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# The Geographic Variation in European Silver Fir (Abies alba Mill.)

## Gas Exchange and Needle Cast in Relation to Needle Age, Growth Rate, Dry Matter Partitioning and Wood Density by 15 Different Provenances at Age 6

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### Abstract

Photosynthesis, respiration and transpiration were studied in one- and two-year-old needles of 15 *Abies alba* (MILL.) provenances at the age of 6 years. Needle cast and nutrient content were registered for the last four year's needles. Differences in all traits could be demonstrated. Especially, differences between provenances in the rate of senescence of the photosynthetic apparatus (needles) where obvious. Thereby provenances from central and eastern Europe showed pronounced decline in photosynthetic capacity and heavy needle losses over needle age compared with provenances from Calabria (southern Italy).

In addition height, diameter, wood density and dry matter partitioning were measured. Provenance differences in all traits could be demonstrated. Thereby seed sources from Calabria (southern Italy) were characterized by a high growth vigor compared with the provenances from central and southeast Europe.

*Key words:* Photosynthesis, respiration, transpiration, dry matter partitioning, growth, wood density, *Abies alba*, provenances, senescence, silver fir decline.

### Summary

Photosynthesis, respiration and transpiration were studied in one- and two-year-old needles of 15 *Abies alba* (MILL.) provenances (respectively 6 from central Europe, 5 from southeastern Europe and 4 from southern Italy/Calabria) at the age of 6 years. In addition, needle cast and nutrient content were registered for the last four year's needles. Gas exchange was measured under controlled conditions (20 °C, 35% relative humidity, 480 $\mu E \cdot m^{-2} \cdot s^{-1}$) on small twigs by using a $CO_2/H_2O$-Porometer (Walz, Effeltrich/FRG). At the end of the sixth growing season the material was analysed for height and diameter growth, wood density and dry matter partitioning.

The results demonstrate significant differences between provenances in almost all traits measured, which mainly could be attributed to regions. Thereby provenances from southern Italy (Calabria) behaved quite differently compared to provenances from the rest of the natural distribution of the species. Differences between provenances from central and southeast Europe were mostly absent.

Photosynthesis of the one-year-old needles was slightly higher for the Calabrian provenances compared with the provenances from the other regions (central and southeastern Europe). For the two-year-old needles, a drastic reduction in photosynthesis was registered for the central and southeast European provenances. By contrast, the Calabrian provenances maintained high rates of photosynthesis. The respiration rates of the one-year-old needles were slightly lower for the Calabrian provenances in comparison to seed sources from the rest of the natural distribution. The two-year-old needles of the Calabrian provenances were characterized by higher rates of respiration.

The Calabrian provenances showed higher transpiration rates. Water use efficiency did not differ between provenances as far as the one-year-old needles are concerned. The two-year-old needles of the Calabrian provenances were characterized by a pronounced better water use efficiency (less units water transpired in order to fix one unit $CO_2$). This indicates overall better water relations and thereby a better adaptation to drought of the Calabrian provenances compared with seed sources from central and southeast Europe.

The big differences in needle cast between provenances could almost entirely be explained by regions. Thereby pronounced losses of older needles were registered in the central and southeast European provenances, whereas the Calabrian seed sources showed merely moderate losses.

The Calabrian provenances were characterized by high growth rates (height, diameter, dry matter and stem volume: respectively 19%, 13%, 45% and 47% above a mean of all provenances) and exhibited a pronounced

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variation within the region. Further, the wood density was slightly below mean (4%).

Provenances from southeastern Europe showed rather low growth rates (height, diameter, dry matter and stem volume: respectively 7%, 3%, 12% and 15% below mean of all provenances). Wood density was 1% above the over all mean. The provenances from this region showed higher needle to twig ratio (7% above mean) compared to the seed sources from the other regions.

The central European seed sources exhibited the lowest growth vigor (height, diameter, dry matter and stem volume: respectively 7%, 6%, 21% and 22% below mean of all provenances). Wood density was 2% above the overall mean.

The results indicate, that the silver fir from central and east Europe are characterized by little variation between provenances, slow growth rates and a rapid development of senescence of the photosynthetic apparatus compared with the Calabrian silver fir. Findings which are discussed in relation to silver fir decline.


### Zusammenfassung

Messungen von Photosynthese, Respiration sowie Transpiration wurden an 6jährigen Weißtannen (*Abies alba* Mill.) von 15 verschiedenen Herkünften (6 aus Zentraleuropa, 5 aus Südosteuropa, 4 aus Calabrien/Süditalien) vorgenommen. Die Gaswechselmessungen wurden an ein- und zweijährigen Nadeln vorgenommen. Zusätzlich wurden Nadelverluste sowie Nährstoffgehalte der vier letzten Nadeljahrgänge ermittelt. Am Ende der 6. Wachstumsperiode wurden Sproßhöhe, Wurzelhalsdurchmesser, Stammvolumen, Holzdichte sowie Trockenmasse und deren Verteilung ermittelt.

Die Ergebnisse zeigten signifikante Unterschiede zwischen den Provenienzen bei fast allen ermittelten Merkmalen. Diese Unterschiede kamen hauptsächlich durch die Provenienzen aus Calabrien zustande, während Unterschiede zwischen Herkünften aus dem gesamten zentral- und südosteuropäischen Raum kaum vorhanden waren.

Die Photosyntheseleistung der 1-jährigen Nadeln lagen bei den calabrischen Provenienzen etwas höher als bei den Herkünften aus Zentral- und Südosteuropa. Die 2jährigen Nadeln der zentral- und südosteuropäischen Provenienzen zeigten gegenüber den 1jährigen Nadeln eine starke Reduktion der Photosyntheseleistung, während dies bei den calabrischen Herkünften nicht beobachtet wurde.

Die Respirationsraten der calabrischen Herkünfte lagen bei den 1jährigen Nadeln geringfügig niedriger als die der zentral- und südosteuropäischen Provenienzen. Bei den 2jährigen Nadeln wurde das Umgekehrte beobachtet.

Die calabrischen Provenienzen waren bei beiden Nadeljahrgängen durch relativ hohe Transpirationsraten gekennzeichnet. Die Wassernutzungseffizienz der 1jährigen Nadeln variierte nicht zwischen den Provenienzen. Bei den 2jährigen Nadeln zeigten die calabrischen Provenienzen eine wesentlich bessere Nutzungseffizienz (weniger Wasser transpiriert pro fixierte Einheit $CO_2$). Dies deutet auf eine gegenüber den zentral- und südosteuropäischen Provenienzen bessere Anpassung an Trockenheit der calabrischen Herkünfte hin.

Mit zunehmendem Nadelalter zeigten die zentral- und südosteuropäischen Provenienzen starke Nadelverluste. Im Vergleich dazu waren die Nadelverluste der calabrischen Herkünfte relativ gering.

Die Untersuchungen deuten darauf hin, daß die zentral- und südosteuropäische Tanne durch eine schnelle Alterung des Photosyntheseapparates im Vergleich zu der calabrischen Tanne charakterisiert ist. Die Ergebnisse werden in Relation zu neueren Theorien zum Tannensterben diskutiert.

Die calabrischen Herkünfte waren durch hohe Wachstumsraten charakterisiert (Höhe, Durchmesser, Trockenmasse und Stammvolumen lagen um 19%, 13%, 45% bzw. 47% über dem Durchschnitt aller Provenienzen). Die Holzdichte lag geringfügig unter dem Durchschnitt (4%).

Provenienzen aus Südosteuropa zeigten ein verhältnismäßig langsames Wachstum (Höhe, Durchmesser, Trockenmasse und Stammvolumen lagen um 7%, 3%, 12% bzw. 15% unter dem Durchscnitt aller Provenienzen). Die Holzdichte lag im Durchschnitt um 1% über dem Mittel.

Die zentraleuropäischen Provenienzen wiesen die geringste Wüchsigkeit auf (Höhe, Durchmesser, Trockenmasse und Stammvolumen lagen um 7%, 6%, 21% bzw. 22% unter dem Durchschnitt aller Provenienzen). Die Holzdichte lag 2% über dem Durchschnitt aller Herkünfte.

Charakteristisch für die Gebiete Südost- und Zentraleuropa war eine relativ geringe Variation zwischen den Provenienzen. Bei allen Eigenschaften wurde dagegen eine große Variation zwischen den Provenienzen in Calabrien nachgewiesen.

Während die südosteuropäischen Provenienzen durch ein signifikant höheres Verhältnis zwischen Nadel- und Sproßmasse gekennzeichnet waren, konnen weder auf Provenienz- noch auf Gebietsebene signifikante Unterschiede im Sproß-Wurzel-Verhältnis nachgewiesen werden.


### Introduction

Provenance trials with European silver fir (*Abies alba* Mill.) demonstrate, that seeds sources from southern Italy (Calabria) are characterized by a pronounced variability and a high vitality and growth vigor. In contrast, all provenances from central Europe show little variability, less vigor, and pronounced signs of "Silver Fir Dieback" (Larsen, 1981, 1986a and b).

The aim of the present investigations is to study the provenance variation in growth rate and dry matter partitioning within and between different regions of the silver fir range. Thereby more information about the geographic variation in European silver fir should be compiled in order to establish better provenance recommendations.

Further, the present investigations aim to study the provenance variation in the basic physiological properties responsible for energy exchange (photosynthesis, respiration and transpiration). These studies are especially designed in order to analyze these properties in relation to ageing of the photosynthetic tissue, since similar studies analysing gas exchange of the youngest needles partly failed to explain the observed large differences in vitality and growth rate between provenances (Mekic, 1988).

Since pronounced needle losses, one of the characteristic signs of silver fir dieback, can be considered as early ageing (senescence) of the needles, the above mentioned gas exchange measurements are compared with provenance-specific variation in needle cast.

### Material and Methods

*Plant material*

The plant material considered of 6-year-old *Abies alba* trees of 15 different provenances listed in *table 1*. The geographic locations are shown in *figure 1*. The numbers are identical to those in a provenance study containing 38 seed sources (Larsen, 1985, 1986b). These earlier studies were able to group the material into 3 provenance regions by means of cluster analysis (Larsen and Schaaf, 1985;

*Table 1.* — *Abies alba* provenances included in the study.

| No. | PROVENANCE, Country | Region(*) | Latitude(°N) | Longitude(°O) | Altitude(m) |
|---|---|---|---|---|---|
| 1 | GARIGLIONE, Italy | C | 39°15' | 16°27' | 1600-1760 |
| 2 | RIBARICA, Bulgaria | S | 42°49' | 24°31' | 1000-1200 |
| 3 | LAPUS, Rumania | S | 47°33' | 24°04' | 700-1000 |
| 5 | SIEGSDORF, F.R.Germany | M | 47°49' | 12°39' | 700- 900 |
| 8 | GOC, Yugoslavia | S | 43°05' | 20°40' | 900-1000 |
| 9 | AVRIG, Rumania | S | 45°40' | 24°26' | 800- 900 |
| 10 | ZWIESEL, F.R.Germany | M | 49°03' | 13°14' | 620- 730 |
| 15 | MAMMA GIUSEPPINA, Italy | C | 39°16' | 16°27' | 1350 |
| 18 | GOBBARIELLU, Italy | C | 38°33' | 16°17' | 1100 |
| 21 | CERASARELLA, Italy | C | 38°33' | 16°18' | 1320 |
| 24 | PESCOPENATARO, Italy | M | 41°36' | 14°13' | 1100-1300 |
| 25 | GESCHWEND, F.R.Germany | M | 48°56' | 9°48' | 400- 500 |
| 30 | OCHSENBODEN, Switzerland | M | 46°17' | 7°33' | 1000-1500 |
| 32 | DONJA STUPCANICA, Yugoslav. | S | 44°07' | 18°40' | 750 |
| 34 | LAVARONE, Italy | M | 45°56' | 11°15' | 1050-1400 |

(*)Grouping into regions according to cluster analysis (LARSEN 1986b, MEKIC 1988):
C: Calabria/southern Italy (Nos. 1, 15, 18, 21)
M: Central Europe (Nos. 5, 10, 24, 30, 34)
S: Southeast Europe (Nos. 2, 3, 8, 9, 32)

Larsen, 1986b; Mekic, 1988). The region "Calabria"/southern Italy (C) is represented with 4 provenances, whereas the regions "Southeast Europe" (S) and "Central Europe" (M) are included with 5 and 6 seed sources respectively (*Table 1*).

The seed was sown in spring 1982, and during the following 6 years the plants were grown in containers under optimal nutrient and water supply. At the time of testing the average height was 64 cm, varying from 48 cm to 99 cm between provenances.

*Test methods*

Photosynthesis (net $CO_2$ uptake), respiration (dark) and transpiration were measured on small twigs by using a $CO_2/H_2O$-Porometer (Fa. Walz, Efféltrich, FRG) as described by Lange (1984). The measurements were made under controlled conditions (20 °C, 35% relative humidity, 480 $\mu E \cdot m^{-2} \cdot s^{-1}$) in a climate chamber. The measurements took place in December 1987. Each provenance was represented by 10 plants, and gas exchange was measured on the current years needles (1987, one-year-old) and on the needles of the previous year (1986, two-year-old).

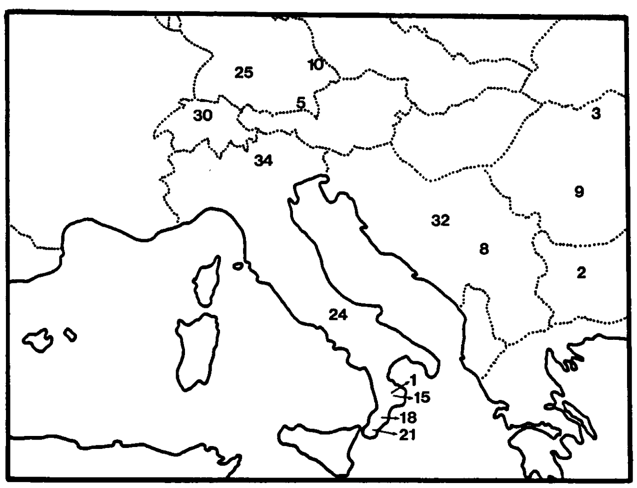


*Figure 1.* — Location of the provenances tested.

All the 150 plants analyzed in the study were registered simultaneously for needle losses. Thereby twigs of the last 4 years (1987, 1986, 1985, 1984) were included.

After the sixth growing season the content of the macro nutrients (nitrogen, phosphorus, potassium, calcium and magnesium) was analysed separately for the last four year's needles (1987, 1986, 1985, 1984). Height and root collar diameter were registred. Further, the soil was carefully removed from the roots, and after 24 hour by 105 °C the dry matter of roots, needles and top was separately registered. Before drying, the stem volume (with bark) was calculated by sectioning each stem in 5 parts. Wood density (dry matter in g/fresh volume in $cm^3$) was measured at the lowermost section (without bark).

## Results

*Photosynthesis*

Table 2 presents the photosynthesis values. The mean values of each provenance are displayed. In the lower part of the table the provenances are grouped into three regions according to *table 1*. Statistical analysis are done by means of analysis of variance (F-ratios are displayed for provenance, respectively region effects). With an overall mean of 2.95 mg $CO_2$ per g needle dry matter and hour, the rate of photosynthesis of the one-year-old needles varies from 2.27 (no. 2) to 3.89 (no. 15). These differences between provenances are highly significant, mainly due to higher photosynthetic rates of the Calabrian provenances (20% above average).

In the two-year-old needles a pronounced differentiation occurs: The four Calabrian provenances are characterized by still high photosynthetic rates (from 2.89 mg to 3.73 mg $CO_2$), whereas the provenances from southeast (from 1.02 mg to 1.49 mg $CO_2$) and central Europe (from 0.49 mg to 2.07 mg $CO_2$) show drastically reduced rates of photosynthesis. With an average rate of 1.83 mg $CO_2$/g and h (all provenances), the mean rate of the Calabrian seed sources is 81% above, whereas the southeastern and central European provenances are exhibiting rates of 37%, respectively, 23% below.

The ratio between photosynthesis of the two- and the one-year-old needles (ratio 2/1) varies highly significant from 0,2 1 (no. 30) to 1.20 (no. 21). Most of the variation is explained by region: The mean ratio of the Calabrian provenances is 0.98, which means, that the two-year needles show 98% of the photosynthesis of the one-year-old needles. In contrast, photosynthesis of the two-year-old needles only make up 48%, respectively 47% compared with the one-year-old needles of the provenances from southeastern and central Europe.

The correlation coefficients between the photosynthesis measurements and the growth parameters (height and dry matter at 6 years, according to *Table 6*) on the provenance level are displayed at the bottom of *table 2*. The photosynthesis rate of the one-year-old needles is not correlated to height growth, and only a weak correlation to dry matter production is obtained. By contrast, significant correlations were registered between height growth and photosynthesis of the two-year-old needles, respectively, the ratio 2/1, and highly significant correlations were obtained by correlating the two parameters with dry matter production (r = 0.77, respectively 0.76).

*Respiration*

*Table 2* shows the respiration rates by levels of provenance and region. With an overall mean of 0.81 mg $CO_2$/g and h, highly significant differences between provenances in respiration rates of the one-year-old needles are demonstrated. These differences are mainly due to differences between regions, since the Calabrian seed sources are showing rather low respiration rates (0.70) compared to the provenances from southeastern and central Europe (0.83 and 0.86 respectively).

The differentiation in respiration rates of the-two-year old needles is less pronounced although significant on both the provenance and the region level. Thereby the Calabrian provenances are characterized by slightly higher respiration levels (0.73) compared with the other regions (0.63 and 0.62). The significant differences in the respiration ratio are mainly explained by regions. With a ratio of 1.07 the Calabrian provenances are slightly increasing their respiration rates from the first to the second needle year; by contrast, the seed sources from the two other regions are decreasing their respiration (0.82 and 0.77).

A negative, significant correlation was found between respiration of the one-year-old needles and dry matter production, whereas no correlations between growth and respiration of the two-year-old needles were obtained. The ratio between the respiration of the two- and the one-year-old needles was significantly correlated with both growth parameters.

*Transpiration*

*Table 3* presents the results of the transpiration measurements by levels of provenance and region together with the main results from the analysis of variance.

The transpiration rates of the one-year-old needles varies from 280 mg $H_2O$/g and h (no. 2) to 506 mg (no. 15) with an overall mean of 375 mg. These highly significant differences can be attributed mainly to differences between regions. The Calabrian provenances exhibit the highest transpiration rates (462 mg), the seed sources from central Europe show intermediate rates (366 mg), whereas the southeast European provenances are characterized by rather low transpiration rates (315 mg).

The rates of transpiration as well as the differentiation between provenances and regions increase in the two-year-old needles. Again most of the variation between provenances can be explained by regional differences. The Calabrian provenances show the highest rates (602 mg), whereas the provenances from the other regions are

*Table 2.* — **Photosyntheses and respiration of one- and two-year-old needles as well as their ratio, by provenance and region.**

| No. | PROVENANCE | Region | Mean values (relative values) 1-year-old | 2-year-old | Ratio 2/1 | Mean values (relative values) 1-year-old | 2-year-old | Ratio 2:1 |
|---|---|---|---|---|---|---|---|---|
| | | | Photosynthesis in mg $CO_2 \cdot g^{-1} \cdot h^{-1}$ | | | Respiration in mg $CO_2 \cdot g^{-1} \cdot h^{-1}$ | | |
| 1 | GARIGLIONE | C | 3.70 (126) | 2.92 (160) | 0.81 (133) | 0.74 ( 92) | 0.76 (117) | 1.05 (122) |
| 15 | MAMMA GIUSEP. | C | 3.89 (132) | 2.89 (158) | 0.81 (133) | 0.83 (102) | 0.75 (116) | 0.94 (108) |
| 18 | GOBBARIELLU | C | 3.45 (117) | 3.66 (200) | 1.08 (178) | 0.58 ( 72) | 0.69 (106) | 1.23 (142) |
| 21 | CERASARELLA | C | 3.14 (106) | 3.73 (204) | 1.20 (198) | 0.67 ( 83) | 0.70 (108) | 1.07 (124) |
| 2 | RIBARICA | S | 2.27 ( 77) | 1.12 ( 61) | 0.49 ( 80) | 0.76 ( 95) | 0.70 (108) | 0.97 (112) |
| 3 | LAPUS | S | 2.75 ( 93) | 1.49 ( 81) | 0.54 ( 88) | 0.92 (114) | 0.64 ( 98) | 0.73 ( 85) |
| 8 | GOC | S | 2.47 ( 84) | 1.02 ( 55) | 0.46 ( 76) | 0.86 (106) | 0.64 ( 99) | 0.82 ( 94) |
| 9 | AVRIG | S | 2.32 ( 79) | 1.08 ( 59) | 0.49 ( 81) | 0.80 (100) | 0.58 ( 89) | 0.81 ( 93) |
| 32 | D. STUPCANICA | S | 2.69 ( 91) | 1.07 ( 59) | 0.42 ( 69) | 0.80 ( 99) | 0.57 ( 87) | 0.76 ( 88) |
| 5 | SIEGSDORF | M | 3.08 (104) | 1.54 ( 84) | 0.51 ( 83) | 0.72 ( 89) | 0.52 ( 80) | 0.75 ( 87) |
| 10 | ZWIESEL | M | 2.66 ( 90) | 1.43 ( 78) | 0.53 ( 87) | 0.94 (116) | 0.77 (118) | 0.85 ( 99) |
| 24 | PESCOPENATARO | M | 3.19 (108) | 2.07 (113) | 0.63 (104) | 0.82 (102) | 0.71 (110) | 0.89 (102) |
| 25 | GESCHWEND | M | 3.35 (114) | 1.96 (107) | 0.58 ( 95) | 0.78 ( 96) | 0.65 ( 99) | 0.91 (105) |
| 30 | OCHSENBODEN | M | 2.54 ( 86) | 0.49 ( 27) | 0.21 ( 34) | 1.02 (127) | 0.49 ( 76) | 0.51 ( 59) |
| 34 | LAVARONE | M | 2.71 ( 92) | 0.96 ( 53) | 0.37 ( 61) | 0.87 (107) | 0.58 ( 89) | 0.69 ( 81) |
| | F: (provenance) | | $5.5^{***}$ | $14.1^{***}$ | $7.1^{***}$ | $3.1^{***}$ | $2.5^{**}$ | $3.6^{***}$ |
| | Calabria | | 3.55 (120) | 3.30 (181) | 0.98 (161) | 0.70 ( 87) | 0.73 (112) | 1.07 (124) |
| | Southeast Europe | | 2.50 ( 85) | 1.15 ( 63) | 0.48 ( 79) | 0.83 (103) | 0.63 ( 96) | 0.82 ( 94) |
| | Central Europe | | 2.92 ( 99) | 1.41 ( 77) | 0.47 ( 78) | 0.86 (106) | 0.62 ( 95) | 0.77 ( 89) |
| | F: (region) | | $25.0^{***}$ | $70.2^{***}$ | $34.1^{***}$ | $7.0^{**}$ | $4.7^{**}$ | $13.0^{***}$ |
| | Over all mean | | 2.95 (100) | 1.83 (100) | 0.61 (100) | 0.81 (100) | 0.65 (100) | 0.86 (100) |
| Correlations with growth parameters on the provenance level | | | | | | | | |
| Height at 6 years | | | $0.40^{ns}$ | $0.62^{*}$ | $0.61^{*}$ | $-0.47^{ns}$ | $0.20^{ns}$ | $0.57^{*}$ |
| Dry matter at 6 years | | | $0.52^{*}$ | $0.77^{***}$ | $0.76^{***}$ | $-0.66^{**}$ | $0.36^{ns}$ | $0.76^{***}$ |

*Table 3.* — **Transpiration and water use efficiency (transpiration/photosynthesis) of one- and two-year-old needles as well as their ratio.**

| No. | PROVENANCE | Region | Mean values (relative values) | | | Mean values (relative values) | | |
|---|---|---|---|---|---|---|---|---|
| | | | 1-year-old | 2-year-old | Ratio 2/1 | 1-year-old | 2-year-old | Ratio 2/1 |
| | | | Transpiration in mg $CO_2 \cdot g^{-1} \cdot h^{-1}$ | | | **Water use efficiency $H_2O/CO_2$** | | |
| 1 | GARIGLIONE | C | 484 (129) | 604 (140) | 1.25 (106) | 134 (104) | 216 ( 52) | 1.71 ( 52) |
| 15 | MAMMA GIUSEP. | C | 506 (135) | 572 (133) | 1.21 (102) | 131 (101) | 214 ( 51) | 1.68 ( 51) |
| 18 | GOBBARIELLU | C | 474 (126) | 574 (133) | 1.23 (104) | 139 (107) | 157 ( 38) | 1.16 ( 36) |
| 21 | CERASARELLA | C | 383 (102) | 656 (152) | 1.77 (150) | 123 ( 95) | 182 ( 44) | 1.49 ( 46) |
| 2 | RIBARICA | S | 280 ( 74) | 394 ( 91) | 1.42 (120) | 124 ( 96) | 426 (102) | 3.39 (104) |
| 3 | LAPUS | S | 366 ( 98) | 352 ( 82) | 0.99 ( 84) | 135 (105) | 321 ( 77) | 2.44 ( 75) |
| 8 | GOC | S | 319 ( 88) | 368 ( 85) | 1.21 (103) | 135 (105) | 686 (165) | 5.11 (156) |
| 9 | AVRIG | S | 299 ( 80) | 335 ( 78) | 1.15 ( 97) | 133 (103) | 359 ( 86) | 2.80 ( 86) |
| 32 | D. STUPCANICA | S | 311 ( 83) | 364 ( 85) | 1.21 (102) | 116 ( 90) | 725 (174) | 6.24 (191) |
| 5 | SIEGSDORF | M | 383 (102) | 373 ( 87) | 0.99 ( 84) | 125 ( 97) | 263 ( 63) | 2.15 ( 66) |
| 10 | ZWIESEL | M | 374 (100) | 411 ( 95) | 1.17 ( 99) | 143 (111) | 607 (146) | 4.08 (125) |
| 24 | PESCOPENATARO | M | 392 (105) | 525 (122) | 1.37 (116) | 127 ( 98) | 516 (124) | 4.03 (124) |
| 25 | GESCHWEND | M | 401 (107) | 415 ( 96) | 1.07 ( 90) | 120 ( 93) | 230 ( 55) | 1.95 ( 60) |
| 30 | OCHSENBODEN | M | 331 ( 88) | 239 ( 56) | 0.73 ( 62) | 135 (105) | 826 (199) | 6.54 (200) |
| 34 | LAVARONE | M | 317 ( 85) | 278 ( 65) | 0.97 ( 82) | 117 ( 91) | 508 (122) | 4.20 (129) |
| | F: (provenance) | | 6.9*** | 9.6*** | 3.6*** | 1.3ns | 2.1* | 2.2* |
| | Calabria | | 462 (123) | 602 (140) | 1.36 (115) | 132 (102) | 192 ( 46) | 1.51 ( 46) |
| | Southeast Europe | | 315 ( 84) | 362 ( 84) | 1.20 (101) | 129 (100) | 503 (121) | 4.00 (122) |
| | Central Europe | | 366 ( 98) | 373 ( 87) | 1.05 ( 89) | 128 ( 99) | 492 (118) | 3.83 (117) |
| | F: (region) | | 31.4*** | 42.0*** | 6.5** | 0.3ns | 5.9** | 5.9** |
| | Over all mean | | 375 (100) | (100) | 1.18 (100) | 129 (100) | 416 (100) | 3.27 (100) |
| Correlations with growth parameters on the provenance level | | | | | | | | |
| Height at 6 years | | | 0.55* | 0.49ns | 0.05ns | 0.54* | -0.54* | -0.57* |
| Dry matter at 6 years | | | 0.63* | 0.63* | 0.27ns | 0.41ns | -0.67** | -0.63** |

characterized by low rates of transpiration (362 mg and 373 mg, respectively).

The ratio between the transpiration rates of the two- and the one-year-old needles (ratio 2/1) gives information about the changes in transpiration rates from the first to the second needle year. The mean ratio of 1.18 shows, that over all provenances the transpiration increase by 18% from the one- to the two-year-old needles. Even though, some provenances exhibit unchanging or even decreasing transpiration rates (nos. 3, 5, 30, 32), these are mainly of central European origin (mean ratio 1.05). Provenances from the Calabrian region show the highest ratios (from 1.25 to 1.77 with a mean of 1.36); the seed sources from southeast Europe are characterized by intermediate ratios (1.20).

Positive correlation between transpiration rates and growth parameters were obtained, whereas the ratio 2/1 did not correlate with growth.

*Water use efficiency*

The ratio between the rates of transpiration and photosynthesis (water use efficiency) tells how many units of $H_2O$ are transpired (used) in order to fix one unit of $CO_2$ (*Table 3*). Low ratios exhibit high water use efficiency and vice versa.

The water use efficiency of the one-year-old needles show with an average value of 129 mg $H_2O$ per mg $CO_2$ no significant differences between provenances and regions. By contrast, the two-year-old needles show significant differences on the provenance level and highly significant differences between regions. These differences are mainly due to pronounced increased ratios by the provenances from southeast (503) and central (492) Europe, whereas the Calabrian seed sources with a mean ratio of 192 exhibit only moderately increased ratios compared with the one-year-old needles.

The ratio between the water use efficiency of the two- and the one-year-old needles gives information about changes in this ecophysiological parameter over needle ageing. Again most of the variation between provenances can be attributed to regional differences. The Calabrian provenances show with a mean ratio of 1.51 only a moderate decrease in water use efficiency from the first to the second year needles. By contrast, the provenances from the other regions exhibit drastic decreases in water use efficiency (4.00 and 3.83 respectively).

The correlation between water use efficiency of the one-year-old needles and growth rates were positive and partly significant, whereas there were significant negative correlations in respect of the two-year-old needles.

*Needle cast*

The results of the needle cast registration are presented in *table 4* as percent of the needles lost divided into needle age (four years), provenance and region.

Needle cast was not observed for one-year-old needles. For the two-year-old needles a certain differentiation occurs, which leads to significant differences on both provenance and region level. The three-year-old twigs are characterized by pronounced and highly significant differences in needle cast between regions. Thereby the Calabrian provenances exhibit rather small losses (average 5%), whereas the seed sources from southeast and central Europe are showing pronounced needle losses (16% and 18% respectively).

These differences are magnified for the four-year-old needles, and differences between provenances and regions are thereby highly significant. While the Calabrian prove-

*Table 4.* — Needle cast on the one-, two-, three- and four-year-old twigs (% needle losses).

| No. | PROVENANCE | Region | Mean values of needle cast in % | | | |
|---|---|---|---|---|---|---|
| | | | 1 year | 2 year | 3 year | 4 year |
| 1 | GARIGLIONE | C | 0 | 7 | 6 | 25 |
| 15 | MAMMA GIUSEP. | C | 0 | 2 | 7 | 29 |
| 18 | GOBBARIELLU | C | 0 | 1 | 4 | 13 |
| 21 | CERASARELLA | C | 0 | 1 | 3 | 16 |
| 2 | RIBARICA | S | 0 | 4 | 12 | 35 |
| 3 | LAPUS | S | 0 | 5 | 14 | 49 |
| 8 | GOC | S | 0 | 3 | 16 | 47 |
| 9 | AVRIG | S | 0 | 8 | 19 | 50 |
| 32 | D. STUPCANICA | S | 0 | 4 | 18 | 43 |
| 5 | SIEGSDORF | M | 0 | 4 | 18 | 38 |
| 10 | ZWIESEL | M | 0 | 2 | 22 | 65 |
| 24 | PESCOPENATARO | M | 0 | 2 | 11 | 44 |
| 25 | GESCHWEND | M | 0 | 2 | 17 | 53 |
| 30 | OCHSENBODEN | M | 0 | 2 | 25 | 58 |
| 34 | LAVARONE | M | 0 | 2 | 18 | 51 |
| | F: (provenance) | | - | 1.8* | 2.8** | 7.8*** |
| | Calabria | | 0 | 3 | 5 | 21 |
| | Southeast Europe | | 0 | 5 | 16 | 45 |
| | Central Europe | | 0 | 3 | 18 | 52 |
| | F: (region) | | - | 3.5* | 9.7*** | 36.6*** |
| | Over all mean | | 0 | 3 | 14 | 41 |
| Correlations with growth parameters on the provenance level | | | | | | |
| Height at 6 years | | | - | -0.16ns | -0.49ns | -0.55* |
| Dry matter at 6 years | | | - | -0.11ns | -0.71** | -0.75** |
| Correlations with gas exchange on the provenance level | | | | | | |
| Photosynthesis (1-y.) | | | - | -0.25ns | -0.64** | -0.57* |
| Photosynthesis (2-y.) | | | - | -0.31ns | -0.89*** | -0.83** |
| Photosynthesis (R-2/1) | | | - | -0.28ns | -0.90*** | -0.85** |
| Respiration (1-y.) | | | - | 0.05ns | 0.72** | 0.85*** |
| Respiration (2-y.) | | | - | -0.10ns | -0.64** | -0.36ns |
| Respiration (R-2/1) | | | - | -0.14ns | -0.86*** | -0.79** |
| Transpiration (1-y.) | | | - | -0.23ns | -0.63* | -0.54* |
| Transpiration (2-y.) | | | - | -0.21ns | -0.90*** | -0.79*** |
| Transpiration (R-2/1) | | | - | -0.09ns | -0.51* | -0.59* |
| Water use eff. (1-y.) | | | - | 0.07ns | -0.02ns | 0.05ns |
| Water use eff. (2-y.) | | | - | -0.04ns | 0.71** | 0.67** |
| Water use eff (R-2/1) | | | - | -0.03ns | 0.69** | 0.64** |

nances are characterized by mean losses of 21%, the provenances from southeast and central Europe had lost on the average 45%, respectively, 52% of the four-year-old needles.

With increasing needle age increasing correlation coefficients between needle cast and growth were registered. The percentage of needle losses on the three- and four-year-old twigs correlated highly significantly with dry matter production; that is, high growth rates are linked with small needle losses and vice versa.

The correlations on provenance level between needle cast over age and the results of the gas exchange measurements (*Tables 2* and *3*) are displayed in the lower part of *table 4*. Since the differentiation in needle cast among provenances is increasing over age, significant correlations with gas exchange parameters are obtained for needle cast at the 3- and 4-year-old but not at the 2-year-old twigs.

Photosynthesis is highly correlated with needle cast, it is however interesting to note, that the correlation coefficients are higher for the two-year-old needles and the ratio 2/1 than for the one-year-old needles. The differences in needle cast (3 year) between provenances can explain more than 80% of the variation in the photosynthesis ratio 2/1 ($R^2 = 0.81$). This relationship between the 2 parameters is displayed in *figure 2*. The provenances are divided into two groups: the central and southeast European provenances (nos. 2, 3, 5, 8, 9, 10, 25, 30, 32, 34) with pronounced needle losses and low ratios, and the Calabrian seed sources (nos. 1, 15, 18, 21) characterized by high ratios and rather small losses of needles. The provenance from central Italy (no. 24) is exhibiting intermediate values.

Needle cast is positively correlated with the respiration rates of the one-year-old needles, but negatively with the rates of the two-year-old needles. The highly significant negative correlations between needle cast and the respiration ratio 2/1 means, that provenances with heavy needle losses are characterized by pronounced reductions in the respiration rates over needle age and vice versa.

Transpiration is negatively correlated with needle cast, which means, that high transpiration rates are linked with small needle losses on the provenance level. The water use efficiency of the one-year-old needles is not correlated

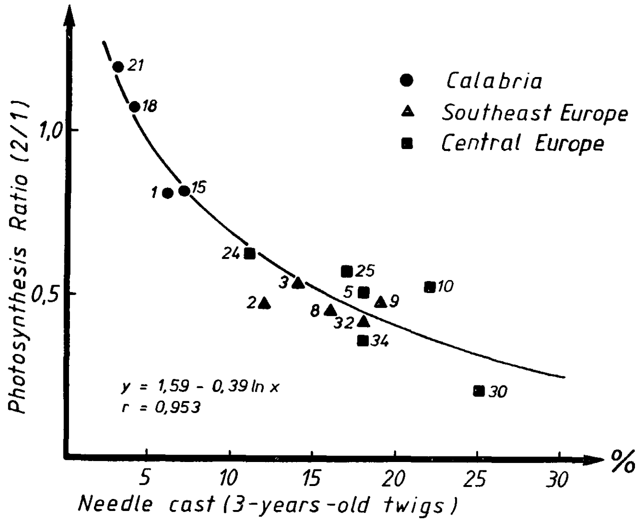


*Figure 2.* — Relation between needle cast (3- year-old needles) and the ratio between photosynthesis of the two- and the one-year-old nedles (Ratio 2/1).

with needle cast. By contrast, water economy of the two-year-old needles is significantly correlated with needle cast on the 3- and 4-year-old twigs.

*Nutrient content*

After the sixth growing season the nutrient content of the needles was analysed separately for each age. Since the analysis were not made on single tree but on provenance level, the statistical analysis are done by regions. *Table 5* shows the results of the nutrient analysis divided into regions and needle age.

An almost linear decrease in N-content over needle age could be demonstrated (from 2.3% to 1.7%). Although no significant differences between regions were obtained, there is a tendency to slightly lower N-content by the Calabrian seed sources.

The K-content also decreases over needle age (from 1.4% to 1.2%). The decrease is less pronounced for the Calabrian provenances, although significant differences between regions could not be found.

*Table 5.* — Nitrogen, potassium, phosphorus, calcium, and magnesium content of the one-, two-, three- and four-year-old needles (% of needle dry matter).

| Region / Nutrient | 1 year | 2 year | 3 year | 4 year |
|---|---|---|---|---|
| Nitrogen | N-content in % of needle dry matter | | | |
| Calabria | 2.26 | 1.98 | 1.83 | 1.66 |
| Southeast Europe | 2.31 | 2.09 | 1.94 | 1.69 |
| Central Europe | 2.38 | 2.08 | 1.92 | 1.71 |
| F: (region) | $0.6^{ns}$ | $1.2^{ns}$ | $1.6^{ns}$ | $0.5^{ns}$ |
| Over all mean | 2.33 | 2.06 | 1.90 | 1.69 |
| Potassium | K-content in % of needle dry matter | | | |
| Calabria | 1.52 | 1.27 | 1.36 | 1.42 |
| Southeast Europe | 1.44 | 1.37 | 1.34 | 1.19 |
| Central Europe | 1.40 | 1.34 | 1.22 | 1.15 |
| F: (region) | $0.6^{ns}$ | $0.4^{ns}$ | $1.5^{ns}$ | $2.3^{ns}$ |
| Over all mean | 1.44 | 1.33 | 1.30 | 1.24 |
| Phosphorus | P-content in % of needle dry matter | | | |
| Calabria | 0.257 | 0.231 | 0.237 | 0.220 |
| Southeast Europe | 0.245 | 0.213 | 0.204 | 0.186 |
| Central Europe | 0.250 | 0.231 | 0.228 | 0.202 |
| F: (region) | $0.4^{ns}$ | $1.5^{ns}$ | $2.8^{ns}$ | $1.8^{ns}$ |
| Over all mean | 0.250 | 0.226 | 0.222 | 0.202 |
| Calsium | Ca-content in % of needle dry matter | | | |
| Calabria | 0.95 | 1.30 | 1.90 | 1.98 |
| Southeast Europe | 0.95 | 1.17 | 1.54 | 1.61 |
| Central Europe | 0.98 | 1.12 | 1.49 | 1.62 |
| F: (region) | $0.1^{ns}$ | $1.1^{ns}$ | $4.3^{*}$ | $4.9^{*}$ |
| Over all mean | 0.96 | 1.19 | 1.61 | 1.71 |
| Magnesium | Mg-content in % of needle dry matter | | | |
| Calabria | 0.131 | 0.102 | 0.122 | 0.137 |
| Southeast Europe | 0.127 | 0.112 | 0.143 | 0.163 |
| Central Europe | 0.117 | 0.088 | 0.104 | 0.115 |
| F: (region) | $2.6^{ns}$ | $4.2^{*}$ | $6.6^{**}$ | $10.4^{**}$ |
| Over all mean | 0.124 | 0.100 | 0.122 | 0.137 |

*Table 6.* — Height, root collar diameter, dry matter, dry matter partitioning, wood density and stem volume by provenance and region.

| No. | PROVENANCE | Region | Means (relative values) | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | | Height (cm) | Root collar diam. (mm) | Dry matter (g) | Needle/twig ratio | Top/root ratio | Wood density g/cm³ | Stem volume cm³ |
| 1 | GARIGLIONE | C | 69.8 (109) | 26.1 (121) | 311 (130) | 0.48 ( 95) | 1.69 (102) | 0.49 ( 93) | 129 (147) |
| 15 | MAMMA GIUSEP. | C | 66.3 (104) | 21.4 ( 99) | 280 (117) | 0.44 ( 87) | 1.56 ( 95) | 0.54 (102) | 104 (119) |
| 18 | GOBBARIELLU | C | 98.8 (155) | 26.9 (125) | 506 (212) | 0.48 ( 95) | 1.74 (105) | 0.52 ( 98) | 189 (216) |
| 21 | CERASARELLA | C | 68.6 (108) | 23.7 (110) | 291 (122) | 0.48 ( 95) | 1.80 (109) | 0.49 ( 93) | 111 (127) |
| 2 | RIBARICA | S | 58.2 ( 91) | 21.2 ( 98) | 224 ( 94) | 0.58 (115) | 1.49 ( 90) | 0.54 (102) | 75 ( 86) |
| 3 | LAPUS | S | 67.2 (105) | 22.8 (106) | 248 (104) | 0.49 ( 97) | 1.62 ( 98) | 0.52 ( 99) | 88 (101) |
| 8 | GOC | S | 57.2 ( 90) | 19.8 ( 92) | 181 ( 76) | 0.54 (107) | 1.74 (105) | 0.54 (102) | 68 ( 78) |
| 9 | AVRIG | S | 68.0 (106) | 22.4 (104) | 258 (108) | 0.59 (117) | 1.67 (101) | 0.50 ( 95) | 90 (103) |
| 32 | D.STUPCANICA | S | 48.1 ( 75) | 18.2 ( 84) | 145 ( 61) | 0.51 (101) | 1.45 ( 88) | 0.56 (106) | 49 ( 56) |
| 5 | SIEGSDORF | M | 58.4 ( 91) | 20.1 ( 93) | 190 ( 79) | 0.58 (115) | 1.56 ( 95) | 0.52 ( 99) | 66 ( 75) |
| 10 | ZWIESEL | M | 58.7 ( 92) | 19.4 ( 90) | 169 ( 71) | 0.48 ( 95) | 1.86 (113) | 0.54 (103) | 64 ( 73) |
| 24 | PESCOPENATARO | M | 54.3 ( 85) | 21.7 (100) | 201 ( 84) | 0.42 ( 83) | 1.64 ( 99) | 0.54 (102) | 69 ( 79) |
| 25 | GESCHWEND | M | 65.4 (102) | 20.8 ( 96) | 232 ( 97) | 0.53 (105) | 1.66 (101) | 0.51 ( 97) | 80 ( 91) |
| 30 | OCHSENBODEN | M | 69.0 (108) | 21.2 ( 98) | 202 ( 85) | 0.45 ( 89) | 1.72 (104) | 0.54 (102) | 82 ( 94) |
| 34 | LAVARONE | M | 51.0 ( 80) | 18.0 ( 83) | 139 ( 58) | 0.51 (101) | 1.56 ( 95) | 0.56 (106) | 48 ( 55) |
| | F: (provenance) | | 17.9*** | 7.9*** | 18.1*** | 5.0*** | 1.3n.s. | 4.7*** | 19.8*** |
| | Calabria | | 76.0 (119) | 24.5 (113) | 347 (145) | 0.47 ( 93) | 1.70 (103) | 0.51 ( 96) | 134 (153) |
| | Southeast Europe | | 59.7 ( 93) | 20.9 ( 97) | 211 ( 88) | 0.54 (107) | 1.60 ( 97) | 0.53 (101) | 74 ( 85) |
| | Central Europe | | 59.4 ( 93) | 20.2 ( 94) | 189 ( 79) | 0.49 ( 97) | 1.67 (101) | 0.54 (102) | 68 ( 78) |
| | F: (region) | | 25.4*** | 23.0*** | 44.3*** | 9.8*** | 1.3n.s. | 7.6*** | 56.9*** |
| | Over all mean | | 63.9 (100) | 21.6 (100) | 239 (100) | 0.50 (100) | 1.65 (100) | 0.53 (100) | 87 (100) |

Significant differences in P-content between regions were not obtained. With decreasing P-content over needle age (from 0.25% to 0.20%), the Calabrian seed sources show less reduction compared to the provenances from the other regions.

A drastic increase in Ca-content over needle age is encountered (from 0.96% to 1.71%). This increase is most pronounced for the Calabrian provenances (108%), while the central and southeast European seed sources only increases their Ca-content over the four years by 65%, respectively 69%.

For all regions the Mg-content is almost constant over needle age. By increasing needle age, however, a differentiation between regions occurs: provenances from southeast Europe show increasingly higher Mg-content compared with provenances from the other regions.

*Height and diameter growth*

*Table 6* presents the results of the height and diameter registration. Height growth varies highly significantly between provenances from 48.1 cm (no. 32) to 98.8 cm (no. 18). The main part of this variation can be attributed to regions: The Calabrian provenances are exhibiting the best height growth with an average of 76 cm (19% above mean), whereas the provenances from the two other regions (southeast and central Europe) are characterized by rather low growth rates (7% below mean). The high variability within the Calabrian seed sources must be mentioned (from 66.3 cm to 98.8 cm).

With a range from 18 cm to 26.6 cm the root collar diameter shows more or less the same variation pattern as height growth, the relative differences between provenances and regions are smaller, however. Highly significant differences between provenances and regions were demonstrated.

*Dry matter partitioning*

The total dry matter (top and root) varies from 139 g to 506 g per plant between provenances (*Table 6*). The most vigorous provenance (no. 18) has produced 3.6 times more dry matter than the slowest growing seed source (no. 34). Most of the variation between provenances can be attributed to regions: The Calabrian seed sources are the most fast growing (45% above the mean of all provenances), whereas the provenances from southeastern and central Europe are less vigorous (12%, respectively 21% below average).

*Table 6* gives furthermore information about the variation in dry matter partitioning within and between regions. Provenance-specific differences in the ratio between needle dry matter and top (without needles) dry matter were demonstrated. This variation could mainly be explained by regions: Whereas the Calabrian and central European provenances are characterized by relative low needle weight in relation to twig weight (7%, respectively 3% below average), the provenances from southeast Europe show high relative needle dry matter (7% above mean of all provenances).

The partitioning of dry matter above and below ground (top/root-ratio) show only little variation, and no significant differences neither between provenances nor regions were obtained, mainly due to a pronounced variation within seed sources.

*Wood density and stem volume*

Wood density varies from 0.49 g/cm³ to 0.56 g/cm³ with highly significance between provenances and regions (Table 6). On an average the Calabrian provenances are exhibiting a slightly lower density (0.51 g/cm³, 4% below average of all seed sources) compared with the provenances from southeastern and central Europe (0.53 g/cm³ and 0.54 g/cm³ respectively, 1% and 2% above mean).

The highest variation of all parameters registered exhibits in stem volume (*Table 6*). The Calabrian provenances are characterized by high volumes (53% above mean), whereas provenances from southeast Europe and from central Europe exhibit a low volume production (15%, respectively 22% below average). The high variation within the Calabrian seed sources (from 104 cm³ to 189 cm³) must be pinpointed.

### Discussion

The results demonstrate significant differences between provenances in almost all traits measured, which could be attributed mainly to regions. Thereby provenances from southern Italy (Calabria) behaved quiet differently compared to provenances from the rest of the natural distribution of the species. Differences between provenances from central and southeast Europe were mostly absent.

The outstanding performance and variability of the Calabrian silver fir are confirmed in a number of provenance experiments (PAVARI, 1951; LÖFTING, 1977; MAYER et al., 1982; LARSEN, 1981 and 1986b; LARSEN and SCHAAF, 1985). The lack of variation between provenances within the central European region is correspondingly found in almost all provenance trials with this species (ENGLER, 1905; LÖFTING, 1954 and 1977; ARBEZ, 1969; VINCENT and KANTOR, 1971; GUNIA et al., 1972; LARSEN, 1981 and 1986b; KORPEL and PAULE, 1984; PAULE et al., 1985).

*Gas exchange and needle cast*

The mean rates of photosynthesis of the one-year-old needles are comparable to results achieved with the same species in the field (MILLER, 1959). The higher rates measured by the Calabrian provenances are partly confirmed by MEKIC (1988), whereas no differences between provenances were demonstrated by LEONHARDT (1986). These rather small differences in photosynthetic rates of the one-year-old needles seem to develop during the year (MEKIC, 1988).

The evidence of an ongoing differentiation in the rate of photosynthesis between provenances during the first year is confirmed by the results from the measurements on the two-year-old needles. Whereas the Calabrian provenances are maintaining almost the same levels of photosynthesis, the two-year-old needles of provenances from central and southeast Europe had lost more than 50% of the photosynthetic capacity compared with the one-year-old needles. MILLER (1959) found a 40% reduction in photosynthesis by four-year-old needles of silver fir grown under a canopy (Bavarian Forest). Reduction in photosynthesis by ageing of the needles are described by *Abies concolor* and *Pinus ponderosa* (FREELAND, 1952) and *Pseudotsuga menziesii* (BRIX, 1971; KÜNSTLE and MITSCHERLICH, 1977).

This provenance-specific loss of photosynthetic capacity over needle ageing explains to a great extent the differences in growth rates between provenances not only in the seedling stage (LARSEN, 1986b, LARSEN and SCHAAF 1985) but also in older field trials (LARSEN, 1981). The reason for the observed outstanding growth of the Calabrian provenances might therefore be explained by a less pronounced decline in photosynthetic capacity with ageing.

The differences in respiration rate between provenances are less pronounced compared with photosynthesis. The significant lower respiration of the one-year-old needles by the Calabrian provenances indicate a relative lower maintenance respiration and is in accordance with the better photosynthetic economy (photosynthesis to respiration ratio) of these provenances found by MEKIC (1988). The significant higher respiration rate of the Calabrian provenances (two-year-old needles) can mainly be attributed to higher metabolic activity, the much higher rates of $CO_2$ fixation, however, indicates a better photosynthetic economy of the older needles too.

Transpiration and photosynthesis of the one-year-old needles are closely correlated on the provenance level, correspondingly differences in water use efficiency between provenances were not obtained. For the two-year-old needles, however, the Calabrian provenances are exhibiting much better water use efficiency compared with seed sources from the other regions. This improved water economy by needle ageing could be a sign of a better adaptation to drought of the Calabrian seed sources, which also could be registered in combination with $SO_2$ stress (LARSEN et al., 1988).

The big differences in needle cast between provenances could almost entirely be explained by regions. The highly significant negative correlation on the provenance level between the photosynthesis ratio (two- to one-year-old needles) and shedding of the three-year-old needles (*Figure 2*) indicates a physiological causality. The cause of needle loss can therefore be explained as an active reaction in order to get rid of photosynthetic tissue, which due to senescence of the photosynthetic apparatus no longer can contribute positively to the energy balance and is definitely contributing negatively to the water balance of the tree.

The causes for the observed reduction in photosynthesis by needle ageing must be found on the physiological level, since the diffusion resistance measured by the transpiration rates is constant, or even increasing by age. In other words, the photosynthesis reduction can not be explained by decreased stomatal aperture. On the other hand, the reduction in photosynthetic capacity over needle age can not be explained by an unbalanced (insufficient) nutrient supply of the older needles, since none of the analysed macronutrients showed specific decline (deficiency) over needle age.

Although it is not possible to discuss and give a physiological explanation of the observed reduction in photosynthesis and thereby following needle cast by means of the present results, natural ageing processes (senescence) of the photosynthetic apparatus can be assumed. Consequently the silver fir from central and eastern Europe is characterized by a rapid development of these senescence phenomena compared with the Calabrian silver fir.

*Growth rate and wood density*

The results demonstrate clearly, that most of the variation in growth rate between provenances can be attributed to regional differences. Thereby silver fir from central and eastern Europe are characterized by slow growth rates and by only little variation between provenances. In contrast, the silver fir from southern Italy/Calabria show high growth rates and a pronounced variation between seed sources. These findings are in accordance with earlier results achieved with the same provenance material (LARSEN and SCHAAF, 1985; LARSEN, 1986b). Since the differences between regions are increasing from age 3 (LARSEN, 1986b) to age 6 (present results), the variation pattern seems to be persisting over time. The outstanding performance of the Calabrian provenances corresponds with results from older field trials published by (PAVARI, 1951; LÖFING, 1977; LARSEN, 1981; MAYER et al., 1982). The limited provenance variation within the central and northeastern part of the fir range is proved in a number of provenance trials (ENGLER, 1905; ARBEZ, 1969; LÖFTING, 1954, 1977; LARSEN, 1981).

The dry matter partitioning is interesting in relation to questions concerning the developmental strategies of different provenances. Since the needle to twig ratio is significantly higher by the southeastern European provenances, they seem to invest more dry matter in producing new photosynthetic tissue than do the provenances from the other regions. By contrast, no significant differences neither between provenances nor between regions were demonstrated in the top root ratio. This ratio is an important parameter concerning adaptation to dry conditions (see LEVITT, 1982) and showed pronounced variation between provenances of *Abies grandis* (LARSEN et al., 1981). By means of this drought resistance trait, differences in drought hardiness between provenances of silver fir could not be demonstrated.

The relative differences in stem volume between provenances are considerably higher than are they by height and root collar diameter (from 55% to 216%, respectively 75% to 155% and 83% to 125%). This indicate, that height and diameter measurements tends to underestimate the differences in (wood) increment. The registered almost two times higher stem volume of the Calabrian provenances compared with the central European seed sources are in close accordance to the results found in yield studies over 22 years in an 45 year old provenance trial (LARSEN, 1981), thus supporting the results achieved in this early test study.

The differences in wood density between provenances and regions demonstrate, that the fast growing provenances are characterized by slightly lower specific density. Although statistical significant, the differences are rather small compared with the large differences in growth rate. It is interesting to note, however, that some fast growing seed sources (no. 15 and 18) show mean density values. Hence, provenance selection for both traits seems possible.

*Silver fir decline*

The pronounced losses of needles by increasing age by the central and southeast European provenances are characteristic symptoms of silver fir decline in older stands in central Europe (VINCENT and KANTOR, 1971; BERCHTOLD et al., 1981; LARSEN, 1981). Further, the area characterized by provenances with pronounced needle losses in this study (central and eastern Europe) is almost identical with the distribution of silver fir dieback in Europe according to LARSEN (1986a). The needle cast registered might therefore be interpreted as an early development of silver fir decline, and the differences in needle cast between provenances could therefore be attributed to provenances specific differences in "resistance" to silver fir decline. Correspondingly, the increase in needle cast after $SO_2$ fumigation was much higher by the central and east European provenances compared with the Calabrian seed sources (LARSEN and FRIEDRICH, 1988).

In a new hypothesis LARSEN (1986a, 1989) assumes, that the silver fir decline in central and northeastern Europe is basically caused by insufficient genetic variation of the species in this region caused by a severe pressure of directional selection in the refugial population during the last glacial period before migrating back to central Europe. The present results fit nicely into this theory, since the observed decline in photosynthetic capacity and the subsequent needle cast (decline) were observed in all provenances in this specific decline "haunted" part of the natural distribution, whose silver fir according to KRAL (1974, 1979, 1980a and b) come from the same refugial population in central or northern Italy. A Calabrian refugium of silver fir is proved by GRÜGER (1977), whose population during the glaciation was able to maintain a higher genetic diversity mainly due to better climatic conditions and higher environmental heterogeneity (see LARSEN, 1986b and 1989 for a more detailed description and explanation).

The existence of these two separate refugial population is proved by means of isozyme polymorphism studies (BERGMANN and KOWNATZKI, 1988). In several isozymes additional alleles were found in the seed sources from southern Italy/Calabria, non-existent outside this area. The intermediate behavior of the provenance from central Italy (no. 24) could be a sign of a introgression zone; an assumption, which is supported by BERGMANN and KOWNATZKI (1988). Recently the theory is strongly supported by analysing the genetic variation (multiplicity and diversity) by means of isozyme studies (BERGMANN et al., 1990).

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# Norway Spruce Cuttings Perform Better than Seedlings of the Same Genetic Origin

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**Abstract**

Growth and survival for seedlings and cuttings of Norway spruce were compared. The two different plant lots originated from the same seed source, and the selection of plants for cutting propagation gave a neglectable reduction of genetic variation. Eight years after planting, both survival and height were superior for cuttings compared to seedlings. The differences in performance for the two plant materials can be explained by differences in morphology and physiology. The results indicate that genetic selection for growth, based on clonal tests, can be improved by using growth in a later stage than from the first eight years when comparing different clones.

*Key words: Picea abies,* seedlings, cuttings, growth.

## Introduction

In Sweden the interest on clonal forestry has been focused on Norway spruce (*Picea abies* (L.) KARST.). An increased growth of about 20% compared to seedlings has been reported (ROULUND et al., 1985).

For the tree breeder it has been important to find methods to test selected cuttings at an early age, mainly due to the problem of aging (KLEINSCHMIDT and SCHMIDT, 1977; WERNER and PETTERSSON, 1981). A clone that is tested for a long time in the field is not usable unless the clone could be maintained in a juvenile status. Early selection is therefore an absolute condition for largescale production of commercial cuttings (ROULUND, 1980; KLEINSCHMIT and SCHMIDT, 1977; FOSTER et al., 1989).

Another reason for making early selections is that cuttings to a large extent are tested in single tree plots. This implies a risk of making incorrect rankings concerning long term growth rates, since competition occurs at 2 m to 3 m stand height in spacings of 2 m x 2 m (GEMMEL, 1988). Clones that start to grow rapidly after planting will thus be favoured ahead of "slow starters".

Cuttings are morphologically different from seedlings depending on the propagation method. KLEINSCHMIDT and SCHMIDT (1977) found that the root/shoot relation was abouth the same for both cuttings and seedlings, while the young cuttings had larger diameter, higher root and shoot weights than seedlings of the same height. It is suggested that this increases the ability to survive damages, such as attacks by pine weevils. The age of the cuttings and the fact that cuttings are physiologically older than seedlings may also influence establishment and growth. ROULUND (1980) points out that plagiotropic growth, caused by taking twigs on old ortets, might be an important factor leading to slow height growth.

Several studies (LAMBETH et al., 1983; HUEHN et al., 1987; BENTZER et al., 1988) report significant correlation between growth and height 3—6 years after planting and growth after 10 to 20 years. Studying old provenance trials MARKLUND (1981) found that survival and mean height at age 13 correlated well with total growth at a 70 year age. However, by using only the height information at age 13 the correlation was relatively weak. The plot size in the experiments was 0.04 ha to 0.08 ha, thus avoiding the most severe problem of competition.

In this report, two series of experiments are presented for comparison of seedlings and cuttings from the same seed source. The selection of cuttings was made so that cuttings and seedlings can be regarded as essentially genetically similar.

The objectives of the study were to provide data on establishment and growth of cuttings in a practical situation and to examine nongenetical growth differences between cuttings and seedlings.

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