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Genetics of dark respiration and its relationship with drought hardiness in coastal Douglas-fir☆

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Abstract

Genetic variation in respiration parameters, and the relationships between respiration and drought hardiness were investigated in coastal Douglas-fir (*Pseudotsuga menziesii* var. *menziesii* (Mirb.) Franco). Material included 3-year-old seedlings from 12 families grown under two treatments: control (well-watered) and drought (moderate drought the second growing season followed by severe drought the next year). Respiratory parameters measured were metabolic heat rate (q) and rate of CO_2 production (R_{CO_2}). Calculated parameters were the ratio of metabolic heat rate to CO_2 production rate (q/R_{CO_2}), specific growth rate (R_{SG}), and Arrhenius temperature coefficients of metabolic heat (μ_q) and CO_2 production (μ_{CO_2}). Growth traits measured were third-year increments of seedling height and diameter.

Means of respiration traits were generally less in the drought treatment than in the control, with the exception of μ_q, which increased under drought. Consistent increase in μ_q and decrease in μ_{CO_2} values in response to drought appear to suggest a differential influence of drought on the temperature dependence of ATP synthesis in catabolic reactions, and ATP breakdown in anabolic reactions or in futile cycles of dark respiration. Metabolic heat rates measured over a wide a range of temperatures (20 to 55°C) differed significantly between control and drought treatments for the most drought sensitive family, but not for drought hardy families.

Variation among the 12 families in q (at 25°C) and μ_{CO_2} were significant ($p<0.05$) when families were grown in the control treatment. Family means for height increments ($r^2=0.43$ to 0.58; $p<0.05$) related negatively to respiration and diameter increments related positively to respiration traits ($r^2=0.34$ to 0.56; $p<0.05$). Temperature coefficient of CO_2 production rate under control treatment was negatively associated with shoot damage ($r^2=0.34$; $p<0.05$) suggesting that respiration traits may be useful for evaluating drought hardiness in this species.

Keywords: Calorimetry; *Psuedotsuga menziesii*; Metabolic heat; Temperature coefficient

1. Introduction

During summer months drought is a major growth limiting factor throughout the natural range of coastal Douglas-fir (*Pseudotsuga menziesii* var. *menziesii* (Mirb.) Franco) [1]. Drought adversely affects the success of natural regeneration of seedlings and limits basal area increments in mature trees [2,3]. Drought

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also is an important factor influencing adaptation in this species, with seed sources from drier sites having shorter growing seasons, slower growth, and smaller top to root ratios than sources from moist sites [4,5,6]. In addition, CO_2 production rates in dark respiration (assessed with an infrared gas analyzer) was found to be higher in sources from wet sites than in sources from dry sites and the rates declined in response to drought stress [7,8]. In a study with open-pollinated families from 35 seed sources of coastal Douglas-fir grown under three drought environments, however, populations from high elevations, but not from drier sites, were more drought hardy [9] suggesting that temperature adaptation may play a role in adaptation to drought.

In recent years, measurements of dark respiration using calorimetry have been used to investigate the influence of metabolic processes on growth and adaptation in plants [10–18]. During respiration in the dark, calorimetry can be used to simultaneously measure the rate of loss of heat from plant tissue (i.e., the metabolic heat rate, q) and carbon dioxide production rate (R_{CO_2}) at defined temperatures. Calorimetrically determined R_{CO_2} in dark respiration has been hypothesized to be an indirect measure of the rate of ATP synthesis in catabolism [16,17,19]. Although metabolic heat is primarily from catabolism, q is not an exclusive measure of ATP synthesis, because a small portion of heat is also generated by futile cycles (i.e., alternative pathway, phosphorylation catalyzed reactions, and adenylate kinase reactions) in dark respiration and anabolic reactions in biosynthesis [19,20].

Two important respiration parameters related to plant growth and survival, specific growth rate (R_{SG}) and the ratio of metabolic heat rate to CO_2 production rate (q/R_{CO_2}) can be derived [12,15] from the measured q and R_{CO_2}. R_{SG} is the rate of incorporation of carbon into new growth per mass of tissue, and is a function of the difference between the metabolic heat rate and CO_2 production rate. The ratio is the metabolic heat energy lost per mole of CO_2 respired during dark respiration and this ratio is inversely related to substrate carbon conversion efficiency [12,16]. When the energy loss is large (i.e., high q/R_{CO_2}), plant cells lose the ability to produce energy at a rate sufficient to maintain cellular structure or form biomass, and plant growth rate is thus limited. A combination of high R_{SG} and low q/R_{CO_2} in two *Eucalyptus* subgenera was strongly associated with high survival and large tree size [21].

The relationship between q (or R_{CO_2}) and temperature (T) can be represented in an Arrhenius plot, where the natural logarithm of q (or R_{CO_2}) is plotted against the reciprocal of absolute T in kiloKelvin [13,17]. At temperatures below 30°C, the plot is linear and the slope is equal to the temperature coefficient of metabolic heat rate (μ_q) or temperature coefficient of CO_2 production rate (μ_{CO_2}). Plants adapted to cold climates tend to show high μ_q values (i.e., large changes in q with increasing temperature) and warm climate plants show high μ_{CO_2} values [13,17,22]. Relative μ_q and μ_{CO_2} values have been shown to be related to adaptation of plants to climatic temperature [16,19].

In a recent common-garden experiment, the Pacific Northwest Tree Improvement Research Cooperative (PNWTIRC) subjected seedling families of coastal Douglas-fir to three moisture stress regimes ('Seedling Drought Physiology Study'). The goals of this study were to identify key physiological mechanisms associated with short-term moisture stress responses in seedlings, evaluate the genetics of drought hardiness, and develop criteria for screening improved families in breeding programs. Because summer drought involves a combination of moisture and temperature stress, understanding the effects of these two climatic factors on drought should provide further insights on mechanisms of drought stress in Douglas-fir. Calorimetry techniques provided an opportunity to determine the influence of normal or stress temperatures independent of moisture-stress on dark respiration of plant tissues. Thus, to investigate metabolic responses to drought stress and potentially identify additional screening traits for drought hardiness, the above respiratory parameters were measured on detached shoots of a subsample of families. The main objectives of this study were as follows:

1. To determine the influence of drought on dark respiration.
2. To assess the extent of genetic variation in dark respiration traits among families of coastal Douglas-fir in a single breeding population.
3. To evaluate genetic relationships between dark respiration traits and drought hardiness.

To our knowledge, this is the first report on family variation in calorimetrically determined respiration

traits in coastal Douglas-fir, and on the influence of drought stress on these traits.

2. Materials and methods

2.1. Plant materials and nursery planting design

The PNWTIRC study included 39 full-sib families of coastal Douglas-fir from southwestern British Columbia (Vancouver Island and the coastal mainland). Parent trees of these families come from environments with low to high levels of available summer moisture. Therefore, the full-sib families obtained by crossing these parents were expected to show differential growth and survival performance in response to drought treatments in nursery beds. Germinated seeds from these families were planted into two custom-built raised nursery beds (20 m long×1.5 m wide×1 m deep) filled with a sandy loam soil to facilitate drainage. The beds were lined at the bottom with landscape cloth to prevent root penetration beyond the beds and with plastic barriers between walled sections of the bed to prevent movement of water between watering regimes. All seedlings were grown the first year under well-watered conditions, with drought treatments begun the second growing season.

The experimental design was a split plot replicated in five blocks. Main plots were two watering regimes applied in the second and third growing seasons: control (well-watered both years) and drought (moderate drought 1 year followed by severe drought the next year). Within each main plot, each family was represented by eight trees in two randomly-located four-tree row plots, with seedling spacing of 8 cm×8 cm. All main plots were surrounded by two rows of buffer seedlings. In addition, some filler seedlings were included in each main plot for predawn xylem water potential (ψ_p) readings to monitor the severity of the drought treatments. At the end of the second growing season, every other seedling in all treatments was harvested. Thus, drought treatments in the third year were applied to only one-half of the original number of seedlings.

All trees were measured for relative increments of height and diameter in the third year ((third year−second year)×100)/second year) and visual injury to shoots (% of foliage and branches brown or dead) at the end of second and third growing seasons. Drought treatments were highly effective with considerable differences between control and drought for ψ_p, shoot damage, and relative growth increment in the third year (Table 1).

Table 1
Predawn xylem water potentials (ψ_p) in control and drought treatments during the third growing season, and the impacts of drought on seedling shoot damage, and relative height and diameter increments

Treatments	ψ_p (MPa)	Shoot damage (%)[a]	Relative increment (%)[a,b]	
Height diameter				
Control	0.64	5	74	37
Drought	2.20	49	51	12

[a] Means for 39 families.

[b] Relative height increment=(seedling height in third year−seedling height in second year)/seedling height in second year. Relative diameter increment=(diameter in third year−diameter in second year)/diameter in second year.

2.2. Plant material used for calorimetric measurements

Seedlings of the 39 families included in the main study were first ranked for drought hardiness based on visual shoot injury resulting from the drought treatment in the second growing season (1997) when mean damage ranged from 14 to 36%. To assess the influence of drought on dark respiration, 10 seedlings (5 blocks×2 seedlings/block×treatments) from the two most drought-hardy and two least drought-hardy families in 1997 were sampled from the control and drought treatments during the third growing season (1998) and subjected to calorimetric measurements of q and R_{CO_2} at 17 and 25°C (N=80; 2 treatments×4 families×10 seedlings/family). In addition, q was measured for these four families in the temperature range of 20–55°C in 5° increments (N=80). The wide range of temperatures made it possible to evaluate impacts of temperature stress on dark respiration. Family means for drought injury in 1998 were 63 and 37% for the least drought hardy families in 1997 (315 and 323, respectively), and were 30 and 46% for the most drought hardy families (135 and 114, respectively).

To evaluate genetic variation in dark respiration traits and the relationships between these traits and drought hardiness, two seedlings from the control treatment of each block were also sampled in the third growing season from each of 12 families sampling the range of visual drought injury in 1997 (i.e., 10 seedlings/family for calorimetric analysis at two test temperatures, 17 and 25°C; N=120). The range in mean drought injury among these 12 families in 1998 was 29 to 68%.

One actively growing, fresh lateral shoot-apex was collected at 8 a.m. from a primary branch in the uppermost whorl of each seedling and placed in an open 15 ml centrifuge tube containing cold, half-strength Hoagland's solution and 1% sucrose. The tubes were maintained near 5°C during the period of storage prior to calorimetric measurements. Fresh samples were collected every day of measurement during June 11–July 17, 1998. Sample collection order and measurements within replicates were randomized. Injury related respiration is negligible with this sampling technique [23].

2.3. Calorimetric measurements

Measurements of metabolic heat rate (q) and CO_2 production rate (R_{CO_2}) were made using a Hart Scientific Model 7707, multi-cell, heat-conduction, differential, scanning calorimeter operated in the isothermal mode [11]. Sections of approximately 100 mg of apical meristem with developing stem and needles were placed in the 1 cm^3 calorimeter ampules and metabolic heat rates measured. Then, 40 ml of 0.4M NaOH in 50 ml vials was placed next to the samples in the ampules and CO_2 production rate measured as an increase in total heat rate [11]. The Arrhenius temperature coefficients of metabolic heat rate (μ_q) and of CO_2 production rate (μ_{CO_2}) in kK were derived following Criddle et al. [13]. The ratio of metabolic heat rate to CO_2 production rate (q/R_{CO_2}) in kJ mol^{-1} and specific growth rate (R_{SG}) were derived from the original variables following Hansen et al. [12,15].

2.4. Analytical methods

To evaluate the influence of drought on dark respiration, differences between the control and drought treatments (four families) were tested for each respiration parameter using the TTEST procedure (Objective 1) [24]. To assess genetic variation in dark respiration traits, measurements of the 12 families in the control treatment were subjected to analyses of variance using a standard General Linear Model (GLM) procedure and the significance of family mean squares tested (Objective 2) [24]. Linear regression was used to relate family means for height and diameter increment (in control and drought treatments) and shoot damage due to drought, to respiration parameters in the control treatment (Objective 3).

3. Results and discussion

Means of respiratory traits measured at 17 and 25°C (over four families) were generally lower for shoot tips sampled from seedlings grown in the drought than in the control treatment (Table 2). The only exceptions are q/R_{CO_2} at 25°C, where the difference was not significant, and μ_q, which is significantly greater in droughted seedlings. The finding that μ_{CO_2} decreased under drought, while μ_q increased, relative to the control treatment, is one of the most intriguing results of this study. This opposite effect on the temperature dependence of R_{CO_2} and q seems to indicate that ATP synthesis and ATP use reactions of the respiratory pathway have responded differently to moisture stress. Although these results on only four families are preliminary, we propose the following two hypotheses to stimulate further investigations of respiratory physiology under moisture stress:

1. Drought decreases the temperature dependence of CO_2 production in dark respiration possibly due to lack of substrate availability, altered substrate (i.e., from carbohydrates to lipids under drought), or lack of sufficient O_2.
2. Drought increases the temperature dependence of q due to increased activity of futile cycles or biosynthesis, but does not increase the average rate of catabolic reactions.

It is important to recognize that q, and thus μ_q, has at least three distinct components: (1) $\mu_{q\ (\text{catabolic})}$, (2) $\mu_{q\ (\text{futile cycles})}$, and (3) $\mu_{q\ (\text{biosynthesis})}$. Calorimetry alone cannot separate these components, or determine the oxidation state of the respiration substrate, thus additional studies are required to verify our results, and subsequent hypotheses.

Table 2
Estimated family means for respiration parameters measured at 17 and 25°C in four coastal Douglas-fir families grown under control and drought treatments[a]

T (°C)	Respiration traits[b]	Treatments	Family				Mean[c]
			135	114	315	323	
17	q	Control	1.80	1.84	2.10	1.78	1.88**
		Drought	1.17	1.31	1.53	1.17	1.29
	R_{CO_2}	Control	4.27	5.59	4.80	4.52	4.79ns
		Drought	4.45	3.24	5.10	3.99	4.17
	q/R_{CO_2}	Control	430	351	503	455	435*
		Drought	281	416	341	335	343
	R_{SG}	Control	28	42.7	34.1	31.1	34.0ns
		Drought	37	21.9	40.5	32.1	32.8
25	q	Control	3.71	3.55	3.70	4.20	3.79**
		Drought	3.08	3.24	2.86	3.04	3.06
	R_{CO_2}	Control	11.1	9.83	10.3	10.8	10.49**
		Drought	8.1	9.43	6.96	7.88	8.12
	q/R_{CO_2}	Control	392	384	382	426	396ns
		Drought	403	387	419	405	403
	R_{SG}	Control	83.7	71.4	74.9	74.7	76.2*
		Drought	56.8	70.4	46.7	55.1	57.5
17 & 25	μ_q	Control	8.42	7.21	7.70	9.33	8.17*
		Drought	10.7	9.85	8.04	10.4	9.86
	μ_{CO_2}	Control	9.75	6.96	8.77	12.5	9.41ns
		Drought	7.19	11.0	5.76	7.85	8.16

[a] Family means for percent shoot damage due to third year drought were: 135 (30%), 114 (46%), 315 (63%), and 323 (37%)
[b] See text for description of these traits. Units of measurement are: q in μW mg^{-1} dry wt; R_{CO_2} in pmol s^{-1} mg^{-1} dry wt; q/R_{CO_2} in kJ mol^{-1}; R_{SG} in pmol s^{-1} mg^{-1} dry wt; μ_q in kK ; μ_{CO_2} in kK.
[c] Significance of difference between control and drought treatment means: ns=not significant; *=$p<0.05$; **=$p<0.01$.

In the absence of a sufficient rate of energy generation to drive anabolism, trees cannot grow or incorporate carbon into structural biomass as indicated by a reduction in R_{SG} values (at 25°C) for all families grown under drought relative to the control. A similar relationship between growth and R_{SG} has been reported in many other plant species [17–19,21,23]. In addition, when q was measured under control and drought treatments over a wider temperature range (20–55°C), the treatment difference was greatest in family 315, which was also the family most sensitive to drought damage (Fig. 1).

Individuals from the wider sample of 12 families grown in the control treatment differed markedly in respiration traits when tested at 17 and 25°C, with a coefficient of variation (CV) never less than 35% (Table 3). CVs and ranges in family means were also large, with family differences significant ($p<0.05$) for q at 25°C and μ_{CO_2}. Thus, considerable genetic variation in respiration traits is apparent. Previous studies in other plant species have also reported high genetic variation in respiration parameters [18,21–23].

Family means for relative height increment in the control treatment were uncorrelated ($r=0.14$) with height increments in the drought treatment, while diameter increments in the control and drought treatments were significantly correlated ($r=0.53$; $p<0.01$). These results suggest that growth response to drought is not consistently associated with inherent growth rate under well-watered conditions. Relative height increments of families in the drought treatment, however, were negatively associated with both q at 25°C ($r^2=58$; $p<0.01$) and μ_{CO_2} ($r^2=0.43$; $p<0.05$) in the control treatment (Fig. 2). Diameter increments under drought, on the other hand, were positively and significantly associated with μ_{CO_2} ($r^2=0.56$; $p<0.01$), but not with q ($r^2=0.01$) in the control. The opposite slopes of the relationships of height and diameter with

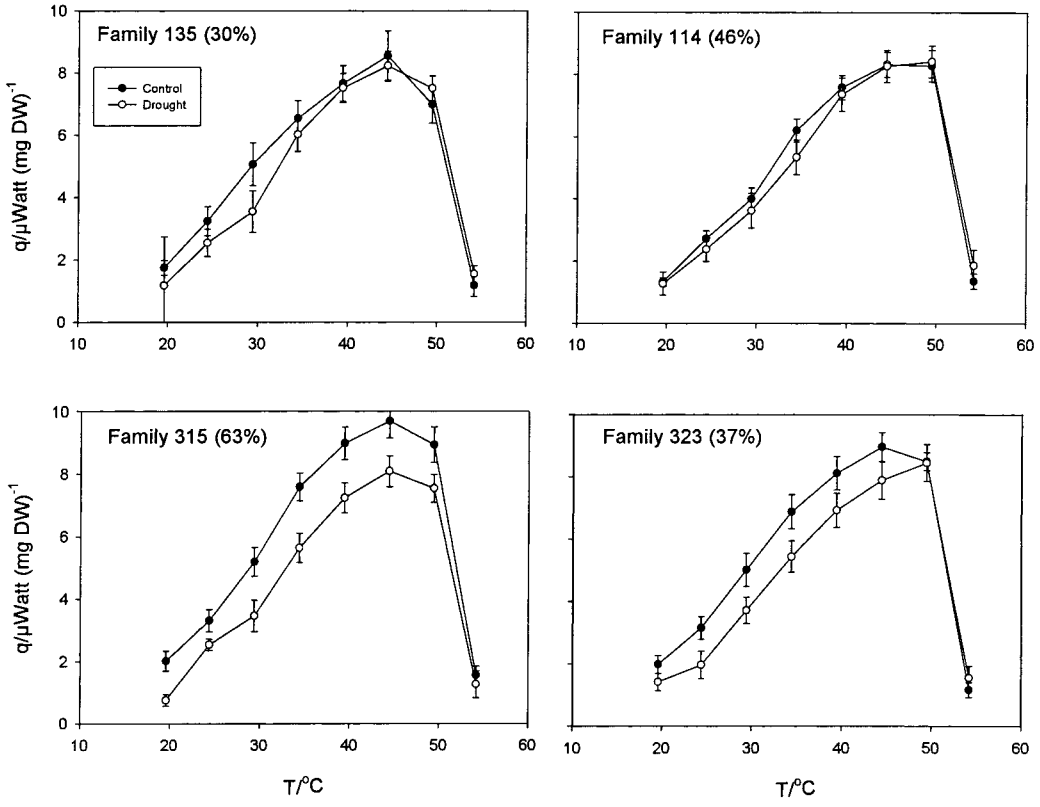

Fig. 1. Change in family means of metabolic heat rate with increasing temperature for four families grown under control and drought treatments. Mean percent damage to shoots from the drought treatment is given for each family in parentheses. Error bars are the standard errors of family means at each measurement temperature.

Table 3
Estimated overall and family means, ranges, and coefficients of variation for respiration traits measured at 17 and 25°C in 12 coastal Douglas-fir families grown under the control (well-watered) treatment

T (°C)	Respiration Traits[a]	Overall[b]			Family[c]	
		Mean	Range	CV[d]	Range	CV[d]
17	q	1.84	0.56–4.26	39	1.42–2.14	11
	R_{CO_2}	5.06	1.80–10.10	39	4.27–6.49	13
	q/R_{CO_2}	413	83–967	48	314–506	16
	R_{SG}	36.4	2.05–93.0	60	20.6–53.9	24
25	q	3.96	1.17–8.11	35	3.39–5.05	14**
	R_{CO_2}	11.1	1.96–30.7	39	9.53–15.3	16
	q/R_{CO_2}	392	101–868	38	311–452	9
	R_{SG}	80	14.1–224	51	61.8–107	16
17 & 25	μ_q	9.36	0.22–21.2	47	7.22–12.3	16
	μ_{CO_2}	9.48	0.07–23.1	49	4.79–12.9	25**

[a] See text for descriptions of traits. For measurement units refer to Table 1.
[b] Based on all 119 seedlings (12 families×2 seedlings/family×5 blocks) from the control treatment.
[c] Based on average values for each of 12 families from the control treatment.
[d] Coefficient of variation in individual seedlings and among 12 family means. Significance of difference among family means: **=p<0.01.

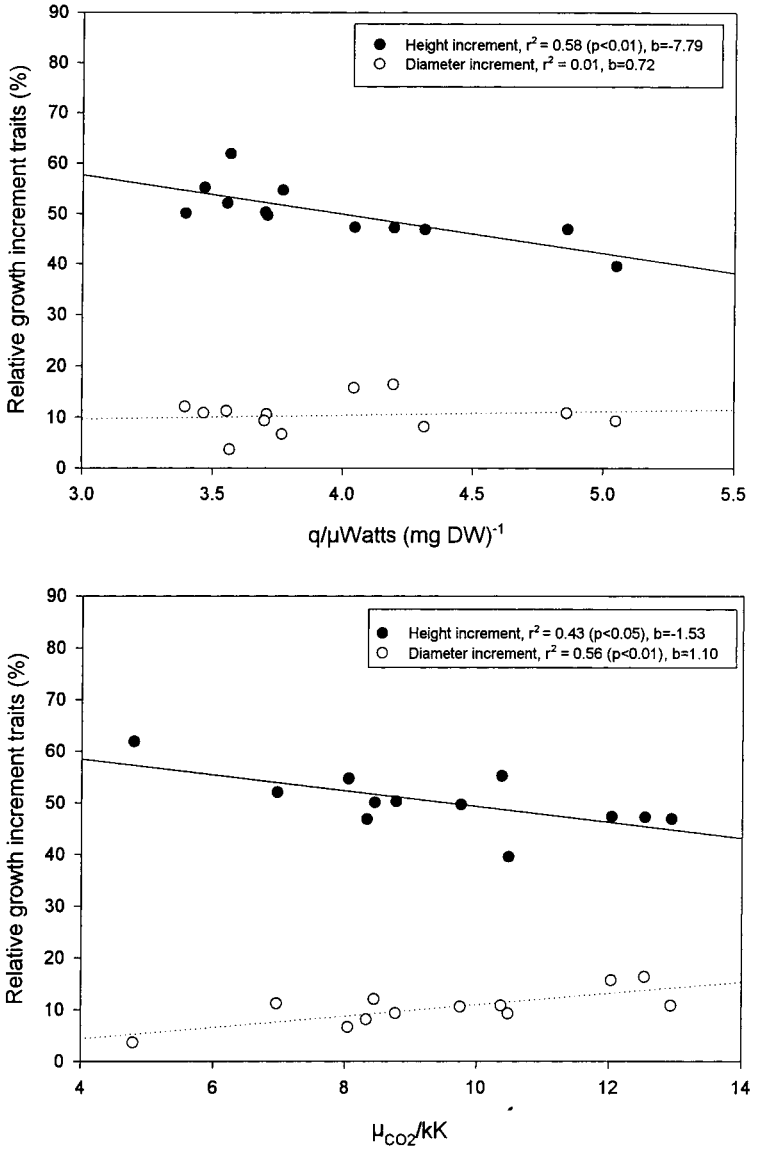

Fig. 2. Linear regressions of family means (12 families) for third year relative height (solid line) and diameter (dotted line) increments in the drought treatment plotted over q and μ_{CO_2} in the control treatment. See footnote in Table 1 for definitions of height and diameter increments.

q or μ_{CO_2} may be related to the timing of the calorimetry measurements (i.e., June 11–July 6, 1998), which were conducted after much of the third-year height growth was completed, but before much of the diameter growth occurred.

Third-year shoot damage was moderately and negatively associated with μ_{CO_2} (r^2=0.34; p<0.05), but not with q (r^2=0.04) measurements made earlier in the growing season (Fig. 3), suggesting that families with the highest μ_{CO_2} are the least susceptible to damage from summer drought. The least damaged families also added the most diameter increments under drought (compare Fig. 3 with Fig. 2). This relationship is consistent with the observed reduction in μ_{CO_2}

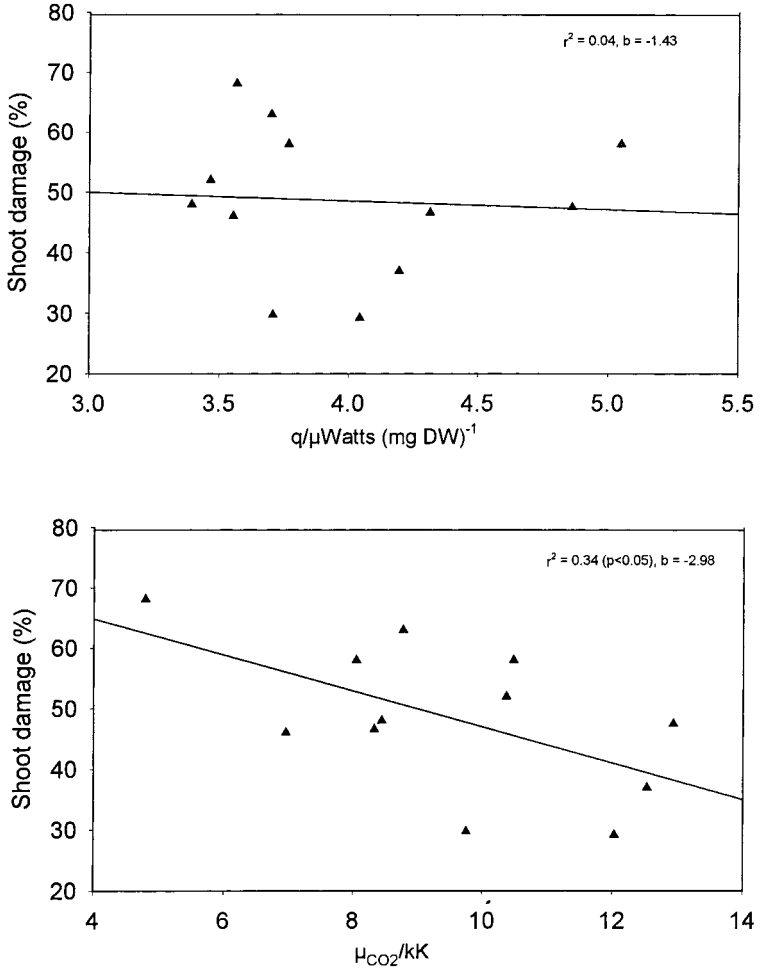

Fig. 3. Family means for third year shoot damage in the drought treatment plotted over q and μ_{CO_2} in the control treatment.

values for three of four families measured under the drought treatment (Table 2). These results suggest that the response of families to severe drought at the seedling stage may be predictable on the basis of simple calorimetric measurements made on seedlings grown in well-watered conditions. The effects of the moderate temperature stress applied during the calorimetric measurement appear to simulate the effects of moisture stress applied in the nursery beds. Obviously, further testing with larger samples of Douglas-fir families is required. In particular, it would be interesting to compare calorimetric parameters of droughted and control seedlings at different times during the course of the growing season as the impact of moisture stress intensifies.

4. Conclusions

This study measured genetic variation in respiration parameters and explored the possibility of using calorimetry to predict drought hardiness in coastal Douglas-fir families. The following conclusions were reached:

1. On average, q, R_{CO_2}, and R_{SG} values were reduced under moisture stress. μ_q values, however, increased and μ_{CO_2} decreased in response to drought.
2. Family means of q in the most drought sensitive family were significantly higher in the control than in drought treatment across the temperature range of 20 to 50°C.

3. All respiration traits showed a high degree of genetic variation among families.
4. Respiration traits determined under mild temperature stress on seedlings grown in the well-watered treatment may be useful for predicting seedling drought hardiness.

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References

[1] J.F. Franklin, R.H. Waring, Distinctive features of the northwest coniferous forests: development, structure, and function, in: R.H. Waring (Ed.), Forests: Fresh Perspectives from Ecosystem Analysis, Oregon State Univ. Press, Corvallis, 1981, p. 59.
[2] S.D. Hobbs, R.H. Byars, D.C. Henneman, C.R. Frost, First-year performance of 1-0 containerized Douglas-fir seedlings on droughty sites in southwestern Oregon, For. Res. Lab., Oreg. State Univ., Corvallis. Res. Pap. 42 (1980) 15.
[3] D.L. Spittlehouse, Determination of the year-to-year variation in growing season water use of a Douglas-fir stand, in: B.A. Hutchinson, B.B. Hicks (Eds.), The Forest-Atmosphere Interaction, 1985, p. 235.
[4] R.K. Hermann, D.P. Lavender, Silvae Genet. 17 (1968) 143.
[5] F.C. Sorensen, Ecology 64 (1983) 696.
[6] R.J. Joly, W.T. Adams, S.G. Stafford, For. Sci. 35 (1989) 987.
[7] J. Zavitkovski, W.K. Ferrell, Bot. Gaz. 129 (1968) 346.
[8] J. Zavitkovski, W.K. Ferrell, Photosynthetica 4 (1979) 58.
[9] T.W. White, For. Sci. 33 (1987) 283.
[10] L.D. Hansen, R.S. Criddle, Thermochim. Acta 160 (1990) 173.
[11] R.S. Criddle, A.J. Fontana, D.R. Rank, D. Paige, L.D. Hansen, R.W. Breidenbach, Anal. Biochem. 194 (1991) 413.
[12] L.D. Hansen, M.S. Hopkin, D.R. Rank, T.S. Anekonda, R.W. Breidenbach, R.S. Criddle, Planta 194 (1994) 77.
[13] R.S. Criddle, M.S. Hopkin, E.D. McArthur, Plant, Cell Environ. 17 (1994) 233.
[14] T.S. Anekonda, R.S. Criddle, W.J. Libby, Can. J. For. Res. 24 (1994) 380.
[15] L.D. Hansen, M.S. Hopkin, D.K. Taylor, T.S. Anekonda, D.R. Rank, R.W. Breidenbach, R.S. Criddle, Thermochim. Acta 250 (1995) 215–232.
[16] L.D. Hansen, M.S. Hopkin, R.S. Criddle, Thermochim. Acta 300 (1997) 183.
[17] B.N. Smith, L.D. Hansen, A.R. Jones, R.S. Criddle, Growth, respiration rate, and efficiency responses to temperature, Chap. 18, in: M. Pessarakli (Ed.), Handbook of Plant and Crop Stress, 2nd Edition, Marcel Dekker, NY, 1998.
[18] D.K. Taylor, D.R. Rank, D.R. Keiser, B.N. Smith, R.S. Criddle, L.D. Hansen, Plant Cell Environ. 21 (1998) 1143.
[19] L.D. Hansen, R.S. Criddle, J.N. Church, B.N. Smith, Global gradients of poikilotherm distribution are explained by temperature responses of energy metabolism, submitted for publication.
[20] R.W. Breidenbauch, M.J. Saxton, L.D. Hansen, R.S. Criddle, Plant Physiol. 114 (1997) 1137.
[21] T.S. Anekonda, R.S. Criddle, M.J. Bacca, L.D. Hansen, Contrasting adaptation of two *Eucalyptus* subgenera is related to differences in respiratory metabolism, Functional Ecol. 13 (1999) 675–682.
[22] R.S. Criddle, T.S. Anekonda, M.J. Bacca, L.D. Hansen, Can. J. For. Res. 26 (1996) 1569.
[23] L.D. Hansen, D.K. Taylor, B.N. Smith, R.S. Criddle, Russian J. Plant Physiol. 43 (1996) 691.
[24] SAS Institute Inc., SAS/STAT guide for Personal Computers, Version 6 Edition, Cary, NC, 1992.