EFFECTS OF ALTERING THE ROOT SYSTEM AND SHOOT SIZE ON THE WATER RELATIONS OF LOBLOLLY PINE (<u>PINUS</u> <u>TAEDA</u> L.) SEEDLINGS UNDER CONTRASTING LEVELS OF SOIL MOISTURE STRESS

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CHAPTER I

INTRODUCTION

The survival and growth of a plant depends on the development of both a root system and a shoot system. Evidence has shown that lateral root cross-sectional area is closely correlated to the stem cross-sectional area (Carlson and Harrington 1986; and APPENDIX B, Figure 1). Plants take up water through a root system and lose it through transpiring leaves. Therefore, it can be inferred that reducing the root system would decrease the amount of water uptake, and that removing leaves from the top, on the other hand, would reduce the total amount of water loss from the plant. It has been reported that severance of portions of a root system lowered leaf water potential, and reduced stomatal conductance and transpiration to an extent corresponding to the amount of severance (Briggs and Wiebe 1982, Aston and Lawlor 1979, Teskey et al. 1983, Thoughton 1974, Blake 1983, Geisler and Ferree 1984, Andrews and Newman 1968, and Brix and Mitchell 1985). Teskey and Hinckley (1985), in their study with Abies amabilis, showed that removal of approximately one-third (31 percent) of the root system had no apparent effect on xylem pressure potential or leaf conductance. When slightly over one-half

(56 percent) of the root system was removed, lower xylem pressure potential and partial closure of stomata were observed. In explaining this result, they hypothesized that the root system was larger than needed for water supply to the leaves due to the moist soil condition. Carlson and others (1987), in a recent field study with loblolly pine saplings, observed significant effects of severing 30 percent of surface-oriented lateral roots on the water relations of the plants. Very little information, however, has been reported about the effects of leaf removal treatments on the water relations of plants. Moreover, most of the previous studies were unable to examine the patterns of response to different soil moisture conditions.

The present study was designed to determine the effects of reductions in root system and shoot size on needle water potential, stomatal conductance, and transpiration, and to examine these treatment effects under low and moderate soil moisture stress in a greenhouse with one-year-old loblolly pine seedlings. This study may provide a better understanding of the basic principles of plant response to varied soil moisture conditions, and nursery practices such as root and top pruning, root wrenching, undercutting, and transplanting.

CHAPTER II

LITERATURE REVIEW

A number of studies concerning the effects of root severance have been reported in recent years. Teskey and Hinckley (1985) studied the relation between root system size and water inflow capacity with 15- to 18-year-old *Abies amabilis* trees and found that in the field under moist soil conditions, removal of approximately one-third (31 percent) of the root system had no apparent effect on xylem pressure potential or leaf conductance. When a larger portion was severed (56 percent), xylem pressure potential and leaf conductance were lowered. In another study with the same species, Teskey and others (1983) showed that severing 54 percent of the root system caused a reduction in both water potential and stomatal conductance; whereas severing 43 percent caused reduction in stomatal conductance but not in leaf water potential.

The effect of disrupting stem sapwood water conduction on the water status was studied by Brix and Mitchell (1985) with 36-year-old Douglas-fir trees under field conditions. They found that reducing sapwood cross sectional area by 42 and 69 percent did not affect the leaf water potential, and only complete removal of sapwood decreased leaf water potential, suggesting that leaf water potential was related to soil water potential rather than to reduction of sapwood and that resistance to water movement in the stem was small compared with that in soil and roots.

A transplanting study with white spruce seedlings was conducted by Blake (1983). Seedlings were root-pruned to 25, 50 and 75 percent of their initial root area immediately prior to transplanting. Results showed that root-pruning caused a statistically significant increase in stomatal resistance 8 days after seedlings were transplanted, but not after 14 days. Root-pruning lowered leaf water potentials by an average of 0.4 MPa, 8 or more days after planting. However, this decrease was not consistantly related to the degree of root pruning.

Geisler and Ferree (1984) studied the effects of root pruning of young 'Golden Delicious' apple trees on water relations, net photosynthesis and growth under greenhouse conditions. An average of 10, 28, or 59 percent of the total root dry weight was removed. Removal of 59 percent of the root system resulted in a 1.3 to 1.5 MPa reduction in leaf water potential 6 hours after the treatment, indicating substantial water stress. Trees with 28 percent of the roots pruned showed 0.4 to 0.5 MPa lower water potentials. Leaf water potential recovered after one day, but was significantly lower in trees with 28 percent and 59 percent of the roots removed than in the control trees 7 and 10 days after root pruning. The 10 percent root pruning treatment had no influence on leaf water potential. Both transpiration and net photosynthesis were reduced 35 and 47 percent by treatments which removed 28 and 59 percent of the roots, respectively. Removal of 10 percent of the roots had no effect on net photosynthesis and transpiration.

A root detachment study in sunflower plants was conducted by Aston (1979). Results showed that decreasing the root surface area by up to 80 percent had either no effect or lowered leaf water potential by up to 0.05 MPa.

Briggs and Wiebe (1982) examined the effects of root pruning on the water relations of Helianthus annuus L. under different soil moisture conditions. They found that the differences in transpiration rates among the pruning treatments produced a significant treatment effect on soil water potentials. The more roots pruned, the wetter the soil. They also found that pruning was not more effective on transpiration in dry soils.

In a root pruning study with wheat under different soil moisture conditions, Andrews and Newman (1968) found that in the wet treatments, pruning 41 percent of the roots (dry weight basis) reduced transpiration by about 25-32 percent. But for the dry treatments, the pruning effects on transpiration were not significant. They suggested this result was due to the effective amount of roots in the pruned and unpruned treatments in the dry regime was approximately the same by the end of the experiment.

Very few studies have been done on the effects of removing leaves. Thoughton (1974) studied the relation between the sizes of the root and shoot system and the development of leaf water deficits (LWD) in plants of Lolium perenne. In this experiment, 50 percent of the roots in term of the total root numbers was cut off at the base of the shoot. He found that the larger the shoot system, the greater the amount of water transpired, so that in a system in which the amount of water was limited, water was depleted more rapidly and the increase in the LWD was more rapid. The other finding, that the larger the root system, the more rapidly LWD developed, was less expected. A regression model was developed as LWD = 5.5 + 2.6 Shoot Removed - 4.7 Root Removed. Thoughton (1974) suggested that the resistance to water uptake occurred in the soil or the root system.

Other defoliation studies were conducted by Sweet and Wareing (1966) and Wareing and Khalifa (1968) with bean (Phascolus vulgaris), maize (Zea mays), and monterey pine (Pinus radiata). These authers found that partial defoliation resulted in increased photosynthetic rates in the remaining leaves. Water relations were not examined in these studies.

CHAPTER III

MATERIALS AND METHODS

The seedlings used were from a single open-pollinated family from a North Carolina source. One-year-old loblolly pine (*Pinus taeda* L.) seedlings from the Weyerhaeuser Company nursery in Fort Towson, Oklahoma were planted in 38-litre plastic pots filled with sandy-loam natural soil on March 10, 1987 in a greenhouse. Seedlings were allowed to grow for four months before the treatments were applied. During this period, they were watered twice each week and fertilized with liquid Peat Lite Special 20:19:18 biweekly. Malathion was applied once to control mites.

Three factors were considered: soil moisture condition (SMC), proportion of roots severed (RS) and proportion of needles removed (NR). Treatments included two levels of SMC (dry and well-watered), and three levels each of RS and NR (0, 33 and 67 percent). The experiment was a 2 X 3 X 3 factorial with 4 replicates and it was arranged in a randomized complete block design.

The replicates were done in series, with measurements for each replicate beginning at one week intervals. Since measurements required 11 days, the replicates overlapped in time.

Preliminary work showed that predawn needle water potential was near -0.6 MPa when seedlings were watered twice each week and -1.0 MPa after 10 days of withholding water. Thus, water was withheld beginning 10 to 12 days before treatments were applied to each replicate. Treatments were begun for replicate one on June 24 and the entire experiment was completed on August 5.

After 10 to 12 days of withholding water, all the seedlings in a replicate, including controls, were partially excavated around the tap roots using a vacuum cleaner, to expose the zone where the lateral roots entered the tap root (APPENDIX B, Figure 2). Diameters of the lateral roots were measured at the point of attachment to the tap root with a caliper, to calculate the total root cross-sectional area of each tree. The holes were covered with damp paper towel, and aluminum foil until root-severing. In the afternoon of the same day of excavation, roots were severed representing 0, 33, and 67 percent of the total lateral root cross sectional area, according to the randomly assigned treatments. Then the soil removed from the pots was used to refill the holes. Needles were removed according to the following treatments: 0, 33, and 67 percent of the total needle numbers. The needles removed based on the total needle numbers were oven dried and weighed, and converted into needle surface area removed on the basis of regression analysis between dry weight and needle surface area (APPENDIX B, Figure 3). The regression equation for needle surface area was based on the method developed by Bingham (1984) using dry weight after 24 hours at 70 °C. No water was added to dry treatment seedlings during the measurement period and the well-watered seedlings continued to be watered twice each week.

Needle water potential was measured on three needle fasicles per seedling at both predawn (300-400, True Solar Time (TST)) and midday (1030-1130, TST) on the day immediately prior to the treatments and 1, 3, 5, and 9 days following the day treatments were applied. Stomatal conductance and transpiration were monitored on three needle fasicles per seedling for each replicate with a Steady State Porometer (Licor Instruments Model 1600) twice a day at 800-830 and 1500-1530 (TST) on the same days as the water potential measurements. Diurnal changes of stomatal conductance and transpiration were monitored at 600, 800, 1000, 1200, 1500, 1700, and 1900 hours (TST) on the third day after the treatments for each replicate. Light intensity, leaf temperature, and relative humidity readings were recorded from the porometer simultaneously.

Following the water relations measurements, seedlings were harvested to determine the actual portions of the root system and needles removed for each of the 18 treatments (Table 1). Data were analyzed using analysis of variance and linear regression methods. The treatment effects were tested with Least Square Difference (LSD) procedures.

TABLE 1

ROOT SEVERANCE AND NEEDLE REMOVAL TREATMENTS

Treatments	SMC	Roots Severed[1] (%)		Needles Removed[2] (%)	
		Assigned	Actual	Assigned	Actual
1	Dry	0	0	0	0
2		0	0	33	38
3		0	0	67	61
4		33	35	0	0
5		33	34	33	41
6		33	34	67	58
7		67	63	0	0
8		67	62	33	31
9		67	66	67	57
10	Well-watered	0	0	0	0
11		0	0	33	31
12		0	0	67	57
13		33	34	0	0
14		33	31	33	34
15		33	36	67	59
16		67	61	0	0
17		67	63	33	33
18		67	60	67	61

[1]percent of the total lateral cross-sectional area.
[2]percent of the total needle surface area.

Regression analysis was used to test the significance of the relationship between the root/shoot balance following treatments and the water relations variables. A value for the root/shoot balance (BAL) was calculated by subtracting the percentage of roots severed (RS) from the percentage of needles removed (NR):

$$BAL = NR - RS$$

The actual values for NR and RS were used and the values for BAL ranged from -63 to 61.

CHAPTER IV

RESULTS

Needle Water Potential

Prior to the RS and NR treatments there was a significant effect of the soil moisture regimes ($P < 0.0001$, APPENDIX A, Table 1). Mean values for predawn needle water potential (PNWP) were -1.24 and -0.64 MPa in the dry and well-watered regimes, respectively. Midday needle water potential (MNWP) was -1.76 MPa in the dry regime and -1.17 MPa in the well-watered regime.

PNWP generally tended to decline from day 1 through day 9 following the RS and NR treatments for some of the treatments (Table 2), but only four of the treatments showed a significant effect of the measurement day ($P < 0.05$, APPENDIX A, Table 2). The decline was greatest in the dry regime from day 5 to day 9 following the reduction treatments. Treatment effects were analyzed separately for each measurement day.

The RS treatments showed a consistently significant effect up to 9 days after the treatments and the response to the RS treatments was influenced by the level of SMC (APPENDIX A, Tables 3a-d). The average effect of severing

TABLE 2

DAILY CHANGES OF PREDAWN NEEDLE WATER POTENTIAL FOR ALL THE TREATMENTS

Soil Moisture Condition	Roots Severed (%)	Needles Removed (%)	Days from the Treatments -1	1	3	5	9
			MPa				
Dry	0	0	-1.27	-1.39	-1.44	-1.54	-1.74
		33	-1.20	-1.30	-1.25	-1.67	-1.45
		67	-1.33	-1.42	-1.35	-1.37	-1.61
	33	0	-1.18	-1.48	-1.59	-1.70	-1.95
		33	-1.20	-1.37	-1.34	-1.41	-1.63
		67	-1.23	-1.49	-1.34	-1.40	-1.56
	67	0	-1.22	-1.82	-1.99	-2.08	-2.27
		33	-1.31	-1.88	-2.01	-2.10	-2.56
		67	-1.18	-1.57	-1.61	-1.59	-1.84
Well-Watered	0	0	-0.66	-0.66	-0.65	-0.64	-0.74
		33	-0.63	-0.62	-0.57	-0.58	-0.69
		67	-0.62	-0.59	-0.57	-0.60	-0.63
	33	0	-0.70	-0.76	-0.75	-0.76	-0.80
		33	-0.62	-0.68	-0.63	-0.72	-0.75
		67	-0.66	-0.67	-0.66	-0.67	-0.70
	67	0	-0.65	-0.87	-0.81	-0.85	-0.85
		33	-0.66	-0.75	-0.71	-0.77	-0.81
		67	-0.61	-0.76	-0.62	-0.65	-0.76

Each value represents the mean of four seedlings.

33 percent of the roots in the dry regime ranged from a 0.02 MPa increase to a 0.12 MPa decrease in PNWP (Table 3). Severing 67 percent of the roots showed a 0.39 to 0.59 MPa decrease in PNWP. In the well-watered regime, PNWP declined 0.06 to 0.09 MPa when 34 percent of the roots were cut and 0.12 to 0.17 MPa when 64 percent of the roots were cut. The effects of the RS treatments were greatest on day 9 in the dry regime and day 1 in the well-watered regime.

PNWP was increased by the NR treatments. The response to the NR treatment was statistically significant ($P < 0.05$) on days 3, 5, and 9 following the treatments and was not significantly affected by the level of the SMC and RS treatments. On the third day, removing 67 percent of the needles showed a 0.18 MPa increase in PNWP (Table 4), and removing 33 percent of the needles produced a 0.11 MPa increase in PNWP. From day 5 through day 9 following the NR treatment, however, the effect of removing 33 percent of the needles was not significant. Removing 67 percent of the needles continued to show at least a 0.20 MPa increase in PNWP through day 9.

There was a strong linear relationship between PNWP and the root/shoot balance in both the dry and well-watered regimes (Figure 1, $P < 0.05$). As the root system decreased in size relative to the shoot, PNWP decreased. The change in PNWP per unit change in the root/shoot balance was over twice as large in the dry regime (0.0056) as in the well-

TABLE 3

PREDAWN NEEDLE WATER POTENTIAL AS AFFECTED BY ROOT SEVERANCE UNDER DRY AND WELL-WATERED REGIMES

SMC	Roots Severed (%)	Days from the Treatments			
		1	3	5	9
		MPa			
Dry	0	-1.37a	-1.35a	-1.52a	-1.60a
	33	-1.45b	-1.43b	-1.50a	-1.72b
	67	-1.76c	-1.87c	-1.91b	-2.19c
Well-watered	0	-0.62a	-0.59a	-0.61a	-0.69a
	33	-0.70b	-0.68b	-0.72a	-0.75b
	67	-0.79c	-0.71b	-0.76a	-0.81c

Each value represents the mean of 12 seedlings; means in each column of each SMC category followed by different letters are significantly different at $P = 0.05$.

TABLE 4

PREDAWN NEEDLE WATER POTENTIAL AS AFFECTED BY NEEDLE REMOVAL

Needle Removed (%)	Days from the Treatments			
	1	3	5	9
	MPa			
0	-1.16 a	-1.20 c	-1.26 b	-1.39 b
33	-1.10 a	-1.09 b	-1.17 ab	-1.26 ab
67	-1.08 a	-1.02 a	-1.05 a	-1.19 a

Each value represents the mean of 24 seedlings. Values followed by different letters are significant at P = 0.05.

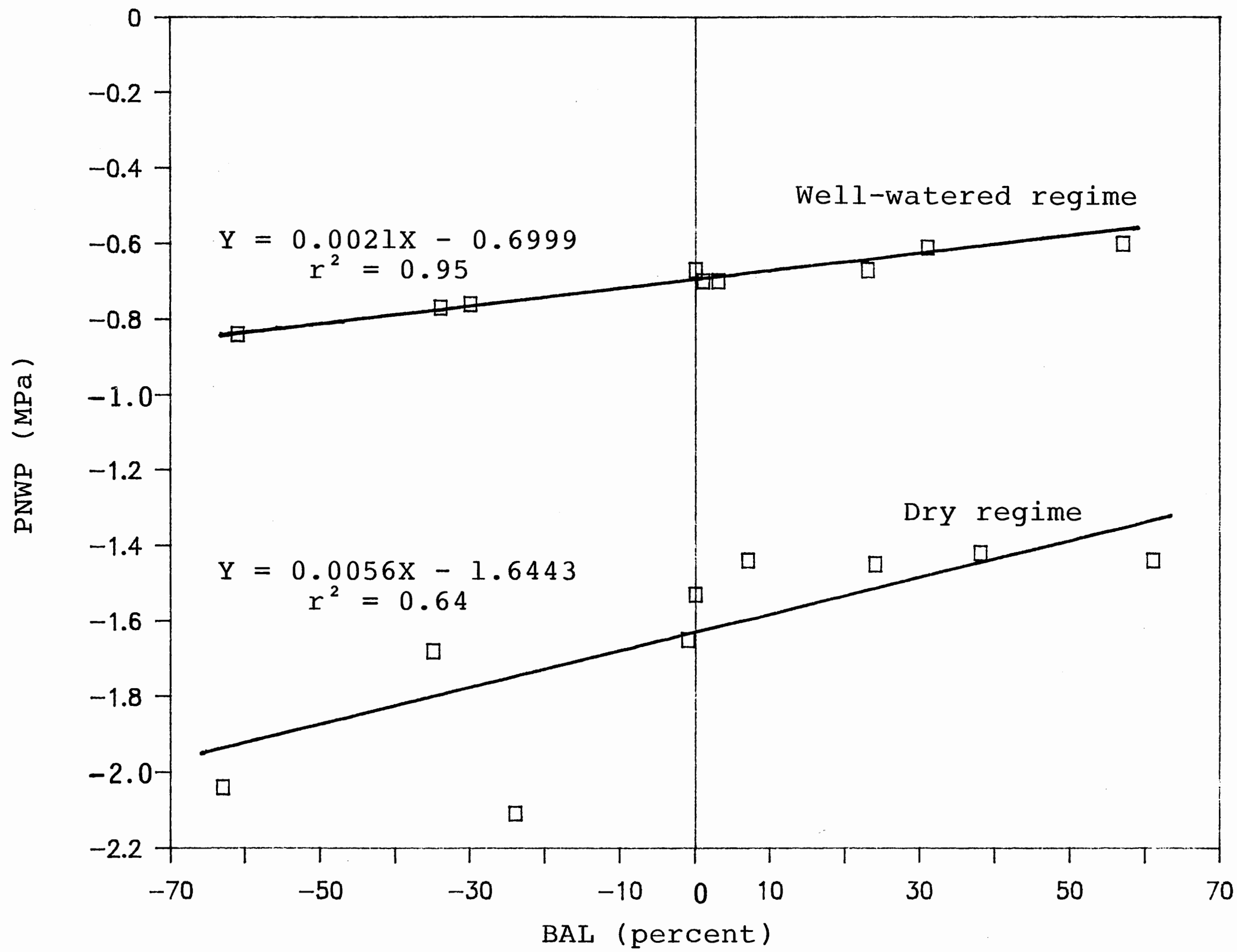

Figure 1. Relationship between Predawn Needle Water Potential (PNWP) and the root/shoot Balance Following the Reduction Treatments (BAL)

watered regime (0.0021). These slopes were significantly different ($P < 0.05$).

The effect of measurement day on MNWP was not significant for any of the treatments (Table 5; APPENDIX A, Table 2); therefore, the data were averaged over the four measurement days for further analyses. MNWP was significantly affected by the RS treatment and the effect of the interaction between RS and SMC or NR treatments was not significant (APPENDIX A, Table 4). Removing 33 percent of the root system showed an overall average decrease in MNWP of 0.08 MPa (Table 6). When the removal of the roots was increased up to 67 percent, a 0.34 MPa reduction in MNWP was observed. In contrast, MNWP was significantly inceased by NR treatments. The effect of the interaction between NR and SMC was not significant. Removing 33 percent of the needles showed a 0.10 MPa increase in MNWP. Removing 67 percent of the needles resulted in an increase of 0.23 MPa in MNWP.

There was a strong linear relationship ($P < 0.0001$) between MNWP and the root/shoot balance in both watering regimes (Figure 2). As the root/shoot balance changed towards a greater reduction in roots than needles, MNWP decreased. For each percent decrease in the root/shoot balance the MNWP decreased 0.0052 MPa in the dry regime and 0.0041 MPa in the well-watered regime. These slopes were not significantly different ($P > 0.46$).

TABLE 5

DAILY CHANGES OF MIDDAY NEEDLE WATER POTENTIAL FOR ALL THE TREATMENTS

Soil Moisture Condition	Roots Severed (%)	Needles Removed (%)	Days from the Treatments -1	1	3	5	9
			-----	-----	MPa	-----	-----
Dry	0	0	-1.83	-1.84	-1.71	-1.87	-1.87
		33	-1.72	-1.61	-1.56	-1.73	-1.62
		67	-1.95	-1.70	-1.59	-1.74	-1.74
	33	0	-1.68	-1.81	-1.87	-2.02	-1.95
		33	-1.73	-1.69	-1.67	-1.75	-1.72
		67	-1.84	-1.73	-1.57	-1.69	-1.69
	67	0	-1.75	-2.18	-2.15	-2.21	-2.38
		33	-1.72	-2.12	-2.00	-2.57	-2.57
		67	-1.64	-1.95	-1.77	-1.89	-1.84
Well-Watered	0	0	-1.10	-1.01	-1.03	-1.15	-1.03
		33	-1.22	-0.98	-1.06	-1.14	-0.98
		67	-1.11	-0.81	-0.84	-0.92	-0.86
	33	0	-1.25	-1.30	-1.19	-1.24	-1.14
		33	-1.12	-1.07	-1.07	-1.13	-1.04
		67	-1.19	-0.96	-0.96	-1.11	-0.99
	67	0	-1.23	-1.50	-1.38	-1.40	-1.19
		33	-1.17	-1.30	-1.24	-1.32	-1.20
		67	-1.17	-1.22	-1.07	-1.15	-1.12

Each value represents the mean of four seedlings.

TABLE 6

EFFECT OF ROOT SEVERANCE AND NEEDLE REMOVAL ON MIDDAY NEEDLE WATER POTENTIAL

Treatment		Water Potential (MPa)
	0	-1.35 a
Roots Severed	33	-1.43 b
(%)	67	-1.69 c
	0	-1.60 c
Needle Removed	33	-1.50 b
(%)	67	-1.37 a

Each value represents 24 seedlings. Values followed by different letters are significantly different at P=0.05 in each treatment category.

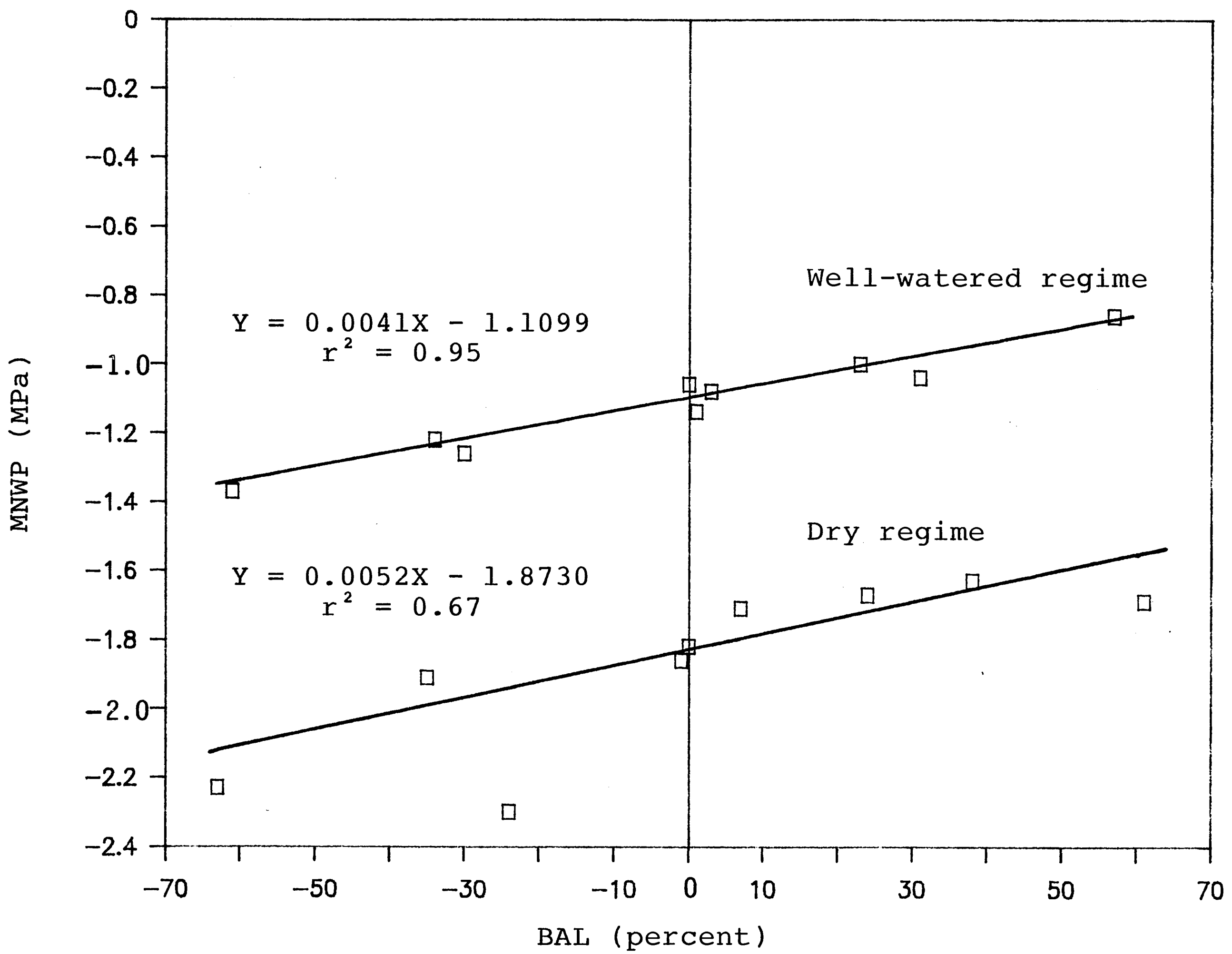

Figure 2. Relationship between Midday Needle Water Potential (MNWP) and the root/shoot Balance Following the Reduction Treatments (BAL)

Stomatal Conductance

Prior to the RS and NR treatments, there was a significant effect of SMC on stomatal conductance at both 800 hours (k_{800}) and 1500 hours TST (k_{1500}). K_{800} was 0.228 $cm.s^{-1}$ in the well-watered regime and 0.101 $cm.s^{-1}$ in the dry regime. K_{1500} was 0.148 $cm.s^{-1}$ in the well-watered regime and 0.048 $cm.s^{-1}$ in the dry regime.

Results indicated that following the RS and NR treatments the effect of measurement day on k_{800} and k_{1500} was not significant (Table 7 and 8; APPENDIX A, Table 2); therefore further analyses were conducted using the average values for the four measurement days. K_{800} was significantly affected by the RS and NR treatments (APPENDIX A, Table 4). None of the treatment interactions significantly affected k_{800}. The average effect of severing 33 percent of the roots was a decrease in k_{800} of 0.24 $cm.s^{-1}$ (Table 9). Severing 67 percent of the roots caused an average decrease of 0.33 $cm.s^{-1}$ in k_{800}. In contrast to the RS treatments, NR treatments increased k_{800} 0.20 and 0.22 $cm.s^{-1}$ when 33 and 67 percent of the needles were removed.

A good linear relationship between k_{800} and the root/shoot balance was found in both watering regimes (Figure 3). Both regression lines showed a significant slope ($P < 0.05$). However, these slopes were significantly different ($P < 0.0008$). In the well-watered regime, altering the root/shoot balance tended to show a greater

TABLE 7

DAILY CHANGES OF STOMATAL CONDUCTANCE AT 800 HOURS
FOR ALL THE TREATMENTS

Soil Moisture Condition	Roots Severed (%)	Needles Removed (%)	Days from the Treatments				
			-1	1	3	5	9
			cm.s^{-1}				
		0	0.117	0.123	0.116	0.097	0.112
	0	33	0.107	0.117	0.141	0.115	0.116
		67	0.104	0.118	0.126	0.100	0.119
		0	0.096	0.107	0.114	0.082	0.100
Dry	33	33	0.099	0.107	0.125	0.091	0.102
		67	0.081	0.118	0.122	0.089	0.096
		0	0.096	0.089	0.093	0.076	0.095
	67	33	0.129	0.103	0.129	0.086	0.093
		67	0.085	0.091	0.108	0.087	0.100
		0	0.219	0.215	0.214	0.199	0.201
	0	33	0.212	0.239	0.246	0.200	0.225
		67	0.209	0.229	0.241	0.242	0.249
		0	0.236	0.169	0.175	0.159	0.168
Well-Watered	33	33	0.206	0.195	0.189	0.165	0.188
		67	0.210	0.215	0.208	0.208	0.235
		0	0.251	0.143	0.166	0.129	0.160
	67	33	0.297	0.182	0.221	0.171	0.198
		67	0.217	0.180	0.183	0.167	0.213

Each value represents the mean of four seedlings.

TABLE 8

DAILY CHANGES OF STOMATAL CONDUCTANCE AT 1500 HOURS FOR ALL THE TREATMENTS

Soil Moisture Condition	Roots Severed (%)	Needles Removed (%)	Days from the Treatments -1	1	3	5	9
			-------------		$cm.s^{-1}$		------------
		0	0.060	0.069	0.080	0.064	0.074
	0	33	0.053	0.071	0.095	0.060	0.070
		67	0.044	0.061	0.088	0.072	0.073
		0	0.040	0.054	0.074	0.055	0.071
Dry	33	33	0.050	0.061	0.086	0.057	0.078
		67	0.046	0.065	0.079	0.055	0.072
		0	0.040	0.053	0.080	0.051	0.053
	67	33	0.054	0.062	0.089	0.064	0.081
		67	0.043	0.055	0.060	0.060	0.066
		0	0.116	0.107	0.153	0.117	0.151
	0	33	0.124	0.138	0.185	0.129	0.170
		67	0.147	0.165	0.189	0.191	0.283
		0	0.162	0.114	0.122	0.094	0.166
Well-	33	33	0.141	0.115	0.159	0.097	0.169
Watered		67	0.144	0.137	0.163	0.145	0.225
		0	0.174	0.083	0.118	0.072	0.113
	67	33	0.165	0.102	0.133	0.088	0.143
		67	0.162	0.101	0.133	0.118	0.133

Each value represents the mean of four seedlings.

TABLE 9

EFFECTS OF ROOT SEVERANCE AND NEEDLE REMOVAL ON STOMATAL CONDUCTANCE AT 800 HOURS

Treatments		Stomatal Conductance ($cm.s^{-1}$)
	0	0.171 a
Roots Severed	33	0.147 b
(%)	67	0.138 c
	0	0.138 b
Needles Removed	33	0.158 a
(%)	67	0.160 a

Each value represents 24 seedlings. Values followed by different letters in each treatment category are significantly different at P=0.05.

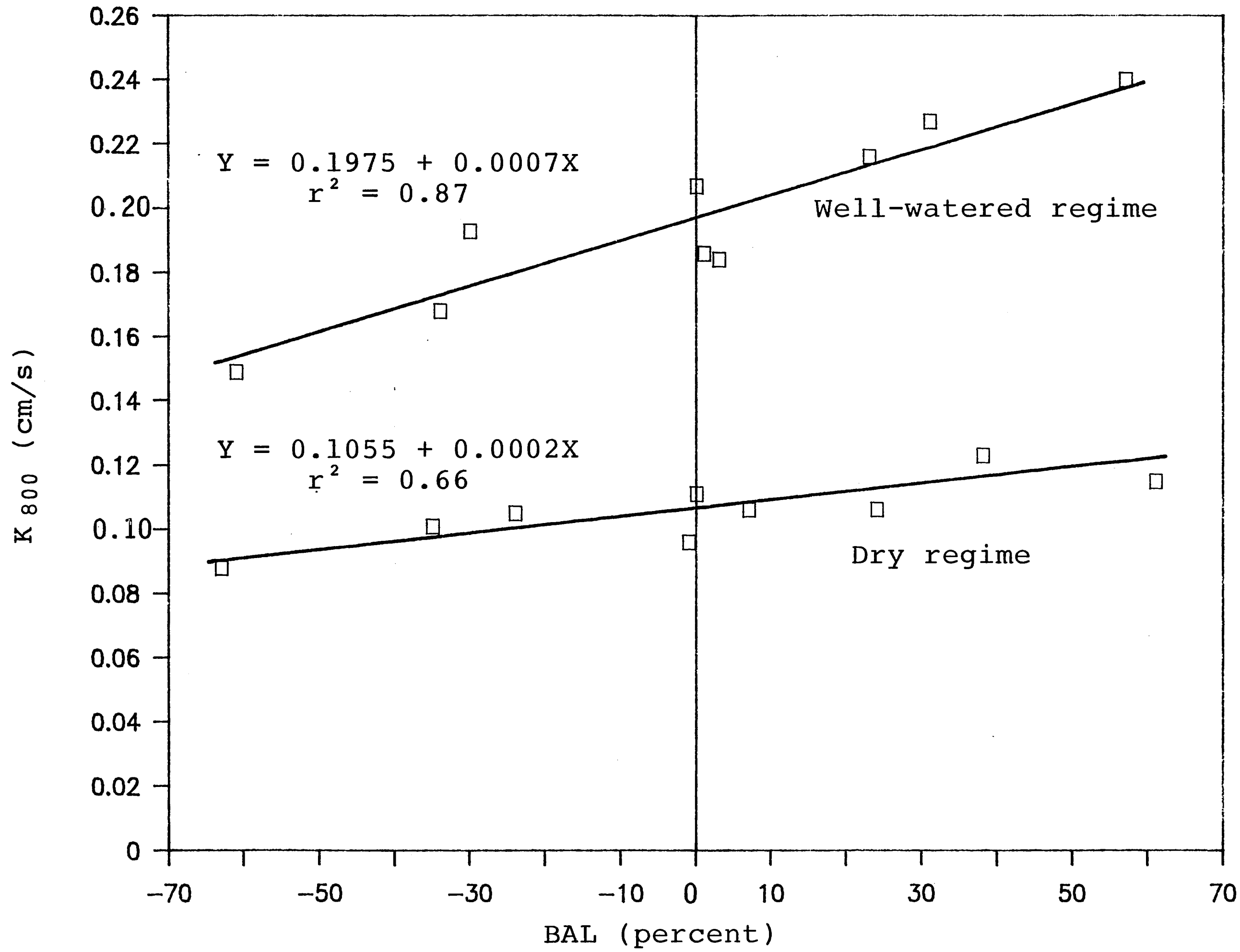

Figure 3. Relationship between Stomatal Conductance at 800 Hours (k_{800}) and the root/shoot Balance Following the Reduction Treatments (BAL)

effect on k_{800}. A unit change in the root/shoot balance resulted in a corresponding change in k_{800} of 0.0007 $cm.s^{-1}$. In the dry regime, a unit change in the root/shoot balance showed a corresponding change in k_{800} of 0.0002 $cm.s^{-1}$.

K_{1500} was also affected by the RS and NR treatments (APPENDIX A, Table 4), but the effects depended on the SMC. In the dry regime the RS and NR treatment effects were not significant (Table 10). In the well-watered regime, severing 33 percent and 67 percent of the roots showed an average 0.039 and 0.060 $cm.s^{-1}$ decrease in k_{1500}. Removing 67 percent of the needles caused an average increase of 0.059 $cm.s^{-1}$ in k_{1500}, but removing 33 percent of the needles did not significantly affect k_{1500}.

There was a strong linear relationship between k_{1500} and the root/shoot balance (Figure 4). Slopes of the relationship in both watering regimes were found to be significant ($P < 0.05$). However, the slope for the well-watered regime was significantly larger than for the dry regime ($P < 0.0001$). In the well-watered regime, a unit change in the root/shoot balance caused a change in k_{1500} of 0.0008 $cm.s^{-1}$. In the dry regime, each percent change in the root/shoot balance resulted in a change of 0.0001 $cm.s^{-1}$ in k_{1500}.

A linear regression analysis was conducted to find the relationship between needle water potential (NWP) and stomatal conductance (k) for each watering regimes. Measurements of both needle water potential and stomatal

TABLE 10

EFFECTS OF ROOT SEVERANCE AND NEEDLE REMOVAL ON STOMATAL CONDUCTANCE AT 1500 HOURS

Treatments			Stomatal Conductance ($cm.s^{-1}$)
Dry	Roots Severed (%)	0	0.073 a
		33	0.045 a
		67	0.049 a
	Needle Removed (%)	0	0.047 a
		33	0.049 a
		67	0.045 a
Well-watered	Roots severed (%)	0	0.140 a
		33	0.101 b
		67	0.080 b
	Needle Removed (%)	0	0.081 b
		33	0.112 ab
		67	0.140 a

Each value represents 12 seedlings. Values followed by different letters in each treatment category are significantly different at P=0.05.

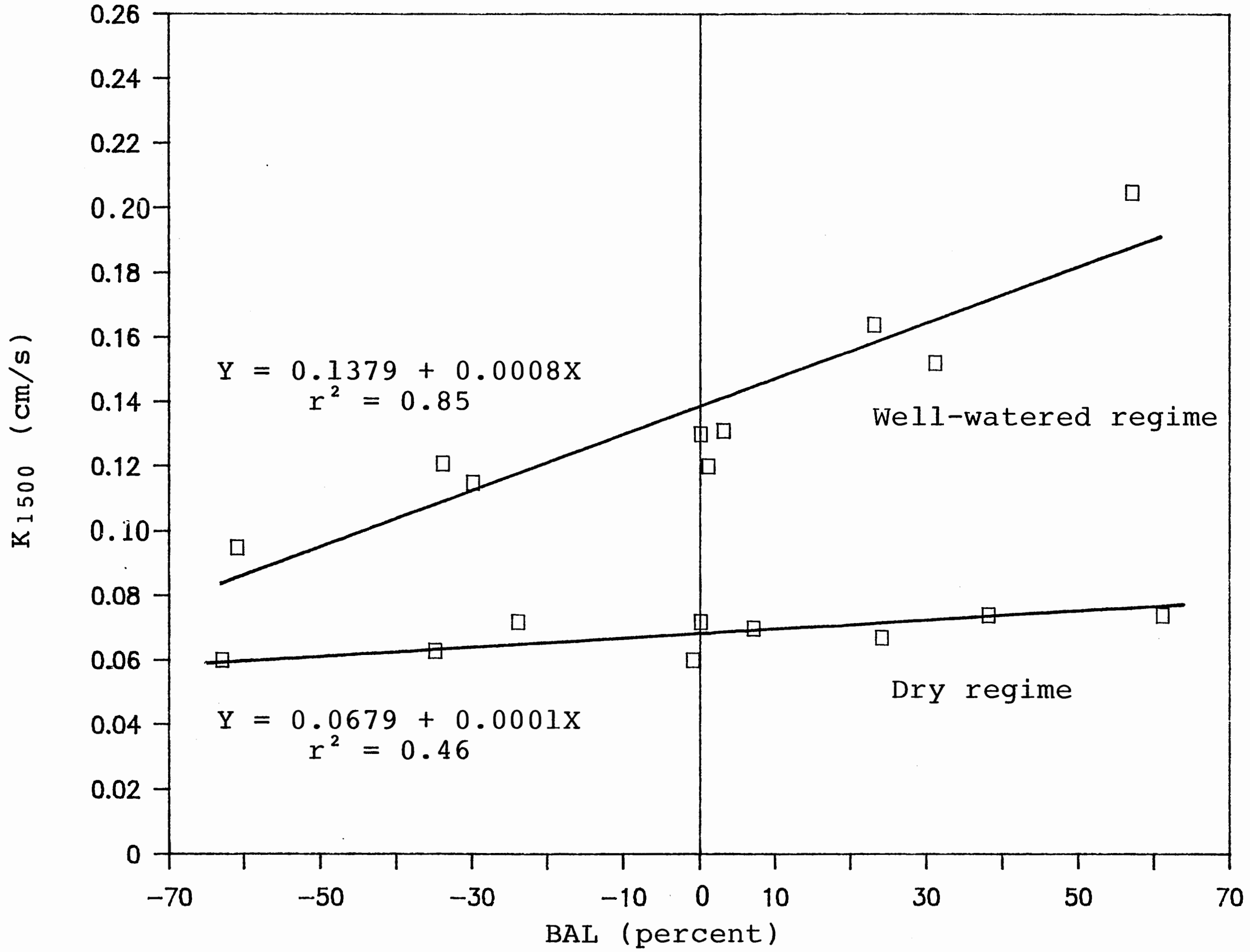

Figure 4. Relationship between Stomatal Conductance at 1500 Hours (k_{1500}) and the root/shoot Balance Following the Reduction Treatments (BAL)

conductance were taken from 1000 to 1130 hours (TST). During this period, absolute humidity deficit was 21.0 gm^{-3}, light intensity was 740 $umol.s^{-1}.m^{-2}$, and air temperature was 33.6 C. K, when ploted over NWP for each SMC category, showed linear relationships (Figure 5). Results indicated that the slope for the well-watered regime was significant ($P < 0.0002$), but the slope for the dry regime was not significant ($P > 0.33$). It was estimated that the threshold value of NWP for stomatal closure ranged between -1.40 and -1.60 MPa.

Transpiration

Before the RS and NR treatments were applied, there was a significant effect of SMC on transpiration ($P < 0.05$) at both 800 hours (TR_{800}) and 1500 hours TST (TR_{1500}). TR_{800} increased from 1.397 $ug.cm^{-2}.s^{-1}$ in the dry regime to 3.294 $ug.cm^{-2}.s^{-1}$ in the well-watered regime. TR_{1500} showed similar response, increasing from 0.947 $ug.cm^{-2}.s^{-1}$ in the dry regime to 2.858 $ug.cm^{-2}.s^{-1}$ in the well-watered regime.

Although TR_{800} and TR_{1500} showed some fluctuation over the four measurement days following the RS and NR treatments (Table 11 and 12), results indicated that only one treatment showed a significant effect of measurement day (APPENDIX A, Table 2). Therefore, the data were averaged over the four measurement days for further analyses.

The response patterns for transpiration were similar to those observed for stomatal conductance (APPENDIX A, Tables

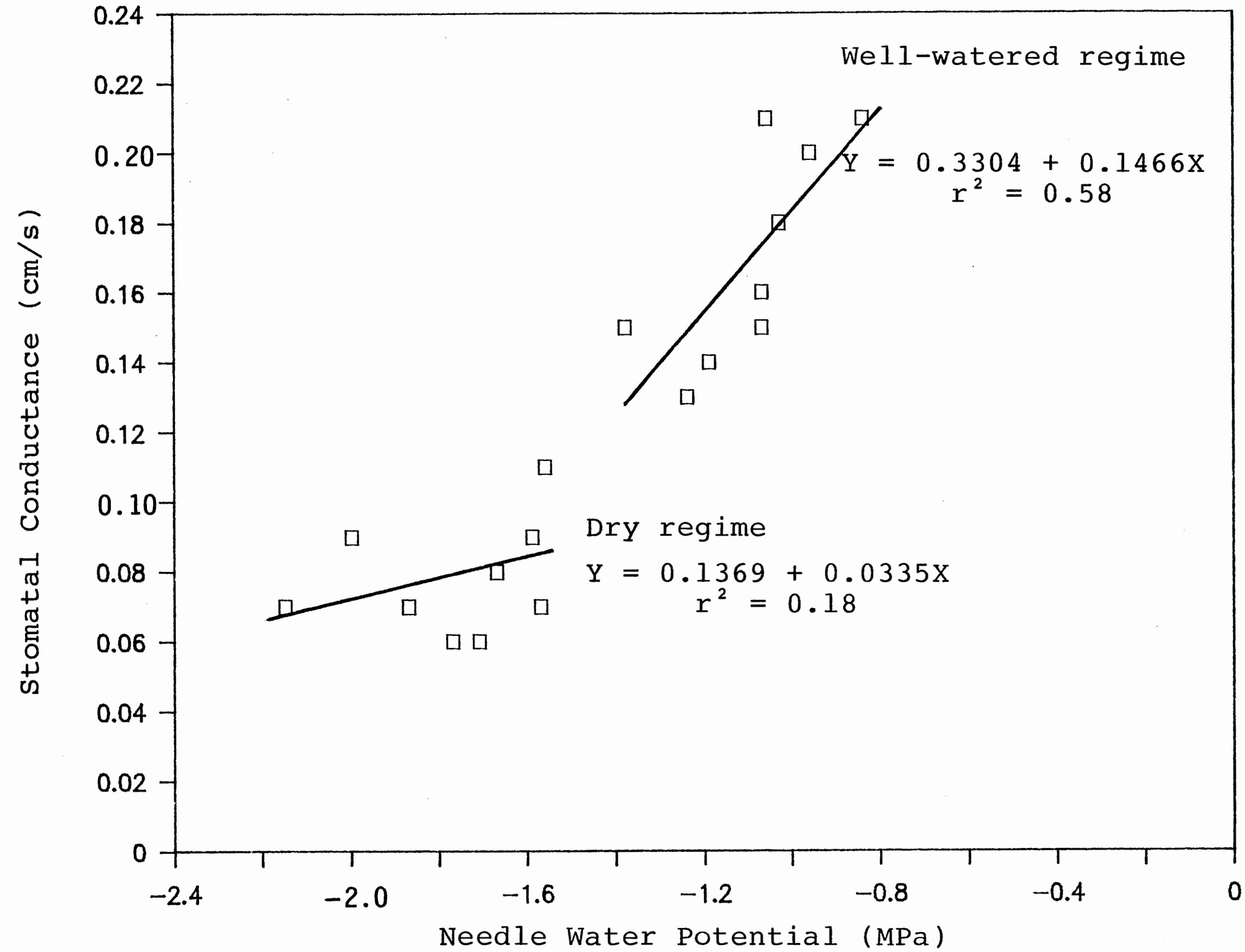

Figure 5. Relationship between Stomatal Conductance and Needle Water Potential

TABLE 11

DAILY CHANGES OF TRANSPIRATION AT 800 HOURS FOR ALL THE TREATMENTS

Soil Moisture Condition	Roots Severed (%)	Needles Removed (%)	Days from the Treatments -1	1	3	5	9
			----------- $ug.cm^{-2}.s^{-1}$ ---------				
		0	1.538	1.376	1.761	1.279	1.442
	0	33	1.674	1.440	2.043	1.572	1.475
		67	1.390	1.317	1.832	1.221	1.502
		0	1.279	1.193	1.712	1.412	1.209
Dry	33	33	1.429	1.216	1.830	1.271	1.260
		67	1.196	1.342	1.819	1.223	1.188
		0	1.128	1.029	1.393	0.890	1.179
	67	33	1.785	1.172	1.938	1.227	1.220
		67	1.157	1.158	1.523	1.188	1.260
		0	3.108	2.424	2.099	2.414	2.442
	0	33	3.042	2.658	3.378	2.471	2.763
		67	2.536	2.551	3.315	2.956	3.152
		0	3.570	2.115	2.484	1.972	2.109
Well-	33	33	3.000	2.120	2.810	2.184	2.251
Watered		67	2.987	2.358	3.147	2.648	2.909
		0	3.609	1.695	2.311	1.659	1.975
	67	33	4.355	2.040	3.034	2.239	2.398
		67	3.435	2.103	2.862	2.148	2.610

Each value represents the mean of four seedlings.

TABLE 12

DAILY CHANGES OF TRANSPIRATION AT 1500 HOURS FOR ALL THE TREATMENTS

Soil Moisture Condition	Roots Severed (%)	Needles Removed (%)	Days from the Treatments -1	1	3	5	9
			----------- $ug.cm^{-2}.s^{-1}$				----------
		0	1.144	1.154	1.419	1.203	1.228
	0	33	1.063	1.264	1.690	1.184	1.244
		67	0.810	1.068	1.492	1.330	1.261
		0	0.746	0.976	1.361	1.037	1.231
Dry	33	33	0.960	1.077	1.488	1.091	1.225
		67	0.873	1.167	1.142	1.025	1.242
		0	0.861	0.927	1.361	0.937	1.001
	67	33	1.142	1.208	1.656	1.335	1.327
		67	0.907	1.011	1.081	0.975	1.254
		0	2.200	2.011	2.594	2.242	2.573
	0	33	2.389	2.428	3.364	2.387	2.997
		67	3.089	2.983	3.268	3.680	4.921
		0	3.045	1.865	2.109	1.735	2.699
Well-	33	33	2.713	2.134	2.889	1.812	3.043
Watered		67	2.768	2.436	2.901	2.645	3.933
		0	3.155	1.509	1.972	1.402	1.981
	67	33	3.188	1.906	2.358	1.459	2.557
		67	3.204	1.811	2.263	2.126	2.146

Each value represents the mean of four seedlings.

5 and 6). The effects of RS and NR on TR_{800} were significant and not affected by the SMC treatments.

Severing 33 percent of the roots resulted in an average decrease in TR_{800} of 0.264 $ug.cm^{-2}.s^{-1}$ (Table 13). When 67 percent of the roots was severed, an average reduction in TR_{800} of 0.369 $ug.cm^{-2}.s^{-1}$ was observed. In contrast, reducing the amount of foliage increased TR_{800}. Removing 33 and 67 percent of the needles caused an average increase in TR_{800} of 0.265 and 0.294 $ug.cm^{-2}.s^{-1}$.

A strong linear relationship was found between TR_{800} and the root/shoot balance in both watering regimes (Figure 6). As the root/shoot balance changed towards a greater reduction in roots than needles, TR_{800} decreased. For each percent decrease in the root/shoot balance, TR_{800} decreased 0.0088 $ug.cm^{-2}.s^{-1}$ in the well-watered regime and 0.0028 $ug.cm^{-2}.s^{-1}$ in the dry regime. These two slopes were significantly different ($P < 0.0008$).

RS and NR treatments did not significantly affect TR_{1500} in the dry regime (Table 14). But in the well-watered regime, reducing 33 percent of the roots showed a decrease of 0.448 $ug.cm^{-2}.s^{-1}$ in TR_{1500}, reducing 67 percent of the roots caused a reduction in TR_{1500} of 0.894 ug.cm-2.s-1. On the other hand, seedlings treated with 33 percent removal of the needles showed an increase in TR_{1500} of 0.328 $ug.cm^{-2}.s^{-1}$, and those with 67 percent removal of the needles showed an increase in TR_{1500} of 0.844 $ug.cm^{-2}.s^{-1}$.

TABLE 13

EFFECTS OF ROOT SEVERANCE AND NEEDLE REMOVAL ON TRANSPIRATION AT 800 HOURS

Treatments		Transpiration ($ug.cm^{-2}.s^{-1}$)
	0	2.167 a
Roots Severed	33	1.903 b
(%)	67	1.802 c
	0	1.771 b
Needle Removed	33	2.036 a
(%)	67	2.065 a

Each value represents 24 seedlings. Values followed by different letters in each treatment category are significantly different at P=0.05.

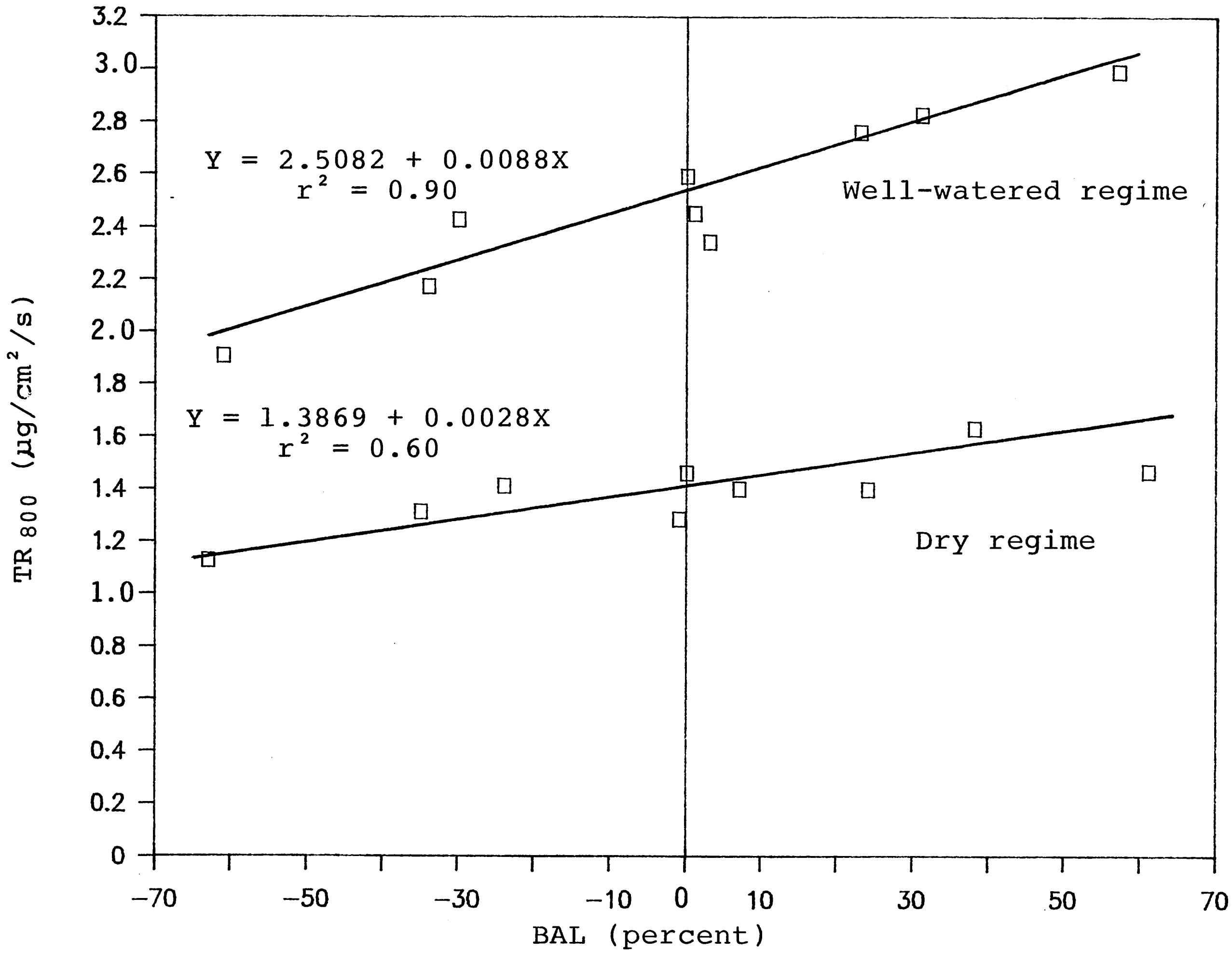

Figure 6. Relationship between Transpiration at 800 Hours (TR_{800}) and the root/shoot Balance Following the Reduction Treatments (BAL)

TABLE 14

EFFECTS OF ROOT SEVERANCE AND NEEDLE REMOVAL ON TRANSPIRATION AT 1500 HOURS

Treatments			Transpiration ($ug.cm^{-2}.s^{-1}$)
Dry	Roots Severed (%)	0	1.308 a
		33	1.182 a
		67	1.229 a
	Needle Removed (%)	0	1.161 a
		33	1.382 a
		67	1.175 a
Well-watered	Roots severed (%)	0	2.891 a
		33	2.443 b
		67	1.977 c
	Needles Removed (%)	0	2.043 c
		33	2.371 b
		67	2.897 a

Each value represents 12 seedlings; Values followed by different letters in each treatment category are significantly different at P=0.05.

There was a linear relationship between TR_{1500} and the root/shoot balance (Figure 7). The slope for the well-watered regime was significant ($P < 0.0002$). The slope for the dry regime was not significant ($P > 0.16$). In the well-watered regime, a unit change in the root/shoot balance resulted in a change in TR_{1500} of 0.0152 $ug.cm^{-2}.s^{-1}$.

Diurnal Changes of Stomatal Conductance and Transpiration

Plots of the diurnal course of environmental data showed that photosynthetic photon flux density (PPFD), absolute humidity deficit (AHD) and air temperature (T) peaked at 1200 hours TST (Figure 8). All times are given in TST.

Transpiration and conductance were generally higher in the well-watered regime than in the dry regime. The effects of the treatments on stomatal conductance and transpiration were more apparent under well-watered conditions than under dry soil conditions. At 600 and 1900 hours, no effects of the root and needle reduction treatments on stomatal conductance and transpiration were observed ($P > 0.05$).

Stomatal Conductance

Essentially, the data showed that the diurnal pattern of stomatal conductance (k) was not changed by RS and NR treatments (Figures 9 and 10). Under dry soil conditions, k increased from 600 hours to a peak at 800 hours and then

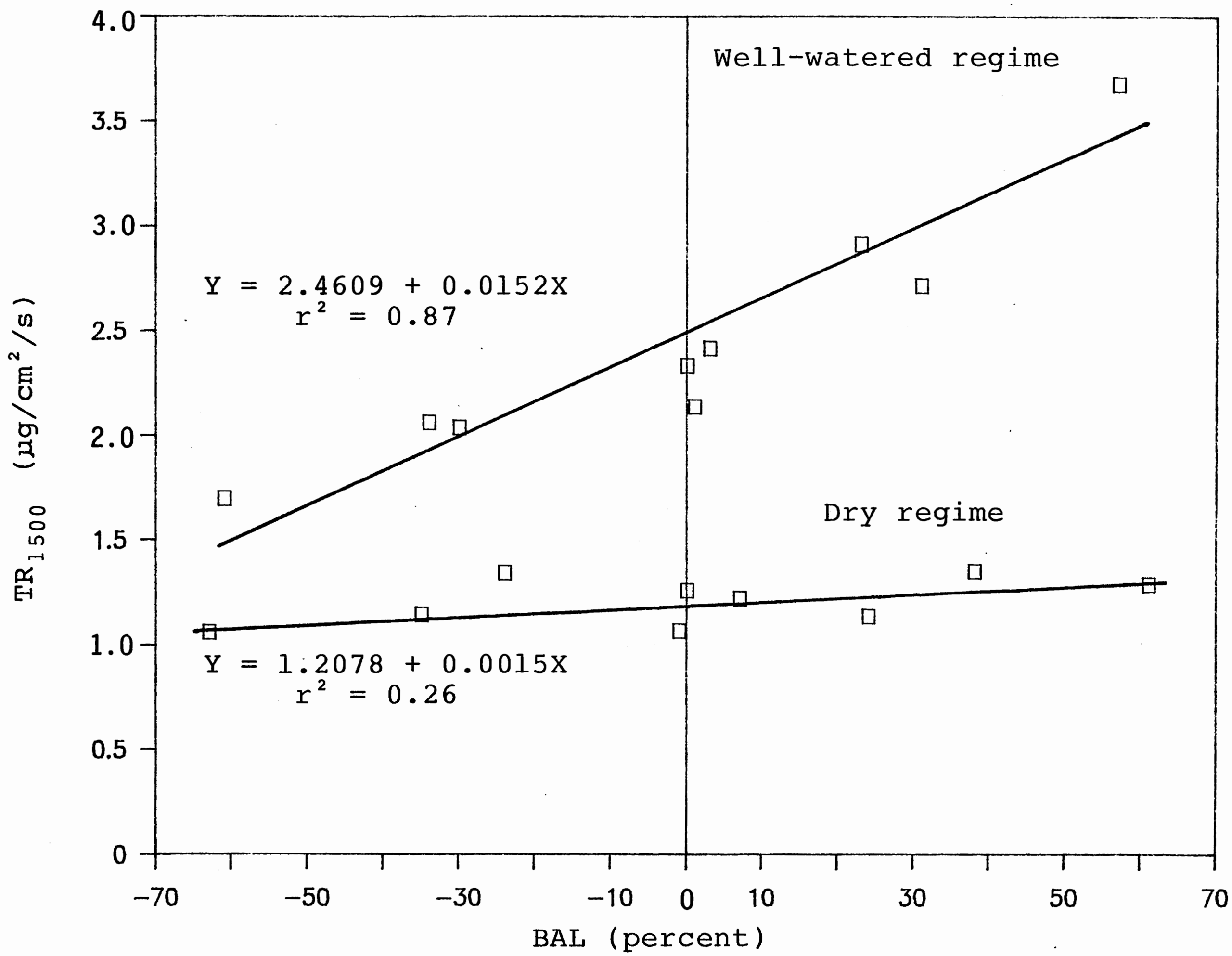

Figure 7. Relationship between Transpiration at 1500 Hours (TR_{1500}) and the root/shoot Balance Following the Reduction Treatments (BAL)

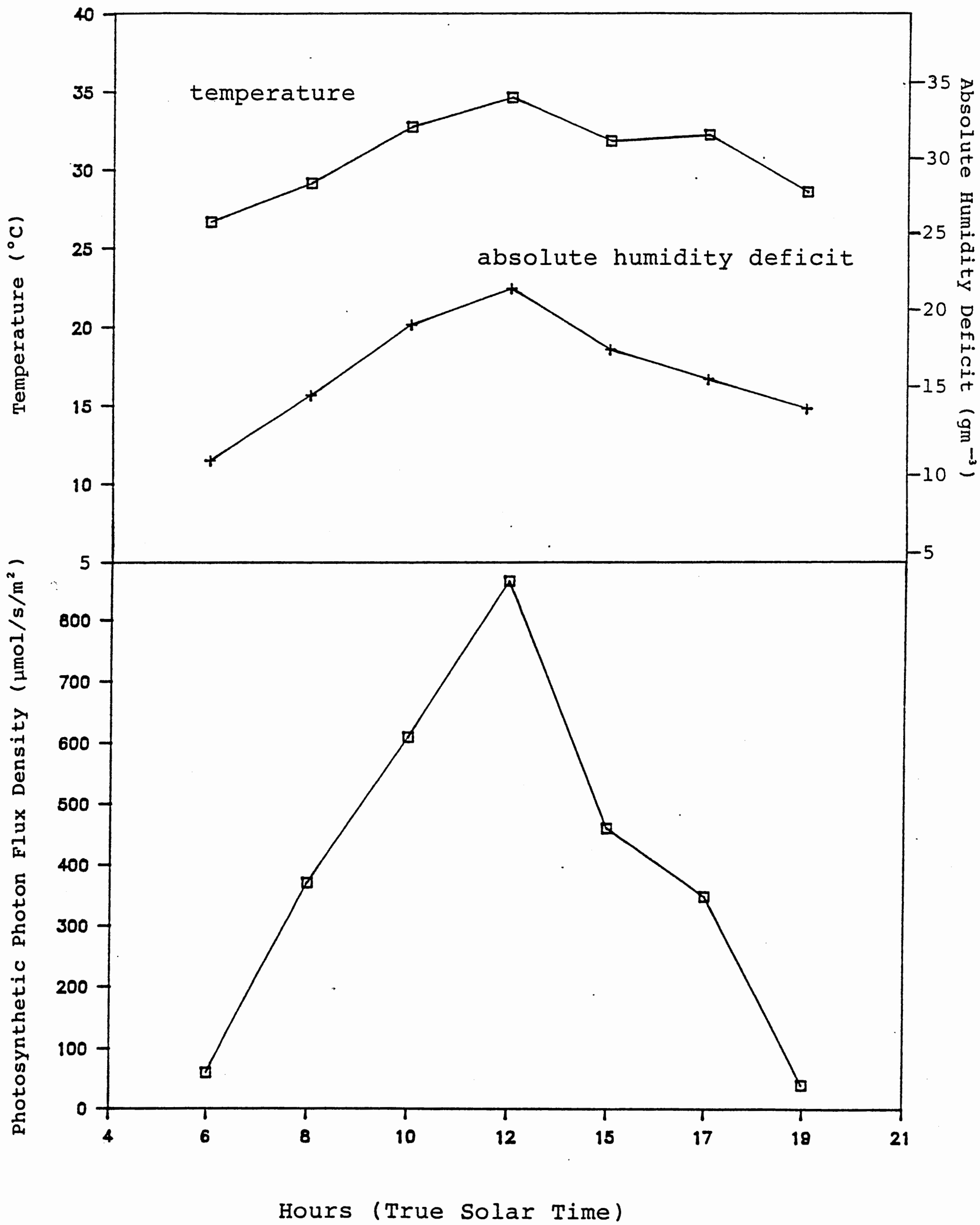

Figure 8. Diurnal Changes of Three Environmental Factors

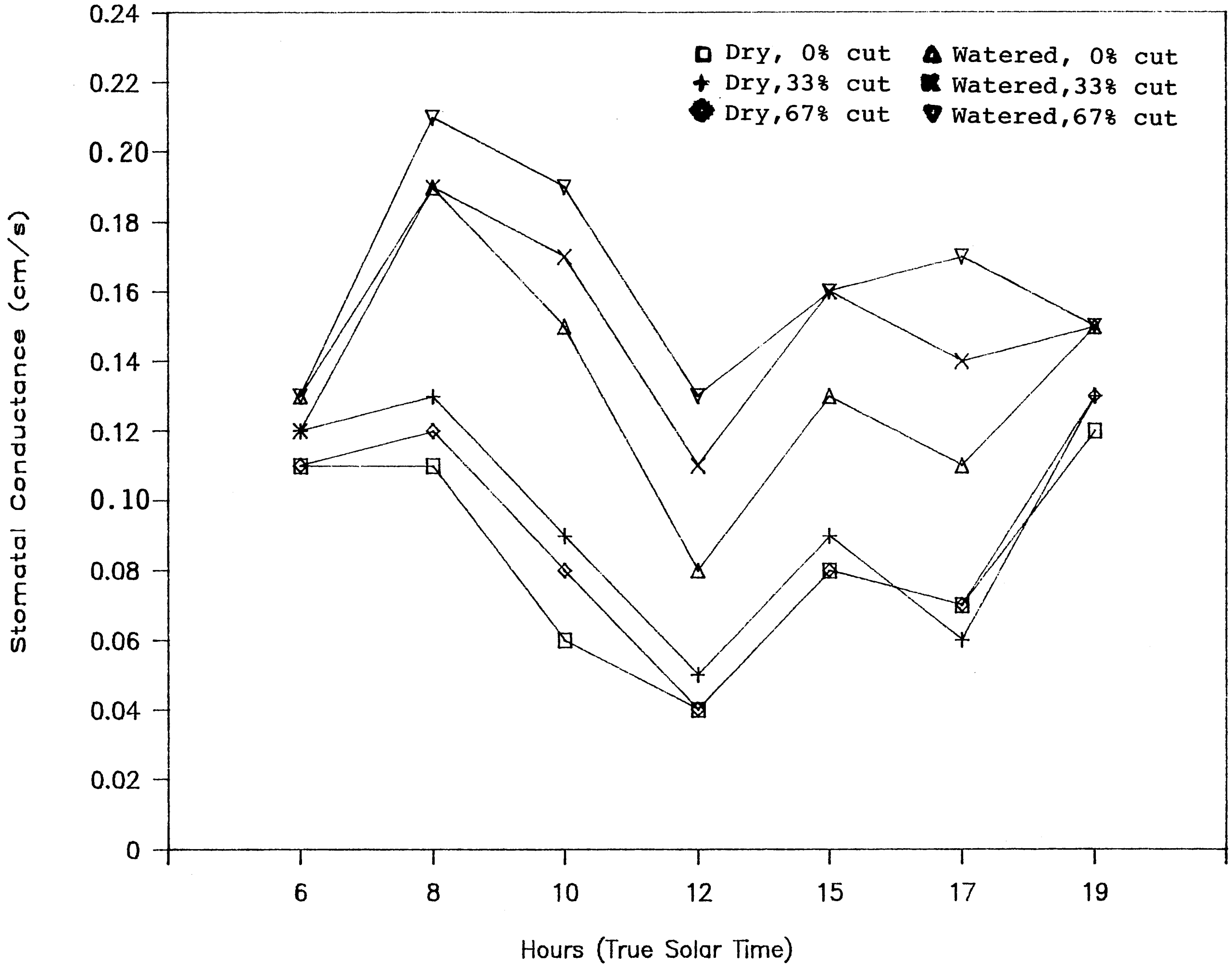

Figure 9. Diurnal Changes of Stomatal Conductance as Affected by Needle Removal

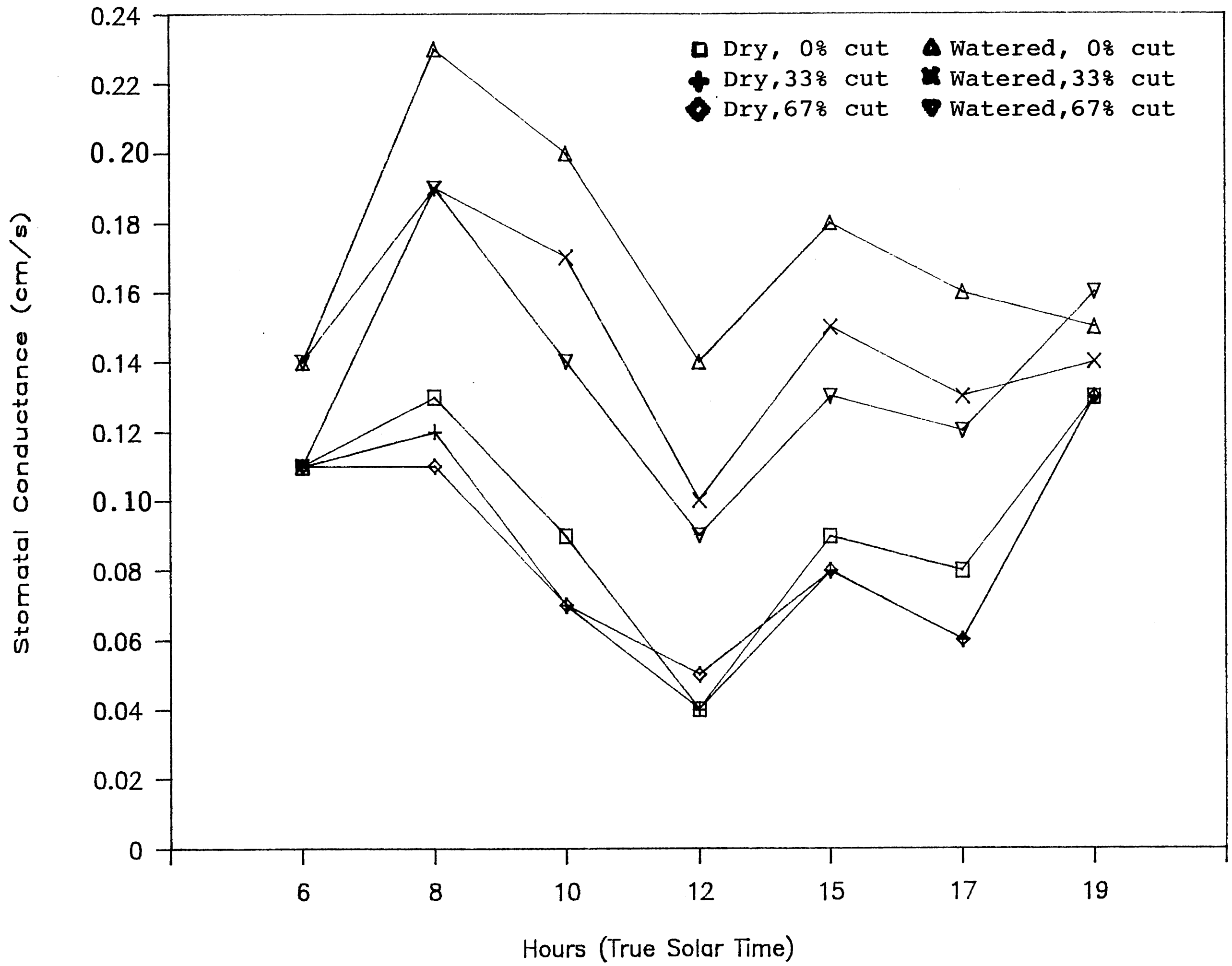

Figure 10. Diurnal Changes of Stomatal Conductance as Affected by Root Severance

declined to a minimum at 1200 hours. K increased from 1200 hours to a maximum value for the dry regime at 1900 hours. Under well-watered conditions, K increased from 600 hours to a maximum at 800 and then declined to a minimum at 1200 hours. K increased again in the afternoon.

A significant effect ($P < 0.05$) of RS and NR treatments was observed during the hours 800-1700 in the well-watered regime and only at 800 and 1000 hours in the dry regime. RS treatments decreased k throughout the day with the largest differences occurring in the well-watered treatments at midday and in the dry regime at 800 hours. The smallest difference occurred at 600 and 1900 hours in both watering regimes. NR treatments, on the other hand, increased k throughout the day with the largest effect occurring in the well-watered treatments at midday and in the dry regime at 1000 hours. The smallest effect occurred in both watering regimes at 600 and 1900 hours.

Transpiration

In the dry soil regime, transpiration started to increase from 600 hours and reached its maximum at 800 hours TST (Figures 11 and 12). Thereafter, it declined gradually until 1700 and increased at 1900. In the well-watered soil transpiration increased until 1000 and steadily declined until 1900. In well-watered soil, however, response to the root severing treatments was different from that in dry soil. All the treatments showed a large effect throughout

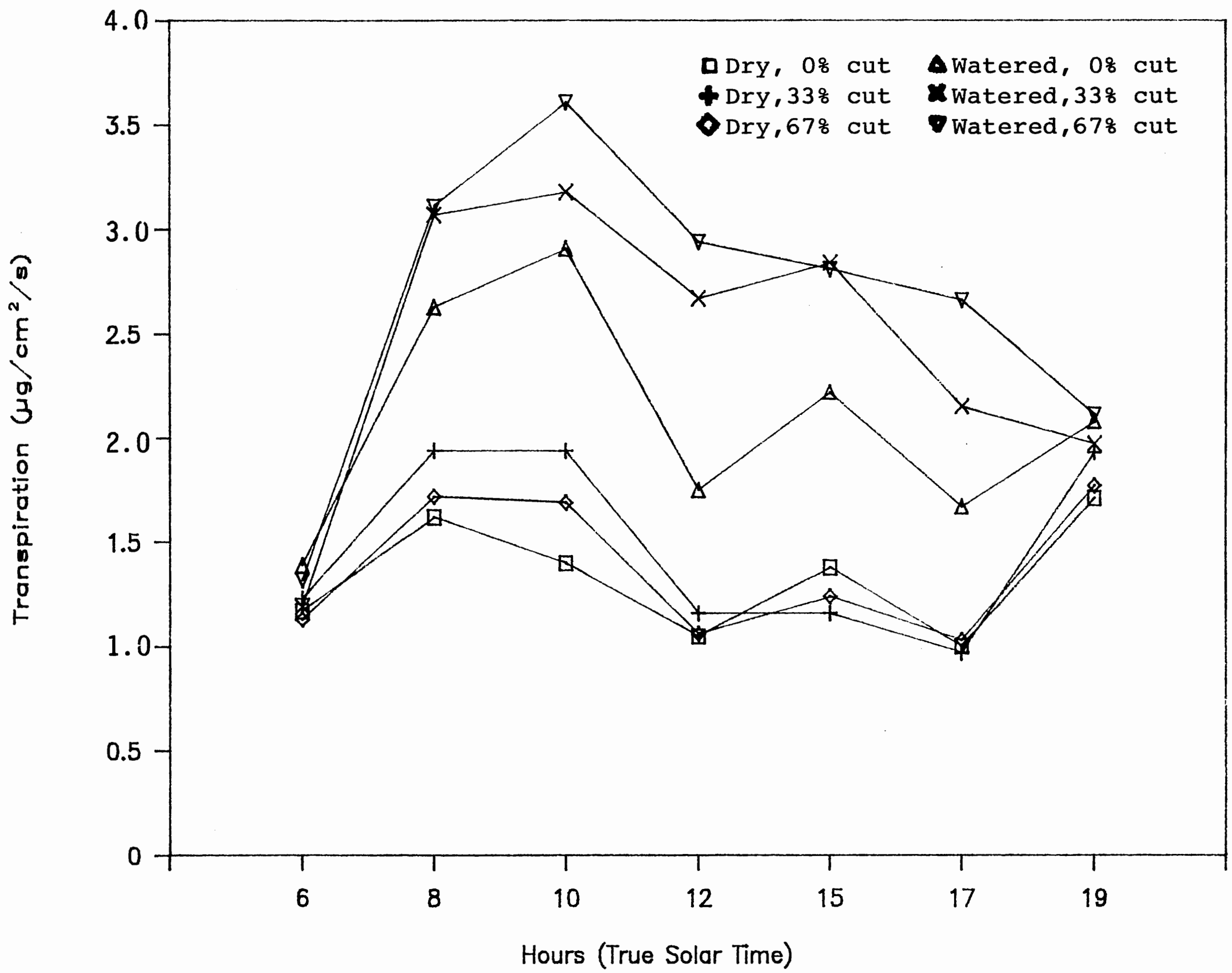

Figure 11. Diurnal Changes of Transpiration as Affected by Needle Removal

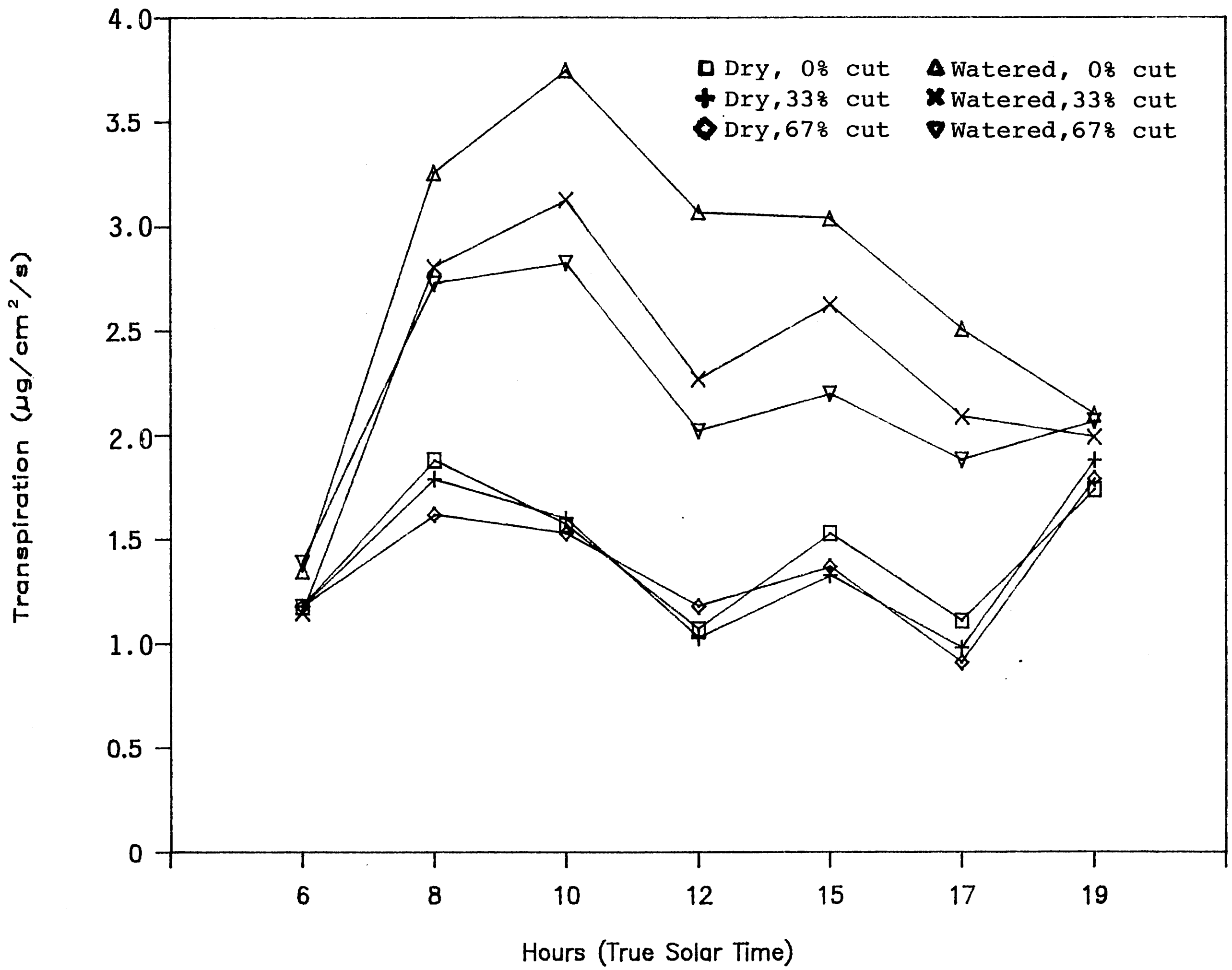

Figure 12. Diurnal Changes of Transpiration as Affected by Root Severance

the day except at 600 and 1900 hours. Although transpiration was much lower in the dry than in the well-watered regime, treatment effects on transpiration were still observed at 800 and 1000 hours. Seedlings with roots severed showed lower values throughout the day. In contrast, seedlings with portions of the needles removed showed higher transpiration throughout the day.

CHAPTER V

DISCUSSION

The daily drop in leaf water potential is the consequence of the loss of water through the transpiring leaves. This study was designed to determine how plant water relations were affected when the water supply/demand relationship was altered. It was assumed that a balanced water supply/demand relationship exists in a normally developed seedling.

A pipe model theory has been suggested to describe the relationship between the stem cross-sectional area and the sum of branch cross-sectional areas. In this theory, a tree was viewed as an assemblage of pipe systems with pipes continuous from the bottom to the top of the tree. The number of interconnected pipes changes and so do their diameters, but the sum of their cross-sectional areas remains constant. In recent years, the pipe model has been applied for predicting canopy leaf area (Waring et al. 1982). Kaufmann and Troendle (1981) found a good linear relationship between the leaf area and the sapwood conducting area in four subalpine forest tree species and stated that this correlation may be based on a physiological balance between demand for water by the crown and the ability of the stem to conduct it. In a more recent study with loblolly and shortleaf pine saplings, Carlson and Harrington (1987) proved that the pipe model also applied to the root system of a tree. The stem cross-sectional area at the root collar was well correlated to the sum of the lateral root cross-sectional areas. This suggests that a bigger basal stem diameter means a correspondingly bigger root system. Thus interupting some of the "pipes" (i.e. cutting some of the lateral roots) would decrease the supply of water to the transpiring demands. In the current study, needle water potential and stomatal conductance were found to be very sensitive to reductions in the root size or the amount of foliage, supporting strongly the pipe model theory (Figures 1, 2, 3 and 4).

The correlation between the stem cross-sectional area and the leaf area and between the stem cross-sectional area and the sum of the lateral root cross-sectional areas indicates a feedback mechanism among the parts of a seedling during its development. This correlation actually represents a physiological balance of the plant supply-conduction-demand system (SCD). Since the stem does not provide the major resistance to water movement, as reported by Brix and Mitchell (1985), it may be inferred that once water enters the root xylem, the rate of water movement inside the undisrupted stem would be increased or decreased in order to maintain an unchanged leaf water potential.

Pipe model theory can be used to interpret the mechanism of physiological balance of the SCD system within a plant. The findings of the current study suggested that any imbalance in the the water supply/demand relationship altered the water relations. For example, as a result of reducing the root system, a decrease in needle water potential was observed.

In contrast to our findings, Teskey and others (1985) in the study with Abies amabilis found that removing 31 percent of the roots did not significantly affect the xylem pressure potential in moist soil conditions and stated that a larger root system than needed had been developed. One possible reason for the difference in findings may be that their work was done with larger trees which were well established in the field, whereas the seedlings in the current study were newly transplanted and less established. It is possible that as trees become more and more established on a site they develop root systems that are larger than needed for water uptake.

Previous work with Douglas-fir indicated that the major resistance to water movement in the plant was not in the stem but elsewhere, perhaps in the roots or soil. Data from the current study supported the hypothesis that the roots were a major source of resistance, since upsetting the balance of roots and shoots by cutting roots significantly affected the plant water potential. It appears that in seedlings that are not fully established the amount of roots for water uptake is closely linked to the water uses of the plant.

In a sunflower root removal experiment, Aston and Lowlar (1979) reported that removing 80 percent of the roots decreased leaf water potential only by 0.05 MPa. They concluded that the root removing treatment possibly increased the influx of water through the remaining roots. The current study's findings did not support their conclusion. The substantial changes in the water relations variables corresponding to the reduction treatments supported the idea that the water uptake of the remaining roots remained unchanged. The results indicated that the amount of uptake or loss of water was directly related to the root and shoot size unless stomatal closure occurred.

Aston (1979), in a root detachment study with sunflower, indicated that the balance between water loss from shoot and uptake by the root was achieved by increasing stomatal resistance. In these findings, a strong linear relationship between stomatal conductance and the root/shoot balance was found at 800 hours for both watering regimes (Figure 6). Reducing the root size decreased k_{800}, but removing needles increased k_{800}. This indicated close stomatal control of water loss. At 1500 hours, the linear relationship was still obvious in the well-watered regime (Figure 8), but in the dry regime, the changes caused by the reduction treatments were very small, suggesting stomatal closure.

A linear relationship between needle water potential and stomatal conductance indicated that stomatal behavior was controlled by the needle water potential (Figure 10). A critical range of needle water potential to trigger stomatal closure was found between -1.40 to -1.60 MPa. For loblolly pine, a threshold leaf water potential for stomatal closure has been reported to range from -0.9 to -1.8 MPa (Teskey and Hinckley 1985).

Response of transpiration to the RS and NR treatments showed the same patterns as stomatal conductance. It was worth noting that at 1500 hours, transpiration showed no response to the reduction treatments in the dry regime probably due to the stomatal closure (Figure 10).

The diurnal response of transpiration was slightly different from that of stomatal conductance. Even when stomatal closure started to occur after 800, transpiration was still increasing because vapor pressure deficit was increasing. Apparently, the decline of transpiration after 1000 was due to the further closure of stomata. Seedlings with portions of the root system severed showed decreased needle water potential which probably triggered stomatal closure, which in turn limited further water loss through transpiration. Compared with the work by Andrews and Newman with wheat (1968) where a 25 to 32 percent reduction was reported in transpiration when 41 percent of the roots was pruned, a corresponding reduction in transpiration of 27 percent was estimated from the current study in the well-watered regime (Figure 10).

It was found in this experiment that the more needles removed, the higher the needle water potential of the remaining needles. Needle removing treatments nearly completely compensated for the effects of partial loss of the root system on water potential, stomatal conductance, and transpiration when the same amount from both roots and top was removed (Figures 1, 3, 5, 7, 8 and 9). No response to needle removing treatment was observed in stomatal conductance and transpiration when the soil was dry enough to result in stomatal closure.

This study showed that seedling water balance could be manipulated by altering the relative proportion of the root system for water uptake and the needles for water loss. Undercutting is often practiced in the nursery to control the shoot growth by subjecting seedlings to water stress. The results of the current study indicated how much moisture stress would result from a given root and shoot reduction treatment. Information like this could be used by forest tree nurseries to refine their root and top pruning practices in order to develop the desired levels of moisture stress in the seedlings. During the process of transplanting, the failure of trees to survive may result from the low capacity of a disturbed root system to support a nearly intact shoot. The current study showed that by removing the same amount of foliage as the roots, seedlings will suffer much less water stress and perhaps better survive the transplanting shock.

The study did not address the question of how long it takes for a seedling to recover from root and shoot pruning treatments. Nine days after treatments there was no indication that recovery was occurring (Tables 2, 5, 7, 8, 11 and 12). Short-term adjustment to stress might include osmotic adjustment. Long-term recovery would presumably involve root and shoot growth in direct relation to the amount needed to reestablish the normal balance between uptake and loss. Further study would be necessary to address those topics.

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APPENDICES

APPENDIX A

TABLES

TABLE 1

ANALYSIS OF VARIANCE FOR PREDAWN NEEDLE WATER POTENTIAL ON PRETREATMENT DAY

Source	d.f.	S.S.	F value	Prob > F
SMC	1	1897.48	741.46	0.0001
RS	2	1.26	0.25	0.7829
NR	2	0.27	0.05	0.9493
SMC*RS	2	6.26	1.22	0.3029
SMC*NR	2	3.77	0.74	0.4837
RS*NR	4	16.09	1.57	0.1958
SMC*RS*NR	4	8.38	0.82	0.5190
Error	51	130.51		

Tests of hypothese were made using four way interaction of block, SMC, RS, and NR as an error term.

TABLE 2

SIGNIFICANCE OF THE EFFECT OF MEASUREMENT DAY ON PLANT WATER RELATIONS VARIABLES FOR EACH TREATMENT

Treatment	Probability > F					
	PNWP	MNWP	SC_{800}	SC_{1500}	TR_{800}	TR_{1500}
1	0.01	0.46	0.87	0.89	0.71	0.95
2	0.55	0.54	0.62	0.68	0.42	0.85
3	0.19	0.60	0.50	0.68	0.31	0.87
4	0.13	0.56	0.62	0.66	0.51	0.77
5	0.03	0.77	0.61	0.52	0.42	0.80
6	0.44	0.55	0.51	0.67	0.47	0.83
7	0.35	0.83	0.70	0.54	0.51	0.77
8	0.04	0.26	0.40	0.28	0.14	0.31
9	0.28	0.67	0.86	0.98	0.83	0.96
10	0.38	0.13	0.90	0.10	0.42	0.47
11	0.05	0.34	0.24	0.40	0.18	0.70
12	0.51	0.28	0.86	0.25	0.42	0.27
13	0.33	0.35	0.92	0.17	0.64	0.47
14	0.41	0.44	0.60	0.06	0.43	0.13
15	0.82	0.11	0.82	0.14	0.49	0.29
16	0.54	0.12	0.52	0.35	0.52	0.61
17	0.27	0.63	0.50	0.39	0.35	0.28
18	0.05	0.38	0.08	0.53	0.04	0.74

Tests of hypothese were made using day*block as an error term; PNWP is the predawn needle water potential; MNWP is the midday needle water potential; SC_{800} and SC_{1500} are stomatal conductance measured at 800 and 1500 hours, respectively; TR_{800} and TR_{1500} are transpiration measured at 800 and 1500 hours, respectively.

TABLE 3a

ANALYSIS OF VARIANCE FOR PREDAWN NEEDLE WATER POTENTIAL ON DAY 1 AFTER TREATMENTS

Source	d.f.	S.S.	F value	Prob > F
SMC	1	3626.86	350.55	0.0001
RS	2	298.80	14.44	0.0001
NR	2	25.92	1.25	0.2944
SMC*RS	2	57.59	2.78	0.0712
SMC*NR	2	0.65	0.03	0.9693
RS*NR	4	36.58	0.88	0.4802
SMC*RS*NR	4	44.17	1.07	0.3823
Error	51	527.65		

Tests of hypothese were made using four way interaction of block, SMC, RS, and NR as an error term.

TABLE 3b

ANALYSIS OF VARIANCE FOR PREDAWN NEEDLE WATER POTENTIAL ON DAY 3 AFTER TREATMENTS

Source	d.f.	S.S.	F value	Prob > F
SMC	1	4237.38	305.16	0.0001
RS	2	395.43	14.24	0.0001
NR	2	120.00	4.32	0.0185
SMC*RS	2	198.11	7.13	0.0019
SMC*NR	2	14.26	0.51	0.6015
RS*NR	4	66.27	1.19	0.3251
SMC*RS*NR	4	28.67	0.52	0.7240
Error	50	708.17		

Tests of hypothese were made using four way interaction of block, SMC, RS, and NR as an error term.

TABLE 3c

ANALYSIS OF VARIANCE FOR PREDAWN NEEDLE WATER POTENTIAL ON DAY 5 AFTER TREATMENTS

Source	d.f.	S.S.	F value	Prob > F
SMC	1	4817.76	222.57	0.0001
RS	2	289.09	6.68	0.0027
NR	2	174.53	4.03	0.0238
SMC*RS	2	123.28	2.85	0.0674
SMC*NR	2	52.79	1.22	0.3040
RS*NR	4	63.98	0.74	0.5699
SMC*RS*NR	4	43.61	0.50	0.7332
Error	50	1082.31		

Tests of hypothese were made using four way interaction of block, SMC, RS, and NR as an error term.

TABLE 3d

ANALYSIS OF VARIANCE FOR PREDAWN NEEDLE WATER POTENTIAL ON DAY 9 AFTER TREATMENTS

Source	d.f.	S.S.	F value	Prob > F
SMC	1	6289.40	237.43	0.0001
RS	2	487.68	9.21	0.0004
NR	2	155.34	2.93	0.0625
SMC*RS	2	239.78	4.53	0.0156
SMC*NR	2	44.76	0.84	0.4356
RS*NR	4	111.78	1.05	0.3886
SMC*RS*NR	4	115.59	1.09	0.3721
Error	50	1324.45		

Tests of hypothese were made using four way interaction of block, SMC, RS, and NR as an error term.

TABLE 4

ANALYSIS OF VARIANCE FOR THE EFFECTS OF TREATMENTS ON MIDDAY NEEDLE WATER POTENTIAL

Source	d.f.	S.S.	F value	Prob > F
SMC	1	11700.75	285.24	0.0001
RS	2	1660.66	20.24	0.0001
NR	2	765.63	9.33	0.0001
SMC*RS	2	135.48	1.65	0.2019
SMC*NR	2	5.43	0.07	0.9360
RS*NR	4	133.08	0.81	0.5240
SMC*RS*NR	4	149.68	0.91	0.4640
Error	51	2092.02		

Analysis was conducted using mean values for measurements on days 1, 3, 5, and 9 following treatments. Tests of hypothese using four way interaction of block, SMC, RS, and NR as an error term.

TABLE 5

ANALYSES OF VARIANCE FOR THE EFFECTS OF TREATMENTS ON STOMATAL CONDUCTANCE

Source	d.f.	0800 S.S.	0800 F value	0800 P > F	1500 S.S.	1500 F value	1500 P > F
SMC	1	1.66	172.35	0.0001	0.84	53.36	0.0001
RS	2	0.15	7.79	0.0011	0.09	8.63	0.0006
NR	2	0.08	4.29	0.0190	0.07	6.81	0.0024
SMC*RS	2	0.04	1.94	0.1536	0.05	4.59	0.0147
SMC*NR	2	0.04	2.06	0.1381	0.07	6.51	0.0030
RS*NR	4	0.02	0.51	0.7306	0.03	1.18	0.3296
SMC*RS*NR	4	0.003	0.08	0.9889	0.01	0.42	0.7942
Error	51	0.49			0.28		

Time (Hours)

Analysis conducted using mean values for measurements on days 1, 3, 5, and 9 following treatments. Tests of hypothese using the four way interaction of block, SMC, RS, and NR as an error term.

TABLE 6

ANALYSES OF VARIANCE FOR THE EFFECTS OF TREATMENTS ON TRANSPIRATION

		Time (Hours)					
Source	d.f.	0800			1500		
		S.S.	F value	P > F	S.S.	F value	P > F
SMC	1	247.36	164.68	0.0001	262.69	146.77	0.0001
RS	2	19.17	6.38	0.0034	30.23	8.45	0.0007
NR	2	14.36	4.78	0.0125	24.46	6.83	0.0023
SMC*RS	2	4.39	1.46	0.2412	21.31	5.95	0.0047
SMC*NR	2	6.98	2.32	0.1083	26.09	7.29	0.0016
RS*NR	4	3.43	0.57	0.6845	9.49	1.33	0.2732
SMC*RS*NR	4	0.12	0.02	0.9992	4.15	0.58	0.6786
Error	51	76.50			91.29		

Analysis was conducted using mean values for measurements on days 1, 3, 5, and 9 following treatments. Tests of hypothese using the four way interaction of block, SMC, RS, and NR as an error term.

APPENDIX B

FIGURES

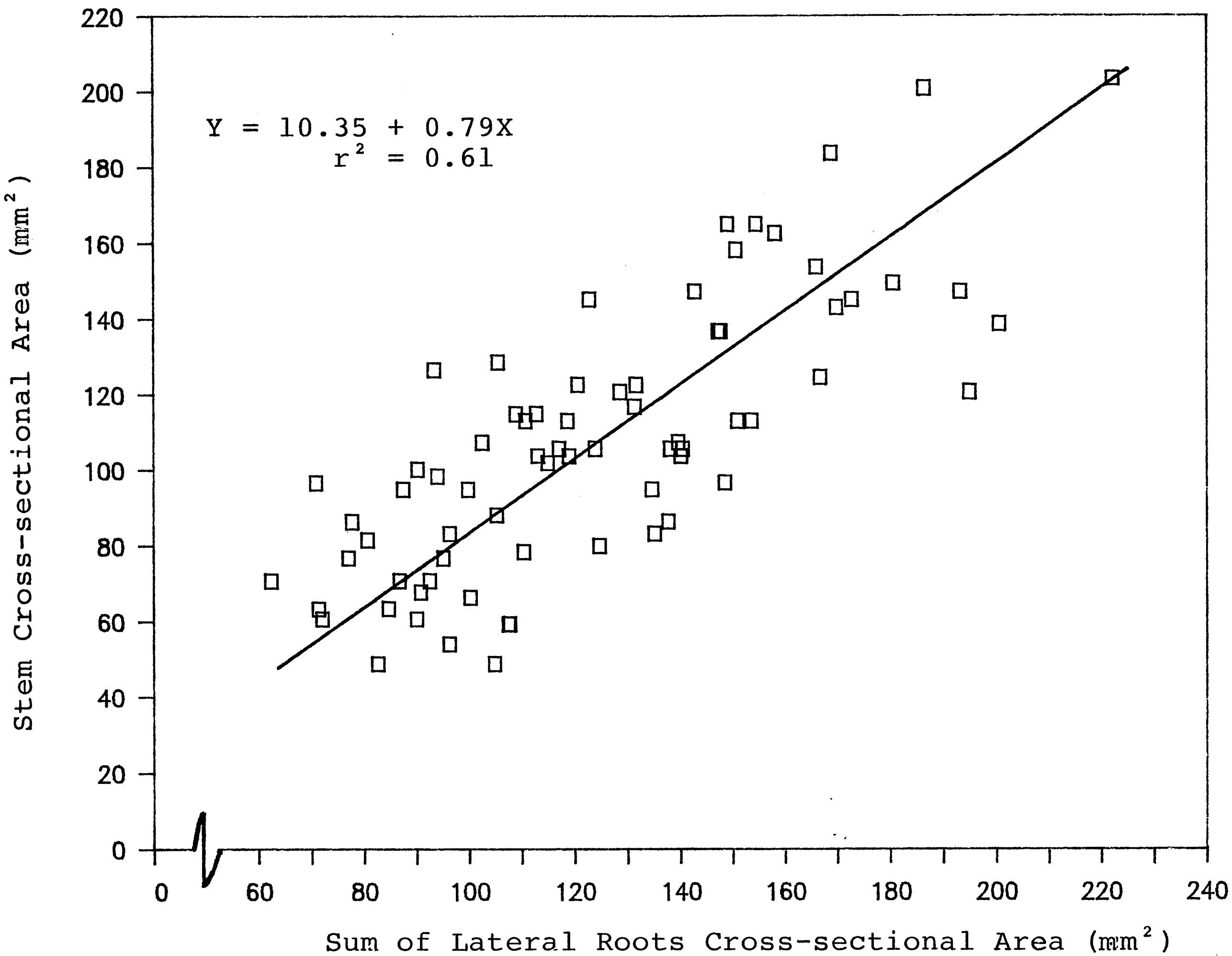

Figure 1. Relationship between Stem Cross-sectonal Area and Sum of Lateral Roots Cross-sectional Area

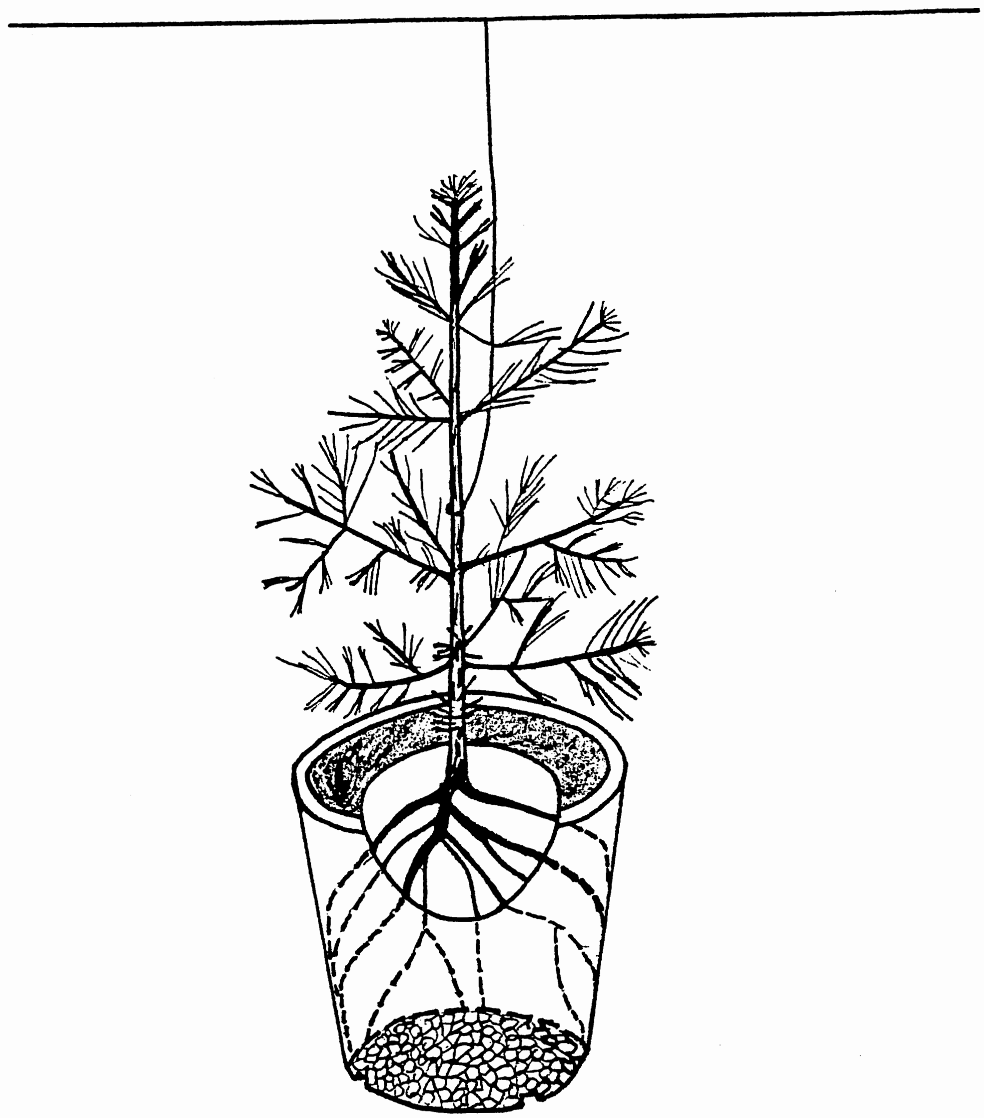

Figure 2. Scheme of the Root Severance Treatments

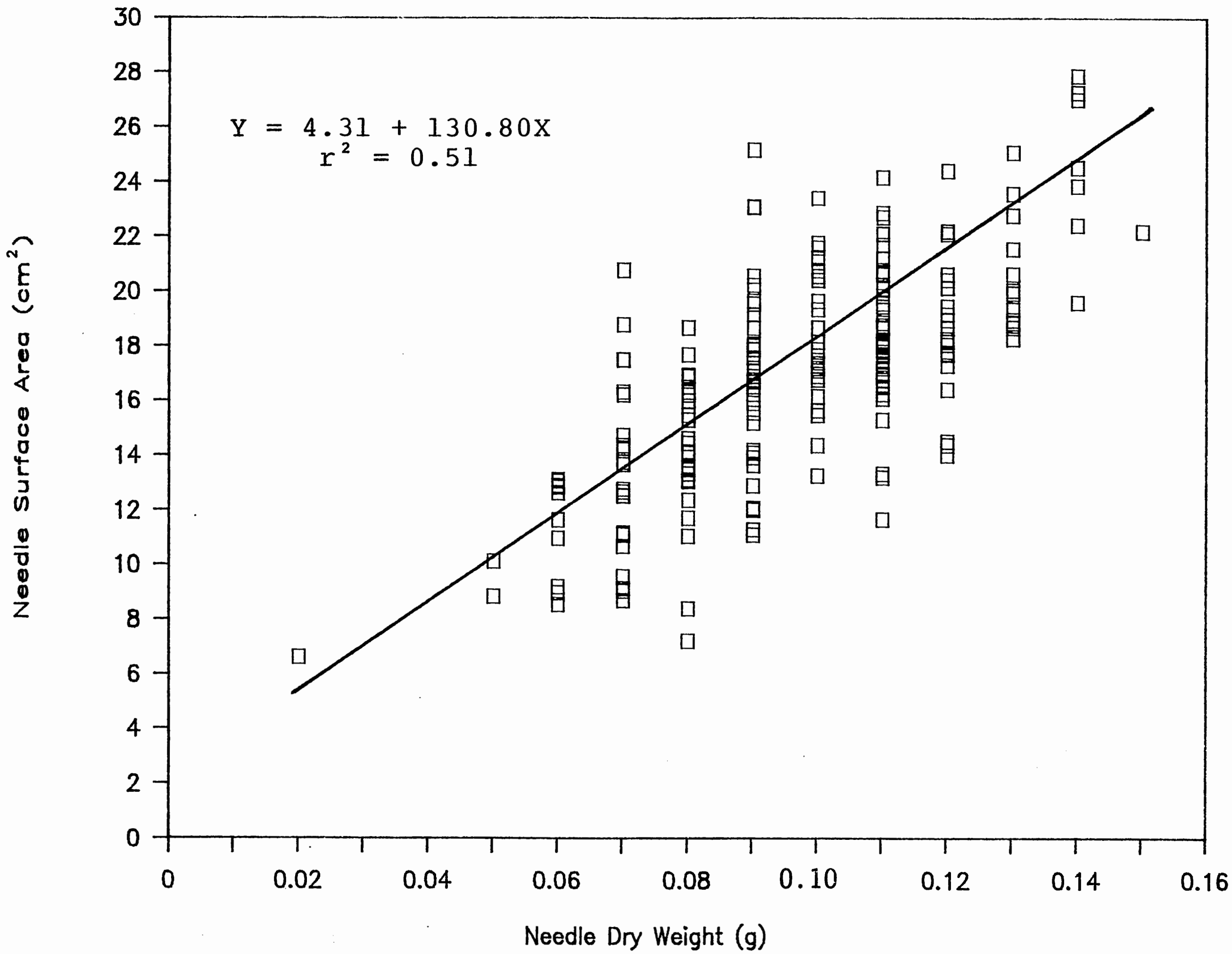

Figure 3. Relationship between Needle Surface Area and Needle Dry Weight

VITA 2

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