

A summary of some studies on *Kalmia angustifolia* L.: a
problem species in Newfoundland forestry

B.D. Titus, S.S. Sidhu and A.U. Mallik
Newfound and Labrador Region – Information Report N-X-296



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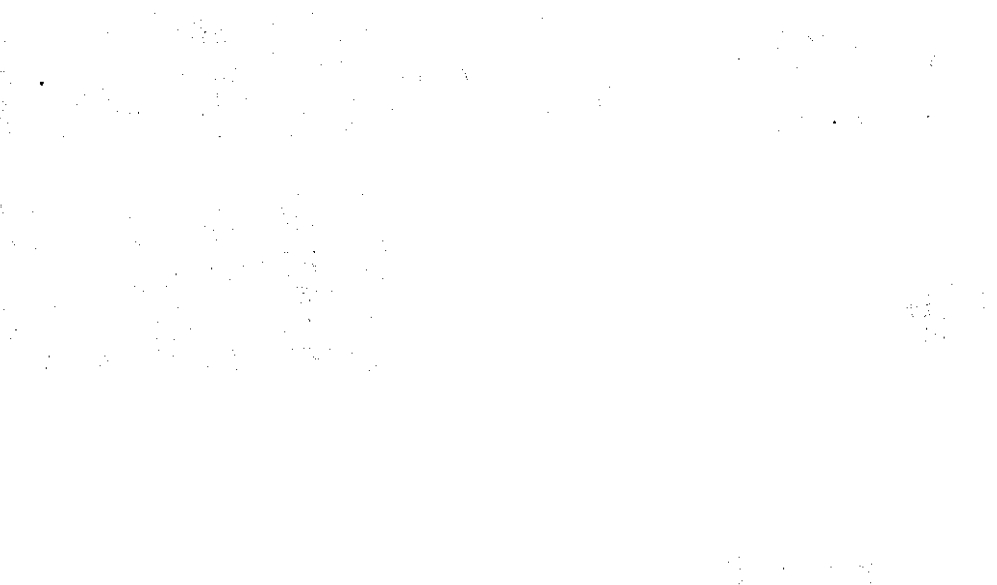
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Cover Caption: **A** cutover in central Newfoundland with a dense **cover** of *Kalmia augustifolia* which impedes natural regeneration of black spruce and inhibits growth of natural or planted conifers (photo by S.S. Sidhu).

Canadian Cataloguing in Publication Data

Titus, B.D.

A summary of some studies on *Kalmia angustifolia* L. : a problem species in Newfoundland forestry.

(Information report: N-X-296)

ISBN 0-662-22920-7

DSS cat. no. Fo-46-15/296E

1. Sheep laurel--Newfoundland. 2. Plant competition--Newfoundland.
3. Black spruce--Diseases and pests--Newfoundland. I. Sidhu, S.S., f1938-
II. Mallik, A.U. (Azim U.) III. Canadian Forest Service, Newfoundland and
Labrador Region. IV. Title. V. **Series:** Information report (Canadian Forest
Service-Newfoundland and Labrador Region): N-X-296.

SB413.K3T57 1995 634.9'752658 C95-900133-6

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ISSN NO. 0704-7657

CAT. NO. Fo46-15/296E

ISBN NO. 0-662-22920-7

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Canadian Forest Service
Newfoundland & Labrador **Region**
P.O. **Box** 6028
St. John's, Newfoundland
Canada A1C 5X8

Telephone No. 709-772-4117

OR

A microfiche edition of **this** publication may **be** purchased from:

Micromedia Inc.
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Printed in Canada



**A SUMMARY OF SOME STUDIES ON *KALMIA ANGUSTIFOLIA* L.:
A PROBLEM SPECIES IN NEWFOUNDLAND FORESTRY**

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**NATURAL RESOURCES CANADA
CANADIAN FOREST SERVICE
NEWFOUNDLAND & LABRADOR REGION
INFORMATION REPORT N-X-296**

ABSTRACT

The ericaceous shrub *Kalmia angustifolia* L. var. *angustifolia* (sheep laurel, lambkill, *Kalmia*) is found in eastern North America, from Newfoundland to Ontario, and south through the New England States to Virginia. It is commonly found as an understory component of black spruce forests, and can proliferate rapidly after stand disturbances such as harvesting, fire or insect attack. Subsequent regeneration and growth of spruce on sites dominated by *Kalmia* is often poor, and a greater understanding of the ecology of *Kalmia* and its interactions with black spruce are required for the management of these problem sites.

Results of a series of field, greenhouse and laboratory studies on the biology of *Kalmia* are presented. The phytological associations of *Kalmia angustifolia* in Newfoundland are described, demonstrating that the species can tolerate a wide range of moisture and nutritional gradients, and can be found in heaths, peatlands, forests and swamps. The shrub is semi-deciduous, with the previous year's leaves supplying photosynthates and nutrients to current growth through translocation.

Vegetative reproduction is the principle method of spread on forested sites and on disturbed sites with intact humus layers. Flowering is greatly reduced on plants growing in mature forests, where they occur in canopy openings. *Kalmia* can produce 15 to 160 million seeds per hectare. Even though up to 45% of these seeds may not be viable, the large output ensures adequate regeneration so long as suitable exposed mineral soil seedbeds are available. Light is required for seed germination. No plants of seed origin were found on forested sites, but they were common on mineral exposed soils. The vegetative buds of *Kalmia* are described in a histological study.

RÉSUMÉ

Kalmia angustifolia L. var. *angustifolia* (kalmia à feuilles étroites), un arbuste de la famille des Éricacées, se retrouve dans l'est de l'Amérique du Nord de Terre-Neuve à l'Ontario et, vers le sud, à travers les états de la Nouvelle-Angleterre jusqu'en Virginie. On le rencontre couramment comme composante de l'étage inférieur des forêts d'épinettes noires; il peut proliférer rapidement après que des peuplements ont été perturbés par la récolte, l'incendie ou une infestation d'insectes. La régénération et la croissance de l'épinette dans les sites dominés par le kalmia sont souvent efficaces; pour aménager ces sites, il importe de mieux comprendre l'écologie du kalmia et ses interactions avec l'épinette noire.

Le présent résumé expose les résultats d'une série d'études sur la biologie du kalmia menées sur le terrain, en serre et en laboratoire. Il décrit les associations phytologiques de *Kalmia angustifolia* à Terre-Neuve et démontre que l'espèce, par sa tolérance à une vaste gamme de gradients d'humidité et de ressources nutritives, fréquente tout aussi bien les landes que les tourbières, les forêts et les marécages. L'arbuste est semi-caduc, les feuilles de l'année précédente alimentant les nouvelles pousses, par translocation, en photosynthates et en substances nutritives.

La multiplication végétative est le principal mode de dispersion du kalmia dans les sites boisés et dans les sites perturbés aux couches humifères intactes. La floraison est fortement réduite chez les plantes qui poussent dans les forêts adultes, où elles se présentent dans les clairières. Le kalmia peut produire de 15 à 160 millions de graines par hectare; bien que jusqu'à 45 % de ces graines ne soient pas viables, cette forte production lui assure une régénération adéquate aussi longtemps qu'il trouve des lits de germination de sol minéral exposé (les graines de kalmia ont besoin de lumière pour germer). Si on n'a trouvé aucune plante née de graines dans les sites boisés, celles-ci étaient communes sur les sols minéraux exposés. Les bourgeons végétatifs du kalmia sont décrits dans une étude histologique.

Kalmia can inhibit black spruce growth through a combination of **nutrient** competition and allelopathic effects. Kalmia can function under low nutritional conditions, but can respond to increased availability by taking up proportionately more nutrients (especially nitrogen), and by concentrating these in important tissues. This shrub is thus able to survive on sites across a wide nutritional range.

Black spruce seeds were found to germinate best in field plots with the Kalmia plants removed and the humus and mineral soil mixed, although removal of the Kalmia and humus without mixing also increased seed germination. In a laboratory study, leaf powder of Kalmia inhibited black spruce emergence from seed. Further, aqueous extracts of the leaves of Kalmia were found to be inhibitory to isolates of *Suillus*, a mycorrhizal fungi, but not to isolates of *Phialocephala*, a genus of pseudomycorrhizae or root pathogens.

From field and greenhouse studies it is apparent that there are no *easy* methods of controlling Kalmia. Light burns, drag scarification, and herbicides were ineffective in the field, where only patch scarification prevented spread of Kalmia into exposed mineral soil. **Likewise**, decapitation, liming and herbicides did not kill Kalmia in a greenhouse experiment. However, shading did inhibit vegetative bud production.

Although this work is mainly a compilation of ecological studies a number of silvicultural **recommendations** can be made. Regardless of what silvicultural options are chosen, consideration should be given to the quality of the site to be reforested: a poor site, even if Kalmia-induced problems are overcome, is still a poor site. Consideration should also be given to economic costs, including **future** wood hauling costs (distance to pulp and sawmills) **as well as** to treatment application **costs** themselves.

Le kalmia peut inhiber la croissance de l'épinette noire par une combinaison de concurrence pour les substances nutritives et **d'effets** allelopathiques. Le kalmia survit dans des conditions de pénurie de substances nutritives, mais peut s'adapter à un accroissement de nourriture en absorbant une proportion plus **élevée** de ces substances (d'azote **en particulier**) et **en les** concentrant dans ses tissus importants. Par conséquent, l'arbuste peut survivre dans des sites aux conditions nutritionnelles très variables.

Les graines d'épinette noire germent le mieux dans des parcelles expérimentales d'où le kalmia a été retiré et où l'humus et le sol minéral ont été **mélangés**, bien que l'enlèvement du kalmia et un humus non mélangé ont aussi favorisé une meilleure germination des graines. Il a été démontré en laboratoire que les feuilles pulvérisées du kalmia ont inhibé l'émergence des graines d'épinette noire; de plus, des extraits aqueux des feuilles de kalmia se sont révélés inhibiteurs pour les isolats de *Suillus*, un champignon des mycorhizes, mais pas pour les isolats de *Phialocephala*, un genre de pseudomycorhize ou de pathogène racinaire.

À la lumière des recherches sur le terrain et **en** serre, il semble qu'il **n'y** ait pas de méthode facile de contrôler le kalmia. Les brûlages légers, le scarifiage par traînage **et** les herbicides se sont montrés inefficaces sur le terrain, où seul le scarifiage de placeaux a empêché la prolifération du Kalmia dans le sol minéral exposé. De la même façon, l'éêtage, le chaulage et l'application d'herbicides n'ont pas **tué** le kalmia dans une expérience **en serre**. Toutefois, l'ombrage a inhibé la production de bourgeons végétatifs.

Bien **que** le présent résumé consiste surtout en une compilation d'études écologiques, il est possible d'en tirer un certain nombre de recommandations sylvicoles. Quelle que soit le traitement sylvicole retenu, il faudra prendre en considération la qualité du site à reboiser : un site peu fertile restera un site peu fertile, même débarrassé des problèmes causés par le kalmia. Il faudra aussi tenir compte des coûts économiques, **y** compris des coûts futurs du remorquage du bois (distance jusqu'aux usines de pulpe et aux scieries) et des coûts directs d'application du traitement.

A holistic approach to forest management is ultimately required so that the "*Kalmia* problem" is prevented rather than cured after the fact by not harvesting sites that will become too problematic to reforest if disturbed. This will require predicting successional pathways and future potential site quality before harvesting takes place.

Pour prévenir le «problème du kalmia» avant d'avoir à le guérir, il importe d'appliquer une approche holistique à l'aménagement forestier en évitant de récolter les sites qui seront trop difficiles à reboiser s'ils sont perturbés. Pour ce faire, avant de récolter un site, il faudra prévoir comment s'y déroulera la succession et quelle sera sa qualité potentielle dans l'avenir.

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ACKNOWLEDGEMENTS

The **original** experimental work **reported** in this publication was designed and carried out in the 1960s and 1970s by a range of researchers including Drs. A.K. Bal, O.A. Olsen, F.C. Pollett, A.W.H. Damman and S. Sidhu. All sections of this publication refer back to the various original contract reports, theses and internal documents produced by these workers and on file in the CFS-NLR office. All uncited experimental work was carried out by Dr. S. Sidhu while on staff at the CFS-NLR office. Present CFS-NLR staff who assisted with the research at the **time as** technicians or students include W. Meades, E.D. Wells, B.A. Roberts, and S. Morgan. The original draft of this manuscript was Written by Dr. S. Sidhu, up-dated by Dr. A.U. Mallik, and then re-written and completed in preparation for publication by **Dr.** B.D. Titus in conjunction with **Drs.** Sidhu and Mallik. The authors wish to thank Drs. R.J. West and M.B. Lavigne of the CFS-NLR for reviewing an original **draft**, and Drs. W. Meades and M. Weber for reviewing the fmal **draft** of the manuscript. **Dr.** J.A. Fortin of l'Université de Montréal, **Dr.** K. Egger of Memorial University of Newfoundland and Drs. J. Bérubé and G. Warren of CFS-NLR assisted with comments on the mycorrhizal research contained in **this** report, and **Dr.** J.E. MacDonald of CFS-NLR provided advice on the micrographs. Mary Gillingham, Joan Rockwood, and Linda Richards typed and laid out the many **drafts of** the manuscript, and production of the fmal report was overseen by Hildegard Dunphy. The third author (Dr. A.U. Mallik) received partial financial assistance from the Natural Science and Engineering Research Council of Canada and the Canada-Newfoundland Forest Resource Development Agreement while working on early **drafts of this** manuscript while a post-doctoral fellow and then a private contractor in Newfoundland.

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1. INTRODUCTION

Kalmia angustifolia L. var. *angustifolia* (sheep laurel, lambkill; hereafter referred to as *Kalmia*¹) occurs over a wide ecological range in Newfoundland, Prince Edward Island, New Brunswick, Nova Scotia, Quebec and Ontario (Hall *et al.* 1973). In the United States it is commonly found in New England and along the coast to the southeastern tip of Virginia, and as far west as Michigan (Fig. 1). There are two varieties of *K. angustifolia*, with var. *caroliniana* (Small) Fern. occurring mainly in North Carolina. A white-flowered variety, *K. angustifolia* L. var. *angustifolia* f. *candida* Fern. was found early this century in the wild on the South Side Hills in St. John's, Nfld., and has since been sighted in a few other locations in Canada and the U.S. (Ebinger 1974, 1988). Other species of *Kalmia* include *K. microphylla* (Hooker) Heller, *K. cuneata* Michaux, *K. hirsuta* Walt. and *K. ericoides* Wright ex Griseb., giving a North American genus with a total of seven species, six varieties, and numerous forms. The two most comprehensive works on the whole genus include a review with an emphasis on taxonomy by Ebinger (1974), and a review with an emphasis on horticulture by Jaynes (1988). The species *K. angustifolia* has been reviewed by Hall *et al.* (1973).

In Newfoundland *Kalmia* commonly occurs as an understory species in nutrient-poor boreal forest types, and also dominates bogs and heathland (or "barrens"). This evergreen ericaceous shrub is an aggressive competitor in disturbed forests in central Newfoundland

(Vincent 1965; van Nostrand 1971; Richardson and Hall 1973a,b; Richardson 1974a,b, 1981), and grows profusely on many poor to medium quality disturbed forest sites, hindering the germination and establishment of black spruce (*Picea mariana* (Mill.) B.S.P.) and reducing the growth of naturally or artificially regenerated seedlings (Candy 1951; van Nostrand 1971; Anon. 1972; Richardson 1975; Wall 1977). A recent provincial survey of plantations in central Newfoundland showed that while no *Kalmia* was found in 44.6% of approximately 6000 regeneration plots, the other 54.4% of plots contained at least some degree of *Kalmia* cover (English and Hackett 1994). In this survey, increased *Kalmia* cover was found to be associated with increased age of plantations. Increased *Kalmia* cover was also associated with decreased total height of black spruce (3 m total spruce height in the absence of *Kalmia* as compared to 1 m for 76-100% *Kalmia* cover for 13 year old plantations). However, it is not yet clear from this survey if *Kalmia* caused the observed reduced spruce height growth, or if *Kalmia* was simply more abundant on poorer sites, and was thus simply an indicator of reduced site quality.

Peterson (1965) was able to demonstrate that aqueous extracts of *Kalmia* leaves inhibited primary root development of black spruce germinants in the laboratory. Similar results were found by Mallik (1987, 1992) for aqueous extracts of *Kalmia* leaves and roots, as well as of litter and soil from beneath *Kalmia* plants. Although it has yet to be demonstrated in the field, it is likely that *Kalmia* suppresses spruce germination through production of allelochemicals, some of which have been identified as phenolic compounds (Zhu and Mallik 1994).

Poor seedling growth on *Kalmia*-dominated sites may be attributed to low soil nutrient availability. Damman (1971) demonstrated that large amounts of N, P and K were immobilized in the ericaceous humus associated with a 65-year old *Kalmia* heath as compared with mature black spruce and balsam fir forest types. Total nitrogen contents of the organic horizons of *Kalmia*, spruce and fir sites were 3070, 1069 and 878 kg ha⁻¹, respectively. However, net availability of nitrogen of samples incubated at 22°C for 100 days gave estimated site availability rates

¹ This name is commonly used amongst foresters in eastern Canada, especially in Newfoundland. Although it is sometimes spelled "kalmia", the use of "*Kalmia*" better reflects the use of a genus epithet as a common name. In light of the references to *K. latifolia* (L.) or mountain laurel in the American forestry literature, and to *K. polifolia* (Wang.) in the Canadian botanical literature it is suggested that in written communications the common name "*Kalmia*" be used only after defining it to the species level, and that the spelling "kalmia" be avoided. However, conversational use of "*Kalmia*" as a common name is less likely to be misunderstood within a Canadian forestry context, where *K. angustifolia* is the only species of operational concern within this genus.

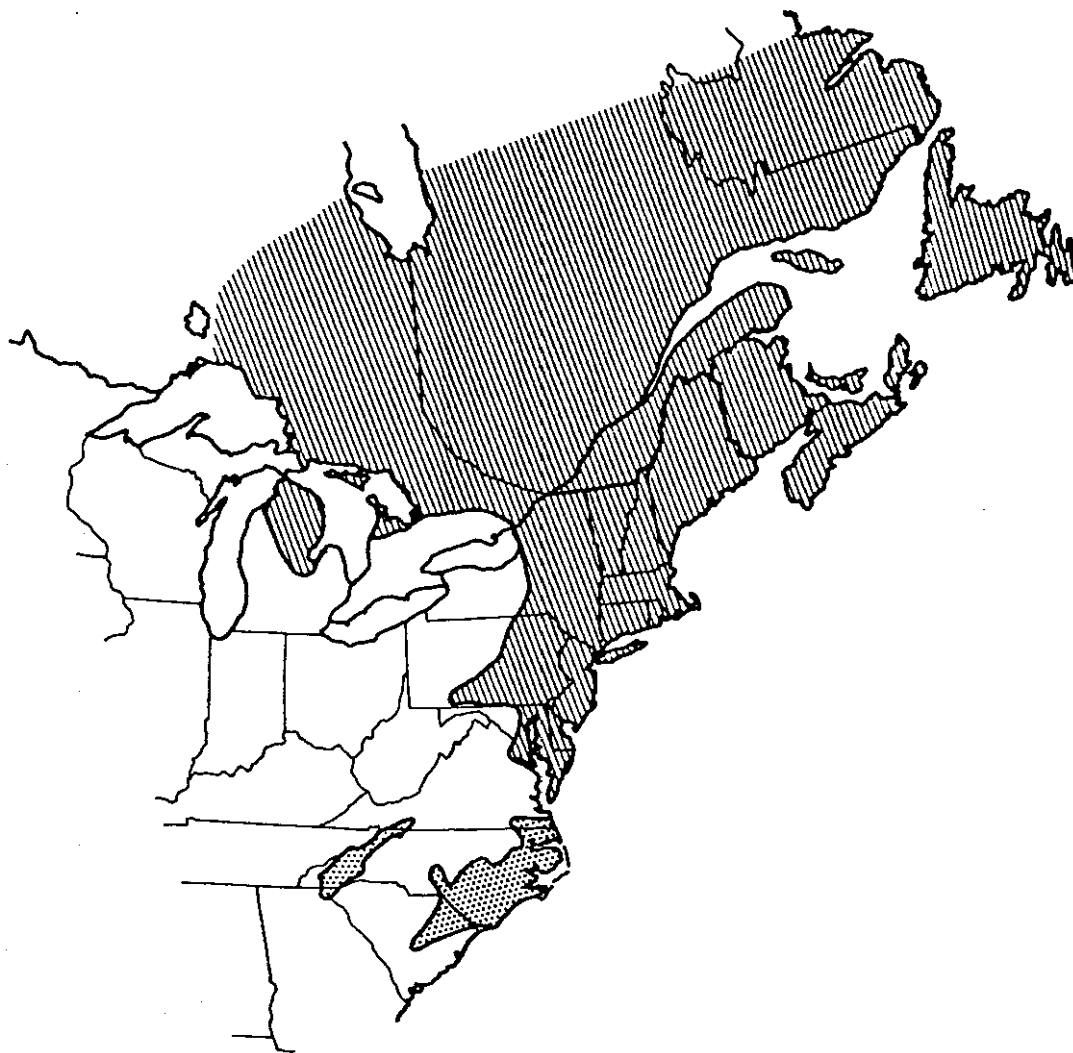


Figure 1. The natural range of *Kalmia angustifolia* var. *angustifolia* in Canada and the eastern United States. The smaller area to the south (dotted pattern) is the range of *K. angustifolia* var. *caroliniana* (after Ebinger 1988, Fig. 2-18, with permission of Timber Press, Oregon)

of 300, 2900 and 3600 mg N ha⁻¹ day⁻¹ for organic horizons from *Kalmia*, spruce and fir sites, respectively (estimated from Table 21 in Damman 1967, and Fig. 4 and Table 14 in Damman 1971). It is also possible that *Kalmia* continues to allelopathically antagonize spruce through inhibition of root production, and/or inhibition of mycorrhizal development. It has recently been shown that seedlings planted adjacent to *Kalmia* plants in the field have lower foliar nitrogen concentrations and different mycorrhizal species associated with them as compared to seedlings planted further away from the shrub (S. Yamasaki², unpublished data). However, cause and effect relationships with respect to *Kalmia*-mycorrhizal relationships require further clarification. As with other members of the Ericaceae, *Kalmia* may therefore out compete spruce seedlings through direct competition for nutrients from a recalcitrant humus and/or through allelopathic suppression of spruce root and/or mycorrhizal development (de Montigny and Weetman 1990, Prescott and Weetman 1994).

Classification of plant communities with *Kalmia* as a component has been conducted by several authors (Damman 1964; Peterson 1964; Strang 1972; Meades 1973; Meades and Moores 1989). Aspects of the plant anatomy of the species were studied by Metcalfe and Chalk (1950) and Mallik (1993). However, specific questions regarding its regeneration, both vegetatively and from seeds, and its competitive advantage over other species have yet to be fully elucidated. An understanding of these factors would help in the formulation of silvicultural prescriptions for controlling *Kalmia*, as to date silvicultural options do not always result in adequate seedling growth. Richardson (1975, 1979) tested several treatments for the control of *Kalmia* to facilitate softwood growth in field experiments, but was not able to demonstrate an effective control measure for *Kalmia*. Difficulty in controlling this weed species on blueberry sites has also been experienced in eastern Canadian provinces (Gagnon 1971).

As *Kalmia* is such an integral component of the forest landscape of Newfoundland, a number of studies have been carried out over the years under the auspices of the Canadian Forest Service. This report provides a summary of some of the research completed under

contract by Drs. A.K. Bal and O.A. Olsen of the Memorial University of Newfoundland, St. John's (Olsen 1974, 1975; Bal 1977) and some aspects of the research carried out at the Newfoundland Forestry Centre on *Kalmia* regarding its (i) general ecology, (ii) reproductive biology, and (iii) competitive advantage over other species, especially spruce. The implications of the research results for forestry operations and silvicultural treatments are discussed, and some recommendations for future research are outlined.

2. ECOLOGY OF *KALMIA ANGUSTIFOLIA*

2.1 Phytosociological Associations of *Kulmiu angustifolia* in Newfoundland

As an oligotrophic species, *Kalmia* tolerates a wide range of moisture regimes (Damman 1967). It is found in a variety of plant communities and site types in Newfoundland including alpine heaths, anthropogenic heaths, forests, peatlands and swamps. It also occurs on climatically exposed sites where *Empetrum nigrum* L. and *Vaccinium vitis-idaea* L. are conspicuous companion species, but with decreased vigour and cover. *Chamaedaphne calyculata* (L.) Moench., *Kalmia polifolia* Wang., *Andromeda glaucophylla* Link. and *Ledum groenlandicum* Ratz. are common associate species on moist to wet sites, and these species may exceed *Kalmia* in abundance and frequency on wet sites (Damman 1967).

An assessment of the site preferences of *Kalmia* and its common associate species is presented in Table 1. Site preference can be inferred from presence value (P.V.) where:

$$P.V. = \frac{\text{no. of relévéés containing a species}}{\text{total no. of relévéés in the association}} \times 100$$

Presence Value Category	Presence Value (%)
+	one occurrence
I	1 - 20
II	21 - 40
III	41 - 60
IV	61 - 80
V	81 - 100

² S. Yamasaki, Dept. of Renewable Resources, Macdonald Campus, McGill University, 21,111 Lakeshore Rd., Ste-Anne-de-Belleve, Québec, H9X 3V9.

Table 1. The ecological distribution of *Kalmia angustifolia* and common companion species in Newfoundland (in Olsen 1974, Table 1, after Damman 1964, 1967, Pollett 1972 and Meades 1973).

	<i>Kalmia angustifolia</i>	<i>Ledum groenlandicum</i>	<i>Vaccinium angustifolium</i>	<i>Empetru m sp.</i>	<i>Vaccinium vitis-idaea</i>	<i>Chamaedaphne calyculata</i>	<i>Andromeda glaucophylla</i>	<i>Kalmia polifolia</i>	
I. HEATH COMMUNITIES									
1. <i>Diapensio-Arctostaphyletum alpinae</i>	II ^a	I	-	V	V	-	-	-	
2. <i>Empetro-Racomitrietum lanuginosae</i>	II	V	V	V	V	I	I	I	
3. <i>Empetro-Potentilletum tridentatae</i>	IV	IV	V	V	V	II	I	+	
4. <i>Luzulo-Polytrichetum commune</i>	+		V	-	-	-	-	-	
5. <i>Luzulo-Empetretum nigrae</i>	II	III	V	IV	III	-	-	-	
6. <i>Kalmietum angustifoliae</i>	V	IV	V	III	III	II	-	I	
7. <i>Kalmio-Alnetum crispae</i>	V	+	V	-	I	-	-	-	
8. <i>Abietetum balsameae hudsoniae</i>	III	II	III	II	II	-	-	-	
9. <i>Kalmio-Myricetum gale</i>	V	IV	V	III	IV	I	-	II	P
10. <i>Kalmio-Spagnetum nemori</i>	V	V	V	IV	IV	III	I	II	
11. <i>Piceetum marianae semiprostratae</i>	V	IV	V	IV	-	-	-	I	
II. PEATLAND COMMUNITIES									
1. <i>Vaccinio-Cladonietum boryi</i>									
a) Eastern Nfld.	IV	III	V	V	V	+	I	I	
b) Central Nfld.	IV	V	II	V	IV	II	-	-	
c) Western Nfld.	V	III	IV	IV	IV	II	II	II	
2. <i>Vaccinio-Empetretum nigri (Northern Nfld.)</i>	-	II	I	V	V	-	I	-	

^a Percent presence value expressed as presence value category, where: + = 1 occurrence; I = 1-20%; II = 21-40%; III = 41-60%; IV = 61-80%; V = 81-100%.

(Cont'd.)

Table 1. (Cont'd.)

	<i>Kalmia angustifolia</i>	<i>Ledum groenlandicum</i>	<i>Vaccinium angustifolium</i>	<i>Empetru m sp.</i>	<i>Vaccinium vitis-idaea</i>	<i>Chamaedaphne calyculata</i>	<i>Andromeda glaucophylla</i>	<i>Kalmia polifolia</i>	
3. <i>Kalmio-Sphagnetum fusci</i>									
a) Eastern Nfld.	V	V	II	V	-	V	IV	V	
b) Central Nfld.	V	V	II	IV	+	V	II	IV	
c) Western Nfld.	V	V	II	IV	I	V	IV	V	
4. <i>Rubeto-Empetretum nigri</i> (Northern Nfld.)	IV	V	II	IV	I	V	IV	V	
5. <i>Calamagrostiето-Sphagnetum fusci</i>									
b) Eastern Nfld.	I	V	+	IV		IV	III	V	
b) Central Nfld.	III	IV	+	II	I	IV	III	V	
c) Western Nfld.	III	V	-		-	IV	III	V	
6. <i>Scirpo-Sphagnetum papillosum</i>									
a) Central Nfld.	-	II				IV	IV	III	-5-
b) Western Nfld.	I	II	-	-		V	IV	II	
7. <i>Scirpo-Sphagnetum subniti</i> (Eastern Nfld.)	I	IV	+	I	-	IV	IV	III	
8. <i>Potentillo-Campylietum stellatae</i>									
a) Eastern Nfld.	-	I	+	-	-	III	III	I	
b) Central Nfld.	-	I	-		-	IV	IV	I	
c) Western Nfld.	+	I		-	-		IV	I	
9. <i>Thalictro-Potentilletum fruticosae</i>	-	-		-	-	-	V	-	
10. <i>Betula-Vaccinietum uliginosi</i> (heath)	-	III	I	V	V		V		
III. FOREST COMMUNITIES									
1. <i>Kalmio-Piceetum</i> (Kalmia-black spruce forest)									
a) Central Nfld.	V	I	V	-	IV	-			
b) Western Nfld.	V	V	V	I	-				

(Cont'd.)

Table 1. (Cont'd.)

	<i>Kalmia angustifolia</i>	<i>Ledum groenlandicum</i>	<i>Vaccinium angustifolium</i>	<i>Empetru m</i> sp.	<i>Vaccinium vitis-idaea</i>	<i>Chamaedaphne calyculata</i>	<i>Andromeda glaucophylla</i>	<i>Kalmia polifolia</i>
2. Piceetum (black spruce-moss forest)								
a) Central Nfld.	V	-	IV	I	-			-
b) Western Nfld.	IV		IV		-			-
3. Abietetum <i>typicum</i> (<i>Pleurozium</i> -balsam fir forest)								
a) Central Nfld.	-		-	-	-	-	-	-
b) Western Nfld.	III	II	IV	-	-			-
4. Abietetum <i>hylocomietosum</i> (Hylocomium-balsam fir forest)								
a) Central Nfld.	-		-	-	-		-	-
b) Western Nfld.	-	-	-	-	-			-
5. Abietetum <i>rubetosum</i> (<i>Rubus</i> -balsam fir forest)								m
a) Central Nfld.	V	-	II	-	-	-	-	-
b) Western Nfld.	-	-	-	-	-	-	-	-
6. Abietetum <i>dryopteretosum</i> (<i>Dryopteris</i> -balsam fir forest)								
a) Central Nfld.	-	-	-	-	-	-	-	-
b) Western Nfld.	-	-	-	-	-	-	-	-
7. Kalmio piceetum <i>sphagnetosum</i> (Sphagnum-Kalmia-black spruce forest; Central Nfld.)	V	II	V	-	III	-	-	-
8. Kalmio piceetum <i>cladonietosum</i> (<i>Cladonia</i> -Kalmia-black spruce forest; Western Nfld.)	V	IV	V	II	III	-	-	-
9. Taxus-Kalmia-black spruce forest (Western Nfld.)	V	V	V	IV	-	-	-	V

(Cont'd.)

Table 1. (Concl'd.)

	<i>Kalmia angustifolia</i>	<i>Ledum groenlandicum</i>	<i>Vaccinium angustifolium</i>	<i>Empetru m sp.</i>	<i>Vaccinium vitis-idaea</i>	<i>Chamaedaphne calyculata</i>	<i>Andromeda glaucophylla</i>	<i>Kalmia polifolia</i>
10. <i>Kalmio piceetum nemopanthetosum</i> (<i>Nemopanthus-Kalmia</i> -black spruce forest; Western Nfld.)	V		V	-	-	-	-	-
11. <i>Abietetum caricetosum</i> (<i>Carex</i> - balsam fir forest; Central Nfld.)	-	-	+	-	-	-	-	-
12. <i>Betuletum kalmietosum</i> (<i>Kalmia</i> - white birch forest; Western Nfld.)	V	V	V	-	-	-	-	-
13. <i>Kalmietosum</i> (heath on West Coast)	V	V	V	IV	III		-	II
IV. SWAMP COMMUNITIES								
a) Western Newfoundland								
1. <i>Larix</i> -alder swamp	III	V	III	-	-	-	-	-
2. <i>Sphagnum robustum</i> -black spruce (bog)	III	III	IV	-	-	+	-	+
3. <i>Piceetum caricetosum</i> (<i>Carex</i> - black spruce; fen)	III	IV	+	-	-	-	-	-
4. <i>Osmundo-Piceetum</i> (<i>Osmunda</i> - black spruce; fen)	II	III	II	-	-	-	-	-
b) Central Newfoundland								
5. <i>Alnetum</i> (alder-black spruce)	III	V	III	-	III	-	-	-
6. <i>Alnetum lycopodietosum</i> (<i>Lycopodium</i> -alder swamp)		-	+	-	-	-	-	-
7. <i>Alnetum caricetosum</i> (<i>Carex</i> - alder swamp)	-	-	-	-	-	-	-	

Kalmia has high presence values in heathland and open forest communities where it often forms a dense shrub layer (Table 1). It attains its greatest cover and vigour on sheltered nutrient-poor sites such as small forest clearings and the bottom of lee slopes where snow cover is deep throughout the winter. However, *Kalmia* is sparse in dense forests of fir and spruce, where mosses dominate the understory species. The abundance of *Kalmia* and associated species in each plant community are described briefly in the following sections (after Olsen 1974). Further data on *Kalmia* and its associated species (expressed as above-ground biomass per unit area) in eight habitats can be found in Mallii (1994), where the same general patterns of *Kalmia* presence were found.

2.1.1. Heath: *Kalmia angustifolia*, *Ledum groenlandicum*, *Vaccinium angustifolium* Ait., *Empetrum nigrum* and *Vaccinium vitis-idaea* are invariably present on heathland sites. In alpine areas *Vaccinium boreale* Halls & Aalders usually replaces *V. angustifolium*. *Chamaedaphne calyculata*, *Andromeda glaucophylla* and *Kalmia polifolia* are only present in moist heathland variants. *Empetrum nigrum* or *E. eamesii* Fern. & Wieg. are dominant on exposed heaths (*Diapensio-Arctostaphyletum* alpinae and *Empetro-Rhacomitrietum* lanuginosae) where *Kalmia* is common (P.V. category II; 21-40% occurrence). The winter snow cover is shallow in these habitats and *Kalmia* displays a procumbent (chamaephytic) rather than upright (nannophanerophytic) life form.

2.1.2. Peatlands: Ericaceous shrubs are ubiquitous within the peatland associations of Newfoundland (Table 1). *Kalmia* is abundant on raised bogs (*Kalmia-Sphagnetum fusci* and *Rubeto-Empetretum nigrae*; P.V. category IV; 61-80% occurrence) and blanket bogs (*Vaccinio-Cladonietum boryi*; P.V. category V; 81-100% occurrence). A notable exception is the northern coastal blanket peat (*Vaccinio-Empetretum nigri*) where *Kalmia* is absent. This absence is possibly related to the occurrence of calcium deposits in the underlying mineral soil.

Although the fen hummocks (*Calamagrostieto-Sphagnetum fuscae*) approximate the ombrotrophic conditions of bogs, *Kalmia* does not exceed a P.V. category of III (41-60% occurrence). This may be because the hummocks are underlain by a nutrient-rich fen substrate within the rooting depth of *Kalmia*.

In mesotrophic bogs (*Scirpo-Sphagnetum papillosum* and *Scirpo-Sphagnetum subniti*) *Kalmia* only occurs sporadically and the shrubs *Ledum groenlandicum*, *Chamaedaphne calyculata*, *Kalmia polifolia* and *Andromeda glaucophylla* are dominant. This trend is continued in mesotrophic and eutrophic fens (*Potentillo-Campylietum stellatae* and *Thalicthro-Potentilletum fruticosae*) where *Kalmia* is completely absent.

Bogs and fens vary widely in both nutrient availability and pH. These two factors may have an influence on the distribution of *Kalmia* on wetlands, as *Kalmia* presence increases with decreasing calcium concentration and increasing acidity (Table 2).

2.1.3. Forests: As in heathland and bogs, *Kalmia* is most common on nutrient poor sites ranging from extremely dry (*Cladonia-Kalmia*-black spruce) to extremely wet conditions (*Sphagnum robustum* - black spruce bog). The presence of *Kalmia* and other woody shrubs declines in forested stands when the density of the tree canopy limits light penetration. While this is true of old dense black spruce stands, it is best illustrated by regenerating balsam fir forests which limit light penetration more effectively than black spruce. *Kalmia*-dominated heaths can replace forests only where satisfactory tree regeneration is both lacking at the time of disturbance, and prevented from taking place soon after disturbance before heath plants spread and become well established. The *Abieto-Piceion* alliance consists of well stocked white birch, black spruce, and balsam fir forests on upland sites. These forests occupy the same range of soil conditions.

However, with few exceptions the history of the site determines which forest cover is present, and the sporadic occurrence of the *Vaccinium angustifolium* group is probably related to disturbance through cutting and/or fire.

Damman (1967) used Sociological Species Groups (SSG) to classify forest vegetation at the alliance level. These groups include species normally occurring together but not necessarily having the same ecological amplitude. *Kalmia* is one of the most prominent species included in the *Vaccinium angustifolium* SSG ground cover of ericaceous shrubs (*Kalmia*-black spruce, *Cladonia-Kalmia*-black spruce, Table 1) where it is found on dry and nutrient poor mineral soils, and shallow oligotrophic peat soils.

Table 2. Variation in moisture, pH and available nutrient concentrations of soil between peatland associations (compiled in Olsen 1974, Table 2, after Pollett 1972).

Peatland Association	<i>Kalmia</i> Presence Value (%)	Water Content (%)	Available Nutrient Concentration (mg g ⁻¹)				pH
			N	P	K	Ca	
<i>Kalmio-Sphagnetum fusci</i> (oligotrophic oceanic and raised bogs)	81-100	90-97	0.036	0.030	0.43	0.54	3.54
<i>Scirpo-Sphagnetum papillosum</i> (mesotrophic bog)	1-20	69-95	0.031	0.024	0.43	2.36	4.22
<i>Potentillo-Campylietum stellatae</i> (eutrophic fens)	0	80-87	0.57	0.012	0.59	7.91	5.47

2.1.4. Swamps: The *Sanguisorba-Piceion* alliance consists of black spruce swamps and fens (alder - black spruce, *Carex*-black spruce and *Osmunda*-black spruce, Table 1). This alliance occurs on wet sites varying in nutrient status from mesotrophic to eutrophic. *Kalmia* occurs sporadically in these associations, and the ground vegetation is dominated by grasses and herbs.

2.2. Phenology

Kalmia is an evergreen shrub. New leaves and flower buds overwinter in an embryonic state, and initiate rapidly during spring growth in late May and early June. Expansion of new leaves and elongation of aerial shoots progresses through June, with the onset of flowering beginning in early July and often continuing into late August. The young leaves and flower buds have numerous glandular hairs projecting from their surfaces which produce a characteristic sweet scent to attract pollinators. The hairs may also serve as a defence against micropredators. *Kalmia* flowers are visited by bees, butterflies, moths and beetles (Lovell and Lovell 1934). As with other ericaceous plants (Reader 1977), bees are probably the most effective pollinators of *Kalmia*. Capsular fruits with five locules are well formed by mid-September and seed dispersal starts by the first week of October (Hall et al. 1973). The leaves produced in one summer season remain on the plant throughout the

first winter and a second growing season, senescing and usually dropping in the autumn before the onset of the second winter (Damman 1971).

2.2.1. Role of Previous Season's Leaves on Growth: The retention of leaves by *Kalmia* for almost two growing seasons raises the question of the role of these overwintering leaves on the following season's growth. It is possible that nutrients stored in these older leaves are made available the following spring to the expanding new shoots and leaves, as has been found for three other ericaceous species (Reader 1978). With *K. latifolia*, it has been suggested that retention of leaves helps to conserve phosphorus on infertile sites (Thomas and Grigal 1976).

A field trial was initiated to determine the role of the previous season's leaves on the growth of the current season (Olsen 1974). An area of vigorously growing *Kalmia* was selected on a sheltered heath near the eastern border of Butterpot Park, eastern Newfoundland (see Appendix I for location of study sites). Three rows of 100 plants each were selected and divided into four 25-plant plots. Four replicates of the following three treatments were applied randomly to the 25-plant plots: (i) 100% of the previous season's leaves removed, (ii) 50% of the previous season's leaves removed; (iii) 0% of the previous season's leaves removed (control).

Table 3. Effect of removal of previous season's leaves on new growth of *Kalmia angustifolia* (after Olsen 1974, Tables 27 and 28).

New growth	Treatment	Mean'	s.d.	F	P
Weight of leaves (g)	100%removal	13.77a	3.35	8.44	<0.05
	50% removal	22.743	3.27		
	0% removal	25.65b	5.61		
Weight of shoots (g)	100%removal	1.41a	0.30	6.27	<0.05
	50% removal	2.12b	0.33		
	0% removal	2.36b	0.73		
Number of shoots per plant	100%removal	5.49a	0.84	5.05	>0.05
	50% removal	6.66a	1.23		
	0% removal	5.61a	1.01		
Length of shoots (cm)	100%removal	1.85a	0.32	14.92	<0.01
	50% removal	2.17ab	0.33		
	0% removal	2.61b	0.59		
Mean weight of shoots per plant (g)	100%removal	0.0565a	0.0326	6.27	<0.05
	50%removal	0.0871b	0.0167		
	0% removal	0.0946b	0.0292		
Mean weight per shoots (g)	100%removal	0.011a	0.0034	13.33	<0.01
	50%removal	0.014ab	0.0032		
	0%removal	0.017b	0.0048		
Weight of seed capsules (g)	100%removal	0.66a	0.4359	1.87	>0.05
	50% removal	0.78a	0.3818		
	0% removal	1.06a	0.1825		

^a Numbers followed by different letters indicates significant differences ($P < 0.05$) using Duncan's Multiple Range test.

The leaves were removed in the late spring (27 and 28 June 1973). Growth of new shoots had commenced on 21 June and new leaves were approximately one centimetre long when the old leaves were removed. Detached leaves were dried at 105°C to a constant weight. The dry weights of removed leaves were 26.4 and 13.9 g per replicate respectively for the 100% and 50%removal treatments.

At the end of the growing season (31 October 1973) the shoots with leaves and seed capsules were harvested. Leaves, new shoots and seed capsules were separated, the number and lengths of new shoots were recorded in the laboratory, and dry weights of all parts were

determined following oven drying at 105°C. All data were subjected to analysis of variance and Duncan's Multiple Range test (Table 3).

It is evident from the results in Table 3 that removal of all of the previous season's leaves significantly ($P < 0.05$) reduced the dry weight of leaves and shoots and the shoot length in the current season. Removal of half of the previous season's leaves did not significantly reduce growth when compared to the control plants. The weight of seed capsules and the number of new shoots were not significantly affected by either of the leaf removal treatments.

The reduced growth may have been due to the loss of photosynthate and nutrients in the previous season's leaves that would otherwise have been translocated to zones of new growth. Regardless of the mechanisms involved, it would appear that the retention of the previous year's leaves may be an adaptation to conditions of **stress** that allow the plant to carry the benefits of the previous year's growth over into the next year, thus conferring a further advantage on an already aggressive competitor of black spruce. Regarding chemical methods of controlling *Kulmiu* on forest sites, the data suggests that (apart from any toxic effects) at least **50%** and preferably 100% defoliation of old leaves is required to have any effect at all on the next years' leaf or shoot growth. However, if only defoliation is achieved through application of herbicides, then the effects of this treatment are likely to be **minimal** after several years.

3. REPRODUCTIVE BIOLOGY OF *KALMLA ANGUSTIFOLIA*

Kalmia normally occupies forest openings but also **occurs** under the closed canopy of mature stands of black spruce, with its dominance increasing towards the forest edge (Figs. 2-4). The dominance of *Kalmia* can increase within a short period of time following clearcutting and/or fire in *Kalmia*-black spruce forest associations through vegetative means, **as** *Kalmia* stems are connected to each other through a tangled mat of underground stolons in the organic soil horizon (Figs. 5 and 6). However, little quantitative information is available on the actual growth rates of *Kulmiu*, or on its reproductive capacity. Several studies were thus initiated to **examine certain** aspects of the reproductive biology of *Kalmia*, and are discussed below in three sections. In the first, the age structure of populations of *Kulmiu* under three site conditions in a strip cutting experiment (van Nostrand 1971) were examined. In the second, the sexual reproductive potential of *Kalmia* was investigated by quantifying seed production in different habitats and determining the conditions required for seed germination under laboratory conditions. Finally, the anatomy of vegetative reproductive organs (rhizomes and vegetative buds) were examined in a histological study.

3.1. Age Structure of *Kalmia angustifolia* Populations in a Forest and on an Adjacent Cutover

A **study** area was located in a black spruce-feather moss forest **type** (Damman 1964, Meades and Moores 1989)

of fire origin located in the southwest Gander watershed (lat. 48°48'N, long. 54°55'W). Soils were ferro-humic podzols which had developed on a well-drained **till** parent material, and were sandy loam in texture and strongly acidic (pH values of **3.05, 4.95, 5.2, 5.05** and 5.10 for the humus, **B2dfhgd, Bzfd, BC, and C** horizons, respectively). A detailed description of the area can be found in van Nostrand (1971).

Parts of the original stand were harvested **14** years previously in a strip cutting experiment, resulting in mature forest adjacent to clearcuts with differing degrees of site disturbance. Three site conditions were thus examined (i) mature undisturbed forest (F); (ii) cutover with soil organic layer intact (C-0); (iii) cutover with mineral soil exposed (C-M).

Fifty points were located along transects at regular **10 m** intervals on areas consisting of each of the above three conditions. The four *Kalmia* stems closest to each sample point were measured for height, and then clipped at ground level and returned to the laboratory in plastic bags. The stems were examined for stoloniferous connections, and transverse sections of stems were prepared using hand sectioning and a wood microtome. The sections were stained with safranin and annual rings were counted using a microscope. The number of annual rings compared very well with the number of swollen nodes on the stems. New *Kulmiu* stems generally originated from underground rhizomes so that many younger stems were connected to one parent, producing a loose aggregate of stems (Figs. 7-10), or "clumps".

The age, stem height and mode of stem origin (seed or vegetative, **differentiated** on the basis of root morphology and the presence or absence of connecting rhizomes; see Figs. 5-10) of *Kalmia* varied noticeably between the three forest site conditions studied. Under the mature forest stand most *Kulmiu* stems sampled were **5-10** years of age (Table 4) and ranged in height from **37** to **85** cm (Fig. 11). Similar heights (**57** and **66** cm) were also found under closed and open canopy black spruce stands in central Newfoundland for *Kulmiu* plants of ages **9** and **10** years old, respectively, **as** compared to the range in height (**77-106** cm) of *Kulmiu* found under more open red pine **stands** (Roberts and Mallik 1994). On the **14** year old cutover sites with an intact organic layer (**C-0**) *Kulmia* continued to grow **profusely** by vegetative means



Figure 2. *Kalmia angustifolia* understory in a mature black spruce forest (S.S. Sidhu).



Figure 3. *Kalmia angustifolia* on a black spruce cutover (S.S. Sidhu).



Figure 4. *Kalmia angustifolia* dominated cutover with black spruce regeneration (S.S. Sidhu).



Figure 5. Excavated dense underground **rhizomes** of *Kalmia angustifolia* showing connections between different clumps (S.S. Sidhu).

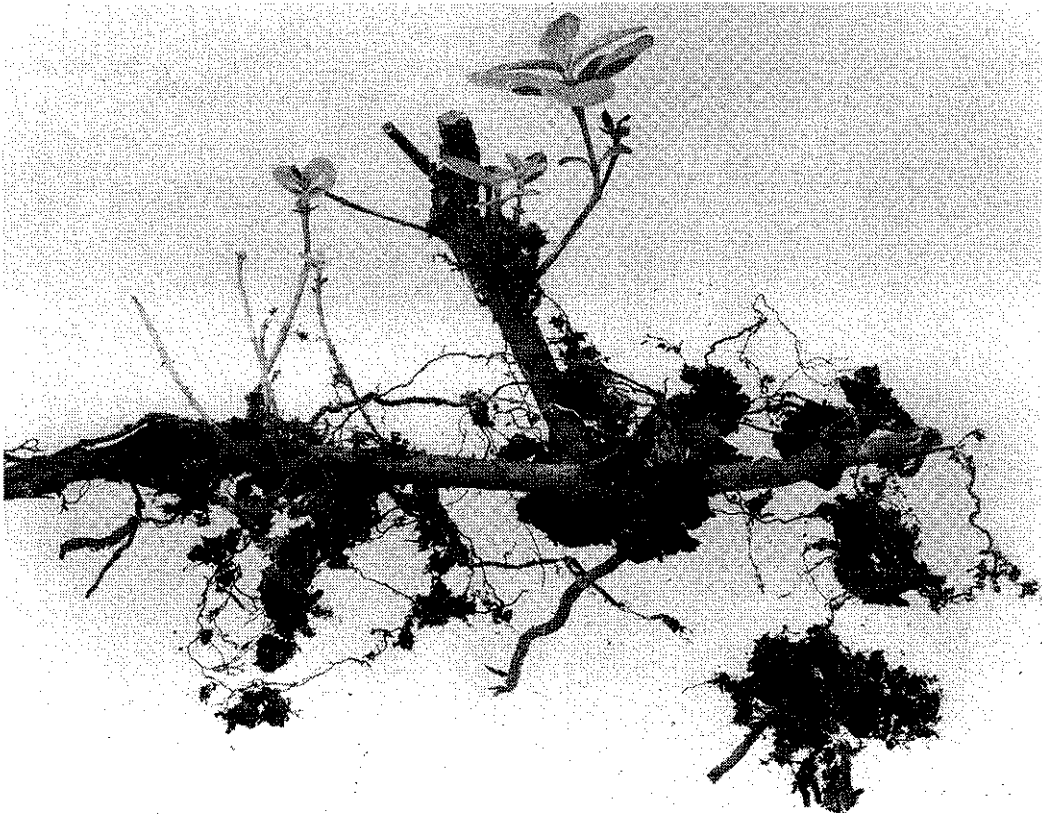


Figure 6. Excavated *Kalmia angustifolia* plant showing profuse vegetative bud development in the vertical stem as well as from the horizontal rhizomes (after Bal 1977, Fig. 2).

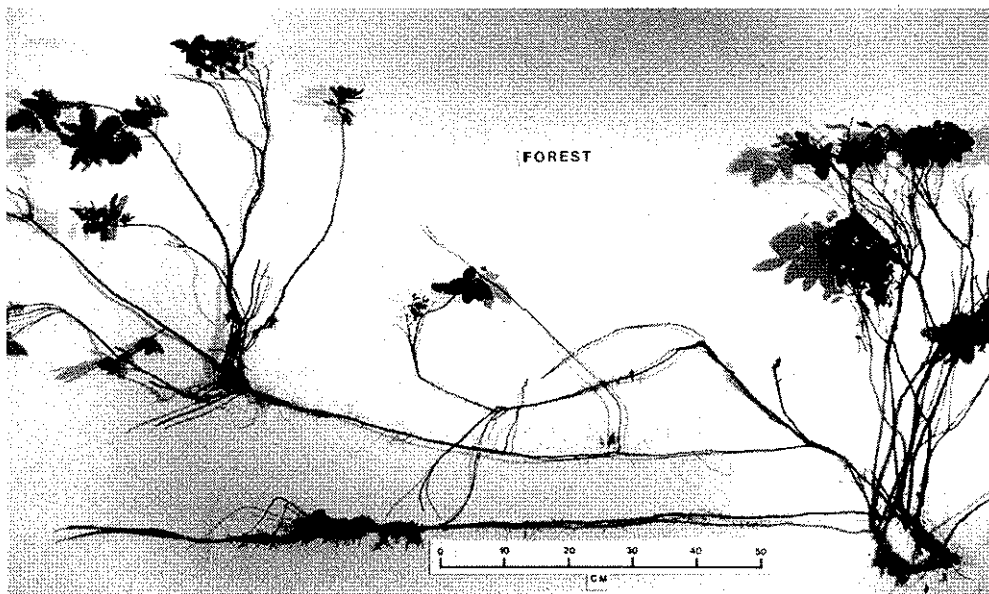


Figure 7. Excavated *Kalmia angustifolia* clumps from the forest sites. Clumps connected by long underground rhizomes (S.S. Sidhu).

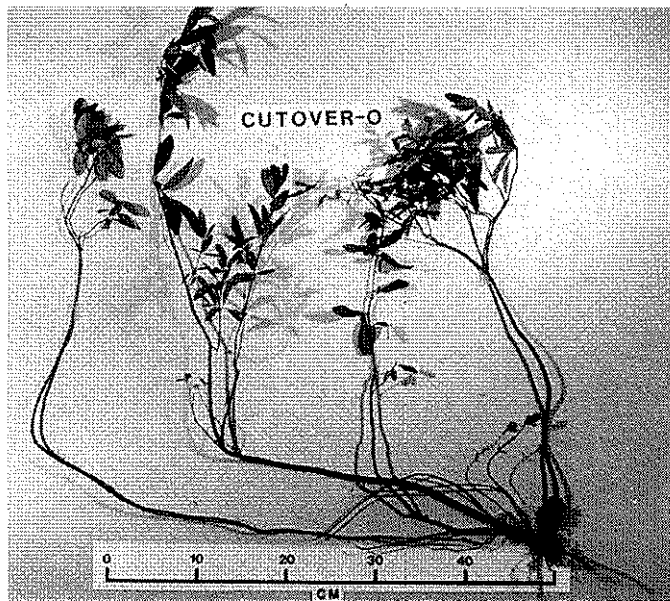


Figure 8. Excavated *Kalmia angustifolia* clump from an undistributed cutover site showing growth by layering and by subterranean long rhizome development (S.S. Sidhu).

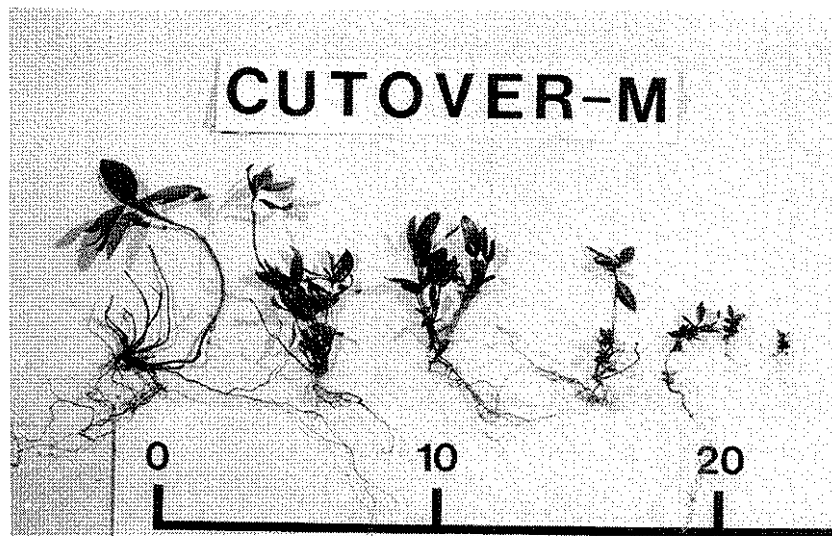


Figure 9. Excavated *Kalmia angustifolia* plants of seed origin from bare mineral soil on disturbed cutover site (S.S. Sidhu).

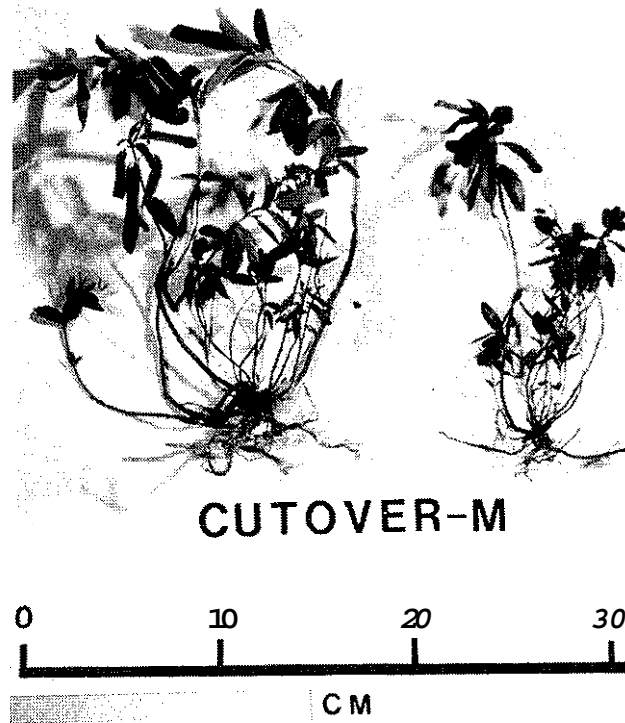


Figure 10. Excavated *Kalmia angustifolia* plants of seed origin greater than 5 years-old showing development of upright clumps and the initiation of long underground rhizomes (S.S. Sidhu).

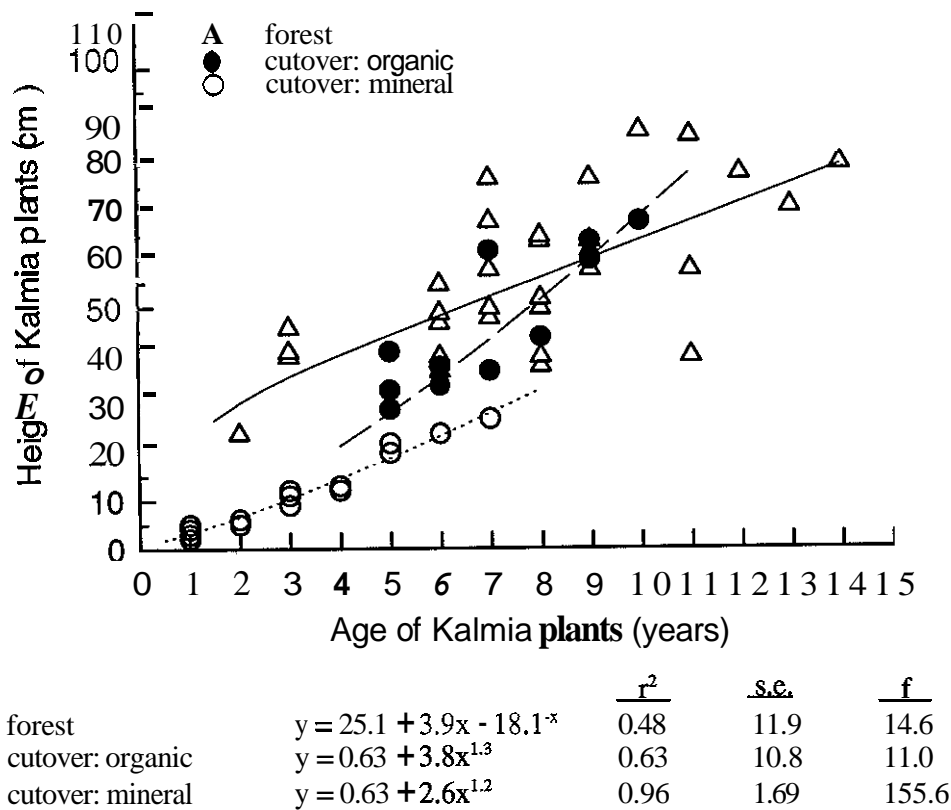


Figure 11. Height/age curves for *Kalmia angustifolia* under three different site conditions (S.S. Sidhu, unpublished data).

Table 4. Percent distribution of *Kalmia angustifolia* plants by age class in a forest and on undisturbed and disturbed cutovers (n = 200 stems per treatment) harvested 14 years previously (S.S. Sidhu, unpublished data).

Origin and Condition of <i>Kalmia</i> Plants	Age Class (years)													
	1	2	3	4	5	6	7	8	9	10	11	12	13	14
Forest	^a	-	-	-	11.5	27.7	25.3	19.2	8.5	7.7 ^b	-	-	-	-
% Seed origin		-	-	-	-		-				-	-	-	-
% Stolon origin			-	-	11.5	27.7	25.3	19.2	8.5	7.7	-	-	-	-
% Alive	-	-	-	-	11.5	27.7	25.3	19.2	8.5	7.1	-	-	-	-
% Dead	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Cutover with undisturbed organic layer	2.6	11.6	12.4	7.2	6.5	13.0	13.6	9.0	6.5	2.1	5.2	2.6	5.1	1.3
% Seed origin	-	-	-	-	-	-	-	-	-	-	-	-	-	-
% Stolon origin	2.6	11.6	12.4	7.2	6.5	13.0	13.6	9.0	6.5	2.1	5.2	2.6	5.1	1.3
% Alive	2.6	11.6	12.4	6.0	5.3	11.8	12.4	9.0	6.5	2.1	5.2	2.6	1.6	1.3
% Dead	-	-	-	1.2	1.2	1.2	1.2	-	-	-	-	-	3.5	
Cutover with mineral soil exposed	29.8	27.7	14.1	9.4	10.4	6.2	2.1	-	-		-	-	-	-
% Seed origin	27.8	22.0	13.1	9.4	10.4	4.6	0.5	-	-		-		-	-
% Stolon origin	2.6	5.7	1.0	-	-	1.6	1.6		-		-		-	-
% Alive	17.3	17.3	11.5	8.9	9.9	6.2	2.1		-		-	-	-	-
% Dead	12.5	10.4	2.6	0.5	0.5	-	-		-		-	-	-	-

^a Dash indicates that no plants were found within this category, and therefore percent distribution is 0.0.

^b Sum of percent distribution by age class may not equal 100 as a result of rounding off errors; distribution of origin and condition of *Kalmia* plants within the three site categories are expressed as a percent of the entire population of *Kalmia* within each site.

(short and long rhizomes³). Conifer regeneration was inhibited, and a thick organic horizon had accumulated. *Kalmia* stem heights ranged from 29 to 68 cm and were 1 to 14 years old. However, where all the organic layer along with the rhizomatous subterranean mass of *Kalmia* had been removed (C-M) *Kalmia* stems were 2-27 cm in height. Most stems were less than five years old, but a small percentage were 6-7 years old. Although not differentiated by presence or absence of humus, *Kalmia* plants 33 cm in height at 5 years of age and 31 cm in height at 9 years of age were found on clearcut black spruce sites with and without fire in Newfoundland (Mallik 1994, Sites 4 and 2). *Kalmia* was shown to have sprouted following a fire in a red pine stand and to have grown from an immediate post-fire height of 5 cm to 27 cm after 1 year to 32 and 33 cm after 2 and 3 years, respectively (Roberts and Mallik 1994).

Conifer regeneration in the present study was adequate and seedlings had grown well and over-topped the *Kalmia* plants. *Kalmia* had not yet fully occupied the site, and there were still mineral-exposed sites available for the germination of conifer as well as *Kalmia* seeds. Long lateral spreading rhizomes were observed on 5-6 year old *Kalmia* seedlings but were absent on younger plants. This suggests that most of the initial invasion of exposed mineral soil by *Kalmia* is by seed, with vegetative reproduction becoming important only after the seedlings are five or more years old. However, reproduction by rhizomes is probably the only means of proliferation and spread in areas where *Kalmia* is already established on continuous organic substrates. Excavations of *Kalmia* plants on 3 different sites in another study (Mallik 1993) suggested that stem-based sprouting and extensive growth of secondary (7-100 cm long) and tertiary (2-6 cm long) rhizomes were mainly responsible for the vegetative spread of *Kalmia*, rather than primary rhizomes (5-30 cm long). However, layering can also contribute somewhat to the vegetative spread of this plant, and the simultaneous presence of the three vegetative means of reproduction (stem sprouting, rhizomes, layering) is thought to contribute to the

comparative resilience of this plant to old-age degeneration (Mallik 1993).

It was observed in this present study that *Kalmia* rhizomes do not readily invade exposed mineral soil (see also Section 5.1). Mechanical site preparation techniques that expose strips or trenches of mineral soil may therefore be advantageous in controlling the vegetative spread of *Kalmia*, or at a minimum in producing spruce planting positions that are protected (at least initially) from encroachment by *Kalmia*. Given the ability of mineral soil strips to prevent rhizome expansion, trenching may establish an effective barrier to rhizome spread, at least in one direction. Repeating this trenching procedure at right angles would produce a "checker board" pattern that may be successful in maintaining *Kalmia*-free "squares" in the short-term. However, mechanical site preparation costs would be increased. More severe humus removal along wider strips through use of blading or a C&H plough may be possible in some areas, especially if underlying mineral soils are nutrient rich and can support spruce seedling growth. However, on poorer sites there is the danger that large-scale redistribution of humus by blading may stop the vegetative spread of *Kalmia* but lead to nutritional problems if seedlings must depend upon impoverished mineral horizons for their nutrient uptake needs.

Mineral soil exposure also has the added advantage of increasing natural tree regeneration. For example, on the undisturbed cutover there were fewer tree seedlings (3.2 seedlings m⁻²) than on exposed mineral soil where there were 80 seedlings m⁻² (Table 5). Fifty-six percent of the tree seedlings were black spruce (*Picea mariana*) and the remaining 44 percent were white birch (*Betula papyrifera* Marsh.). The least number of tree seedlings were found in the forest (0.8 seedlings m⁻²).

3.2. Sexual Reproduction in *Kalmia angustifolia*

In spite of the availability of a vast quantity of seed, *Kalmia* seedlings were virtually absent under the forest stand and on the cutover site with the intact organic layer (C-0) in the previous study. This prompted the initiation of an investigation on the reproductive potential of *Kalmia* by seed versus vegetative means on the same site. The sexual reproductive potential of *Kalmia* was then further investigated in seven different habitats in the

³ cf. terminology in Mallik (1993) where rhizomes are described as *primary* (short, 5-30 cm in length, thick, woody), *secondary* (long, 7-100 cm in length, slender, soft, containing many vegetative buds and responsible for vegetative spread of plant; arise from primary rhizomes) and *tertiary* (small, 2-6 cm, arise at distal ends of secondary rhizomes).

Table 5. Mean density (\pm s.d.) of *Kalmia angustifolia* and tree seedlings under three site conditions (S.S. Sidhu, unpublished data).

Forest site condition	Diameter ^a per clump (cm)	No. of clumps ^b per m ²	No. of stems/clump ^a	Average No. of <i>Kalmia</i> Stems ^c		Tree Seedlings ^b	
				Per m ²	Per ha	Per m ²	Per ha
Forest	111.9 \pm 56.7	0.32 \pm 0.47	31 \pm 21	10	1.0 \times 10 ⁵	0.8 \pm 0.22	8 \times 10 ³
Cutover with organic layer intact	85.2 \pm 35.8	0.52 \pm 0.50	25 \pm 11	13	1.3 \times 10 ⁵	3.2 \pm 0.62	3.2 \times 10 ⁴
Cutover with mineral soil exposed	28.0 \pm 19.0	1.80 \pm 0.77	12 \pm 7	22	2.2 \times 10 ^{5d}	80.0 \pm 6.1	8 \times 10 ^{5d}

^a Mean of 20 clumps.

^b Mean of 20 quadrats (1 m \times 1 m).

^c Mean no. of stems = (average no. of clumps/m²) \times (average no. stems/clump).

^d Assuming 1 ha of bare mineral soil; in reality, this situation does not occur and bare mineral soil is found in patches of various sizes, depending upon disturbance history.

field. Finally, the conditions required for seed germination were determined under laboratory conditions, and *Kalmia* seeds were sown on test plots in the field.

3.2.1. *Kalmia* Fruit and Seed Production in a Forest and on an Adjacent Cutover: Twenty sampling points were established at 10 metre intervals along two transects on each of the three site conditions (forest, cutover with intact organic layer and cutover with organic layer removed) examined previously (see Section 3.1). A one metre square quadrat was centred on each sampling point and the following data recorded: (i) diameter of the clump closest to the sampling point; (ii) number of clumps per quadrat (clumps were included if one-half or greater of the clump occurred in the quadrat); (iii) number of fruiting and number of non-fruiting stems per clump (number of stems in clump nearest the sample point \times the number of clumps per quadrat); (iv) number of seed capsules per fruiting stem (seed capsules on fruiting stem nearest to sample point); (v) number of viable seeds per capsule (seeds from 50 individual capsules were extracted and counted; the seeds were then mixed and the presence or absence of embryos determined on 10 replicates of 100 seeds each, using a dissecting microscope).

Kalmia was most frequent on the cutover treatment with exposed mineral soil, and was least frequent under the uncut mature forest (Table 5). The size of individual clumps of *Kalmia* decreased from the forest to the undisturbed cutover (C-0) to the cutover with mineral soil exposed (C-M). In the forest, *Kalmia* was mostly restricted to forest openings, and individual clumps were easily identifiable. On the undisturbed cutover, the increased availability of light stimulated new growth which resulted in an increase in the number of clumps as well as in stem density (stems m⁻²; Table 5). Excavations of *Kalmia* root systems revealed that the younger clumps were connected to the older clumps by underground rhizomes (Fig. 7), and thus it is evident that the new clumps and stems were produced vegetatively. By contrast, no difference in percent cover of *Kalmia* was found in a 60-year old black spruce stand with a canopy cover of 65-75% as compared to an adjacent 7-year old clearcut in central Newfoundland⁴.

⁴ 57% and 54% *Kalmia* cover for Sites 1 and 2, respectively, from Table 2 in Mallik (1994); clearcut site harvested 7 years previously; origin of plants not given.

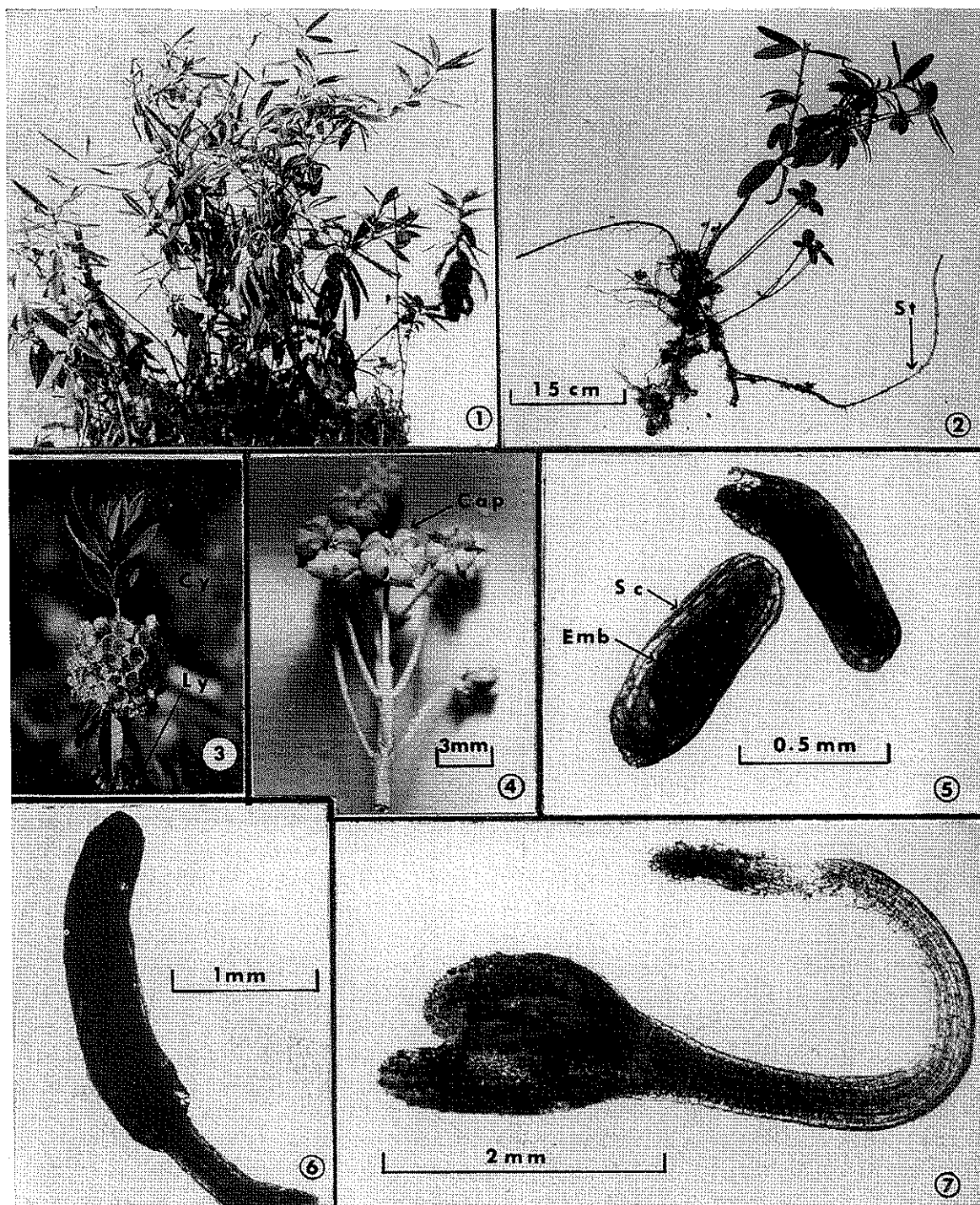


Figure 12. Reproduction in *Kulmiu unguistifoliu* (S.S. Sidhu):

1. general habitat of the above ground part of *Kulmia*;
2. *Kulmiu* with exposed rhizome stolon (St) and fine roots;
3. a flowering twig with current year's (Cy) and last year's (Ly) flowers;
4. a branch of *Kulmiu* with mature capsule (Cap);
5. seed of *Kalmia* showing seed coat (Sc) and embryo (Emb);
6. newly germinated seed showing radicle;
7. subsequent stage of germination showing radicle and plumule (developing into primary leaves)

Table 6. Mean stem density and seed production (\pm s.d.) in *Kalmia angustifolia* under three site conditions (S.S. Sidhu, unpublished data).

Forest site condition	Stem density (stems m ⁻²)	% Stems with seed capsules ^a	No. capsules per stem ^b	No. seeds per capsule ^c	% Seeds with embryo ^d	No. of Seeds with Embryo	
						Per m ²	Per ha
Forest	10	12.6 \pm 12.7	25.4 \pm 9.1	72 \pm 49	64.7 \pm 4.7	1.49 \times 10 ³	1.49 \times 10 ⁷
Cutover with organic layer intact	13	49.2 \pm 19.1	38.4 \pm 8.4	97 \pm 62	67.3 \pm 4.9	1.60 \times 10 ⁴	1.60 \times 10 ⁸
Cutover with mineral soil exposed	22	0	-	-	-	-	-

^a Mean of 20 clumps.

^b Mean of 20 stems.

^c Mean of 50 capsules.

^d Based on 10 replicates of 100 seeds each.

The percentage of *Kalmia* stems with seed capsules (Table 6) varied significantly under the three forest conditions (12.6% in the uncut forest, 49.2% in the C-0 treatment and none in the C-M treatment). The absence of flowering and fruiting stems under exposed mineral soil conditions was probably due to the younger age of the plants (maximum age of 7 years). From the data in Table 6 it was calculated that *Kalmia* produced approximately 1490 and 16 000 seeds m⁻² (1.49 \times 10⁷ and 1.60 \times 10⁸ seeds ha⁻¹) during a single growing season in the forest and undisturbed cutover (C-0) treatments, respectively. The lower seed production in the forest was a result of fewer flowering stems and fewer seeds per capsule as compared to the undisturbed cutover treatment. By contrast, in another study in central Newfoundland (Mallik 1994) the percent of flowering stems was much lower in a mature black spruce stand (1%) and on an adjacent cutover (10%), although viable seed production was similar and was estimated to be 1586 and 8275 seeds m⁻², respectively (assuming total seed production of approximately 1824 and 15 613 seeds m⁻², with viability of 87% and 53%, respectively). Hall *et al.* (1973) report finding 181.9 seeds per *Kalmia* capsule, 4.3 capsules per corymb and 9.1 corymbs per stem, for a theoretical production rate of 7118 seeds per

stem, although germination rates were low (44%). Assuming that the plants sampled were from blueberry fields and that they were similar in morphology and density (13 stems m⁻²) to plants on the undisturbed cutover, this would be equivalent to a viable seed production of approximately 40 715 viable seeds m⁻². A low germination rate of *K. angustifolia* seeds (approximately 50%) is also reported by Jaynes (1968a), who in another study found that only 36% of flowers in controlled crosses formed capsules with viable seed (Jaynes 1968b).

The average number of seeds per capsule in the present study varied from 72 to 97 (Table 6). Fully mature seeds of *Kalmia* are elliptical in shape, 0.70-0.80 mm in length and 0.15-0.20 mm in width. The seed coat is striated on the surface (Fig. 12) and there is a large embryo towards the narrow end of the seed cavity. Only 65 to 67% of the seeds examined from the forest and undisturbed cutover, respectively, contained embryos (Table 6). This suggests a minimum of a one-third reduction in the reproductive capacity of *Kalmia* in the black spruce-feather moss forest type in Newfoundland. However, much of this reduction in viability is compensated for by the prolific production of millions of seeds per hectare, which is

Table 7. Proportion of fruiting and non-fruiting stems, mean number of capsules per fruiting stem and mean number of seeds per capsule of *Kalmia angustifolia* in seven habitats (after Olsen 1974, Tables 22, 23 and 25).

	Habitat Types							
	Basin Bog ^a		Dwarf ^b - shrub bog	<i>Kalmia</i> ^c - <i>Vaccinium</i> heath	Exposed ^d heath	Sheltered ^e heath	<i>Kalmia</i> - black ^f spruce forest	Burned ^g black spruce forest
	Margin	Hummock						
% Fruiting stems	-	≤ 1	1	1	1	27	2	7
% Non-fruiting	-	≥ 99	99	99	99	73	98	93
Mean no. ^h of capsules per fruiting stem	8.10	-	12.36	7.32	6.04	14.26	29.56	47.12
Mean height of fruiting stems (cm)	19.11	-	14.40	19.39	16.58	33.92	56.06	28.47
Mean seeds per capsule ^j	143.4 (95.1)	-	136.7 (54.7)	159.3 (98.9)	159.1 (104.3)	116.3 (101.6)	163.0 (80.1)	152.1 (94.0)

^a **Basin bog:** 4 km west of Foxtrap access road on Trans-Canada Highway (T.C.H.) (53°02'W, 47°15'N); Altitude: 260 m; Slope: level.

^b **Dwarf-shrub bog:** 2 km west of Donovan's Overpass on T.C.H. (52° 51'W, 47°32'N); Altitude: 200 m; Slope: level.

^c ***Kalmia-Vaccinium* heath:** 2 km west of Donovan's Overpass on T.C.H. (52°51'W, 47°32'N); Altitude: 200 m; Slope: level.

^d **Exposed heath:** 4 km west of Foxtrap access road on T.C.H. (53°01'W, 47°15'N); Altitude: 260 m; Slope: level.

^e **Sheltered heath:** 3 km west of Foxtrap access road on T.C.H. (53°00'W, 47°16'N); Altitude: 260 m; Slope: 20°E.

^f ***Kalmia-black spruce forest:*** 3 km west of Donovan's Overpass on the T.C.H. (53°06'W, 47°30'N); Altitude: 200 m; Slope: level.

^g **Burned black spruce forest:** 8 km north of Bay Bulls (53°37'W, 47°24'N); Altitude: 175 m; Slope: level.

^h Mean of 50 stems.

ⁱ **Only** 1 plant out of 332 on the basin bog hummock was a fruiting stem, so 50 fruiting stems from the adjacent margin were used to examine fruiting behaviour.

^j Standard deviation in brackets.

more than adequate **for** reproduction when a suitable substrate for establishment is present.

Absence of embryos may be due to pollination failure or intra-clonal incompatibility. From their study of the pollination and pollinating agents of *Kalmia*, Lovell and Lovell (1934) concluded that the flowers of *Kalmia* are generally cross-pollinated by insects but may also be wind pollinated. These authors did not comment on the viability of pollen at the time of dehiscence. Jaynes (1968a) concluded that selfing either resulted in no seed formation or in fewer seeds per capsule in *Kalmia*. The predominantly vegetative means of reproduction of *Kalmia* under natural conditions can result in the establishment of the same clone over a large forest area, and possible intra-clonal incompatibility and absence **or** scarcity of suitable pollinating insects could result in a reduction in seed viability in Newfoundland.

3.2.2. *Kulmiu* Fruit and Seed Production over a Range of Habitats: Additional extensive field observations also indicated the absence of *Kalmia* plants of seed origin in forests, heathlands and bogs in spite of the presence of an abundance of seed-bearing *Kalmia* plants. Some of the characteristics of fruit capsule and seed production by *Kalmia* were thus examined across a range of different habitats.

A representative plot (2 m x 2 m) was selected in each of seven habitats including a basin bog, dwarf shrub bog, *Kalmia*-*Vaccinium* heath, exposed *Kalmia* heath, sheltered *Kalmia* heath, *Kalmia*-black spruce forest, and burned black spruce forest (full site descriptions can be found in Olsen 1974; the *Kalmia*-black spruce and the burned black spruce forests were used for further sampling and trials in Sections 4.2.1 to 4.2.3). The number of single stems on which current season seed capsules were produced and the number of non-fruiting stems in each plot were counted. Fifty fruiting stems were then collected **from** each habitat (except for the basin bog hummock in which case the seeds were collected from near the margin of the bog where flowering stems were produced in greater numbers than **on** the hummock itself). The stems were all clipped at ground level and returned to the laboratory where stem heights were measured, and the number of new seed capsules were counted. Ten unopened capsules were **selected from** each of the seven habitats. The capsules

were then opened and the very small seeds placed in a gridded **container** and counted with the aid of a dissecting microscope. The results of the above measurements are presented in Table 7.

The fruiting behaviour **of** *Kalmia* differed markedly between the seven habitats sampled. Only one fruiting stem was found in a plot of 333 plants in the basin bog hummock habitat and very few were present in the dwarf shrub bog, the exposed *Kalmia* heath, and the *Kalmia*-*Vaccinium* heath. Some increase in the percent of fruiting stems was found in the *Kalmia*-black spruce forest habitat and in the burned black spruce forest. Fruiting was heaviest in the sheltered *Kalmia* heath where approximately 27% of the plant stems produced fruit. However, the highest number of capsules and clusters of capsules per plant were found in the *Kalmia*-black spruce forest and burned spruce forest. Only half **as** many capsules were produced on fruiting plants from the sheltered *Kalmia* heath and dwarf shrub bog. In the other habitats, capsule production dropped even further. From the counts of the number of seeds in mature, unopened capsules it is evident that the number of seeds per capsule is quite uniform between sites, although the large standard deviations of the means indicates that there is considerable variation on any given site (Table 7).

This data can be contrasted with another study of eight sites (Mallik 1994) in which the percent of fruiting stems were less than 1% in a mature spruce forest, 10% on an adjacent cutover, 5% in an open canopy black spruce forest, 36% in a *Kalmia* heath that had developed on a burned cutover, 21% in a burned red pine stand, 7% in a burned *Kalmia*-*Sphagnum* bog heath, 15% in a twice burned wet *Kalmia*-*Cladina* heath, and 7% in an adjacent forest-heath ecotone⁵. It is notable that the heaths all had a much higher proportion of flowering stems (7-36%) than in the present study (1%), with the exception of the sheltered heath (27%). However, in both studies the proportion of flowering stems in a mature spruce forest was 2% or less. Although the deep shade of a mature spruce stand hinders flower development, it is clear that the importance of sexual reproduction varies greatly between sites, depending **on** environmental conditions other than just the degree of shading.

⁵ Estimated from Fig. 3 in Mallik (1994)

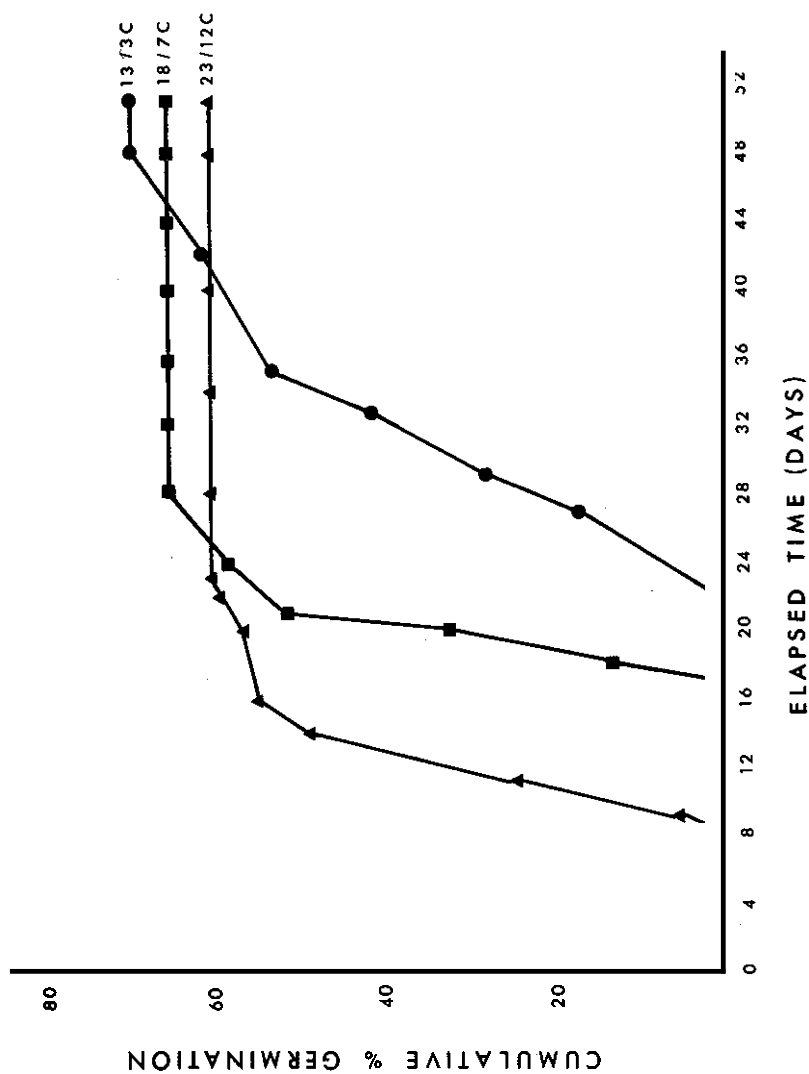


Figure 13. Cumulative percent of germination of seeds of *Kalmia angustifolia* without cold treatment at three different temperature cycles under variable light conditions (● 13 hrs daylight at 3°C; ■ 18 hrs daylight at 7°C; ▲ 23 hrs daylight at 12°C) (S.S. Sidhu, unpublished data).

3.2.3 *Kalmia* Seed Germination in the Laboratory:

From the above studies it is evident that vast numbers of *Kalmia* seeds can be produced in certain habitats. However, even though 15-160 million *Kalmia* seeds ha⁻¹ were produced annually in two of the site treatments of the strip cutting experiment (Table 6; Sections 3.1 and 3.2.1), *Kalmia* plants of seed origin were only found on the cutover with exposed mineral soil microsites (Table 4). In this treatment *Kalmia* seedlings were present at a density of 22 stems m⁻², which is theoretically equivalent to 220 000 stems per hectare of bare mineral soil (Table 6) some 14 years after disturbance. The fate of the millions of seeds produced and the conditions necessary for germination and survival were thus investigated using seed from capsules collected from the cutover with an intact organic layer (C-0). Seeds were extracted from this bulk sample and subjected to varying environmental treatments under controlled laboratory conditions.

Four replicates of 50 seeds each (with embryos) were exposed to three temperature cycle treatments either under alternating light and dark conditions or complete darkness. The three temperature treatments were based upon 30 year averages for climatic data from Gander (Anon. 1975) and were: (i) 13°C/3°C (16 h/8 h; average daily maximum and minimum temperature of May and October); (ii) 18°C/7°C (16 h/8 h; average daily maximum and minimum temperature for June and September); (iii) 23°C/12°C (16 h/8 h; average daily maximum and minimum temperature for July and August).

The light cycle coincided with the maximum temperature cycle and the dark cycle with the minimum temperature cycle. The two light treatments were: (i) alternate 16 hours light and 8 hours dark; (ii) complete dark.

The seeds were placed on a double layer of filter paper (Whatman No. 42) in 100 x 15 mm glass petri dishes and soaked with 5 mL of distilled water. For germination tests in complete darkness the petri dishes were wrapped in a double layer of aluminum foil and the number of germinated and ungerminated seeds determined at the end of three weeks. However, petri dishes exposed to alternate light and dark treatments were assessed on alternate days and germinated seeds removed from the petri dishes after counting. The observations for light:dark cycle treatments were continued for 50 days, at which time half of the ungerminated seeds were treated with gibberellic acid (400 ppm) and the other half with

a cold treatment (1°C for two weeks). Following these two further treatments, the seeds were re-exposed to their respective temperature and light treatments. Germination counts were then continued for a further two weeks.

The effect of the duration of cold treatments (stratification) on the subsequent germination of *Kalmia* seeds was studied in a second experiment. Three replicates of 50 seeds each were sown in a soil mixture (one part sand:one part peat:one part peat moss, pH = 4.2) wetted with distilled water. After exposures of 2, 3, 4 and 6 weeks to 1°C the pots were transferred to growth chambers with alternating temperature and light conditions (27°C for 16h/21°C for 8h, with 16 hours of light and 8 hours of darkness). New germinants were counted on alternate days for 50 days.

The results of the effect of temperature, light and cold treatment on the germination of *Kalmia* seeds are given in Figure 13 and Table 8. Seventy percent of the seeds germinated at temperatures comparable to the mean May and October temperatures (13°/3°C) under alternate light and dark conditions. There was no germination at the same temperature in the absence of light. The germination of June-September temperatures (18°C/7°C) and July-August temperatures were 65% and 60% respectively under alternate light and dark conditions. There were no significant differences ($P > 0.05$) in the final percent of germinants between the three temperature cycles (Table 8), although the rates of germination differed (Fig. 13). There was little or no seed germination in the absence of light at these temperatures.

Flemer (1949) used light conditions in culturing seeds and embryos of *K. latifolia*. However, Jaynes (1971) was the first to conclusively demonstrate that *K. angustifolia* seeds required light to germinate. The results of the present study suggest that better germination of *Kalmia* seeds can be expected in well lighted openings in the forest, or when the forest cover is removed. Seeds must be lodged on or just under the soil surface so that there is adequate light, but only a small proportion may actually germinate. Once established, however, a single individual has the potential to produce large numbers of new plants through vegetative reproduction.

Using seeds from southern New Jersey, Nichols (1934) observed dormancy in seeds of *Kalmia angustifolia*. Jaynes (1971) found that dormancy in seeds of *K. hirsuta*, *K. latifolia* and *K. cuneata* could be broken

Table 8. Mean cumulative percent germination(\pm s.d.) of *Kalmia angustifolia* seeds after 50 days with and without cold treatment at four different temperature cycles under variable light conditions (S.S. Sidhu, unpublished data).

Treatments	Light Period Temperature/Dark Period Temperature			
	13°C/3°C	18°C/7°C	23°C/12°C	27°C/21°C
Without cold treatment^a				
Alternate light (16 hrs) and dark (8 hrs) conditions	70 ^b \pm 3.8	65 ^b \pm 8.1	60 ^b \pm 14.5	-
Complete darkness (24 hrs)	0 \pm 0.0	0 \pm 0.0	1.5 \pm 3.0	
With cold treatment (1°C)^c				
2 Weeks, alternate light & dark	-	-	-	57 \pm 6.9
3 Weeks, alternate light & dark	-	-	-	56 \pm 8.3
4 Weeks, alternate light & dark	-	-	-	57 \pm 14.8
6 Weeks, alternate light & dark	-	-	-	66 \pm 13.3

^a Germination tests in petri dishes.

^b Means not significantly different (P > 0.05).

^c Mermination tests in water-soaked soil.

after stratification or after a brief exposure to high temperatures (80-90°C). However, *K. angustifolia* seeds exposed to 80" and 90°C for 1-10 minutes did not show any improvement in germination. Similarly, stratification for two, three, four or six weeks at 1°C failed to improve the germination rate of *K. angustifolia* seeds. As he was not able to detect any dormancy in *K. angustifolia* seeds collected from northern sources, Jaynes (1971) concluded that dormancy in *K. angustifolia* seems to be an adaptation for survival in the southern latitudes where warm fall temperatures could lead to germination but then death with ensuing winter temperatures. In more northern latitudes, fall temperatures would not be warm enough for newly fallen seed to germinate.

The present study supports the results of Jaynes (1971) as the ungerminated seeds were tested for dormancy, but did not respond to cold treatment or to application of gibberellin (400 ppm GA), and finally deteriorated. There was an indication, however, that 30-40% of the visually healthy seeds tested had embryos that were not

viable. The estimated values of reproductive capacity in this present study (Table 6) may therefore not be attained in the field, and seed germination trials are needed to understand the exact role of seed in the establishment of *Kalmia* on new sites in the field.

As the results of the earlier field study showed that approximately 65% of seeds produced had embryos (Table 6), and as the above germination tests showed that about 70% of these seeds with embryos were potentially viable (Table 8), it would appear that only about 45% of *Kalmia* seed produced had the potential to germinate. However, such large numbers of seed were produced that in spite of this significant reduction in sexual reproductive potential, approximately 4 and 60 million seeds were still estimated to be viable under forest and cutover conditions, respectively. Further reductions in seed viability in *Kalmia* may be caused by parasitism. For example, overwintered capsules from the 1977 growing season were collected near St. John's, Newfoundland at Logy Bay on 30 May 1978. Most of

the capsules had **dehisc**ed, but 74.5% (111 capsules from a sample of 149) were infected by the possible fungal parasite *Diplodina* sp.⁶. Black-brown fruiting bodies and/or hyphae were present on the capsules, **enmeshing** the overwintered seeds and preventing dispersal. Twelve of these capsules (8.3%) did not dehiscce at all, and were all diseased and undersized. A total of only 25% of the capsules were free of disease.

3.2.4 Kalmia Seed Germination in the Field Trials in controlled greenhouses or growth chambers may help to define optimal conditions for seed germination, but in the field a full range of environmental and microsite conditions interact to determine germination rates and ultimately *Kalmia* seedling establishment rates. To test *Kalmia* seed germination rates under field conditions, 200 seeds were sown in the fall of 1974 in 25 cm x 25 cm quadrats on the surface of each of the twenty sampling points established earlier under the three forest and cutover conditions (Section 3.2.1) in the strip cutting experiment. Germination was then assessed in the summer of 1975. A total of 12 000 seeds were sown in the field plots in the three forest and cutover site conditions. However, these seeds produced only two seedlings, both of which were found in quadrats on exposed mineral soil on cutovers (C-M). This result was consistent with the field observation that although all *Kalmia* establishment on the undisturbed cutover with an intact organic layer (C-0) was from underground rhizomes or stolons, *Kalmia* establishment on the cutover with exposed mineral soil (C-M) was mostly from seedlings (Table 4). Indeed, assuming a success rate in the field of **two** *Kalmia* seedlings established for every 4000 seeds applied, then 440 million viable seeds ha⁻¹ would be required to produce the theoretical potential of the 220 000 seedlings ha⁻¹ found earlier on exposed mineral soil (Table 6). This lies within the potential production capabilities of the estimated 4 to 60 million viable **seeds** ha⁻¹ yr⁻¹ over the 14 year period from the time of disturbance to time of estimating *Kalmia* density (*i.e.* a **total** of 56 to 840 million viable seeds over 14 years), assuming that the seeds could blow from the forest and undisturbed cutover onto the exposed mineral

soil site, and that seed production and germination rates were consistent from year to year. Regardless of the assumptions used in the quantification of the establishment **rate** of *Kalmia* by seed, it certainly cannot be assumed that **this** species does not spread by seed (especially after disturbance), or that this successional mechanism is unimportant.

Viable *Kalmia* seed that does not germinate may build up in the soil seed bank. It has been estimated that surface soil samples from beneath a red pine stand in central Newfoundland were capable of producing up to 8306 seedlings m² in a greenhouse, which were "almost entirely *Kalmia*" (Mallik and Roberts 1994), which is equivalent to **83** million seedlings ha⁻¹. This vast number of *viable* seeds in the soil reserve is obviously a function of both annual seed production rates and the length of time that seeds are able to remain viable in the soil. **As** approximately 57 million seeds ha⁻¹ are produced at this same red pine site⁷, one conclusion that can be drawn is that *Kalmia* **seeds** do not remain viable for long periods of time in the soil. However, **as** seed bank data is not presented by humus or by soil depth in Mallik and Roberts (1994), this assumption cannot be examined further. Although very different from natural field conditions, Jaynes (1982) showed that *K. angustifolia* **seed** germination rates decreased from 92% to 22% after 16 years storage at 4°C under laboratory conditions.

Scarification was recommended earlier **as** a site preparation technique for restricting the vegetative spread of *Kalmia* through breaking up the continuity of the humus layer (Section 3.1). However, it is clear that this treatment may also lead to germination of *Kalmia* **seeds** on the resultant exposed mineral soil. Furthermore, anecdotal observations from exposed **mineral** soil on roadsides, landings, and older scarified sites in central Newfoundland suggest that the *Kalmia* densities found on mineral soil in the field **survey** (22 stems m⁻² **after** 14 years) and the seeding trial (1.6 seedlings m⁻² after 1 growing season) can be observed on some sites. However, spread by seed into mineral soil exposed by scarification has not yet been observed in the field to be extensive enough **or** in high enough densities to cause immediate concern.

⁶ Identification by Dr. M.P. Corlett of the Centre for Land and Biological Resource Research (CLBRR), Research Branch, Agriculture Canada, Saunders Building, Central Experimental Farm, Ottawa, Ontario, K1A 0C6. Specimen suggestive of *Diplodina eurhododendri* Voss, a Ceolomycete.

⁷ Estimated for Site 5 from Fig. 8 in Mallik (1994).

Until it is demonstrated to the contrary, the benefits of scarification before planting for increasing spruce seedling growth and survival and for controlling vegetative spread of *Kalmia* across bare mineral trenches seems to outweigh any subsequent disadvantages that might arise through increased germination of *Kalmia* in the exposed mineral soil produced by mechanical site preparation. However, the *Kalmia* densities measured in this study suggest that the situation requires continued monitoring in the field, as the potential for the spread of *Kalmia* by seed onto exposed mineral soil after scarification may exist when high seed viability and good germination conditions exist. The field survey demonstrated that approximately 50% of the *Kalmia* plants of seed origin were only 1 or 2 years old on mineral soil exposed 14 years previously (Table 4). This may suggest that the environmental conditions required for viable seed production and successful germination and establishment do not arise regularly. Alternatively, the fairly steady increase in establishment from seed over time after a delay of seven years from disturbance, along with the lack of evidence for germination in humus, may also suggest that *Kalmia* is autoallelopathic and that some period of time is required for allelochemicals to leach out of even exposed mineral soil before germination can take place. If the latter is the case, preliminary surveys for seed-origin *Kalmia* should begin in plantations which were scarified at least seven years previously. Notwithstanding the potential for spread from seed, further questions concerning *Kalmia* germination on exposed mineral soil can await field evidence that mechanical site preparation solves an immediate spruce establishment problem (production of *Kalmia*-free planting microsite and control of *Kalmia* spread by rhizomes) in the short-term while at the same time leading to another problem (*Kalmia* spread by seed) in the long-term, if indeed *Kalmia* can come to fully occupy the exposed mineral soil around a planting microsite and inhibit spruce growth before canopy closure is reached.

3.3 Vegetative Reproduction in *Kalmia angustifolia*

Kalmia is relatively slow in developing sexual reproductive tissue as compared to other ericaceous species (Bell and Burchill, 1955). From casual field

observations and the results of the above studies it is apparent that *Kalmia* can produce vast numbers of seeds from flowering stems. These stems are more abundant under canopy openings in forests or on cutovers than under the shade of dense, fully closed canopies of black spruce. However, the seed produced may have a potential maximum germination rate of less than 50%, and even then only seeds that fall on exposed mineral soil are likely to germinate and give rise to new seedlings.

While seed production likely plays a pioneering role in establishing *Kalmia* on mineral soil after natural disturbances such as fire (e.g. see soil seed reserve data in Mallik and Roberts 1994), *Kalmia* can spread rapidly by the growth of rhizomes through the humus after fire or harvesting. This is especially true once it becomes well established (depending on site and forest conditions). However, under mature forest canopies the production of rhizomes may be slow. Once produced, the rhizomes can elongate very rapidly before protruding above ground and producing new upright stems at various nodes consisting of vegetative clumps (Figs. 6 and 7). Sub-terranean shoots serve to enlarge the clump diameter, and vegetative spread is brought about by the growth of long as well as short rhizomes, with long rhizomes measuring from a few centimetres to over two metres in length. This growth of long rhizomes can result in the formation of new clumps several metres away from the original "parent" clump. Both short and long rhizomes can be initiated in one summer, overwinter, and then begin to develop new clones the following summer.

The development of rhizomes is very common in old plants in forest openings and on undisturbed cutovers (Fig. 8). By contrast, plants on mineral soil on cutovers are predominantly of seed origin (Fig. 9). The growth of clumps for the first five years is mostly through production of short rhizomes or adventitious buds, after which time production of long rhizomes begins.

To study the anatomy and histology of rhizomes and vegetative buds of *Kalmia*, various tissue sections were prepared (Bal 1977). Rhizome parts and vegetative buds were fixed in formal:acetic acid:alcohol (FAA) and Camoy's solution (Jensen 1962). Tissues were then dehydrated in alcohol:tertiary butyl alcohol series and

embedded in paraplast, and sections were stained with **safranin-aniline** blue, **safranin-light** green, and haematoxylin-Bismark brown. For cytochemical studies, sections were treated with Millon's reagent (for localization of proteins), periodic acid-Schiff (for polysaccharide) and KI-I, (for starch) following procedures outlined in Jensen (1962).

Transverse sections of a rhizome are shown in Figure 14. The epidermis is characterized by the presence of multicellular trichomes (Fig. 15), which have also been found in vegetative buds. The apical cells of the trichomes are densely stained, which suggests high cytoplasmic activity and possibly the presence of polyphenolic compounds. More detailed work at the cytochemical and ultrastructural level needs to be done to determine the functional **role** of the trichomes, as these structures may be involved in the secretion of possible allelopathic substances. Indeed, trichomes (as surficial glands on the under sides of leaves) have been suggested **as** the source of allelopathic compounds in another member of the Ericales, *Empetrum hermaphroditum* (Zackrisson and Nilsson 1992).

The outer surface of the epidermis shows bristle-like projections of unknown function (Fig. 16). The cortex is about ten cell layers thick, which is followed by a sclerenchymatous sheath of two to three layers (Fig. 14). The phloem tissue next to it is followed by the cambium and the **xylem**, which consists of large vessels **as** well as rays. The cells of the pith (or medulla) are thick walled, and characterized by large cavities which are formed by the breakdown of cell walls (Figs. 14, 17 and 18). In sections they appear to be empty. It **is** possible, however, that these cavities are filled with some substance that has been leached out during the fixation and embedding procedures. Alternatively, they may serve as air pockets to ensure aerobic conditions in the underground rhizome (Hall *et al.* 1973). **The** other cells of the pith have large granules which stain with periodic acid-Schiff's and KI-I, as well as Millon's reagent, and are thus likely large amyloplasts containing starch **as** well as small amounts of proteins (Figs. 17 and 18).

The pith cavities can be seen to extend to many cells in length when **viewed** in longitudinal section (Fig. 19). The presence of the remnants of cell walls suggests that these

cavities are lysigenous in origin. The central cavity or cavities of *Kalmia* stems and rhizomes have been observed previously (Hall *et al.* 1973; Metcalfe and Chalk 1950). Breakdown of cell walls may be related to mobilization of nutrients from storage granules. Such breakdown of cell walls is observed in the seed endosperm tissue of barley during early stages of germination (Jones 1969). A seasonal appearance of lysigenous cavities could support the hypothesis that nutrients in the cavities were stored in granules prior to mobilization for growth. The true nature of the **intercellular** connections should be examined in detail at the ultrastructural level to determine if they are plasmodesmata. These communication channels may be of great importance in mobilizing reserve nutrients when demand for new vegetative growth is made in the plant.

Vegetative buds at a very rudimentary stage can frequently be seen in longitudinal section (Fig. 20). These buds have a vascular supply, as well as trichomes in the tunica layer. Two kinds of underground vegetative buds were found. One **type** was slender with an average diameter of 5 mm, and the other was thicker and about twice that size. Both were virtually identical in all other respects, and the thicker bud is shown in Figure 21. The apical meristem in both cases was composed of small isodiametric cells. Abundant trichomes were present on the leaf primordia and all around the epidermal surface. The larger buds showed breakdown of cell walls in the pith, and were probably an early appearance of the lysigenous cavities. It is possible that the two different sizes of buds observed represent different stages in growth.

The gradual development of leaf primordia can be seen in a cross section through the apical meristem of a large bud (Fig. 22).

Although **this** preliminary study on the vegetative reproduction of *Kalmia* has provided some basic anatomical facts that suggest certain physiological processes, future histophysiological studies should be undertaken to determine the quiescent areas of the rhizome and the buds. Investigations on the function of trichomes in relation to the secretion of possible allelopathic compounds should also be carried out in the future.

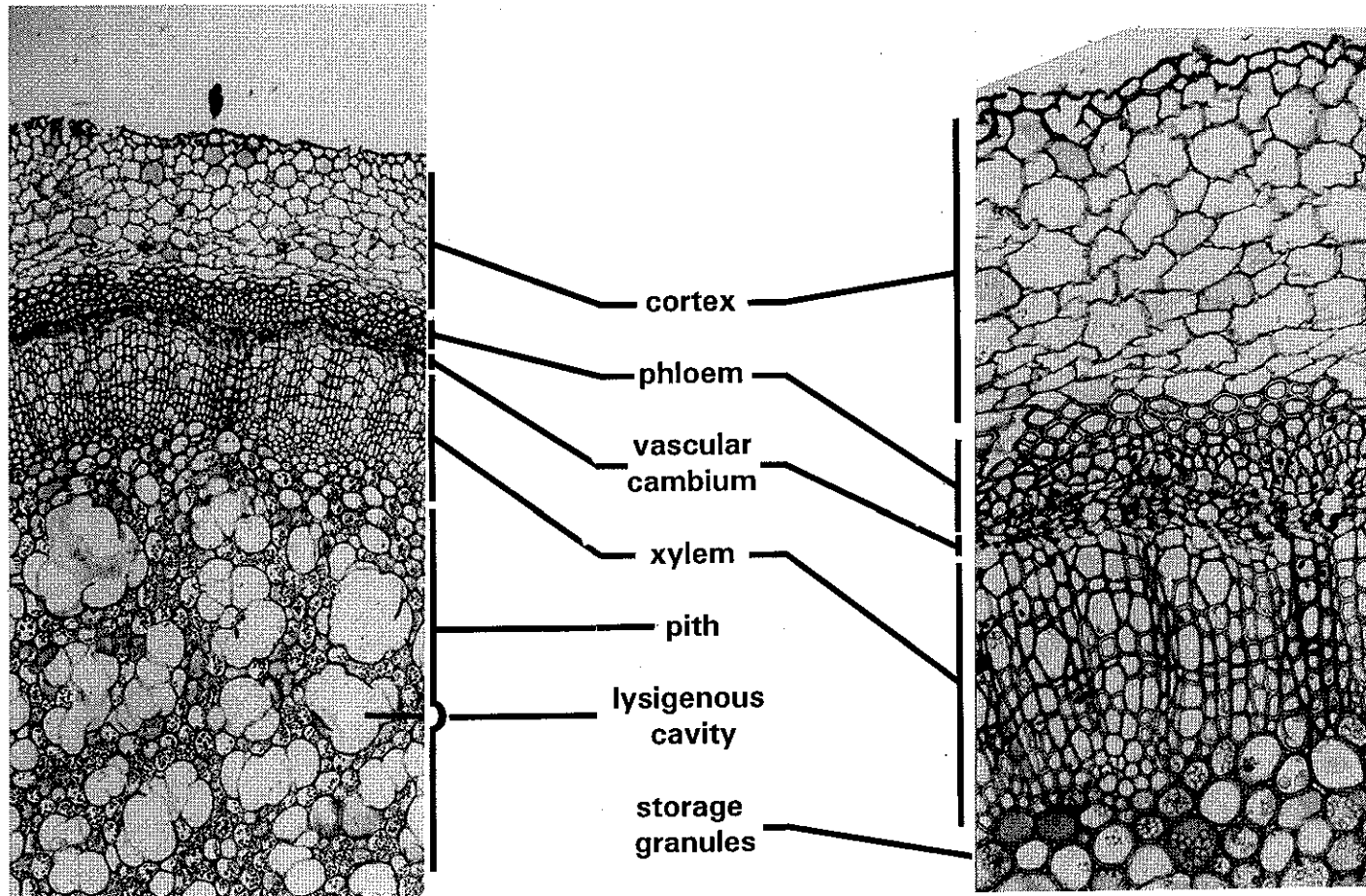


Figure 14. Transverse sections (80X on **left**, 200X on **right**) of a portion of a *Kalmia angustifolia* rhizome showing distribution of tissues (*after* Bal 1977, Figs. 3 and 6).

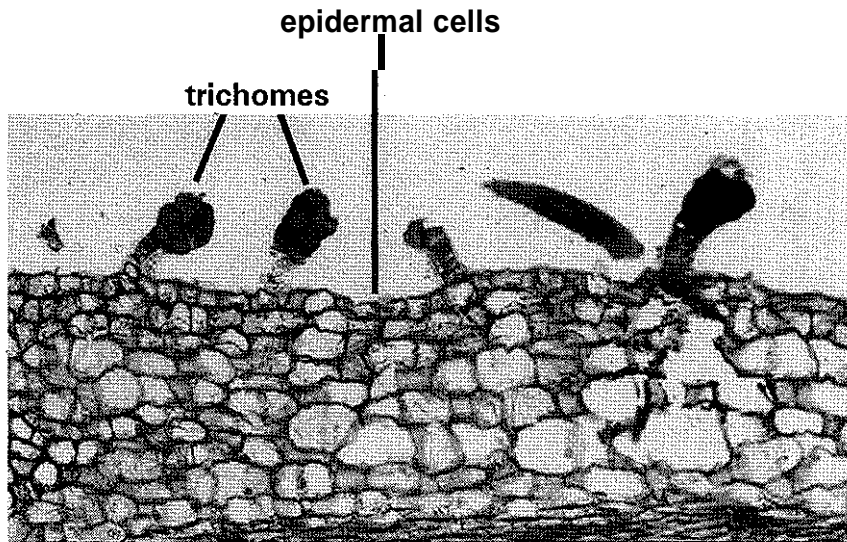


Figure 15. Epidermal trichomes (200X) of *Kalmia angustifolia* (after Bal 1977).

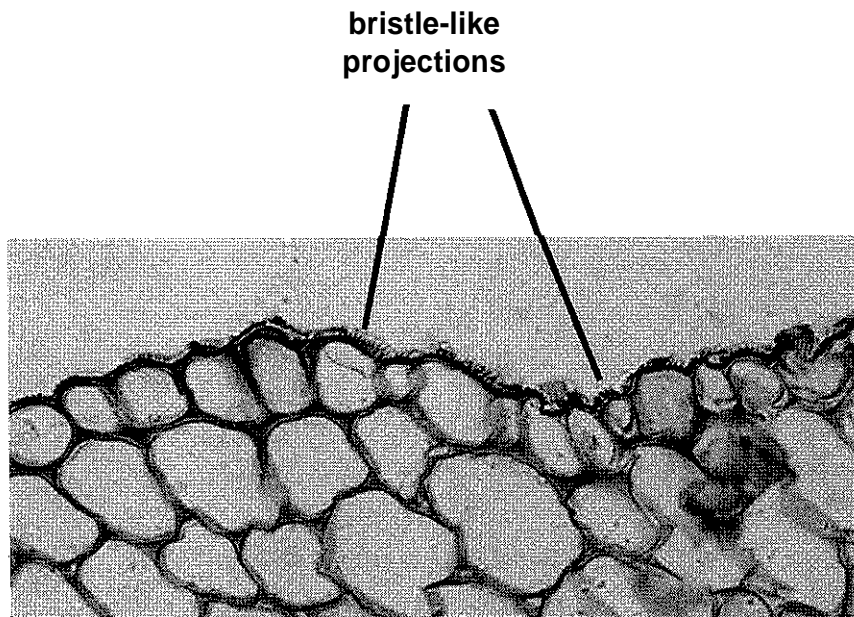


Figure 16. Transverse section (500X) of a *Kalmia angustifolia* rhizome, showing bristle-like structures on the surface of the epidermal cells (after Bal 1977, Fig. 5).

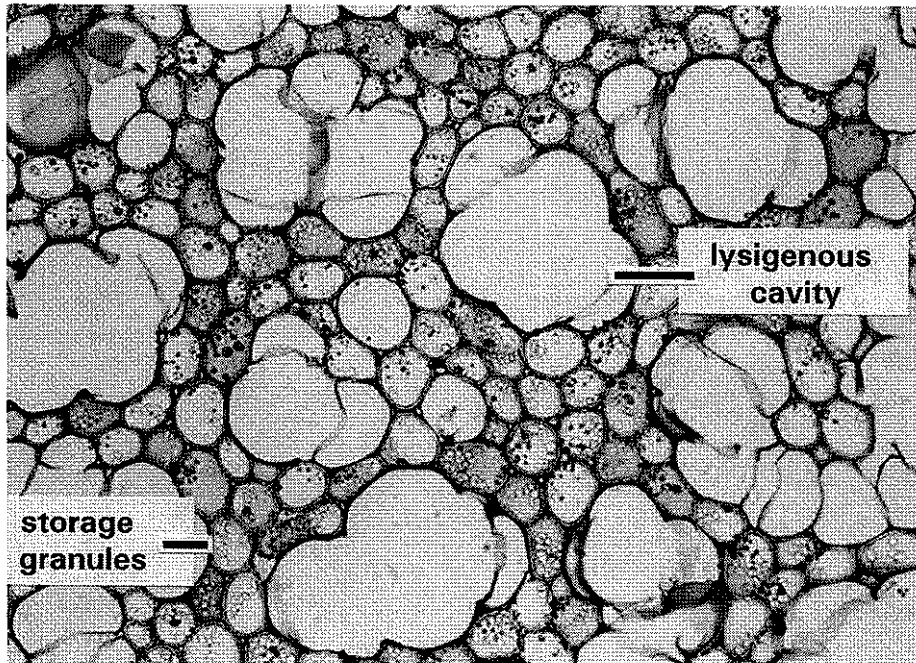


Figure 17. Transverse section (200X) of a *Kalmia angustifolia* rhizome, showing the pith. Note the lysigenous cavities and pith cells with large storage granules (after Bal 1977, Fig. 7).

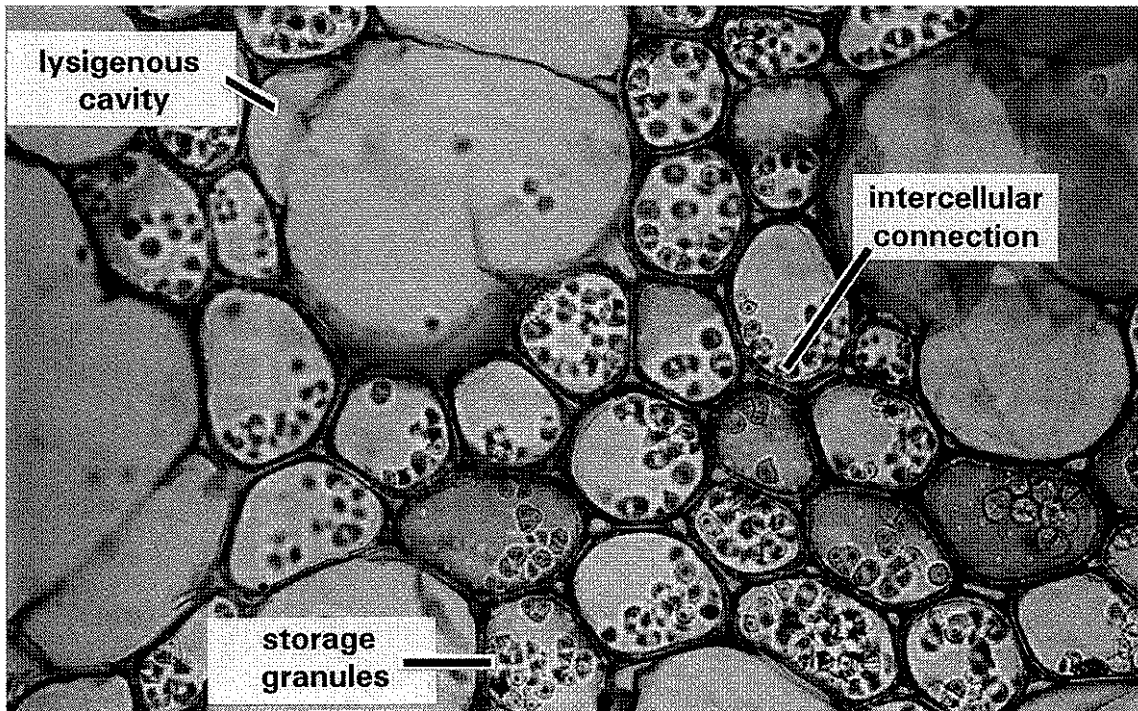


Figure 18. Transverse section (500X) of a *Kalmia angustifolia* rhizome, showing the pith. Note the lysigenous cavities, pith cells with large storage granules, and profuse intercellular connections between pith cells (after Bal 1977, Fig. 8).

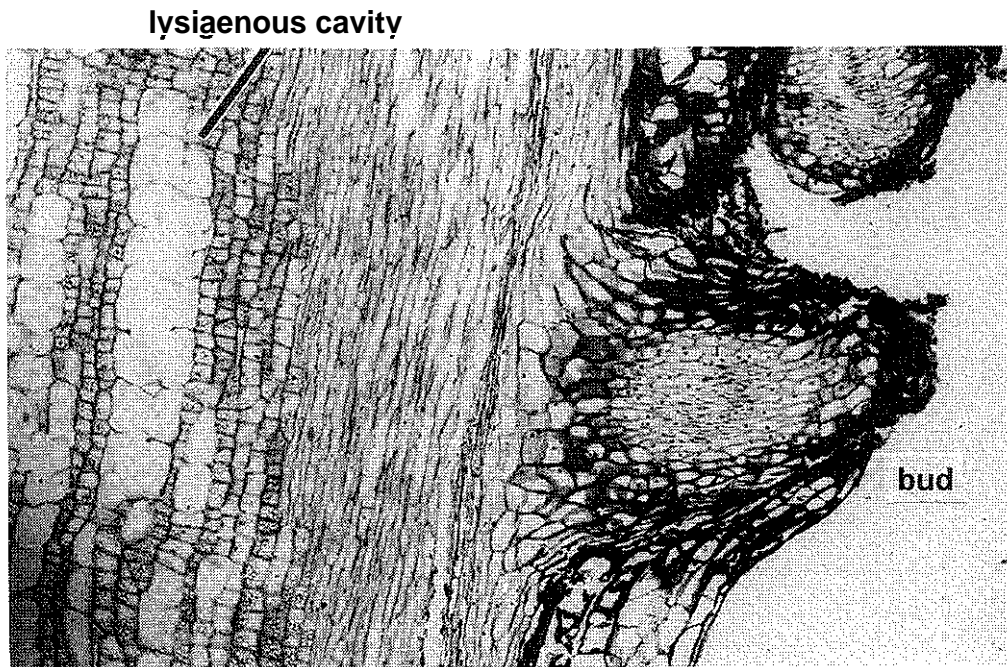


Figure 19. Longitudinal section of a rhizome of *Kulmiu angustifolia*, showing the continuity of the lysigenous cavities and remnants of the cell walls (200X). The intact cells contain storage granules (after Bal 1977, Fig. 9).

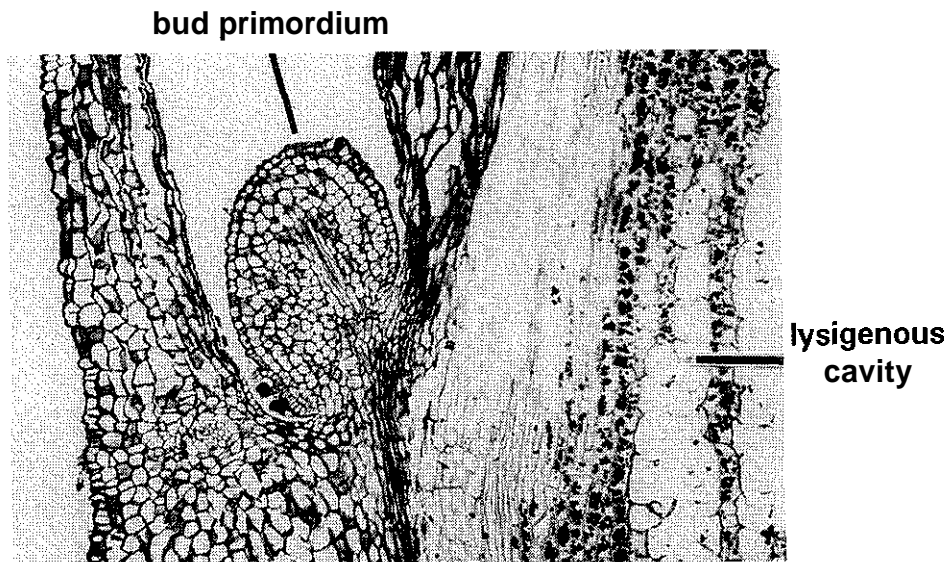


Figure 20. Longitudinal section of a rhizome of *Kulmia angustifolia* (200X) showing a bud primordium (also illustrated in Mallik 1993, Fig. 4, after Bal 1977, Fig. 10).

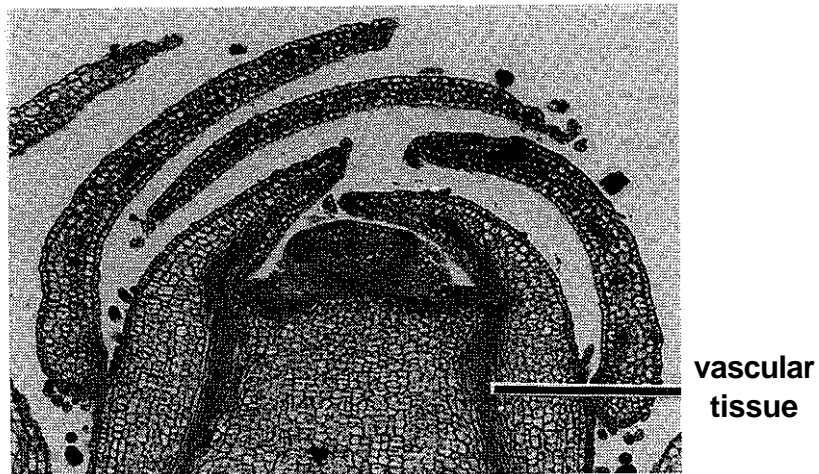


Figure 21. Longitudinal section (80X) through a thick vegetative underground bud of *Kalmia angustifolia* (after Bal 1977, Fig. 12).

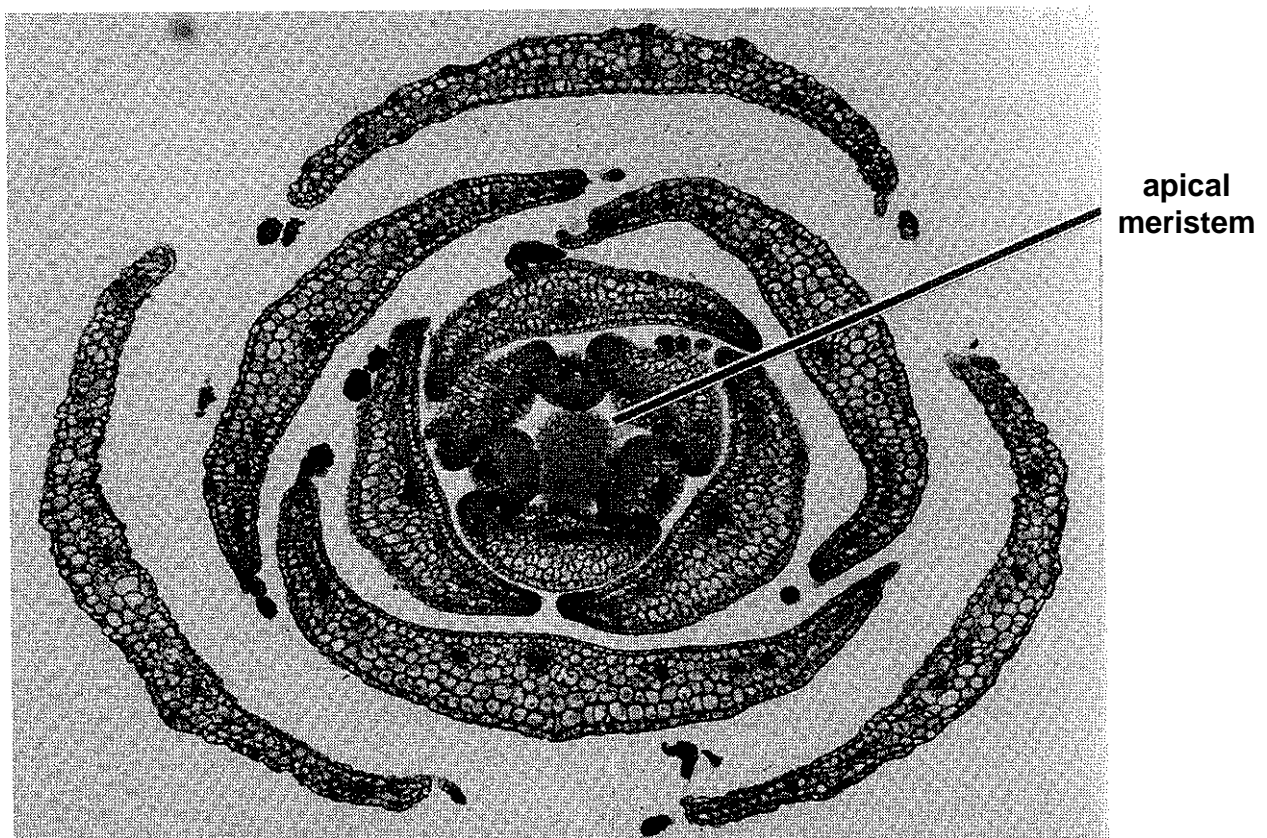


Figure 22. Transverse section through the apical meristem of a *Kalmia angustifolia* bud (90X). Note the presence of trichomes (after Bal 1977, Fig. 13).

4. INHIBITION OF BLACK SPRUCE REGENERATION BY *KALMIA ANGUSTIFOLIA*

The abundant growth of *Kalmia* on cutovers is known to adversely affect regeneration of black spruce. Two mechanisms have been suggested to contribute to this phenomenon: (i) nutrient competition, and (ii) allelopathy.

4.1. Nutrient Competition

The profuse growth of *Kalmia* and other ericaceous shrubs can result in the limitation of environmental factors vital for successful black spruce regeneration. For example, *Kalmia* and other understory species immobilize soil nutrients in living tissue and in detritus which would otherwise be available to black spruce. Damman (1971) showed that *Kalmia* heaths have a much thicker litter layer than black spruce or balsam fir forests. Most of the litter input from *Kalmia* was found to originate from root and rhizome mortality. The roots of *Kalmia* can penetrate to a depth of 67 cm (Peterson 1964), thus defining the extent of the rootable zone from which nutrients can potentially be taken up and immobilized. Damman (1971) examined changes in site conditions with respect to nutrient contents of litter under different cover types and found that the humus on *Kalmia* sites had twice the amount of total nitrogen, more phosphorus, but lower potassium and calcium compared to humus on balsam fir sites. More importantly, however, net nitrogen mineralization rates of incubated humus from the *Kalmia* site were negligible. The possibility therefore remains that poor spruce growth in the field is as much a function of lack of nutrient availability as it is of allelopathy.

The results of a study to quantify the nutrient accumulation by *Kalmia* plants growing on peatlands are described in the following sections, where the productivity of eight peatland communities on Crooked Bog (near Badger, central Newfoundland) were determined during July and August 1969 (Olsen 1974, after Pollett *et al.* 1970, Pollett 1972). Only the results from three communities (*Kalmia-Sphagnum fuscum*, *Betula michauxii*, and *Lonicera villosa-Rosa nitida*) were considered pertinent to the autecology of *Kalmia*,

and will be referred to as *Kalmia-Sphagnum*, *Betula* and *Lonicera-Rosa* communities respectively.

The Crooked Bog complex was classified using the techniques of the Zurich-Montpellier School (Pollett *et al.* 1970, Pollett 1972). Sites were selected within the defined communities and a 25 cm³ sample of peat including the above ground vegetation was removed and divided into its constituent parts. The wet and dry weights of all species comprising the sample were recorded, as well as the living and dead components of the peat substrate. Specimens for chemical analysis were then retrieved in close proximity to the sample site.

The floristic compositions of the three communities are given in Table 9. The *Kalmia-Sphagnum* community occupied an ombrotrophic raised bog with a pH range of 3.2 to 4.6. The community was dominated by ericaceous dwarf shrubs, indicating relatively dry conditions. The *Betula* community included some of the most nutrient rich sites on Crooked Bog, and was underlain by a compact sedge-wood peat with the water table near or at the surface. The pH ranged from 4.5 to 5.6. Lichens were rare in this community, probably because of the high water table. The *Lonicera-Rosa* community was typical of forest-peat margins. The substrate was usually composed of a shallow woody-sedge peat with a pH of 4.6 to 5.0.

Kalmia is usually most abundant on oligotrophic sites such as raised bogs and decreases to sporadic occurrences in fens. This is reflected in a *Kalmia* biomass of 150.72 g m⁻² for the *Kalmia-Sphagnum* community as compared to 16.32 and 17.76 g m⁻² for *Betula* and *Lonicera-Rosa* communities, respectively (Table 10).

The mineral content of *Kalmia* in all three communities is summarized in Table 10, where it is compared to the total mineral content (mg m⁻²) of the biomass of the community, expressed on an area basis. *Kalmia* immobilized substantial quantities of mineral elements, especially nitrogen. However, the accumulation by *Kalmia* of a particular element was not the same in all communities. For example, the fraction of the total nitrogen accumulated by *Kalmia* in the two fen (*Betula* and *Lonicera-Rosa*) communities was in proportion to the fraction of the total plant biomass made up by

Table 9. Plant species found within *Kalmia-Sphagnum*, *Betula* and *Lonicera-Rosa* communities on Crooked Bog, Badger (in Olsen 1974, pp. 7-9, after Pollett 1972).

Vascular plants	Mosses	Liverworts	Lichens
1. <i>Kalmia-Sphagnum</i> community			
<i>Kalmia angustifolia</i>	<i>Sphagnum fuscum</i>	<i>Mylia anomala</i>	<i>Cladonia rangiferina</i>
<i>K. polifolia</i>	<i>S. rubellum</i>	<i>Lepidozia reptans</i>	<i>C. mitis</i>
<i>Rubus chamaemorus</i>	<i>Polytrichum schreberi</i>	<i>Cephalozia connivens</i>	<i>C. pyxidata</i>
<i>Vaccinium oxycoccus</i>	<i>Pleurozium schreberi</i>	<i>Odontoschisma</i>	<i>C. arbuscula</i>
<i>V. angustifolium</i>	<i>Dicranum bergeri</i>	<i>sphagnii</i>	<i>C. coccifera</i>
<i>Chamaedaphne calyculata</i>	<i>Aulacomnium palustre</i>		<i>Cetraria islandica</i>
<i>Andromeda glaucophylla</i>			
<i>Drosera rotundifolia</i>			
<i>Scirpus cespitosus</i>			
<i>Empetrum nigrum</i>			
<i>Sarracenia purpurea</i>			
<i>Larix laricina</i>			
<i>Ledum groenlandicum</i>			
2. <i>Betula</i> Community			
<i>Betula michauxii</i>	<i>Campylium stellatum</i>	<i>Cladopodiella fluitans</i>	<i>Cladonia rangiferina</i>
<i>Calamagrostis inexpansa</i>	<i>Sphagnum papillosum</i>	<i>Pellia fabroniana</i>	
<i>Solidago uliginosa</i>	<i>S. pulchrum</i>	<i>Cephalozia connivens</i>	
<i>Lonicera villosa</i>	<i>S. plumulosum</i>		
<i>Lycopodium inundatum</i>	<i>S. warnstorffii</i>		
<i>Selaginella selaginoides</i>	<i>Calliergon stramineum</i>		
<i>Vaccinium oxycoccus</i>			
<i>Sarracenia purpurea</i>			
<i>Scirpus cespitosus</i>			
<i>Kalmia angustifolia</i>			
<i>K. polifolia</i>			
<i>Carex oligosperma</i>			
<i>Aster radula</i>			
<i>Rhynchospora alba</i>			
<i>Schizaea pusilla</i>			
<i>Chamaedaphne calyculata</i>			
<i>Andromeda glaucophylla</i>			
<i>Drosera rotundifolia</i>			
<i>Ledum groenlandicum</i>			
<i>Juniperus communis</i>			

(Cont'd.)

Table 9. (Concl'd.)

Vascular plants	Mosses	Liverworts	Lichens
3. <i>Lonicera-Rosa</i> community			
<i>Kalmia angustifolia</i>	<i>sphagnum pulchrum</i>	<i>Riccardia palmata</i>	
<i>Myrica gale</i>	<i>S. magellanicum</i>		
<i>Alnus rugosa</i>	<i>S. recurvum</i>		
<i>Equisetum fluviatile</i>	<i>S. palustre</i>		
<i>Ledum groenlandicum</i>	<i>Bryum pseudo-</i>		
<i>Carex lasiocarpa</i>	<i>triquetrum</i>		
<i>C. livida</i>			
<i>C. rostrata</i>			
<i>C. michauxiana</i>			
<i>Lonicera villosa</i>			
<i>Rosa nitida</i>			
<i>Vaccinium oxycoccus</i>			
<i>Sanguisorba canadensis</i>			
<i>Aster radula</i>			
<i>Chamaedaphne</i>			
<i>calyculata</i>			

Kalmia. However, in the bog (*Kalmia-Sphagnum*) community *Kalmia* immobilized relatively less nitrogen per unit of plant weight produced than the other species in the community. In the bog community, the only element which was immobilized in *Kalmia* in approximately the same proportion as its biomass was phosphorus. All other elements were present in lower proportions. In most instances, proportions of immobilization of minerals by *Kalmia* was greater in the fen communities. This was especially so for sodium, which was present in *Kalmia* in the *Lonicera-Rosa* community at over three times its proportion of biomass.

The total nutritional content of three other ericaceous shrubs (*Kalmia polifolia*, *Ledum groenlandicum* and *Andromeda glaucophylla*) on Crooked Bog were also determined and expressed on an area basis (mg m⁻²). Results are presented in Appendix II.

Analyses of the nutrient concentrations (nutrient content as a percent of dry weight) in the roots, stems and leaves of *Kalmia* from the three communities on Crooked Bog

are presented in Table 11. On all sites the nutrient concentrations were generally greatest in the leaves and decreased in the stems and roots. However, there were differences in nutrient concentrations between the three communities. Not surprisingly, nitrogen concentrations in all three plant components increased from the *Kalmia-Sphagnum* to the *Betula* to the *Lonicera-Rosa* communities, reflecting the nutritional transition from bog (nutrient poor) to fen (nutrient rich). Differences in nitrogen concentrations between stems and roots were very small, but concentrations increased three-fold in the leaves. However, the phosphorus concentration in the leaves of *Kalmia* decreased slightly from the *Kalmia-Sphagnum* bog to the *Lonicera-Rosa* fen community, although values for the *Betula* fen community were, surprisingly, one third those of the other two communities. The phosphorus concentrations in the roots and stems of *Kalmia* were similar in all three communities. The concentration of phosphorus in the leaves was three times that of the roots and stems, with the exception of the *Betula* community where all concentrations were approximately the same. Potassium

Table 10. Contribution of *Kalmia angustifolia* to total biomass (g m^{-2}) and nutrient composition (mg m^{-2}) of biomass in three bog communities on Crooked Bog, Badger (in Olsen 1974, Table 3, after Pollett 1972).

	Community Type								
	<i>Kalmia-Sphagnum</i>			<i>Betula</i>			<i>Lonicera-Rosa</i>		
	Contribution by <i>Kalmia</i>			Contribution by <i>Kalmia</i>			Contribution by <i>Kalmia</i>		
	Total	Biomass	% ^a	Total	Biomass	%	Total	Biomass	%
Biomass ^b	2 028.48	150.72	7.43	2007.04	16.32	0.81	2726.40	17.76	0.65
N ^c	9 858.75	483.74	4.91	17 218.33	158.01	0.92	18 737.32	114.49	0.61
P	468.60	36.67	7.82	367.58	3.77	1.03	843.16	5.02	0.60
K	3 291.00	70.81	2.15	1721.08	14.03	0.82	1854.80	5.42	0.29
Ca	2 038.33	71.87	3.53	5 158.26	29.19	0.57	3 679.12	16.97	0.46
Mg	1208.36	41.84	3.46	1280.87	6.22	0.49	1614.45	7.71	0.48
Mn	411.91	20.77	5.04	208.45	2.16	1.04	468.85	-	-
Fe	191.28	8.21	4.24	4 825.10	0.47	0.01	713.12	1.25	0.18
Na	2 359.85	89.58	3.80	2 296.25	13.17	0.57	2 867.23	61.30	2.14
Zn	93.41	3.46	3.70	71.96	0.55	0.76	125.95	0.77	0.61

^a Weight of *Kalmia* expressed as a percent of total biomass in community.

^b g m^{-2} .

^c All nutrients expressed as mg m^{-2} .

Table 11. Concentration of nutrients (as percent of dry weight) in leaves, stems and roots of *Kalmia angustifolia* from three bog communities on Crooked Bog, Badger (in Olsen 1974, Table 4, after Pollett 1972).

Nutrient concentration (% of dry wt)	Plant part	Community Type		
		<i>Kalmia-Sphagnum</i>	<i>Betula</i>	<i>Lonicera-Rosa</i>
N	leaf	1.22	1.37	1.68
	stem	0.39	0.47	0.55
	root ^a	0.28	0.42	0.50
P	leaf	0.077	0.023	0.069
	stem	0.028	0.029	0.027
	root	0.022	0.024	0.021
K	leaf	0.410	0.450	0.179
	stem	0.090	0.117	0.012
	root	0.030	0.054	0.009
Ca	leaf	0.210	0.375	0.190
	stem	0.070	0.065	0.090
	root	0.040	0.060	0.080
Mg	leaf	0.090	0.098	0.108
	stem	0.030	0.037	0.038
	root	0.025	0.034	0.033
Mn	leaf	0.023	0.038	-
	stem	0.010	0.013	-
	root	0.014	0.015	-
Fe	leaf	0.011	0.002	0.010
	stem	0.012	0.004	0.005
	root	0.005	0.002	0.008
Na	leaf	0.152	0.094	0.145
	stem	0.073	0.076	0.086
	root	0.055	0.058	0.088
Zn	leaf	0.002	0.003	0.003
	stem	0.004	0.003	0.004
	root	0.002	0.002	0.004

^a Root = rhizome + roots.

concentrations were greatest in the leaves, and generally declined quite sharply from leaves to stems to roots. The values for potassium in all components were much lower in the *Lonicera-Rosa* community than in the other two communities. Concentrations of calcium in leaves were greatest in the *Betula* community, stem concentrations were greatest in the *Lonicera-Rosa* community, and root concentrations rose markedly from the bog through the two fen communities. The concentrations of micronutrients (Fe, Na, Zn and Mn) were very small and did not vary considerably between communities or plant components. However, the iron concentration was approximately four times greater in the *Kalmia-Sphagnum* than in other communities. In general, the concentration of nutrients increased from roots to stems to leaves, except for zinc which was found in the highest concentration in stems.

From the nutritional data for these three communities it would appear that *Kalmia* is less able to compete with other wetland species for mineral nutrients when nutrient availability is lower (*i.e.* on the bog), but above some threshold of nutrient availability it is able to respond by taking up proportionately more nutrients (Table 10) and by increasing nutrient concentrations (especially nitrogen) in important tissues (Table 11). This suggests that *Kalmia* is adapted to functioning under low nutritional conditions, but can also respond to increased nutrient availability by increasing nutrient uptake and then tissue concentrations, and can thus grow across a range of sites of varying nutritional quality. The same ability of *Kalmia* to function across a wide range of site qualities is also apparent within forest communities, as *Kalmia* can be found from nutritionally poor *Cladonia-Kalmia*-black spruce sites through to richer moist black spruce-feathermoss and *Kalmia*-birch sites (Meades and Moores 1989⁸). However, as yet no work has been carried out to quantify how well *Kalmia* out-competes black spruce for nutrients on forested sites.

4.2. Allelopathy

The hypothesis that plants influence each other by chemical means (other than mineral nutrition) has long been a subject of scientific research. However, there is

still no consensus as to the direct or indirect harmful effects of such chemical compounds. Some authors consider allelopathic interactions between plants to be of great importance in natural or managed plant communities (*e.g.* Muller 1974; Rice 1984) while others conclude that the existence of such allelopathic interactions have not yet been demonstrated unambiguously under field conditions (*e.g.* Harper 1977⁹). Within this context, allelopathy must be considered as only one of a range of possible interacting mechanisms by which *Kalmia* out-competes spruce in the field (*cf.* hypotheses outlined in de Montigny and Weetman 1990, and Prescott and Weetman 1994).

Allelopathy has been suggested as a competitive mechanism for several heath shrubs. A possibly analogous situation to that of *Kalmia*-black spruce interactions occurs in the U.K., where growth of *Picea sitchensis* (Bong.) Carr. can be considerably reduced or "checked" during reforestation of upland *Calluna* heaths. This is thought to be the result of the release of a mycotoxin from living mycorrhizal roots of *Calluna* which inhibit the growth of conifer mycorrhizae and thus severely affect the ability of softwood to take up mineral nutrients from the soil (Handley 1963; Robinson 1971, 1972). Other studies have indicated that *Calluna* has an inhibitory effect on the germination of seeds of some grass and herb species (Roff 1964; Mantilla *et al.* 1975; Read and Jalal 1980). Other possible chemical interactions among heathland plants have been reported by Hobbs (1984). Two other species of the order Ericales that may inhibit conifer regeneration and/or growth through allelopathy are *Gaultheria shallon* in the Pacific Northwest of North America (de Montigny and Weetman 1990, Prescott and Weetman 1994) and *Empetrum hermaphroditum* in Sweden (Zackrisson and Nilsson 1992).

Peterson (1965) first demonstrated that leaf extracts of *Kalmia* were inhibitory to the primary root growth of black spruce seeds germinated in petri dishes. Phytotoxic substances from leaves, roots, and litter of *Kalmia* or soil

⁹ See pp. 369-381, especially p. 371; see also comments in book review by Harper (1975) the *Quarterly Review of Biology* 50:493-495.

⁸ Sites SK #21, SM/M #17 and BK #29, respectively.

from beneath *Kalmia* were also shown to inhibit primary root growth of black spruce germinants (Mallik 1987, 1992). Humus from beneath *Kalmia* was shown to decrease the germination rate of black spruce in another study (Prévost 1994), but not germinant morphology except for shoot:root ratio. Similar inhibitory effects of organic matter from *Kalmia*-dominated sites on primary root growth of conifer germinants have been reported for balsam fir (Thompson and Mallik 1989) and red pine (Mallik and Roberts 1994). Recent evidence suggests that the inhibitory substances may include phenolic compounds (Zhu and Mallik 1994), notably o-hydroxyphenylacetic, p-hydroxybenzoic, vanillic, p-coumeric, gentisic, syringic, ferulic and m-coumaric acids (ordered by increasing toxicity). However, in all but one of the above studies in which seeds were placed in petri dishes with *Kalmia* extract (Zhu and Mallik 1994) the extract solutions were not adjusted for pH (cf. Harper 1977) and therefore caution must be used in interpretation of the data from the earlier germinant work.

while inhibition of germination is a potent competition mechanism in natural ecosystems, the planting of non-regenerated sites with conifer seedlings is a routine step in forest management. It does not necessarily follow that the allelopathic mechanisms acting against germinating seeds are the same as the allelopathic mechanisms acting against one- to three-year old conifer planting stock. To date only three studies have been carried out that investigate possible allelopathic interactions between conifer planting stock and *Kalmia* plants. In all cases a "stair-step pot experiment" was used to continuously circulate leachate through pots containing planted black spruce, larch, or red pine seedlings (Mallik 1987, 1992, Mallik and Roberts 1994). A vertical row of pots containing *Kalmia* were placed between pots of sand planted with seedlings to create a "*Kalmia* treatment", and seedling growth was compared with that of "control" seedlings grown in non-interrupted vertical rows of pots of sand. Although the authors conclude that *Kalmia* leachate caused an allelopathically-induced reduction in seedling growth, inherent weaknesses in the "stair-step" design do not eliminate the possibility that differences in seedling growth were simply the result of differences in leachate nutrient concentrations (cf. Harper 1977), or the continuous circulation of leachate for 4 to 8 months which may have led to the unrealistic concentrating of allelochemicals to levels far in excess of those

experienced in the field. It thus cannot be definitively proven that reported decreases in seedling growth parameters were not the result of a decrease in available nutrients in the soil solution as the result of *Kalmia* plants taking up nutrients from the leachate, rather than adding allelochemicals to it.

Rice (1984) has summarized the properties of a wide range of allelopathic compounds that occur in nature. The mechanism of growth inhibition by allelopathic compound(s) is complex and may affect any number of processes and structures such as cell division, elongation and ultra-structure hormone-induced growth, membrane permeability, mineral uptake, stomatal opening, respiration, protein synthesis, and inhibition or stimulation of specific enzymes. The following sections describe studies carried out to determine if allelopathic interactions between *Kalmia* and black spruce might occur, and if so, at what stage of seedling development. Work included (i) a field trial on the germination of black spruce seed applied to a combination of manipulated site treatments, (ii) a greenhouse study on the germination of black spruce seed following the addition of ericaceous litter, and (iii) a laboratory study on the effect of leaf water extracts on the growth of two fungal symbionts isolated from black spruce from the field.

4.2.1. Black Spruce Seed Germination in *Kalmia*-Dominated Stands: An experiment on the establishment of black spruce from seed was set up in a burned black spruce forest with a representative ground cover of *Kalmia* north of Bay Bulls, near St. John's, to test the hypothesis that *Kalmia* inhibits the regeneration of black spruce (Olsen 1974). An adjoining area with *Vaccinium angustifolium* ground cover was selected as a *Kalmia*-free control.

Twenty 1 m² plots were located (sixteen in the *Kalmia* area and four in the *Vaccinium* area) and five treatments were randomly assigned to each of four replicates.

The five treatments were as follows:

- (i) *Kalmia* and soil undisturbed
- (ii) *Kalmia* removed by clipping stems at ground level, but soil undisturbed;

Table 12. Percent germination and establishment of black spruce seedlings on adjacent *Kalmia angustifolia* and *Vaccinium angustifolium* heaths (after Olsen 1974, Table 30).

Treatments	Date of Count		
	25 July	10 August	14 November
<i>Kalmia</i> not removed, soil undisturbed	0 -	0.43" (0.36)	1.20 (0.96)
<i>Kalmia</i> removed, soil undisturbed	0 -	0 -	1.40 (1.12)
<i>Kalmia</i> removed, humus and mineral soil mixed	6.43 (1.92)	10.30 (2.20)	10.43 (2.20)
<i>Kalmia</i> removed, humus removed	3.47 (1.32)	4.37 (1.88)	2.90 (1.60)
<i>Vaccinium</i> not removed, soil not disturbed	0.20 (0.16)	1.33 (1.04)	1.80 (1.72)

^a Mean of 750 seeds sown per plot in each of 4 replicates, for a total of 3,000 seeds per treatment; s.e. of mean in brackets.

- (iii) *Kalmia* removed by clipping stems at ground level. Humus layer cut up and mixed with underlying mineral soil;
- (iv) *Kalmia* removed by clipping stems at ground level. Humus layer cut up and removed, and level of mineral soil restored by adding surface mineral soil from beneath another area of *Kalmia*;
- (v) *V. angustifolium* and soil surface undisturbed (control treatment).

Black spruce seeds were planted in ten rows per plot, with 75 seeds per row (750 seeds per plot). The seeds were placed in very shallow furrows which were then thinly covered with substrate from the treatment in which they were sown on 20-22 June. Seedling emergence counts were made on 25 July, 10 August and 14 November and results are presented in Table 12.

The survival counts from the field trial were small and the largest germination rate was only about 10% (313 live spruce germinants from 3000 seeds). Differences between replicates for each treatment were fairly consistent, suggesting certain general trends. The highest germination counts on 25 July were found in the plots in which humus and mineral soil had been well mixed. Higher germination was probably due to the water-retaining effect of the humus in the mineral soil. The second highest count was in the mineral soil plots. As some germination did occur in the *V. angustifolium* control plot, it is possible that the absence of germination in the remaining *Kalmia* plots indicates the presence of germination-inhibiting substances in the litter of *Kalmia*. On 10 August, germination had occurred in the plots with undisturbed *Kalmia* but not in the plots where *Kalmia* was removed but plots were otherwise undisturbed, suggesting that shading may have enhanced germination. However, the number of black spruce

seedlings in the *V. angustifolium* plots was higher than in the comparable *Kalmia* plots. The number of seedlings on mineral and on mixed humus and mineral soil continued to increase. In the November count, seedlings appeared for the first time in the plots cleared of *Kalmia*. In all other plots (except those of exposed mineral soil where an actual decrease was noted) the number of emergents increased. The decrease in number of spruce seedlings in plots with exposed mineral soil was attributed to frost heaving as several frosts had occurred and frost-thrown seedlings were observed.

Generally, the data suggests that black spruce is indeed capable of germinating under *Kalmia* in the field and surviving for at least one growing season, although germination rates were very low. Regarding any allelopathic effect of *Kalmia* leaf throughfall, any toxic effects are little greater than those exhibited by *Vaccinium*. The fact that removal of the *Kalmia* canopy only improved germination a small amount suggests that seedbed conditions (including humus toxicity) were virtually as important as *Kalmia* throughfall in inhibiting spruce germination. Not only did the humus exhibit some degree of inhibition, but this inhibition was also present, although to a lesser extent, on the bare mineral soil when the humus was removed. There is thus a trend of decreasing inhibition to spruce establishment moving from *Kalmia* throughfall effects to humus and to mineral soil effects. However, germination dramatically increased when the humus and mineral soils were mixed. This may have been the result of a physically more receptive seedbed (moisture and thermal conditions). Alternatively, it is possible that allopathic throughfall from *Kalmia* leaves was eliminated, and decomposition processes in the humus were enhanced because of soil mixing so that allelochemicals were biologically degraded.

This present trial was too short-term to draw firm conclusions regarding allelopathy. Although germination rates were measured, subsequent seedling growth was not. However, the data do suggest that some mixing of humus and mineral soils using mechanical scarification techniques is advisable as a site preparation treatment in reforestation programs if direct seeding is to be carried out. Although the use of "mulchers" is likely to be prohibitive in Newfoundland as a result of costs and potential machine damage on stony sites, the use of trenching equipment may be advisable, especially where

these machines are used in such a way as to produce some bare mineral soil as a conifer seed bed, as well as mixed humus and mineral soil.

4.2.2. Black Spruce Seedling Germination and Seedling Growth in Ericaceous Litter: In order to further investigate the role of allelopathy in inhibiting spruce regeneration by seed, an experiment was established to determine the effects of a simulated cover of ericaceous litter on germination and growth of black spruce seedlings in a greenhouse (Olsen 1975). The ericaceous species used were *Kalmia angustifolia*, *Vaccinium angustifolium*, and *Ledum groenlandicum*¹⁰.

Soil was obtained from a burned black spruce forest north of Bay Bulls, near St. John's. The largely organic surface soil was collected from a grass covered area to avoid the presence of ericaceous leaf material. The soil was screened and mixed to ensure uniformity and was placed in plastic pots of approximately 11.5 cm diameter. Fifty black spruce seeds were planted in each pot and covered with approximately 3 mm of soil. A spacing disc was used during planting to ensure uniform seed distribution in each pot. The soil surface area was 104 cm² per pot.

In an earlier study on the amount of leaf litter produced by various ericaceous species in a burned black spruce forest it was determined that a "light" *Kalmia* cover produced an average leaf litter fall of 34.72 g m⁻², which is equivalent to 0.72 g per 12.5 cm² greenhouse pot. To simulate a realistic ericaceous litter effect, 1, 2, 3 and 4 g of air dried, current leaf material were selected as the appropriate treatments, with a control in which no leaf material was added to the soil surface.

¹⁰ In a separate experiment Olsen (1975) also tested black spruce germination in petri dishes on filter paper after addition of water extracts of *Kalmia angustifolia*, *Ledum groenlandicum*, *Chamaedaphne calyculata*, *Myrica gale* and *Rhododendron canadense* and all were inhibitory when 1 g of leaves were extracted in 40 mL of water overnight (pH and osmotic potential were not controlled). This work from Olsen (1975) on *Rhododendron* is erroneously referred to as "A.U. Mallik and S.S. Sidhu unpubl. data" in Mallik and Roberts (1994).

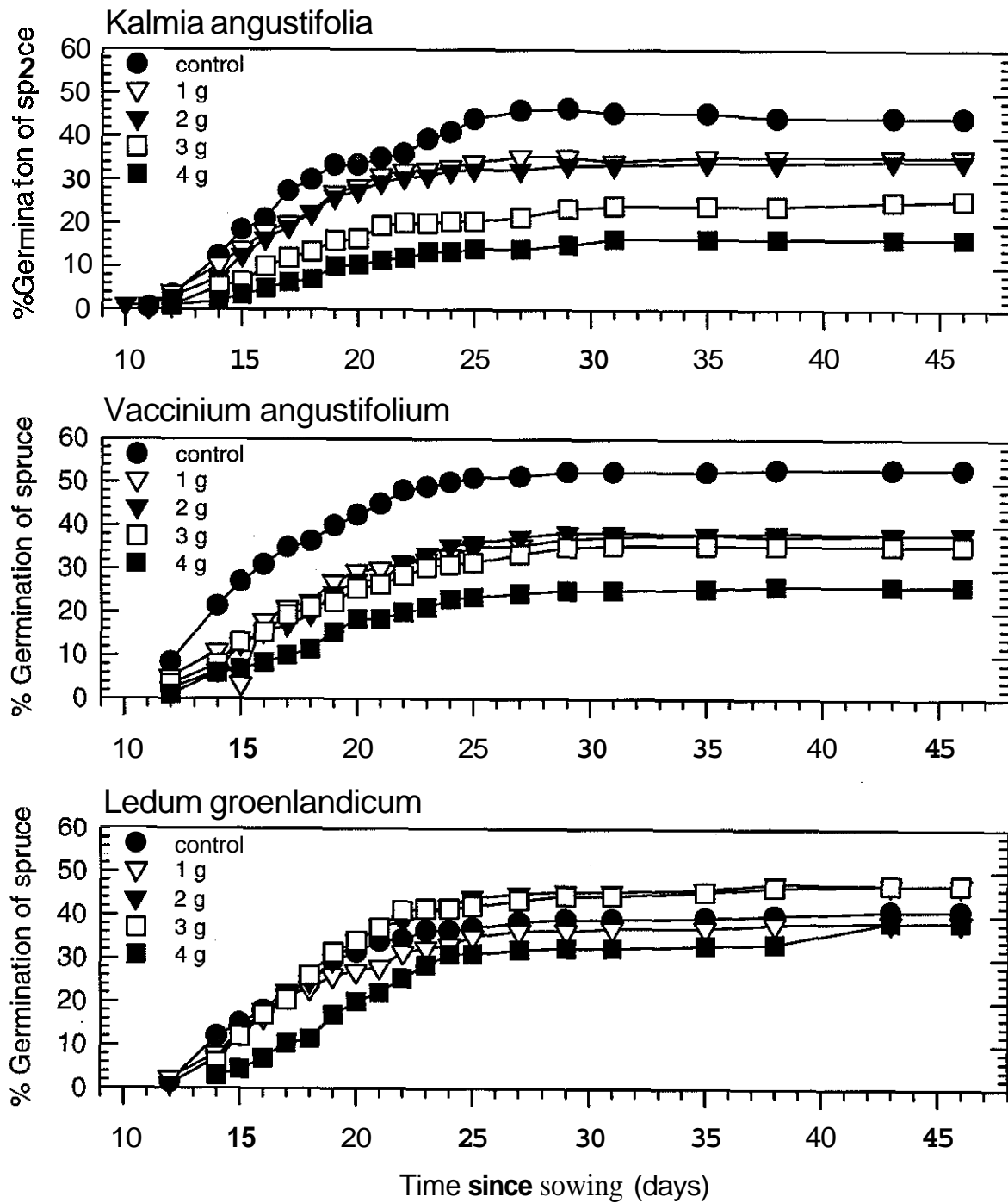


Figure 23. Effect of *Kalmia angustifolia*, *Vaccinium angustifolium* and *Ledum groenlandicum* leaf powder on emergence of *Picea manana* seedlings grown in the greenhouse (after Olsen 1975 Appendix Table 1).

Current season's leaves were air dried and ground finely with a mortar and pestle before being added to the pots. The ground leaf material was spread uniformly over the soil surface after the black spruce seeds had been sown and covered with soil. The experiment was set up in a split plot design with species as the main plot. Each treatment was replicated four times and dosage treatments were randomized within each main species plot. **One** hundred mL of water was added to each pot per watering to provide uniform leaching of the leaf material. The pots were observed for seedling emergence, and once this began daily germination counts were taken for the **first 15 days**, then at 2 day intervals for an additional 20 days, by which time emergence was complete.

Percent emergence over time for the five treatments within each species treatment is presented in Figure 23. The final percent emergence for all treatments is given in Table 13. An analysis of variance was performed on the **final** date of emergence data (Table 14), and shows that dosage treatments within species treatments **were** highly significantly different, but that species effect was not significant. The species treatment interaction was significant at the 5% level.

The **results** indicate that ground leaf litter of both *Kalmia* and *V. angustifolium* inhibited the rate **of** germination and **total** seedling emergence as compared to the control treatment, while that of *L. groenlandicum* did not. With *Kalmia* the degree of inhibition increased with the amount of leaf litter added. The same trend was evident for *V. angustifolium* but the degree of inhibition by the 1, 2 and 3 g treatments did not differ significantly ($P > 0.05$) from each other, although all four litter treatments caused a marked inhibitory effect as compared to the control, with the 4 g treatment producing the greatest amount of inhibition. Seedling emergence in the untreated control treatments was lower for *L. groenlandicum* than for the other two species, and consequently the emergence of black spruce appeared to be less inhibited. However, increased amounts of *L. groenlandicum* ground leaf litter did not lead to as large differences in seedling emergence as with the other two species. Overall, *Kalmia* leaf litter was most inhibitory towards black spruce seed germination, followed by *V. angustifolium* and then *Ledum groenlandicum*.

As in the previous field germination trial (Section 4.2.1), it is interesting to note that *V. angustifolium* was only slightly less inhibitory than *Kalmia* to black spruce seed germination, even though this is not generally perceived to be the case in forestry. The results of both the field and greenhouse trials raise several possibilities: (i) *V. angustifolium* is as allelopathically toxic as *Kalmia* towards germinating black spruce seeds but *V. angustifolium* has not been recognized in the field as being such a strong allelopathic spruce competitor as *Kalmia* because it is not found in such abundance on disturbed forest sites where natural regeneration of spruce has been poor; (ii) any allelopathic effect of *Kalmia* is more from longer-term leaf decomposition products than from leaf throughfall, whereas that of *V. angustifolium* is from throughfall or shorter-term leaf decomposition products (the two leaves are very different in structure); (iii) *Kalmia*-induced inhibition of spruce seed germination in the field is more the result of allelochemicals in the litter from root/rhizome and/or mycorrhizal symbionts than leaf exudates.

The implications for silviculture of this study are simply that the presence of ericaceous leaves alone may inhibit black spruce seed germination. As in the previous section, direct seeding with black spruce on untreated sites with a heavy cover of *Kalmia* (and to a lesser extent *Vaccinium* and *Ledum*) may not be successful because of the potential for germination failure.

4.2.3. Effect of Leaf Extracts of *Kalmia angustifolia* on Growth of Mycorrhizal Fungi: It was hypothesized that water soluble leachates from *Kalmia* leaf litter adversely affect the growth of black spruce seedlings by inhibiting the growth and development of mycorrhizal fungi on the roots of black spruce. To test this hypothesis two studies were carried out. In the first, the roots of *Kalmia* and black spruce and their mycorrhizae from a burned black spruce forest north of Bay Bulls and an unburned *Kalmia*-black spruce forest near Donovan's Overpass were stained and examined. In the second, root fungi from the spruce were isolated and treated with *Kalmia* leaf extracts (Olsen 1975).

In the first study, optimal stain or stain combinations and a staining schedule were determined for producing root

Table 13. Final percent germination of black spruce seeds after 46 days under different amounts of simulated ericaceous leaf litterfall (*after* Olsen 1975, Table 15).

Species	Simulated Ericaceous Litterfall (g powdered leaf)				
	0	1	2	3	4
<i>Kalmia</i>	48.5 ^a	36.0	34.5	25.5	16.5
<i>angustifolia</i>	(5.7)	(5.3)	(2.2)	(3.5)	(3.5)
<i>Vaccinium</i>	53.00	38.00	38.30	35.50	26.00
<i>angustifolium</i>	(1.7)	(5.5)	(2.6)	(3.1)	(4.6)
<i>Ledum</i>	42.00	38.50	47.00	47.00	33.50
<i>groenlandicum</i>	(9.1)	(5.3)	(5.1)	(4.4)	(1.3)

^a Mean of 50 seeds sown per pot in each of four replicates, for a total of 200 seeds per treatment; s.d. in brackets.

Table 14. **Results** of ANOVA on the effect of simulated ericaceous leaf litterfall on percent black spruce seedling emergence (*after* Olsen 1975, Table 16).

source	df	ss	mss	F Values from Statistical Tables		
				Experimental	5%	1%
Species	2	228.40	114.20	2.03	5.14	10.92
Error A	6	336.80	56.13	-	-	-
Treatments	4	795.10	198.78	11.82 ^a	2.63	3.89
Species x trts.	8	292.10	36.51	2.71 ^b	2.21	3.04
Error B	36	605.20	16.81	-	-	-
Total	59	2260.60	-	-	-	-

^a Significant at the 1% level.

^b significant at the 5% level.

sections in which root tissue could be clearly differentiated from any fungus present. Formalin-acetic acid-alcohol (FAA) and Zirkle's reduced chromic fluid were both tested as potential killing and fixing fluids. It was concluded that in combination with a suitable stain, Zirkle's reduced chromic fluid gave the best **results** for differentiating fungi from root tissue cells. After killing and fixing, *Kalmia* root segments were dehydrated in a tertiary butyl alcohol series and embedded in paraffin (Tissuemat) using standard procedures, sectioned at **10** microns, fixed to slides with Raupt's adhesive and deparaffined in xylol. A number of stain combinations were tested on tissue sections killed and fixed in both FAA and Zirkle's fluid, but were not found to give satisfactory results (Safranin-fast green; Safranin, aqueous-picro aniline blue, aqueous; Safranin in cellosolve-picroaniline blue, aqueous; Stoughton's thionin and orange G; Orsellinic BB¹¹; Orsellinic BB and crystal violet, full strength; Simmons and Shoemaker's Pianezze III B; Safranin aqueous-anilineblue in cellosolve). However, other stain combinations were relatively satisfactory and gave good definition of the various tissues in *Kalmia* root sections (Gurr's safranin and picro aniline blue "rapid"; Trypan blue in glacial acetic acid; Sharp's Pianezze III B; Orsellinic BB and crystal violet, diluted ten times). It was concluded that the diluted Orsellinic BB and crystal violet stain gave the best **results** for *Kalmia* roots, following killing and **fixing** with Zirkle's reduced chromic fluid.

Roots were collected from each of the two habitats (a *Kalmia*-black spruce forest and a burned black spruce forest). Roots from 10 plants at each site were sectioned transversely and stained with trypan blue or Orsellinic BB plus crystal violet diluted ten times. Careful examination indicated that the *Kalmia* roots were uniformly **free** from fungal invasion (Fig. 24). One greenhouse-grown plant of *Kalmia* was found with mycorrhizae in one or two small roots, however, and was sectioned, stained and ectotrophic mycorrhizae were positively identified (Figs. 25 and 26).

Black spruce roots collected from the burned black spruce forest site were found to have many roots with mycorrhizae which were evident to the naked **eye**, but some roots were uninfected (Fig. 27). These were sectioned and stained most successfully with Gurr's safranin plus picro aniline blue or Orsellinic BB and diluted crystal violet. In the microscope sections, the mycorrhizal fungus formed a thick, continuous layer surrounding the cortical tissues of the root. The fungal hyphae also penetrated as a **thin** layer between the outer cortical cells to form a network separating the cells from each other (Fig. 28).

In the second study, the hypothesis that *Kalmia* leaf extracts inhibit the growth of black spruce mycorrhizae was tested, using fungi isolated from the roots of black spruce. Pieces of root visibly affected with mycorrhizae were surface sterilized in 3% sodium hypochlorite for **four** minutes, then plated on malt agar. Plates were incubated in darkness at room temperature.

Two species of fungi were isolated. These were tentatively identified by comparison with reference samples¹². One was a species of *Suillus* (possibly *S. granulatus*) which is a genus known to form mycorrhizal associations with black spruce and the other was *Phialocephala dimorphospora*¹³ or *P. fortinii*,

¹² Obtained from Dr. J.A. Fortin, then of the Faculté de foresterie et de géomatique, l'Université Laval, Ste-Foy, Quebec; now Directeur, Institut de Recherche en Biologie Végétale (I.R.B.V.) l'Université de Montréal, 4101 Sherbrooke Est, Montréal, Québec, H1X 2B2.

¹³ Previously known as *Mycelium radialis atrovirens*, which used to refer to a group of sterile, darkly-pigmented fungi commonly isolated from roots and classified with the "Imperfect Fungi" as they were never observed to produce either asexual or sexual fruiting bodies. Conidial stages were eventually observed, and two taxa were identified *Phialocephala dimorphospora* Kendrick, and *P. fortinii* Wang & Wilcox. The term *M.r.a.* was used in the original work (Olsen 1975), and unfortunately it is not possible to determine now which of the two *Phialocephala* species **this** could refer to.

¹¹ Spelling from Windholz, M., ed. 1983. The Merck Index - An Encyclopedia of Chemicals, Drugs and Biologicals (10th edition). Merck & Co., Inc., Rathway, N.J. 1463 pp.; alternate spellings *orseillin* and *oreseillin* can also be found.

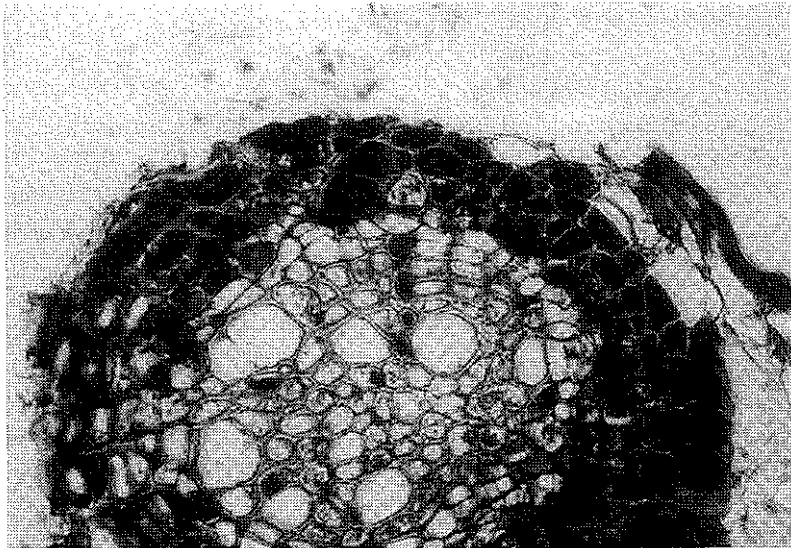


Figure 24. Cross section *Kalmia angustifolia* root (560X). Mycorrhizae absent. Stained with trypan blue (after Olsen 1975, Fig. 8).

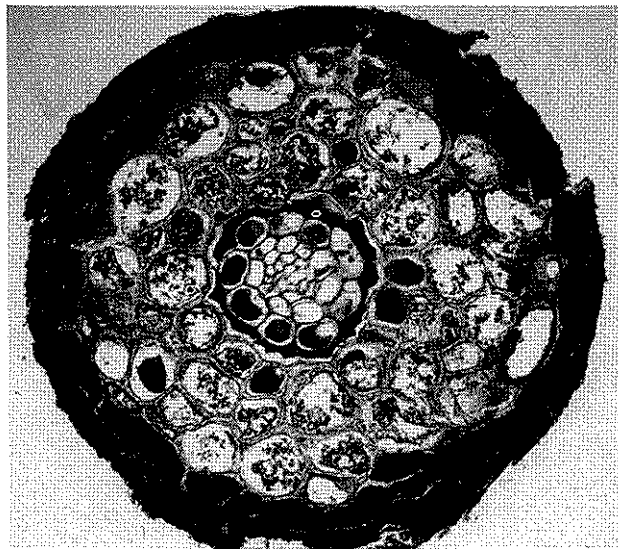


Figure 25. Cross section of *Kalmia angustifolia* root (224X). Mycorrhizae present. Note fungal sheath surrounding root and net between cortical cell walls. Stained with Orsellinic BB plus diluted crystal violet (after Olsen 1975, Fig. 9).

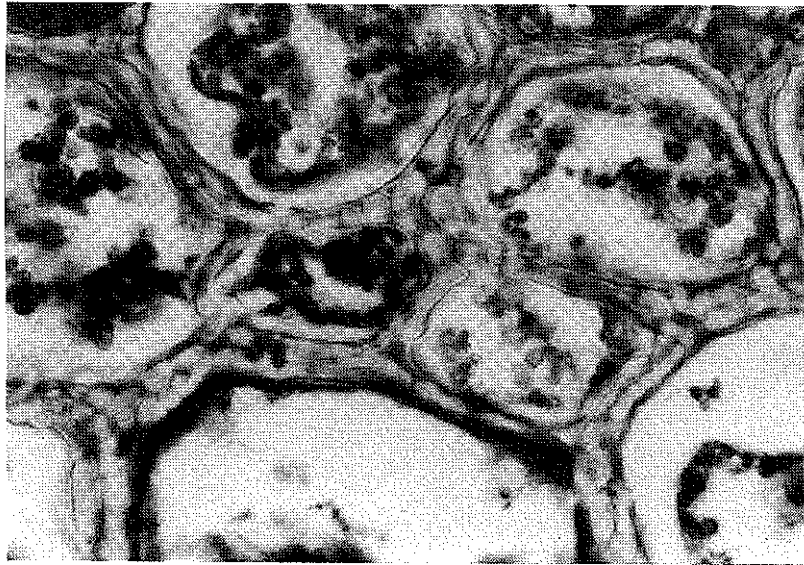


Figure 26. Cross section of *Kalmia angustifolia* root (1400X). Mycorrhizae present. Enlargement of the cortical cell region to show fungal hyphae between the cells. Stained with Orsellinic BB plus diluted crystal violet (after Olsen 1975, Fig. 10).

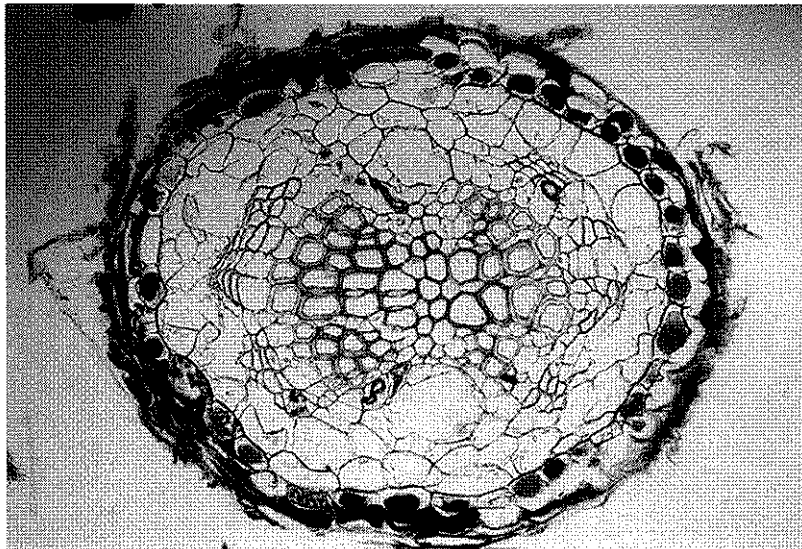


Figure 27. Cross section of *Picea mariana* root (224X). Mycorrhizae absent. Stained with Orsellinic BB plus diluted crystal violet (after Olsen 1975, Fig. 6).

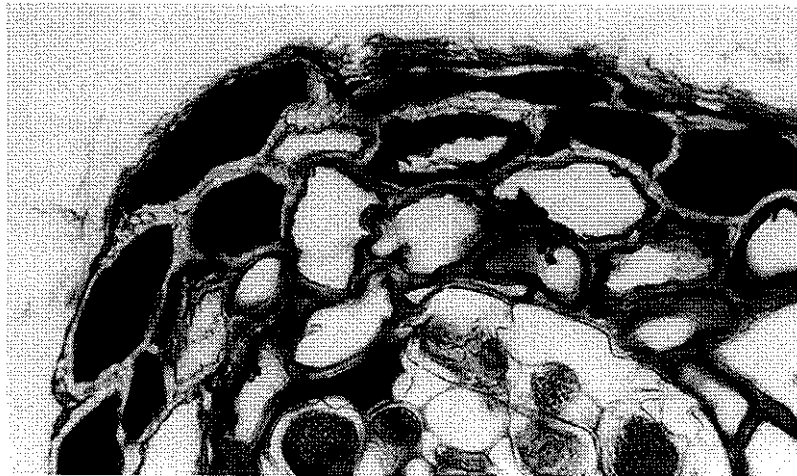


Figure 28. Cross section of *Picea mariana* root (560X). Mycorrhizae present. Note fungal sheath surrounding root and net between cortical cell walls. Stained with Orsellinic BB plus diluted crystal violet (after Olsen 1975, Fig. 7).

ubiquitous inhabitants of **humus** in boreal forests whose symbiotic relationships with plant roots range from pseudomycorrhizal to pathogenic (Wilcox and Wang 1987). Two isolates of *Suillus* (No. 4 and No. 5) and two isolates of *Phiulocephala* (No. 6 and No. 12) were selected for the experiments. Each isolate was cultured on malt agar to which *Kulmia* leaf extract was added.

To obtain the leaf extract, 100 grams of air-dried, finely ground leaves of *Kulmiu* were soaked in 500 mL of sterile distilled water for 16 h, then filtered through a Millipore bacteriological filter. Double strength malt agar (500 mL) was prepared with sterile distilled water and autoclaved. The *Kulmiu* leaf filtrate was added to the malt agar and made up to one litre with sterile distilled water. The **medium** was dispensed into sterile petri plates (about 20 mL in each). A parallel set of plates was prepared from malt agar alone for use as controls.

Nine control plates each of malt agar and **nine** plates each of malt agar plus *Kalmia* leaf extract were inoculated with one of the four isolates (*Suillus* sp. isolates No. 4 and No. 5 and *Phiulocephalus* sp. isolates No. 6 and No. 12) for a total of 72 plates. A 2 mm diameter disc of inoculum was placed in the centre of each plate. The plates were incubated at 18°C in a refrigerated incubator. As soon as growth was evident, **daily** measurements were taken of colony diameters. Two measurements were taken at right angles to each other on each colony and averaged. The plates were inoculated on 12 March and readings were continued until 5 April for the slowest growing cultures.

The measurements taken from the **nine** replicate plates of each treatment on the same day were averaged and results are presented graphically in Figure 29.

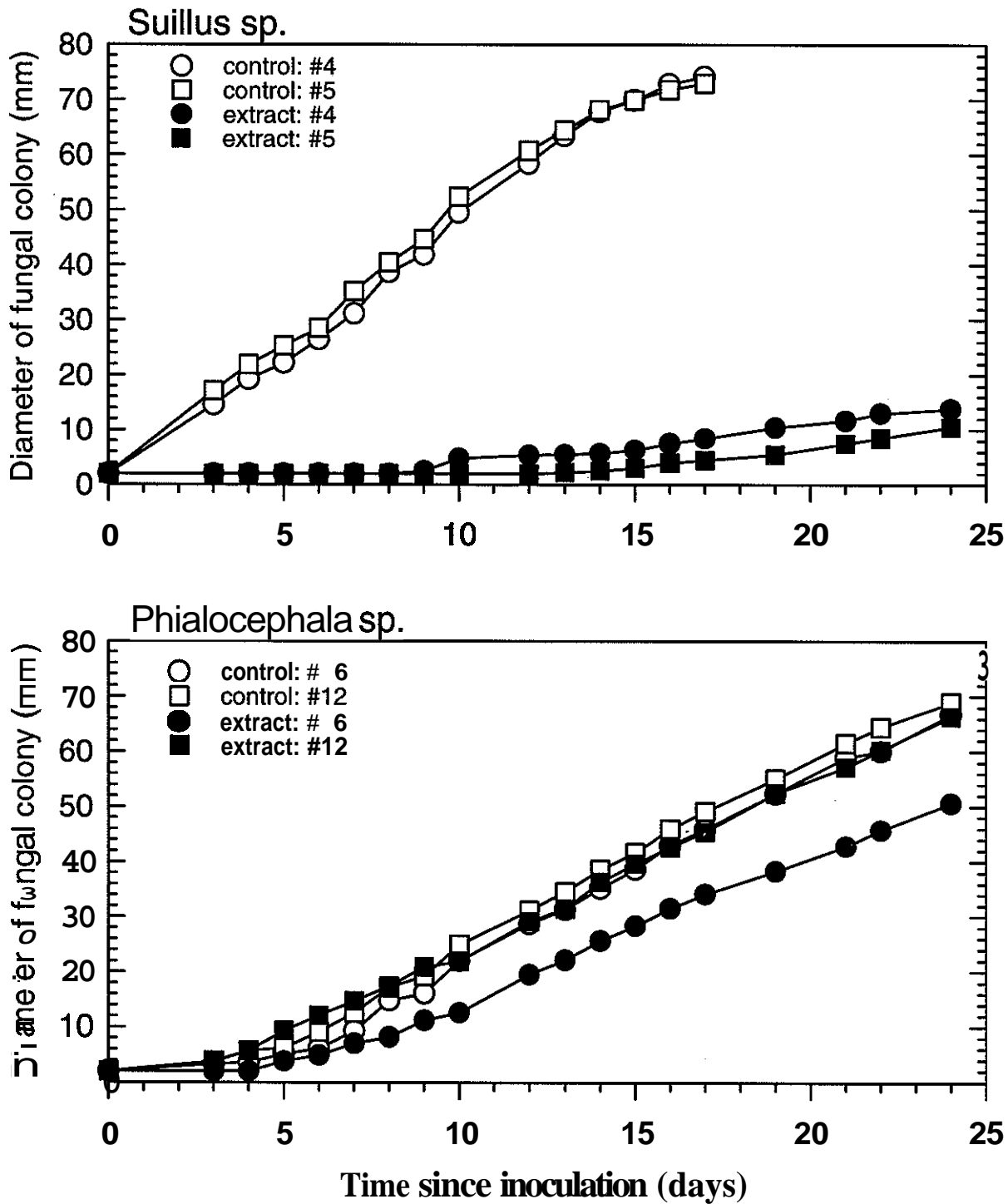


Figure 29. Effect of *Kalmia angustifolia* leaf extracts on the growth of black spruce mycorrhizal fungi (*Suillus* sp. isolates #4 and #5) and a possible root pathogen (*Phialocephala* sp. isolates #6 and #12) (after Olsen 1975, Table 17).

This experiment demonstrated that the *Suillus* sp. isolates No. 4 and No. 5 did not differ from each other in growth rate, but that the growth of both was markedly inhibited by the addition of aqueous leaf extracts of *Kalmia* to the malt agar substrate. Growth was visible soon after inoculation in the control colonies and proceeded steadily until the plates were filled. Visible growth was not evident in the plates containing the *Kalmia* leaf extract until 7 to 13 days had elapsed (Fig. 29) and the rate of growth was much slower compared to the control plates.

The response of *Phialocephala* sp. isolates No. 6 and No. 12 were very different from the *Suillus* sp. isolates in that although the *Phialocephala* sp. isolates did not differ from each other in their rate of growth, the presence of *Kalmia* leaf extract did not affect their growth rate (Fig. 29). The only apparent difference was the production of a distinct band of red colour only in the malt agar plus *Kalmia* substrate, about 2 mm wide and just at the edge of the advancing mycelium.

The results of this experiment can only be regarded as preliminary. However, if *Suillus* is beneficial to the establishment and growth of black spruce seedlings in the field, and if a water soluble substance in the leaf litter of *Kalmia* can affect the growth of *Suillus* under natural soil conditions as it does in culture, then one effect of *Kalmia* on the growth of black spruce may be exerted through the prevention or inhibition of *Suillus* mycorrhizal relationships established by black spruce, which could lead to seedling nutrient and/or water stress. On the other hand, *Phialocephala* species are potential root pathogens. As the growth rate of *Phialocephala* in culture was not affected by *Kalmia* leaf extracts, it may be that the ability of *Phialocephala* to colonize black spruce roots is not decreased by the presence of *Kalmia* in the field. In summary, the possibility exists that at least a proportion of *Kalmia*-induced black spruce "check" occurs by *Kalmia* inhibiting mycorrhizal growth on black spruce while at the same time having no effect on a potential pathogen, or at best pseudomycorrhiza. Further research on mycorrhizae may be more important in leading to a greater understanding of the mechanisms of *Kalmia*-induced "check" than in developing practical operational treatments for dealing with these problem

sites. Although it would be useful if "*Kalmia*-resistant" strains of mycorrhizae could be found that increased spruce growth in the field, a number of important steps must be taken before seedling inoculation becomes operational. At an experimental level these include (i) identification of "*Kalmia*-resistant" strains of mycorrhizae, (ii) production of inoculum for experimental purposes, (iii) long-term evidence that successful inoculation leads to improved survival and growth of black spruce as compared with non-inoculated seedlings in the presence of *Kalmia* in the field, and (iv) identification of which strains of mycorrhizae perform best on which site types, and under what conditions. The operational conditions would then have to be created under which large-scale inoculation could successfully take place, with resultant long-term improved seedling performance in the field. This would best be managed under a larger scale inoculation program in which mycorrhizae were being used to enhance seedling performance in general, and not only on *Kalmia*-dominated sites.

5. CONTROL OF *KALMIA ANGUSTIFOLIA*

Several mechanical and chemical methods to control *Kalmia* have been tested under field and greenhouse conditions with the aim of finding a control method that would be cost effective, efficacious, long lasting (5+ years), environmentally safe and ecologically acceptable. Herbicides, cultivation and scarification are commonly used to control forest weeds. Although 2,4-D effectively controls the aerial stems of *Kalmia* (Engler 1947, 1948), its effect on underground rhizome-bearing vegetative buds has not been studied previously. The following sections summarize field and greenhouse experiments carried out in Newfoundland to examine control methods.

5.1. Field Trial

A field trial was established in 1974 near Gambo Pond, central Newfoundland (Richardson 1975, 1979). The following 7 treatments were randomized and replicated 3 times, and applied to approximately 100 m² plots (10.1 m x 10.1 m):

- i) **SFI patch scarification**¹⁴ (pulled by a D-6 tractor);
- (ii) drag scarification with anchor chain and spiked drums (pulled by a D-6 tractor);
- (iii) herbicide (0.7 kg 2,4-D ha⁻¹);
- (iv) prescribed burn (with furnace oil or fuel sprayed over entire plot);
- (v) herbicide (0.7 kg 2,4-D ha⁻¹) + SFI patch scarification;
- (vi) prescribed burn + SFI patch scarification;
- (vii) control (no treatment).

The plots were assessed in 1974 before and after the treatments were applied, and again in 1976 for black spruce regeneration, density of *Kalmia*, other vegetation cover and percent surface disturbed and exposure of the mineral horizon (Bal 1977). In 1976 three plants from each of three plots per treatment were carefully excavated with their rhizomes intact and the following parameters measured: height of plant, number of leaves, number of flowers, length of rhizome unearthed, number of vegetative buds on rhizomes.

The immediate effects of the treatments two months after application are presented in Table 15. All treatments except burning alone considerably reduced the density of *Kalmia* stems. Burning destroyed all aerial growth but fresh shoots had appeared on the *Kalmia* plants at the time of the survey. All treatments considerably reduced the cover of *Kalmia* with the exception of the SFI patch scarification, where the screening produced by the SFI affected only a proportion of the total soil surface. However, the SFI in combination with burning produced a greater reduction in plant cover than any other treatment. Drag scarification with anchor chains and spiked drums was also partially effective in reducing plant cover. Naturally regenerated black spruce were present on the site, and these were also affected by the treatments. However, these natural seedlings were shorter than the ericaceous cover (<30 cm in height) even though they were up to 20 years old, and the aim was not to enhance this natural regeneration but to control *Kalmia* and then plant and seed the treatment plots with black spruce.

¹⁴ A variety of patch scarifiers are available, and the SFI is very similar to models produced by Leno and Bräcke.

The differences in soil disturbance produced by the two scarification treatments is evident in Table 15. The anchor chains did not expose appreciably more mineral soil than the SFI, yet caused more than twice as much surface disturbance because most of the organic mantle was scraped off and deposited in uneven piles elsewhere across the treatment plots.

Results of the 1976 field survey, carried out two years after treatment, are summarized in Table 16. The SFI patch scarification treatment seemed to be effective in controlling *Kalmia* around the planting microsite. In all other cases regeneration of new *Kalmia* plants was apparent. Even in herbicide treated plots vigorous new growth was observed, with the plants having healthy, abundant leaves and profuse flowering. However, bialophos has recently shown some promise in controlling *Kalmia* in the field, with virtually no stems resprouting after up to two years in some treatments (Jobidon 1991).

Overall, this present field trial demonstrates the difficulty of controlling *Kalmia* operationally, although the site was extremely poor in quality, and heavily invaded by *Kalmia*. However, the trial does emphasize the importance of good scarification in providing *Kalmia*-free planting microsites (cf. Section 3.1). The relatively light burns produced in this trial were not beneficial, but this does not necessarily preclude the use of fire as a potential control mechanism, especially if burns are deep enough to kill *Kalmia* rather than stimulate vegetative reproduction. At the same time, a deep burn could also seriously reduce the nutrient capital of the site through destruction of the humus layer, and operational prescribed burning should be preceded by an experimental burning program. As *Kalmia* has a waxy cuticle, application of herbicides dependent on foliar uptake for their action are not likely to be as successful as herbicides that are taken up by roots. However, as the use of herbicides in forestry is decreasing nationally as regulations become more restrictive, and as only glyphosate is presently registered for forestry use in Newfoundland, it is unlikely that chemical control methods will offer a long-term operational treatment, but for legislative rather than biological reasons.

Table 15. Effects of control treatments on *Kalmia angustifolia*, natural black spruce regeneration and remaining vegetation two months after treatment application at Gambo Pond, central Newfoundland (after Richardson 1975, Table 1).

Treatment	<i>Kalmia</i>				Black Spruce Regeneration				Other Vegetation		Scarification	
	stems m ⁻²		Percent cover		Percent stocking		stems ha ⁻¹		% Cover		% Exposed mineral soil	% Surface disturbance
	before	after	before	after	before	after	before	after	before	after		
SFI	874	279	64	31	60	47	4250	3 000	19	20	13	32
Anchor chains	810	182	63	11	60	28	3800	1300	19	5	16	78
Herbicide	715	22A	57	12	65	68	5225	5950	23	13	-	-
Burning	835	1042	51	19	53	1	3 275	25	24	12	-	-
Herbicide + SFI	688	176	52	16	66	69	4875	4350	23	15	17	36
Burning + SFI	858	505	48	5	54	1	3600	25	23	3	8	40

Table 16. Mean number and size of aerial and subterranean portions of *Kalmia angustifolia* two years after application of control treatments at Gambo Pond, central Newfoundland (*after* Bal 1977, Table 1).

Treatment	Height (cm)	No. of leaves	No. of flowers	Rhizome length	No. of buds on rhizomes	Comments
SFI	0	0	0	0	0	no <i>Kalmia</i> growing; a few blueberries 10 cm in height
Anchor chains	28	22.6	2	70	0.7	few plants, most without flowers
Herbicide	70	33	30	50	0.7	abundant new growth from rhizomes, plants vigorous, flowering profusely
Burning	12	13	3	>40	2.3	all plants fairly short, abundant dead <i>Kalmia</i> shoots about 1% in flower
Herbicide + SFI	52.5	40	2	> 134	2.4	plants tall with abundant foliage
Burning + SFI	11	59	1	> 50	0	plants small, a few blooms
Control	15	38	3	49	0	plants abundant, not many flowers, more organic matter (lichens, etc.)

Table 17. Number and size of aerial and subterranean portions of *Kalmia angustifolia* 85 days after application of control treatments in a greenhouse experiment (*after* Bal 1977, Table 2, p. 7).

Treatment	Number of plants	Average height (cm)	Rhizome length (cm)	Number of Vegetative Buds		Total no. of vegetative buds
				Below ground	Above ground	
Control	8	27	16	8	5	13
Lime	9	29	40	7	4	11
Decapitation	10	-	18	-	12	12
1% 2,4-D	8	-	40	0	0	0
2% 2,4-D	9	-	56	5	0	5
3% 2,4-D	12	-	30	0	0	0
Shade	10	18	48	-	1	1

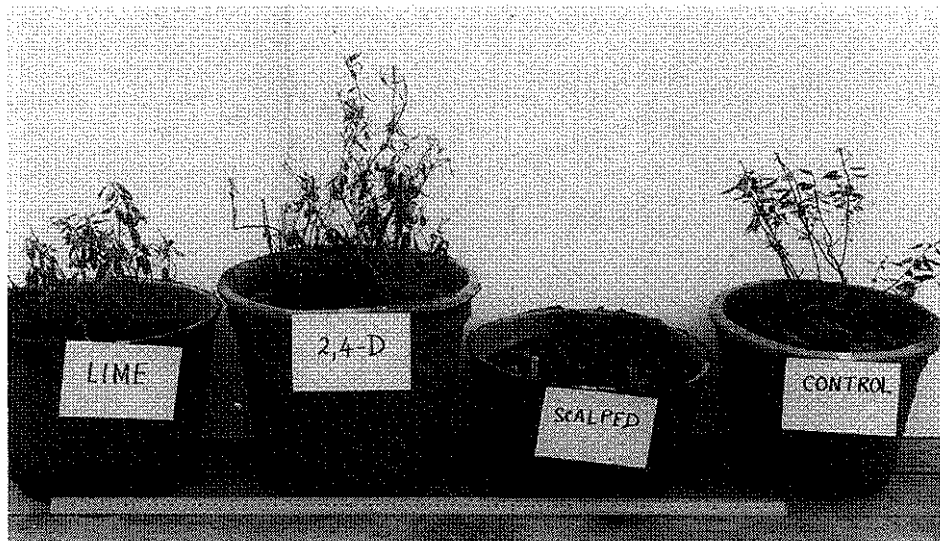


Figure 30. Samples from a greenhouse experiment showing **l**ied, 2,4-D treated, decapitated and control pots after **e**ight months. New regeneration **o**f buds occurred in decapitated pots **a**s well as in the 2,4-D treated pots (*after* Bal 1977, Fig. 1).

5.2 Greenhouse Experiment

Healthy *Kalmia* plants were collected from the Gambo Pond field trial (Section 5.1) on 20 July 1976 and potted in their original soil in 45 cm diameter pots (Bal 1977). The plants were allowed to acclimatize for 10 days until 30 July 1976 in a greenhouse. Eight to 10 plants were selected for each of the following treatments:

- (i) control (normal light, over $53.82 \text{ kcd sr m}^{-2}$)¹⁵;
- (ii) shade ($4.3 \text{ kcd sr m}^{-2}$);
- (iii) decapitation (all aerial shoots removed);
- (iv) lime (plants potted in 1:1 mixture of soil and agricultural lime);
- (v) 1% 2,4-D¹⁶ (sprayed until the leaves were wet);
- (vi) 2% 2,4-D;
- (vii) 3% 2,4-D.

After 85 days the plants were excavated and various parameters including the number of vegetative buds recorded.

The results of the greenhouse experiment are summarized in Table 17. Liming of the soil did not visibly affect the plants. Some of the leaves turned brown due to accidental contact with lime, but in general the plants were healthy. Even after eight months plants showed no appreciable differences from the control treatment (Fig. 30). Mature *Kulmiu* plants seem to be tolerant of high pH values and even produced several vegetative buds. The initial pH of soil leachate after mixing with lime was 12, but within three weeks the pH dropped to 6.7 and remained constant at that level under normal watering conditions. Even if effective, the costs of operationally liming at rates required to alter pH would likely be prohibitive.

Decapitation of aerial shoots was found to initiate more vegetative bud formation overall than the other

treatments, but not the control (Table 17). However, all the buds were above ground, with some originating from the base of the cut shoots, while others originated from horizontal rhizomes. In a similar greenhouse experiment, Mallik (1991) also concluded that decapitation, or cutting above-ground stems, with or without burning, were not effective methods for controlling *Kulmiu*.

The 1%, 2% and 3% concentrations of 2,4-D showed equal effectiveness in killing the aerial parts of *Kalmia* (Table 17) which turned brown in 2-3 weeks and ultimately dried off. Some vegetative buds may have withstood or perhaps never were in contact with the herbicide, as new shoots were observed in all 2,4-D treated pots after eight months. This greenhouse study thus mirrors the results of the field trial for herbicide treatments. Although it is clear that 2,4-D can be a potent killer of the shoots of *Kalmia* plants, the regeneration of new buds can still take place after treatment. It is thus evident that some rhizomatous tissue can remain viable after treatment and later produce buds, and for chemical control to be effective it is essential that all regenerative tissue be killed. For the reasons given earlier, it is unlikely that herbicide applications will provide a long-term operational control treatment for *Kalmia* in Newfoundland.

Low light intensity was found to inhibit vegetative bud production. However, the effect was not absolute at $4.3 \text{ kcd sr m}^{-2}$, as some buds were produced. While this could reflect the nutritional status of the plants, the 2,4-D treated plants (where the tops had browned off) also showed similar effects. Since the decapitated plants produced more buds, the inhibition of bud development may not be directly linked to the photosynthetic efficiency of the aerial shoot. Some hormonal mechanism may be involved in bud production in the rhizome. This hypothesis is substantiated by the earlier histological studies of the rhizome (Section 3.3) in which stored food reserves in the rhizome were observed which could be mobilized when required for new bud development. Regardless of the mechanism involved, the reduction in bud production under low light intensity is consistent with the observation in the field that there are fewer *Kalmia* stems under mature closed forest canopies than in direct sunlight (Section 3.1). Two silvicultural implications can be inferred from this. First, thinning in stands when *Kulmiu* is present should be avoided, so that

¹⁵ Where 1 foot candle = 10.764 lux (Ix); 1 lux = 1 lumen m^{-2} (lm m^{-2}) = 1 candela steradian m^{-2} (cd sr m^{-2}); lighting for the two treatments were originally reported as (i) over 5,000 ft. candles, and (ii) 400 ft. candles.

¹⁶ Concentrations of 2,4-D were higher than the recommended dose for forestry use.

Kalmia spread within the stand is minimized. This should help to minimize the further spread of *Kulmiu* once the stand is harvested. Secondly, consideration should be given to ways of achieving canopy closure in the next rotation as quickly as possible so that natural shading will reduce the spread of *Kulmia*. Silvicultural alternatives for achieving early canopy closure include: (i) planting as soon as possible after harvesting; (ii) planting the largest stock possible; (iii) planting either just *Kalmia* patches or whole sites at higher densities; (iv) spot fertilizing seedlings a year or two after planting once seedlings have become established, although application of fertilizer early on may necessitate further applications at a later date if nutrient deficiencies arise before canopy closure is reached.

6. SUMMARY AND CONCLUSIONS

Information presented in this report describes the phytosociological associations of *Kalmia angustifolia* in Newfoundland. The species tolerates a wide range of moisture and nutritional gradients, and can be found in heaths, peatlands, forests and swamps. The shrub is semi-deciduous, with the previous year's leaves supplying photosynthates and nutrients to current growth through translocation.

Vegetative reproduction is the principle method of regeneration on forested sites and on disturbed sites with intact humus layers. Regeneration takes place through the extensive growth of rhizomes through the humus layer, and also through the development of adventitious buds on rhizomes. Flowering is greatly reduced on plants growing in mature forests, where they occur in canopy openings. *Kalmia* can produce 15 to 160 million seeds per hectare, but up to 45% of these seeds may not be viable. Light is required for seed germination, and no plants of seed origin were found on forested sites. *Kulmiu* seeds do not germinate on humus in forest stands or on cutovers, but do germinate on exposed mineral soil surfaces on cutovers, under which conditions most *Kulmiu* regeneration takes place through seed germination. The vegetative buds of *Kulmiu* are further described in a histological study.

Kulmiu can inhibit black spruce growth through a combination of nutrient and allelopathic competition. *Kulmiu* can function under low nutritional conditions,

but can respond to increased availability by taking up proportionately more nutrients (especially nitrogen), and by concentrating these in important tissues. This shrub is thus able to survive on sites across a wide nutritional range.

Black spruce seeds were found to germinate best in field plots with *Kulmiu* plants removed and the humus and mineral soil mixed, although removal of *Kalmia* plants and humus without mixing also increased seed germination rates. In a laboratory study, powdered *Kulmia* leaves inhibited black spruce seed germination. Further, aqueous extracts of the leaves of *Kalmia* were found to be inhibitory to isolates of *Suillus*, a mycorrhizal fungi, but not to *Phiulocephulu*, a pseudomycorrhiza or root pathogen.

From field and greenhouse studies it is apparent that there are no easy methods of controlling *Kulmia*. Light burns, drag scarification, and herbicides were ineffective in the field, where only patch scarification prevented spread of *Kalmia* into exposed mineral soil. Likewise, decapitation, liming and treatment with herbicides did not kill *Kulmiu* in a greenhouse experiment. However, shading did inhibit vegetative bud production.

Although this work is not exhaustive, is a compilation of smaller studies rather than a complete study in itself, and contains mostly ecological studies, a number of silvicultural recommendations and comments can be made. However, these recommendations are based solely on the experimental results presented, and are therefore not complete or exhaustive. The recommendations are listed below, ordered by the section of the report from which they are drawn:

1. Site preparation treatments that remove foliage but do not kill rhizomes (e.g. herbicides, light burns) will only temporarily reduce *Kalmia* growth, and then only if defoliation is virtually complete (Section 2.2.1 cf. Sections 5.1, 5.2);
2. Trenching or similar mechanical site preparation treatments should not only improve the seedling planting microsite in general, but should prevent *Kulmia* spread by rhizomes across strips of exposed mineral soil exposure, at least in the short-term (Section 3.1 cf. Section 5.1). Making two passes at

90 degrees to produce a "checkerboard" pattern may further restrict *Kalmia* spread, but will double site preparation costs. As the humus layer represents an accumulation of nutrient capital, more radical humus removal (blading; C&H plough) should only be used on richer sites where the mineral horizons are capable of supplying adequate nutrients to seedlings. In all cases, planting in the "hinge" position at the humus-mineral interface is recommended, unless local experience suggests otherwise. However, as *Kalmia* has the potential to re-invade bare mineral soil by seed in the long-term (Section 3.1, 3.2.1, 3.2.4), older scarified sites should be monitored to determine if invasion of *Kalmia* by seed has a detrimental effect on plantations.

3. Seeding with black spruce should only take place after scarification, preferably using techniques that mix the mineral and humus horizons (Section 4.2.1)
4. Planting seedlings adjacent to *Kalmia* even on scarified sites should be avoided wherever possible, as *Kalmia* leaf leachates may inhibit beneficial mycorrhizal symbionts (Section 4.2.3).
5. Light burning will not control *Kalmia* (Section 5.1). However, it may be that heavier prescribed burns that kill underground rhizomes could be used to control *Kalmia*, so long as sites are not nutritionally impoverished to an unacceptable level in the process. The fact that *Kalmia* and black spruce have co-existed since glaciation and yet extensive naturally occurring *Kalmia* heaths do not seem to have arisen on previously forested sites in central Newfoundland as a result of natural forest fires alone suggests that wild fire plays an important role in succession that has largely been eliminated through fire suppression activities but that could possibly be reintroduced through the use of prescribed burning.
6. Herbicides must kill underground rhizomes and reproductive tissue and not just above-ground parts in order to be effective (Sections 5.1 and 5.2 cf. Section 2.2.1). The potential for use of herbicides must be weighed against long-term registration concerns.
7. Liming and cutting of above ground stems will not control *Kalmia* (Section 5.2 cf. Section 2.2.1).

8. Mechanical scarification can control the spread of *Kalmia*, at least in the short-term (Section 5.1 cf. Section 3.1).

9. Silvicultural treatments to achieve canopy closure as soon as possible so that *Kalmia* is suppressed by shading (Section 5.2) should be applied. Consideration should be given to some combination of: (i) planting as soon as possible after harvesting; (ii) planting the largest stock possible; (iii) planting either just *Kalmia* patches or whole sites at higher densities; (iv) spot fertilizing seedlings once they have become established, although further fertilizer applications may be required to reach canopy closure. Conversely, thinning should not be carried out where *Kalmia* is present in the understory, especially on poorer quality sites.

Regardless of which silvicultural options are chosen, consideration should be given to the quality of the site to be treated: a poor site, even if *Kalmia*-induced problems are overcome, will still be a poor site. Future wood hauling costs (distance from site to pulp and sawmills) as well as treatment application costs themselves should be given consideration. A medium or even poorer quality site adjacent to a mill may warrant more investment than a good site that is far from a mill.

7. ON-GOING AND FUTURE RESEARCH

Since the completion of the contracts (Olsen 1974, 1975; Bal 1977) and the studies summarized in this report, further research has been carried out on *Kalmia* in the Newfoundland and Labrador Region. Topics studied to date include further laboratory and greenhouse work on the allelopathic relationship between *Kalmia* and black spruce germinants and seedlings (Mallik 1987, 1992; Zhu and Mallik 1994) and mycorrhizae, and relationships between *Kalmia* and balsam fir (Thompson and Mallik 1989) and red pine (Mallik and Roberts 1994). Autecological relationships of *Kalmia* (Mallik 1994) and its vegetative reproduction (Mallik 1993) have been surveyed in the field. The response of *Kalmia* to control measures such as herbicides, burning and mulching (Mallik 1990) have been studied in the greenhouse. A major field trial was established to test scarification, herbicide and fertilizer effects on *Kalmia*

and three softwood species (Titus and Meades 1988). In order to **quantify** the amount of disturbed sites dominated by Kulmiu in central Newfoundland, remote sensing techniques using air-borne and satellite imagery (Gillespie *et al.* 1993; Titus *et al.* 1993; Franklin *et al.* 1994a,b) are being developed. Work has also been carried out on the biochemical changes in Kulmiu foliage in response to environmental stress (Zhang 1993; Titus *et al.* 1993). Studies on Kalmiu **leaf** litter decomposition, soil nitrogen availability through the growing season in the field, and on humus decomposition processes are on-going.

Although the research carried out on Kulmiu in the Newfoundland and Labrador Region over the past 30 years has led to a much greater understanding of its ecology, practical solutions for achieving good rates of black spruce growth on some *Kalmia*-dominated sites are still lacking. As these sites are largely of poor to medium quality, large financial investments in reforestation techniques are not warranted, and further research in mulching, fertilization and liming are unlikely to be practical because even if they proved successful they would increase reforestation costs substantially. Likewise, with the continuing reduction in the operational **use** of herbicides across Canada it is unlikely that eradication of *Kalmia* by chemical means, including the **use** of biologically produced toxins (e.g. Jobidon 1991) will ever become wide-spread in Newfoundland where only glyphosate is presently licensed for forestry use. Although there is evidence for allelopathic suppression of black spruce mycorrhizae in the greenhouse (Zhu and Mallik, unpublished data) and the field (S. Yamasaki¹⁷, unpublished data), further research along this line is only warranted within the larger context of the application of mycorrhizal inoculation for reforestation in Newfoundland in general. While mycorrhizal research may increase understanding of the mechanisms of *Kalmia*-black spruce interactions it is unlikely to have a major impact on reforestation programs **unless** mycorrhizal strains that improve spruce growth in the field in the long-term can be operationally produced and applied to seedlings.

Economic reforestation prescriptions could include scarification followed by seeding, and therefore more research on this combination of treatments is warranted. In particular, the use of alternate species to black spruce such as jack pine or eastern larch may increase site productivity, although at the moment these are not considered desirable pulpwood or sawlog species within the province. As much of the Kulmia problem may be nutritional in nature, the use of conifer mixtures or the addition of birch or nitrogen-fixing alders may go some way towards increasing softwood productivity. In these cases, a series of long-term field trials are required, with appropriate in-depth scientific investigations. As Kulmiu is a fire-adapted species, research on fire ecology and prescribed burning is also warranted.

Routine description of site types is a pre-requisite for the accurate and consistent application of silviculture prescriptions. Although the present ecological classification system for Newfoundland (Meades and Moores 1989) describes successional pathways following disturbance, further work is needed to help operational foresters determine **the** quality of disturbed sites, and to consistently identify them in the field. This will require research on the succession of Kulmiu following disturbance, and on the effect of Kulmia on the growth and yield of stands of black spruce.

Operational foresters ultimately require a methodology by which problem sites can be identified and prioritized for reforestation investments based on predicted site productivity, and future timber supply requirements. Even more importantly, forest managers need to be able to predict **before** disturbance which stands will become problem sites following harvesting, so that pre-harvest silvicultural prescriptions can be made. As it is generally the poorer sites on which *Kalmia* is most problematic there must be a threshold level below which harvesting is not economical, not because the volume of timber cannot be extracted economically, but because the costs of reforesting poor sites once Kulmia is well established become prohibitive. Forest inventory, harvesting and reforestation concerns must be addressed together, as only then can forest management proceed in full confidence of being able to rationally **assure** an adequate level of reforestation and subsequent tree growth on these problem sites.

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¹⁸ Square brackets indicate that pages not numbered in original.

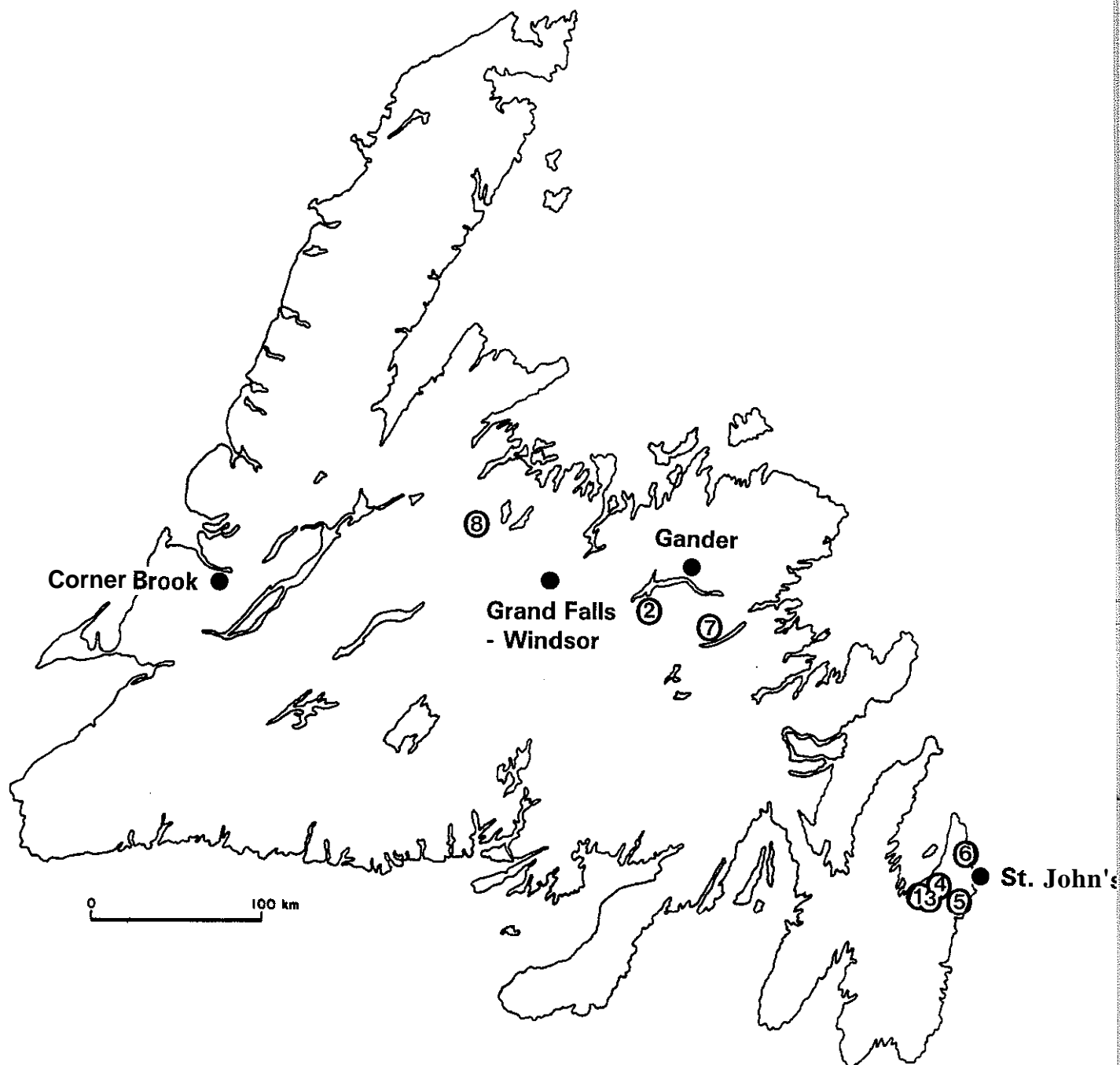
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APPENDICES

Appendix I. Location of *Kulmiu angustifolia* study sites and sampling locations.



Site 1: Butterpot Park
Site 2: southwest Gander watershed
Site 3: Foxtrap
Site 4: Donovan's Overpass

Site 5: Bay Bulls
Site 6: Logy Bay
Site 7: Gambo Pond
Site 8: Crooked Bog

Appendix I. Location of *Kalmia angustifolia* study sites and sampling locations (Concl'd.)

Section Number	Study site and sampling location	Section Number	Study site and samuline location
2.2.1	Role of previous season's leaves on growth: field trial near eastern border of Butterpot Park, Avalon Peninsula (Site 1: 47°24'N 53°02'W)	3.3	Vegetative reproduction in <i>Kalmia angustifolia</i> : <i>Kalmia</i> samples from Gambo Pond field trial (Site 7: 48°39'N 54°29'W)
3.1	Age structure of <i>Kalmia angustifolia</i> populations in a forest and on an adjacent cutover: field sampling on southwest Gander watershed strip cutting experiment (Site 2: 48°48'N 54°55'W)	4.1	Inhibition of black spruce regeneration by <i>Kalmia angustifolia</i> : Nutrient competition: plant samples from Crooked Bog, near Badger (Site 8: 49°08'N 56°07'W)
3.2.1	Kalmia fruit and seed production in a forest and on an adjacent cutover: field sampling on southwest Gander watershed strip cutting experiment (Site 2: 48°48'N 54°55'W)	4.2.1	Black spruce seedling germination and growth in a Kalmia-dominated stand: field tial established on burned black spruce forest site north of Bay Bulls (Site 5: 47°24'N 53°37'W)
3.2.2	Kalmia fruit and seed production over a range of habitats: seven habitats near St. John's Foxtrap (Site 3): exposed heath (47°25'N 53°01'W), sheltered heath (47°26'N 53°00'W), basin bog hummock (47°25'N 53°02'W) Donovan's Overpass (Site 4): dwarf shrub bog (47°32'N 52°51'W), <i>Kalmia</i> - <i>Vaccinium</i> heath (47°32'N 52°51'W), <i>Kalmia</i> -black spruce forest (47°30'N 53°06'W) north of Bay Bulls (Site 5): burned black spruce forest (47°24'N 53°37'W)	4.2.2	Black spruce seedling germination and growth in ericaceous litter: soil samples from burned black spruce forest site north of Bay Bulls, near St. John's (Site 5: 47°24'N 53°37'W)
		4.2.3	Effect of leaf extracts of <i>Kalmia angustifolia</i> on mycorrhizal fungi: <i>Kalmia</i> and black spruce root samples & burned black spruce forest site north of Bay Bulls, near St. John's (Site 5: 47°24'N 53°37'W), and <i>Kalmia</i> -black spruce forest near Donovan's Overpass (Site 4: 47°30'N 53°06'W)
3.2.3	Kalmia seed germination in the laboratory: <i>Kalmia</i> seed from southwest Gander watershed strip cutting experiment (Site 2: 48°48'N 54°55'W); <i>Kalmia</i> seed from Logy Bay, near St. John's (Site 6: 47°38'N 52°40'W)	5.1	Control of <i>Kalmia angustifolia</i> : field trial: re-measurement of Gambo Pond field tial (Site 7: 48°39'N 54°29'W)
3.2.4	Kalmia seed germination in the field: field trial established on southwest Gander watershed strip cutting experiment (Site 2: 48°48'N 54°55'W)	5.2	Control of <i>Kalmia angustifolia</i> : greenhouse trial: plants collected from Gambo Pond field trial (Site 7 48°39'N 54°29'W)

Appendix II. Total nutrient content of biomass of ericaceous species from three bog communities on Crooked Bog, Badger expressed on an area (mg m^{-2}) basis (in Olsen 1974, Appendix Table 1, after Pollett 1972).

Nutrient content (mg m^{-2})	Species	Plant Community		
		<i>Kalmia-Sphagnum</i>	<i>Betula</i>	<i>Lonicera-Rosa</i>
N	<i>Kalmia angustifolia</i>	483.73	158.01	114.49
	<i>Ledum groenlandicum</i>	627.40	312.02	598.08
	<i>Kalmia polifolia</i>	164.77	16.53	128.02
	<i>Andromeda glaucophylla</i>	357.25		
P	<i>Kalmia angustifolia</i>	36.67	3.77	5.02
	<i>Ledum groenlandicum</i>	48.87		36.67
	<i>Kalmia polifolia</i>	10.46	0.71	4.74
	<i>Andromeda glaucophylla</i>	79.87	4.33	-
K	<i>Kalmia angustifolia</i>	70.81	14.03	5.42
	<i>Ledum groenlandicum</i>	117.79	62.67	29.09
	<i>Kalmia polifolia</i>	31.50	1.75	11.12
	<i>Andromeda glaucophylla</i>	309.52		-
Ca	<i>Kalmia angustifolia</i>	71.87	29.19	16.97
	<i>Ledum groenlandicum</i>	157.45	100.51	160.56
	<i>Kalmia polifolia</i>	49.97	1.74	18.94
	<i>Andromeda glaucophylla</i>	600.83		
Mg	<i>Kalmia angustifolia</i>	41.84	6.22	7.71
	<i>Ledum groenlandicum</i>	27.01		77.04
	<i>Kalmia polifolia</i>	13.59	2.96	10.21
	<i>Andromeda glaucophylla</i>	140.70	8.75	-
Mn	<i>Kalmia angustifolia</i>	20.77	2.16	
	<i>Ledum groenlandicum</i>	16.43	10.60	44.08
	<i>Kalmia polifolia</i>	4.97	0.39	10.21
	<i>Andromeda glaucophylla</i>	43.07		
Fe	<i>Kalmia angustifolia</i>	8.21	0.47	1.25
	<i>Ledum groenlandicum</i>	6.20		9.81
	<i>Kalmia polifolia</i>	0.87	0.65	1.20
	<i>Andromeda glaucophylla</i>	14.08	1.05	
Na	<i>Kalmia angustifolia</i>	89.58	13.17	61.30
	<i>Ledum groenlandicum</i>	87.61	49.87	157.49
	<i>Kalmia polifolia</i>	24.90	1.93	43.95
	<i>Andromeda glaucophylla</i>	184.42		
Zn	<i>Kalmia angustifolia</i>	3.46	0.55	0.77
	<i>Ledum groenlandicum</i>	7.08	2.12	7.96
	<i>Kalmia polifolia</i>	1.27	0.08	0.60
	<i>Andromeda glaucophylla</i>	8.92		