EFFECTS OF POPULATION, ENVIRONMENT AND THEIR INTERACTION ON SASKATOON BERRY (*Amelanchier alnifolia* Nutt.) SEED GERMINATION

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To determine the effects of population, environment and their interaction on the variability of seed germination, seeds of 27 random native Alberta populations of Saskatoon berry (*Amelanchier alnifolia* Nutt.) were collected over 3 yr. Each year the seeds were stratified at 3°C for 84 d and then germinated at 25/10°C light(16h)/dark. Among the populations, mean seed germination after 4 wk ranged between 7 and 67%. Ecoregion and moisture condition at the site of origin did not significantly influence germinability. Of the total variance, 56% was contributed by population while the year and the population-year interaction contributed 0.3% and 17.5%, respectively. Over years the rank order of the populations was maintained. Three populations of diverse origin, grown in a common nursery, produced seeds with significantly different germination. Therefore, germination in *A. alnifolia* can largely be considered a genetically controlled character which is influenced to a limited extent by yearly environmental fluctuation.

Key words: Saskatoon berry, *Amelanchier alnifolia* Nutt., germination, population-environment interaction

[Effets de la population, de l'environnement et de leurs interactions sur la germination des graines de la petite poire (*Amelanchier alnifolia* Nutt.).]

Titre abrégé: Germination des graines de la petite poire.

Nous avons recueilli les graines de 27 populations albertaines indigènes de petite poire (*Amelanchier alnifolia* Nutt.) choisies au hasard pendant trois ans, afin de déterminer les effets de la population, de l'environnement et de leurs interactions sur la variabilité de la germination. Chaque année, les semences ont été stratifiées à 3°C pendant 84 jours puis laissées à germer à 25/10°C (jour de 16 h/nuit). Parmi ces populations, la germination moyenne après quatre semaines oscillait entre 7 et 67%. La région écologique et les conditions d'humidité à l'endroit d'origine n'influaient pas significativement sur la capacité de germination. Sur la variance totale observée, 56% était due à la population tandis que l'année et l'interaction population-année n'expliquaient que 0,3 et 17,5% de la variation respectivement. Le classement relatif des populations est demeuré stable d'une année à l'autre. Trois populations d'origines différentes, cultivées dans une pépinière commune, ont produit des semences présentant des caractéristiques de germination significativement différentes. Par conséquent, la germination chez *A. alnifolia* peut être considérée comme un caractère génétique sur lequel les fluctuations annuelles de l'environnement peuvent exercer un effet limité.

Mots clés: Petite poire (*Amelanchier alnifolia* Nutt.), germination, interaction population-environnement

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Native Saskatoon-berry, *Amelanchier alnifolia* (Nutt.), is common throughout Alberta in open woods, forest edges, and along streambanks and roadsides. Although widely adapted, it prefers dry sites and good exposure to the sun. The species is considered a primary invader, produces edible fruits, browse-favored by animals, and is useful in the revegetation of disturbed lands (Watson et al. 1980). *A. alnifolia* is not currently being used to its full potential due to problems associated with dormancy in the seed material (McLean 1967; Fedkenheuer and Heacock 1980; King et al. 1983) and difficulty in propagation through vegetative means (Harris 1961; Everett et al. 1978; Fedkenheuer and Heacock 1980; Hermesh and Cole 1983). The seeds have embryo dormancy (Crocker and Barton 1931) and seed coat impermeability (Hilton et al. 1965). Attempts to break seed dormancy through a wide range of cold stratification treatments and/or scarification using concentrated acids have generally produced very poor and often inconsistent results (Heit 1971; Brinkman 1974; Cram 1978; Watson et al. 1980; Fedkenheuer and Heacock 1980; King 1983; Anonymous 1985; Belcher 1985). Germination tests on seeds from various Alberta populations indicated significant differences in response to various stratification and scarification treatments (unpublished data). However, over 2 yr the seeds collected from some areas germinated consistently better under all treatments suggesting variability among populations for germination. The present experiments were undertaken to determine the extent of this variability, as well as the effects of population, environment and their interaction on germination.

MATERIALS AND METHODS

Mature, fully ripened, dark-red pomes of *A. alnifolia* were collected in each of 3 yr (1984–1986) from 27 native populations in northern Alberta, isolated from each other by at least 50 km (Fig. 1). Excepting populations 1, 2 and 3 which were grown at the Alberta Environmental Centre nursery in Vegreville, each population represented one collection site about 25 m^2 in area. In most cases the seeds were collected from one bush. Care was taken to collect seeds from the same bush in subsequent years. The place of origin, ecoregion to which the collection site belongs, moisture condition of the site and year of collection for each population are presented in Table 1. Pomes were collected between 9 and 23 Aug. in 1984, between 28 July and 28 Aug. in 1985 and between 5 and 19 Aug. in 1986. The seeds were hand cleaned without scarifying or damaging the seed coat, surface sterilized by dipping into 4% sodium hypochlorite for 2 min, then rinsed with sterile distilled water. The sterilized seeds were then layered in a tray between cheese cloth and moistened vermiculite. To prevent moisture loss, the trays were sealed in plastic bags and stratified at 3°C for 84 d. The stratification period chosen represents a minimal treatment since the recommended period is 90-120 d (Belcher 1985). After stratification, well-developed and undamaged seeds of each population were counted into groups of 25. To test germination, the seeds were placed between two moistened Whatman no. 1 filter papers in a 9-cm petri dish. The petri dishes were placed in a growth chamber set to light/dark cycles of 25/10°C (the average summer temperature for northern Alberta) with 16 h light provided by wide-spectrum bulbs (285 $\mu E\ m^{-2}\ s^{-1}$ intensity). The filter papers were kept moist by adding sterile water when necessary. In all 3 yr the experiments were conducted using a completely randomized design with eight replications. Germination was recorded three times a week for four consecutive weeks. Cumulative germination after each week was used to determine the magnitude of the components of variance. Since the cumulative germination data were found to be normally distributed (plotting) and the variances were homogeneous (Bartlett's test) it was not necessary to transform the data for analyses of variance.

Experiment I

Seeds of populations 4 through 10 were collected over a 3-yr period (Table 1). Cumulative germination data from these populations were subjected to a random effects (Model II) analysis of variance described in Table 2. The σ_p^2, σ_y^2 and σ_{py}^2 values were calculated to represent population, year and population-year interaction variances, repectively. The ranks of the seven population means in the 3 years were used to calculate Spearman's Rank Correlation Coefficients.

Experiment II

The 1984 and 1986 data, obtained from populations 1, 2 and 3 originating from three different locations, but growing in one site (AEC nursery)

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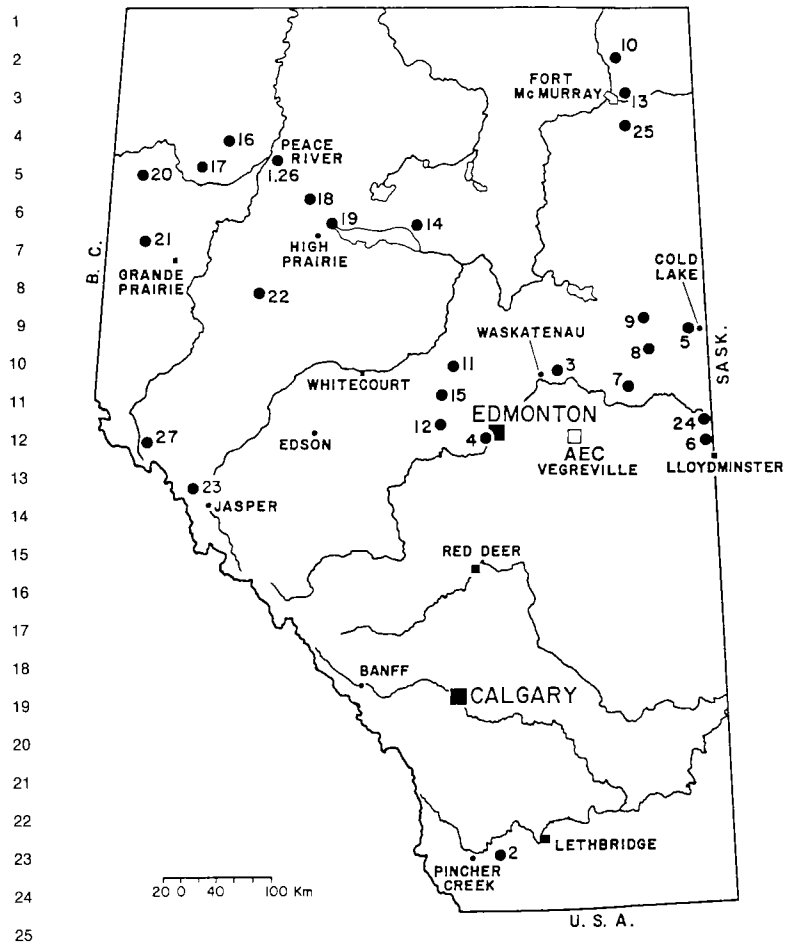

Fig. 1. *Amelanchier alnifolia* collection sites in Alberta.

since 1977, were used to determine the effects of population, year and their interaction. In this case, the effects of the three populations and 2 yr were considered fixed (Model I). The population means were compared by using Tukey's studentized range test at 5%. In 1985 the plants from the three populations were moved to another AEC nursery.

Experiment III

In 1985, seeds were collected from 24 isolated populations belonging to the Aspen Park Land (APL), Boreal Foot Hills (BFH), Boreal Forest Mixed Wood (BFMW), and Subalpine (SA) ecoregions, and to wet and dry moisture conditions (Table 1). The cumulative germination data were used to determine the effect of these environmental factors. The range, mean and standard deviation for germination of the populations were determined. After observing significant F-values in the fixed effects (Model I) ANOVA, the sample means for each population were subjected to Tukey's studentized range test for comparison.

RESULTS

Experiment I

The effects of population and population-year interaction for cumulative seed germination after each week were significant for *A.*

Table 1. Origin, ecoregion,, moisture condition and year of collection of the *A. alnifolia* seed populations included in the three experiments

Population† Code	Place of origin	Ecoregion‡	Moisture condition	Year of collection 1984	1985	1986
1	Peace River	BFMW	×§	✓		✓
2	Pincher Creek	FG	×	✓		✓
3	Waskatenau	APL	×	✓		✓
4	Edmonton	APL	Moist	✓	✓	✓
5	Cold Lake	BFMW	Moist	✓	✓	✓
6	Alcurve	APL	Dry	✓	✓	✓
7	St. Paul	APL	Moist	✓	✓	✓
8	Moose Lake	BFMW	Dry	✓	✓	✓
9	Iron River	BFMW	Moist	✓	✓	✓
10	Mildred Lake	BFMW	Dry	✓	✓	✓
11	Freedom	BFMW	Dry		✓	
12	Wabamun Lake	BFMW	Moist		✓	
13	MacDonald Island	BFMW	Moist		✓	
14	Slave Lake	BFH	Moist		✓	
15	Gunn	BFH	Dry		✓	
16	Queen Elizabeth Park	BFMW	Moist		✓	
17	Dunvegan	BFMW	Moist		✓	
18	Winagami Lake	BFMW	Moist		✓	
19	Hillard's Bay	BFMW	Moist		✓	
20	Moonshine Lake	BFH	Moist		✓	
21	Saskatoon Island	APL	Moist		✓	
22	Williamson Park	BFMW	Moist		✓	
23	Jasper	SA	Moist		✓	
24	Sand Beach	APL	Dry		✓	
25	Gregoire Park	BFMW	Moist		✓	
26	Peace River	BFMW	Dry		✓	
27	Willmore Wilderness Park	SA	Moist		✓	

†See Fig. 1 for location in Alberta.
‡Ecoregions were described by Strong and Leggat (1981).
APL = aspen park land, BFH = boreal foot hills, BFMW = boreal forest mixed wood, FG = fescue grass, SA = subalpine.
§Grown in the Alberta Environmental Centre nursery, Vegreville since 1977 under dryland prairie conditions.

Table 2. Sources of variation, degrees of freedom, expected mean squares, and calculations for *F* ratio in exp. I

Sources	df	EMS†	*F*
Population	6	$\sigma^2+8\sigma^2_{py}+24\sigma^2_{p}$	MS_P / MS_{PY}
Year	2	$\sigma^2+8\sigma^2_{py}+56\sigma^2_{y}$	MS_Y / MS_{PY}
Population × year	12	$\sigma^2+8\sigma^2_{py}$	MS_{PY} / MS_E
Error	147	σ^2	

†The mean squares were estimated taking populations and years as random effects.

alnifolia (Table 3). The year effect was not significant in all 4 wk. Population variance (σ^2_p) was the largest and contributed most to the germination variance in all 4 wk (Table 4). The contribution of population to total variance increased (42–56%) as germination progressed, while a reduction in variance was observed for the year (σ^2_y) (5–0.3%) and the population-year interaction (σ^2_{py}) (23–18%) components (Table 4). The error variance

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Table 3. Sources of variation, and mean squares for germination over the 4 wk (exp. I)

Sources	Mean squares			
	1st week	2nd week	3rd week	4th week
Population	325.2***	396.5***	417.4***	444.7***
Year	133.8NS	67.0NS	72.9NS	54.9NS
Population × year	57.5***	48.8***	50.8***	49.2***
Error	8.1	7.6	7.7	7.9

***$P < 0.001$; NS, not significant at 5%.

Table 4. Sources of variation, variance components and percentage of total variance (in parentheses) over the 4 wk (exp. I)

Sources	Variances			
	1st week	2nd week	3rd week	4th week
Population	11.2	14.5	15.3	16.5
	(41.6)	(52.5)	(53.1)	(55.6)
Year	1.4	0.3	0.4	0.1
	(5.2)	(1.1)	(1.4)	(0.3)
Population × year	6.2	5.2	5.4	5.2
	(23.1)	(18.9)	(18.8)	(17.5)
Error	8.1	7.6	7.7	7.9
	(30.1)	(27.5)	(26.7)	(26.6)

Table 5. Spearman's rank correlation coefficients calculated from the population means after 2 (top) and 4 wk (bottom) of germination (exp. I)

Year	1984	1985	1986
1984	—	0.89**	0.75*
1985	0.89**	—	0.82*
1986	0.79*	0.96***	—

*, **, *** $P < 0.05$, $P < 0.01$, $P < 0.001$, respectively.

(σ^2) remained relatively unchanged (30–27%) over the 4 wk. There were also highly significant year to year rank correlation coefficients (Table 5).

Experiment II

Population and year had significant effects on germination of the three populations grown in the Alberta Environmental Centre nursery (Table 6). The population-year interaction effect was not significant. Mean germination of the three populations ranged from 55 to 44%. During the initial 2 wk seeds borne on plants originating from Pincher Creek and the Peace River area germinated significantly better than the ones borne on the Waskatenau plants (Table 7). After the third week only the Pincher Creek population was significantly different from the Waskatenau population. Mean germination was significantly greater for seeds collected in 1984 than in 1986 (Table 7).

Experiment III

Seeds collected in 1985 from the BFH, BFMW and APL ecoregions did not differ significantly in germinability (Table 8). Over the 4-wk period, seeds collected from the SA ecoregion germinated significantly less than seeds from the BFMW ecoregion. The moisture condition of the collection site did not have a significant influence on seed germination (Table 8). However, there were significant differences among seed populations (Table 9). Populations 17, 24, 16, 20, 12 and 9 (in descending order of germination) germinated more than 50% within the first 2 wk, whereas populations 21, 23, 11, 15, 14 and 7 germinated less than 20% during that period. For all 24 populations included in this test most of the germination occurred during the initial two weeks. Germination during the next two weeks increased by a maximum of 7%.

DISCUSSION

Population was by far the greatest determinant of seed germination (dormancy) in *A. alnifolia* as indicated by the highly significant population mean square, the larger variances and the

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Table 6. Sources of variation, degrees of freedom and mean squares for germination over the 4 wk (exp. II)

Source	df	Mean squares			
		1st week	2nd week	3rd week	4th week
Population	2	81.4***	64.5***	42.3**	27.8*
Year	1	1102.1***	1017.5***	901.3***	816.8***
Population × year	2	26.5	7.3	2.8	1.5

*, **, *** $P < 0.05$, $P < 0.01$, $P < 0.001$, respectively.

Table 7. Mean germination percentage over 4 wk of the three *A. alnifolia* seed populations collected from AEC nursery in 1984 and 1986 (exp. II)

Year†	Mean germination (%)			
	1st week	2nd week	3rd week	4th week
1984	62	65	66	66
1986	24	28	31	33
Population				
2 (Pincher Creek)	51*a*	55*a*	55*a*	55*a*
1 (Peace River)	45*a*	48*a*	48*ab*	49*ab*
3 (Waskatenau)	33*b*	38*b*	42*b*	44*b*

†Year means within each column are significantly different (ANOVA).
a, b Population means followed by the same letters within a column are not significantly different (Tukey's 5%).

Table 8. Mean germination percentage of seed collected from four ecoregions and two moisture conditions over the 4 wk (exp. III)

Ecoregion†	N	Mean germination (%)			
		1st week	2nd week	3rd week	4th week
BFMW	112	30*a*	37*a*	37*a*	39*a*
APL	40	22*a*	28*ab*	28*ab*	31*ab*
BFH	24	22*a*	26*ab*	28*ab*	29*ab*
SA	16	21*a*	23*b*	23*b*	24*b*
		Moisture condition‡			
Moist	136	28	33	34	35
Dry	56	24	30	31	33

†BFMW = boreal forest mixed wood, APL = aspen park land, BFH = boreal foot hills, SA = subalpine.
a, b Ecoregion means followed by same letters within a column are not significantly different (Tukey's 5%).
‡Means for moisture conditions in a column are not significantly different (ANOVA).

high proportion of the variance attributed to population in exp. I. The significant differences in germination can be attributed to genotypic differences among the populations because: over the 3 years, care was taken to obtain fully mature seeds from the same plants of isolated populations; seeds from all populations were collected at the same time; only well-developed seeds were included in the test; the same method was used to test germination; and a low proportion of the variance was contributed by year (environment) and population-year interaction. Significant rank correlation coefficients indicate that the populations maintained their rank over the 3 yr (Table 5). This suggests that the rank for germination is not influenced by yearly environmental fluctuations. The idea that genetic differences are the main cause of variation in germinability is further supported by the significant differences observed among the three populations growing at the Alberta Environmental Centre nursery (exp. II). These populations were subjected to the same environmental conditions, and therefore the observed differences can only be due to genetic influence.

For the present set of experiments the seeds were collected over a large and diverse area. Therefore, differential influences of the

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Table 9. Mean cumulative percentage germination for 24 isolated populations of *A. alnifolia* belonging to four ecoregions over the 4 wk (exp. III)

Population code	Ecoregion†	Mean germination (%)			
		1st week	2nd week	3rd week	4th week
17	BFMW	57*a*	65*a*	66*a*	67*a*
24	APL	54*ab*	60*ab*	62*ab*	63*a*
16	BFMW	50*abc*	57*ab*	57*ab*	58*ab*
20	BFH	48*abc*	57*ab*	60*ab*	64*a*
12	BFMW	45*abc*	50*bc*	50*bc*	55*abc*
19	BFMW	38*bcd*	42*cd*	43*cd*	45*cd*
9	BFMW	37*bcde*	50*bc*	50*bc*	50*bc*
13	BFMW	28*def*	31*def*	31*def*	33*de*
27	SA	28*def*	30*def*	30*def*	31*ef*
5	BFMW	26*def*	29*ef*	30*def*	31*ef*
8	BFMW	25*efg*	34*de*	34*de*	36*de*
26	BFMW	25*efg*	34*de*	34*de*	37*de*
18	BFMW	24*efg*	29*ef*	30*def*	34*de*
25	BFMW	24*fg*	28*efg*	28*efg*	28*efg*
10	BFMW	23*fg*	29*ef*	30*def*	34*de*
6	APL	22*fg*	25*efg*	25*efgh*	25*efgh*
22	BFMW	22*fgh*	25*efg*	25*efgh*	28*efg*
4	APL	18*fghi*	29*ef*	30*def*	35*de*
23	SA	14*fghij*	15*gh*	15*ghi*	16*ghi*
21	APL	12*ghij*	18*fgh*	18*fghi*	19*fgh*
11	BFMW	10*hij*	12*h*	14*hi*	15*hi*
15	BFH	8*ij*	11*h*	12*hi*	17*ghi*
14	BFH	8*ij*	10*h*	11*i*	14*hi*
7	APL	3*j*	5*h*	5*i*	5*i*
	Range	3-57	5-65	5-66	5-67
	Mean	27	32	33	35
	SD	15.6	16.8	17.2	17.2

†APL = aspen park land, BFH = boreal foot hills, BFMW = boreal forest mixed wood, SA = subalpine.
a-j Population means followed by same letters within a column are not significantly different (Tukey's 5%).

immediate environment on seed germination were expected (McCullough and Shropshire 1970; Urbanska and Schultz 1986). However, there were no significant differences in germination between dry and moist sites and among ecoregions (exp. III). This suggests that such environmental factors have only a minor effect on seed germination of *A. alnifolia*. Furthermore, out of the six populations that germinated more than 50%, four belonged to the BFMW, one to the BFH and one to the APL ecoregions. The six populations that germinated less than 20% also belonged to all four ecoregions (Table 9). These observations further emphasize that the wide range of germinability among the 24 populations (7-67%) cannot be due mainly to the differential effects of the environment under which the seeds had developed.

The highly significant effect of year and relatively large mean square for this component compared to population observed in exp. II was contrary to the observation in exp. I. This discrepancy may be due to the limited (55-44%) inherent variability among the three populations included in exp. II. The three populations were included based on their geographic origin (isolated by distance) and not on their diversity in germination. Another reason may be the production of hybrid seeds among the three genotypes while growing in one nursery. The natural cross pollination in this species has been estimated at 20% (Davidson 1988, pers. commun.). Transplanting these plants to another nursery in 1985 may also have adversely influenced the 1986 germination which would also explain the nonsignificant population-year interaction effect.

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A wide range of germination was obtained using a pretreatment comprising only 84 d of cold stratification and no scarification. It is possible that this new method produced high germination in some populations. However, the marked effect of population on seed germination suggests that the diverse populations (genotypes) rather than the method used was the key to obtaining such a wide range.

In summary, the experiments suggest a genetic basis for seed germination in *A. alnifolia*. Germination can, to a limited extent, be influenced by yearly environmental fluctuations. It is suggested that a genetic basis for variation in seed germination (dormancy) as well as the significant population-year interaction effect on this trait may have been responsible for the inconsistent and nonrepeatable results obtained by earlier researchers while developing a method for breaking *A. alnifolia* seed dormancy. Although the germination percentage (or dormancy) of a natural *A. alnifolia* stand cannot be predicted on the basis of environmental factors prevailing in that area, it will be possible to select genotypes with superior germinability through screening.

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