Genetic variation of ecophysiological traits in red alder (*Alnus rubra* Bong.)

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We examined the genetic variation of ecophysiological traits within and among 40 red alder (*Alnus rubra* Bong.) provenances (two families per provenance) in a common-garden experiment in the summer of 1993. The provenances were representative of the entire species range in British Columbia, Canada. We found significant genetic variation among provenances ($P < 0.001$) in photosynthetic rate (A), mesophyll conductance (g_m), transpiration rate (E), stomatal conductance (g_{sw}), stomatal sensitivity to water vapour pressure deficit ($SENS_{VPD}$), intercellular to ambient CO_2 concentration ratio (C_i/C_a), and midday xylem water potential (ψ). Photosynthetic water-use efficiency, however, did not differ significantly among provenances. There were no significant differences between families within provenance for any of these variables. A weak but significant geographic trend was detected in ecophysiological traits: ψ, A, g_m, and E increased, and $SENS_{VPD}$ decreased, from southeast to northwest. Photosynthetic rate, E, g_m, g_{sw} and ψ were positively related to each other, but negatively correlated with $SENS_{VPD}$. C_i/C_a was negatively correlated with g_{sw}. These correlations indicate that red alder might have undergone genetic differentiation in drought resistance.

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Dans une expérience en arboretum à l'été 1993 sur 40 provenances d'aulne de l'Orégon (*Alnus rubra* Bong.), nous avons examiné la variabilité génétique de caractères écophysiologiques entre les familles de même provenance (deux familles par provenance) ainsi qu'entre les provenances. L'origine des provenances couvrait l'aire de distribution de l'espèce en Colombie-Britannique, Canada. Nous avons trouvé des différences génétiques significatives entre les provenances ($P < 0,001$) dans les mesures de taux photosynthétique (A), de conductance du mésophylle (g_m), de transpiration (E), de conductance stomatique (g_{sw}), de sensibilité des stomates au déficit de pression de vapeur ($SENS_{VPD}$), du rapport des concentrations en CO_2 intercellulaire et ambiant (C_i/C_a) et de potentiel hydrique du xylème de midi (ψ). L'efficacité d'utilisation de l'eau, par contre, n'était pas significativement différente entre les provenances. Nous n'avons trouvé aucune différence entre les familles d'une même provenance dans les variables mesurées. Nous avons détecté une tendance géographique significative mais faible dans les caractères écophysiologiques : ψ, A, g_m et E augmentaient, et $SENS_{VPD}$ décroissait, du sud-est au nord-ouest. Le taux de photosynthèse, E, g_m, g_{sw} et ψ étaient corrélés positivement entre eux, mais négativement avec $SENS_{VPD}$. Les variables C_i/C_a et g_{sw} étaient corrélées négativement entre elles. Ces corrélations indiquent que l'aulne de l'Orégon pourrait avoir subi une différentiation génétique dans sa résistance à la sécheresse.

[Traduit par la Rédaction]

Introduction

Red alder (*Alnus rubra* Bong.) is the most abundant hardwood tree species in the Pacific Northwest and coastal Alaska. Its ability to fix atmospheric nitrogen (Atkinson and Hamilton 1978), excellent growth characteristics (Gordon 1978), and the increasing utilization of its wood for furniture, paper, etc. (Harrington 1984) make red alder the most important commercial hardwood species in the region. Red alder occurs naturally from southern California (34°N) to southeastern Alaska (60°N) and is generally found within 200 km of the ocean and at elevations below 750 m (Harrington 1994). Within its natural range, climatic and edaphic conditions vary considerably. Annual precipitation ranges from 400 to 5600 mm, extreme temperature ranges from −30 to 46°C, and soils vary from well-drained gravels or sands to water-logged clays or organic soils (Harrington 1990). This

environmental diversity has led to adaptive differentiation among red alder populations in growth, phenology, and morphology (Ager et al. 1993; DeBell and Wilson 1978; Lester and DeBell 1989).

Physiological processes reflect the interaction between the genotype and the environment. Studies of variation in ecophysiological traits (inheritable physiological characteristics that can be affected by and that can adapt to the environment) may provide fundamental information on mechanisms of adaptation. Knowing the extent and geographic patterns of genetic variation in important ecophysiological variables is of great value in developing effective genetic improvement strategies and silvicultural prescriptions, and in the protection of genetic diversity. Significant genetic variation in water relations and gas exchange have been reported for a number of coniferous tree species, e.g., loblolly pine (*Pinus taeda* L.) (Bilan et al. 1977; Boltz et al. 1986) and Monterey pine (*Pinus radiata* D. Don) (Bennett and Rook 1978; Sands et al. 1984). Boltz et al. (1986) have found
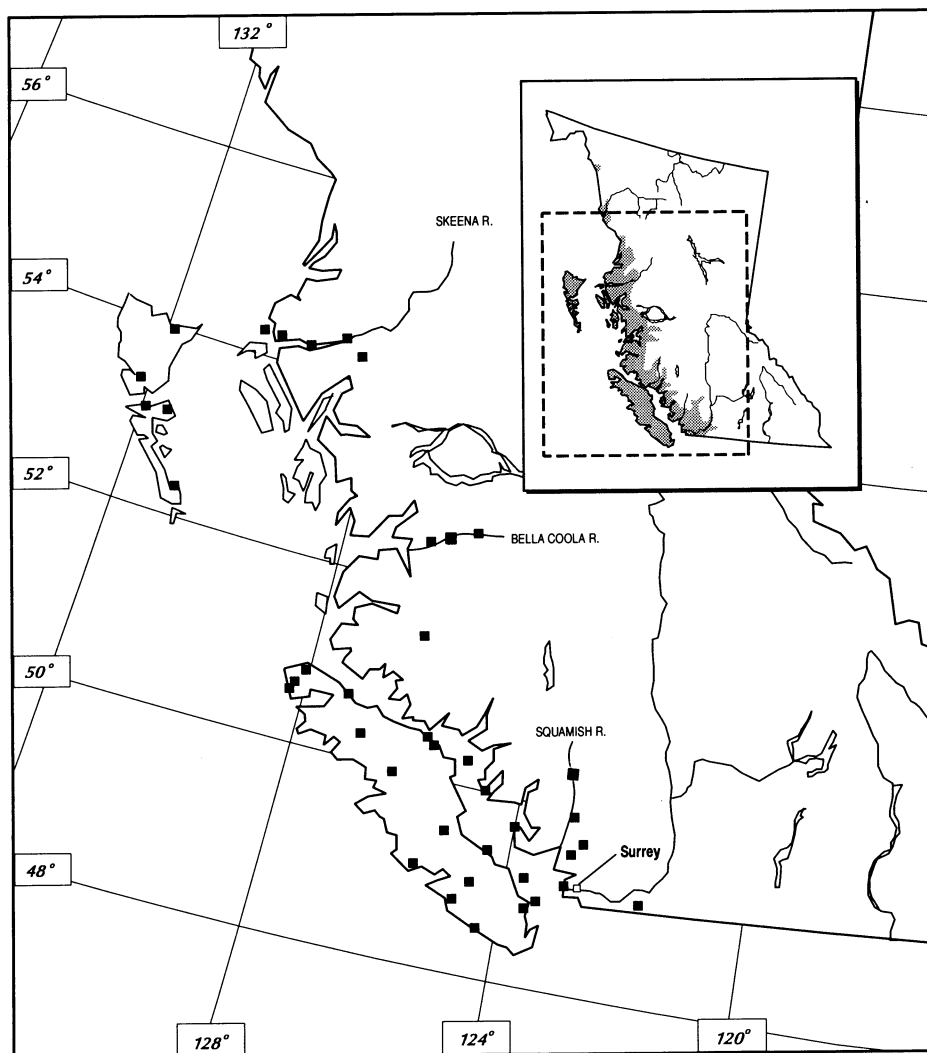
FIG. 1. Geographic distribution of red alder in British Columbia, and locations of provenance samples.

that *Pinus taeda* seedlings from a fast-growing Florida provenance have higher rates of net photosynthesis than slower growing provenances from Arkansas to Oklahoma, or Texas. Significant genetic variation in water relations and gas exchange is also reported for mature ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.) (Cregg 1993). Genetic variation in ecophysiological variables in hardwood tree species, however, has not received much attention. In this study, we examine the genetic variation of ecophysiological traits within and among 40 widely scattered red alder provenances representing the species range in British Columbia. Intercorrelations among the ecophysiological variables are discussed in the context of adaptation mechanisms of red alder.

Materials and methods

Plant materials and experimental design

Forty provenances of red alder (*Alnus rubra* Bong.) were selected from a common-garden installation at the B.C. Ministry of Forests Nursery in Surrey (details described by Xie and Ying 1994). The chosen provenances cover the entire species range in British Columbia, Canada (Fig. 1). Two families per provenance and two individuals per family were used in the current experiment. The experiment was replicated in two blocks, and seedlings were 2 years old and about 2 m tall at the time (August 18–September 4 1993). The seedlings were not fertilized or watered during the whole year of 1993.

Measurements and calculations of ecophysiological traits

Semi-diurnal (09:00–16:00) variation in ecophysiological variables was examined at the beginning of the experiment in order to determine appropriate time periods for further sampling (data not presented). Xylem water potential (ψ) was low and stable between 12:30 and 15:00. Therefore, all subsequent measurements were taken during this time period. Xylem water potential measurements were taken in day blocks, whereby one individual from each family and each provenance was measured on each measuring day. Other ecophysiological variables (such as photosynthesis) varied with time of day. Photosynthesis and stomatal conductance became very low around noon. Heavy dew early in the morning prevented reliable gas exchange measurements before 09:00. Therefore, all subsequent gas exchange measurements were taken between 09:00 and 11:40. Gas exchange was also measured in blocks of one individual per family per provenance, but each block took more than 1 day. The sequence of measurements for families and provenances within the same block was random. The use of measurement blocks and the randomization of the measuring sequence were designed to avoid the systematic errors in assessing genetic variation in gas exchange variables that would occur as a result of fluctuations in environmental conditions.

Xylem water potentials were measured using a portable Scholander pressure chamber (PMS Instrument Company, Oreg., U.S.A.). One twig from each sample seedling (at about 120 cm height) was cut and the xylem water potential was measured

TABLE 1. Effects of provenance and family on midday ψ, A, g_m, g_{sw}, WUE, C_i/C_a, E, and SENS$_{VPD}$

Variable	Family				Provenance		
	MSS$_{residual}$	MSS	F	$P > F$	MSS	F	$P > F$
SENS$_{VPD}$	8.8528	9.6811	1.14	0.2874	35.9707	3.72	0.0001
E	0.5474	0.3134	0.57	0.9798	1.9730	6.30	0.0001
g_{sw}	35.1619	31.6457	0.90	0.9899	87.0257	2.75	0.0010
A	7.9865	6.2851	0.79	0.8110	26.5505	4.22	0.0001
WUE	0.9859	0.9006	0.91	0.6206	1.2955	1.44	0.1284
g_m	131.9884	89.1106	0.68	0.9269	434.6474	4.88	0.0001
C_i/C_a	0.0048	0.0025	0.53	0.9905	0.0071	2.79	0.0008
ψ	0.4931	0.6465	1.31	0.1334	3.6436	5.64	0.0001

NOTE: The degrees of freedom are 40 for family and 39 for provenance. The degrees of freedom for the residual are 120 for ψ, 160 for C_i/C_a, and 158 for all others. 'MSS', 'F', and '$P > F$' stand for mean sum of squares, F-statistics, and probability for greater F-values, respectively.

immediately. This measurement is a good estimate of the water potential of the twig (Ritchie and Hinckley 1975).

Gas exchange rates of CO_2 and H_2O were measured using an ADC LCA-3 open system and a PLC B broadleaf chamber (Analytical Development Company Limited, Hoddesdon, England). A photosynthetically active photon flux density of 1000 µmol·m^{-2}·s^{-1} was provided by a halogen cool-spot lamp (OSRAM Canada Ltd., Mississauga, Ont.) powered by a 12-V heavy duty gel battery. To determine the sensitivity of stomata to changes in evaporative demand, two measurements were taken on each sample at different relative humidities (low; 30–45%, and high; 70–85%). The relative humidities were later converted to water vapour pressure deficit (VPD). Carbon dioxide concentration inside the cuvette was controlled at 335 ± 10 µL·L^{-1}. We were unable to control the temperature in the leaf chamber, although we were very much aware of the effects that temperature can have on gas exchange variables. The temperature effects, however, were taken into account by using temperature as a covariate in statistical analyses. In addition, an infrared filter on the chamber minimized the heating of the leaf inside the chamber during measurements.

Net photosynthesis (A), stomatal conductance to H_2O (g_{sw}), transpiration rate (E), and intercellular CO_2 concentration (C_i) were determined as described by von Caemmerer and Farquhar (1981). Mesophyll conductance (g_m) was determined according to Fites and Teskey (1988). Photosynthetic water-use efficiency (WUE) was calculated as A/E. Intercellular to ambient CO_2 concentration ratio was calculated as C_i/C_a, where C_a is the CO_2 concentration in the cuvette. Stomatal sensitivity to H_2O vapour pressure deficit (SENS$_{VPD}$) was defined as $\Delta r_{sw}/\Delta VPD$, where stomatal resistance $r_{sw} = 1/g_{sw}$. The reason for using r_{sw} instead of stomatal conductance (g_{sw}) is that r_{sw} changes linearly with VPD where g_{sw} has a curvilinear relationship with VPD (Q.L. Dang et al., unpublished).

Statistical analyses

All ecophysiological variables but ψ were subjected to analysis of covariance (ANOCOVA); the covariates were: time of day, air temperature, and VPD. The purpose of ANOCOVA is to improve the precision of the F-test (Hicks 1982). The linear model for ANOCOVA is:

$$Y = B + P + B \times P + F(P) + B \times F(P) + \text{covariates}$$

where B, P, and $F(P)$ are, respectively, block, provenance, and family within provenance. Adjusted mean squares and means were used for the F-test and presentation where covariate(s) had a significant effect on the ecophysiological variable concerned. Significant covariates were temperature and VPD for WUE and g_{sw}, and time and temperature for all other variables except C_i/C_a which did not have any significant covariate ($P > 0.05$). Treatment effects on C_i/C_a, therefore, were analyzed using analysis of variance

(ANOVA). The linear model for C_i/C_a is the same as the one for ANOCOVA, except that the term "covariates" is dropped. Since ψ was very stable during the time period of measurements, ψ was also analyzed using ANOVA. The linear model for ψ is:

$$Y = D + P + D \times P + F(P) + D \times F(P)$$

where D, P, and $F(P)$ are, respectively, day, provenance, and family within provenance. Family was considered as nested within provenance in both ANOCOVA and ANOVA. The effects of block were considered as fixed while provenance and family had random effects. All analyses were conducted using the General Linear Model of SAS for Unix systems. The use of blocks was for the purpose of error control and thus the effects of block and interactions associated with it were not presented. The coefficient of variance (standard deviation/mean) and relative range ((maximum − minimum)/mean) were used as measures of between-provenance variation in each variable.

Stepwise multiple regression analysis was conducted to examine geographic patterns of ecophysiological variables. Latitude, longitude, and elevation of provenance origin, and their squares and cross products, were used as independent variables. The use of combinations of latitude, longitude, and elevation was intended to take into account correlations between them (e.g., the southeast to northwest geographic orientation of coastal B.C.) and possible curvilinear relationships between ecophysiological variables and latitude, longitude, and elevation. The probability used for a variable to enter the equation was 0.10.

Some intrinsic intercorrelations were expected for the ecophysiological variables. For example, photosynthetic rate should be positively correlated with mesophyll conductance. Considering the general southeast–northwest geographic pattern of red alder distribution in B.C. (Fig. 1), correlations between latitude and longitude can also be expected. To assess geographic trends of ecophysiological traits as inter-correlated sets of variables, we also conducted canonical correlation analysis (CANCORR). Different from multiple regression analysis, CANCORR allows the entry of both sets of dependent (ecophysiological) and independent (geographic) variables, and assesses intrinsic intra- and inter-set correlations simultaneously.

CANCORR analyzes the correlations between a set of independent and a set of dependent variables. It is particularly efficient when dependent variables and (or) independent variables are correlated with each other, as is the case described in the above paragraph. CANCORR extracts canonical variables (linear combinations of original variables) from each data set (i.e., independent and dependent data sets) so that the first pair of canonical variables (one from each data set) are the most highly correlated among all possible linear combinations. The second pair of canonical variables are the second most highly correlated and at the same time are not correlated with the first pair, and so

TABLE 2. Minimum, maximum, and mean values; coefficient of variability (CV = standard error/mean); and relative range (RR = range/mean) of ecophysiological variables (provenance means) in red alder

Variable	Minimum	Maximum	Mean	CV (%)	RR (%)
$SENS_{VPD}$ $(s \cdot m^{-2} \cdot mol\ H_2O^{-1} \cdot kPa^{-1})$	1.73	11.20	5.16	41.09	183.53
E (mmol $H_2O \cdot m^{-2} \cdot s^{-1}$)	0.79	3.12	2.01	24.88	115.92
g_{sw} (mmol $H_2O \cdot m^{-2} \cdot s^{-1}$)	43.84	149.03	83.61	24.84	125.78
A (μmol $CO_2 \cdot m^{-2} \cdot s^{-1}$)	2.08	10.9	6.72	26.93	131.25
g_m (mmol $CO_2 \cdot m^{-2} \cdot s^{-1}$)	8.27	46.39	28.50	25.69	133.75
C_i/C_a	0.65	0.79	0.72	4.17	19.44
ψ (MPa)	-1.38	-1.13	-1.25	5.34	20.00

TABLE 3. Stepwise multiple regression analysis of ecophysiological variables against latitude, longitude, and elevation, and their squares and cross products

Dependent	Independent	r^2	F	$P > F$	Equation
$SENS_{VPD}$	Latitude	0.1745	8.05	0.0073	$28.94 - (0.47 \times lat.)$
g_m	Latitude	0.1128	4.83	0.0341	
	Elevation	0.0780	3.57	0.0668	$-57.31 + (1.65 \times lat.) + (0.0099 \times elev.)$
ψ	Latitude^2	0.1709	7.84	0.0080	$-16.12 + (1.4 \times 10^{-3} \times lat.^2)$

NOTE: The geographic variables listed in this table were those that entered and remained in the equation at 0.10 probability. F, F-statistics; $P > F$, probability for greater F-values.

TABLE 4. Correlations (r) between ecophysiological variables (above), and between ecophysiological variables and geographic variables (below the diagonal) in red alder

	$SENS_{VPD}$	E	g_{sw}	A	WUE	g_m	ψ	C_i/C_a
$SENS_{VPD}$	—	$-0.7645*$	$-0.5598*$	$-0.7111*$	-0.1464	$-0.7419*$	$-0.5966*$	0.2691
E	$-0.7645*$	—	0.4670*	0.9039*	-0.0263	0.9054*	0.5342*	0.0440
g_{sw}	$-0.5598*$	0.4675*	—	0.3809*	0.2456	0.3764*	0.3054*	$-0.4481*$
A	$-0.7111*$	0.9039*	0.3809*	—	0.3793*	0.9234*	0.5679*	-0.0490
WUE	-0.1464	0.0263	0.2456	0.3793	—	0.1536	0.1223	$-0.3563*$
g_m	$-0.7419*$	0.9054*	0.3764*	0.9234*	0.1536	—	0.5869*	-0.1732
ψ	$-0.5966*$	0.5342*	0.3054*	0.5679*	0.1223	0.5869*	—	-0.2318
C_i/C_a	0.2691	0.0440	$-0.4481*$	-0.0490	$-0.3563*$	-0.1732	-0.2318	—
Latitude	$-0.4181*$	0.2459	0.2829	0.2267	-0.1643	0.3358*	0.4133*	-0.0007
Longitude	$-0.3662*$	0.1978	0.3399*	0.1135	-0.2518	0.2024	0.3192*	-0.0557
Elevation	-0.0271	0.0744	0.0341	0.1497	0.2898	0.1597	-0.0919	-0.1775

NOTE: Significant r-values are 0.304 at $P = 0.05$ and 0.393 at $P = 0.01$ ($n = 40$). *Indicates $P < 0.05$.

on (Dillon and Goldstein 1984; SAS Institute Inc. 1988). As part of CANCORR analysis in SAS, canonical redundancy analysis outputs the proportion of the total within-set variance (e.g., the total variance of ecophysiological variables) that is explained by the canonical variables of the opposite data set (e.g., geographic variables) (SAS Institute Inc. 1988).

Results

Genetic variation

There were highly significant differences among different provenances in mid-day ψ, A, g_m, g_{sw}, C_i/C_a, E and $SENS_{VPD}$, but no significant between-provenance differences in WUE were detected (Table 1). Differences between provenances were very large, as shown by large values of coefficient of variability and relative range of provenance means (Table 2). The relative range for $SENS_{VPD}$, for example, was as high as 183%. There were no significant differences between families within provenance in any of the ecophysiological variables (Table 1).

Geographic pattern

Multiple regression analysis (Table 3) showed that $SENS_{VPD}$ decreased, but g_m and ψ increased with increases in latitude (i.e., ψ became less negative). Mesophyll conductance increased with elevation. These correlations were not strong, however. The largest coefficient of multiple determination was only 0.19 (0.1128 + 0.0780 for g_m, Table 3). Other variables did not show any significant geographic patterns.

Canonical correlation analysis showed strong intercorrelations between geographic variables and between ecophysiological variables. The correlations between geographic variables were 0.835 between latitude and longitude, -0.314 between latitude and elevation, and -0.363 between longitude and elevation. These correlations reflected the southeast–northwest geographic pattern of red alder distribution in B.C., and also indicated that the elevations of provenance samples decreased from southeast to northwest. The correlations between ecophysiological variables were as high as 0.923 (Table 4). Some of the correlations were intrinsic

TABLE 5. Canonical correlation analysis of the relationships between ecophysiological variables and geographic locations of provenance origin

Canonical correlation	Standard error	Approx F	Num df	Den df	$P > F$
0.6972	0.0823	1.688	24	85	0.0420
0.5220	0.1164	1.130	14	60	0.3519
0.3732	0.1378	0.836	6	31	0.5517

NOTE: Approx F, F approximation; Num df, degrees of freedom of the numerator of F-ratio; Den df, degrees of freedom for the denominator of F-ratio; $P > F$, probability for greater F-values.

characteristics of the variables and were expected (e.g., correlations between A and g_m); others may have reflected adaptation mechanisms of the species (discussed later). These within-set correlations were much stronger than the correlations between the two data sets (Table 4). The largest between-set correlation was only -0.4181 (between $SENS_{VPD}$ and latitude; Table 4). This rendered canonical correlation analysis more appropriate than multiple regression in examining the geographic patterns of ecophysiological variables in red alder.

The three canonical correlations (r) were sequentially 0.6972, 0.522, and 0.373. The first canonical correlation was statistically significant, whereas the other two were not significant (Table 5). The first ecophysiological canonical variable was closely and positively correlated with ψ, g_m, E, and A, and negatively correlated with $SENS_{VPD}$ (Table 6). The first geographic canonical variable primarily represented latitude but also had a strong correlation with longitude (Table 6). The first pair of canonical variables, therefore, could be interpreted as indicating that midday ψ, g_m, A, and E increased, and that $SENS_{VPD}$ decreased from southeast to northwest. Latitude had a greater impact than longitude on this trend. Canonical redundancy analysis suggested that this trend could only explain 18% of the total between-provenance variation in ecophysiological variables. This was in general agreement with the results of regression analysis for $SENS_{VPD}$, g_m and ψ. Regression analysis, however, failed to reveal this trend for E and A (Table 3).

The second and third canonical correlations were not significant ($P > 0.35$) (Table 5) and thus no interpretations were pursued.

Intercorrelations among ecophysiological traits

The correlation matrix between ecophysiological variables (Table 4) showed that provenances with more sensitive stomata (i.e., higher $SENS_{VPD}$) tended to have lower E, A, g_m, g_{sw}, and ψ. Lower g_{sw} was also associated with higher C_i/C_a ratios, but with lower E, A, g_m and ψ. Net photosynthesis, g_m, E, g_{sw}, and ψ were positively related to each other, but negatively related to $SENS_{VPD}$. WUE was positively related to A but negatively related to C_i/C_a.

Discussion

Provenances of red alder were significantly differentiated in all ecophysiological traits examined except WUE (Table 1). The between-provenance differences in ecophysiological variables were large (Table 2). Provenance means for g_m ranged from 8.27 to 46.39 mmol $CO_2 \cdot m^{-2} \cdot s^{-1}$. Mesophyll conductance represents the photosynthetic capacity after stomatal limitations have been accounted for (Fites and Teskey 1988). The actual photosynthetic rates (also provenance

TABLE 6. Correlations (r) between ecophysiological variables in red alder and their canonical variables (ECOPHYS1 to 3), and between the geographic variables of provenances and their canonical variables (GEOGRAP1 to 3)

	ECOPHYS1	ECOPHYS2	ECOPHYS3
$SENS_{VPD}$	$-0.5426*$	$0.3255*$	$-0.5002*$
E	$0.3582*$	-0.0993	$0.3900*$
g_{sw}	-0.1257	-0.2140	$0.8421*$
A	$0.4366*$	0.1342	$0.3489*$
WUE	0.0229	$0.6012*$	0.2198
g_m	$0.5867*$	0.0673	$0.4661*$
C_i/C_a	0.0031	-0.0242	$-0.6239*$
Ψ	$0.5458*$	$-0.3246*$	0.0592

	GEOGRAP1	GEOGRAP2	GEOGRAP3
Latitude	$0.8496*$	$-0.5260*$	0.0394
Longitude	$0.4446*$	$-0.8477*$	0.2894
Elevation	0.0229	$0.6882*$	$0.7252*$

NOTE: Significant r-values are 0.304 at $P = 0.05$ and 0.93 at $P = 0.01$. *Indicates $P < 0.05$.

means) ranged from 2.08 to 10.90 $\mu mol\ CO_2 \cdot m^{-2} \cdot s^{-1}$ (Table 2). These results indicate a strong genetic differentiation among provenances of red alder in potential productivity. Stomatal sensitivity to VPD ranged from 1.73 to 11.20 $s \cdot m^{-2} \cdot mol\ H_2O^{-1} \cdot kPa^{-1}$. Stomatal sensitivity to VPD represents the direct response of the guard cells to evaporative demand. This feed-forward regulation of stomatal conductance can be very advantageous, particularly for trees growing in environments with low atmospheric humidity (Ludlow 1980). Stomatal conductance to water vapour ranged from 43.8 to 149.0 $mmol \cdot m^{-2} \cdot s^{-1}$. Although the large differences in $SENS_{VPD}$ and g_{sw} resulted in significant differences in E between provenances, the between-provenance differences in WUE were not significant. This is because provenances with higher $SENS_{VPD}$ and lower g_{sw} had lower A and g_m.

Our data suggest that there is genetic differentiation in drought resistance in red alder. Photosynthesis, g_m, g_{sw}, and midday ψ were positively related to each other, but negatively correlated with $SENS_{VPD}$. Garden and Hibbs (1993) have also reported a positive relationship between A and ψ for this species. The significant between-provenance difference in A, g_m, ψ, g_{sw}, $SENS_{VPD}$, and C_i/C_a, and the above correlations indicate that red alder probably had undergone differentiation in drought resistance and drought had affected both stomata and mesophyll. These correlations could have been caused by differences in root to shoot ratios among different provenances, and thus differences in drought resistance. Ager (1987) has found that provenances of red alder from higher elevation allocate more resources to roots and nodules. The provenances that had lower A, g_m, g_{sw}, and midday ψ in association with higher $SENS_{VPD}$, might have had greater leaf area per unit root area, resulting in higher sensitivity to water stress. Bunce (1981) has observed that species with greater leaf area per unit area of roots have lower g_{sw} and are more sensitive to changes in humidity than those with smaller leaf area per unit area of roots. A higher rate of photosynthesis, however, should be expected for the provenances with greater leaf to root ratios when they grow under nonwater stress conditions. The higher shoot to root ratio would then translate into higher productivity. Indeed, red alder grows best on wet sites (Hook et al.

1987). The provenances with higher A, g_m and midday ψ, on the other hand, might have had smaller leaf to root ratios and, therefore, would have been more suitable for drier environments. Further studies are needed to test the hypothesis on genetic differentiation in shoot to root ratio and its relationship to drought resistance in red alder.

The lower g_{sw} and higher $SENS_{VPD}$ in provenances with more negative midday ψ might have been triggered by water stress. Indeed, the data of Pezeshki and Hinckley (1982, 1988) indicate that both leaf resistance and sensitivity to VPD in red alder increase in response to drought. Comparison of our midday ψ measurements (-1.38 to -1.18 MPa) with the solute potentials (-1.27 to -0.80 MPa) reported for water-stressed red alder (Pezeshki and Hinckley 1988) suggests that the seedlings in this study indeed experienced water stress. In drought resistant species, WUE normally increases in response to water stress as a result of greater deceases in stomatal conductance than g_m. There were, however, no significant differences in WUE among provenances of red alder with different g_{sw} and g_m, suggesting that the stomata in red alder were not sensitive enough to achieve a more efficient utilization of water when the trees were under water stress. The insensitive stomata may represent a serious constraint on red alder growing in dry environments. Our results can be considered as an ecophysiological explanation of why a lack of precipitation in the growing season is a major limit to the range of red alder (Harrington 1994).

Red alder has showed a weak but significant southeast to northwest geographic trend in ecophysiological traits. Multiple regression analysis showed that g_m and ψ significantly increased, but $SENS_{VPD}$ decreased, with increases in latitude (Table 3). Canonical correlation analysis (CANCORR) showed that A, g_m, E, and midday ψ increased, but $SENS_{VPD}$ decreased, from southeast to northwest (Table 6). Latitude had a greater impact than longitude. In this sense, CANCORR results generally supported those from regression analysis. The canonical correlation analysis, however, also suggested that the geographic patterns of $SENS_{VPD}$ were much more complicated than that indicated by regression analysis. Considering the complicated intercorrelations between ecophysiological variables (Table 4) and between geographic variables, we think that CANCORR was more reliable than regression analysis. Therefore, the southeast–northwest trend may represent a general geographic pattern of changes in ecophysiological variables in red alder. This trend suggests that ecophysiological adaptation in red alder may have occurred along the environmental gradient from southeast to northwest (e.g., in moisture and temperature). However, this trend is very weak. Canonical redundancy analysis has shown that differences in latitude, longitude, and elevation of provenances could only explain 18% of total between-provenance variations in the ecophysiological variables. The largest combined r^2 in the multiple regression analysis was also only 0.19 (Table 3). In other words, more than 80% of the total between-provenance variation in ecophysiological traits is not related to the general geographic trend. Considering the complexity of the geography of the sampling area (Fig. 1), however, this is not surprising. But this result may have important implications for the wise utilization of seed resources of red alder in reforestation programs and for gene conservation. It suggests that the micro-environmental conditions of the seed source may be more important in determining the physiological performance of red alder than

its geographic location. The correlations among ecophysiological variables suggest that moisture conditions deserve particular consideration, but other factors may also be important. The lack of site-specific environmental information for each provenance has prevented us from examining the possible relative contributions of different environmental factors to the genetic differentiation of ecophysiological traits in red alder. Further studies in this area are warranted.

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