2005

Revegetating Blackwoods Campground, Acadia National Park: Emphasis on Natural Regeneration of Red Spruce and Balsam Fir

Cristin O'Brien

REVEGETATING BLACKWOODS CAMPGROUND, ACADIA NATIONAL PARK: EMPHASIS ON NATURAL REGENERATION OF RED SPRUCE AND BALSAM FIR

By

Cristin L. O'Brien

B.A. University of Maine, 2000

B.S. Univeristy of Maine, 2000

A THESIS

Submitted in Partial Fulfillment of the

Requirements for the Degree of

Master of Science

(in Horticulture)

The Graduate School

The University of Maine

August, 2005

Advisory Committee:

Reeser C. Manley, Assistant Professor of Horticulture, Advisor

Michael S. Greenwood, Ruth Hutchins Professor of Tree Physiology

Ivan J. Fernandez, Professor of Plant, Soil & Environmental Sciences

REVEGETATING BLACKWOODS CAMPGROUND, ACADIA NATIONAL PARK: EMPHASIS ON NATURAL REGENERATION OF RED SPRUCE AND BALSAM FIR

By Cristin L. O'Brien

Thesis Advisor: Dr. Reeser C. Manley

An Abstract of the Thesis Presented
in Partial Fulfillment of the Requirements for the
Degree of Master of Science
(in Horticulture)
August, 2005

Blackwoods Campground in Acadia National Park has a declining vegetative understory, characterized by a lack of tree seedling recruitment and shrub populations. This project was embarked upon to identify limiting factors to tree seedling establishment and shrub survival. From these studies, management plans will be developed for revegetating the campground understory.

To better understand the factors that inhibit successful seedling establishment, we investigated the effects of varying soil moisture levels on seed germination, seedling survival and seedling dry mass accumulation for red spruce and balsam fir. We also studied the effect of organic layer depth on seedling growth for both species.

Our experimental results and observations indicate that a tree seedling population in the understory of Blackwoods Campground is attainable with natural seed inputs and current light levels, but that additional watering is required. Red spruce and balsam fir seed germination significantly decreased below a threshold of 25% soil moisture (based

ACKNOWLEDGMENTS

I am grateful to my committee - Reeser Manley, Mike Greenwood and Ivan Fernandez - for their continual support, guidance, and advice that have been essential in the completion of this thesis. My fellow graduate students, faculty and staff members have also been invaluable in helping make this process successful. I wish to thank the National Park Service and the Department of Plant, Soil and Environmental Sciences for their funding and research support. And a special thank-you to Dad, Mom, my brother Sean, and all my wonderful friends for inspiration, patience, and emotional reinforcement.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

Chapter One: *Abies balsamea* and *Picea rubens* Seed Germination and Seedling Growth as Affected by Six Watering Treatments and Depth of the Organic Horizon

1. Introduction

Blackwoods Campground in Acadia National Park is on the eastern coastline of Mount Desert Island (MDI), Maine. The campground contains 314 campsites and sees roughly 100,000 visitors per year (Visitor Use Statistics, Acadia National Park, 2002). Soils are described as frigid Typic and Lithic Haplorthods, frigid Lithic Udorthents, and frigid Aeric Haplaquods. The major soil series are a Lyman-Tunbridge complex, 0 to 15 percent slope, very stony; a Naskeag-Schoodic complex, 0 to 8 percent slope, very stony; and a Hermon-Colton outcrop complex, 3 to 15 percent slope, very stony (Jordan 1998). Rock outcroppings are common throughout the campground. Mineral soil is derived from glacial till, mostly of granitic minerology, and the overlaying organic horizon ranges in thickness from less than one centimeter to more than 30cm.

Picea rubens Sarg. (Red Spruce), *Picea glauca* (Moench) Voss (White Spruce) and *Abies balsamea* (L.) Mill. (Balsam Fir) dominate the overstory, interspersed with several other coniferous species, including *Picea mariana* (Mill.) BSP (Black Spruce) *Pinus strobus* L. (White Pine), *Tsuga canadensis* (L.) Carr. (Canadian Hemlock) and *Thuja occidentalis* L. (Eastern White Cedar) and deciduous hardwoods such as *Acer rubrum* L. (Red Maple), *Acer pensylvanicum* L. (Striped Maple), *Betula papyrifera* Marsh. (Paper Birch), *Betula alleghaniensis* Britt. (Yellow Birch) and *Fraxinus nigra* Marsh. (Black Ash). While the overstory is well developed (this area was not affected by the fire of 1947 that burned much of Bar Harbor and MDI), there is a distinct lack of understory vegetation in areas between most campsites, both of tree seedlings and of shrub species.

Based on literature research and initial observations at the site, five main hypotheses were developed to help explain the lack of forest understory: 1) lack of viable seed input, 2) trampling of seedlings and small shrubs by campers, 3) smothering of seedlings by fresh leaf litter, 4) thick organic horizons which prevent root penetration, and 5) lack of adequate moisture.

The first important factor to forest regeneration is seed input from mature canopy trees. Hundreds of newly sprouted spruce and fir seedlings, as well as birch, maple and ash were observed every spring throughout the campground. While we did not count cone crops or collect seed rain for analysis, our observations of seedlings every spring suggest that seed input from reproducing canopy trees is not the most limiting factor inhibiting regeneration.

Trampling of vegetation has detrimental effects on plant growth and survival, and hinders restoration projects (Sauer 1998; Matthes et al. 2003). Coniferous seedlings are tiny with thin needles, difficult to distinguish above the coniferous litter, twigs and cones on the soil surface, and are therefore easily overlooked and stepped on. This effect of trampling was explored within the campground by caging five, $1m^2$ areas and leaving equivalent reference plots uncaged (See Appendix A). Large seedling mortality in both caged and un-caged plots suggests that while trampling is known to inhibit seedling regeneration, it is not most limiting factor within Blackwoods, leading us to look more closely at other hypotheses.

Undecomposed leaf litter adversely affects seedling survival by blocking light, preventing root penetration, and limiting water availability (Moore 1926; Koroleff 1954; Walsh and Voigt 1977; Schimpf and Danz 1999; Simard et al. 2003). The campground is a mixed deciduous/ coniferous stand and the type of leaf litter varies throughout the site. Advanced regeneration appears to be independent of litter type - first year seedlings have been observed in the litter of all stand types, but very few seedlings persist.

The thickness of the organic layer may affect *Picea rubens* and *Abies balsamea* seedling survival (Klein et al. 1991). Early growth of roots through the organic soil and into mineral soil is important for successful establishment to withstand summer drought (Place 1955) and for survival in successive years (Burdett et al. 1983). Intact organic horizons, 2cm thick, significantly reduced first and second year seedling survival of *Abies balsamea* compared to the same forest settings with the organic layer removed (Cornett et al. 1998). This decline in survival may be explained by a decreased ability of balsam fir roots to penetrate needle litter compared with mineral soils. Moore (1926), found seedling root penetration hindered by the tough, elastic nature of humus, and he observed that radicle penetration became more difficult as the soil dried. This suggests an interaction between moisture content and the ability of seedling roots to penetrate organic soils.

Water is of primary importance to seed germination for imbibition and continued growth. Fully imbibed balsam fir and red spruce seeds lose water slowly in dry soils, but when evaporative losses do occur, the seeds are able to re-imbibe and germinate when water is again available (Baldwin 1934; Thomas and Wein 1985). The ability to withstand water loss and remain viable is critical for seeds of northeastern forests attempting to germinate in surface organic soils because most species do not maintain a presence in the seedbank beyond one year (Baldwin 1934; Houle 1992; Farmer 1997). In his site descriptions of Mount Desert Island, Moore noted that: "[The organic] upper surface dries out rapidly after a rain. Water either runs off as from a thatch roof, or goes straight down through." (Moore 1926, p. 197). Many researchers have attributed high conifer seedling mortality to drought, both from desiccation and root inhibition caused by toughening of the organic soil as it dries (Moore 1926; Baldwin 1934; Place 1955; Walsh and Voigt 1977; Royo et al. 2001; Lee et al. 2004). Thus, thick organic horizons may be inhibitory to seed germination and growth because of low water availability and retention, which will also contribute to the inability of seedling roots to penetrate the soil surface.

Organic horizons are generally acidic because decomposing litter releases organic acids (Williams and Gray 1974), but a hypothesis on pH effects was not considered because organic soil samples from Blackwoods Campground consistently measured pH 3.7 or 3.8, and mineral soils averaged pH 5.5. These measurements fall within suiTable ranges and indicate that pH is not a limiting factor to seed germination or continued growth of spruce and fir (Baldwin 1934; McIntosh and Hurley 1964; Abouguendia and Redmann 1979; Scherbatskoy et al. 1987).

The objectives of our experiments were to assess the effects of water availability in organic soils on seed germination and seedling development of *Picea rubens* and *Abies balsamea*, and to investigate effects of depth of the organic layer, independent of moisture stress, on seedling growth.

2. Methods and Materials

2.1 Effects of soil moisture on germination of *Abies balsamea* and *Picea rubens* under controlled light and temperature

2.1.1 Experimental Design

We used a Generalized Randomized Complete Block Design (GRBD), with two species (*Abies balsamea* and *Picea rubens*), 6 watering treatments (80%, 70%, 60%, 50%, 40%, and 30% of field capacity), and two blocks (separate growth chambers) with two replicates per chamber, equaling 12 experimental units per replication (6 of each species), 24 units per chamber, and 48 units total. We determined seed viability using four replicates of 100 seeds of each species on moist germination cloth.

2.1.2 Seed

We purchased seed from F. W. Schumacher Co., Inc. (Sandwich, MA) in the winter of 2001-02. *A. balsamea* was of Lake States provenance, *P. rubens* was of Nova Scotia, Halifax County provenance. *A. balsamea* seed was soaked in distilled water for 24 hours, wrapped in cheesecloth and moist sphagnum moss and stratified at 4°C from April 6, 2002 to June 19, 2002 (stratification treatment suggested by Dirr and Heuser, 1987). *P. rubens* does not require stratification (Farmer 1997) and seed was kept cool and dry until the sowing date. When removed from stratification, the medium containing the *A. balsamea* seed had developed a thick, white mold. To remove unfilled seeds, all seeds were placed in water after stratification, and floating seeds were skimmed off and discarded (approximately 40-50% of the seed was discarded in this manner). Viability trial germination means were 79.5% and 67.3 % for *P. rubens* and *A. balsamea*, respectively.

2.1.3 Growing Medium and Containers

Seeds were sown in black, 13.5 cm square thermoformed pots, 6.5 cm deep (TLC Polyform, Inc.). The growing medium was organic horizon material dug from under a spruce/fir canopy within Loop A of Blackwoods Campground. The top 10 cm were removed and sieved through a 5mm wire mesh screen and homogenized. Five sub-samples were taken at the beginning of the experiment and analyzed by the Maine Soil Testing Service at the University of Maine, Orono for pH, N, C and C/N ratio, as well as several macro and micro nutrient concentrations (Table 1). After sieving, the soil was fluffy with a fibrous texture, many coniferous needles still distinguishable from more decomposed matter.

All pots were filled with approximately 900 cm^3 of moist soil and lightly packed by hand. They were placed in deep pans and watered from above, then soaked in the pans of water for ten minutes to saturate the medium. Pots were removed from the pans, placed on a wire rack, and allowed to drain for one hour. They were then randomly assigned to block, species and treatment levels, labeled, and weighed while saturated. These weight measurements were used as pot weight at saturation values, and watering treatments were calculated based on percentages of these values. The total water-retention capacity of this soil was 400% of its dry weight.

Seeds were sown June 20, 2002. A grid of 25, 8-penny nails driven into a block of pine was used as a template for seed placement by gently pressing the nail heads onto the

						Exchangeables (cmol/kg, aka millequivalents/100g)							Extractable (mg/kg, or ppm)			
Soil	**pHw**	**%LOI**	**N**	**C**	**C/N**	**Ca**	**K**	**Mg**	**Na**	**Ac.**	**Base**	**CEC**	**P**	**Al**	**Fe**	**Mn**
Organic	3.7	89.5	1.14	49	42.98	10.45	2.45	6.38	1.19	11	64.78	31.9	103	80	37	220
Mineral	5.5	1.1	0.034	0.61	17.94	0.304	0.036	0.099	0.034	0.4	52.56	0.9	2.6	39	8.5	4.7
Acceptable Range	4.3-4.5	10.0-12.0	0.27-0.31	3.5-3.7	12-13	0.83-1.09	0.04-0.07	0.11-0.19	0.043-0.06				3.0-6.0	208-275	23-35	6.6-9.0

Table 1. Soil was removed from Blackwoods Campground, sieved, and four samples were taken of each soil type to be analyzed at the Maine Soil Testing Service, University of Maine, Orono. Results presented are all four samples pooled.

Model	Photoperiod	Day Temp.	Night Temp.	PAR	RH	RH Range
E-54B (Chamber 1)	16 Hour	23.7 - 24.7°C	17.2 – 17.7°C	62-68 μmol $m^{-2}s^{-1}$	99.7%	80-110%
MB-60B (Chamber 2)	16 Hour	23.6 - 23.8°C	12.1 – 12.4°C	128-138 μmol $m^{-2}s^{-1}$	88.8%	70-100%

Table 2. Environmental conditions recorded in two growth chambers manufactured by Percival Scientific, Inc. (Boone, Iowa). Data was recorded by a CR10X data logger (Campbell Scientific, Inc. Logan, Utah) from seed sowing on June 20, 2002 to seedling harvest on October 2, 2002. Temperature, PAR and RH values are averages

soil surface to create indentations (no deeper than 5mm). Seeds of the assigned species were placed into each well, but were not covered or driven into the soil. After germinating, many seeds had difficulty piercing the soil surface. We created a small hole with a toothpick and encouraged the radicle to grow down into it.

2.1.4 Watering Treatments

Pots were watered when they reached within ±5 % of target treatment levels, approximately 80%, 70%, 60%, 50%, 40%, or 30% of their weight at saturation (Table 3). After sowing, all pots were bottom watered and misted on top with an atomizer – this minimized seed movement and facilitated germination counts. Each pot was weighed individually and assessed daily.

Target watering treatment	*Actual range of percent pot weights at re-watering*	*Approximate soil moisture level corresponding to target treatment*
80 %	75 - 84	75 %
70 %	68 - 73	63 %
60 %	58 - 64	50 %
50 %	46 - 53	38 %
40 %	40 - 46	25 %
30 %	33 - 34	13 %

Table 3. Target treatment levels were percentages of saturated pot weight. The range of actual pot weights at re-watering are for the growth chamber study only. Approximate soil moisture values were calculated based on eight replicate soil samples that were weighed at saturation and again after oven drying. They showed consistently that 20% of the weight at saturation was soil, and 80% was water (±1%).

2.1.5 Growth Chambers

Two growth chambers (Percival Scientific, Inc.,Boone, Iowa, Models E-54B and MB-60B) were considered blocks to help control for environmental differences that exhistesd between them. Both chambers were set with a 16-hour photo period, 25°C days and 15°C nights, close to optimal germination conditions for both species (Greenwood 2004, unpublished data). Hourly temperature and light intensity values, as well as relative humidity were measured and recorded by a CR10X data logger (Campbell Scientific, Inc. Logan, Utah; Table 2).

2.1.6 Data Collection

The experiment was concluded after 15 weeks (October 2) when the seedlings were harvested for weighing. Data collected included daily germination, daily weight of each pot and watering frequency, seedling dry weights at the conclusion of the experiment, and root: shoot ratios of dry mass. Germinated seeds were marked with colored toothpicks to prevent duplication of counts. We used daily counts of germination to calculate the number of days it took for each seed to germinate (from the sowing date). We attempted to measure actual water stress of the seedlings with a pressure bomb and found the young stems to be too fragile for the process.

2.1.7 Campground Soil Collection

Soil samples from two campsites within Loop A were collected to determine campground soil moisture levels for comparison with the levels used in our experiments.

Soil was collected on five dates between July 28 and September 8, 2003, the typical period of late summer drought. A trowel was used to excavate three clods from each site, approximately 5-7cm deep and 5-7cm across, as intact as possible. The samples were immediately placed into individual, sealable plastic bags and labeled. All samples were then placed into another plastic bag, which was also sealed, to preserve moisture content during transport back to the lab. The bags of soil were weighed on an analytical balance prior to being opened, then the soil was removed and placed into a paper bag (also pre-weighed) for drying, and the empty plastic bags were re-weighed. All paper bags of soil were placed into the oven for drying at 40°C until they reached a constant weight. By subtracting bag weights from total weights, we calculated the weight of soil and the weight of water in the soil at collection.

Dry soil sample weights were used to calculate soil weight at field capacity (based on replicate sampling revealing that pots of organic soil at field capacity dried to 20% of their original weight, thus water comprised 80% of total weight). The weight of soil samples at the time of collection was divided by the estimated weights at field capacity to calculate the percent saturation of the samples. These values ranged between 10 and 49% soil moisture (Table 4).

Date Sample Collected	**Site #**	**Range of Estimated % Soil Moisture**	**Estimated % Soil Moisture**
July 28, 2003	123 160	18 – 34% 10 – 13%	23% 11%
August 4, 2003	123 160	19 – 31% 24 – 19%	19% 15%
August 11, 2003	123 160	21 – 49% 21 – 54%	36% 31%
August 25, 2003	123 160	13 – 16% 10 – 15%	14% 13%
September 8, 2003	123 160	15 – 21% 11 –26%	18% 16%

Table 4. Soil Samples were collected from Blackwoods Campground and analyzed for moisture content by weighing before and after oven drying. An estimate of percent soil moisture was calculated to compare with drought levels used in our experiments.

2.2 Effects of soil moisture on germination of *Abies balsamea* grown outdoors with natural moisture withheld

2.2.1 Experimental Design

The growth chambers were unavailable for a repetition of the previous experiment, so we conducted a second experiment outside using ambient temperature, light and humidity conditions, and we tested lower water levels than in the chambers. We were going to use a Completely Randomized Design (CRD) with both *P. rubens* and *A. balsamea*, but two weeks after sowing the *P. rubens* seed began to disappear in large numbers. The cause of this disappearance may have been wind, the method of watering, or predation (though there were no visible signs of bird or rodent damage). Thus, the experiment was reduced to a CRD using only *A. balsamea* seed at 5 treatment levels, with four replicates of each watering level (20 experimental units in all). Experimental units were checked for germination and pot weight daily.

2.2.2 Seed

A. balsamea (Lake State Provenance, F. W. Schumacher Co., Inc.) was soaked for 24 hours in distilled water with 20% hydrogen peroxide wash to reduce mold growth, wrapped in moist cheese cloth, and stratified at 4°C from March 5th to June 18th. Seed was sown on June 19, 2003 (see 2.1.3 for description of medium and containers). Viability trials of the seed were conducted in the lab using moist filter paper in Petri dishes. Five replicates of 25 seeds were sown and germination means were 59 and 78% for *P. rubens* and *A. balsamea*, respectively.

2.2.3 Watering Treatments

These were similar to the growth chamber experiment, but with target treatment values assigned at 60%, 50%, 40%, 30%, and 20% of pot weight at saturation (Table 5). Lower values were selected to try to distinguish at what level seed germination and seedling survival become severely limited. Eight extra pots with soil were prepared, saturated with water, drained, and weighed. They were then transferred to an oven at 60ºC until a constant weight was reached. The difference between pot weight at saturation and pot weight after oven drying is the amount of water the soil was able to hold. Dividing this by the remaining weight of the soil we calculated that water comprised 80% of the weight at pot saturation. Thus, the 20% treatment is nearly equivalent to oven dry soil.

Target watering treatment	*Approximate soil moisture% of target trt.*	*Range of % pot weights at re-watering*
60 %	50	63 – 53
50 %	38	52 – 42
40 %	25	42 – 38
30 %	13	35 – 30
20 %	0	23 - 20

Table 5. Target treatment levels were percentages of saturated pot weight. Approximate soil moisture values were calculated based on eight replicate soil samples that were weighed at saturation and again after oven drying. They showed consistently that 20% of the weight at saturation was soil, and 80% was water (±1%). Percent of pot weight at re-watering had greater ranges for this outdoor experiment than within the growth chambers because of faster drying times and difficulty predicting water losses between measurements.

2.2.4 Shade House

A shade house was constructed using four, eight-foot segments of 4" x 4" pressure treated pine set two feet into the ground, and supporting a square grid of 2x4's set at 18" intervals covered with a canopy of blue fiberglass. The canopy was built to extend beyond experimental units and exclude natural rainfall, and pots were placed on plywood raised above ground level with bricks to prevent water seepage. PAR values beneath the canopy during June on a cloudless day from noon to 1pm ranged between 420 and 541 μmol $m^{-2}s^{-1}$, with a mean of 492 (approximately 25% of full sunlight).

2.2.5 Data Collection

The experiment was concluded on September 9, 2003 when all living seedlings were carefully removed from the soil, washed and placed into envelopes (all seedlings for each experimental unit were pooled). Seedling roots and shoots were oven dried to a constant weight at 40°C. Data collected include daily germination, daily weight of each pot and watering frequency, seedling dry weights at the conclusion of the experiment, and root: shoot ratios of dry mass. Germinated seeds were marked with colored toothpicks to prevent duplication of counts.

2.3 Effects of soil moisture on seedling survival

2.3.1 Experimental Design

A 2x2x3 factorial design was used, with two species, two age groups, and three watering treatments, replicated six times, totaling 72 total experimental units.

2.3.2 Plant Material and Soil

A. balsamea and *P. rubens* germinated seeds from the viability trial (section 2.2.2) were planted into Ray Leach Superstubby Cells (Hummert International, Earth City, MO), 18 of each species. The tubes were 3.5 cm in diameter and 13.5cm deep (118cm^3), filled with sieved organic soil as described above. A second batch of seed was germinated and planted to create seedling groups of two ages, one month apart. On September 11, 2003 the first batch was two months old and the second batch was one month old, and they were moved into the greenhouse under high pressure sodium lamps (Ballast S51, 400 Watts, 1.7 amps, Sylvania LU400 bulbs, General Electric) set to a 14 - hour photo period. Average daily temperatures ranged from 16°C to 27°C.

2.3.3 Watering Treatments

Initially, tubes were re-watered when they reached the target treatment levels of 60, 40 and 30% of saturated tube weight. After 40 days there were no visible treatment differences, and only three seedlings had died. A new approach was adopted and all experimental units were thoroughly soaked overnight on November 19, 2003. Tubes were not re-watered again until December 12, 2003 when the older *P. rubens* seedlings showed signs of severe water stress. All tubes were re-saturated with water to determine if the stressed seedlings were beyond recovery. Daily weights were still collected and needle appearance described. The tubes were not watered again and units were observed until January 16, 2003, at which time all seedlings were dead.

2.4 Effects of soil organic horizon depth on *Abies balsamea* and *Picea rubens* seedling development

2.4.1 Experimental Design

A 2x7 factorial design was used, with two species and 7 organic horizon depths, replicated three times, totaling 42 experimental units.

2.4.2 Plant Material

Germinated seeds from viability trials (see 2.1) were planted in organic soil from the campground and kept in a growth chamber with a 16-hour photoperiod, 24°C days and 12°C nights for one month before being transplanted into PVC pipes in August 2002 (see 2.4.4). Four seedlings of a single species were carefully transplanted into each pipe and watered immediately. The pipes were left outside under a shade cloth (with an average of 638 μmol $m^{-2}s^{-1}$, ~33% of full sunlight) for the remainder of the growing season and through early December. The experiment was checked daily and each pipe was watered with approximately 450 mL of water when the top 3cm felt dry to the touch.

On December 10^{th}, 2002, all pipes were moved inside a Quonset greenhouse at 4°C to prevent freezing death during cold winter months above ground. They were returned to the shade house in April of 2003 and maintained the same as the pervious summer, through December 15, 2003 at which time they were thawed in the greenhouse and seedlings harvested.

2.4.3 Soil

The mineral soil for this experiment was excavated from Blackwoods Campground behind campsite 7. Patches of sod were peeled back, revealing coarse mineral soil that was sieved through a 5mm wire mesh screen to remove rocks and homogenize the soil. Five sub-samples of this homogenized soil were collected, and analyzed by the Maine Soil Testing Service at the University of Maine, Orono for pH, N, C and C/N ratio, as well as several macro and micro nutrient concentrations (Table 1). The organic soil was obtained in the same manner as described for the experiment in 2.1.3.

2.4.4 Containers and Supporting Manifold

Containers were made from 4" diameter PVC pipe with end caps. The pipes were cut into two-foot lengths, then all segments were cut in half length-wise; five drainage holes were drilled into each end cap. Each 2' segment of pipe, now cut in half, was fitted with an end cap and duct-taped together along the seams on the sides and around the bottom. Next, 10cm of perlite was added in the bottom for drainage. Mineral soil was poured into each pipe to a pre-drawn line, and organic soil was placed on top (and gently packed down) to equal organic soil depths of 0, 5, 10, 15, 20, 25, and 30cm. A lip of 5cm was left above soil surfaces to allow for watering.

The supporting manifold was made of 1"x 2" spruce strapping cut into 3' and 4' segments, notched, and pieced together to produce a grid of 5 1/2" squares (6 squares x 8 squares) to accommodate 48 PVC pipe containers. Legs 1.5' high were added at the corners and the entire structure was screwed together with sheet rock screws.

2.4.5 Seedling Harvest

The pipes were left outside until December 15, 2003 when they were brought into the greenhouse and allowed to thaw for one week at approximately 20°C. Harvest began on December 22, 2003 and was completed December 30, 2003. The end caps and one strip of duct tape was removed, then the two halves of each pipe were hinged open. Seedling roots were carefully removed from the soil, rinsed, measured primary root length, and divided into roots and shoots. Seedling roots and shoots from each experimental unit were pooled, placed into two envelopes, and oven dried at 70°C for two weeks until no further loss of weight was detected when weighed (Sartorius Analytical Balance, Model A1205).

2.5 Statistical Analyses

All experiments were all analyzed with analysis of variance (ANOVA) using SAS 9.0 (SAS Institute Inc. 2002). Data transformations were made when necessary and noted in the results. Treatments were considered significant when the Pr value fell below 0.05 ($\alpha = 0.05$), and treatment differences were determined using Tukey's pair-wise comparisons. ANOVA tables are presented in Appendix B.

3. Results

3.1. Effects of soil moisture on seed germination and early growth

3.1.1 Comparative effects of moisture on seed germination of *Abies balsamea* and *Picea rubens* grown in a controlled environment

There was a significant species difference (Pr>F .0305) between *Picea rubens* (red Spruce, RS) and *Abies balsamea* (Balsam Fir, BF) seed germination, with RS averaging 73% and BF averaging 66% germination (the viability trial averages were 80 and 67%, respectively). There was also a significant effect of moisture treatment (Pr>F

.0029). Tukey's pair-wise comparisons of treatment levels across both species suggest a decreasing trend in germination as moisture levels decreased. The driest treatment was significantly different from the others (Figure 1), and may indicate a soil moisture level between treatments 5 and 6 (25% - 13% soil moisture content) to be the minimum threshold required for good germination of both species.

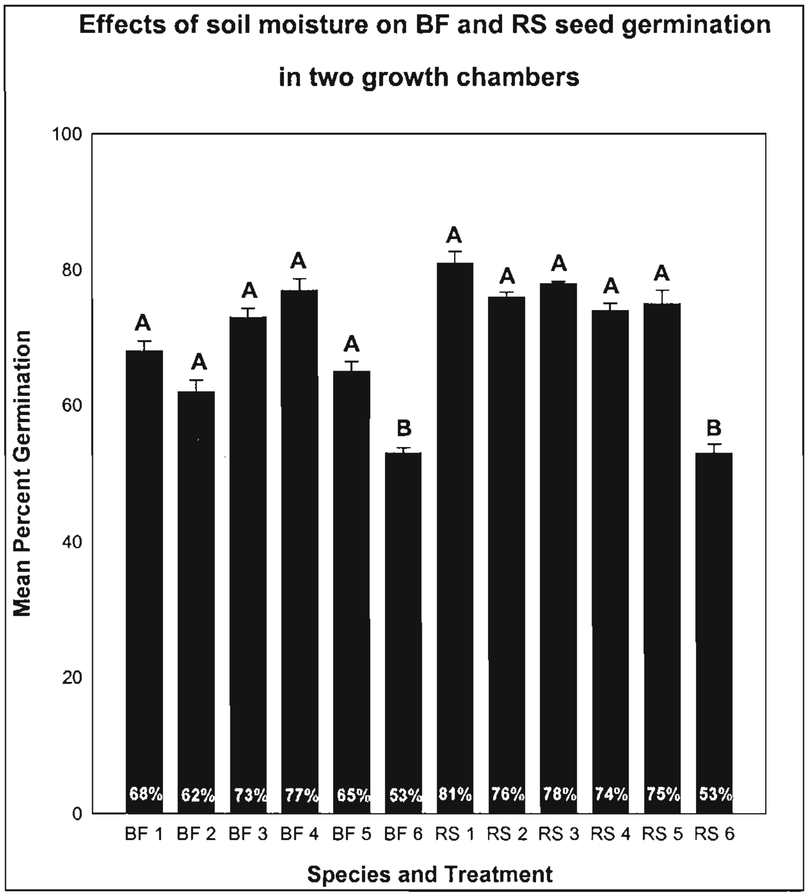

Figure 1. Seed germination for BF and RS under six watering treatments in a controlled environment. Different letters indicate statistically significant treatment differences. Treatment numbers correspond to percent soil moisture as follows: 1 = 75%, 2 = 63%, 3 = 50%, 4 = 38%, 5 = 25%, 6 = 13%.

Rate of germination was evaluated based on the number of days it took for each seed to germinate (this excluded seeds that did not germinate). We found a significant species difference in germination rate, and also significant treatment differences (Pr>F

0.0013 and Pr>F 0.0012, respectively - see Table 6). Tukey's comparisons placed the two driest soil moisture treatments (13% and 25%) in separate categories and grouped the four other treatments together. We observed that seeds in the driest treatments germinated in a distinct pattern of 2-3 days immediately after they were watered (Figure 2). This observation agrees with the findings of Thomas and Wein (1985) that the seeds of these two species are able to withstand drought and germinate once water is again available.

	Species	
Soil Moisture	*BF*	*RS*
75%	12.24 ± 0.92 a	4.00 ± 0.94 a
63%	11.61 ± 0.84 a	3.56 ± 0.84 a
50%	10.86 ± 0.66 a	4.53 ± 0.82 a
38%	10.80 ± 0.62 a	2.75 ± 0.73 a
25%	13.10 ± 1.15 b	6.97 ± 1.20 b
13%	17.48 ± 1.45 c	9.83 ± 1.40 c

Table 6. Mean number of days to germination ± SE for BF and RS seeds under 6 watering treatments. Means with different letters indicate significant treatment effects (Pr>F 0.0012). There was also a significant species difference (Pr>F 0.0013).

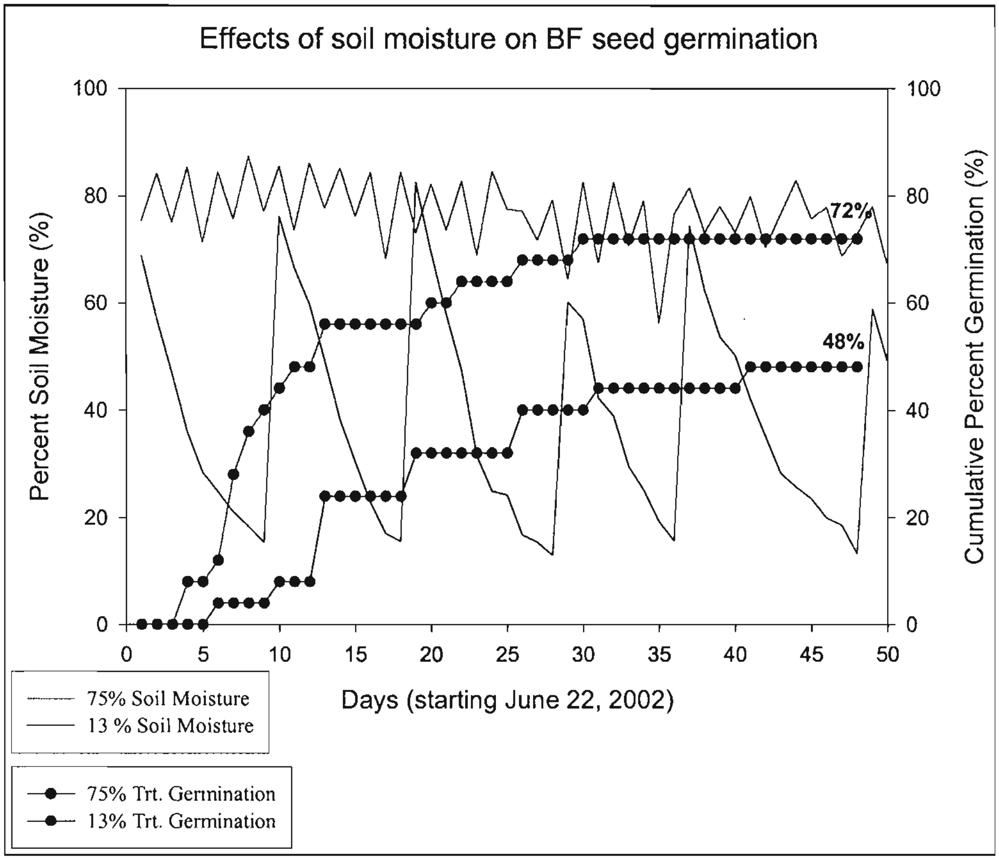

Figure 2. For both species there appeared to be a step-wise pattern to seed germination in the driest treatment. Shown here are two examples of BF (individual pots from the wettest and driest treatments, 75% and 12.5% soil moisture, respectively). For lines representing percent soil moisture, increases in soil moisture correspond to watering events. It can be seen that for the 13% soil moisture treatment, seeds germinated in flushes only several days after being watered.

3.1.2 Effects of soil moisture on BF seed germination grown outdoors

When grown outdoors in the same containers and soil type as within the growth chamber, but with ambient temperature, humidity, wind, and approximately 33% of full sunlight (based on average readings of 638 μmol $m^{-2}s^{-1}$ and the assumption full sunlight is 2000 μmol $m^{-2}s^{-1}$), the effects of water stress are enhanced. It should be noted that we added a drier treatment, nearly equivalent to oven-dry weight. Treatment differences were highly significant (Pr>F 0.0001): Tukey's test revealed 60% trt (80% germ) > 50% trt (59% germ) > 40% trt (37% germ) > 30 & 20% trt (4% & 7%, respectively) (Figure

3). Germination in the driest treatment only occurred immediately after a watering followed by a cloudy, cool, and humid week. Without the cool, cloudy weather to preserve the soil's surface moisture, these seeds would not have germinated.

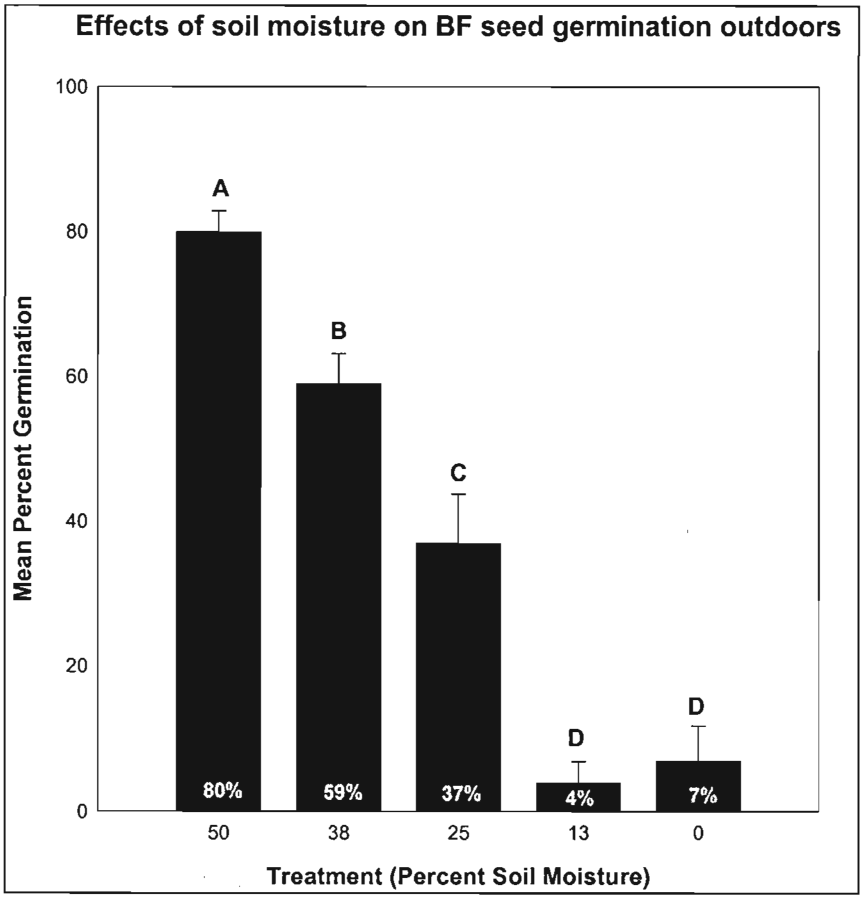

Figure 3. Seed germination for BF under 5 watering treatments, grown outdoors. Treatments with different letters represent statistically significant differences by Tukey's pair-wise comparisons. Each bar represents four replicates pooled.

3.2 Seedling Growth (Dry Mass Accumulation)

<u>3.2.1 Comparative effects of moisture on seedling dry mass of BF and RS grown in a controlled environment (using Weighted Least Squares because of unequal variance)</u>

There is a significant effect of watering on dry weight of seedlings (Pr > F 0.0409 - using block*trt as the error term) and a highly significant block effect (Pr>F 0.0001). The block effect is suspected to come from light differences between the two growth chambers (PAR values for the smaller chamber [block 1] averaged 62-68 μmol $m^{-2}s^{-1}$ and the larger chamber [block 2] averaged 128 to 138 μmol $m^{-2}s^{-1}$, see Table 2). In addition, there were highly significant block*species (Pr>F 0.0001) and block*trt (Pr>F 0.0001) interaction effects.

BF seedlings produced significantly more dry mass accumulation in the brighter chamber (Table 7). RS seedlings were more variable in their response to the different light conditions and were not discernibly different between the two chambers. The interactions show that BF seedlings respond to an increase in low light levels (3% to 7% of full sunlight) more efficiently than RS, and that both species have differing growth responses to the watering treatments along the gradient tested.

There was no overall statistical difference in dry mass accumulation between species found using the block*species MSE as the error term, though the data indicate a clear distinction (Table 7). When treatment levels were removed from the model to examine only block and species effects, the analysis does show highly significant species variation (Pr > F 0.0001). The small replication within treatments and prominent block effect that resulted in a block*species interaction (most outstanding for BF) may be masking statistical variation between the species when treatments are included in the model (Figure 4).

Treatment	*Growth Chamber 1*		*Growth Chamber 2*	
(Soil Moisture)	*BF*	*RS*	*BF*	*RS*
75%	270 ± 40	180 ± 7	400 ± 30	210 ± 10
63%	260 ± 30	230 ± 3	360 ± 20	150 ± 10
50%	200 ± 10	190 ± 30	340 ± 10	190 ± 20
38%	270 ± 20	180 ± 10	360 ± 20	170 ± 10
25%	230 ± 60	200 ± 40	390 ± 10	170 ± 10
13%	210 ± 1	160 ± 3	290 ± 3	100 ± 5

Table 7. Mean dry weights (mg) ± SE of 15-week old BF and RS seedlings, grown under 6 watering treatments in environmentally controlled growth chambers (means were calculated using 5 random seedlings from each experimental unit).

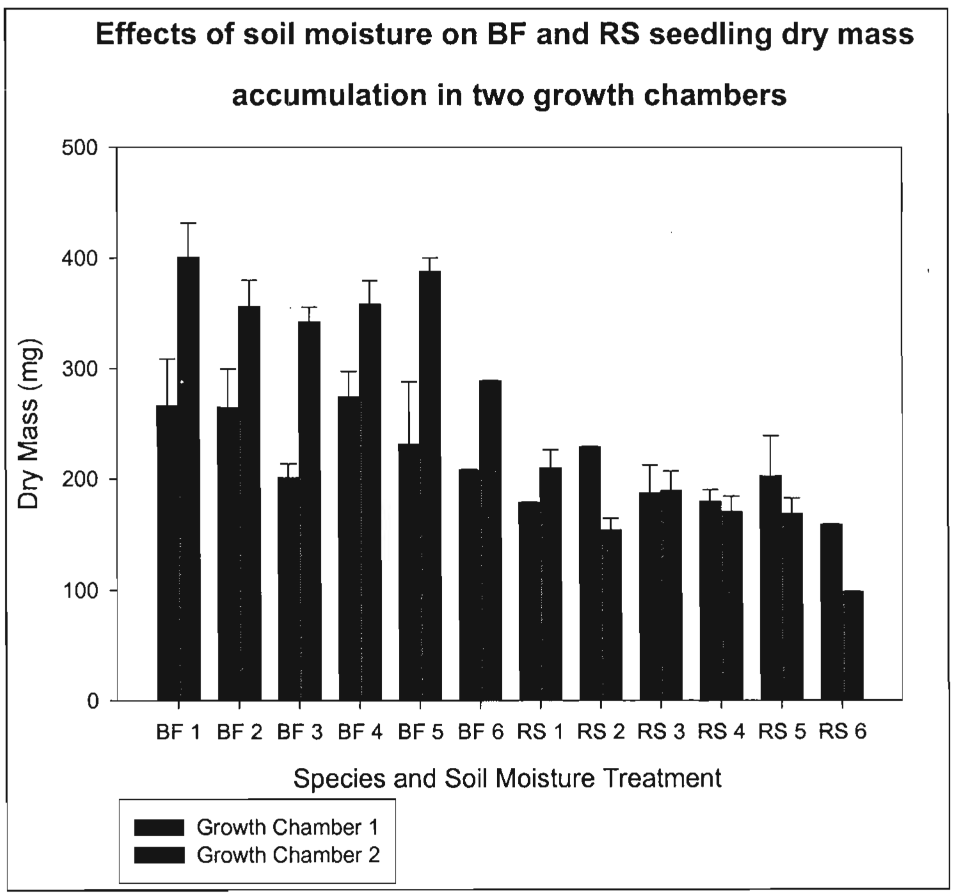

Figure 4. Dry mass for BF and RS seedlings at 15 weeks of age, grown under six different watering treatments in two growth chambers (considered separate blocks). Each bar represents the mean of two replicates, and each replicate is the weight of 5 seedlings pooled together.

3.2.2 Effects of moisture on seedling dry mass of BF grown outdoors

There was a highly significant treatment effect (Pr > F 0.0006) between the 60, 50 and 40% treatments (equaling 50%, 38% and 25% of total soil moisture capacity) with each level earning a separate Tukey ranking (Figure 5). The driest two treatments could not be included in this portion of the analysis because only one experimental unit in the 30% treatment, and none in the 20% treatment, had any surviving seedlings at the end of the experiment.

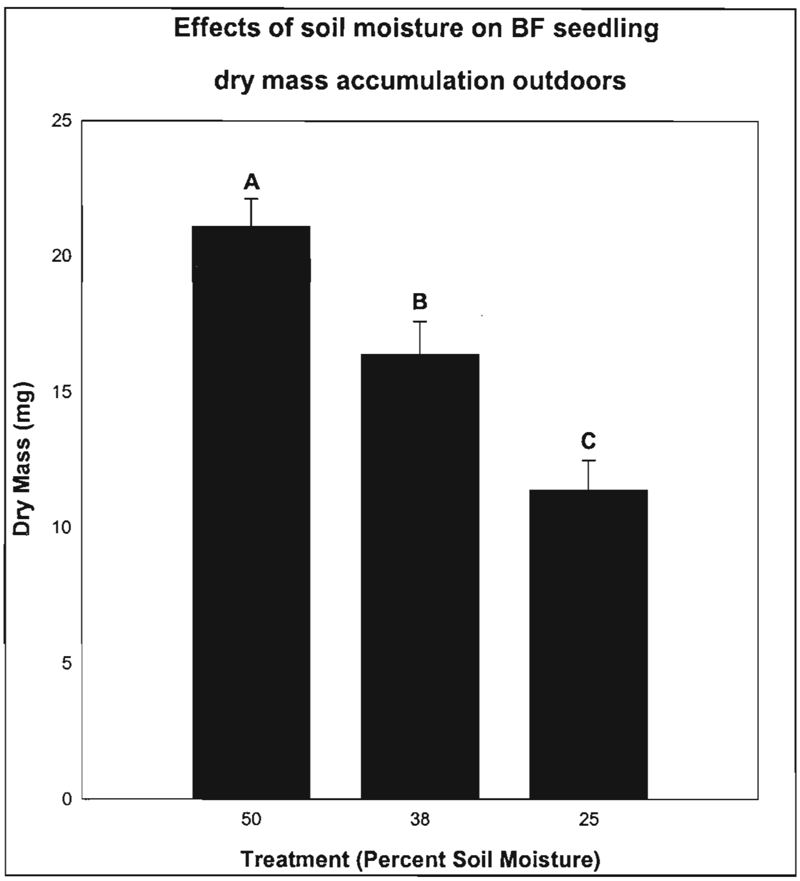

Figure 5. Dry mass for BF seedlings at 11.5 weeks of age, grown outside in partial shade under three different watering treatments. Each bar represents one average seedling (calculated as the mean of all seedlings in each treatment). All treatments were significantly different. [Note: Two treatments could not be included because the 30% treatment had only one replicate and 20% had no replicates with surviving seedlings.]

3.3 Root:Shoot Ratios

3.3.1 Comparative root:shoot ratios (by dry mass) between BF and RS grown in a controlled environment

Only the block*species and block*treatment interaction terms were statistically significant (Pr >F 0.0002 and 0.0186, respectively). The block*species interaction appears to be significant because root:shoot mean ratios between BF and RS in Chamber 1 were 0.58 and 0.24, respectively, whereas Chamber 2 ratios were 0.53 and 0.36, much closer in numerical value (Table 8). The block*treatment interaction appears to be caused by the differing response of BF between the two chambers, displaying a general increasing trend of root:shoot dry mass allocation in block 1, and a decreasing trend in block 2. RS shows consistently higher root:shoot ratios in the brighter chamber, indicating more allocation of dry mass to roots when light is more available (Figure 6). RS does not display a linear relationship to watering levels. The raw data indicates a significant species difference, but when using block*species MSE as the error term there is no statistical significance (Pr > F 0.2091). Small replication and the large block effect may be masking true species differences in this analysis. An analysis of root:shoot rations with treatments removed did show a significant species difference (Pr > F 0.0001).

Treatment	*Growth Chamber 1*		*Growth Chamber 2*	
(Soil Moisture)	*BF*	*RS*	*BF*	*RS*
75%	0.50 ± 0.10	0.26 ± 0.07	0.59 ± 0.02	0.33 ± 0.04
63%	0.42 ± 0.04	0.24 ± 0.003	0.52 ± 0.01	0.43 ± 0.09
50%	0.63 ± 0.04	0.22 ± 0.03	0.59 ± 0.06	0.29 ± 0.08
38%	0.63 ± 0.05	0.29 ± 0.04	0.52 ± 0.02	0.40 ± 0.03
25%	0.55 ± 0.003	0.18 ± 0.05	0.48 ± 0.05	0.33 ± 0.03
13%	0.79 ± 0.004	0.30 ± 0.02	0.48 ± 0.05	0.38 ± 0.04

Table 8. Mean root:shoot ratios ± SE of 15-week old BF and RS seedlings, grown under 6 watering treatments in environmentally controlled growth chambers.

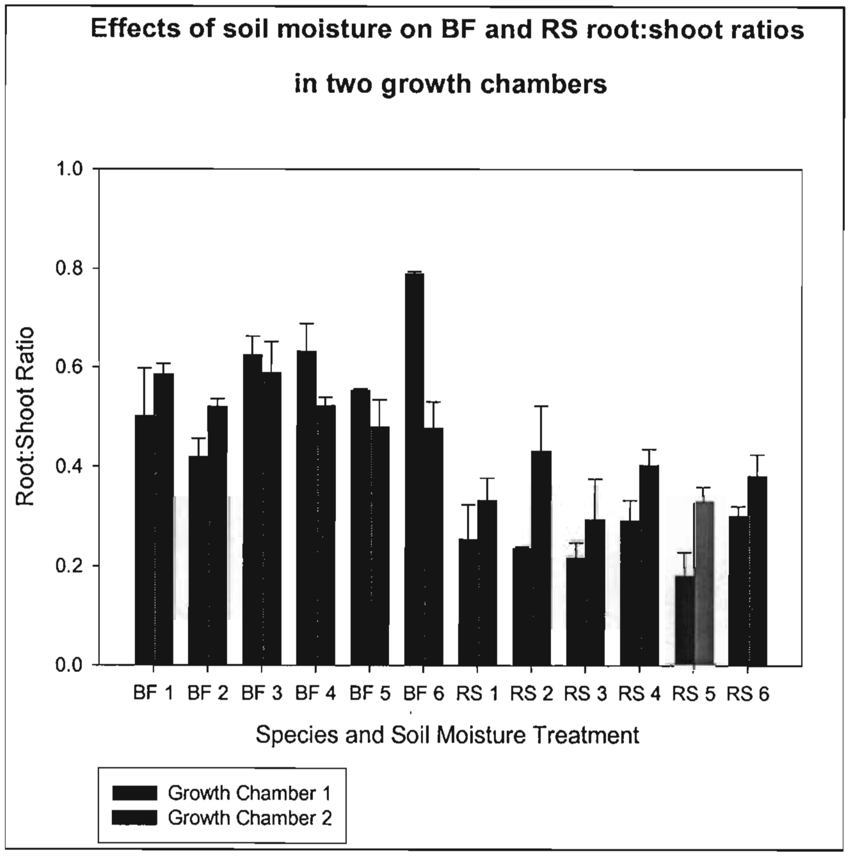

Figure 6. Root:shoot ratios of BF and RS at 15 weeks of age grown under controlled environmental conditions in two growth chambers. Each bar represents five seedlings pooled.

3.3.2 Root:shoot ratios (by dry mass) of BF grown outside

Only the 60, 50 and 40% treatments could be analyzed for root:shoot ratios due to lack of seedling survival in the 30 and 20% treatments. Root:shoot ratios decreased with moisture stress ($Pr > F$ 0.0009) and Tukey's comparison placed the 60 and 50% treatments together in one grouping, the 40% in a second group as significant from both 50 and 60% (Figure 7). In drier conditions, BF appears to allocate fewer resources to roots than shoots. Light may be an important factor in this effect and account for the different trends in root:shoot ratios between the two growth chambers. The size of the pots may also play a role because the bottom is only 5cm from the soil surface - if given more space to expand downward, perhaps the roots would have shown more growth to reach available water lower in the soil profile. The physical restriction of growing through the organic soil after it dries and become hard is also an important consideration.

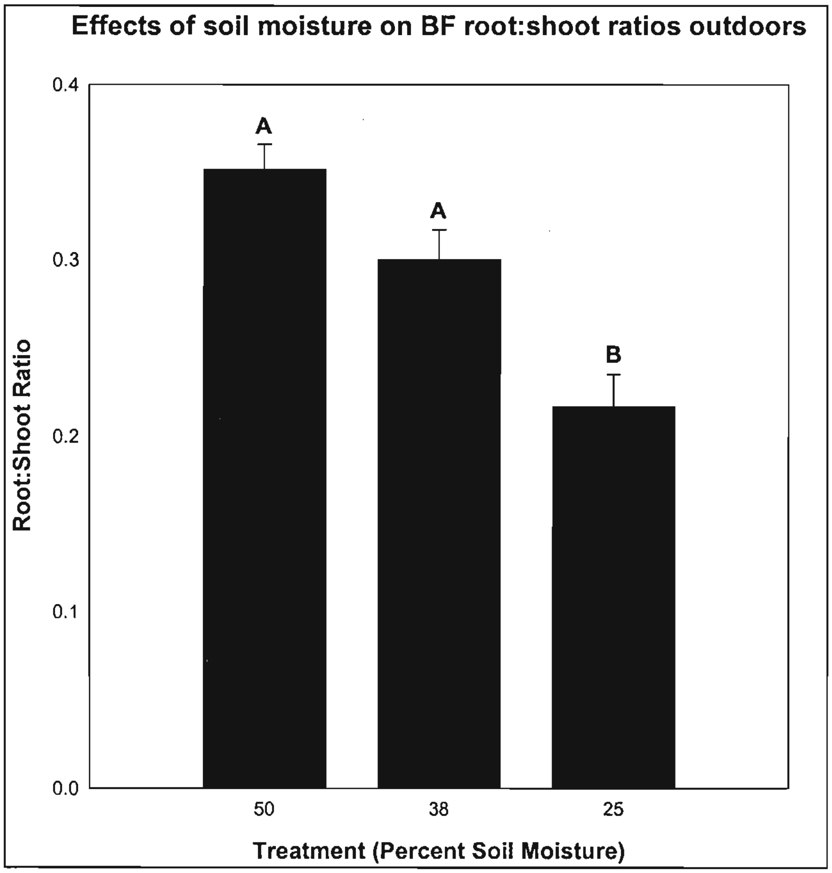

Figure 7. Root:shoot ratios (by dry mass) for BF seedlings at 11.5 weeks of age, grown outside in partial shade under three different watering treatments. Treatments with different letters represent statistically significant differences by Tukey's pair-wise comparisons. Each bar represents one average seedling (calculated as the mean of all seedlings in each treatment).

3.4 Effects of drought on BF and RS seedling survival at different ages

BF and RS seedlings (in individual cells) were of two different ages when treatments began - half were one month old and half were two months. During the initial six weeks that watering treatments were imposed, only four seedlings died (two were older RS in the driest treatment). All cells were watered to field capacity at the start of week eight, and after an additional three weeks without being watered, most of the older

RS seedlings (now 5 months of age) appeared stressed beyond recovery (needles browning and some had dropped). When saturated with water the second time, only one of the older RS seedlings remained alive. All BF and all of the 4 month old RS seedlings (minus one) survived the first drought period (Table 9). The difference in survival between 4 and 5 month old RS seedlings during drought is very striking and suggests that RS seedlings differ in their drought tolerance based on root and shoot morphology that varies with the age of the seedling. RS seedlings exhibit indeterminate shoot growth, which correlates to lower root:shoot ratios as the seedlings age (results reported in 3.3.2). These findings also suggests that BF seedlings are more suited to tolerate late summer drought because of higher root:shoot ratios than RS seedlings after 4 months of age (resulting from a contrasting growth habit of setting bud after a finite amount of shoot growth). It should be noted that most of the BF of both ages in the original 50% and 25% soil moisture treatments began to break bud and flush at varying times between weeks eight and twelve. These new leaves began showing signs of stress before established cotyledons during the second drought cycle, but the presence of new growth did not appear to cause earlier seedling death. All BF seedlings died within the same four-day period, starting four weeks after the last watering, when the soil reached near oven-dry weight. There was no pattern of death associated with the initial watering treatments, or bud break, but there was an age distinction. The older seedlings died towards the beginning of the four day window, the younger seedlings died at the end.

Days to death	13	16	39	71[‡]	74	88	92[‡]	99	101	107	111	115	118	123	127	Mean Days to Death
RS 1	1		1	1	1	2		9	1	1			1			88
RS 2						1					1	1	2	8	5	121
BF 1														12	6	124
BF 2		1													17	121

Table 9. Number of RS and BF seedlings, in individual super stubby cells, that died the indicated number of days after beginning the experiment. The numbers 1 and 2 following species identification represent the age group of the seedlings - five and four months of age, respectively, on 9/11/03 when the experiment began. [‡] Previous to day 71, three watering treatments were imposed and cells were watered when they reached 60, 40, and 30% of their saturated weight. All cells were soaked overnight to fully re-saturate the soil on day 71, and again on 92, with no supplemental watering in between or after day 92.

3.5 Effects of organic layer depth on BF and RS seedling growth

3.5.1 Seedling dry weight vs. organic layer depth

BF and RS significantly differed (Pr>F 0.0001) in response to variation in organic layer depth, with RS seedlings weighing more than BF in all but the straight mineral soil treatment (Figure 8). The increased accumulation may in part be attributable to the growth pattern differences mentioned in 3.4.1, where RS seedlings put on indeterminate growth until fall arrives, while BF seedlings produce a short epicotyl and set bud relatively early. The light under the outdoor canopy (about 638 $\mu mol\ m^{-2}s^{-1}$) was 5-10x higher than in the growth chambers. The increased light, coupled with the increased growing time, may explain this species difference, opposite from what was found in the growth chamber experiment (3.2.1).

There was also a highly significant difference in dry mass accumulation among organic depth treatments (Pr>F 0.0001). Tukey's pair-wise comparisons placed all treatments with organic matter in the same rank, while the one treatment of straight mineral soil separated into a different rank. The dramatic difference in seedling growth between presence and absence of organic soil can be explained by nutritional differences. The campground's organic soil contains more than adequate nutrient content while the mineral soil has less than required, as shown by the acceptable ranges listed in Table 1.

In addition to the species and treatment differences, there was also a significant species*treatment interaction (Pr>F 0.0057). BF showed a continually increasing trend in dry mass accumulation with increasing organic layer depth, while RS seedlings increased sharply to the 15cm depth treatment, then decreased again (Figure 8). In the deeper organic layers (20 – 30cm), water saturation at the base of the O horizon may have impeded growth by limiting oxygen availability to the roots, causing the decrease in RS growth response.

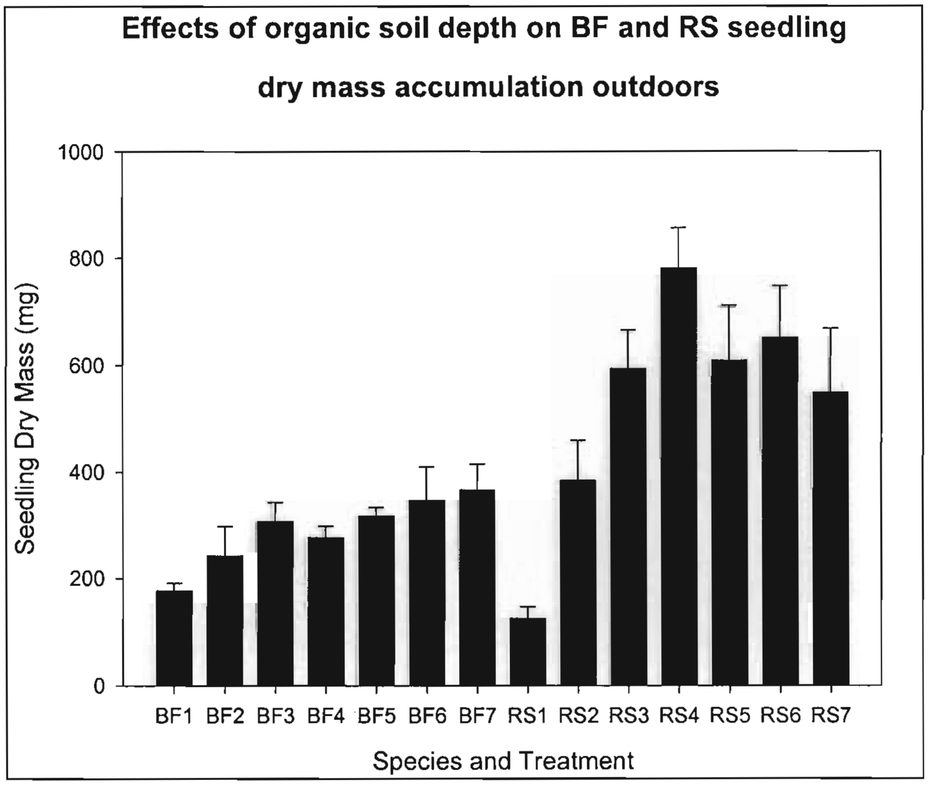

Figure 8. BF and RS seedling mean dry mass at two years of age. Treatment levels correspond to organic layer depth as follows: 1 = 0cm, 2 = 5cm, 3 = 10cm, 4 = 15cm, 5 = 20cm, 6 = 25cm, and 7 = 30cm.

3.5.2 Comparative root:shoot ratios (by dry mass) between BF and RS in varying organic layer depths

There was a significant species difference (Pr>F 0.0001) in root:shoot ratios between BF and RS. BF seedlings had consistently higher ratios than RS, with the exception of RS seedlings in the mineral soil (Figures 9 & 10). RS seedlings, in the presence of organic matter, put nearly twice as much dry mass into shoots as into roots while BF seedlings are nearly equal in dry mass accumulation between roots and shoots.

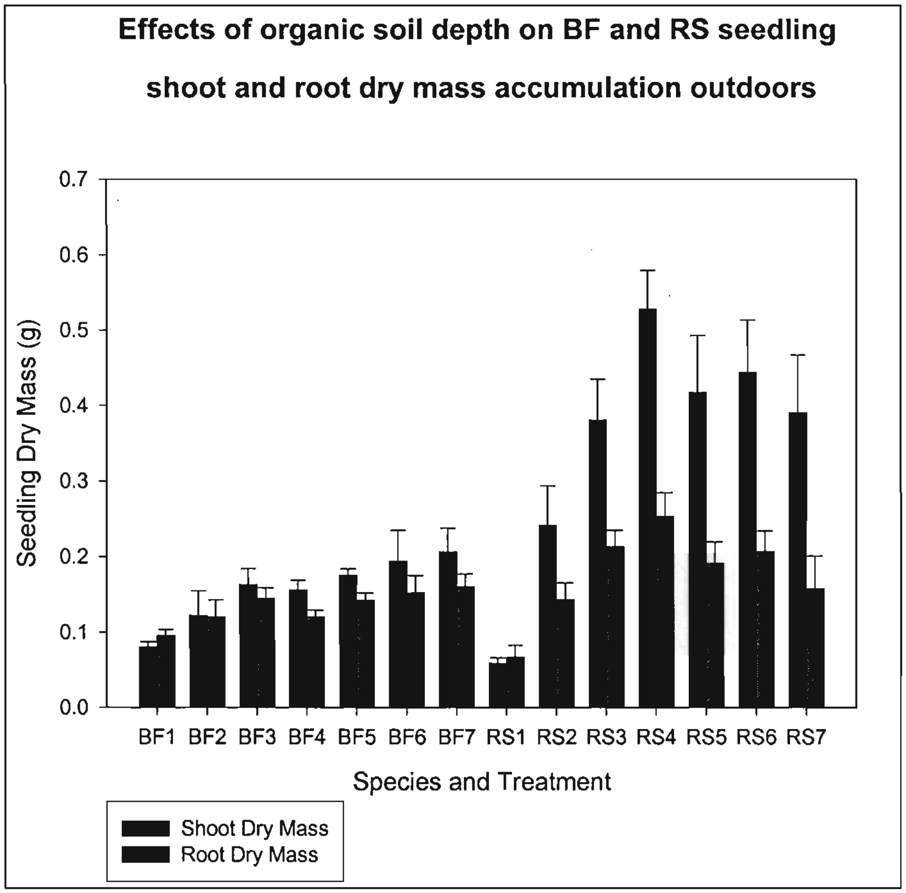

Figure 9. Mean dry mass, separated by roots and shoots, of two-year old BF and RS seedlings. Treatment levels correspond to organic layer depth as follows: 1 = 0cm, 2 = 5cm, 3 = 10cm, 4 = 15cm, 5 = 20cm, 6 = 25cm, and 7 = 30cm.

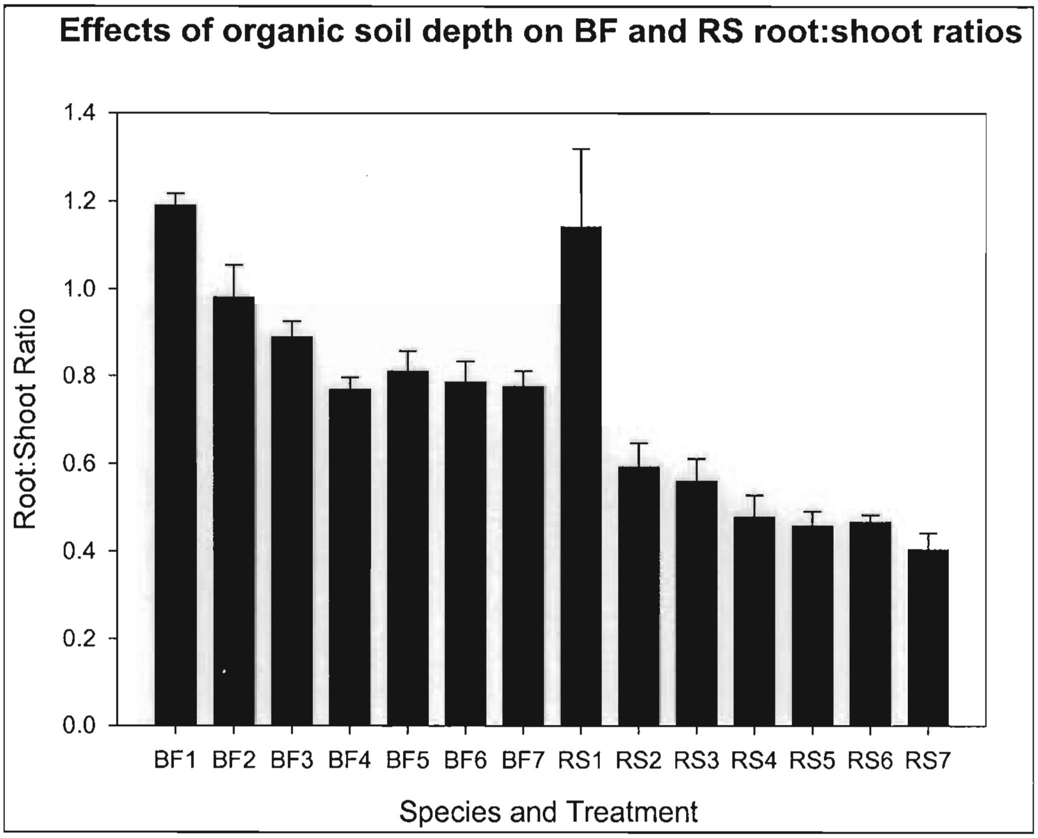

Figure 10. Two-year old BF and RS seedlings' mean root:shoot ratios. Treatment levels correspond to organic layer depth as follows: 1 = 0cm, 2 = 5cm, 3 = 10cm, 4 = 15cm, 5 = 20cm, 6 = 25cm, and 7 = 30cm.

Root:shoot ratios decrease significantly with an increase in organic layer depth (Pr>F 0.0001, Figure 10). BF and RS seedlings grown in mineral soil had the highest root:shoot ratios. Root:shoot ratios in BF decreased up to 15cm of organic horizon where they appeared to even out, while RS seedling root:shoot ratios continued to decrease to 30cm of organic matter (Figure 10). Both species favored shoot mass accumulation over root mass as the depth of the organic matter (and available mineral nutrition) increased, with RS ratios showing greater proportional shoot growth than BF. With both species pooled to examine only treatment effect, Tukey's pair-wise comparisons analysis reveals a strong decreasing trend in root:shoot ratios with increasing organic matter (Figure 11).

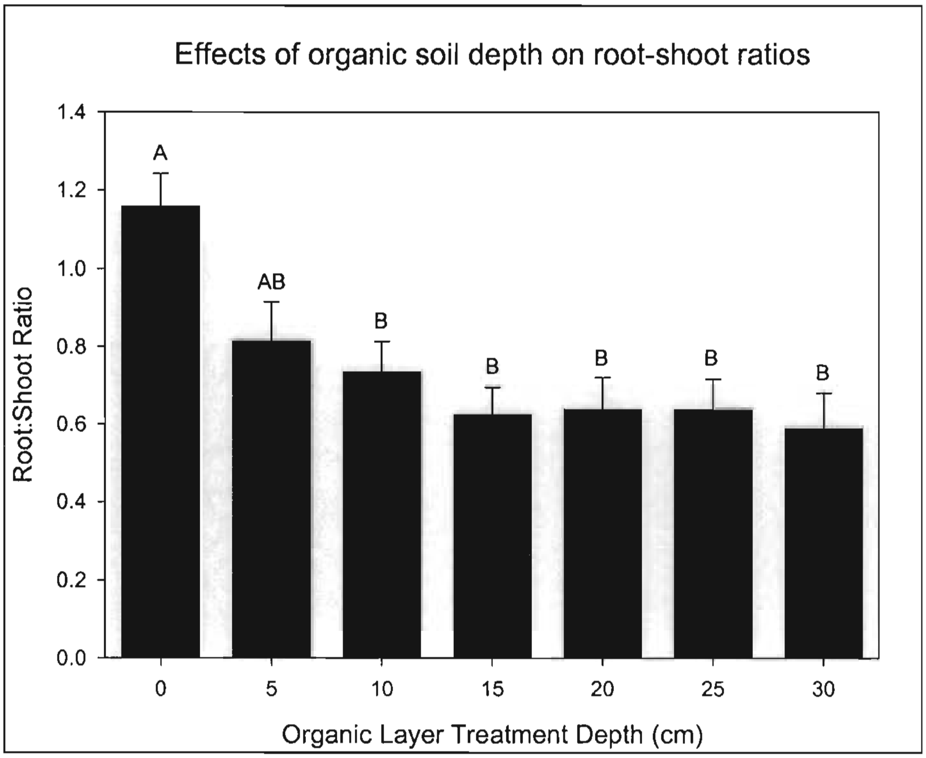

Figure 11. Mean root:shoot ratios for BF and RS seedlings at two years of age, pooled by species across seven organic soil depth treatments. Treatments with different letters represent statistically significant differences by Tukey's pair-wise comparisons. Each bar represents a mean of six samples.

4. Discussion and Conclusions

In some stands of mixed balsam fir and red spruce, *P. rubens* dominates seed production (e.g. nearly triple that of *A. balsamea*, Randall 1974) and under some conditions new seedling numbers are proportional to seed production (McIntosh and Hurley 1964). *P. rubens* seedlings apparently do not survive as well as *A. balsamea*, and advance regeneration in the understory is often primarily of *A. balsamea* (McIntosh and Hurley 1964; Randall 1974; Randall 1976; Brissette 1996). In an old-growth spruce-fir forest dominated by *P. rubens*, 82% of the seedlings smaller than 2.5 feet in height were spruce, and only 6% were fir. However, seedling populations greater than 5 feet in height averaged only 4% spruce and 96% fir (McIntosh and Hurley 1964). High *P. rubens* seedling mortality appears to occur early in development during the first several growing seasons, but little is known about possible causes.

Light levels in the forest understory can be very low. Single-point light readings taken in Blackwoods during the summer solstice (mid-June, 2003, see 2.1.5) ranged from full sun readings of almost 2000 μmol $m^{-2}s^{-1}$, to dense shade readings as low as 20 μmol $m^{-2}s^{-1}$. A single location does not, however, remain at the same level throughout the day, and three days of consecutive PAR readings taken at 8am, noon, and 4pm under cloudless conditions were averaged. The lowest average PAR for a site (of 23 locations measured) was approximately 161 μmol $m^{-2}s^{-1}$. Low light levels do not inhibit *P. rubens* or *A. balsamea* seed germination (Baldwin 1934), but light does affect growth response of both species. The light compensation point, below which level respiration costs are greater than the energy gained from photosynthesis, is probably between 20 and 30 μmol $m^{-2}s^{-1}$ for *P. rubens* (Jagels and Day 2004), and 10 to 25 μmol $m^{-2}s^{-1}$ for *A. balsamea*

(Landhäusser and Lieffers 2001). Light within Blackwoods is therefore not likely to remain at or below the compensation point for an amount of time long enough to cause mortality for either species.

In our experiments, we found differences in seedling growth between *P. rubens* and *A. balsamea* in response to light intensities. PAR levels during seed germination and seedling development in the growth chambers (see 2.1) averaged 68 μmol $m^{-2}s^{-1}$ in chamber 1 and 120 μmol $m^{-2}s^{-1}$ in chamber 2, equaling approximating 3% and 7% of full sunlight (estimation based on full sun value of 2000 μmol $m^{-2}s^{-1}$). There was a significant growth response difference between the two chambers for *A. balsamea*, which we attribute to the light differences. *P. rubens* growth (dry weight) was similar in both chambers, while *A. balsamea* nearly doubled its dry mass accumulation at 120 μmol $m^{-2}s^{-1}$. Night temperatures were 5°C cooler in the bright chamber, which may have had a confounding effect, but is an unlikely cause of *A. balsamea*'s greater growth.

In the forest, older seedlings and saplings of *A. balsamea* have a higher growth rate than *P. rubens* (as measured both by diameter at breast height increase per year, and annual leader growth), both in a shaded understory and in large gaps where seedlings are released (Oosting and Billings 1951; McIntosh and Hurley 1964; Meng and Seymour 1992; Battles and Fahey 2000). *A. balsamea*'s greater capacity to use light at low levels may result from an increased ability to capture light, caused by needle arrangement (Mike Day, personal communication). *P. rubens*, throughout its life, has radially arranged, small, narrow needles that may shade each other. *A. balsamea*, on the other hand, has slightly broader, flat needles arranged in two rows, perpendicular to incoming radiation. This arrangement begins with the first cotyledons that emerge, 4-5 leaves that remain nearly perfectly horizontal. As *A. balsamea* ages under full sun conditions, needles on outer branches will alter their position and more closely resemble a semi-radial arrangement on the upper side of the stem. Shaded branches maintain the flat arrangement to take best advantage of the light they receive (personal observations).

Our experiment studying the effect of depth of the organic layer (see 2.4) shows that *P. rubens* is capable of greater growth rates than *A. balsamea* under some conditions, which agrees with the findings of Greenwood and McConville (2002). Our results after two growing seasons showed that *P. rubens* seedlings gained twice as much dry mass as *A. balsamea* seedlings across all treatments with organic matter (excluding the mineral soil treatment where seedling growth for both species was almost zero), and *P. rubens* shoots averaged more than twice the length of *A. balsamea* shoots. This contrasting growth trend between our results with potted trees and performance reported in the forest shows that *P. rubens* can exhibit growth superior to *A. balsamea*. The seedlings growing in organic matter did not experience water stress and were grown at approximately 33% of sunlight, allowing *P. rubens* to take full advantage of its indeterminate growth habit as a young seedling. During the first several growing seasons, *P. rubens* may continue to put on shoot growth until the onset of fall when environmental cues initiate bud set. *A. balsamea*, however, will grow only a fixed amount before setting bud, even in full sun and favorable conditions for continued growth. *A. balsamea* may continue root growth through the fall, but shoot growth is halted once buds have formed. This growth difference is important not only in considering light, but becomes critical when considering moisture requirement differences between these two species.

With light requirements above the compensation point, the most limiting factor for *P. rubens* and *A. balsamea* seed germination and seedling survival is moisture stress (Baldwin 1934; Place 1955). In our controlled environment experiments examining germination and survival at different moisture levels we found *P. rubens* and *A. balsamea* seed germination to be significantly reduced only below a threshold of about 25% soil moisture content (Figure 1). Seeds in the 13% moisture treatment of both species averaged a germination rate of 50%; above 25% soil moisture, seed germination for *P. rubens* and *A. balsamea* averaged 74% and 67%, respectively. This experiment was repeated outdoors for *A. balsamea* only, under ambient temperature, humidity, wind, and approximately 25% sunlight. Germination responses to the same moisture levels decreased; at 13% soil moisture only 4% of the *A. balsamea* seed germinated, and at 38% only 37% germinated (compared to 62% in the controlled experiment, Figures 1 & 3).

The differences observed in germination response to the same treatment levels between indoors and out may be due to the manner in which the organic soil dried. In the growth chamber, pots experienced limited air movement and the soil dried fairly evenly. Outdoors, with wind, brighter light, and higher temperatures (max. 24.7 °C in the growth chamber, 35 °C outside), the surface of the soil and the sides would have dried faster than the center of the block. Soil water treatments were based on overall pot weight; thus imposition of the same treatment level between the two experiments did not result in equal moisture stress experienced by the seed on the organic soil surface because moisture distribution throughout the pots was not uniform. The difference in results may also be attributable to the assistance we gave seed radicles in the growth chambers by making small toothpick holes for them to penetrate into the soil.

Seedling survival of *A. balsamea* was also very different between these two experiments. Both *A. balsamea* and *P. rubens* had very high survival rates in the growth chambers, averaging 98 and 97% respectively across all treatments. When this experiment was repeated outdoors, the survival rate dropped significantly (Table 10). With soil remaining at or above 50% soil moisture, the seedling survival rate was 93%, but mortality increased as water availability decreased, and only 17% survived at 13% soil moisture, and 0% in the 0% soil moisture treatment. This decreasing trend is not surprising, and is expected, but this drop in survival rate was not expressed in the growth chambers, even in the 13% soil moisture treatment. This contrast between experimental results for *A. balsamea* survival may be due to the difference in soil drying between the controlled environmental settings in growth chambers, and ambient wind and temperature fluctuations outside. Additionally, not all BF seeds in outdoor pots were treated with a small toothpick hole to aid in radicle penetration. This penetration assistance may have had a greater effect on survival than surface drying because if seeds were given an opportunity to reach moister soil they might have survived.

A. balsamea seedlings in the campground probably undergo conditions more equivalent to our outdoor germination and survival trial, thus the low number of *A. balsamea* seedlings found at Blackwoods is most likely due to lack of water. Campground soil samples were estimated to be as low as 25% soil moisture (see 2.1.6), the level at which *A. balsamea* experienced only 37% germination in pots outdoors, and 63% survival.

Species and Location	*% Soil Moisture*	*% Survival*	*Average % Survival*
BF - Chamber	75	94	
BF - Chamber	63	100	
BF - Chamber	50	100	98
BF - Chamber	38	100	
BF - Chamber	25	100	
BF - Chamber	13	96	
RS - Chamber	75	97	
RS - Chamber	63	99	
RS - Chamber	50	95	97
RS - Chamber	38	100	
RS - Chamber	25	99	
RS - Chamber	13	90	
BF - Outside	50	93	
BF - Outside	38	80	
BF - Outside	25	63	50
BF - Outside	13	17	
BF - Outside	0	0	

Table 10. Percent seedling survival of BF and RS in growth chambers, and BF outdoors, after fifteen weeks with indicated soil moisture treatments. Survival calculations based on number of seeds germinated per treatment and number of living seedlings at the end of the experiment.

While we do not have data comparing *P. rubens* and *A. balsamea* seedling responses in the experiment conducted outdoors, other comparative studies of seedling drought resistance of these two species illustrate interesting differences. The experimental drying cycles imposed on *P. rubens* and *A. balsamea* growing individually in super stubby cells (see 2.3) revealed that *A. balsamea* seedlings at four and five months of age are more drought resistant than *P. rubens* seedlings at five months of age, able to withstand a drying cycle that reached near 0% soil moisture. Observations also imply that the difference in *P. rubens* seedling age from four months to five resulted in decreased drought resistance, thought to be because of lower root:shoot ratios with the additional growing time (see Table 6 for root:shoot ratios of 15-week-old *P. rubens* and *A. balsamea* seedlings).

Greenwood and McConville (2002) also found a distinct age-related response of *P. rubens* and *A. balsamea* to drought cycles. Water was withheld from 60 and 150-day-old seedlings of both species (growing in individual conical stubby cells) until stress symptoms were visible. Seedlings were re-watered and observed for survival. 60-day-old seedlings of *P. rubens* and *A. balsamea* had similar mortality rates of 70 and 80%, respectively, as well as similar root:shoot ratios of 0.30 and 0.44. *P. rubens* seedling dry weights at 150 days averaged 4 times greater than *A. balsamea* and were the first to show symptoms of stress. *P. rubens* mortality in seedlings 150-days-old increased to 88% and root:shoot ratios had decreased to 0.29, while *A. balsamea* mortality dropped to 0 and the root:shoot ratio had increased to 0.69 (Greenwood and McConville 2002). This change in root:shoot ratios and difference in dry weights is a reflection of the growth pattern differences between indeterminate *P. rubens* seedlings and determinate *A. balsamea*, and is the likely explanation for the striking contrast in survival at 150 days of age.

P. rubens seedlings cannot be conditioned to withstand drought. Seiler and Cazell (1990) found that two-year-old *P. rubens* seedlings subjected to drought cycles did not exhibit osmotic or stomatal adjustments as compared to continuously well-watered seedlings, and seedlings from both treatments showed equal rates of photosynthesis upon drought initiation. *P. rubens* seedlings did show almost complete recovery from drought (measured as photosynthetic activity) 24 hours after being re-watered. While no physiological adjustments appear to have occurred, the repeated drought treatments did alter seedling growth, causing a reduction in the root/shoot ratio of treated *P. rubens* seedlings compared to the well-watered seedlings.

P. rubens seedlings may survive as well as or better than *A. balsamea* in situations where light and moisture are not limited, demonstrated by this research and a study of seedling recruitment in two clear-cut areas of a spruce-fir stand (Randall 1976). One clear-cut area was left with fallen slash and the existing understory largely intact, the other area was burned to remove slash and the seedling bank. Nine years after canopy removal, the unburned opening contained 1,520 spruce seedlings per acre and 5,780 fir (nearly four times more fir) – the burned area contained 1,120 spruce seedlings per acre and only 440 fir (nearly three times more spruce). Both species were able to establish more seedlings in the unburned area where slash provided shade, resulting in cooler soil surface temperatures and soil moisture retention. However, *P. rubens* was far more successful than *A. balsamea* in the burned site. *P. rubens* appears to be a better pioneer species, surviving relatively better on mineral seedbeds. In the wild, this increased growth potential by *P. rubens* over *A. balsamea* is rarely realized because of fierce competition for mineral nutrition and water in low light level environments. *P. rubens* may rarely grow at full potential in densely shaded understories where indeterminate growth is not supported.

P. rubens produces good seed crops every 3 to 8 years (Blum 1990); *A. balsamea* produces good seed crops every 2-4 years (Frank 1990). In a mixed spruce-fir forest in Eastern Maine, annual spruce seed production over 6 years was more than triple that of fir seed (Randall 1974). However, *A. balsamea* exhibits relatively greater growth, and dominates the understory seedling population. *P. rubens* continues to remain an important part of this forest type and lives an average of 200 years, while *A. balsamea* live approximately 100 years, only half the life span (Kozlowski 1971). Though it may take 200-250 years for an individual *P. rubens* to reach the canopy, the tree would still have nearly 100 years of life after this to grow larger and produce seed to retain a presence in the understory. This is evidenced in the Penobscot Experimental Forest in east-central Maine where Brissette (1996) found 14 to 22 adult spruce trees more than 31cm in diameter at breast height (DBH) in all selection cut areas, and no fir greater than 30cm.

5. Summary

Picea rubens and *Abies balsamea* are the dominate overstory trees in Blackwoods Campground, Acadia National Park. Both of these species co-exist in stands throughout northeastern North America, each possessing different strategies for maintaining their presence in the forest. *P. rubens* produces more seed than *A. balsamea*, resulting in more first-year seedlings. However, young balsam fir seedlings show better resistance to drought than red spruce, attributable to smaller shoots and higher root:shoot ratios. *A. balsamea* also grows faster than *P. rubens* in competitive understory environments, allowing *A. balsamea* to dominate the seedling population. Red spruce seedlings, though fewer in number than balsam fir, persist until a gap opens in the canopy and are able to grow either to achieve canopy status or they will survive several periods of oppression until another gap opens. This strategy is successful because red spruce has a much longer life span, nearly double that of balsam fir. In addition, red spruce seedlings have the capacity for much greater growth than balsam fir if light and moisture conditions are favorable.

In conclusion, our experimental results and observations indicate that a tree seedling population in the understory of Blackwoods Campground is attainable with natural seed inputs and current light levels, but that additional watering is required. Watering is necessary not only for direct plant growth, but also to promote successful root penetration through organic soils. Both *A. balsamea* and *P. rubens* will maintain a presence in the campground with watering assistance, and protection from damaging behaviors from campers.

Chapter Two: Suitability of eleven native shrubs for planting at campsite locations in Blackwoods Campground, Acadia National Park

1. Introduction

1.1 The History of Blackwoods

Blackwoods Campground, located within Acadia National Park, is on the eastern coastline of Mount Desert Island, Maine. It began in 1936 when John D. Rockefeller, Jr. donated the site to the Park with his approval to build a campground on the land. His donation came after the procurement of funding for road construction, with his desire that the motor road into a campground be contrasting to the public roads of Mount Desert Island. He envisioned campers arriving on a wooded road to set the stage for a camping experience in the forested setting. The name Blackwoods is from 'black woods,' referring to the dense shade cast by the spruce and fir canopy.

Construction on the first section (Loop A) began in 1938. The Civilian Conservation Corps, established by Franklin D. Roosevelt, performed much of the preparatory work of clearing land for road construction, well drilling, and the installation of utility lines. Construction was interrupted by WWII and was resumed following the war by other labor sources. Loop A opened to the public in 1946 and was not affected by the great fire of 1947 that burned much of Bar Harbor and Mount Desert.

Loops B and C were included in original campground plans, with the purpose of having two loops open for camping every season and one closed for repairs, both to infrastructure and vegetation. Loop B was constructed from 1956-1959 by "Mission 66" under the direction of NPS Director Conrad Wirth. The construction of Loop C was never realized and no current plans exist to construct it (Foulds 1996).

1.2 The Purpose and Use of the Campground

Blackwoods is one of only two locations (Seawall is the other) where people can stay overnight within the park. Blackwoods contains 314 campsites and sees roughly 100,000 visitors per year (Visitor Use Statistics, Acadia National Park, 2002). Beyond a simple place to pitch a tent, the campground offers bathroom facilities (no showers), water taps with potable water for drinking, trash disposal bins, limited firewood, and an amphitheater. A recently added bus service shuttles campers throughout the park during peak summer months. During July and August it is common for the campground to be full every night.

1.3 Current Vegetation Conditions

Picea rubens Sarg. (Red Spruce), *Picea glauca* (Moench) Voss (White Spruce) and *Abies balsamea* (L.) Mill. (Balsam Fir) dominate the overstory, interspersed with several other coniferous species, including *Picea mariana* (Mill.) BSP (Black Spruce) *Pinus strobus* L. (White Pine), *Tsuga canadensis* (L.) Carr. (Canadian Hemlock) and *Thuja occidentalis* L. (Eastern White Cedar) and deciduous hardwoods such as *Acer rubrum* L. (Red Maple), *Acer pensylvanicum* L. (Striped Maple), *Betula papyrifera* Marsh. (Paper Birch), *Betula alleghaniensis* Britt. (Yellow Birch) and *Fraxinus nigra* Marsh. (Black Ash). While the overstory is well developed, there is a distinct lack of understory vegetation, both of tree seedlings and shrubs, throughout much of the campground (Figure 12). Understory decline is more advanced in Loop A than Loop B, which is thirteen years younger than Loop A, is occupied by fewer campers and campers with less equipment (Foulds 1996), and is only open from Memorial Day in late May, through Labor Day in early September. Lower sections of Loop A remain open year-round).

The scarcity of understory vegetation within Loop A creates less desirable camping conditions due to the lack of visual privacy and noise buffering between sites (Figures 13 & 14). We hypothesized that the lack of understory shrubs is due to human influences, both direct and indirect, but that with proper labeling and education these impacts can be alleviated.

Plants around the perimeter of campsites are crushed by cars, pulled out of the ground for firewood or marshmallow sticks, and stepped on. Shrubs are also impacted by compacted soils where people regularly walk, and other human activities. We did not attempt to directly measure camper activity, though I made observations when camping in Blackwoods to collect data.

Chapter 1 focused on re-populating the understory with tree seedlings that will replace the overstory as it ages and canopy gaps open. This chapter focuses on planting shrubs around the perimeter of campsites to create visual screens and to define campsite boundaries. The purpose of this research was to evaluate native shrub species and their suitability for planting at campsites. This evaluation would lead to a management report for park service scientists to assist with revegetation efforts.

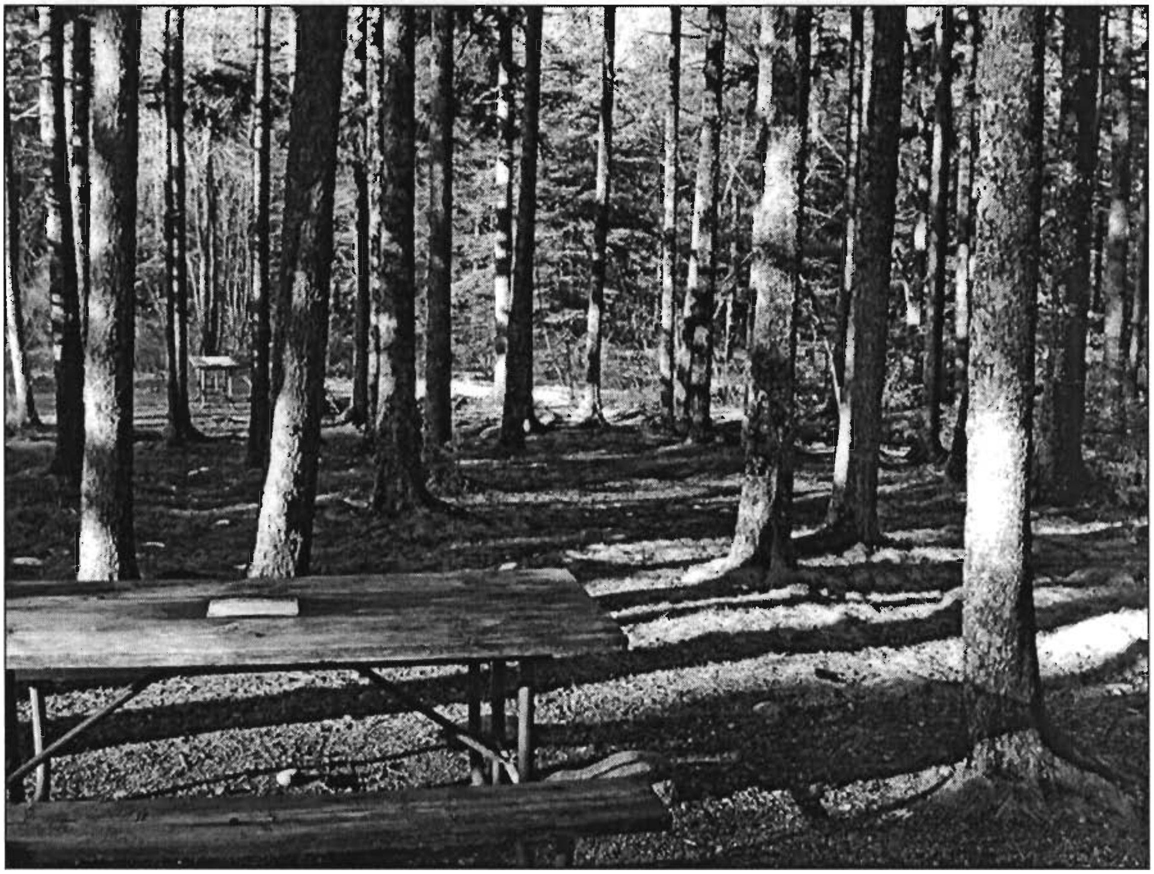

Figure 12. Campsite 42 within Loop A, October 2001. The camera is looking north into Campsite 41.

Figure 13. Campers pitching tents in Campsite 47 of Loop A in October of 2001. The camera is looking east into Campsites 46 and 38 where other tents and vehicles are clearly visible because there are no shrubs or tree seedlings in the understory to provide visual screening.

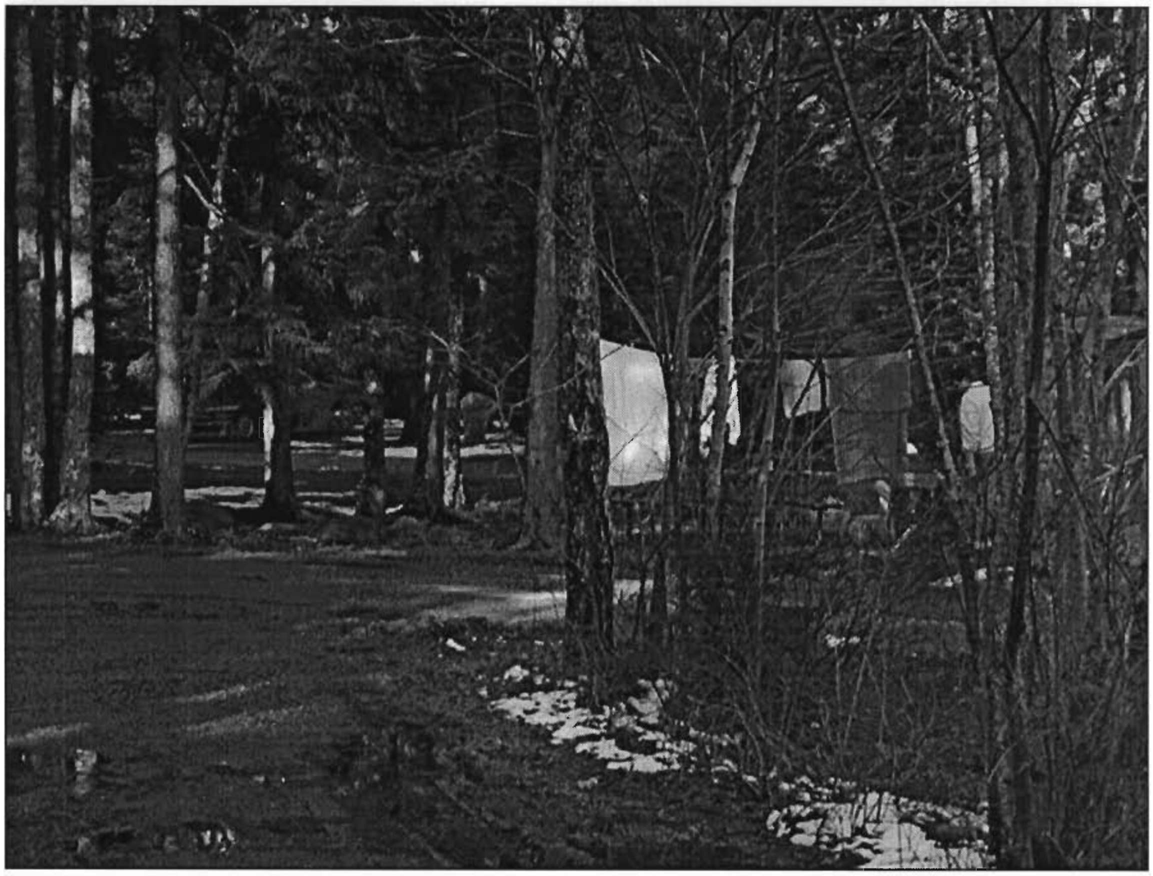

Figure 14. Campsite 52 in Loop A, looking west into Campsites 45 and 36. This image was taken in October of 2001 after leaf drop. Several deciduous shrubs are visible in the foreground, though they are insufficient to provide visual screening during the growing season.

2. Methods and Materials

2.1 Campsite planting

2.1.1 Campsite selection

Loop A was chosen for the location of planting trials - it is in a greater state of decline than Loop B because it is older and used more heavily. Campsite numbers were selected randomly to determine planting sites. Campsite 56 was added to ensure sampling that included a wet location. At the time of planting, two of the pre-selected sites had been closed for ant studies, and the nearest site was chosen as substitute. One additional site, #53, was found to have no possible spot for planting and was removed from the list, leaving a total of 22 campsites for study. Appendix C contains the complete list of campsites studied.

2.1.2 Plant material

Both Loop A and Loop B were surveyed along three transect lines for tree and shrub species. Table 11 displays the taxa found and identified. Shrubs for evaluation were selected from this list with the following requirements: they must be native to the park, they must be tolerant of semi-urban conditions (soil compaction and drought), and they must be available for use in the study. Several shrubs that were excellent candidates for plantings (ie: *Gaylussacia baccata* (Wang.) K Koch and *Nemopanthus mucronata* (L.) Trel. could not be included because specimens were unavailable. The final eleven species selected for planting at campsites are listed in Table 12. These plants are not only native to the park but are native to the campground itself. Acadia National Park maintains a small plant nursery of native species with park provenance, and from their stock five shrubs were available. Plants not available from the park nursery were purchased in the spring of 2002 from Pierson Nurseries, Inc., in Biddeford, Maine. All plants were containerized in 1-3 gallon pots.

*Latin Name**	*Common Name*
Abies balsamea (L.) Mill.	Balsam Fir
Acer pensylvanicum L.	Striped Maple
Acer rubrum L.	Red Maple
Acer saccharum Marsh.	Sugar Maple
Acer spicatum Lam.	Mountain Maple
Amelanchier arborea (Michx.) Fern.	Downy Serviceberry
Amelanchier canadensis (L.) Medic.	Shadbush
Amelanchier laevis Wieg.	Smooth Shadbush
Betula alleghaniensis Britt.	Yellow Birch
Betula papyrifera Marsh.	Paper Birch
Comptonia peregrina (L.) Coult.	Sweetfern
Cornus racemosa Lam.	Witherod Viburnum
Diervilla lonicera Mill.	Bush Honeysuckle
Fraxinus nigra Marsh.	Black Ash
Fraxinus pennsylvanica Marsh.	Green Ash
Gaylussacia baccata (Wang.) K Koch	Black Huckleberry
Ilex verticillata (L.) Gray	Winterberry Holly
Myrica pensylvanica Loisel.	Bayberry
Nemopanthus mucronata (L.) Trel.	Mountain Holly
Picea glauca (Moench) Voss	White Spruce
Picea mariana (Mill.) BSP	Black Spruce
Picea rubens Sarg.	Red Spruce
Pinus strobus L.	White Pine
Physocarpus opulifolius (L.) Maxim.	Ninebark
Quercus rubra L.	Red Oak
Rosa carolina L.	Carolina Rose
Rubus sp. L.	Raspberry or Blackberry
Sambucus canadensis L.	American Elderberry
Sorbus americana Marsh.	American Mountain Ash
Spiraea alba Du Roi var. *latifolia* (Ait.) Dippel	Meadowsweet
Thuja occidentalis L.	Eastern White Cedar
Tsuga canadensis (L.) Carr.	Canadian Hemlock
Vaccinium corymbosum L.	Highbush Blueberry
Vaccinnium angustifolium Ait.	Lowbush Blueberry
Viburnum dentatum L.	Arrowwood
Viburnum nudum L. var. *cassinoides* L. Torr. Gray	Wild Raisin

Table 11. List of tree and shrub species found within Blackwoods Campground when surveyed in the fall of 2001.
*Full notation from Gray's Manual of Botany (Fernald 1950)

Species – Latin Name	Common Name	Zone	P	S	SC	DH
*Ilex verticillata**	Winterberry Holly	3b		S	R	I
Rosa carolina†	Carolina Rose	4b	S	S	I	R
Sambucus canadensis	American Elderberry	3a	S	S	R	R
Vaccinium corymbosum	Highbush Blueberry	3	S	R	R	I
*Myrica pensylvanica**	Northern Bayberry	4b		R	R	R
Cornus racemosa	Gray Dogwood	3a	S	S	I	R
Diervilla lonicera	Bush Honeysuckle	3a		R	R	R
Comptonia peregrina	Sweetfern	2		R	S	R
Spiraea alba var. *latifolia**	Meadowsweet	3a		S	R	R
*Viburnum dentatum**	Arrowwood	2	S	R	I	R
Viburnum nudum var. *cassinoides**	Witherod Viburnum	2	S	R	R	I

Table 12. Shrub species selected for campsite planting trials within Loop A of Blackwoods Campground to evaluate growth under varying light, moisture, and soil conditions. Plants denoted by an asterisk were provided by the Acadia National Park Nursery and are of park provenance. All other plants were purchased from Pierson Nurseries, Inc., Biddeford, Maine.
† Only nine specimens were available - they were randomly assigned to nine of the twenty-two pre-selected campsites.
Abbreviations: P = pollution, S = salt, SC = soil compaction, DH = drought/heat
Stress Tolerance: R = resistant, I = intermediate, S = sensitive (Hightshoe 1988)
Zone letters indicate USDA cold hardiness

2.1.3 Planting Area Selection and Installation

At each campsite selected for evaluation, planting areas were approximately 3x3m in size, and located in a spot not designated for use by a vehicle, the picnic table or a tent. Digging with shovels and other hand tools in Blackwoods is nearly impossible due to excessive roots and rocks. We used a 12-inch gas-powered auger to drill planting holes on July 15, 2002.

Soil samples were collected from the bottom of each hole, taking care to sample the mineral soil and as little of the organic surface horizon as possible. Samples were combined into a site-composite if the soil appeared uniform. Soils appearing different in texture or color were treated as individual samples and analyzed separately. Soil was allowed to air-dry, sieved through a 2mm wire mesh, and submitted for pH and available nutrients testing at the Maine Soil Testing Service, University of Maine, Orono. (For analysis results see Appendix D).

After holes were dug and soil samples extracted, one shrub of each species was delivered to all 22 sites and each plant was randomly assigned to one of eleven planting holes. In campsites containing more than one soil type, we recorded which species was planted in each soil type for possible correlations with growth later in the experiment. Shrubs were planted July 15, 16, and 17, 2002.

To prevent excessive trampling or other damage by campers, 4 wooden stakes were driven into the ground around the perimeter of the planting and circled twice with orange nylon twine. A small, plastic 3x4" sign, "Revegetation Project", was suspended on a nylon cord around each enclosure. In some instances, roots and rocks in the soil prevented staking and only three corners could be established to form a triangular enclosure, sometimes excluding one or two plants from the fenced area.

Plantings were mulched in the fall of 2002 with chip mulch produced in the campground from fallen trees. Mulch was spread within the fenced area to a depth of approximately 2 inches, leaving areas immediately around plant stems clear. The mulch conserved soil moisture and served to draw attention to the planted shrubs.

2.1.4 Watering

All shrubs were irrigated during the first growing season, mid July through September 2002, using a watering truck equipped with a 50-gallon tank and hose. Each plant received a gallon of water per week except during weeks of heavy rainfall. In 2003 watering was restricted to August.

2.1.5 Light Measurements

In addition to soil samples, light readings were also collected for correlation with plant growth response. Photosynthetic photon flux ($\mu mol/m^2s$) readings were taken using a hand-held basic quantum meter (Apogee Instruments, Inc., Logan, Utah).

Readings were collected at 8am, 12pm, and 3pm during three cloudless days just before the summer solstice (June 16, 17, and 18, 2003). At each campsite the sensor was placed on the ground within the planting area, oriented vertically. Light conditions within each plot were highly variable and readings were taken in full sun and deepest shade. If full sun was not available, several bright spots were measured and the highest reading was recorded. Measurements were not taken within the shade of the shrubs themselves.

There were a total of 18 light measurements recorded for each planting site (two readings, three times a day, for three days). The highest and lowest light readings for each sampling time were averaged. The resulting nine means for each planting (corresponding to the nine sampling times) were again averaged to create one light value estimate per site. These estimates were used to rank planting sites, from highest to lowest light exposure, and approximate the level of difference between them.

2.1.6 Growth Measurements

Plant growth for each shrub was evaluated after two growing seasons. Growth was determined by calculating the change in volume of each plant between measurements taken in the spring and fall of 2003.

The volume of each specimen was calculated from three measurements. Plant height was measured using a metal yardstick from the base of the stem (where mulch was absent), vertically to the highest point of the shrub, without artificially extending stems by holding them. The next measurement was of the widest horizontal part of the shrub (measurement was taken with the ruler parallel to the ground). The location of widest section was usually estimated visually when standing above the plant looking down, and then measured. If it could not easily be identified by sight, several measurements were taken to determine the largest width. The third measurement was another width, perpendicular to the first. These three values, height, largest width, and perpendicular width, were multiplied to estimate the volume of each shrub.

All shrubs were measured on May 2, 2003 and again on November 1, 2003. Only shrubs at sites 56, 74, 95, 123, and 160 were measured on June 13, 2005 due to time restrictions. These five sites were originally selected for part of a volunteer program of pest monitoring and represented a cross section of site conditions within the campground. The 2003 fall volume estimate was divided by the 2003 spring volume estimate to give the magnitude of change (a magnitude less than 1 indicated a decrease in size, equaling 1 indicated no change, equaling 2 indicated a doubling in size, etc…). This method generated numbers easy to interpret and analyze, whereas growth estimates left as volumetric values covered a very large scale and were difficult to interpret.

2.1.7 Statistical Analysis

Shrub growth was analyzed using Excel X for Mac (Microsoft 2001). Regression analysis compared magnitude of growth for each shrub species with estimated light rankings and measured soil characteristics (% LOI, pH, and P, K, Mg, Ca, and Na concentrations) across all campsites. Correlations were considered significant when the Pr value fell below 0.05 ($\alpha = 0.05$). For regression analysis results, see Appendix E.

3. Results and Discussion

3.1 Statistical Results

There were no significant correlations between growth and either light or soil properties for any shrub species. This lack of correlation prevents us from making regression line predictors for specific shrubs at any campsite with known light and soil conditions. However, based on our observations of plants in the campground we can still provide valuable information and recommendations.

3.2 Shrub Survival

Table 13 shows the number of shrubs that were dead or in serious decline after two years in the campsite plantings. *Comptonia peregrina* appears to be poorly suited for campsite planting because of high mortality, however this species is abundant throughout the campground and thrives in colonies along the roadsides and near restrooms. We can attribute the low survival of *C. peregrina* in this trial to poor quality plants, not a poorly adapted species. At the time of installation the plants were small with very few roots, and the potting soil completely fell apart from when removed from the pots. The plants appeared to have been just dug from the ground without sufficient time to establish roots before being planted, leaving them especially vulnerable to establishment stress.

Diervilla lonicera performed disappointingly, with half of the plants dead or in severe decline after two years. These were also low quality plants, excessively pot-bound with almost no soil in the pots. We had difficulty removing them from the containers and breaking the root masses before planting. There are large colonies of *D. lonicera* in Balckwoods Camground, especially around the restroom areas, which suggests that this is also an excellent candidate for campsite plantings in sunny areas.

Species – Latin Name	Shrub deaths	Shrubs in serious decline	Total	% dead or declining
Ilex verticillata	1	1	2	9%
Rosa carolina	0	3	3	33%
Sambucus canadensis	1*	2	3	14%
Vaccinium corymbosum	0	5	5	23%
Myrica pensylvanica	2	1*	3	14%
Cornus racemosa	1	1	2	9%
Diervilla lonicera	4	7	11	52%
Comptonia peregrina	8 dead, 7 missing	1	16	73%
Spiraea alba var. *latifolia*	1	1	2	9%
Viburnum dentatum	1	2	3	14%
Viburnum nudum var. *cassinoides*	0	1*	1	5%

Table 13. Number of shrubs that were dead or were in serious decline on July 12, 2004, two years after planting. A total of nine *R. carolina* were planted, and twenty-two of all other species. Plants denoted by an asterisk could clearly be attributed to human influences (pulled out of the ground, run over by a car, sat on, etc…). These numbers do not reflect an entirely destroyed planting at campsite #47.

No *Vaccinium corymbosum* had died after two years, but five shrubs were near death. This is due to extensive herbivory (determined to be by hares). The damage we observed ranged from the removal of several stem tips to complete defoliation. Many shrubs showed no disturbance, but those that were attacked in one or both seasons suffered severe damage that will likely kill the plants.

3.3 Plant Performance

We measured plant growth at three separate times to provide information about overall performance. Data collected on plant growth (presented as magnitude of change with a value >1 indicating growth, a value =1 indicating no change, and a value <1 indicating a decline in size) is summarized in Tables 14 & 15. Table 14 includes all living shrubs at all planting areas, measured at the beginning and end of the 2003 growing season. Table 15 contains data specific to only five locations and compares shrub size at the beginning of 2003 with the beginning of 2005. This smaller selection of locations was chosen because they were sites that have been closely monitored by a volunteer since installation. We also chose to narrow the scope of our investigation to allow closer investigation of all variables for each of these sites (PAR, pH, and other soil factors).

While general trends appear (for example, *Cornus racemosa* had positive growth at all locations), we have reservations about how accurately the data reflects actual plant growth. We estimated volumes using one height and two width measurements, and within these estimated volumes there were highly variable amounts of negative space. Other methods of measurement were discussed prior to measuring, as well as throughout experiments, but none were entirely satisfactory. One method involved measuring three terminal shoots on each shrub. While perhaps more accurate in quantifying actual growth, in the campground setting we were not willing to take the risk of losing data because terminal shoots might be damaged by campers, herbivory, winterkill, or insect damage. The tendency of *Sambucus canadensis* to replace the previous year's stems with new shoots each year during establishment also excluded use of this method.

Species	Lowest	Highest	Mean	# of Shrubs	% Survival
Ilex verticillata	0.4	7.0	2.5	22	100%
Rosa carolina	1.3	3.2	1.8	9	100%
Sambucus canadensis	0.9	24.5	8.5	22	100%
Vaccinium corymbosum	0.4	5.8	2.1	21	95%
Myrica pensylvanica	0.7	3.5	1.7	21	95%
Cornus racemosa	1.6	28.4	8.6	22	100%
Diervilla lonicera	0.9	5.6	1.6	21	100%
Comptonia peregrina	0.006	7.2	1.9	16	73%
Spiraea alba var. *latifolia*	1.2	11.2	5.0	22	100%
Viburnum dentatum	0.4	19.1	3.9	22	100%
Viburnum nudum var. *cassinoides*	1.0	13.4	4.9	22	100%

Table 14. Magnitude of change for all 22 campsite plantings after one growing season. Change was calculated by dividing volume estimates measured November 1, 2003 by volume estimates measured May 2, 2003. Values do not include shrubs that died. The number of plants included in the mean are indicated.

Species	Lowest	Highest	Mean	# of Shrubs
Ilex verticillata	0.1	20.1	4.8	5
Rosa carolina	0.7	0.9	0.8	2
Sambucus canadensis	0.001	4.8	1.4	5
Vaccinium corymbosum	0.08	1.5	0.8	4
Myrica pensylvanica	0.007	2.2	0.8	4
Cornus racemosa	4.8	17.3	12.7	4
Diervilla lonicera	0.1	3.3	1.0	4
Comptonia peregrina	-	-	-	0
Spiraea alba var. *latifolia*	0.4	20.8	6.2	5
Viburnum dentatum	0.3	9.2	2.9	4
Viburnum nudum var. *cassinoides*	2.2	15.6	7.3	4

Table 15. Magnitude of change for five selected campsites (56, 74, 95, 123, 160) after two full growing seasons. Change was calculated by dividing volume estimates measured June 13, 2005 by volume estimates measured May 2, 2003. Values do not include shrubs that died. The number of plants included in the mean are indicated.

3.4 Recommendations

While our measurements do not lead to statistical formulas for recommendations, observations provide valuable information about proper site location for individual species. Based upon our observations of plant performance and problems, Table 16 summarizes our recommendations for campsite plantings.

Species – Latin Name	*Common Name*
Cornus racemosa	Gray Dogwood
Ilex verticillata	Winterberry Holly
Sambucus canadensis	American Elderberry
Spiraea alba var. *latifolia*	Meadowsweet
*Diervilla lonicera**	Dwarf Bushhoneysuckle
*Comptonia peregrina**	Sweetfern
Myrica pensylvanica	Northern Bayberry

Table 16. Recommended shrubs for planting at campsites in Blackwoods Campground. An asterisk denotes plants that performed poorly in our trials but are recommended for more extensive trials based on the performance of natural colonies in the campground, many in areas adjacent to our plantings.

3.4.1 Recommended Species

Cornus racemosa was perhaps the most versatile species examined. Nearly all shrubs established well, and after the second growing nearly every plant had more than doubled in size, with a mean increase in size of 8.6 times. After two full growing seasons, at the five locations re-sampled four plants had increased more than 4-fold, with a mean increase of 12.7 times. The shrub at campsite 74 was missing in June of 2005, but had been in moderate condition when observed in July of 2004, thus I cannot explain the disappearance. This species showed very few problems, one shrub had a small amount of powdery mildew and another experienced minor leaf herbivory from small, unidentified black caterpillars. When observed in the spring of 2004, only two shrubs had died. One had been pulled out of the ground, roots and all, the other died for unknown reasons. Gray stemmed dogwood appears to do well in all conditions tested and can be planted nearly anywhere in the campground. It also has beautiful orange and red fall colors that can be enjoyed by the brave souls who camp in late October.

Ilex verticillata grows throughout the campground, most often in wet areas. All but one planted shrub survived through to July 2004. Most plants appeared healthy and average growth increase was 2.5 times at the end of the first growing season in 2003, and 4.8 times by the spring of 2005. The only problem noticed was a small bit of powdery mildew on one plant and some dieback in mid-June of 2005, presumed to be winterkill. This plant is especially recommended for wetter areas where many other species will not perform well – but it is highly versatile and will also grow in moderately dry areas once established. Winterberry holly can grow 6-8 feet in height and should be planted towards the back of any planting to prevent it shading out smaller species.

Sambucus canadensis in Loop A grows mostly along the perimeter road, or in the forested area above campsites 6,8,and 9. The shrubs planted for evaluation did well, with an average increase in size of 8.5 times at the end of 2003. The five shrubs re-measured in late spring of 2005 only averaged an increase of 1.4 times between May of 2003 and June of 2005, due to the *S. canadensis'* habit of replacing old stems with new growth from the ground every year. This observed pattern could be due to transplant stress as new roots are grown and the plant becomes established. Shrubs previously established in the campground did show some shoot growth coming from the ground, but the majority of new growth came from existing above ground stems. We also spotted suckers growing up to two feet away from plants at all 5 sites measured in June of 2005. *S. canadensis* has a colonizing growth habit and may be good for monoculture plantings around individual campsites. It is often a large shrub with mature height quite variable between 5 and 12 feet and will grow in locations ranging from full sun to mostly shady.

Spiraea alba var. *latifolia* is recommended for planting. There were only three fatalities, and by the end of the first growing seasons all plants had grown with an average increase of five times. At the beginning of season three (June, 2005), the mean had increased to 6.2 (with only one shrub actually decreasing in size). We noticed one plant with a small amount of gall damage at campsite 90, and there was a little powdery mildew after the wet spring in 2004, but no serious problems. *S. alba* var. *latifolia* prefers sunny locations, though it will tolerate partial shade, and will grow in both wet and dry locations once established.

3.4.2 Specific Recommendations

Diervilla lonicera in our plantings did not perform well, with a 50% mortality rate and disappointing growth. As previously discussed, this was caused by severely potbound plants at the time of planting. The plants we purchased were very pot bound, with completely constrained root balls and no soil left in the pots. Had these been better quality stock I expect our results would have been very positive. *D. lonicera* is well suited to the campground and can be seen growing profusely around bathroom facilities and roadsides where there is more sun. *D. lonicera* should not be planted in deep shade, but a location receiving partial to full sun will support healthy colonies.

Comptonia peregrina specimens in this study performed very poorly, with more than 50% dying before the end of the second growing season and few survivors showing signs of establishing well. This disappointing performance is attributable to the condition of the initial plants, described in section 3.1.2. *C. peregrina* is a hardy shrub that appears in colonies throughout the campground and Mount Desert Island, especially along roadsides. With quality seedlings and placement in sun/partial sun it will establish very well and be a vigorous grower. It should also be noted that this species only grows 2 to 3 feet in height and will not provide a full visual screen.

Myrica pensylvanica showed a small but consistent increase in size between May and November of 2003, averaging a magnitude of change of 1.7. Over time the picture changed a bit and the five plants examined in June of 2005 averaged a decrease in size. *M. pensylvanica* had few insect/disease problems, only one plant appeared to have a leaf mining insect. Three shrubs died, but two showed signs of vegetative spreading by the summer of 2004. There are large colonies of *M. pensylvanica* around the amphitheatre between Loops A & B, as well as several roadside locations within Loop A, suggesting that this is a suitable plant for the campground but that successful establishment and growth require full or nearly full sun.

3.4.3 Species to avoid

Viburnum dentatum and *Viburnum nudum* var. *cassanoides* were evaluated for planting but both have been eliminated from this list due to the increasing problem of *Pyrrhalta viburni* Paykull (Viburnum Leaf Beetle) in Maine. There are severe signs of damage to *V. dentatum* visible at Park Headquarters, and while damage within the campground appears to still to be minimal, we observed egg cases present on both *Viburnum* species in Loop A. In other regards these shrubs are well adapted to campground conditions, but the beetles will become an increasing problem and will threaten not only newly planted shrubs, but also shrubs currently established throughout the campground.

Vaccinium corymbosum should not be planted because it is prone to herbivory (determined to be caused by hares). The damage we observed ranged from the removal of several stem tips to complete defoliation. Growth at the end of 2003 was a promising average of 2.1 (a doubling in size). The five plantings re-evaluated in June of 2005, however, averaged a decrease with a mean of 0.8 because of extensive damage by hares and poor recovery. The high-bush blueberry also does not grow well in wet areas (such as campsite 56), but our reservations about the shrub are largely because of herbivory problems.

Rosa Carolina did not have the benefit of being planted at all campsites due to limited availability. Nine shrubs were planted and all survived, but none appeared to be thriving and several were nearly completely defoliated from insect damage. Roses in general tend to be riddled with pests, from galls and rusts to caterpillar and other insect infestations (Dirr 1990). The roses growing wild in the campground also displayed insect damage, though not as severely as the specimens we planted for evaluation. The plants we purchased for the experiment were pot-bound (not as significantly as the *Diervilla lonicera*), and this may be a factor causing poor establishment and extra stress, making the shrubs more susceptible to damage. The poor performance of both planted and established shrubs is the cause for removing it from the list of recommended shrubs. After one growing season, shrubs nearly doubled in size, but of the 5 locations re-measured in 2005, only two of four roses remained alive, and both had decreased in size.

4. Summary

We evaluated eleven native shrub species in very austere conditions for their suitability to plant at campsites within Loop A of Blackwoods Campground. Mineral soil is nutritionally poor (see Appendix D) and the soil was not amended, nor was fertilizer applied. Our results may not fully represent the potentials of these species, because they were still in the establishment phase while most data was being collected, as well as the difficulties with our chosen method of measurement, discussed in 3.3.

During establishment, plants grow roots into the surrounding soil to draw water and nutrients from the soil in sufficient quantities to support existing shoots, as well as new growth. During this phase most plants will reduce shoot growth in favor of root growth, thus falsely indicating small increases in size when only shoots are measured. In the campground where there is summer drought and low nutrition, shrubs may still be struggling to establish, a full three years after being planted. An argument could be made that fertilizer would have enhanced plant growth and possibly shortened this establishment period. However, increased shoot growth with fertilizer during late July into August without sufficient supplemental watering might have caused more shrubs (with inadequate root systems) to die during those dry summer weeks.

The seven species on our final list of recommendations have either proven their vigor in natural stands throughout the campground, or proven their suitability by showing positive shoot growth and good health, even given the harsh conditions imposed. Once fully established, these shrub species will be able to revegetate the sparse understory of Blackwoods Campground and help restore campsite privacy and beauty.

Bibliography

Abouguendia, Z. M. and R. E. Redmann (1979). Germination and early seedling growth of four conifers on acidic and alkaline substrates. Forest Sci. **25**(2): 358-360.

Ahlgren, C. E. and I. F. Ahlgren (1981). Some effects of different forest litters on seed germination and growth. can. J. For. Res. **11**: 710-714.

Ammer, C., R. Mosandl and H. E. Kateb (2002). Direct seeding of beech (*Fagus sylvatica* L.) in Norway spruce (*Picea abies* [L.] Karts.) stands - effects of canopy density and fine root biomass on seed germination. Forest Ecology and Management **159**: 59-72.

Baldwin, H. I. (1934). Germination of the red spruce. Plant Physiology **9**: 491-532.

Battles, J. J. and T. J. Fahey (2000). Gap dynamics following forest decline: a case study of red spruce forests. Ecological Applications **10**(3): 760-774.

Björkman, O. and S. B. Powles (1984). Inhibition of photosynthetic reactions under water stress: interaction with light level. Planta **161**: 490-504.

Blum, B. M. (1990). *Picea rubens* Sarg. Red Spruce. Silvics of North America: Volume 1. Conifers. Agriculture Handbook 654. Washington, D.C., USDA Forest Service. **1**: 250-259.

Brissette, J. C. (1996). Effects of intensity and frequency of harvesting on abundance, stocking and composition of natural regeneration in the Acadian Forest of Eastern North America. Silva Fennica **30**(2-3): 301-314.

Brix, H. (1979). Effects of plant water stress on photosynthesis and survival of four conifers. Can. J. For. Res. **9**: 160-165.

Burdett, A. N., D. G. Simpson and C. F. Thompson (1983). Root development and plantation establishment success. Plant and Soil **71**: 103-110.

Cornett, M. W., K. J. Puettmann and P. B. Reich (1998). Canopy type, forest floor, predation, and competition influence conifer seedling emergence and early survival in two Minnesota conifer-deciduous forests. Can. J. For. Res. **28**: 196-205.

Dirr, M. A. (1990). Manual of Woody Landscape Plants: Their Identification, Ornamental Characteristics, Culture, Propagation, and Uses. Champaign, Illinois, Stipes Publishing Company.

Farmer, R. E., Jr. (1997). Seed Ecophysiology of Temperate and Boreal Zone Forest Trees. Delray Beach, Florida, St. Lucie Press.

Fernald, M. L. (1950). Gray's Manual of Botany. Boston, American Book Company.

Fisher, R. F. and D. Binkley (2000). Ecology and Management of Forest Soils, John Wiley & Sons, Inc.

Foulds, E. H. (1996). Cultural Landscape Report for Blackwoods and Seawall Campgrounds Acadia National Park. Boston, Massachusetts, Olmsted Center for Landscape Preservation.

Frank, R. M. (1990). *Abies balsamea* (L.) Mill. Balsam Fir. Silvics of North America: Volume 1. Conifers. Agriculture Handbook 654. Washington, D.C., USDA Forest Service. **1:** 26-35.

Greenwood, M. S. and D. McConville (2002). A comparative study on the effects of temperature and moisture stress on the germination and seedling survival of balsam fir and red spruce. CFRU Annual Report, University of Maine.

Grossnickle, S. C. and S. Fan (1999). Genetic variation in response to drought of interior spruce (*Picea glauca* (Moench) Voss x *P. engelmannii* Parry ex. Engelm.). Scandinavian Journal of Forest Research **14**: 251-261.

Grossnickle, S. C. and J. Heikurinen (1989). Site Preparation: Water relations and growth of newly planted jack pine and white spruce. New Forests **3**: 99-123.

Grossnickle, S. C. and J. E. Major (1994). Interior spruce seedlings compared with emblings produced from somatic embryogenesis. III. Physiological response and morphological development on a reforestation site. Can. J. For. Res. **24**: 1397-1407.

Hawkins, B. J., H. J. Guest and D. Kolotelo (2003). Freezing tolerance of confiner seeds and germinants. Tree Physiology **23**: 1237-1246.

Helenius, P., J. Louranen, R. Rikala and K. Leinonen (2002). Effect of drought on growth and mortality of actively growing norway spruce container seedlings planted in summer. Scandinavian Journal of Forest Research **17**: 218-224.

Hightshoe, G. L. (1988). Native Trees, Shrubs, and Vines for Urban and Rural America. New York, Van Nostrand Reinhold Co.

Houle, G. (1992). The reproductive ecology of *Abies balsamea*, *Acer saccharum* and *Betula alleghaniensis* in the Tantaré Ecological Reserve, Québec. Journal of Ecology **80**: 611-623.

Jagels, R. and M. E. Day (2004). The adaptive physiology of *Metasequoia* to Eocene high-latitude environments. The Evolution of Plant Physiology - from whole plants to ecosystems. A. R. Hemsley and I. Poole. London, UK, Elsevier Academic Press.

Johnson, D. W., H. Van Miegroet, S. E. Lindberg, D. E. Todd and R. B. HArrison (1991). Nutrient cycling in red spruce forests of the Great Smoky Mountains. Can.. J. For. Res. **21**: 769-787.

Jordan, G. B. (1998). Soil Survey of Hancock County Area, Maine, USDA, NRCS, Maine Agriculture & Forest Experiment Station and Maine Soil and Water Conservation Commission.

Klein, R. M., T. D. Perkins, J. Tricou, A. Oates and K. Cutler (1991). Factors affecting red spruce regeneration in declining areas of Camels Hump Mountain, Vermont. American Journal of Botany **78**(9): 1191-1198.

Koroleff, A. (1954). Leaf Litter as a Killer. Journal of Forestry **52**: 178-182.

Kozlowski, T. T. (1971). Growth and development of trees, Vol 1: Seed germination, ontogeny and shoot growth. NY, Academic Press.

Kozlowski, T. T. (2002). Physiological ecology of natural regeneration of harvested and disturbed forest stands: implications for forest management. Forest Ecology and Management **158**: 195-221.

Landhäusser, S. M. and V. J. Lieffers (2001). Photosynthesis and carbon allocation of six boreal tree species grown in understory and open conditions. Tree Physiology **21**: 243-250.

Landis, R. M. and D. R. Peart (2005). Early performance predicts canopy attainment across life histories in subalpine forest trees. Ecology **86**(1): 63-72.

Lee, C. S., J. H. Kim, H. Yi and Y. H. You (2004). Seedling establishment and regeneration of Korean red pine (*Pinus densiflora* S.et Z.) forests in Korea in relation to soil moisture. Forest Ecology and Management **199**: 423-432.

Leverenz, J. W. (1995). Shade shoot strudture of conifers and the photosynthetic response to light at two CO_2 partial pressures. Functional Ecology **9**: 413-421.

Marchand, P. J., F. L. Goulet and T. C. Harrington (1986). Death by attrition: a hypothesis for wave mortality of subalpine *Abies balsamea*. Can. J. For. Res. **16**: 591-596.

Matthes, U., J. A. Gerrath and D. W. Larson (2003). Experimental restoration of disturbed cliff-edge forests in Bruce Peninsula National Park, Ontario, Canada. Restoration Ecology **11**(2): 174 - 184.

McIntosh, R. P. and R. T. Hurley (1964). The Spruce-Fir Forests of the Catskill Mountains. Ecology **45**(2): 314-326.

Meng, X. and R. S. Seymour (1992). Influence of soil drainage on early development and biomass production of young, herbicide-released fir-spruce stands in north central Maine. Can. J. For. Res. **22**: 955-967.

Minnesota, E. C. L. o. (1974). Book catalog of the Environmental Conservation Library, Minneapolis Public Library. Chicago, American Library Association.

Moore, B. (1926). Influence of certain soil and light conditions on the establishment of reproduction in northeastern conifers. Ecology **VII**(2): 191-220.

Oosting, H. J. and W. D. Billings (1951). A comparison of virgin spruce-fir forest in the Northern and Southern Appalachian system. Ecology **32**(1): 84-103.

Papageorgiou, K. (2001). A combined park management framework based on regulatory and behavioral strategies: Use of visitors' knowledge to assess effectiveness. Environmental Management **28**(1): 61-73.

Parent, S., M.-J. Simard, H. Morin and C. Messier (2003). Establishment and dynamics of the balsam fir seedling bank in old forests of northeastern Quebec. Can. J. For. Res. **33**: 597-603.

Peters, S., S. Boutin and E. Macdonald (2003). Pre-dispersal seed predation of white spruce cones in logged boreal mixedwood forest. Can. J. For. Res. **33**: 33-40.

Place, I. C. M. (1955). The influence of seed-bed conditions on the regeneration of spruce and balsam fir. Bull.117. Ottawa, Canada, Department of Northern Affairs and National Resources, Forestry Branch - Forest Research Division.

Randall, A. G. (1974). Seed dispersal into two spruce-fir clearcuts in Eastern Maine. Research in the Life Sciences **21**(8): 1-15.

Randall, A. G. (1976). Natural regeneration in two spruce-fir clearcuts in Eastern Maine. Research in the Life Sciences **23**(13): 1-10.

Royo, A., L. Gil and J. A. Parados (2001). Effect of water stress conditioning on morphology, physiology and field performance of *Pinus halepensis* Mill. seedlings. New Forests **21**: 127-140.

Sauer, L. J. (1998). The Once and Future Forest: A Guide to Forest Restoration Strategies, Island Press.

Scherbatskoy, T., R. M. Klein and G. J. Badger (1987). Germination responses of forest tree seed to acidity and metal ions. Environmental and Experimental Botany **27**(2): 157-164.

Schimpf, D. J. and N. P. Danz (1999). Light passage through leaf litter: variation among northern hardwood trees. Agricultural and Forest Meterology **97**: 103-111.

Seiler, J. R. and B. H. Cazell (1990). Influence of water stress on the physiology and growth of red spruce seedlings. Tree Physiology **6**: 69-77.

Simard, M.-J., Y. Bergeron and L. Sirois (2003). Substrate and litterfall effects on conifer seedling survivorship in southern boreal stands of Canada. Can. J. For. Res. **33**: 672-681.

Sokol, K. A., M. S. Greenwood and W. H. Livingston (2004). Impacts of long-term diameter-limit harvesting on residual stands of red spruce in Maine. Northern Journal of Forestry **21**(2): 69-73.

Thomas, P. A. and R. W. Wein (1985). Water availability and the comparative emergence of four conifer species. Canadian Journal of Botany **63**: 1740-1746.

Walsh, R. P. D. and P. J. Voigt (1977). Vegetation litter: an underestimated variable in hydrology and geomorphology. Journal of Biogeography **4**: 253-274.

Williams, S. T. and T. R. G. Gray (1974). Decomposition of litter on the soil surface. Biology of Plant Litter Decomposition. C. H. Dickinson and G. J. F. Pugh. New York, Academic Press. **2:** 611-632.

APPENDICES

Appendix A

OBSERVATIONS OF 1m^2 CAGES AND REFERENCE PLOTS WITHIN LOOP A OF BLACKWOODS CAMPGROUND TO ASCERTAIN THE EFFECTS OF EXCLUDING TRAMPLING ON TREE SEEDLING RECRUITMENT

The sites were selected for diversity of conditions, including a high-traffic walkway, a remote low-traffic area, and a site covered with deciduous leaf litter. The cage and the adjacent, uncaged reference plot in an open location between campsites 146 and 149 had very little success, with one maple seedling in July 8, 2002 that was gone by September. The next year there were again no seedlings. The cage with deciduous leaf litter near campsite 82 had 11 maple and 26 birch seedlings in July of 2002, but only 8 maple and 13 birch by September, showing a distinct drop in seedling numbers. The reference plot to this cage, also covered with deciduous litter, started with 2 maple and 12 birch seedlings. September observations found 1 maple and only 4 birch, as well as 1 Picea, apparently late to germinate. Two cages, not covered by deciduous litter, were dominated by spruce seedlings. The first cage, placed in campsite 66, contained 27 spruce and 5 maple seedlings in early July of 2002. By September of the same year seedling counts had dropped to 2-4 spruce and only 1 maple. The reference plot showed a similar decline from 13 spruce and 3 maples in July to 0 spruce and 2 maples in September. The other cage, in the woods behind campsite 32, began with 13 new spruce seedlings, one spruce appearing to be 2-4 years old (though still less than 10cm high), 1 fir and 1 ash. Only two young spruce, the same older spruce, and one fir survived to September. There is no September data for the reference plot beside the cage. A summary of these results is presented in Table 17.

Cage location	July 8, 2002	August 27, 2002	May 3, 2003	July 12, 2004
Cage @ site 66	27 spruce 5 maple	2 spruce 1 maple	3 spruce 1 ash	0 spruce seen
Reference plot	13 spruce 3 maple 1 unidentified	0 spruce seen 2 maple	1 maple	
Cage @ 82/84 Deciduous litter	11 maple 26 birch	8 maple 13 birch	17, mix of ash and maple	
Reference plot	2 maple 12 birch	1 maple 4 birch 1 spruce		
Cage @ 97/98	4 birch 3 maple 1 fir	4 birch 3 maple 1 fir	6 maple breaking bud 1 fir	Several birch and maple Several little spruce – 1 fir
Reference plot	3 birch 6 maple 1 fir, several yrs old	6 birch 5 maple	5 maple 1 ash 1 fir, tattered, several yrs old	
Cage @ 146	1 maple	0	0	
Reference plot	1 unidentified	0	0	Lots of tiny spruce
Cage @ 32/29	13 spruce 1 ash 1 fir	1 older spruce 1 spruce 2 fir	7 spruce 1 spruce 2-4 yr 1 fir yr old	Lots of small spruce only 1-3 weeks old
Reference plot	6 spruce 4 fir		2 spruce yr old 1 spruce 2-4 yr 3 fir yr old	1 spruce 3-4 yr

Table 17. Location of five cages placed within Loop A of Blackwoods Campground and seedling counts on indicated dates.

Notes: Plot at site 66 was covered with 30-40% moss; plot between sites 82 & 84 contained lots of deciduous litter; plot behind sites 32 and 29 was very shady with lots of rocky ledge and exposed roots.

Appendix B

CHAPTER ONE ANALYSIS OF VARIANCE

Abies balsamea and *Picea rubens* seed germination
under 6 watering treatments, in growth chambers N:48

Source	Sum-of-Squares	DF	Mean-square	F value	P
Block	16.3333333	1	16.3333333	2.14	0.1563
Species	40.3333333	1	40.3333333	5.29	0.0305
Treatment	188.9166667	5	37.7833333	4.96	0.0029
Block*species	4.0833333	1	4.0833333	0.54	0.4714
Species*trt	42.6666667	5	8.5333333	1.12	0.3768
Block*trt	13.6666667	5	2.7333333	0.36	0.8717
Block*species*trt	48.9166667	5	9.7833333	1.28	0.3037

Days to germination of *Abies balsamea* and *Picea rubens*
under 6 watering treatments, in growth chambers N:799

Source	Sum-of-Squares	DF	Mean-square	F value	P
Species	1.29245898	1	1.29245898	12.19	0.0013
Treatment	2.71489841	5	0.54297968	5.12	0.0012
Species*trt	0.10840422	5	0.02168084	0.20	0.9585

Abies balsamea seed germination under 5 watering
treatments, outdoors N:20

Source	Sum-of-Squares	DF	Mean-square	F value	P
Water trt	17284.80000	4	4321.20000	53.13	<.0001

Dry mass of *Abies balsamea* and *Picea rubens* seedlings,
15 weeks of age, under 6 watering treatments, in growth chambers N:48

Source	Sum-of-Squares	DF	Mean-square	F value	P
Block	350.3696395	1	350.3696395	350.37	<.0001
Species	496.0406288	1	496.0406288	496.04	<.0001*
Treatment	591.6718045	5	591.6718045	118.33	<.0001*
Block*species	613.0668632	1	613.0668632	613.07	<.0001
Species*trt	60.1257956	5	12.0251591	12.03	<.0001
Block*trt	8.6964875	5	1.7392975	1.74	0.1640
Block*species*trt	3.1302139	5	0.6260428	0.63	0.6815

*Dry mass of *Abies balsamea* and *Picea rubens* seedlings, 15 weeks of age, under 6 watering treatments, in growth chambers, using Type III MS, block*trt and block*species as Error terms for treatment and species, respectively N:48

Source	Sum-of-Squares	DF	Mean-square	F value	P
Treatment	123.7782860	5	24.7556572	5.60	0.0409
Species	172.5279600	1	172.5279600	3.04	0.3315[§]

[§]Dry mass of *Abies balsamea* and *Picea rubens* seedlings, 15 weeks of age, under 6 watering treatments, in growth chambers, with treatment removed to examine just species differences N:48

Source	Sum-of-Squares	DF	Mean-square	F value	P
Block	0.02455265	1	0.02455265	15.39	0.0003
Species	0.17590987	1	0.17590987	110.29	<.0001
Block*species	0.05785185	1	0.05785185	36.27	<.0001

Dry mass of *Abies balsamea* seedlings, 11.5 weeeks of age,
under 5 watering treatments, outdoors N:12

Source	Sum-of-Squares	DF	Mean-square	F value	P
Treatment	0.00018727	2	0.00009364	19.30	0.0006

Root:shoot ratios of *Abies balsamea* and *Picea rubens* seedlings,
15 weeks of age, under 6 watering treatments, in growth chambers N:42

Source	Sum-of-Squares	DF	Mean-square	F value	P
Block	0.00971511	1	0.00971511	2.11	0.1589
Species	0.77297219	1	0.77297219	168.21	<.0001*
Treatment	0.05854150	5	0.05854150	2.55	0.0551*
Block*species	0.08976652	1	0.08976652	19.53	0.0002
Species*trt	0.05115221	5	0.05115221	2.23	0.0847
Block*trt	0.07785179	5	0.07785179	3.39	0.0186
Block*species*trt	0.04732684	5	0.04732684	2.06	0.1060

*Root:shoot ratios of *Abies balsamea* and *Picea rubens* seedlings, 15 weeks of age, under 6 watering treatments, in growth chambers, using Type III MS, block*trt and block*species as Error terms for treatment and species, respectively N:42

Source	Sum-of-Squares	DF	Mean-square	F value	P
Treatment	0.05854150	5	0.01170830	0.75	0.6190
Species	0.77297219	1	0.77297219	8.61	0.2091[§]

[§] Root:shoot ratios of *Abies balsamea* and *Picea rubens* seedlings, 15 weeks of age, under 6 watering treatments, in growth chambers, with treatment removed to examine just species differences N:48

Source	Sum-of-Squares	DF	Mean-square	F value	P
Block	0.00971511	1	0.00971511	1.24	0.2718
Species	0.77297219	1	0.77297219	98.54	<.0001
Block*species	0.08976652	1	0.08976652	11.44	0.0015

Root:shoot ratios of *Abies balsamea* seedlings, 11.5 weeks of age,
Under 5 watering treatments, outdoors N:12

Source	Sum-of-Squares	DF	Mean-square	F value	P
Treatment	0.03687339	2	0.01843669	16.85	0.0009

Dry mass of *Abies balsamea* and *Picea rubens* seedlings, 2 years of age, under 7 organic layer depth treatments N:42

Source	Sum-of-Squares	DF	Mean-square	F value	P
Species	2.51415846	1	2.51415846	35.98	<.0001
Treatment	6.38927489	6	1.06487915	15.24	<.0001
Species*trt	1.64473064	6	0.27412177	3.92	0.0057

Root:shoot ratios of *Abies balsamea* and *Picea rubens* seedlings, 2 years of age, under 7 organic layer depth treatments N:42

Source	Sum-of-Squares	DF	Mean-square	F value	P
Species	589.3711693	1	589.3711693	589.37	<.0001
Treatment	193.4543233	6	32.2423872	32.24	<.0001
Species*trt	7.3801505064	6	1.2300251	1.23	0.3210

Appendix C

NATIVE SHRUB EVALUATION CAMPSITE LOCATIONS
AND NEW CAMPSITE NUMBERS

Campsites planted for native shrub evaluation	*New campsite number*
7	A6
17	A15
28	A25
22	A20
38	A35
47	A42
56	A50
74	A67
75	A68
90	A83
92	A85
95	A88
96	A89
106	A98
110	A103
117	A111
123	Was eliminated – now adjacent to A115
124	A116
130	A123
141	A134
154	A145
160	A152

Table 18. List of campsites where native shrubs were evaluated. Campsites were re-numbered in the Spring of 2005, and several campsites were closed. The numbers that existed during the duration of this study were utilized throughout this document. This table presents the most current numbering of these locations for future use.

Appendix D

SOIL ANALYSIS RESULTS FOR SAMPLES COLLECTED FROM EACH CAMPSITE WHERE NATIVE SHRUBS WERE PLANTED

Sample Number	*Campsite Number*	*Soil pH*	*% LOI*	*P*	*K*	*Mg*	*Ca*	*Na*	*Species*
1	7	4.9	8.6	5.2	83	83	434	35	
2	17	5.2	4.9	2.4	49	28	181	16	CR
3	17	5.1	3.8	2.6	42	26	154	14	All others
4	28	5.8	9.4	4.0	152	112	1435	33	
5	33	5.1	4.6	3.3	37	37	163	17	
6	38	4.2	8.3	4.3	60	47	124	33	
7	47	4.8	8.3	4.8	87	26	138	30	VD, DL
8	47	5.2	6.0	3.3	53	21	122	28	All others
9	56	5.1	8.0	3.6	58	36	219	43	
10	74	5.3	2.4	0.9	20	6	61	8	
11	75	5.3	2.3	1.8	36	21	130	15	
12	90	5.1	5.7	3.8	56	31	194	20	
13	92	5.3	6.2	2.2	32	16	106	18	
14	95	5.5	2.1	1.1	28	11	75	11	
15	96	5.2	1.8	1.4	17	9	69	10	DL, SC, CP, SL
16	96	5.1	1.7	0.9	18	6	59	9	All others
17	106	5.4	2.1	1.2	29	12	108	11	
18	110	5.3	4.6	2.1	47	22	150	17	VN, CP
19	110	4.3	27.5	8.1	96	96	369	49	RC, IV, VC, MP, DL, SL
20	110	4.4	11.8	3.9	54	44	185	30	VD, SC, CR
21	117	4.7	4.4	2.3	33	23	91	15	
22	123	5.2	3.1	2.1	30	18	95	12	
23	124	5.2	3.1	1.5	31	12	73	13	
24	130	4.8	6.0	3.2	39	25	125	23	
25	141	4.8	6.0	1.7	38	14	76	16	CR, CP, MP
26	141	5.1	4.4	1.2	34	9	67	13	All others
27	154	5.3	3.7	1.2	34	16	147	13	
28	160	3.7	55.4	20.0	254	187	280	168	SC, VC
29	160	4.0	9.1	4.2	80	38	98	36	IV, DL, VD
30	160	4.9	13.4	1.3	44	13	84	27	VN, SL, CP
31	160	4.3	15.6	3.6	66	26	97	34	CR, MP

Table 19. Analysis results for soil samples taken on July 15, 2002 when planting shrubs at campsite locations. For campsites with multiple soil samples, the species' planted in each soil type are indicated by the first letters of their genus and the specific epitaph (ie: IV = *Ilex verticillata*).
Analysis performed by the Maine Soil Testing Service, University of Maine, Orono. pH was measured in distilled water. Organic matter was measured by loss on ignition (LOI) at 375°C. Available nutrients were extracted in pH 4.8 ammonium acetate (Modified Morgan method) and measured by plasma emission (ICP). Nutrient levels are expressed as parts per million (ppm or mg/kg) on a dry soil basis.

Appendix E

CHAPTER TWO REGRESSION TABLES

Ilex verticillata

	df	SS	MS	F	Significance F
Regression	8	10.4017	1.30021	0.30666	0.95
Residual	13	55.1185	4.23989		
Total	21	65.5202			

	Coefficients	Standard Error	t Stat	P-value
Intercept	8.558	13.505	0.634	0.537
PAR	0.000	0.003	0.062	0.952
pH	-1.025	2.483	-0.413	0.687
%LOI	0.133	0.197	0.677	0.510
P	0.164	1.308	0.126	0.902
K	-0.005	0.085	-0.061	0.952
Mg	-0.051	0.090	-0.568	0.580
Ca	0.003	0.011	0.258	0.801
Na	-0.043	0.115	-0.369	0.718

Sambucus canadensis

	df	SS	MS	F	Significance F
Regression	8	388.8	48.6	1.03	0.461
Residual	13	613.1	47.16		
Total	21	1002			

	Coefficients	Standard Error	t Stat	P-value
Intercept	-35.863	35.12	-1.02	0.326
PAR	-0.002	0.007	-0.26	0.801
pH	10.132	6.809	1.488	0.161
%LOI	2.003	1.111	1.803	0.095
P	-2.319	4.316	-0.54	0.600
K	-0.420	0.319	-1.32	0.211
Mg	0.135	0.305	0.444	0.664
Ca	0.014	0.029	0.493	0.630
Na	0.088	0.417	0.211	0.836

***Rosa carolina*§**

	df	SS	MS	F	Significance F
Regression	3	0.652	0.217	0.776	0.565
Residual	4	1.119	0.28		
Total	7	1.771			

	Coefficients	Standard Error	t Stat	P-value
Intercept	-0.649126	3.332	-0.19	0.855
PAR	-0.001888	0.001	-1.27	0.274
pH	0.5126928	0.621	0.826	0.455
%LOI	0.05606459	0.043	1.298	0.264

***Rosa carolina*§**

	df	SS	MS	F	Significance F
Regression	5	1.128	0.226	0.701	0.676
Residual	2	0.643	0.322		
Total	7	1.771			

	Coefficients	Standard Error	t Stat	P-value
Intercept	1.710	1.406	1.216	0.348
P	0.280	1.198	0.234	0.837
K	-0.046	0.075	-0.61	0.604
Mg	-0.025	0.100	-0.25	0.825
Ca	0.005	0.006	0.792	0.512
Na	0.055	0.047	1.171	0.362

§Due to the small replication of *Rosa carolina*, all 8 variables could not be analyzed in one regression because there were only 8 surviving shrubs, so pH, %LOI and light values were conducted as one analysis and soil nutrients were a separate analysis of the same data.

Vaccinium corymbosum

	df	SS	MS	F	Significance F
Regression	8	9.283	1.16	0.332	0.937
Residual	12	41.91	3.493		
Total	20	51.2			

	Coefficients	Standard Error	t Stat	P-value
Intercept	13.212	13.87	0.953	0.359
PAR	0.003	0.003	1.148	0.274
pH	-2.030	2.524	-0.8	0.437
%LOI	0.081	0.179	0.454	0.658
P	-0.919	1.204	-0.76	0.460
K	-0.026	0.085	-0.3	0.766
Mg	-0.006	0.082	-0.07	0.943
Ca	0.004	0.010	0.362	0.724
Na	0.036	0.108	0.335	0.743

Myrica pensylvanica

	df	SS	MS	F	Significance F
Regression	8	3.933	0.492	0.757	0.646
Residual	12	7.799	0.65		
Total	20	11.73			

	Coefficients	Standard Error	t Stat	P-value
Intercept	-0.266	5.183	-0.05	0.960
PAR	0.000	0.001	-0.36	0.727
pH	0.311	0.960	0.324	0.752
%LOI	-0.102	0.073	-1.4	0.187
P	0.642	0.541	1.186	0.259
K	-0.022	0.042	-0.51	0.619
Mg	-0.011	0.035	-0.3	0.769
Ca	0.001	0.005	0.177	0.862
Na	0.027	0.047	0.570	0.579

Cornus racemosa

	df	SS	MS	F	Significance F
Regression	8	172.8	21.59	0.457	0.865
Residual	13	614.4	47.26		
Total	21	787.1			

	Coefficients	Standard Error	t Stat	P-value
Intercept	16.537	46.01	0.359	0.725
PAR	-0.011	0.008	-1.42	0.179
pH	-1.453	8.578	-0.17	0.868
%LOI	-0.415	1.153	-0.36	0.724
P	3.690	4.535	0.814	0.431
K	0.093	0.327	0.284	0.781
Mg	-0.056	0.308	-0.18	0.859
Ca	-0.010	0.035	-0.29	0.776
Na	-0.192	0.408	-0.47	0.645

Diervilla lonicera

	df	SS	MS	F	Significance F
Regression	8	6.956	0.869	0.329	0.938
Residual	12	31.68	2.64		
Total	20	38.64			

	Coefficients	Standard Error	t Stat	P-value
Intercept	5.82	11.53	0.50	0.62
PAR	0.00	0.00	0.11	0.91
pH	-0.73	2.12	-0.35	0.74
%LOI	0.01	0.20	0.06	0.95
P	1.26	1.01	1.24	0.24
K	-0.06	0.05	-1.04	0.32
Mg	-0.12	0.10	-1.21	0.25
Ca	0.01	0.01	1.13	0.28
Na	0.02	0.09	0.20	0.84

Comptonia peregrina

	df	SS	MS	F	Significance F
Regression	8	25.35	3.169	0.786	0.631
Residual	7	28.22	4.031		
Total	15	53.57			

	Coefficients	Standard Error	t Stat	P-value
Intercept	32.738	19.49	1.680	0.137
PAR	0.006	0.005	1.185	0.275
pH	-5.156	3.508	-1.47	0.185
%LOI	-0.136	0.365	-0.37	0.721
P	0.246	1.382	0.178	0.864
K	-0.408	0.213	-1.91	0.097
Mg	-0.094	0.092	-1.03	0.337
Ca	0.041	0.020	2.073	0.077
Na	0.342	0.208	1.643	0.144

***Spiraea alba* var. *latifolia**

	df	SS	MS	F	Significance F
Regression	8	74.96	9.37	0.823	0.597
Residual	13	148	11.38		
Total	21	222.9			

	Coefficients	Standard Error	t Stat	P-value
Intercept	-26.143	23.19	-1.13	0.280
PAR	-0.006	0.005	-1.29	0.219
pH	6.498	4.304	1.510	0.155
%LOI	0.063	0.258	0.245	0.811
P	-0.226	1.795	-0.13	0.902
K	-0.066	0.185	-0.36	0.726
Mg	0.134	0.148	0.902	0.383
Ca	-0.012	0.019	-0.63	0.541
Na	0.104	0.198	0.526	0.608

Viburnum dentatum

	df	SS	MS	F	Significance F
Regression	8	11.32	1.414	0.339	0.935
Residual	13	54.2	4.17		
Total	21	65.52			

	Coefficients	Standard Error	t Stat	P-value
Intercept	1.849	14.03	0.132	0.897
PAR	-0.001	0.003	-0.27	0.793
pH	0.283	2.611	0.108	0.915
%LOI	0.419	0.507	0.827	0.423
P	-0.017	1.200	-0.01	0.989
K	-0.014	0.066	-0.21	0.834
Mg	-0.018	0.089	-0.2	0.846
Ca	0.000	0.011	-0.02	0.983
Na	-0.071	0.138	-0.51	0.615

Viburnum nudum* var. *cassinoides

	df	SS	MS	F	Significance F
Regression	8	103.4	12.92	0.794	0.618
Residual	13	211.5	16.27		
Total	21	314.8			

	Coefficients	Standard Error	t Stat	P-value
Intercept	51.073	28.15	1.815	0.093
PAR	-0.001	0.005	-0.1	0.922
pH	-8.097	5.233	-1.55	0.146
%LOI	0.192	0.628	0.306	0.765
P	2.385	2.297	1.038	0.318
K	-0.211	0.235	-0.89	0.387
Mg	-0.232	0.178	-1.3	0.215
Ca	0.034	0.023	1.477	0.164
Na	-0.088	0.270	-0.33	0.749

BIOGRAPHY OF THE AUTHOR

Cristin Louise O'Brien was born in Bangor, Maine. She graduated Salutatorian from John Bapst Memorial High School in Bangor, Maine in 1995. She attended The University of Maine, Orono and graduated *summa cumme laude* in 2000 with a Bachelor of Arts in Studio Art with an Art History Minor, a Bachelor of Sciences in Landscape Horticulture with a Science Concentration, and was awarded High Honors for her artistic Honors Thesis entitled "Walls and Patterns." She became a member of Phi Kappa Phi, Phi Beta Kappa, Alpha Zeta and Golden Key fraternities.

Cristin worked for a year at DownEast Magazine as the Design and Editorial Assistant, she then returned to The University of Maine to pursue graduate studies in Landscape Horticulture in the department of Plant, Soil and Environmental Sciences.

After completing her degree she will be joining the Community Relations department at Eastern Maine Healthcare Systems as a Communications Specialist. Cristin is a candidate for the Master of Science degree in Landscape Horticulture from the University of Maine in August, 2005.