CHLOROSIS IN PLANTED WHITE SPRUCE AT LIMESTONE LAKE, ONTARIO

R.D. WHITNEY and V.R. TIMMER1

GREAT LAKES FOREST RESEARCH CENTRE

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1Professor of Forest Soils Faculty of Forestry University of Toronto 45 St. George Street Toronto, Ontario M5S 1A1.

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Great Lakes Forest Research Centre
Canadian Forestry Service
Department of the Environment
P.O. Box 490
Sault Ste. Marie, Ontario
P6A 5M7

ABSTRACT

A severe chlorosis that developed in 1977, some 10 years after white spruce (Picea glauca [Moench] Voss) were planted at Limestone Lake, Ontario, was related to severe drought periods in 1975 and 1976. In these two years unusually dry conditions prevailed during May, when precipitation was only 17% and 13% of normal. After a return to normal moisture conditions, the chlorotic trees regained their green color, although some chlorosis remained. None of the most severely chlorotic trees in 1977 had died by 1980. Heavy mortality of fine feeder roots, probably resulting from the water deficit, was directly related to nitrogen deficiency in the needles. Fertilizing of affected trees in 1977 did not improve needle color or N-content of needles over controls, an indication that there was no N deficiency in the soil. Above-average incidence of Armillaria root rot, excessively deformed roots, unsuitable seed provenance, frost killing of new shoots, aphid-like damage, brown spots of unknown cause in the inner bark, and some nematode species, may also have contributed to the chlorosis.

RESUME

En 1977, une grave chlorose attaquait les épinettes blanches (Picea glauca [Moench] Voss) plantées au lac Limestone (Ontario) quelque dix ans auparavant; la situation a été attribuée à l'intense sécheresse des années 1975-1976. Au cours de ces deux années, le mois de mai avait été particulièrement sec, les précipitations n'ayant été que de 17 et de 13% du volume habituel. Au retour des conditions normales d'humidité, les arbres ont repris leur couleur verte, bien que la maladie ait laissé encore des traces. Aucun des arbres les plus touchés en 1977 n'était mort en 1980. La perte d'un grand nombre de radicelles, sans doute à cause de la sécheresse, a été directement La fertilisation des arbres attribuable à une carence en azote dans les aiguilles. malades en 1977 n'a pas entraîné une amélioration de la couleur ni une augmentation de la teneur en azote des aiguilles, après comparaison avec le groupe témoin. Ce résultat montre qu'il y avait suffisamment d'azote dans le sol. D'autres facteurs ont pu contribué à la propagation de cette maladie: l'incidence plus élevée que la normale du pourridié-agaric, la déformation excessive des racines, un mauvais choix dans la provenance des graines, le gel des nouvelles pousses, les dommages causés par les pucerons, la présence (de cause inconnue) de taches brunes dans l'écorce interne et certaines espèces de nématodes.

ACKNOWLEDGMENTS

The assistance of H.E. Foster in providing disease records on the plantations and in reviewing literature, of B.E. Smith in obtaining feeder roots from the plantations and analyzing them, and of M.J. Applejohn and R.J. Sajan in classifying feeder roots, is gratefully acknowledged. The authors also wish to thank G.I. Marek for his unflagging interest and for providing historical records of the plantations, B.J. Stocks for providing weather records and Dr. R.V. Anderson for supplying identifications and other information on nematodes.

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INTRODUCTION

A general chlorosis was found in the fall of 1977 in two white spruce (Picea glauca [Moench] Voss) plantations totalling 500 ha in northwestern Ontario, near Limestone Lake (Fig. 1). Nursery stock (2+2 and 3+0) had been planted in the spring of 1967 and some in-planting was done in failure spots in 1970 with similar stock.

In October 1977, the trees ranged from 1 to 2 m in height, and many were uniformly chlorotic. Some were obviously yellower than others, but mortality was sparse. There were a few dark green trees scattered over one of the plantations (Gretel Creek), none of which developed chlorosis. These were larger (4-6 m tall) white spruce of natural origin.

The sites were sandy loams and clay loams with limestone outcrops. The area was cut over prior to 1940 and fires in 1940 and 1948 removed much of the organic layer. Heavy growths of grasses, herbaceous species and shrubs were reduced with an aerial application of brush-kill (2,4-D and 2,4,5-T) in 1969 over parts of the plantations and hand cleaning was conducted on parts of them in 1976 and 1977.

METHODS

In October 1977² the trees were divided into four classes: (1) no chlorosis-green (2.5 G 5/2)³ needles, long leader (not reduced); (2) light chlorosis-unhealthy, lightly yellow green (5 GY

2The chlorosis was first considered severe by Mr. G.T. Marek, Forest Management Supervisor, Ontario Ministry of Natural Resources, Nipigon in August, 1977.

Resources, Nipigon in August, 1977.

3According to Munsell color charts (Anon. (1963).

6/4), reduced leader; (3) moderate chlorosis--unhealthy, distinctly yellow green (2.5 GY 6/4), reduced leader; (4) heavy chlorosis--unhealthy, yellow (5 Y 8/6), much reduced leader; (5) dead, needles reddish brown (2.5 YR 5/8). Ten trees of each of the four classes of living trees were pulled out on each of the two affected plantations (Gretel Creek and Cedar Mountain), for a total of 80 trees. Total height and height increment over the last five years were measured. The main roots of each tree were examined in detail for signs of Armillaria mellea (Vahl ex Fr.) mycelial fans beneath Kumm. infection: the bark, and yellow stringy decay in root Roots were also examined for deformation. Each stem was examined by cutting longitudinally into the bark from ground level to approximately 40 cm above the ground, for irregular, resinous brown spots (approx. 1 to 10 mm across), and for smaller (approx. 0.5 to 1 mm in diam.) circular brown spots, possibly caused by aphids (aphid-like damage), both in the middle cortex tissues. Each of the above factors was rated for severity on a scale of 1 to 5 as follows: (1) none; (2) 1-25%; (3) 26-50%; (4) 51-75%; (5) 76-100% of roots or stem cross-sectional area affected. Other root or stem damage such as Hylobius spp. tunnels, bark beetle exit holes, frost damage, root rot of unknown cause, and necrotic bark areas or resinosis were also noted. Representative decayed and stained roots were taken to the laboratory in Sault Ste. Marie for culturing and identification of causal fungi.

In each of four successive years beginning in 1977, samples of feeder roots were taken to the laboratory in Sault Ste. Marie from each of two trees in each chlorosis class from each plantation, for determination of proportions that were healthy, unhealthy or dead. Samples were always taken in October. Feeder roots

were considered healthy if they were smooth and plump, and if a mycorrhizal mantle was present; they were unhealthy if they were shrivelled, dark brown or black, even if the cortex was still white as viewed under the microscope. If the cortex was brown or black the feeder root was considered dead.

Precipitation records from a nearby weather station at Cameron Falls⁴ operated by the Atmospheric Environment Service, Department of the Environment, Winnipeg, Manitoba, were obtained from B.J. Stocks, Fire Research Officer at the Great Lakes Forest Research Centre.

Physical and chemical soil properties were described from a soil pit in the Cedar Mountain Plantation. Standard techniques were used to determine macronutrients in current needles of 10 trees of each chlorosis class in each of four years (1977-1980 inclusive).

Soil and root samples from each of two chlorotic trees on each plantation were sent to Dr. R.V. Anderson, Biosystematics Research Institute, Ottawa, for nematode analyses in 1978 and 1979.

To determine the future condition of chlorotic trees, 10 trees in each chlorosis class, including those with no chlorosis (Class 1), were marked in each plantation in October, 1977. Height increment was recorded on each tree back to 1973 on the Gretel Creek plot and to 1972 at Cedar Mountain. The same trees were again rated for chlorosis and height increments were measured in October of each year up to and including October, 1979 at Cedar Mountain, and to October, 1980 at Gretel Creek.

RESULTS

Progress of the Chlorosis

Examination of the chlorotic trees in 1978 revealed continued heavy chlorosis in May and June. However, in October, 1978, chlorosis had decreased noticeably since the previous year, even on the older needles. The average chlorosis rating of chlorotic trees rated in 1977 decreased from 3.0 to 2.5 on both plantations over the 12-month period (Table 1). Chlorosis ratings again increased in 1979, especially in Class 2. Trees remained at about this level of chlorosis in October 1980. It is noteworthy that some of the green trees (Class 1) in 1977 were somewhat chlorotic in 1979 and 1980. All 20 trees with the most severe chlorosis (Class 4) in 1977 were still alive in 1980.

Tree Growth

Height increment in 1973 was quite uniform for all trees within each plantation (Fig. 2a,b). Beginning in 1976 there was a general downward trend in height increment in both plantations and these reductions were greatest in the trees that were most chlorotic (Class 4) in 1977. In 1978, when the chlorosis generally began to improve, average height increments of trees in all classes except Class 4 improved. It was noted that trees destined to be chlorotic (Classes 2-4) in 1977 began growing more slowly than green (Class 1) trees as early as 1974 at Gretel Creek and 1973 at Cedar Mountain.

Drought Conditions

Precipitation records at nearby Cameron Falls indicated below-average precipitation for the two growing seasons between May, 1975 and October, 1976 (Fig.

⁴About 16 km from the further of the two plantations (Cedar Mountain).

Table 1. Average change in chlorosis rating of 10 trees in each chlorosis class over a four-year period.

		Gretel	Creek	Cedar Mountain							
Foliage Condition	1977	1978	1979	1980	1977	1978	1979	1980			
			Av	erage chl	orosis ra	ting					
Green	1.0a	1.0	1.1	1.2	1.0	1.0	1.2	1.2			
Light chlorosis	2.0	1.7	1.8	1.7	2.0 3.0	1.4 2.5	1.7 3.0	2.0 2.8			
Mod. chlorosis Heavy chlorosis	3.0 4.0	2.3 3.5	2.5 3.7	3.8	4.0	3.6	3.5	3.2			
Avg of chlorotic	3.0	2.5	2.7	2.6	3.0	2.5	2.7	2.7			

^aTrees were initially (1977) selected in these classes (see text for rating criteria).

beginning May, 1975 and May, 1976, this area received, respectively, only 87% and 70% of normal rainfall, levels considered very low for the entire growing season. During both summers, July, August, and September monthly rainfall averages ranged between 51% and 77% of normal, and averages during the critical May period when new feeder roots would normally be forming were only 17% and 13% of normal in each of these two years (Table 2). June rainfall was better, at 141% and 121% of normal.

Following the two very dry growing seasons of 1975 and 1976, nearby Cameron Falls recorded a wet summer in 1977, when 118% of normal precipitation was received in the period from May to October, inclusive. In 1978 the dry conditions returned when only 80% of normal precipitation fell during the May to October period and only 75% of normal precipitation fell during the entire year. Precipitation in the area was average in 1979; in 1980, May and June were very dry while precipitation was above average from July to October.

Armillaria Root Rot

Armillaria root rot, diagnosed on the basis of mycelial fans on the cambium, rhizomorphs on or in the bark, yellow stringy decay in the root wood, heavy resinosis in the root collar area, and cultures from representative roots, was present in the roots of 53% and 20% of all chlorotic trees at Cedar Mountain and Gretal Creek, respectively, in 1977 (Table 3). At Cedar Mountain 80% of the trees in the most severe chlorosis class (4) were attacked by A. mellea and infected trees had an average severity rating of 4.3 on a 1 to 5 scale (Table 3) where the rating of 5 indicates 75-100% of roots or root collar girdled and killed by A. mellea mycel-Apparently eight out of 10 trees sampled in chlorosis Class 4 would have died from the A. mellea attack. Similarly, five and three out of the 10 trees each in chlorosis classes 3 and 2 with average severity ratings of 3.0 and 4.0, respectively, would probably also have died from A. mellea. One green tree in the Cedar Mountain plantation was lightly

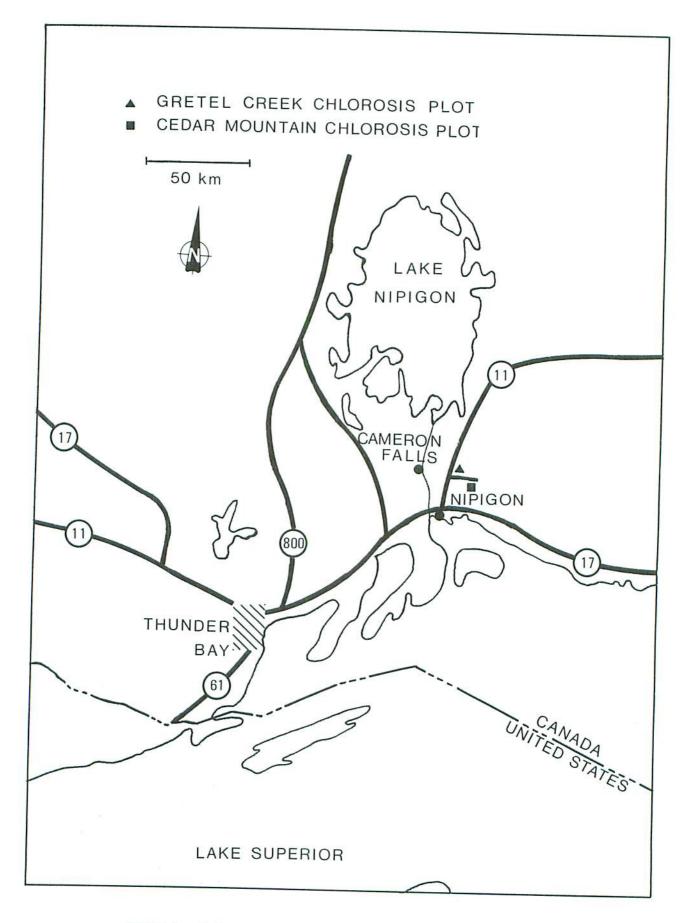
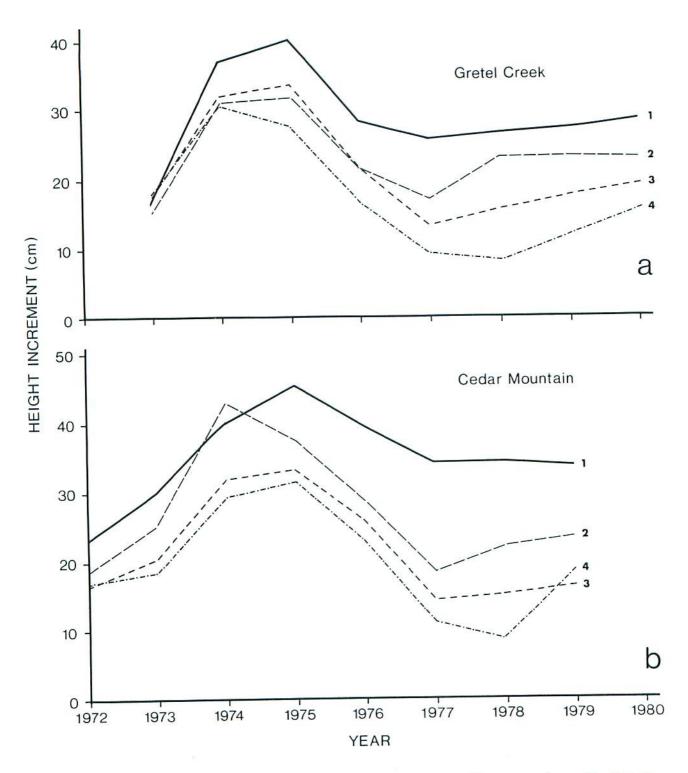


Figure 1. White spruce chlorosis study, Limestone Lake, Ontario.



Figures 2a and 2b. Average annual height growth of 10 white spruce trees in each of four chlorosis classes (see text for class descriptions) from 1972 to 1980 at Limestone Lake, Ontario.

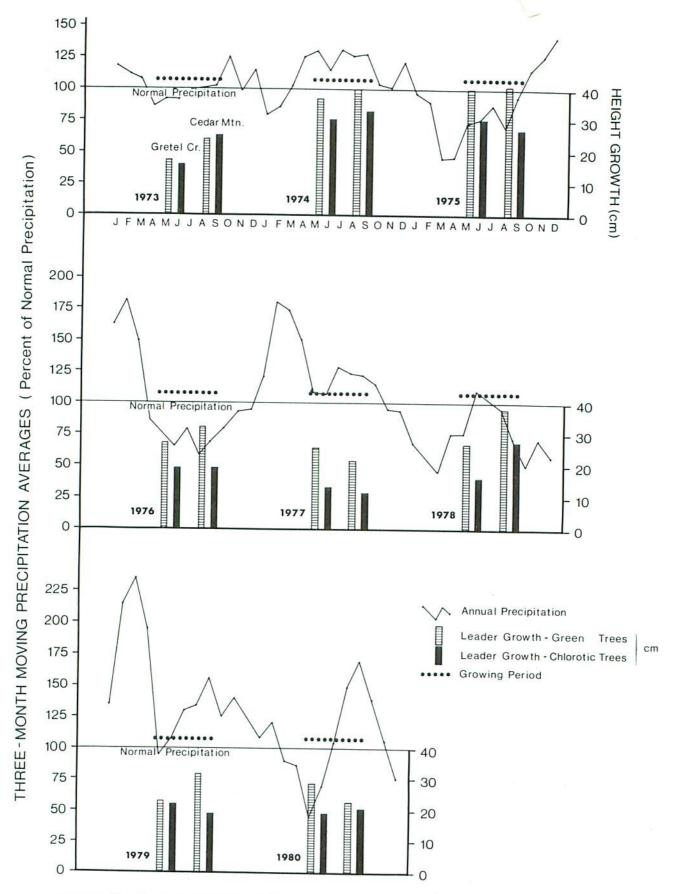


Figure 3. Monthly three-point moving averages of precipitation from Cameron Falls (16 km from the furthest plot), and average annual height growth of 30 chlorotic and 10 green trees on each of two plots at Limestone Lake, Ontario from 1972 to 1980 inclusive.

Table 2. Monthly percentage of normal precipitation at Cameron Falls, Ontario weather station.^a

	Jan.	Feb.	Mar.	Apr.	Мау	June	July	Aug.	Sept.	0ct.	Nov.	Dec.
					% of	normal	precip	itation				
1973	83	131	125	69	67	147	62	91	150	69	155	74
1974	122	58	80	176	118	95	124	177	68	131	102	77
1975	188	21	59	64	17	141	70	56	77	159	118	97
1976	194	199	151	94	13	121	62	51	59	107	73	99
1977	112	155	273	93	89	144	87	155	129	84	132	71
1978	78	23	71	47	107	73	151	88	49	66	35	111
1979	25	247	367	81	140	67	118	205	78	185	116	129
1980	134	61	171	34	58	43	110	163	174	179	58	91

^aBased on records from Atmospheric Environment Service, Department of the Environment, Winnipeg, Manitoba.

attacked by A. mellea. At Gretel Creek, 50% and 10% of trees in chlorosis classes 4 and 3, respectively, were attacked by A. mellea, which itself could have caused Lightly chlorotic and the chlorosis. green trees were not attacked. The pattern of A. mellea attack in both plantations indicated that root rot by this fungus is more prevalent in the trees with the most severe chlorosis; however, there are some severely chlorotic trees with no A. mellea attack, especially at Gretel Creek. One tree in chlorosis class 3 in the Cedar Mountain plantation was heavily attacked by Polyporus tomentosus Fr., a common root-rotting fungus in spruce trees older than 25 years (Whitney 1977).

Root Deformation

Averages of 53% and 80% of root systems of chlorotic trees examined at

Gretel Creek and Cedar Mountain, respectively, were deformed (Table 3), most likely at the time of planting. Root deformation was much more severe at Cedar Mountain than at Gretel Creek but not all chlorotic trees had deformed roots.

Brown Spots

Irregular, resinous brown spots of various shapes and sizes (up to approx. 1 cm across) were found in the middle bark of basal stem portions (chiefly) of 43% of the trees at Gretel Creek and 97% of those at Cedar Mountain (Table 3). These spots were as abundant in green, non-chlorotic trees as in chlorotic trees at Gretel Creek, but were slightly less prevalent in green trees than in chlorotic trees at Cedar Mountain. The cause of the brown spots is unknown, but examination by A.H. Rose, an entomologist at the Great Lakes

Table 3. Proportion of trees affected and intensity of Armillaria root rot, root deformation, aphid-like damage, and brown spots in 10-year-old planted white spruce at Limestone Lake in October, 1977.

		А. п	ellea	Defor	rmation		id-like mage	Brown	n spots
Chlorosis class ^a	No. of trees	gb	Rtg.c	8	R†g.	Ø	Rtg.	Z	R†g.
Gretel Creek									
Ī	10	0	1.0	30	2.0	0	1.0	70	2.0
2	10	0	1.0	60	2.3	40	2.0	40	2.3
3	10	10	4.0	30	2.7	30	3.0	50	2.6
4	10	50	4.6	70	2.9	30	2.3	40	2.5
Avg of 2-4		20	3.2	53	2.6	33	2.4	43	2.5
Cedar Mountain									
1	10	10	2.0	50	2.6	30	2.5	90	2.0
2	10	30	4.0	60	3.2	40	4.0	90	2.3
3	10	50	3.0	90	2.8	40	3.5	100	2.0
4	:0	80	4.3	90	3.3	67	3.0	100	2.4
Avg of 2-4		53	3.8	80	3.1	49	3.5	97	2.2

aSee text

Forest Research Centre, of non-chlorotic white spruce of comparable age from the Kirkwood Management Unit, Thessalon, Ontario, revealed similar irregular, resinous spots in the middle bark, except that they were clear instead of brown.

Smaller circular brown spots, about 0.5 mm in diameter, were quite prevalent in the same tissues as the larger irregular spots above. These smaller spots were not resinous and were considered possibly

to be punctures made by aphids. Smaller brown spots were seldom found in non-chlorotic trees (30% of trees at Cedar Mountain and 0% at Gretel Creek). A.H. Rose could not confirm these small brown spots as being made by aphids.

Feeder Roots

Between 70% and 95% of recoverable feeder roots were dead or unhealthy on

bPercentage of trees having this defect

CDamage rating. (1) none; (2) 1-25%; (3) 26-50%; (4) 51-75%; (5) 76-100% of roots or stem surface affected.

representative chlorotic trees in October, 1977, the time of most severe chlorosis (Table 4). High proportions (75-80%) of feeder roots were also dead or unhealthy on green trees in the affected plantations. Feeder roots of trees in a nearly unaffected white spruce plantation were almost all healthy with only 6% dead or unhealthy (Table 4). In October, 1978 average proportions of feeder roots that were dead or unhealthy had dropped to less than 50% in all chlorotic trees and only 15% of feeder roots were dead or unhealthy on green trees at Cedar Mountain. Proportions of feeder roots dead or unhealtny again increased in succeeding years, averaging nearly 50% on chlorotic trees in both plantations in 1979 and 51% and 64% at Gretel Creek and Cedar Mountain, respectively, in 1980.

Soil Characteristics

Soils in the Cedar Mountain plantation were characterized by red, acid, loamy textured mineral horizons over calcareous parent materials derived from dolomitic limestone (Sibley formation) (Table 5). Prolific rooting was confined to the shallow organic surface horizon.

Physical properties (Table 6) indicated typical clay enrichment in the B horizons. The pH increased with depth, to the carbonate-rich Ck horizon. The soil was relatively low in organic matter; however, the cation exchange capacity was moderately high because of the clay-rich horizons.

The nutrient status was generally low for N and P (Table 7) in comparison with that of other soils in the area⁵. Calcium and Mg levels were higher, presumably because of dolomitic parent materials. The

eluviated A-horizon exhibited relatively lower nutrient levels than the B-horizons, because of leaching.

Macro-nutrient concentrations in current needles from the same trees measured over a four-year period indicate that the status of P, K, Ca, and Mg was not affected by the chlorotic condition (Fig. 4a,b). However, the severity of chlorosis was associated with decreasing N levels. Differences in N-levels between chlorosis classes decreased each year from 1977 to 1980, confirming the field observations that the trees were recovering. Even trees with the severest chlorosis (Class 4) had increased N concentrations in 1978 in comparison with 1977.

Correlations of nutrient concentrations in current needles (Table 8) tend to confirm that the degree of chlorosis was related to tree N status rather than to the other macro-nutrients. Mean annual height growth was closely related to foliar N. Nitrogen and P uptake were also negatively related to feeder root mortality. The higher r-values for feeder root mortality suggest that height growth and chlorosis were secondary effects when compared with feeder root mortality.

Nematodes

Nematode species and numbers of each were determined by Dr. R.V. Anderson, Biosystematics Research Institute, Ottawa, in the base of two chlorotic trees, one each from classes 3 and 4, from each plantation on 31 October 1978 and on 17 August 1979. Several species of nematodes were found and Dr. Anderson indicated that the 1978 samples from Gretel Creek contained sufficient Hemicycliophora minor Wu (sheath nematode) to be possibly contributing to the symptoms. He further indicated that Cephalenchus emarginatus (Cobb), Bello

⁵Timmer, V.R. 1981. Unpublished data.

Table 4. Proportions of feeder roots dead or unhealthy on representative a trees in each chlorosis class in two white spruce plantations over a four-year period.

Fallers		Grete	Creek		Cedar M	Mountain		
Foliage condition ^b	1977	1978	1979	1980	1977	1978	1979	1980
			% of fee	der roots	dead or u	ınhealthy		
Green	80	35	46	31	75	15	62	60
Light chlorosis	70	50	39	52	90	44	66	66
Mod. chlorosis		20	57	47		36	49	74
Heavy chlorosis	75	65	68	53	95	50	29	51
Avg of 2-4	73	45	55	51	93	43	48	64
Nearby healthy trees					6	24	62	62

 $^{^{\}rm a}$ About 500 feeder roots from each of two different trees in each plantation were counted in October of each year.

Table 5. Generalized profile description of an Orthic Gray Luvisol at the Cedar Mountain plantation, Limestone Lake, Ontario.

Horizon	Depth (c)	Description
L-H	4-0	Semi-decomposed organic material; abundant very fine to medium roots; abrupt smooth boundary; pH 5.7
Ae	0-11	Reddish brown (5 YR 5/3 m); loam; weak subangular blocky; very friable; few fine roots; clear wavy boundary; 6-15 cm thick; pH 4.9
B†1	11-25	Red (2.5 YR 4/6 m); clay loam; weak to moderate fine subangular blocky; friable; few fine roots; clear wavy boundary; $18-33$ cm thick, pH 5.3
B†2	25-26	Reddish brown (2.5 YR 4/4m); clay; moderate fine subangular blocky; friable; few roots; gradual wavy boundary; $38-50$ cm thick; pH 5.6
С	36-48	Dark reddish brown (2.5 YR $3/4$ m); clay loam; medium subangular to angular blocky; firm to very firm; very few roots; clear wavy boundary; pH 7.5
Ck	48+	Reddish brown (2.5 YR 4/4 m); loam; medium angular blocky; very firm; no roots; smooth boundary; pH 7.8

bsee text.

Table 6. Physical and chemical properties of soil profile at the Cedar Mountain site, Limestone Lake, Ontario.

			Texture				
Horizon	Depth (cm)	Sand (%)	Sil+ (%)	Clay (%)	рН	Organic carbon (%)	Cation exchange capacity (meq/100 g)
L-H	4-0	-	-	- -	5.7	13.0	u=
Ae	0-11	43	37	20	4.9	0.5	6.5
B+1	11-25	32	33	35	5.3	0.9	11.5
B+2	25-36	29	30	41	5.6	1.2	13.5
С	36-48	35	31	34	7.5	0.8	13.0
Ck	48+	45	31	24	7.8	0.3	4.4

Table 7. Nutrient status of mineral soil horizons at the Cedar Mountain site, Limestone Lake, Ontario.

				Exchangeablec	
	Total N ^a	Available pb	K	Ca	Mg
Horizon	(%)	(mg/100 g)		(meq/100)	
Ae	0.05	1.20	0.09	1.37	0.51
B+1	0.06	1.20	0.12	5.14	1.94
B+2	0.09	0.53	0.11	4.94	1.80
С	0.07	0.66	0.13	10.48	5.35
Ck	0.03	0.66	0.09	5.30	3.66

aSemi-micro Kjeldahl procedure

Table 8. Simple correlations (r) between nutrient concentration of current-year needles and chlorosis intensity, annual height increment and feeder root mortality for 1977, 1978 and 1979 (n = 12).

N	Р	K	Ca	Mg
.62	.04	.07	.02	•17
.71**	.06	19	18	31
76**	77**	.66	.45	.67
	.71**	.71**	.71** .0619	.62 .04 .07 .02 .71** .061918

^{**}Significant at 1% level.

Medium Strength Bray method

 $^{^{\}text{C}}\text{Extracted}$ with 1 $^{\text{N}}$ ammonium acetate.

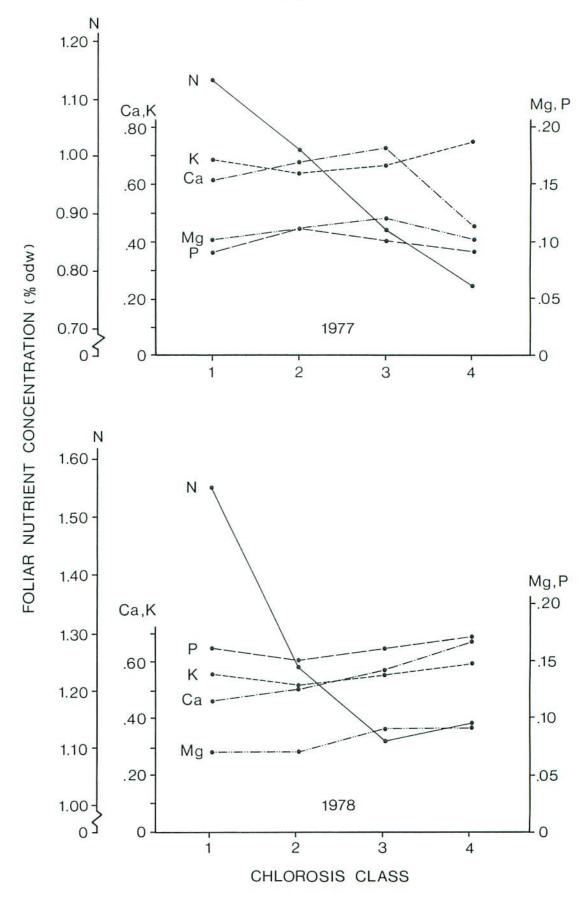


Figure 4a (caption on next page)

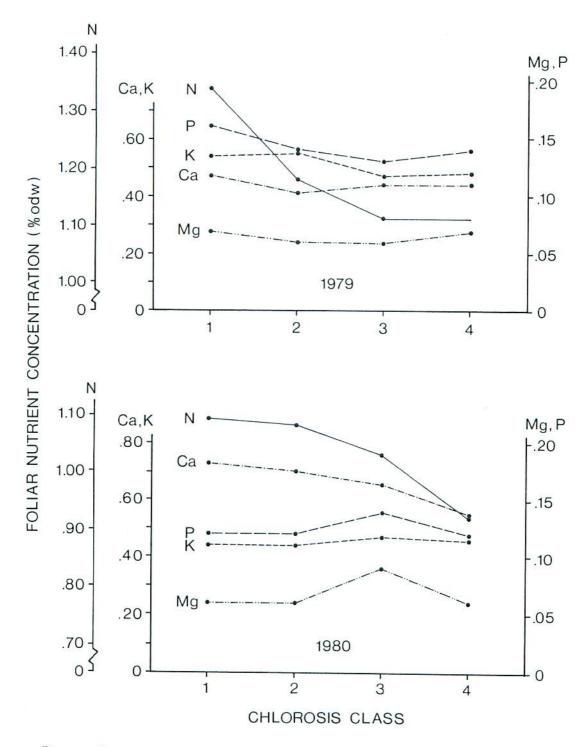


Figure 4b

Figure 4. Foliar nutrient concentrations of major nutrient elements in 10 trees of each chlorosis class (see text) on the Cedar Mountain plot at Limestone Lake, Ontario in a) 1977 and 1978 (left) and b) 1979 and 1980 (above).

and Geraert, a known parasite of spruce, was found in low numbers in the 1979 samples.

DISCUSSION AND CONCLUSIONS

The chlorosis that was general throughout the two plantations in 1977 and early 1978 decreased considerably in late 1978. In 1979 chlorosis increased slightly and it remained close to the 1979 level in 1980, though not necessarily on the same trees. Height increment improved in 1978 and continued at a fairly steady rate in 1979 and 1980.

Although there were several factors affecting the health of the trees, such as an abnormally heavy attack of Armillaria mellea, deformed roots, and frost damage on many new shoots in 1977 and 1980, the only factor consistently associated with the severe chlorosis of 1977 was heavy feeder root mortality. An average of 83% of feeder roots were dead or unhealthy on chlorotic trees in 1977, while only 44% were dead on the significantly improved trees in 1978. It appeared that the higher numbers of living feeder roots in 1978 were associated with N assimilation, reduction of the chlorotic condition and improved growth.

Although total N was low in the soil at Cedar Mountain (in comparison with other nearby soils), there was apparently sufficient available N for the foliage level to increase when feeder roots again became functional. The negative correlation of N in current-year needles with the percentage of dead feeder roots further suggests the malfunctioning feeder roots as a major factor in the chlorosis syndrome.

Unusually high feeder root mortality has been associated with other diseases

such as littleleaf disease of shortleaf echinata Mill.) (Jackson pine (Pinus In littleleaf disease, affected trees did not assimilate some nutrients, especially nitrogen, in quantities considered normal for healthy trees (Copeland Tanz (1979), investigating the 1952). same white spruce chlorosis at Limestone Lake, found N concentrations improved to near normal and chlorosis much less pronounced in both treated and control trees following N application in early 1978. This indicated that the soil was not deficient in N, but that as a result of mortality of feeder roots, the trees were unable to assimilate N, a condition similar to that reported by Roth et al. (1948) in littleleaf disease.

While a chief cause of rootlet mortality in littleleaf disease is apparently Phytophthora cinnamoni Rands, the main cause of this mortality in white spruce chlorosis appears to be lack of moisture. Lack of soil moisture and nutrient deficiencies were apparently important factors in deteriorating white spruce plantations in Quebec (Paine 1960). Precipitation in the Limestone Lake area was much below normal in the growing seasons of 1975 and 1976 and this was especially so in the early part of the growing season (May) when roots would be regenerating.

Extreme drought conditions prevailed at nearby Cameron Falls from 1 May to 5 June 1975 and from 1 May to 12 June 1976. The May 1975 rainfall, 17% of normal, was lower for that month at Cameron Falls than at any other weather station in Ontario, and although June rainfall was above normal, the monthly averages for the other growing season months did not exceed 77% of normal in either of the two years. The occurrence of two extremely dry spring and summer periods in successive years must be very unusual and this was probably the factor contributing most to feeder root

death, and indirectly to the chlorosis. Demands on the meagre moisture supplies by an abundance of grasses, small shrubs and herbs, and the lack of reserves in the well drained sites, would tend to aggravate the effects of drought. An initial effect of drought in the trees was reduced height increment. As the drought extended into the second year (1976), feeder roots apparently became desiccated and died, resulting in very poor nutrient absorption, especially of N, and chlorotic foliage. Even in green trees (Class 1), high proportions of feeder roots were affected, an indication that the condition affecting them (drought) was general, and that these trees might eventually have become chlorotic as well, had the drought conditions persisted. Only a few roots were found in soil horizons below the humus, the bulk of fine feeder roots being in the latter lay-When the humus became dry from the severe drought, insufficient moisture was present to maintain these vital feeding roots in a viable state. Zobel and Goddard (1955) also indicated drought as the main factor causing poor survival of Florida provenances of loblolly pine (Pinus taeda L.) in a droughty area in Texas.

Root regeneration of white spruce following sustained drought conditions is apparently slow when moisture conditions return to normal (Day and MacGillivray 1975), as occurred in 1977. Apparently during this period of very high feeder root mortality with little or no replacement, nutrient absorption was so low that the foliage became chlorotic. The return to normal moisture conditions in 1977 eventually resulted in regeneration of feeder roots, a decrease in chlorosis, and an improvement in tree growth in 1978. A similar recovery was noted by Denyer and Riley (1964) in drought-affected black spruce (Picea mariana [B.S.P.] Mill.) and white spruce when moisture conditions returned to above normal following two years of severe drought in forested areas in Saskatchewan. They also noted heavy feeder root mortality in affected trees. It has been observed that drought symptoms develop in trees only after several years of accumulated moisture deficits, and that a number of wet years are required to restore average tree growth following the drought (Holloway 1954, Gass 1977).

Other stress factors such as Armillaria root rot, root deformation from faulty stock or planting techniques, late spring frosts, and perhaps aphid and nematode parasitism, when combined with the very poor feeder roots, may also have contributed to the chlorosis, to reduced leader growth and to some mortality.

Twenty-six percent of the 80 trees initially examined for defects on the two plantations were attacked to varying degrees by A. mellea; most of these trees would probably have died from the root rot before reaching maturity. The very high proportion of trees attacked by this root parasite could be due to the previous severe drought conditions (Boyce 1961).

The few natural white spruce in the Gretel Creek plantation, all of which remained non-chlorotic even at the height of the chlorosis in 1977, may have been better adapted (more deeply rooted) to this site than the planted trees. Although the provenance of the planted trees was not known, the presence of limestone ecotypes in white spruce (Teich and Holst 1974) suggests that the planted trees may have been from a provenance less compatible with this site.

It was noted that the increases in average chlorosis ratings in 1979 and 1980 were coincident with increases in feeder root mortality. This suggests that the mild yellowing frequently observed in

white spruce foliage, especially in the autumn, may be caused by interference in nutrient absorption because of feeder root mortality.

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