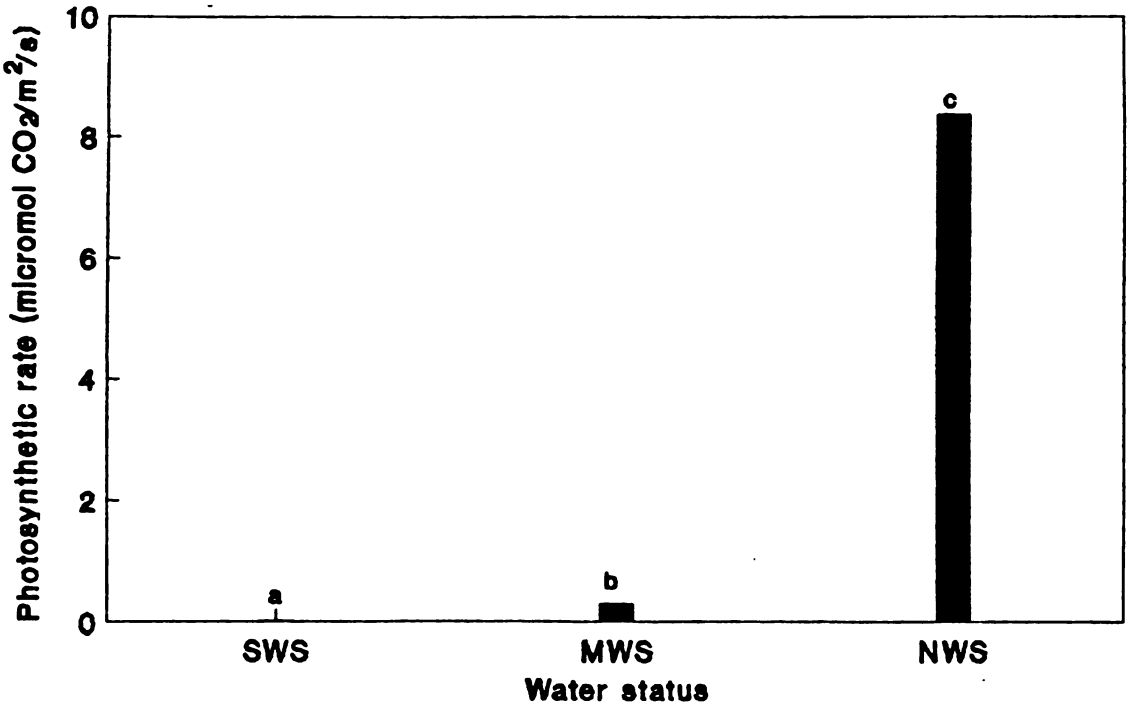

Figure 27. The effect of water status on photosynthetic rate after 2.5 months in the greenhouse study. Any means with the same letter are not significantly different by Duncan's multiple range test at the 5 % level. SWS= severe water stress; MWS= moderate water stress; NWS= no water stress.

Table 31. Correlations between physiological characteristics in the greenhouse study **

	Leaf water potential	Stomatal conduct.	Trans. rate	Photosyn.
Leaf water potential		-.74	-0.81	-0.79
Stomatal conductance			0.87	0.87
Transpiration				0.90

** = all correlations are significant at the 1 % level.

negatively correlated with stomatal conductance, transpiration, and photosynthesis. As leaf water potential became more negative, stomatal conductance, transpiration, and photosynthetic rates decreased. Stomatal conductance, on the other hand, correlated positively with transpiration and photosynthesis. As stomatal conductance increased, transpiration and photosynthetic rates were enhanced.

Variance Component Estimation

The variance component attributable to clones between sites was smaller in comparison to the variance component accounted for by clones within sites for height, diameter, shoot biomass, root biomass, and root-shoot ratio (Table 32). Despite the fact that clones between sites were not the major source of variation, their contribution to the total variation was high for height and shoot biomass. For physiological traits, the contribution of clones between sites, as well as clones within sites seemed to be of less significance. The major source of variation for these characteristics was residual error.

Stability Assessment

The stability or plasticity parameters were assessed only for the characteristics which showed site origin of clones-treatment interactions. Since the only treatment that interacted with clones was water status, the stability parameters referred to this treatment. Clones from the dry

Table 32. Variance component estimation for characteristics measured in the greenhouse study

Characteristics	Variance component (% of total)					
	σ^2_{BS}	σ^2_{WS}	σ^2_{WC}	σ^2_{NC}	σ^2_{WNC}	σ^2_{E}
Height	13.5	27.4	10.1	1.2	1.6	46.3
Diameter	3.0	30.15	6.5	1.8	9.5	49.1
Leaf area	0	21.0	0.8	1.6	11.6	65.0
SLW	0	11.8	3.6	4.9	17.3	62.5
Shoot biomass	9.7	19.7	9.4	1.6	0	59.7
Root biomass	1.1	24.6	15.0	1.4	4.2	53.8
Root-shoot ratio	3.1	10.9	12.0	0	13.4	60.7
Leaf water potential	10.0	12.3	15.0	0.3	3.6	58.2
Stomatal conductance	0	2.2	3.3	0.7	0	93.8
Transpiration	1.2	8.6	0	0	0	90.3
Photosynthesis	0	0	2.6	0.2	3.8	93.4

Table 33. Stability parameters of two populations of eastern cottonwood across three soil water levels

Characteristics	Population	b	Sd^2
Height	Dry site	0.93	0.1146
	Wet site	1.07	0.1949
Diameter	Dry site	0.90	79.0937
	Wet site	1.10	113.9021
Shoot biomass	Dry site	0.90	0.0470
	Wet site	1.10	0.0706

site had smaller **b** and σ_d^2 values than those from the wet site for all characteristics examined. Clones from the wet site were more responsive to favorable water conditions than those from the dry site, which is indicated by the higher **b** values. In addition, clones from the wet site were more plastic in response to changes in water status in comparison with those from the dry site as shown by higher values of σ_d^2.

DISCUSSION

Water stress has a profound effect upon plant growth. Cell enlargement and differentiation are all reduced by water deficit with the obvious result being a reduction in plant size (Kramer, 1983; Kramer and Kozlowski, 1979).

Despite the fact that the severe water stress (SWS) treatment in experiment one only occurred during the first three months after its establishment (Table 2), the resulting water deficit reduced height and diameter growth of eastern cottonwood profoundly. During the first three months after planting, the highest recorded soil water potential in the SWS treatment was -0.07 MPa. Thereafter plants in all water treatments were essentially in well-watered conditions due to the adequate amount of rainfall (Table 2). Supplemental irrigation was added quite rarely for the moderate water stress (MWS) and no water stress (NWS) treatments from this period of time until the end of the growing season. MWS had apparently no significant effect on reducing height and diameter growth.

The results of experiment two were similar to those of experiment one. Height and diameter growth were affected by water deficit in a significant way. In this experiment, plants in the SWS treatment experienced quite severe water deficit until the end of July (Table 7). As a matter of fact the drought this year was the worst drought to occur in Michigan in recent years (United States, Department of

Commerce, 1988). The lowest recorded soil water potential in the SWS treatment was -0.1 MPa. Again, from August until the end of the experiment, all water treatments were in well-watered conditions. Additional irrigation for the MWS and NWS treatments was only rarely needed.

Water deficit also had significant effects upon leaf area and SLW. Leaf enlargement is more severely affected by water deficit than other physiological processes such as photosynthesis and transpiration (Boyer, 1976). This field plot experiment clearly showed that water deficit had a dramatic impact on leaf area of eastern cottonwood. Water stress reduced leaf area even with moderate water stress. SLW was also very sensitive to changes of water status.

It has long been documented that soil water status affects leaf water potential, stomatal conductance, transpiration, and photosynthesis (Hsiao, 1973; Boyer, 1976; Farquar and Sharkey, 1982; Schulze, 1986). The results of this field plot study substantiated the previous findings, except for photosynthesis. Leaf water potential, stomatal conductance, and transpiration were all reduced by decreasing water availability.

Stomatal conductance has long been recognized as a key variable influencing leaf gas exchange through its regulation of water vapor and CO_2 diffusion. Researchers have attempted to correlate stomatal conductance to leaf water potential. However, there is accumulating evidence that under field conditions (mild water stress), the

decrease in stomatal conductance is not associated with a change in leaf water potential. For example, Osonubi (1985) found that substantial decreases in stomatal conductance of cowpea (Vigna unguiculata L.) were independent of leaf water potential. Blackman and Davies (1985) also found an independence of stomatal conductance with leaf water potential in maize plants subjected to soil drying. Cock et al. (1985) observed decreased stomatal conductance in unirrigated cassava (Manihot esculenta Crantz.) plants even though the leaf water potential was slightly higher than that of well-irrigated plants.

In the field plot study the correlation between leaf water potential and stomatal conductance was very low (-0.15), indicating that stomatal conductance was independent of leaf water potential, even though both stomatal conductance and leaf water potential decreased as water deficit increased. A number of researchers have suggested that stomatal conductance decreases only after a threshold of leaf water potential is attained (Hsiao and Acevedo, 1974; Turner, 1974, Baldocchi et al., 1985; Teskey and Hinckley, 1986).

The correlation between stomatal conductance and photosynthesis found in the field plot study was moderate (0.45). Water status also had little effect on photosynthesis in this regard. Farquhar and Sharkey (1982) discussed this matter extensively, and suggested that stomata generally function to minimize water loss, while

only marginally limiting photosynthesis. In addition, stomatal closure is not the only mechanism by which water deficit influences photosynthesis (Boyer, 1971; Hsiao, 1973; Jones, 1985; Nicolodi et al, 1988; Teskey et el, 1986).

The correlation between leaf water potential and photosynthesis was also low (-0.15). Some researchers have observed this phenomenon and proposed that photosynthesis responds to soil water depletion independent of leaf water status alterations, presumably through a still unknown signal coming from the roots (Passioura, 1980; Bates and Hall, 1982; Turner et al., 1985; Schulze, 1986). In conifers Grieu at al. (1988) found that increasing soil drought affected stomatal conductance and mesophyll photosynthesis independently. The result with relatively mild water deficit in this field plot experiment was in agreement with the previous findings. Water stress had a significant effect on stomatal conductance, but had little influence on photosynthesis.

It is surprising that the effect of nitrogen fertilization on growth was not significant, even though unfertilized plants grew less. It has been reported that nitrogen fertilization improved the growth of eastern cottonwood in the field. For example, Blackmon and White (1972) found that applying nitrogen fertilizer (150 lb/acre) to a six-year old eastern cottonwood increased diameter, basal area, and volume growth by 200 %. Curlin (1967) observed that a large increase in growth at one-year of age

resulted from nitrogen fertilization. Blackmon (1977) reported that eastern cottonwood's response to nitrogen was related to age. When nitrogen fertilizer was applied to a plantation at age four (336 kg N/ha) diameter growth increased by 33 % over unfertilized treatments. Fertilizing at ages two and three resulted in no responses. Nitrogen fertilization was reported to increase photosynthetic capacity in a Douglas-fir stand (Brix, 1971; Brix, 1972). However, nitrogen fertilization has also been reported to have no significant effect on photosynthetic rate (Brix and Ebell, 1969; Helms, 1964).

Since the nitrogen content in the soil of the field plot in this study was relatively low (Table 1), it was expected that the added nitrogen would result in increased growth rates. This discrepancy could in part be due to the high coefficient of variation in the sub-plot that resulted in an inability to detect any significant differences between nitrogen levels. The plantation might also be merely unresponsive to the added nitrogen at such a young age, as was also observed by Blackmon (1977). At this young age competition among plants was not a significant factor, and the nitrogen demand might be met by indigenous soil nitrogen.

The greenhouse study was designed to be similar to the field experiment, but with more severe water stress in the SWS and MWS treatments. As expected, water stress affected all growth and physiological characteristics measured. The

water deficit occurring in this experiment reduced the growth and inhibited physiological processes of eastern cottonwood in a dramatic fashion. This is not surprising since a lack of moisture inhibits enzyme activities, affects membrane conformation, and influences all other physiological processes, the end result being a decrease in growth (Teskey and Hinckely, 1986; Kramer, 1983; Kramer and Kozlowski, 1979).

In the greenhouse study most of the effects of water status were not independent, but rather varied according to the rate of nitrogen applied. Nitrogen fertilization was of little significance in influencing growth and physiological processes under water stress, but had considerable effects under favorable water conditions. Plants respond to nitrogen fertilization depending on other environmental factors, such as the availability of water supply (Kramer and Kozlowski, 1979).

Water serves as the medium for diffusion and mass flow of nutrients to plant roots. Nutrient movement may be seriously limited in soils with a low moisture content, since that reduces hydraulic conductivity and thereby mass flow and pathways for nutrient diffusion (Ballard and Cole, 1974; Viets, 1972).

Moisture deficiency affects nitrogen metabolism of plants both directly and indirectly in many complex ways, often resulting in a moisture-nitrogen interaction in growth. The direct effects are through inhibition of the

biosynthesis of nitrogen-dependent compounds such as protein. Indirect effects include reduction in nitrogen uptake, because nitrogen cannot be absorbed from dry soil. (Brix, 1979; Hsiao, 1973; Naylor; 1972).

An interaction of moisture and nutrients in tree growth depends on whether moisture changes affect the relationship of nutrient supply and demand in plants. It is conceivable that demand is reduced more than availability, thus improving the mineral nutrient status of plants. Also, nutrient storage within plants may overcome brief limiting periods of nutrient uptake, providing a clear case of moisture-fertilizer interaction in which fertilization would affect growth under favorable soil moisture but not when moisture becomes deficient (Brix, 1979).

The results of the greenhouse study basically verified the finding in other fertilization studies. Growth and physiological processes are more affected by nitrogen when plants are under well-watered conditions, except that root biomass declined as nitrogen levels increased irrespective of water status.

Water stress profoundly affected shoot biomass and root biomass in this study. Root-shoot ratios for plants under water stress were higher than those under favorable soil moisture conditions. Root growth is oftentimes less affected by water stress than shoot growth, resulting in an increase in root-shoot ratios (Kramer, 1983). This increase in root-shoot ratio observed under water deficit is

generally believed to be due to greater water stress developing in the shoot (Kramer, 1983). A higher root-shoot ratio under water stress was also reported in eastern cottonwood (Farmer, 1970 b) and hybrid poplar (Mazzoleni, 1985). It has also been demonstrated in many species that shoot growth is affected more by water stress than root growth, resulting in a higher root-shoot ratio (Kramer, 1983; Kramer and Kozlowski, 1979).

As mentioned before, root growth declined with the increase of nitrogen rates regardless of water status. Root-shoot ratios tended to decline as the rate of nitrogen applied increased, particularly under favorable moisture conditions. This was shown by the negative slopes of regression lines. It has been known that fertilization, particularly heavy fertilization, causes a reduction in carbohydrates and an increase in nutrient content in the plant. Plants respond by producing proportionally more shoot and less root materials, resulting in a low root-shoot ratio. By contrast, a lack of nutrient (nitrogen) availability leads to low concentrations of limiting nutrients and to accumulation of carbohydrates. Plants respond by increasing proportional allocation to root growth, resulting in a higher root-shoot ratio (Bloom et al., 1985).

In many forest tree species nutrient availability affects carbon allocation, with more carbon being

allocated to the root in poor nutrient soil (Keyes and Grier, 1981; Grier et al., 1981).

As with the field plot study, water stress reduced leaf area in the greenhouse study. Unlike the field experiment, however, nitrogen fertilization increased leaf area significantly. The effect of nitrogen was more profound under favorable soil moisture conditions than under water deficit. The water status and nitrogen treatments also had a significant influence on SLW. Plants lacking water and nitrogen had a lower SLW than those under favorable conditions. An inverse relationship between SLW and nitrogen availability has been observed in other species (Gulmon and Chu, 1981; Longstreth and Nobel, 1980; Osman et al., 1977). A lack of available nitrogen has been related to a reduction in the proportions of sugar and protein. Therefore, the remaining insoluble materials (cell wall materials) constitute a much greater portion of the dry matter in nitrogen-deficient plants (Shimsi, 1970; Radin and Parker, 1979).

In the greenhouse study water stress inhibited all physiological processes. The effect of water deficit upon stomatal conductance, transpiration, and photosynthesis in eastern cottonwood has been previously documented. Under water stress, stomatal conductance, transpiration, and photosynthesis are reported to decrease (Bonner, 1967; Farmer, 1969; Kelliher and Tauer, 1980; Regehr et al., 1975; Scarascia-Mugnozza et al, 1986; Schulte, 1985).

Water deficit can decrease photosynthesis either by decreasing conductance to diffusion of carbon dioxide, or by affecting the photosynthetic and respiratory mechanisms (Boyer, 1976; Hinckley et al. 1981). Changes in stomatal conductance during water stress have a major impact upon photosynthesis. It has been reported in a number of studies that there is a strong correlation between stomatal conductance and photosynthesis during severe drought. Generally, as leaf water potential becomes more negative, both stomatal conductance and photosynthetic rate decrease (Boyer, 1976).

In eastern cottonwood, transpiration at various degrees of water stress was found to be primarily controlled by stomatal conductance (Kelliher, et al., 1980). Regehr et al.(1975) found that stomatal conductance and transpiration of eastern cottonwood paralleled the decline in net photosynthetic rate. The result of the greenhouse study seems in agreement with those found in other experiments. Leaf water potential, stomatal conductance, transpiration, and photosynthesis were strongly intercorrelated. However, the complete lack of photosynthesis in the SWS treatment indicates that it was due to more than just stomatal closure. The photosynthetic process itself was likely affected (Boyer, 1971; Hsiao, 1973; Jone, 1985; Teskey et al., 1986).

Despite the fact that stomatal conductance is believed to be a factor limiting photosynthetic rate, some

researchers have suggested otherwise (Farquar and Sharkey, 1982). Even though there is a strong correlation between stomatal conductance and photosynthetic rate, it appears more likely to represent an adjustment of stomatal conductance to match the intrinsic photosynthetic rate rather than a causal relationship. According to a theoretical model for stomatal control, the stomata may minimize daily transpiration for a given daily carbon gain. In other words, if a certain amount of water can be acquired for transpiration, stomata should act to maximize photosynthesis within this constraint (Cowan and Farquhar, 1977).

Under favorable soil moisture conditions nitrogen fertilization seemed to enhance stomatal conductance and transpiration. Nitrogen deficiency has been reported to reduce stomatal conductance in maize (Ryle and Hesketh, 1969), cotton (Longstreth and Nobel, 1980; Ryle and Hesketh, 1969, sugar beet (Nevins and Loomis, 1970) and rice (Yoshida and Coronel, 1976).

Childers and Cowart (1935) found a 30 % decrease in the rate of transpiration of nitrogen-deficient apple leaves. This reduction in transpiration occurred despite greater pore area per unit leaf area in the nitrogen-deficient leaves. The leaves of nitrogen-deficient bean (Phaseoulus vulgaris L) transpired less than nitrogen-supplied plants (Shimsi, 1970).

Photosynthetic rate was enhanced by increasing the nitrogen level in pine seedlings (van den Driessche and Wareing, 1966), Douglas-fir (Brix, 1971, 1972) and cotton (Wong, 1979). In other studies, however, no apparent increase of photosynthetic rate was reported. Kozel et al. (1983), for example, found that wheat plants having nitrogen deficient chloroplasts are photosynthetically at least as active as those with normal chloroplasts. A study with maize plants grown with different nitrogen concentrations also indicated no significant differences in photosynthetic rate. In this later study the photosynthetic rate was low due to the low level of illumination during the growth period, which could possibly explain the lack of significant differences between nitrogen concentrations (Fernandez and Manero, 1983; Bouma, 1970).

It is not yet clear as to how nitrogen affects stomatal conductance, transpiration and photosynthesis, but it is likely to be mediated through chlorophyll content of the leaves. An accumulating evidence indicates that there is an intimate relationship between chlorophyll content of the leaf and stomatal function. Nitrogen deficiency causes the following chain of effects: low chlorophyll content, low photosynthetic rate, high concentration of CO_2 in mesophyll spaces, and stomatal closure (Shimsi, 1970). Disruption of nitrogen nutrition has been known to affect all nitrogen-dependent plant constituents such as chlorophyll (Kramer and Kozlowski, 1979).

In the greenhouse experiment, the lack of significant differences in photosynthetic rates between the different nitrogen treatments may have been due to high temperatures that resulted from the lack of air movement (Table 19). During the measurement of photosynthesis, temperature was around 33 ^{o}C. High temperatures have direct effects on the synthesis and activity of enzymes, and have indirect effects through changing stomatal conductance for CO_2. Stomata tend to close with increasing temperature, the closure results from a stomatal response to an increased vapor deficit (Kramer and Kozlowski, 1979; Berry and Bojrkman, 1980). Under the same well-watered condition, photosynthetic rates of the greenhouse-grown plants were considerably lower than those of field-grown plants. The low photosynthetic rates of the greenhouse-grown plants may also have been due to low SLWs, which resulted from the high temperature and relatively low level of illumination during leaf development.

The average SLW of the field-grown plants under well-watered conditions was 1.13 times greater than that of the greenhouse-grown plants under the same soil moisture condition. This difference was probably due to low levels of illumination and higher temperatures in the greenhouse environment during leaf development. PARs measured in August were 2510 and 1165 μmol $m^{-2}s^{-1}$ for the field and greenhouse environments, respectively. The average daily

temperatures in the greenhouse were higher than those in the field (See Table 3 and 19).

It has been well documented that SLW or leaf thickness is influenced by light intensity and temperature. For example, Nelson and Ehlers (1984) found that SLW of populus hybrids grown in the field was 1.5 to 1.8 times than that of greenhouse-grown plants. This was primarily due to the greater average PARs in the field. The thickness of Populus x euramericana leaves increased about 30 % when the temperature was decreased from 25 to 16 ^{o} C (Pieter 1974 cited by Nelson and Ehlers, 1984). The SLW of Festuca arundinaca decreased as much as 13 % due to an increase in temperature from 10 to 25 ^{o} C (Nelson et al., 1978). Both thickness and SLW decreased as growth temperatures were raised for Glycine max and Gossypium hirsutum (van volkenburg and Davis, 1977).

SLW is often associated with photosynthetic rate (Nelson and Ehlers, 1984; McMillen and McClendon, 1983; Chabot et al. 1979). When the data of well-watered treatments from both field and greenhouse experiments were pooled, the correlation coefficient for the relationship between photosynthetic rate and SLW was 0.69. Nelson and Ehlers (1984) found slightly higher coefficients of correlation for hybrid poplar. The results of this experiment indicated that one of the major effects of the growth environment on photosynthetic rate is likely a result of changes in leaf thickness or SLW.

The SWS and MWS treatments of the greenhouse study were more severe than the corresponding treatments in the field. In the greenhouse experiment, GE-interactions for several growth and physiological characteristics were detected. Despite the fact that GE-interactions were significant, plants from the dry site grew more slowly than those from the wet site, indicating that the nature of interaction was not changes in direction, but rather changes in magnitude of differences. In addition, the variance components of GE-interactions appeared to be small in relation to the total variation. Similar results were reported by Farmer (1970b), who found that clone-moisture interactions were significant for growth, but the variance components for GE-interaction were relatively small. In another study, clone-moisture interaction for growth was not detected (Broadfoot and Farmer, 1969).

In both field and greenhouse studies, however, GE-interactions with regard to nitrogen fertilization were not of great importance. This finding was in conflict with that reported by Curlin (1967), who found that the clone-nitrogen interaction was very strong.

It is interesting to note that plants collected from the wet site consistently grew faster than those from the dry site in both field plot and greenhouse studies, even though in the greenhouse study the differences between the two populations were statistically significant only in the well-watered condition.

Compared with the plants from wet habitats, plants growing in dry habitats usually are smaller and their leaves are usually smaller and thicker. In addition, they tend to have deeper root systems and lower transpiration rates (Kramer and Kozlowski, 1983). A number of studies that have been done in forest tree species indicate that there are genetic differences between plants growing in dry habitats and those growing in wet habitats with regard to growth and physiological characteristics. For example, Pinus sp. from xeric locations had a lower rate of shoot growth than those from mesic habitats (Venator,1976; Wells and Wakely, 1966; Woesner, 1972a, 1972b; Wright and Bull, 1963). Transpiration of Douglas-fir from dry sites was found to be lower than that from wet site (Zavitkovski and Ferrell, 1968). On the other hand, Feret (1982) found that the growth of Pinus ponderosa grown under water stress did not differ significantly between xeric site type and mesic site type. Photosynthetic rate of Douglas-fir from dry sites was not significantly different from that of wet sites (Zavitkovski and Ferrell, 1968).

Kelliher and Tauer (1980) found that there were differences between clones of eastern cottonwood from dry sites and those from wet sites for growth and stomatal conductance when they were grown under water stress. Height and stomatal conductance were higher for clones from the dry site than those from the wet site.

In the present study plants from the dry site grew more slowly than those from the wet site, particularly in the field plot experiment. It appears that there is genetic differentiation between the two populations with regard to growth. The existence of genetic differentiation between these populations is substantiated by the amount of variation attributable to clones between sites. For example, in experiment two of the field plot study, more than 45 % and more than 30 % of the total phenotypic variation for height and diameter, respectively, were accounted for by between population differences.

By contrast, SLW and physiological traits were hardly affected at all by the site origin of clones. In other words, the original site of the population had little or no effect on the variation of these traits. Environmental factors, on the other hand, were the major cause of the existing variation. These traits may be of less significance for the adaptation of eastern cottonwood in the habitats being studied.

Plants from the dry site appear to be better adapted for slower growth than those from the wet site, due to the lack of water and nutrient availabilities. In sand dune environments plants always experience water deficit, particularly during dry weather conditions. The primary source of water for plants in dune habitats is from direct rainfall, but because the mechanical nature of the soils restricts their ability to retain water, the major factors

limiting their growth in these situations are the water-holding capacity of the soil and the soil resistance to surface evaporation (Ranwell, 1972). Furthermore, dune soil is very poor in nutrients (McGee et al., 1981; Grime, 1977).

By contrast, the floodplain from which the wet-site plants were collected possesses different soil conditions. In floodplains plants never experience severe water stress and floodplain soils are nutrient rich. Eastern cottonwood found in this habitat grows very rapidly (McGee et al., 1981).

McGee et al. (1981) reported somewhat similar results. They found the existence of genetic differentiation between populations of eastern cottonwood originated from sand dune, strip mine and floodplain for several growth characteristics such as height, root weight, specific leaf area, and shoot root ratio. They also found that the pattern of transpiration and photosynthesis as influenced by water deficit was different between the three populations studied.

Slower growth and higher root-shoot ratios for plants from the dry site seem to have adaptive significance. Sand-dune populations experience drought and nutrient limitation more frequently than floodplain plants and selection favors slower growth and higher root-shoot ratios for survival in the sand dune (McGee et al, 1981).

It has been well-documented that plants adapted to poor habitats have slow growth rates (Chapin, 1980; Grime and Hunt, 1975). Slow growth rates may enable the plant to

survive between occasional pulses of nutrient supply, whereas more rapidly growing plants may exhaust their nutrient reserves, leading to a complex of nutrient deficiency symptoms (Bradshaw, 1969).

In this present study it was found that there was no significant difference in root-shoot ratio between dry site and wet site plants. The importance of high root-shoot ratios for plants growing in poor habitats has been elaborated by Chapin (1980). Plants from infertile habitats maximize nutrient intake to a greater extent through high root-shoot ratios than through high root-absorption capacities. Many plants occurring in poor habitats are found to have high root-shoot ratios as a response, in part, to a lack of nutrient availability. On the other hand, plants from nutrient-rich habitats show considerable phenotypic plasticity in root-shoot ratio and generally have higher ratios at low availability and low ratios at high availability than do plants from a poor-nutrient habitat.

In this study it was found that plants from the wet site were more plastic than those from the dry site for characteristics such as height, diameter, and shoot biomass. Higher growth and higher plasticity values for plants from the wet site indicate that this population tends to adapt to more favorable conditions, in the present case to more favorable soil moisture conditions. According to Bradshaw (1965) phenotypic plasticity is one of the mechanisms by

which a species or genotype can maximize fitness. Phenotypic plasticity could itself be under genetic control.

The result of this experiment has an important implication from a practical standpoint. Selection of plant materials for improvement programs or plantation establishment in marginal lands needs to be undertaken cautiously. Populations from what we classify as dry sites may not be as drought resistant as expected. In addition, plants from dry sites may not grow better in marginal sites than those from wet sites. Plants from dry sites seem unresponsive to changes in more favorable conditions. Ideally, genotypes desirable for plantations are those having a high growth rate and a low plasticity across different environmental conditions (Shelbourne, 1972). As far as the populations used in this study are concerned, there was no evidence that plants collected from the dry site outperformed those from the wet site under any water conditions.

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