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THE UNIVERSITY OF ALBERTA

THE EFFECTS OF RIGHT-OF-WAY CLEARING ON A SUBARCTIC UNDERSTORY SHRUB: THE REGROWTH RESPONSE OF *SALIX ARBUSCULOIDES* ANDERSS. OVER THREE GROWING SEASONS.

BY

TERESA DE GROSBOIS

A THESIS
SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH
IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE
OF MASTER OF SCIENCE

DEPARTMENT OF GEOGRAPHY

EDMONTON, ALBERTA
SPRING 1989

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ISBN 0-315-52803-6

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NAME OF AUTHOR: Teresa de Grosbois

TITLE OF THESIS: The effects of right-of-way clearing on a Subarctic understory shrub: the regrowth response of *Salix arbusculoides* Anderss. over three growing seasons.

DEGREE: Master of Science

YEAR THIS DEGREE GRANTED: Spring, 1989

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"You can't always get what you want;
but if you try sometimes
you might find
you get what you need."

M. Jagger,
K. Richard

THE UNIVERSITY OF ALBERTA

FACULTY OF GRADUATE STUDIES AND RESEARCH

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled

THE EFFECTS OF RIGHT-OF-WAY CLEARING ON A SUBARCTIC UNDERSTORY SHRUB: THE REGROWTH RESPONSE OF *SALIX ARBUSCULOIDES* ANDERSS. OVER THREE GROWING SEASONS.

Submitted by: TERESA DE GROSBOIS

in partial fulfilment of the requirements for the degree of: MASTER OF SCIENCE

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Date: March 23, 1989

To Andrew

(for keeping the houseplants alive)

ABSTRACT

An homogeneous 3.4 ha area of black spruce forest was selected for study at a site 10 km north of Fort Norman N.W.T. A 25-m-wide corridor was cleared in the spring of 1985 to simulate a seismic line or pipeline disturbance. *Salix arbusculoides*, the dominant erect deciduous shrub found in this area, was monitored for three growing seasons after canopy removal. Regrown shrubs on the cleared right-of-way were compared to undisturbed shrubs in an adjacent black spruce stand, which served as a control sample.

High rates of productivity, primarily in stem growth [illegible] owing clearing, which was most pronounced in the second growing se[illegible] egrown right-of-way shrubs attained dry weights equal to control shrubs by the second growing season. Leaf biomass relative to both ground cover and shrub canopy volume was higher for right-of-way shrubs in all three years. This suggests that shading and gas exchange capabilities per unit area of ground, equalled or exceeded undisturbed shrubs over the period of the study.

Leaf area was not consistent among the three years in either area. Control shrubs' leaves were significantly smaller in 1985 relative to 1986 and 1987. Leaves on the right-of-way shrubs in 1985 and 1986 were significantly larger than in 1987. This was reflected in comparisons of the two sampling areas among years. Relative to control shrubs leaves were significantly larger on right-of-way shrubs in 1985; virtually identical in size in 1986 and smaller for the right-of-way shrubs in 1987.

Right-of-way shrubs were consistently shorter in height, however by the third growing season this difference was negligible. Canopy volume was only significantly less in right-of-way shrubs in the first growing season, when right-of-way shrub volume was an average of 85% of control values. By the second growing season, right-of-way shrubs had attained canopy volumes no different from control shrubs.

ACKNOWLEDGEMENTS

The completion of this thesis has been as simple and straightforward as determining beforehand which side of the bed to get up on. As a result there are many people to thank. Foremost I must thank my Supervisor Peter Kershaw primarily for always being willing to buy a broke student a beer; and secondly for assistance in almost every aspect of this project. His constant willingness to listen to arguments (and more arguments....) and ideas, and his patience have been greatly appreciated. Linda Kershaw provided the original idea for this project, as well as the preliminary year of data collection. To Frances Reintjes I owe many thanks, not only for the excellent field and lab assistance but also for her continual friendship and encouragement. Field assistance was also provided by many of the SEEDS workers, especially Gary Demeriez and Bonnie Gallinger. Growth chamber assistance from Andrew Fox, Mark Seemann, Sabine Nolte and Lee Weisling was also greatly appreciated. Thanks also to Eric Kershaw for carrying equipment and samples to and from the study site.

Unlike many Masters students, I have had the assistance and advice of my committee members, Ron Eyton of Geography and John Hoddinott of Botany, throughout the course of this study. For all of their help and guidance I am very grateful. Thanks also Ron, for all of the moral support and for continuously letting me borrow your SAS manuals. Advice and information regarding various aspects of this project were also provided by George LaRoi and Walter Moser of Botany, Mike Ranger of Geology and Greg Henry of Geography. A special thanks to Rudi Kroon and Hermann Barthel of the Botany Phytotron for their friendship, advice and constant willingness to help with the many problems encountered in the course of these studies (not to mention all the free coffee...).

Funding for this project was provided by The Boreal Institute for Northern Studies and by NOGAP. Logistical support was also provided by the Department of Geography. I would also like to thank the department for supporting me with a Graduate Teaching Assistantship during the coarse of my degree. A special thanks to George Pemberton of the Department of Geology who not only allowed me the use of his computer, laser printer and lab facilities, but also provided part-time work for me while I completed the final stages of this thesis. Thanks also to Kevin Evans for editing this work.

On the personal side I must thank my husband Andrew Fox for his constant support, encouragement and criticism; and for always making me coffee in the morning. My parents have always been an inspiration to me for their love of knowledge and for their patience in dealing with nine children. Although growing up with eight older siblings can sometimes be difficult (hand-me-downs take on a whole new meaning!), my family has always been there with encouragement, advice and friendship. I would not trade them for anything (not even a 1965 hard-top Corvette!).

Gerard Courtin (G.M.C.) of Laurentian University was the first person to introduce me to the notion that plants can be interesting and exciting (when they survive to the end of the study that is!), for which I will always be grateful. When I leave here I will miss the interaction and friendship I have had with my fellow graduate students, especially Bonnie Gallinger and my office mates Francien Niekus, Val Sloan, Val Johnson, Lauren Crooks, Mark (Hank) Seemann, Sabine Nolte, Astrid Berthold and Kevin Evans. I must also thank my 'sweat-sisters' Frances Reintjes, Barb Shaw, Shawna Vossler, Gesche Schmidt and Astrid Berthold for keeping me sane. My house mate Andy Haden is owed many thanks for both his friendship and for never complaining about how often he ended up doing my dishes. To Bob Skoye thanks not only for help in writing the opening sentence of these acknowledgments, but also for always knowing what to say and when to say it. Finally, thank-you Mr. Christie for making Oreo ice-cream.

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CHAPTER I

INTRODUCTION

This study was completed as one facet of a larger multi-disciplinary research effort. The 'Studies of the Environmental Effects of Disturbances in the Subarctic' (SEEDS) project was designed to: 1. create a human-induced disturbance and monitor both biotic and abiotic changes which result and; 2. administer test reclamation treatments and evaluate their effectiveness. The long-term goal of the project is to develop and test a predictive model for site recovery on Subarctic transport corridors (Kershaw, 1988). Following disturbance, natural recovery processes also operate. Regrowth of plants from intact root stocks can rapidly occur following right-of-way clearing.

This thesis has been completed as two separate papers. The first deals with the productivity (biomass production) of the shrub *Salix arbusculoides* Anderss. recovering after canopy removal. This paper is intended to be useful in a predictive capacity for reclamation planning/ modelling. The second paper provides a description and comparison of shrub morphology changes at both a canopy and a leaf level, as a result of the environmental alterations caused by the disturbance.

S. arbusculoides was chosen as the focus for this study because it is one of the dominant erect understory shrubs in the study area, having an observed cover of 1.6% (Kershaw, L.J., 1988). Results of these studies have broader geographical application however, since the species is one of the most common erect deciduous shrubs in upland Boreal and Subarctic ecosystems throughout the area west of Hudson Bay (Porsild and Cody, 1980). Although currently considered to be endemic to North America, Argus (1973) maintains that further study may confirm it to be conspecific with the Siberian *Salix boganidensis* Tracy. which is common in many areas of the central and eastern Soviet Arctic and northern Subarctic (Volkova et al., 1966). *S. arbusculoides* is well documented for its ability and propensity to naturally recolonise disturbances including: roads, borrow pits, bladed slopes, and rights-of-way (Farrington, 1988; Kershaw and Kershaw, 1987) and mine sites (Brady, 1984; Ebersole, 1985).

This work complements that of Kershaw et al. (1988) which also considered regrowth in *S. arbusculoides* on an individual shrub basis (i.e., the same individuals were used in pre- and post-harvest comparisons). The current study differs in that comparisons were made with control shrubs for each year, in order to separate responses to disturbance from those resulting from natural annual variations in the environment. Environmental variability can be significant in the Subarctic biome, in both the short- and long-term (Kershaw, 1988).

Study area

An homogeneous 4.3 ha area of decadent black spruce (*Picea mariana* (Mill.)BSP) forest was selected for study at a site 10 km north of Fort Norman, Northwest Territories, which is situated at the confluence of the Mackenzie and Great Bear Rivers (Figure 1). A 25-m-wide right-of-way was cleared at the beginning of the 1985 growing season to simulate a transport corridor disturbance such as a seismic line, winter road, power line or pipeline (Plate 1, Figure 2). The portion of the right-of-way utilised in this study was oriented north-south.

The open-canopied black spruce forest (Plate 2) attains a maximum height of 7.2 m and averages 1.8 m if one includes all individuals of greater than 0.5 m (Schotte, 1988). *S. arbusculoides* dominates the erect shrub stratum, averaging 96 cm in height (Kershaw et al., 1988). Soils in the area are Gleysolic Turbic Cryosols (Kershaw and Evans, 1986). The active layer below the organic layer in the soil,

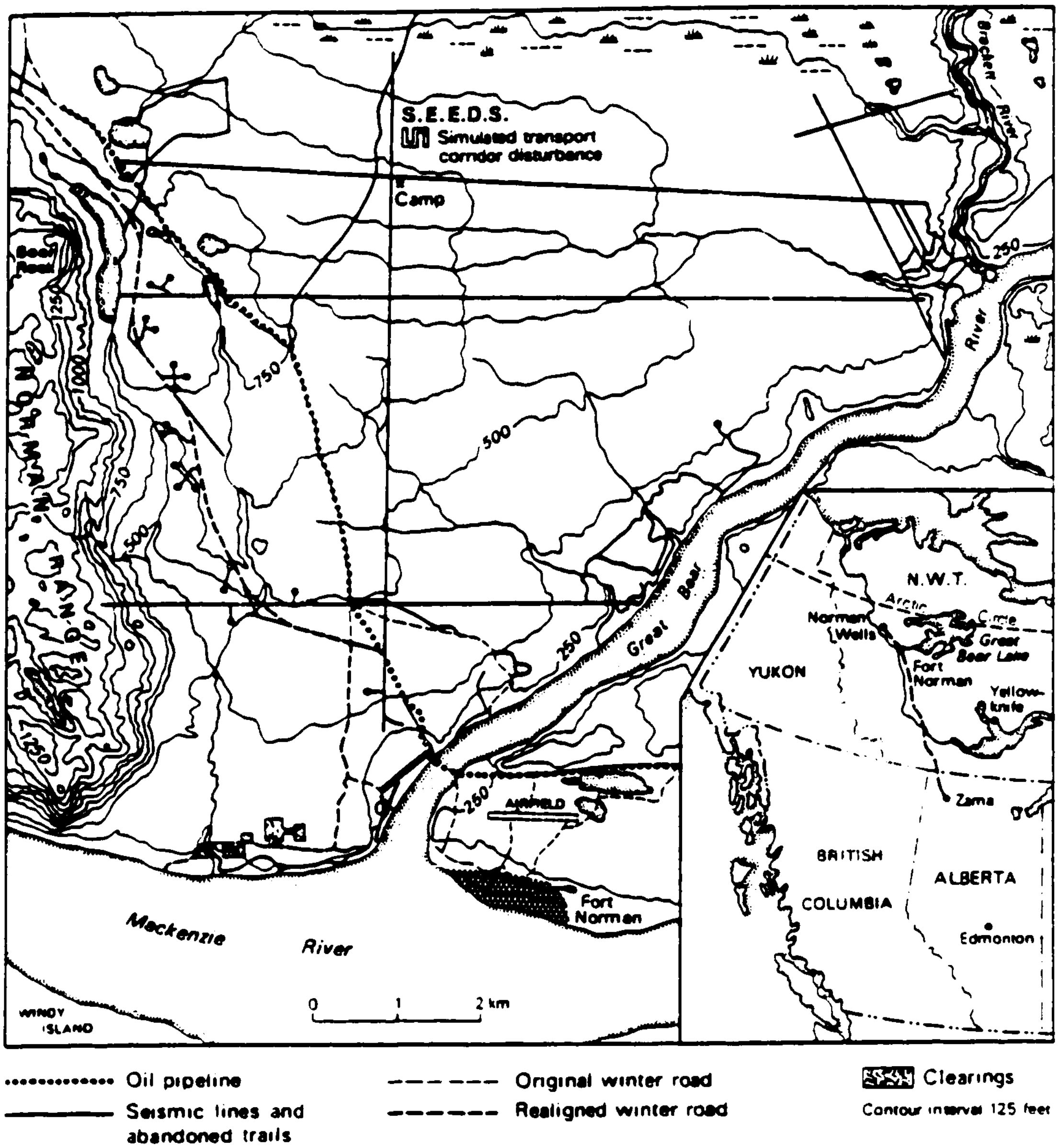
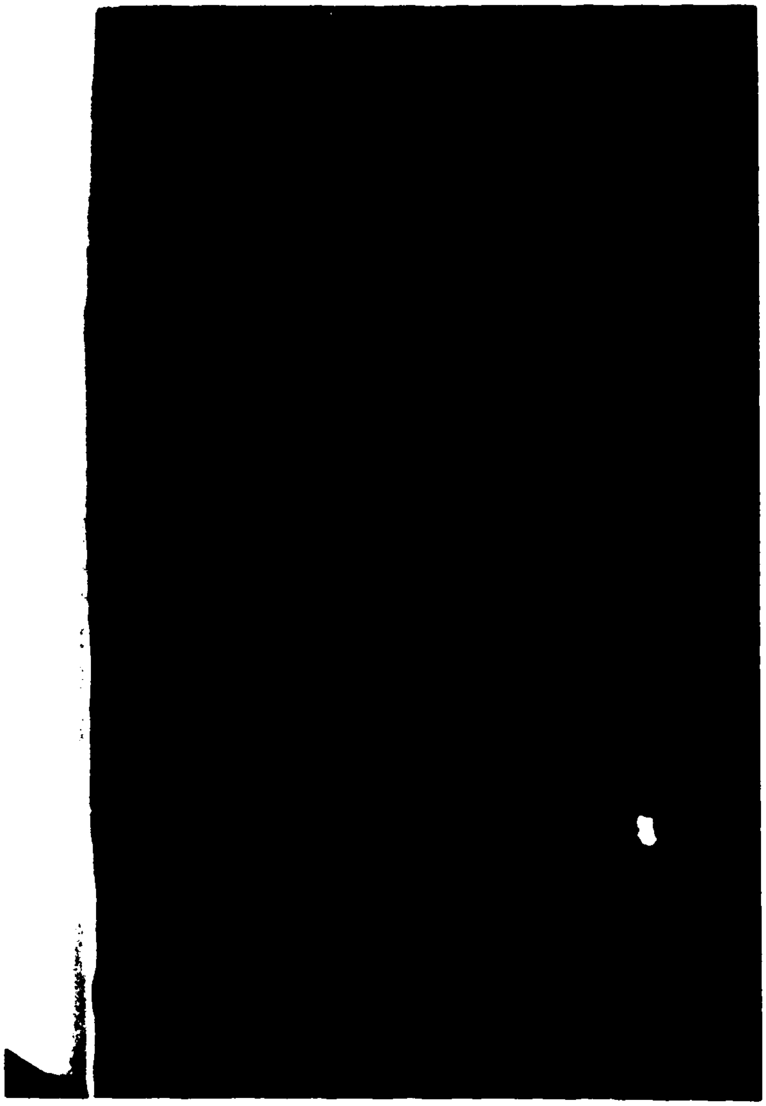


Figure 1. Location of the simulated transport corridor disturbance installed for the project – Studies of the Environmental Effects of Disturbances in the Subarctic (SEEDS), Fort Norman, N.W.T.

Plate 1

View of study site located 10 km north of Fort Norman, N.W.T. (looking south). A north/south oriented seismic line can be seen running west of the study site. Sampling of shrubs was conducted on the first right-of-way and adjacent control area (on right/ west side of photo).



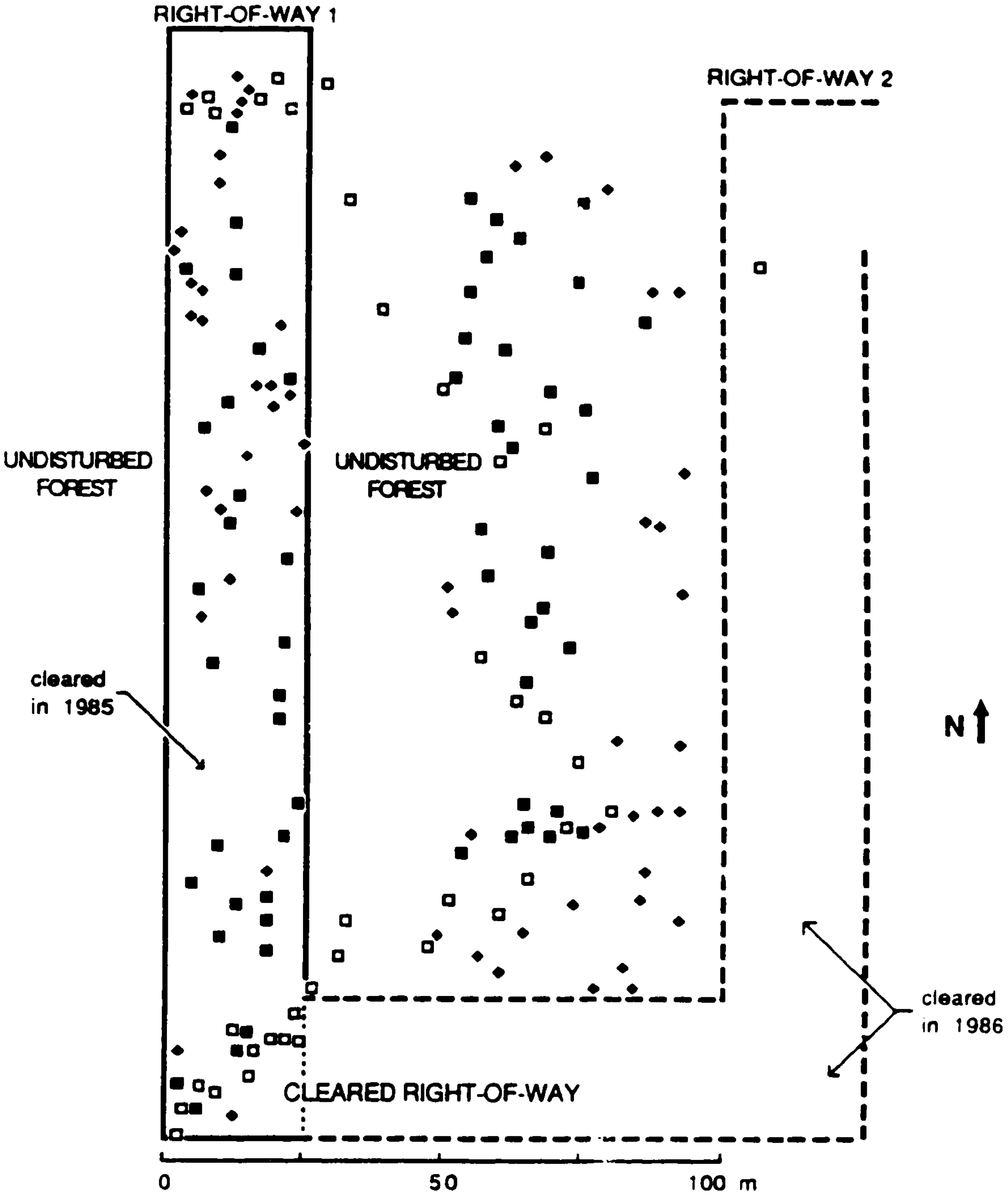


Figure 2. Schematic representation of the study area including relative locations of the cleared right-of-way and undisturbed control areas. Sample locations are indicated for 1985 (□), 1986 (◆), and 1987 (■).

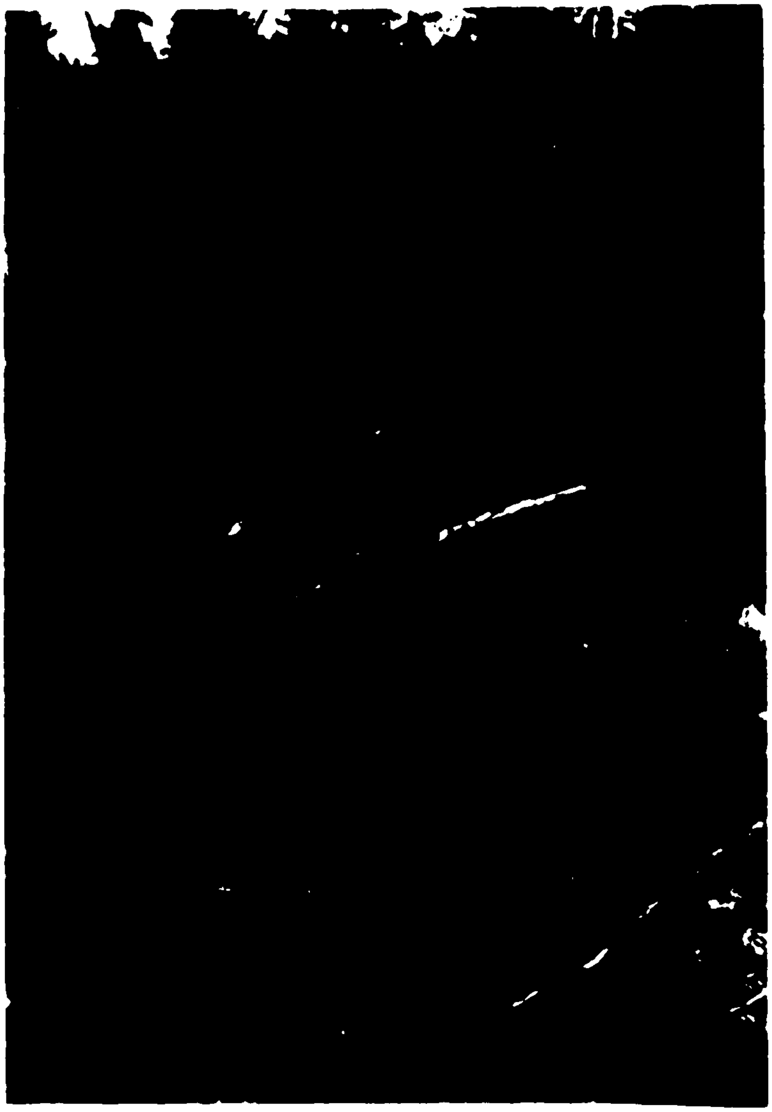


Plate 2

Open-canopied black spruce forest typical of undisturbed study site.

which was observed to be the primary rooting zone for *S. arbusculoides*, is typically water-saturated (Kershaw and Evans, 1986; Evans et al., 1988). The following mean and standard deviation levels for macro-nutrients within the O_m soil horizon on the right-of-way were 19488.5 ± 3935.3 mg/kg for calcium, 2453.7 ± 521.8 mg/kg for magnesium, 115.9 ± 134.9 mg/kg for sodium and 8.6 ± 7.4 mg/kg for potassium (Evans et al., 1988) Although variable on the site, these nutrient levels are consistently within the range (Evans, pers. comm., 1988) which Pritchett and Fisher (1987) suggest will not inhibit plant growth.

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CHAPTER II

ABOVE-GROUND BIOMASS DISTRIBUTION

Introduction

The Subarctic of western Canada has been influenced by both man-induced and natural disturbances. Natural disturbances, especially wildfires are considered important to the maintenance of Subarctic ecosystems (Dyrness et al., 1986).

Recent discoveries of non-renewable resources in the North have resulted in an increase in human-induced disturbances associated with resource exploration and to a lesser extent, development. Recovery from disturbances has been studied from two perspectives: natural recovery; and revegetation through planting means. Many of the studies documenting natural recovery of disturbed areas have taken place in tundra regions (e.g., Ebersole, 1987; Hernandez, 1973; Kershaw and Kershaw, 1987) whereas few have involved Subarctic regions (e.g., Farrington, 1988; Younkin and Marten, 1987). Considerable work has been done on revegetation as a means of preventing thermal degradation of permafrost, alluvial erosion and slope instability in disturbed areas such as seismic lines, pipelines and other linear corridors in the Subarctic (e.g., Cargill and Chapin, 1987; Densmore and Holmes, 1987; Gartner et al., 1983; Hernandez, 1973; Johnson, 1981; Johnson et al., 1981; Strang, 1973; Younkin, 1976). Seed application studies have involved the use of both native (e.g., Hernandez, 1973; Younkin, 1976; Gartner et al., 1983) and commercially-available seed mixes of agronomic grasses and forbs (e.g., Strang, 1973; Johnson, 1981; Johnson et al., 1981), although most revegetation programmes to date have utilised only agronomic species (e.g., Wishart, 1988). Vaartnou (1988) indicates that many agronomic cultivars are not adaped to northern environments as their success often declines after the first growing season. Younkin and Marten (1987) also point out that the establishment of a dense cover of agronomic grasses may inhibit the reestablishment of better-adapted and more ecologically desirable native species, thus revegetation programmes using native species may be more successful.

Shrubs may provide better ground cover than herbaceous (non-woody) plants because their greater height allows for increased leaf production per plant resulting in a greater leaf-area-index (i.e., the total leaf surface area relative to the ground cover of a plant). An increased total leaf area (evaporative surface) would result in greater potential for evapotranspiration per unit area of ground covered by the shrub. Increased evapotranspiration speeds drying of soils. This is beneficial because wet soils have greater thermal conductivity (Oke, 1983). Increased ground shading from the shrub canopies would reduce the net radiation at the ground (e.g., Haag and Bliss, 1974). These factors, when combined, result in reduced thermal degradation of the permafrost. Several studies have attempted shrub reestablishment in disturbed areas using shrub cuttings. Willows (*Salix* spp.) have proven to be successful in these studies because of their high rooting capacity (Chmelar, 1974; Densmore and Zasada, 1978; Densmore and Holmes, 1987; Densmore et al., 1987; Holloway and Zasada, 1979). The main limitations of this method are: 1. the intensive labour required in planting; and 2. the smaller shrub size obtained with cuttings over the short-term (e.g., Densmore et al., 1987) relative to regrown shrubs (Kershaw et al., 1988).

One alternative to shrub reestablishment by planting methods that has received only minimal attention is the utilisation of shrub regrowth from pre-disturbance rootstocks. Shrubs can store considerable carbohydrate reserves in their below-ground parts (roots, root-crowns, rhizomes), which they can reallocate to above-ground material when necessary. Utilisation of stored root carbohydrates can result in rapid shoot growth, thus plant species that have underground reservoirs of carbohydrates can regenerate considerably faster than those which must start from seed (Blaisdell and Mueggler, 1956) or from shrub cuttings (Younkin, 1976). The tendency for a plant species to store carbohydrates below-ground can be indicated by the ratio of below-ground to above-ground biomass (dry weight), which is referred to as the root to shoot biomass ratio. Although there is a great deal of spatial and seasonal variability in the root to shoot biomass ratio of Arctic plant species, Dennis and Johnson (1970) note that this ratio is consistently high (greater than 5 to 1). They reason that this is an adaptation to facilitate regrowth when necessary. Evidence exists that shrub regrowth will occur naturally on disturbances, as Hernandez (1973) found that most shrub reestablishment on a disturbed delta in the Barrow Alaska region, was regeneration from predisturbance rootstock. Post-fire recovery research also supports a resprouting stategy from pre-fire root stock (Black and Bliss, 1978; Smith and Sparling, 1966). *Salix* spp. were successful in the study of Black and Bliss (1978), as they found that after the first fifteen years of post-fire recovery the canopy was predominantly *S. glauca* and *S. pulchra* (both erect species).

Utilisation of this regrowth in shrubs may be advantageous where short (shrub/ herb) ground cover is desired. Vegetative regeneration occurs primarily in early successional shrubs and biennial herbs, as according to Bryant and Chapin (1986) late successional plant species do not regrow as well. This is also true of plant species adapted to low resource environments (Bryant et al., 1983). Zasada (1986) noted that all broad leaf deciduous species can produce some basal sprouts after top removal, although in many species the ability to resprout declines with the age of the individual. Alternatively, conifers tend not to resprout well, only reproducing vegetatively in undisturbed or marginal sites. White spruce is a notable exception, as it has been observed to produce new shoots when some living branches are left on the stump. Resprouting after fire has also been the subject of study, although there tends to be greater microsite variation following fire than after clear-cutting (Zasada, 1986). Many fires in black spruce ecosystems however, are similar to clear-cut harvesting in that they are either crown or ground fires of enough intensity to kill overstory trees while leaving at least part of the organic layer intact (Viereck, 1983). The main complication in comparing fire to clearing disturbances is that fire may improve site conditions by warming the active layer and increasing mineralisation of nutrients in the soil (Dyrness et al., 1986).

This use of vegetative regrowth in land reclamation may [illegible] actical solution for all purposes. In many situations, rootcrowns remaining below ground level could be subject to sufficient stress that they would not survive the disturbance. Farrington (1988) suggests that *S. arbusculoides* roots can withstand some mechanical stress however, as much of the recolonisation of this species on borrow pits excavated in slopes was through rafting of the organic mat. Thus the preservation of these rootstocks could prove to be an important planning step in areas which are susceptible to thermal degradation and slumping such as south-facing and/ or ice-rich slopes.

Salix spp. are commonly used for shrub revegetation as they have the ability to grow well from whip plantings (e.g., Chmelar, 1974; Densmore and Zasada, 1978), and also have a propensity for natural recolonisation (e.g., Brady, 1984; Ebersole, 1985; Elliott et al., 1987; Hernandez, 1973 ; Kershaw and Kershaw, 1987; McKendrick, 1987). Members of the genus are well recognised for their ability to produce biomass through coppicing after denudation. Most studies which have documented this coppice production have dealt with objectives such as biomass production for energy uses (Pearce, 1984; Stott et al., 1981), or browse production (Bryant and Chapin, 1986; Wolff, 1978). Kershaw et al. (1988) have shown that *S. arbusculoides* has considerable potential for regrowth; they examined the regrowth response to denudation on an individual shrub basis (i.e., the same shrubs were used in pre- to post- harvest comparisons). On average, in only one growing season following denudation to ground surface, the shrubs produced 11.5 times more current annual growth biomass; they attained canopy radii of 75% of their original size; and they produced 673% more basal stems per coppice (an average increase from 7 to 43 stems).

The objective of this study was to monitor biomass changes which occurred in *S. arbusculoides* over a three-year-period after the removal of both the black spruce-dominated tree canopy and the understory shrub canopy. Denuded shrubs in the right-of-way were compared to shrubs in an adjacent undisturbed forest (as opposed to original pre-disturbance shrub vigour as in the study of Kershaw et al. (1988)). Increased growth rates of denuded plants relative to control plants were expected for two reasons: 1. the use of stored root carbohydrates for compensatory growth, especially in the first growing season following canopy removal; and 2. the potential for increased photosynthesis with the removal of the shade-producing black spruce canopy. As well, improved microclimate on the right-of-way as evidenced by the greater active layer depths (Gallinger and Kershaw, 1988), may have allowed for a greater period of active carbohydrate cycling in right-of-way shrubs. As a result of these expectations the following null hypotheses were generated for testing:

Ho_1. no biomass production differences would exist between right-of-way and control shrubs in all three years, for all plant parts;

Ho_2. no differences in leaf biomass relative to ground cover (Leaf Biomass Index) would exist between right-of-way and control shrubs;

Ho_3. no differences in leaf biomass relative to canopy volume (Leaf Biomass Density) would exist between right-of-way and control shrubs;

Methods

Field and lab methods

At the beginning of the 1985 growing season before any plants had broken dormancy, a north/ south oriented right-of-way was cleared of erect vegetation to the ground surface (Plate 1). This involved the removal of all plants greater than 25 cm in height. The two sampling areas were the cleared right-of-way and a nearby undisturbed forest stand which served as a control. Sample sites were randomly selected from each sampling area separately. Twenty (in 1985) or thirty (in 1986 and '87) sample sites were selected from each area. The shrub stool (i.e., the coppice, seemingly from one root crown) nearest each sample site was collected. Occasionally, shrubs were found growing intertwined at the base, in which case the sample may have included more than one plant. Shrub samples were collected at the end of the first, second and third growing seasons after canopy removal. Time of sampling was determined by typical growth phenology: after full leaf expansion and prior to leaf senescence. The dimensions of each shrub (height, maximum diameter and diameter perpendicular to the maximum diameter) were measured and the above-ground portion of each shrub was collected for detailed laboratory

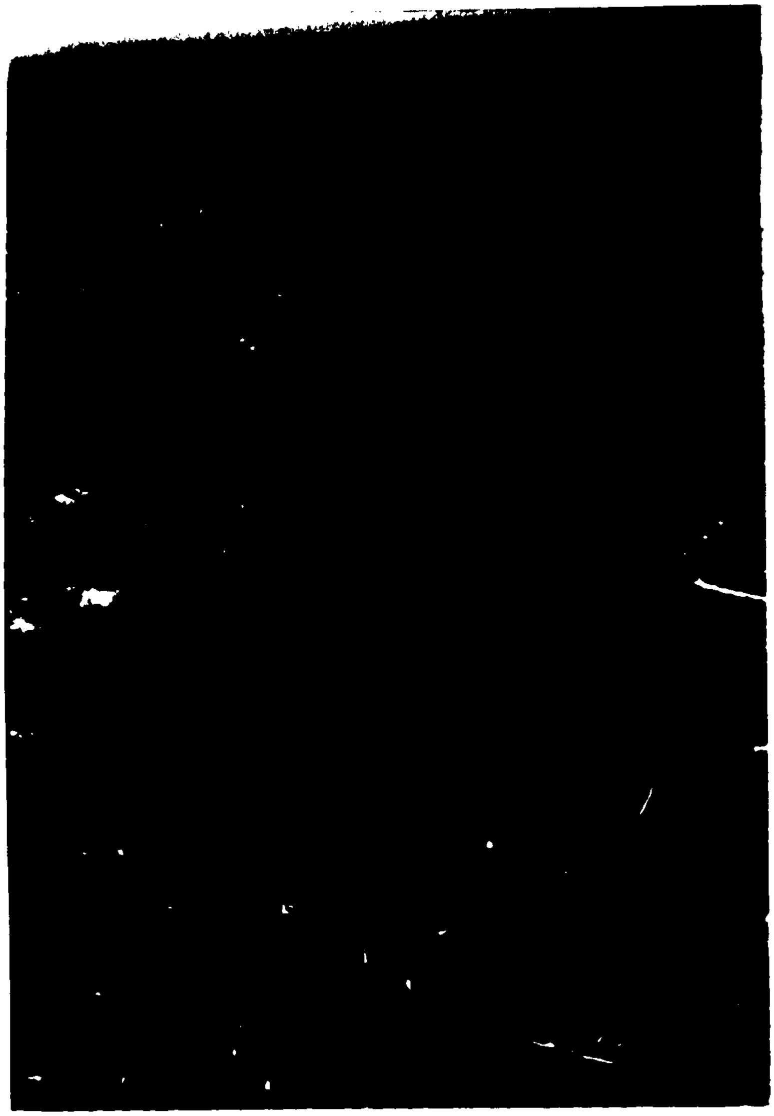


Plate 1

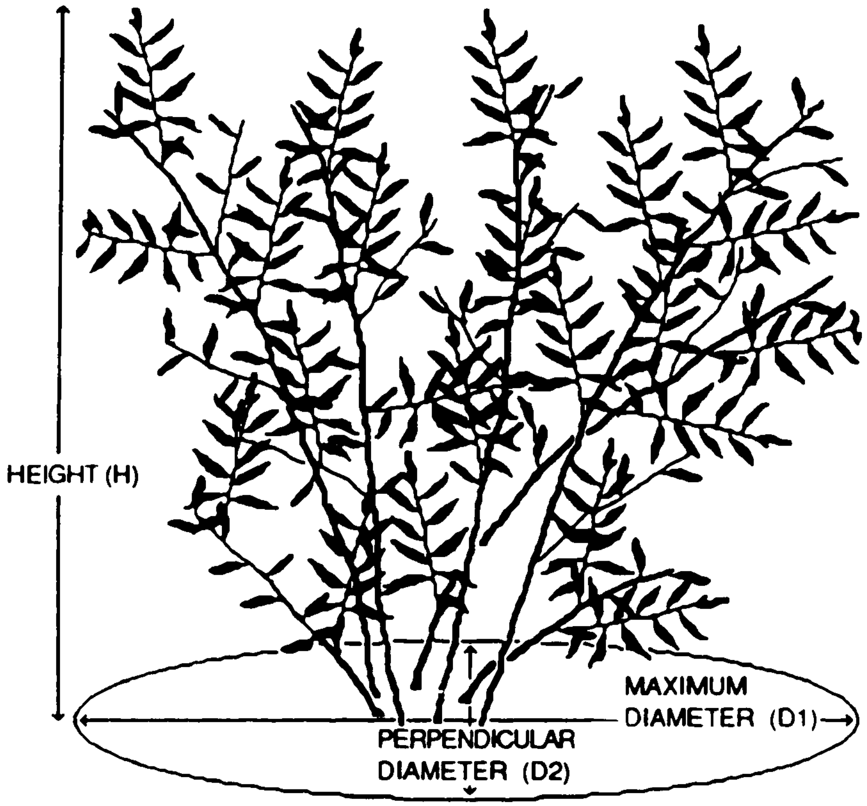
East side of the right-of-way involved in this study, which was cleared in 1985. Photo taken in 1987 (looking north).

analysis. In the case of very large individuals, a subsample (the subsample comprising a minimum of 20% of the total fresh weight) was analysed. Each shrub (or subsample) was then separated into its component parts: current growing season stems and leaves, and stems produced prior to the growing season of sampling. For purposes of simplicity these will be referred to as leaves, new stems and old stems. *S. arbusculoides* is a spring-blooming willow, and since sampling occurred late in the growing season, catkins (the flowering structure of willows) were typically not present on the shrubs. Any that were present were included in the calculation of total and new growth (total current annual growth) parameters, rather than being treated as an individual component part. All materials were oven-dried and weighed for biomass determination. Estimates of total dry weights and dimension parameters for subsamples were calculated based on the ratio of total green weight to subsample green weight.

Statistical Analysis

All analyses for this study were completed using SAS on the University of Alberta MTS (Michigan Terminal System) mainframe. For all sample distributions the Shapiro Wilk normality test was carried out because it was the most appropriate test for sample sizes of less than 50 (Shapiro and Wilk, 1965). Skewness and kurtosis were also calculated using PROC UNIVARIATE on SAS (SAS Institute Inc., 1985a).

Shrub ground cover ([1], Figure 1) was calculated as an ellipse using the maximum canopy diameter (D1) and perpendicular to the maximum canopy diameter (D2). Canopy volume ([2], Figure 1) was treated as a cylinder and calculated as the quotient of height and ground cover. An indication of ground shading ability in terms of leaf biomass, was determined by calculating dry weight of leaves per unit area of ground ([3], Figure 1), a



GROUND COVER (GC) = Π (D1÷2) X (D2÷2) [1]
CANOPY VOLUME (CVOL) = GC X H [2]
LEAF BIOMASS INDEX (LBI) = LEAF DRY WEIGHT ÷ GC [3]
LEAF BIOMASS DENSITY (LBD) = LEAF DRY WEIGHT ÷ CVOL [4]

Figure 1. Canopy dimensions used in the calculation of canopy volume (m^3), leaf biomass index ($g \cdot m^{-2}$) and leaf biomass density ($g \cdot m^{-3}$).

term referred to in this study as leaf biomass index (LBI). An indication of leaf biomass density (LBD) was then determined by calculating leaf dry weight relative to canopy volume ([4], Figure 1).

Frequency distributions of both the biomass and shrub dimension parameters were non-normal, being right-skewed (i.e., the right tail of the distribution drawn out) and leptokurtic (i.e., having more items at the mean and tails and fewer in intermediate regions than a normal distribution). Log_{10} transformations corrected this problem and allowed the use of analysis of variance (ANOVA) using the GLM procedure on SAS (SAS Institute Inc., 1985b). Hochberg's (1974) GT2 means difference test was then carried out, because this test accepts unequal sample sizes.

Results

All comparisons were made in a stratified manner. First each area was considered separately to observe differences in the three years of sampling (i.e., yearly variation), then each year was considered separately to observe differences in the two sampling areas for any given year (i.e., areal variation).

Yearly variation

As indicated in Table 1, control shrubs' biomass for all of the component plant parts remained consistent over the three year period. Although total above-ground shrub biomass (Figure 2) was not considered significantly different between any of the thr years among right-of-way samples, significantly more new growth (Figure 3) was produced in the second year, as compared to the first or third years. This increas

TABLE 1

Summary of ANOVA results and Hochburg means difference (GT2) test groupings for comparisons of component plant parts[a] (mg·shrub^{-1}) of *Salix arbusculoides* on the basis of area and year.

	df[b]	totals	new growth	leaves	new stem	old stem
YEARLY VARIATION:						
Control						
F-value	2	2.00	0.01	0.01	0.01	2.70
PR>F[c]		0.1427	0.9869	0.9888	0.9948	0.0739
Right-of-way						
F-value	2	2.31	4.81	3.16	10.19	2.50
PR>F		0.1067	0.0110*	0.0321*	0.0001***	0.0895
GT2 groupings			('86,'87)	('86,'87)	('85,'87)	
			('85,'87)	('85,'87)	('86)	
AREAL VARIATION:						
1985						
F-value	1	21.97	1.09	1.51	0.07	11.25
PR>F		0.0001***	0.3036	0.2278	0.7997	
0.0019**						
1986						
F-value	1	0.04	7.71	3.86	27.07	3.64
PR>F		0.8378	0.0075**	0.0545	0.0001***	0.0618
1987						
F-value	1	0.53	0.33	0.46	1.50	1.01
PR>F		0.4713	0.5695	0.4984	0.2265	0.3188

[a] all comparisons based on $\log_{10}$ transformed data

[b] df = degrees of freedom, sample sizes were n=20 in 1985 and n=30 in 1986 and 1987

[c] probability of theoretical F value exceeding calculated F value; F significant at the following probabilities: 0.05 (*), 0.01(**) and 0.001(***).

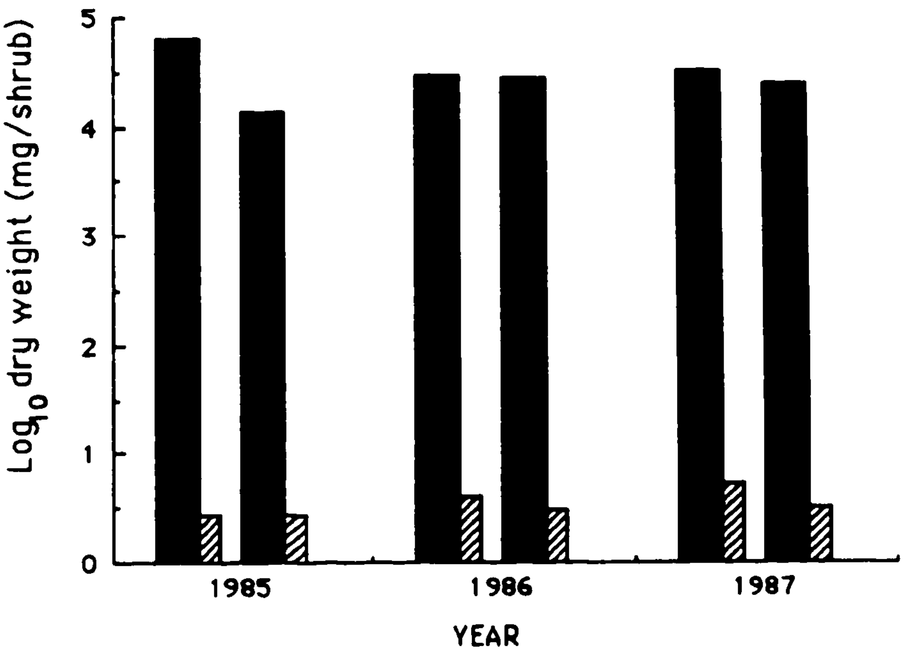


Figure 2. Mean $\log_{10}$ dry weight of total phytomass (mg/shrub) of *Salix arbusculoides* in 1985, 1986 and 1987. ■ Control, ■ Right-of-way and ▨ Standard deviation.

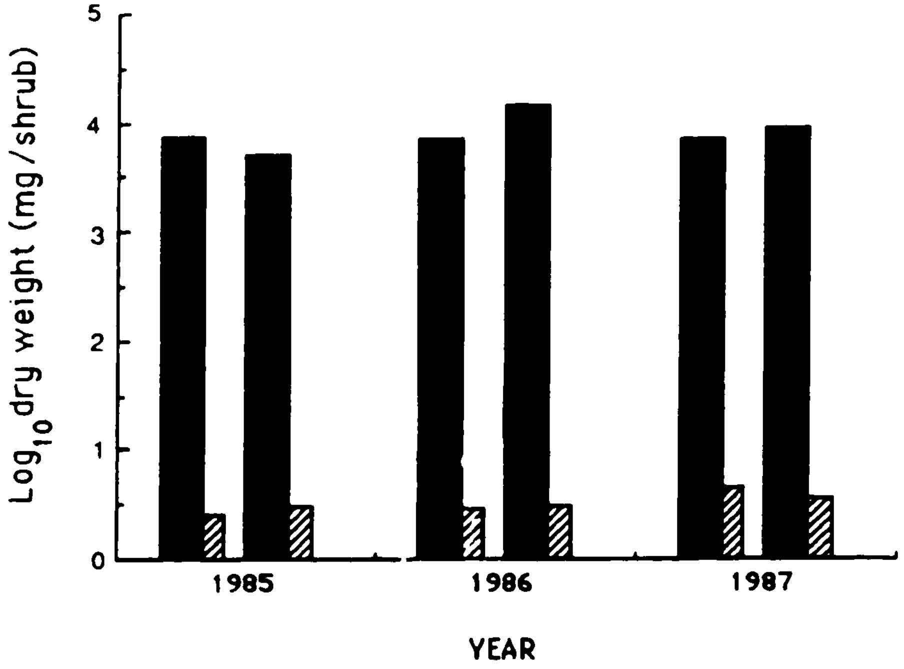


Figure 3. Mean $\log_{10}$ dry weight of new growth (mg/shrub) of *Salix arbusculoides* in 1985, 1986 and 1987. ■ Control, ■ Right-of-way and ▨ Standard deviation.

right-of-way new growth in the second growing season was primarily production of stems (Figure 4), whereas the increase in leaf biomass (Figure 5) was not as great. Leaf biomass for right-of-way samples was greatest in 1986 however this sample was only considered to be significantly greater than the 1985 right-of-way sample. The dry weight of old stems (Figure 6) increased in right-of-way shrubs linearly over the three growing seasons. This was expected because every year the old stem parameter includes the previous year's new stem biomass; this increase was not significant however. For right-of-way shrubs leaf biomass index (LBI) increased significantly in 1986 relative to the other 2 years (Table 2, Figure 7). Control shrubs had no significant changes in the LBI over the three-year-period.

Areal variation

If the right-of-way and control areas are compared among years, the changes in right-of-way samples are reemphasised. In 1985 old stems were significantly less on right-of-way plants as a result of the removal of most of the woody shrub canopy at the beginning of that season. This is reflected in a significantly lower total dry weight in right-of-way shrubs in this growing season. Although the dry weights of the component plant parts (new growth, new stems and leaves) produced on the shrubs during the 1985 growing season (Figures 3 to 5) were consistently lower on the right-of-way, this difference from control samples was not significant in any case (Table 1). In 1986, the new growth component weights were consistently higher on the right-of-way shrubs, but not significantly so in the case of leaf biomass. Although old stem dry weight still averaged less on right-of-way shrubs in 1986 (Figure 6), this was no longer significant (Table 1). Total shrub weights were also no different in 1986 (Figure 2, Table 1). In 1987,

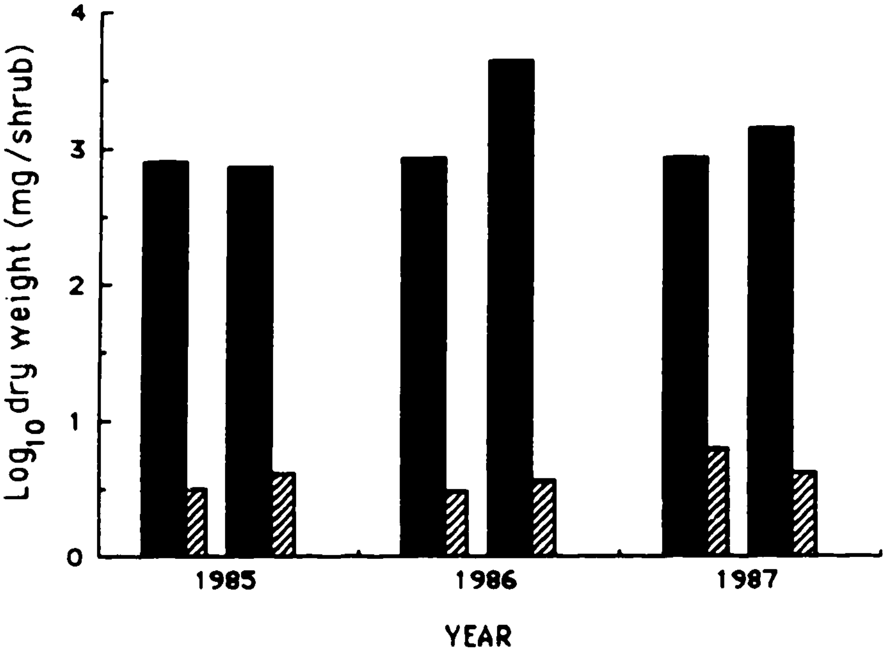


Figure 4. Mean $\log_{10}$ dry weight of new stems (mg/shrub) of *Salix arbusculoides* in 1985, 1986 and 1987. ■ Control, ■ Right-of-way and ▨ Standard deviation.

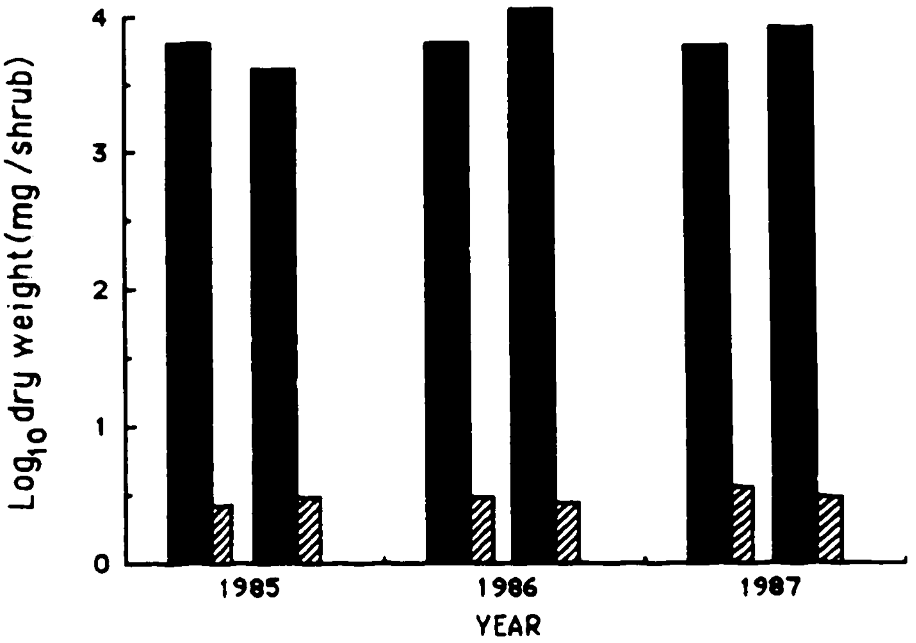


Figure 5. Mean $\log_{10}$ dry weight of leaves (mg/shrub) of *Salix arbusculoides* in 1985, 1986 and 1987. ■ Control, ■ Right-of-way and ▨ Standard deviation.

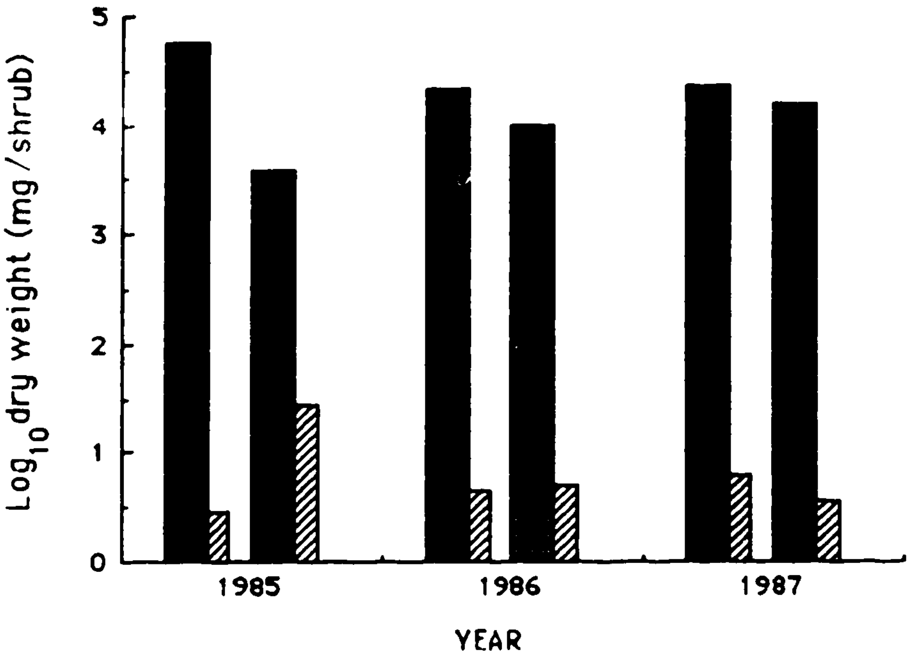


Figure 6. Mean $\log_{10}$ dry weight of old stems (mg/shrub) of *Salix arbusculoides* in 1985, 1986 and 1987. ■ Control, ■ Right-of-way and ▨ Standard deviation.

TABLE 2

Summary of ANOVA results and Hochburg means difference (GT2) test groupings for leaf biomass index and leaf biomass density[a] of *Salix arbusculoides*

	df[b]	leaf biomass index[c]	leaf biomass density[d]
YEARLY VARIATION:			
Control			
F-value	2	1.95	3.86
PR>F[e]		0.1492	0.0252*
GT2 groupings			('85, '86) ('86, '87)
Right-of-way			
F-value	2	5.80	1.05
PR>F		0.0047**	0.354
GT2 groupings		('85, '87) ('86)	
AREAL VARIATION:			
1985			
F-value	1	9.14	33.53
PR>F		0.0046**	0.0001***
1986			
F-value	1	41.67	37.03
PR>F		0.0001***	0.0001***
1987			
F-value	1	5.22	11.26
PR>F		0.0261*	0.0014**

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[a] all comparisons based on $\log_{10}$ transformed data

[b] df = degrees of freedom, Sample sizes were n=20 in 1985 and n=30 in 1986 and 1987

[c] leaf biomass index = $g \cdot m^{-2}$

[d] leaf biomass density = g·r

[e] probability of theoretical F value exceeding calculated F value; F Significant at the following probabilities: 0.05 (*), 0.01(**) and 0.001(***)

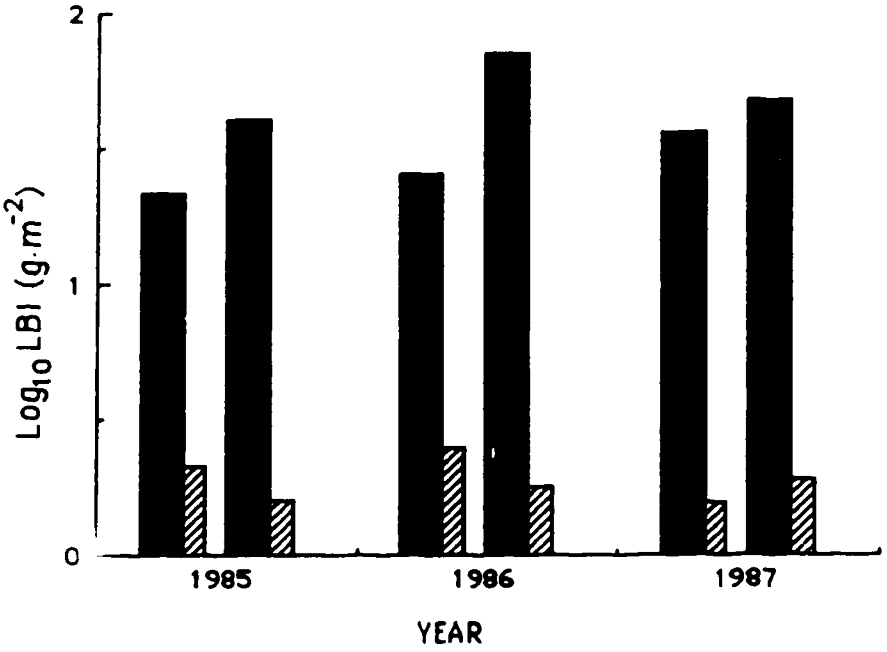

Figure 7. Mean $\log_{10}$ Leaf Biomass Index ($g \cdot m^{-2}$) of *Salix arbusculoides* in 1985, 1986 and 1987. ■ Control, ■ Right-of-way and ▨ Standard deviation.

right-of-way shrubs did not have significantly different biomass distributions from the control shrubs in any way. Thus, within three growing seasons following disturbance, regrown shrubs attained sizes and growth rates equal to undisturbed shrubs.

In all three years the right-of-way shrubs had a larger LBI than control shrubs with the greatest increase in 1986 and the least difference in 1987. Right-of-way shrubs consistently had greater leaf biomass density (LBD) than control shrubs (Figure 8) with the greatest differences in the first and second growing seasons. Although no differences occurred among the three years for right-of-way shrubs, the leaf biomass density did increase consistently over the three years for control shrubs, causing the smallest difference between the sampling areas to occur in the third growing season of recovery.

Discussion

The significant regrowth potential of *S. arbusculoides* was confirmed by the fact that the right-of-way shrubs attained a total above-ground biomass not significantly different from that of undisturbed control shrubs by the [illegible] growing season following right-of-way construction. This recovery of size was primarily as a result of increased stem production. This increased growth rate on right-of-way shrubs, especially in the second growing season, may be a result of several factors: 1. increased light quantity resulting from canopy removal (e.g., Haag and Bliss, 1974) allowing greater photosynthetic production; 2. faster thaw rates of the right-of-way active layer (Gallinger and Kershaw, 1988) creating a longer period of carbohydrate cycling; and 3. increased usage of stored root carbohydrates to compensate for the loss of above-ground biomass (i.e., compensatory growth) (e.g., Bryant and Chapin, 1986; Pearce, 1984).

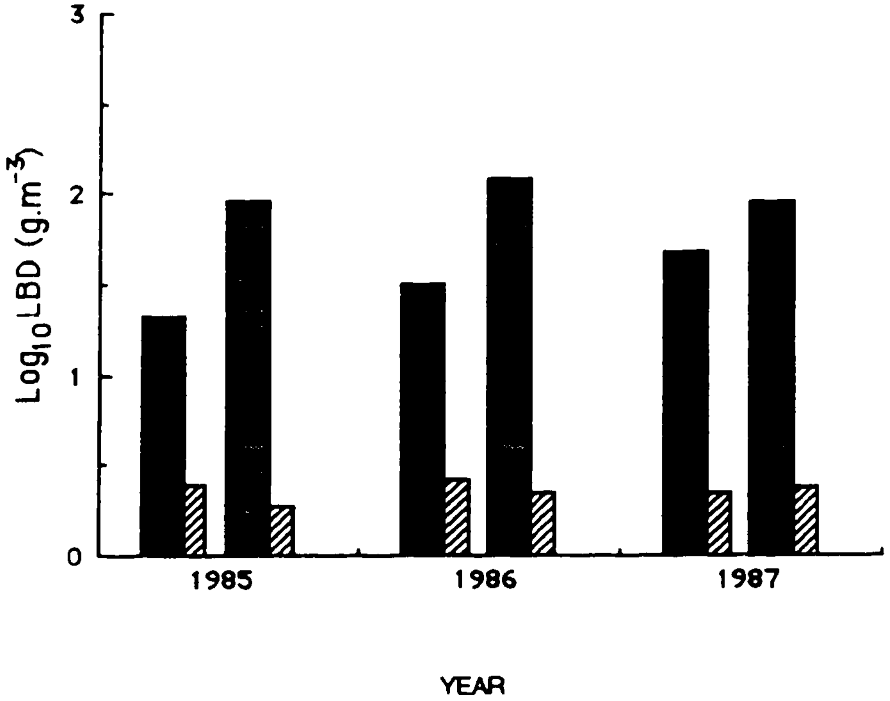

Figure 8. Mean log$_{10}$ Leaf Biomass Density (g·m^{-3}) of *Salix arbusculoides* in 1985, 1986 and 1987. ■ Control, ■ Right-of-way and ▨ Standard deviation.

The first two factors are related as increased light quantity and subsequently increased temperature result in significant increases in productivity (Nilsson and Eckersten, 1983).

Current annual growth (new growth) was greatest in 1986, the second growing season of recovery, on right-of-way shrubs. This sample had a significantly greater mean than both the 1986 control sample and the 1985 right-of-way sample. This increase in biomass production was primarily observed in current annual stem growth (new stems) and only minimally and not significantly so, in leaves. This suggests that compensatory growth occurs primarily in the second growing season. By the third season, the right-of-way shrubs no longer had significantly greater new growth than the control, suggesting a return to a more typical growth rate dependent primarily on photosynthesis for production of above-ground biomass. This similar growth rate in the third year of recovery suggests that the quantity of light available for photosynthesis may be similar in both areas (i.e., the right-of-way light quantity does not exceed the control by any significant amount).

The fact that right-of-way shrubs did not exceed control shrubs in the amount of new growth during the first year as would have been expected, may be because of a time lag between denuding and the initiation of growth. Lags in the initiation of regrowth of 4 to 6 weeks have been observed in temperate shrubs following fire (Leege and Hickey, 1971). This amount of time would comprise a substantial portion of the 1985 growing season at the Subarctic SEEDS site. The season during which denudation is carried out is critical: with the best regrowth occurring after spring and fall (relative to summer) denudation as these are the periods when stored carbohydrates in the below-ground plant portions are most abundant (Buttery et al., 1959; Jones and Laude, 1960; Leege and Hickey, 1971).

Maximum below-ground carbohydrate storage is most often in fall just prior to senescence (Trilica, 1977) thus denuding the shrubs in the fall rather than the spring would result in more substantial growth the following spring (i.e., the first growing season after harvesting) with little lag in the initiation of regrowth (Leege and Hickey, 1971).

The timing of resprouting is likely also affected by moisture availability and temperature (Laude et al., 1961; Plumb, 1961; Plumb, 1963). In the years subsequent to the year of disturbance, these conditions were probably met earlier in the growing season on the less shaded right-of-way than in the control area due to greater heating and thawing of first the snowpack, and then the active layer. The greater thaw rates on the right-of-way indicated by Gallinger and Kershaw (1989) support this argument. This may be due to both the greater net radiation at the ground with the lack of canopy (e.g., Haag and Bliss,1974) and the shallower snowpack which may exist in the cleared area (e.g., Rouse, 1976). This was not likely as pronounced the year of disturbance because snow melt would have proceeded at the same rate in both areas prior to right-of-way clearing which took place toward the end of the snow-melt period. Thus conditions conducive to the breaking of dormancy may have existed sooner in the second and third growing seasons on the right-of-way (relative to both 1985 right-of-way conditions and control conditions in all three growing seasons), as a result of this earlier ground exposure and active layer thaw.

Although minimal (but not significant) increases in leaf weight were observed for right-of-way shrubs, leaf weight remained relatively consistent throughout the study; the right-of-way shrubs never significantly exceeding the control shrubs. This suggests that harvesting does not reduce leaf production and thus the photosynthetic potential is not significantly altered. Biomass allocation may therefore change, but the potential for biomass production appears to remain constant.

For revegetation purposes it is beneficial not only to know how large, in terms of dry weight, a shrub will regrow, but also how well it will provide ground cover. The ability for a shrub to provide ground cover is important for two reasons: 1. increased ability to shade the ground and prevent excessive thaw of the permafrost; and 2. an increased evapotranspirative surface to facilitate the removal of water from the active layer.

Canopy characteristics can be important to the understanding of how effectively a shrub provides shade. The most commonly used parameter for estimating ground cover effectiveness is leaf area index (LAI). This is the total leaf area (cm^2) over the total basal ground cover (cm^2) and is thus a dimensionless measure. Harper (1977) describes leaf area index as the area of photosynthetic surface expanded over an area of ground, which suggests it is a parameter which indicates the gas exchange capabilities (for both photosynthesis and transpiration) of a plant. Odum (1983) however, describes it in more simple terms, as an indication of the biomass density of a plant. Because the measurement of total leaf surface area for a number of shrubs is extremely time consuming, leaf area index was not determine in this study.

As a substitute for leaf area, leaf biomass was used in indices of ground cover. Although this meets with the description of Leaf Area Index as a biomass density measure, it is questionable if this also provides an adequate estimate of gas exchange surface and the evapotranspirative potential relative to ground cover. This is because leaves which develop under shaded conditions can have a different structure than leaves which develop in full sun-light (Boardman, 1977). Should there be a sun/ shade differentiation between leaves in the two sampling areas, two things can be expected which would affect the use of leaf biomass in an index of ground cover: 1 sun leaves are thicker; and 2. sun leaves tend to have a greater number of stomata per surface area for increased gas exchange (Boardman, 1977). Thus as leaf weight increases in sun leaves so does the capacity for gas exchange. Although it is not known if the leaf weight: surface area ratio and gas exchange capacity are linearly related, it is possible that in the event of a shade/ sun leaf differentiation, biomass provides a better index than leaf area. There is some evidence in the literature to support this idea, as previous studies on *Salix* spp. canopies have shown that beyond a certain leaf area index, the light extinction coefficient (the rate of light attenuation) begins to decrease (Cannell et al., 1987; Eckersten, 1984). Eckersten (1984) attributed this to changes in the properties of shaded leaves at the base of the canopy. Preliminary data used to compare leaf area to thickness on *S. arbusculoides* suggest that if there is a difference in leaf thickness between the sampling areas it is not a significant one. This is most likely a result of the fact that the black spruce canopy occupies only 13% cover and provides very little shade to the upper portions of erect shrubs. Thus any shade leaves present would only be found at the base of the shrub canopies.

The calculation of leaf biomass index (LBI) in this study was intended to be comparable to leaf area index as it is primarily an indication of the mass of leaves vertically covering a given area of ground. Leaf biomass density (LBD) is a refinement of LBI since it includes shrub height. It may be important to include height in a parameter intended to infer how much shade a canopy provides, as the solar altitude at these northern latitudes is typically low, never exceeding 48.5° throughout the growing season. Thus light incident upon the canopy is always at an oblique angle rather than from directly above. Right-of-way shrubs exceeded control shrubs in both these parameters in all comparisons, although the least differences were observed in the third growing season suggesting the right-of-way values are slowly approaching control levels. Thus the shading and gas exchange capacities of regrown shrubs are expected to always equal or exceed undisturbed shrubs. The significant increase in these factors in the first growing season is of special interest, as Younkin (1976) indicates that good plant recovery in the first year is important to disturbance reclamation.

Conclusions

With respect to the hypotheses stated in the introduction the following conclusions can be made:

Hypothesis 1

The null hypothesis that no biomass production differences would occur between the sampling areas can be rejected as high rates of productivity occured in *S. arbusculoides* following total above-ground harvesting. The majority of this increase in growth occured in the second growing season after a spring harvest as a result of stem production. As expected, old stem biomass was lower in right-of-way shrubs as a result of its removal during clear-cutting.

Hypotheses 2 and 3

The null hypotheses that both leaf biomass index and leaf biomass density would not change following harvesting must be rejected, as both increased for right-of-way shrubs after harvesting. These values slowly begin to approach those for unharvested shrubs within three growing seasons of harvesting. Thus shading and gas exchange capabilities in regrown shrubs are expected to equal or exceed undisturbed shrubs for the period of recovery.

On the basis of these observations it can be concluded that vegetative regrowth is a viable and predictable option for revegetation planning. *Salix arbusculoides* has an excellent propensity for natural vegetative regeneration following clear-cutting. The substantial biomass production and denser shrub canopies after regeneration make it a prime candidate for ground stabilisation. It meets with Younkin and Martens (1987) criteria that recovery must be substantial within the first growing season and provide a stable self maintaining vegetative cover. Farrington (1988), indicated that the species was able to recolonise borrow pits through rafting of surface material, suggesting that the rootstocks are capable of surviving considerable mechanical stress. This may make it an excellent candidate for surface material replacement programmes: an approach which warrants further investigation.

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CHAPTER III

LEAF AND CANOPY MORPHOLOGY

Introduction

The morphology of individual plants within a species can be highly variable both locally and over the entire range of the species. Arctic plants, because of their high degree of adaptation to the environment, can exhibit very different morphologies than plants of the same species grown under different conditions (Mooney and Billings, 1961; Saville, 1972). These morphological differences have, in some cases, been significant enough to raise taxonomic questions. *Carex aquatilis* Wahlenb var. *stans* (Drej.) Boott. which is now considered to be a smaller Arctic variety of *Carex aquatilis* (Porsild and Cody, 1980) was once treated as the separate species *Carex stans* Drej. (Porsild, 1964) because of its morphological differences. Shrubs also have these morphological differences as the work of Zhuikova (1959: as cited in Bliss, 1962) indicated that several species of *Vaccinium* in the U.S.S.R. had different forms of shrub growth in different habitats. The specific responses of individual species to environmental stresses can also vary considerably. Chapin and Shaver (1985) noted that responses to manipulations of temperature, light and nutrient availability varied considerably for twelve Arctic plant species, depending on the niche each occupied.

Two environmental factors which have been observed to affect plant morphology are light quality (specifically the ratio of red to far-red light) and wind. Wind, which is well reviewed in Nobel (1981), has been observed to cause thicker, smaller and shorter leaves, reduced plant height and increased lateral branching. Light quality, which is also well reviewed in Morgan and Smith (1981), has been shown to affect leaf expansion, morphology and anatomy; stem production and plant growth form.

Light quality changes may be further explained as follows. Within canopies red (R) light is strongly attenuated whereas far-red (FR) light is not. The relative amounts of R and FR are often calculated as the ratio of quantum flux of 10 nm bandwidths centred at 660 and 730 nm, which is referred to as *zeta* (e.g., Holmes and Smith, 1977a). *Zeta* is considerably higher after canopy clearing (Holmes and Smith, 1977a; Smith, 1981). The relative quantity of light in these wavebands affects the plant bichromatic pigment phytochrome. In response to absorbed red light P_r (phytochrome red) is converted to its chemically active form P_{fr} (phytochrome far-red) and in response to FR light, P_{fr} is converted to its chemically inactive form P_r (Smith, 1982). This phytochrome photoequilibrium (the ratio of P_{fr} to total P) is linearly related to *zeta* (Smith and Holmes, 1977) and concomitantly both are linearly related to many plant developmental processes (Morgan and Smith, 1981). The fact that sun conditions exist on the right-of-way is evident. The canopy presumably provides shade conditions (i.e. *zeta* of less than 1) as Ross et al. (1986) found that beneath *Picea* spp.-dominated stands of less than 10% shoot cover, *zeta* was consistently less than one. It is possible however that the upper portions of the shrubs in the control stand may be in sun conditions (*zeta* of greater than one) for a large portion of the day.

Although shade developmental conditions most often cause leaf areas to be larger, the opposite response, or no response at all, have also been observed (Goulet and Bellefleur, 1986; Holmes and Smith, 1977b). Low *zeta* (shade) has also been observed to cause increased stem production, specifically internode elongation, which appears to happen at the expense of leaf development (Holmes and Smith, 1977; Smith, pers. comm., 1988). This increased stem development may affect the relative canopy dimensions (Grime, 1981) as well as the ratio of stem to leaf biomass production. Canopy volume however, is not expected to change significantly, because total biomass is not significantly reduced (see chapter 2). As a result of the clear-cutting undertaken at the study site in the spring of 1985, microenvironmental conditions changed. Gallinger and Kershaw (1988) noted increased thaw rates and Kershaw (1988) recorded higher daily windspeeds, warmer soil temperatures and higher net radiation during the growing season on the cleared right-of-way.

The objectives of this study were first to describe the shrub morphology of *S. arbusculoides* at this latitudinal location and second to monitor, over a three-year-period, the changes in morphology resulting from the removal of both the black spruce-dominated tree canopy and the understory shrub canopy. Denuded shrubs in the right-of-way were compared to shrubs in an adjacent undisturbed forest. In summary, changes in leaf and shrub canopy morphology were expected for one of two primary reasons: 1. because there may have been differences in light quality between the two sampling areas; and 2. because improved microclimatic conditions on the right-of-way may have allowed for a greater period of leaf or shoot expansion. As a result of these expectations the following null hypotheses were generated for testing:

Ho_1. no leaf area differences would exist between right-of-way and control shrubs;

Ho_2. no differences in the ratio of leaf to current annual stem dry weight would exist between right-of-way and control shrubs;

Ho_3. no height differences would exist between right-of-way and control shrubs;

Ho_4. canopy volume of right-of-way shrubs would not be less than control shrubs;

Ho_5. no differences in the ratio of shrub height to average diameter would exist between right-of-way and control shrubs;

Methods

Field and lab methods

Sample sites were randomly selected in a stratified manner (i.e., random locations were determined for each sampling area separately) from a right-of-way cleared in 1985 and from a nearby undisturbed forest stand which served as a control. Twenty (in 1985) or thirty (in 1986 and 1987) sites were selected from each area and the nearest shrub to each site was considered as one sample. The timing of sampling was determined by typical growth phenology: after full leaf expansion and prior to leaf senescence. The dimensions of each shrub (height, the maximum diameter and the diameter perpendicular to the maximum diameter) were measured. The above-ground portion of each shrub was then collected and current annual stem and leaf growth were separated and oven dried. Above-ground portions of shrubs were then collected and current annual stem and leaf growth were separated and oven dried. The length and width of 10 randomly-selected leaves were then recorded for comparison of leaf sizes.

Statistical Analysis

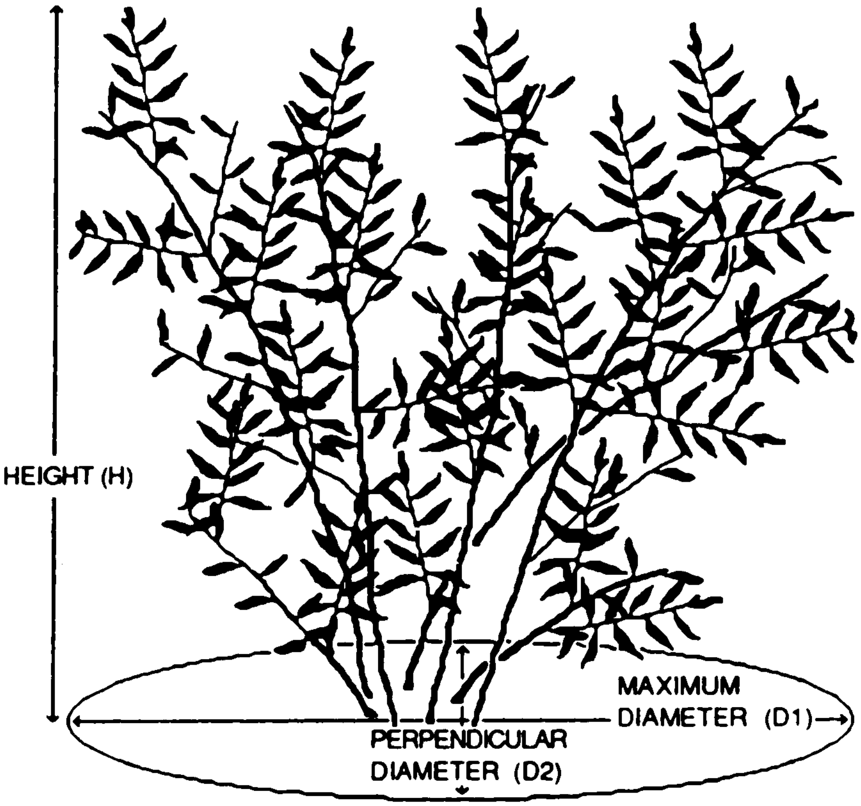
All analyses for this study were completed using SAS on the University of Alberta MTS (Michigan Terminal System) mainframe. For all sample distributions the Shapiro Wilk normality test was carried out because it is the most appropriate test for sample sizes of less than 50 (Shapiro and Wilk, 1965). As well, skewness and kurtosis were calculated using PROC UNIVARIATE or SAS (SAS Institute Inc., 1985a).

To calculate leaf areas, a subsa[illegible] 40 leaves were traced on graph paper in order to determine their exact area, thus [illegible] a data set which included leaf length, width and area. Using these data and the formula for determining the area of an ellipse, an analogue for calculating leaf area was created using the General Linear Models procedure in SAS (SAS Institute Inc., 1985a). The leaf area analogue which had an R-squared value of 0.974 when compared with the true leaf areas, was:

$$\text{LEAF AREA } (\text{cm}^2) = \pi(\text{LEAF LENGTH}/2) \times (\text{LEAF WIDTH}/2) \times 0.863 - 0.092 \quad [1]$$

Shrub ground cover ([2] Figure 1) was calculated as an ellipse using the maximum canopy diameter (D1) and a measurement perpendicular to the maximum canopy diameter (D2) (Figure 1). Canopy volume was treated as a cylinder ([3] Figure 1). The ratio of canopy height to ground cover was also calculated to compare canopy morphology.

Frequency distributions of the majority of shrub dimension parameters were non-normal, being right-skewed (i.e., the right tail of the distribution drawn out) and leptokurtic (i.e., having more items at the mean and tails and fewer in intermediate regions than a normal distribution). Log_{10} transformations best corrected this problem and allowed the use of analysis of variance (ANOVA) employing the GLM procedure on SAS (SAS Institute Inc., 1985b). Hochberg's (1974) GT2 means difference test was then carried out, because this test allows for unequal sample sizes. In some cases untransformed samples had greater probabilities of being normal than transformed (although both were within acceptable limits), so in the presentation of typical leaves (Figure 2) and typical canopies (Figure 7) means of the sample with the greatest probability of being normal were used. Leaf width which was not independently used in means comparisons was, in two samples, so skewed that Log transformation failed to provide normality. In these cases the median of the untransformed data was used in the presentation of typical leaves.



$$\text{GROUND COVER (GC)} = \Pi\,(\text{D1} \div 2) \times (\text{D2} \div 2) \quad [2]$$

$$\text{CANOPY VOLUME (CVOL)} = \text{GC} \times \text{H} \quad [3]$$

Figure 1. Canopy dimensions used in the calculation of canopy volume (m^3).

Results

All comparisons were made in a stratified manner. First each area was considered separately to observe differences in the three years of sampling (i.e., yearly variation, then each year was considered separately to observe differences in the two sampling areas for any given year (i.e., areal variation).

Leaf area (Figure 2, Table 1), which ranged from a mean of 1.3 to 2.9 cm^2, was not consistent among the three years in either area. On control shrubs, leaves were significantly smaller in 1985 relative to 1986 and 1987. On the right-of-way shrubs, 1985 and 1986 leaves were significantly larger than 1987 leaves. This was reflected when comparing the two sampling areas for each year. Relative to control shrubs, leaves were significantly larger on right-of-way shrubs in 1985; virtually identical in size in 1986 and smaller on the right-of-way shrubs in 1987.

The ratio of leaf to current annual stem biomass production (LV:ST) was consistent in control samples over the three-year period (Figure 3). Although this ratio was consistently lower for right-of-way samples, this difference was not considered significant in 1985. In 1986, stem production was so great for right-of-way shrubs that the mean LV:ST ratio for this sample was smaller than both the other two years for right-of- way samples and the control sample for that year.

Canopy height (Figures 4 and 7) did not change significantly within either sampling area over the three-year-period. In all three years right-of-way shrubs were shorter than control shrubs. A similar response was observed in canopy volumes (Figures 5 and 7). Over the three-year period canopy volumes increased slightly for the right-of-way shrubs and decreased slightly for the control shrubs. Neither trend was significant but it did result in the largest and only significant difference between the

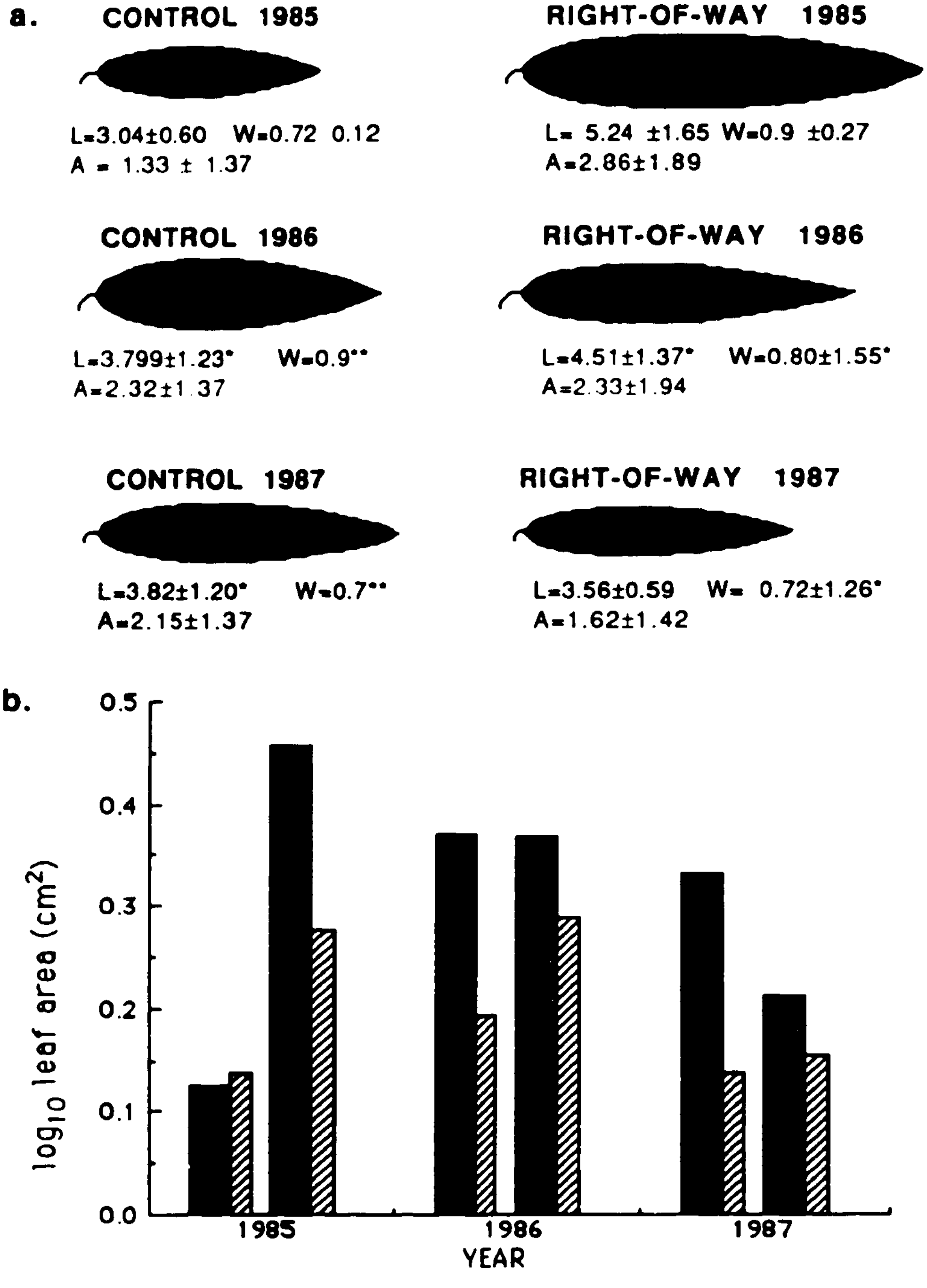


Figure 2a. Typical leaf area (A), length (L) and width (W) in cm. Based on: sample mean, log transformed sample mean (*), or sample median (**) depending on which had the greatest probability of normality. 2b. Mean $\log_{10}$ Leaf Area of *Salix arbusculoides* in 1985, 1986 and 1987. ■ Control, ■ Right-of-way and ▨ Standard deviation.

TABLE 1

Summary of ANOVA results and Hochburg means difference (GT2) test groupings forshrub dimensions[a] of *Salix arbusculoides*

	df[b]	leaf area (cm^2)	$\frac{\text{leaf biomass}}{\text{stem biomass}}$	canopy height (cm)	canopy volume (m^3)	$\frac{\text{canopy height}}{\text{mean diameter}}$
YEARLY VARIATION:						
Control						
F-value	2	14.69	1.12	2.21	1.21	0.85
PR>F[c]		0.0001***	0.3302	0.1173	0.3053	0.4326
GT2 groupings		('85) ('86, '87)				
Right-of-way						
F-value	2	6.61	19.33	1.81	1.27	0.95
PR>F		0.0023**	0.0001***	0.1717	0.2877	0.3906
GT2 groupings		('85, '86) ('87)	('85, '87) ('86)			
AREAL VARIATION:						
1985						
F-value	1	22.23	1.35	31.21	19.57	5.18
PR>F		0.0001***	0.2533	0.0001	0.0001***	0.0289*
1986						
F-value	1	0.00	82.01	5.30	3.72	0.23
PR>F		0.9617	0.0001***	0.0252*	0.0591	0.6319
1987						
F-value	1	10.14	23.60	5.69	1.30	5.65
PR>F		0.0024**	0.0001***	0.0178*	0.2596	0.0209*

[a] all comparisons based on $\log_{10}$ transformed data

[b] df = degrees of freedom, Sample sizes were n=20 in 1985 and n=30 in 1986 and 1987

[c] probability of theoretical F value exceeding calculated F value: F Significant at the following probabilities: 0.05 (*), 0.01(**) and 0.001(***)

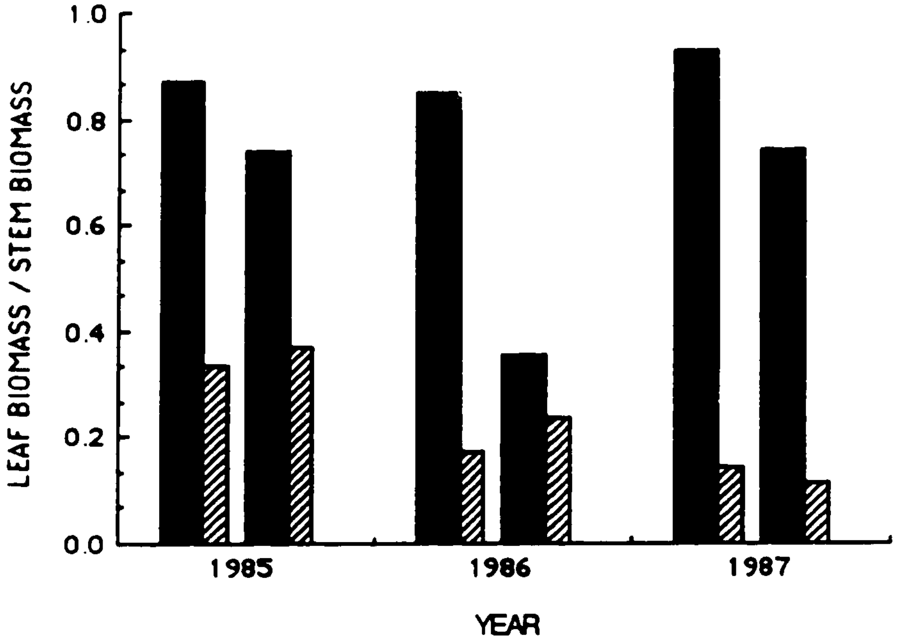


Figure 3. Mean $\log_{10}$ leaf to current annual stem biomass ratio of *Salix arbusculoides* in 1985, 1986 and 1987. ■ Control, ■ Right-of-way and ▨ Standard deviation.

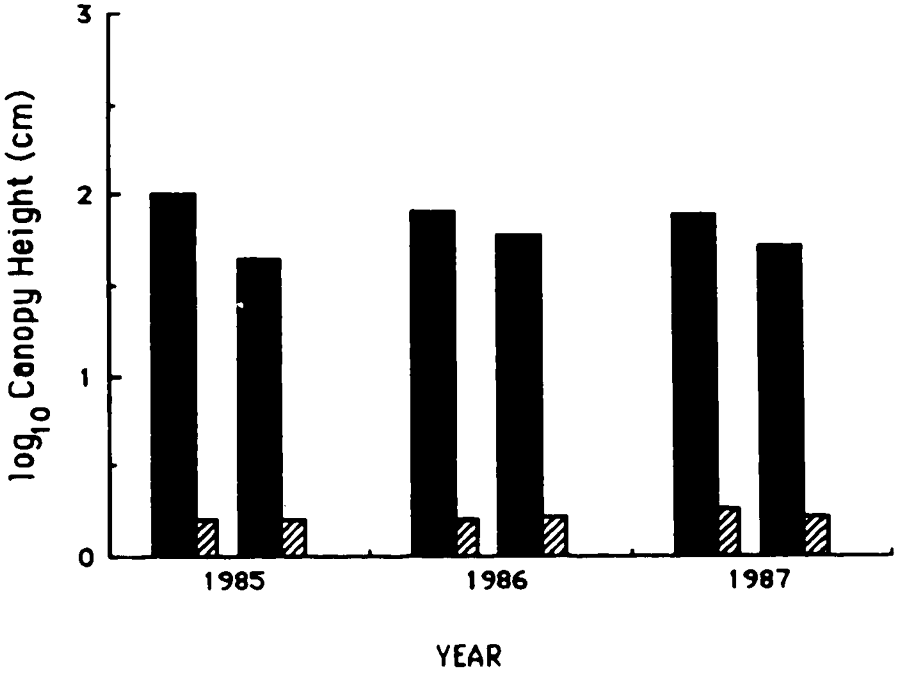


Figure 4. Mean $\log_{10}$ canopy height (cm) of *Salix arbusculoides* in 1985, 1986 and 1987. ■ Control, ■ Right-of-way and ▨ Standard deviation.

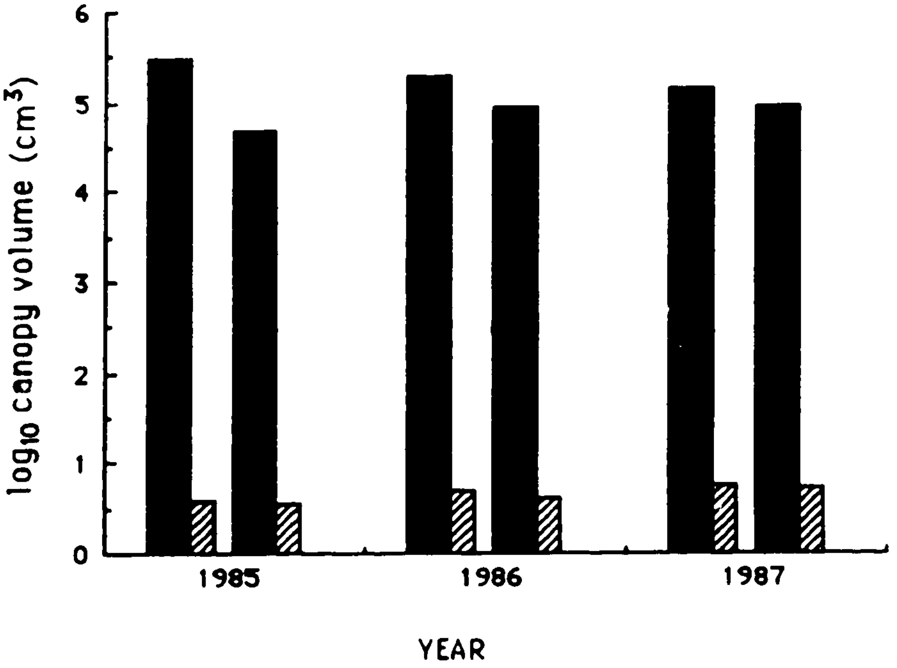


Figure 5. Mean $\log_{10}$ canopy volume (cm^3) of *Salix arbusculoides* in 1985, 1986 and 1987. ■ Control, ■ Right-of-way and ▨ Standard deviation.

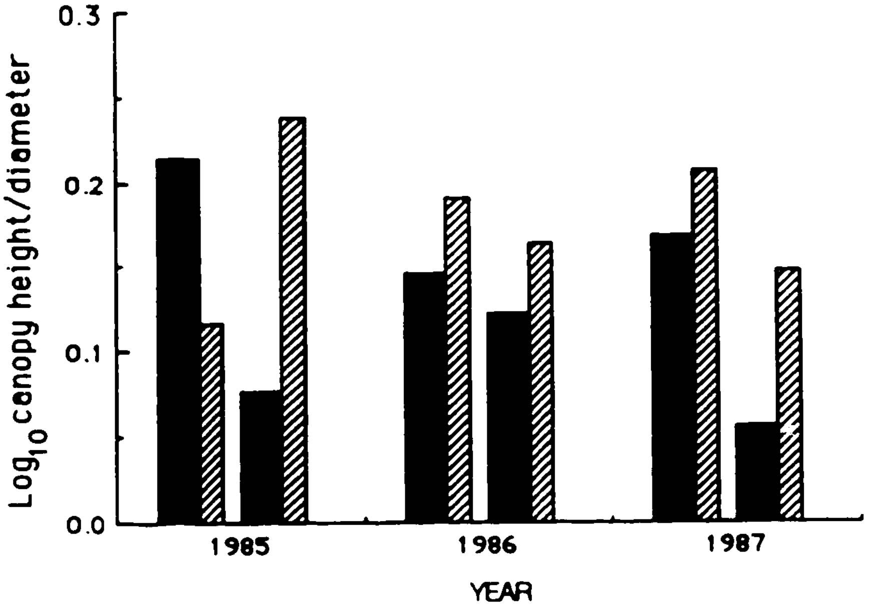
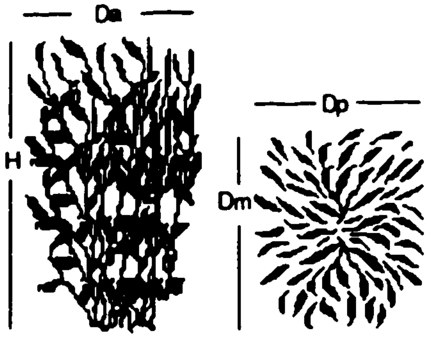


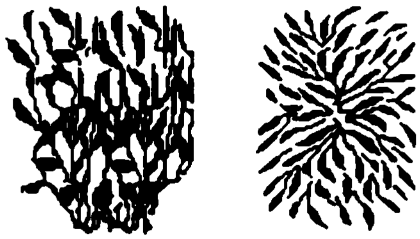
Figure 6. Mean $\log_{10}$ height to mean diameter ratio of *Salix arbusculoides* in 1985, 1986 and 1987. ■ Control, ■ Right-of-way and ▨ Standard deviation.

CONTROL 1985



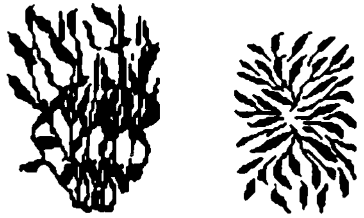
H = 102.33 ± 1.58 *
Dm = 71.10 ± 1.70 *
Dp = 56.42 ± 22.75
CVOL = 294171 ± 3.77 *
Da = 63.76 ± 12.2

CONTROL 1986



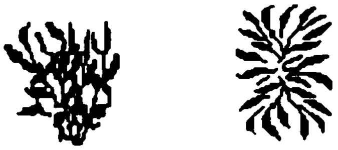
H = 79.43 ± 1.61 *
Dm = 75.97 ± 31.47
Dp = 52.58 ± 26.95
CVOL = 187241 ± 4.8 *
Da = 64.28 ± 29.21

CONTROL 1987



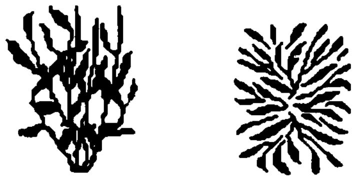
H = 72.44 ± 1.94 *
Dm = 60.74 ± 1.81
Dp = 39.65 ± 2.09 *
CVOL = 135487 ± 5.81 *
Da = 50.19 ± 1.95 *

RIGHT-OF-WAY 1985



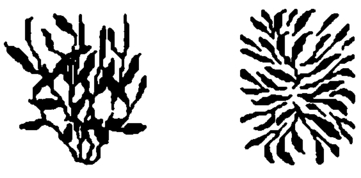
H = 43.65 ± 1.59 *
Dm = 47.79 ± 21.53
Dp = 30.70 ± 1.75 *
CVOL = 45656 ± 3.56 *
Da = 39.25 ± 11.6

RIGHT-OF-WAY 1986



H = 58.88 ± 1.64 *
Dm = 50.85 ± 1.59 *
Dp = 36.87 ± 1.75 *
CVOL = 86437 ± 4.0 *
Da = 87.72 ± 1.67 *

RIGHT-OF-WAY 1987



= 52.48 ± 1.65 *
Dm = 54.85 ± 1.80 *
Dp = 37.51 ± 1.94 *
CVOL = 84938 ± 5.3 *
Da = 46.18 ± 1.9 *

Figure 7. Typical canopy morphology based on averages of untransformed and log transformed (*) data. Dimensions in cm include height (H), maximum diameter (Dm), perpendicular to the maximum diameter (Dp) and average diameter (Da).

two sampling areas to be in 1985, the growing season following clear-cutting, when the mean right-of-way canopy volume was lower than for the control. The canopy volumes of shrubs in the two areas tended to become more similar as time passed, resulting in the least difference in 1987.

The relative canopy dimensions (Figure 6) did not have a similar trend. The mean ratio of height to average canopy diameter was consistently lower for right-of-way shrubs but not significantly so in 1986. This suggests that although canopy volume of right-of-way shrubs approached that of control shrubs as time passed, the right-of-way shrubs maintained a lower, broader canopy morphology, for at least the first three growing seasons.

Discussion

Argus (1973) described *S. arbusculoides* as ranging in height from 1 to 6 m in Alaska and the Yukon. The typical heights of 72 to 100 cm measured for undisturbed shrubs, suggest that at this location the species is in the smaller end of its size range. Raup (1947) described the species for the southwest Mackenzie valley region as forming shrubs or small trees, up to 7 meters high, with tall slender trunks up to 5 cm in diameter. Thus, the typically low broad coppiced growth form present on the study site may not be typical for the entire Subarctic range of the species.

The lack of shading in the clear-cut right-of-way may result in changes in light quality (specifically the red : far-red ratio referred to a *zeta*). Increased light quantity and subsequently increased temperature on the right-of-way should promote increases in productivity (Nilsson and Eckersten, 1983), whereas changes in light quality are more likely to affect shrub morphology. Changes in light quality can be affected by solar angle, sky conditions and season (Ross et al., 1986; Smith, 1982) and are thus not as predictable and linear as increases in light quantity. In this case due to the north-south orientation of the right-of-way, both photosynthetically active radiation (PAR) and *zeta* may have been considerably higher after canopy removal.

The average wind speed at a 3 m height was 1.62 (± 1.67 standard deviation) $m \cdot s^{-2}$ higher on the cleared right-of-way during the 1987 growing season. Although wind data is not yet available for 1985 and 1986, it is likely that conditions were also windier on the right-of-way in these years as the spruce canopy would tend to reduce wind in the control. Windy conditions tend to cause smaller leaf sizes (Whitehead, 1963). In 1985 right-of-way shrub leaf areas were not smaller, thus it is unlikely that the leaf area differentiation observed was initiated by wind.

Responses to light quality are more varied. Sun leaves typically have smaller leaf areas than shade leaves, however this is not always the case as in a few species they have either been larger or exhibited no difference (Go et and Bellefleur, 1986; Holmes and Smith, 1975; McLaren and Smith, 1978). Leaf area on right-of-way shrubs was significantly greater than for control shrubs in 1985, however the control sample for 1985 had considerably smaller leaves than the control samples in the two subsequent years of sampling. 1985 may have been a climatic anomaly at the study site however, as it was cooler and possibly had a shorter growing season than 1986 or 1987 (Kershaw, pers. comm., 1989). This may have resulted in less energy being allotted to the production of leaves in 1985 than in the two subsequent growing seasons. Average right-of-way leaf area consistently decreased over the three-year-period relative to the control. As there was no change in leaf biomass over this same period, it is likely that this was a morphological change rather than a decrease in overall leaf expansion and production. As productivity (see chapter 2) did not decrease after harvesting, it is unlikely that the change in microclimatic conditions on the right-of-way were limiting on this species. Thus, it is not likely that this decrease in average leaf area over the course of time, is simply a physical response to a degeneration in growing conditions. Three possibilities exist: 1. *S. arbusculoides* does not respond to light quality changes by altering leaf area, in which case the variations observed would be due to other physical influences; 2. *S. arbusculoides* responds to shade light quality by increasing leaf area, in which case 1985 would be typical and 1986 and 1987 atypical; or 3. *S. arbusculoides* responds to shade light quality by decreasing leaf area, in which case 1987 would be typical and 1985 and 1986 atypical.

If the first possibility were the case, the substantial increase in leaf area in the first year could be a regrowth response to produce greater photosynthetic tissue. No evidence can be found in the literature to support this thesis however, and this would not explain why control leaves were larger in 1987. The second possibility of shade leaves being larger which is the most typical response cited in the literature (e.g., Goulet and Bellefleur, 1986), may be possible if 1986 and 1987 are atypical years. This may be the case as compensatory growth was greatest in 1986. The third case of shade leaves being smaller is also possible. Any given shrub may contain leaves of both sun and shade morphology (Whatley and Whatley, 1980). In 1985 when the right-of-way shrubs were shortest (averaging 43.7 cm), and presumably contained fewer leaf strata, individual shrubs may have contained more sun than shade leaves (i.e., more and larger leaves) resulting in higher averages. As canopy height increases averaging over 50 cm in 1986 and 1987, the possibility for shading within an individual canopy increases. Thus in 1986 and 1987 the number of shade leaves (which would be smaller than sun leaves in *S. arbusculoides* given these results) relative to the number of sun leaves in any given right-of-way shrub would continue to increase with time, causing the average values to decrease. Because leaf density (LBD, see chapter 2) remained higher for right-of-way shrubs, shading may be more pronounced resulting in the right-of-way average falling below the control average in 1987.

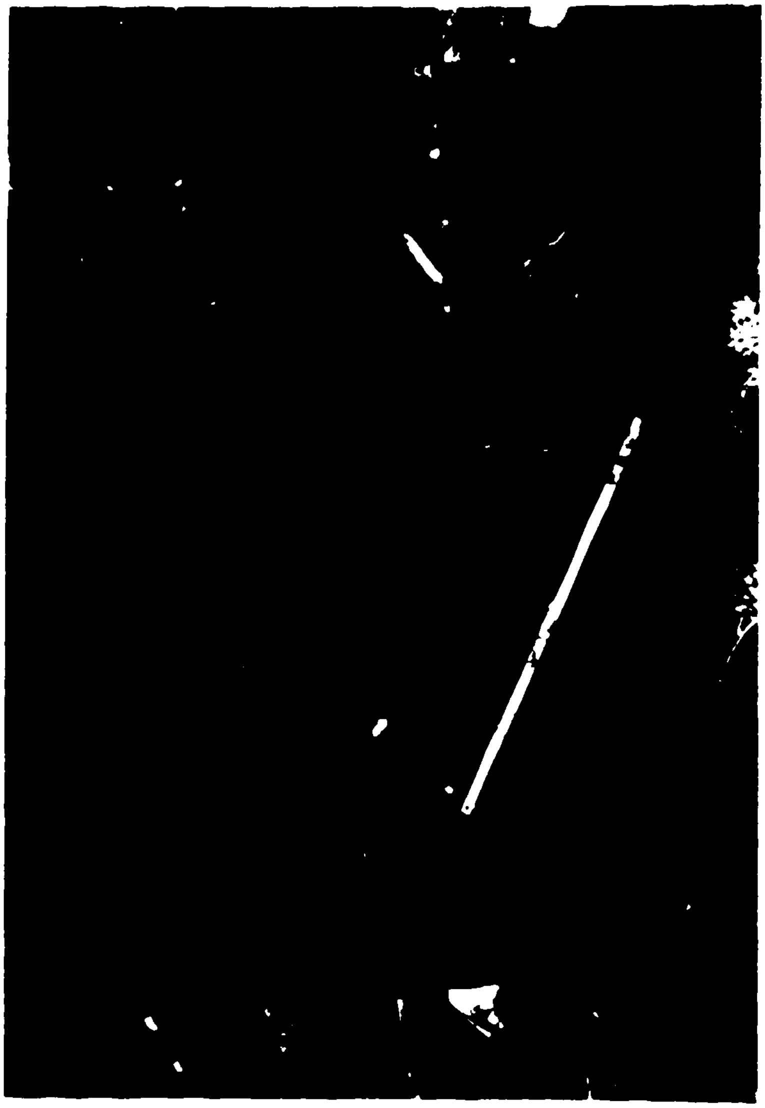
Although low R:FR can result in an increase of stem production which appears to happen at the expense of leaf development (Holmes and Smith, 1977b; Smith, pers. comm., 1988), the opposite response was observed in this study. The leaf to stem biomass ratio was lower for the unshaded right-of-way shrubs in all but the first growing season of recovery. Although it is possible that this was a result of changes in other environmental conditions this may still be a R:FR response as the lower leaf:stem ratio noted by Holmes and Smith (1977b) has only been observed in "weed" species. Plants growing within a grain-crop canopy would benefit by producing longer stems to position leaves higher up within the crowded canopy. They speculate that this type of adaptation may not exist in species which typically grow beneath a forest canopy as reduction in leaf production would not be of any advantage.

Although canopy volume was only significantly smaller for right-of-way shrubs in the first growing season of regrowth, canopy height remained lower in all three years. This resulted in the H/Dx ratio tending to be lower for right-of-way shrubs as reflected in the shrubs illustrated in plates 1 and 2. This relationship may have occurred for three reasons: 1. low R:FR can cause plants to exhibit a more upright morphology which would cause the control shrubs to be taller and less broad; 2. increased wind can cause reduced height (Wheeler and Salisbury, 1979) and increased lateral branching (Mitchell et al., 1975); and 3. increased basal sprouting (coppicing) in response to the shrub canopy removal, which would broaden the canopy. Increased coppicing as a result of denudation does occur in *S. arbusculoides*, as Kershaw et al. (1988) noted an increase of 673% in the number of basal stems per coppice, in one growing season after above-ground harvesting. It is possible that increased

Plate 1

Typical low, dense, coppiced right-of-way shrub in second growing season of recovery (meter stick for scale).

(Photo compliments of B. Gallinger)



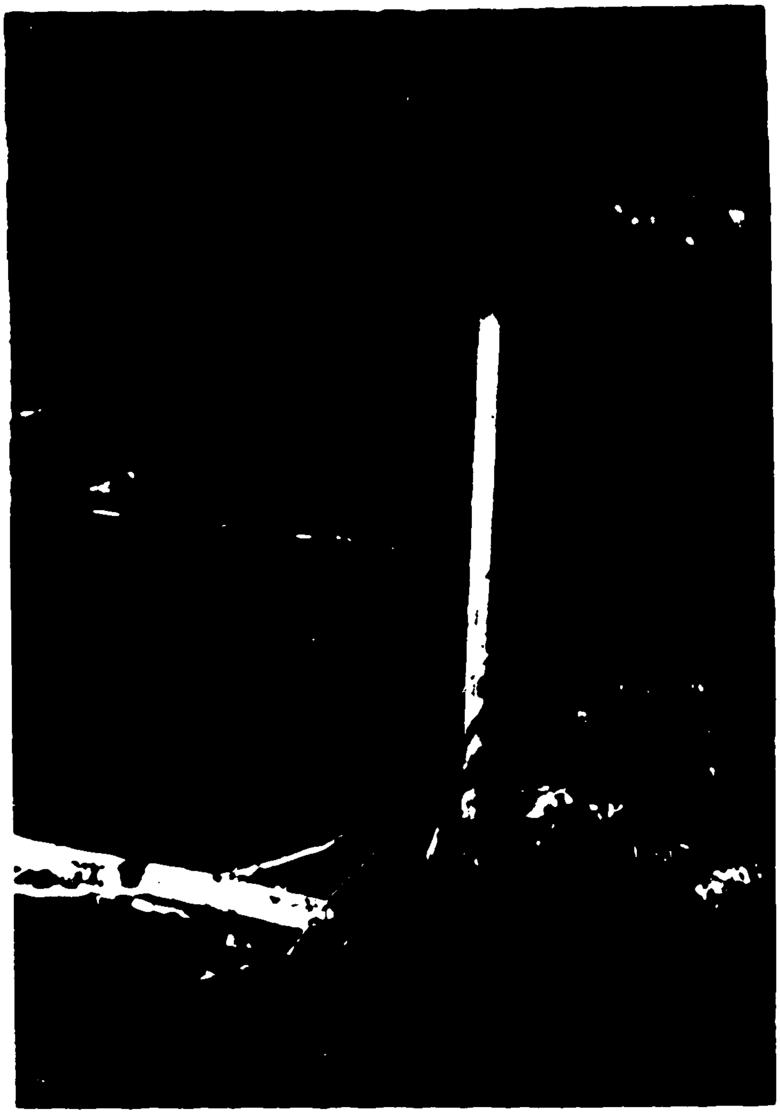


Plate 2

A typical shrub from the understory of the undisturbed control (meter stick for scale).

coppicing, rather than simply being a physical response to harvesting, may also be phytochrome mediated. A number of studies have found that the number and vigour of shrubs sprouting from tree boles or stumps was greatest under sunny conditions (Smith, H.C., 1965; Vogt and Cox, 1970). A similar phenomenone may occur in some graminoid species. The *zeta* ratio has been shown to effect tiller (basal shoot) production. Reduced tillering has been observed in plants growing under controlled conditions in low *zeta* levels (shade) either at the end of day or during the main period of daylight (e.g., Casal et al., 1985: Casal et al., 1987; Casal, 1988; Deregibus, 1983).

Conclusions

With respect to the null hypotheses stated in the introduction the following conclusions can be made:

Hypothesis 1

The null hypotheis that no leaf area differences would exist between right-of-way and control shrubs, must be rejected. Leaf area varied significantly between the study areas, however this was not consistent and absolute conclusions cannot be made without further investigation. Based on the evidence presented it appears most likely that *S. arbusculoides* produces smaller leaves in response to shade, but that the ratio of sun to shade leaves within an individual canopy decreases with time.

Hypothesis 2

The null hypothesis that no differences in the ratio of leaf to current annual stem dry weight would exist between right-of-way and control shrubs mus be rejected, as it was higher in right-of-way shrubs. If this was a R:F response it is opposite to the response found by Holmes and Smith (1977b), possibly because of their suggestion that shade-tolerant plants within a forest canopy may not respond in the same manner as the "weed" species involved in their study. It is also possible that *S. arbusculoides* has no canopy morphology response to changes in light quality and that this is a response to some other environmental factor.

Hypothesis 3

We must reject the third null hypothesis because shrubs were shorter in height on the right-of-way.

Hypothesis 4

Shrub canopy volume of right-of-way shrubs was only significantly less than control shrubs in the first growing season of recovery, thus the null hypothesis that no height differences would be observed must be rejected.

Hypothesis 5

The ratio of shrub height to the average diameter was consistently lower in right-of-way shrubs, thus the null hypothesis that no height/diameter differences would be observed must be rejected. Thus, as canopy volume was not lower, it can be concluded that the right-of-way shrubs had lower, broader morphologies. It cannot be concluded however, that this is either a response to windier conditions, a *zeta* response, or a physical response to cutting.

With reference to the overall objectives of this project, the following observations can be made: 1. *S. arbusculoides* in the Fort Norman area is smaller and more branched than can be expected for other areas within its range (Raup, 1947); and 2. the morphology of *S. arbusculoides* changes in response to clear-cutting. Although this may be simply a physical response to both the cutting of the shrubs and the changed microclimatic conditions following disturbance, there is evidence to suggest that *S. arbusculoides* responds to changes in R:FR.

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CHAPTER IV

RESEARCH OVERVIEW

Salix arbusculoides has an excellent propensity for natural vegetative recovery following clear-cutting. Within two growing seasons, regrown shrubs attained total biomass and canopy volumes which were not considered significantly less than control shrubs. The primary differences exhibited in regrown shrubs were morphological. Right-of-way shrubs tended to be shorter, broader and denser than control shrubs. Leaf area also varied between the right-of-way and control shrubs. As light quality, specifically the ratio of red to far-red light (*zeta*), is well documented as affecting plant morphology (Morgan and Smith, 1981), the following questions arise: 1. Does the black spruce canopy of 13% ground cover provide shade quality light (i.e., *zeta* < 1)? and 2. Does *S. arbusculoides* respond to changes in *zeta*, and if so, how? Attempts at studying these questions were [illegible], however this research was not outlined in the main text of this thesis and is instead summarised below.

Study site light conditions

Light conditions at the study site have been recorded during the 1987 growing season with a LICOR spectral radiometer. Ross et al. (1986) had great variability in light conditions at the ground surface beneath mature evergreen stands, thus an attempt was made to record light conditions under a variety of conditions to fully represent all possible quantities and qualities of light present. Both light quantity (PAR) and light quality were recorded on the cleared right-of-way and within the control at several different times of day, and at both the ground surface and at the tops of shrub canopies. Problems with instrument calibration were encountered during this exercise which may limit the amount of usable data which was obtained. It is expected however, that zeta levels within the black spruce stand will reflect shade conditions as the solar altitude at this northerly latitude is low throughout the growing season. This may not result in light quantity (PAR) being reduced however, because of the open nature of the canopy which allows for a considerable amount of diffuse light. It is also expected that a mathematical model for estimating the amount of shade provided by the black spruce canopy on both a daily and seasonal basis can be created using the sun angle and forest canopy cover and height.

Responses of *S. arbusculoides* to *zeta* levels

Gas exchange

In conjunction with light measurements recorded at the tops of shrub canopies, gas exchange (photosynthesis, respiration and transpiration) was measured on shrubs at the study site during the 1987 growing season. Measurements were recorded on three leaves at different positions on the shrub canopy to give an indication of gas exchange at the individual leaf (as opposed to the entire shrub) level. Control shrubs had greater variability but similar average levels of net photosynthesis. Interpretation of these results was difficult because several environmental conditions other than light are known to vary between the two sampling areas, and replication of these results was low due to time constraints. As a result it was difficult to make conclusions based on field measurements alone and growth chamber studies were attempted to provide a controlled comparison to this field work

Controlled-environment growth chamber studies were designed to quantify the photosynthetic and morphological responses of *S. arbusculoides* to variation in *zeta* ratios. Shrub cuttings from the study area were returned to the University of Alberta Phytotron facility and placed in aerated water to root. Only cuttings which had both root and shoot development are being used since it was determined from earlier attempts at establishing shrub whips that many break bud but do not root and subsequently die within the first growing season. The best shrub whip survival has been obtained using whips of 10 to 15 cm length obtained from the middle portion of one-year-old growth. Whips from the tip of the new growth were not as successful, possibly due to insufficient cambium present for rooting; whereas whips from the basal portions of the one-year-old growth may not have been as successful as a result of the cambium being too old to produce roots (Kroon, pers. comm., 1989). Two treatments were established involving equal amounts of photosynthetically active radiation (approximately 190 $\mathrm{uE \cdot m^{-2} \cdot s^{-1}}$) and differing *zeta* ratios (*zeta* $< 1 = 0.74$ and *zeta* $> 1 = 5.49$). It was hoped that gas exchange could be recorded on the shrub cuttings to determine if photosynthetic differences occur at either the leaf or the total shrub level. This treatment had to [illegible] however, due to equipment failure which eli[illegible] treatment effect. Unfortunately it could not be attempted an additional tim[illegible]e constraints. It is difficult to predict what the results of this study would ha[illegible]n, as various photosynthetic responses to specific *zeta* conditions are recorded in the literature. McLaren and Smith (1978) state that sun plants of *Rumex* sp. had twice the photosynthetic rate of shade plants on a unit area basis. Hoddinott and Hall (1982) however, found that both sun- and shade-grown plants of *Phaseolus* sp. had higher rates of photosynthesis under shade conditions.

Morphology

In conjunction with the growth chamber studies for gas exchange, it was hoped that morphological changes could also be monitored. Leaf area and density (leaf weight per unit area, as outlined in Goulet and Bellefleur, 1986) were to be examined to determine if and how leaves of these species respond to light quality. Stem length would also have been recorded since low levels of *zeta*, over the entire light period have been shown to increase stem elongation (Morgan and Smith, 1976; Holmes and Smith, 1977). It is not known if increased stem elongation results in greater stem biomass allocation, and if so, if this increase in stem tissue is at the expense of other plant components. Evidence in the literature does support differences in biomass allocation since higher shoot / root weight ratios have been observed in shade plants (Hoddinott and Hall, 1982; McLaren and Smith, 1978). Biomass allocation would therefore have been determined, to observe any differences between above / below ground and leaf / stem biomass distribution. Based on field observation and controlled environment experiments, some plant species in full sun or high *zeta* ratio conditions, have prolific branching, whereas in shade or given short periods of exposure to far-red light at the end of the day, these same species have apical dominance and suppressed axillary bud growth (e.g., Bogorad and McIlrath, 1960; Kasperbauer, 1971; Tucker and Mansfield, 1972). To observe weather *S. arbusculoides* responds to shade light quality by exhibiting apical dominance the number of branches produced and their relative distance from the apex would also have to have been recorded.

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APPENDIX 1
Summary statistics of biomass parameters

		UNTRANSFORMED DATA				LOG10 TRANSFORMED DATA	
PARAMETER	n	MAX	MIN	MEAN	STANDARD DEVIATION	ANTILOG MEAN	LOG10 STANDARD DEVIATION
TOTAL SHRUB BIOMASS(g/shrub)							
Control '85	20	327.00	10.54	100.91	92.31	65.464	0.444
R.O.W. '85	20	47.64	1.01	20.35	15.67	13.931	0.439
Control '86	31	276.30	1.26	61.13	71.09	30.130	0.586
R.O.W. '86	30	222.40	2.84	52.66	67.33	28.054	0.485
Control '87	30	1694.00	1.36	128.18	315.73	32.584	0.731
R.O.W. '87	30	186.40	1.37	44.30	48.68	24.547	0.514
TOTAL CURRENT ANNUAL GROWTH (g/shrub)							
Control '85	20	47.00	0.87	11.34	11.71	7.228	0.416
R.O.W. '85	20	28.05	0.53	8.25	7.96	5.093	0.479
Control '86	31	29.56	0.43	10.38	8.75	6.839	0.449
R.O.W. '86	30	141.10	2.60	28.76	39.97	15.031	0.471
Control '87	30	172.00	0.54	20.12	35.37	6.918	0.647
R.O.W. '87	30	69.78	0.54	16.42	18.41	8.491	0.540
LEAVES (g/shrub)							
Control '85	20	43.10	0.66	9.58	10.25	6.223	0.425
R.O.W. '85	20	23.21	0.50	6.57	6.07	4.120	0.473
Control '86	31	26.67	0.38	9.00	7.57	5.929	0.447
R.O.W. '86	30	95.04	1.37	18.34	24.39	10.209	0.448
Control '87	30	66.42	0.49	13.79	17.67	5.907	0.603
R.O.W. '87	30	55.92	0.49	13.74	14.56	7.534	0.525
CURRENT ANNUAL (NEW) STEMS (g/shrub)							
Control '85	20	7.98	0.13	1.49	1.90	0.834	0.481
R.O.W. '85	20	9.49	0.03	1.68	2.32	0.750	0.613
Control '86	31	5.16	0.05	1.39	1.33	0.845	0.488
R.O.W. '86	30	69.39	0.50	10.49	16.38	4.529	0.560
Control '87	30	93.75	0.06	5.35	17.32	0.815	0.797
R.O.W. '87	30	13.86	0.05	3.04	3.77	1.374	0.606
NON-CURRENT ANNUAL (OLD) STEMS (g/shrub)							
Control '85	20	291.60	6.97	89.84	81.79	56.620	468
R.O.W. '85	20	42.01	0.00	12.09	11.57	37.670	454
Control '86	31	249.90	0.59	50.75	63.59	21.830	0.660
R.O.W. '86	30	95.25	0.24	23.87	29.17	9.890	0.683
Control '87	30	1634.00	0.81	110.43	303.10	22.390	0.781
R.O.W. '87	30	116.60	0.83	27.90	30.68	14.870	0.546

		UNTRANSFORMED DATA				LOG10 TRANSFORMED DATA	
PARAMETER	n	MAX	MIN	MEAN	STANDARD DEVIATION	ANTILOG MEAN	LOG10 STANDARD DEVIATION
LEAF BIOMASS INDEX (g/shrub)							
Control '85	20	70.19	4.31	27.44	18.07	21.670	0.327
R.O.W. '85	20	99.39	14.39	44.09	20.41	39.990	0.200
Control '86	31	138.20	8.67	30.41	24.22	25.120	0.257
R.O.W. '86	30	306.40	21.78	83.10	61.51	69.340	0.252
Control '87	30	74.68	3.87	38.06	20.85	31.550	0.299
R.O.W. '87	30	442.50	16.36	60.63	75.69	50.000	0.267
LEAF BIOMASS DENSITY (g/shrub)							
Control '85	20	110.60	4.37	30.65	28.42	21.180	0.388
R.O.W. '85	20	220.40	18.69	105.33	53.61	90.150	0.273
Control '86	31	476.70	8.04	50.88	85.63	31.700	0.352
R.O.W. '86	30	1532.00	28.21	183.00	292.56	118.030	0.346
Control '87	30	218.00	2.67	55.08	42.59	43.850	0.359
R.O.W. '87	30	1264.00	20.85	144.63	233.60	88.510	0.376

APPENDIX 2

Summary statistics of morphological parameters

PARAMETER	n	UNTRANSFORMED DATA MAX	MIN	MEAN	STANDARD DEVIATION	LOG10 TRANSFORMED DATA ANTILOG MEAN	LOG10 STANDARD DEVIATION
LEAF AREA (cm^2)							
Control '85	20	2.02	0.67	1.39	0.41	1.330	0.136
R.O.W. '85	20	8.45	0.88	3.41	1.97	2.870	0.275
Control '86	31	7.50	1.05	2.54	1.44	2.360	0.196
R.O.W. '86	30	6.21	0.64	2.83	1.73	2.330	0.288
Control '87	30	4.58	1.19	2.25	0.77	2.150	0.136
R.O.W. '87	30	3.16	0.79	1.72	0.61	1.62	0.153
LEAF LENGTH (cm)							
Control '85	20	3.90	1.90	3.04	0.60	2.99	0.089
R.O.W. '85	20	8.40	2.40	5.24	1.65	4.98	0.145
Control '86	31	6.90	3.00	3.75	1.09	3.80	0.090
R.O.W. '86	30	8.60	2.70	4.73	1.50	4.5[illegible]	0.137
Control '87	30	5.[illegible]	2.50	3.88	0.70	3.82	0.079
R.O.W. '87	30	4.80	2.50	3.56	0.59	3.51	0.073
LEAF WIDTH (cm)							
Control '85	20	0.90	0.40	0.72	0.12	0.71	0.082
R.O.W. '85	20	1.50	0.50	0.92	0.27	0.88	0.134
Control '86	31	3.10	0.60	1.07	0.55	0.99	0.158
R.O.W. '86	30	2.80	0.40	0.88	0.49	0.80	0.190
Control '87	30	1.50	0.70	0.88	0.19	0.87	0.083
R.O.W. '87	30	1.10	0.50	0.74	0.17	0.72	0.099
CANOPY HEIGHT (cm)							
Control '85	20	210.00	48.00	112.58	48.51	102.30	0.200
R.O.W. '85	20	85.00	15.00	48.63	20.27	44.70	0.202
Control '86	31	175.00	29.00	88.13	40.95	79.30	0.207
R.O.W. '86	30	186.00	20.00	65.84	33.95	58.70	0.214
Control '87	30	161.00	22.00	87.62	45.28	75.00	0.259
R.O.W. '87	30	110.00	15.00	58.79	25.85	52.70	0.217
MAXIMUM CANOPY DIAMETER (cm)							
Control '85	20	170.00	21.00	80.47	40.00	70.85	0.232
R.O.W. '85	20	81.00	18.00	47.79	21.53	42.66	0.219
Control '86	31	150.00	7.00	75.97	31.47	67.30	0.254
R.O.W. '86	30	126.00	18.00	56.48	27.78	50.48	0.201
Control '87	30	181.00	14.00	70.86	38.09	60.67	0.258
R.O.W. '87	30	147.00	11.00	63.31	32.74	54.70	0.255

		UNTRANSFORMED DATA				LOG10 TRANSFORMED DATA	
PARAMETER	n	MAX	MIN	MEAN	STANDARD DEVIATION	MEAN	STANDARD DEVIATION
CANOPY DIAMETER PERPENDICULAR TO THE MAXIMUM DIAMETER (cm)							
Control '85	20	100.00	18.00	56.42	22.76	51.29	0.202
R.O.W. '85	20	89.00	12.00	35.42	19.55	30.69	0.243
Control '86	31	137.00	5.00	52.58	29.95	44.67	0.283
R.O.W. '86	30	122.00	11.00	42.96	26.14	36.85	0.243
Control '87	30	177.00	6.00	50.59	36.72	39.63	0.319
R.O.W. '87	30	101.00	8.00	45.52	27.46	37.50	0.288
GROUND COVER (m^2							
Control '85	20	1.11	0.06	0.407	0.325	0.289	0.401
R.O.W. '85	20	0.52	0.02	0.157	0.137	0.103	0.444
Control '86	31	1.61	0.003	0.368	0.317	0.237	0.522
R.O.W. '86	30	1.21	0.02	0.239	0.284	0.521	0.430
Control '87	30	2.52	0.01	0.375	0.496	0.189	0.559
R.O.W. '87	30	17	0.01	0.291	0.301	0.161	0.536
CANOPY VOLUME (m^3)							
Control '85	20	2.23	0.028	0.564	0.608	0.294	0.576
R.O.W. '85	20	0.284	0.005	0.084	0.082	0.046	0.551
Control '86	31	2.647	0.001	0.405	0.524	0.187	0.682
R.O.W. '86	30	2.246	0.004	0.232	0.471	0.086	0.601
Control '87	30	3.648	0.002	0.461	0.751	0.142	0.764
R.O.W. '87	30	1.131	0.001	0.225	0.300	0.086	0.725
LEAF TO STEM BIOMASS RATIO							
Control '85	20	67.62	2.83	10.92	14.57	7.46	0.336
R.O.W. '85	20	21.22	1.35	7.69	6.53	5.48	0.371
Control '86	31	12.34	2.10	7.49	2.62	7.01	0.170
R.O.W. '86	30	10.12	1.03	2.67	1.97	2.26	0.236
Control '87	30	13.75	0.10	8.69	3.16	8.47	0.150
R.O.W. '87	30	11.44	3.06	5.80	2.10	6.21	0.147
CANOPY HEIGHT TO MEAN CANOPY DIAMETER RATIO							
Control '85	20	3.36	1.09	1.70	0.53	1.64	0.117
R.O.W '85	20	2.67	0.56	1.37	0.75	1.19	0.238
Control '86	31	4.83	0.56	1.54	0.78	1.40	0.190
R.O.W. '86	30	2.82	0.68	1.43	0.58	1.33	0.164
Control '87	30	3.52	0.344	1.63	0.73	1.47	0.207
R.O.W. '87	30	1.84	0.50	1.20	0.38	1.14	0.148

APPENDIX 3

Glossary of terms

active layer: the upper portion of soil in a permafrost zone, which experiences seasonal freezing and thawing

biennial: a plant which requires two years to complete its life cycle

biomass: the dry weight of living material expressed as a weight per sampling unit (in this study: mg per shrub)

borrow pit: a pit which has had aggregate material extracted from it for road building or other berm construction

catkin: a scaly spike of flowers; the flowering structure of willow

compensatory growth: growth by the redistribution of stored root carbohydrates, in response to removal of plant tissue

coppice: *n.* a shrub or small tree having numerous basal stems; *v.* basal sprouting

early successional species: opportunistic species which colonise available areas quickly, but which are often replaced by other plants in the long term

herb: non-woody plant

herbaceous: non-woody

late successional species: species which are well adapted to an environment, which can out-compete other species for available resources to form a stable self-maintaining state.

macro-nutrient: a nutrient required by plants in large quantities (relative to micro-nutrients): i.e calcium, potassium, nitrogen, phosphorus, magnesium and sulphur

net-radiation: the balance between total incoming and outgoing long and short wave radiation at a surface

phenology: the timing or periodicity in the life-cycle, in relation to seasonal climatic change; e.g., the timing of leaf expansion, flowering, senescence

phytochrome: a plant bichromatic pigment believed to mediate many plant developmental processes

root-crown: the subsurface node from which branching and rooting occur

rhizome: an underground stem used as a means of vegetative propagation or storage organ

Tiller: *n.* a shoot from the base of a stem, sucker; *v* to put forth stems from the root

senescence: the act of entering dormancy (leaf fall in deciduous species)

shrub: a woody perennial plant of low height (2 m is commonly accepted as a height maximum for Subarctic species)

shrub stool: a coppice

vegetative regeneration: site or plant recovery from intact below ground plant parts, excluding seed (sexual) propagation

weed: an unwanted plant which invades cultivated ground

zeta ratio: the ratio of quantum flux of 10 nm bands centred at 660 (red) and 730 nm (far-red)