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The Effect of Boron Deficiency on the Wood Quality of *Pinus radiata* D. Don[*1]

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라디아타소나무에 있어서 硼素의 缺乏이 材質에 미치는 影響[*1]

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摘 要

New Zealand 남섬의 Canterbury지방과 Nelson 지방의 硼素 缺乏地域과 硼素 施肥地域에 生育하고 있는 라디아타소나무의 解剖學的 差異를 調査하였다. 즉 假導管의 길이, 放射方向의 假導管 內徑, 放射方向 細胞壁의 두께를 早, 晩材別로 測定하였고 光學顯微鏡 및 電子顯微鏡 特性을 觀察하였다.

晩材에서는 假導管의 길이에 硼素 缺乏地域과 施肥地域 間에 有意差가 認定되었으나, 早材에서의 假導管의 길이 및 假導管의 內徑 및 假導管壁의 두께는 早, 晩材 모두에서 有意差가 認定되지 않았다. 그러나 硼素 缺乏地域에서 生育된 리디아타소마누에서는 細胞壁의 剝離現象 및 木質化가 덜된 部分에 많이 觀察되었고, 찌그러진 細胞의 多數出現 및 細胞의 크기가 不均一한 것이 많이 出現되었으며 細胞壁의 間層이 넓었음이 觀察되었다.

INTRODUCTION

Boron is one of the essential micronutrients for plant growauth. The level of boron required for the growth varies considerably. Far example, grass and cereal crops require low levels, whereas tree crops require substantially high levels(Crane and Borough, 1987 ; Schon and Blevins, 1990). There is usually no large difference between the upper limit of its requirement and the toxic level (Gupta et al., 1985 ; Will. 1985 ; Hunter et al., 1987).

The greater required level of boron for dicotyledons than monocotyledons may be due to the differences in membrane properties between two plants whether the effect of boron on plant membrane is a direct or indirect one

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(Pilbeam and Kirkby, 1983).

The function and mode of action of boron remain unknown and utilization is quess work.

Boron is quite immobile in plant so that this element to developing sinks may be a problem(Crane and Borough, 1987; Schon and Blevins, 1990). The role of boron has been considered in several aspect. It is known to be associated with metabolism, transport or action of auxin-type hormones (Robertson and Loughman, 1974) and regulation of membrane function(Pollard et al., 1977). This information on the effect of boron on plant growth comes largely from studies with agricultural and horticultural plants, but those with forest trees are limited. The scope of the roles of boron to plant assess critically various roles. From the surveys in the many books, reviews and research paper the following putative major roles may be listed; (a) cell wall bonding and lignifcation, (b) cell division, (c) nucleic acid and enzyme regulation and (d) nutrient metabolism.

Cell wall bonding and lignification

A lack of lignification in certain vascular tissue is frequently observed from the stem of plant grown under inadequate supply of boron (McIlath and Skok, 1964). Dugger(1983) has been pointed out that boron may react with hydroxyl-rich compounds existing in cellular membranes, boric acid may be directly involved in membrane activity or serve as a building unit for cell wall polysaccharide biosynthesis. This effect of boron is also supported with the other works(Gauch and Dugger, 1952; Spurr, 1957; Lee and Aronoff, 1966; Starck, 1963; Kouch and Kumazawa, 1976; Lewis, 1980).

Cell division and enlargement

Skok(1957) proposed that the functions of boron are primarily in differentiation and maturation of plant cells rather than cell division.

Boron is required for cell elongation rather than cell division(Starck, 1963). Albert(1975) reported that under the boron deficient conditions, cell division and root elongation stopped, followed by effects such as reduced DNA synthesis, and Cohen and Lepper(1977) noted that the cessation of root elongation due to the boron deficiency was caused by a failure of cell division in meristematic cells, not by the failure of cellular elongation. The limiting effect of boron deficiency on root growth is also associated with both cell division and cell enlargement(Kouchi and Kumazawa, 1976; Dugger, 1983). Some other works (Gauch and Dugger, 1952; Spurr, 1957; Jackson and Chapman, 1975; Middleton et al., 1978, 1980; Pilbeam and Kirkby, 1983; Jarvis, 1984; Gupta et al., 1985) suggested that the boron acts as a regulator for cell division and elongation.

Nucleic acid and enzyme regulation

Lewis(1980) suggested that the potential role for boron is regulator hydroxylase and oxydase activities of the phenolases involved in the biosynthesis of caffeic and hydroxyferulic acids.

Pilbeam and Kirkby(1983) reported that the damage of apical meristems occured when boron was withheld, and involvement of boron in nucleic acid metabolism was sug-

gested.

Although boron is not considered to be a constitutive component of specific plant enzymes; Boron does play as a role in enzymatic regulation and, therefore, is involved in regulating plant growth and development (Dugger; 1983). Jarvis et al.(1984) reported that the most significant finding concerning the interaction between IAA and boron was that the position of the optimum response to either variable dependent upon the value of the other.

Nutrient metabolism

Gauch and Dugger(1952) reported that boron is involved in protein metabolism. in fact, boron deficient plants had more soluble nitrogenous compounds as well as higher sugar level than control plants.

Boron deficient roots absorbed less phosphate with reduced ^{32}P-labelling of the nucleotide fraction and increased labelling of the hexosephosphates when compared with contrals (Robertson and Loughman; 1974).

The origin of this role for boron depended on the selection of sucrose as a mobile and storage carbohydrate since, compared with the acyclic sugar alcohols that was accumulated other algal groups, sucrose forms only a very weak complex with boron(Lewis, 1980).

Boron deficiency, as well as possibly causing an inhibition of uracil biosytheses, is thought to inhabit the action of uridine diphosphate glucose(UDPG) pyrophosphorglase, the enzyme that catolyses UDPG formation (Pilbeam and Kirkby, 1983). Correction of boron deficiency enhanced the uptake of phosphorous by the trees(Hopmans and Flinn, 1984).

Boron deficiency in tree crops was first recognised and described in New Zealand in 1962(Will et al., 1963; Stone and Will, 1965). Raitio's(1983) description in *Pinus sylvestris* emphasized abundant resin flow and various disturbances in apical dominances as the first external evidences. The terminal bud become small, malformed, retarded in expansion or dead. Adjacent lateral bud may or may not be similarly affected(Stone and Will, 1965; Stone, 1987; Borough et. al., 1987). The most prominent symptoms of boron deficiency are resin flow, bud, shoot or tip die back(Stone and Will, 1965; Will, 1985; Stone, 1987; Borough et al., 1987; Carter and Brockley, 1987) and discoloration of the leader, swelling of leading shoots and multileadered, bush crown(Walker et al., 1955; Whittington, 1957, 1958; Stone and Will, 1965; Raitio, 1983; Stone, 1987). Unopened fascicles are often shed and rapid dessication often makes the unlignified stem to crook or to curl into an inverted U-, T- and S- shape(Stone and Will, 1965; Raitio, 1983; Will, 1985; Crane and Borough, 1987).

Browning or red-browning of cells were often occurred in the pith tissue of the leader in boron deficient trees(Kolari, 1979; Raitio, 1983; Carter and Blockley, 1987; Crane and Borough, 1987) and the othar clearly discernible symptom in the pith tissue was the formation of cell cavities(Raitio, 1983; Stone, 1987).

But the most important function of boron in trees should be conjecturred lignification of cell wall and cell division, enlargement,

maturation and differentiation(McIlath and Skok, 1964; Jackson and Chapman, 1975; Gupta, 1985; Downed and Turvey, 1987; Dugger, 1983; Harris, unpublished).

Anatomical effect of boron were usually reduced growth and necrosis(Starck, 1963; Blaser et al, 1967) and accumulation of material and changes in cell wall thickness(Gauch and Dugger, 1952; Blaser et al., 1967; Kouchi and Kumazawa, 1976). Extreme development involved grossly distorted and hypertrophied ray cells(Downes aud Turvey, 1987; Harris, unpublished) associated with misshapen and irregular tracheid sometimes traumatic resin canals(Harris, unpublished).

From time to time, many sawmillers, especially worked Canturbury area, have been petitioned for us to overcome the logs that distort off the saw, and which yield sawn timber that warps severely on drying.

At last, we recognised the presence of compression wood and the area of boron deficiency as a contributing to these problem. On the way, the athors were racking their brain to find a solution to the problem as for the first step, we carried out this study in order to investigate anatomical differenuces boron deficient and fertilized wood.

MATERIALS AND METHOD

Sampling

Sixteen radiata pine(*Pinus radiata*. D. Don.) trees were felled down to investigate the anatomical properties.

Twelve trees were cut from Ashley forest and four trees were cut from Nelson forest, and the discs to investigate anatomical properties were cut down from diameter of breast height(1.4m from ground) of each trees. Half of them were brought from boron deficient area and the other half were fertilized area.

Sample blocks(appr. 1×1×1cm) were prepared for measuring the lumen diameter and cell wall thickness and match sticks(2−3cm long) for tracheid length from earlywood and latewood of each tree.

Measurement

Thin cross sections(30−50μm in thickness) were cut with sliding microtome, stained in toluidine blue solution(0.5% toluidine blue 0+1% barac) and mounted in glycerol. Measurement were made using a microscope (Carl Zeiss, Photomicroscope II), thirty two measurement of radial lumen diameter and radial wall thickness(double wall thickness), at the each disc, respectively, were investigated. Earlywood and latewood cells were measured.

The means of each set of thirty two measurement were used in subsequent analysis.

The pieces cut from ealywood and latewood were macerated in a 1:1/v:v mixture of glacial acetic acid and hydrogen peroxide at 90−100℃ for 8−10 hours. After washing the samples were stained with 1% safranin soluton, and followed by mounting in glycerol. Tracheid length were measured using digital measuring wheel(Leitz) fifty tracheids each.

Status of sampling forest and discs were shown in table 1.

The data were analysed using analysis of variance for between treatments data and analysis are shown in table 2 and 3.

Table 1. Quantitative effect of boron deficiency on cell characteristics.

Samples		Length(mm)*		Diameter(um)**		Thickness***	
		B^-	B^+	B^-	B^+	B^-	B^-
A	E	2.797	3.046	26.18	34.77	5.15	7.18
	L	2.226	2.523	11.84	19.11	6.45	7.08
B	E	2.762	3.149	20.76	26.39	5.95	9.48
	L	2.166	2.340	8.85	13.72	6.75	9.22
C	E	1.782	2.422	26.14	28.35	7.72	6.96
	L	1.668	2.230	14.28	15.16	5.72	8.33
D	E	2.894	2.939	19.81	29.63	4.64	6.30
	L	2.267	2.618	8.73	15.21	6.50	8.29
E	E	2.903	3.277	20.35	30.09	4.79	6.80
	L	2.078	2.416	9.23	14.36	6.17	8.18
F	E	2.852	2.988	24.62	20.03	5.27	8.54
	L	2.228	2.274	10.18	14.85	6.80	9.32
me	E	2.665	2.970	22.98	29.74	5.59	7.54
an	L	2.106	2.400	10.51	15.40	5.38	8.40

* Tracheid length
** Radial lumen diameter
*** Radial Cell Wall Thickness
B^- : Boron deficient
B^+ : Boron fertilizer
E : early wood
L : Late wood

Table 2. Average diameter of tested disc.(cm)

		B^+	B^+	Remarks
	GL*	34	28	
Black I	B.H.**	24	20	
	B.G.C.***	20	18	
	GL*	30	26	
Block II	B.H.**	20	18	
	B.G.C.***	17	17	

*GL : Ground level
**B.H. : Breast height(1.5m from ground level)
***B.G.C. : Base green crown

RESULT AND DISCUSSION

At the late wood in the breast height, average tracheid length were 2.1mm in boron deficient wood and 2.4mm in borom fertilized wood, redial wall thickness were 5.4um, and 8.4um, and radial lumen diameter were 10.5um and 15.4um respectively. Much Differences between boron deficient and fertilized wood were found, but analysis of varience between treatment does not support this result as shown table 2 for radial lumen diameter and radial wall thickness besides

Table 3. Quantitative effect of boron deficiency on wood cell characteristics

	Thick ness of tracheid Wall		Length of tracheids		Diameter of tracheid lumen	
	−B	+B	−B	+B	−B	+B
Ground level						
Summer wood	8.3	8.8	1621	2120	22	17
Spring wood	7.0	9.8	1754	2557	17	22
Breast height						
Summer wood	8.7	10.5	2006	2662	15	16
Spring wood	6.4	7.2	2235	2657	22	26
Base green crown						
Summer wood	5.4	8.0	1508	2478	12	13
Spring wood	3.1	6.3	1711	2614	17	24

Measurement in micrometres(μm)
−B=boron deficient
+B=boron fertilised

Table 4. Analysis of variance for the differences between boron deficient and ferti$lized wood in earlywood

Sourse	Tracheid length			Lumen diameter		Wall thickness	
	df	MS	F	MS	F	MS	F
Block	2	0.0517		31.309		0.539	
Treat	1	0.1206	0.060^{ns}	29.223	0.188^{ns}	0.296	0.799^{ns}
Residual	2	0.0079		6.546		3.498	
Total	5						

Table 5. Analysis of variance for the difference between boron deficient and fertilized wood in latewood

Sourse	Tracheid length			Lumen diameter		Wall thickness	
	df	MS	F	MS	F	MS	F
Block	2	0.2149		10.038		0.908	
Treat	1	0.1262	0.010**	18.180	0.139^{ns}	0.602	0.613^{ns}
Residual	2	0.0013		3.168		1.713	
Total	5						

**Significantly difference at 99% confidence level

tracheid length that shows significant difference at 99% confidence level.

At the earlywood, average tracheid length were 2.7mm in boron deficient wood and 3.0mm in fertilized wood, radial wall thickeness were 5.6um and 7.5um, and radial lumen diameter were 5.4um and 8.4um each. Much differences between boron deficient and fertilized wood could be found too, but no significan difference between treatment could be supported as shown table 3.

The main reason for the no significant between control and boron deficiency may be probably depend on the limited samplings, unfortunately one of the earlier designed block had destructed with the storm in 1980, therefore, we could not got sampling at there. Spurr(1957) reported that the amount of boron in the plant had a pronounced effect on cell wall thickness. Under boron deficiency most of the collenchyma cell walls are markedly thinner apparentely because of a localized carbohydrate deficiency. But other tissues in the same sections showed an opposite response; the cell walls of the phloem parenchyma and the ground parenchyma become thicker.

Harris(1981) noted the low contrast between earlywood and latewood in radiata pine means that neither tracheid diameter nor cell wall thickness differs greatly across an annual growth layer. It is apparent that although latewood tracheid are by no means strongly radialy compressed nor especially thick walled compared with early wood tracheid. Also he assested, in his unpublished paper, latewood was very weakly developed in all boron deficient trees with only slight cell wall thicking, compared with earlywood, and little reduction in radial diameter. But, Knight et al.(1983) reported the opposite result applied boron had no obvious effect on the parameters measured.

Harris(1965) reported that the average tracheid length of latewood in radita pine much vary from 3.3mm to 4.7mm. The regional tracheid length variance, in accordance with Cown and McConchie(1983) were 2.8mm in Canterbury and Nelson district. Kibblewhite(1982) worked that the tracheid length was 3.3mm, wall thickness was 8.0 μm and lumen diameter was 40.0 μm in slab wood of radiata pine. Orman and Harris(1965) reported that the tracheid diameter in radiata to pine was 41.4 μm in earlywood and 30.4 μm in latewood, and the cell wall thickness was 2.6 μm in early wood and 5.0 μm in latewood.

But as you know, all of these results were based on the no boron deficient samples, and radiata pine have a wide range of tracheid types(Kibbiewhite 1982).

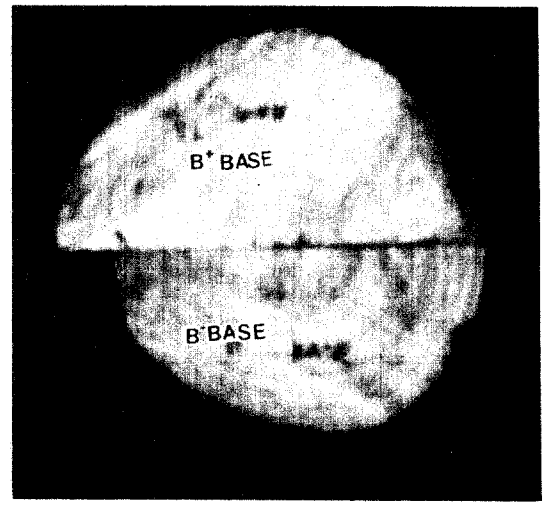

Fig. 1. Different diameter between radiata pines grown boron fertilized and deficient area at ground level

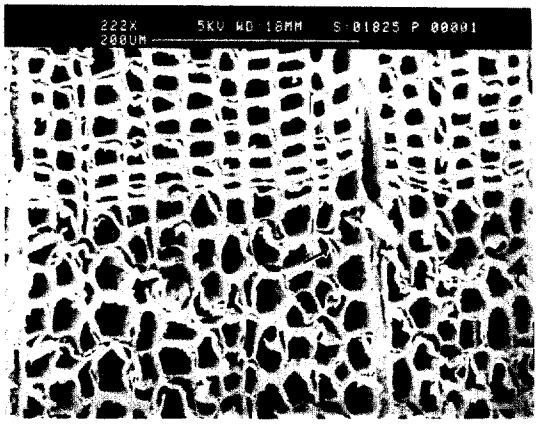

Fig. 2. Delaminated tracheid walls were much occured in radiata Pine grown in boron deficient area (SEM 222 X)

The results shown in table 3 shows similar or a little bit shorter in tracheid length, but for smaller in cell lumen diameter on the contrary much thicker in cell wall thickness those previous results.

One of main variance in confirmation of cell walls between boron deficient and fertilized wood is much occurance of delaminated cell wall in boron deficient wood as shown in Fig. 2. Spurr(1957) reported that under boron defi$ciency the fine structure of the walls became coarse in celery. IN contrast to normal collenchyma, in boron deficient collenchyme, there are fewer lamellae. Starck(1963) suggested that the cross section of cell wall of boron deficient collenchyma, sunflower did not reveal microfibrilar structure. And also Slack and Whittington(1964) said boron was concentrated with cell wall bonding, followed with many other works which was apparently a neccessary component of cell wall or cellular membrane(Jackson and Chapman, 1975; Dugger, 1983; Gupta et al., 1985).

The delamination of cell wall could be due to differences in chemical compositions of the wall, in ultrastructure of the wall and orientation of wall microfibrils. But there were no previously published information available on eht effect of boron deficiency on the chemical composition and ultrastructure of wood cell wall of forest trees.

Many of those works on celery, sunflower, field bean and so on supported that the cell wall would be delaminated in the case of boron deficiency. And also Raitio(1983) suggested that the primary phloem cells in roots were thin walled and swollen, the vascular cylindar of the root had developed cavities and protoxylem was poorly lignified(Fig. 3).

The darkening and formation of cavities in pith agreed well with the review of Stone (1987) and Raitio(1983). In boron deficient wood, we frequently could found the col-

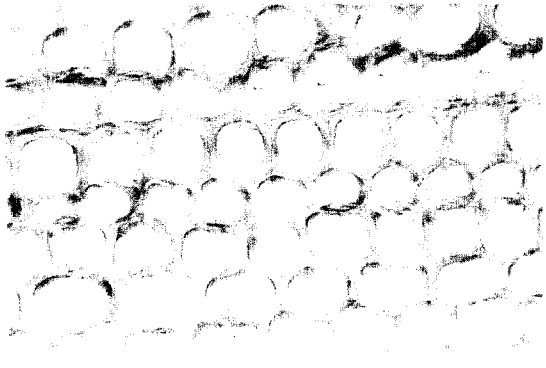

Fig. 3. Thin walled tracheid could be observed in boron deficient radiata pine

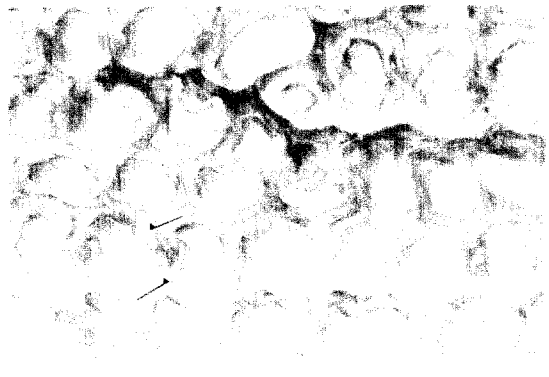

Fig. 4. In boron deficient wood, frequently could be found the collapsed misshapen irregular tracheid

lapsed cells shown in Fig. 4.

Spurr(1957) suggested that the boron apparently affected the rate and process of carbohydrate condensation into wall material. Cell wall responses to boron deficiency implicate boron as a morphogenetic agent affecting the development of specific form of the cell walls of the plants. Pollard et al. (1977) reported that boron plays an essential role in the regulation of the function of higher plant membranes. IN boron deficient vascular plant, the observed quantitative reduction in lignin should be accompanied by a qualative change in composition(Lewis, 1980). Harris(unpublished) found that extreme development involved distorted and hypertropied ray cells, associated with misshapen and irregular tracheid and sometimes traumatic resin canals.

The wood anatomy of *pinus nigra* showed no abnormal features. Latewood was regular, and strongly developed, indicating a much denser type of timber than that bring produced by *pinus radiate*(Cown and McConchie, 1983; Harris, unpublished).

Exact role of boron in the regulation of plant metabolism still unclearly(Pilbeam and Kirkby, 1983). Suggestions have been made that boron effects cell growth and maturation through its regulaton of enzyme activity of certain path way and of cell membrane permeability.

The trees which grown in boron deficient soil grew slowly in height and diameter than those of fertilized soiles(Fig. 1 and Table 4). The reason, we supposed, would be based on the swollen lumen diameter, shorten length and uneven sized tracheids(Table 1).

Blaser(1967) reported that the abnormality in structure, cell shape, wall confirmation and rigidity are described for both primary and secondary tissue in boron deficient *Thuya*.

The abnormal shapes of cells suggest symplastic walls, even in the secondary tracheids which develop thick pitted walls. In *Thuja Plicata* the short tracheids and abundant abnormal wood parenchyma probably account for the weak stems of boron deficient plants. In boron deficient tomato root tips, cell walls suffered on irregular thickening, followed by a rugged or serrated structure(Kouch and Kumazawa, 1976). And also Harris(unpublished) reported that the wood Kumazawa, 1976). And also Harris(unpublished) reported that the wood structure and properties of trees grown under conditions of boron deficiency relate purely to the stem malformation associated with that condition. But there were no obvious differences between wood from boron deficient tree and wood from similary malformed trees grown on normal soils.

Dugger(1983) suggested that the effect occurred because the abnormalities in the formation of cell walls prevented the cells from becoming organized for mitosis.

CONCLUSION

The anatomical differences between boron dificient and fertilized *Pinus radiata* D. Don, grown at the Ashley forest in Canterbury and the Nelson forest in Nelson were investigated, Tracheid length, radial luman diameter and radial wall thickness in earlywood and latewood were measured. Optical, photomicroscopic and scanning electronic microscopic characteristics were also observed.

The results obtained in boron deficient wood are summerized as follow;

1. Tracheid length in latewood are shorter than that in boron fertilized wood.
2. Delaminated and unlignifed cell walls are found
3. Cellapsed, uneven sized and thin walled cells are found
4. Broad cell wall cavities were observed too.

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