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Water-soluble Thiols in Spruce Seedlings from Provenances of Different Sea Levels¹⁾

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Summary

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This paper shows the connections between the SH concentration of young spruces and their genetic source regarding to sea-level. Spruces from mountaineous regions supply their F₁-generation from the beginning with a higher SH-concentration than spruces from lower regions. If kept longer at a certain sea-level this feature disappears again.

Zusammenfassung

GUTTENBERGER H., BERMADINGER E., GRILL D. & HOLZER K. 1992. Wasserlösliche Thiolverbindungen in Fichtensämlingen verschiedener Seehöhen-Herkunft. – *Phyton* (Horn, Austria) 31 (2): 217–226. – Englisch mit deutscher Zusammenfassung.

In dieser Arbeit werden die Zusammenhänge zwischen dem SH-Gehalt in den Nadeln junger Fichten mit ihrer genetischen Herkunft verglichen. Berglagenfichten zeigen anfangs höhere SH-Gehalte in ihrer F₁-Generation als Tallagenfichten. Werden die Fichtensämlinge für längere Zeit in einer bestimmten Seehöhe belassen, verlieren sich diese Unterschiede wieder.

¹⁾ Dedicated to Prof. Dr. Otto HÄRTEL on the occasion of his 80th birthday.

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Introduction

The water-soluble thiols in spruce (*Picea abies* [L.] Karst.) needles consist to a prevailing part of glutathione (GSH) and to a minor part (normally 5%) of cysteine (GRILL & ESTERBAUER 1973a) and γ -glutamyl-cystein (SCHUPP & RENNENBERG 1988). The absolute concentration and the relationship of its components are subjected besides to a diurnal rhythm (SCHUPP & RENNENBERG 1988) mainly to a seasonal rhythm (GRILL & ESTERBAUER 1973 b, ESTERBAUER & GRILL 1978). Thiols have manifold tasks in metabolism (RENNENBERG 1982). Their interaction with proteins must be mentioned as one of the most important ones. GSH acts as stabilizer to the SH/SS quotient; thus the function of proteins is guaranteed, whereas GSH has a repairing effect by resolving S-S groups strongly built up by stress (ESTERBAUER 1976). Therefore it was obvious to LEVITT & al. 1961 to examine the connection between SH-groups and stress. The thiols were conceded a main position in stress hypothesis (LEVITT 1980). GRILL & ESTERBAUER 1973 b, ESTERBAUER & GRILL 1978, GRILL & al. 1982, GRILL & al. 1987 connected the increase of the GSH concentration in winter with greater stress, which is a special burden to evergreen plants during that season; furthermore they also observed a higher protein-SH-concentration in winter (PFEIFHOFER & al. 1988).

Because of its natural occurrence within a broad sea-level zone the European spruce is exposed to very different climates, so that the genetic adaption to higher regions of the Alps – in connection with a shorter vegetation period – also goes along with a proportionate stress disposition (SCHMIDT – VOGT 1986). GRILL & al. 1988, GRILL & al. 1990, PFEIFHOFER & al. 1987 refer the higher SH-concentrations which they found at a higher sea-level to the stress situation in that region. Based on examinations of different mountain- and valley-provenances and alternate plantations GRILL & al. 1988 drew the conclusion, that climate factors are dominate responsible for higher thiol quantities in mountaineous regions and there is no genetically fixed feature of mountain provenances. These results were gained from spruces which had already been cultivated either in valley- or

Table 1

Data of the origins of the serie 1980/81. Explanation in the text.

origin = provenances of the mothertrees; asl = altitude above sea level [m] of the mothertrees; NOB = number of buds, values > 650 = mountainous type, < 650 and > 370 = middle region type, < 370 lower region type (cp. HOLZER 1967, 1975, 1981); type = phenological-physiological behaviour of the seedlings (cp. HOLZER 1981); group = F₁-generation of the mothertrees, classified on the annual length of the shoots: 1 = $\leq$ 3 mm, 5 = $\geq$ 30 mm; Ø = average of the classification in groups; B = Burgenland, C = Carynthia, LA = Lower Austria, S = Salzburg, St = Styria, T = Tyrol, UA = Upper Austria. Explanation in the text.

in mountain-regions for some years. But the seedlings could possibly also still have attributes – as information from the mothertree – which make them develop a thiol concentration that corresponds to the origin of the seeds. That would signify a higher thiol concentration in seedlings from the seeds from higher areas compared to those from lower regions. But such a genetically conditioned thiol concentration could be dominated by the local stress situation in the following years.

Origin	asl [m]	NOB	type
Breitenfurth, LA	600-900	249	low
Hopfgarten, Kelchsau, UA	1100	665	high
Hopfgarten, Wertendorf, UA	1700	424	middle
Innsbruck, Gnadenwald, T	400-900	271	low
Innsbruck, Leutschach, T	1300	731	high
Innsbruck, Nassenreith, T	1500	804	high
Kelchsau, UA	1600	675	high
Kitzbühel, T	1200	482	middle
Kitzbühel, T	1000	402	middle
M. Lankowitz, Piber, St	600	276	low
M. Lankowitz, Pölzen, St	1000-1400	719	high
Mariazell, Walster, St	1000-1200	387	middle
Matrei i. O., T	1600-1700	737	high
Mauterndorf, Muhr, S	1400	755	high
Mauterndorf, St. Michael, S	1000	529	middle
Mitterndorf, St	1350-1550	682	high
Mitterndorf, Kairisch, St	800	352	low
Neuberg, Niederalpl, St	900-1300	716	high
Oberwart, Pinkafeld, B	300-600	305	low
Schneegattern, S	600	246	low
Silian, T	1700-1800	641	middle
St. Pölten, Schlauching, LA	400	295	low
Villach, Hermagör, C	1400	613	middle
Villach, Hermagor, C	700	203	low
Zwettl, Rosenau, LA	650	289	low

Material and Methods

For these investigation series there was planting material of spruces from two different sowing times at disposal. The seeds were taken from mothertrees from various Austrian areas at different sea-levels. The questioning was not only limited by investigation of the origin from different sea-levels, but also referred to the ecotypes within one origin. This becomes an important fact if the F_1 -generation of a mother-tree is investigated. Within the seedlings from one mother-tree one can distinguish plant groups of montane type, middle region type, and lower region type. A helpful tool for classifying a tree is the determination of the vegetation period (HOLZER 1981) a short vegetation period refers to the mountainous type and groups with a long vegetation period refer to the lower region type.

All trees were cultivated in the tree-nursery „Tulln“ at 350 m asl.

In the first series of tests 1980/81 (appendage of 25 origins of spruces from harvest 1971, sawing 1980, sampling 1981), all descendants of one origin were used as a mixed sample for the determination of thiols, because there was too little substance for a further more differentiated determination of the descendants (tab. 1).

In the series of tests 1986/88 there was plenty of planting material available for checking the dependence of the SH content upon the origin of the phenological-physiological behaviour of the single plants. For that purpose the single groups (mountainous type and lower region type) were graded by classifying them within one origin according to the size of the plants in the year of harvest. The dependence of the plant size on the development of the end bud during the first year is clearly ensured (HOLZER 1981). The series taken for these investigations comprised altogether 65 origins; 25 of them were at disposal as annual plants and also as biennial plants; additionally 40 origins were examined only as biennial seedlings. Because of the annual length of shoots five groups could be distinguished fairly safely (tab. 2a, 2b); from 1 = mountainous type to 5 = lower region type. In both test series the plants were taken from the seed beds at the beginning of winter and they were kept wrapped in order to have them available at the moment of investigation. The sorting of the plants within the selected origins and afterwards the dispatch of the postal parcels to Graz for carrying out the thiol analyses took place in the course of January (resp. in March in test series 2b). Because of preliminary examinations we know that the alterations of the thiol content under these conditions of transportation are insignificant and neglectable concerning our question. In the lab the spruces were taken immediately out of the box and separated according to the age classes. In each case only the last needle age class examined. As a rule there was plenty of needle material available for the investigations, and only in some cases several samples had to be mixed up. Annual plants were mainly blended. But there was taken into consideration that they corresponded to one type, which means mountainous or lower region.

The determination of the water-soluble thiol compounds was carried out according to GRILL & ESTERBAUER 1973a and GRILL & al. 1982: 1 g of spruce needles (fresh weight = FW) was homogenized (Ultraturax, 30 s at 24 000 rpm) in 25 ml aqueous ascorbin acid solution. 5 ml of the filtered extract are added to 4.5 ml 0.2 M phosphate buffer and 0.5 ml DTNB-reagent (30 mg 2,2'-dinitro-5,5'-dithiobenzoeic acid, dissolved in 10 ml 0.2 M phosphate buffer, pH 7.0). The extinction of the arising yellow staining is measured in 1 cm cuvettes at 412 nm against 5 ml phosphate buffer and 5 ml extract (E_{412}). At a second measurement the extinction of 9.5 ml phosphate

Table 2 a

Data of the origins of the series 1986/88; a = one year old seedlings, b = two years old seedlings. Correlation-coefficient between the average size of the plants and the NOB: $r = -0.89 ***$ (one year old seedlings), and $r = -0.89 ***$ (two years old seedlings); correlation-coefficient between the two dates of sawing (1986/1988) $r = 0.92 ***$ Explanation in the text.

Abbreviations see tab. I

Origin	asl [m]	type	NOB	Group a					Ø	Group b					Ø
				1	2	3	4	5		1	2	3	4	5	
Bad Ischl, UA	900-1300	middle	631	44	109	32	5	-	1.99	58	93	28	4	-	1.88
Bad Mitterndorf, St	1300-1400	high	820	54	15	3	-	-	1.29	47	66	17	-	-	1.77
Brandenberg, T	1300	middle	617	16	97	61	2	-	2.28	43	100	66	41	13	2.55
Gosau, UA	1300-1400	high	771	48	79	3	-	-	1.65	88	58	20	3	-	1.63
Gosau, UA	1400-1500	high	826	56	81	6	-	-	1.65	120	78	28	2	3	1.66
Groß Reifling, St	1300-1400	high	739	56	97	9	-	-	1.71	94	108	38	6	-	1.82
Groß Reifling, St	1300-1400	middle	604	24	42	19	3	-	2.01	54	55	36	14	-	2.06
Großarl, S	1400-1500	high	698	30	42	37	9	-	2.21	43	66	31	6	2	2.04
Großarl, S	1500-1600	middle	610	-	41	34	4	-	2.53	64	64	24	6	1	1.84
Hallein/Adnet, S	500	low	244	-	21	74	53	6	3.28	7	49	79	58	34	3.28
Hintersee, UA	900-1300	low	363	17	138	108	14	-	2.43	6	108	99	32	5	2.69
Inst-Roppen, T	1700-1850	middle	546	18	66	36	13	3	2.39	23	106	55	26	16	2.58
Kindberg, St	950	low	344	-	20	74	63	16	3.43	-	31	54	47	36	3.52
Lainsach/Göls, St	950	low	339	4	8	59	39	5	3.29	5	29	54	41	23	3.32
Leutasch, T	1500-1600	high	762	87	105	13	-	-	1.72	84	74	33	23	-	1.97
Mitterndorf, St	900-1300	middle	618	47	82	23	-	-	1.84	93	84	20	18	-	1.83
Mitterndorf, St	1300-1400	high	761	56	43	-	-	-	1.43	75	55	29	5	-	1.78
Mühlbach, S	1500-1600	high	772	29	14	2	-	-	1.40	54	26	23	1	-	1.75
Neuberg, St	1300-1400	high	911	48	17	-	-	-	1.26	115	60	11	2	-	1.47
Pölla-graben, St	900-1300	low	341	11	35	17	2	1	2.20	26	35	26	8	-	2.17
Pölsen, St	1200-1400	high	823	39	83	14	4	-	1.88	111	82	21	2	-	1.60
Rathhof, St	900	low	297	7	68	64	8	3	2.55	15	19	27	23	-	2.69
Schlachitzgraben/Göls, St	700	low	282	-	3	60	62	17	3.65	-	24	46	49	30	3.57
Straßburg, C	600	low	330	8	25	52	28	-	2.88	-	10	40	42	17	3.54
Villach, C	1500-1600	high	752	68	52	17	-	-	1.63	64	45	32	6	5	1.91

buffer and 0.5 ml DTNB-reagent is measured against 10 ml phosphate buffer (E_2). The SH-content is calculated according to the formula:

$$\frac{E_1 - E_2}{6800} = M \text{ SH/g FG}$$

The determination of the dry weight resulted from drying the needles at 105° C up to weight constancy.

The static evaluation was carried out at a PC using the statistic programme NCSS (Unisoft Comp.) according to Student's t-test. In the tables highly significant distinctions ($P = \text{probability of error} < 0,01\%$) are marked with ***, significant distinctions ($0,1 < P < 1\%$) are marked with ** and distinctions of low significance ($1 < P < 5\%$) are marked with *. Not significant distinctions ($P > 5\%$) are marked with °.

Results and Discussion

The basic requirement for examining the thiol content is its execution during a physiologically stable period of the spruces. We chose the time of winter rest from January to February. Outside such stable periods the thiol concentration would vary too much because of the different states of development of the spruces with mountaineous and lower region characters. This problem always occurs with eco-physiological examinations of spruces of different sea-level (GRILL & al. 1988, BERMADINGER & al. 1989). As GRILL & al. 1973 a, b, ESTERBAUER & GRILL 1978 stress and what can also be seen in other papers (e. g. PFEIFHOFER & al. 1988, GRILL & al. 1987 etc.), the thiol content in winter is dependent on the prevailing temperature. As the results of the test series show, the thiol concentration in both series is differently high (tab. 3). The causes can be found in the above mentioned climatic conditions, as the winter of 1981/82 was essentially colder than the relatively warm winter of 1987/88.

The statistic examination of both test series (1980/81 and 1986/88) revealed that the thiol concentration in needles of spruce seedlings can be correlated to the origin of the seed grain, although all seedlings grew up at 350 m asl. Mountaineous seedlings showed significant respectively partly statistically secured higher SH-values – both relating to dry and also to fresh weight – than seedlings from lower region provenance (compare tab. 3). Hereby the correlations with sea-level show up more clearly than coordination to low region and mountaineous types being based on the number of buds (= NOB): Statistic examination had only correlations with $P > 5\%$. The value of the NOB corresponds to the average duration of the vegetation period, in the course of which higher values indicate a higher source sea level (HOLZER 1967, 1975, 1981, 1988). The NOB of the descendants, which was defined on the occasion of a further investigation (HOLZER 1985), correlates more or less well with the origins (tab. 1). The values of both series in tab. 3 show annual seedlings at the series 1981/82 but biennial

Table 2b

Data of the origins and the examined groups of the series 1986/88, two years old seedlings; correlation-coefficient between the average size of the plants and the NOB: $r = -0.93$ *** Explanation in the text.

Abbreviations see tab. I

Origin	asl [m]	type	NOB	Group					O
				1	2	3	4	5	
Bad Aussee, UA	1000	middle	381	-	18	116	86	56	3.65
Felfering, Gurk, C	1450	low	411	-	33	65	51	50	3.59
Gosern, Obersee, UA	850-880	middle	463	-	20	105	92	58	3.68
Gosau, UA	1300-1400	high	691	77	114	45	8	-	1.93
Großarl, Grafenberg, S	1600-1700	high	768	37	47	12	2	-	1.79
Großarl, Kronau, S	1450	middle	567	32	117	103	30	3	2.49
Großarl, St. Johann, S	1500-1600	middle	610	36	46	45	24	11	2.56
Hallein, Adnet, S	900-100	low	303	-	52	104	69	16	3.20
Hallein, Adnet, S	500	low	246	-	7	49	68	40	3.86
Hermagor, C	1300-1400	high	731	73	59	36	13	7	2.05
Hermagor, C	1500-1600	middle	639	65	66	48	11	-	2.03
Hermagor, C	500-600	middle	661	66	59	25	8	6	2.03
Hintersee, UA	1000-1100	middle	377	10	46	97	71	36	3.29
Hohe Wand, LA	1000	middle	438	8	100	157	61	17	2.94
Hohe Wand, LA	700-800	middle	399	4	49	123	44	19	3.11
Innsbruck, Gaistal, T	1500-1600	middle	629	32	102	60	12	5	2.40
Innsbruck, T	1460-1560	middle	648	67	156	50	4	-	1.98
Kohlehen, St	1000	high	398	11	64	104	32	-	2.74
Milstatt, C	1400-1600	high	790	37	63	19	1	1	1.89
Milstatt, C	1400-1600	high	702	44	45	11	-	-	1.67
Neuberg, Krampen, St	1300-1400	high	822	41	44	10	8	2	1.95
Obervellach, C	1480-1500	high	832	157	98	14	-	-	1.47
Offensee, UA	800	low	350	-	5	88	87	32	3.69
Offensee, Rindbach, UA	940-1060	low	358	-	41	103	68	27	3.34
Offensee, Rindbach, UA	940-1060	low	359	-	19	61	41	26	3.50
Offensee, UA	700-900	low	308	-	12	50	56	73	3.99
Orth, UA	900-960	low	322	-	20	80	57	39	3.59
Rosenau, UA	950	middle	393	5	43	97	34	3	2.93
Rosenau, UA	950	middle	422	2	83	131	59	4	2.93
Schwarzach, S	1650	middle	625	22	26	13	7	1	2.12
Silian, T	1500	middle	547	16	88	110	38	9	2.75
Villach, Gerlitz, C	1500-1600	high	852	39	46	21	2	3	1.95
Waydhofen/Ybbs, LA	970	low	328	-	67	91	32	17	3.00
Windischgarsten, UA	1300	high	796	72	83	29	8	1	1.89
Windischgarsten, UA	1300	high	839	133	75	20	5	2	1.60
Braunau, UA	300-600	low	240	3	44	86	61	12	3.17
Oberwart, B	400	low	309	3	36	117	51	28	3.28
Mauterndorf, S	1500	high	667	29	73	37	6	5	2.23
St. Michael/Lg, S	1600-1700	high	710	103	83	21	4	1	1.67
Innsbruck, T	1360-1420	high	871	126	157	10	2	-	1.64

ones at the series 1988. An evaluation of annual seedlings from the series 1986/88 produced no statistically secured statement, as too many groups and also origins had to be blended because of the small material quantity.

If one tries to get further information within the F_1 -generation of the same origin by classifying the seedlings being based on the periods of

Table 3

Water SH-content, average and SD [$\mu\text{M SH/g FW}$]; n = number of examined seedlings; significance of the correlation between the provenances of the mother trees. Explanation in the text.

Provenance	$\mu\text{M SH/g FW}$ 1981/82	n	$\mu\text{M SH/g FW}$ 1986/88	n
High	1.31 ± 0.39	7	0.81 ± 0.14	37
Middle	0.97 ± 0.16	9	0.75 ± 0.13	34
Low	0.70 ± 0.24	9	0.70 ± 0.13	32
Correlation	Significance			
High/Low	**		***	
High/Middle	*		o	
Low/Middle	*		o	

vegetation in mountainous and lower types, no statistically secured relations can be stated. That means, that mountainous types (group 1, tab. 2a, b) within the F_1 -generation of one origin do not have more thiols than the lower region types (group 5). At least the differences are so small, that they cannot be parted from each other statistically. It is evident therefore that the characteristic feature „higher thiol content“ e. g. of a origin of higher sea-level obviously comprises the whole number of descendants, even if the F_1 -generation is split up in different phenotypes.

The mean value of the seedlings' affiliation to the groups 1–5 comp. tab. 2a and 2b naturally shows a correlation to the origin of the trees, as descendants with prevailing mountainous type come from mountainous regions so that descendants with a mean value under 3 (mountainous type) have higher thiol contents than with a mean value above 3 (lower region type). This subdivision of descendants of one origin could possibly have shown a result, if the completion of growth before resp. at the end of September had really been checked. The development of the increase length as sign for classifying mountainous and lower region forms is subject to many factors such as e. g. root damages, insect infection etc., so that it could not serve exclusively as a safe and unequivocal criterion for the classification to a tree type even though HOLZER 1981 could show up statistical correlations.

Although all seedlings from all origins were cultivated at the same sea level (350 asl) it is obviously that the genetic information is transferred to the young trees via their seeds so that they behave like mountainous or low

region origins as far as their thiol content is concerned. Even if this does purely phenotypically not appear at the descendants. This quality of higher thiol concentration and origin from higher sea-level disappears at longer cultivation at a certain sea-level (GRILL & al. 1988). According to LEVITT's stress hypothesis (1980) this implies that mountaineous provenances supply their descendants from the beginning with a better protection against stress in higher regions than lower ones.

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Recensio

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Fünf Jahre nach dem ersten Band (vgl. die Rezension in *Phyton* 26 (2): 317, 1986) ist nun erfreulicherweise auch der zweite und letzte Band der *Mountain Flora of Greece* herausgekommen und damit diese Flora eines der bisher botanisch am schlechtesten bekannten Bergländer Europas abgeschlossen worden. Einiges hat sich gegenüber dem ersten Band verändert: Ein Coeditor hat mitgearbeitet, der Verlag wurde gewechselt und schließlich ist der neue Band um ca. 150 Seiten umfangreicher.

Über den berücksichtigten Raum und die Art der Präsentation vgl. die eingangs zitierte Rezension. Für die Benützung des Werkes wesentliche Teile der allgemeinen Einleitung aus Band 1 sind übernommen bzw. adaptiert worden. Insbesondere sei darauf hingewiesen, daß die Liste mit den Namen der Berge und den Höhenangaben revidiert worden ist; die zugehörige Karte ist auch nochmals abgedruckt.

Der Band beginnt mit dem zweiten Teil der Dicotylen ab den *Gentianaceae* und enthält an großen Familien u. a. *Lamiaceae*, *Scrophulariaceae* und *Asteraceae*. Dann folgen die Monocotylen mit *Liliaceae* s. l. [*Dioscoreales*, *Asparagales* exkl. *Amaryllidaceae*, *Liliales* exkl., *Iridaceae*], *Poaceae*, *Cyperaceae* u. a. Gut illustriert sind die Gattungen *Nepeta*, *Thymus*, *Taraxacum* (Achänen) und *Carex* (Schläuche). Auch auf den „Griechischen Bergtee“ von den taxonomisch schwierigen Sippen aus *Sideritis* sect. *Empedoclia* (*Lamiaceae*) ist Augenmerk gerichtet (3 Abbildungen). 34 Seiten Schriftenverzeichnis und das Namensregister bilden den Abschluß.

Band 2 enthält 1054 anerkannte Taxa im Range von Arten und Unterarten; zusammen mit Band 1 sind in der Flora 1980 Taxa berücksichtigt, das ist ca. ein Drittel der Gefäßpflanzenflora Griechenlands (p. XIII). Wieder ist ca. ein Drittel der Arten dieser Flora nicht oder nicht in dieser Form (andere Rangstufe, anderer Name) für Griechenland in der Flora Europaea angegeben.

Die *Mountain Flora of Greece*, zu deren erfolgreichem Abschluß man A. STRID gratulieren darf, wird sicherlich die floristische, systematische und pflanzengeographische Forschung in Griechenland und den angrenzenden Ländern sehr stimulieren.

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Zoologisch-Botanische Datenbank/Zoological-Botanical Database

Digitale Literatur/Digital Literature

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