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GROWTH, PHYSIOLOGY, AND FINE-ROOT DYNAMICS
OF TWO HYBRID POPLAR CLONES
GROWN UNDER FOUR LEVELS OF IRRIGATION

by

Carlos Firkowski

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ABSTRACT

GROWTH, PHYSIOLOGY, AND FINE-ROOT DYNAMICS OF TWO HYBRID POPLAR CLONES GROWN UNDER FOUR LEVELS OF IRRIGATION

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A field plantation of two physiologically, morphologically, and phenologically contrasting poplar clones, "Eugenei", a Populus x euramericana hybrid and "Tristis", a P. tristis x P. balsamifera hybrid, grew under four different levels of soil moisture for three years. Height and diameter growth were measured during three growing seasons. Leaf senescence and bud activity were observed during one growing season. Biomass production was statistically different between clones and among treatments. Phenological variability also was induced by different soil water regimes in the Eugenei treatments. Volume of Tristis trees averaged 0.08 and 0.5 dm³ at the end second and third growing seasons with no significant differences among the moisture treatments. Eugenei non-irrigated treatment reached 1.0 and 6.6 dm³ at the end of the second and third growing seasons, respectively. Growth of the highest irrigated Eugenei treatment was 3.3 times larger than the non-irrigated treatment for both seasons.

Physiological parameters such as photosynthesis rate, stomatal conductance, transpiration rate and leaf water potential were measured during the second growing season from August to October. Few significant physiological differences were detected among Tristis treatments, although leaf water potential declined with increasing water stress. The Eugenei clone was very sensitive to water supply; stomatal conductance, photosynthesis rate and leaf water potential declined with increasing water stress.

Observation of fine roots (up to 3 mm diameter) was accomplished with minirhizotrons and a color video recording system. Only the high water and non-irrigated treatments of both clones were used for this study. Fine roots were observed from September to November of the third growing season. Differences between clones were observed in root distribution, branching habit, growth rate, and life span. Irrigation had an opposite effect in each clone. In terms of the absolute number of fine roots, irrigation promoted development of more roots in Eugenei, but had a detrimental or no effect on Tristis. The most significant difference in the fine root system was observed in the Tristis treatments. The non-irrigated trees had six times more branched roots, with laterals three times closer together than the irrigated treatment. This Tristis characteristic of growing a larger root system was a major reason why the non-irrigated treatment coped with drought conditions so well. By increasing water uptake, overnight turgor recovery of leaves

and high transpiration rate was possible.

Technical aspects of the minirhizotron and video recording system are discussed and photographs of typical and atypical root images are also shown.

**This dissertation is dedicated to
my wife, Margarida, for her
love and support**

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INTRODUCTION

Water is an essential component for plant life and it also is one of the environmental factors that more strongly regulates plant existence and distribution on the earth's surface. As a plant component, water may constitute up to 90% of the protoplasm; it is indispensable for chemical reactions as a reactant or media; and it is also responsible for the maintenance of cell turgescence (Kramer and Kozlowski 1979). The universal importance of water is once again recalled here, as the main issue of this dissertation is the effects of water on plant growth.

Most afforestation and reforestation programs have been established to satisfy the enormous need for lumber, fiber, and biomass. Intensive culture methods have enabled foresters to grow trees quickly by using, among other things, a species growth potential more effectively (McAlpine et al 1966; McAlpine and Brown 1967; Gordon 1975 and 1976; Wittwer et al 1978). The silvicultural system called short-rotation intensive culture (SRIC) combines the use of fast growing tree species planted under high density, intensive management, often with irrigation and/or fertilization, rotations of 5 - 10 years, and vegetative regrowth (coppice) after repetitive harvest.

Short-rotation poplar plantations are one of the most widely studied systems in parts of Canada and the USA (Zsuffa et al. 1977). Large biomass increments can be obtained in such close-spaced, intensively managed, frequently and repeatedly harvested plantations (Larson et al. 1976; Zavitkovski et al. 1976). Poplars are ideal for short-rotation systems because they grow fast and uniformly, regenerate by coppicing, and respond favorably to intensive culture.

Short-rotation intensive culture of any applicable species demands precise information on ranges of environmental factors required for maximum growth. Hybrid poplar, one of the most promising tree species for use in SRIC (Dickmann et al. 1975; Papadopol 1982; Zavitkovski et al. 1976; Zsuffa and Anderson 1970), is highly productive only on sites that can adequately supply its growth requirements (Baker and Broadfoot 1976; Dickmann and Stuart 1983; Dickmann et al. 1987). Understanding how environmental factors affect plant morphology and physiology is a vital step in increasing productivity of SRIC plantations (Isebrands et al. 1983). Silvicultural practices are based on physiological principles; by understanding these principles, the physiologist can suggest ways to manipulate plant growth to attain better yields.

Studies made in controlled-environmental conditions may define basic requirements and responses to them. However, the applicability of such results to the field is often

restricted. Plants growing under field conditions may respond differently to the environment than plants growing under controlled conditions (Jordan and Ritchie 1971; Nelson and Ehlers 1984). Photosynthesis rate, leaf water potential, stomatal responses, and plant morphology may vary greatly between plants grown in greenhouses and in field plantations. Understanding plant growth based on field experimentation is, therefore, a crucial practical tool required to place the right species on the right site and manipulate it for maximum growth.

Productivity can be increased in single trees or, more desirably, per unit of land area in a number of ways. Leaf area index can be increased through higher plant densities and intensive culture, producing greater photosynthetic surface and, as a consequence, more biomass production (Larson and Gordon 1969). The effective length of the growing season can also be increased by selection of genotypes with extended growing periods. Another way of increasing usable biomass is by directing growth to the stem instead of having large amounts of branch biomass (Larson and Isebrands 1972).

With the increase of productivity more pressure is exerted upon some of the site factors responsible for plant growth. Water is one of the crucial site factors in poplar plantings because high growth rates are strongly dependent on high water availability (Dickmann and Stuart 1983; Kennedy and Henderson 1976; Zsuffa et al. 1977). In

dry years, survival declines and growth rate of young plantations may be reduced up to 90% (Broadfoot 1967; Blackmon 1976; Rose et al. 1981). Because of competition from other uses, particularly agriculture, it is impossible to establish SRIC plantations only on the best sites; there is the need to utilize marginal land. Michigan has large areas of sandy soil that experience drought during part of the growing season. Such areas can support a SRIC plantation only if water availability is increased.

Silvicultural techniques, such as mechanical and chemical weed control, greatly increase available water in young plantations, resulting in high survival and growth rate (Kennedy and Henderson 1976; McKnight 1970). Increasing available water by irrigation may only be economically justifiable in cases where it can create new commercial forest land or increase the probability of producing a commercial forest crop (Blackmon 1976; Hansen 1983; Papadopol 1982). Erosion control, effluent disposal, insurance against drought, and water quality should also be considered when irrigation is used (Hansen et al. 1980; Rose et al. 1981; Rose and Kallstrom 1976).

Poplar responses to soil moisture conditions have been obtained mostly from studies in controlled environments (Ceulemans and Impens 1980; Domingo and Gordon 1974; Harkov and Brennan 1980). Little has been done at the field level on physiological responses of hybrid poplar growing in soils with annual drought periods. There is evidence that the

accumulation of poplar biomass can be appreciably increased under favorable soil conditions (Farmer 1970; Papadopol 1970; Zavitkovski 1979). However, the responses of a variety of poplar clones in terms of tolerance to drought and reaction to different soil moisture conditions, imply that there is a complex genetically controlled relationship between internal growth factors and the environment (Dickmann et al. 1979; Ceulemans et al. 1980; Pallardy and Kozlowski 1981; Mazzoleni 1985).

The objective of my research has been to conduct further study on the effects of water on physiological processes of poplar in a field plantation managed under intensive culture. This experiment, established in 1984, eventually became part of the Michigan State University/Department of Energy - Short Rotation Woody Crops Program project in 1986. Two physiologically, morphologically, and phenologically contrasting hybrid poplar clones (Isebrands et al. 1983; Michael 1984; Nelson and Ehlers 1984) were chosen for comparison of plant strategies. Clone "Eugenei", a Populus x euramericana (= P. nigra x P. deltoides) hybrid, is included in the section Aigeiros, and is known by it's fast growth rate and resistance to canker diseases. Clone "Tristis #1", a hybrid between P. tristis and P. balsamifera from the section Tacamahaca, is known to be adapted to dry soil conditions and it is cold and canker resistant.

The general goal of this research was to determine how different levels of soil moisture affect growth and

physiological processes, especially water relations, and fine root growth. Hopefully, the results will add significant information to current knowledge and lead to a better understanding of plant-environment interactions in SRIC plantations.

CHAPTER I. GROWTH AND YIELD

Introduction

Silvicultural techniques either stimulate greater growth or redirect it to a more useful and valuable form. Some environmental factors can be easily manipulated to increase production. For example, spacing or density greatly affects growth and/or form by changing the growing space available to each tree. Weed control and fertilization require more economic input, but they are also very effective in increasing yield. Irrigation, although economically questionable, does produce a marked growth response in most cases and can be an option for the practice of short-rotation, intensive culture (SRIC) forestry (Zavitkovski 1979).

Plantations managed under SRIC techniques are particularly responsive to site factors. The expression of the growth capacity of a tree species under high density is more than often restricted by limitations in available nutrients, water, oxygen, etc. Site factors can, although at some cost, can be improved. If fossil fuel prices increase, the use of wood for energy will increase and increased silvicultural inputs in SRIC will be feasible (Szego and

Kemp 1973; Rose 1975 and 1977).

Water is a site factor that strongly limits productivity of SRIC plantations on many sites. The results of Rawitz et al. (1966), Ek and Dawson (1976), Cooley (1978), Sinclair and Burger (1979), and Zavitkovski (1979), showing greater growth and high survival rate of hybrid poplar under a regular water supply, are illustrative of the importance of water. Although field experiments where water supply is controlled are restricted, the few examples available indicate that supplemental water can greatly increase yield.

This study will present data on two hybrid poplar clones managed under SRIC techniques and growing under four different levels of soil moisture for three growing seasons. Height, diameter, volume growth, leaf senescence, and bud set will be discussed. Growth variables are related to certain physiological variables and plant water status in the following chapter.

Materials and Methods

A plantation of Populus x euramericana cv. "Eugenei" (NC 5326) and P. tristris x P. balsamifera cv. "Tristis #1" (NC 5260) was established in May of 1984. Figure 1.1 is a map of the experimental area showing the plantation layout and equipment details.

A homogeneous area, considering slope and soil type, was

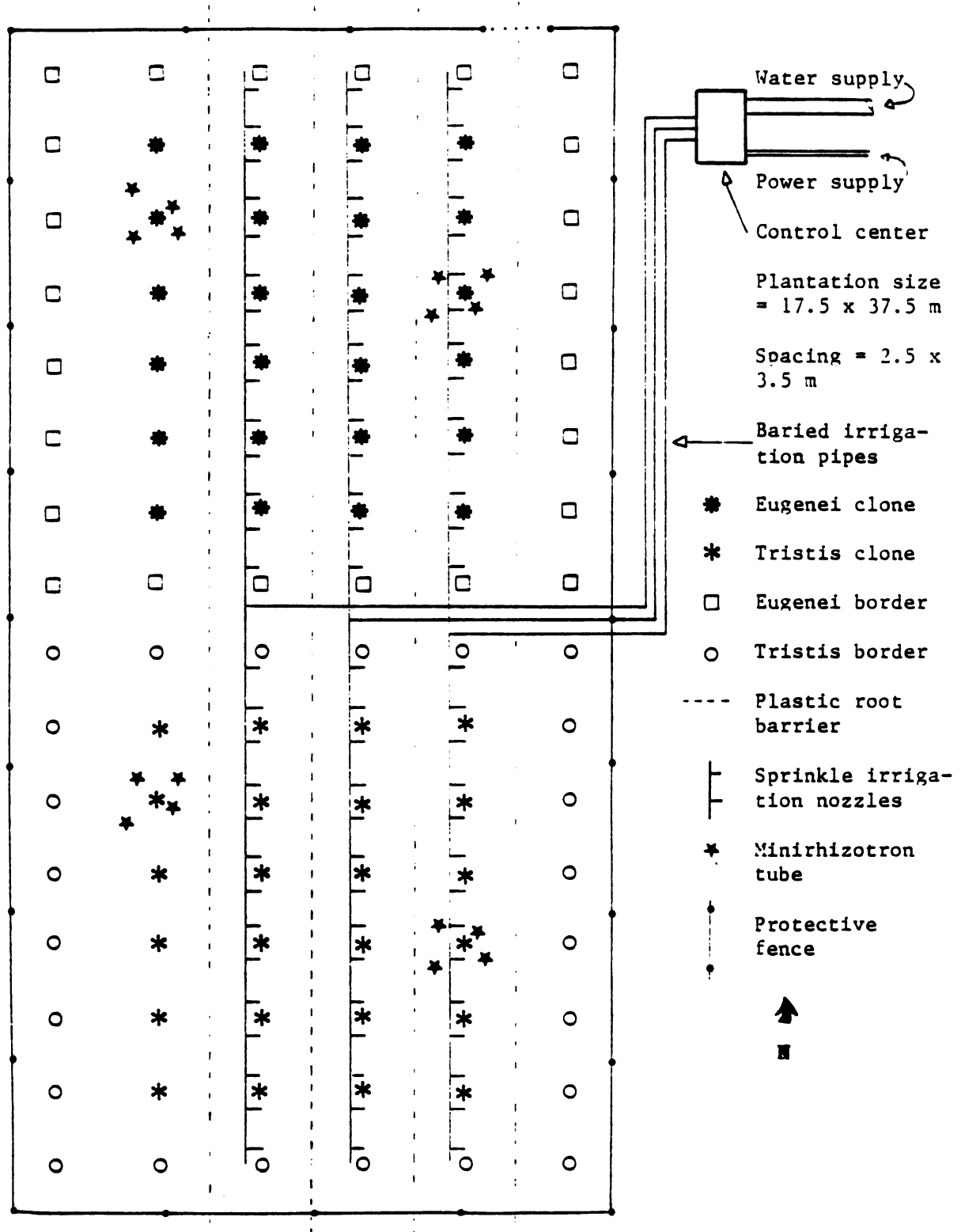


Figure 1.1. Layout of experimental plantation.

chosen at the Michigan State University Tree Research Center. The soil is a sandy loam of the Owosso series, well drained and moderately permeable in the upper horizon. Chemical analysis showed no deficiency in levels of nitrogen, phosphorus, and potassium.

The experimental area was plowed and roto-tilled prior to planting. Trenches 40 m long were opened with a Ditch Witch trencher and plastic root barriers were installed between treatments to restrict roots to their own soil moisture regime. The placement of a double wall of impermeable plastic (6 MIL gauge, approximately 0.16 mm thick) to a depth of 60 cm was presumed to be enough to avoid root growth out of the treated area for the first few years. Faulkner's (1976) studies of five-year-old hybrid poplar (*P. x euramericana*) show that the root system was strongly horizontally oriented between 5 and 20 cm, occasionally to 35 cm deep. Baker and Blackmon (1977), studying one-year-old eastern cottonwood (*P. deltoides*), also observed most of the root biomass in the upper part of the soil, with 84% of it in the first 20 cm of the soil and up to 94% of it within the top 30 cm.

Dickmann et al. (1980) showed that large diameter poplar cuttings have a higher chance of survival and grow better than small diameter cuttings. All cuttings were 25 cm long; Eugenei cuttings were 13-15 mm in diameter while Tristis cuttings were 10-12 mm. Cuttings used in the plantation protective boundary were smaller in diameter. Cuttings with

cankers and insect damage were rejected and a minimal bud number of four was maintained.

Unrooted cuttings were soaked in water for 24 hours before being planted. Planting occurred on May 9, 1984 and cuttings were set at a depth of about 20 cm by using a cylindrical planting bar 2 cm in diameter. During the next three days each cutting received 2 l of water a day in the morning hours. Extra cuttings for replacement were also planted on the same day next to the experimental plot and treated the same manner.

The plantation consisted of four rows (treatments east-west oriented) with six plants per row (replications south-north oriented) of each clone and a protective boundary of 24 plants around each plot. Trees were spaced 2.5 m apart in rows and rows were 3.5 m apart, which represents a total experimental area of 840 m^2 equivalent to 1,142 trees/ha.

Weeds were controlled with the herbicide glyphosate ("Roundup" from Monsanto). The application of the herbicide solution was made with a back-mounted sprayer. The herbicide, along with a surfactant and dye were used at the manufacturer's specified concentrations. Four or five applications a year during the first three years were necessary to maintain the plot weed-free. Young poplar plants were protected from the sprayed solution with cardboard cylinders placed around them.

Rabbit damage occurred during the winter of 1984/85, mostly in plants from the protection border. One Eugenei and

two Tristis treatment plants died due to rabbit damage, and they were replaced by plants of at least the same size in early spring of 1985. Border plants that died were also replaced. Repetitive deer damage to the tip of young shoots and leaves also occurred in early and mid spring of 1985. A fence 2.5 m high had to be installed around the plantation to avoid more serious deer browsing. Figure 1.2 is a photograph of the field plantation in mid-September of 1985. Some details of plant size can be observed and a rough comparison between height growth of Tristis (front) and Eugenei trees (back) may be made.



Figure 1.2. View of the plantation in mid-September of 1985 showing protective fence, Tristis treatments (front), and Eugenei treatments (back).

A buried 130 m long triple wired cable was installed to supply power to the irrigation control equipment. An irrigation system was installed in the late spring of 1985. It consisted of three 24-hour Dayton Programmable Time Switchers of seven days capacity and five minutes minimum operation time. Asco Shut Off valves (110 v and 6 w) were connected to and regulated by each timer. At pre-established timer intervals each Asco valve was triggered allowing water to flow into the sprinklers. The control center with timer, valves, and some of the equipment used for data collection is shown in Figure 1.3.

Two opposing sprinklers were used for each measured tree, located 30 cm from the stem and 20 cm in height. Figure 1.4 exemplifies the location and operation of a typical sprinkler. Each sprinkler was regulated to deliver one liter per minute by reducing water pressure with taps and pipe diameter. The three treatments delivered 40, 20, and 10 l of water per tree per day during the 1985 growing season. The volume of 40 l per tree per day corresponded to 32 mm per tree per week. The fourth treatment, the control, received no water and represented natural environmental conditions. The delivered water volume was doubled for the 1986 growing season since water needs increased due to tree and crown size. Thus, the well irrigated treatment was maintained at 80 l per tree per day, the medium irrigated received 40 l, and the low irrigated only 20 l. Treatments were designated as: "NC"= natural conditions. for the

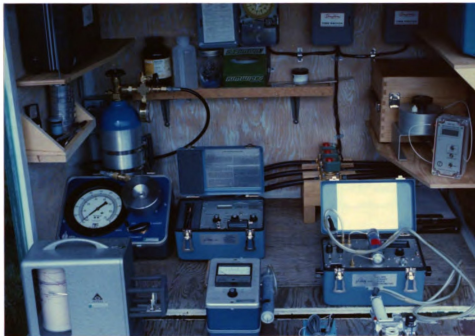


Figure 1.3. Control center with timers, valves, and other equipment used in data collection.



Figure 1.4. Disposition and operation of irrigation sprinklers on Eugenei clone during June 1985.

control; "LW" = low watered; "MW" = medium watered; and "WW" = well watered.

Irrigation started when mid-summer drought was detected in the beginning of July 1985. The water potential of four leaves from two plants of each clone was measured with a PMS pressure chamber three times a week. Irrigation started when the averages of the weekly measurements did not show complete recovery to a non-stressed condition. The above condition was observed only in few leaves of some Tristis plants. Eugenei plants appeared to be more influenced by the environment, with all measured plants and leaves having some signs of stress during early July.

Weekly observations of soil moisture content were done at two depths (0-5 and 10-15 cm). Soil samples were taken randomly at two trees per treatment in both clones. At each location, three samples were mixed together resulting in a single sample per depth. A sample was taken at 30 cm from the tree stem perpendicular to the sprinklers and two other at 60 cm from the stem in the same direction. Percent soil moisture content was then calculated by difference in weight of fresh and oven-dry (105 °C) samples. Soil samples were taken during the intensive data collection period, from August to mid-September of 1985.

Measurements of growth and physiological parameters started in August 1985. Height increments were measured every week from August to mid-September. Diameter increments were measured every two weeks at 10 cm above the root collar

for the same period. Growth observations were done only on Eugenei plants since Tristis plants did not show any measurable increment during the period.

Leaf senescence was evaluated weekly by counting the number of yellow leaves in the Eugenei clone. On Tristis plants, leaf senescence evaluation followed a different methodology, since the clone did not show any abscission of yellow leaves. The only observation made on Tristis leaves was the time when leaves turned brown. Time of bud set was observed only on Eugenei plants because Tristis plants set bud in late June. Total annual height and diameter were recorded at the end of each of the three growing seasons (1984, '85, and '86) for both clones.

Data analysis was based on a completely randomized field design. Because of the nature of the treatments, which included irrigated and non-irrigated trees and the use of plastic root barriers, it was impractical to establish an experiment in a true randomized disposition. Analysis of variance was used to detect differences among treatments. When treatment means were significantly different separation was made by the Least Significant Difference (LSD).

Smallian equations using diameters measured at the base, at one and two thirds of the tree height were used to calculate volume increments.

Environmental data was obtained from three different sources. Percentage of possible hours of sunshine was

compiled from the Lansing Airport weather station. Daily precipitation was recorded at the Tree Research Center (TRC) weather station. Relative humidity at 04:00 AM and at 10:00 AM was compiled from a one-week-cylindrical thermohygrometer installed at the control house at the field experiment. Maximum and minimum daily temperature were also obtained from the same thermohygrometer, except for a few times when data from the TRC weather station had to be used because of failure in the graphic recording.

Results

Average soil moisture contents for August and September 1985 are shown in Figure 1.5 for the Eugene1 treatments and in Figure 1.6 for the Tristis treatments. Weekly treatment values represent an average of two trees and two depths. The sharp definition of treatments reflected the effects of summer drought and irrigation.

Eugene1 and Tristis clones have a very distinctive annual shoot growth patterns. Tristis height growth began in the third or fourth week of April and bud set occurred in the last week of June. No differences among treatments were observed in the Tristis clone in the time of bud set for the 1985 or 1986 growing seasons. A few trees from each treatment set bud by the third week of June but the majority

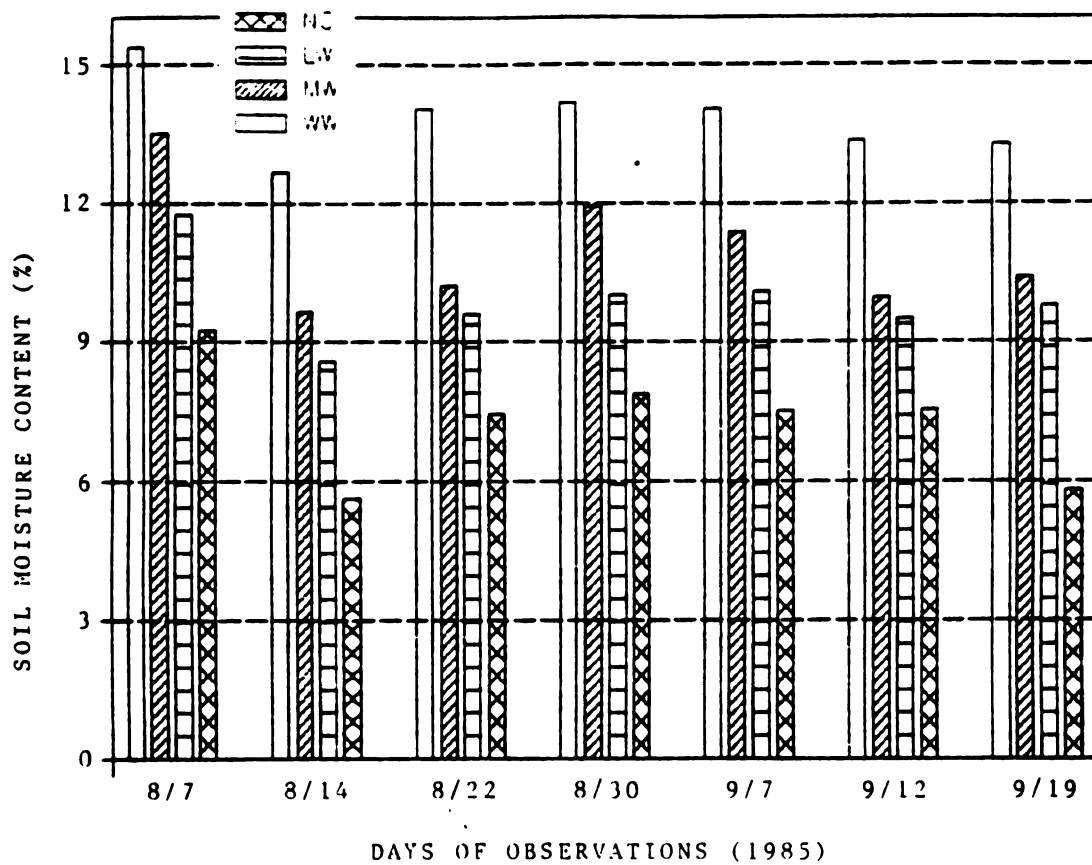


Figure 1.5. Treatment differences in soil moisture content (percent of wet weight) averaged over two depths (0-5 and 10-15 cm) for Eugenei during August and September 1985 (WW well watered; MW medium watered; LW low watered; NC natural conditions).

of trees of all treatments completed bud set by the fourth week, although some bud activity was observed in the first week of July. Height growth stopped in almost all plants in a matter of two weeks.

Eugenei started height growth one week later than Tristis did, but it continued growing until the beginning of fall. This clone had a five-month long growing season, while Tristis grew for two to two and a half months. Bud set time in Eugenei was strongly influenced by treatments (Figure 1.7). The drier the soil, the sooner buds set. Plants grown under natural conditions set bud approximately two weeks before any treated plants.

The simple field observations of Eugenei leaf senescence illustrated in Figure 1.8 show slight differences in the amount and pattern of leaf abscission. While trees in the irrigated treatments shed a few leaves in the beginning of the season, abscission in the NC trees was higher. The WW trees increased their rate of leaf abscission toward the end of the season, whereas the NC treatment had a slower rate of increase. The values presented in Figure 1.8 are absolute leaf numbers of different size plants. Thus, the higher initial number of shed leaves in the NC treatment represents even a higher value in terms of percentage of the total leaf number. The WW treatment had the largest number of leaves still to be shed during early October, while NC treatment had none. The other two irrigated treatments were intermediate. The WW treatment shed all of its leaves by the

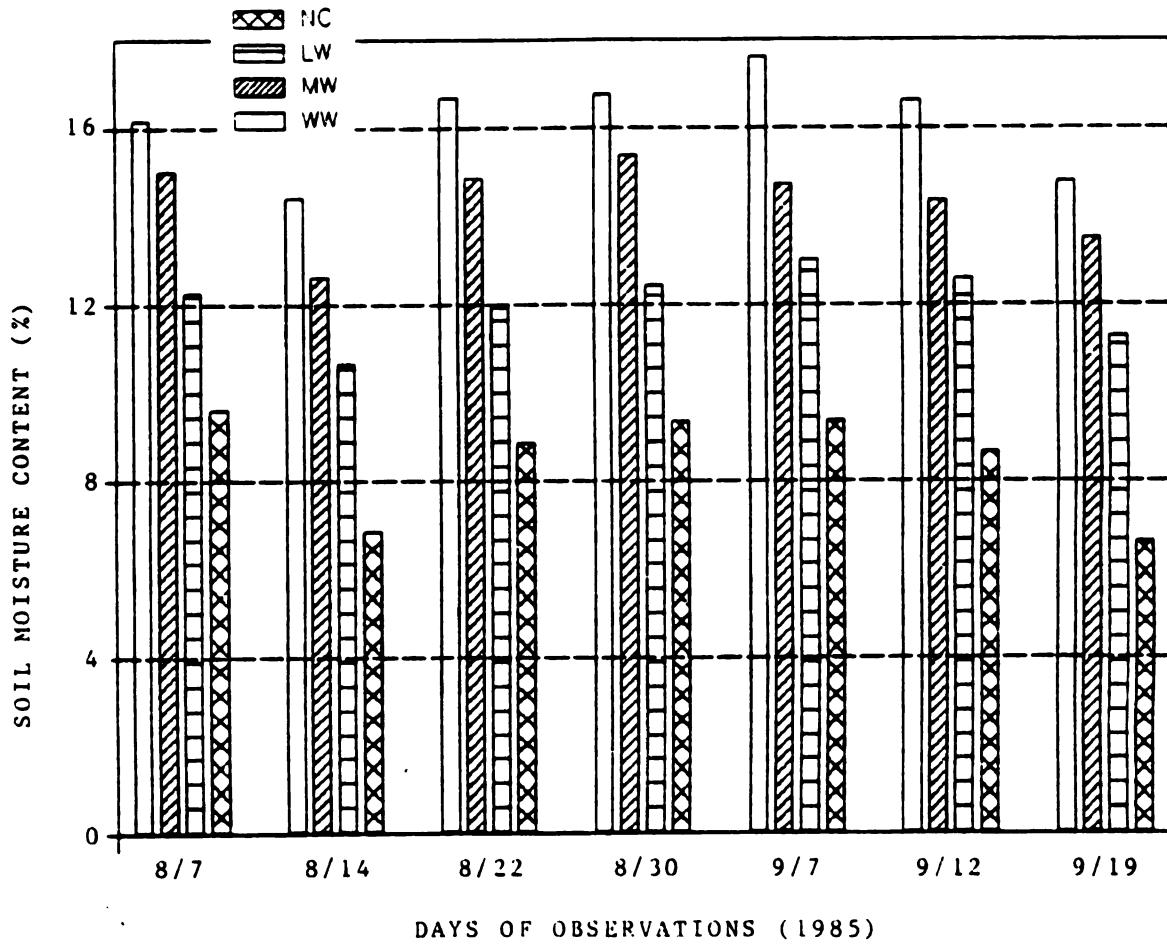


Figure 1.6. Treatment differences in soil moisture content (percent of wet weight) averaged over two depths (0-5 and 10-15 cm) for Tristis during August and September 1985 (WW well watered; MW medium watered; LW low watered; NC natural conditions).

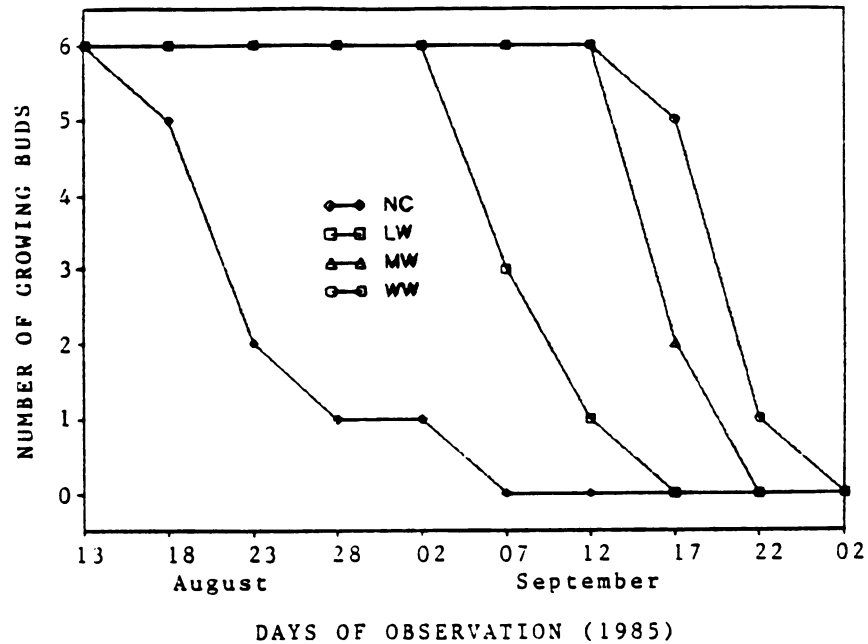


Figure 1.7. Variation among Eugenei treatments in bud setting time (WW well watered; MW medium watered; LW low watered; NC natural conditions).

end of October.

Leaf senescence of Tristis plants did not differ among treatments. Leaves were not shed periodically as in Eugenei; rather leaves were retained until they turned brown. Leaf color started to change in all plants during the second and third day of September. Starting with many small necrotic areas, leaves turned completely brown in a matter of days. All leaves of Tristis plants had been shed before the end of September.

Height of both Eugenei and Tristis clones at the end of each of the three growing seasons is summarized in Figures 1.9 and 1.10. No differences in height were shown in either

clone at the end of the first growing season, since no irrigation treatment had not been applied. Eugenei height growth was significantly altered by irrigation treatments during the second and third growing seasons. Trees in the WW treatments grew the most, MW and LW treatments were intermediate, and the NC treatment grew the slowest. Differences at the end of the 1985 and 1986 growing seasons were significant at 1% level of probability; the NC mean was always different from the irrigated treatment means.

Tristis treatments did not differ in height at the end of the first growing season, as expected, nor after the

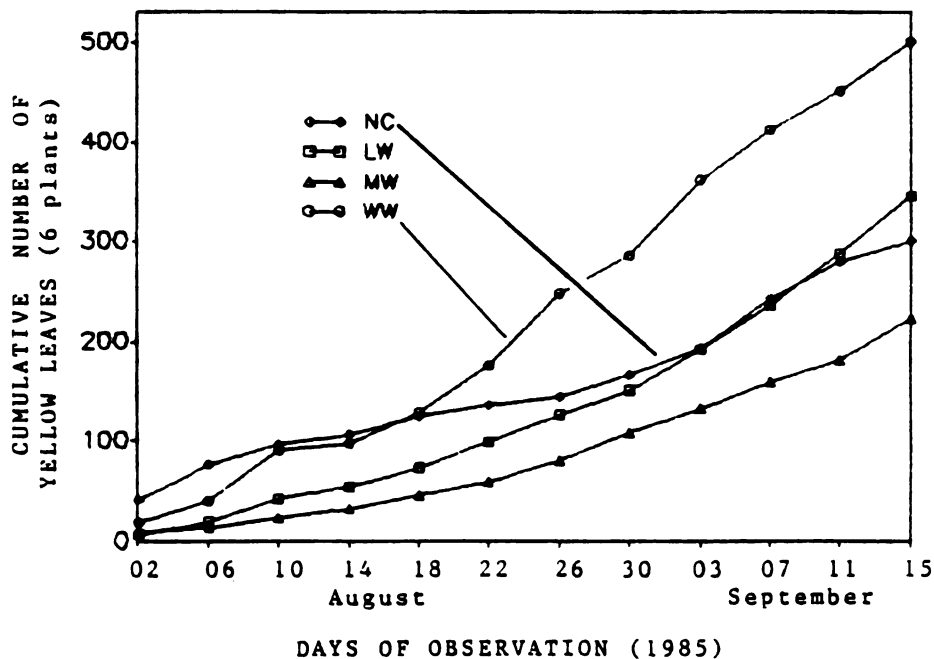


Figure 1.8. Variation among treatments of Eugenei clone in shedding and senescence of leaves (WW well watered; MW medium watered; LW low watered; NC natural conditions).

second season (Figure 1.10). A significant difference in height was detected between WW and LW treatments at the 1% level of probability for the 1986 season; however, there was no significant difference between the control and the irrigated treatments for the same season. Thus, the slower growth of LW treatment cannot be attributed to low water supply, but rather to other unknown causes.

Annual diameter growth of Eugenei treatments is presented in Table 1.1. No differences were detected at the end of the first growing season, as expected. The second and third seasons showed the same trend as shown by height growth. The WW and NC treatments were the only treatments that were significantly different at the end of the 1985 season. However, the NC treatment mean differed from all other irrigated treatment means at 1% level of probability at the end of the third season.

Treatment diameter growth responses of the Tristis clone were similar to those for height growth. No differences among treatments for any of the three growing seasons were detected (Table 1.2), although there is some variation between means.

Periodic height increments of Eugenei treatments after irrigation was implemented and the behavior during the more intense data collection period is shown in Figure 1.11. Data from Tristis is not shown because it had already set bud. Weekly increments of irrigated plants were always higher than the controls. NC increments decreased constantly from

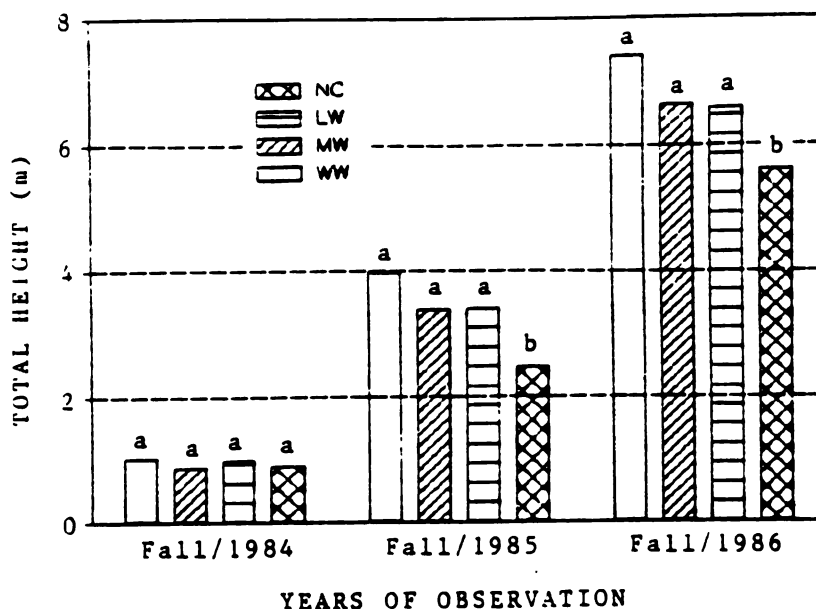


Figure 1.9. Treatment differences in the total height of Eugenei after the 1984, 1985, and 1986 growing seasons (WW well watered; MW medium watered; LW low watered; NC natural conditions). Bars topped with the same letter are not significantly different ($p = 0.01$, LSD).

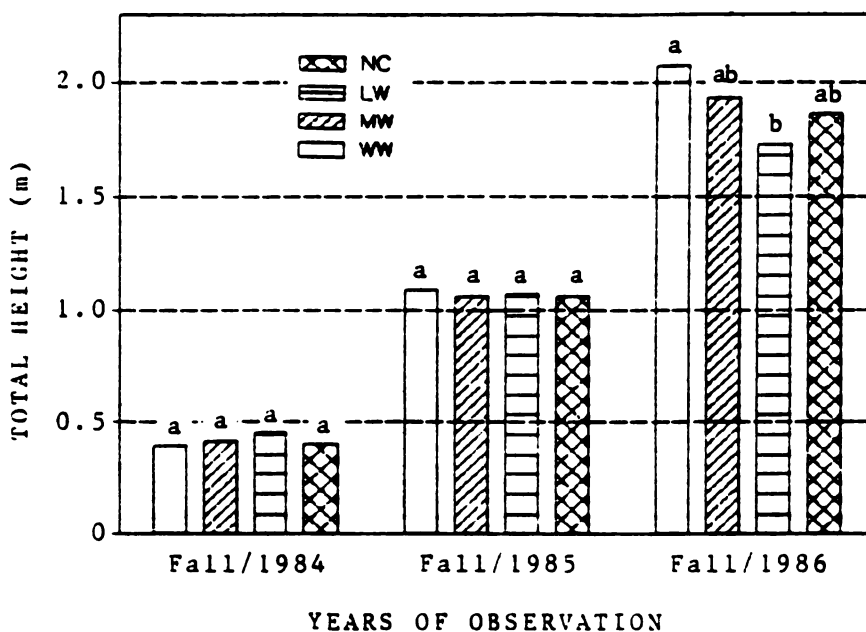


Figure 1.10. Treatment differences in the total height of Tristis after the 1984, 1985, and 1986 growing seasons (WW well watered; MW medium watered; LW low watered; NC natural conditions). Bars topped with the same letter are not significantly different ($p = 0.01$, LSD).

first week to the last, when they were almost zero, whereas the irrigated treatments were showing higher, though somewhat variable, weekly increments. The WW treatment had a mean increment of 25 cm during the last week of August, or more than 4 cm a day. During the last three weeks increments were, respectively, 4, 8, and 28 times higher, as an average, in the irrigated plants than in the NC treatment. Significant differences between NC and the watered treatment means at the 5% level of probability were detected in all measurements.

Table 1.1 Total annual diameter growth of Eugenei after each of three growing seasons.

Year	Significance ¹ of F-value	Treatment means ²			
		WW	MW	LW	NC
		 cm			
1984	ns	2.1a	1.9a	2.0a	1.9a
1985	**	5.6a	4.7ab	4.8ab	3.9b
1986	**	11.1a	10.0a	10.1a	7.4b

1

ns not significant.

** significant at $p = 0.01$ level.

2

Means followed by the same letter do not differ from each other based on the least significant difference. WW well watered; MW medium watered; LW low watered; NC natural conditions.

Periodic height growth of Eugenei obeyed a very specific pattern. In the NC treatment height increment decreased regularly through time. Such decreases were due in part to the early bud setting. The irrigated treatments showed two peaks of growth in response to environmental conditions in 1985 (see Figures 1.12, 1.13, 1.14, 1.15, and 1.16). Precipitation of about 36 mm, high minimum temperatures, low maximum temperatures, and high relative humidity during the third week of August greatly improved growth conditions. Because of such environmental conditions, the best increment was observed during the last week of August. However, only

Table 1.2 Total annual diameter growth of Tristis after each of three growing seasons.

Year	Significance ¹ of F-value	Treatment means ²			
		WW	MW	LW	NC
		 CM			
1984	ns	1.1	1.1	1.0	1.0
1985	ns	1.7	1.7	1.6	1.6
1986	ns	3.3	3.0	2.8	3.1

¹

ns not significant.

²

WW well watered; MW medium watered; LW low watered; NC natural conditions.

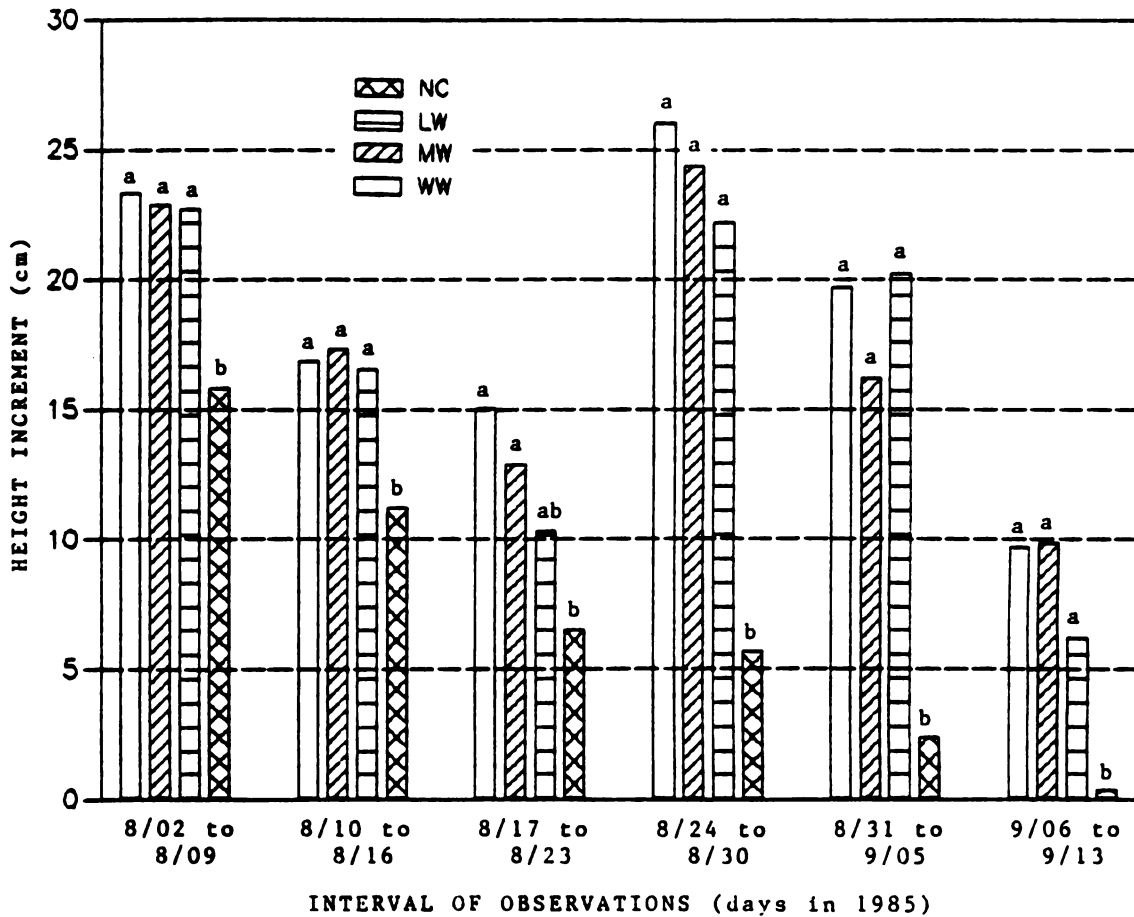


Figure 1.11. Treatment differences in periodic height increments of Eugenei during August and part of September (WW well watered; MW medium watered; LW low watered; NC natural conditions). Bars topped with the same letter are not significantly different ($p = 0.05$, LSD).

irrigated trees were able to recover from the poor conditions during the third week of August.

Periodic diameter increment of Eugenei plants were measured at two week intervals (Figure 1.17). A consistent pattern of growth among treatments could not be observed, since measurement of some trees were null or even negative. Negative diameter increments were considered null. Variation among treatments was higher than for height, but a general trend can be observed: irrigated plants always showed significantly better diameter growth than the NC plants for all three observation intervals, except for the LW treatment during the second measurement.

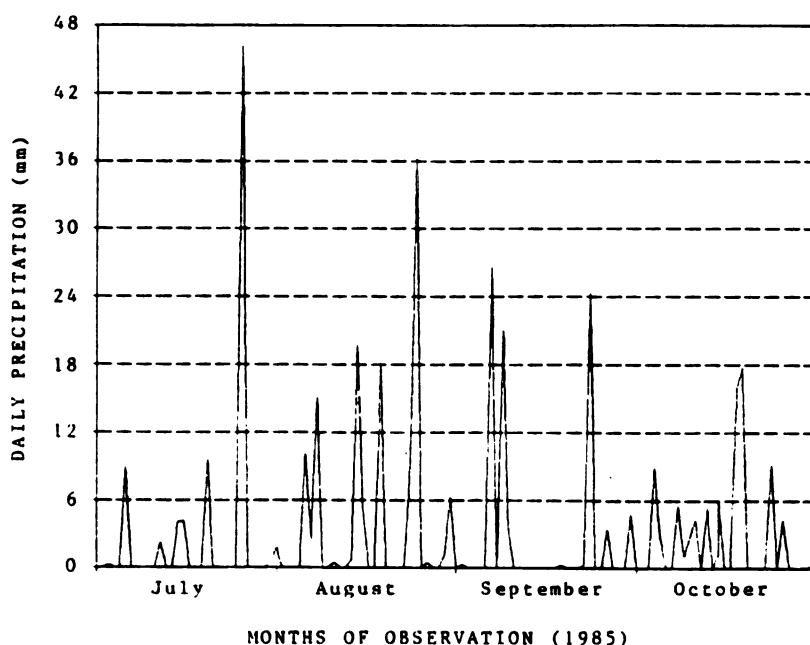


Figure 1.12. Daily precipitation during the 1985 study season.

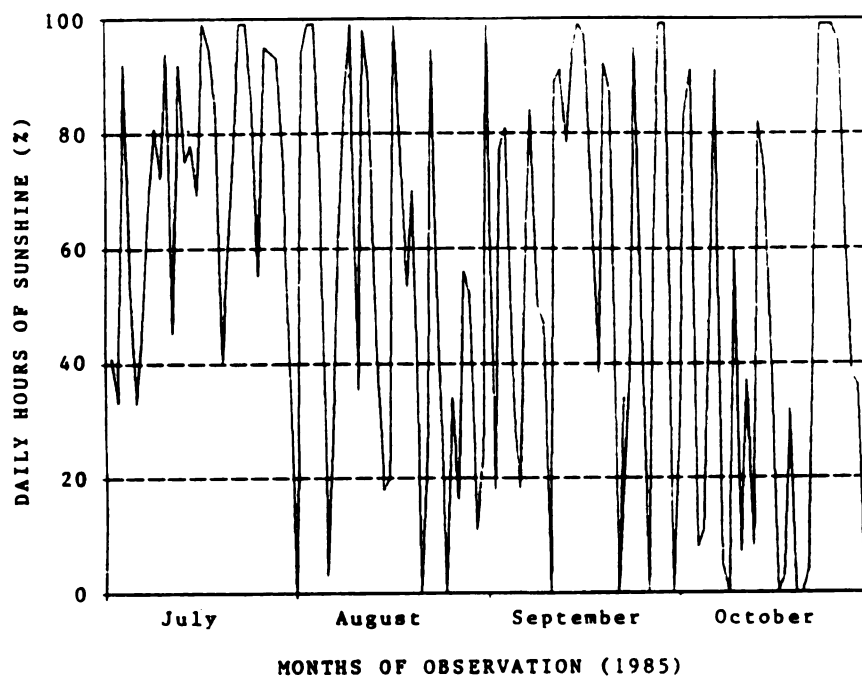


Figure 1.13. Daily percentage of total possible hours of of sunshine during the 1985 study season.

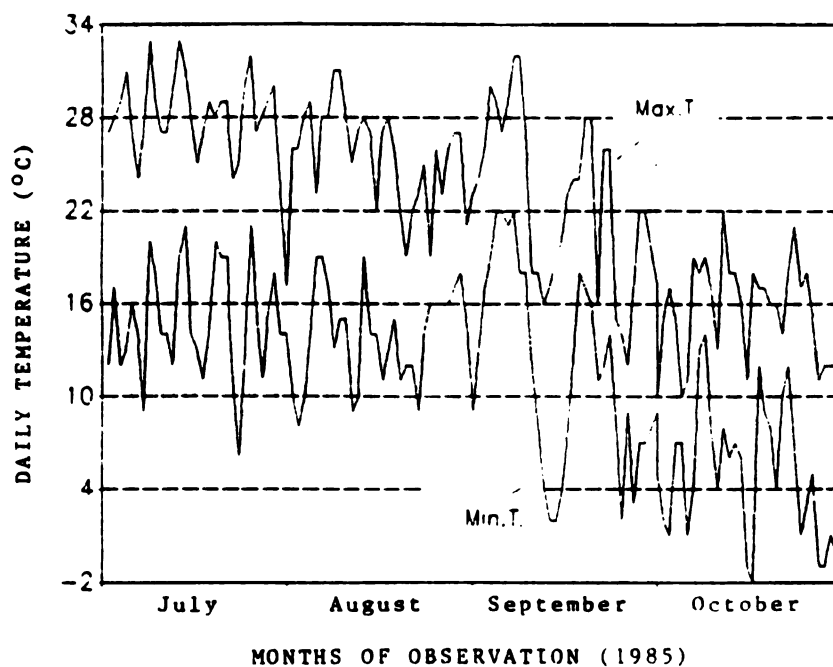


Figure 1.14. Daily maximum and minimum temperatures during the 1985 study season.

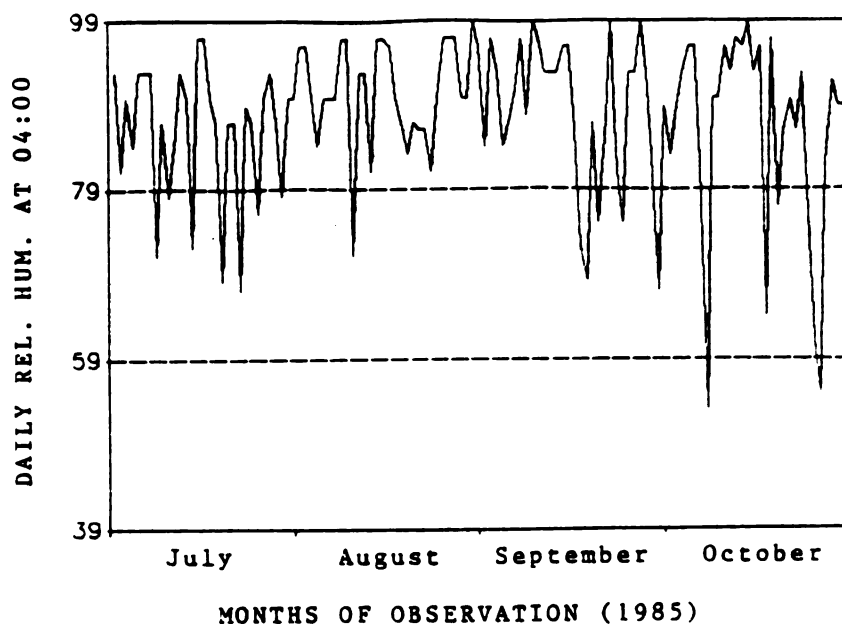


Figure 1.15. Daily relative humidity at 04:00 AM during the 1985 study season.

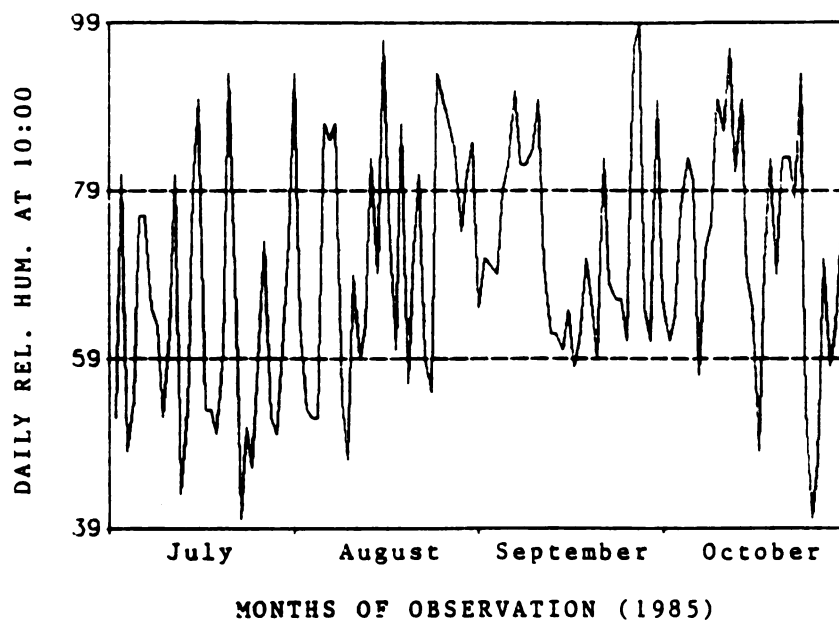


Figure 1.16. Daily relative humidity at 10:00 AM during the 1985 study season.

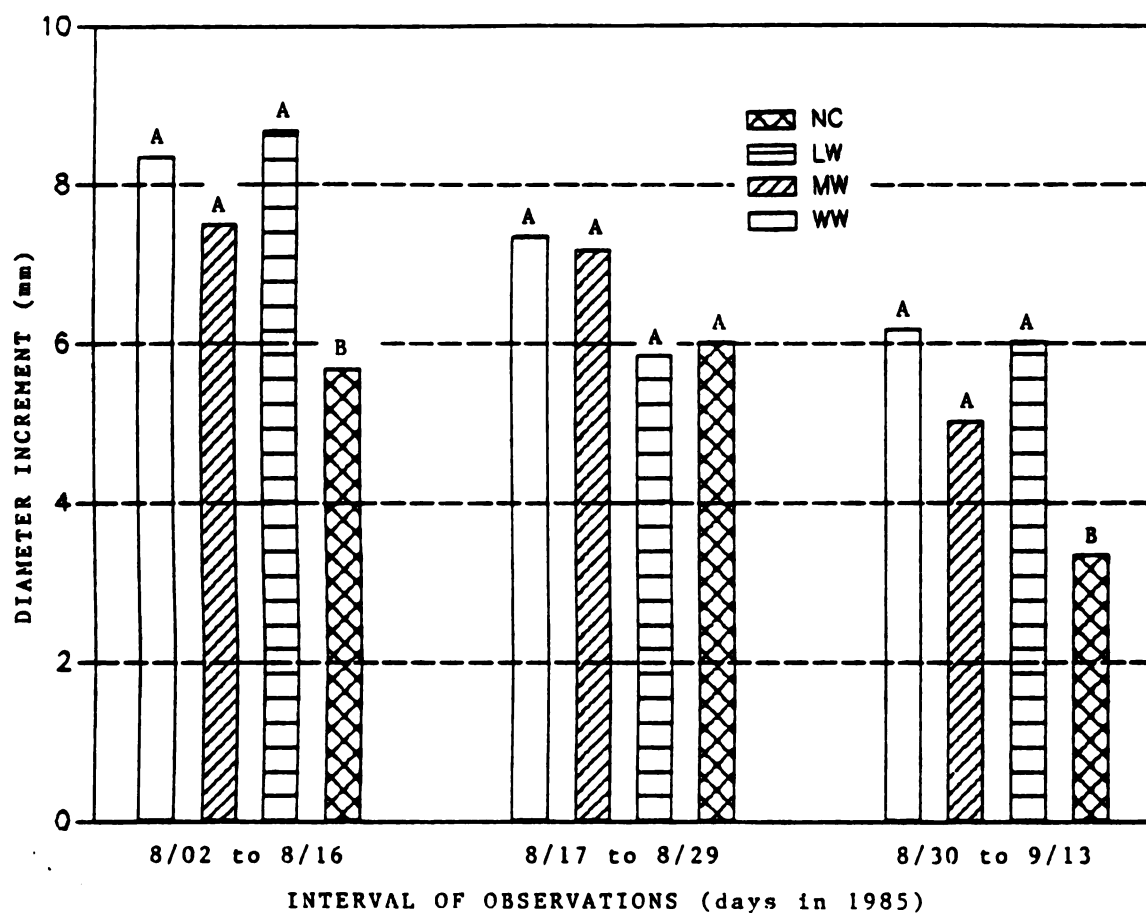


Figure 1.17. Treatment differences in periodic diameter increments of Eugenei during August and part of September (WW well watered; MW medium watered; LW low watered; NC natural conditions). Bars topped with the same letter are not significantly different ($p = 0.05$, LSD).

Total height and diameter growth of Eugenei treatments during the intensive measurement period are shown by Figures 1.18 and 1.19, respectively. The average increment of WW, MW, and LW treatments represents two and half times more growth than the NC treatment during August to mid-September. Such growth represents 1 m per 45 days or, even more impressively, over 2 cm a day. Analysis of variance detected significant differences among Eugenei treatments at the 1% level of probability. Diameter increments for the period summarized in Figure 1.19 were not as variable. The NC treatment mean was 15 mm while the mean for the irrigated treatments was 20 mm, only 33% higher. Despite the small variance, differences among treatments were significant at a 5% level of probability. Even though diameter increment was smaller in the NC treatment, it did not decrease at the same rate as height did, regardless of bud set time. During the last week of measurements NC diameter increments were still quite high when compared with the average of irrigated treatments. The NC height increment mean was 2.3 times smaller than the height increment mean of the irrigated treatments. On the other hand, the diameter increment mean of the NC treatment was less than 1.8 times smaller when compared to the mean of irrigated treatments. Thus, the NC treatment maintained more or less the same rate of diameter growth for a longer time in the season than it did for height growth.

The Tristis clone did not have any measurable growth

during the period of intense data collection. Height growth stopped one to one and half months prior to measurements. Diameter growth was minimal (less than 2 mm) or did not occur at all.

Growth variations among treatments and between clones were more dramatic when volume of average trees were compared. Tristis volume growth data corresponds to averages of all four treatments, since they did not vary significantly. Tristis volume during the 1985 season reached 0.08 dm^3 and 0.5 dm^3 during the following season. Eugenei volume did vary significantly among treatments. During the

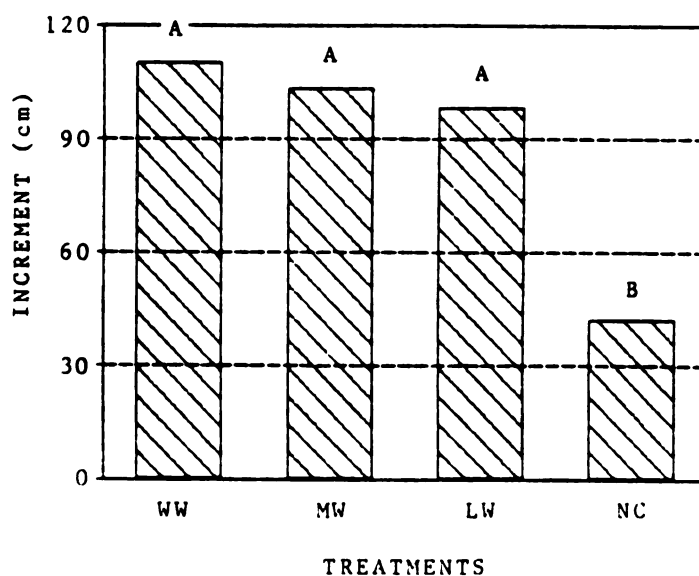


Figure 1.18. Treatment differences in total height increment of Eugenei during the period from 8/02 to 9/13 of the 1985 growing season (WW well watered; MW medium watered; LW low watered; NC natural conditions). Bars topped with the same letter are not significantly different ($p = 0.01$, LSD).

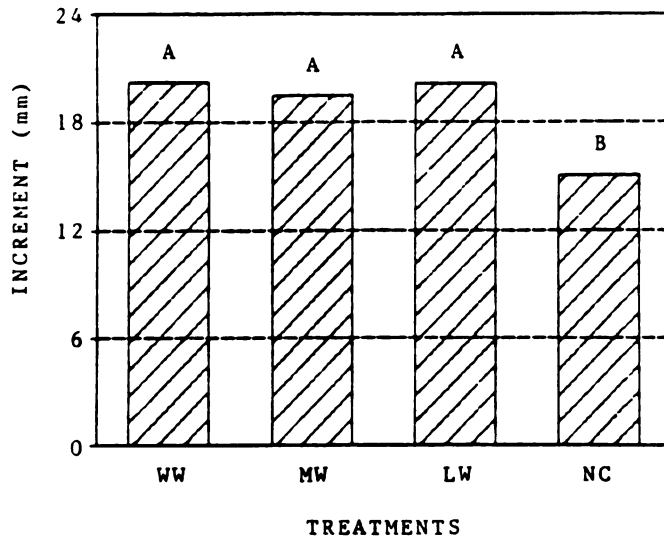


Figure 1.19. Treatment differences in total diameter increment of Eugenei during the period from 8/02 to 9/13 of the 1985 growing season (WW well watered; MW medium watered; LW low watered; NC natural conditions). Bars topped with the same letter are not significantly different ($p = 0.05$, LSD).

1985 season volume reached 3.2 dm^3 for the WW treatments but only 1.0 dm^3 for NC treatments. MW and LW treatments were intermediate between the extremes. During the 1986 season, the WW treatment reached 22.3 dm^3 , whereas the natural conditions treatments reached only 6.6 dm^3 . A volume growth differential of approximately 42 and 45 times was attained when comparing the WW treatment of Eugenei and Tristis overall means for the 1985 and 1986 seasons, respectively. When comparisons are made between volumes of the NC Eugenei treatment and the Tristis overall means, volume was approximately 13 times higher.

Discussion

The Eugenei and Tristis clones showed strong differences in the annual pattern of growth. Variation in the time of bud break and set, height and diameter growth, and type of leaf senescence occurred throughout both of the seasons studied. The Tristis clone was less plastic, maintaining a similar behavior regardless of water regime. Variation in the Eugenei clone was substantial due to differences in soil moisture regime, and as a general rule the more water available the better it grew.

Time of bud break was just slightly variable between clones. As an average, Tristis started bud activity one week before Eugenei, while temperatures were slightly colder, although there were trees from both clones growing during the first week of observable shoot activity. Bud opening is a physiological process dependent upon critical temperatures for initiation of shoot growth (Kramer and Kozlowski 1979). Plants that are moved to lower latitudes, such as Tristis, tend to start growing earlier than in their place of origin, because critical temperatures are reached earlier.

Time of bud set differed significantly between clones and among Eugenei treatments. Bud set is a physiological process that is strongly determined by photoperiod (Vince-Prune 1975). Pauley and Perry (1954) studied various poplar clones and found that the timing for bud setting was

correlated with the environmental conditions of the provenance of origin. Genotype traits of the parental species of the hybrids clones used in this study could contribute to their contrasting behavior. The Tristis clone is a putative hybrid of P. balsamifera and an exotic Himalayan species (P. tristis) , both from cold climates. In contrast, the Eugenei clone is a more southerly tree, originating in France, from a cross between P. deltoides and P. nigra.

Populus balsamifera is defined by Nitsch (1957) as being induced to dormancy by short days. Larson and Isebrands (1972) found that growth cessation of Tristis early in the season is an inherited response of the genotype to the photoperiod. When days become shorter after the summer solstice, Tristis stops growth and begins to go into dormancy. Eugenei, on the other hand, grows almost up to the end of summer, when days are short and temperatures cool. But Eugenei is a hybrid of species from lower and warmer latitudes than Tristis.

The lack of variation in bud set time among treatments in the Tristis clone cannot be directly attributed to any factor. At the time of bud set no treatment had been applied during the 1985 season. Right after irrigation started and bud activity was ceasing, a strong nitrogen fertilization at a rate of 100 k/ha was applied in an attempt to promote a second flush (Dykstra 1974). However, no responses were detected in any treatment, which suggests that a stronger

factor than water availability or a high nitrogen level was ruling.

Studies done with the Tristis clone at higher latitudes (Rhineland, WI approximately 46 degrees north latitude) showed terminal buds being set by the end of July or beginning of August in one study (Michael 1984) and by mid-August in two others (Dawson et al. 1976; Isebrands et al. 1983). A speculative reason why Tristis set bud earlier in East Lansing (approximately 42.5 degrees north latitude) than Rhineland is because the day length was too short to support continued growth even at the summer solstice. A given day length in East Lansing will occur later in the season at higher latitude; thus, the Tristis clone continues to grow in Rhineland while it is setting bud in East Lansing. However, during the abnormally warm and slightly dry 1987 growing season, most of the Tristis plants set bud during the end of June, unusually early. Then, probably due to continued high temperatures and abundant rainfall, more than half of the plants reflushed, some more than once. Thus, under special circumstances in more southern latitudes, Tristis becomes recurrently flushing rather than strictly determinate, whereas in northern latitudes it is indeterminate, though not as much so as Eugenei.

Variation in the time of bud set of Eugenei was due to treatment differences in water availability. Water deficit is known to cause profound effects on the internal physiological status of plants (Kramer and Kozlowski 1979).

Under stress conditions shoot growth is immediately reduced (Hansen and Phipps 1983). Leaf senescence is strongly affected when various hormonal changes (specially in ABA and ethylene) trigger abscission and also terminal bud formation (Osborne 1973; Apelbaum and Yang 1981; Ackerson 1982). Number of leaves per plant, although not directly evaluated in this study, is also a very important factor that can alter growth behavior. Trees of the NC treatment had proportionally fewer green leaves that were healthy and photosynthetically active than the other treatments. An early bud set time due to low soil moisture regime, accompanied by a high rate of leaf senescence, influenced growth of the NC treatment negatively.

The time of the year that Tristis shed all leaves is comparable to the observation by Michael (1984), if the environmental effects of latitude are considered. Leaf senescence and other growth variables of Tristis were unaffected by soil moisture. Thus, the plant's internal physiological balance adjusted to moisture deficits indicating a substantial drought tolerance in this clone (Mazzoleni 1985). Another explanation may be related to the root/shoot ratio of Tristis trees (Michael 1984); its extended root system is more than enough to supply water to a restricted crown, even in adverse drought conditions. Poplars from the Tacamahaca section generally have a higher water use efficiency, when compared to poplars from the Aigeiros section, which also contributes to the drought

tolerance shown by Tristis (Blake 1981).

Height growth observed by Gottschalk (1984) on a two-year-old unirrigated planting of Eugenei was very similar to that reported in this study. The average growth in height of the NC treatment for the second growing season was 2.5 m and Gottschalk reported an average of 2.54 m for the same age. Diameter growth attained in this study by the NC treatment, 3.9 cm was higher than the 2.3 cm average obtained in the Gottschalk study, but his trees were planted at a much higher density.

Tristis growth was very poor when compared with results from other areas of the country. Trees growing in irrigated and fertilized close spaced plantations near Rhineland, WI attained average values of 1.9 m in height at two years (Zavitkovski et al. 1976; Ek and Dawson 1976), whereas Tristis trees in this study attained the same height one year later, at the end of the third growing season. Mean height of Tristis plants in East Lansing was approximately half of that attained in Rhineland after three growing seasons due primarily to early bud set in East Lansing. Diameter growth was 2.3 cm and 3.4 cm for the second and the third season, respectively, in the closer-spaced Wisconsin study; it was 1.6 cm and 3.1 cm for the same respective growing seasons in the present research.

Although some studies may indicate that diameter is more affected by drought (Dickmann 1979; Gottschalk 1984), this observation was not substantiated in this study. The present

results indicate that height growth of Eugenei was more deeply affected than diameter growth during the period of observation. Height increments were significantly different in all observations, some even at the 1% level of probability. Diameter increments were significantly different in two out of three cases and only at a 5% level of probability.

As a general rule for the Eugenei clone, height growth in the irrigated treatments was proportional to the volume of supplied water. However, diameter growth did not follow the same rule precisely. The LW treatment trees grew more in diameter than the trees in the MW treatment, and in some occasions, almost as well as the ones in the WW treatment. The reason for such behavior may be that trees in the LW treatment had more available space to grow than the ones in the MW treatment. Although trees of LW treatment were shorter in height than MW or WW trees, they had large crowns with abundant leaves (Figure 1.8). The space left unoccupied by the slow-growing NC treatment trees was promptly used by the trees in the LW treatment. Another factor was a possible dominance of the WW treatment trees over the ones in the MW treatment. Even considering the ample spacing of 3.5 x 2.5 m, the large WW trees may have caused some shading of the small MW ones.

Rawitz et al. (1966) working with Populus deltoides and P. x euramericana cv. I-214, respectively obtained, 185% and 92% more biomass in the irrigated treatments than in the

controls at the end of four growing seasons. The results in the present study with Eugenei are even more impressive, with irrigated trees reaching up to 330% more volume than the control trees. Papadopol (1982), working with four clones of P. x euramericana, obtained biomass values that were strongly influenced by irrigation. The best clone had more than double the basal area when irrigated. Dry biomass was more than three times higher in the irrigated treatment when compared to the control. Cooley (1978) further reported that effluent irrigation proved to be effective in increasing poplar production; height growth of the hybrid P. canescens x P. tremuloides was nearly doubled after growing for three years under effluent irrigation.

Irrigation of intensively cultured poplar plantations can also be analysed in terms of energy balance. A study done by Zavitkovki (1979) using production values of the Tristis clone showed that irrigation brought 43% more net energy in a 10-year-old plantation. Net energy was what remained after the energy equivalence of inputs such as operations, fertilization, irrigation, equipment, etc were subtracted from the total energy produced. Furthermore, the results from Rawitz et al (1966) with a four-year-old poplar indicate that the beneficial effect of irrigation became more and more pronounced as the age of trees increased. Irrigation costs may appear high during the first years, but as the difference between treatments increases, the situation becomes more favorable. Results from intermediate

age plantations (less than 10 years) may be even better, with higher monetary returns than those shown by Zavitkovski (1979).

The economic interest in irrigation is to boost productivity so that the final cost per unit is lower compared with other alternatives. Mace et al. (1975) presents a hypothetical analysis of cost per unit produced in irrigated and non-irrigated forest plantations, and he makes some interesting points. First, land costs are reduced since irrigation produces higher yields per unit area. Second, protection costs are reduced, since a smaller area need be protected. Third, average transportation costs are reduced, since a smaller production area can be closer to the mill. Fourth, less land is required for the same production when irrigation is used, which reduces the problem of adverse market influences that forces land prices up. Finally, property taxes and other taxes or costs that are based on unit of land area are also reduced.

This study also reinforce the importance of matching the poplar clone to the site. On droughty sites, especially in northern latitudes, Tristis would be preferred over Eugenei. On the other hand, Eugenei will outperform Tristis on the moister sites, especially in more southern latitudes in the Lake States. There is a need to expand this knowledge base to other poplar clones, however, so that genetic diversity can be maintained in plantations in the region.

CHAPTER II. PHYSIOLOGY AND WATER

Introduction

Lack of water is probably the most common problem encountered by plants and water deficits may affect physiological processes directly and/or indirectly (Kramer 1962; Kramer and Kozlowski 1979; Hall 1981). The plant's sensitivity and responses to the stress imposed by water deficits may vary according to genus, species, provenances, individuals, plant age, site, time of the year, and plant organ (Luukkanen and Kozlowski 1972; Ceulemans et al. 1978a, b; McGee et al. 1981; Pallardy and Kozlowski 1981; Scholz and Stephan 1982; Shulte and Marshall 1983; Morgan 1984).

Zahner (1968), emphasizing the importance of water for plants, estimated that 80 to 90% of the variation in plant growth can be attributed to inadequate water supply. During persistent droughts, water stress can reduce and even stop plant growth (Larson 1980). Lack of cell turgidity is the first major effect of water deficit (Hsiao 1973; Zimmermann 1978; Morgan 1984), followed by metabolic changes and modifications in substrate production, all leading to reduction in growth and development (Kramer and Kozlowski

1979; Fitter and Hay 1981; Kramer 1983). But other effects such as stomatal closure (Kelliher and Tauer 1980; Ackerson and Herbert 1981) and reduction in photosynthesis rate are also important (Brix 1979). Since their internal physiological equilibrium is modified (Ackerson 1981), plants subjected to water stress will experience other indirect effects. Changes in the balance of growth regulators and water potential causes reduction in root (Dixon et al. 1980; Heth 1980) and stem growth (Hansen and Phipps 1983), and increases leaf abscission (Daveport et al. 1980). Late bud break and/or early bud set may also be a plant response to water stress (Larson 1980). Under severe drought conditions, a final and more dramatic effect can be plant death (Kelliher et al. 1980; Hansen and Phipps 1983).

Inadequate water supply affects not only the quantity of growth but also quality in terms of wood density, cell wall thickness, and chemical composition (Chen and Sung 1983; Berlin et al. 1982). Physiological interdependence may be exemplified by the relation between nitrogen deficiency and water stress. Plants that appear to be well supplied with water show symptoms of water stress when nitrogen is deficient (Radin and Ackerson 1981; Radin et al. 1982). There is also evidence that insect (Ferrel 1978) and disease resistance (Bier 1959) is decreased when plants experience water stress. In sum, water deficits cause many modifications in plant growth, physiology, biochemistry, morphology, and anatomy, with their most significant

influence probably on gas exchange of the leaf.

The physiological role of water as an important and indispensable environmental component is still not well understood. As a rule, irrigation in SRIC plantations is still done without the basic knowledge that advocates the use of it. Irrigation of any sort depends on information of how much, when, and at what interval water should be applied. The answer to such questions lies in the measurements of the plant-soil-environment system that may reflect the plant condition necessary for a higher growth capacity.

Environmental measurements are often difficult to interpret because of the dynamic nature of plant-soil relationships. Plants are often not entirely in equilibrium with the environment and observations of only one factor cannot clearly reflect this relationship (Boyer 1969). The current methods to evaluate the necessity for irrigation developed for agricultural crops and may not be suitable for use with forest crops. Unknown root distribution, lack of functions relating soil moisture to tree growth, and difficulties in obtaining accurate and representative measurement are some reasons why specific methods for evaluating water relations of SRIC tree plantations should be developed. Indispensable for such a task is, however, the understanding of water physiology, water balance, and water requirements to provide a more clarified idea and view of the subject.

Given the above considerations, a field study using fast growing poplar clones was initiated. Poplars are interesting subjects of study because of their substantial water requirement and adaptive responses to avoid severe water deficits (Domingo and Gordon 1974; Smith and Gatherum 1974; Pieters and Zima 1975; Kelliher et al. 1980). Two poplar clones, contrasting in terms of water use and drought tolerance, were compared while submitted to four different field soil moisture regimes. Data on physiological parameters generated under defined soil moisture regimes is analyzed, discussed, hopefully leading to a better understanding of the role of water in tree growth.

Materials and Methods

The present research was carried on using the same field experiment described in Chapter I. Data collection started in early August 1985, during the plantation second growing season, soon after irrigation was implemented. Observations were made of photosynthesis capacity, leaf transpiration, leaf stomatal conductance, and leaf water potential before and after sunrise. Some physiological data were collected on the same day, while other physiological observations, because of logistical problems and inappropriate weather conditions, had to be taken on different dates. All observations were in a completely

randomized order with respect to clones, treatments, and replications. Forty-eight numbers representing all trees in the experiment were drawn before every measurement to establish a sequential order. When measurements were done on more than one leaf per tree, they were always in sequence from top to bottom of the crown.

Photosynthesis: The radioactively-labeled carbon dioxide (now on referred as RLCD) technique used in this study was modified by Michael (1984) from that described by Incoll and Wright (1969) and McWilliam et al. (1973). The handpiece developed by Michael (1984) and used here allows adaxial and abaxial light interception during the measurements. Descriptions of the gas system, handpiece, field operation, and assay for radioactivity can be found in Michael et al. 1985.

Measurements were taken on sunny or partly sunny days. From 10:00 AM to 2:00 PM photosynthesis of one leaf from all trees from both clones and four treatments could be measured. According to various studies (Regehr et al. 1975; Nelson and Michael 1982; Isebrands et al. 1983; Reich 1983; Gottschalk 1984; Michael 1984) photosynthesis greatly varies in the tree crown and there is no defined leaf position representative of whole-tree photosynthesis. Given this fact, young fully expanded leaves with theoretically the highest photosynthetic capacity were chosen for sampling (Larson and Gordon 1969; Dickmann 1971). The Eugenei clone

leaves measured were of LPI (leaf plastochron index; Larson and Isebrands 1971) equal to 9 - 15 in the middle upper part of the crown. The Tristis clone leaves were not referred to with an LPI notation, since height growth and production of new leaves had ceased when measurements began. The Tristis leaves measured were also from the upper crown.

Radioactively-labeled carbon dioxide was simultaneously administered on both abaxial and adaxial surfaces to a 0.503 cm^2 area midway between the leaf tip and base free of large veins, while the leaf was held in its natural orientation. A leaf had to fulfill five requirements to be selected for measurements: positioned at the right height, fully exposed, visually healthy, from the south face, and with surface perpendicular to the sun.

The radioactive leaf samples were counted in a liquid scintillation spectrometer (Packard Tri-Carb model 2002) in wide and narrow channels and corrected for background radiation. Photosynthesis rate (P_g) expressed in $\text{mg CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ was calculated using the formula from Nelson et al. (1982).

Leaves from both clones and treatments that had been applied with RLCD were collected in the first and fifth measurement for an estimation of the clone leaf density. After having their area measured they were oven-dried (105°C) and weighted.

Transpiration Rate and Stomatal Conductance: Leaf transpiration and stomatal conductance were measured with a

Li-Cor Steady State Autoporometer (model LI-1600) on sunny or partially sunny days between 10:00 AM and 2:00 PM. The LI-1600 model utilizes a technique which automatically incorporates actual leaf temperature to calculate stomatal diffusive resistance, eliminating calibration difficulties. Observations were made on three leaves per tree in both clones and in all four treatments during the first and second measurement date. Only one leaf per tree was sampled during the following six measurement dates. Leaves that had been previously sampled for photosynthesis were not eligible for measurements of transpiration rate and stomatal conductance. One battery charge was enough to operate the equipment for the entire observation day. Environmental parameters such as leaf temperature, photosynthetically active radiation (PAR), and relative humidity were also recorded when measuring the second (intermediate) leaf of each tree.

The selection of measurable leaves varied between clones, since growth patterns were different. The leaves measured in the Eugenei clone were one of the first fully expanded leaves below the terminal bud, a leaf in the middle of the crown, and a leaf at the bottom of the crown not showing any signs of senescence. The Tristis clone also had three leaves measured for the first two observations, but because of its growing pattern, selected leaves were from the bulk of fully expanded and healthy ones from the middle of the crown. Observations were made in the central part of

one leaf lamina half, avoiding concentrations of large veins. After the first two observation dates, only one leaf among the first fully expanded ones below the terminal bud was measured.

Stomatal conductance values reported here are from the abaxial surface. The Eugenei and Tristis clones have stomata on both leaf surfaces, but fewer on the adaxial than the abaxial surface (Siwecki and Kozlowski 1975; Pallardy and Kozlowski 1979). The autoporometer measures stomatal diffusive resistance (sec/cm); however, its reciprocal, stomatal conductance (cm/sec), which is the most commonly used expression, was used in this study.

Leaf Water Potential: A PMS-Instruments Co. pressure chamber, which according to Boyer (1969) is probably the most rapid, simple, and accurate field method for estimating leaf water potential, was used in this study. Measurements were done at dawn (from 6:00 to 7:00 AM) and mid-morning (from 9:30 to 10:30 AM) on one leaf per tree of all replications, treatments, and clones.

An attempt to measure more than one leaf per tree was made, but because of time restrictions and the large number of measurements some adjustments were necessary. One mature and healthy leaf in the upper part of the crown was measured at dawn and another at around 10:00 AM. When photosynthesis measurements were done on the same day, they started after the mid-morning leaf water potential determination had been

completed.

Data analysis was based on a completely randomized field design. Analysis of variance was used to detect differences among treatments. When treatments means were significantly different separation was made by the Least Significant Difference (LSD). Correlation coefficients were calculated when required for further interpretation.

Results

Photosynthesis rate varied significantly between clones and there was a trend of decreasing photosynthesis with decreasing water treatments. Eugenei treatments varied significantly only at the end of the growing season (Figure 2.1). In Tristis a significant variation among treatments occurred only in the beginning of the data collection period (Figure 2.2). Photosynthesis rates attained by Eugenei were 43% higher than those attained by Tristis if all measurements are considered. Only on August 22 did the average photosynthesis rate of Tristis exceed that of Eugenei. The Eugenei irrigated treatment averages for the five observations were 31% higher than the NC treatment average, while the Tristis irrigated averages were only 11% higher than the NC average.

Tristis treatments showed constantly decreasing values of photosynthesis through time, whereas Eugenei

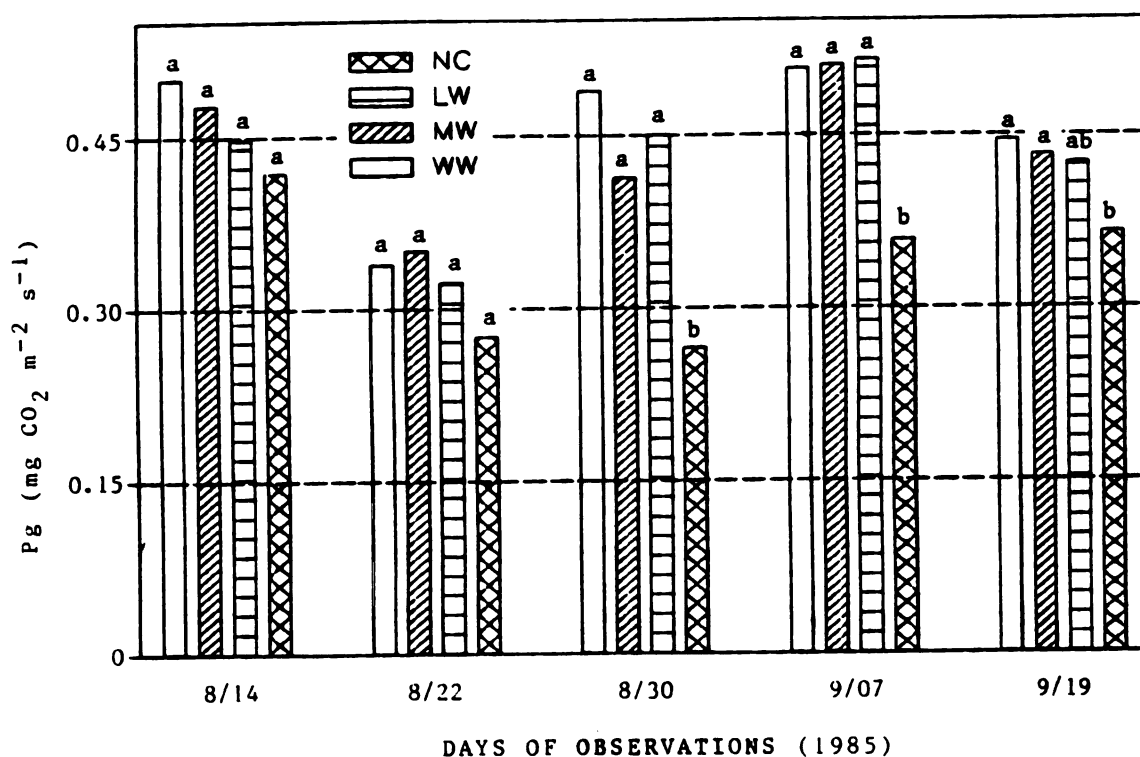


Figure 2.1. Differences among *Eugenei* treatments in estimates of photosynthesis using radioactively labeled carbon dioxide during August and September of 1985 (WW well watered; MW medium watered; LW low watered; NC natural conditions). Bars topped with the same letter are not significantly different ($p = 0.01$, LSD).

photosynthesis rates were not so affected. Eugenei photosynthesis rates varied closely about the average ($CV = 14\%$), whereas Tristis rates were more variable ($CV = 34\%$). Both clones attained more or less the same maximum photosynthetic rates, although at different dates. Minimum rates were also attained on different dates.

Eugenei showed significant differences among treatments in transpiration rates on all eight measurements dates (Figure 2.3). Tristis behaved differently (Figure 2.4); only in two observations were significant differences at the 5% level of probability detected. However, for both clones the differences do not in any way seem related to the treatments. When averages of all treatments of both clones are considered, transpiration rates of Eugenei were slightly less than those observed in Tristis.

Environmental conditions such as PAR, leaf temperature, and relative humidity measured with transpiration rate are shown in Figure 2.5. A close positive relationship between variation in transpiration rate and leaf temperature was observed; for every increment in temperature there is a corresponding increment in transpiration rate in both clones and in all treatments.

Transpiration of Eugenei varied little among replications within each treatment ($CV\% = 6.2$), resulting in significant differences among treatments at the 1% level of probability in all eight observations. Tristis was more variable between replications ($CV\% = 8.6$), so

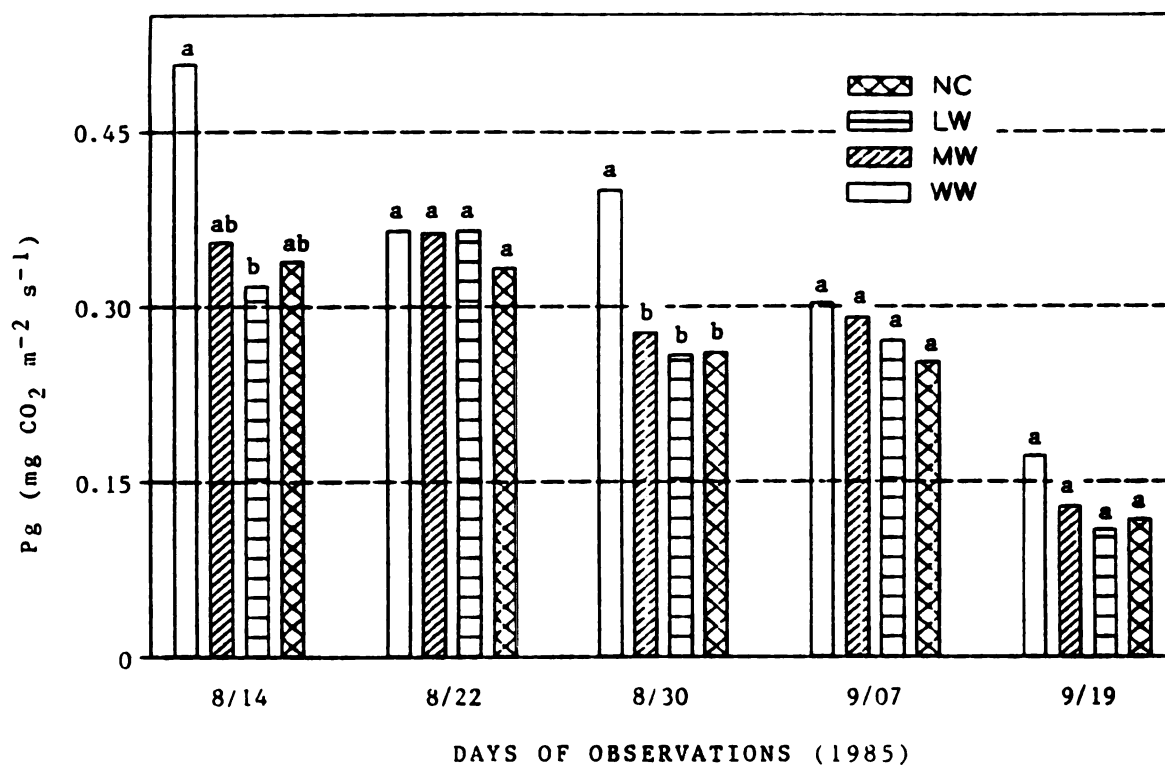


Figure 2.2. Differences among Tristis treatments in estimates of photosynthesis using radioactively labeled carbon dioxide during August and September of 1985 (WW well watered; MW medium watered; LW low watered; NC natural conditions). Bars topped with the same letter are not significantly different ($p = 0.05$, LSD).

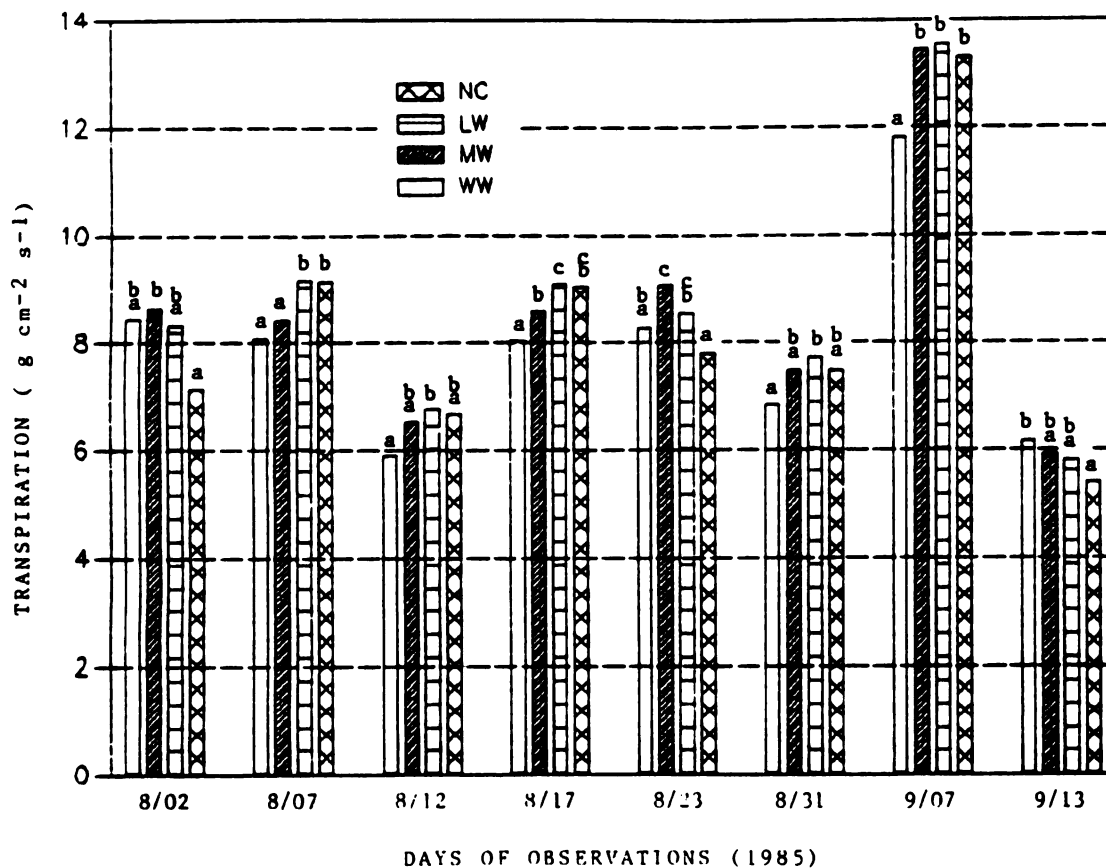


Figure 2.3. Differences among Eugenei treatments in transpiration rate during August and September of 1985 (WW well watered; MW medium watered; LW low watered; NC natural conditions). Bars topped with the same letter are not significantly different ($p = 0.01$, LSD).

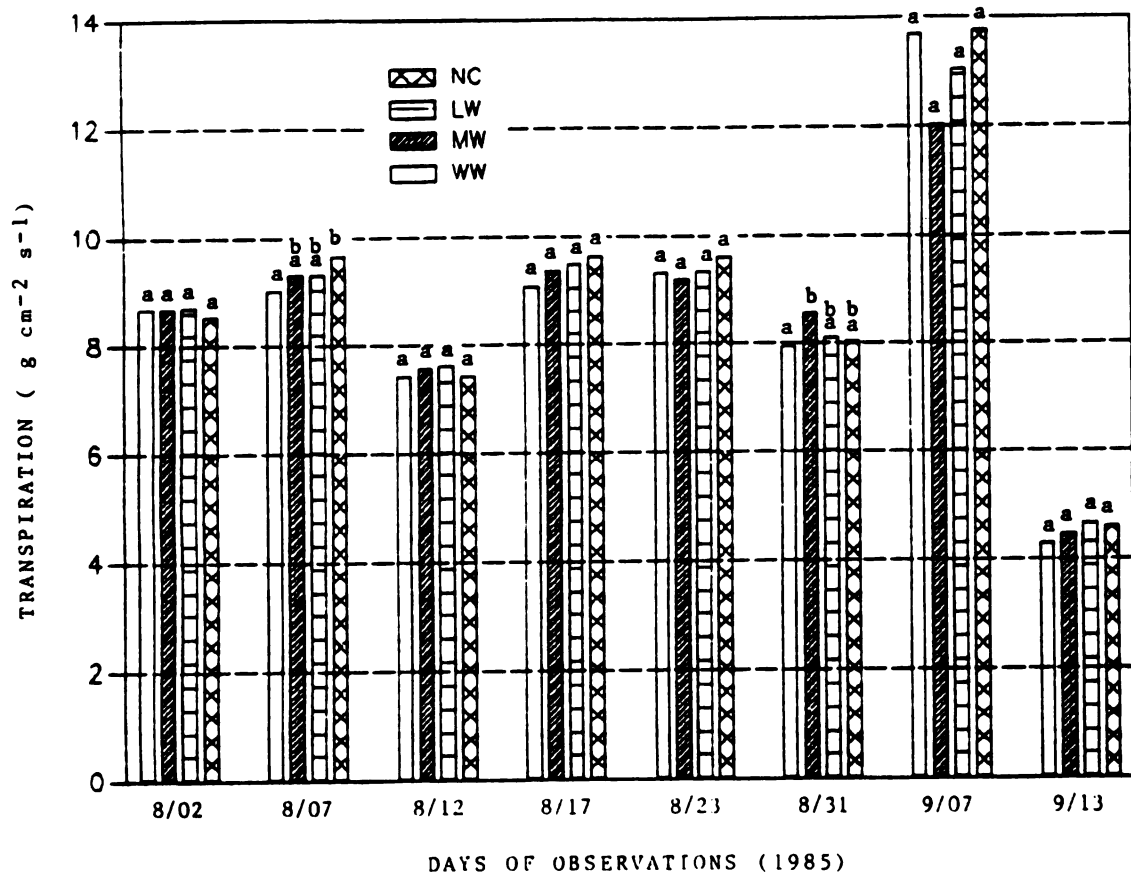


Figure 2.4. Differences among Tristis treatments in transpiration rate during August and September of 1985 (WW well watered; MW medium watered; LW low watered; NC natural conditions). Bars topped with the same letter are not significantly different ($p = 0.05$, LSD).

significant differentiation among treatments was not possible to detect.

While transpiration did not show any consistent pattern with treatment, stomatal conductance was almost always related to treatments in Eugenei, with differences at the 1% level of probability detected in all eight measurements (Figure 2.6). With the exception of the last measurement on September 13, it is apparent from the data that the more the tree is supplied with water the greater is the stomatal conductance.

Stomatal conductance of Tristis did not appear to be affected by the treatments, with all but one measurement showing no significant differences (Figure 2.7). The same pattern observed with transpiration rate was also observed with stomatal conductance; stomatal behavior was inconsistent with the soil moisture regimes. During half of the time WW treatment had higher stomatal conductance, and during the other half it had lower rates when compared to the NC treatment.

Stomatal conductance follows closely the pattern of leaf temperature (Figure 2.5) in Eugenei and Tristis. Approximately a 25% difference in stomatal conductance occurred between clones; Eugenei had an average of 0.24 cm/s while Tristis clone attained only 0.18 cm/s. Abnormally high values of transpiration observed on the seventh measurement date were also observed for stomatal conductance for both clones.

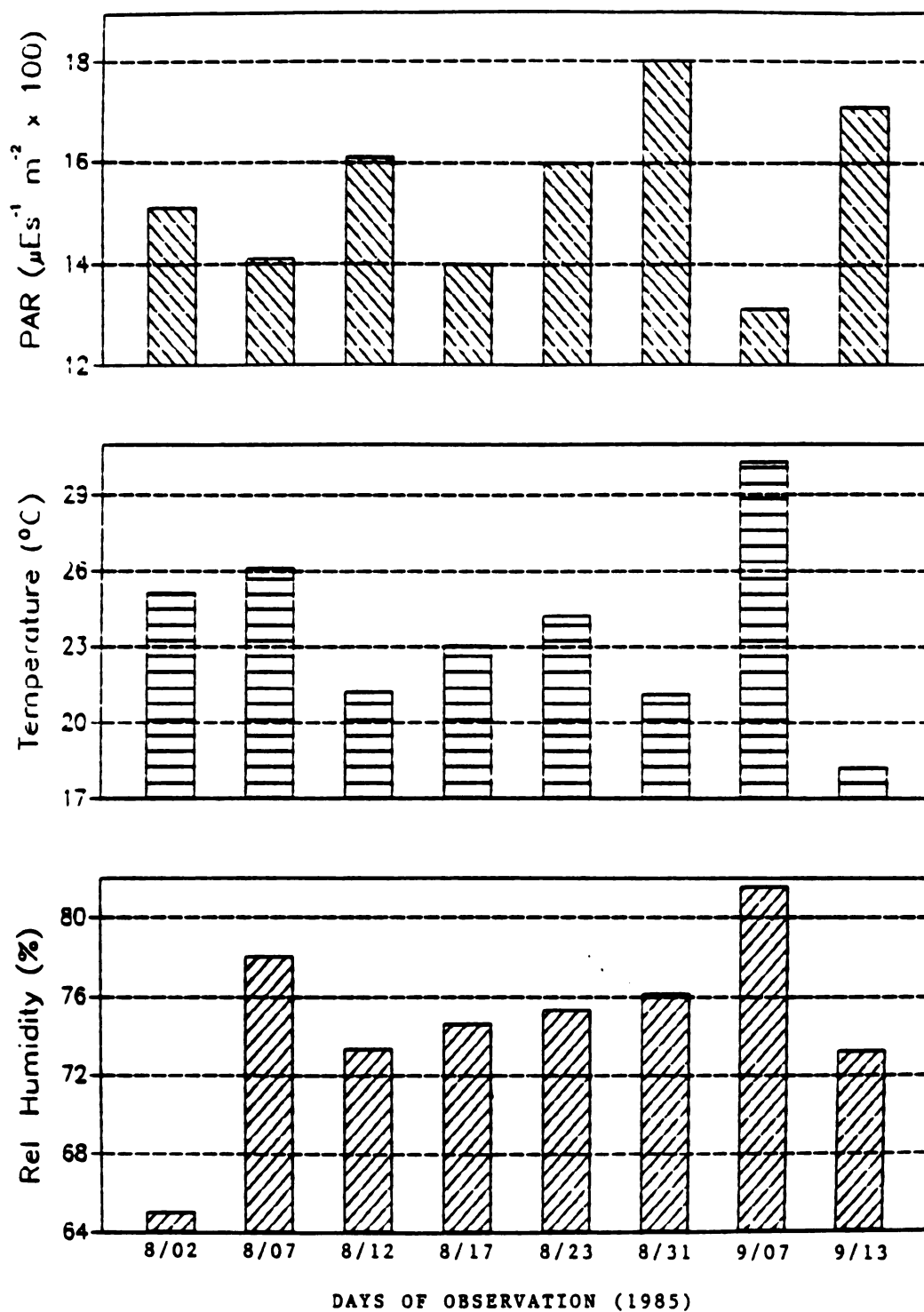


Figure 2.5. Average environmental conditions during transpiration rate and stomatal conductance measurements in August and September of 1985.

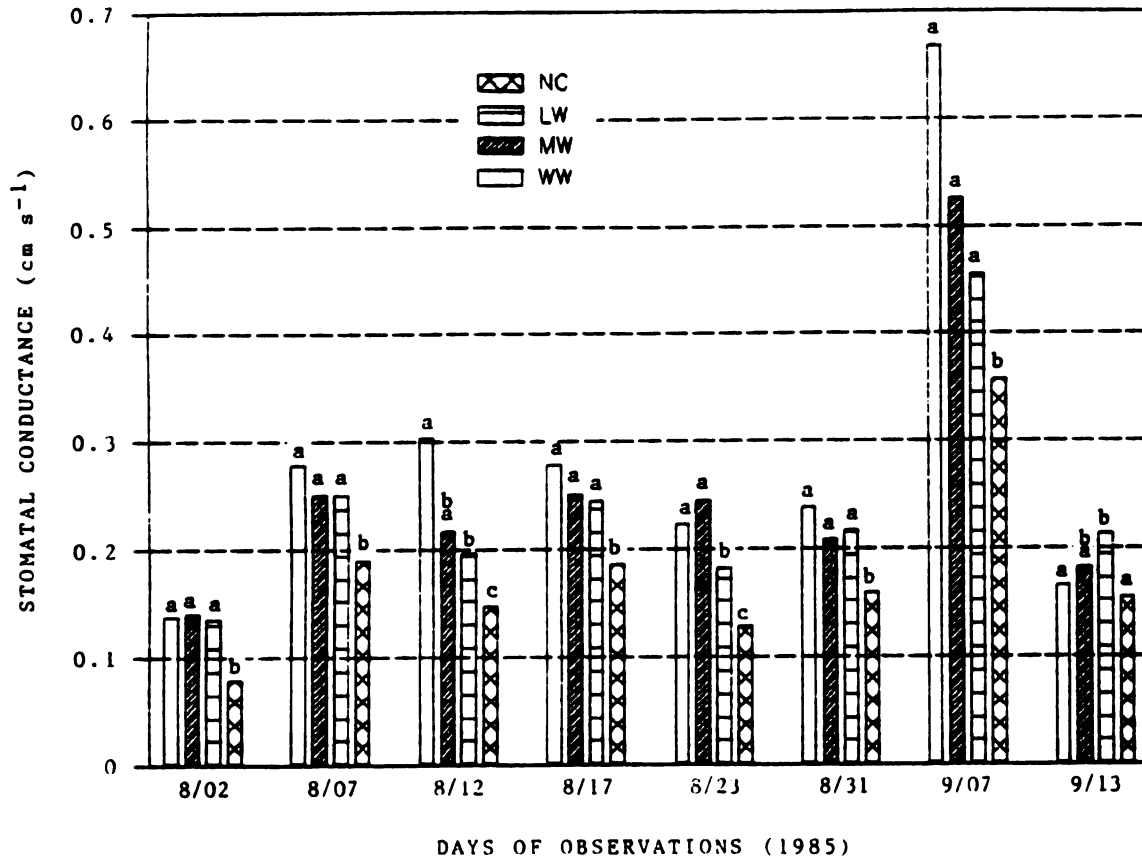


Figure 2.6. Differences among Eugenei treatments in stomatal conductance during August and September of 1985 (WW well watered; MW medium watered; LW low watered; NC natural conditions). Bars topped with the same letter are not significantly different ($p = 0.01$, LSD).

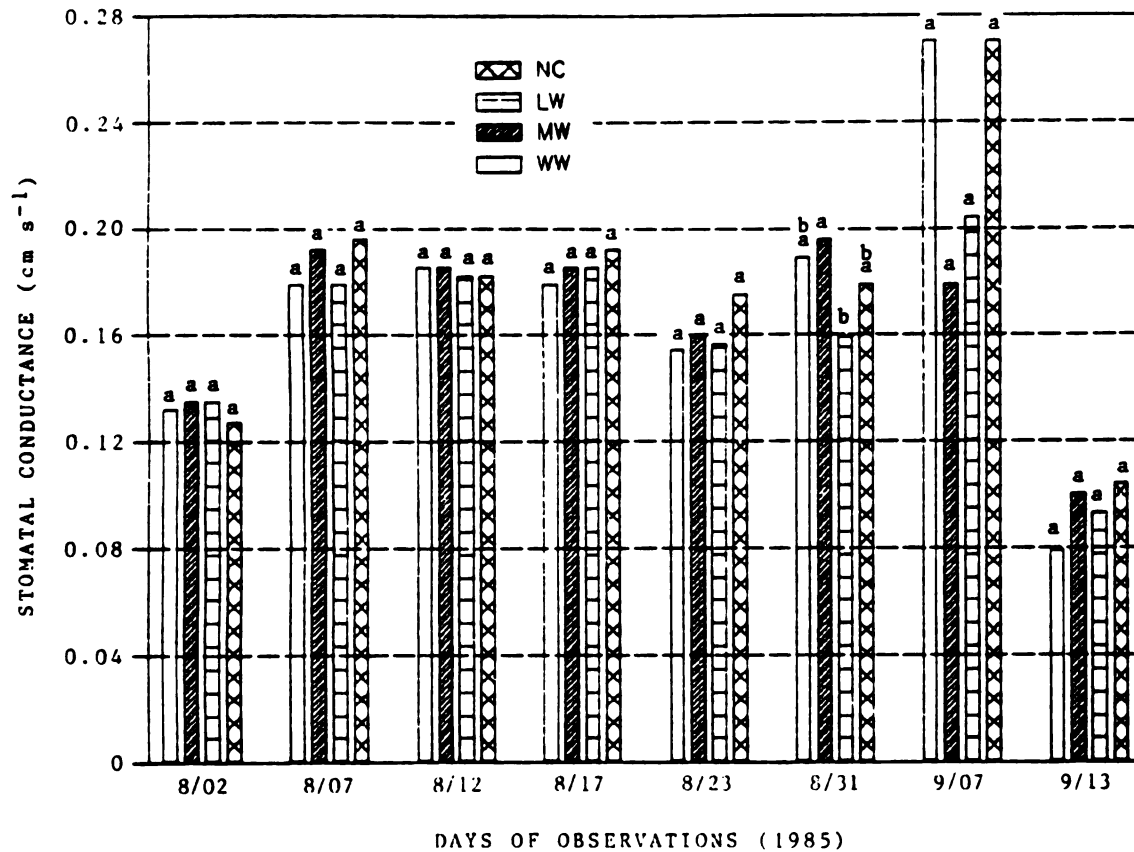


Figure 2.7. Differences among Tristis treatments in stomatal conductance during August and September of 1985 (WW well watered; MW medium watered; LW low watered; NC natural conditions). Bars topped with the same letter are not significantly different ($p = 0.05$, LSD).

Dawn water potential in Eugenei was significantly different at the 1% level of probability among treatments on four out of the six measurement dates (Figure 2.8). In Tristis only the last measurement showed any significant variation due to treatment (Figure 2.9). The Eugenei responses were always consistent with the treatments; the higher the water deficits the lower the water potential, regardless of the time of observation. While Tristis did not show a significant response of leaf water potential to soil water, there was a tendency for the LW treatment to have a lower water potential.

Mid-morning leaf water potential of both Eugenei (Figure 2.10) and Tristis (Figure 2.11) were remarkably similar. Both clones were affected by the treatments when measured at approximately 10:00 AM. Water potential values at mid-morning have the same pattern of variation in both clones, but Eugenei generally showed higher water deficits. The general average for Tristis was approximately -0.8 MPa while for Eugenei the average was -1.2 to -1.3 MPa. The lowest value attained by Tristis was -1.1 MPa and by Eugenei -2.5 MPa. Tristis also had the highest values when compared to Eugenei. As a general trend, Tristis was less variable and showed lower water deficits than Eugenei.

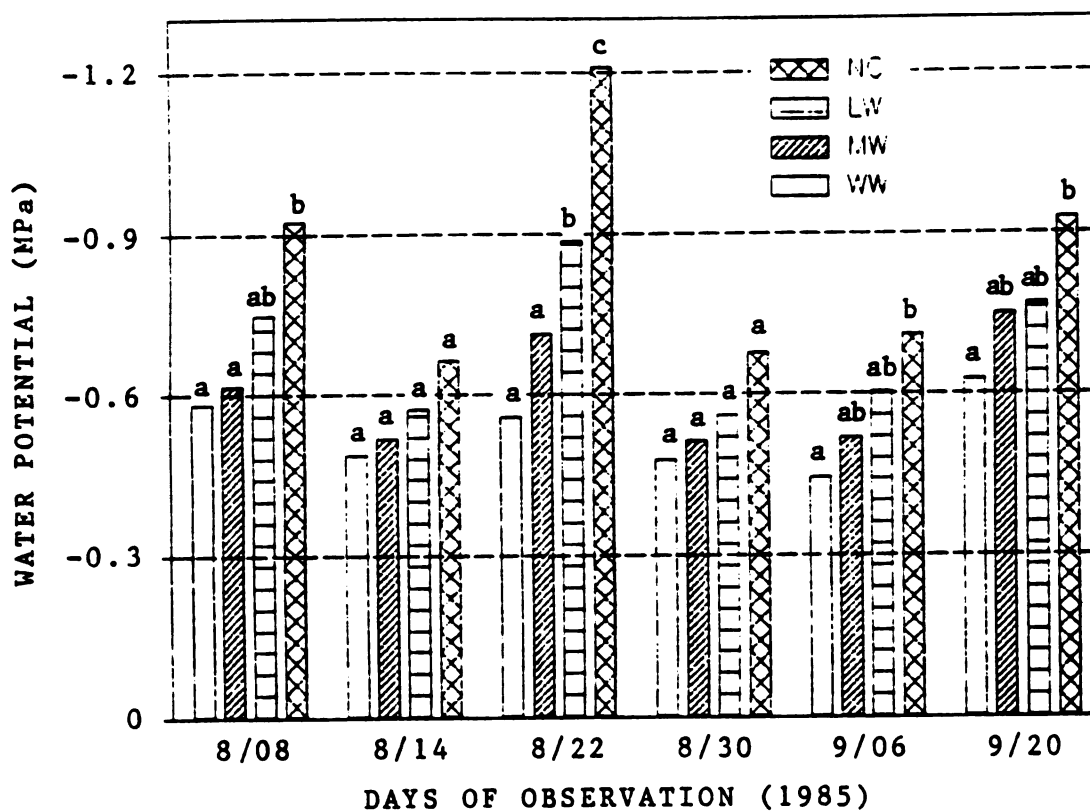


Figure 2.8. Differences among treatments in leaf water potential obtained before sunrise for Eugenei during August and September of 1985 (WW well watered; MW medium watered; LW low watered; NC natural conditions). Bars topped with the same letter are not significantly different ($p = 0.01$, LSD).

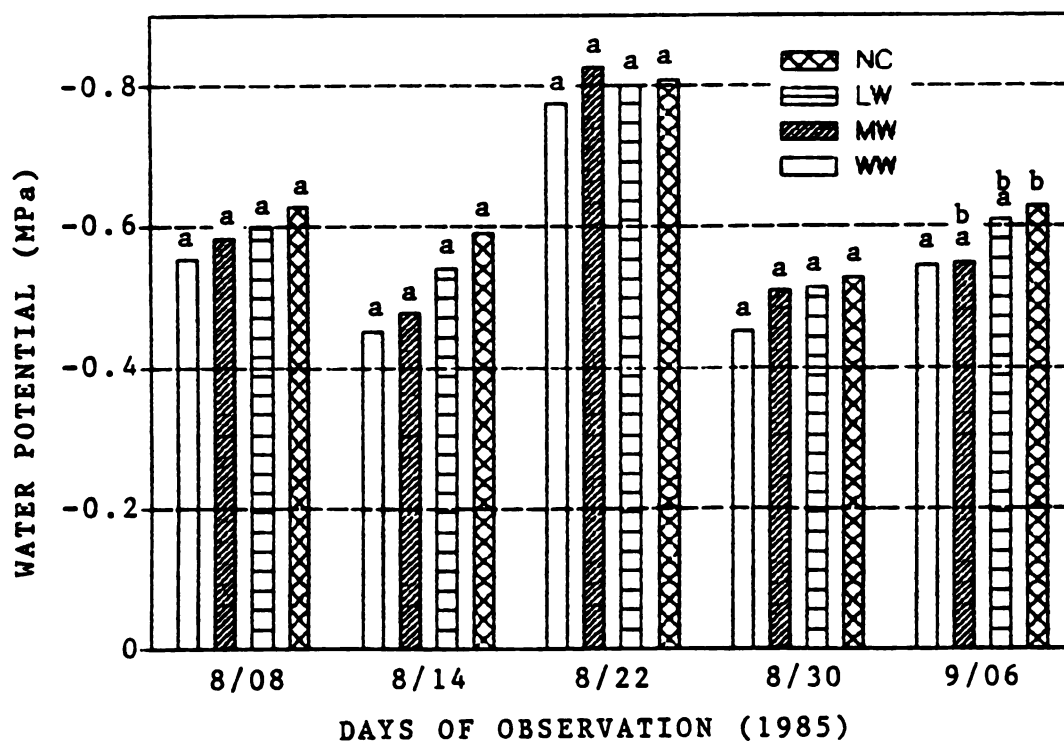


Figure 2.9. Differences among treatments in leaf water potential obtained before sunrise for Tristis during August and September of 1985 (WW well watered; MW medium watered; LW low watered; NC natural conditions). Bars topped with the same letter are not significantly different ($p = 0.01$, LSD).

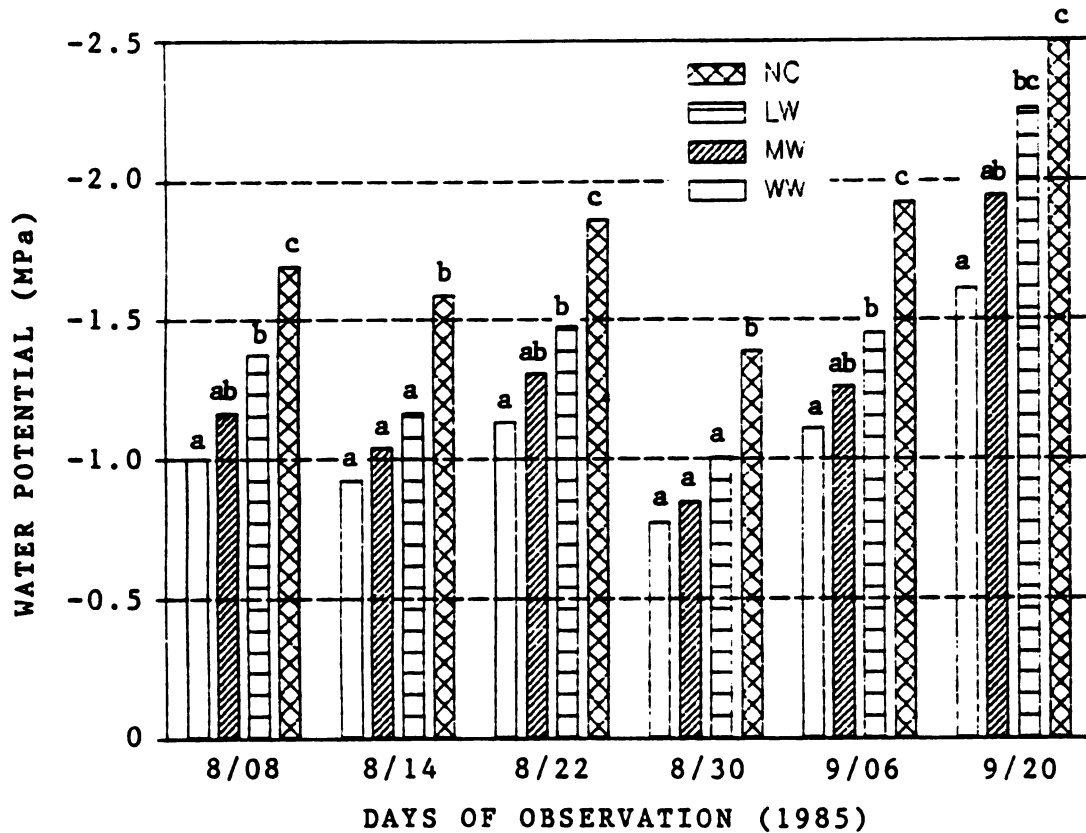


Figure 2.10. Differences among treatments in leaf water potential obtained at 10:00 AM for Eugenei during August and September of 1985 (WW well watered; MW medium watered; LW low watered; NC natural conditions). Bars topped with the same letter are not significantly different ($p = 0.01$, LSD).

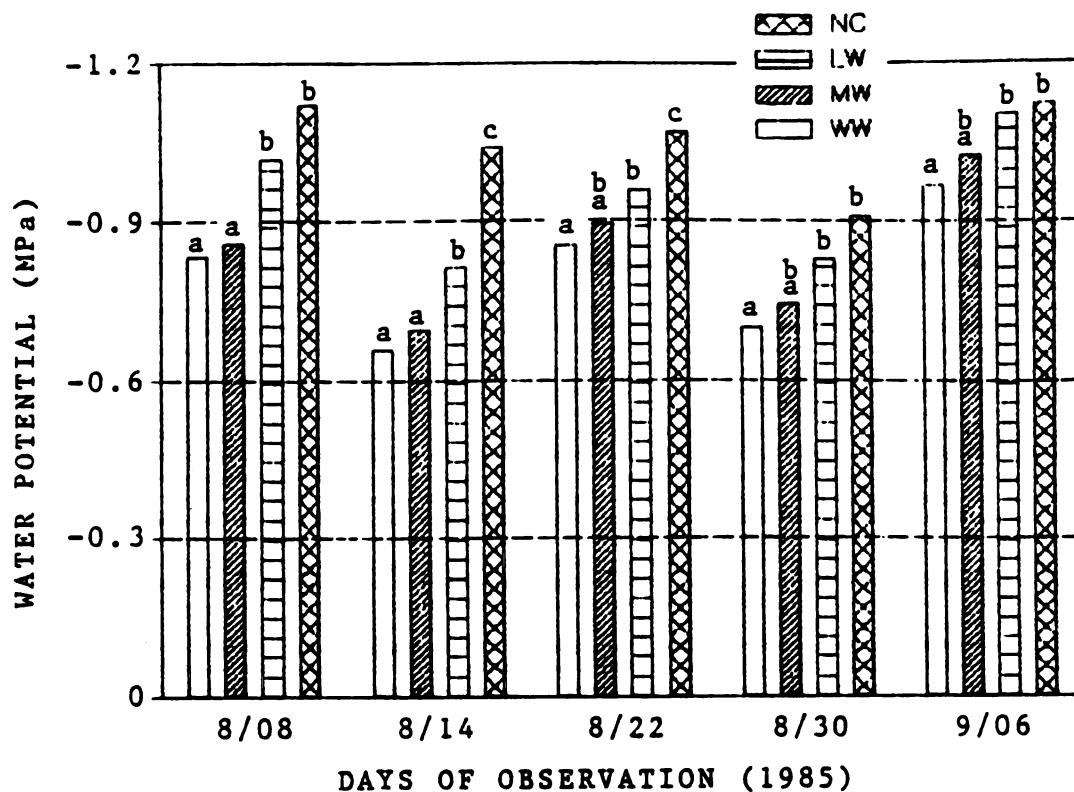


Figure 2.11. Differences among treatments in leaf water potential obtained at 10:00 AM for Tristis during August and September of 1985 (WW well watered; MW medium watered; LW low watered; NC natural conditions). Bars topped with the same letter are not significantly different ($p = 0.01$, LSD).

Discussion

The negative effects of water deficit on photosynthesis rate of hybrid poplar are well known (Domingo and Gordon 1974; Smith and Gatherum 1974; Regehr et al. 1975). Also well known is the variability in the responses among hybrids and clones (Ceulemans and Impens 1980; Ceulemans et al. 1980). Eugenei is a hybrid from Populus deltoides, a species physiologically very sensitive to water stress (Regehr et al 1975). Photosynthesis, stomatal conductance, and transpiration are substantially modified by drought in this clone. Tristis, on the other hand, is a clone adapted to drier conditions (Isebrands et al 1983). This basic difference between Eugenei and Tristis in response to water deficit was reflected in the behavior of the physiological parameters measured in the field.

The variation in photosynthesis rate in Eugenei was related to soil water content, as indicated by water potential before sunrise; high photosynthetic values were associated with low values of leaf water potential. The lowest photosynthetic values of Eugenei occurred during a day when the highest leaf water deficits before sunrise were observed (August 22). Mid-morning leaf water potential did not show a relation with photosynthesis rate, although mid-morning leaf water potential was very consistent with the soil water regime. There was also a close relation between

photosynthesis rate and stomatal conductance in the Eugenei treatments. Larcher (1980) suggested that the most important factor that regulates photosynthesis under a critical leaf water potential is stomatal movement.

There was no relation between the pattern of photosynthesis and the pattern of stomatal conductance in Tristis. Some studies (Chatier et al. 1970; Jones and Slatyer 1972; Samsuddin and Impens 1978; Ceulemans and Impens 1980) have indicated that the most significant components of the total leaf resistance to carbon dioxide diffusion could be the internal resistances. O'Toole et al. (1977) found that increases in carboxylation and mesophyll resistance may also be non-stomatal factors which mediate reduction in photosynthesis and transpiration. Ceulemans and Impens (1980), while studying several poplar clones, found great variability between stomatal resistance (R_s) and internal resistance (R_i) to carbon dioxide. Ratios from 2.5 up to 23.5 of R_i/R_s were observed, suggesting that there is difference in the degree of importance of stomatal control over gas exchange.

Stomatal movement in Tristis apparently had little or no effect on photosynthetic carbon dioxide uptake, even though it affected transpiration rate. Morphological and anatomical leaf differences affect internal resistances to carbon dioxide diffusion. Ridge et al (1986) studied leaf growth characteristics of fast growing hybrid poplars and their parents. They found that the hybrids have a greater total

leaf area because they had larger leaves than the parents due to either larger cells or large cell number per leaf. The thinner and more succulent Eugenei clone leaves may offer a smaller resistance (small R_i/R_s ratio) to carbon dioxide diffusion from the ambient air to the reaction sites in the chloroplasts (Holmgren et al 1965), making stomatal resistance more important for gas exchange. In Tristis stomatal resistance to gas exchange may be small compared to internal resistances (high R_i/R_s ratio). In such a case, varying stomatal conductance may have little effect on the rate of carbon dioxide fixation, but be efficiently affecting transpiration rate.

The photosynthesis rates obtained in this study were similar range to previous studies. Photosynthesis averaged 0.42 and 0.29 $\text{mg CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ in Eugenei and Tristis, respectively, over the period of August 14 to September 19. Photosynthesis rates obtained using RLCD and compared to the IRGA technique were found to be 5% (Michael 1984) and 8% (Nelson et al. 1982) higher than net photosynthesis. Average net photosynthesis in this study reduced by 8% would be 0.39 and 0.27 $\text{mg CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ while maximum net photosynthesis rates observed were 0.58 and 0.64 $\text{mg CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ for Eugenei and for Tristis, respectively, rates which are comparable to other studies. Field-grown Populus deltoides leaves measured under laboratory conditions had net photosynthesis ranging from 0.29 to 0.86 $\text{mg CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ (Regehr et al. 1975; Drew and Bazzaz 1979).

Dickmann et al (1975) reported a maximum net photosynthesis of $0.4 \text{ mg CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ in individual leaves of hybrids of P. x euramericana grown in a growth chamber. In a study done with several different poplar hybrids grown in a growth chamber, individual leaves showed net photosynthesis rates ranging from 0.17 to $0.53 \text{ mg CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ (Ceulemans et al. 1980).

When photosynthesis rate is expressed in units of leaf weight, the difference between Eugenei and Tristis clones become greater. The leaf area ratio of Tristis was 0.0062 g/m^2 compared to 0.0054 g/m^2 for Eugenei, values that are similar to other values observed by Nelson and Ehlers (1984). When averaged for the entire period of measurements are considered, Eugenei clone showed a 43% higher rate of photosynthesis per unit of leaf area than Tristis. If photosynthesis is expressed on a leaf weight basis, the average photosynthetic capacity of Eugenei was 65% higher than that of Tristis.

The general trend of declining photosynthesis through time in Tristis was expected since a visual senescence process started in the beginning of September and concluded by the end of September. Eugenei maintained high levels of photosynthesis because its foliage stayed healthy up to the last measurement. Total leaf shedding in Eugenei did not occur until October 20 in the WW treatment. Autumnal photosynthesis in several poplar clones continues until hard frost kill the leaves and contributes to late-season plant

growth and build-up of reserve pools (Nelson et al. 1982; Isebrands et al. 1983).

Control of water deficit is accomplished in three ways by a plant: increased absorption, decreased transpiration, and/or internal redistribution (Kozlowski 1968; Hall 1981). Water losses are commonly shown to be effectively reduced mainly by stomatal closure (Barrs 1968; Slatyer and Lake 1966; Allerup 1960; Shimshi 1963; Kramer 1983), although, some studies (Darlington and Cirulis 1963; Yamada et al. 1964; Pallas and Bertrand 1966) show that large amounts of water can be lost after hydroactive stomatal closure has occurred. Cuticular transpiration, the second possible main route for water losses, has been investigated for several plants and ranges from 10 to 90% of total transpiration (Crafts 1968). Variation in how these two loss-routes account for the total transpiration is determined by many factors among leaf age, morphology, anatomy and stomatal functionability.

Stomatal sensitivity to leaf water potential may be an adaptation of clones such as *Eugenei* that enables it to maintain a large leaf area without losing an excessive amount of water under light drought conditions. The influence of the vertically oriented leaf disposition of *Eugenei* would reduce light interception, effectively minimizing irradiation stress (Michael 1984) and consequently reducing transpiration rate.

Eugenei appeared to have weaker stomatal control of

transpiration rate than Tristis. Correlation coefficients between transpiration rate and stomatal conductance (Tristis ' r '= 0.81 and Eugenei ' r '= 0.71) reinforce the above conclusion. Transpiration rate and stomatal conductance in Tristis do not correlate with the leaf water potential or the modified soil moisture regime, whereas for Eugenei transpiration rate is inversely correlated with leaf water potential.

Considering the above, it appears that plants with an impermeable cuticle will show a greater dependence of transpiration rate on stomatal movement (Burrows and Milthorpe 1976). Then, such plants should have an apparent relation between stomatal condition and water status. However, even though Tristis had a lower stomatal conductance than Eugenei, it transpired at a higher rate. Even with higher transpiration rates, its water deficit did not increase at mid-morning measurements. Jordan and Ritchie (1971) found that transpiration of stressed cotton plants was maintained at a high rate despite a soil drought, perhaps due to an extensive root system. The same explanation may well fit the case of Tristis trees. Results from Chapter 3 indicate that Tristis trees under natural conditions treatment grew a larger and more branched root system.

Stomatal function is affected by environmental factors such as light intensity, CO_2 concentration, vapor pressure deficit gradient, leaf temperature, leaf water potential and

other internal factors (Allaway and Milthorpe 1976; Elving et al. 1972; Hsiao et al. 1973; Mansfield and Jones 1971; Pallas and Wright 1973; Raschke 1972 and 1975; Watts 1977). Prediction of stomatal behavior based on environmental factors could have, for some species, a practical use when studying plant water relationships, photosynthesis, and transpiration. However, a general field relation between stomatal behavior and the environment has not yet been clearly identified, possibly due to the multi-environmental effects (light, leaf water potential, air humidity, leaf temperature, carbon dioxide concentration, and endogenous substances) and interdependent-physiological reactions (photosynthesis, respiration, and transpiration rates) (Hall et al. 1976; Itai and Benzione 1976).

The relationship of stomatal movement to leaf water potential is not always clear. Pallardy and Kozlowski (1979) found under certain unclear situations stomatal resistance increased with a reduction of water deficit, probably due to other factors overriding the effects of leaf water potential and stomatal aperture. Furthermore, stomatal response to water deficit may only occur after certain levels of stress have been reached (Dale 1961), or stomata may not open promptly or as wide after severe water stress is relieved (Iljin 1957). Barrs (1968) considered the complexity of stomatal control and concluded that initially stomatal activity is affected by internal and external factors, but when stress progresses and becomes severe, water overrides

everything else and becomes the main factor. Barrs recommends the use of another more accurate parameter than stomatal aperture to measure plant water status.

No significant differences in transpiration rate or stomatal conductance among leaves from various crown positions in my study could be detected in trees of the same treatment. Stomatal conductances, although variable among different leaves and shoots of Tristis, were also not different statistically in a study reported by Nelson and Michael (1982). Drew and Bazzaz (1979) found that stomate ability to function appears to be unaffected by leaf senescence. In the present study leaves from the top, middle and bottom of the crown had similar values and followed the same pattern for the first and second observation date. Thus, the six following measurements of both transpiration rate and stomatal conductance were done on only one mature leaf.

Although leaf water potential reflected perfectly the soil water regime in almost all treatments in both clones, its effect on physiology and growth was variable. Tristis height and diameter growth (see Chapter I), transpiration rate and stomatal conductance were not significantly affected by treatments and their respective leaf water potentials. Smith and Gatherum (1974), studying several aspen-poplar hybrids in controlled environment, found that increases in soil moisture (from -1.5 to -0.03 MPa) were accompanied by increases in, among other variables,

photosynthesis and stomatal conductance. Such responses were clearly observed in Eugenei treatments, but not so in those of Tristis.

Dawn leaf water potential of Eugenei did not indicate an overnight recovery of turgor on the least irrigated and NC treatments to the same levels as the heaviest irrigation treatment, whereas Tristis apparently was able to recover from the daily water deficit in almost all cases. Even with a higher transpiration rate than Eugenei, water was supplied to Tristis leaves at a rate that brought the leaf water potential of all treatments to the same level. Sucoff and Heisey (1978) implied that dawn leaf water potential is better related to height growth than readings made at 1:00 PM, and in this study the same relationship was observed for both clones.

Eugenei apparently is a hybrid that does not exert an effective control over water deficits. Every physiological process I measured was reduced as water availability declined. Since Eugenei is a clone sensitive to water stress, transpiration rate, stomatal conductance and photosynthesis, all processes leading to plant growth, were reduced in each treatment. When water deficit reached extremes, plants from the non-irrigated treatment began to shed leaves and set bud (see Chapter 1) in order to cope with drought. Tristis was, however, able to exert control over water deficit by increasing internal water supply. This clone is drought tolerant and maintained more or less the

same level of physiological activity and growth (see Chapter 1) regardless of the treatment. The non-irrigated Tristis plants were often completely relieved from water stress during night because these plants developed a larger and intense branched root system (see Chapter 3).

The methods for field evaluation of photosynthesis using radioactive-labeled carbon dioxide (RLCD) are fast and minimally disturb or change the environment surrounding the leaf as compared to the infrared gas analysis (IRGA) method (Incoll and Wright 1969; Shimshi 1969; McWilliam et al 1973; Incoll 1977). The RLCD technique does present some problems, though. An important disadvantage is that dark respiration cannot be measured. Possible sources of error are physical and chemical discrimination against $^{14}\text{CO}_2$ at mesophyll diffusion and carboxylation sites (Van Norman and Brown 1952; Incoll 1977), dilution of $^{14}\text{CO}_2$ by the CO_2 evolved from respiration (Incoll 1977), and photorespiration of $^{14}\text{CO}_2$ already fixed (D'Aoust and Calvin 1972).

Results of controlled environment and field measurements showed that results from RLCD were to be quite similar to those obtained by IRGA (Biscoe et al. 1977; Austin and Longden 1967); it often slightly underestimates gross photosynthesis (Nelson et al. 1982; Michael 1984). In this study, the RLCD method proved to be advantageous because it provided the large number of measurements and replications necessary to compare treatment and clonal effects on photosynthesis. New and more sophisticated IRGA

portable equipment is now available and possibly will eliminate the use of the radioactive-labeled carbon dioxide technique for field evaluation of photosynthesis.

CHAPTER III - FINE ROOT DYNAMICS

Introduction

Productivity can be defined as the amount of carbon fixed in the form of organic matter in a period of time. Even if not always considered, the below-ground growth of roots, mainly root depth and density, is part of and often controls productivity (Cowan 1965; Bohm et al. 1977). Observation of a plant root system growing in a natural environment is complicated because it is shielded from view by the soil matrix. Thus, one of the most inadequately understood components of primary productivity is the growth, development, and death of roots.

Morphological and physiological functions undoubtedly vary within the root system of a tree species. A tree root system presents a continuous integration of morphological and functional characteristics, thus any classification based on size is arbitrary (Leshem 1965; Ford and Deans 1977). Although size classification may be arbitrary, it is very useful in studies of perennial plants. A tree root system can be divided into structural roots and fine or feeder roots, the latter being most responsible for the absorption of water and nutrients (Lyr and Hoffman 1967;

Trappe and Fogel 1977).

Variation in the root system among species is a well known fact. Morphological characteristics as well as physiological functions such as absorption of nutrients may also vary in sources or ecotypes (Gardner 1960; Jahromi et al. 1976a; 1976b). Brown (1969) found differences in the development of primary and secondary roots of various Scotch pine sources. Van Buijtenen et al. (1976), studying loblolly pine sources, concluded that dry-zone sources had a deeper and wider root system than the wet-zone sources. Respiration rate, as well as other physiological functions, was found to be significantly different among shortleaf pine sources (Allen 1969). Faulkner and Fayle (1978) and Gordon and Promnitz (1976) rationalized that there are many differences in root development (branching, growth, length, etc.) amongst poplar clones, while Farmer (1970) reported that there were genetic differences in the root:shoot ratio among 30 cottonwood clones investigated. Medve (1970) found differences among 8 sources of red maple in fine roots rather than in the first order roots. He suggested that more attention should be directed to fine roots rather than to gross root morphology.

It was suggested that fine roots could be those up to 3 mm in diameter (Moir and Batchelard 1969). Fine roots can also be further categorized as fine roots of rapid turnover rate, and fine roots that will undergo secondary thickening. Not using an arbitrary diameter classification may lead to a

false idea and interpretation of the root system; e.g., equal root masses can be achieved by a multi-branched fine root system or by a sparsely branched coarse root system.

In large trees fine roots represent a small part of the total dry biomass at a given time. However, because of their high turnover rate, the fine root budget may represent more than 50% of all carbon fixed per year (Agren et al 1980; Grier et al. 1980). Knowledge about the magnitude of below-ground turnover is of special importance with respect to quantitative carbon balance, but also reveals the adaptive implications of an ephemeral yet profuse component of the root system.

Many environmental, genetic, and physiological factors influence root growth, distribution, morphology, and longevity (Cadwell 1976; Atkinson 1980). Root growth cycles are variable according to species, and may or may not be related to shoot growth (Ford and Deans 1977; Kummerow et al. 1978) or to the level of photoassimilates (Zaerr et al. 1973). Roots can grow in early spring (Morrow 1950; McClaugherty et al. 1982), during hot and dry summers in Israel (Leshem 1965), and/or during late fall when cold conditions have induced shoot dormancy (Head 1973).

Water excess or deficits greatly affect the development and functions of the root system (Bryant 1934; Kramer 1951 and 1983; Kawase and Whitmoyer 1980). Deficits of water directly affect growth rate, suberization of root tips, and reduction of absorptive capacity (Newmann 1966; Kaufmann

1968), but most of our knowledge in this area is from fruit trees and annual crops (Beukes 1984; Meyer and Barrs 1985; Layne et al. 1986). Fewer studies of the effects of water availability on root growth have been done forest trees and results also have indicate the same general negative influence of water on root development in either excess or deficit (Leshem 1965; Kaufmann 1968).

Knowing the rates of death, decay, and regeneration of new roots over a time period, and how every process is controlled, are important steps towards understanding the entire physiological process of carbon allocation. An increase in the life time of fine roots suggests that large amounts of fixed carbon may be directed: instead of going belowground to fine roots it could go above ground to boles. Consequently, the possibility of manipulating factors which determine the life-span of fine roots is of great physiological silvicultural. Torrey (1976) concluded that "manipulation of the root system, of its size and shape and physiology, by genetic means together with selection and field testing, offer an almost unexplored avenue to the improvement of plant growth and productivity."

Studies of root systems in the past have been accomplished by various methods (Bates 1937; Upchurch 1951; Bennett and Doss 1960; Melhuish 1968 Melhuish and Lang 1968; Rogers 1968a; Aycock and Mckee 1975; Bohm et al. 1977; Bohm 1979; Gregory 1979; Richards 1984; Itoh 1985). Excavation *in situ*, growing plants in special containers, soil coring,

trench profiles, underground chambers (rhizotron), and transparent tubes (minirhizotron and microrhizotrons) are some of the most commonly used methods.

Destructive methods present some disadvantages since they are time consuming and demand the eventual separation of live roots from other organic matter (Russel 1977). With the exemption of rhizotrons, these methods do not allow measurements to be repeated at any particular location, with temporal variation being confounded with spatial variation. Rhizotrons also allow growth, longevity, and decay of a particular fine root to be monitored at almost any time interval (Sanders and Brown 1978; Upchurch and Ritchie 1983 and 1984; Van Noordwijk et al. 1985). However, non-destructive methods also present some disadvantages, the worst being that the glass or plastic of an observation window or tube creates an artificial interface and displacement of roots (Itoh 1985). The negative effect is that root growth is promoted in the soil-glass or soil-plastic interface in comparison to the bulk soil (Taylor and Bohm 1976; Voorhees 1976; Bragg et al. 1983), overestimating root distribution and root density. Each method has distinctive advantages and disadvantages that should be addressed, keeping in mind the specific objectives of the experiment (Bohm et al. 1977).

Minirhizotron tubes, a color microvideocamera, and a video recording system was the chosen method for this study due to various reasons. A study of perennial plants must be

done during all phases and seasons of plant growth and the minirhizotron image recording technique appears to be a very promising way of accomplishing this. Another advantage of the method is that it allows for fast and frequent observations of many replications under natural soil and environmental conditions.

The objective of the present study was to observe fine root growth, longevity, and morphology (branching) of two physiologically contrasting poplar clones growing under two different soil moisture regimes. As a pionner study of forest tree roots with minirhizotrons and a video recording system, particular aspects of the use and limitations of the technique will be reported and discussed.

Materials and Methods

The present research was carried out using the same field experiment described in Chapter I. Only the extreme treatments, i.e., well watered (Eugenei well watered - Eww and Tristis well watered - Tww) and natural conditions (Eugenei natural conditions - Enc and Tristis natural conditions - Tnc) were subject to fine root observations. Four minirhizotrons around two trees of each clone were installed during September of 1985 (see Figure 1.1). However, image recording started one year later, due primarily to unavailability of the required equipment.

Minirhizotrons were 90 cm long tubes of butyrate

plastic, 5.1 cm in diameter. The bottom of each tube was air-tight, sealed with a rubber stopper and silicone glue. The 20 - 25 cm left above-ground was spray painted black first, to prevent light from reaching the roots, and then white to reflect heat, and temporarily sealed with a rubber stopper. Each minirhizotron was installed vertically, the first was placed at 30 cm from the tree stem at 90 degrees (west), the second at 60 cm and 135 degrees, the third at 90 cm and 180 (south) degrees and finally the fourth at 120 cm and 225 degrees (Figure 3.1).

Field installation of tubes was accomplished by manually extracting a soil core with a improvised auger. Aluminum pipe augers had to be constantly repaired and sharpened and with the help of a hammer they bored a 70 - 80 cm deep hole slightly smaller than required for a minirhizotron. Most of the minirhizotrons were placed at the maximum depth (70 - 75 cm) but some, because of stones and hard clay, could not be placed that deep. The correct diameter hole was produced using a sharp-edged old minirhizotron tube manually pushed in the hole as a reamer. After a circular wire brush was used to roughen up the sides of the hole and remove any smeared soil, the plastic tubes were slipped in.

The effect of the soil-plastic interface was minimized by insuring that no compaction occurred when tubes were installed. Small gaps between the tube and bulk soil, mostly in the upper 20 cm layer, were filled with the same soil



Figure 3.1. Field installed minirhizotrons at 30 cm intervals in one of the Eugenei well watered treatment trees.

which had been removed from the top portion. After the first rain more soil was placed around the tubes, which helped to form a satisfactory minirhizotron bedding. Extra care was taken to assure that the soil adjacent to the tubes was similar in all properties to the bulk soil surrounding the minirhizotrons.

Constant attention was given to weed control prior to and during the image collecting period. The weed control method was similar to the one described in Chapter I, except that it was applied at shorter intervals, soon after the first small weed plants were spotted. The area adjacent to

the minirhizotrons had to be completely weed-free because of the practical impossibility of differentiating poplar fine roots from weed roots.

Images were recorded with a portable, battery-operated color microvideo camera (Circon MV-9011), 4.8 cm in diameter and 44 cm in length. The camera was modified to include a right angle lighted objective, lenses and a prism, providing a 20 mm wide x 12 mm high field of view. Lighting was provided by four incandescent lamps (3 W and 12 V), two on each side of the prism. Camera control was through a Circon Color Bore Inspection System model MV-9380. The entire optical system was lowered into the minirhizotrons using a calibrated aluminum rod. The rod was marked at approximately 12 mm intervals in order to have slightly overlapping images.

Steady two to three second images were recorded on a Panasonic VHS video cassette recorder model NV-8420 while being monitored with a small 3 x 2 cm Hitachi black and white monitor. Batteries when fully recharged last for one day of recording and monitoring. The VCR, batteries, monitor, and camera controls were assembled in a storage box mounted on a two wheeled frame.

The equipment was used under harsh conditions of variable humidity, high temperature, and much dust. High temperatures were the worst problem encountered for the VCR. Darker images were obtained during observation days with high temperatures. A security circuit shut down the VCR many

times when mid-day temperatures were high, stopping the work for half an hour each time.

Minirhizotron images were taken weekly on 11 occasions from the middle of August to the beginning of November. Due to numerous problems, primarily equipment failure, the three first observations could not be used. Recording was made on four faces of each minirhizotron in a predetermined order of both faces (north, east, south, and finally west) and tubes.

Image recording took approximately four hours when everything was working properly. Image processing (data collection) was done in the laboratory using a portable Curtis Mathes VCR model JV 7731 and a regular 19' color television. A transparent plastic grid placed over the television screen helped in data collection. The grid, equivalent to 0.5 x 0.5 mm, was made based on a minirhizotron image of a metric scale projected on the television screen. Laboratory work was very time demanding and tedious, since field observation produced approximately 3,200 individual images each day. Although most of the images had no signs of roots or root growth, some time had to be spent on them.

The following root parameters were observed and recorded in each image containing fine roots (up to 3 mm in diameter): root diameter, number of roots oriented in an angle greater than 45 degrees (vertical roots - VR) and number of horizontal roots (HR). If a root branched while intersecting the minirhizotron it was counted as a root and

each branch was counted also as a root. When root tips were observed, then root length was recorded. Branching pattern, color, brightness, appearance and death were also aspects observed in each image. Damage from organisms and total disappearance of fine roots were rarely observed.

The video quality was good enough to identify and count roots greater than 0.03 mm in diameter when lighting and contrast were at the best. The color image on a regular television produced a sufficiently sharp picture to differentiate old and new roots from a convenient 3.5 m viewer distance. The old roots were a distinct light brown to caramel color, some with darker areas of shed rhizodermis (see Figure A1 in Appendix). The new roots were a bright white, sometimes transparent, or with a dark cream central cylinder, and very sharp edged. Dead roots were also, after some training, possible to identify mainly due to the aspect and color. Dead roots were a homogeneous brown color, clearly without brightness and without a sharp edge (see Figure A2 in Appendix). The use of color, brightness, and edge is necessary for the description of a root because there may be strong image variation from one tape to another. A given root can appear brown on one tape and monitor but whiter in the following tape. When water bubbles appeared (see Figure A3 in Appendix) they caused some difficulties in visualizing the very fine roots in the 0.1 to 0.2 mm diameter class.

Results

The Eugenei well watered (Eww) treatment showed more or less constant values of total number of fine roots (TNFR in Tables 3.1 to 3.3), with the exception of the first and the two last observations (Figure 3.2). The fine root system increased during the end of summer, attaining a maximum during mid-October and declining thereafter. Exactly the same pattern can be observed in both vertical (VR) and horizontal (HR) roots (Figure 3.3). The average ratio of VR/HR of all eight dates was 1.2, indicating that there are slightly more vertical than horizontal roots. Accumulated values for the upper profile resulted in a V/H ratio of 1.2 (Table 3.4), a bottom profile V/H ratio of 1.4 and a UP/BP ratio of 1.1.

Eugenei natural conditions (Enc) treatment was quite different from Eww in terms of TNFR. The Enc treatment produced almost 2.5 times fewer fine roots in the minirhizotron profile than the well watered treatment (Figure 3.4). The growing pattern of the fine-root system was also different from the well watered treatment; TNFR started to increase later and did not show any substantial decrease by November. The fine root habit shown by V/H ratio changed dramatically under natural conditions (Figure 3.5). The average V/H ratio of the upper profile was 1.3 and the bottom profile ratio was 0.99. In contrast to the results of the well watered treatment, it is the upper profile that

Table 3.1. Fine root distribution in the upper profile (0 to 24 cm, UP), bottom profile (25.2 cm to bottom, BP) and total number of fine roots (TNFR) per observation in Eugenei and Tristis well watered and natural conditions treatments during September, October and first week of November, 1986.

Treatment ¹		Observations							
		1	2	3	4	5	6	7	8
		No. of fine roots.....							
	UP	151	167	172	169	182	176	146	98
Eww	BP	117	156	172	161	192	172	126	74
	TNFR	268	323	344	330	374	348	272	172
.....									
	UP	54	84	84	107	119	121	119	118
Enc	BP	12	15	14	32	41	41	37	35
	TNFR	66	99	98	139	160	162	156	153
.....									
	UP	80	105	86	86	96	80	62	47
Tww	BP	39	39	32	27	28	29	22	16
	TNFR	119	144	118	113	124	109	84	63
.....									
	UP	133	136	123	132	129	114	87	57
Tnc	BP	19	24	27	36	34	35	20	15
	TNFR	152	160	150	168	163	149	107	82

1

Eww Eugenei well watered; Enc Eugenei natural conditions; Tww Tristis weel watered; Tnc Tristis natural conditions.

Table 3.2. Vertical and horizontal fine root distribution in the upper profile (0 to 24 cm), bottom profile (25.2 cm to bottom) and total number of fine roots (TNFR) per observation in Eugenei well watered and natural conditions treatments during horizontal roots during September, October and first week of November, 1986.

1 Treat.	2 Root Type	Observations							
		1	2	3	4	5	6	7	8
		No. of fine roots.....							
	V/UP	73	81	86	84	98	93	73	48
Eww	V/BP	62	87	95	91	120	108	74	38
	V/TNFR	135	168	181	175	218	201	147	96
									
	H/UP	78	86	86	85	84	83	73	50
Eww	H/BP	55	69	77	70	72	64	51	36
	H/TNFR	133	155	163	155	156	147	124	86
									
	V/UP	34	47	46	60	71	72	72	71
Enc	V/BP	6	6	7	18	23	21	18	14
	V/TNFR	40	53	53	78	93	93	90	85
									
	H/UP	20	37	38	47	48	49	47	47
Enc	H/BP	6	9	7	14	18	20	19	21
	H/TNFR	26	46	45	61	66	69	66	68

1

Eww Eugenei well watered; Enc Eugenei natural condition;
Tww Tristis well watered; Tnc Tristis natural conditions.

2

V/UP vertical roots of upper profile; V/BP vertical roots of bottom profile; V/TNFR total number of vertical fine roots; H/UP horizontal roots of upper profile; H/BP horizontal roots of bottom profile; H/TNFR total number of horizontal fine roots.

Table 3.3. Vertical and horizontal fine root distribution in the upper profile (0 to 24 cm), bottom profile (25.2 cm to bottom) and total number of fine roots (TNFR) per observation in Tristis well watered and natural conditions treatments during horizontal roots during September, October and first week of November, 1986.

1 Treat.	2 Root Type	Observations							
		1	2	3	4	5	6	7	8
		No. of fine roots.....							
	V/UP	45	64	52	49	53	46	38	32
Tww	V/BP	28	33	28	25	24	25	19	15
	V/TNFR	73	97	80	74	77	71	57	47
									
	H/UP	35	41	34	37	43	34	24	15
Tww	H/BP	11	6	4	2	4	4	3	1
	H/TNFR	46	47	38	39	47	38	27	16
									
	V/UP	79	85	75	82	82	75	56	35
Tnc	V/BP	15	20	25	32	31	34	19	14
	V/TNFR	94	105	100	114	113	109	75	49
									
	H/UP	54	51	48	50	47	39	31	22
Tnc	H/BP	4	4	2	4	3	1	1	1
	H/TNFR	58	55	50	54	50	40	32	23

1

Eww Eugenei well watered; Enc Eugenei natural condition;
Tww Tristis well watered; Tnc Tristis natural conditions.

2

V/UP vertical roots of upper profile; V/BP vertical roots of bottom profile; V/TNFR total number of vertical fine roots; H/UP horizontal roots of upper profile; H/BP horizontal roots of bottom profile; H/TNFR total number of horizontal fine roots.

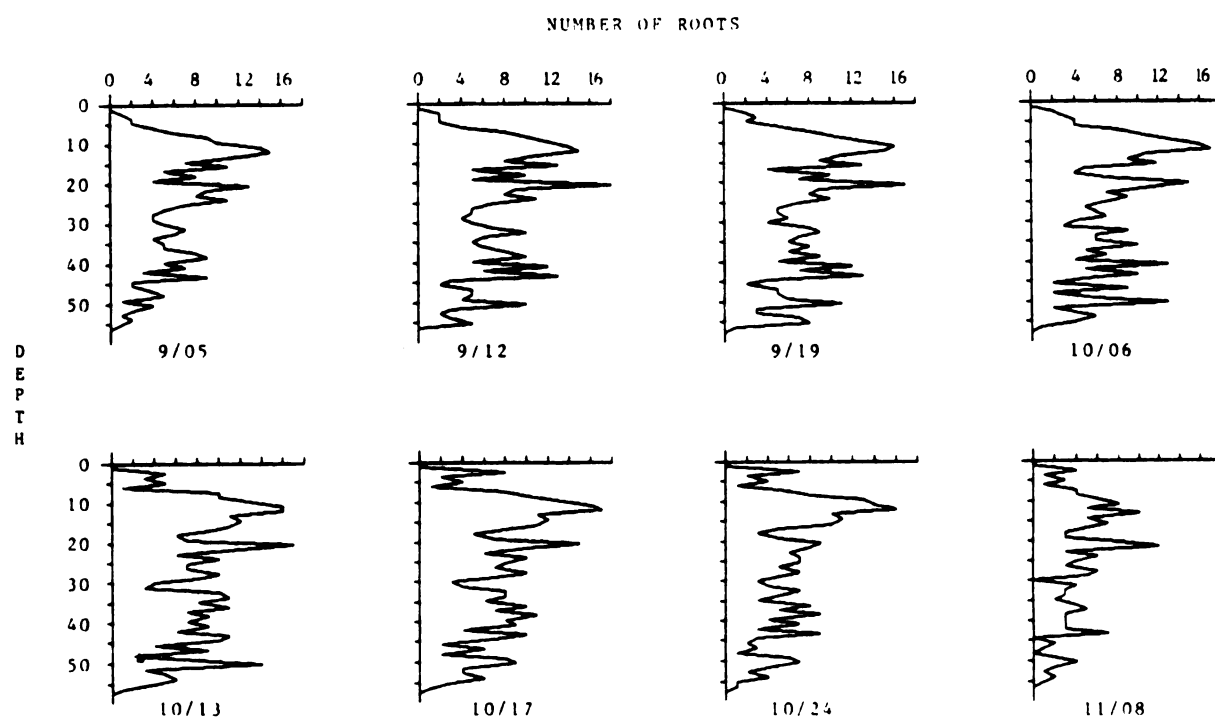


Figure 3.2. Weekly changes in fine root distribution (up to 3 mm in diameter) in the Eugenei well watered treatment during September, October and first week of November, 1986 (depth in cm).

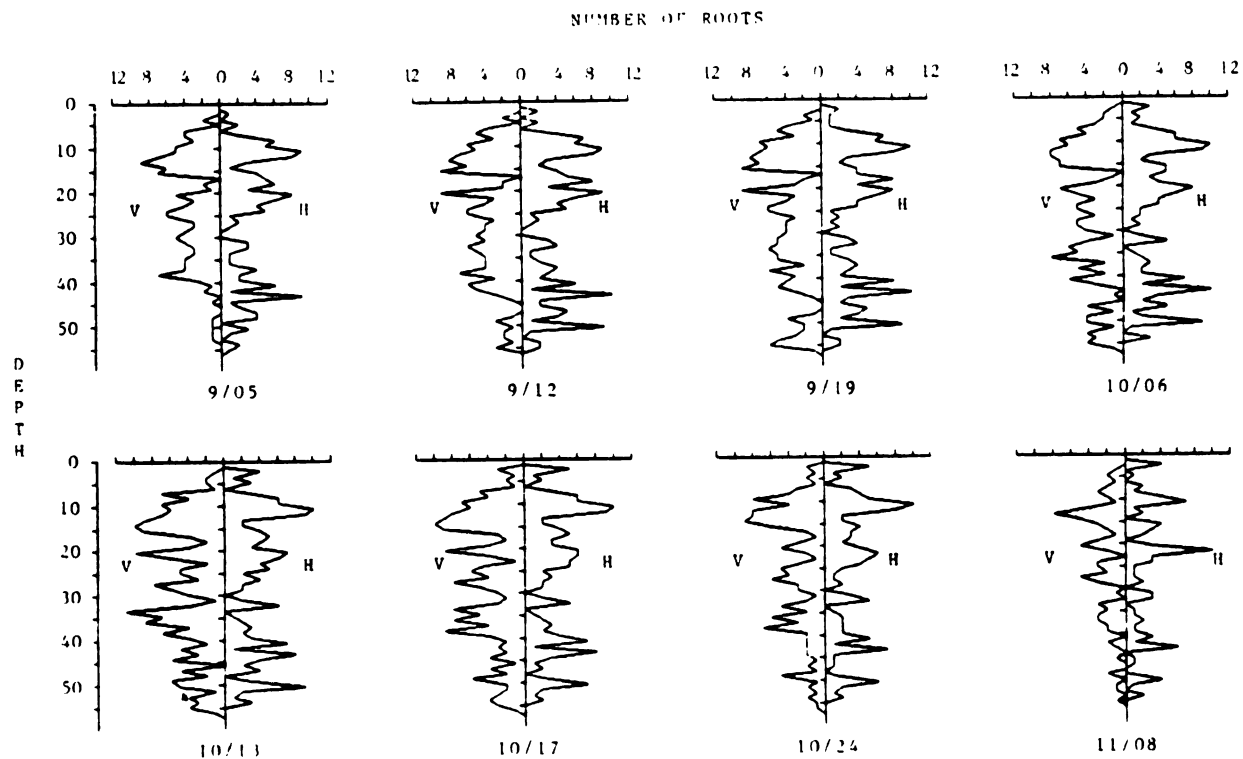


Figure 3.3. Weekly changes in fine root distribution (up to 3 mm in diameter) in the Eugenei well watered treatment during September, October and first week of November, 1986 (V= vertical roots; H= horizontal roots; depth in cm).

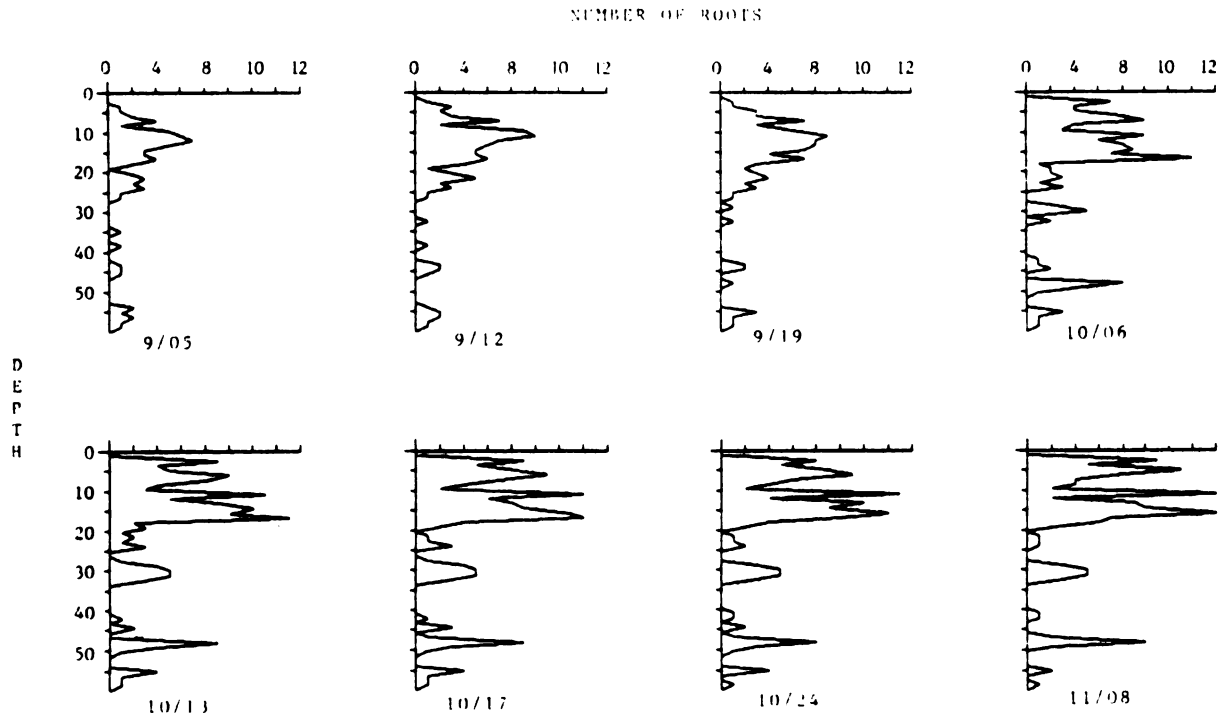


Figure 3.4. Weekly changes in fine root distribution (up to 3 mm in diameter) in the Eugenei natural conditions treatment during September, October and first week of November, 1986 (depth in cm).

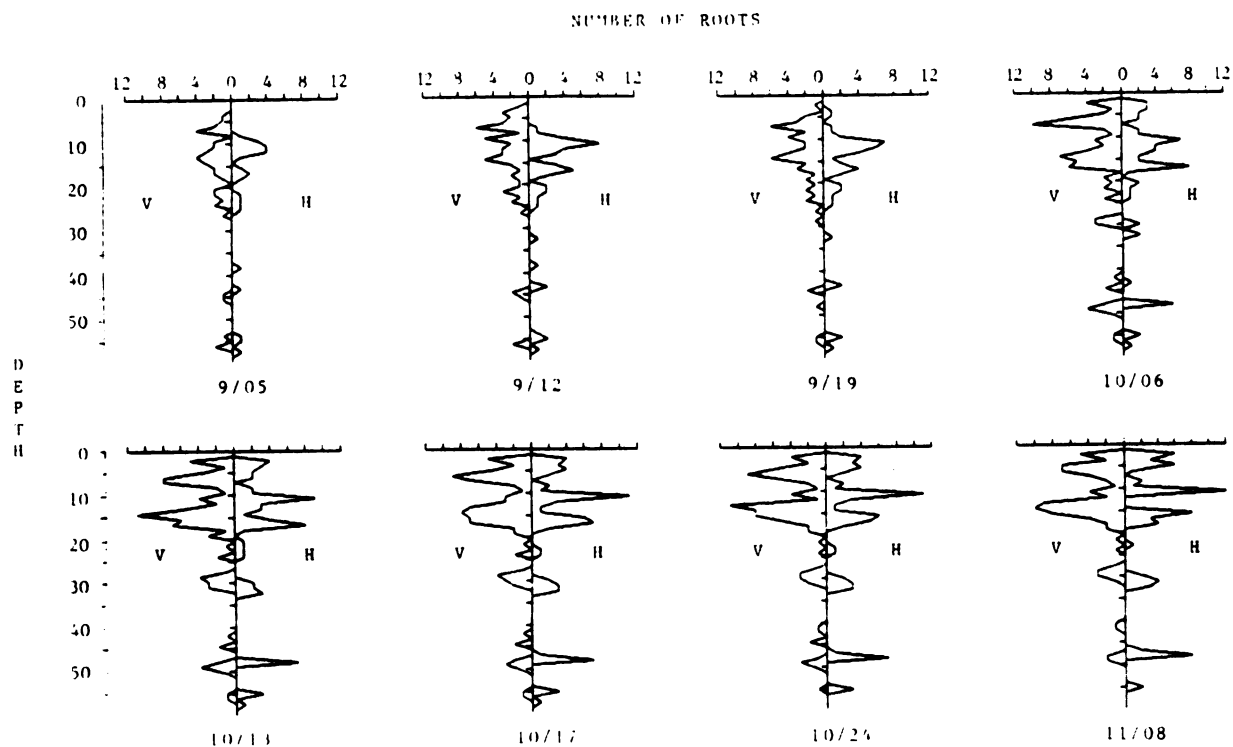


Figure 3.5. Weekly changes in fine root distribution (up to 3 mm in diameter) in the Eugenei natural conditions treatment during September, October and first week of November, 1986 (V= vertical roots; H= horizontal roots; depth in cm).

Table 3.4. Fine root characteristics (averages of eight observations) in Eugenei and Tristis well watered and natural conditions treatments, 1986.

Treatment	1 2 TNFR	3 Root Type		V/H Ratio ⁴
		Vertical	Horizontal	
Eww	303	163	140	1.2
Enc	129	73	56	1.3
TwW	109	72	37	1.9
Tnc	140	95	45	2.1

1

Eww Eugenei well watered; Enc Eugenei natural conditions; TwW Tristis well watered; Tnc Tristis natural conditions.

2

Average of total number of fine roots of all observations per treatment.

3

Vertical roots were those oriented at an angle greater than 45 degrees and horizontal roots were those oriented at an angle less than 45 degrees.

4

Ratio of the average vertical fine roots and horizontal fine roots.

contained more vertical roots under drought conditions. Another contrast with the well watered treatment is that the root system of Enc was mostly in the upper portion of the soil, resulting in a UP/BP ratio of 3.6.

The Tristis well watered (Tww) treatment showed a constant TNFR up to the middle of October and from then on it slowly decreased (Figure 3.6). Tristis as a general rule had more fine vertical roots than horizontal ones; the upper profile V/H ratio was 1.4 and the bottom profile ratio 5.6 (Figure 3.7). The average of eight observations resulted in a V/H ratio of 1.9. The UP/BP ratio was 2.8, indicating that the Tww treatment, similar to Enc, had almost 3 times more fine roots close to the soil surface.

The Tristis natural conditions (Tnc) treatment, like the well watered treatment, also showed a more or less constant TNFR up to the middle of October and from then on it slowly decreased (Figure 3.8). As a general average, the Tnc had 29% more fine roots in the minirhizotron profile than the Tww treatment. However, it also had 10% fewer fine roots in the bottom profile, resulting in a eight-observation average UP/BP ratio of 4.3. The V/H ratio in the bottom profile was 9.5, indicating that for every ten fine roots, nine were vertical (Figure 3.9). The upper portion V/H ratio of 1.7 was similar to the one obtained in the well watered treatment. Tristis under natural conditions produced more vertical roots, considering the entire profile for all observations, resulting in a V/H ratio of 2.1.

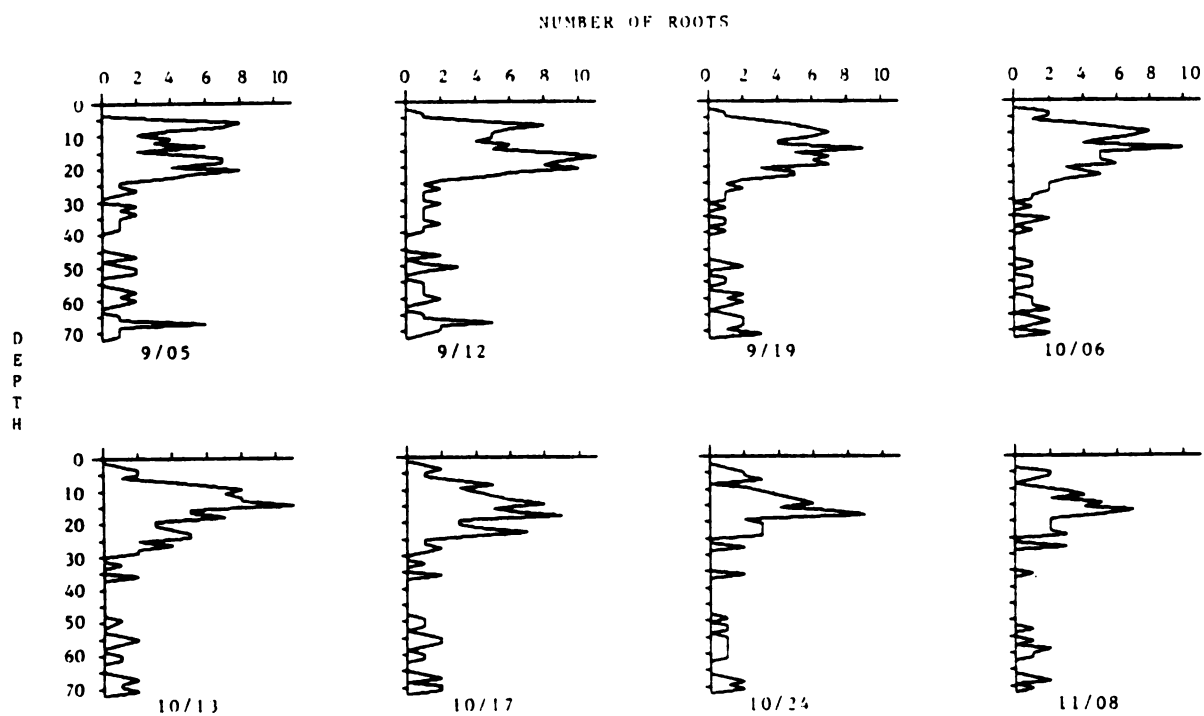


Figure 3.6. Weekly changes in fine root distribution (up to 3 mm in diameter) in the Tristis well watered treatment during September, October and first week of November, 1986 (depth in cm).

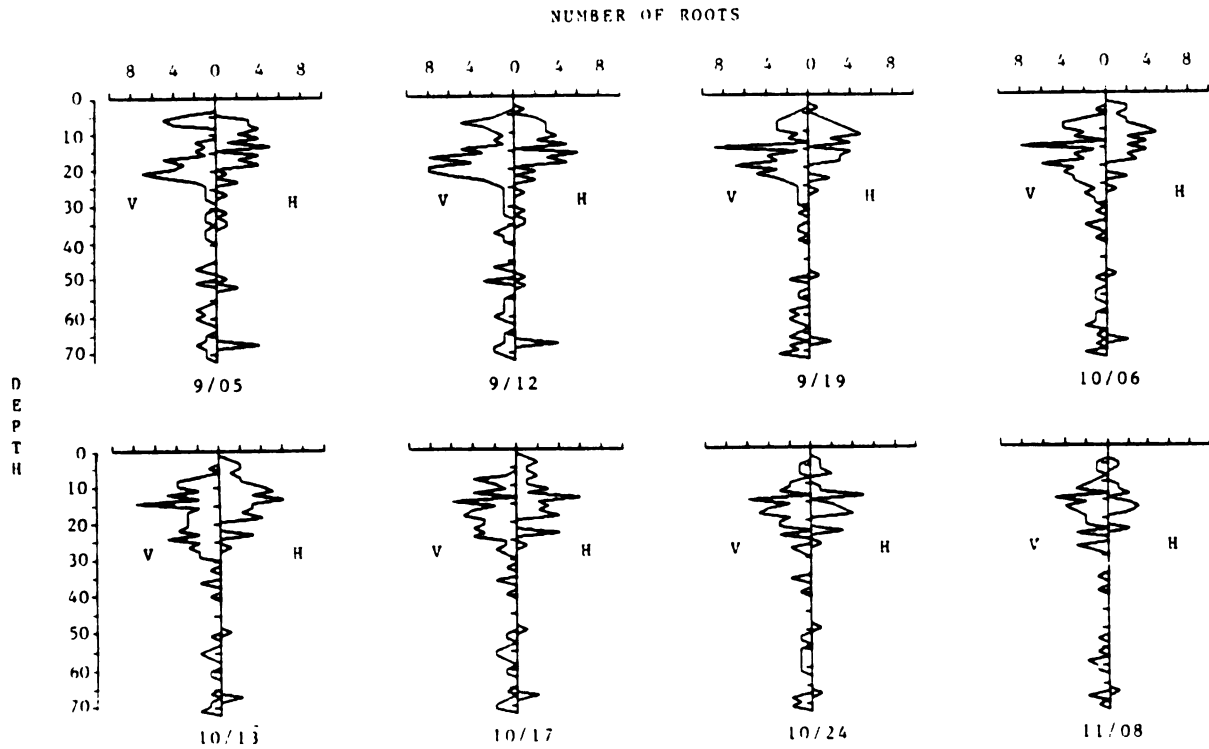


Figure 3.7. Weekly changes in fine root distribution (up to 3 mm in diameter) in the Tristis well watered treatment during September, October and first week of November, 1986 (V= vertical roots; H= horizontal roots; depth in cm).

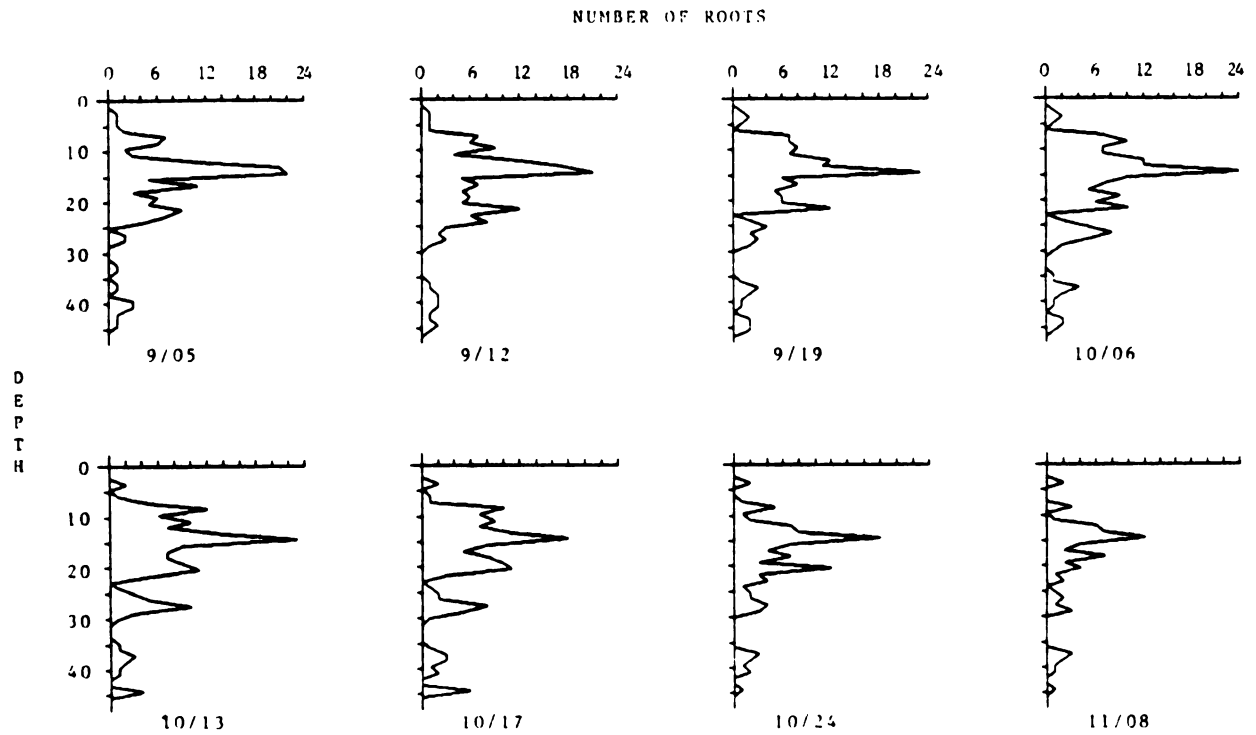


Figure 3.8. Weekly changes in fine root distribution (up to 3 mm in diameter) in the Tristis natural conditions treatment during September, October and first week of November, 1986 (depth in cm).

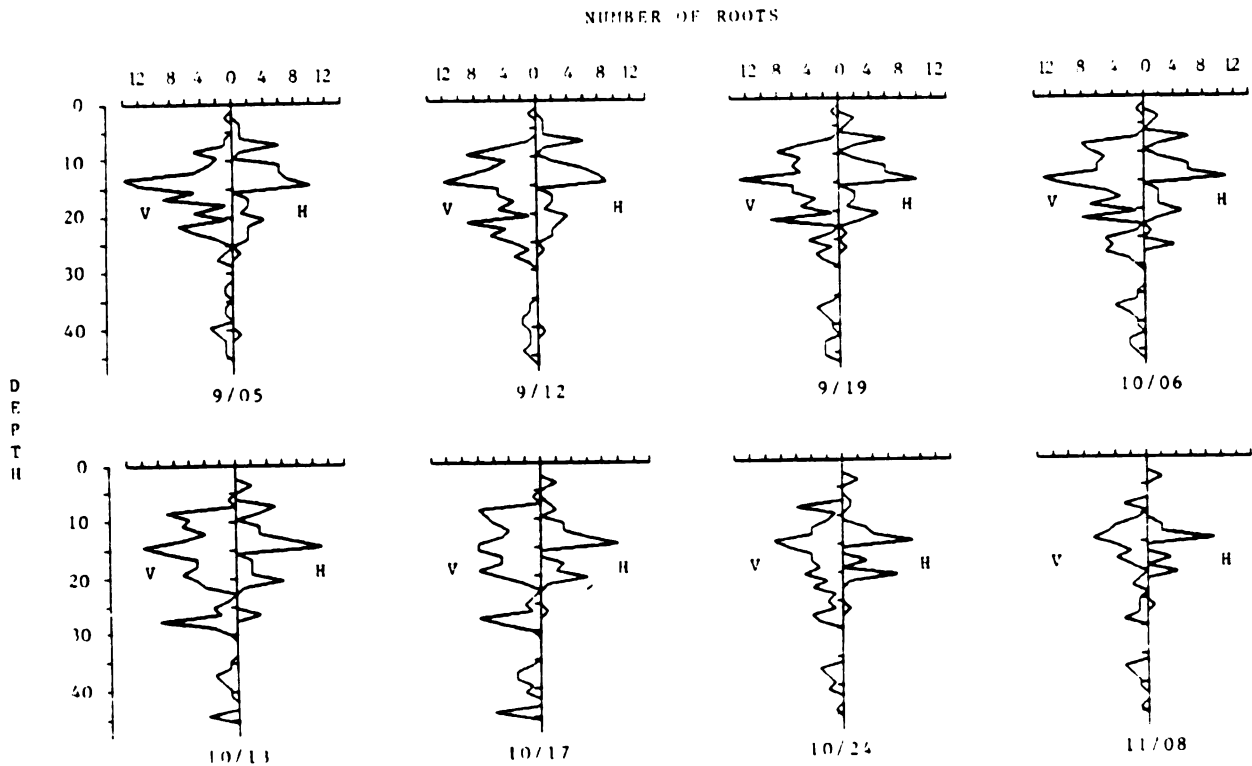


Figure 3.9. Weekly changes in fine root distribution (up to 3 mm in diameter) in the Tristis natural conditions treatment during September, October and first week of November, 1986 (V= vertical roots; H= horizontal roots; depth in cm).

Table 3.5 shows fine root diameter distribution as averages of eight periodic observations throughout the minirhizotron profile. The average diameter of fine roots was smaller in the well watered treatments compared to natural condition treatments. The upper profile average fine root diameter was greater than that at the bottom in all treatments, except for the Tnc, which had finer roots in the top soil and thicker roots deeper. Both clones and treatments had approximately 90% of all observed fine roots below 0.9 mm in diameter.

The majority of fine roots did not grow in diameter (Table 3.6), with approximately 5% of all roots showing some diameter growth during the entire observation period. Small diameter roots had a variable and slow growth rate and only a few of the upper diameter class roots had growth rates high enough to be observed bi-weekly. However, most of the time it was difficult to measure any diameter growth.

Weekly changes in average fine root diameter of all four treatments are shown in Table 3.7, and indicate changes due to root growth and death. Since diameter growth of fine roots was so small that can be neglected, changes in diameter averages indicate shedding or appearance (extension of fine roots). Changes were contrasting in Eugene1 treatments. While Eww shed roots of average diameter, Enc shed thicker ones through the period. Both Tristis treatments shed fine roots at a higher rate than coarser roots, changing the average diameter dramatically from the

Table 3.5. Average fine root diameters by depth and diameter class distribution in the minirhizotron profile in Eugenei and Tristis well watered and natural conditions treatment, 1986.

Treat- ment ¹	Overall Mean Diameter ²	Depth (cm)		Freq./Diam. Class(%)	
		0-24	> 25	0.0-0.8	0.9-3.0
		 mm			
Eww	0.37	0.44	0.30	94	6
Enc	0.45	0.46	0.37	89	11
Tww	0.38	0.40	0.35	90	10
Tnc	0.42	0.36	0.65	91	9

1

Eww Eugenei well watered; Enc Eugenei natural conditions; Tww Tristis well watered; Tnc Tristis natural conditions.

2

Means of eight periodic observation of four entire profiles from four minirhizotrons.

first to the last observation date. Tww roots increased in diameter 33% while Tnc doubled.

The majority of fine roots did not die. Some already existing roots died, others grew, and just a few grew and died during the eight observations. Intense precipitation during the last week of September and the first days of October hindered the maintenance of weekly observation intervals (e.g., between third and fourth observations). Such unusual precipitation, of 3.2 times the September average, was probably the cause of profuse root growth, mostly in Enc, but also in Eww. However, almost no new roots were observed in Tristis treatments following the rains.

Only nine Eugenei roots varying from 0.1 to 0.3 mm, appeared and died during the entire observation period. The approximate average lifespan was 5 weeks. Most of the dying roots already existed in the profile when observations began, and they were mostly from the 0.2 to 0.6 mm diameter class.

In the Eugenei natural conditions treatment, eleven fine roots, mostly in the 0.2 to 0.5 mm diameter class, and a few larger ones died during the entire period (average lifespan of 3.8 weeks). Most of the already existing roots that died were larger ones (0.6 - 0.8 mm).

The 31 roots in the Tristis well watered treatment that appeared and died during the observation period were small, mostly of 0.2 - 0.4 mm, and had an average lifespan of

Table 3.6. Mean weekly diameter increments of fine roots and percentage of growing roots in Eugenei and Tristis well watered and natural conditions treatment, 1986.

Treat. ¹	Diameter class		Growing Roots ²
	0 - 0.8	> 0.9	
	 mm/week		
Eww	0.03	0.06	8%
Enc	0.03	0.10	5%
TwW	0.04	0.20	3%
Tnc	0.05	0.15	5%

1

Eww Eugenei well watered; Enc Eugenei natural conditions; TwW Tristis well watered; Tnc Tristis natural conditions.

2

Percentage of total fine roots that showed any measurable growth over eight observations.

approximately 2.3 weeks. The majority of these roots appeared before the September rainy period. Later in the season most of the roots that died were from the 0.1 to 0.4 mm diameter class.

The Tristis natural conditions treatment also was similar to the well watered one. Twenty nine roots in the 0.1 to 0.3 mm class appeared and died, mostly before the third measurement. The life span of these roots was approximately 2.6 weeks. The late death of existing roots was mostly in the 0.1 to 0.2 mm diameter class.

Most of the new root growth in the Eugenei well watered occurred after the third measurement (after the September rainy period). Nearly 20 new roots appeared during this period; most of them grew very fast in length (5 - 8 mm a week). Such fast growing roots were 0.5 - 0.8 mm in diameter and unbranched. Figures 3.10 and 3.11 are photographs of some of these fast growing fine roots. Small diameter roots (0.2 - 0.4 mm) grew slower in length (0.1 to 0.3 mm per week). Branching occurred in approximately 30% of the roots. Root branches were of second and third order, alternating in straight roots at intervals of approximately 3 - 5 mm.

The Enc treatment also had most of its new root growth after the rainy period. More than 40 new and unbranched roots 0.4 to 0.8 mm in diameter grew at the very fast rate of 10 - 15 mm during the first week. During the following week the growth rate declined to 4 - 6 mm and continued to decline thereafter. Branching was observed in approximately

Table 3.7 Average diameter of fine roots during eight observations in Eugenei and Tristis well watered and natural conditions treatments, 1986.

Date	1 Treatments			
	Eww	Enc	TwW	Tnc
	 mm			
9/05	0.37	0.47	0.34	0.32
9/12	0.36	0.46	0.34	0.36
9/19	0.34	0.48	0.37	0.37
10/06	0.35	0.49	0.35	0.42
10/13	0.38	0.46	0.37	0.43
10/17	0.39	0.41	0.41	0.40
10/24	0.39	0.44	0.40	0.46
11/08	0.38	0.39	0.46	0.60

1

Average fine root diameters of four entire profiles from four minirhizotrons. Eww Eugenei well watered; Enc Eugenei natural conditions; TwW Tristis well watered; Tnc Tristis natural conditions.

15% of roots and second order roots were at intervals of 5 - 7 mm on the primary root, farther apart than in the Eww treatment.

Almost no growing root tips were observed in both Tristis treatments after the rainy period and length growth rate cannot be characterized because of the few and extremely variable examples. The most striking difference between the treatments in Tristis was in the branching pattern. Approximately 5% of all fine roots had second order branch roots in the Tristis well watered treatment. Intervals between secondary branches were 10 to 15 mm. In contrast, more than 30% of roots branched, almost one fourth of them with both second and third order roots, in the Tristis natural conditions treatment. Secondary branches were much closer than in the Tww treatment, varying from 3 to 5 mm.

Branching occurred mostly in straight roots and was alternate (Figure 3.12), rarely opposite (Figure 3.13). Lateral roots normally appeared on the outside surface of curved roots, although laterals could also grow from the inside root surface. Normally branch roots were somewhat smaller in diameter than the main root (Figures 3.12 and 3.14); rarely large diameter roots (0.9 to 1.2 mm) produced very fine 0.1 to 0.3 mm branch roots as shown in Figure 3.15.

Roots that had high growth rate were those with massive root tips, a white to cream color, and a very shiny sharp

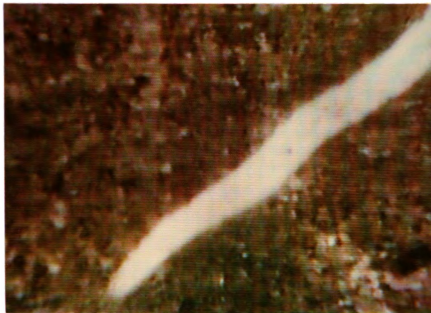


Figure 3.10. Fast-growing fine root tip (1.4 mm diameter) in Tristis natural condition treatment after the late September rainy period, 1986 (photograph represents 17.4 x 11.6 mm).



Figure 3.11. Fast-growing lateral roots (three 0.5 mm and one 0.7 mm diameter) in Tristis natural conditions treatment after the late September rainy period, 1986 (photograph represents 17.4 x 11.6 mm).

edge appearance (Figure 3.10). Roots of slower growth rate were crooked, with small tips, and a cream to light brown color. Dead and decayed roots left a black stain in the white sand particles that remained for a long period, even after being "washed" by percolating soil water (Figure 3.16).

Two examples of weekly root growth and correspondent rates are shown in the sequences of photographs in Figures 3.12 and 3.14 and an example of a dead branched root is shown in Figure 3.17.

Discussion

The general pattern of root distribution shown by the minirhizotron window is similar to that found in other studies. The majority of fine roots were localized in the upper portion of the soil. Moir and Bachelard (1969) found most of the fine roots of various Pinus radiata plantations in the upper 15 cm of soil. Baker and Blackmon (1977) observed that young Populus deltoides had 84% of their total root biomass in the upper 20 cm of the soil and up to 94% of it above 30 cm. Faulkner (1976), studying five-year-old hybrid poplar, determined that the root system was strongly horizontally oriented, localized mostly in the upper 20 cm of the soil. When both clones and treatments of the present study were considered, approximately 66% of fine roots were

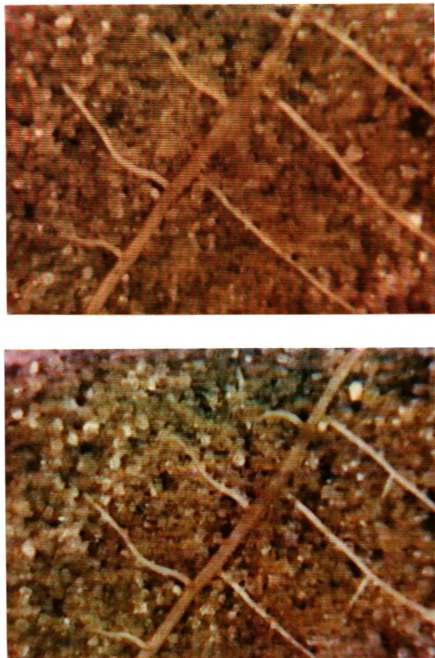


Figure 3.12. Development of two third order lateral branches (ca. five days old), 1.2 and 0.8 mm in length in Eugenei natural conditions treatment (photograph represents 17.4 x 11.6 mm).



Figure 3.13. Normally observed root branching pattern in Eugenei well watered treatment. Note rare opposite laterals (photograph represents 17.4 x 11.6 mm).

localized in the upper 24 cm of soil.

Percentages of roots in a layer of the profile may not exemplify the behavior of roots systems well, especially when very different sizes trees are being compared (see Chapter I). Although the percentage of roots in the upper profile was smaller in Eww than Enc, the absolute number in Eww was larger than any other treatment due to the large size of the trees. The same tendency also was observed in Tristis treatments; the smaller the tree (see Chapter I), the larger the percentage of roots in the upper soil profile. However, the same principal does not apply when



Figure 3.14. Sequence showing a lateral root growing 3.9 mm during the first week and 1.3 mm during the following week in Eugenei natural conditions treatment (photograph represents 11.6 x 8.7 mm).



Figure 3.15. Rare fine root branching pattern in Tristis well watered treatment (photograph represent 17.4 x 11.6 mm).



Figure 3.16. Transparent root stains from roots presumably dead for six months in Eugenei well watered treatment (photograph represent 17.4 x 11.6 mm).



Figure 3.17. Dead main root and four laterals that can be indentified by their fuzzy edge, homogeneous color, and lack of depth and brightness in Tristis well watered treatment (photograph represent 17.4 x 11.6 mm).

absolute values are considered.

Irrigation had an opposite effect in the two clones. When absolute numbers of fine roots are considered, Eugenei responded similarly to other studies. Gregory (1979) found that irrigation promoted a more intensive rooting in the upper soil profile in two agricultural crops. Tristis treatments in the present experiment responded to irrigation in a more peculiar way; irrigation inhibited or did not affect root production under well watered conditions. Layne et al (1986) observed also that irrigated peach trees developed fewer fine roots in the upper soil profile. The Tristis natural conditions treatment had 30% more fine roots

than the watered treatment, suggesting some adaptability of the clone to drought conditions.

Attention should be paid to how comparisons are made between root systems. The delineation of the upper portion of the soil is relative and variation in it can modify the perception root distribution. Ratios of UP/BP show that under irrigation rooting is more deeply distributed (Eww 1.1 - Enc 3.6; Tww 2.8 - Tnc 4.3), whereas more fine roots appeared in the top soil under natural conditions. Layne et al. (1986) found that non-irrigated peach trees also produced more fine roots (absolute number) in a shallow profile (120 cm) when compared with irrigated trees. However, they were apparently comparing trees of similar size (not mentioned), whereas in the present experiment there was tremendous size difference. The same ratios obtained in this study would not be obtained if another soil limit was chosen, or if rooting depth was proportional to above ground dimensions.

The TNFR responses to irrigation varied differently in each clone. Eugenei had more fine roots than Tristis, but the large size of Eww trees had a strong determinant effect on the average. When non-irrigated treatments are compared the relation reversed, and Tnc had effectively more fine roots than Enc.

Root orientation was less variable both among treatments and clones. Eugenei, independent of the soil moisture regime, had approximately the same number of horizontally

and vertically oriented fine roots. Tristis also maintained a ratio of 2:1 of vertically to horizontally oriented fine roots independent of the treatment. The small variation in the weekly treatment ratios, indicated by a general coefficient of variation of approximately 12%, suggests that the orientation of the fine root system was determined by the clone rather than by the environment.

Root system growth is difficult to quantify and characterize because growth cycles of individual roots may or may not be independent. Johnson-Flanagan and Owens (1985) found that various white spruce roots had different growing cycles. Secondary thickening may be observed only in a few roots (Head 1973) and changes of color due to suberization are variable among same age roots. Rogers and Head (1968) reported that during summer apple fine roots changed to a brown color one or two weeks after appearance through degeneration and shedding of the epidermis and primary cortex (Figure A1). In the present study some fine roots changed color from a light cream (Figure 3.10) to a light brownish yellow color (Figure 3.13) during the week after their appearance whereas some others did not change at all during the whole period.

According to Root and Root System Terminology (Sutton and Tinus 1983), roots turn to a brownish color in consequence of suberization (deposition of suberin in thin lamellae) or metacutization (massive deposition of suberin in cell walls and cell contents) or development of a

secondary endodermis (associated with suberization). Shedding of the epidermis and root cortex seems to be associated with secondary thickening and occurs more or less at the time of endodermis formation (Head 1973), although it may be visually difficult to spot any signs of tissue differentiation in very fine roots 0.1 to 0.3 mm in diameter. All the roots in the present study which appeared to be shedding dead tissue were growing in diameter. The amount of dead tissue shed by roots growing in diameter could account, according to Rogers (1968b), for up to half of the stele tissue. Large and fast growing roots observed in this study also shed considerable amounts of tissue. However, according to Head (1973) and to the results of the present study, very few fine roots (5%) undergo any secondary thickening, so shedding may not be an important process in fine roots.

Root extension growth, observed mostly in *Eugenei*, was as variable as values reported in the literature and it seems to depend on both genetic and environmental factors (Russel 1977). Extremely fast extension growth rates of 5 to 6 cm/day in honey locoust were reported by Lyr and Hoffmann (1967). Intermediate rates for apple trees of 4 to 5 cm/week were observed by Rogers and Head (1968). Fast growing poplar roots in the present study had growth rates of up to 2 cm/week, but often they were much less. Extremely slow growth rates (0.1 to 0.3 mm/week) were also observed, primarily in very fine roots. Although some extremely fast

growth rates were observed right after the unusually high September rain, such extension rates were not sustained for long periods (Wilcox 1962).

Turnover rate of fine roots varies on a daily, weekly, monthly or even a yearly basis (Head 1973; Ford and Deans 1977; Kummerow et al. 1978; Persson 1978 and 1979; Marshall and Waring 1985). The life span of fine roots is determined by factors such as season of appearance and extension, starch content, level of respiration, soil temperature, frost or flooding, genotype, etc. In general, a fine root can be compared to a battery with a limited charge: it can last for a long time under optimum growth conditions or it can wear out fast when growth conditions are not appropriate (low photosynthesis, high soil temperature, drought, flooding, etc.).

Although Eugenei fine roots lived, on average, two weeks longer than those of Tristis, variance among individual observations hampers any general conclusion. Drought conditions did not have any noticeable effect on the life span of Tristis fine roots. The number of roots that appeared and died during the observation period, however, seems to have been genetically controlled. Tristis had three times more fine roots that appeared and died than Eugenei. Thus, the dynamics of the fine root system of Tristis was more intense, since this clone spent more photoassimilates in growing numerous fine roots, the life span of which was slightly shorter than in Eugenei. An index, determined by

multiplying the inverse of turnover rate by the number of fine roots, gave a production ratio of approximately 5.4:1 when Tristis and Eugenei clones were compared.

The position of root hairs has been considered variable and they may originate at different sites (Bogar and Smith 1965). Observations by Head (1973) can be generalized in that fast growing roots have root hairs away from the root tip (some millimeters) and slow growing ones have them very near the tip. Fruit trees such as avocado and pecan have roots that may not have root hairs at certain times of the year (Woodroof and Woodroof 1934; Smith and Wallace 1954). Johnson-Flanagan and Owens (1985) found that white spruce have what can be described as elongation roots without hairs and absorbing ones with root hairs. Upchurch and Ritchie (1984) report that root hairs of maize could be identified when root tips were in contact with the minirhizotron surface.

Poplar roots may or may not have root hairs at certain times. Intensive observations were made in the present study to locate root hairs, especially in the root type exemplified by Figure 3.10, but without success. Thus, root hairs were either too small to be resolved with the videoequipment used, or they were absent from the roots during the period of observation.

Russell (1977) suggests that under field conditions variation of water supply is the principal cause for differences in root distribution. Intensity of root

branching and root depth are the two most important characteristics of root systems that enhance water uptake (Russell 1977). The reason the Tnc treatment physiologically coped with drought conditions so well seems to be associated with the significant increase of fine root branching. The root branching habit of any species under constant environmental conditions is closely predictable. Alterations in environmental conditions may lead to considerable changes in the number of laterals per unit of length and in their individual lengths (Russel 1977). Intensive root branching of Tnc in response to water stress seems to be the factor that enabled the plants to maintain normal levels of growth. On the other hand, intensive branching also appears to be associated with high levels of organic matter and mycorrhizal infection (Head 1973).

The lack of branches in the fast growing roots observed in Eww and Ens after the rainy period was remarkable. More than 50 roots from both treatments were carefully analyzed and all lacked laterals. Unusual summer rains also promoted vigorous fine root growth in chaparral shrubs (Kummerow et al. 1978), although they did not mention root branching. The time of the year, root type, or endogenous substances, specifically cytokinins and auxins, may affect root branching capacity (Goodwin and Morris 1979). High levels of cytokinins due to large root tips (Yoshida and Oritani 1972) and low levels of above-ground produced auxins normally occur during fall. It has been demonstrated that cytokinins

inhibit lateral root production (Short and Torrey 1972; Bottger 1974) and auxins produced by the shoot promote root branching (Goodwin and Morris 1979).

Seasonal root growth may be generally described by three overlapping phases based on the export of photosynthates. Root growth begins with the export of previous year photosynthates during pre-budbreak phase. There is little or no root growth during shoot elongation, since photosynthates are diverted to newly forming shoots. Finally, photosynthate export to roots resumes after shoot growth stops and a second root growing phase is observed (Loach and Little 1973, Russell 1977). The Eugenei clone behaved more or less according to the above. Little root growth occurred during August and part of September. A major root growth phase followed the rainy period at the end of September and early in October. Eugenei treatments showed root extension growth late, after leaves had fallen. In contrast, there were no signs of a major pulse of root growth in Tristis treatments during the whole observation period.

Data derived from a few minirhizotron tubes is inappropriate for a statistical analysis, since it produces profile sequences with many zeros. A great number of minirhizotrons is required in order to provide accumulated data that can then be transformed or non-parametrically analyzed for better results and consistent comparisons. Perhaps a minimum of six minirhizotrons with two profiles each facing the tree stem would generate consistent data to

form a single replication. Six minirhizotrons at a distance from the stem with a great probability of root interception (60 to 90 cm for both clones at the age of two) might provide even greater values of TNFR than of those obtained in this study.

Minirizhotron root studies of single trees require knowledge of root distribution in order to place minirhizotrons and extrapolate profile data to the entire tree root system. Studies of crops roots are not made in single plants but rather on dense plantations where there is more or less the same root density throughout the area. Tubes at 30 cm from the tree stem in Eugenei had roughly three times more fine root interception than those at 120 cm. However, we lack knowledge of how to relate such observations to the entire tree root system. It is necessary to have studies that uncover such relations in order to use the full and promising potential of the minirhizotron technique.

The image quality and the data consistency which derive from minirhizotrons can be maintained if the tubes are fixed in the soil in a way that they cannot rotate even slightly while being manipulated. Better profile images and less interface effect may be obtained from minirhizotrons installed in holes where the soil structure is maintained in a more natural form. Smoothened soil surfaces, besides preventing clear visualization of very fine roots, also seem to have a detrimental effect on fine root growth.

Color cameras of greater resolution are already being used and results generated by the respective images will provide a clearer characterization of fine roots, especially with regard to color, state of life, mycorrhiza, and root hairs. Depth of focus is still a problem since it is difficult to achieve a clear visualization of thick roots (0.8 mm and up).

The laboratory analysis of minirhizotron images can be reduced if, instead of having one tape for each day of observation or for each large group of minirhizotrons, the recording of one treatment, or even better, one minirhizotron is done in a separate tape for each observation day. Tapes will thus have profiles of one or of a few minirhizotrons on various dates which will facilitate the tedious counting and checking work.

SUMMARY AND CONCLUSIONS

Plants which are susceptible to water deficits may respond to drought by changing growth rate, hormonal balance, physiological activity, reproduction, etc. Eugenei and Tristis have different inherent ways of coping with water deficits, and so responded differently to various levels of irrigation. Eugenei is a sensitive clone and showed growth and physiological responses modified by the soil water regime. Tristis, being a more tolerant clone, was not strongly affected.

Differences in water availability caused noticeable modifications in growth and physiology of the Eugenei clone. Eugenei was unable to exert control over increasing water deficits, and physiological functioning was reduced. Under extremely harsh conditions height growth ceased and buds set, leaves were shed to reduce transpiration, and photosynthesis rate declined significantly. When water was supplied in abundance, very high rates of growth were achieved.

Irrigation of Tristis did not increase vegetative growth since this clone was able to control water deficits. The increase of the supply of available water in Tristis grown under droughtly conditions was associated with the growth of a profuse and much-branched fine root system. Physiological

activity of Tristis plants was maintained more or less constant throughout the various soil water regimes.

Stomatal movement in Tristis was not related to the imposed irrigation treatments. Stomatal movement in Eugenei, however, reflected the existing water conditions. The relation of stomatal conductance to transpiration, photosynthesis, or sometimes to leaf water potential varied greatly from one clone to another and from one treatment to another.

Root growth was different between clones and related to the growth strategy of each clone. Eugenei had some root growth during early fall because the shoot was still actively growing. Tristis had almost no late season root growth since above-ground growth had ceased in mid-summer.

The morphology of the fine root system may help to explain the differential drought tolerance among species. The fine root system habit of Tristis plants might have contributed to its drought tolerance by growing twice the number of vertically oriented fine roots than Eugenei.

Concluding, the idea that Eugenei grows very well when its growth requirements are supplied in abundance was reinforced in this study. Tristis, on the other hand, is a more conservative, adaptable species that, although having a smaller growth capacity, was able to cope with the variations in the environment.

The study of fine roots of forest trees by using minirhizotrons and a video recording system showed to be a

promising technique for gathering fine root information. The technique is outstanding for constant and rapid observation of fine root development and for the study of fine root morphology.

APPENDIX



Figure A.1. A large 2.3 mm diameter root showing signs of diameter growth and shedding of the rhizodermis in Eugenei natural conditions treatment (photograph represents 17.4 x 11.6 mm).



Figure A.2. Water bubbles on the external minirhizotron surface hampers visualization of the very fine (0.05 to 0.2 mm) roots (photograph represent 17.4 x 11.6 mm).

Table A.1 Accumulated number of fine roots per image (12 mm) of four minirhizotrons and four faces in Eugenei well watered treatment.

Image	No. of fine roots/observ.															
No.	Horizontal								Vertical							
	1	2	3	4	5	6	7	8	1	2	3	4	5	6	7	8
1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2	1	2	2	3	4	5	5	4	0	0	0	1	1	3	2	0
3	0	1	1	1	1	1	1	0	2	2	2	2	2	1	1	1
4	2	2	1	2	3	2	2	1	0	0	1	2	2	2	2	2
5	0	1	1	0	0	0	0	0	4	4	4	3	1	1	1	1
6	2	3	3	3	3	3	3	2	4	5	5	5	7	5	3	2
7	6	7	7	6	6	6	4	1	3	3	3	4	4	4	4	3
8	5	6	6	6	6	6	5	4	5	6	7	7	7	7	8	2
9	9	9	10	10	10	10	10	7	5	5	6	6	6	6	4	1
10	8	8	8	9	9	9	8	1	7	7	7	8	7	8	8	4
11	3	3	3	3	2	2	2	2	9	8	8	8	9	9	8	8
12	1	2	2	2	2	2	2	0	6	6	7	7	10	10	9	5
13	4	4	4	5	4	4	4	4	7	9	9	7	9	9	6	3
14	5	5	4	5	5	5	3	3	0	0	0	0	4	3	2	2
15	6	8	8	3	4	3	3	3	2	2	2	1	2	2	1	1
16	3	3	4	4	3	3	2	0	1	2	3	3	4	4	3	3
17	8	9	8	8	7	6	4	3	5	9	9	7	10	9	5	5
18	6	6	6	6	6	6	6	10	3	3	3	5	6	4	2	2
19	4	4	4	4	4	5	5	3	4	4	4	3	2	1	1	0
20	5	5	4	4	5	5	4	3	6	6	6	5	5	5	3	3
21	1	1	1	2	2	2	2	1	6	6	6	5	5	6	5	3
22	2	2	2	2	4	3	1	1	3	3	3	3	3	4	4	2
23	1	1	1	1	2	2	1	1	3	4	4	5	8	8	6	5
24	0	0	2	2	2	2	2	2	4	4	4	5	6	5	3	3
25	0	0	0	0	0	0	0	0	5	5	4	4	4	3	3	0
26	3	3	2	2	2	2	3	3	4	4	5	1	1	2	1	1
27	3	4	4	5	6	5	5	3	3	6	5	4	4	3	2	0
28	1	1	1	0	0	0	0	0	3	5	6	6	11	8	5	3
29	1	1	1	1	1	1	1	1	4	4	5	5	7	5	2	2
30	1	2	3	2	2	2	2	1	4	4	5	8	9	8	6	3
31	4	4	4	3	3	3	2	2	4	4	2	2	4	4	3	3
32	2	3	3	2	2	2	2	1	7	7	6	5	7	9	7	2
33	2	2	2	2	3	4	2	1	3	3	3	2	4	4	2	2
34	6	6	8	7	7	7	5	3	1	6	4	6	2	2	2	0
35	1	1	2	2	1	1	1	1	2	5	5	3	5	3	2	2
36	9	10	10	10	8	8	7	6	0	3	3	0	3	2	2	1
37	1	2	3	4	4	3	1	0	1	1	1	1	6	4	2	0
38	2	2	2	2	2	1	1	1	0	0	0	0	0	1	1	1
39	4	5	5	5	4	2	1	1	0	0	0	4	5	4	2	0

-continuation of Table A.1

[illegible]

Table A.2. Accumulated number of fine roots per image (12 mm) of four minirhizotrons and four faces in Eugenei natural conditions treatment.

Image	No. of fine roots/observ.															
No.	Horizontal								Vertical							
	1	2	3	4	5	6	7	8	1	2	3	4	5	6	7	8
1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2	0	0	0	3	4	4	4	6	0	1	1	4	5	5	4	5
3	0	0	1	3	3	3	3	3	1	3	0	1	1	2	2	2
4	0	0	1	2	2	4	4	6	1	2	2	2	3	4	5	7
5	0	0	0	2	2	2	2	1	2	3	3	6	8	9	9	7
6	0	1	1	0	0	0	0	0	4	6	6	10	8	7	6	4
7	1	1	1	2	2	2	2	2	0	1	2	2	2	2	2	2
8	3	4	2	2	2	1	1	1	2	5	4	1	1	1	1	1
9	4	8	7	7	9	11	11	12	2	2	2	3	4	3	4	4
10	4	4	6	4	3	3	3	0	3	3	2	2	2	3	1	2
11	1	3	4	4	3	1	1	0	4	3	4	4	6	7	11	9
12	0	0	1	2	1	1	1	0	3	5	6	7	11	8	8	10
13	1	3	2	2	4	6	6	8	2	2	2	5	6	7	8	8
14	2	5	4	8	8	7	5	4	2	1	3	6	7	7	5	4
15	1	2	2	1	1	2	2	4	1	2	1	0	1	2	2	2
16	0	0	0	0	0	0	0	0	0	1	2	2	3	2	2	2
17	0	2	2	2	1	0	0	0	2	1	1	1	0	0	0	0
18	1	2	2	1	1	0	0	0	2	3	2	2	1	1	1	1
19	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0
20	1	1	1	1	1	1	1	0	2	2	2	2	2	2	1	1
21	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0
22	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0
23	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1
24	0	0	0	0	0	0	0	0	0	0	1	3	4	4	3	3
25	0	0	0	2	2	2	2	2	0	0	0	3	3	3	3	3
26	0	0	0	0	2	3	3	4	0	0	0	0	3	2	2	1
27	0	1	1	2	3	3	3	3	0	0	0	0	0	0	0	0
28	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
29	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
30	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
31	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
32	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
33	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
34	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
35	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1
36	1	2	2	1	0	0	0	0	0	0	0	0	0	0	0	0
37	0	0	0	0	0	0	0	0	1	2	2	2	2	2	2	0
38	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0
39	0	0	0	0	0	1	1	2	0	0	0	0	0	0	0	0

-continuation of Table A.2

[illegible]

Table A.3. Accumulated number of fine roots per image (12 mm) of four minirhizotrons and four faces in Tristis well watered treatment.

Image No.	Horizontal								Vertical							
	1	2	3	4	5	6	7	8	1	2	3	4	5	6	7	8
1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0
3	0	1	1	2	2	2	1	0	0	0	0	0	0	0	0	0
4	0	0	0	2	2	1	1	1	3	1	1	1	1	0	1	1
5	3	2	1	1	1	1	1	1	5	2	2	0	0	1	1	1
6	6	3	2	2	2	2	2	0	4	5	3	2	2	0	1	1
7	4	3	3	2	2	1	0	0	0	3	3	4	4	8	0	0
8	2	3	4	4	4	1	0	0	0	2	3	4	4	7	2	1
9	4	4	5	5	5	3	1	1	0	1	1	2	2	6	2	2
10	1	2	2	2	3	1	1	1	2	2	2	3	5	4	3	3
11	5	5	4	4	6	6	5	2	1	1	0	0	2	5	0	0
12	0	0	0	2	3	2	0	0	2	5	9	8	8	8	6	5
13	4	6	4	4	3	3	2	2	1	3	1	1	2	8	2	2
14	2	3	3	2	2	2	3	3	5	8	4	3	3	5	4	4
15	4	5	3	3	4	4	4	2	3	4	3	2	3	5	5	3
16	0	0	0	0	0	0	0	0	4	8	7	6	3	8	2	2
17	1	2	0	0	0	0	0	0	7	8	3	3	3	5	3	2
18	0	0	0	0	0	0	0	0	5	6	5	4	4	2	3	2
19	2	2	2	2	3	4	3	2	2	3	3	3	2	0	0	0
20	0	0	0	0	0	0	0	0	1	2	2	3	5	3	3	3
21	0	0	0	0	0	0	0	0	1	1	1	2	2	2	0	0
22	1	1	1	1	1	1	1	0	1	1	1	1	3	1	1	1
23	0	0	0	0	0	0	0	0	1	1	1	2	2	8	3	3
24	0	0	0	0	0	0	0	0	0	1	1	1	2	5	1	1
25	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1
26	1	1	0	0	0	0	0	0	1	1	0	0	0	0	0	0
27	0	0	0	0	0	0	0	0	1	1	1	1	1	0	0	0
28	1	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0
29	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
30	0	0	0	0	0	0	0	0	1	1	1	1	2	2	1	1
31	0	0	0	0	0	0	0	0	1	2	1	0	0	0	0	0
32	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0
33	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1
34	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
35	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
36	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
37	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
38	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
39	0	0	0	0	0	0	0	0	2	2	0	0	0	0	0	0

[illegible]

Table A.4. Accumulated number of fine roots per image (12 mm) of four minirhizotrons and four faces in Tristis natural conditions treatment.

Image	No. of fine roots/observ.															
No.	Horizontal								Vertical							
	1	2	3	4	5	6	7	8	1	2	3	4	5	6	7	8
1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2	0	0	0	0	0	0	0	0	1	1	1	1	0	0	0	0
3	1	1	2	2	2	2	2	2	0	0	0	0	0	0	0	0
4	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0
5	1	1	0	0	0	0	0	0	1	0	0	0	1	1	0	0
6	6	6	6	6	5	1	1	0	1	1	1	1	0	0	0	0
7	1	1	2	2	3	2	1	0	5	5	5	8	9	8	6	3
8	0	0	0	0	0	0	0	0	2	9	8	7	6	7	1	0
9	6	2	2	2	3	3	0	0	3	4	5	5	7	6	2	1
10	6	6	6	6	3	3	3	2	5	6	6	6	4	4	4	4
11	7	8	6	6	7	6	4	2	14	9	5	6	7	5	4	5
12	10	9	10	11	11	10	9	9	12	12	13	13	12	8	9	7
13	0	0	0	0	0	0	0	0	5	5	6	10	9	8	7	4
14	2	2	2	2	2	0	0	0	9	5	6	5	5	5	4	2
15	2	2	2	2	3	3	3	3	1	3	3	3	5	5	4	4
16	1	1	1	2	2	2	0	0	5	5	5	7	7	8	3	2
17	4	4	5	5	6	6	7	4	1	1	1	1	5	5	5	0
18	2	3	3	2	1	1	1	0	7	9	9	8	4	2	2	1
19	2	2	0	0	0	0	0	0	5	4	0	0	0	0	4	2
20	2	2	1	1	0	0	0	0	2	6	1	1	1	1	1	0
21	0	0	0	0	0	0	0	0	0	3	4	5	3	2	2	1
22	1	1	1	4	3	1	1	1	1	1	1	4	2	1	1	1
23	0	0	0	0	0	0	0	0	2	3	3	5	10	8	4	1
24	0	0	0	0	0	0	0	0	0	1	2	2	3	5	3	3
25	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0
26	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
27	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
28	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
29	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0
30	0	0	0	0	0	0	0	0	1	1	1	1	1	1	0	0
31	0	0	0	0	0	0	0	0	1	1	3	4	3	3	3	3
32	0	0	0	0	0	0	0	0	0	2	2	2	2	3	2	2
33	0	0	0	0	0	0	0	0	3	2	1	1	1	1	1	1
34	1	1	0	0	0	0	0	0	2	1	1	1	1	2	2	1
35	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0
36	0	0	0	0	0	0	0	0	1	1	2	2	0	0	0	0
37	0	0	0	0	0	0	0	0	1	2	2	2	4	6	1	1
38	0	0	0	0	0	0	0	0	0	1	2	1	0	0	0	0
39	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

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