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Variation of Alnus rubra for Nitrogen Fixation Capacity and Biomass Production[1])

By PH. A. MONACO,*) T. M. CHING**) and K.K. CHING*)

Oregon State University, Corvallis, Oregon 97331

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Summary

To test half-sib families of *Alnus rubra* BONG. for biomass production and nitrogen assimilation capacity, seeds were collected from two parent trees selected from each of five natural populations between Newport and Corvallis in western Oregon. The seedlings were germinated and grown in a greenhouse with or without indigenous inoculant at two nitrogen fertilizer levels. At age 5 weeks before inoculation, seedling size and weight among families and sources differed little. However, at age 14 weeks, seedlings inoculated with indigenous endophyte grew 10 to 15 times larger than noninoculated seedlings. Differences in biomass production and nitrogen assimilation between families and sources in the inoculated group indicate genetic variability and the possibility of gain by selection. Because progeny from sources with site indices of 95 and 65 performed better in this experiment than those from sites with indices of 100 and 110, site index should not be the sole selection criterion for nitrogen-fixing capacity and biomass production in *A. rubra*.

Key words: *Alnus rubra*, tree improvement, genetic selection, nitrogen-fixation.

Zusammenfassung

Samen von je zwei selektierten Elternbäumen aus fünf natürlichen Populationen von *Alnus rubra* BONG. zwischen Newport und Corvallis in West-Oregon wurden gesammelt, um Halbgeschwister-Familien bezüglich ihrer Biomasse-Produktion und Stickstoff-Assimilationskapazität zu testen. Nach dem Auskeimen wurden die Samen im Gewächshaus mit oder ohne am Standort gewonnene Strahlenpilz-Suspension bei zwei Stickstoffdüngerstufen angezogen. Im Alter von fünf Wochen vor der Beimpfung differierten die Sämlingshöhen und -gewichte zwischen Familien und Herkünften nur gering. Im Alter von 14 Wochen waren die mit standorteigener Pilzsuspension beimpften Sämlinge 10 bis 15 mal so groß wie die nicht beimpften. Unterschiede in der Biomasse-Produktion und Stickstoffassimilation zwischen Familien und Herkünften in der beimpften Gruppe deuten auf eine genetische Variation und die Möglichkeit eines Selektionsgewinnes hin. Weil die Nachkommenschaft von Herkünften mit Standortindexen von 95 und 65 in diesem Versuch besser abschnitten, als die von Standorten mit einem Index von 100 und 110, sollte der Standortindex nicht das alleinige Selektionskriterium für die Stickstoff-Fixierungskapazität und Biomasseproduktion bei *Alnus rubra* sein.

Introduction

Nitrogen-fixing plants in managed forests may increase wood production tor timber, fiber, and energy (BOND, 1977; SMITH, 1978; STETTLER, 1978). *Alnus rubra* BONG. or red alder is a moderately fastgrowing and widely distributed nitrogen-fixing hardwood tree in the Pacific Northwest (BURNS and HARDY, 1975; FRANKLIN and PECHANEC, 1968; TARRANT, 1978). As predominant hardwood in the Northwest, *A. rubra* may be a useful silvicultural tool for maximizing forest yield (BERG and DOERKSEN, 1975; DEBELL, STRAND, and REUKEMA, 1978; GORDON, 1978). Oregon alone has 79 million m³ of *A. rubra* (U.S. Forest Service, 1977). In addition to economic value as sawtimber, *A. rubra* is an efficient and valuable nonleguminous nitrogen-fixer. The fixed nitrogen causes the rapid growth of *A. rubra*, and the accretion of nitrogen to the soils increases the productivity of associated species (ATKINSON and HAMILTON, 1978; FRANKLIN and PECHANEC, 1968; MILLER and MURRAY, 1978).

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* Department of Forest Science.
** Department of Crop Science.

Although many tree-improvement programs are being conducted in the western United States, most involve conifers. With the increasing value of forest products, the potential of *A. rubra* should be explored. CAMPBELL and CHING (1980) studied the effect of thermoperiod on *A. rubra* from different elevations and geographic sources. DEBELL and WILSON (1978) investigated geographic and racial variation among 10 transplanted provenances of native *A. rubra* seedlings. STETTLER (1978) discussed the possibility of improving *A. rubra* and the potential of a breeding program.

However, results specific for improvement selection of *A. rubra* have not been reported. Therefore, to increase the productivity and usability of this hardwood species, we initiated a project to breed superior *A. rubra* through selection by testing progeny from five natural populations.

Materials and Methods

Five natural populations of *A. rubra*—diverse in elevation, slope aspect, and tree age--were selected in the Oregon Coast Range (lat. 44° 30' N, long. 123° 30' W). The five sites were within a 48-km radius of Marys Peak, 25 km west of Corvallis. All populations were at least 80% *A. rubra* and had good stand quality as determined by straigthness of stem, crown cover, and little observable biotic or abiotic damage. Average tree age, height, and diameter were determined by standard mensurational methods; from these stand data, a site index was assigned to each population according to the site index curves (height at age 50) developed for *A. rubra* (WORTHINGTON *et al.*, 1960).

From each of the three populations with high site indices (A, E, and G), two parent trees were selected as having growth characteristics "superior" to the immediately adjacent trees and the stand population. Tree improvement programs in the Pacific Northwest often use tree diameter, age, apparent health, stem form, height, and availability of seed cones, to select genetically superior trees.

The two remaining populations of lower site indices (B and C) were designated as controls, and two average trees in each site were selected for comparison. *Table 1* summarizes the characteristics of the 5 sites and the 10 parent trees.

In early November, open-pollinated cones were collected from all parent trees and air-dried for 2 wks at room temperature (21°C) until scales opened. Then seeds were collected and stored in jars at 2° C. The stratified seeds were germinated in a greenhouse with a controlled day/night temperature of 24°/18° C.

Four replicates of 100 seeds each from the 10 trees (or families) were weighed; each replication was germinated between moistened filter papers, which were placed in covered plastic boxes over moistened, sterile perlite. The natural day-lenght (February through May) was supplemented by a 4,400-lux flourescent photoperiod for a total light period of 16 hr. Seeds were counted as germinated when the radicle was half the lengh of the seed coat. Germination counts were made every 2 days and terminated on day 12.

The germinated seeds were planted in disinfected 55-cm³ tubes filled with perlite: vermiculite: Lite-gro*) (2:1:1 v/v) and were covered with rock grit. Seedlings were grown in the greenhouse, watered regularly, and fertilized twice weekly with a one-fourth strength nutrient solution supplemented with 20 ppm NH_4NO_3 (*Table 2*). After 5 wks (two-leaf stage), 10 seedlings per family were sampled for shoot length and weight, root length and weight, number of leaves, and total nitrogen content by the micro-Kjeldahl method. Because the oven-dried plants were small, nitrogen was analyzed by pooled samples of 10 seedlings from each family.

*) Available from J. M. McConkey & Co., Inc., Box 309, Sumner, WA 98390.

Table 1. — Site description and characteristics of selected parent trees.

	Source									
	A		B		C		E		G	
Elevation (m)	518		610		200		275		122	
Aspect	West		East		West		North		East	
Slope position	Middle		Bottom		Bottom		Upper		Bottom	
Site index +	95		80		75		110		100	
Parent tree number	1	2	3	4	5	6	7	8	9	10
Tree height (m) Stand Avg.	23		23		15		26		21	
DBH (cm)	27.1	26.7	45.0	39.0	21.2	16.7	24.6	22.1	26.1	29.3
Stand Mean	18.8		28.7		15.5		15.8		14.8	
Age*	26	28	43	46	23	22	26	23	25	25
Stand Mean	27		39		22		25		24	
Rings/cm	0.94	1.05	0.96	1.18	1.08	1.32	1.06	1.04	0.96	0.85
Stand Mean	1.45		1.35		1.39		1.78		1.65	

+ Determined by tree height at given age and normal yield tables for red alder.
* Number of growth rings at breast height plus three.

Table 2. — Nitrogen-free nutrient solution (one-fourth strength) as modified from MOORE (1974).*

Compound	Final concentration (ppm)
Macronutrients	
$CaCl_2 \cdot 2H_2$	183.7
KCl	93.0
$MgSO_4 \cdot 7H_2$	123.2
KH_2PO_4	34.0
Micronutrients	
H_3BO_3	0.7150
$MnCl_2 \cdot 4H_2O$	0.4525
$ZnSO_4 \cdot 7H_2O$	0.0550
$CuSO_4 \cdot 5H_2O$	0.0200
$Na_2MoO_4 \cdot 2H_2O$	0.0063
$CoCl_2 \cdot 2H_2O$	0.0125
FeEDTA (sodium salt)	5.0000

* Supplemented with NH_4NO_3 as required for treatments.

The remaining seedlings were grouped into four treatments, each containing 40 seedlings per family: high nitrogen (20 ppm NH_4NO_3) plus and minus inoculum.

For the inoculated treatments, nodules were collected from the five selected sites and surface-sterilized for 2 min in 1% NaOCl. After being copiously rinsed with water, the nodules were homogenized in water for 2 min at setting 30 in a Virtis homogenizer, then diluted to a solution containing 50 mg·ml^{-1} of fresh nodule. Each seedling tube was inoculated with 1 ml of the indigenous nodule suspension.

For 4 wks, all seedlings were fertilized twice weekly; then nitrogen was discontinued for the low-nitrogen treatment. At age 14 wks, 10 seedlings per family from each inoculated treatment and 3 seedlings from the noninoculated treatments were sampled and analyzed in the same manner as the seedlings evaluated at age 5 wks.

Additional data were collected on fresh weight of nodules per plant and nitrogenase activity as assayed by the acetylene-reduction method (HARDY *et al.*, 1968). To assay nitrogenase activity, whole seedlings in 55-cm^3 tubes were incubated in the greenhouse in cylindrical, air-tight chambers with 0.12 atm of acetylene generated from calcium carbide and water. During a 1-h incubation period, 0.5-ml gas samples were taken at 30 min and 60 min. Sampling of all seedlings was limited to a period of 4 h commencing 4 h after the supplemented photoperiod in order to reduce nitrogenase variation caused by diurnal fluctuation (GORDON and WHEELER, 1978; WHEELER, 1969, 1971). Ethylene (C_2H_4) production was measured on a Carle gas chromatograph (Model 311) equipped with a flame-ionization detector.

Results

Many growth criteria differed significantly between families and sources during germination and at age 14 wks, but not for the 5-wk-old seedlings, none of which were inoculated. Seed weight ranged from 63.6 mg/100 seeds for source A to 42.6 mg/100 seeds for source G *(Table 3)*. Germination index, which is an indicator of seedling vigor, and percentage of germination were highest for sources C and A, respectively, and again lowest from source G. Except for percentage of germination and germination index for source A, these criteria varied considerably between the two families of each source.

In the inoculated seedlings seed sources performing well at germination generally exhibited superior growth at age 14 wks. Progeny from sites A and C grew tallest and produced both the most plant dry biomass *(Fig. 1A)* and nodule fresh weight *(Fig. 1B)*. In accord with the trends at germination, the two families from site G generally performed poorly in these growth criteria. Sources A and C also exhibited the highest acetylene-reduction rates *(Fig. 1C)* and assimilated the most nitrogen *(Fig. 1D)*.

The inoculated seedlings receiving the high-nitrogen treatment produced the most dry biomass *(Fig. 1A)*. Shoot length and dry weight and total biomass differed significantly between the two nitrogen treatments, both in the inoculated and noninoculated seedlings. The shoot-to-root ratio, nodule fresh weight, and root dry weight, also differed significantly between nitrogen levels of inoculated seedlings. In noninoculated seedlings, leaves per plant also differed significantly as a result of differing nitrogen levels. Student t-tests were used to test for differences between N treatments within inoculum treatments using a pooled varience estimate, S_P^2, from the two samples *(Table 4)*.

Excluding the contaminated control seedlings, plants in the noninoculated treatments had small chlorotic leaves, little stem elongation, and a small shoot-to-root ratio *(Ta-*

Table 3. — Seed weight and germination by sources and families of red alder.*

	Source A			Source B			Source C			Source E			Source G		
Seed Measurement	Fam. 1	Fam. 2	Avg.	Fam. 3	Fam. 4	Avg.	Fam. 5	Fam. 6	Avg.	Fam. 7	Fam. 8	Avg.	Fam. 9	Fam. 10	Avg.
Mean weight per 100 seeds (mg)	58.3^{c}	68.9^{a}	63.6^{a}	62.0^{b}	49.3^{d}	55.6^{ab}	45.6^{e}	55.2^{c}	50.4^{bc}	58.0^{c}	43.3^{e}	50.6^{bc}	50.5^{d}	34.7^{f}	42.6^{c}
Mean germination in 12 days (%)	64.0^{bc}	68.3^{b}	66.4^{a}	63.8^{bcd}	52.8^{e}	58.25^{ab}	56.8^{e}	90.3^{a}	73.50^{a}	57.5^{cde}	42.8^{f}	50.13^{b}	57.3^{de}	32.8^{g}	45.0^{b}
Germination index*	235^{b}	236^{b}	236^{a}	229^{b}	170^{cd}	200^{a}	181^{cd}	316^{a}	248^{a}	203^{bc}	152^{de}	117^{a}	198^{bc}	117^{e}	157^{b}

+ Within a given row, means followed by the same letter are not statistically different at the 5% level of probability (Duncan's Multiple Range Test).

* Germination index = number of seeds germinated on a specific day × weighted speed of germination on the specific day.

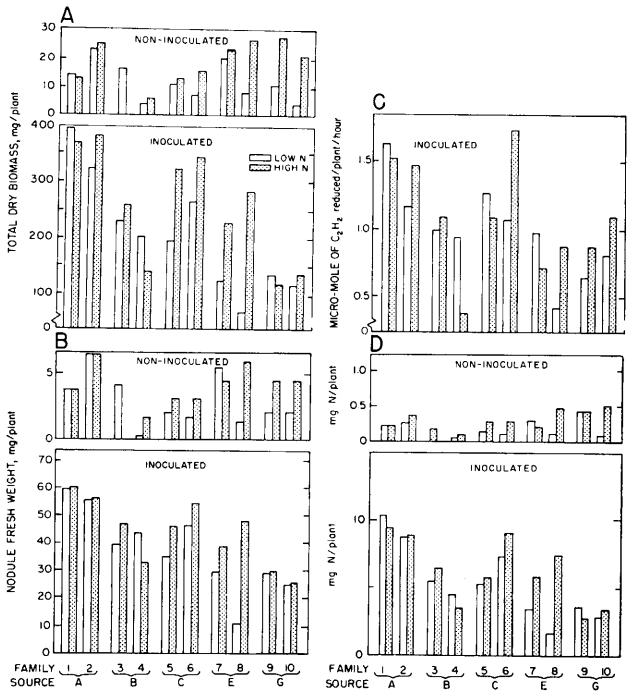

Figure 1. — Average total dry biomass (mg) of seedlings at age 14 wks by family and source (A). Average nodule fresh weight (mg) at age 14 wks by family and source (B). Average rate of acetylene reduction (micro-moles plant^{-1} h^{-1}) at age 14 wks by family and source (C). Average nitrogen assimilated by seedlings at age 14 wks by family and source (D).

ble 4). Progeny of sources A and C, which had superior growth when inoculated, did not show superiority without inoculum.

Discussion

The effect of levels of combined nitrogen agrees with findings on other nonleguminous nitrogen-fixing species (Bond, 1977). Treatment with the higher nitrogen level (20 ppm) increased total dry biomass and nitrogen accumulation per plant. The specific nitrogenase activity was less for the inoculated high-nitrogen seedlings than for the low-nitrogen seedlings (22.9 versus 24.7 μmoles per h per gram of fresh nodule weight). Contrary to previous reports (Bond, 1977; Hughes and Gessel, 1968), however, the higher nitrogen (20 ppm) treatment increased nodule fresh weight. Nitrogen assimilation indicated that the progenies from trees selected on sites A and C were more efficient, apparently because of nodule weight per plant, number of leaves per plant, and the nitrogen-fixation rate per plant. These might be used for selection criteria in discerning the progeny's ability to produce biomass and assimilate nitrogen.

The experimental results confirm other studies showing natural genetic variation in *A. rubra* (Campbell and Ching 1980; DeBell and Wilson, 1978) and indicate the possibility of genetic gain by selection. The progeny tests that many growth characteristics varied more between than within sources, indicating ecotypic variation. In this study, we found that it is difficult to predict superior populations by using only site index curves for *A. rubra.* Conventional site indices based on height apparently do not indicate growth potential of a source; under greenhouse conditions, progeny from sites of low indices (e.g., source C) performed better than seedlings from sources E and G with high site indices.

The experimental results may truly express genetic potential of a particular plant-endophyte ecotype, since the greenhouse conditions often remove environmental stresses. Other investigators (Bond, 1974; Dijk, 1979; Hall *et al.,* 1979) have found that there are likely to be specific endophyte strains. Because the best genotypes usually are found on the better sites, guidelines for tree improvement programs often recommend tree selection from high quality sites. However, our findings show that selection of *A. rubra* from such sites may preclude some superior genotypes.

In working with *A. rubra,* tree breeders may select from a variety of ecotypes, cross-inoculate and self-inoculate the selections with endophytes from different site origins, and grow them under various environmental conditions. Plant-endophyte combinations for maximizing biomass production and nitrogen assimilation can then be identified and selected for use on appropriate sites. Forest managers must fully utilize the genetic resources of *A. rubra* and its microsymbiont on different forest sites and wastelands.

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Table 4. — Mean growth criteria for inoculated and noninoculated seedlings at age 14 wks after growth at high and low nitrogen levels.

	Growth Criteria							
Treatment	Shoot length (cm)	Root length (cm)	Shoot/root ratio	Shoot weight (mg)	Root dry weight (mg)	Total dry biomass (mg)	Number of leaves per plant	Nodule fresh weight (mg)
Plus Inoculum								
High N_2	13.00**	13.60	0.987*	209.50*	48.20**	260.00**	9.4	44.30*
Low N_2	11.20	12.92	0.897	168.12	36.84	202.00	9.2	37.50
Minus Inoculum								
High N_2	1.87**	8.96	0.237	12.33**	6.67	18.90**	6.7**	4.30
Low N_2	1.10	9.40	0.190	6.07	5.93	12.00	4.9	2.90

*, ** Within a given pair in each column, treatment means are significantly different at the 5 and 1 percent levels of probability, respectively.

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Intraspecific Genetic Variation of Quercus rubra L., Northern Red Oak[1])

By S. E. SCHLARBAUM and W. T. BAGLEY[2])

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Summary

Growth and phenological characteristics of *Quercus rubra* L. indicated that intraspecific genetic variation is discontinuous with the exception of dormancy processes. Changes in growth rate likely reflects genetic differences among populations due to different site or climatic requirements. Variation in leaf flushing dates among populations may be due to different requirements in the prerequisite number of hours at cold temperatures to initiate spring growth. Genetic controls of dormancy processes were selected for in response to photoperiod and temperature regimes. A high degree of winter leaf retention is prevalent in western populations. Rate of individual tree growth within a provenance can be predicted at an early age. Inherent growth potential is not associated with any of the phenological characteristics studied.

Key words: Northern red oak, *Quercus rubra*, genetic variation, provenance test, phenology.

Zusammenfassung

Wachstums- und phänologische Merkmale von Roteiche (*Quercus rubra* L.) zeigen, daß die intraspezifische genetische Variation, mit Ausnahme von Ruheprozessen, diskontinuierlich ist. Beschleunigung oder Unterdrückung des Wachstums spiegeln wahrscheinlich genetische Unterschiede zwischen Populationen infolge unterschiedlicher Standortansprüche wider. Variation zwischen Populationen in Blattaustriebsdaten mag auf unterschiedliche Voraussetzungen in der notwendigen Stundenzahl bei kühler Temperatur, die das Frühjahrswachstum initiieren zurückzuführen sein.

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[2]) Former Graduate Research Asst. (presently Graduate Research Assist., Dept of Agronomy, Colorado State University, Fort Collins, CO 80523) and Assoc. Prof., respectively, Dept. of Forestry, Fisheries, and Wildlife, Univ. of Nebraska, Lincoln, NE 68583. The authors wish to acknowledge R. F. MUMM and W. J. WAYNE, Professors of Agronomy and Geology, respectively, Univ. of Nebrtska-Lincoln and H. B. KRIEBEL, Prof. of Forestry, Ohio Agricultural Research and Development Center, Wooster, Ohio for their assistance in this study.