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Reaction of *Larix gmelinii* Roots Under Low Soil Temperatures in Northern Parts of Central Siberia

PROKUSHKIN Stanislav G.[1]*, PROKUSHKIN Anatoly S.[1], STASOVA Victoria V.[1], MORI Shigeta[2], SAKAMOTO Yasuaki[3], QUORESHI Ali M.[4] and KOIKE Takayoshi[4]

[1] V.N.Sukachev Institute of Forest, Siberia Branch of The Russian Academy of Science, Akademgorodok, Krasnoyarsk 660036, Russia
[2] Forestry and Forest Products Research Institute (FFPRI), Tohoku Research Center, Morioka 020-0123, Japan
[3] FFPRI, Hokkaido Research Center, Sapporo 062-8516, Japan
[4] Hokkaido University Forests, FSC, Sapporo 060-0809, Japan

Abstract

This study examined how permafrost soils affect morphology, anatomy and metabolism of Dahurian larch (*L. gmelinii*) roots at five different sites in northern parts of Central Siberia. Field monitoring using custom-made rhizotrons showed that there were three different periods for seasonal root growth. Root growth was most active in the latest season (mid-July to late August) when soil-temperature and moisture were favorable. Use of an artificial watering treatment revealed that the larch root was developing resulted in even root growth throughout the growing season. The larch trees developed superficial root systems on permafrost soils and each root stretched into the warm mounds of soil. Moreover, *L. gmelinii* generated adventitious roots following litter accumulation. Comparative analysis of anatomic root structures between *L. gmelinii* growing on the permafrost and *L. sibirica* from southern region showed some interspecific differences; e.g. prevalence of other fine root tips, in the number and diameter of growth roots, inter-cell spaces and cell layers. Analysis of biochemical characteristics of fine roots of *L. gmelinii* demonstrated that the level of free amino acids on colder soils was 1.5-2 times higher than on warmer soils. Conversely, protein nitrogen content was 1.5-2 times larger in warmer soils. These anatomical, morphological and physiological features were discussed from the viewpoint of the adaptive growth characteristics for *L. gmelinii* against severe climate conditions in the permafrost region.

Key words: larch, permafrost, soil temperature, root system, root anatomy, root metabolism.

Introduction

Larix gmelinii (Rupr.) Rupr. is dominant in the permafrost zone of the northern part of central and eastern Siberia (Abaimov *et al.* 1997). Soil temperature in the region, according to observations of Savvinov (1976) is the coldest in the northern hemisphere. Soil temperatures are affected by micro-relief elements and sharply decrease with depth. Positive temperature season does not last more than 30-40 days. During such short growing season, a deficit of biologically active soil-temperatures may be crucial for tree growth in the harsh continental climate of Central Siberia (Dimo 1972, Pozdnyakov 1986). For example, irrespective of much sunlight income trees growing on the north facing slopes often suffer from lack of biologically active temperatures (Yanagihara *et al.* 2000, Koike *et al.* 2001). Therefore, the main limiting factor for growth and development of plants in this region might be low soil-temperature.

Information on the formation process and functions of *L. gmelinii* roots in permafrost soils in relation to low temperatures are fairly limited. Recently, a field study on the old *L. gmelinii* forests in central Siberia showed that stand biomass and net primary production were 39 Mg $hr^{-1}yr^{-1}$ and 1.8 Mg $hr^{-1}yr^{-1}$ respectively, and the biomass allocation to roots reached 43% (Kajimoto *et al.* 1999). This large carbon allocation to roots seems to be an adaptive feature of the larch especially in severely cold environments. Meanwhile, it should be noted that the effect of low temperatures in permafrost conditions on plant roots is likely a result of long-term rather than short-term effects. In northern parts of Central Siberia, sharp and short-term temperature fluctuations in rhizosphere are not observed, but roots are exposed to continuously low positive temperatures (3-8°C) during the growing season (Abaimov *et al.* 1997). Therefore, so-called "Sellie's reaction" characteristic for short-term stress is unlikely to be observed. Resistance of the roots to low temperatures may be

(Received; May 14, 2001: Accepted; Jan. 18, 2002) *Corresponding author: instiute@forest.akadem.ru

explained by molecular-genetic mechanisms due to permanent and/or repeated effect of low positive temperature - "prolonged stage of adaptation", providing profound and directed structural and functional changes in the root system (Drozdov *et al.* 1984, Burdon 1988, Stuart 1991, Pakhomova 1995, Sudachkova 1998).

Many transformations in structure and function of *L. gmelenii* root systems have been found in providing useful information on root vitality under low below-ground temperatures (Savvinov 1976, Pozdnyakov 1986, Kajimoto *et al.* 1999). These changes were found in; 1) morphological and anatomical structures, 2) shifts in proportion between different types of root tips, 3) timing and intensity of root formation and growth, 4) sizes of absorption surface and capacity of absorption of nutrients (Prokushkin, 1982, Abaimov *et al.* 2000).

Roots are responsible for the whole organism's resistance to unfavorable conditions as well as its productivity (Kursanov 1960, Orlov 1971, Koshelkov 1971). A complex change of root parameters is an integral indicator that describes root adaptation at any level of organization - subcellular, cellular, tissue, organ and population (Levitte 1980, Schlee 1988, Thompson *et al.* 1989, Edreva 1992). All these changes in roots are directed toward maintenance of homeostasis in the plants in these low temperature conditions (Kursanov 1960, Sudachkova 1998). Due to the important role that the larch roots play in whole-tree-level adaptation to stress, it was proposed that underground organs comprising special structure, metabolism and functions should be assumed as a self-regulating and balanced system, whose stability and plasticity on cold soils would be achieved due to the maintenance of its subsystem constancy, namely the idea of function – structure (Fig. 1).

The objective of this study was to investigate the adaptive strategies of *L. gmelinii* in the extremely harsh conditions of Northern Siberia, while focusing on particular characteristics of roots. Firstly, seasonal patterns of root growth at different positions on the mountain slope and in earth hammock with different moisture stress was described. Secondary, root morphology and anatomical traits between *L. sibirica* and *L. gmelinii* were compared. Finally, to ascertain the role of nitrogen for growth and development of roots, the growth processes of roots under field condition and analyzed the allocation of nitrogen elements in newly formed roots of *L. gmelinii* under permafrost conditions were monitored.

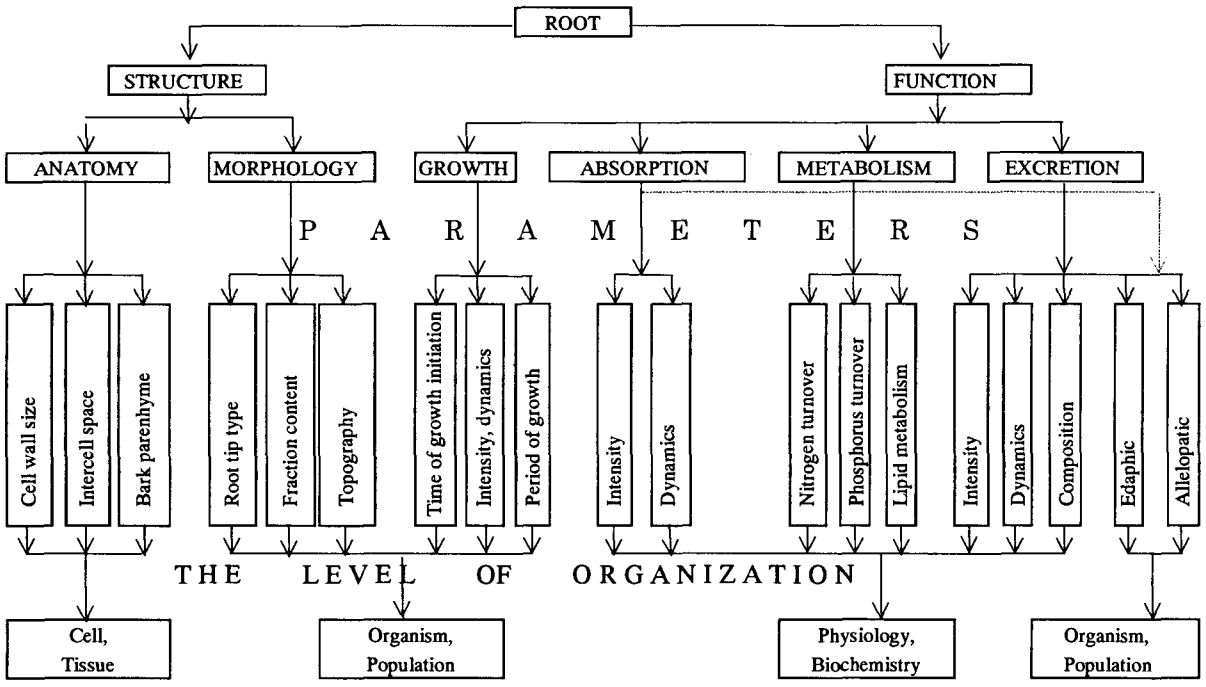

Fig. 1. Levels of structural and functional adaptation pathways of larch roots to low soil-temperature

Material and methods

1. Study sites

The study was carried out on five sample plots of *L. gmelenii* forests (G1 - G5) at the Evenkia experimental station of V.N. Sukachev Institute of Forest (64°19'N, 100°13E; 200 m a.s.l.). They were situated in the middle part of the Nizhnyaya Tunguska River near the Tura settlement (Table 1). *L. gmelenii* forests are common to the zone of continuous permafrost in this area of Central Evenkia. These sample stands were characterized by relatively slow growth of trees, lower productivity and even-aged structure (except for G5 with selective cutting in 1940s). All the stands were established after a strong ground fire occurred in 1902 (Abaimov *et al.* 1996). According to Abaimov *et al.* (1996), more productive tree stands were formed in the middle or upper parts of the southwestern slope (G2 - G4). On the bottom of the valley (G1), active soil layer depth was much thinner due to significant moss-lichen cover thickness, and the productivity of this stand was the lowest despite the high tree density (Table 1).

To compare the features of morphology, anatomy and developmental processes of root systems between larch species, a 25-year-old stand (S1) of *L. sibirica* Ledeb was selected in a forest-steppe zone where soils freeze seasonally. Rooting depth in the stand was 100-130 cm, but the highest quantity of live roots corresponded to the Ao layer (Table 1).

2. Root growth observations

For long-term observations, the glass-box method seemed most suitable way for determining of tree root growth even in frozen soil (Orlov 1968, Turner *et al.* 1982). Instead of the previous method, we used a custom-made rhizotron consisting of dense chromatographic paper (FN-3, Russia) instead of glass. Although the glass-box prevents water penetration through soil capillary and sometimes causes damage to roots, our modified method was working well to monitor the same roots during four years (1993-1996) where there were no serious disturbances in either the root or soil environment. In

Table 1. Stand characteristics of the six sampling plots

Plot No.	Location, larch stand type	Tree stand characteristics: composition / age (yrs)	mean: H, m / DBH (cm)	Depth, cm: moss cover / litter	root layer	Larch root capacity in ($g\ dm^{-3}$): root layer / one tree
G1	River valley area: dwarf shrub-*Sphagnum*	100% L.g.** / 72-92	4.2 / 4	10-12 / 9-13	15-20	0.428 / 0.64±0.13
G2	Terrace above river valley: dwarf shrub	90% L.g. 10% B / 72-92	6.1 / 6.2	0-1.5 / 2-4	50-70	0.93 / 1.32±0.20
G3	Middle part of SW slope: *V. vitis-idaea* – feathermoss	100% L.g. / 72-92	8.2 / 6.6	7-10 / 2-3	25-35	0.69 / 1.35±0.18
G4	Near top part of SW slope: *V. vitis-idaea* - *L. palustre* - feathermoss	100% L.g. / 72-92	10.7 / 9	6-11 / 5-9	25-35	0.45 / 1.40±0.07
G5	Surface of terrace a river valley: *L. palustre* - *V. uliginosum*	100%L.g. rareB / 41-285	8.9 / 9.1	8-12 / 3-5	25-40	0.584 / 1.50±0.33
S1*	Larix sibirica sylviculture of 1978: Grasses	100% L.s. / 25-30	10 / 12	0 / 3-5	100-130	1.635 / n/o

Notes: S1* is located in forest-steppe zone near Krasnoyarsk;

** - L.g. – *Larix gmelinii* (Rupr.) Rupr.; L.s. – *Larix sibirica* Ledeb., B – *Betula pendula* ; n/o – not observed.

addition, spatial patterns of root systems were investigated in the well-developed earth hammock area (Kajimoto *et al.* 1999); main roots of two seedlings of *L. gmelinii* occurred between the mounds were traced from the basal portions to the tip parts.

Field monitoring of the root growth started in late August of 1993, when the terminal number of roots was counted. The ends of their tip parts were also marked for the next year's measurements. At the beginning of the next growing season (May 1994), some root tips (n=5-7) were selected for measurements, and in latter periods already 10-15 root tips had been used. Root growth monitoring was continued for four years in the five types of *L. gmelinii* stands (G1 – G5) together with the measurement of soil temperature (Table 1).

During summer periods (July and early August) of two years (1995-1996), the watering treatment (10 $L \cdot m^{-2}$) was carried out every 3-5 days to avoid water deficit in the forest floor and litter in larch stands with dwarf shrub-*Sphagnum* and *V. vitis-idaea*-feathermoss larch stands (G1 and G3, respectively). Sampling plot G1 was characterized by colder conditions of soil and called "cold". Sampling plot G3, which had warmer soil conditions, was therefore called "warm".

Spatial distribution and density of larch roots in upper soil horizons in accordance with the distance from the tree stump were examined using the method described by Abaimov *et al.* (1997). Soil samples were taken and washed to determine contents of roots. The roots were then divided into fractions (> 1 mm and < 1 mm). The latter fraction of fine roots was further divided into alive roots (with white and light-brown surface) and dead roots (dark, wrinkled, with died off cortex parenchyma). Moreover, among the live fine roots, absorbing roots with clavate, bifurcated and coral-like tips and growing tips, were separated since their physiological roles in absorbing nutrients were different. The amounts of root tips of these different types were determined in 1 g of fresh mass using a binocular microscope with magnification x 4-8 in five replications.

3. Study of morphology and anatomy of roots

For anatomical study, only first-order growth roots were examined. They were fixed in Karnua mixture (Salyaev 1958, 1962; Shemakhanova 1962). Cross sections of 10 roots were cut 3-4 mm from the tips. At this section, the cells generally stopped growing and progressed to the next phase of development – differentiation, according to our preliminary analysis. The root samples were fixed with FAA (formalin: acetic acid: 50% ethanol = 5: 5: 90). After washing under running water for 4 hours, they were dehydrated in ethanol series and embedded in paraffin. Ten to fifteen μ m thick serial transverse and longitudinal sections were cut with a sliding microtome (Leitz, Germany). They were stained with safranin "O" (1% solution in 50% ethanol) and fast green (0.1% solution in 95% ethanol), and were then examined under a light microscope. The cross sections were mounted in glycerine and examined using a microscope. For each section we measured the following parameters: thickness and the number of cell layers in exodermis and cortex parenchyma and diameters of their cells, intercellular spaces and the cell wall thickness of cortex parenchyma. The measurement was carried out along two different radii using an ocular micrometer (x 200-1000 magnification). Statistical analysis was made by ANOVA (Doerfel 1969).

4. Biochemical analyses

For biochemical analyses, fine absorbing and conductive roots of *L. gmelenii* were sampled during the period with maximal activity (late July - early August). These samples (50-60 g) were oven-dried at 105°C to keep before the analyses.

Total nitrogen and nitrogen contained in protein were determined according to the Kjeldal procedure with a slight modification (Yermakov *et al.* 1972). Total, soluble and storage carbohydrates' contents were determined by oxidation with a mixture of phenol in concentrated sulphuric acid with further colorimetric detection of the optic density of the solution. Solution density was measured by a colorimeter KFK-3 (Russia) at wavelengths of 490 nm. The content of free amino acids was measured using an Amino acid analyzer (AAA-339M, Czech

Table 2. Edaphic conditions of sampling plots

Plot No.	Average July temperatures on different depth from surface, °C							pH		Contents of available forms, mg 100 g^{-1} dry soil	
	0 cm	5 cm	10 cm	15 cm	20 cm	25 cm	30 cm	water solution	KCl solution	N - NH_4^+	P - P_2O_5
G1	30.1	14.2	13.6	11.5	3.3	1.6	ice	6.10	5.04	1.62	2.26
G2	35.0	21.2	20.0	14.8	9.2	5.9	5.5	6.30	4.70	0.14	0.86
G3	30.2	17.5	14.9	9.2	5.8	1.7	ice	6.90	5.50	0.22	0.41
G4	28.0	14.8	8.7	6.7	3.5	1.4	ice	6.80	6.20	0.78	0.85
G5	25.7	12.6	8.9	6.5	2.6	0.8	ice	5.60	5.30	0.12	0.31
S1	26.4	17.8	15.4	14.7	10.3	6.9	6.8	5.60	5.30	2.45	3.82

Republic). Organic acids were quantified by the paper chromatography method (solvents: n-butanol-acetate-water, 4:1:5 v/v).

Results and discussion

Biologically active temperatures in rhizosphere (>9° C) were observed only in the crowberry-bearberry larch forest (G2, Table 2). Temperature regime of rhizosphere was mainly dependent on thickness of moss-litter layer and slope position (Table 1, 2). Therefore, low temperature and rather shallow active soil layer may limit vertical distribution of root systems and stock of physiologically active fine roots (Table 1). From these observations, the temperature seems to act as a key factor in the formation process and spacing of root systems of *L. gmelinii*, since nutritional regimes in the larch ecosystems were almost similar and unlikely influenced root functioning to a greater extent (e.g. Schulze *et al.* 1995).

Seasonal growth activity of the larch roots was independent on the root penetration depth. Root growth starts usually at a soil temperature above 1-3°C, and finishes in August or early September when soil temperature decreases below 1-2°C (Prokushkin *et al.* 1988, Abaimov *et al.* 2000). Meanwhile, above ground organs have already entered the dormant phase after needle-shedding. This phenomenon can

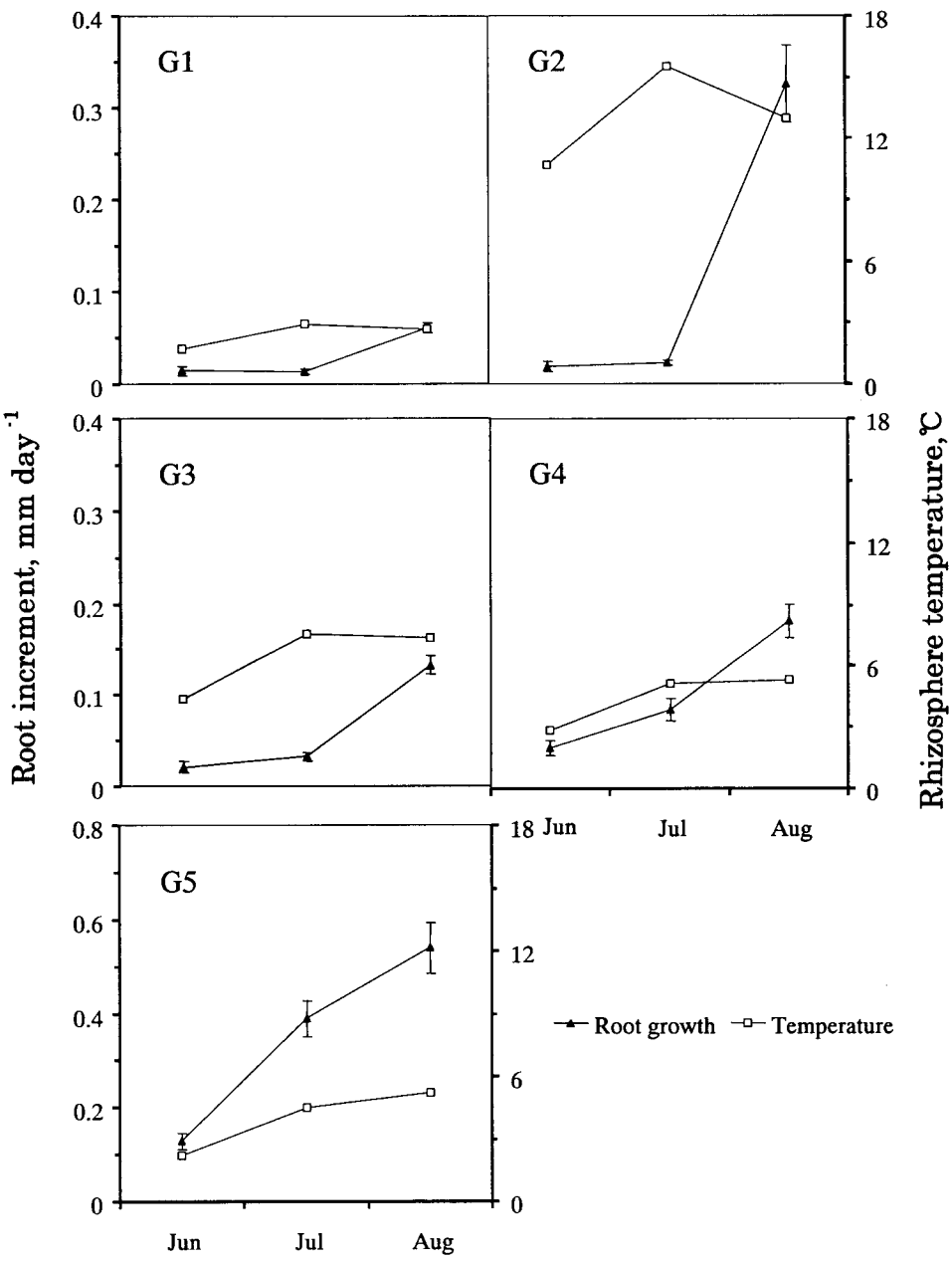

Fig. 2. Root increment and soil-temperature in five different larch stands during growing season of 1996. Sample plot G5 had different first y-axis valuation. Vertical bars represent SD value.

be specially marked as one of the growth characteristics of the developmental pattern of larch root system in this permafrost region.

Moreover, in spite of the higher humidity of lower soil horizons near the front of permafrost, water deficit occurred in the shallower surface of the active soil layer. Root growth in the upper horizons seemed to be limited by not only the temperature regime but also water deficit during summer. In fact, three different periods for seasonal root growth (Fig. 2) were observed. In early summer (June), root growth was mainly limited by low soil temperature. In the middle of growing season (July and the first decade of August), root growth was enhanced by relatively high temperature, but was partially limited due to a lack of soil water. At the end of the season (late August), intensive root growth continued under high temperature and wet soil conditions. In this period, the increment rate of roots was: 0.05-0.1 mm day^{-1} in *Sphagnum*-dominated larch stands of the river valley (G1) and 0.3-0.5 mm day^{-1} in well-warmed larch stands on the terraces (G2 and G5).

The watering experiment showed that limitation by water deficit was reduced considerably (Fig. 3). Root growth was rarely interrupted during the growing season indicating that the dynamics of root growth was mainly regulated by only temperature in rhizosphere and/or the physiological status of individuals.

The most intensive root growth of larch was usually found in the upper horizons due to the relatively high temperature regimes. This feature

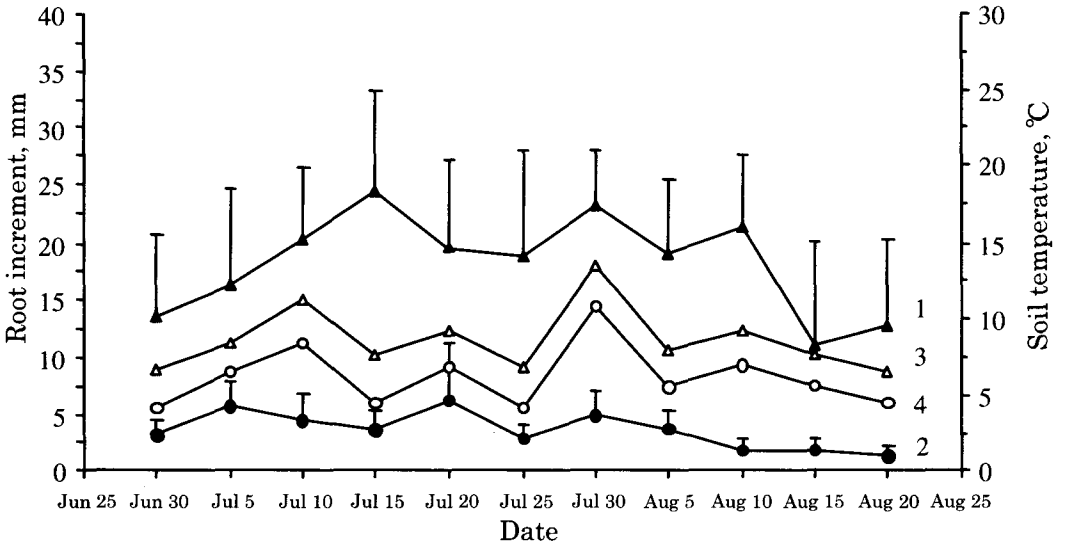

Fig. 3. Growth dynamics of *Larix gmelinii* roots and average soil-temperature in root zone during growing season of 1996 under artificial treatment of water: 1 – larch root increment on "warm" site (G3); 2 – larch root increment on "cold" site (G1); 3 – rhizosphere temperature on "warm" site; 4 – rhizosphere temperature on "cold" site. Vertical bars represent standard deviation.

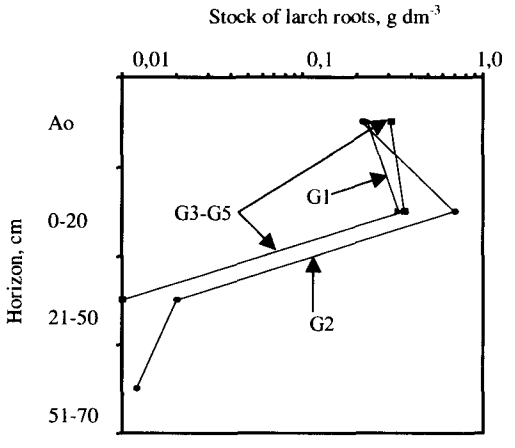

Fig. 4. Distribution of *Larix gmelinii* fine roots in soil profiles on sample plots located in different larch stands. Ao represents litter including L, F and H layers. Following values are the depth of soil where fine root sampling was performed. G1—G5 are reffed to Table 1.

stimulates the unique pattern of shallow fine root distribution due to temperature gradient as shown in Figure 4. Moreover soil temperature might cause overall shallow and superficial root system of *L. gmelenii* with well-developed lateral roots (Abaimov *et al.* 1997; Kajimoto *et al.* 1999). The majority of the lateral roots grow upward and explore well-warmed mounds demonstrating positive thermotropism. Likewise this pattern was typical for the larch trees growing on the well-developed earth hammock areas: tap root has a short period of vertical growth, and upon reaching the permafrost table may expand horizontally or die. This was apparent in the G1, G3 and G4 sampling plots, where the depth of active layer was less than 25-35 cm (Table 2).

The largest section of physiologically active fine roots was distributed in the upper 20 cm soil layer (Fig. 4), and surprisingly high portion was concentrated in the litter layer. Horizontal distribution of roots showed that a minimal number of roots were in adjacent areas to each stem with a radius of 0.5 m. Root density increased and reached a maximum at the distance of 1.0-1.5 m from the tree stump. In this zone, fine roots mostly occurred adventitiously from the newly formed lateral roots above the root neck following litter accumulation. It may be possible that rate of formation and growth of these roots would determine larch viability and resistance in decreasing temperature conditions of growing moss-lichen cover. The small portion of live fine roots (mainly growth ones) was found actually within frozen soils. This phenomenon may have been due to a greater degree of summer precipitation (e.g. in July and early August of 1993 and 1996) resulting in the roots being able to penetrate into thawed permafrost horizons. The roots that penetrated into the frozen soil appeared to have been in a state of anabiosis for some years (in our case two years), but remained alive (they had thin cortex and living cortex parenchyma).

Among fine roots of *L. gmelinii*, physiologically active root tips (clavate and growth tips) were most numerous which was independent on site conditions. There was a very small amount of coral and bifurcated root tips (Table 3). The lower soil temperature conditions, especially for stand G1, led to a significant increase in the number of healthy growing root tips while yielding a decrease in the number of clavate root tips. These roots may have contributed to the increase of the area's water and nutrient absorption. No tendency was found in the changes of proportion between bifurcated and coral root tips in site-dependency. Similar results were reported for Scots pine (*Pinus sylvestris*) in south taiga in Siberia (Prokushkin 1982, Abaimov *et al.* 1997).

Table 3. Quantitative and qualitative contents of larch root tips in different larch stands (pcs g^{-1} fresh root weight)

Plot No.	Tip types*				Total
	Growth	Claviform	Furcate	Coral	
G1	257±22 / 6	276±13 / 6	8±3 / 8	3±1 / 8	543±11 / 22
G2	159±22 / 0	533±15 / 3	14±6 / 8	4±1 / 12	711±38 / 23
G3	177±38 / 0	369±12 / 0	2±2 / 0	0 / 8	548±40 / 21
G4	180±20 / 0	350±28 / 4	2±1 / 8	1±1 / 9	533±40 / 23
G5	167±23 / 0	280±28 / 4	0 / 7	0 / 11	447±37 / 23
S1	120±14 / 0	814±54 / 3	7±1 / 5	1 / 0	945±44 / 8

Note: Figures above line – quantity of alive tips; figures under line – quantity of dead tips

The proportion of dead fine roots was very small (3-5%), which was likely to be caused by prolonged period of root life span in these conditions. *L. sibirica* in the forest-steppe zone may have relatively different quantitative and qualitative ratio of fine root types. In particular, this larch produced 1.2-1.5 more root tips than *L. gmelinii* and clavate type was most numerous (approximately 85% of total, Table 3).

A clear and robust response to soil-temperature was also found in morphology of growth root tips for *L. gmelinii*. These root tips are usually small - 2-3 cm in length and about 1 mm in diameter (except so-called "searching" roots). In some cases, however, the diameter was 1.5-3.0 mm and the length was 6-7 cm. They were referred to as "large" growth roots. Size and the number of these tips were different depending on the site conditions (Table 4). Namely growth roots were greater in number in the colder site (G1) and fewer in the other warmer sites (G2 and G4). Trees in the G3 plot all had enlarged growth roots in comparison with trees in the other stands. In the stand G5, the large and ordinary growth roots were different primarily in length only. Trees of *L. sibirica* on the forest-steppe site (S1) did not form such large growth roots.

"Large" and ordinary growth roots were also different in anatomical structure (Table 4). In all cases, the greater diameter of large roots was a result of changes in all tissues, including exodermis and cortex parenchyma (Photos 1-10). It should be noted that the size of cortex parenchyma was a result of an increasing number of cell layers as well as an increase in cell dimensions. Exodermis thickness was determined by an increase in cell diameter. Cell wall thickness in parenchyma of large growth roots was found to be slightly less than in tips of ordinary growth roots. On the other hand, intercellular spaces of large growth roots were 1.5-2.0 times larger in the ordinary roots.

In this study, for anatomical analysis, only ordinary growth root tips were used. Growth root diameter, parenchyma cell diameter, parenchyma thickness and intercellular spaces in root tips increased in four *L. gmelinii* stands (G1, G3, G4, G5)

Table 4. Summary of anatomical characteristics of growth roots of *L. gmelinii* and *L. sibirica*

	Plot No.					
	G1	**G2**	**G3**	**G4**	**G5**	**S1**
Root diameter, mm	624.9±30.6	544.1±96.5	826.8±67.3	521.8±23.5	682.3±29.7	495.5±37.6
	1848.7±	1079.4±	-	971.7±231.2	887.6±59.0	-
	Exodermise:					
Thickness, mm	31.9±2.41	40.7±5.1	34.4±4.3	25.6±2.5	32.6±2.3	26.2±1.4
	57.8±11.4	57.1±9.8	-	62.1±3.8	44.2±1.6	-
Cell number	2.1±0.2	2.6±0.2	2.1±02	1.7±0.1	2.0±0.2	2.1±0.1
	3.0±0.4	2.7±0.4	-	2.2±0.6	2.1±0.2	-
Cell diameter, mm	15.8±0.4	16.1±1.7	16.2±0.6	15.0±0.8	16.3±0.5	12.6±0.6
	18.9±1.5	21.4±1.7	-	28.1±2.2	21.0±0.6	-
	Bark parenhyme:					
Thickness, mm	126.5±8.8	119.7±11.1	185.8±13.1	111.2±6.9	154.9±7.4	105.7±7.2
	477.5±102.2	246.9±49.3	-	271.4±7.9	198.7±25.8	-
Cell number	4.8±0.1	5.9±0.4	6.0±0.4	4.6±0.2	6.1±0.2	4.3±0.2
	12.0±1.7	8.2±0.5	-	7.0±0	7.5±0.6	-
Cell diameter, mm	26.3±1.7	19.6±2.1	29.9±1.3	25.9±1.0	25.4±0.8	24.4±0.6
	40.0±5.5	29.4±4.8	-	36.6±2.8	26.4±0.8	-
Cell wall thickness, mm	2.4±0.3	1.7±0.1	1.6±0.1	1.6±0.3	1.7±0.1	2.1±0.2
	2.0±0.3	1.5±0.1	-	1.8±0.1	1.5±0.1	-
Intercell space size, mm	3.3±0.2	1.5±0.3	4.1±0.4	1.9±0.1	1.9±0.1	2.5±0.2
	7.3±0.4	3.2±1.3	-	3.7±0.1	3.7±0.1	-

Note: Figures above line – prevailing roots of medium diameter; figures under line - "large" roots;
– - "large" roots were not observed.

with lower soil temperatures. In addition, growth roots had thinner cell walls, and some thickening of the cell walls was observed only in one stand, G1, which was probably due to an over-moistened environment.

Comparisons of anatomical root parameters between *L. gmelinii* and *L. sibirica* showed that *L. gmelinii* had larger growth root diameter, exodermis and parenchyma thickness because of an increase in the number of cell layers and cell dimension (Table 4). In contrast, the cell walls of *L. gmelinii* roots were sufficiently less thick than that of *L. sibirica*. These results suggested that the roots of *L. gmelinii* in extreme temperature conditions facilitated the absorption of nutrients and endured anaerobic conditions in early summer and autumn.

Correlation analysis of anatomical root structures of *L. gmelinii* and edaphic factors showed a positive correlation between thickness of root exodermis and average soil temperature of July, at different depths: 0, 5, 10, 15 and 20 cm (correlation coefficient - r = 0.74, 0.74, 0.87, 0.79 and 0.81 respectively). The exodermis thickening with the increase in temperature occurred mainly because of the growth of cell layers (r = 0.83, 0.78, 0.92, 0.90, 0.84), whereas cell diameter recorded slightly large: r values which ranged from 0.16 to 0.42. Thickness of cortex parenchyma in the larch growth roots appeared to be correlated with July's average temperature of moss-lichen cover and of rhizosphere (r = -0.56, -0.51, -0.48, -0.61, -0.57). However, increasing parenchyma thickness was accompanied by a decrease in the average diameter of its cells. These average and slight degrees of correlations indicated that the formation of anatomical structure of the larch growth roots in July was influenced by not only temperature, but also nutrients. It may be also associated with a shortage of available forms of nitrogen and phosphorus in the soils (Table 2). In stands with enhanced nutrient supply, we registered a decrease in root diameter, the number of cell layers and the average cell diameter in exodermis, and the number of cell layers of cortex parenchyma and its thickness (r = -0.26...– -0.33; -0.45...– -0.11; -0.49...– -0.29; -0.43...– -0.49; -0.83...– -0.67). Simultaneously, trophic improvement affected an increase in cell wall thickness in cortex parenchyma (r = -0.85...– -0.93).

Biochemical analysis showed that total carbohydrate content of fine roots was much higher in *L. gmelinii* than that of the larch of southern regions (Sudachkova, 1998). Even under better

Table 5. The quantitative and qualitative contents of carbohydrates in *L. gmelinii* fine roots during growing season (mg g^{-1} dry mass) in five sample plots (SP)

Plot No.	Soluble carbohydrates		Insoluble carbohydrates (starch)
	monosaccharides	oligosaccharides	
G1	24.3±0.5	6.0±0.2	20.0±0.3
G2	10.3±0.3	2.3±0.2	19.3±0.3
G3	6.0±0.2	2.0±0.2	35.6±0.4
G4	9.3±0.3	3.7±0.1	20.6±0.4
G5	35.3±0.4	9.3±0.2	45.9±0.4

Table 6. Contents of organic acids in *L. gmelinii* fine roots (μg g^{-1} dry mass)

Ogranic acid	Plot No.				
	G1	G2	G3	G4	G5
Galacturonic	504.5	807.3	302.8	252.3	662.3
Citric	201.7	428.9	252.3	151.1	403.5
Malic	883.3	941.9	588.6	765.3	1000.9
Succinic	785.1	1020.4	549.4	981.3	667.0
Oxalic	530.0	706.6	441.6	588.6	594.2
Fumaric	494.6	777.3	353.3	565.3	734.6
Total	3399.2	4682.4	2438.0	3303.9	4112.5

hydrothermal conditions in the permafrost region, the amount of carbohydrates in larch roots from sampling plots G2-G4 were found to be declining (Table 5). The amount of insoluble storage sugars in total carbohydrates was high and low depending on the site conditions. Among the soluble carbohydrates, monosaccharides were abundant, and oligosaccharides were always small in number. Both monosacharides and oligosaccharides contents were higher in fine roots from colder environments.

Qualitative composition of organic acids in roots of *L. gmelinii* was found to be similar among the sampling plots. However, their total contents reached a maximum value in the stands G1 and G5 (Table 6). In all stands, malic and succinic acids were predominant. The other acids were generally low in concentration. The broad spectrum of organic acids and their high quantity in physiologically active roots may have been connected with the intensive metabolism of carbohydrates transported from aboveground organs and the high activity of Krebs cycle as well as ornithine and glyoxalate cycles in roots.

Physiologically active roots during the period of their maximal growth contained more than 20 amino acids (Table 7). Among them, primary amino acids were the highest in content, where as the more complex amino acids (i.e. aromatic and heterocyclic) were lower in concentration. In all cases, the amino acid content of roots taken in colder sites was 1.5-2.0 times that in other warmer sites. This may have been related to the slow utilization of amino acids in protein synthesis and reduction of protein nitrogen contents: protein N was 25% of total N in the colder site (G1), and about 50 % in warmer stands (G2-G5)(Table 8). This suggests that *L. gmelinii* roots, as well as the other of cold-resistant plants, are characterized by the specifics of their nitrogen metabolism.

Table 7. Contents of free amino acids in *L. gmelinii* fine roots (μg g^{-1} dry mass)

Amino acids	Plot No.				
	G1	G2	G3	G4	G5
Cysteic	160.4	174.9	210.2	199.6	215.7
Aspartate	85.5	74.9	100.3	72.4	82.0
Threonine	16.2	16.2	16.2	11.3	24.3
Serine	83.0	90.1	71.3	66.4	96.3
Asparagine	46.6	23.3	23.3	-	116.6
Glutamate	519.7	363.9	545.5	207.7	487.9
Glutamine	775.2	227.5	144.5	72.4	313.1
Glycine	47.3	45.2	49.4	47.3	43.8
α- Alanine	267.1	236.0	209.5	150.4	317.4
Citrulline	371.0	92.5	223.3	79.1	97.0
α-Aminobutirate	68.9	9.9	36.4	9.9	16.2
Valine	53.7	32.2	26.8	21.2	59.5
Cystine	857.5	60.7	284.7	72.4	91.6
Methionine	21.2	-	11.3	-	-
Isoleucine	32.5	24.7	22.2	17.3	37.4
Leucine	32.5	38.1	24.4	27.2	54.9
Tyrosine	53.0	31.8	37.4	26.5	33.8
Phenylalanine	25.4	30.0	20.1	14.8	35.6
β-Alanine	13.4	16.6	10.6	16.6	16.7
γ-Aminobutirate	70.6	59.0	65.0	44.8	238.2
Ornithine	38.1	32.8	27.2	35.7	32.8
Lysine	30.3	30.3	30.3	30.3	42.4
Histidine	618.3	13.4	18.3	13.4	23.5
Arginine	70.6	5.3	43.8	1.8	195.0
Total	3758.0	1729.3	2252.0	1238.5	2671.7

Table 8. Contents of nitrogen and phosphorus in the samples of fine larch roots (mg g^{-1} dry mass)

Plot No.	Nitrogen		Phosphorus
	Total	Protein*	Total
G1	9.24±0.56	2.96±0.33 25	1.90±0.10
G2	11.80±0.60	5.24±0.40 44	2.34±0.10
G3	8.90±0.10	5.09±0.30 57	2.55±0.08
G4	12.70±0.65	5.96±0.35 47	2.02±0.03
G5	9.00±0.65	4.28±0.02 48	1.73±0.04
S1	14.3±0.48	7.54±0.52 53	2.34±0.11

* - Figures above line – absolute value; figures under line – % of total nitrogen

Conclusions

Our findings suggested that soil-temperature regime combined with soil moisture significantly influenced the root system development of *L. gmelinii*. Superficial root system, ability to explore warmer mounds and occurrence of adventitious roots were all probably due to the constraints of low soil-temperature. Anatomical structures also indicated that a sharp decline in soil temperature along with greater soil depth increased root diameters, intercellular spaces and cell sizes in the cortex and parenchyma of roots. Nitrogen metabolism of roots under low soil-temperature conditions was characterized by protein synthesis inhibition, which resulted in higher amino acid contents. These changes were more apparent for *L. gmelinii* than the less cold-resistant larch species of the southern regions, *L sibirica*, suggesting a greater capacity of *L. gmelinii* to survive in harsh permafrost environments.

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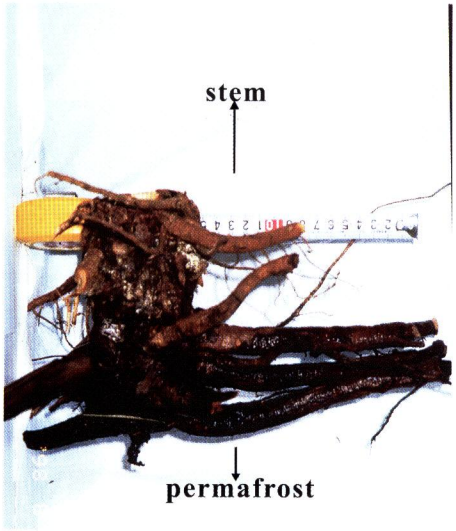


Photo. 1. *L. gmelinii* root system from G1 site. Tap root and lower lateral roots are dead. Upper adventitious roots have horizontal development.

Photo. 2. Soil profile along larch tree trunk up to permafrost layer from S1 site. Upper permafrost boundary occurred in litter. Active mineral soil layer is absent. Temperature in immediate space of permafrost was 0.2. Most part of adventitious roots is developed in litter layer in depth 10-20 cm from surface.

Photo. 3. Examples of root system of *L. gmelinii* trees of different age (103, 88, 84 from left to the right) and vital status from G1 site. All trees have dead lower part roots.

Photo. 4. Example of growth roots of *L. gmelinii* from G3. Bottom right part shows "large" growth roots. In center of photo, "ordinary" roots are presented.

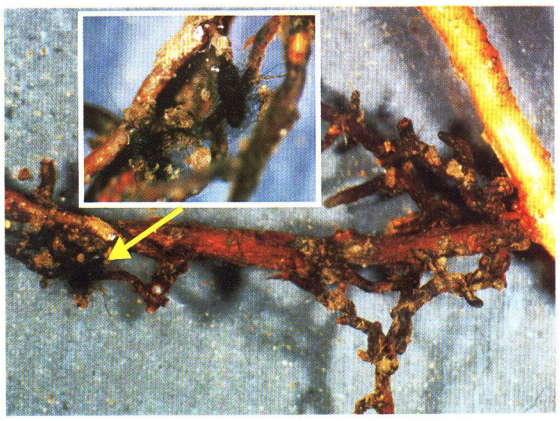


Photo. 5. Fine root of larch infected with ectomycorrhiza (*Cenococcum geophilum*)

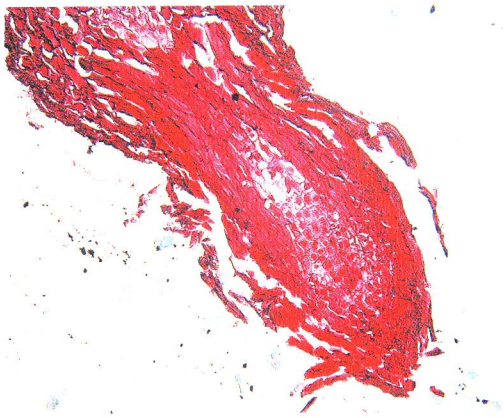
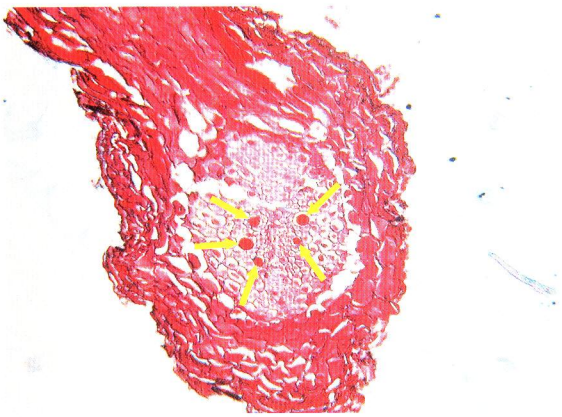


Photo. 6. Longitudinal section of lateral (or branch) root



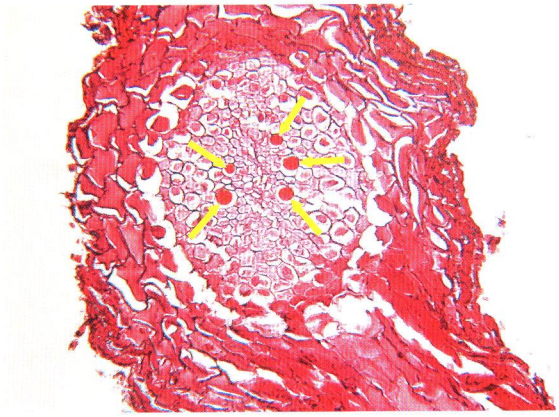


Photo. 7. 8. Unknown substances stained with safranin "O"

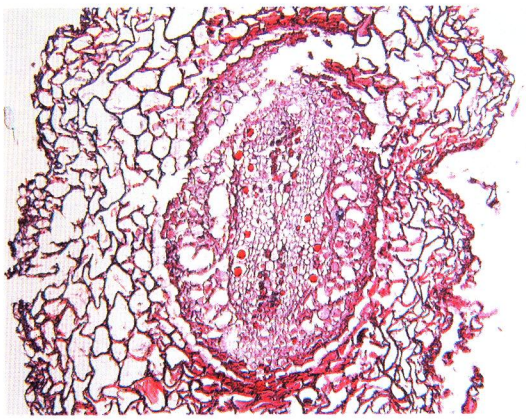


Photo. 9. Root showing development of Hartig net

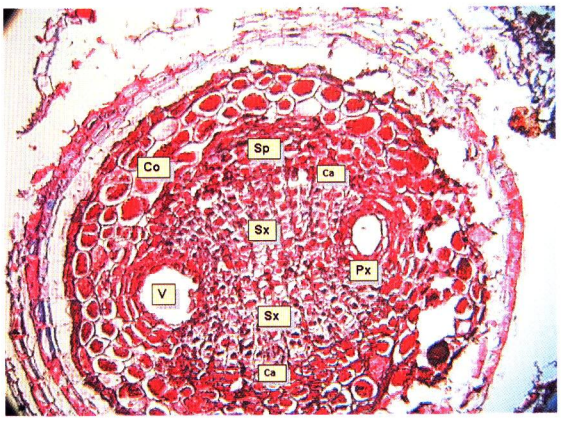


Photo. 10. Vessels in xylem tissue
Co : cortex, V : vessel, Px : primary xylem, Sx : secondary xylem, Sp : secondary phloem, Ca : cambium