

AN ABSTRACT OF THE DISSERTATION OF

Eladio H. Cornejo-Oviedo for the degree of Doctor of Philosophy in Forest Science presented on December 9, 1999. Title: Regeneration Aspects of Three Mexican *Pinus* Species: Field and Greenhouse Studies.

Abstract approved:

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William H. Emmingham

In a field study, seedlings of Arizona pine (*Pinus arizonica* Engelm.), Apache pine (*P. engelmannii* Carr.), and Durango pine (*P. durangensis* Mart.) were planted in an open area and in canopy gaps of four forested sites of a pine-oak forest in the Sierra Madre Occidental in the state of Durango, Mexico. Competing vegetation in half of the study plots was treated with glyphosate before planting to test the effects of competition on survival, growth, and water relations. After two years in the open area, significant herbicide effects were detected only for the survival of *P. engelmannii* and *P. durangensis*. Stem height and diameters were significantly different between treated and untreated plots only for *P. engelmannii*. Midday xylem water potential in *P. durangensis* was significantly different between treated and untreated plots, and morning and midday stomatal conductance rates of *P. engelmannii* were significantly different between treated and untreated plots 21 months after planting. In the canopy gaps, significant herbicide effects were detected only for the survival of *P. durangensis*. There was little understory vegetation in canopy gaps, therefore, treated and untreated plots did not differ in seedling growth or water relations among the species.

In a greenhouse study, seedlings of *P. arizonica*, *P. engelmannii*, *P. durangensis*, and Pacific ponderosa pine (*Pinus ponderosa* var. *ponderosa* Laws.) were subjected

to well-watered and water-stressed treatments over three replicated drying cycles in the dormant season. The volumetric water content ranged between 67 and 36% in the well-watered treatment, and between 8.0 and 2.0% in the water-stressed treatment. Statistically, no water stress effect was found on seedling growth except for *P. durangensis*, and biologically the effect was marginal. Xylem water potential and stomatal conductance were measured in needle fascicles at the end of two drying cycles. The water stress caused significant and highly significant treatment and diurnal differences for water potential and stomatal conductance on most of the species in those two cycles. A predawn water potential threshold associated with less than 50% of the maximum midday stomatal conductance was found for each species. The threshold for the three Mexican pine species ranged from -0.6 to -0.8 MPa while *P. ponderosa* var. *ponderosa* had a higher threshold at -1.1 MPa.

Through tree planting, the uncertainties of the natural regeneration process are avoided. Successful regeneration of forested sites in the Sierra Madre Occidental will require reduction in overstory stocking, control of competing vegetation where necessary and prevention of livestock grazing.

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Regeneration Aspects of Three Mexican *Pinus* Species:
Field and Greenhouse Studies

by

Eladio H. Cornejo-Oviedo

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DEDICATION

I would like to dedicate this dissertation to:

My parents Eladio Cornejo-Lugo and Ma. Guadalupe Oviedo de Cornejo

My sisters, brothers, sisters in law, brothers in law, nieces, and nephews.

The people of the Comunidad El Tarahumar y Bajíos del Tarahumar,
Tepehuanes, Durango.

The people of my country: México.

Regeneration Aspects of Three Mexican *Pinus* Species: Field and Greenhouse Studies

1. INTRODUCTION ¹

Mexico's native forests are biologically and economically important. Their great diversity of pines, potential for carbon sequestration, and the importance of forest products to local and regional economies make the study of native forests an imperative. However, forest vegetation management and pine seedling physiology are poorly understood. This study examined basic aspects of pine seedling physiology and application of herbicides as a means of improving nursery practices and regeneration methods.

Native commercial forests in Mexico comprise 53.9 million ha (27.4% of the total area), with 30.4 million ha in temperate forests and 23.5 million ha in tropical forests (SARH, 1994). Mexico's biodiversity is widely recognized (Rzedowski, 1991, 1993; Bye, 1995). Fifty-two pine species have been identified in the temperate forests (Perry, 1991), the most diverse pine population in the world (Hawksworth and Bailey, 1989; Styles, 1993). The net carbon sequestered (tons of Carbon ha⁻¹; t C ha⁻¹) in temperate forests was approximately 98 to 134 t C ha⁻¹ in 1995. This level was between that for tropical forests (148 to 182 t C ha⁻¹) and commercial pine plantations (97 to 101 t C ha⁻¹). Because temperate forests have a larger proportion of their total timber volume in commercial species and offer the largest benefit to landowners, Masera et al. (1995) contended that managing these forests is the most profitable and promising option for carbon sequestration.

¹The format used for this dissertation follows that of the journal *Forest Ecology and Management*

Approximately 80% of Mexican forest land is held in one of two forms of community-based corporate ownership (Alcorn and Toledo, 1995). These forms, recognized by Mexican agrarian law, are called *ejido* and *comunidad*. The *ejido* is a land grant that was created in 1917 after the Mexican revolution. The *comunidad* is an organized pre-existing entity. Members' rights are recognized if they can demonstrate prior longstanding, community-based use of the land and water (Alcorn and Toledo, 1995).

In Mexico, timber production can be enhanced by improving on traditional silvicultural systems (Castilleja and Goebel, 1995). However, selective cutting of pine forests generally has been the preferred method for harvesting. Selective cutting is then followed by poor natural pine regeneration, proliferation of noncommercial oak species (Negreros and Snook, 1984), overstocked pine stands ($> 20 \text{ m}^2 \text{ ha}^{-1}$) with multiple cohorts and low growth rates (Faeth et al. 1994), and destruction by fires. Therefore, it is important to understand regeneration dynamics, given the current popularity of selective harvesting and fire suppression, and the resultant overstocking in stands. Musálem-Santiago et al. (1987) stated that, because of its inherent shade intolerance, natural pine regeneration is successful mostly on sites with no more than $10 \text{ m}^2 \text{ ha}^{-1}$ of residual basal area after harvest. In many cases management plans have ignored the natural processes of forest succession, competition, and regeneration establishment (Jardel-Peláez, 1985; Jardel-Peláez and Sánchez-Velásquez, 1989). Field studies of pine ecophysiology are essential for helping to preserve the rich pine diversity in Mexico (Rundel and Yoder, 1998).

In the United States, Tinus and Owston (1984) stated that physiological research improved survival and growth of container-grown seedlings. In Mexico, Mexal et al. (1994) reported that low quality seedlings are produced with the polyethylene bag-container system because irrigation is inadequate and poorly distributed, and often seedlings are produced with poor root to shoot ratios. Mexican nursery managers need to understand basic elements of seed biology and seedling physiology if they are to improve the quality of their stock (Mexal, 1996).

In Mexico, pine-oak forests occur throughout the Sierra Madre Occidental (SMOC), on sites with a blend of contrasting geological, climatological, and topographical characteristics (Rzedowski, 1978). The SMOC has a continental climate with a pronounced drought period in early spring (March through May). More than 50% of the annual rain falls from July to September. Fall is drier, followed by some rain or snow from December through February. In the SMOC, Arizona pine (*Pinus arizonica* Engelm.), Apache pine or pino real (*P. engelmannii* Carr.), and Durango pine (*P. durangensis* Mart.) are widely distributed and economically valuable.

Forest vegetation management is poorly understood and applied in the SMOC. Forest vegetation management may be defined as controlling the rate and course of secondary forest succession by 1) planting or promoting the establishment of desired species, and 2) removing or inhibiting the growth or establishment of undesirable plants (Wagner and Zasada, 1991). Spraying herbicide is a way of controlling secondary succession on a given site. Competing vegetation is treated with herbicide, soil moisture and nutrients become available to seedlings planted on the site (Newton and Preest, 1981; Nambiar and Sands, 1993). Capó-Arteaga and Newton (1991) observed in northeastern Mexico and Oregon that consistent improvement in survival and growth occurred in both locations when both herbs and shrubs were controlled prior to planting pines native to both areas.

Seedling water relations of *P. arizonica*, *P. engelmannii*, and *P. durangensis* are poorly understood. Woodward (1998) stated that the opening and closing of stomata not only regulate the rate of water loss and plant water-use efficiency, but may also help increase seedling survival and competitive ability.

With more knowledge about seedling physiology, forest managers can more effectively match stock types to particular planting sites. The research described in this dissertation concentrated on the effects of seedling planting practices and the application of herbicides as means for understanding the role of cover in pine regeneration in the SMOC. Basic aspects of pine seedling physiology were examined, including diurnal patterns of plant water potential and stomatal conductance, and stomatal thresholds under soil water-stress conditions. This dissertation includes the results of field and greenhouse studies.

The objectives of the field study were to evaluate: 1) survival; 2) absolute stem height, stem diameter, and volume growth rates; and 3) plant water potential and stomatal conductance rates of *P. arizonica*, *P. engelmannii*, and *P. durangensis*. Seedlings of these species were grown for two years in plots with and without herbicide treatments, in an open area and in the canopy gaps of four forested sites.

The objectives of the greenhouse study were to evaluate the influences of water stress on: 1) relative stem height and stem diameter growth rates; 2) shoot and root dry-mass ratios; 3) plant water potential and stomatal conductance rates of pine seedlings during the dormant season; and 4) determine a range of predawn plant water potential for the point at which less than 50% the maximum midday stomatal conductance occurred. Seedlings of *P. arizonica*, *P. engelmannii*, *P. durangensis*, and Pacific ponderosa pine (*Pinus ponderosa* var. *ponderosa* Laws.) were used for all greenhouse measurements.

2. EARLY SURVIVAL, GROWTH, AND WATER RELATIONS OF THREE *PINUS* SPECIES PLANTED IN A PINE-OAK FOREST IN DURANGO, MEXICO.

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2.1 Abstract

Ten- to thirteen-month-old seedlings of Arizona pine (*Pinus arizonica* Engelm.), Apache pine (*P. engelmannii* Carr.), and Durango pine (*P. durangensis* Mart.) were planted in an open area and in canopy gaps of a pine-oak forest in Durango, Mexico. Survival, growth, and water relations of seedlings were evaluated for two growing seasons. Competing vegetation in half of the study plots was treated with glyphosate, a non-residual herbicide, before planting to test the effects of competition on survival, growth, and water relations. After two years in the open area, *P. arizonica* and *P. engelmannii* had higher survival rates than *P. durangensis*. Significant herbicide effects, however, were detected only for the survival of *P. engelmannii* and *P. durangensis*. The tallest seedlings, i.e., *P. arizonica* and *P. durangensis*, grew more in stem height, and the shortest seedlings, *P. engelmannii*, grew more in stem diameter. Stem height and diameters were significantly different between treated and untreated plots only for *P. engelmannii*. Midday xylem water potential in *P. durangensis* was significantly different between treated and untreated plots in the spring (21 months after planting); morning and midday stomatal conductance rates of *P. engelmannii* were significantly different between treated and untreated plots in that spring. Treated and untreated plots showed no differences across the three species for xylem water potential during the summer (26 months after planting). Summer-maximum rainfall likely prevented soil dessication regardless of weed control treatments. In the canopy gaps, seedling survival was moderately high (>60%) for all species, however significant herbicide effects were detected only for *P. durangensis*. There was little understory vegetation in canopy gaps (sprayed and unsprayed), therefore, herbicide treatments had little effect on seedling growth for any of the pines. Similarly, herbicide treatments had little effect on xylem water potential and stomatal conductance rates in spring and xylem water potential in the summer.

2.2 Introduction

Approximately 27.4% (53.9 million ha) of the total land area in Mexico is covered by native, commercial forest with nearly 30.4 million ha of that in temperate forests (SARH, 1994). The diversity of Mexico's pine species is widely recognized (Hawksworth and Bailey, 1989; Perry, 1991; Styles, 1993).

In Mexico, managing the native temperate forest is economically feasible and can increase carbon sequestration (Masera et al. 1995). Timber production can be enhanced by improving silvicultural systems (Castilleja and Goebel, 1995). However, selective cutting of pine forests generally has been the preferred method for harvesting. Selective cutting is then followed by poor natural pine regeneration, proliferation of noncommercial oak species (Negreros and Snook, 1984), overstocked pine stands ($> 20 \text{ m}^2 \text{ ha}^{-1}$) with multiple cohorts and low growth rates (Faeth et al. 1994), and destruction by fires. Therefore, it is important to understand regeneration dynamics, given the current popularity of selective harvesting and fire suppression, and the resultant overstocking in stands. Musálem-Santiago et al. (1987) stated that, because of its inherent shade intolerance, natural pine regeneration is successful mostly on sites with no more than $10 \text{ m}^2 \text{ ha}^{-1}$ of residual basal area after harvest. In many cases management plans have ignored the natural processes of forest succession, competition, and regeneration establishment (Jardel-Peláez, 1985)

Natural pine regeneration has been successfully established in uneven-aged systems in the southeastern portion of the United States (Cain, 1991; Shelton and Murphy, 1994; 1997). Their studies involved prolific pine species; evaluation of seed-crop production, identification of the year and season for harvesting; manipulation of the stand structure by reducing pine and hardwood densities mechanically and chemically; and mechanical preparation of the seedbed.

To ensure pine regeneration, the silvicultural needs of desirable species should be linked to environmental conditions (Spittlehouse and Stathers, 1990). Plant metabolism is influenced by light intensity, nutrient and soil moisture availability, soil temperature, vapor pressure deficit, and competition dynamics on a given site (Spomer, 1973). Regeneration is most successful in an environment that promotes seedling establishment and growth (Margolis and Brand, 1990). The goal of any management program should be to identify the regeneration method that provides the most suitable niches for a given site and species (Tesch and Helms, 1992). Forest vegetation management may be defined as guiding the secondary forest succession to create the suitable regeneration niche for a desired species, stand structure, and growth rate. In addition, management involves controlling the rate and course of secondary forest succession by planting or promoting the establishment of the desired species and by removing or inhibiting the growth or establishment of undesirable plant species (Wagner and Zasada, 1991).

Spraying herbicide is a way of modifying the secondary succession on a given site. After undesirable, competing vegetation is treated with herbicide, demands on soil moisture and nutrients decrease, hence they become available to seedlings planted on the site (Newton and Preest, 1981; Nambiar and Sands, 1993). Capó-Arteaga and Newton (1991) observed in northeastern Mexico and Oregon that consistent improvement in survival and growth occurred in both locations when both herbs and shrubs were controlled prior to planting pines native to both areas.

Open areas can be used to control the rate and course of secondary succession by favoring the establishment of shade-intolerant species. These areas may result from natural or human disturbances, and are characterized in early successional stages by the presence of ruderal plants with short life spans and high seed production (Radosevich and Osteryoung, 1987). Herbaceous and forb species (*Cruciferae* or *Compositae*)

characterize the early successional stages in abandoned fields (Bazzaz, 1996).

Canopy gaps or openings are regeneration niches formed by natural disturbances such as disease, insects, fire, or tree fall. Shade-tolerant species colonize small openings, while shade-intolerant species become established in large canopy gaps or openings (Whitmore, 1989). In a single-tree selection system, small gaps are created by harvesting mature trees. However, the successful regeneration of shade-intolerant pine species in an uneven-aged system relies, among other factors, on the regulation of the residual basal area. Guldin and Baker (1998) working with loblolly pine (*Pinus taeda* L.) found that overstocked residual basal areas ($>17.0 \text{ m}^2 \text{ ha}^{-1}$) will suppress regeneration. Understocked residual basal areas ($<10.0 \text{ m}^2 \text{ ha}^{-1}$), however, will encourage an irregular shelterwood arrangement.

Pines and oaks are easily regenerated in the summer-wet and winter-dry climate in the Sierra Madre Occidental (SMOC) of Mexico (Smith et al. 1997). In the SMOC, the pine-oak forest is found in a variety of geological, climatological, and topographical regions (Rzedowski, 1978; Ferrusquía-Villafranca, 1993). Stagnated understory vegetation is commonly observed in these forests. Similar understory conditions have been reported for Apache pine (*Pinus engelmannii* Carr.) and Arizona pine (*Pinus arizonica* Engelm.) stands in Arizona (Barton, 1994), and *P. taeda* and shortleaf pine (*Pinus echinata* Mill.) in uneven-aged stands in Arkansas (Tappe et al. 1995).

Pines are pioneer species that frequently invade after fires. Changes in the disturbance regime can alter this pattern of the invasion (Richardson and Bond, 1991). Fire suppression has changed the disturbance regime in the SMOC. For example, a pine-oak stand subjected to fire suppression after 1945 had a mean fire interval (MFI) of 15.3 to 46.0 years (Fulé and Covington, 1994, 1995). The previous long-term MFI

of would have been 3.8 to 5 years.

In the SMOC, fire suppression encouraged a clumped pattern of overstory trees, with a high density of small-diameter trees and an increase in the proportion of sprouting oak species. In contrast, the uninterrupted fire regime induced a random pattern to a uniform pattern of overstory trees and a relatively open stand (Fulé and Convington, 1998).

In the SMOC, *P. arizonica*, *P. engelmannii*, and Durango pine (*P. durangensis* Mart.) are widely distributed and economically valuable. They are commonly found together or associated with other conifer or oak species.

P. arizonica, (a three-needle pine), is restricted to elevations from 2,500 to 2,800 m in moist, cool valleys and mesas with deep, well-drained soils.

P. engelmannii, (a three-needle pine), grows at elevations of 1,900 to 2,600 m. Although it can be found in dry climates and poor soils on eastern slopes, it also grows in cool, moist valleys and mesas with deep soils or in the semitropical-temperate climate of the western slopes (Yeaton et al. 1983; Perry, 1991; García-Arévalo and González-Elizondo, 1998). The juvenile seedling stage has a "grass stage," which is typical of fire-resistant species (Mirov, 1967; McCune, 1988; Barton, 1993; Barton, 1995).

P. durangensis, (a six-needle pine), is found at 2,400 to 3,200 m in semi-humid to humid climates, and on a variety of slopes, mesas, and creeks (Perry, 1991; García-Arévalo and González-Elizondo, 1998).

Open areas created by fire or agricultural activities are common and are occupied by herbaceous vegetation. The reforestation of these areas is seen as a means for controlling soil erosion, rather than for timber production. The canopy gaps created by extensive selective cutting are often occupied by undesirable species. Both open areas and canopy gaps offer an opportunity to study some aspects of pine regeneration. Field research of pine ecophysiology is imperative for helping to preserve the rich pine diversity in Mexico (Rundel and Yoder, 1998). Therefore, a field study was conducted to begin to understand the survival, growth, and water relations of *P. arizonica*, *P. engelmannii*, and *P. durangensis* seedlings planted in an open area and canopy gaps in a pine-oak forest in the SMOC. The null hypothesis was that reduction of competition by the use of herbicide would not significantly affect survival, growth, and water relations of these seedlings.

The specific objectives were to evaluate the influence of reduction in herbaceous cover and presence of overstory on::

- 1) survival,
- 2) absolute stem height, stem diameter, and volume growth rates, and
- 3) plant water potential and stomatal conductance rates.

Seedlings of these species were grown for two years in plots with and without herbicide treatments, in an open area and in the canopy gaps of four forested sites.

2.3 Materials and methods

2.3.1 Area description

The planting sites were within the Comunidad El Tarahumar y Bajíos del Tarahumar (Tarahumar), Tepehuanes, Durango, Mexico (Fig. 2.1). Elevations in this region of the SMOC range from 2,052 to 2,650 m (INEGI, 1992). Stratigraphically, lower and upper volcanic complexes are found in the SMOC. The lower complex is intensely faulted and is compounded by andesitic materials, including lavas and pyroclastic sheets. The upper, discontinuous complex is compounded by extensive silicic ignimbrite (Ferrusquía-Villafranca, 1993). Litosols and regosols are the most common soil types, and sandy-loam and clay-loam soils are widely distributed, with depths ranging from 0.5 to 2.0 m (UAF "Tepehuanes," 1995).

Mean annual rainfall is 909.93 mm (Fig. 2.2), with peaks in summer and early winter. Little rain falls in spring. Precipitation was less than the mean annual in 1995, 1996, and 1997 (25.1%, 32.2%, and 3.4%, respectively). 1998 precipitation (up to November) was about 41.0% less than the mean annual and no rain fell during April of that year. August 1998 rainfall was 35.7% less than the 195.8 mm expected for that month (Conagua and Cornejo-Oviedo, unpublished data).

Mean annual air temperature is 10.3 °C (Fig. 2.2). July and August are the warmest and December is the coldest. April of 1998 was cooler than normal (7.25 vs 9.41°C), however. August of that year was just below average (14.26 vs 14.93 °C; Conagua and Cornejo-Oviedo, unpublished data).

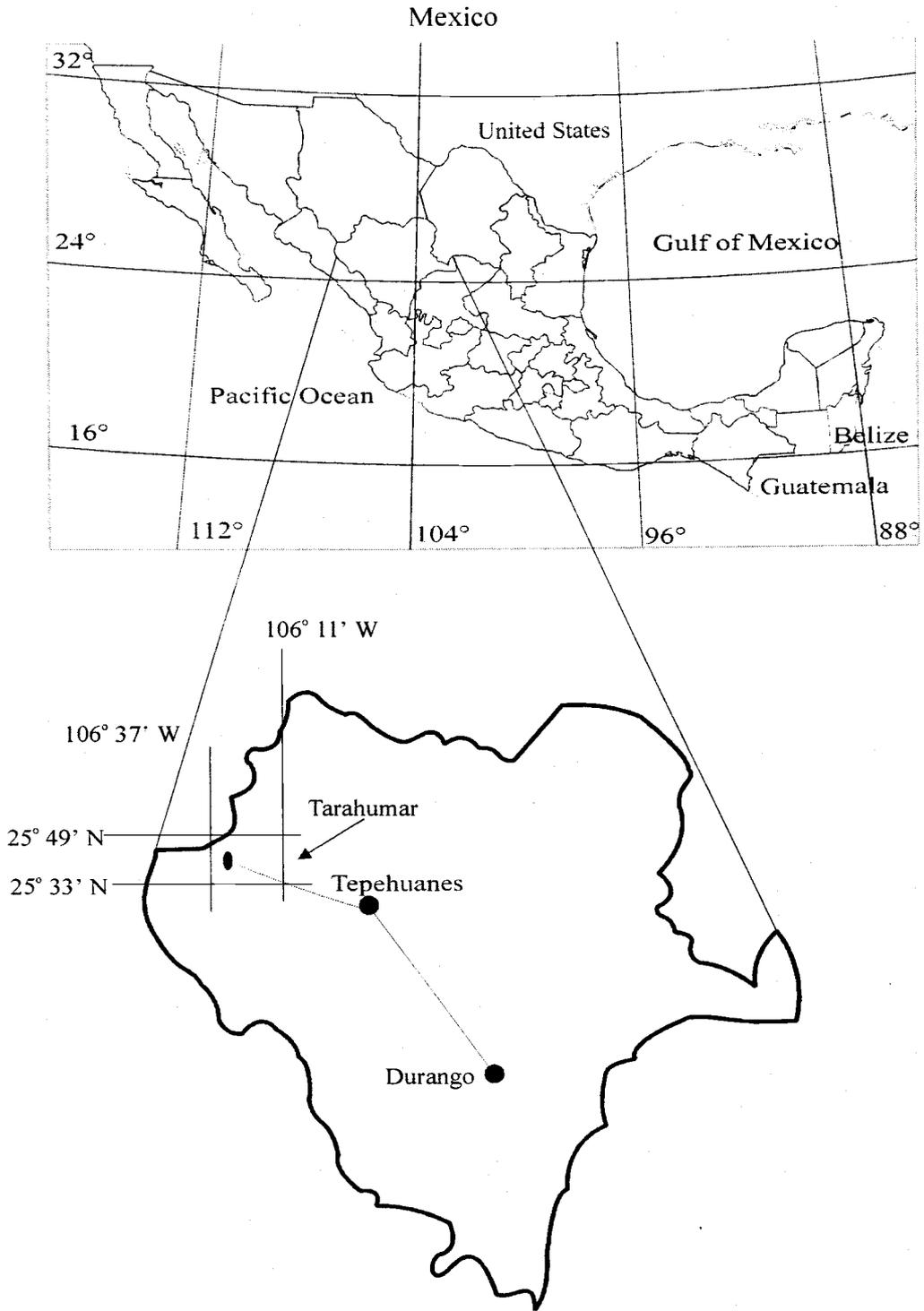


Figure 2.1 Geographical location of Comunidad El Tarahumar y Bajíos del Tarahumar, Tepehuanes, Durango, Mexico.

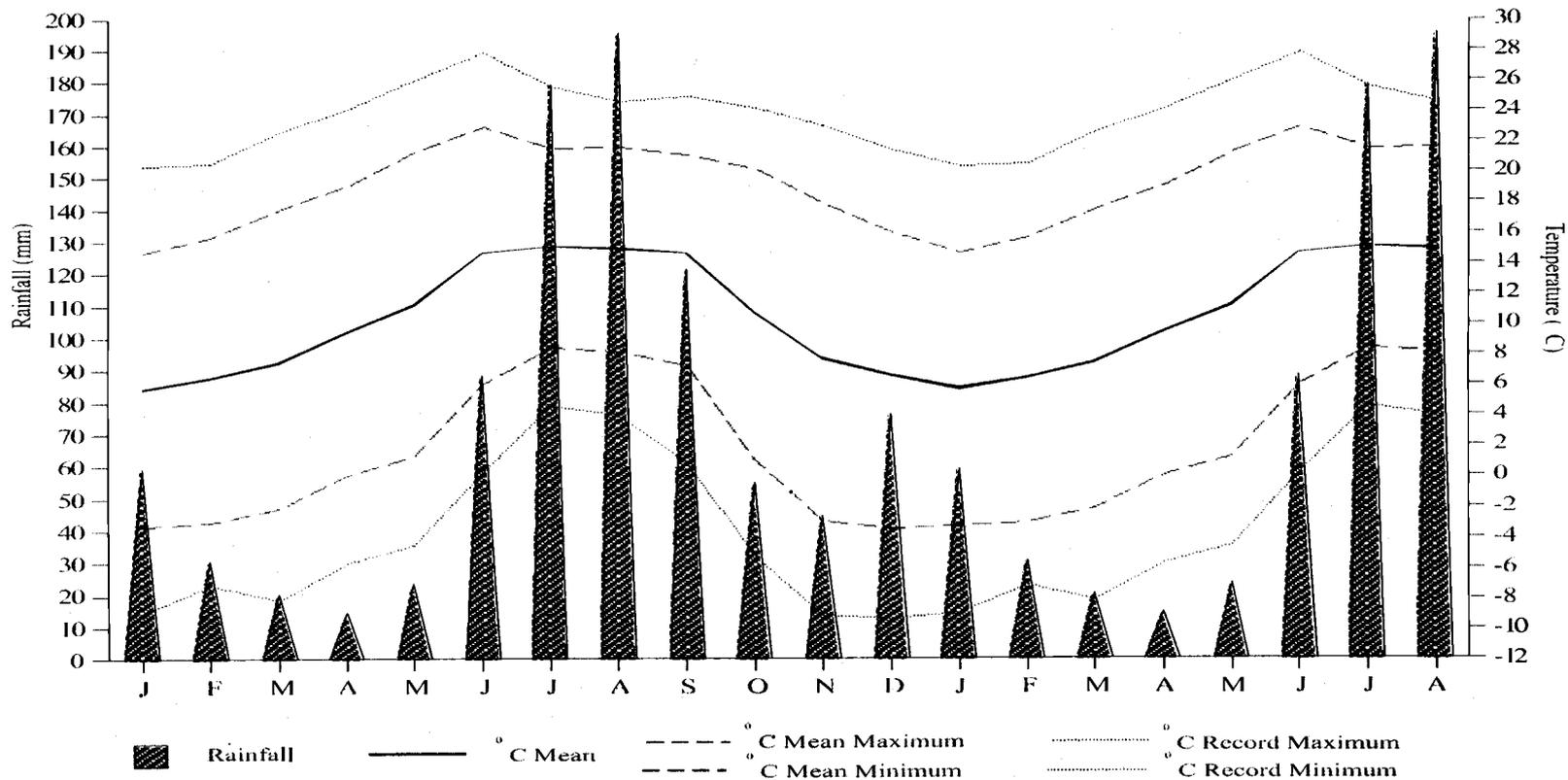


Figure 2.2 Monthly mean rainfall, mean temperature, mean monthly maximum and minimum temperatures, and monthly record maximum and minimum temperatures at the El Tarahumar weather station (25° 38' N; 106° 21' W; 2,435 m). (n=28 years). Values are shown for a 20-month period to display the seasonal sequence.

In Tarahumar, the forest is classified as pine-oak, following the vegetation classification system of Rzedowski (1988). Cones, needles, leaves, branches, stems, and flowers were collected from trees, shrubs, and herbaceous plants in four forested sites and three open areas in the summer of 1997. Personnel from the Centro Interdisciplinario de Investigación para el Desarrollo Integral Regional (CIIDIR) Unidad Durango del Instituto Politécnico Nacional (CIIDIR-IPN) identified the species composition according to González-Elizondo et al. (1991) and García-Arévalo and González-Elizondo (1998).

The upland pine-oak forests in Tarahumar were a complex blend of communities heavily influenced by site conditions and disturbance history. Three vegetation strata were recognized: 1) a tree stratum, with a diameter breast height (DBH) ≥ 5 cm, was composed of *Alnus sp.*, *Arbutus xalapensis*, *Garrya laurifolia*, *Juniperus deppeana*, *Pinus arizonica*, *P. ayacahuite*, *P. durangensis*, *P. leiophylla*, *P. lumholtzii*, *P. strobiformis*, *P. teocote*, *Pseudotsuga mensiezii*, *Quercus crassifolia*, *Q. migosa*, and *Q. sideroxyla*; 2) a shrub stratum (DBH < 5 cm) comprising *Alnus sp.*, *Arbutus xalapensis*, *Garrya laurifolia*, *Juniperus deppeana*, *Pinus ayacahuite*, and *Quercus sideroxyla*; and, 3) an herbaceous stratum (height ≤ 1.50 m) that included *Astragalus sp.*, *Cyperus fendlerianus*, *Geranium sp.*, *Lotus sp.*, *Pteridium aquilinum*, and *Salvia sp.* In general, shrub and herbaceous strata were not well-developed in the forest understory.

In open areas and fallow agricultural fields, the herbaceous stratum was composed of *Aegopogon sp.*, *Castilleja sp.*, *Chenopodium graveolens*, *Commelina sp.*, *Cyperus manimae*, *Geranium sp.*, *Gnaphalium spicatum*, *Juncus sp.*, *Lupinus sp.*, *Potentilla thurberi*, *Prunella vulgaris*, *Salvia laevis*, *Sisyrinchium sp.*, and *Tagetes micrantha*.

2.3.2 Seedling acquisition and seed sources

The nursery manager from Union de Ejidos y Comunidades Forestales y Agropecuarias "Gral. Emiliano Zapata" (UNECOFAEZ), Santiago Papasquiario (25° 02' N; 105° 25' W), Durango, Mexico propagated and donated the seedlings for this study. Forest managers from Unidad de Administración Forestal "Tepehuanes" (UAF "Tepehuanes") collected pine seed from several local wild stands in the Tepehuanes region (Table 2.1). Seedlings were grown in styroblocks (Number 7; Stuewe & Sons, Inc.) with 160 conical cells of 121 cm³ each (cell depth = 20 cm; top diameter = 3.1 cm). *P. arizonica* and *P. engelmannii* seedlings were 10 months old, *P. durangensis*, 13 months old, when planted.

Table 2.1 Geographical location of Mexican pine seed sources from Durango, Mexico.

Species	Location	Latitude	Longitude
		N	W
<i>Pinus arizonica</i>	La Cebadilla, Canelas	25° 07'	106° 26'
<i>Pinus durangensis</i>	Comunidad Río y Papudos, Canelas	25° 02'	106° 32'
<i>Pinus engelmannii</i>	Ejido San José de la Cruz, Santiago Papasquiario	25° 03'	106° 22'

2.3.3 Experimental designs and planting procedures

Seedlings of *P. arizonica*, *P. engelmannii*, and *P. durangensis* were planted on five sites, from July 17 to 31, 1996 (during the rainy season). One open area and four forested sites were chosen. The seedlings were transported in an open truck to Tarahumar, where they were irrigated and kept under shade.

2.3.3.1 Open area

The open area had been cleared and used for growing corn. Several years ago, it was abandoned as a farm field, revegetated (Table 2.2), and was heavily grazed by free-roaming cattle. The site covered 0.15 ha and was at 2590 m (25°39' 31" N; 106° 20' 06" W) with a NE aspect and a 10% slope. The herbaceous vegetation was uniform and abundant (Table 2.2) and covered 70 to 80% of the ground. The area was adjacent to Las Conchitas, one of the four forested sites (Fig. 2.3). Twelve planting plots (8-x-8 m each) were established in a completely randomized design (Fig. 2.3). Six of the plots were chosen for herbicide treatment. Glyphosate (Coloso 480™) was applied at a rate of 2% active ingredient (a.i.) to the herbaceous vegetation, from a 15-liter backpack sprayer on July 23-24, 1996, before planting.

The seedlings were planted, with shovels and mattocks, on a 1-x-1 m spacing in each plot. Three groups of four seedlings each (12 seedlings for each three species) were randomly assigned within each plot (Fig. 2.4). Seedlings were planted in groups of 4 so that they could be thinned and still retain the random distribution. Even though this uniform distribution simplified the planting operation and future identification of the seedlings, it may have had a statistical confounding effect. In addition, 28 buffer seedlings were planted around each plot, for a total of 768 seedlings in the open area. At planting, the area was fenced to exclude livestock.

Table 2.2 Species composition of the herbaceous vegetation in the open area.

Family	Species
Boraginaceae	<i>Lithospermum sp.</i>
Chenopodiaceae	<i>Chenopodium graveolens</i> L.
Compositae	<i>Gnaphalium spicatum</i> Lam. <i>Tagetes micrantha</i> Cav
Cruciferae	<i>Brassica campestris</i> L.
Cyperaceae	<i>Cyperus manimae</i> HBK
Geraniaceae	<i>Geranium sp.</i>
Graminieae	<i>Aegopogon sp.</i>
Iridaceae	<i>Sisirynchium sp.</i>
Juncaceae	<i>Juncus tenuis</i> <i>Juncus liebmannii</i> Macbr.
Labiatae	<i>Salvia laevis</i> Benth <i>Prunella vulgaris</i> L.
Leguminosae	<i>Lupinus sp.</i>
Rosaceae	<i>Potentilla thurberi</i> A. Gray
Scrophulariaceae	<i>Castilleja sp.</i>

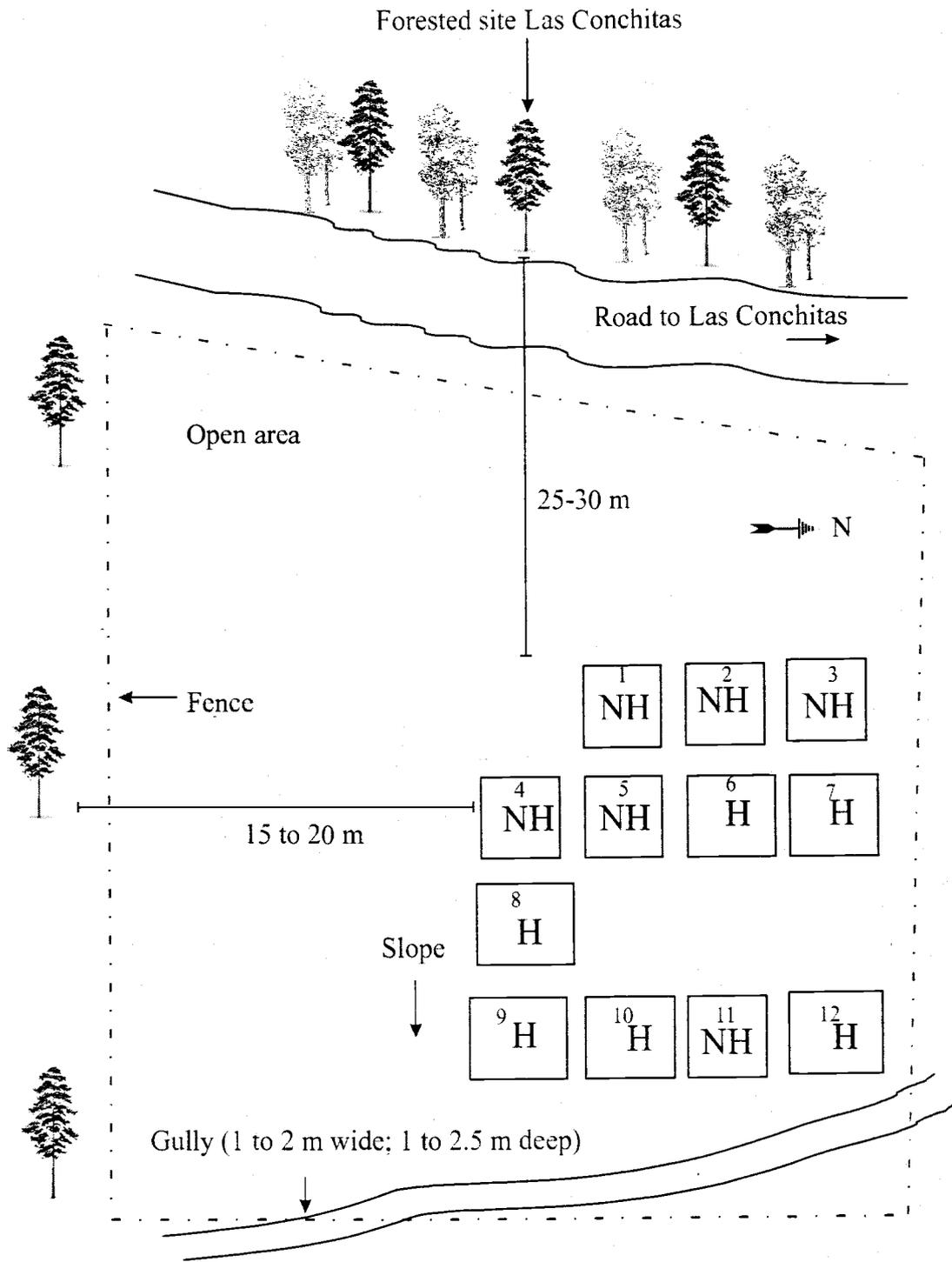
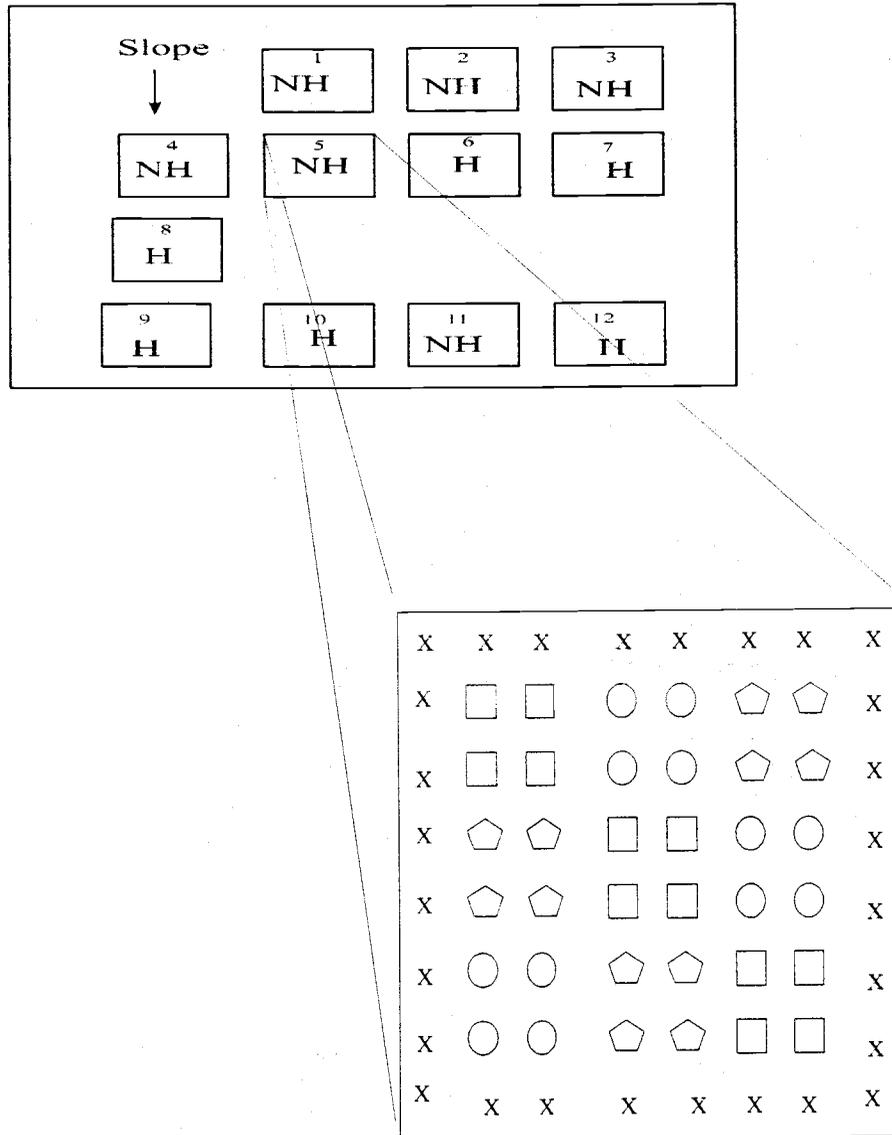


Figure 2.3 Layout of herbicide and no herbicide treatments in the open area at Tarahumar.

Open area



□ *P. arizonica* ○ *P. engelmannii* ◡ *P. durangensis*
 X Buffer seedlings

Figure 2.4 Species arrangement inside the 8-x-8-m plot. Seedlings were planted on a 1-x-1m grid.

2.3.3.2 Forested sites

The four forested sites had recently been harvested selectively (Table 2.3 contains the physical description of each site). Site index for all forested sites was 12 to 18 m (100-year basis), and was determined by using naturally regenerated trees that had become dominant (UAF "Tepehuanes," 1994, 1995). The trees probably had been suppressed a long time, undoubtedly leading to an underestimate of true site index. Thinning removal in 1994 and 1995 ranged from 23 to 29% of the volume (Table 2.4). In general, "selective" harvest entailed removing the dominant conifers without concurrent removal of hardwoods or thinning in lower crown classes.

Each forested site was sampled via three randomly distributed circular plots (0.1 ha each) during July of 1997. In these plots, heights and diameters were measured for all trees of all species with DBH \geq 5 cm. In two of the three plots at each site, cores were extracted for estimating the age at DBH (ADBH) and periodic annual radial increment at DBH (DPAI) in two to three pines of each diameter class \geq 15 cm (at 5-cm intervals). ADBH was estimated by counting the annual rings from the pith to the bark. The width of the last ten rings was measured to estimate PAI:

$$\text{DPAI} = \frac{(\text{width of the last ten rings}) * 2}{10} \quad \text{Equation 1}$$

Overstory species composition was similar across all four forested sites, except for Tijera del Santo Niño (Table 2.5). Pine and oak species were the most common overstory species found on the sites.

Table 2.3 Physical characteristics of the selected forested sites at Tarahumar.

Sites (name)	Latitude N	Longitude W	Elevation (m)	Aspect	Slope %	Area [†] (ha)
El Cercado	25°40' 11"	106°19' 32"	2585	NE	20	9
Las Conchitas	25°39' 31"	106° 20' 06"	2590	E	15	19.8
Tijera del Santo Niño	25°36' 35"	106° 19' 58"	2720	E	38	5.69
Arroyo del Cristo	25°39' 28"	106°20' 57"	2610	NE	20	12.1

Latitude and longitude were estimated using a Magellan GPS 300. Altitude was measured with a Thommen altimeter-barometer. Aspect was determined using a compass and the slope was measured with a Haga altimeter.

[†]= taken from the forest management program for Tarahumar (UAF "Tepehuanes," 1994, 1995).

Table 2.4 Pine volumes before and after selective harvest, and total tree basal area in the forested sites.

Site	Year Harvested	Volume before harvest [†] (m ³ ha ⁻¹)	Volume removed (m ³ ha ⁻¹)	Volume after harvest (m ³ ha ⁻¹)	Tree basal area [‡] (m ² ha ⁻¹)
El Cercado	1994	113.8	26.86	86.94	24.04
Las Conchitas	1994	102.3	24.24	78.06	22.91
Tijera del Santo Niño	1995	196.3	55.94	140.36	25.01
Arroyo del Cristo	1995	128.5	30.58	97.92	24.68

[†]=all volume numbers were taken from the forest management program for Tarahumar. Volume numbers before selective harvest were calculated based on a forest inventory for El Cercado and Las Conchitas in 1994 and for Tijera del Santo Niño and Arroyo del Cristo in 1995 (UAF "Tepehuanes," 1994; 1995).

[‡]= tree basal area was measured around the area occupied by the canopy gap-planted seedlings of this study.

Table 2.5 Overstory and understory species composition and understory ground cover in the four forested sites.

Site	Overstory species	Understory species	Cover (%)
El Cercado	<i>Pinus arizonica</i> , <i>P. durangensis</i> , <i>P. leiophylla</i> , <i>P. strobiformis</i> , <i>P. teocote</i> , <i>Quercus crassifolia</i> , <i>Q. sideroxyla</i> , and <i>Arbutus xalapensis</i> .	<i>Juniperus deppeana</i> , <i>Arbutus xalapensis</i> , <i>Salvia sp.</i> , <i>Astragalus sp.</i> , and <i>Lotus sp.</i>	5 to 10
Las Conchitas	<i>Pinus arizonica</i> , <i>P. leiophylla</i> , <i>P. teocote</i> , <i>P. strobiformis</i> , <i>Quercus sideroxyla</i> , <i>Q. crassifolia</i> , and <i>Arbutus xalapensis</i> .	<i>Juniperus deppeana</i> , <i>Arbutus xalapensis</i> , and <i>Salvia laevis</i> .	5 to 10
Arroyo del Cristo	<i>Pinus arizonica</i> , <i>P. durangensis</i> , <i>P. leiophylla</i> , <i>P. strobiformis</i> , <i>Quercus sideroxyla</i> , and <i>Juniperus deppeana</i> .	<i>Juniperus deppeana</i> , <i>Arbutus occidentalis</i> , <i>Pteridium aquilinum</i> , <i>Salvia sp.</i> , <i>Solanum sp.</i> , <i>Commelina dianthifolia</i> , <i>Cyperus fendlerianus</i> .	5 to 10
Tijera del Santo Niño	<i>Pinus arizonica</i> , <i>P. durangensis</i> , <i>P. strobiformis</i> , <i>Q. sideroxyla</i> , <i>Arbutus xalapensis</i> , <i>Juniperus deppeana</i> , <i>Pseudotsuga menziesii</i> , and <i>Alnus sp.</i>	<i>Juniperus deppeana</i> , <i>Arbutus xalapensis</i> , and <i>Pteridium aquilinum</i> .	5 to 20

Species native to mesic environments, such as *Pseudotsuga menziesii* and *Alnus sp.*, were found at Tijera del Santo Niño (Table 2.5). Understory species were also similar across all four forested sites. *Juniperus deppeana*, *Arbutus xalapensis*, *Salvia sp.*, and *Pteridium aquilinum* were the most common understory species across all sites. Understory ground cover (%) was similar at the four sites, except for Tijera del Santo Niño, where the understory ground cover was slightly higher (Table 2.5).

Las Conchitas, Tijera del Santo Niño, and Arroyo del Cristo had similar values of overstory density (trees ha⁻¹; Fig. 2.5B, E, F), which were higher than that of El Cercado (Fig. 2.5A). Basal area values (m² ha⁻¹) were very similar across the four sites (Table 2.4; Fig. 2.5C, D, G, H). *Pinus spp.* dominated at three sites. At Tijera del Santo Niño, however, pine and oak species shared the space almost equally (Fig. 2.5E, G). However, hardwood tree species in the 35- to 60-cm diameter-size classes covered 8.9258 m² ha⁻¹ of basal area, which represents 64.60% of the total hardwood basal area at Tijera del Santo Niño.

Across all sites, the diameter distribution (trees ha⁻¹) of pine in the overstory followed an inverse j-shaped curve, except for the 5-cm diameter class (Fig. 2.5A, B, E, F). However, basal area distributions were irregular across all sites (Fig. 2.5C, D, G, H), except for El Cercado. There, a bell-shaped curve was seen in the 10- to 40-cm diameter classes (Fig. 2.5A). In Las Conchitas, a mid-story of about 607 trees ha⁻¹ of pine and hardwood tree species was found around the 10- to 15-cm diameter classes.

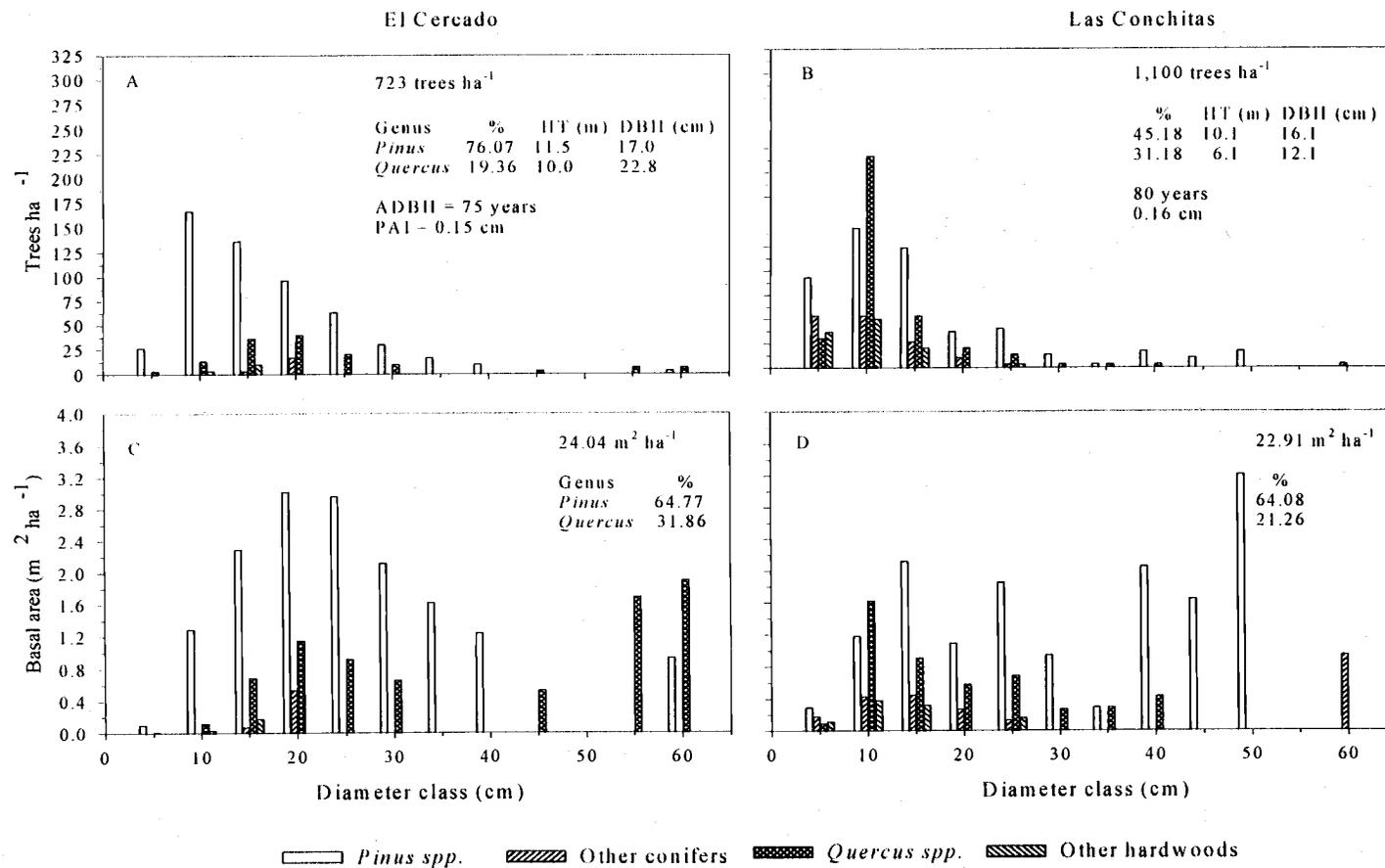


Figure 2.5 Overstory density, diameter structure, genus composition, age at DBH (ADBH), and periodic annual increment (PAI) of the forested sites at Tarahumar.

Tijera del Santo Niño

Arroyo del Cristo

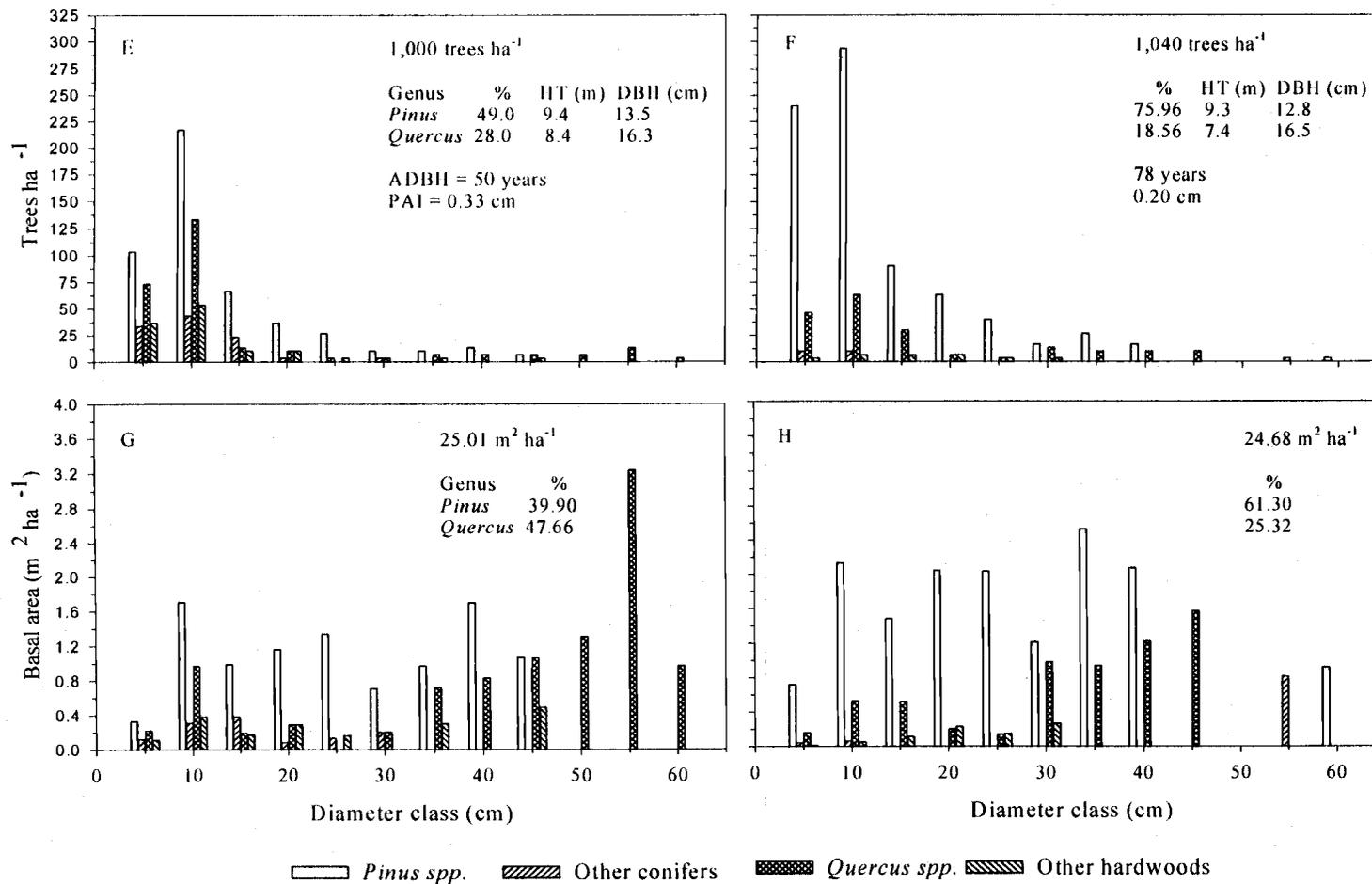


Figure 2.5 continued.

Heights and DBH of pine and oak species were similar across all sites, except for Tijera del Santo Niño. The average height of dominant pine trees (diameter-size class ≥ 35 cm) was 18 to 22 m at El Cercado. Average heights for dominant pine trees ranged between 19 and 22 m at Las Conchitas. At Tijera del Santo Niño, average height of dominant pine and oak trees was 19 to 22 m, and 16 to 20 m, respectively. Dominant pine trees averaged 22 m tall at Arroyo del Cristo. The DBH of the oaks was greatest (22.8 cm) at El Cercado (Fig. 2.5A, C). Stand age also was similar for all sites except at Tijera del Santo Niño, which was about 25 to 30 years younger. PAI also was higher at Tijera del Santo Niño (Fig. 2.5E,G).

A randomized complete block experimental design was used for the four forested sites. At each site, twelve planting plots (8-x-8 m) were established on selected canopy gaps of different sizes and shapes (Fig. 2.6A-D). The size of the canopy gaps ranged between 64 and 320 m², which represented a combination of conditions left by cutting a single mature tree, logging operations, and the natural arrangement of standing overstory trees left after selection cutting. The shapes included circles, ellipses, and irregular strips. The criteria used for selecting the canopy gaps included the presence of herbaceous and shrub vegetation and a lack of established pine regeneration. Herbicide treatment plots were assigned to six of the twelve gaps (Fig. 2.6A-D) and the same treatments were applied as in the open site. In addition, axe cuts were made into the cambial layers of nearby, undesirable hardwood trees, at 0.3 m aboveground. Approximately 2 ml of Estamine™ (2,4-D amine as the active ingredient) was injected into the exposed tissues.

The same planting procedure was followed as with the open site (Fig 2.4). A total of 768 seedlings (including buffer seedlings) were planted at each forested site during July of 1996. To protect the seedlings from cattle damage, a four-strand barbed wire fence was placed around each forested site.

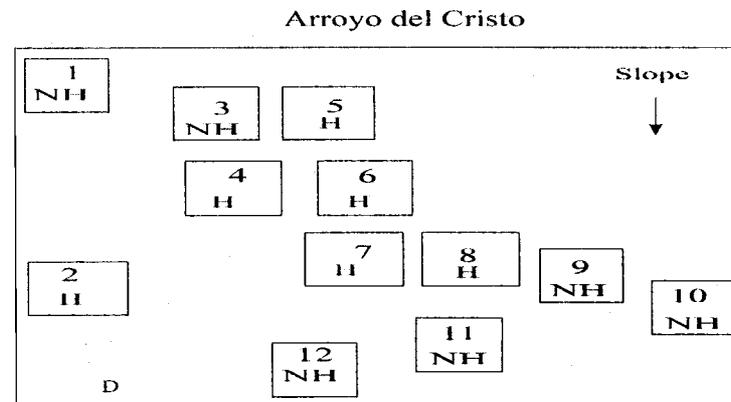
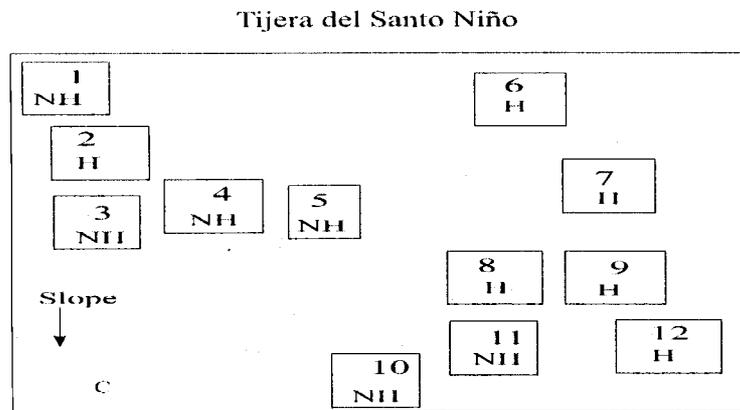
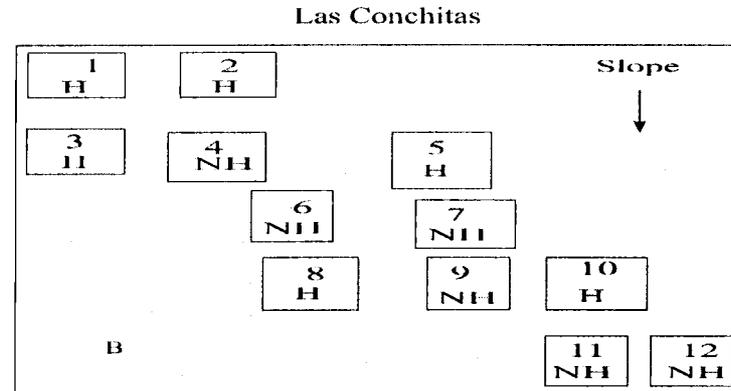
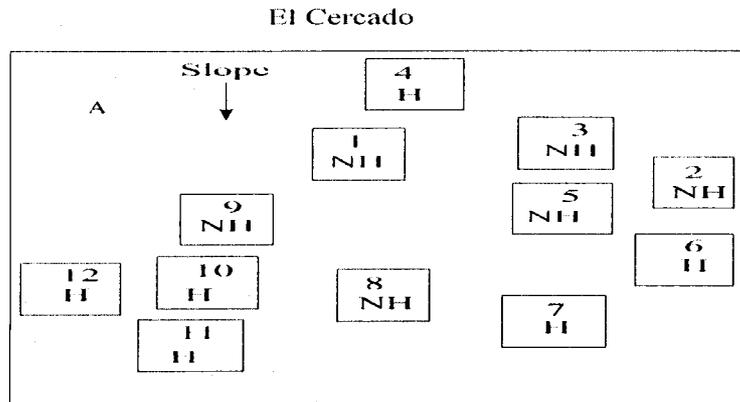


Figure 2.6 Layout for no herbicide (NH) and herbicide (H) treatments for the four forested sites at Tarahumar.

2.3.4 Height and diameter measurements, and evaluation of survival and causes of mortality

After eighty dead seedlings were replaced with the same stock type, initial height and diameter measurements were taken during August of 1996 in the open site and forested sites (Tables 2.6, 2.7, and 2.8). Stem heights were measured from the root collar to the apical bud (to the nearest mm); stem diameters were taken at the ground line (to the nearest 0.1 mm). Stem heights and diameters were also measured from June 30 to July 4, 1997 (at the end of the first growing season), and from August 17 to 21, 1998 (at the end of the second growing season). Buds had already set at those times. Seedling volume (cm³) was calculated with the formula for a cone ($V = \frac{1}{3} \pi * \text{diameter}^2 * \text{height}$). The same stock type had been used for the open area and the forested sites. However, statistical tests showed that the initial stem height of the three *Pinus* species planted in the open area was smaller (Table 2.6) than the initial stem height of those species planted in the four forested sites (Tables 2.7 and 2.8). The initial stem diameter of *Pinus arizonica* seedlings was smaller (0.35 cm) in the herbicide treatment than in the no-herbicide (0.45 cm) treatment at El Cercado (Table 2.7).

Absolute stem height growths rates for the first and the 2-year period (ASHTG1 and ASHTG2, respectively), were calculated as follows:

$$\text{ASHTG1} = \frac{(\text{ht}_2 - \text{ht}_1)}{t_2 - t_1} \quad \text{Equation 2}$$

where:

ht₁ = initial stem height (1996),

ht₂ = stem height after the first growing season (1997),

t_1 = year planted (1996),

t_2 = year after the first growing season (1997), and

t_3 = year after the second growing season (1998).

In like manner, absolute growth rates were calculated for stem diameters and volumes after the first (ASDIG1, and AVOG1, respectively) and second growing seasons (ASDIG2, and AVOG2, respectively).

At the end of each growing season, survival rates were assessed for each plot. Three causes for mortality were recorded: 1) drought, indicated by brown needles; 2) injury by mammals, with stems clipped off at 45° angles; and 3) weevil damage, with girdling about the bark of the tap root.

Table 2.6 Initial stem height and stem diameter of three *Pinus* species planted in an open area with no herbicide and herbicide treatments at Tarahumar.

Species	Height (cm)(SE)		Diameter (cm)(SE)	
	Treatments			
	No Herbicide	Herbicide	No Herbicide	Herbicide
<i>P. arizonica</i>	11.8 (0.63)	8.9 (0.35)	0.44 (0.012)	0.40 (0.017)
<i>P. engelmannii</i>	6.1 (0.55)	4.7 (0.15)	0.46 (0.023)	0.47 (0.016)
<i>P. durangensis</i>	20.9 (1.04)	20.4 (1.53)	0.38 (0.009)	0.37 (0.020)

SE= standard error. n = 6 plots.

Table 2.7 Initial stem height (HT) and stem diameter (DIA) of three *Pinus* species planted in two of the forested sites, El Cercado and Las Conchitas, with no herbicide (NH) and herbicide (H) treatments at Tarahumar.

Species	Site							
	El Cercado				Las Conchitas			
	HT		DIA		HT		DIA	
	(cm)		(cm)		(cm)		(cm)	
	(SE)		(SE)		(SE)		(SE)	
Species	Treatments				Treatments			
	NH	H	NH	H	NH	H	NH	H
<i>Pinus arizonica</i>	12.5 (0.28)	13.3 (0.50)	0.45 (0.007)	0.35 (0.008)	15.1 (0.35)	13.5 (0.98)	0.39 (0.007)	0.38 (0.006)
<i>Pinus engelmannii</i>	8.1 (0.41)	6.9 (0.24)	0.49 (0.022)	0.43 (0.021)	7.0 (0.23)	6.3 (0.29)	0.46 (0.007)	0.48 (0.013)
<i>Pinus durangensis</i>	23.9 (0.65)	27.4 (1.0)	0.40 (0.003)	0.40 (0.011)	24.7 (0.89)	25.4 (0.55)	0.40 (0.008)	0.41 (0.011)

SE= standard error. n = 6 plots.

Table 2.8 Initial stem height (HT) and stem diameter (DIA) of three *Pinus* species planted in two of the forested sites, Tijera del Santo Niño and Arroyo del Cristo, with no herbicide (NH) and herbicide (H) treatments at Tarahumar.

Species	Site							
	Tijera del Santo Niño				Arroyo del Cristo			
	HT		DIA		HT		DIA	
	(cm)		(cm)		(cm)		(cm)	
	(SE)		(SE)		(SE)		(SE)	
Species	Treatments				Treatments			
	NH	H	NH	H	NH	H	NH	H
<i>Pinus arizonica</i>	14.2 (0.73)	15.7 (0.58)	0.40 (0.011)	0.40 (0.006)	14.6 (0.66)	16.0 (0.77)	0.39 (0.005)	0.39 (0.007)
<i>Pinus engelmannii</i>	7.0 (0.22)	6.7 (0.29)	0.48 (0.021)	0.43 (0.018)	7.2 (0.31)	5.3 (0.20)	0.43 (0.022)	0.43 (0.009)
<i>Pinus durangensis</i>	22.4 (0.80)	24.2 (1.10)	0.37 (0.013)	0.37 (0.013)	25.3 (0.91)	21.9 (1.04)	0.40 (0.016)	0.36 (0.009)

SE= standard error. n = 6 plots.

2.3.5 Water relations

To determine xylem water potential and stomatal conductance, six seedlings for each treatment-species combination were randomly selected from the open site, as well as from the forested sites at Las Conchitas and Arroyo del Cristo. The same seedlings were used in spring (April 15 to 17, 1998) for xylem water potential and stomatal conductance, and in summer (August 25 to 27, 1998) for xylem water potential. The sites were measured on separate days in each season. The spring mornings were frosty, followed by sun at midday and clear evenings. Summer mornings typically were mild, with partly or mostly cloudy skies by midday, followed by thunderstorms in the afternoon or night.

Xylem water potential (ψ) was measured with a pressure chamber (PMS Instrument, Co. Corvallis, OR) using a one-year-old fascicle from each seedling and following standard procedures (Johnson and Nielsen, 1969; Ritchie and Hinckley, 1975; Day and Walsh, 1980). Readings were taken at 0400 h (pre-dawn; ψ_{PD}), 1200 h (midday; ψ_{MD}), and 1600 h (evening; ψ_{EV}).

Stomatal conductance (g_s) was recorded only in the spring at 0800 h (morning; g_{sMO}), 1200 h (midday; g_{sMD}), and 1600 h (evening; g_{sEV}). Conductance was measured with a steady state porometer (LI-1600M, LI-COR, Inc., Lincoln, NE).

Water potential readings were correlated to stomatal conductance measurements on the same seedling by selecting another one-year-old fascicle, which was then marked so that it could be re-measured later in the day. The fascicle was identified by marking its sheath with a waterproof red marker. All the needles in a fascicle were placed as a bundle across the cylindrical chamber of the porometer. Fascicles were collected at the end of each measurement day.

To adjust stomatal conductance readings for leaf area, the total surface area was estimated for a 5-cm-long needle (the diameter of the cylindrical chamber was 5 cm) by measuring the radius of an interior face of the needle. It was assumed that the fascicle shape approximated a cylinder form (Haller, 1965; Johnson, 1984; Shelton and Switzer, 1984; Svenson and Davies, 1992). The needle radius was measured with an electronic digital caliper (MAX-CAL, Fowler & NSK) to the nearest 0.01 mm.

Leaf temperature was determined with a chromel-constantan thermocouple, and air and leaf temperatures (T_{air} and T_{leaf} , respectively) were assumed to be equal. Photosynthetic active radiation (solar radiation in the wave band of 400 to 700 nm absorbed by the chloroplast for photosynthesis; PAR), and relative humidity (RH) were assessed with an LI-190S-1 quantum sensor and a Vaisala HUMICAP[®], respectively. These sensors were mounted in a LI-COR steady state porometer. Vapor pressure deficit (VPD) values were estimated according to Percy et al. (1989) and Grantz (1990).

2.3.6 Statistical analyses

To meet analysis of variance (ANOVA) assumptions, the residuals must be independent and normally distributed with a constant variance (Sabin and Stafford, 1990). The arc sine square root transformation was used for survival and causes of mortality, the square root transformation for absolute growth rates and plant water potentials, and $\log_e(y + 1)$ transformation was used for stomatal conductance values. The Statistical Analysis System (SAS, version 6.12 software package; see Appendix I) was used to analyze experiments in the open site and in the forested sites. Because of the inherent differences in morphology, the statistical analyses were done by species. Herbicide and interaction effects were compared at $\alpha = 0.05$.

For the open area, treatment means for absolute growth rates were compared with Student's t-test. Treatment effects also were compared for survival rates by stem diameter class after the second growing season. The Student's t-test used six replications. The herbicide effect was tested for predawn and midday plant water potential, and for morning and midday stomatal conductance. To adjust seedling growth to initial seedling size, a covariate was included in the model. For each species and growing season, a matrix of three response variables (absolute stem height, stem diameter, and volume growth) by three initial seedling sizes (covariates; stem height, stem diameter, and stem height:stem diameter ratio (H:D)) was used to identify a significant covariate.

If the herbicide effect was not significant by including the covariate (non significant covariate effect), the unadjusted means were reported. When the covariate by treatment interaction was significant, a test for unequal treatment slopes was performed and a test for treatment differences was done for a minimum of three values of the covariate. This applied for the covariate by treatment interaction found for the absolute stem diameter growth of *P. engelmannii* after the second growing season.

For the forested sites, the herbicide effect on survival and growth rates was tested using a randomized complete block design with four replicates. Like in the open area, the initial seedling stem height, stem diameter, and the H:D ratio were used as covariates for seedling growth. In this case, if the herbicide effects were not significant with the covariate, but the covariate was significant and yielded a significant interaction, that interaction was displayed to interpret the relationship between the response variable (growth) and the covariate at given treatment. In addition, the herbicide effect on plant water potential and stomatal conductance was tested using a randomized complete block design with two replicates.

The randomized complete block design model was:

$$y_{ij} = \mu + \beta_i + \tau_j + \varepsilon_{ij} \quad \text{Equation 3}$$

where:

y_{ij} = response variable in the j^{th} treatment in the i^{th} block,

μ = overall mean,

β_i = random effect associated to the i^{th} block,

τ_j = added effect of the j^{th} treatment, and

ε_{ij} = random error associated with the unit on the j^{th} treatment in the i^{th} block.

All Students t-tests, ANOVA, and regression line comparison tables are included in Appendix II. When the herbicide effect was only significant in the forested sites, least square means were back-transformed and its error bars (asymmetrical) were displayed. In case the herbicide effect was not significant, the arithmetic mean and its error bars were computed. Only significant herbicide effects (p-value < $\alpha = 0.05$) are presented and discussed in the following sections.

2.4 Results

2.4.1 Open area

2.4.1.1 *Survival*

Survival of all three species in the open area was higher in the plots where herbicide had been applied. This relation persisted through both growing seasons (Fig. 2.7A, B, C). Survival was greater for *P. arizonica* and *P. engelmannii* than for *P. durangensis* after each growing seasons. Among species, there was no herbicide effect on survival after the first season (*P. arizonica* p-value=0.1529; *P. engelmannii* p-value=0.1669; *P. durangensis* p-value=0.1458). However, a highly significant herbicide effect was found for survival of *P. engelmannii* seedlings after the second season (p-value=0.0095; Fig. 2.7B). For this species, seedling survival in the herbicide plots was higher (78.6%) than in untreated plots (42.8%). Similarly, a significant herbicide effect was found for survival of *P. durangensis* seedlings after the second growing season (p-value=0.0477; Fig. 2.7C), i.e., 26.6% in the herbicide treatment versus 7.1% in the no-herbicide treatment. A higher survival rate for *P. arizonica* persisted in the herbicide plots (83%) than in the no-herbicide plots (61.4%) after the second growing season.

P. durangensis was the species most damaged in the open area. Seedlings of this species had brown needles and showed signs of wilting. The seedlings apparently were not suitable for the operational environment of the open area.

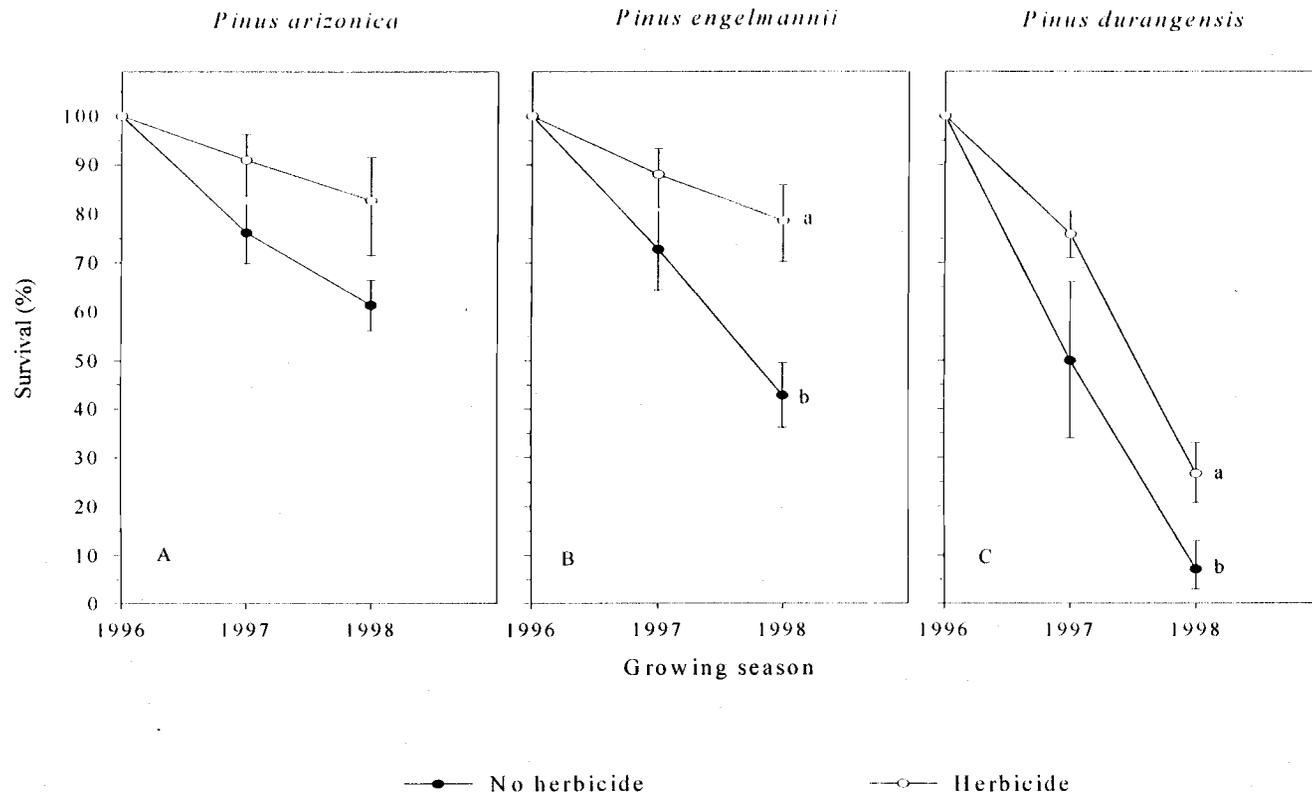


Figure 2.7 Seedling survival of three *Pinus* species in the no herbicide and herbicide treatments for planted year (1996) and two growing seasons (1997 and 1998) in an open area at Tarahumar. Survival rates with different lowercase letter are significantly different at $\alpha = 0.05$. Vertical bars represent standard error of the arithmetic mean. (n = 6).

2.4.1.2 Absolute stem height, stem diameter, and volume growth rates

In general, there was no herbicide effect for absolute stem height, stem diameter, and volume growth rates among species in the open area after the first growing season ($p\text{-value} > \alpha = 0.05$; Appendix II and Fig. 2.8). However, the no-herbicide and herbicide treatment effects differed for stem height in *P. durangensis* and for volume in *P. arizonica* after the first season ($p\text{-value}=0.0135$ and 0.0457 , respectively; Fig. 2.8C, D). For both stem height and volume, values for the no-herbicide treatment were higher than for the herbicide treatment (height = 3.44 and 1.41 cm yr^{-1} ; volume = 1.81 and 1.11 $\text{cm}^3 \text{yr}^{-1}$, respectively).

In comparison, the herbicide effect was highly significant for the absolute stem height growth rate of *P. engelmannii* after the second season ($p\text{-value}=0.0078$; Fig. 2.8B). For this species, the absolute stem height growth rate with herbicide was higher (3.58 cm yr^{-1}) than without (1.87 cm yr^{-1}). The other two species also showed positive responses to weed control, though not significantly (Fig. 2.8A, C).

After the second growing season, the absolute stem diameter growth of only *P. engelmannii* depended on initial stem height. A covariate by treatment interaction was found for absolute stem diameter growth, and treatment slopes were significantly different ($p\text{-value}=0.0422$; Fig. 2.9). Therefore, the response for stem diameter growth of *P. engelmannii* was positive and higher with herbicide than without. Because treatment slopes were significantly different, the minimum and maximum values, and the mean of the initial stem height of *P. engelmannii* were selected for comparing the treatments for absolute stem diameter growth (Fig. 2.9).

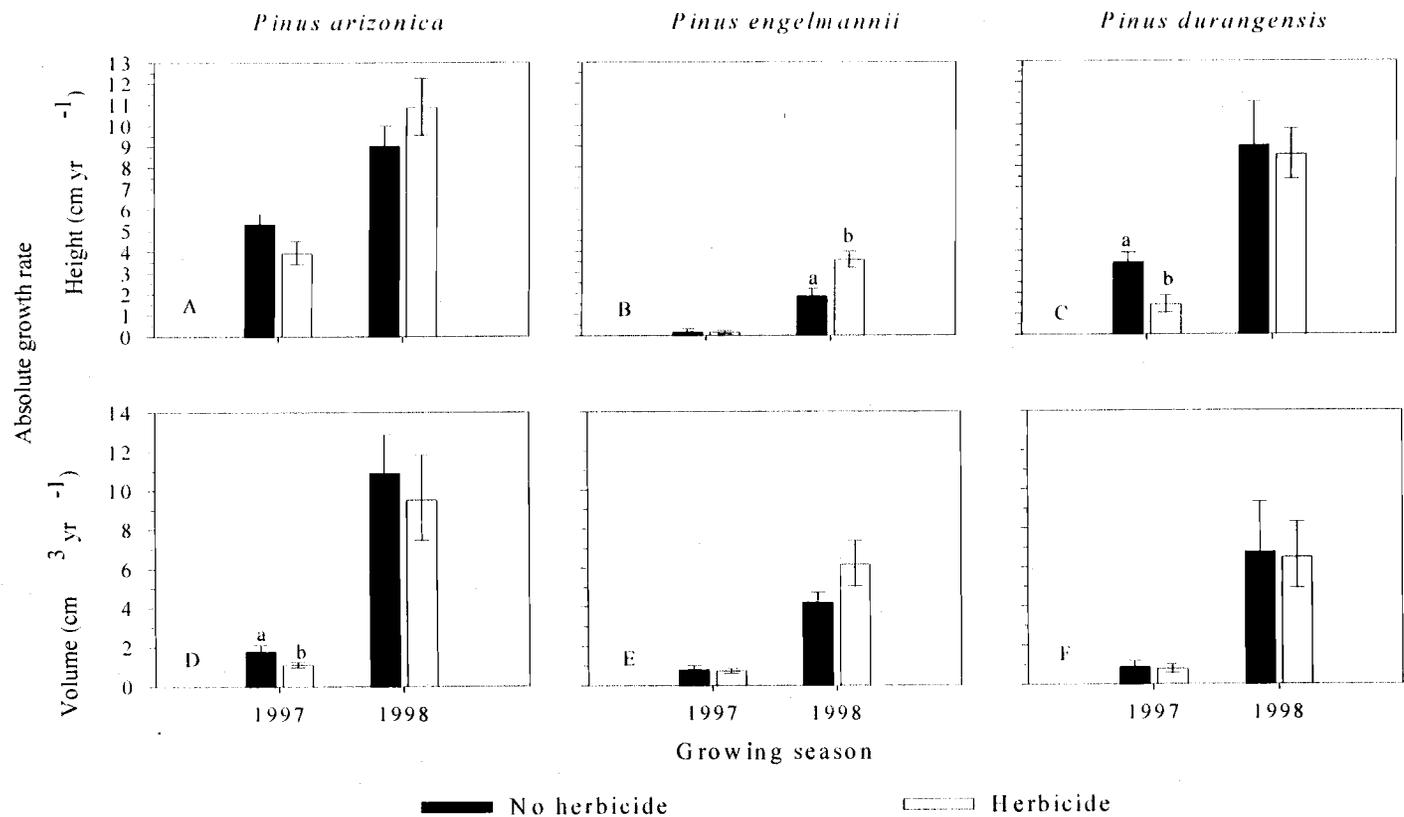


Figure 2.8

Absolute stem height and volume growth rates of three *Pinus* species in the no herbicide and herbicide treatments for two growing seasons (1997 and 1998) in an open area at Tarahumar. Absolute growth rates with different lowercase letter are highly significant different at $\alpha=0.05$. Vertical bars represent standard error of the arithmetic mean. (n=5 and 4 in the no herbicide treatment for *Pinus durangensis*, all others n=6).

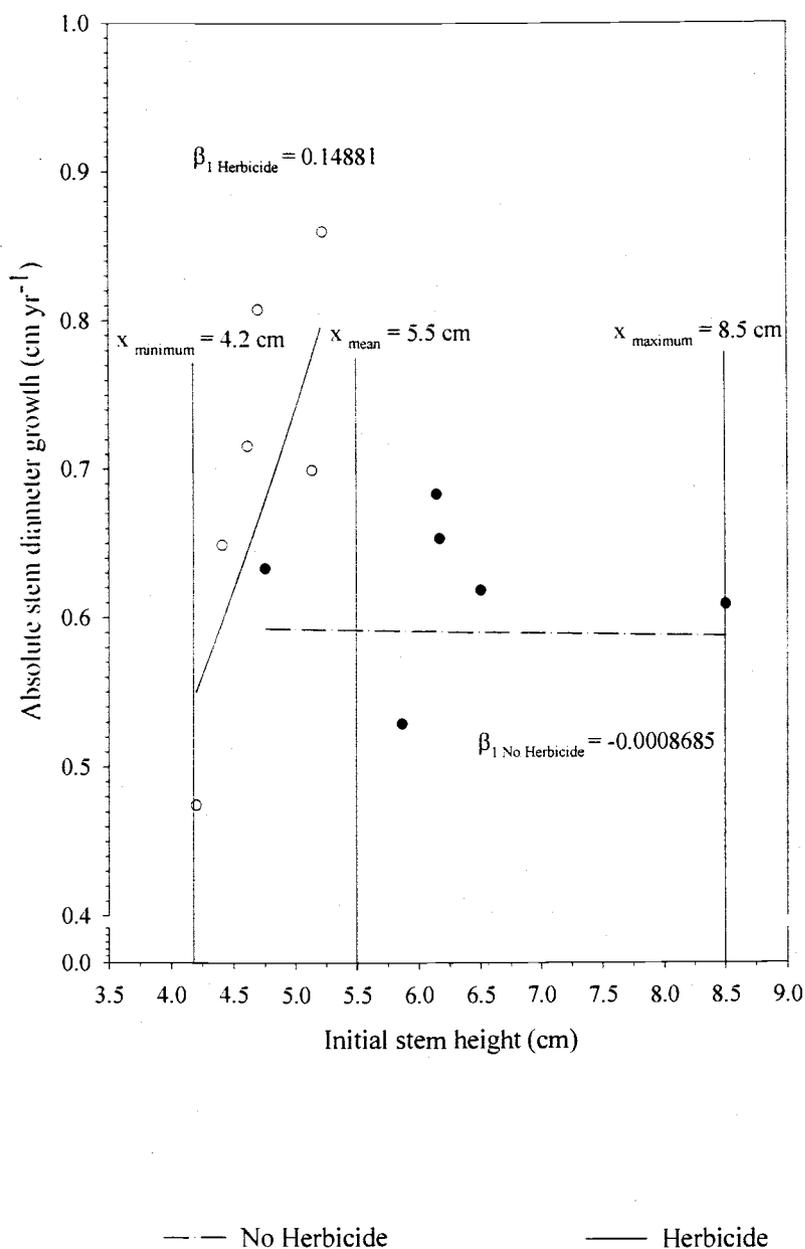


Figure 2.9 Regression lines with slopes of the no herbicide (filled circles) and herbicide (empty circles) treatments for absolute stem diameter growth of *P. engelmannii*, and comparison of the regression lines at three values of the initial stem height (covariate). Each scattered point represents a replication and each replication includes the mean of 12 seedlings.

No treatment differences were found at the minimum value (p-value=0.6416; Table 2.9). However, the herbicide effect was significant for the mean and maximum values of the initial stem height of *P. engelmannii* (p-value=0.0211 and 0.0279, respectively).

Table 2.9 Treatment mean comparisons for the absolute stem diameter growth at the minimum, maximum, and mean values of the initial stem height of *P. engelmannii*.

	Initial stem height (cm)		
	Minimum	Mean	Maximum
	4.2	5.5	8.5
Treatment	Absolute stem diameter growth (cm yr ⁻¹)		
No Herbicide	0.59 a	0.59 a	0.58 a
Herbicide	0.55 a	0.87 b	1.91 b

Means with the same letter are not significantly different at $\alpha = 0.05$.

Stem diameter appeared to influence the ability to respond to weed control. The largest seedling displayed the highest over-all survival, but smaller initial-size classes consistently had better survival if weeds were controlled. This result was not as evident in the largest seedlings after the second growing season (Fig. 2.10).

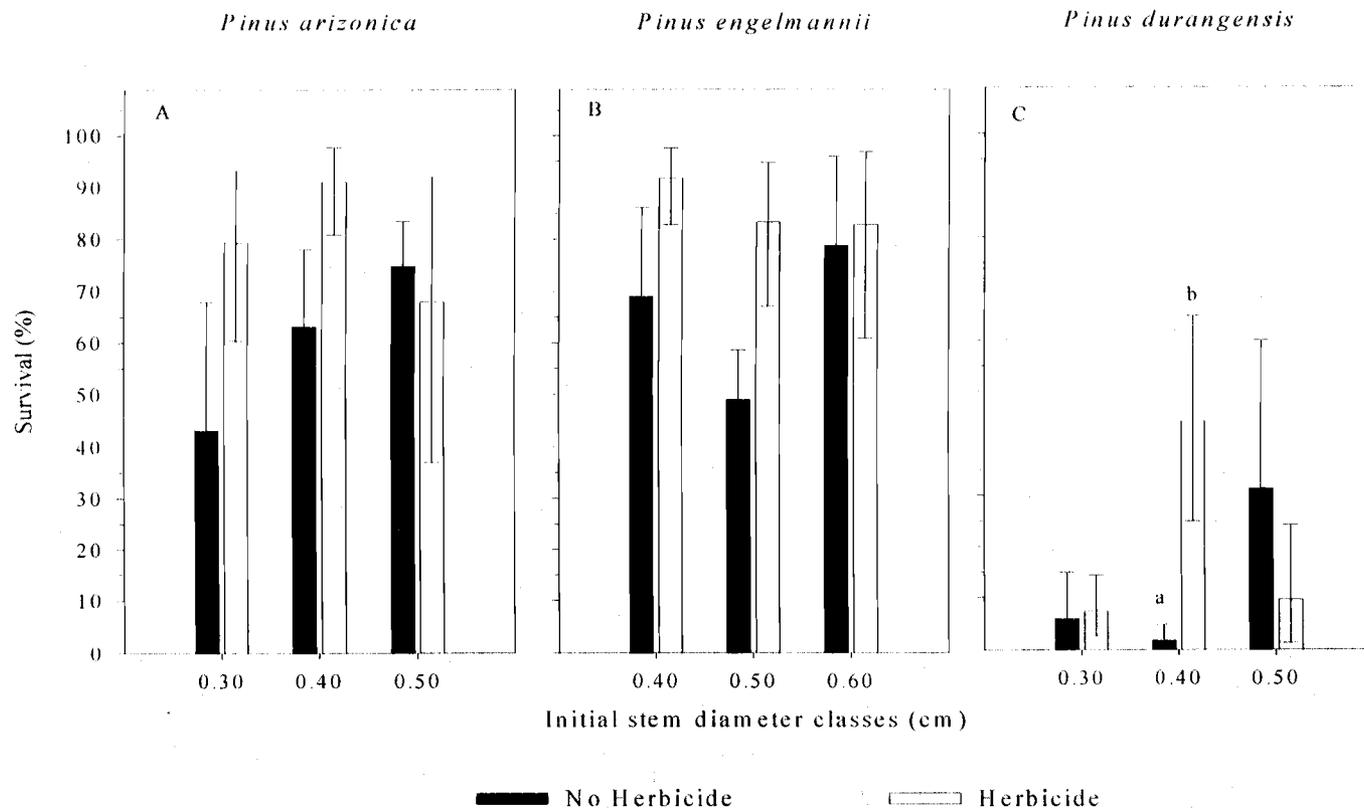


Figure 2.10 Survival rates of three *Pinus* species in the no herbicide and herbicide treatments by stem diameter classes after the second growing season in an open area at Tarahumar. Survival rates with different lowercase letter are significantly different at $\alpha=0.05$. Vertical bars represent standard error of the arithmetic mean ($n=4$ to 6 plots). Note: The initial diameter classes of *P. engelmannii* ranged between 0.40 and 0.60 cm.

In the 0.40-cm initial stem diameter class, survival rates were significantly higher in treated (44.3%) than in untreated (1.9%) plots of *P. durangensis* (p-value=0.0237; Appendix II and Fig. 2.10C). Similarly, *P. arizonica* seedlings in the 0.30- and 0.40-cm stem diameter classes had higher survival rates in the herbicide plots (79.4 and 91.1%, respectively) than in those without herbicide after the second growing season (43.2 and 63.2%, respectively; Fig. 2.10A). Likewise, *P. engelmannii* seedlings in the 0.40-cm stem diameter class had higher survival rates in the plots treated with herbicide (91.7%) than in those without herbicide treatment (69.0%).

2.4.1.3 Seedling water relations

During the early-spring drought of 1998, xylem water potential followed a typical diurnal pattern across treatments and species, with higher values at predawn, decreasing at midday, and stabilizing in the evening (Fig. 2.11A-C). Predawn xylem water potentials ranged between -0.64 and -0.86 MPa, midday values between -1.31 and -2.61 MPa across species and treatments. A highly significant herbicide effect was found for xylem water potential of *P. durangensis* seedlings at midday (p-value=0.0012; Fig. 2.11C). These seedlings had higher plant water potential in plots where herbicide was sprayed (-1.31 MPa) than in untreated plots (-2.61 MPa).

A delayed stomatal opening pattern was observed among the species on April 15, 1998. Early morning readings for stomatal conductance were lower than midday readings, which may reflect the effect of the low temperatures (frost) during the hours previous to the morning measurements (Fig. 2.11D-F).

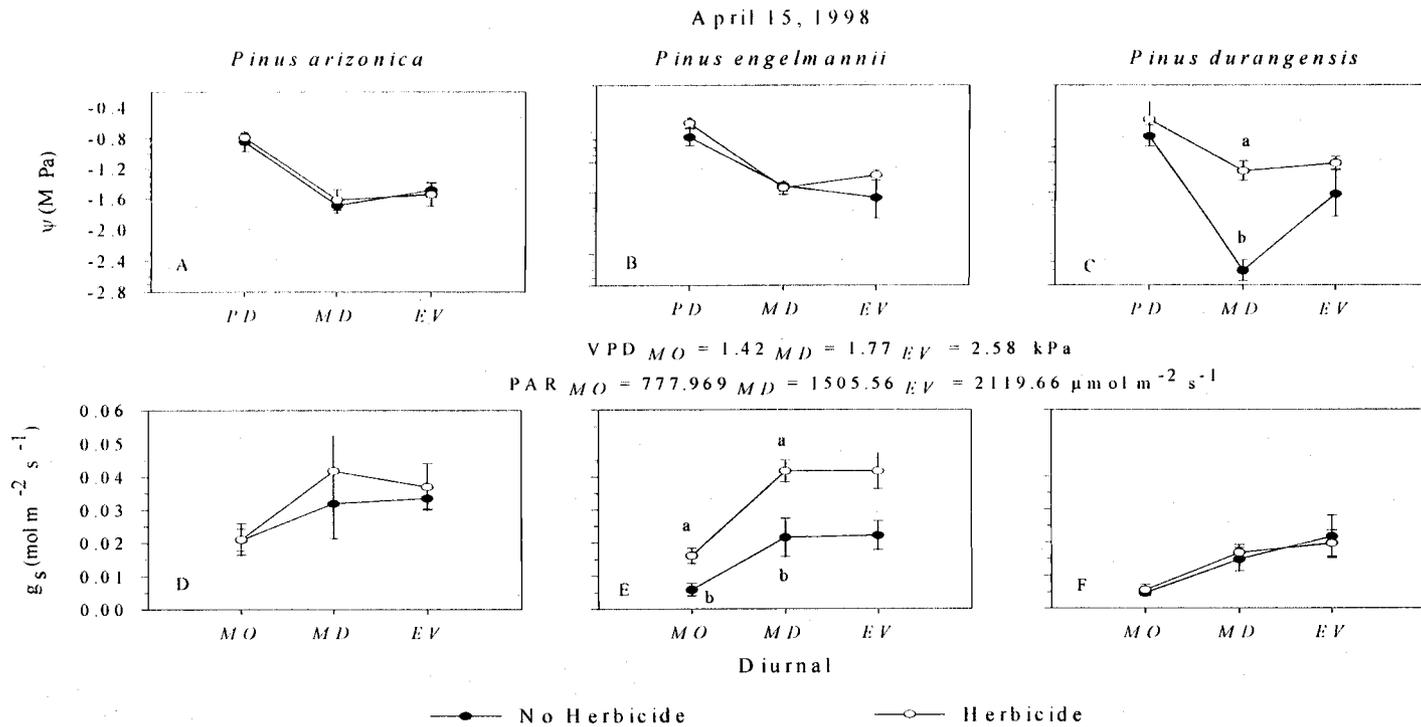


Figure 2.11 Diurnal xylem water potential (ψ) and stomatal conductance (g_s) for April 15, 1998 of three *Pinus* species in an open area at Tarahumar. Diurnal labels are *PD*= predawn, *MO*= morning, *MD*=midday and *EV*=evening. Vapor pressure deficit (VPD) and photosynthetically active radiation (PAR) are indicated for each diurnal period. Xylem water potential and stomatal conductance with different lowercase letter are significantly different at $\alpha=0.05$. Vertical bars represent standard error of the arithmetic mean. ($n = 3$ to 6 seedlings for *Pinus durangensis*; $n = 6$ seedlings for the others).

A significant herbicide effect was found for stomatal conductance in *P. engelmannii* in the morning (p-value=0.0061) and at midday (p-value=0.0158) during Spring 1998 (Fig. 2.11E). These seedlings had higher stomatal conductance in treated plots ($g_{sMO} = 0.16 \text{ mol m}^{-2} \text{ s}^{-1}$ morning, and for both midday and evening, $g_s = 0.41 \text{ mol m}^{-2} \text{ s}^{-1}$) than in untreated plots ($g_{sMO} = 0.06 \text{ mol m}^{-2} \text{ s}^{-1}$ morning, and for both midday and evening, $g_s = 0.21 \text{ mol m}^{-2} \text{ s}^{-1}$).

During the summer rainy season of 1998, higher values of xylem water potential were recorded at predawn and midday compared with those of the early-spring drought season. Predawn water potentials were relatively high across species, irrespective of weed control (between -0.52 and -0.88 MPa). Similarly, midday values were moderate and similar for *P. arizonica* and *P. durangensis* (-1.16 and -1.46 MPa) regardless of the competing vegetation. In contrast, midday xylem water potential of *P. engelmannii* was slightly than those of *P. arizonica* and *P. durangensis* (-0.81 and -1.12 MPa).

There was no significant herbicide effect for xylem water potential in any of the species during the summer of 1998 (p-value $> \alpha = 0.05$; Appendix II). Even though, midday higher water potentials were recorded for all species in treated plots (Fig. 2.12A, B, C), predawn and evening xylem water potentials were similar between herbicide and no-herbicide plots and among the species. The regrowth of the herbaceous vegetation, the summer rains, and the exclusion of grazing may have reduced the differences between treated and untreated plots after the second growing season in the open area.

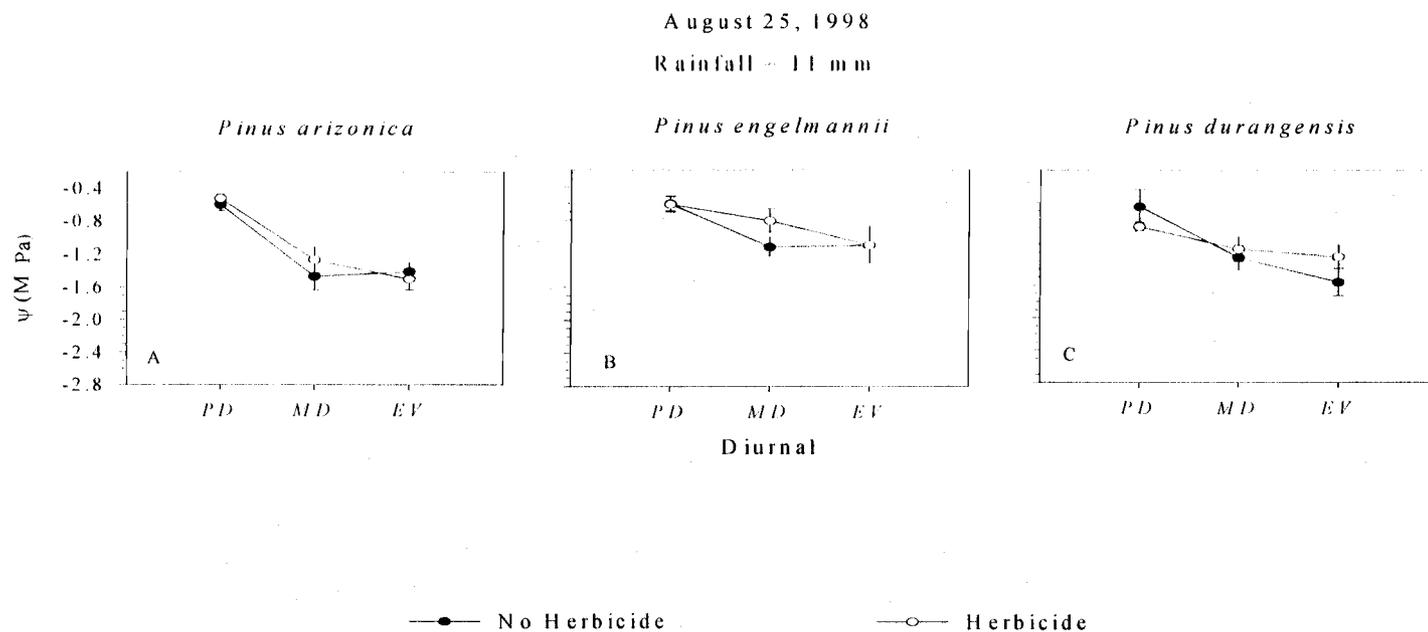


Figure 2.12 Diurnal xylem water potential (ψ) for August 25, 1998 of three *Pinus* species an open area at Tarahumar. Diurnal labels are *PD*=predawn, *MD*=midday, and *EV*=evening. Rainfall for August 25, 1998 is displayed, and rainfall accumulated for the previous 24 days was 115 mm. The precipitation was recorded at the El Tarahumar weather station, which is found within 10 km from the open area. Vertical bars represent standard error of the arithmetic mean. ($n = 3$ to 6 seedlings for *P. durangensis*; $n = 6$ seedlings for the others).

2.4.2 Forested sites

2.4.2.1 Survival

In general, seedling survival was greater for *P. arizonica* and *P. engelmannii* than for *P. durangensis* in the canopy gaps after each growing season. No herbicide effects were found for survival of *P. arizonica* and *P. engelmannii* seedlings after both seasons ($p\text{-value} > \alpha = 0.05$; Appendix II, and Fig. 2.13A, B). These forested sites had light understory herbaceous cover, hence the small change associated with herbicide treatment. However, a significant herbicide effect was found for survival of *P. durangensis* seedlings after both first and second growing seasons ($p\text{-value}=0.0443$ and $p\text{-value}=0.0121$, respectively; Fig. 2.13C). This species had higher survival rates in gaps treated with herbicide (89%) than in untreated gaps (85%) after the first growing season, but survival decreased after the second season. The herbicide effect persisted, nevertheless, and higher seedling survival still was found in gaps with herbicide (67%) than in gaps without (61%).

At plot level, mortality in *P. arizonica* appeared to be caused primarily by drought (21.14%) and clipping by small mammals (12.6%) after the second season. In *P. engelmannii* the main causes of mortality were drought (21.6%) and root girdling (7.4%), whereas *P. durangensis* seedlings were killed by drought (24.6%) and clipping by small mammals (25.0%).

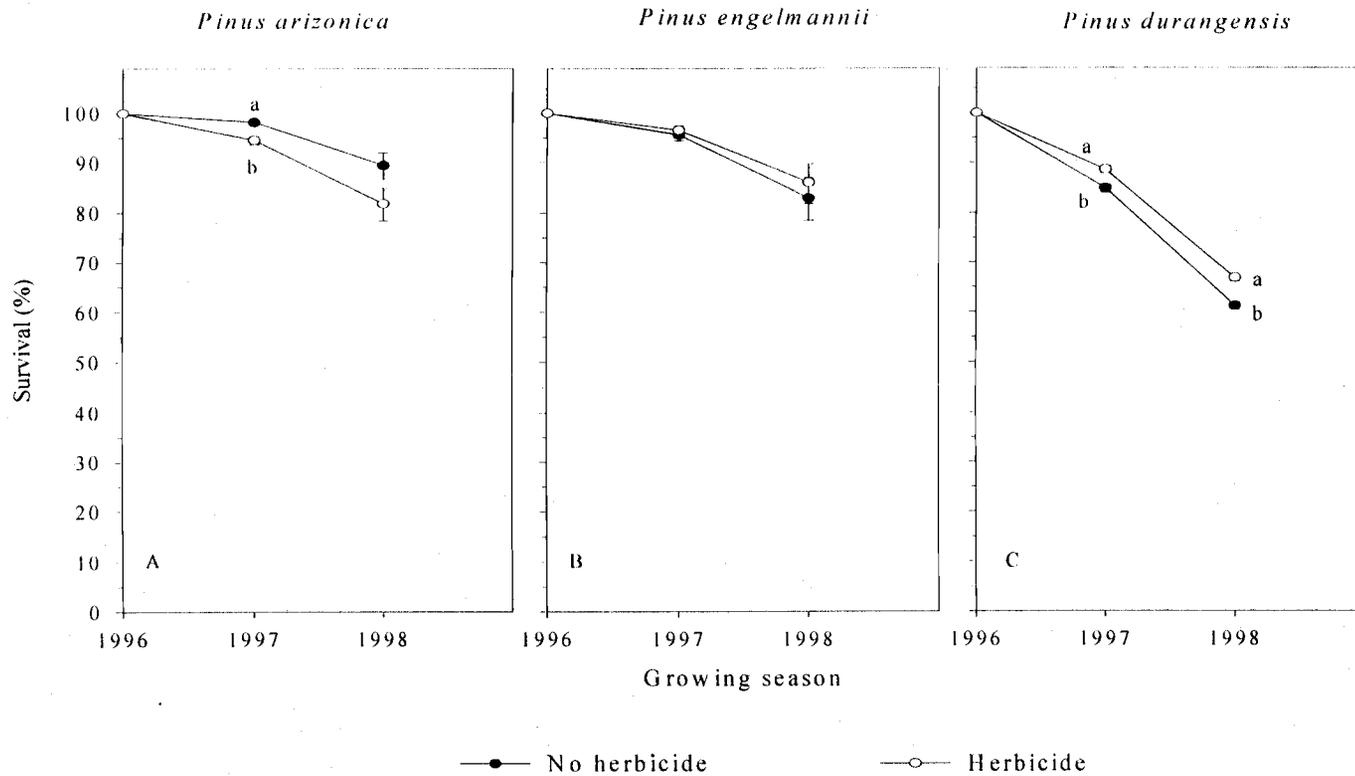


Figure 2.13 Seedling survival of three *Pinus* species in the no herbicide and herbicide treatments for planted year (1996) and two growing seasons (1997 and 1998) in the canopy gaps of four forested sites at Tarahumar. Survival rates with different lowercase letter are significantly different at $\alpha=0.05$. Vertical bars represent standard error of the least square means. ($n = 4$).

2.4.2.2 Absolute stem height, stem diameter, and volume growth rates

During each growing season, absolute growth rates of the three pine species reflected a minimal response to the weed control treatment. Growth trends followed from initial seedling size, which was related to basic species characteristics. Tall seedlings, i.e., *P. arizonica* and *P. durangensis*, grew more in stem height than did short seedlings, a species with a grass stage, i.e., *P. engelmanni* that increased more in stem diameter than did tall seedlings (Fig. 2.14A-I).

There was no herbicide effect on absolute stem height, stem diameter, and volume growth rates when the initial stem height, diameter, and stem height:stem diameter ratio (H:D) were included as covariates during each growing seasons. Although the covariate was positively associated with seedling growth in several tests across species and in both seasons (Appendix II), the covariate did not account for a significant proportion of the variation in any of the tests to detect a significant herbicide effect. However, for *P. arizonica*, the initial H:D ratio by herbicide interaction for absolute stem diameter growth was consistent and detected after the second growing season (p-value = 0.0053; Fig. 2.15). A group of six seedlings was detected as outliers and deleted to rerun the analysis. The interaction became marginally significant (p-value = 0.0414) when the outliers were deleted. In general, the stem diameter growth increased with small H:D ratios.

For *P. durangensis*, the initial height by herbicide interaction was detected for absolute volume growth. The interaction was consistent after both the first (p-value = 0.0217) and the second (p-value = 0.0160; Fig. 2.15) seasons. A group of eight seedlings was detected as outliers and deleted to rerun the analysis. The interaction was not significant (p-value = 0.3538) when the outliers were deleted from the analysis. In general, the volume growth increased with large initial stem height.

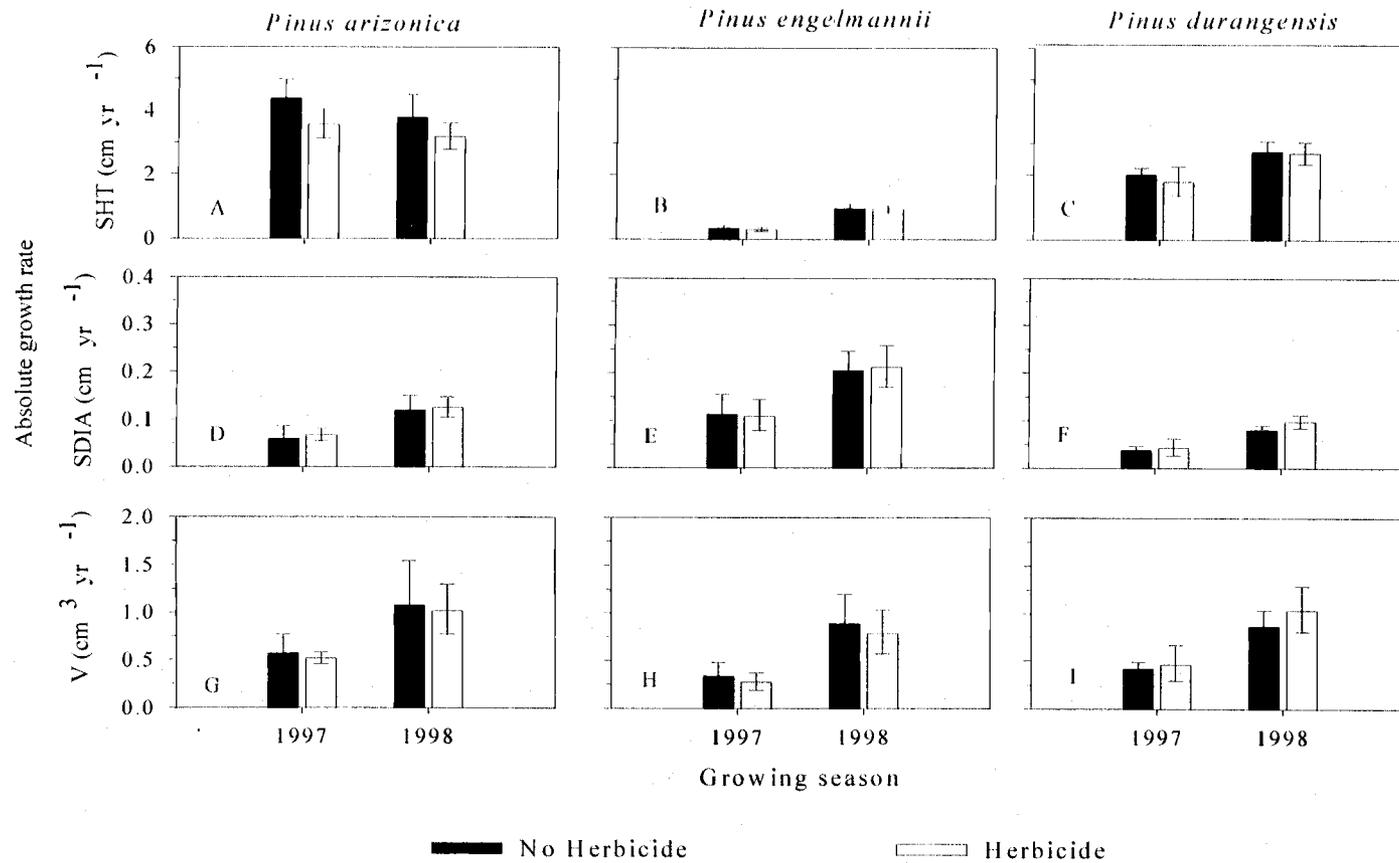


Figure 2.14 Absolute stem height (SHT), stem diameter (SDIA), and volume (V) growth rates of three *Pinus* species in the no herbicide and herbicide treatments for two growing seasons (1997 and 1998) in the forest canopy gaps of four forested sites at Tarahumar. Vertical bars represent standard error of the arithmetic mean (n = 4).

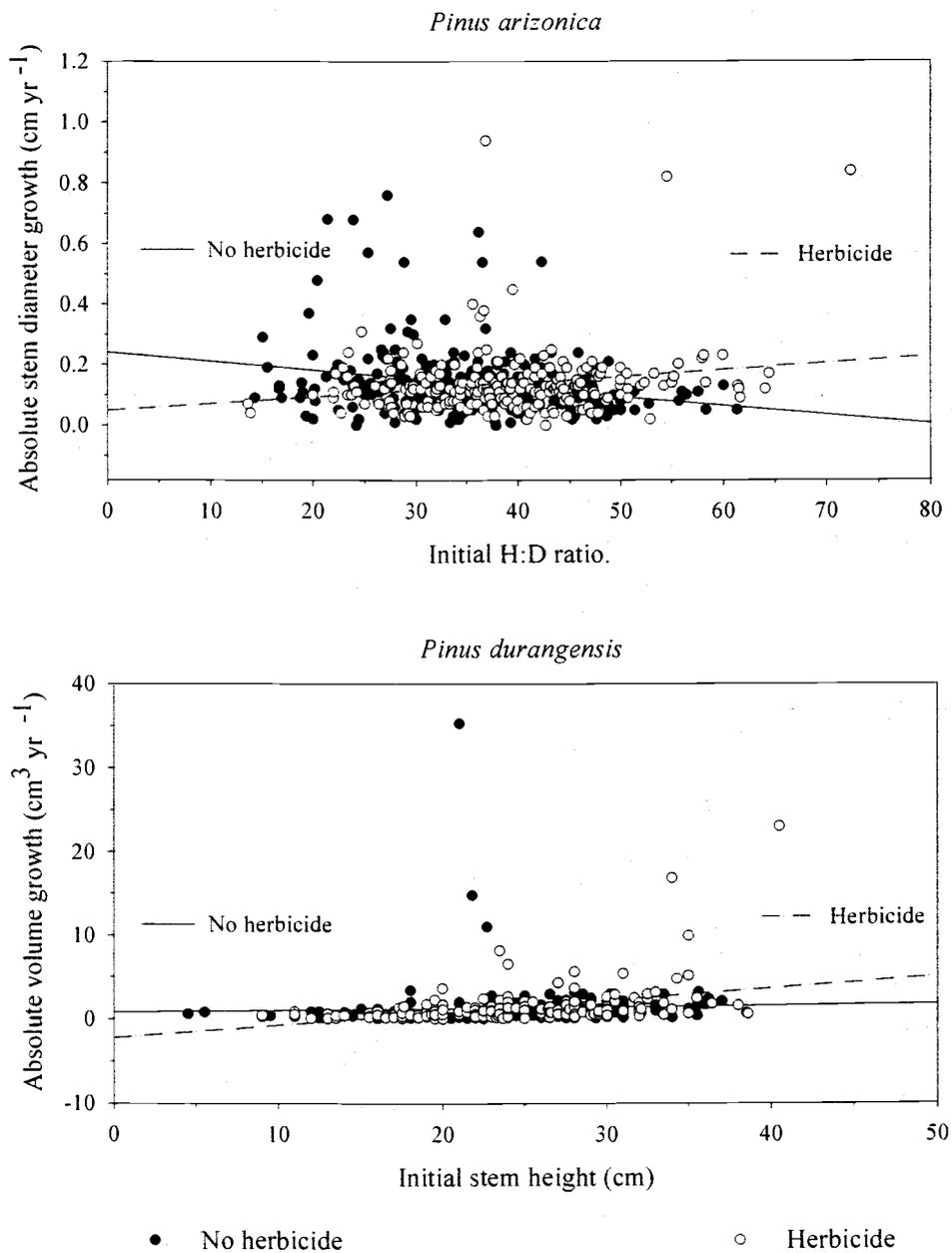


Figure 2.15 Interactions for the initial H:D ratio by herbicide for the absolute stem diameter growth of *P. arizonica* (top) and for the initial stem height by herbicide for the absolute volume growth (bottom) of *P. durangensis* after the second growing season.

Over-all, survival responses to weed control in the canopy gaps were small and inconsistent, with no herbicide effect for seedling survival by stem diameter classes among species (p -value $> \alpha = 0.05$; Appendix II and Fig. 2.16A, B, C). *P. arizonica* seedling survival was high ($>80\%$), regardless of weed control treatment across the 0.30-, 0.40-, and 0.50-cm stem diameter-size classes (Fig. 2.16A). Similarly, *P. engelmannii* survival was moderately high for the no- herbicide treatment (64%) and high for the herbicide treatment (89%) in the 0.30-cm stem diameter class. Seedling survival also was high ($> 85\%$) for both herbicide treatment among the 0.40-, 0.50-, and 0.60-cm diameter classes (Fig. 2.16B). Survival of *P. durangensis* seedlings was slightly higher (not significant) for the 0.30- and 0.40-cm classes in the herbicide treatment (70.4 and 76%, respectively) than in the no herbicide treatment (66 and 62%, respectively; Fig. 2.16C).

2.4.2.3 Seedling water relations

Xylem water potential showed a typical diurnal pattern across species on April 16 and 17, 1998, at the two forested sites. Predawn xylem water potential was low ($\psi < -1.0$ MPa) for all species and both herbicide treatments (Fig. 2.17A, B, C). Midday xylem water potentials had further decreased, and ranged between -1.57 and -2.23 MPa across species and treatments. In the evening, seedlings showed signs of recovery, and xylem water potential was -1.37 to -1.84 MPa. Despite its low predawn readings, *P. arizonica* showed a significant effect (p -value=0.0409) between plots with the no-herbicide treatment (-1.16 MPa \pm 0.09) and those treated with herbicide (-1.26 MPa \pm 0.08). No significant differences were found for xylem water potential for the other two species, predawn (p -value=0.7011 and 0.0715, respectively) or at midday (p -value= 0.7602 and 0.8361, respectively).

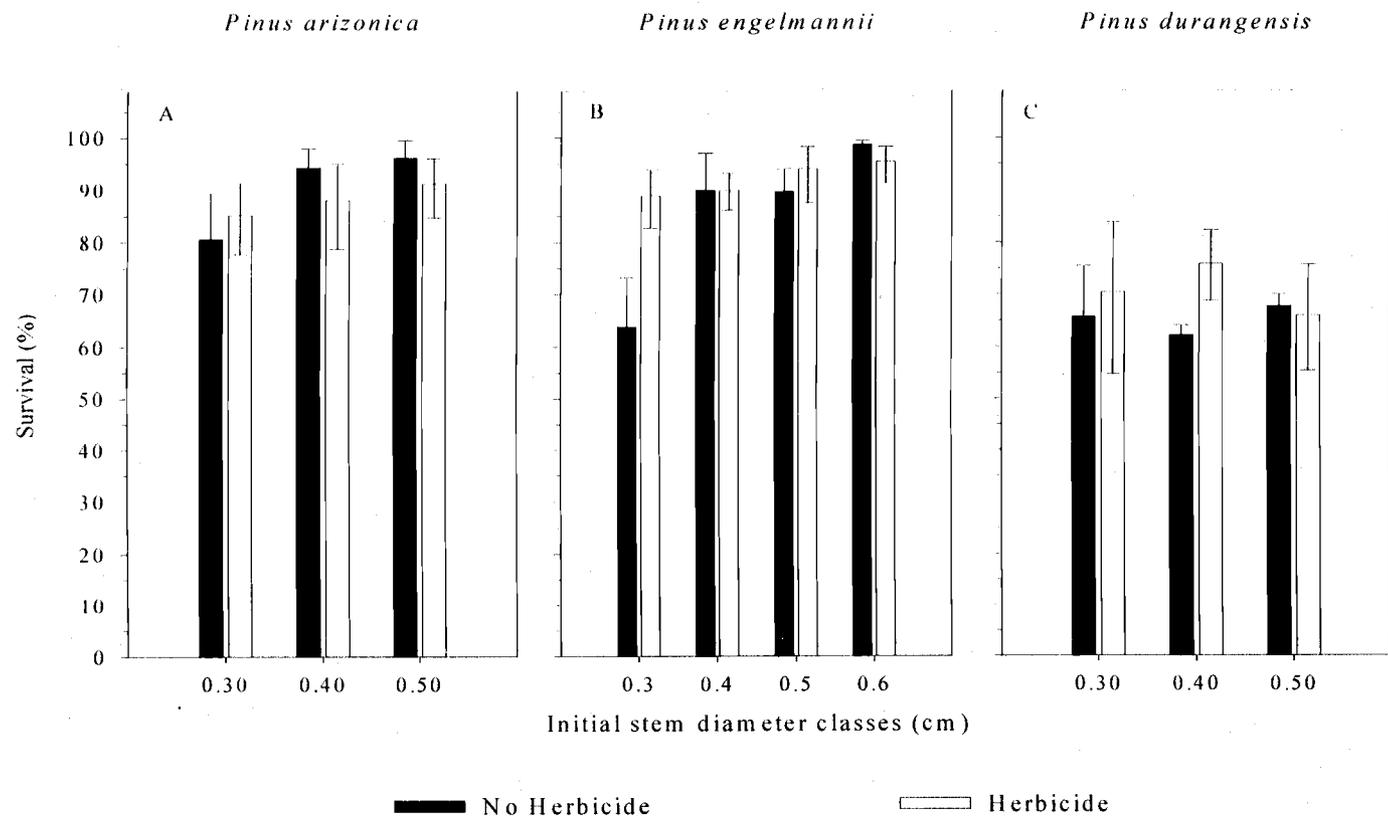


Figure 2.16 Survival rates of three *Pinus* species in the no herbicide and herbicide treatments by stem diameter classes after the second growing season in four forested sites at Tarahumar. Vertical bars represent standard error of the arithmetic mean (n = 4).

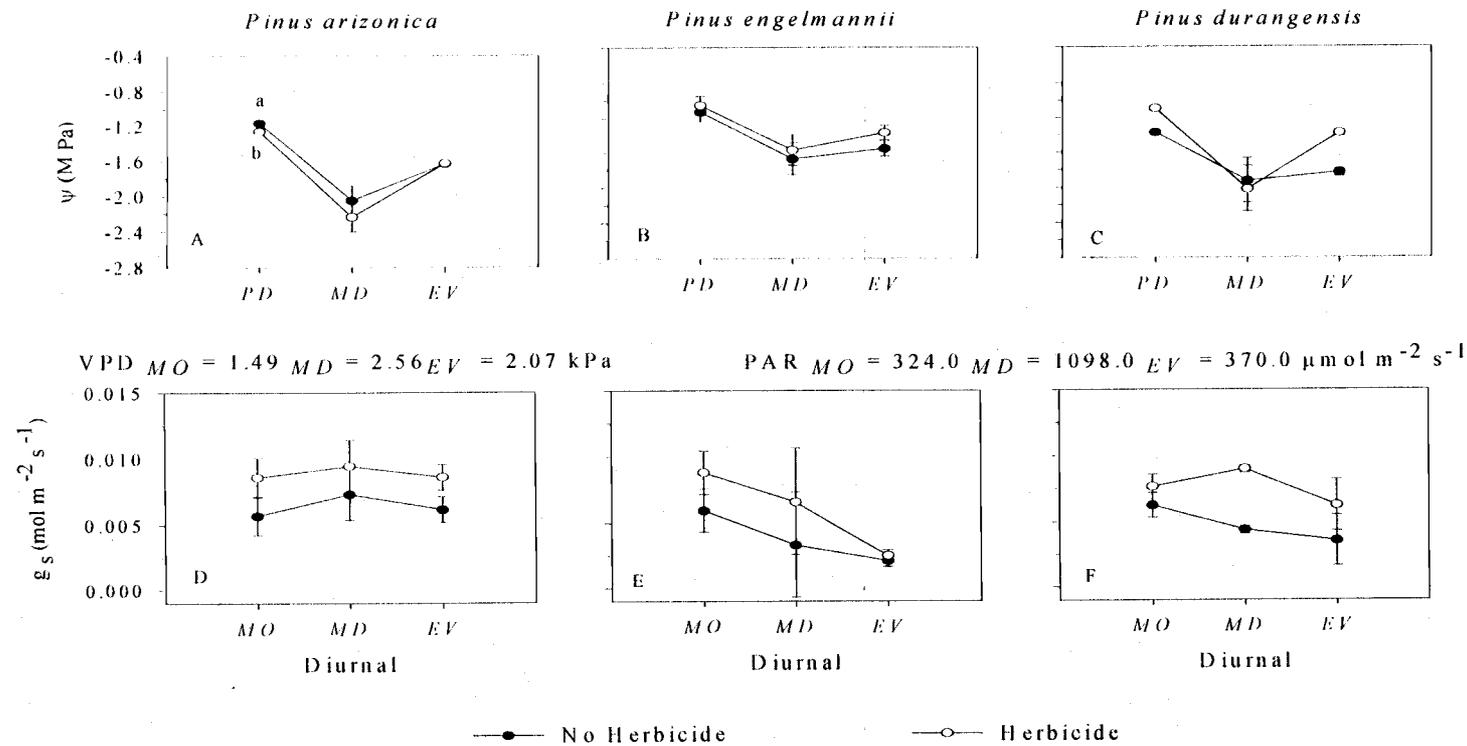


Figure 2.17 Diurnal xylem water potential (ψ) and stomatal conductance (g_s) for April 15, 1998 of three *Pinus* species in two forested sites at Tarahumar. Diurnal labels are *PD*=predawn, *MO*=morning, *MD*=midday, and *EV*=evening. Vapor pressure deficit (VPD) and photosynthetically active radiation (PAR) are indicated for each diurnal period. Xylem water potentials with different lowercase letter are significantly different at $\alpha = 0.05$. Vertical bars represent standard error of the least square means. ($n = 2$ sites).

Stomatal conductance was low across species and treatments during the spring of 1998 at the two forested sites ($g_s < 0.01 \text{ mol m}^{-2} \text{ s}^{-1}$). The stomatal conductances for *P. arizonica* and *P. durangensis* were similar, increasing from morning to midday, then declining in the evening. In contrast, conductance in *P. engelmannii* seedlings decreased from morning to evening (Fig. 2.17D, E, F). No significant differences among species were found for stomatal conductance in the morning and at midday (p-value $> \alpha = 0.05$; Appendix II). Instantaneous values of PAR were the highest at midday.

Xylem water potential for all species also followed a typical diurnal trend on August 26 and 27, 1998. Predawn readings were similar across species and treatments and were higher than in the spring. Potentials ranged between -0.59 and -0.89 MPa, with no significant differences between treatments (Fig. 2.18A, B, C).

In contrast, midday xylem water potential varied among species. *P. engelmannii* seedlings had the highest midday potentials, in both no-herbicide and herbicide treatments ($\psi = -1.16 \text{ MPa}$ and $\psi = -1.39 \text{ MPa}$, respectively; p-value = 0.5108). In comparison, *P. arizonica* had the lowest midday readings without and with herbicide ($\psi = -1.65 \text{ MPa}$ and $\psi = -2.04 \text{ MPa}$, respectively; p-value = 0.0329). Potentials for *P. durangensis* were between those of *P. engelmannii* and *P. arizonica* (no-herbicide $\psi = -1.30 \text{ MPa}$ and herbicide $\psi = -1.67 \text{ MPa}$; p-value = 0.2283; Fig. 2.18A, B, C).

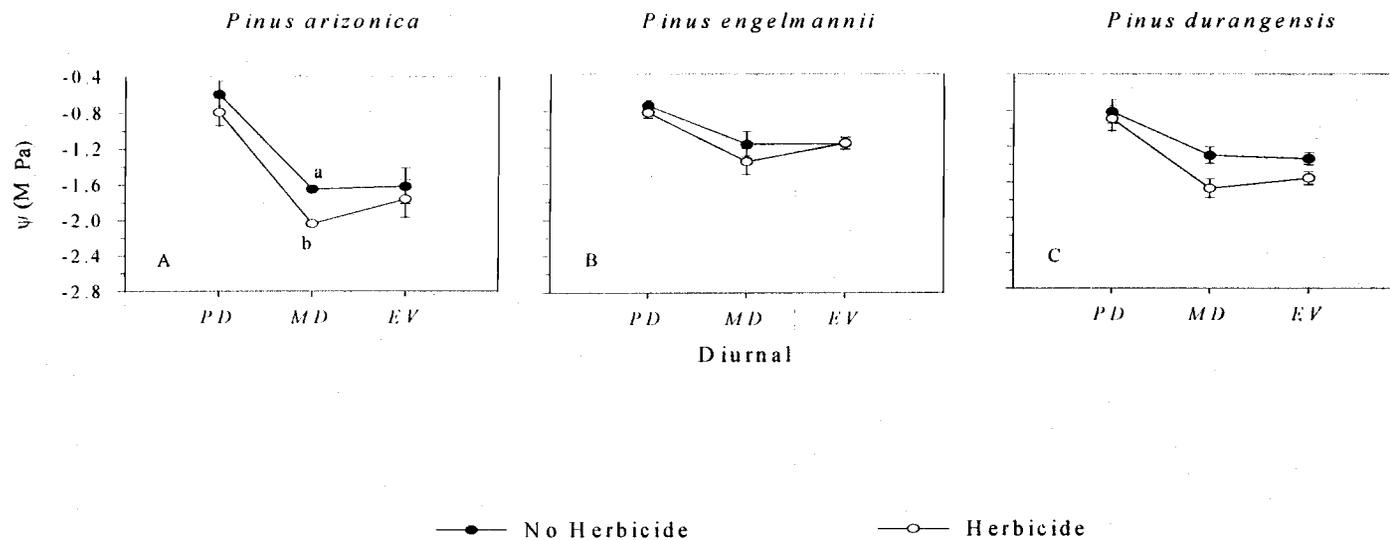


Figure 2.18 Diurnal xylem water potential (ψ) for August 25, 1998 of three *Pinus* species in two forested site at Tarahumar. Diurnal labels are *PD*=predawn, *MO*=morning, *MD*=midday, and *EV*=evening. No precipitation was recorded in August 26 and 27, however the rainfall accumulated previous to these dates was 126 mm. Rainfall was recorded at the El Tarahumar weather station, which is found within 10 km from the two forested sites sampled. Xylem water potentials with different lowercase letter are significantly different at $\alpha = 0.05$. Vertical bars represent standard error of the least square means (n = 2 sites).

2.5 Discussion

2.5.1 Open area

2.5.1.1 Survival

Vegetation management can free soil resources to improve survival and growth of desirable species by reducing the size and number of competing vegetation (Walstad and Kuch, 1987). In this open-area study, survival rates for *P. engelmannii* and *P. arizonica* seedlings after two seasons were significantly higher in the herbicide-treated plots (36%) than in the untreated plots (22%) despite recovery of green cover after a period of release. A similar trend was observed for *P. durangensis*, but with lower survival rates than *P. engelmannii* and *P. arizonica*.

The difference in seedling survival because of herbicide treatment may be due, in part, to higher soil water potential values on the treated plots. At two grass-seeded sites on the east side of the Sierra Nevada mountains, in Nevada and California, Eckert (1979) reported that survival of one-year-old *P. ponderosa* seedlings was significantly higher (67%) in herbicide-treated (atrazine at 6.72 kg ha⁻¹) plots than in untreated plots after two growing seasons. He attributed the positive herbicide effect on seedling survival to the higher soil water potential found at soil depth of 15 cm in the treated plots (-0.2 MPa) than in the untreated plots (-1.5 MPa). Soil water potential continued to decline during the summer in the untreated plots, beginning from planting time in mid-July (Eckert, 1979).

In this study, soil water potential and vegetation cover were not systematically measured after the herbicide was applied in the open area. However, I believe that more soil moisture was available to the seedlings in the weeded plots,

because I observed that the herbicide reduced the competing herbaceous vegetation by 60 to 70% in the first growing season. In addition, planting was done during the rainy season of 1996 at Tarahumar, so summer rainfall may have alleviated soil moisture deficiencies at the beginning of the first growing season.

Soil moisture measurements were made in herbicide-treated and untreated plots by Heidmann (1969) on a site in Arizona. That site had a rainfall pattern similar to the one at Tarahumar. The author reported that herbicide-treated plots in Arizona were significantly moister than the untreated plots at 20-cm soil depths from mid-August of 1961 to October of 1962, except for periods with precipitation during the winter. Higher gravimetric soil water content was found in the herbicide-treated plots (26 to 30%) than in the untreated plots (11.5%) during the spring and early-summer drought season of 1961. However, during the spring to summer of 1962 (an unusually dry year), the gravimetric soil water content quickly approached the potted *P. ponderosa* wilting point of 8.8% in the untreated plots (Heidmann, 1969). Similarly, Larson and Schubert (1969) in Arizona reported that plots without competing grasses such as Arizona fescue (*Festuca arizonica* Vasey) and mountain muhly (*Muhlenbergia montana* (Nutt.) Hitchc.) had a higher gravimetric water content (20 to 27%) than grassy plots (10 to 15%), at a 10-cm soil depth. Soil water potential quickly approached -1.5 MPa in the grassy plots during spring and early-summer drought seasons (Larson and Schubert, 1969). Likewise, the positive relationship between soil water availability and seedling survival in herbicide-treated plots has been documented for slash pine (*Pinus elliottii* Engelm.; Baker, 1973), *P. ponderosa* (Tappeiner II and Radosevich, 1982), and *P. taeda* (Zutter et al. 1986).

The positive herbicide effect of reducing competing vegetation and promoting higher seedling survival in this study is also found in other pine plantation research. When herbicide was used to reduce herbaceous competition in

plantations of *P. taeda* in Alabama and Georgia, Creighton et al. (1987) reported that seedling survival in 4 of the 13 plantations significantly increased in the treated plots compared with the untreated plots. The herbicide effect was observed after two and three growing seasons at two of those plantations and after five growing seasons in the other two plantations (Creighton et al. 1987). Their work was done in an area of even rainfall distribution with slight summer maximum.

After evaluating four methods of applying the herbicide hexazinone to control herbaceous vegetation in a *P. ponderosa* plantation in northeastern Oregon, Oster et al. (1995) reported a significant positive herbicide effect on seedling survival when herbaceous vegetation was reduced. After five growing seasons, seedling survival was higher with these two herbicide treatments (60 and 63%, respectively) than without (18%). Likewise, in a study of 13 *P. taeda* plantations in Oklahoma and Arkansas, Yeiser and Williams (1996) reported that seedling survival was significantly higher in the herbicide-treated plots than in untreated plots at ten of those plantations after one growing season, and at all the plantations after five growing seasons.

The effect of herbicide application on seedling survival response also can be positive when plots contain shrub competition. In the mixed conifer forest of the Sierra Nevada, in California, Tappeiner II and Radosevich (1982) found that one-year-old seedlings of *P. ponderosa* planted on forest openings with uniform cover of bear mat (*Chamaebatia foliolosa* Benth) had higher survival in herbicide treated plots (71%) than in untreated plots (13%) after three growing seasons.

On a north aspect of a mixed conifer forest in northeastern Mexico, Capó-Arteaga and Newton (1991) reported that seedling survival after two growing seasons was higher for Mexican white pine (*Pinus ayacahuite* Shaw.),

Montezuma pine (*P. montezumae* Lamb.), and *P. ponderosa* seedlings planted in herbicide-treated plots than in untreated plots. However, treated and untreated plot differences for survival were much greater for *P. ayacahuite*, *P. ponderosa*, *P. montezumae*, Sugar pine (*P. lambertiana* Dougl.), and Hartweg pine (*P. hartwegii* Engelm.) on a south aspect in southwestern Oregon. Seedling survival in Oregon of all those species, except *P. ponderosa*, was significantly correlated with the first-year (1985) soil condition index (SCI = soil moisture / soil temperature + 10). Higher soil moisture availability and cool soil temperatures, therefore, were associated with higher survival after two growing seasons ($r = 0.773$ to 0.850 ; Capó-Arteaga and Newton, 1991).

In contrast, some studies in pine plantations have shown no positive herbicide effect on seedling survival. After pre- and post-planting applications of six herbicides were tested at a wind-throw site dominated by herbaceous vegetation in northeast Oregon, Dimock et al. (1983) reported that no herbicide effect was found in seedling survival of *P. ponderosa* after two growing seasons. Average survival rates were 55 and 58% in the untreated and treated plots, respectively. The lack of herbicide effect was attributed to above normal precipitation in August of 1976 (which exceeded the monthly normal by 5.6 cm), and to the combination of abundant precipitation with cooler weather, which reduced the evaporative demand in the treated plots. In Georgia, Nelson et al. (1985) reported that no herbicide effect was found for seedling survival in a longleaf pine (*Pinus palustris* Mill.) plantation after four growing seasons. Seedling survival averaged 83 and 87.5% in the untreated and treated herbicide plots, respectively. The authors had no explanation for the lack of response.

In Arizona, Elliot and White (1987) reported that *P. ponderosa* seedlings survived equally well, either in plots seeded with four grasses and two forbs, or in hand-weeded plots free of competing vegetation. The lack of survival differences

between plot types was attributed to transplant shock, poor planting stock, and the spring-early summer drought. About 90% of the mortality was after the first growing season, with 51% of the mortality occurring before plant competitors were seeded (Elliot and White, 1987).

In this study, despite the positive herbicide effect on survival, *P. durangensis* had low survival after two growing seasons. Causes of mortality, other than from herbaceous competition, may have included seedling quality (slender stems and short crowns), transportation, handling, and water stress during and after planting. Consequently, most of the *P. durangensis* seedlings showed signs of wilting and lost most of their fascicles after the first growing season. Although the seedlings were planted during the rainy season, rainfall amounts for the planting year (1996) and for the second growing season were 32.2 and 41.0% less (up to November 1998) than the expected annual mean (909.9 mm) at Tarahumar (Conagua and Cornejo-Oviedo, unpublished data). This lack of rainfall may have contributed to poor survival rates for *P. durangensis*.

2.5.1.2 Absolute stem height and stem diameter growth rates, and survival-initial stem diameter class relationship

Differences in growth rates of trees are related partly to species genetics and their manifestation on a given site (Helms and Rutter, 1979). In this study, *P. durangensis* seedlings were three months older than the *P. arizonica* and *P. engelmannii* seedlings. The inherently more rapid growth rate of *P. durangensis*, plus the use of older stock led to disproportionately larger seedlings in this study.

The juvenile grass stage of *P. engelmannii* (Mirov, 1967; McCune, 1988; Barton, 1993; 1995) allows the species to resist surface fires and survive on xeric environments. The grass stage is characterized by short, thick terminal

buds surrounded by needles up to 30 cm long, and a carrot-like root system. The long needles protect the terminal bud against surface fire while the root system stores carbohydrates. A juvenile grass stage has also been documented for longleaf pine (*Pinus palustris* Mill.) in the southeastern United States (Wahlenberg, 1946; McCune, 1988) and *P. montezumae* in Mexico (Capó-Arteaga and Newton, 1991). This stage may persist for 2 to 9.5 years, with an average of 6 years (Wahlenberg, 1946). However, this stage can be interrupted by promoting stem height growth, which responds quickly to clearing of competing vegetation, either manually (Pessin, 1939; 1944), chemically (Nelson et al. 1982; 1985; Creighton et al. 1987; Edwards et al. 1995), or completely (manually and chemically; Boyer, 1989; Capó-Arteaga and Newton, 1991).

In this study, reducing the competing vegetation, prompted stem height growth of *P. engelmannii* that was 91.4% greater in the herbicide-treated plots than in the untreated plots after two growing seasons. In the same way that herbicide treatment improved survival, I believe that the positive height growth response of *P. engelmannii* could be explained by site resource availability in the treated plots.

The positive height growth response to reduced competition was documented in a plantation of *P. palustris* in Georgia by Nelson et al. (1982). The authors reported that where competing vegetation was reduced with one herbicide application at planting time, seedlings of *P. palustris* were significantly taller (87.4%) in the herbicide-treated plots than in untreated plots after two growing seasons. The seedlings in that study plantation remained significantly taller (84.5 and 53.2%) in the treated plots than in the untreated plots after four (Nelson et al. 1985) and five (Creighton et al. 1987) growing seasons, respectively.

Combining mechanical and chemical treatments to reduce competing vegetation can interrupt the juvenile grass stage in some pine species. In Georgia, Boyer (1989) reported that when five plantations of container-grown *P. palustris* seedlings were treated with one of two pre-planting treatments, i.e., complete overstory removal with one mechanical pass (low) or two mechanical passes (high) with either a chopper or harrow for brush control, and with one of two post-planting treatments, i.e., herbicide or no herbicide, the seedlings were taller (80.5%) in the low-herbicide combination than in the low-no herbicide combination after five growing seasons. However, the seedlings were only 33% taller in the high-herbicide combination than in the high-no herbicide combination. Capó-Arteaga and Newton (1991) reported that the grass stage of *P. montezumae* growing on south aspects was interrupted by manually removing the shrub vegetation and treating the remaining stumps with herbicide. This complete-removal treatment minimized competing vegetation and maximized solar radiation. After two growing seasons, *P. montezumae* seedlings were taller in the complete-removal plots than in untreated plots in northeastern Mexico (110.3%) and in southwestern Oregon (59%) (Capó-Arteaga and Newton, 1991).

Edwards et al. (1995) reported that a single herbicide application at planting reduced the herbaceous competing vegetation and promoted the stem height growth of *P. palustris* during the second growing season in a plantation in North Carolina. Clason (1997) reported that stem height growth of *P. palustris* planted in Louisiana showed no response to the reduction of competing vegetation with herbicide after the first growing season. He found significant herbicide effect on height growth in year two. In this study, stem height growth of *P. engelmannii* responded significantly and positively in the herbicide-treated plots over two growing seasons. Therefore, I concluded that the grass stage of *P. engelmannii* could be shortened if vegetation management was incorporated in reforestation projects in the SMOC.

The positive seedling height growth response to reduced competition is a result of increased soil moisture availability in the herbicide-treated plots. In a *P. taeda* plantation in Alabama, Zutter et al. (1986) reported that gravimetric soil moisture content decreased with increasing biomass production. Even though soil moisture varied significantly across blocks due to soil texture, seedling height growth increased with soil moisture ($r = 0.922$) after the first growing season (Zutter et al. 1986). Similarly, Newton and Preest (1988) reported significantly lower xylem water potential of Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) seedlings as soil water availability increased to a depth of 90 cm in the complete elimination of competing, grasses, broad-leafed herbs, and mixed vegetation plots (three herbicide applications).

Seedling stem height growth may also be response to increased soil nutrient availability when competing vegetation was reduced by herbicides. In a *P. lambertiana* plantation in California, Eckert (1979) reported that the top growth was 140% larger in herbicide-treated plots than in untreated plots after two growing seasons. Nitrate-nitrogen ($\text{NO}_3\text{-N}$) availability also was higher in treated plots (49 kg ha^{-1}) than in untreated ones (4 kg ha^{-1}) at a 30-cm soil depth. In Canada, Sutton (1975) found that seedlings of white spruce (*Picea glauca* (Moench) Voss) had a 38% higher stem height increment and higher foliar concentration of N in herbicide treated plots than in untreated plots after two growing seasons. Similarly, in a Monterey pine plantation (*Pinus radiata* D. Don) in Australia, Woods et al. (1992) reported that needle-N concentration was significantly higher in treated plots (16 mg g^{-1}) than in the untreated ones (13 mg g^{-1}) after two growing seasons. However, there was no reduced-competition effect on stem height growth.

Nambiar and Sands (1993) stated that the roots of herbaceous vegetation were most dense in the upper 10-cm soil depth ($32 \text{ to } 44 \text{ cm cm}^{-3}$), which

is the major cause for the negative water balance in a tree seedling during the first year after planting. To overcome this negative water balance, the tree must develop a deeper root system and extract water from deeper soil horizons. It is difficult to differentiate the competition of water versus nutrients on a site when both are limiting, because water content influences soil nutrient availability and plant uptake (Nambiar and Sands, 1993). In this study, even though these relationships were not evaluated, I believe that they probably had an additive effect that resulted in the positive response for the stem height growth of *P. engelmannii* in the herbicide-treated plots after two growing seasons.

In this study, the positive response of absolute stem diameter growth of *P. engelmannii* to herbicide treatment depended on initial stem height. After two growing seasons, initially taller seedlings had higher absolute stem diameter growth in herbicide-treated plots than in untreated plots. By culling seedlings shorter than 6 cm at the nursery and reducing the competing vegetation with herbicides at planting, greater stem diameter growth may be expected, at least for *P. engelmannii*. Stem diameter increases as a result of cambial growth, which depends on current-year photosynthates. Cambial growth occurs later in the season after the carbohydrate sink of the apical meristem subsides. By reducing the competing vegetation, seedlings can grow foliage during the early part of the growing season and still have conditions favorable for radial growth late in the growing season (Lanner, 1985).

In a plantation of *P. palustris* in Georgia, Nelson et al. (1985) reported that seedling stem diameters were significantly larger (23%) in the treated plots (one-time herbicide application at planting) than in untreated ones after four growing seasons. In this same plantation, the herbicide effect for stem diameters remained after five growing seasons (Creighton et al. 1987). In a *P. taeda* plantation in Alabama, Zutter et al. (1986) reported that seedlings of *P. taeda* were significantly

larger (63.7%) in diameters in treated plots (one-time herbicide application after planting) than in untreated plots after two growing seasons. Yeiser and Williams (1996) reported that the stem diameter of *P. taeda* seedlings was significantly larger in treated plots, by 60 and 28.5%, after one and five growing seasons, respectively. When a complete shrub treatment, i.e., manual removal and chemical treatment of the stumps, was used in Mexico and Oregon, Capó-Arteaga and Newton (1991) reported that the relative diameter increment of all the species (*P. ayacahuite*, *P. hartwegii*, *P. lambertiana*, *P. montezumae*, and *P. ponderosa*) was higher in plots that received the complete herbicide treatment than in plots without it.

Although, the slow stem diameter response of *P. arizonica* and *P. durangensis* to reduced competition could have been attributed to planting, the response by these species to resource availability on-site may simply require more than two growing seasons. In California, McDonald et al. (1994) reported that the mean stem diameter of *P. ponderosa* seedlings was significantly larger in herbicide-treated plots than in untreated plots after five growing seasons. In addition, the loss of fascicles by *P. durangensis* seedlings may have contributed to reduced carbohydrate production needed for cambial growth.

In this study, the relationship found between initial stem height and absolute stem diameter growth in *P. engelmannii* was similar to the relationship found between initial stem height and stem height growth reported by Tuttle et al. (1987; 1988) for *P. taeda* in Alabama. He noted that the initial stem height was significantly correlated with seedling height growth after two growing seasons. At good sites, seedlings with initial heights of 10.6 to 25.4 cm grew more than those shorter than 10.6 cm or taller than 25.4 cm (Tuttle et al. 1987).

In this study, the relationship between absolute stem diameter growth and initial stem height in the treated plots was associated with the relationship found between seedling survival after two seasons and initial stem diameter class. Seedlings of *P. arizonica*, *P. engelmannii*, and *P. durangensis*, with initial stem diameters of 0.40 cm, had higher survival rates in the treated plots than in the untreated ones. These findings support the concept that large seedling survive and grow better than small ones. This idea has been subjected of several studies for defining the target seedling morphological characteristics that would maximize survival and growth in a given site (Rose et al. 1990). In addition, stem diameter may be a good predictor of outplanting survival (Mexal and Landis, 1990) because it is associated with seedling root volume, which is also useful when forecasting survival and growth after outplanting (Rose and Haase, 1995; Rose et al. 1997). The target morphological characteristics have not been studied for *P. arizonica*, *P. engelmannii*, and *P. durangensis* seedlings to be planted in the SMOC.

In Georgia, Lauer (1987) found that seedlings of *P. palustris* in the > 2.1-cm in initial diameter class were 37 and 100% taller than those seedlings within the initial classes of 1.91 to 2.1 cm and 1.6 to 1.8 cm, respectively, after two growing seasons. However, no differences in survival were found among diameter classes (Lauer, 1987). In Louisiana, Barnett (1991) reported that the survival rate for container-grown seedlings of *P. palustris* was higher in classes 1 and 2 (0.50 to 0.55 cm, and 0.40 to 0.45 cm, respectively) than in class 3 (0.30 to 0.35 cm). Seedlings from classes 1 and 2 were also significantly larger (13.2%) in stem diameter than those from class 3 after one and a half growing seasons. A similar grading system for *P. arizonica*, *P. engelmannii*, and *P. durangensis* seedlings would help select the best planting stock for the SMOC.

Enhancing stock quality may be integrated with vegetation management. South et al. (1993) reported that when seedlings were graded by stem diameter prior to planting and herbicide applications were used to control the competing vegetation, a larger diameter seedling would grow more than a smaller diameter seedling. Likewise, a bigger seedling with no herbicide treatment would grow equal to or greater than a smaller seedling in a plot treated with herbicide. Thus, it is possible that a significant seedling survival and growth could be gained if seedlings are graded and if a vegetation management is applied. Similar relationships have been reported for *P. radiata* in New Zealand (Albert et al. 1980) and for Sitka spruce (*Picea sitchensis* (Bong.) Carr.) in Scotland (Nelson, 1990).

Tree improvement may be incorporated into this integrated scheme of stock quality and vegetation management. McDonald et al. (1994) reported that seedlings of *P. ponderosa* from seed collected in a control-pollinated breeding orchard were significantly taller than those from seed collected from either wild stands or superior trees from progeny tests, regardless of the competing vegetation. Control-pollinated seedlings were taller (51.5 cm) and had thicker stem diameters (1.27 cm) in the treated plots than in untreated ones (47.0 cm and 1.12 cm, respectively) after two growing seasons.

The positive effects of integrating nursery culture and vegetation management may be amplified by incorporating fertilization at planting time. In a *Pseudotsuga menziesii* plantation in Oregon, Rose and Ketchum (1997) reported that applying slow-release fertilizer at planting, stem diameter responded significantly after the second growing season. Although the weed control by fertilization interaction was not significant, these treatments had an additive effect on stem diameter growth (Rose and Ketchum 1997). In Tarahumar, a comprehensive research program is needed to enhance seedling quality and evaluate outplanting performance in several sites with

different vegetation management schemes. This research program must be compatible with the objectives and economical resources of the landowners of Tarahumar and elsewhere in the SMOC.

2.5.1.3 Water relations

In the Pacific Northwest, soil moisture is the primary limiting factor for seedling survival and growth (Hobbs and Owston, 1985). Because needles are subject to transpirational demands from the atmosphere, establishing functional connections through the soil-plant-atmosphere continuum is a priority for initial survival and growth. Intimate contact between roots and soil water, low resistance to water flow into and within the seedling, and control of excessive water loss from stomata are important attributes favoring the survival and rapid growth of newly planted tree seedlings (Margolis and Brand, 1990). Ritchie and Hinckley (1975) and Hinckley et al. (1978) stated that predawn water potential provides a measure of the soil water potential experienced by the seedling and indicates the plant's water stress level at the start of the day.

I planned to measure xylem water potential after the first growing season (summer 1997), however, the one-year-old fascicles showed signs of wilting and were not vigorous enough for these measurements. The wilted fascicles were produced while the seedlings were in the nursery and probably they had lost turgidity and vigor during the planting process. The current-year fascicles were completing their development during the summer of 1997. This was especially true for *P. durangensis* seedlings, which lost the majority of their nursery fascicles after the first growing season. During the early-spring drought season (April of 1998) and during the summer rainy season (August of 1998) at Tarahumar (21 and 26 months after planting, respectively), I measured xylem water potential on fascicles that grew

in 1997. During the early-spring drought season, water potentials were moderate at predawn (between -0.64 and -0.86 MPa) among the species, and lower at midday. The majority of the readings were around -1.5 MPa at midday, regardless of herbicide use, except for *P. durangensis* in the untreated plots.

Photosynthesis and stomatal conductance of pine seedlings can be reduced substantially when xylem water potential reaches a threshold often found near -1.5 MPa. For example, stomatal closure in *P. ponderosa* seedlings occurred when water potential values were between -1.65 and -1.73 MPa (Lopushinsky, 1969). Likewise, photosynthetic rates were reduced by 50% in *P. ponderosa* seedlings when plant water potentials readings were either -1.5 MPa (Cleary, 1971) or between -1.3 and -1.8 MPa (Bunce et al. 1979). During the first 13 days of a drought treatment, stomatal conductance rates were reduced from 0.033 to 0.011 mol m⁻² s⁻¹ in seedlings of Greg pine (*P. greggii* Engelm.); predawn water potential was between -1.0 and -2.0 MPa (Vargas-Hernández and Muñoz-Orozco, 1991). Carbon dioxide uptake also was negligible in Rocky mountain ponderosa pine (*P. ponderosa* var. *scopulorum* Engelm.) and *P. engelmannii* seedlings when plant water potential was about -2.0 MPa (Barton and Teeri, 1993).

The predawn conditions may have not entirely halted stomatal closure and photosynthesis in the early morning hours of April 15, 1998 because there was a marked contrast between predawn and midday plant water potential. I hypothesized that the lower values for xylem water potential at midday may have induced stomatal closure and reduced photosynthesis at midday (Fig. 2.11). The significantly higher midday water potential for seedlings of *P. durangensis* in the treated plots could be explained by the reduction of the competing vegetation after the first growing season. In addition, seedlings in the untreated plot were probably under water stress after the first growing season and their root systems were not able to

supply enough water for their demanding fascicles. Therefore, xylem cavitation may have occurred, which probably induced embolism formation and fascicle desiccation. The midday water potential values also may have been an artifact of sampling fewer seedlings in the untreated plots ($n = 3$) than in the treated plots ($n = 6$), because seedling survival was higher in those treated plots after the second growing season.

During the summer rainy season, the higher predawn xylem water potential values may have reflected the recharge of the soil profile compare to the early-spring drought. However, midday values of xylem water potential approached stomatal closure threshold for these species (-1.2 to -1.5 MPa ; Fig. 2.12). This may have been caused by a higher transpirational demand because of higher midday temperatures that characterized the summer rainy season at Tarahumar. I suspect that the lack of treatment effect and the diurnal trends during the summer reflect the regrowth of the herbaceous vegetation in the treated plots after two seasons.

Predawn and/or midday xylem water potentials in pine seedlings have shown significantly positive responses to reducing the competing vegetation with herbicides. These responses were observed within two (Nelson et al. 1981) and five months (Carter et al. 1984; Sands and Nambiar, 1984) after the competing vegetation was controlled. This positive response decreased with seedling age or time since treatment (Sands and Nambiar, 1984). However, these positive significant responses sometimes were still detected after two or three growing seasons (Lanini and Radosevich, 1986; Newton and Preest, 1988).

In a plantation of *P. taeda* in Arkansas, Nelson et al. (1981) found that predawn water potentials were significantly higher in the treated plots (-0.4 to -0.5 MPa) than in the untreated plots (-1.5 MPa) five months after planting. Similarly, in *P. taeda* plantations at Piedmont and in the Coastal plains of Alabama,

Carter et al. (1984) reported that predawn water potentials were consistently and significantly higher when herbaceous and arborescent vegetation was eliminated completely within 1.5 m of the crop seedlings (-0.27 to -0.81 MPa) versus without it (-0.39 to -1.06 MPa). This was true at least for the Piedmont site two months after the competing vegetation was eliminated. Diurnal xylem water potential also was significantly higher in treated plots during a day that represented a severe dry period. Water potential in these plots was lowest (-1.73 MPa) at midday (Carter et al. 1984).

In three Australian plantations of *P. radiata* that were 5, 16, and 28 month-old, Sands and Nambiar (1984) reported that the diurnal xylem water potential trend on a typical dry summer day diverged distinctly, with higher values in the treated, five-month-old plots (less negative than -1.0 MPa) than in the untreated ones (-1.0 to -2.0 MPa). In contrast, the diurnal xylem water potential trend in the 28-month-old, treated plots converged, with values (-0.5 to -1.5 MPa) similar to that of the untreated plots on the same day. The difference between trends in those plantations was because seedlings in the five-month-old plantation were more stressed in the untreated plots, with their roots confined to the upper 25-cm soil depth where the weeds competed the most for soil water. In contrast, seedlings at the 28-month-old plantation probably had developed deeper root systems beyond the upper 25-cm soil depth, thereby tapping soil water from deeper zones in the soil profile. These trends for diurnal xylem water potential were consistent in both five- and 28-month-old plantations on two more dry days, before rain fell (Sands and Nambiar, 1984).

At Tarahumar, xylem water potential was measured at 21 months post planting on a typical day in the early-spring drought. The xylem water potential trends for *P. arizonica* and *P. engelmannii* were very similar to those reported for the 28-month-old Australian plantation by Sands and Nambiar (1984). Thus, *P.*

arizonica and *P. engelmannii* seedlings may have developed root systems adequate for escape from 25-cm soil depth.

When mechanical and chemical treatments were used to reduce the competing effect of shrub vegetation in a mixed conifer plantation in California, Lanini and Radosevich (1986) reported that predawn and midday values of water potential for *P. ponderosa* seedlings differed among three shrub canopy volumes (SCV; low = 0 to 1000 m³ ha⁻¹; medium = 1000 to 2000 m³ ha⁻¹; high = > 2000 m³ ha⁻¹) after four years. Predawn and midday water potential values were significantly higher in the low SCV than in the high SCV during June and July after only two and three growing seasons. Similarly, after competing vegetation was controlled in a *Pseudotsuga menziesii* plantation, with three consecutive applications of herbicide in three growing seasons, Newton and Preest (1988) reported that a positive response and higher overall values of xylem water potential were recorded in those plots with complete elimination of competition after three growing seasons.

The delayed opening of stomata in the early morning hours of April 15, 1998, was probably due to cold temperatures of the previous night. Temperature records from the weather station at Tarahumar reveal a mean annual minimum temperature (T_{\min}) of -5.7°C (n = 28 years) for April. Thus, freezing temperatures are not uncommon for this region. Frost was observed at the open site early in the morning on April 15, 1998.

Stomatal behavior responds to various stimuli, including light, intercellular carbon dioxide concentration, vapor pressure deficit, leaf water potentials, and hormonal signals (Farquhar and Sharkey, 1982; Hinckley and Braatne, 1994). Stomatal conductance can be delayed by low temperatures in the early morning hours (Drew et al. 1972) or the previous night (Kaufmann, 1982).

The delayed stoma opening in this study was similar to that reported by Drew et al. (1972). A pressure-infiltration technique was used to monitor changes in stomatal opening in branches of two *P. ponderosa* var. *scopulorum* trees in the Santa Catalina Mountains, of Arizona. High infiltration indices were recorded in November in the early morning hours after the air temperature abruptly fell to -7°C earlier in the morning. Opening of the stomata was delayed in the morning, with a gradual opening as the air temperature increased. Although soil moisture was available, root absorption may have been inhibited by the low soil temperatures at the 15-cm soil depth. On some April mornings, stomata remained closed because temperatures well below freezing interrupted the normal opening processes even in the presence of abundant light (Drew et al. 1972). In Engelmann spruce (*Picea engelmannii* Parry ex. Engelm.) and lodgepole pine (*Pinus contorta* var. *latifolia* Engelm.) trees, temperatures the previous night that were below about 4°C reduced leaf conductance the next day (Kaufmann, 1982). In addition, Lopushinsky and Max (1990) reported that stomatal conductance (0.009 to $0.013 \text{ mol m}^{-2} \text{ s}^{-1}$) was negligible in *P. ponderosa* seedlings when the soil temperature was between 5 and 10°C , regardless of the presence of new root growth.

The rationale is uncertain for stomatal behavior during spring measurements of *P. engelmannii* seedlings in the treated plots. After stomata opening was delayed in the morning, the seedlings apparently had better water balances, and higher stomatal conductances were recorded in the treated plots than in the untreated ones. Perhaps the root system for the seedlings in the herbicide-treated plots had already escaped to a greater soil depth ($> 20\text{-cm}$) allowing them to reach soil moisture from deeper soil horizons. Even though the stomatal conductance measurements showed a better water balance of the seedlings in the herbicide-treated plots, there was not herbicide effect on predawn water potentials in April 15, 1998 (Fig. 2.11). Probably, the herbicide effect was masked by the frost that occurred in the morning of

April 15. More intensive stomatal conductance measurements and their seasonal integration may help answer this question.

2.5.2 Forested sites

2.5.2.1 Survival

In general, seedling survival was moderate to high for seedlings planted in the canopy gaps of the forested sites. Across treatments, *P. arizonica* and *P. engelmannii* had higher seedling survival (> 80%) than *P. durangensis* (64%) after the second growing season. However, seedling survival of *P. durangensis* was significantly higher in the treated plots than in the untreated ones, after both growing seasons.

The herbicide effect on *P. durangensis* may be explained in two ways. First, even though the amount of existing understory vegetation cover was low in the canopy gaps before treatment, spraying the scant vegetation still released site resources and improved seedling survival. Second, survival steadily declined, from 87% after the first growing season to 64% after the second growing season. This declining rate of survival may suggest that other factors unrelated to the herbicide effect were causing the differences in survival. The herbicide effect was probably found by chance rather than being a true effect.

Apparently, *P. durangensis* seedlings were affected not only by planting shock but also by the presence of small mammals. Seedling desiccation and clipping of the stem at a 45° angle were the most common causes for mortality of *P. durangensis* in the canopy gaps after the second growing season. *P. engelmannii* seedlings were most susceptible to tap root girdling by pine weevils.

Few studies have investigated the survival of pine seedlings planted in canopy gaps or openings where the competing vegetation was controlled. Such studies were limited by the site conditions and species involved in the systems, but these investigations provide an insight about pine seedling survival in openings similar to this study. In a mixed pine-hardwood forest under single-tree selection management in Arkansas, Wahlenberg (1948) reported that the survival of naturally regenerated *P. taeda* after two growing seasons was 90% in openings ranging from 16.0 to 81.0 m². These gap sizes represented the typical size of an opening left after a mature tree was removed in a single-tree cut. Seedling survival was also 90% in larger openings (>121 m²) after the second growing season. However, seedling survival decreased to 66% in the small openings (16.0 to 81.0 m²) and remained at about 75% and 79% in the mid-size (121.0 to 283.0 m²) and large (\geq 405.0 m²) openings, respectively, after the fifth growing season (Wahlenberg, 1948).

In a 55-year-old *P. echinata* forest in Georgia, Jackson (1959) planted *P. taeda* and *P. echinata* seedlings in openings of six different sizes (1.8, 16.4, 46.0, 89.4, 148.0, and 222.0 m²), and competing vegetation was eradicated for three years. Seedling survival was moderate to high (55 to 82%) for both species across the six opening sizes after the second growing season. However, seedling survival decreased to between 12 and 26% in the three smallest opening sizes, (1.8, 16.4, and 46.0 m²) and remained moderate (46 to 59%) in the three largest sizes (89.4, 148.0, and 222.0 m²) after the sixth growing season. When the hardwood basal area was reduced from 26.0 to 15.0 m² ha⁻¹ (42.3%) in an immature *P. taeda* and *P. echinata* stand mixed with sweetgum (*Liquidambar styraciflua* L.), red oak (*Quercus falcata* Michx.), and post oak (*Q. stellata* Wangenh) in eastern Texas, Ferguson (1963) reported that the survival of underplanted *P. taeda* seedlings after two growing seasons was higher in the reduced basal area hardwood plots (70%) than in the control basal area plots (24%).

In a mixed conifer forest of the Sierra Nevada in California, McDonald (1976) reported that the established natural regeneration for *P. ponderosa* was 2,125 and 3,706 seedlings ha⁻¹ in stands treated with single- and group-tree selection cuts, respectively, after the ninth growing season. These densities represented 23.8 and 41.4%, respectively, of the maximum natural regeneration reached in a shelterwood cut (8,945 seedlings ha⁻¹) after the ninth growing season. Although the *P. ponderosa* seedlings survived in the single-tree cuts after nine growing seasons, the majority of them lacked vigor because of insufficient light and soil moisture. These circumstances also applied to the group selection cuts, with areas of 63.6, 254.5, and 572.5 m², but the seedlings were robust and vigorous in the center of the largest openings (572.5 m²) (McDonald, 1976).

In a mixed pine-hardwood forest in South Carolina, Waldrop (1991) reported that where *P. taeda* seedlings were planted in openings of 405 and 1,350 m² and competing was controlled, seedling survival was high >80% throughout the first growing season. However, seedling survival was 6% higher in the smaller openings, regardless of weed control measures. Higher, direct sunlight that reached into the center and northwest quarter of the 1,350 m² openings may have contributed to the lower seedling survival because mortality was associated with water stress in the larger openings after the first growing season.

After reviewing studies and aspects associated with the operational environment and vegetation of group-tree selection openings in California, McDonald and Fiddler (1991) stated that the environmental conditions are not as extreme in openings compared with less-sheltered sites. Trees around the openings provided shade and reduced temperatures, and in general, temperatures were not as extreme as in a less-protected site. However, late spring frosts could occur in the openings because of cold-air ponding. In addition, the roots of surrounding trees could

expand quickly and use the site resources released in the opening. In general, survival was poor for naturally-seeded seedlings, but good for planted seedlings.

In this study, therefore, the early moderate to high survival of *P. arizonica*, *P. engelmannii*, and *P. durangensis* found in the small openings (natural and left by selective cutting) was similar to that found in small openings by Wahlenberg (1948), Jackson (1959), and Waldrop (1991). Seedling survival will probably decrease in subsequent growing seasons, as was reported by Wahlenberg (1948) and Jackson (1959) after five and six, respectively, growing seasons. Survival is a short-term outcome because minimum light-intensity requirement for early seedling establishment can be met under dense canopies (Tesch and Mann, 1991). In the long term, however, the surrounding trees may negatively interfere as seedling requirements for soil moisture and light increase (Radosevich and Osteryoung, 1987). More time is needed to confirm the early survival trends found in this study at Tarahumar.

2.5.2.2 *Absolute stem height, stem diameter, and volume growth rates, and survival-initial stem diameter class relationship*

In general, seedlings of *P. arizonica*, *P. engelmannii*, and *P. durangensis* had slow growth rates in the canopy gaps of the forested sites after both the first and second growing seasons. Stems heights, stem diameters, and volume growth rates were higher for the three species, (except for the height growth rate of *P. arizonica*) after the second growing season than after the first growing season. These higher growth rates in the second season may have been because the seedlings were recovering from planting shock in the first growing season. The growth rates increased equally, regardless of herbicide treatment. This lack of an herbicide effect reflected the initially low understory vegetation cover; the application of herbicide did not make a difference for seedling growth after either growing season.

The slow growth response of naturally regenerated and planted seedlings in small openings that resulted from single- and group-tree selection cuts was documented by Wahlenberg (1948) in Arkansas. The author reported that naturally regenerated seedlings of *P. taeda* were 71.5% taller in the larger openings ($\geq 405.0 \text{ m}^2$) than in the smaller openings (16.0 to 81.0 m^2) after the third growing season. This effect persisted and seedlings in the large opening remained 94.0% taller after the fifth growing season. Seedling stem diameters as well were 80.5% and 104.2% larger in the large openings than in the small ones after the third and fifth growing season, respectively (Wahlenberg, 1948).

In Georgia, Jackson (1959) reported that planted seedlings of *P. taeda* and *P. echinata* had marginal annual height increment growth in smaller openings (1.8, 16.4, 46.0, and 89.4 m^2) after the second growing season. Increment growth ranged from 10.2 to 16.5 cm for *P. taeda*, and from 8.9 to 12.7 cm for *P. echinata* in those openings. In contrast, the height increment growth was greater in the larger openings (148.0 and 222.0 m^2). Growth within these openings ranged from 25.4 to 43.2 cm for *P. taeda*, and from 15.2 to 23.5 cm for *P. echinata* after the second growing season. The annual height increment peaked in the larger openings after the third growing season. Thus, *P. taeda* and *P. echinata* seedlings had 123.0 and 144.0%, respectively, higher height values in the 148.0 m^2 openings than in smaller openings. In addition, height values were 346.0 and 266.2% higher, for *P. taeda* and *P. echinata* seedlings, respectively, in the 222.0 m^2 openings than in the four smallest openings. Seedling stem diameters also were low, ranging from 0.3 to 0.6 cm across species among the small openings. In contrast, stem diameters ranged from 0.5 to 0.8 cm in the 148.0 and 222.0 m^2 openings across species after the second growing season. These stem-diameter differences between the small and large openings clearly diverged after the sixth growing season. Stem-diameter was suppressed and growth was marginal for both species in the small openings. In contrast, stem diameter ranged

from 1.9 to 3.5 cm across species in the large openings after the sixth growing season (Jackson, 1959).

In eastern Texas, Ferguson (1963) reported that underplanted *P. taeda* seedlings after two growing seasons were 76 cm taller when the hardwood basal area was reduced by 42.3%, from 26.0 to 15.0 m² ha⁻¹. Seedling height decreased as the residual basal area increased after two growing seasons. For naturally regenerated *P. palustris* seedlings in Alabama, overstory residual basal areas ranged from zero (no overstory competition) to 20.6 m² ha⁻¹ (Boyer, 1963) and between zero and 11.45 m² ha⁻¹ (Boyer, 1993). Negative relationships were found between stem diameter and the overstory residual basal areas. After the fourth growing season, stem diameter was 98.4% larger for the zero overstory residual basal area than for basal area of 20.6 m² ha⁻¹. After seven seasons, stem diameter was 129.2% larger in the zero basal areas (Boyer, 1963). The growth of grass-stage species like *P. palustris* was suppressed by the high levels of overstory residual basal area. Light overstory densities of about 6.87 m² ha⁻¹ may have accounted for about 70% of the size difference from the zero and 20.6 m² ha⁻¹ basal areas (Boyer, 1963).

In California, McDonald and Abbott (1994) reported that the height of naturally regenerated *P. ponderosa* seedlings in openings of 66.0, 263.0, and 590.0 m² differed significantly between the smallest and largest openings after the ninth growing season. Seedlings in the largest opening were 62.3% taller than those growing in the smallest opening. Growth of pine seedlings increases as the size of the opening increases or the overstory competition is reduced. In the forested sites at Tarahumar, light and soil moisture availabilities were not evaluated for cause-effect relationships between seedling growth and resources in the gaps left by the single-tree cuts. However, soil moisture and light generally increase from the forest edge to the center of the openings (McDonald and Abbott, 1994). To identify some aspects of the

relationship between seedling growth and site resources in canopy gaps, one must understand the competing relationships between surrounding trees and seedlings planted in the gaps. For example, the maximum root radius reported for mature *P. ponderosa* ranges from 6.1 to 25.6 m, and from 15.5 to 22.2 m for *P. palustris* (Stone and Kalisz, 1991). Seedlings growing within the range of these root radii probably would encounter more limited soil moisture.

In a mixed-conifer forest in the Sierra Nevada of California, Ziemer (1964) measured soil moisture depletion along a transect between the forest and a one-year-old opening. Moisture increased in the soil profile from the forest toward the center of the opening, and from June to September. The soil profile was nearly at field capacity (35 to 40%) in both the forest and the opening in June. As the season advanced, soil moisture was quickly depleted, progressing from the forest to the opening, reaching its maximum depletion rates in early September. In September, soil moisture was about 10 to 15% from the soil surface to the 76-cm soil depth in the forest. In contrast, at 3.4 and 6.8 m from the canopy drip line of the forest, soil moisture was between 15 and 20% at the 15-cm soil depth. However, at the 76-cm soil depth, soil moisture ranged between 25 and 35% at 3.4, 6.8, and 13.7 m of the canopy drip line. The highest soil moisture (30 to 35%) was available about 13.7 m from the drip line, and from 20-cm to 107-cm soil depth (Ziemer, 1964).

Competition for soil water by lateral roots of understory and overstory vegetation may also limit soil water availability to seedlings planted in the forest understory (Childs, 1985). Apparently, soil moisture depletion is due to water absorption by tree roots and probably impacts the growth of *P. ponderosa* seedlings in small openings (McDonald and Abbott, 1994).

Among the natural regeneration of *P. palustris* in twelve tree-fall gaps (between 1257.0 and 1963.5 m²) in Florida, Brockway and Outcalt (1998) reported that the number of seedlings was significantly higher at distances ≥ 16 m from the canopy gap edges. Fine root biomass at the 20-cm soil depth was significantly reduced at distances ≥ 16 m from canopy gap edges. They defined the seedling exclusionary zone, the area between canopy gap edges and the beginning of the root gap, that resulted from the intraspecific competition between the root systems of mature trees and seedlings for soil resources.

Light and nitrogen availabilities also are influenced by surrounding trees. In California, Oliver and Dolph (1992) found that height growth after five years for naturally regenerated *P. ponderosa* seedlings was 154% greater at 58% of full sun (residual basal area of 9 m² ha⁻¹) than at 34% (basal area of 23 m² ha⁻¹). In Georgia Palik et al. (1997) found that nitrogen availability (NH₄+NO₃) and seedling biomass (above- and below-ground) of planted *P. palustris* were significantly and negatively associated with overstory basal area after the first growing season in Georgia. In addition, seedling biomass was positively associated with the gap light index (an index of the percent cumulative seasonal light availability relative to light availability in the open; Canham et al. 1990)).

Four gap sizes (1067, 1225, 1553, and 2027 m²) and equal areas of those gaps in an undisturbed overstory were studied by Palik et al. (1997). Seedlings of *P. palustris* were planted in a crossed design within nine 2-m² quadrants in each pair gap-undisturbed overstory. Prior to planting, the quadrants were treated with herbicide and hand-weeded periodically. The authors found that biomass of the planted *P. palustris* seedlings increased slowly as the overstory basal area decreased from 27 to 9 m² ha⁻¹. However, seedling biomass began to increase at about 8 m² ha⁻¹ after the first growing season. Similarly, nitrogen availability was low in basal areas of 10 to 27 m²

ha⁻¹, but nitrogen began to increase at about 7 m² ha⁻¹. Seedling biomass also remained low between 28 and 66% of a gap light index, but, increased quickly beyond the 68% gap light index.

In this study, the residual basal areas after the selective cutting (22.91 to 25.01 m² ha⁻¹) were apparently too great to promote better growth of the planted seedlings after two growing seasons. Pine and oak trees will probably continue to suppress stem height and diameter growth of the *P. arizonica*, *P. engelmannii*, and *P. durangensis* seedlings in subsequent growing seasons. In addition, the small openings left by the selection cuttings may receive more side shade from surrounding trees, thus limiting light for the planted seedlings.

The lack of herbicide effect found for the relationship between seedling survival and initial stem diameter is probably due partially to the small amount of understory vegetation initially. In addition, the retention of high basal areas did not decrease survival across the different initial stem diameter classes, regardless of the use of herbicide.

2.5.2.3 *Water relations*

The lack of an herbicide effect on predawn and midday water potentials during the spring and summer sampling days may reflect the low level of understory vegetation. Because sampling took place 21 and 25 months after the seedlings were planted, and three to four years after the selective cutting, this delay may have influenced the chances of determining an herbicide effect on water balance of the planted seedlings. Also, roots of associated trees near gaps may have already penetrated the soil and utilize site resources.

The seedlings had initially low water potential values during the two, typical days of the early-spring drought at Tarahumar. Values peaked at -1.57 and -2.23 MPa at midday. These levels exceeded the known water potential threshold of -1.5 MPa at which point stomatal closure may occur (Lopushinsky, 1969) or where photosynthetic rates can be reduced by 50% (Cleary, 1971) in *P. ponderosa*. The low predawn water potential may reflect the lack of precipitation that characterized the early-spring drought at Tarahumar. Interestingly, *P. engelmannii* had higher midday water potential values than did *P. arizonica* and *P. durangensis*. Probably, the water potential at midday induced stomatal closure because low levels of conductance were recorded on the same day, regardless of herbicide control. However, low levels of instantaneous PAR also were recorded at midday ($1098 \mu\text{mol m}^{-2} \text{s}^{-1}$), never reaching the light saturation point of $2,200 \mu\text{mol m}^{-2} \text{s}^{-1}$ that was reported for *P. ponderosa* by Tinus (1970). Therefore, low light levels may not have stimulated stomatal opening, which could be an additional effect of the low conductance of the seedlings planted at Tarahumar.

In this study, predawn water potential values were moderate (-0.59 and -0.89 MPa) for the three pine species in the two sampled days during the summer rainy season of 1998. However, these values were higher than those during the early-spring drought of 1998. In addition, midday summer water potential values were close to the -1.5 MPa threshold, ranging from -1.16 to -2.04 MPa across species. However, *P. engelmannii* had higher water potential at midday than the other species. Apparently, moderate predawn water potentials readings taken during the summer rainy season may indicate that some soil moisture was supplied to the planted seedlings, which allowed them to recover from the diurnal fluctuations of the previous day. Prior to the summer sampling days, 126 mm of rainfall were recorded at the Tarahumar weather station. The station is located within 10 km of the forested sites. Perhaps

some rain reached the sampled forested sites and allowed the seedlings to maintain moderate predawn water potentials.

Even though predawn water potentials were measured only on two days in the early-spring drought and in the summer rainy season, the values apparently followed the moisture availability in the seedling root zone that the rainfall probably supplied. Low predawn readings were recorded in the early-spring drought, moderate values during the rainy season. Similarly, Brandeis (1998) reported that predawn plant water potentials steadily declined for underplanted seedlings of *Pseudotsuga menziesii*, grand fir (*Abies grandis* (Dougl.) Lindl.), western red cedar (*Thuja plicata* Donn ex. D. Don), and western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) in 50-year-old stands of *Pseudotsuga menziesii* thinned to a certain residual basal area, e.g., low (16.0 to 18.3 m² ha⁻¹), medium (18.4 to 20.6 m² ha⁻¹), or high (25.2 to 26.3 m² ha⁻¹) in western Oregon. This declining trend in predawn readings was carried across all species as the growing season advanced from months of high precipitation (May and June) to months of low precipitation and high evaporative demand (July and August). Even though the residual overstory density was negatively associated with predawn water potentials across all species, the relationship was not strong.

In the forested portion of this study, because the understory vegetation was initially low and the overstory residual basal area was very uniform across the forested sites, it was difficult to elucidate clearly the competing effects on the water balance of the planted seedlings. There is a great need to understand the competing effects of understory and overstory densities on the water relations of planted seedlings and advanced regeneration in the forests of Tarahumar.

2.6 Conclusions

2.6.1 Open area

In the field studies at Tarahumar, the survival of *P. arizonica*, *P. engelmannii*, and *P. durangensis* seedlings after two growing seasons was enhanced by applying herbicide to reduce the competing herbaceous vegetation in an abandoned agricultural field. Reducing the herbaceous vegetation also increased stem height and diameter growth of *P. engelmannii* in the treated plots after two growing seasons. More time is needed to confirm the long-term survival and growth trends found after the second growing season.

Furthermore, initial seedling size influenced the survival of the three species; larger seedlings survived better. The initial size combined with the herbicide application also yielded a larger stem diameter in *P. engelmannii*. Therefore, it is important to begin a comprehensive research program that integrates stock quality and vegetation management if land owners and forest managers wish to accomplish successful reforestation efforts at Tarahumar and elsewhere in the SMOC.

Although, my data were insufficient to specify the relationships between seedling survival and growth, and seasonal precipitation and temperature, I did not find evidence to suggest these three Mexican pine species were behaving differently than pines in southeastern and western USA. Specifically, herbicide treatments that substantially reduce the volume of heavy stands of competing herbs and grasses will result in better survival and growth of healthy seedlings planted in open areas.

A better understanding of the seasonal pattern of soil moisture and temperature, and their effects on seedling growth in open areas will help understand the seasonal seedling growth and define windows of opportunities for changing the competitive relationship between crop seedlings and weed plants.

2.6.2 Forested sites

This study provided insight into the survival and growth of planted seedlings under the current selective cutting practices at Tarahumar. Herbicides had no effect on survival and growth of seedlings planted in canopy gaps, natural openings and those openings left by the selective cutting, because understory vegetation was already suppressed by overstory trees. Although the survival of *P. arizonica* and *P. engelmannii* was moderate after the second growing season, other studies have shown that survival of pine species may decline for five or six growing seasons in small gaps ($< 46.0 \text{ m}^2$) or in areas with high residual basal areas ($> 20 \text{ m}^2 \text{ ha}^{-1}$). Therefore, survival and growth of planted seedlings will be optimized if the size of the gap is large enough to avoid the seedling exclusionary zone ($> 16 \text{ m}$ radius) and increased site resources are available to planted seedlings.

At Tarahumar, the current practice of the selective cutting does not insure regeneration of the pine forest. Even though desirable stand composition relies on natural regeneration, there is a lack of experience and knowledge about seed-crop production, favorable physical and biological characteristics of the seedbed, timing of seedbed preparation, reducing overstory density to allow seedling emergence, and controlling the amount of seed predation by insects and animals.

Even when natural regeneration is successfully established, control of intraspecific or interspecific competition is not achieved to improve survival and

growth of the established seedlings. Therefore, these conditions lead to overstocked stands with increasing volume of low value oak trees and stagnated growth of pines. In many cases these stands appear ideal candidates for stand-replacement fires.

This study provided insight for incorporating artificial regeneration into the current silvicultural practices at Tarahumar. Through tree planting, the natural seedling establishment process is avoided, but, a nursery-produced seedling must meet morphological and physiological characteristics to overcome an apparently harsh operational environment and competition at a given site. In addition, the current cutting practices select pine trees suitable for saw timber-diameter sizes, thereby leaving behind small pine trees and hardwoods of all sizes in the stands. These practices promote forest structures that are unsuitable for natural regeneration or planted seedlings. There is a great need for understanding other forms of silvicultural practices that not only ensure survival and growth of planted seedlings, but also reduce overstocked stands and stagnated tree growth at Tarahumar.

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3. EFFECTS OF WATER STRESS ON SEEDLING GROWTH, WATER POTENTIAL, AND STOMATAL CONDUCTANCE OF FOUR *PINUS* SPECIES.

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3.1 Abstract

In a greenhouse study, we investigated the response of growth and water relations of seedlings of Arizona pine (*Pinus arizonica* Engelm.), Apache pine or pino real (*Pinus engelmannii* Carr.), Durango pine (*Pinus durangensis* Mart.), and Ponderosa pine (*Pinus ponderosa* Laws.) subjected to stressing treatments. The two treatments were well-watered and water-stressed, conducted over three replicated drying cycles during the dormant season. The well-watered treatment ranged between 67 and 36% of volumetric water content of the growing media; the water content in media of the stress treatment ranged between 8.0 and 2.0% of volumetric water content. Due to inherent species differences in morphology and physiology, the level of water stress at the end of the drying cycles was not the same for all species. Xylem water potential and stomatal conductances were measured in needle fascicles at the ends of two drying cycles. Statistically, no water-stress effect was found on seedling growth, except in *P. durangensis*. Biologically, the effect was marginal. Water stress caused significant and highly significant treatment and diurnal differences in plant water relations in at least three of the species during those two cycles. At midday, stomatal conductance was reduced significantly (by more than 60%) in the water-stress treatment. For each species, a maximum midday stomatal-conductance value was defined, based on the mean and standard deviation of midday conductance in the well-watered treatment over the three drying cycles. This maximum value was used as the baseline (100%) from which relative values were estimated for conductance readings in the well-watered and water-stress treatments. For each species, I identified a predawn water potential range associated with less than 50% of the maximum midday stomatal conductance.

3.2 Introduction

Seven thousand plant species have been identified in Mexico's temperate forests (Rzedowski, 1991,1993; Bye, 1995), including 52 pine species (Perry, 1991). These forests contain the highest concentration (24%) of Mexico's flora diversity (Rzedowski, 1991,1993), and the fifty-two pine species represent the greatest variety of pine species in the world (Hawksworth and Bailey, 1989; Styles, 1993).

Pine-oak forests are found throughout the Sierra Madre Occidental (SMOC) on a wide variety of geological, climatological, and topographical sites (Rzedowski, 1978; Ferrusquía-Villafranca, 1993). In the SMOC, the summer rainy season is followed by little precipitation in fall, winter, and spring. A pronounced droughty period occurs from late winter to late spring. Arizona pine (*Pinus arizonica* Engelm.), Apache pine (*P. engelmannii* Carr.), and Durango pine (*P. durangensis* Mart.), are the major, economically valuable species in that region (Martínez, 1948; Perry, 1991). The needles of these trees have stomata arranged in rows on their dorsal and ventral surfaces (García-Arévalo and González-Elizondo, 1998). These pines are classified within the *Ponderosae* subsection of genus *Pinus* by Perry (1991). Recently, Rehfeldt (1999) reviewed the systematics of the *Ponderosae* subsection of the southwestern United States. He placed *P. engelmannii* and *P. durangensis* in the "engelmannii" and "quinquefoliata" groups, respectively. He located *P. arizonica* in a subgroup within the "scopulorum" group where Rocky mountain ponderosa pine (*Pinus ponderosa* var. *scopulorum*) was placed. He concluded that the systematics of the subsection is not fully understood.

In the SMOC, *P. arizonica* (a three-needle pine) is confined to elevations of 2,500 to 2,800 m. in moist, cool valleys and mesas with deep and well-drained soils (Perry, 1991; García-Arévalo and González-Elizondo, 1998).

P. engelmannii (a three-needle pine), is found in a wide ecological range (1,900 to 2,600 m) from the dry climate and poor soils of the eastern slopes, to cool, moist valleys and mesas with deep soils at higher elevations. This species also grows on sites with a semitropical-temperate climate on the western slopes (Yeaton et al. 1983; Perry, 1991; García-Arévalo and González-Elizondo, 1998). The juvenile seedling of *P. engelmannii* is characterized by a "grass stage," (Mirov, 1967; McCune, 1988; Barton, 1993, 1995).

P. durangensis (a six-needle pine), is found from 2,400 to 3,200 m, in semi-humid and humid climates, and on a variety of slopes, mesas, and creeks (Perry, 1991; García-Arévalo and González-Elizondo, 1998).

Little is known about the morphological and physiological characteristics needed for pine seedlings to survive and grow on a given site in Mexico. Mexal et al. (1994) reported that seedlings used in reforestation usually are propagated in polyethylene bag-container nurseries. This system produces low-quality stock because irrigation is inadequate and poorly distributed, and seedlings often have a poor root to shoot ratios. Another factor that contributes to poor stand establishment is the inability to match seedling characteristics to the operational environment on the plantation site. However, seedling quality could be improved by converting from polyethylene bag-containers to a fixed-geometry (containerized) system (Mexal et al. 1994). In addition, Mexal (1996) stated that Mexican nursery managers need to understand basic aspects about seed biology and seedling physiology.

Seedling morphology and physiology can be changed via water-stress conditioning in containerized systems. In Washington state, for example, Tanaka and Timmis (1974) reported that five-month-old Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) seedlings that were subjected to water stress at predawn water

potentials of -0.8 and -1.7 MPa had significantly increased cold tolerance. In Oregon, Khan et al. (1996) reported on four- to five-month-old *Pseudotsuga menziesii* seedlings treated with a moderate water stress regime (17 to 53% volumetric water content) showed optimal bud development, and stem heights, and diameters. In contrast, seedlings treated with too much (65%) or too little water (7%) did not have those optimal characteristics.

The irrigation schedule must be evaluated if one is to successfully alter seedling morphology and physiology. Weighing the containers is the most common way to monitor moisture content in containerized nursery systems (Landis et al. 1989). The weight of a container decreases noticeably during evapo-transpiration. At a predetermined container weight the irrigation process is triggered again (Landis et al. 1989). This technique has been used for assessing water stress regimes in seedlings of *Pseudotsuga menziesii* (Tanaka and Timmis, 1974; Khan et al. 1996), red pine (*Pinus resinosa* Ait; Becker et al. 1987), and western hemlock (*Tsuga heterophylla* (Raf.) Sag.; O'Reilly et al. 1989; Grossnickle et al. 1991).

Nursery managers could also incorporate this weighing method for designing an irrigation schedule. However, stomatal behavior during dormancy is not well understood in *P. arizonica*, *P. engelmannii*, and *P. durangensis* seedlings. Stomata open and close in order to regulate the rate of water loss and plant water use efficiency (Woodward, 1998). This mechanism also helps to increase survival and competitive ability during seedling establishment. Even though physiological research has contributed toward improving survival and growth of container-grown seedlings in the United States (Tinus and Owston, 1984), the diurnal behavior of stomata in water-stressed Mexican pine species has not been studied. A knowledge of water relations in these species during the dormant season could help explain their ecological distribution and also lead to improvements in nursery practices and planting success.

The threshold of stomatal regulation differs among species and with the degree of adaptation to a particular habitat (Larcher, 1995). In a greenhouse study, carbon dioxide uptake was negligible in seedlings of *P. engelmannii* when plant water potential reached -2.0 MPa during February and March (Barton and Teeri 1993). During the first 13 days of a drought treatment, stomatal conductance rates were reduced from 0.033 to 0.011 mol m⁻² s⁻¹ in seedlings of Greg pine (*P. greggii* Engelm.); predawn water potential was between -1.0 and -2.0 MPa (Vargas-Hernández and Muñoz-Orozco, 1991).

In the United States, Pacific Ponderosa pine (*P. ponderosa* var. *ponderosa* Laws.) is found from the mountains of southern California (on both sides of the Sierra Nevada-Cascade crest), north to Canada (Wells, 1964). A maritime climate characterizes the Pacific region, with wet winters and dry summers (Steele, 1988). At lower elevations (152 to 1,524 m) in California, the Pacific variety grows best on northern and eastern aspects, along protected creeks and canyons. At higher elevations (762 to 1,828 m), the species grows well on all aspects, but is best on southern and western aspects at its upper limit (2,438 m; Roy and McDonald, 1973). A second variety, Rocky Mountain Ponderosa pine (*P. ponderosa* var. *scopulorum* Laws.) grows east of the summit of the northern Rocky Mountains, and from the southern and central Rockies to the Black Hills of South Dakota (Wells, 1964). The continental climate of this region means less winter rainfall than in the maritime climate, but convective storms provide summer precipitation (Steele, 1988).

A threshold of stomatal closure in var. *ponderosa* seedlings has been measured at water potential values of -1.65 to -1.73 MPa from December to February (Lopushinsky, 1969). Photosynthetic rates in this variety can also be reduced when plant water potentials readings are -1.73 MPa after the growing season (Cleary, 1971).

In a greenhouse study of seedlings under well-watered and water-stress treatments, Kaufmann (1977) reported that the transpiration rate of Monterey pine (*Pinus radiata* D. Don) under well-watered conditions followed a bell-shaped pattern with a peak at noon. Transpiration rates for pines kept under water stress for 12 days were suppressed, with a small peak around 1000 h, then a decline from noon to evening. In Australia, seedlings of eucalyptus (*Eucalyptus marginata* Donn. ex Sm.) were grown under well-watered conditions (Stonema et al. 1994). The diurnal pattern of photosynthesis rates had an increasing curvilinear form, with a plateau at noon. In contrast, the photosynthesis rates of seedlings grown under water stress for 12 days were suppressed, with a small peak around 0800 h followed by a steady decline the rest of the day.

Even though the overall water-stress effects on the transpiration and photosynthesis rates were statistically tested in the two previously described studies, the water stress effects on those rates at midday or any other time were not examined. The MIXED procedure of the Statistical Analysis System (SAS) has been improved to allow for modeling a covariance structure for repeated measurements (Littell et al. 1998). Variances at individual times and correlations between measurements taken at different times on the same seedling can now be better estimated. Two repeated measurements close in time on the same seedling are often more highly correlated than measurements made farther apart in time. In earlier methods, i.e. analysis of contrast variables and univariate analysis of variance either avoided the issue of repeated measurements or ignored it. These improvements allow to test the overall water stress effects and the effects at midday or at any other given time (Littell et al. 1998).

The overall objective in this greenhouse study was to gain information about the morphology and physiology of *P. arizonica*, *P. engelmannii*, and *P. durangensis*.

A better understanding of basic seedling biology could help in improving nursery activities and reforestation efforts in the SMOC. *P. ponderosa* was included in this study as a reference species. The newly improved statistical methods were used to testing for overall water-stress effects, plus at midday on plant water potential and stomatal conductance values.

The specific goals of this study were to:

- 1) determine the water-stress effect on relative stem height and diameter growth rates, and on the shoot and root dry-mass ratios of four *Pinus* species;
- 2) characterize plant water potential and stomatal conductance of seedlings subjected to well-watered and water-stressed treatments;
- 3) determine the overall and midday water-stress effects on plant water potential and stomatal conductance of seedlings in the stress treatment, and
- 4) determine a range of predawn plant water potential values at which less than 50% of the maximum midday stomatal conductance is achieved.

3.3 Materials and methods

3.3.1 Seed acquisition and seedling propagation

Forest managers from UAF "Tepehuanes", Durango, collected seed from the Mexican pine species from in wild stands (Table 3.1). The seed source for *P. ponderosa* was zone 526, "El Dorado", in the Sierra Nevada of California (elevation of 1,676 m). Total precipitation in El Dorado County is about 1,651 mm per year (Anonymous, 1998).

Seedlings of *P. arizonica*, *P. durangensis*, *P. engelmannii*, and *P. ponderosa* were grown in expanded polystyrene containers (Number Eight: 80 conical cells, 133 cm³ each; Stuewe & Sons, Inc., Corvallis, OR) from March to September 1997, at the Georgia-Pacific nursery at Cottage Grove, OR. Cells were filled with a mix of 90% peat moss and 10% perlite, using a vibration based flat filler. The media volume for each cell was about 117 cm³. A total of sixteen containers were sown (two to three seeds per cell): four containers with *P. ponderosa*, the second week of March, 1997, and four for each Mexican pine species, on the last week of March, 1997. After sowing, a 1.0-cm layer of quartz gravel was spread over each cell. After the seedlings emerged, they were thinned to one per cell. At the nursery, the seedlings were irrigated and fertilized (7-40-17, 15-16-17, and 6-30-30) following Georgia-Pacific's irrigation and fertilization schedules.

3.3.2 Experimental design and greenhouse environment

Six-month-old seedlings were transferred to the west greenhouses at Oregon State University (OSU), Corvallis, OR, in September of 1997, and arranged in a randomized complete-block experimental design.

Table 3.1 Seed sources of the four *Pinus* species.

Pine species	Location	Latitude N	Longitude W
<i>P. arizonica</i>	La Cebadilla, Canelas, Durango, Mexico	25° 07'	106° 26'
<i>P. durangensis</i>	Comunidad Río y Papuos, Canelas, Durango, Mexico	25° 02'	106° 32'
<i>P. engelmannii</i>	Ejido San José de la Cruz, Santiago Papasquiario, Durango, Mexico	25° 03'	106° 22'
<i>P. ponderosa</i>	EI Dorado County, CA USA	25° 03'	106° 22'

The two greenhouse benches were the experimental blocks and the containers were the experimental units. Each species was a whole-plot treatment, which was split into two subplots. These replicated subplot treatments were: 1) well-watered and 2) water-stressed. Treatment confounding may have occurred because the experimental units were based on the whole-plot randomization. Each container was rotated clockwise weekly to minimize any environmental effects during the experiment.

Photosynthetically active radiation (PAR) and relative humidity (RH) were measured with an LI-190S-1 quantum sensor and with a Vaisala HUMICAP[®], respectively, mounted in a steady state porometer (LI-COR, Inc., Lincoln, NE). During the course of the experiment, midday PAR ranged from 310 to 440 $\mu\text{mol m}^{-2} \text{s}^{-1}$. The

photo period was extended to 14 h with 400 W high-pressure sodium lamps (PAR = $610 \mu\text{mol m}^{-2} \text{s}^{-1}$) (Thimijan and Heins, 1983). RH ranged from 42 to 78.8%, with a mean of $59.82 \% \pm 1.08\%$. Day and night temperatures were $23.6 \text{ }^\circ\text{C} \pm 0.13 \text{ }^\circ\text{C}$ and $17.3 \text{ }^\circ\text{C} \pm 0.12 \text{ }^\circ\text{C}$, respectively.

3.3.3 Media water retention curve and water stress regimes

A water retention curve for the growing medium (Fig. 3.1) was determined by analyzing a bulk sample at the Soil Physics Lab, Department of Crop and Soil Science, OSU. The gravimetric ($\theta_{g\text{gm}}$) and volumetric water contents ($\theta_{v\text{gm}}$) of the growing media were obtained for two subsamples, at 0.001, 0.005, 0.01, and 0.1 MPa with a pressure plate apparatus (Soil Moisture Equipment Corp., Goleta, CA); and at 1.5 MPa with a pressure membrane extractor. To determine the target moisture levels for the well-watered and water stressed treatments, the mass of the polystyrene containers was monitored for each treatment-species combination. The definition of the gravimetric water content of the growing medium ($\theta_{g\text{gm}}$) was based on the following equation, and according to Khan (1993):

$$\theta_{g\text{gm}} = \left[\frac{(\text{TMC}) - (\text{mec} + \text{mdgm} + \text{mgr} + \text{ms})}{\text{mdgm}} \right] 100 \quad \text{Equation 1}$$

where:

TMC = total mass of a polystyrene container, including the masses of the container with dry growing medium, gravel, water, and 80 seedlings,

mec = mass of an empty polystyrene container,

mdgm = mass of dry growing medium in the 80 cells,

mgr = mass of the gravel in the 80 cells, and

ms = mass of 80 seedlings.

Equation [1] was redefined as:

$$\theta_{ggm} = \frac{(\theta_{vgm})(\rho_w)}{\rho_{gm}} \quad \text{Equation 2}$$

where:

θ_{vgm} = volumetric-water content of the growing medium, as defined by the water retention curve for a given water stress,

ρ_w = density of water, and

ρ_{gm} = bulk density of the growing medium.

Equation [1] also was rearranged to estimate the mass of a polystyrene container for a desired water stress regime:

$$MC_{ws} = [(\theta_{ggm})(mdgm)] + (mec + mdgm + mgr + ms) \quad \text{Equation 3}$$

where:

MC_{ws} = mass of a polystyrene container for the desired water-stress regime,

$\theta_{g gm}$ = gravimetric water content (%) of the growing medium for the regime,

mec = mass of an empty polystyrene container,

mdgm = mass of dry growing medium in the 80 cells,

mgr = mass of the gravel in the 80 cells, and

ms = mass of 80 seedlings.

The polystyrene containers were weighed on a 12-kg temperature-compensated spring dial scale (Douglas Homs, Co., Belmont, CA). Because the *P. ponderosa* seedlings were larger than the others, their irrigation scheduled varied from that of the Mexican pine species to compensate for this discrepancy.

3.3.4 Drying cycles

A drying cycle was defined as the length of time for when MC_{ws} to reach the desired level for the well-watered or water-stress treatment. Irrigation in the well-watered treatment was scheduled for *P. ponderosa* when MC_{ws} was between 7.5 and 5.7 kg, which corresponded to a $\theta_{v gm}$ of 67 to 37%. The well-watered treatment for the Mexican species was defined as $MC_{ws} = 6.5$ to 5.4 kg, which represented a $\theta_{v gm}$ of 56 to 36%. The water-stress treatment for *P. ponderosa* was defined as $MC_{ws} = 3.8$ kg ($\theta_{v gm} = 2\%$). The desired MC_{ws} for the other species was 3.8 kg ($\theta_{v gm} = 8\%$). At the end of each drying cycle, the values of the volumetric water content of the water-stress treatment were considered cautiously because the weighing method in this study probably underestimated the true value of the hygroscopic water in the growing media.

Hand-irrigation schedules were used for the three drying cycles. The first cycle, in 1997, ran from November 9 to 20 (12 days), the second from November 25 to December 3 (10 days), and the third, in 1998, from January 11 to 21 (11 days; Fig. 3.2 and 3.3). Following the first cycle, the water-stress treatment was sustained for two to three days after water potential and stomatal conductance were measured.

Afterward, those seedlings were watered to field capacity, then allowed to dry to the desired level for the water-stress treatment of the second drying cycle. Five weeks elapsed between the second and the third drying cycle, during which time plants in both water treatments were irrigated to field capacity twice a week.

3.3.5 Sampling procedure

Four seedlings were randomly sampled (without replacement) from each treatment combination (species X watering treatment) to evaluate treatment effects at the end of each drying cycle. To define the seedling population size (N), the containers were mapped by assigning an Arabic numeral to each cavity, beginning at the upper left corner of the map (Fig. 3.4). Two external columns (1 to 7 and 74 to 80) and two external rows (8 to 69 and 13 to 73) were excluded from the seedling population and designated as buffer. The remaining 46 seedlings, on the interior, made up the sampling population. Each seedling was randomly numbered, and was considered the observational unit. Seedlings were flagged for physiological measurements.

3.3.6 Morphological measurements and phytomass estimation

Before the first drying cycle started (IH) and after the third drying cycle ended (FH; Fig. 3.2), stem heights and diameters were recorded for four seedlings randomly selected from each treatment combination (initial measurements in Table 3.2). The stem height was measured from the root collar to the terminal bud to the nearest 1 mm. Stem diameter at the root collar was measured with a digital caliper (nearest 0.1 mm).

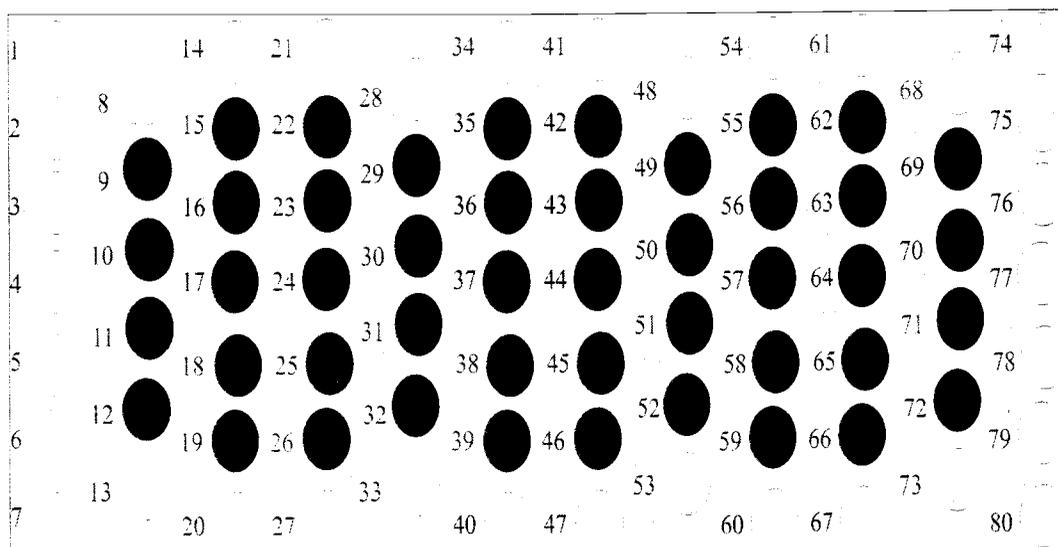


Figure 3.4 Top view of a styrofoam container with buffer seedlings (empty circles) and the population of seedlings from which the sampled seedlings were taken (filled circles, N=46).

Mean relative growth rates for stem height (RGRHT) and stem diameter (RGRDIAM) were calculated as follows (Ledig, 1974; Hunt, 1990):

$$\text{RGRHT or RGRDIAM} = \frac{(\ln \text{ ht } 2 - \ln \text{ ht } 1)}{t_2 - t_1} \quad \text{Equation 4}$$

where:

ht₁ = initial stem height (cm) or stem diameter (mm),

ht₂ = final stem height (cm) or stem diameter (mm),

t₁ = initial week (November 9, 1997),

t₂ = last week (January 21, 1998), and

ln = the natural logarithm to the base *e*.

Fresh and dry shoot and root masses were measured for those four seedlings, to the nearest whole gram. After shoots and roots were separated, the growing medium was washed from the fresh roots. The shoots and roots were oven-dried in paper bags for 72 h at 105 °C. The final total shoot to total root dry-mass ratios (FSH:ROTDRA) were estimated as follows:

$$\text{FSH:ROTDRA} = \frac{\text{total shoot dry mass}}{\text{total root dry mass}} \quad \text{Equation 5}$$

3.3.7 Physiological measurements

Xylem water potential (ψ) was measured in fascicles with a pressure chamber (PMS Instruments, Co., Corvallis, OR), according to Johnson and Nielsen (1969), Ritchie and Hinckley (1975), and Day and Walsh (1980). Four seedlings were selected randomly (without replacement) for each treatment combination at the end of each drying cycle (Fig. 3.2). Each bench-block was measured one day apart. Water potential was evaluated diurnally, at 0400 h (predawn, ψ_{PD}), 1200 h (midday, ψ_{MD}), and 1600 h (evening, ψ_{EV}).

Stomatal conductance (g_s) was measured at the same time as xylem water potential, using a steady state porometer (LI-1600M, LI-COR, Inc., Lincoln, NE). For these readings, a different fascicle from the same seedling was used. This fascicle was identified by marking its sheath with a waterproof red marker. Conductance measurements were taken at 0800 h (morning, g_{sMO}), and 1200 h (midday, g_{sMD}) for the first cycle, and at 0800 h, 1200 h, and 1600 h (evening, g_{sEV}) for the second and third cycles.

All needles in a fascicle were placed as a bundle across the cylindrical chamber of the porometer so that both interior and exterior needle surfaces were exposed. The fascicles were collected at the end of each measurement day. To adjust stomatal conductance readings for leaf area, the total surface area of a 5-cm needle length was estimated (because the diameter of the cylindrical chamber was 5 cm), as it was assumed that the fascicle shape approximated a cylinder form (Haller, 1965; Johnson, 1984; Shelton and Switzer, 1984; Svenson and Davies, 1992). The radius of an interior face of each needle was measured to the nearest 0.01 mm with an electronic digital caliper (MAX-CAL, Fowler & NSK).

3.3.8 Statistical analyses

The morphological and physiological variables were transformed to meet analysis of variance (ANOVA) assumptions that the residuals were independent and normally distributed with a constant variance (Sabin and Stafford, 1990). Square-root transformation was used for xylem water potentials. All relative growth rates and dry mass ratios were \log_e -transformed, according to Poorter and Garnier (1996). Stomatal conductance was transformed with $\log_e(y + 1)$. SAS version 6.12 software package (Appendix I) was used to test two models. A PROC GLM procedure was followed for the morphological variables. The water-stress effect on the morphological variables was tested with the randomized complete block-design model and the physiological variables were assessed with PROC MIXED procedure. This procedure accounted for fixed effects from treatments and random effects from blocks, thus allowing a covariance structure to be defined for repeated measurements (Bennington and Thayne, 1994; Littell et al. 1996; Newman et al. 1997). A covariance structure was selected, based on likelihood ratio tests, and graphical display of the repeated measurements of the physiological variables, and by using a goodness-of-fit Schwarz Bayesian criterion (SBC) (Wolfinger, 1993; Dawson et al. 1997; Littell et al. 1998).

At the end of the first drying cycle, only two repeated measurements were taken for xylem water potential and stomatal conductance. The first measurement was taken at predawn (xylem water potential) or in the morning (stomatal conductance); the second at midday for both xylem water potential and stomatal conductance. Thus, the data were analyzed as a randomized complete-block design with a split plot model of repeated measurements. At the end of the second and third drying cycles, three repeated measurements including evening were made. Thus, the data of the second and third drying cycle was analyzed as in the first drying cycle. The analysis tested the water stress effect on physiological variables at a given time. Data were analyzed by species within a drying cycle.

The model for morphological variables was:

$$y_{ij} = \mu + \beta_i + \tau_j + \varepsilon_{ij} \quad \text{Equation 7}$$

where:

y_{ij} = post-treatment seedling size or phytomass in the j^{th} treatment in the i^{th} block,

μ = overall mean size or phytomass of all observations,

β_i = random effect associated with the i^{th} block,

τ_j = added effect of the j^{th} treatment, and

ε_{ij} = random error associated with the unit on the j^{th} treatment in the i^{th} block.

The model for physiological variables was:

$$y_{ijkl} = \mu_{ik} + r_l + \alpha_i + d_{ij} + \beta_k + (\alpha\beta)_{ik} + \varepsilon_{ijkl} \quad \text{Equation 8}$$

where:

y_{ijkl} = water potential in the i^{th} treatment in the k^{th} time in the l^{th} block,

μ_{ik} = the mean of ik^{th} treatment*diurnal combination,

r_l = the l^{th} block effect,

α_i = the effect of i^{th} treatment. (a fixed parameter),

d_{ij} = the random effect associated with the j^{th} subject in treatment i^{th}
(subject was defined by treatment within block),

β_k = the effect of the k^{th} time. (a fixed parameter),

$(\alpha\beta)_{ik}$ = the ik^{th} treatment*diurnal interaction effect. (a fixed
parameter), and,

ε_{ijkl} = a random error associated with the j^{th} subject in treatment i^{th} at
time k in the l^{th} block.

Treatment differences were compared at $\alpha = 0.05$ for both morphological and physiological variables. Orthogonal contrasts were estimated to compare least square means when diurnal main effects (overall effects across the two treatments) were significant at $\alpha = 0.05$. The contrasts compared ψ_{PD} versus ψ_{MD} and versus ψ_{EV} ; and g_{sMO} versus g_{sMD} and versus g_{sEV} . When the interaction effect (treatments X diurnal) was significant, treatment least square means were contrasted at a given diurnal period. All least square means were back-transformed and 95% confidence limits (CL) were estimated. The back-transformed means were biased, and the back-transformed CL asymmetrical. All ANOVA tables are included in Appendix II.

For each species, a maximum midday stomatal conductance value was defined based on the mean (\bar{x}) and standard deviation (SD) of the midday conductance in the well-watered treatment over the three drying cycles. The maximum midday

conductance value for both *P. arizonica* and *P. durangensis* was defined by $\bar{x} + 2*(SD)$. The maximum midday conductance value for both *P. engelmannii* and *P. ponderosa* was defined by $\bar{x} + SD$. The maximum values were used as the baseline conductance (100%) from which relative values were estimated for the conductance readings in both treatments. A nonlinear model with four parameters was used to describe the relationship between the relative values of the maximum midday stomatal conductance and predawn xylem water potential for a given species. The nonlinear model was:

$$y = k_1 + (\beta_0 / 1 + e^{-(x - k_2) / \beta_1}) \quad \text{Equation 9}$$

where:

y = relative value of the maximum midday stomatal conductance,

k_1 , k_2 , β_0 , and β_1 = parameters of the model,

x = predawn xylem water potential, and

e = exponential function.

PROC NONLIN of SAS was followed to estimate the parameters of the model (Appendix I). The parameters had different starting values, and scatter and residual plots were used in the analysis. ANOVA tables are included in Appendix II.

3.4 Results

Inherent morphological differences were observed among the four pine species at the beginning of the treatments. The seedlings of *P. ponderosa* were the tallest with an average height of 29.4 cm (Table 3.2). The shortest seedlings were those of *P. engelmannii* (average of 12.1 cm). Among the Mexican pine species, *P. durangensis* was the tallest (20.6 cm), followed by *P. arizonica* (14.7 cm). Of the four species, *P. engelmannii* had the largest stem diameter (0.51 cm) followed by *P. ponderosa* (0.44 cm), and *P. durangensis* and *P. arizonica* (0.39 and 0.41 cm, respectively; Table 3.2). Although, no measurements of total leaf area per plant were taken, the large seedlings probably had more leaf area.

These size differences contributed to unequal water-stress levels among the species at the end of the three drying cycles presumably because large seedlings had greater leaf area surface (Fig. 3.3). For example, in the water-stress treatment at the end of the first drying cycle (among the Mexican pines), the containers of *P. arizonica* weighed the most (3.86 kg; 8.70% volumetric water content); those of *P. durangensis* were the lightest (3.45 kg; 1.30% volumetric water content) (Fig. 3.3). Values for *P. engelmannii* were intermediate (3.72 kg; 6.22% volumetric water content).

Even though the initial heights of *P. arizonica* and *P. engelmannii* seedlings were similar, *P. arizonica* had shorter needles (17.5 cm versus 30 cm long). This variation in size may have been a factor in the way these transpired and used water at the end of the cycles. *P. ponderosa* seedlings were taller than all the Mexican species and were probably transpiring at higher rates. The container weight of *P. ponderosa* was 3.80 kg, which corresponded to a volumetric water content of 2.0% at the end of the first drying cycle (Fig. 3.3).

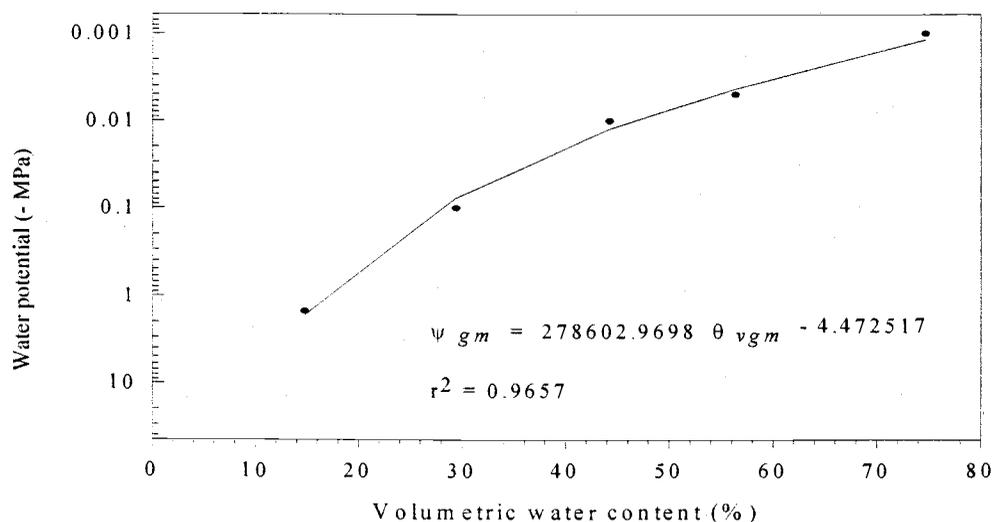


Figure 3.1 Water retention curve for a growing media mix of 90% peat moss and 10% perlite.

Table 3.2 Initial mean and its standard error (SE) of the stem height and stem diameter of the four *Pinus* species in the well-watered and water-stressed treatments.

Variable Species	Treatments							
	Well-watered				Water-stressed			
	Stem height (cm) SE		Stem diameter (cm) SE		Stem height (cm) SE		Stem diameter (cm) SE	
<i>P. arizonica</i>	15.50	0.75	0.41	0.014	13.93	0.94	0.41	0.010
<i>P. engelmannii</i>	12.81	2.20	0.51	0.010	11.44	0.44	0.51	0.024
<i>P. durangensis</i>	20.62	0.37	0.38	0.015	20.69	0.19	0.41	0.012
<i>P. ponderosa</i>	29.44	1.56	0.45	0.004	29.31	0.81	0.43	0.079

n = 2 blocks.

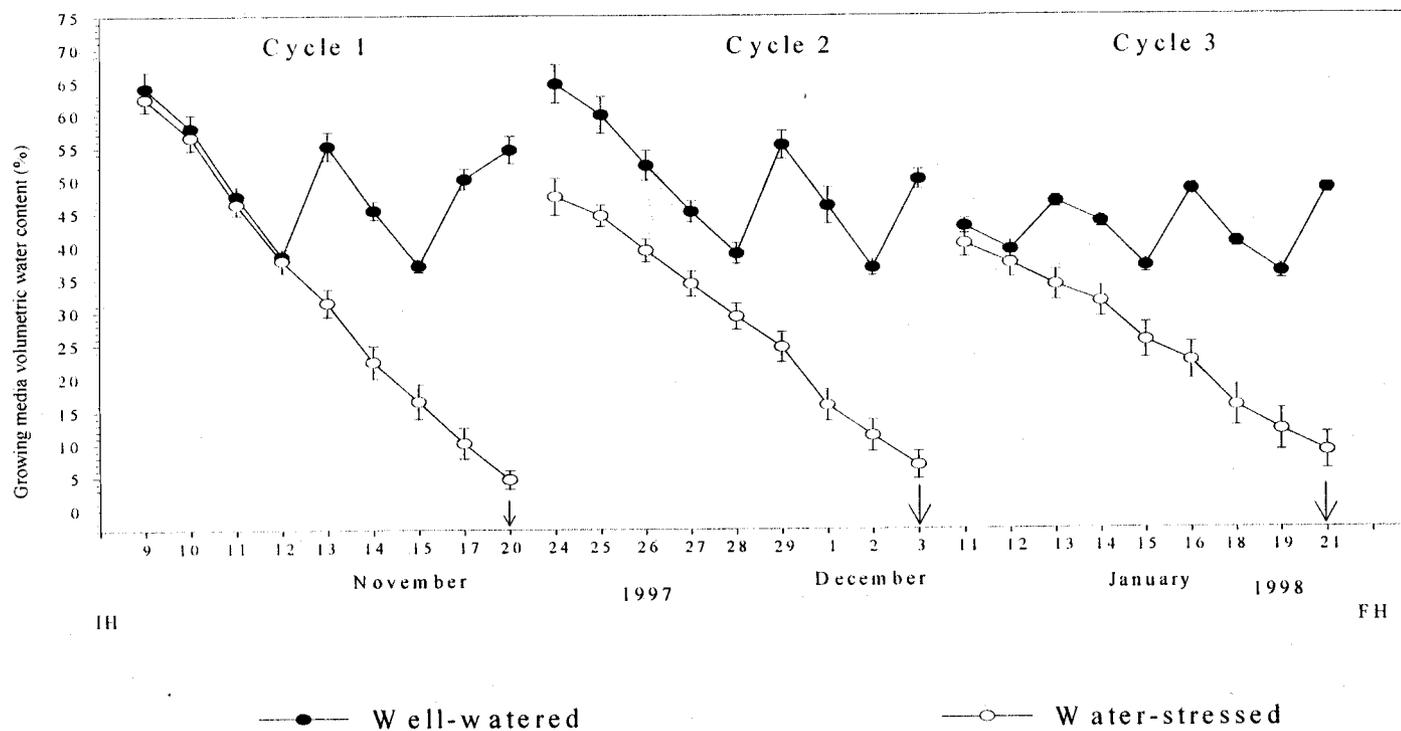


Figure 3.2 Growing media volumetric water content for well-watered and water-stressed treatments over three drying cycles. IH = initial seedling morphological measurements and harvest. FH = final seedling morphological measurements and harvest. Arrows indicate when xylem water potential and stomatal conductance were measured. Vertical bars represent standard error of the mean (n = 8). Note: The scale on the x axis (time) is not uniform.

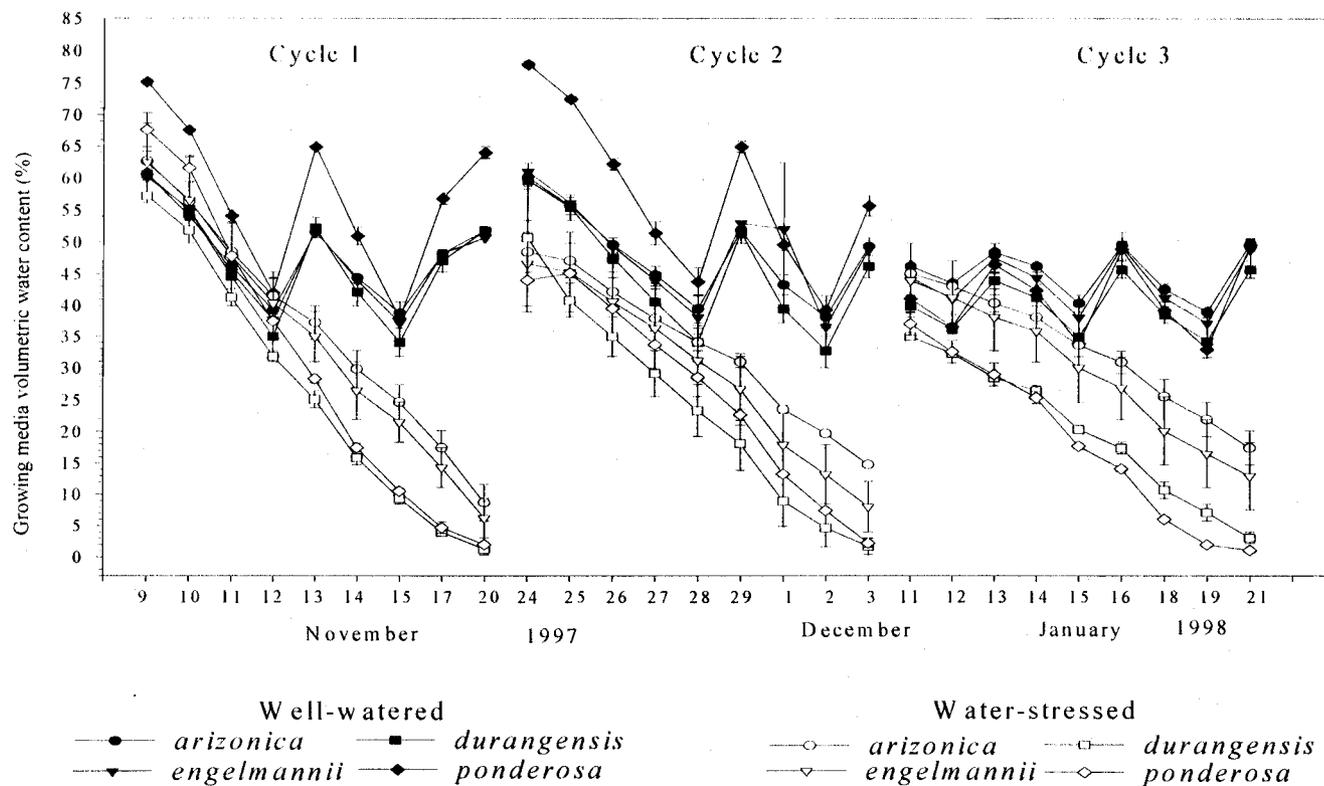


Figure 3.3 Growing media volumetric water content of four *Pinus* species under well-watered and water-stressed treatments over three drying cycles. Vertical bars represent standard error of the mean ($n = 2$). Note: *P. ponderosa* had a different watering regime.

The degree of stress experienced by species at the end of each drying cycle was: *P. arizonica* < *P. engelmannii* < *P. durangensis* < *P. ponderosa* (Fig. 3.3). This arrangement may reflect the physiological behavior measured for xylem water potential and stomatal conductance at the end of each drying cycle. During the third drying cycle, the well-watered treatment was not irrigated properly and became drier (Fig. 3.2 and 3.3). Therefore, the data were inconsistent, and were not used in ANOVA for water-stress effects at the end of the third drying cycle. However, predawn water potential and midday conductance readings from the third drying cycle were included for the nonlinear regression analysis.

3.4.1 Seedling morphology

In general, the seedling morphology of any species was not affected by the level of water stress imposed throughout the three drying cycles ($p\text{-value} > \alpha = 0.05$; Table 3.3 and Appendix II). The one exception was for the relative stem diameter growth rate of *P. durangensis* seedlings. The well-watered treatment yielded higher relative stem diameter growth than the water-stress treatment ($1.01120 \text{ cm cm}^{-1}\text{week}^{-1}$ versus $1.00224 \text{ cm cm}^{-1} \text{ week}^{-1}$; Table 3.3). Even though relative diameter growth of *P. durangensis* had a highly significant water-stress effect, the difference between the well-watered and water-stress treatments was not biologically relevant.

No water-stress effect was seen in the final total shoot to total root dry-mass ratio (FSH:ROTDRA; $p\text{-value} > \alpha = 0.05$; Table 3.3 and Appendix II). The FSH:ROTDRA for *P. arizonica* seedlings was smaller than for the other pines in both treatments (Table 3.3).

Table 3.3 Relative stem height and stem diameter growth rates (RGRHT and RGRDIAM, respectively), and final total shoot to total root dry mass ratio (FSH:ROTDRA).

Species	Morphological Variable					
	RGRHT (cm cm ⁻¹ week ⁻¹)		RGRDIAM (cm cm ⁻¹ week ⁻¹)		FSH:ROTDRA	
	Treatments		Treatments		Treatments	
	Well-watered	Water-stressed	Well-watered	Water-stressed	Well-watered	Water-stressed
<i>P. arizonica</i>	0.9941	1.0074	1.0073	0.9962	1.4917	1.5598
<i>P. engelmannii</i>	0.9718	0.9743	1.0246	1.0324	2.0176	1.9730
<i>P. durangensis</i>	1.0029	1.0023	1.0112	1.0022**	2.1453	2.3830
<i>P. ponderosa</i>	1.0071	1.0062	1.0099	1.0100	1.9388	1.9436

** = highly significant differences p-value = 0.0086.

Because of the lack of a water stress effect on total shoot to total root dry-mass ratios, we combined the total shoot and root dry masses from the well-watered and water-stress treatments. As a result, *P. arizonica* had the lowest shoot to root ratio, or vice versa the highest root to shoot ratio (Fig. 3.5). In contrast, *P. durangensis* had the highest shoot to root ratio. *P. engelmannii* and *P. ponderosa* were similar and intermediate to the other pines.

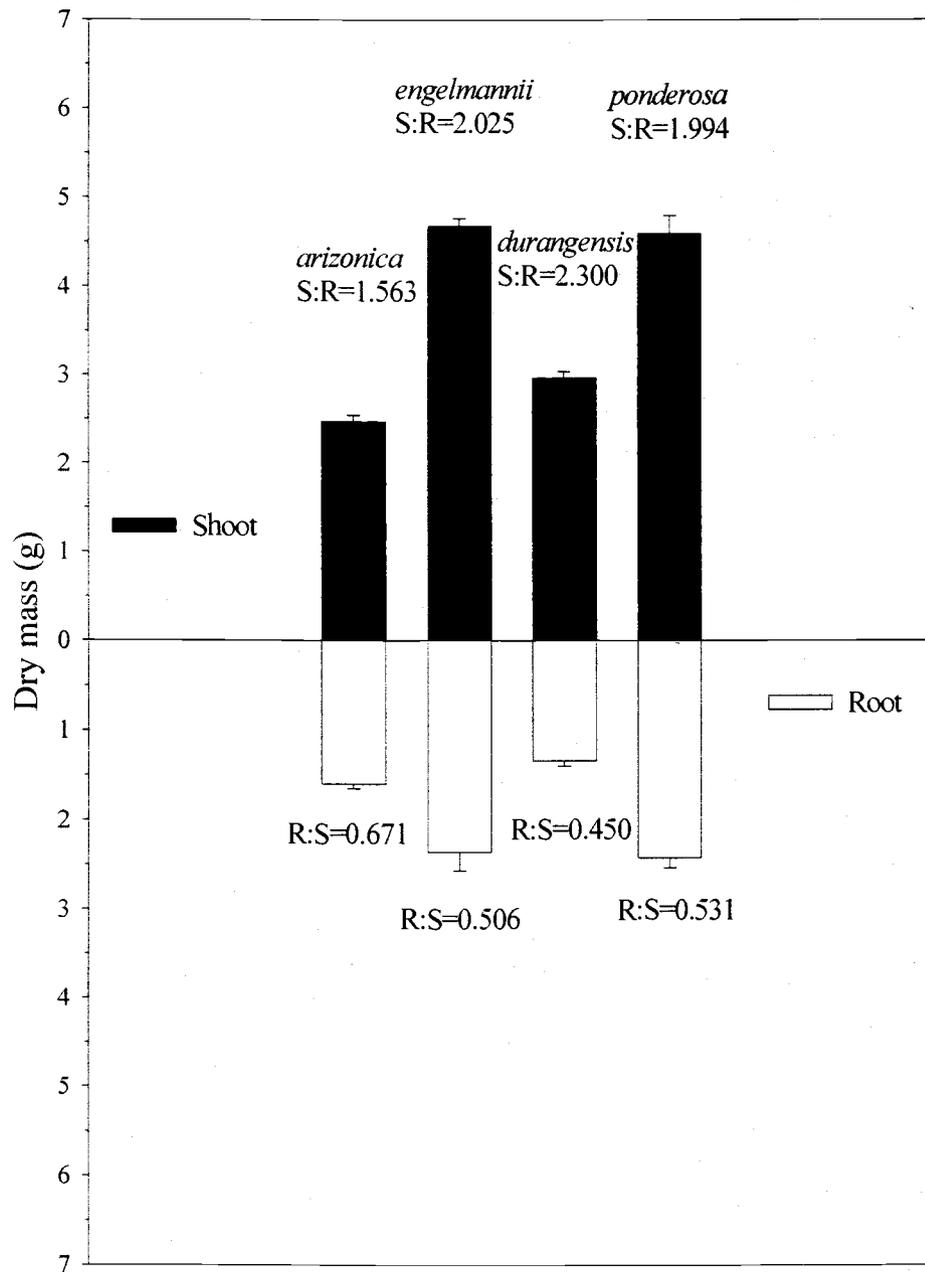


Figure 3.5 Total shoot and root dry mass of four *Pinus* species at the final harvest. The total shoot to total root ratio (S:R) and the total root to total shoot ratio (R:S) are included for each species.

3.4.2 Physiological response

The physiological response to the water-stress treatment varied among species at the end of the first and second drying cycles. The patterns for diurnal xylem water potential and stomatal conductance followed that of the water-stress levels reached at the end of each drying cycle (Fig. 3.6; 3.7). Water potential values in the well-watered treatment were relatively constant, fluctuating between -0.4 and -0.8 MPa during the day. Those values for *P. durangensis* and *P. ponderosa* were slightly depressed at noon, but began to recover in the evening (Fig. 3.6C; 3.7C).

In the water-stress treatment, values also closely followed the pattern of stress, as measured by the weighing method at the end of the first and second cycles (Fig. 3.6; 3.7). *P. arizonica* seedlings were the least stressed seedlings, while *P. ponderosa* showed the greatest stress (Fig. 3.6A, D; 3.7A, D). Stress was intermediate in seedlings of *P. engelmannii* and *P. durangensis* (Fig. 3.6B, C; 3.7B, C). As expected, predawn values for all species were higher than those measured at midday and evening.

At the end of the first drying cycle, stomatal conductance rates during the day varied by treatment, regardless of species (Fig. 3.6E, F, G, H). Stomatal conductance was lower in all species subjected to the water-stress treatment, except for *P. arizonica* seedlings. Those seedlings had similar conductance rates for both well-watered and water-stress treatments at the end of the first drying cycle (Fig. 3.6E).

First Drying Cycle

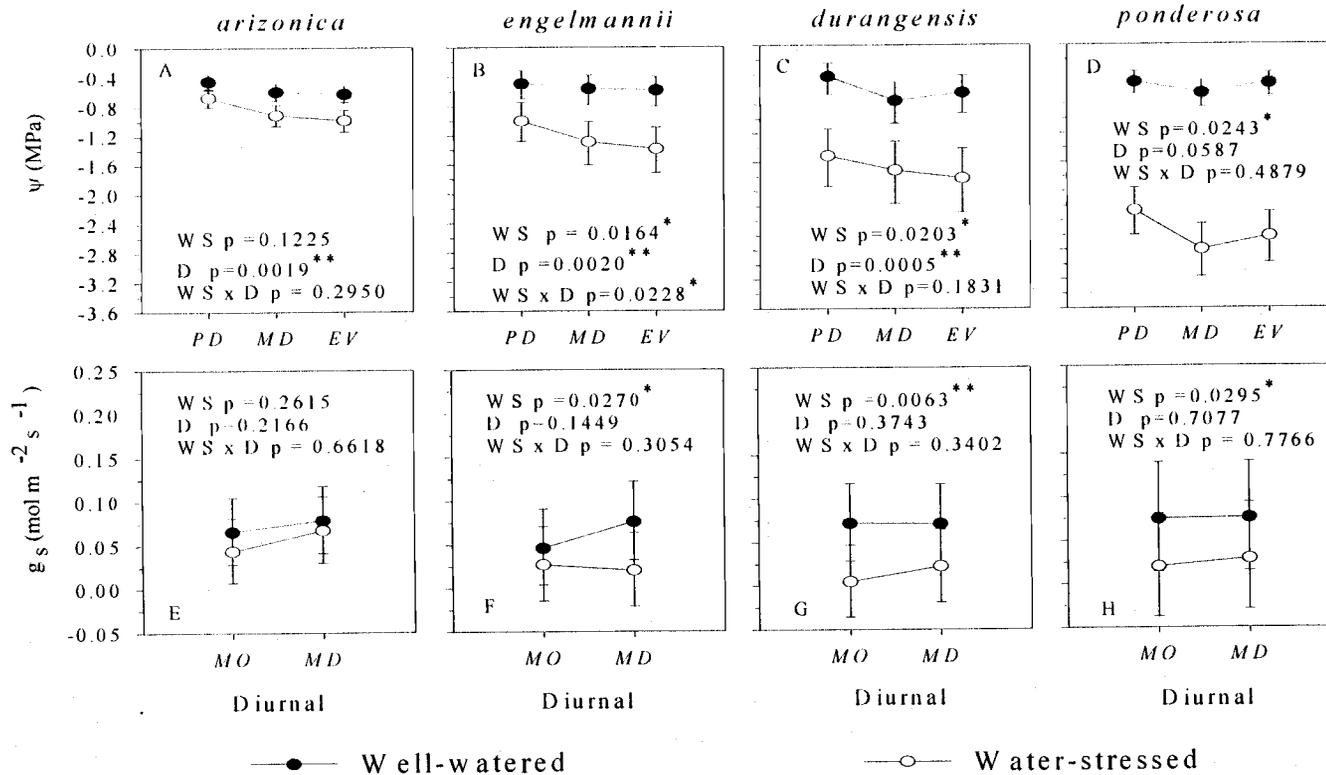


Figure 3.6 Diurnal xylem water potential (ψ) and stomatal conductance (g_s) of four *Pinus* species in the well-watered and water-stressed treatments at the end of the first drying cycle. Diurnal labels are *PD* = predawn, *MO* = morning, *MD* = midday, and *EV* = evening. Water stress (WS) and diurnal (D) main effects and interaction effect (WS x D) are included in each inset. * = significant differences p -value $< \alpha = 0.05$. ** = highly significant differences p -value $< \alpha = 0.01$. Vertical bars represent 95% CL of least square means. ($n = 2$).

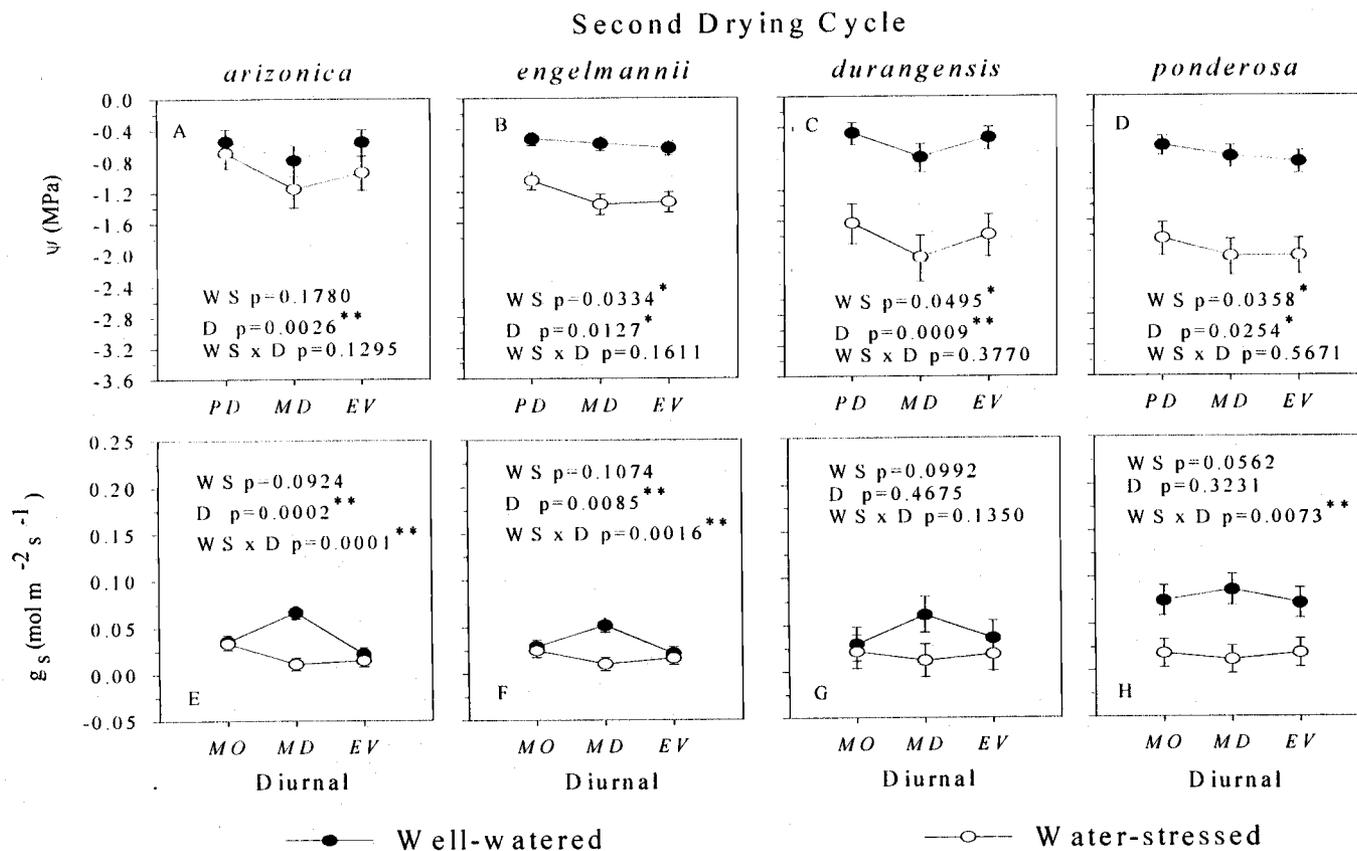


Figure 3.7 Diurnal xylem water potential (ψ) and stomatal conductance (g_s) of four *Pinus* species in the well-watered and water-stressed treatments at the end of the second drying cycle. Diurnal labels are *PD*=predawn, *MO*=morning, *MD*=midday, and *EV*=evening. Water stress (WS) and diurnal (D) main effects and interaction effect (WS x D) are included in each inset. * = significant differences p -value $< \alpha = 0.05$. ** = highly significant differences p -value $< \alpha = 0.01$. Vertical bars represent 95% CL of least square means. ($n = 2$).

At the end of the second drying cycle, stomatal conductance rates across all species in the well-watered treatment tended to increase from morning to midday, then declined toward evening (Fig. 3.7E, F, G, H). In contrast, conductance rates in the water-stress treatment declined from morning to midday, and began to recover by evening. Much higher rates were recorded for *P. ponderosa* in the well-watered treatment than in the water-stress treatment (Fig. 3.7H)

At the end of the first cycle, a water stress-diurnal interaction effect was found in *P. engelmannii* seedlings (Fig. 3.6B). In *P. durangensis* the water-stress and diurnal effects were significant and highly significant, respectively (Fig. 3.6C). Only the water-stress effect was significant for *P. ponderosa* seedlings (Fig. 3.6D). Likewise, the diurnal effect was the only significant one in *P. arizonica* seedlings (Fig. 3.6A; and Appendix II).

For each diurnal period, the water stress-diurnal interaction effect found for *P. engelmannii* seedlings was characterized by a significantly higher (p-value = 0.0001) mean water potential in the well-watered treatment ($\psi_{PD} = -0.49$, $\psi_{MD} = -0.56$, and $\psi_{EV} = -0.58$ MPa) than in the water-stress treatment ($\psi_{PD} = -0.99$, $\psi_{MD} = -1.29$, and $\psi_{EV} = -1.39$ MPa; Fig. 3.6B). The water-stress effect in *P. durangensis* and *P. ponderosa* yielded an overall water potential mean that was lower in the water-stress treatment ($\psi = -1.67$ and -2.56 MPa, respectively) than in the well-watered treatment ($\psi = -0.59$ and -0.56 MPa, respectively; Fig. 3.6C, D).

The diurnal xylem water potential effect in *P. arizonica* seedlings showed highly significant differences between the mean predawn potential ($\psi_{PD} = -0.55$ MPa) and those at midday and evening ($\psi_{MD} = -0.74$ and $\psi_{EV} = -0.78$ MPa; p-value = 0.0009 and 0.0012; respectively). Similarly, the mean predawn values for *P. durangensis* seedlings ($\psi_{PD} = -0.88$ MPa) were as significantly different from those at midday ($\psi_{MD} = -1.18$ MPa; p-value = 0.0135) and in the evening ($\psi_{EV} = -1.15$ MPa; p-value = 0.0002).

Water-stress effects for *P. engelmannii*, *P. durangensis*, and *P. arizonica* seedlings were found only for stomatal conductance rates at the end of the first drying cycle (Fig. 3.6F, G, H, and Appendix II). The overall mean for conductance in well-watered *P. engelmannii* and *P. ponderosa* was significantly higher ($g_s = 0.0594$ and 0.0738 mol m⁻² s⁻¹, respectively) than in water-stressed seedlings ($g_s = 0.0228$ and 0.0240 mol m⁻² s⁻¹, respectively). For *P. durangensis*, the overall mean conductance for well-watered seedlings was significantly higher ($g_s = 0.0700$ mol m⁻² s⁻¹) than for water-stressed seedlings ($g_s = 0.0126$ mol m⁻² s⁻¹).

The physiological responses of the seedlings in the second drying cycle were similar to those at the end of the first cycle. Water stress effects were significant for water potentials in *P. engelmannii*, *P. durangensis*, and *P. ponderosa* seedlings (Fig. 3.7B, C, D). A significant diurnal effect was found for *P. engelmannii* and *P. ponderosa* (Fig. 3.7B, D), and the diurnal effect was highly significant for *P. arizonica* and *P. durangensis* (Fig. 3.7A, C, and Appendix II). The overall mean water potential values in *P. engelmannii*, *P. durangensis*, and *P. ponderosa* were higher for well-watered seedlings ($\psi = -0.58$, -0.59 , and -0.75 MPa, respectively) than for water-stressed seedlings ($\psi = -1.24$, -1.82 , and -1.99 MPa, respectively).

During the day, overall predawn readings for *P. arizonica*, *P. engelmannii*, and *P. ponderosa* were significantly higher ($\psi_{PD} = -0.61, -0.76, \text{ and } -1.16$ MPa, respectively; $p\text{-value} < \alpha = 0.05$) than at midday ($\psi_{MD} = -0.95, -0.93, \text{ and } -1.35$ MPa, respectively) and in the evening ($\psi_{EV} = -0.74, -0.95, \text{ and } -1.39$ MPa, respectively). However, only the overall mean for predawn values in *P. durangensis* was highly significant higher ($\psi_{PD} = -0.96$ MPa; $p\text{-value} = 0.0006$) than for midday ($\psi_{MD} = -1.35$ MPa).

A highly significant water stress by diurnal interaction was found for stomatal conductance in *P. arizonica*, *P. engelmannii*, and *P. ponderosa* at the end of the second cycle (Fig 3.7E, F, H, and Appendix II). The midday mean for conductance in well-watered *P. arizonica* and *P. engelmannii* was significantly higher ($g_{sMD} = 0.0668$ and 0.0523 mol m⁻² s⁻¹, respectively; $p\text{-value} = 0.0001$) than in the water-stressed seedlings ($g_{sMD} = 0.0112$ and 0.0108 mol m⁻² s⁻¹, respectively). In contrast, the water stress by diurnal interaction effect in *P. ponderosa* was highly significant in each diurnal period ($p\text{-value} < \alpha = 0.01$). In this species, the mean stomatal conductance for each diurnal period was higher in the well-watered treatment ($g_{sMO} = 0.0735$, $g_{sMD} = 0.0849$, and $g_{sEV} = 0.0714$ mol m⁻² s⁻¹) than in the water-stress treatment ($g_{sMO} = 0.0183$, $g_{sMD} = 0.0114$, and $g_{sEV} = 0.0185$ mol m⁻² s⁻¹).

In summary, the water-stress treatment reduced midday stomatal conductance by more than 60% in *P. engelmannii*, *P. durangensis*, and *P. ponderosa* seedlings at the end of the first drying cycle (Table 3.4). However, only 14.8% reduction in midday conductance was due to water-stress in *P. arizonica* during the first drying cycle. Clearly, the species arrangement (in order of degree of stress) and physiological behaviors were artifacts of the stress levels at the end of the drying cycles.

Table 3.4 Midday stomatal conductance (g_{sMD}) in the well-watered and water-stressed treatments, reduction of the midday stomatal conductance, and predawn xylem water potential (ψ_{PD}) in the water-stressed treatment of the four *Pinus* species at the end of both first and second drying cycles.

Variables	First drying cycle				Second drying cycle			
	Treatments		g_{sMD} reduction	ψ_{PD} (MPa)	Treatments		g_{sMD} reduction	ψ_{PD} (MPa)
	Well-watered	Water-stressed			Well-watered	Water-stressed		
Species	g_{sMD} (mol m ⁻² s ⁻¹)	g_{sMD} (mol m ⁻² s ⁻¹)	(%)	(MPa)	g_{sMD} (mol m ⁻² s ⁻¹)	g_{sMD} (mol m ⁻² s ⁻¹)	(%)	(MPa)
<i>P. arizonica</i>	0.0789	0.0672	14.83	-0.67	0.0668	0.0112**	83.00	-0.69
<i>P. engelmannii</i>	0.0746	0.0254	66.00	-0.99	0.0523	0.0118**	79.35	-1.05
<i>P. durangensis</i>	0.0696	0.0211	69.70	-1.51	0.0603	0.0119	80.30	-1.63
<i>P. ponderosa</i>	0.0754	0.0280	63.00	-2.27	0.0849	0.0114**	86.60	-1.84

** = highly significant differences p-value < α = 0.01.

The water-stress treatment was related to a 70% reduction in the midday stomatal conductance for all species at the end of the second drying cycle (Table 3.4). The majority of these latter reductions were highly significant. Predawn water potential values lower than -1.0 MPa apparently can reduce midday conductance by more than 60%. This is consistent at least in *P. engelmannii*, *P. durangensis*, and *P. ponderosa*.

The stomatal conductance values from the well-watered treatments were combined for the three drying cycles in order to define the maximum midday conductance for each species. The highest value was for *P. arizonica* at 0.11 mol m⁻²s⁻¹. *P. engelmannii* had the lowest maximum value, at 0.070 mol m⁻² s⁻¹. The maximum midday values were 0.10 and 0.090 mol m⁻² s⁻¹ for *P. ponderosa* and *P. durangensis*, respectively. The relationship between relative conductance and predawn water potential also reflected the level of water stress reached by each species over the three drying cycles (Fig. 3.8, 3.9). For example, the values for conductance and predawn water potentials overlapped for *P. arizonica*, regardless of treatments (Fig. 3.8A). This species was the least stressed. In contrast, the most stressed species was *P. ponderosa*, which showed a clustering pattern for that same relationship (Fig. 3.9B). The patterns for *P. engelmannii* and *P. durangensis* were intermediate (Fig. 3.8B, 3.9A).

The nonlinear model used to fit the relative conductance and predawn water potential predicted a 60.7% of the maximum midday conductance when predawn water potential was about -0.6 MPa in *P. arizonica* (Table 3.5). However, maximum midday conductance was reduced quickly when predawn water potential was -0.7 to -0.8 MPa. At potentials greater than -0.8 MPa, the maximum value stabilized.

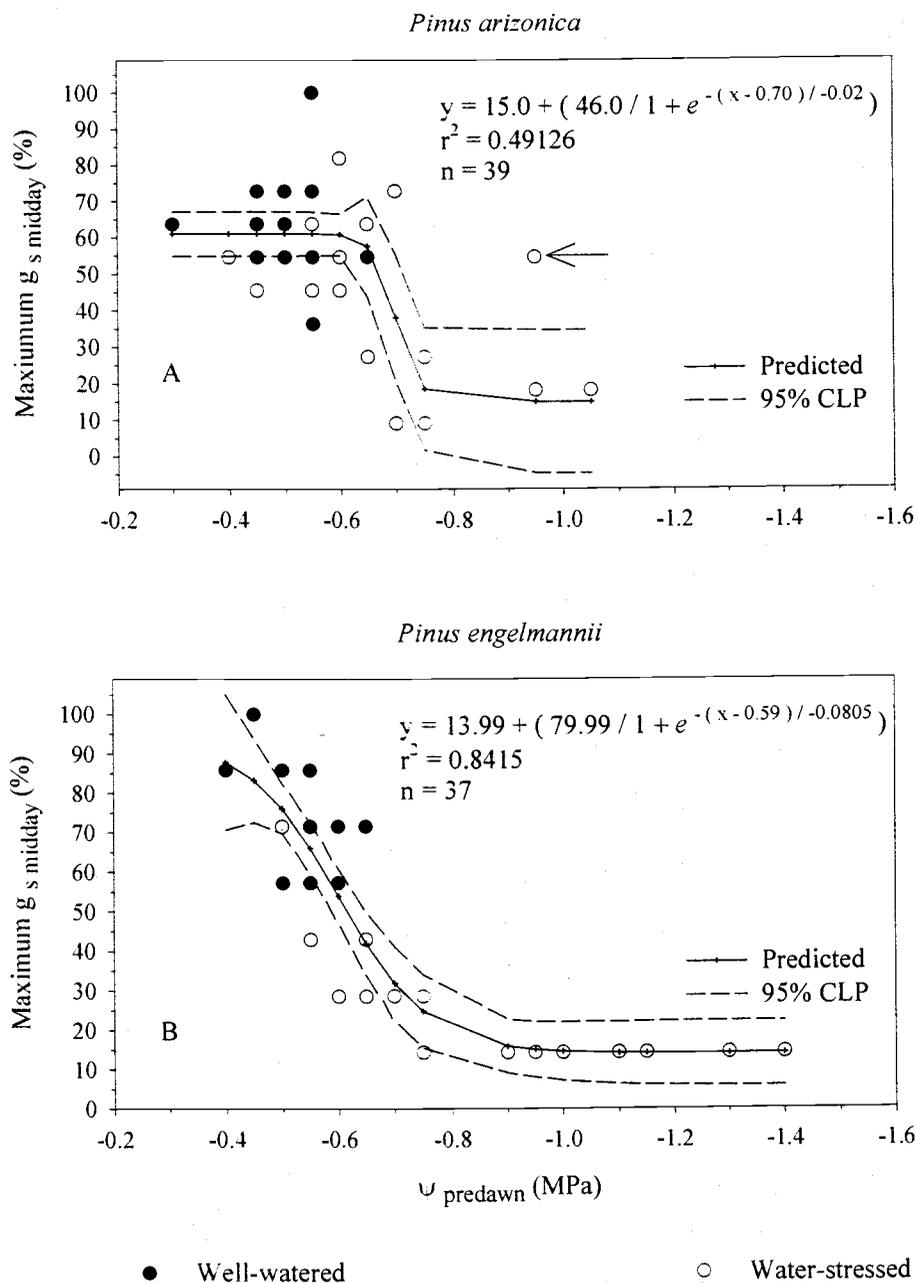


Figure 3.8 Relationship between the maximum midday stomatal conductance (g_s , %) and predawn xylem water potential (ψ) of *P. arizonica* and *P. engelmannii* for the well-watered and water-stressed treatments. In the scatter plot, each point represents a pair of values from one seedling. The arrow is pointing an outlier in A. 95% confidence limits of the predicted values (CLP) are shown in each inset.

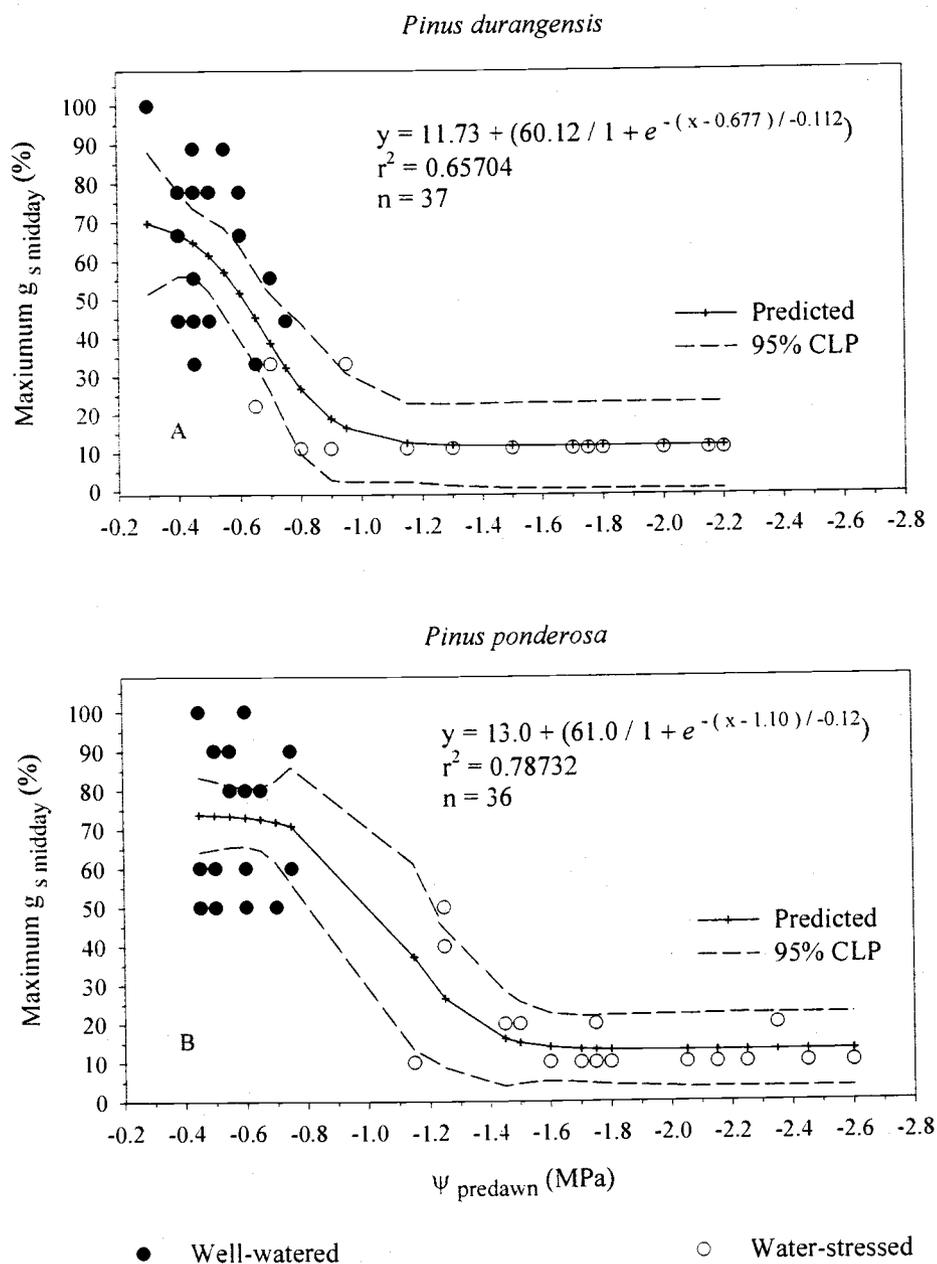


Figure 3.9 Relationship between the maximum midday stomatal conductance (g_s , %) and predawn xylem water potential (ψ) of *P. durangensis* and *P. ponderosa* for the well-watered and water-stressed treatments. In the scatter plot, each point represents a pair of values from one seedling. 95% confidence limits of the predicted values (CLP) are shown in each inset.

Table 3.5 Predicted values of the maximum midday stomatal conductance of four *Pinus* species.

Predawn water potential (-MPa)	Species			
	<i>arizonica</i>	<i>engelmannii</i>	<i>durangensis</i>	<i>ponderosa</i>
	Maximum g_s midday (%)	Maximum g_s midday (%)	Maximum g_s midday (%)	Maximum g_s midday (%)
0.4	61.0	87.08	67.18	73.82
0.5	61.0	74.27	61.58	73.59
0.6	60.7	51.50	51.73	73.07
0.7	38.0	30.24	38.71	71.90
0.8	15.31	19.48	26.76	69.37
0.9	15.0	15.66	18.95	64.31
1.0	15.0	14.48	14.91	55.52
1.1	15.0	14.13	13.08	43.50
1.2		14.03	12.29	31.48
1.3		14.00	11.96	22.69
1.4		13.99	11.82	17.63
1.5			11.77	15.10
1.6			11.75	13.93
1.7			11.74	13.41
1.8			11.73	13.18
1.9			11.73	13.08

For *P. engelmannii* and *P. durangensis*, the model predicted values of 51.50 and 51.73%, respectively, when predawn water potential was about -0.6 MPa (Table 3.5). Similarly, predicted values were 30.24 and 38.71% of the maximum midday conductance when predawn water potential was about -0.7 MPa. In *P. engelmannii*, the maximum midday conductance continued to decline at potentials of -0.8 to -0.9 MPa, then stabilized beyond -1.0 MPa. In *P. durangensis*, the maximum midday conductance declined from -0.8 to -1.2 MPa, then stabilized past -1.3 MPa.

In *P. ponderosa*, 55.52% of maximum midday conductance was predicted when predawn water potential was about -1.0 MPa (Table 3.5). Maximum conductance continually decreased from 55.52 to 22.69%, which corresponded to predawn water potentials of -1.0 to -1.3 MPa. The maximum midday conductance began to stabilize beyond -1.4 MPa.

3.5 Discussion

3.5.1 Seedling morphology

The seedling morphology was not modified by the water stress treatment in this study. The lack of a water-stress effect in most of the morphological variables could have resulted from two factors. First, the time period in this study corresponded to the non-growing season for these species (November 1997 to January 1998). Secondly, the seedlings were subjected to only a short period of water stress.

Because the species were grown in the same water regime at the Georgia Pacific's nursery and the lack of water stress effect on the morphology in this study, the species showed its own inherent morphology. For example, seedlings of *P. arizonica* had the lowest shoot to root dry-mass ratios (Fig. 3.5). In contrast, *P. durangensis* allocated disproportionately more phytomass to the shoot than to the root system. The shoot dry mass in *P. engelmannii* seedlings reflected the grass stage characteristic of this species. In some instances, a well-developed shoot was not even observed. The aboveground dry mass was, in fact, composed of needles up to 30 cm long that surrendered a large, thick terminal bud and a short stem. *P. ponderosa* seedlings had the second smallest total shoot to a dry mass ratio of the four pine species.

Levitt (1956) contended that water stress during the hardening-off period does not increase hardiness. He mentioned that plants grown under drier conditions may be able to harden more deeply. In the SMOC, seedlings are planted during the summer rainy seasons, the plants are actively growing, and seedling mortality is high because of the transportation, storage, handling, and planting processes (Mexal, 1996). Heidmann and King (1992) stated that producing seedling

in containers would provide flexibility because seedlings could be planted in spring or fall when the stock is dormant.

A comprehensive research program could identify the target morphological characteristics of planting stock for a variety of conditions in the SMOC. This research would design an optimum schedule for seedling production, so that seedlings could be planted in the spring, summer, or fall, and on a variety of sites.

3.5.2 Physiological response

The diurnal patterns for xylem water potential and stomatal conductance were typical of those seen by other researchers (Ritchie and Hinckley, 1975; Hinckley et al. 1978). These patterns closely followed the levels of stress at the end of both drying cycles. In general, well-watered seedlings of *P. arizonica*, *P. engelmannii*, *P. durangensis*, and *P. ponderosa* had higher overall xylem water potential and stomatal conductance than did water-stressed seedlings at the end of both cycles.

The typical diurnal pattern for xylem water potential, under well-watered conditions, was characterized by initially high, predawn values, which decreased toward midday and then began to increase again by evening. By midday, the water potential readings decreased in proportion to the atmospheric evaporative demand around the seedlings. Under water-stress conditions, however, the diurnal pattern began with lower predawn water potentials, which decreased at midday according to evaporative demand, and then began to recover later in the evening. These two patterns applied only for *P. engelmannii*, *P. durangensis*, and *P. ponderosa* under both treatments (Fig. 3.6 and 3.7). *P. arizonica* seedlings showed this pattern only under well-watered conditions, because conditions were not sufficiently stressful to induce the water stress behavior at the end of two drying cycles.

The diurnal patterns for water potential described in this study are somewhat similar to those reported in an Arizona greenhouse by Heidmann and King (1992) for two-year-old *P. ponderosa* var. *scopulorum* seedlings. Seedlings were exposed to well-watered conditions and 112 days of drought starting August 7, 1984. After the 112 days of drought were complete in November, predawn water potential values in the well-watered seedlings were between -0.25 and -0.5 MPa and decreased to around -1.25 MPa at midday. In contrast, predawn values in stressed seedlings were much lower (-2.5 MPa), and remained at about the same level at midday.

The typical diurnal patterns of stomatal conductance to be expected under well-watered conditions and low evaporative demand present a bell-shaped form. When predawn water potential is very low as a result of water stress, however stomatal conductance is drastically reduced (Hinckley et al. 1978). In this study, the diurnal patterns of stomatal conductance from the well-watered and water-stress treatments were similar to those described during transpiration of two-year-old *P. radiata* seedlings grown in a Colorado greenhouse by Kaufmann (1977). The author reported that well-watered seedlings showed a bell-shaped pattern for transpiration. Predawn water potential in the water-stress treatment was lower than -1.5 MPa, which resulted in stomatal closure to reduce transpiration. Seedlings treated by 12 days of water-stress had a small peak in transpiration at around 1000 h, and were suppressed the rest of the day. Also, in a greenhouse study in Arizona Heidmann and King (1992) reported that in four sampled days during the fall, the stomatal conductance rates of well-watered two-year-old *P. ponderosa* var. *scopulorum* seedlings reached a maximum between 1100 and 1400 h, in contrast water stressed seedlings had negligible conductance. Similar diurnal trends have been described in a greenhouse study by Stoneman et al. (1994) in Australia for photosynthesis rates of two-month-old seedlings of jarrah (*Eucalyptus marginata* Donn ex Sm.) subjected to well-watered and water stress treatments.

The maximum stomatal conductance rates found in well-watered six-month-old seedlings of this study ranged from 0.070 to 0.110 mol m⁻² s⁻¹ across the four pine species. These conductance values averaged one third of those reported by Heidmann and King (1992) in a greenhouse study in Arizona. They reported that maximum daily conductance rates of well-watered two-year-old *P. ponderosa* var. *scopulorum* averaged 0.363 mol m⁻² s⁻¹ on a sample day in November 1984. This great contrast might be attributed to differences in seedling age, growing media, and specific greenhouse environments in Arizona and Oregon. However, the maximum daily conductance rate in the water-stress treatment (0.040 mol m⁻² s⁻¹) reported on a sample day of November in Arizona was in the range of the maximum morning readings (0.020 and 0.0570 mol m⁻² s⁻¹) recorded in the water-stress treatment across the four pine species at the end of both drying cycles in this study.

Farquhar and Sharkey (1982) and Hinckley and Braatne (1994) reported that stomatal respond to stimuli such as light, CO₂ concentrations in intercellular spaces, humidity, leaf water potentials, and hormonal signals. Using the recent improvements in the PROC MIXED of SAS, I found that the water-stress effect on stomatal conductance at midday was significant at the end of both drying cycles, at least for *P. engelmannii*, *P. durangensis*, and *P. ponderosa*. Maximum midday stomatal conductance of the well-watered seedlings was properly associated with their predawn xylem water potentials, and I was able to identify a threshold at which stomatal conductance was reduced.

Passioura (1996) asserted that short-term physiological responses are not related to adaptive strategies. Rather, they are reactions for maintaining activities and conditioning the seedling to a survival mode. The stomatal threshold for having less than 50% maximum midday conductance was estimated to be at -0.7 MPa for *P. engelmannii*. Negligible carbon uptake was recorded in *P. engelmannii* seedlings when

plant water potential was about -2.0 MPa (Barton and Teeri, 1993). The threshold in *P. durangensis* for less than 50% maximum midday conductance was at -0.7 MPa. Beyond this, the maximum conductance continued to decline from -0.8 to -1.0 MPa, where it began to stabilize. Few previous results are available for comparison in these species. The only report available is that of Vargas-Hernández and Muñoz-Orozco (1991) for nine-month-old *P. greggii* seedlings in a greenhouse study in Mexico. They reported that when predawn water potential values ranged -1.0 and -2.0 MPa, stomatal conductance rates reduced from 0.033 to 0.011 mol m⁻² s⁻¹ during the first 13 days of water stress. Although *P. greggii* is not related to the *Ponderosae* subsection, the reported potential values for this species are the most similar to those of *P. engelmannii* and *P. durangensis* found in this study.

In this study, the 50% conductance threshold for *P. ponderosa* var. *ponderosa* was predicted at a predawn water potential of -1.1 MPa. This value is consistent with the threshold for stomatal closure (-1.65 to -1.73 MPa) in the dormant season (Lopushinsky, 1969). It appears to be a bit lower threshold than the -1.73 MPa ambient water potential values at which 50% of the maximum photosynthesis was recorded in two-year-old *P. ponderosa* var. *ponderosa* seedlings (Cleary, 1971). The seedlings had set bud at the time the measurements were taken. These differences could be attributable to the differences in instrumentation and the fact that one is based on predawn water potential while the other is based on ambient water potential.

In this study, the seed source of *P. ponderosa* var. *ponderosa* was from El Dorado County, which is located on the western slopes of the Sierra Nevada, CA (average annual precipitation of 1,651 mm; Anonymous, 1998). Seedlings from this seed source are characterized for having higher stomatal conductance than seedlings derived from an interior-derived parent. In a greenhouse study in Colorado, Monson and Grant (1989) compared stomatal conductance rates of three-year-old seedlings

derived from two crosses during the growing season. One of the crosses was between two parents native to coastal habits in El Dorado, County CA (*ponderosa* x *ponderosa*). The other cross was between a maternal parent from El Dorado County and a paternal parent native to interior montane habitats in Niobraro County, WY, variety *scopulorum* (*ponderosa* x *scopulorum*). In general, seedlings from the *ponderosa* x *ponderosa* cross had higher stomatal conductance rates ($0.151 \text{ mol m}^{-2} \text{ s}^{-1}$) than seedlings from the *ponderosa* x *scopulorum* cross ($0.07 \text{ mol m}^{-2} \text{ s}^{-1}$) over a range of leaf-to-air water vapor concentration differences (Monson and Grant, 1989). The *ponderosa* variety has evolved in a more mesic environment, in contrast to the xeric environment of the *scopulorum* variety (Grant et al. 1989).

The results for *P. arizonica* were somewhat inconsistent and inconclusive because seedlings never reached highly stressed conditions. Approximately 60.7% of the maximum midday conductance was predicted when predawn water potential was -0.6 MPa. Lower values of maximum conductance (38.0 and 15.31%) occurred when predawn water potential was -0.7 to -0.8 MPa. In this study, the low shoot to root ratios that characterized *P. arizonica* seedlings may have helped maintain higher xylem water potentials than in the other species, even in the water stress treatments. Prolonging the water-stress treatment to achieve more moisture stress, may be necessary to definitively determine a comparable 50% conductance threshold for this species.

In this study, *P. arizonica*, *P. engelmannii*, and *P. durangensis* apparently had similar thresholds for less than 50% maximum midday conductance. Differences in physiological behavior and water-stress conditions preclude drawing firm conclusions about these Mexican pine species, but the results may be useful helping to describe their responses to water stress after they are transplanted in the field.

These four pine species have morphological and physiological attributes for avoiding and tolerating dehydration. The adaptations a plant uses for avoiding dehydration can postpone detrimental water stresses whereas plants tolerate dehydration by developing a means for functioning under those water-stress conditions (Pallardy et al. 1995). Plants possess an integrated set of avoidance and tolerance attributes, and often present both kinds of adaptations.

Among the Mexican pine species, *P. arizonica* had the lowest shoot to root ratios while *P. durangensis* had the highest ratios. The morphological attributes of *P. arizonica* helped to avoid dehydration. With shorter stems and less-exposed phytomass, the transpiration demand may have been reduced, and water absorbed by the root system needed to travel over a shorter distance. In contrast, larger shoots and open crown of *P. durangensis* quickly depleted the water in the growing media. Despite the morphological differences between *P. arizonica* and *P. durangensis* in this study, the stomatal threshold was similar for both species. *P. engelmannii* had an intermediate shoot to root ratio, and its stomatal threshold was similar to that found in *P. arizonica* and *P. durangensis*. In addition, *P. engelmannii*'s juvenile grass stage may be an adaptive attribute for avoiding dehydration.

The large shoots and root systems of *P. ponderosa* var. *ponderosa* maximize CO₂ uptake in well-watered conditions. However, this could be a disadvantage under water-stress conditions, if water absorbed by the root system is insufficient to supply the transpirational demand of the large shoot. This can lead to cavitation and failure of the water conductivity system. However, the plant water potential threshold for stomatal closure found for this species was much lower than for the Mexican species. *P. ponderosa* var. *ponderosa* variety apparently can withstand lower water potentials, despite the differences in morphology.

The mechanisms associated with stomatal behavior are complex and dynamic, and are difficult to elucidate in a greenhouse study. Further research could help in understanding the dynamics associated with hydraulic conductivity and vapor pressure deficits in these Mexican pine species.

3.6 Conclusions

The seedlings used in this experiment were grown under uniform greenhouse conditions, and their morphology was not affected by the water stress treatment imposed after they were dormant. Thus, shoot to root ratios showed their own natural inherent morphology. Among the Mexican pine species, *P. arizonica* had the lowest total shoot to root dry mass ratio and *P. durangensis* had the largest total shoot to root dry mass ratio. *P. engelmannii* and *P. ponderosa* var. *ponderosa* were between *P. arizonica* and *P. durangensis*. Seedlings of *P. ponderosa* var. *ponderosa* appeared to develop about equal biomass in shoots and roots.

Significant water stress effects were found for plant water potential and stomatal conductance at the end of two drying cycles. Because the water stress treatment yielded significant reductions of midday stomatal conductance, a maximum midday stomatal conductance for the well-watered seedlings was defined for each species. Midday conductances were associated with decreasing predawn water potential. We used 50% of maximum midday conductance as a comparison "threshold".

Under the experimental conditions of this study, the stomatal thresholds for less than 50% of the maximum midday stomatal conductance for *P. arizonica*, *P. engelmannii*, and *P. durangensis* ranged from -0.6 to -0.8 MPa. However, the morphological attributes (e.g., shoot to root ratios) associated with this threshold may provide different strategies for avoiding dehydration. Because *P. arizonica* and *P. engelmannii* had small and intermediate, respectively, shoot to root ratios and because their associated predawn water potential thresholds for stomatal closure were high, these species are recommended for planting on north and northeastern slopes (low to mid elevations) in the SMOC.

The large shoot to root ratios of *P. durangensis* probably mean that the species is better suited for mesic, rather than xeric sites. However, the predawn water potential threshold for stomatal closure was high in this species, too. Therefore, this species may be able to sustain some degree of water deficit. *P. durangensis* could probably be successfully established on north and northeastern slopes (mid to high elevations) in the SMOC on deeper soils where the water supply was not limiting.

A comprehensive research program is needed to develop the target morphological characteristics of seedlings to be planted in the SMOC. This research could be used to design irrigation schedules for producing adapted stock types to be planted in the spring, summer, or fall on a variety of sites. Using predawn water potential readings to predict midday stomatal conductance, irrigation schedules and conditioning regimes (using water stress) could be devised for optimizing seedling performance. This information could then be coupled with the weighing method to more efficiently regulate the amount of water and time between irrigations needed for different species and stock types. Nursery managers should also consider the inherent species differences in morphology and physiology. In this way, planting stock could be tailored to fulfill the requirements for survival and growth on a given plantation site in the SMOC.

3.7 References.

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4. IMPLICATIONS FOR MANAGEMENT

4.1 Field study

4.1.1 Open area

Our findings have implications for reforestation of sites that have been cleared by either natural or anthropogenic disturbances. If reforestation is needed in such sites and high seedling survival and good growth is desired, forest managers may incorporate the use of herbicides to reduce competing vegetation and release site resources to planted seedlings. In this study, the survival of *P. engelmannii* and *P. durangensis* was enhanced by applying herbicides. In addition, the stem height and diameter growth of *P. engelmannii* was higher in the herbicide-treated plots than in untreated plots after two growing seasons.

In addition, nursery and forest managers need to link the stock type and nursery seedling condition to planting site conditions. In this study, seedlings of *P. engelmannii* with stem heights ≥ 5.5 cm had a greater stem diameter growth when they were planted in the herbicide-treated plots after two seasons. This implies that establishing quality control over seedlings produced at the nursery and controlling the competing vegetation at the planting site could lead to better survival and growth.

4.1.2 Forested sites

In general, seedling survival was moderately high ($> 60\%$) for all the species in the small canopy gaps, however the seedling growth rates after two years were slow even where the scant amounts of competing vegetation were controlled. Even though seedling survival was good in the canopy gaps after the two growing

seasons, I expect poor survival in the long run because the gaps were small (<0.04 ha) and residual stocking in the adjacent forests was high (> 22 m² ha⁻¹). Several authors have documented that seedling survival and growth in small canopy gaps decreased through five or six growing seasons. This implies that artificial regeneration could be used to regenerate canopy gaps left by selective cutting instead of waiting for the establishment of the natural regeneration. Gap size should, however, be at least 0.1 ha and competing hardwoods should be eliminated to give seedlings enough site resources to prosper until the next harvest entry.

Through tree planting, the uncertainties of the natural regeneration process are avoided. If forest managers wish to successfully regenerate a forested site at Tarahumar, forest managers need to adjust overstory stocking, control competing vegetation where necessary and prevent livestock grazing. A density diagram such as those developed by Drew and Flewelling (1979) Ernst and Knapp (1985), Long (1985), Long and Daniel (1990), Guldin (1991), Cochran (1992), Long (1995), O'Hara (1996) and Schulte et al. (1998) would be a useful tool in reducing tree density in overstocked stands. A stand density diagram must include a mixed species approach because oak densities have increased due to selective harvesting of pine trees species and fire suppression.

Effective management of large areas at Tarahumar will require utilization of both small diameter conifers and oaks of all sizes. Small conifers could be used to produce charcoal, hand-crafted items, and wood for framing. Oak species could be used to produce charcoal, wood flooring or wood kitchen cabinets.

At Tarahumar, dysgenic selection is probably serious due to repeated selective harvesting. There is a great need to study this aspect of silviculture in order to maintain a desirable genetic pool.

New avenues must be attempted for finding a balance between economical development and conservation of the pine-oak forest of Tarahumar and elsewhere in the SMOC. New silvicultural alternatives are being tested in the United States (Baker et al. 1996; Curtis et al. 1998; Oliver and Powers, 1998) and Canada (Arnott et al. 1995; Coates et al. 1997; Hollstedt and Vyse, 1997). Results from these studies may provide a starting point for testing of silvicultural alternatives for the SMOC. Perhaps, an adaptive management approach would be useful to test silvicultural systems along with range management and agricultural systems.

4.2 Greenhouse study

The greenhouse study has implications for understanding a basic pine seedling physiological behavior to improve nursery practices in the SMOC. In the greenhouse study, the inherent seedling morphology of the Mexican pine species influenced the degree of stress that the seedlings reached at the end of the drying cycles. Among the Mexican pine species, *P. arizonica* had the smallest total shoot to root dry mass ratios. This species maintained higher plant water potentials regardless of water stress than *P. durangensis* at the end of two drying cycles. This implies that the same irrigation schedule cannot be used for these species either in research studies or in nursery practice.

Improving stock quality for enhanced survival and growth of planted seedlings may hinge on using irrigation schedules that match the phenology and physiology of the species with the desirable morphological characteristics needed for a given site. Monitoring seedling conditions in the nursery by assessing xylem water potential or the weighing method could be use to develop more effective irrigation schedules for each species, however, fixed volume containers should replace plastic bags as a growing system.

Hopefully, this study will lead to a good research program aimed at defining the morphological and physiological target characteristics needed for successful survival and growth of seedlings planted in the SMOC.

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APPENDICES.

Appendix I. SAS programs.

SAS program for survival 1997 and 1998 in the open for the field study.

```
options ps=60 ls=80 pageno=1;
proc format;
  value block 2='COOA';
  value treat 1='NH' 2='H';
  value spe 1='a' 2='e' 3='d';
  value damsev 1='alive' 2='drought' 3='clipped' 4='root-borer';
data mor97;
  infile 'c:\sas\fieldstu\coa.dat';
  input block treat spe plot damsev ht96pl dia96pl ht97pl dia97pl ht98pl dia98pl
  htdi96pl htdi97pl htdi98pl sedpro97; format block block.; format treat treat.; format
  spe spe.; format damsev damsev.; sur=sedpro97/100; sutra=arsin(sqrt(sur));if
  damsev=1;
proc sort;
by spe;
proc ttest;
by spe; class treat; var sutra; run;
```

```
options ps=60 ls=80 pageno=1;
proc format;
value block 2='COOA';
value treat 1='C' 2='H';
value spe 1='a' 2='e' 3='d';
value dameig 1='alive' 2='drought' 3='clipped' 4='root-borer' 5='unknown';
data fie;
infile 'c:\sas\fieldstu\coa98.dat';
input block treat spe plot dameig sedpro98;
format block block.;format treat treat.;format spe spe.; format dameig dameig.;
sur=sedpro98/100; sutra=arsin(sqrt(sur)); if dameig=1;
proc sort;
  by spe treat;
proc sort;
  by spe;
proc ttest;
  by spe;
  class treat;
  var sutra; run;
```

SAS program for absolute shoot height, stem diameter, and volume in the open area for the field study.

```

options ps=60 ls=80 pageno=1;
proc format;
  value site 2='COOA';
  value treat 1='C' 2='H';
  value spe 1='ar' 2='en' 3='du';
  value damsev 1='alive' 2='drought' 3='clipped' 4='root-borer';
  value dameig 1='alive' 2='drought' 3='clipped' 4='root-borer' 5='unknown';
data fie98;
  infile 'c:\sas\fieldstu\cooagro98.dat';
  input site treat spe plot sedl ht96 diam96 ht97 diam97 damsev ht98 diam98 dameig;
  format site site.; format treat treat.; format spe spe.; format damsev damsev.;
  format dameig dameig.; di96cm=diam96/10; di97cm=diam97/10;
  di98cm=diam98/10;
  abgrht1=(ht97-ht96)/1; abgrht2=(ht98-ht96)/2; abgrdi2=(di98cm-di96cm)/2;
  sqabght2=sqrt(abgrht2); lht96=log(ht96); lht97=log(ht97); lht98=log(ht98);
  rgrht2=(lht98-lht96)/2; orrgrht2=exp(rgrht2); ldi96=log(di96cm); ldi98=log(di98cm);
  rgrdi2=(ldi98-ldi96)/2; orrgrdi2=exp(rgrdi2); sqabgdi2=sqrt(abgrdi2);
  vo96=((3.141592654*(di96cm**2))*ht96)/12;
  vo97=((3.141592654*(di97cm**2))*ht97)/12;
  vo98=((3.141592654*(di98cm**2))*ht98)/12;
  abvogr2=(vo98-vo96)/2; sqabvgr2=sqrt(abvogr2); lvo96=log(vo96);
  lvo97=log(vo97);
  lvo98=log(vo98); diaca=(0.05*round((di96cm-10)/0.05))+10;
  diaca2=(0.1*round((di96cm-10)/0.1))+10; heica=(5*round((ht96-10)/5))+10;
  htdica2=(5*round((htdi96-10)/5))+10; htdica3=(10*round((htdi96-10)/10))+10;
  if dameig=1;
proc sort; by spe; proc ttest; by spe; class treat; var sqabght2 sqabgdi2 sqabvgr2;
run;
proc sort; by treat spe plot; proc means noprint;
  by treat spe plot; var sqabvgr2; output out=means1 mean=sqabvgr2;
proc sort data=means1; by treat spe;
proc means noprint data=means1; by treat spe;
  var sqabvgr2; output out=means2 mean=sqabvgr2 stderr=se n=no_plots;
data; set means2; x1=sqabvgr2+se; x2=sqabvgr2-se; x3=x1**2;
  x4=x2**2; abvogr2=sqabvgr2**2; upse=x3-abvogr2; lose=abvogr2-x4;
proc sort; by spe treat; proc print; by spe; id treat;
  var no_plots abvogr2 upse lose;
run;

```

SAS program for the analysis of covariance of the absolute stem diameter growth of *P. engelmannii* after the second growing season in the open area.

```

options ps=60 ls=80 pageno=1;
proc format;
value site 2='COOA'; value treat 1='2NH' 2='1H'; value spe 1='ar' 2='en' 3='du'; value
damsev 1='alive' 2='drought' 3='clipped' 4='root-borer'; value dameig 1='alive'
2='drought' 3='clipped' 4='root-borer' 5='unknown';
data fie98;
  infile 'c:\sas\fieldstu\cooagro98.dat';
  input site treat spe plot sedl ht96 diam96 ht97 diam97 damsev ht98 diam98 dameig;
  format site site.; format treat treat.; format spe spe.; format damsev damsev.; format
dameig dameig.;
  if spe=1 or spe=3 then delete; lht96=log(ht96); sqht96=ht96**2; di96cm=diam96/10;
  di97cm=diam97/10; di98cm=diam98/10; sqht96=ht96**2; abgrht2=(ht98-ht96)/2;
  sqabght2=sqrt(abgrht2); abgrdi2=(di98cm-di96cm)/2; sqabgdi2=sqrt(abgrdi2);
  if dameig=1 and spe=2;
proc sort;
by treat spe plot;
proc means noprint;
by treat spe plot;
  var sqabght2 sqabgdi2 di96cm ht96 htdi96 abgrdi2 lht96;
output out=means1 mean=sqabght2 sqabgdi2 di96cm ht96 htdi96 abgrdi2 lht96;
proc sort; by spe;
proc glm;
by spe;
class treat;
model sqabgdi2= treat ht96*treat /solution;
estimate 'B1-B2' ht96*treat 1 -1;
estimate 'h-nh at 4.2' treat 1 -1 ht96*treat 4.2 -4.2;
estimate 'h-nh at 5.5' treat 1 -1 ht96*treat 5.5 -5.5;
estimate 'h-nh at 8.5' treat 1 -1 ht96*treat 8.5 -8.5;
run:

```

SAS program for xylem water potential in the open area for the field study.

```
options ls=80 ps=60 pageno=1;
proc format; value block 2='COOA' ; value treat 1='NH' 2='H'; value spe 1='ar'
2='du' 3='en'; value diur 1='PD' 2='MD' 3='EVE';
data winter;
infile 'c:\sas\fieldstu\wasprinopen.dat';
title2 'water potentials winter 1998';
input block treat spe diur plot seed1 sedl wapote; format block block. treat treat. spe
spe. diur diur.; waabs=abs(wapote); sqwapo1=sqrt(waabs); if diur=2;
proc sort;
by spe;
proc ttest;
title3 'testing for herbicide effect on midday water potential';
by spe;
class treat;
var sqwapo1;
run;
```

SAS program for stomatal conductance in the open area for the field study.

```
options ls=80 ps=60 pageno=1;
proc format; value site 2='COOA' 3='COFO' 5='AC'; value treat 1='C' 2='H'; value spe
1='ar' 2='du' 3='en'; value diur 1='1mo' 2='2md' 3='3ev'; data field;
infile 'c:\sas\fieldstu\fieldstomata.dat'; title2 'stomata conductance data winter 1998';
input site treat plot spe sedl diur flow t_cuv t_leaf es rh ea vpd light rawgs surfa2
trans;
format site site. treat treat. spe spe. diur diur.;
if site=2 then delete; surf=surfa2/10; gs=rawgs/1000; gs1=gs/surf; lgs1=log(gs1+1);
if spe=2; proc sort; by site spe treat plot sedl; PROC TRANSPOSE prefix=stoma
out=sto1; by site spe treat plot sedl; var lgs1; proc sort data=sto1;
by site spe treat; proc means noprint data=sto1; by site spe treat;
var stomal stoma2 stoma3; output out=menas mean=stomal stoma2 stoma3
stderr=se1 se2 se3 n=no_plots;
proc sort;
by spe;
proc glm;
by spe;
class site treat;
model stomal stoma2=site treat;
run;
```

SAS program for survival 1997 in the forested sites for the field study.

```

options ps=60 ls=80 pageno=1;
proc format;
  value site 1='CER' 3='COFO' 4='TSN' 5='AC';
  value treat 1='C' 2='H';
  value spe 1='a' 2='e' 3='d';
  value damsev 1='alive' 2='drought' 3='clipped' 4='root-borer';
data mor97;
  infile 'c:\sas\fieldstu\morta974blo.dat';
  input site treat spe plot damsev ht96pl dia96pl ht97pl dia97pl ht98pl dia98pl
        htdi96pl htdi97pl htdi98pl sedpro97;
  format site site.; format treat treat.; format spe spe.; format damsev damsev.;
  sur=sedpro97/100; sutra=arsin(sqrt(sur))*morta=100-sedpro;*mort=morta/100;
  *mortra=arsin(sqrt(mort)); if damsev=1;
proc sort;
  by block treat spe; proc means noprint; by block treat spe; var sutra;
output out=means mean=sutra;
proc sort data=means; by spe;
proc glm data=means; by spe; class block treat; model sutra= block treat;
means treat / clm;
run;
proc sort;
  by site spe treat;
proc means noprint;
  by site spe treat;
  var sutra;
output out=menas mean=sutra stderr=sutrase;
proc sort data=menas;
  by spe treat;
proc means noprint data=menas;;
  by spe treat;
  var sutra;
output out=menas2 mean=sutra stderr=sutrase n=no_blo;
data;
  set menas2; x1=sutra+sutrase; x2=sutra-sutrase; x3=sin(x1); x4=(x3**2)*100;
  x5=sin(x2); x6=(x5**2)*100; sur=sin(sutra); orsur=(sur**2)*100; upse=x4-orsur;
  lose=orsur-x6;
proc print;
  var spe treat no_blo sutra orsur sutrase upse lose;
run;

```

SAS program for survival 1998 in the forested sites for the field study.

```

options ps=60 ls=80 pageno=1;
proc format;
value site 1='CER' 3='COFO' 4='TSN' 5='AC';
value treat 1='NH' 2='H';
value spe 1='a' 2='e' 3='d';
value dameig 1='alive' 2='drought' 3='clipped' 4='root-borer' 5='unknown';
data fie;
infile 'c:\sas\fieldstu\surv984blo.dat';
input site treat spe plot dameig sedpro;
format site site.; format treat treat.; format spe spe.; format dameig dameig.;
sur=sedpro/100; sutra=arsin(sqrt(sur)); morta=100-sedpro; mort=morta/100;
mortra=arsin(sqrt(mort)); if dameig=1; proc sort; by site treat spe; proc means noprint;
by site treat spe;
var sutra;
output out=means mean=sutra;
proc sort data=means;
by spe;
proc glm data=means;
by spe;
class site treat;
model sutra= site treat;
run;
proc sort;
by site spe treat;
proc means noprint;
by site spe treat;
var sutra;
output out=menas mean=sutra stderr=sutrased;
proc sort data=menas;
by spe treat;
proc means noprint data=menas;;
by spe treat;
var sutra;
output out=menas2 mean=sutra stderr=sutrased n=no_blo;
data; set menas2; x1=sutra+sutrased; x2=sutra-sutrased; x3=sin(x1); x4=(x3**2)*100;
x5=sin(x2); x6=(x5**2)*100; sur=sin(sutra); orsur=(sur**2)*100; upse=x4-orsur;
lose=orsur-x6; proc print;
var spe treat no_blo sutra orsur sutrased upse lose;
run;

```

SAS program for seedling growth after two growing seasons in the forested sites for the field study.

```

options ps=60 ls=80 pageno=1;
proc format; value site 1='ER' 3='OFO' 4='TSN' 5='AC'; value treat 1='1NH' 2='2H';
value spe 1='ar' 2='en' 3='du'; value damsev 1='alive' 2='drought' 3='clipped' 4='root-
borer'; value dameig 1='alive' 2='drought' 3='clipped' 4='root-borer' 5='unknown';
data fie98;
  infile 'c:\sas\fieldstu\standgro98a.dat';
  input site treat spe plot sedl ht96 diam96 ht97 diam97 damsev ht98 diam98 dameig;
  format site site.; format treat treat.; format spe spe.; format damsev damsev.;
format dameig dameig.; di96cm=diam96/10; di97cm=diam97/10;
di98cm=diam98/10;
htdi96=ht96/di96cm; sqht96=htdi96**2; htdi97=ht97/di97cm; htdi98=ht98/di98cm;
ah1=(ht97-ht96)/1; ah2=(ht98-ht96)/2; abgrht2=(ht98-ht96)/2;
sqabght2=sqrt(abgrht2);
lht96=log(ht96); lht97=log(ht97); lht98=log(ht98); rgrht2=(lht98-lht96)/2;
orrgrht2=exp(rgrht2); ldi96=log(di96cm); ldi98=log(di98cm); rgrdi2=(ldi98-ldi96)/2;
orrgrdi2=exp(rgrdi2); abgrdi2=(di98cm-di96cm)/2; sqabgdi2=sqrt(abgrdi2);
vo96=((3.141592654*(di96cm**2))*ht96)/12;
vo97=((3.141592654*(di97cm**2))*ht97)/12;
vo98=((3.141592654*(di98cm**2))*ht98)/12; abvogr2=(vo98-vo96)/2;
sqabvgr2=sqrt(abvogr2); lvo96=log(vo96); lvo97=log(vo97); lvo98=log(vo98);
rgrvo1=(lvo97-lvo96)/1; rgrvo2=(lvo98-lvo96)/2; diaca=(0.05*round((di96cm-
10)/0.05))+10; diaca2=(0.1*round((di96cm-10)/0.1))+10; heica=(5*round((ht96-
10)/5))+10; htdica2=(5*round((htdi96-10)/5))+10; htdica3=(10*round((htdi96-
10)/10))+10; if dameig=1;
proc sort; by site treat spe plot; proc means noprint; by site treat spe plot;
var sqabght2 sqabgdi2 sqabvgr2 di96cm ht96 vo96 htdi96 abgrdi2;
output out=means1 mean=sqabght2 sqabgdi2 sqabvgr2 di96cm ht96 vo96 htdi96
abgrdi2 n=no_sedl;
proc sort data=means1; by site treat spe; proc means noprint data=means1;
by site treat spe; var sqabght2 sqabgdi2 sqabvgr2 di96cm ht96 vo96 htdi96 abgrdi2;
output out=means2 mean=sqabght2 sqabgdi2 sqabvgr2 di96cm ht96 vo96 htdi96
abgrdi2 n=no_plot;
proc sort data=means2;
by spe;
proc glm data=means2;
by spe;
class site treat;
model sqabght2= site treat;
run;

```

SAS program for the analysis of covariance of the absolute stem diameter growth of *P. arizonica* in the forested sites of the field study.

```

options ps=60 ls=80 pageno=1;
proc format; value site 1='ER' 3='OFO' 4='TSN' 5='AC'; value treat 1='NH' 2='H';
  value spe 1='ar' 2='en' 3='du'; value damsev 1='alive' 2='drought' 3='clipped' 4='root-
borer'; value dameig 1='alive' 2='drought' 3='clipped' 4='root-borer' 5='unknown';
data fie98;
  infile 'c:\sas\fieldstu\standgro98a.dat';
  input site treat spe plot sedl ht96 diam96 ht97 diam97 damsev ht98 diam98 dameig;
  format site site.; format treat treat.; format spe spe.; format damsev damsev.; format
dameig dameig.; di96cm=diam96/10; di97cm=diam97/10; di98cm=diam98/10;
  htdi96=ht96/di96cm; htdi97=ht97/di97cm; htdi98=ht98/di98cm; abgrht2=(ht98-
ht96)/2;
  sqabght2=sqrt(abgrht2); abgrdi2=(di98cm-di96cm)/2; sqabgdi2=sqrt(abgrdi2);
  vo96=((3.141592654*(di96cm**2))*ht96)/12;
  vo97=((3.141592654*(di97cm**2))*ht97)/12;
  vo98=((3.141592654*(di98cm**2))*ht98)/12;
  abvogr2=(vo98-vo96)/2; sqabvgr2=sqrt(abvogr2);
  diaca=(0.05*round((di96cm-10)/0.05))+10;
  diaca2=(0.1*round((di96cm-10)/0.1))+10;
  heica=(5*round((ht96-10)/5))+10;
  htdica2=(5*round((htdi96-10)/5))+10;
  *htdica3=(10*round((htdi96-10)/10))+10;
  if dameig=1 and spe=1;
proc sort data=fie98;
  by spe;
proc glm data=fie98;
  by spe;
  class site treat plot;
  model sqabvgr2= site treat site*treat site*plot(treat) htdi96 htdi96*treat/solution;
  test h= treat site*treat e=site*plot(treat);
run;

```

SAS program for xylem water potential in the forested sites for the field study.

```
options ls=80 ps=60 pageno=1;
proc format; value site 3='COFO' 5='AC'; value treat 1='NH' 2='H'; value spe 1='ar'
2='du' 3='en'; value diur 1='PD' 2='MD' 3='EVE';
data winter; infile 'c:\sas\fieldstu\wasprinsites.dat'; title2 'water potentials winter 1998';
input site treat spe diur plot seed1 sedl wapote; format site site. treat treat. spe spe. diur
diur.; waabs=abs(wapote); sqwapo1=sqrt(waabs); proc sort;
by site spe treat plot sedl;
PROC TRANSPOSE prefix=wapo out=wal;
by site spe treat plot sedl; var sqwapo1;
proc sort data=wal; by site spe treat;
proc means noprint data=wal; by site spe treat; var wapo1 wapo2 wapo3;
output out=menas mean=wapo1 wapo2 wapo3 stderr=se1 se2 se3 n=no_plots;
proc sort; by spe;
proc glm; by spe; class site treat; model wapo1 = site treat;
run;
```

SAS program for stomatal conductance in the forested sites for the field study.

```
options ls=80 ps=60 pageno=1;
proc format; value site 2='COOA' 3='COFO' 5='AC'; value treat 1='C' 2='H'; value spe
1='ar' 2='du' 3='en'; value diur 1='1mo' 2='2md' 3='3ev';
data field;
infile 'c:\sas\fieldstu\fieldstomata.dat';
title2 'stomata conductance data winter 1998';
input site treat plot spe sedl diur flow t_cuv t_leaf es rh ea vpd light rawgs surfa2
trans;
format site site. treat treat. spe spe. diur diur.; if site=2 then delete; surf=surfa2/10;
gs=rawgs/1000; gs1=gs/surf; lgs1=log(gs1+1);
proc sort; by site spe treat plot sedl;
PROC TRANSPOSE prefix=stoma out=sto1; by site spe treat plot sedl; var lgs1;
proc sort data=sto1; by site spe treat;
proc means noprint data=sto1; by site spe treat;
var stoma1 stoma2 stoma3;
output out=menas mean=stoma1 stoma2 stoma3 stderr=se1 se2 se3 n=no_plots;
proc sort; by spe;
proc glm;
by spe;
class site treat;
model stoma1=site treat;
run;
```

SAS program for mean relative growth rate of seedling caliper diameter and height in the greenhouse study.

```

options ls=80 ps=60 pageno=1;
proc format; value spe 1='ar' 2='du' 3='en' 4='po';v alue treat 1='well-watered'
2='water-stressed';
data field1; infile 'c:\sas\grehouse\htdiam.dat';
input block spe treat styro $ sedl iht idiam fht fdiam; format spe spe. treat treat.;
  idia1=idiam/10; fdia1=fdiam/10; lnidi1=log(idia1); lnfdi1=log(fdia1);
  rgrdiam1=((lnfdi1-lnidi1)/11); backdia1=exp(rgrdiam1); lniht=log(iht); lnfht=log(fht);
  rgrhight=((lnfht-lniht)/11);
if spe=4;
proc sort;
  by block spe treat;
proc means noprint;
  by block spe treat;
  var rgrdiam1 rgrdiam2;
  output out=mean1 mean=rgrdiam1 rgrdiam2 n=no_sedl;
run;
proc sort data=mean1;
  by spe;
proc mixed data=mean1;
  title3'diameter in cm';
  by spe;
  class block treat;
  model rgrdiam1= treat;
  id block spe treat;
  random block;
  lsmeans treat / cl;
  make 'lsmeans' out=lmean3 noprint;
data new3;
  set lmean3; rgrdia =exp(_lsmean_); lo95cl=exp(_lower_); up95cl=exp(_upper_);
  u95ci=up95cl-rgrdia; l95ci= rgrdia-lo95cl;
  drop _effect_; drop _se_; drop _df_; drop _t_; drop _pt_; drop _alpha_;
proc sort;
  by spe treat;
proc print;
  by spe;
  id treat;
  var rgrdia u95ci l95ci up95cl lo95cl; run;

```

SAS program for seedling phytomass analysis from the greenhouse study.

```

options ls=80 ps=60 pageno=1;
proc format;
  value spe 1='ar' 2='du' 3='en' 4='po' 5='mexpines'; value treat 1='control' 2='stress';
data field2;
  infile 'c:\sas\grehouse\phytomass.dat';
  input block spe treat styro $ sedl ishfreq irofreq ishdry irodry fshfreq frofreq fshdry
frodry; format spe spe. treat treat.;
  itodrywe=ishdry+irodry; ftodrywe=fshdry+frodry;
  rodywera=((irodry/itodrywe)+(frodry/ftodrywe))/2;
  shdywera=((ishdry/itodrywe)+(fshdry/ftodrywe))/2;
  lrodyw1=log(rodywera);lshdyw1=log(shdywera);
if spe=4;
proc sort data=field2;
  by block spe treat sedl;
proc means noprint;
  by block spe treat;
  var lshdyw1 lrodyw1 ;
  output out=means2 mean=lshdyw1 lrodyw1 n=no_sedl;
proc sort data=means2;
  by spe;
proc mixed data=means2;
  by spe;
  class block treat;
  model lrodyw1 = treat;
  id block spe treat;
  random block;
  lsmeans treat / cl;
  make 'lsmeans' out=lmean1 noprint;
data new1;
  set lmean1; rotdry=exp(_lsmean_); lo95cl=exp(_lower_); up95cl=exp(_upper_);
  u95ci=up95cl-rotdry; o95ci=rotdry-lo95cl;
  drop _effect_; drop _se_; drop _df_; drop _t_; drop _pt_; drop _alpha_;
proc sort;
  by spe treat;
proc print;
  by spe;
  var treat rotdry u95ci o95ci up95cl lo95cl;
run;

```

SAS program for water potentials analysis of the first cycle from the greenhouse study.

```

options ls=80 ps=60 pageno=1;
proc format; value spe 1='ar' 2='du' 3='en' 4='po'; value treat 1='control' 2='stress';
  value diur 1='1predawn' 2='2md' 3='3eve';
data water1; libname save 'c:\'; infile 'c:\sas\grehouse\wanew11.dat';
title3 'water potential data from the 1st cycle';
input block spe treat styro $ sedl diur wapote;
format spe spe. treat treat. diur diur.; waabs=abs(wapote); sqwapo1=sqrt(waabs);
proc sort; by block spe treat diur;
proc means noprint; by block spe treat diur; var wapote sqwapo1;
output out=means1 mean=wapote sqwapo1 n=no_sedl;
proc sort data=means1; by spe;
proc mixed data=means1; by spe;
  title4 'analysis with the first two contrast';
  class block treat diur;
  model sqwapo1 = treat diur treat*diur;
  id block spe treat diur;
  random block block*treat / type=vc;
  repeated / type=AR(1) sub=treat(block);
  contrast '1 pd vs 12&4PM' diur 2 -1 -1;
  contrast '2 pd vs 12PM' diur 1 -1 0;
  contrast '1 drpd vs dr12&4PM' diur 2 -1 -1 treat*diur 0 0 0 2 -1 -1;
  contrast '2 drpd vs dr12PM' diur 1 -1 0 treat*diur 0 0 0 1 -1 0;
proc sort data=means1; by spe;
proc mixed data=means1; by spe; title4 'analysis with the second two contrast';
  class block treat diur;
  model sqwapo1 = treat diur treat*diur;
  id block spe treat diur;
  random block block*treat / type=vc;
  repeated / type=AR(1) sub=treat(block);
  contrast '3 pd vs 4PM' diur 1 0 -1;
  contrast '4 12PM vs 4PM' diur 0 1 -1;
  contrast '3 drpd vs 4PM' diur 1 0 -1 treat*diur 0 0 0 1 0 -1;
  contrast '4 dr12PM vs dr4PM' diur 0 1 -1 treat*diur 0 0 0 0 1 -1;
run;
make 'lsmeans' out=meanspe;
data new1; set meanspe; ormeanwa=(_lsmean_**2)*-1; or95lo=(_lower_**2)*-1;
  or95up=(_upper_**2)*-1; drop _effect_; drop _se_; drop _df_; drop _t_; drop _pt_;
  drop _alpha_;proc print; run;

```

SAS program for stomatal conductance analysis of the second cycle from the greenhouse study.

```

options ls=80 ps=60 pageno=1;
proc format;
  value spe 1='ar' 2='du' 3='en' 4='po'; value treat 1='control' 2='drought';
  value diur 1='18-10AM' 2='2-2PM' 3='4-6PM';
data stomata2; libname save 'c:\';
infile 'c:\sas\grehouse\stomnew2.dat';
title2 'stomata conductance data from the 2nd cycle';
input block spe treat styro $ sedl diur flow cuv_T leaf_T RH quan stocon sueal trans;
format spe spe. treat treat. diur diur.;
surf=sueal/10; gs=stocon/1000; gs1=gs/surf; sqgs1=sqrt(gs1); lgs1=log(gs1+1);
proc sort; by block spe treat diur;
proc means noprint; by block spe treat diur; var gs1 lgs1;
  output out=means2 mean=gs1 lgs1 n=no_sedl;
proc sort data=means2; by spe;
proc mixed data=means2; title4 'G=VC R=AR(1)'; by spe; class block treat diur;
  model lgs1 = treat diur treat*diur;
  id block spe treat diur;
  random block block*treat / type=vc; repeated / type=AR(1) sub=treat(block);
  lsmeans treat|diur / cl;
make 'lsmeans' out=meanspe noprint;
contrast '1 8AM vs 12&4PM' diur 2 -1 -1;
contrast '2 8AM vs 12PM' diur 1 -1 0;
contrast '1 dr8AM vs dr12&4PM' diur 2 -1 -1 treat*diur 0 0 0 2 -1 -1;
contrast '2 dr8AM vs dr12PM' diur 1 -1 0 treat*diur 0 0 0 1 -1 0;
data new4;
set meanspe;
or95lo=(2.718281828459045**_lsmean_)-1;
or95lo=(2.718281828459045**_lower_)-1;
or95up=(2.718281828459045**_upper_)-1;
drop _effect_ ; drop _se_ ; drop _df_ ; drop _t_ ; drop _pt_ ; drop _alpha_ ;proc print;
run;

```

SAS program for the nonlinear regression of *Pinus arizonica*

```

options ls=80 ps=60 pageno=1;
data ar2; input wapd gspromax @@; list; cards;
0.30 63.64 0.40 54.55 0.40 54.55 0.45 72.73 0.45 63.64 0.45 72.73 0.45 72.73 0.45
45.45 0.45 54.55 0.45 63.64 0.50 54.55 0.50 63.64 0.50 72.73 0.50 63.64 0.50 72.73
0.55 100.00 0.55 63.64 0.55 54.55 0.55 72.73 0.55 36.36 0.55 63.64 0.55 63.64 0.55
45.45 0.60 54.55 0.60 54.55 0.60 81.82 0.60 45.45 0.60 54.55 0.65 63.64 0.65 54.55
0.65 27.27 0.65 54.55 0.70 9.09 0.70 72.73 0.70 9.09 0.75 27.27 0.75 9.09 0.95 18.18
0.95 54.55 1.05 18.18
;
proc nlin method=marquardt data=ar2;
title3 'testing for a sigmoid 4 parameters model for Pi ar';
parms b0=30 to 100 by 5 b1=-0.02 to -0.01 by 0.01 x0=0.50 to 0.80 by 0.1 y0=10 to
20 by 1.0;
x2=(wapd-x0)/b1;
z1=exp(-x2);
model gspromax =y0+(b0/(1+z1));
der.y0 =1+(b0/(1+z1));
der.b0 =y0+(1/(1+z1));
der.b1 =y0+(-z1*b0/(1+z1)**2);
der.x0 =y0+(-wapd*z1*b0/(1+z1)**2);
output out=B1 sse=sse p=yhat r=resid student=rstu l95m=l95m u95m=u95m;
proc univariate normal plot data=B1;
title4 'test for normality';
var resid;
proc plot;
plot resid*yhat='*' / hpos=60 vpos=40 vref=0;
plot gspromax*wapd='O' yhat*wapd='P' l95m*wapd='M' u95m*wapd='M' / overlay;
plot rstu*wapd='*' / hpos=60 vpos=40 vref=2.5 0 -2.5;
proc sort;
by wapd gspromax;
proc print;
var wapd gspromax resid rstu ;
proc means data=ar2 noprint css;
var gspromax;
output out=B2 css=css n=nr_obs;
DATA;
SET B1(OBS=1); SET B2(OBS=1);
RSQ = 1 - SSE/CSS;
MSE = SSE/(nr_obs-4);
proc print; run;

```

SAS program for the nonlinear regression of *Pinus engelmannii*

```

options ls=80 ps=60 pageno=1;
data en2; input wapd  gspromax @@; list; cards;
0.40 85.71 0.45 100.00 0.50 85.71 0.50 85.71 0.50 57.14 0.50 57.14 0.50 71.43 0.50
71.43 0.50 71.43 0.50 85.71 0.55 85.71 0.55 71.43 0.55 57.14 0.55 42.86 0.55 71.43
0.55 71.43 0.60 57.14 0.60 71.43 0.60 57.14 0.60 28.57 0.65 42.86 0.65 28.57 0.65
71.43 0.70 28.57 0.70 28.57 0.75 14.29 0.75 28.57 0.90 14.29 0.95 14.29 0.95 14.29
1.00 14.29 1.00 14.29 1.10 14.29 1.10 14.29 1.15 14.29 1.30 14.29 1.40 14.29
;
proc nlin method=marquadt data=en2;
title3 'testing for a sigmoid 4 parameters model for Pi en';
parms b0=75 to 100 by 1 b1=-0.08 to -0.12 by 0.01 x0=0.40 to 0.70 by 0.02 y0=10 to
16.0 by 2;
x2=(wapd-x0)/b1;
z1=exp(-x2);
model gspromax =y0+(b0/(1+z1));
der.y0 =1+(b0/(1+z1));
der.b0 =y0+(1/(1+z1));
der.b1 =y0+(-z1*b0/(1+z1)**2);
der.x0 =y0+(-wapd*z1*b0/(1+z1)**2);
output out=B1 sse=sse p=yhat r=resid student=rstu l95m=l95m u95m=u95m;
proc univariate normal plot data=B1;
title4 'test for normality';
var resid;
proc plot;
plot resid*yhat='*' / hpos=60 vpos=40 vref=0;
plot gspromax*wapd='O' yhat*wapd='P' l95m*wapd='M' u95m*wapd='M' / overlay;
plot rstu*wapd='*' / hpos=60 vpos=40 vref=2.5 0 -2.5;
proc sort;
by wapd gspromax;
proc print;
var wapd gspromax resid rstu ;
proc means data=en2 noprint css;
var gspromax;
output out=B2 css=css n=nr_obs;
DATA;
SET B1(OBS=1); SET B2(OBS=1);
RSQ = 1 - SSE/CSS;
MSE = SSE/(nr_obs-4);
proc print;
run;

```

SAS program for the nonlinear regression of *Pinus durangensis*

```

options ls=80 ps=60 pageno=1;
data du2; input wapd  gspromax; list; cards;
0.30 100.00 0.40 44.44 0.40 66.67 0.40 77.78 0.40 44.44 0.45 77.78 0.45 77.78 0.45
33.33 0.45 44.44 0.45 55.56 0.45 33.33 0.45 88.89 0.50 77.78 0.50 77.78 0.50 44.44
0.55 88.89 0.60 77.78 0.60 66.67 0.65 33.33 0.65 22.22 0.65 33.33 0.70 55.56 0.70
33.33 0.75 44.44 0.80 11.11 0.90 11.11 0.95 33.33 1.15 11.11 1.30 11.11 1.50 11.11
1.50 11.11 1.70 11.11 1.75 11.11 1.80 11.11 2.00 11.11 2.15 11.11 2.20 11.11
;
proc nlin method=marquardt data=du2;
  title3 'testing for a sigmoid 4 parameters model for Pi du';
  parms b0=60 to 100 by 2 b1=-0.02 to -0.09 by 0.01 x0=0.4 to 0.8 by 0.02 y0=10 to 14
  by 2;
  x2=(wapd-x0)/b1;
  z1=exp(-x2);
  model gspromax =y0+(b0/(1+z1));
  der.y0 =1+(b0/(1+z1));
  der.b0 =y0+(1/(1+z1));
  der.b1 =y0+(-z1*b0/(1+z1)**2);
  der.x0 =y0+(-wapd*z1*b0/(1+z1)**2);
  output out=B1 sse=sse p=yhat r=resid student=rstu l95m=l95m u95m=u95m;
proc univariate normal plot data=B1;
  title4 'test for normality';
  var resid;
proc plot;
  plot resid*yhat='*' / hpos=60 vpos=40 vref=0;
  plot gspromax*wapd='O' yhat*wapd='P' l95m*wapd='M' u95m*wapd='M' / overlay;
  plot rstu*wapd='*' / hpos=60 vpos=40 vref=2.5 0 -2.5;
proc sort;
  by wapd gspromax;
proc print;
  var wapd gspromax resid rstu ;
proc means data=du2 noprint css;
  var gspromax;
  output out=B2 css=css n=nr_obs;
DATA;
  SET B1(OBS=1); SET B2(OBS=1);
  RSQ = 1 - SSE/CSS;
  MSE = SSE/(nr_obs-4);
proc print;
run;

```

SAS program for the nonlinear regression of *Pinus ponderosa*

```

options ls=80 ps=60 pageno=1;
data po2; input wapd  gspromax @@; list; cards;
0.45 50.00 0.45 60.00 0.45 100.00 0.50 60.00 0.50 90.00 0.50 50.00 0.55 80.00 0.55
90.00 0.60 80.00 0.60 60.00 0.60 80.00 0.60 100.00 0.60 100.00 0.60 60.00 0.60 50.00
0.65 80.00 0.70 50.00 0.75 60.00 0.75 90.00 1.15 10.00 1.25 40.00 1.25 50.00 1.45
20.00 1.50 20.00 1.60 10.00 1.70 10.00 1.75 10.00 1.75 10.00 1.75 20.00 1.80 10.00
2.05 10.00 2.15 10.00 2.25 10.00 2.35 20.00 2.45 10.00 2.60 10.00
;
proc nlin method=marquardt data=po2;
  title3 'testing for a sigmoid 4 parameters model for Pi po';
  parms b0=60 to 100 by 1 b1=-0.12 to -0.24 by 0.01 x0=1.0 to 1.5 by 0.02 y0=9 to 13.0
  by 0.5;
  x2=(wapd-x0)/b1;
  z1=exp(-x2);
  model gspromax =y0+(b0/(1+z1));
  der.y0 =1+(b0/(1+z1));
  der.b0 =y0+(1/(1+z1));
  der.b1 =y0+(-z1*b0/(1+z1)**2);
  der.x0 =y0+(-wapd*z1*b0/(1+z1)**2);
  output out=B1 sse=sse p=yhat r=resid student=rstu l95m=l95m u95m=u95m;
proc univariate normal plot data=B1;
  title4 'test for normality';
  var resid;
proc plot;
  plot resid*yhat='*' / hpos=60 vpos=40 vref=0;
  plot gspromax*wapd='O' yhat*wapd='P' l95m*wapd='M' u95m*wapd='M' / overlay;
  plot rstu*wapd='*' / hpos=60 vpos=40 vref=2.5 0 -2.5;
proc sort;
  by wapd gspromax;
proc print;
  var wapd gspromax resid rstu ;
proc means data=po2 noprint css;
  var gspromax;
  output out=B2 css=css n=nr_obs;
DATA; SET B1(OBS=1); SET B2(OBS=1);
  RSQ = 1 - SSE/CSS;
  MSE = SSE/(nr_obs-4);
proc print;
run;

```

Appendix II. Student's t-test and analysis of variance (ANOVA) tables for the field and greenhouse studies.

Student's t-test for the open area.								
Species	Variable	T ¹	n	Mean	SE ²	t-value	DF ³	Pr> t
<i>P. arizonica</i>	Survival 97	NH ⁴	6	1.0611	0.0708	1.5470	10	0.1529
		H ⁵	6	1.2648	0.1111			
	Survival 98	NH	6	0.9000	0.0527	1.6831	10	0.1233
		H	6	1.1413	0.1333			
	ASHTG1 ⁶	NH	6	2.3126	0.0975	1.9131	10	0.0848
		H	6	1.9875	0.1391			
	ASDIG1 ⁷	NH	6	0.4575	0.0408	0.2667	10	0.7952
		H	6	0.4698	0.0217			
	AVOG1 ⁸	NH	6	1.3438	0.1105	2.2813	10	0.0457
		H	6	1.0527	0.0638			
	ASHTG2 ⁹	NH	6	3.0079	0.1536	1.128	10	0.2856
		H	6	3.2962	0.2043			
	ASDIG2 ¹⁰	NH	6	0.7370	0.0298	0.0377	10	0.9707
		H	6	0.7354	0.0307			
	AVOG2 ¹¹	NH	6	3.3038	0.2848	0.4816	10	0.6405
		H	6	3.0849	0.3542			

¹= treatments; ²= standard error; ³= degree of freedom; ⁴= no herbicide; ⁵= herbicide; ⁶= absolute stem height growth after the first growing season = (stem height 97-stem height 96)/1; ⁷= absolute stem diameter growth after the first growing season = (stem diameter 97-stem diameter 96)/1; ⁸= absolute volume growth after the first growing season = (volume 97-volume 96)/1; ⁹= absolute stem height growth after the second growing season = (stem height 98-stem height 96)/2; ¹⁰= absolute stem diameter growth after the second growing season = (stem diameter 98 - stem diameter 96)/2; ¹¹= absolute volume growth after the second growing season = (volume 98-volume 96)/2.

Species	Variable	T	n	Mean	SE	t-value	DF	Pr> t
<i>P. arizonica</i>	PDWSP98 ¹	NH	6	0.9177	0.0699	0.4018	10	0.6963
		H	6	0.8867	0.0326			
	MDWSP98 ²	NH	6	1.2975	0.0404	0.4247	10	0.6800
		H	6	1.2693	0.0528			
	MOSTSP98 ³	NH	6	0.0209	0.0032	0.0658	10	0.9488
		H	6	0.0213	0.0048			
	MDSTSP98 ⁴	NH	6	0.0315	0.0103	0.6513	10	0.5295
		H	6	0.0409	0.0102			
	PDWSU98 ⁵	NH	6	0.7548	0.0520	0.4581	10	0.6567
		H	6	0.7257	0.0365			
	MDWSU98 ⁶	NH	6	1.2113	0.0697	0.8711	10	0.4041
		H	6	1.1261	0.0687			

1 = predawn xylem water potential for the spring of 1998;

2 = midday xylem water potential for the spring of 1998;

3 = morning stomatal conductance for the spring of 1998;

4 = midday stomatal conductance for the spring of 1998;

5 = predawn xylem water potential for the summer of 1998;

6 = midday xylem water potential for the summer of 1998.

Species	Variable	T	n	Mean	SE	t-value	DF	Pr> t	
<i>P. arizonica</i>	Survival 98 0.30 cm DIA ¹ class	NH	5	0.7174	0.2518	1.1667	8	0.2769	
		H	5	1.0995	0.2094				
	Survival 98 0.40 cm DIA class	NH	6	0.9193	0.1641	1.5684	10	0.1479	
		H	6	1.2687	0.1507				
	Survival 98 0.50 cm DIA class	NH	6	1.0463	0.1055	0.2299	10	0.8228	
		H	6	0.9699	0.3153				
<i>P. engelmannii</i>	Survival 98 0.40 cm DIA class	NH	6	0.9808	0.2081	1.1997	10	0.2579	
		H	6	1.2791	0.1359				
	Survival 98 0.50 cm DIA class	NH	6	0.7757	0.0954	1.7594	10	0.1090	
		H	6	1.1497	0.1899				
	Survival 98 0.60 cm DIA class	NH	4	1.0931	0.2757	0.1349	8	0.8960	
		H	6	1.1444	0.2493				
	<i>P. durangensis</i>	Survival 98 0.30 cm DIA class	NH	5	0.2462	0.1507	0.1521	8	0.8829
			H	5	0.2749	0.1143			
		Survival 98 0.40 cm DIA class	NH	6	0.1339	0.0862	2.6646	10	0.0237
			H	6	0.7287	0.2059			
		Survival 98 0.50 cm DIA class	NH	5	0.5943	0.2912	0.7933	8	0.4505
			H	5	0.3141	0.1997			

¹ = diameter class.

Species	Variable	T	n	Mean	SE	t-value	DF	Pr> t
<i>P. engelmannii</i>	Survival 97	NH	6	1.0216	0.0909	1.4907	10	0.1669
		H	6	1.2160	0.0935			
	Survival 98	NH	6	0.7134	0.0678	3.1996	10	0.0095
		H	6	1.0897	0.0960			
	ASHTG1	NH	6	0.4086	0.1546	0.1846	10	0.8572
		H	6	0.3733	0.1124			
	ASDIG1	NH	6	0.5558	0.0292	0.6965	10	0.5020
		H	6	0.5820	0.0236			
	AVOG1	NH	6	0.8963	0.1030	0.3526	10	0.7317
		H	6	0.8517	0.0731			
	ASHTG2	NH	6	1.3681	0.1211	3.3172	10	0.0078
		H	6	1.8933	0.1019			
	ASDIG2	NH	6	0.7684	0.0158	1.3294	10	0.2132
		H	6	0.8173	0.0331			
	AVOG2	NH	6	2.0580	0.1163	1.6227	10	0.1357
		H	6	2.4830	0.2347			

Species	Variable	T	n	Mean	SE	t-value	DF	Pr> t
<i>P. engelmannii</i>	PDWSP98	NH	6	0.9299	0.0608	1.3935	10	0.1936
		H	6	0.8260	0.0430			
	MDWSP98	NH	6	1.2299	0.0282	0.1941	10	0.8499
		H	6	1.2389	0.0368			
	MOSTSP98	NH	6	0.0059	0.0018	3.4241	10	0.0065
		H	6	0.0159	0.0023			
	MDSTSP98	NH	6	0.0213	0.0057	2.9819	10	0.0138
		H	6	0.0408	0.0032			
	PDWSU98	NH	6	0.7814	0.0537	0.0322	10	0.9749
		H	6	0.7840	0.0611			
	MDWSU98	NH	6	1.0579	0.0559	1.6741	10	0.1251
		H	6	0.9009	0.0775			

Species	Variable	T	n	Mean	SE	t-value	DF	Pr> t
<i>P. durangensis</i>	Survival 97	NH	6	0.7855	0.1633	1.5773	10	0.1458
		H	6	1.0569	0.0543			
	Survival 98	NH	6	0.2703	0.0981	2.2556	10	0.0477
		H	6	0.5422	0.0700			
	ASHTG1	NH	5	1.8552	0.1199	3.0650	9	0.0135
		H	6	1.1887	0.1706			
	ASDIG1	NH	5	0.3205	0.0384	0.0749	9	0.9419
		H	6	0.3245	0.0379			
	AVOG1	NH	5	0.9446	0.1508	0.3278	9	0.7506
		H	6	0.8807	0.1260			
	ASHTG2	NH	4	5.3588	0.3336	0.2194	8	0.8318
		H	6	5.2792	0.1997			
	ASDIG2	NH	4	0.9721	0.0644	0.1151	8	0.9112
		H	6	0.9624	0.0543			
	AVOG2	NH	4	3.7501	0.6403	0.1051	8	0.9189
		H	6	3.6691	0.4653			

Species	Variable	T	n	Mean	SE	t-value	DF	Pr> t
<i>P. durangensis</i>	PDWSP98	NH	3	0.9249	0.0751	0.6748	6	0.5250
		H	5	0.7992	0.1334			
	MDWSP98	NH	3	1.6165	0.0418	5.7649	6	0.0012
		H	5	1.1477	0.0565			
	MOSTSP98	NH	3	0.0046	0.0008	0.4075	6	0.6978
		H	5	0.0055	0.0016			
	MDSTSP98	NH	3	0.0146	0.0034	0.4882	6	0.6428
		H	5	0.0166	0.0023			
	PDWSU98	NH	4	0.8017	0.1220	1.1247	3.3	0.3369
		H	6	0.9423	0.0271			
	MDWSU98	NH	4	1.1230	0.0675	0.0662	8	0.9488
		H	6	1.1304	0.0780			

Analysis of covariance for the absolute stem diameter growth (ASDIG2) of *P. engelmannii* after the second growing season in the open area.

Species	Variable	SV ¹	DF ²	SS ³	MS ⁴	F-value	Pr > F
<i>P. engelmannii</i>	ASDIG2	H ⁵	1	0.01310405	0.01310405	4.66	0.0630
		HT96	1	0.01602751	0.01602751	5.69	0.0441
		H x HT96	1	0.01640611	0.01640611	5.83	0.0422
		Error	8	0.02251981	0.00281498		
		Total	11	0.04764904			
	ASDIG2	H	1	0.01310405	0.01310405	4.66	0.0630
		H x HT96	2	0.01797248	0.00898624	3.19	0.0957
		Error	8	0.02251981	0.00281498		
		Total	11	0.04764904			

1 = source of variation; 2 = degrees of freedom; 3 = sum of squares; 4 = mean square; 5 = herbicide effect. HT96 = initial stem height. (covariate).

Parameter		Estimate	T for H ₀ : Parameter = 0	Pr > T	Std Error of Estimate
INTERCEPT		0.7739395296	6.23	0.0003	0.12420984
TREAT	H	-0.6573280693	-2.16	0.0630	0.30466092
	NH	0.0000000000			
H x HT96	H	0.1488073180	2.53	0.0355	0.05890148
	NH	-0.0008685366	0.04	0.9653	0.01935256
B1-B2		0.14967585	2.41	0.0422	0.06199924
H-NH at 4.2		-0.02868948	-0.48	0.6416	0.05932169
H-NH at 5.5		0.16588913	2.86	0.0211	0.05798931
H-NH at 8.5		0.61491669	2.68	0.0279	0.22932173

ANOVA for the four forested sites in the field study.

Species	Variable	SV	DF	SS	MS	F-value	Pr > F
<i>P. arizonica</i>	Survival 97	Site	3	0.06787213	0.02262404	18.44	0.0195
		H	1	0.02055153	0.02055153	16.75	0.0264
		Error	3	0.00368069	0.00122690		
		Total	7	0.09210435			
	Survival 98	Site	3	0.12863552	0.04287851	5.72	0.0929
		H	1	0.02436258	0.02436258	3.25	0.1691
		Error	3	0.02247968	0.00749323		
		Total	7	0.17547778			
	ASHTG1	Site	3	0.22864960	0.07621653	1.44	0.3858
		H	1	0.08636150	0.08636150	1.63	0.2914
		Error	3	0.15879264	0.05293088		
		Total	7	0.47380374			
	ASDIG1	Site	3	0.02993770	0.00997923	5.40	0.0998
		H	1	0.00038804	0.00038804	0.21	0.6780
		Error	3	0.00554604	0.00184868		
		Total	7	0.03587178			
AVOG1	Site	3	0.14102760	0.04700920	2.59	0.2275	
	H	1	0.00296286	0.00296286	0.16	0.7132	
	Error	3	0.05444167	0.01814722			
	Total	7	0.19843214				

Species	Variable	SV	DF	SS	MS	F-value	Pr > F
<i>P. arizonica</i>	ASHTG2	Site	3	0.47110239	0.15703413	11.42	0.0378
		H	1	0.05416350	0.05416350	3.94	0.1414
		Error	3	0.04126087	0.01375362		
		Total	7	0.56652677			
	ASDIG2	Site	3	0.02995313	0.00998438	32.03	0.0089
		H	1	0.00012169	0.00012169	0.93	0.5764
		Error	3	0.00093518	0.00031173		
		Total	7	0.03100999			
	AVOG2	Site	3	0.66683536	0.22227845	19.83	0.0176
		H	1	0.00181351	0.00181351	0.16	0.7145
		Error	3	0.03363336	0.01121112		
		Total	7	0.70228222			

Species	Variable	SV	DF	SS	MS	F-value	Pr > F
<i>P. arizonica</i>	PDWSP98	Site	1	0.00577756	0.00577756	736.5	0.0234
		H	1	0.00189162	0.00189162	241.1	0.0409
		Error	1	0.00000784	0.00000784		
		Total	3	0.00767702			
	MDWSP98	Site	1	0.00020415	0.00020415	0.03	0.8857
		H	1	0.00415689	0.00415689	0.67	0.5630
		Error	1	0.00619359	0.00619359		
		Total	3	0.01055463			
	MOSTSP98	Site	1	0.00006299	0.00006299	14.87	0.1615
		H	1	0.00000818	0.00000818	1.93	0.3971
		Error	1	0.00000424	0.00000424		
		Total	3	0.00007540			
	MDSTSP98	Site	1	0.00009830	0.00009830	13.09	0.1717
		H	1	0.00000432	0.00000432	0.58	0.5869
		Error	1	0.00000751	0.00000751		
		Total	3	0.00011012			
	PDWPSU98	Site	1	0.00109176	0.00109176	0.07	0.8336
		H	1	0.01461734	0.01461734	0.96	0.5086
		Error	1	0.01525443	0.01525443		
		Total	3	0.03096353	0.03096353		
	MDWPSU98	Site	1	0.01045788	0.01045788	190.5	0.0460
		H	1	0.02055896	0.02055896	374.6	0.0329
		Error	1	0.00005489	0.00005489		
		Total	3	0.03107173			

Species	Variable	SV	DF	SS	MS	F-value	Pr> F
<i>P. engelmannii</i>	Survival 97	Site	3	0.06177384	0.02059128	7.16	0.0701
		H	1	0.00112148	0.00112148	0.39	0.5766
		Error	3	0.00862836	0.00287612		
		Total	7	0.07152369			
	Survival 98	Site	3	0.11223754	0.03741251	2.88	0.2040
		H	1	0.00372121	0.00372121	0.29	0.6296
		Error	3	0.03895435	0.01298478		
		Total	7	0.15491309			
	ASHTG1	Site	3	0.06191069	0.02063690	2.65	0.2221
		H	1	0.00342305	0.00342305	0.44	0.5546
		Error	3	0.02334264	0.00778088		
		Total	7	0.08867638			
	ASDIG1	Site	3	0.05794354	0.01931451	6.23	0.0836
		H	1	0.00009561	0.00009561	0.03	0.8718
		Error	3	0.00930304	0.00310101		
		Total	7	0.06734220			
	AVOG1	Site	3	0.20424295	0.06808098	6.79	0.0750
		H	1	0.00711290	0.00711290	0.71	0.4614
		Error	3	0.03006841	0.01002280		
		Total	7	0.24142426			

Species	Variable	SV	DF	SS	MS	F-value	Pr> F
<i>P. engelmannii</i>	ASHTG2	Site	3	0.03665337	0.01221779	0.65	0.6350
		H	1	0.00061734	0.00061734	0.03	0.8680
		Error	3	0.05658507	0.01886169		
		Total	7	0.09385578			
	ASDIG2	Site	3	0.04168697	0.01389566	5.60	0.0955
		H	1	0.00008880	0.00008880	0.04	0.8621
		Error	3	0.00744963	0.00248321		
		Total	7	0.04922540			
	AVOG2	Site	3	0.43148696	0.14382899	9.13	0.0511
		H	1	0.00691907	0.00691907	0.44	0.5549
		Error	3	0.04725445	0.01575148		
		Total	7	0.48566048			

Species	Variable	SV	D F	SS	MS	F- value	Pr> F
<i>P. engelmannii</i>	PDWSP98	Site	1	0.00008261	0.00008261	0.02	0.9197
		H	1	0.00132363	0.00132363	0.26	0.7011
		Error	1	0.00514212	0.00514212		
		Total	3	0.00654835			
	MDWSP98	Site	1	0.00138150	0.00138150	0.14	0.7742
		H	1	0.00157693	0.00157693	0.16	0.7602
		Error	1	0.01007518	0.01007518		
		Total	3	0.01303361			
	MOSTSP98	Site	1	0.00016604	0.00016604	31.99	0.1114
		H	1	0.00000795	0.00000795	1.53	0.4327
		Error	1	0.00000519	0.00000519		
		Total	3	0.00017917			
MDSTSP98	Site	1	0.00003311	0.00003311	1.04	0.4944	
	H	1	0.00001064	0.00001064	0.33	0.6669	
	Error	1	0.00003197	0.00003197			
	Total	3	0.00007573				
PDWPSU98	Site	1	0.00183601	0.00183601	0.80	0.5355	
	H	1	0.00190727	0.00190727	0.83	0.5295	
	Error	1	0.00229621	0.00229621			
	Total	3	0.00603949				
MDWPSU98	Site	1	0.00579204	0.00579204	0.74	0.5479	
	H	1	0.00732075	0.00732075	0.93	0.5108	
	Error	1	0.00783267	0.00783267			
	Total	3	0.02094546				

Species	Variable	SV	DF	SS	MS	F-value	Pr> F
<i>P. durangensis</i>	Survival 97	Site	3	0.08318304	0.02772768	52.63	0.0043
		H	1	0.00588441	0.00588441	11.17	0.0443
		Error	3	0.00158049	0.00052683		
		Total	7	0.09064794			
	Survival 98	Site	3	0.05386775	0.01795592	78.97	0.0024
		H	1	0.00676257	0.00676257	29.74	0.0121
		Error	3	0.00068215	0.00022738		
		Total	7	0.06131246			
	ASHTG1	Site	3	0.32118888	0.10706296	3.68	0.1567
		H	1	0.01415083	0.01415083	0.49	0.5360
		Error	3	0.08738496	0.02912832		
		Total	7	0.42272467			
	ASDIG1	Site	3	0.02190029	0.00730010	3.75	0.1532
		H	1	0.00018574	0.00018574	0.10	0.7776
		Error	3	0.00584100	0.00194700		
		Total	7	0.02792703			
	AVOG1	Site	3	0.18129192	0.06043064	2.45	0.2401
		H	1	0.00172311	0.00172311	0.07	0.8085
		Error	3	0.07386661	0.02462220		
		Total	7	0.25688164			

Species	Variable	SV	DF	SS	MS	F-value	Pr> F
<i>P. durangensis</i>	ASHTG2	Site	3	0.21789232	0.07263077	7.18	0.0698
		H	1	0.00069866	0.00069866	0.07	0.8097
		Error	3	0.03034525	0.01011508		
		Total	7	0.24893623			
	ASDIG2	Site	3	0.00711447	0.00237149	5.51	0.0974
		H	1	0.00157559	0.00157559	3.66	0.1517
		Error	3	0.00129218	0.00043073		
		Total	7	0.00998223			
	AVOG2	Site	3	0.21183123	0.07061041	4.98	0.1102
		H	1	0.01418440	0.01418440	1.00	0.3911
		Error	3	0.04257334	0.01419111		
		Total	7	0.26858897			

Species	Variable	SV	DF	SS	MS	F-value	Pr> F
<i>P. durangensis</i>	PDWSP98	Site	1	0.00526090	0.00526090	26.66	0.1218
		H	1	0.01549707	0.01549707	78.53	0.0715
		Error	1	0.00019734	0.00019734		
		Total	3	0.02095531			
	MDWSP98	Site	1	0.00362402	0.00362402	0.22	0.7206
		H	1	0.00114009	0.00114009	0.07	0.8361
		Error	1	0.01644159	0.01644159		
		Total	3	0.02120570			
	MOSTSP98	Site	1	0.00017211	0.00017211	102.1	0.0628
		H	1	0.00000194	0.00000194	1.15	0.4774
		Error	1	0.00000169	0.00000169		
		Total	3	0.00017574			
	MDSTSP98	Site	1	0.00006348	0.00006348	416.9	0.0312
		H	1	0.00002070	0.00002070	135.9	0.0545
		Error	1	0.00001350	0.00001350		
		Total	3	0.00008433			
	PDWPSU98	Site	1	0.00133105	0.00133105	0.12	0.7889
		H	1	0.00170231	0.00170231	0.15	0.7636
		Error	1	0.01122374	0.01122374		
		Total	3	0.01425709			
	MDWPSU98	Site	1	0.00526092	0.00526092	1.61	0.4250
		H	1	0.02326648	0.02326648	7.12	0.2283
		Error	1	0.00326981	0.00326981		
		Total	3	0.03179721			

Analysis of covariance for the absolute stem diameter growth (ASDIG2) of *P. arizonica* and for the absolute volume growth (AVOG2) of *P. durangensis* after the second growing season in the forested sites.

Species	Variable	SV	DF	SS	MS	F-value	Pr > F
<i>P. arizonica</i>	ASDIG2	Site	3	1.32440413	0.44146804	49.61	0.0001
		H	1	0.06260458	0.06260458	1.57	0.2176
		Site x H	3	0.03635768	0.01211923	0.30	0.8225
		Site x Plot (H)	40	1.59588291	0.03989707	4.48	0.0001
		H:D 96	1	0.03496032	0.03496032	3.93	0.0481
		H x H:D 96	1	0.07001691	0.07001691	7.87	0.0053
		Error	425	3.78205012	0.00889894		
Total	474	7.17005405					
<i>P. durangensis</i>	AVOG2	Site	3	5.07815131	1.69271710	6.80	0.0002
		H	1	1.04946560	1.04946560	1.45	0.2359
		Site x H	3	0.80553960	0.26851320	0.37	0.7747
		Site x Plot (H)	40	28.9911094	0.72477774	2.91	0.0001
		HT96	1	10.0614055	10.0614055	40.42	0.0001
		H x HT96	1	1.45969676	1.45969676	5.86	0.0160
		Error	314	78.1632204	0.24892745		
Total	363	131.342552					

Species	Variable	SV	D F	SS	MS	F-value	Pr> F
<i>P. arizonica</i>	Survival 98 0.30 cm	Site	3	0.28352254	0.09450751	17.80	0.0205
		H	1	0.00728957	0.00728957	1.37	0.3259
		Error	3	0.01592540	0.00530847		
		Total	7	0.30673752			
	Survival 98 0.40 cm	Site	3	0.26554395	0.08851464	6.07	0.0864
		H	1	0.02476633	0.02476633	1.70	0.2835
		Error	3	0.04375002	0.01458334		
		Total	7	0.33406027			
	Survival 98 0.50 cm	Site	3	0.27787068	0.09262356	6.22	0.0838
		H	1	0.02237438	0.02237438	1.50	0.3077
		Error	3	0.04466416	0.01488805		
		Total	7	0.34490922			
<i>P. engelmannii</i>	Survival 98 0.30 cm	Site	3	0.13700824	0.0446694	1.77	0.3255
		H	1	0.18633105	0.18633105	7.22	0.0746
		Error	3	0.07745888	0.02581963		
		Total	7	0.40079817			
	Survival 98 0.40 cm	Site	3	0.16447402	0.05482467	1.19	0.4437
		H	1	0.00000174	0.00000174	0.00	0.9955
		Error	3	0.13769728	0.04589909		
		Total	7	0.30217305			
	Survival 98 0.50 cm	Site	3	0.20112561	0.06704187	6.96	0.0726
		H	1	0.01244507	0.01244507	1.29	0.3382
		Error	3				
		Total	7				

Species	Variable	SV	D F	SS	MS	F-value	Pr> F
<i>P. engelmannii</i>	Survival 98 0.60 cm	Site	3	0.08353656	0.02784552	3.72	0.1544
		H	1	0.02054479	0.02054479	2.75	0.1960
		Error	3	0.02243584	0.00747861		
		Total	7	0.12651719			
<i>P. durangensis</i>	Survival 98 0.30 cm	Site	3	0.34598271	0.11532757	3.31	0.1757
		H	1	0.00487749	0.00487749	0.14	0.7330
		Error	3	0.10440535	0.03480178		
		Total	7	0.45526555			
	Survival 98 0.40 cm	Site	3	0.05313730	0.01771243	1.93	0.3011
H		1	0.04368595	0.04368595	4.77	0.1170	
Error		3	0.02750055	0.00916685			
Total		7	0.12432380				
	Survival 98 0.50 cm	Site	3	0.08297331	0.02765777	1.29	0.4199
H		1	0.00078508	0.00078508	0.04	0.8605	
Error		3	0.06439172	0.02146391			
Total		7	0.14815012				

ANOVA tables for greenhouse study.

Species	Variable	Source of Variation	NDF ¹	DDF ²	Type III	Pr > F
<i>P. arizonica</i>	RGRHT ³	Water stress	1	1	8.20	0.2138
	SHDWRF ⁴	Water stress	1	1	0.00	0.9953
	RGRDIAM ⁵	Water stress	1	1	28.64	0.1176
	RODWRF ⁶	Water stress	1	1	0.03	0.8986
	ψ (1 st cycle)	Water stress	1	1	26.33	0.1225
		Diurnal	2	4	44.46	0.0019**
		WS x D ⁷	2	4	1.68	0.2950
	g_s (1 st cycle)	Water stress	1	3	1.90	0.2615
		Diurnal	1	3	2.44	0.2166
		WS x D	1	3	0.23	0.6618
	ψ (2 nd cycle)	Water stress	1	1	12.12	0.1780
		Diurnal	2	4	37.45	0.0026**
		WS x D	2	4	3.56	0.1295
	g_s (2 nd cycle)	Water stress	1	1	59.90	0.0818
		Diurnal	2	4	140.32	0.0002**
		WS x D	2	4	404.40	0.0001**

¹ = numerator degree of freedom;

² = denominator degree of freedom;

³ = $(\ln \text{ final stem height} - \ln \text{ initial stem height})/11$;

⁴ = $[(\text{initial shoot dry mass}/\text{initial total dry mass}) + (\text{final shoot dry mass}/\text{final total dry mass})]2$;

⁵ = $(\ln \text{ final stem diameter} - \ln \text{ initial stem diameter})/11$;

⁶ = $[(\text{initial root dry mass}/\text{initial total dry mass}) + (\text{final root dry mass}/\text{final total dry mass})]2$;

⁷ = water stress-diurnal interaction;

ψ = xylem water potential;

g_s = stomatal conductance ;

** = highly significant differences $P < \alpha = 0.01$.

Species	Variable	Source of Variation	NDF	DDF	Type III	Pr > F
<i>P. engelmannii</i>	RGRHT	Water stress	1	1	0.57	0.5878
	SHDWRF	Water stress	1	1	0.14	0.7687
	RGRDIAM	Water stress	1	1	8.88	0.2061
	RODWRF	Water stress	1	1	0.21	0.7268
	ψ (1 st cycle)	Water stress	1	1	1497.17	0.0164*
		Diurnal	2	4	43.27	0.0020**
		WS x D	2	4	11.25	0.0228*
	g_s (1 st cycle)	Water stress	1	3	13.98	0.0334*
		Diurnal	1	3	2.60	0.2053
		WS x D	1	3	1.00	0.3920
	ψ (2 nd cycle)	Water stress	1	1	362.54	0.0334*
		Diurnal	2	4	15.73	0.0127*
		WS x D	2	4	2.98	0.1611
	g_s (2 nd cycle)	Water stress	1	1	36.42	0.1045
		Diurnal	2	4	19.43	0.0087**
WS x D		2	4	50.64	0.0014**	
<i>P. durangensis</i>	RGRHT	Water stress	1	1	0.88	0.5204
	SHDWRF	Water stress	1	1	0.72	0.5531
	RGRDIAM	Water stress	1	1	5538.3	0.0086**
	RODWRA	Water stress	1	1	0.72	0.5516
	ψ (1 st cycle)	Water stress	1	1	982.56	0.0203*
		Diurnal	2	4	84.58	0.0005**
		WS x D	2	4	2.67	0.1831
	g_s (1 st cycle)	Water stress	1	3	41.36	0.0076
		Diurnal	1	3	1.18	0.3561
		WS x D	1	3	1.38	0.3248
	ψ (2 nd cycle)	Water stress	1	1	164.80	0.0495*
		Diurnal	2	4	64.34	0.0009**
		WS x D	2	4	1.26	0.3770
	g_s (2 nd cycle)	Water stress	1	1	39.95	0.0999
		Diurnal	2	4	0.70	0.5494
WS x D		2	4	3.51	0.1317	

* = significant differences $P < \alpha = 0.05$. ** = highly significant differences $P < \alpha = 0.01$.

Species	Variable	Source of Variation	NDF	DDF	Type III	Pr > F	
<i>P. ponderosa</i>	RGRHT	Water stress	1	1	0.01	0.9297	
	SHDWRF	Water stress	1	1	3.78	0.3025	
	RGRDIAM	Water stress	1	1	0.00	0.9977	
	RODWRF	Water stress	1	1	3.44	0.3149	
	ψ (1 st cycle)	Water stress	Diurnal	1	1	685.86	0.0243*
			Diurnal	2	4	6.26	0.0587
			WS x D	2	4	0.86	0.4879
	g_s (1 st cycle)	Water stress	Diurnal	1	3	21.69	0.0187*
			Diurnal	1	3	0.32	0.6134
			WS x D	1	3	0.10	0.7701
	ψ (2 nd cycle)	Water stress	Diurnal	1	1	315.97	0.0358*
			Diurnal	2	4	10.54	0.0254*
			WS x D	2	4	0.66	0.5671
	g_s (2 nd cycle)	Water stress	Diurnal	1	1	190.93	0.0460*
			Diurnal	2	4	0.17	0.8521
WS x D			2	4	23.53	0.0061**	

* = significant differences $P < \alpha = 0.05$. ** = highly significant differences $P < \alpha = 0.01$.

ANOVA tables for the relationship between midday stomatal conductance and predawn water potential by species in the greenhouse study.

Species	SV ¹	DF ²	SS ³	MS ⁴	Parameters	SE ⁵
<i>P. arizonica</i>	Regression	4	121318.25338	30329.5633	$2_0 = 46.0$	13.79
	Error	35	8526.67272	243.61922	$2_1 = -0.02$	31.90
	Uncorrected	39	129844.92610		$k_1 = 0.70$	45.94
	Corrected	38	16760.46444		$k_2 = 15.0$	0.2742
<i>P. engelmannii</i>	Regression	4	109270.00856	27317.5021	$2_0 = 79.99$	1.4148
	Error	33	4605.29794	139.55448	$2_1 = -0.0804$	3.1617
	Uncorrected	37	113875.30650		$k_1 = 0.5996$	4.6553
	Corrected	36	29063.54697		$k_2 = 13.99$	0.2145
<i>P. durangensis</i>	Regression	4	85615.277062	21403.8192	$2_0 = 60.12$	1.6505
	Error	33	10064.377538	304.981138	$2_1 = -0.1123$	4.7064
	Uncorrected	37	95679.654600		$k_1 = 0.6766$	6.3787
	Corrected	36	29345.576503		$k_2 = 11.73$	0.2570
<i>P. ponderosa</i>	Regression	4	106781.83025	26695.4575	$2_0 = 61.0$	1.8564
	Error	32	7918.16975	247.44280	$2_1 = -0.12$	9.5179
	Uncorrected	36	114700.00000		$k_1 = 1.10$	7.9262
	Corrected	35	37230.55556		$k_2 = 13.0$	0.1595

1 = source of variation; 2 = degrees of freedom; 3 = sum of squares; 4 = mean square; 5 = standard error.