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Incorporating *Chenopodium berlandieri* into a Seasonal Subsistence Pattern: Implications of Biological Traits for Cultural Choices.

Sara Halwas^{1*} and Anne C. Worley²

Abstract. Local ecological knowledge of culturally important plants informed food choices by Indigenous peoples across North America. Recovery of such knowledge through ecological and genetic studies of contemporary populations increases understanding of variation in seasonal availability and economic value, potentially enhancing interpretation of the archaeobotanical record. We compared habitat, seed yield, and nutritional value of seed in up to ten wild populations of net-seed goosefoot (*Chenopodium berlandieri*) from four survey regions in Manitoba, North Dakota, Missouri, and Ohio with evidence of pre-contact cultivation and domestication of *C. berlandieri*. We assessed cultivation impacts and variation in seasonal timing by growing seed from three Manitoban populations in two common gardens. Population density, plant size, and seed yield increased six-fold from north (Manitoba) to south (Ohio) in wild populations, with genetic differences between Manitoban populations remaining evident in gardens. However, cultivation (e.g., watering, weeding) in well-worked soil extended timing of seed harvest and increased seed yield beyond the range of wild populations. Nutritional profiles from five populations were similar across the survey regions but differed from domesticated quinoa in their higher fiber and slightly lower energy content. Our results suggest that both plasticity and genetic factors influence productivity of *C. berlandieri* populations as a seed source. Genetic variation in seasonal timing would have provided choice between populations and flexibility in incorporating *C. berlandieri* into a seasonal subsistence strategy. Simple cultivation techniques would have substantially increased yield, thereby enhancing reliability and economic returns.

Keywords: *Chenopodium berlandieri*, pre-contact cultivation, Manitoba, economic potential, phenology

Introduction

Over the last 20 years, understanding of Indigenous pre-European contact (hereafter pre-contact) food procurement and production practices has grown substantially. In general, plant use forms a continuum from harvesting wild edible plants to growing fully domesticated plants within current industrial agricultural systems (Ford 1985). Between these extremes lies a broad range of cultivation and management practices used to ensure availability of favored foods or plant parts used for medicine, fuel, construction, or rituals. Cultivation practices include watering, weeding, transplanting,

tilling, burning, selective harvesting, and sowing stored seed (Deur and Turner 2006; Smith 2001).

Pre-contact cultural groups across North America employed various cultivation techniques in food procurement and production (e.g., Anderson 2005; Raviele and Lovis 2014). In southern Manitoba (Figure 1), Late Pre-contact cultural groups (ca. 3000–400 BP) incorporated wild and domesticated native plants and tropical cultigens into mixed subsistence strategies (Boyd and Surette 2010; Deck and Shay 1992; Quaternary Consultants 2013). Domesticated maize, beans, squash, and

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wild rice were combined with wild berries, nuts, and seeds, including net-seed goosefoot (*Chenopodium berlandieri*) (Boyd et al. 2014; Deck and Shay 1992; Lints 2012; Quaternary Consultants 2013).

Understanding how plants were incorporated into daily subsistence patterns first recognizes that human decisions are informed by broad environmental and local habitat information, plant traits (underlying

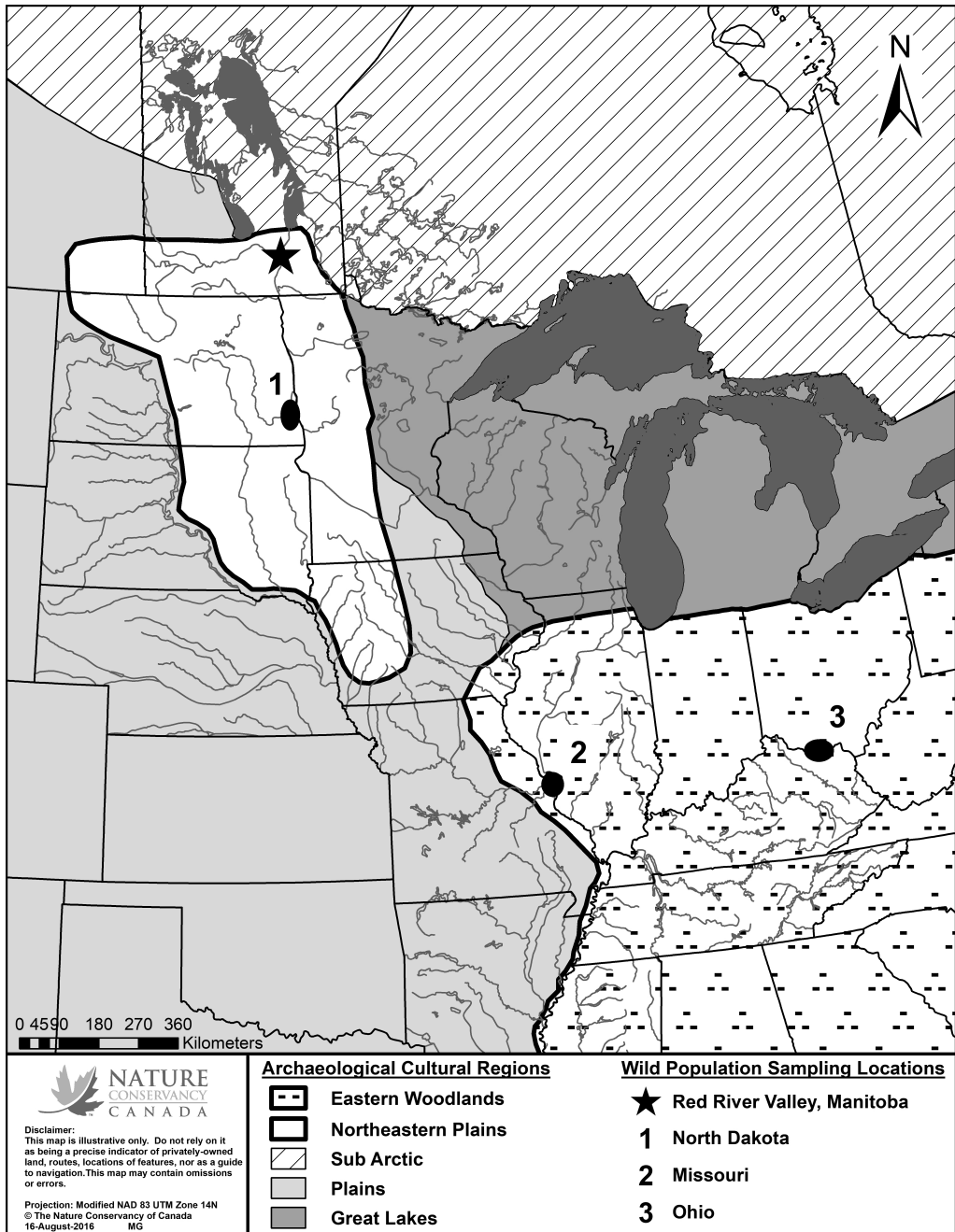


Figure 1. Map indicating sampling locations of wild *Chenopodium berlandieri* populations in southern Manitoba, North Dakota, Missouri, and Ohio in relation to broad archaeological cultural regions.

genetics), cultural preferences, and social goals (Chase 1989; Cruz et al. 2014; Turner and Peacock 2006). Understanding species phenology or timing of growth stages, differences in availability or traits between populations, and practices that ensure reliability of favored plant parts can inform our interpretation of plants incorporated into mixed subsistence systems. For instance, Okanagan people in British Columbia use the flowering of the prickly pear (*Opuntia fragilis*) to indicate saskatoon (*Amelanchier alnifolia*) ripening (Lantz and Turner 2003:266). Historically, the Natchez in southwestern Mississippi broadcast sowed wild *Chenopodium* (*choupichoul*) seed (Smith 2011), while Indigenous peoples in California coupled broadcast sowing with seasonal burning to improve wild *Chenopodium* stand regeneration (Anderson 2005:262).

Our paper explores net-seed goosefoot use in southern Manitoba. Net-seed goosefoot was domesticated in the Eastern Woodlands approximately 3800 years ago (Smith 1984). The use of domesticated goosefoot spread outward from the Eastern Woodlands along with other Eastern Woodland cultural influences (Windham and Calabrese 1998:275). Domesticated goosefoot was used by Mill Creek peoples in Iowa ca. 1000–800 BP (Jones 1993), and intensive harvesting of wild goosefoot is known from Late Woodland/Plains Village sites in the Dakotas ca. 800–600 BP (Adair 2003; Benn 1974; Michlovic and Schneider 1993). A large cache of domesticated *C. berlandieri* subsp. *jonesianum* seeds recovered in southern Ontario extends use of this domesticate to Canada by 2900 BP (Crawford et al. 2018).

Evidence of cultural connections between Manitoba and Late Woodland/Plains Village peoples from the Dakotas has been identified at the Lockport site (ceramic wares, bison scapula hoes, bell shaped storage pits; Deck and Shay 1992; Flynn 2002) and the Forks site (ceramic wares;

Flynn and McKinley 2004; Quaternary Consultants 1999). The recovery of small quantities of undomesticated *C. berlandieri* seeds at these Manitoba sites is associated with mixed subsistence economies (Boyd and Surette 2010) and raises the possibility that intensification or cultivation of *C. berlandieri* spread to pre-contact Manitoba communities through connections from North Dakota.

Scientific studies on natural populations of food plants can access ecological knowledge that may have informed past cultural decision-making. For instance, modern harvest experiments on wild lambsquarters (*C. album*) (Munson 1984) and *C. berlandieri* (Asch and Asch 1977; Smith 1987) in Eastern Woodlands populations indicate wild seed yields are similar to cultivated cereal crops. Seed from a single *C. berlandieri* plant collected in the Eastern Woodlands was also nutritionally comparable to its domesticated relative and current super food quinoa (*Chenopodium quinoa*) (Smith 1987). Comparable research has not been conducted in the Northeastern Plains and direct effects of cultivation on phenology and seed yield of *C. berlandieri* remain unexamined for any region. Such studies can extend our knowledge of potential cultivation practices of non-domesticated species.

We explore ecological, phenological, economic, and nutritional aspects of *C. berlandieri* as potential criteria that may have influenced seed use by pre-contact cultural groups. We focus on the Lockport (EaLf-1) and the Forks (DILg-33:08A) sites in the Red River valley of southern Manitoba because previous detailed plant remains analyses conducted at both sites present the possibility that *C. berlandieri* may have been intensively harvested or cultivated (Deck and Shay 1992; Halwas 2017; Quaternary Consultants 2013). Manitoba data are placed within the broader geographic and cultural context through a comparison with data gathered from the Northeastern Plains

(North Dakota) and the Eastern Woodlands (Missouri and Ohio). Areas included in the study are within close proximity to archaeological sites with cultural ties to Manitoba and intensive use or cultivation of domesticated *C. berlandieri*.

Objectives and Hypotheses

Our first objective is to document location, habitat, and plant characteristics of *C. berlandieri* within the Northeastern Plains and Eastern Woodlands regions. We hypothesize that populations occupy similar habitats and plants have similar biomass and seed yields across the survey region.

The second objective is to describe the phenology and yield of extant *C. berlandieri* populations in a common garden setting in Manitoba to determine optimal timing for leaf and seed harvest. In addition, we use common gardens to explore the effects of cultivation on wild seed, and genetic differences between populations. We hypothesize that plants originating from different populations have similar phenology, especially with regard to seed maturation, making seed harvest fairly uniform across the Red River valley. Further, we expect that low-level cultivation (weeding and watering) will increase plant size and seed yield relative to wild populations.

The third objective is to describe the economic potential of using wild collected seed as a food resource. Yield and cleaning rates for Manitoba populations are compared to published values for the Eastern Woodlands (Smith 1987), while nutritional value of wild seed across the study area is compared to published values for domesticated quinoa. We hypothesize that harvest yield (kg/ha) and cleaning rate for seed (kilograms of cleaned seed produced in an hour) are comparable across all populations within the study region, and that the nutritional value of wild seed is similar across the survey region and to domesticated quinoa.

Methods

Population Survey

To place Manitoban populations of *Chenopodium berlandieri* within the context of its wider geographic range, we searched for populations in the Northeastern Plains and the Eastern Woodlands regions. The Northeastern Plains included sub-regions Red River Valley of Manitoba and eastern North Dakota. The Eastern Woodlands included the central Missouri/Illinois and southern Ohio sub-regions. Targeted areas were near to known archaeological sites where *C. berlandieri* was intensively used or domesticated (e.g., Michlovic and Schneider 1993) and in the disturbed soils typical of *C. berlandieri* occurrence (Clemants and Mosyakin 2003).

We searched potential habitat locations in Manitoba for a few days in July, August, and September, when *Chenopodium* is fully-grown and easily distinguished from surrounding species. All suitable areas were investigated by field walking. The Assiniboine River floodplain and surrounding areas were targeted in 2010 and the Red River Valley floodplain in 2011.

We searched the southern sub-regions for three weeks starting at the end of September 2011. The search focused on the Red River Valley and tributaries in North Dakota, the Missouri/Mississippi River Confluence in east-central Missouri, and tributaries of the Ohio River in southern Ohio.

Population size was estimated from approximate area covered, and populations with more than 50 plants were sampled. Transects were spaced at one- or five-meter intervals across the length of the population and between 30 and 60 plants were sampled, depending on extent of the population. Plants were measured for total height and diameter (widest distance between lateral branches) in the field. In Manitoba populations, plants were cut at

the base of the stem and placed in cloth bags with a 0.3 mm mesh size or paper bags to air dry. Total dry above-ground biomass and total dry seed mass were measured. In USA populations, plants were measured for height and diameter in the field. Seeds were then stripped off the plant and placed in a mesh bag to air dry. Once dry, total seed mass was measured.

Common Garden Experiments

Growing plants in a single environment (hereafter common garden) standardizes broad-scale environmental effects on plants, allowing for more accurate documentation of genetic differences (Conner and Hartl 2004). Populations of wild collected seed were grown in two common gardens over two years. Plants in each common garden were grown from subsamples of seed collected from individual plants (hereafter maternal lines) from wild Manitoban populations, Delta Marsh (DM), St. Vital (SV), and Aubigny (AB).

The first common garden was at the Arboretum field site on the University of Manitoba Fort Gary campus (hereafter Arboretum). This site is within city limits and is relatively sheltered by trees from prevailing winds. The soil matrix is easy to till and comprises laminated deposits of fine sand/loam/clay from numerous Red River flooding events (Don Flaten, personal communication 2016; Ehrlich et al. 1953).

The second common garden was the Glenlea Agricultural Research Station (hereafter Glenlea). This open field site just south of Winnipeg is approximately two kilometers west of the Red River. The soil matrix varies from heavy to fine lacustrine clays that also developed through episodic river flooding by the Red River followed by long periods of drying. This area contains patches of alkalized and degraded soils due to many years of heavy agricultural use (Ehrlich et al. 1953; Manitoba Agriculture 2011). Lack of shelter from wind, rain, and sun causes heavy clay soil to dry out

quickly, forming a very hard surface with deep cracks.

The first (2011) experiment was designed to characterize the phenology of *C. berlandieri*. Seeds from populations DM and SV were started on June 1 or 2 in the Crop Technology Center (CTC) greenhouse at the University of Manitoba; 89 seedlings from 25 maternal lines were transplanted June 15 across both common gardens. Seedlings were planted so there was only one seedling per maternal line per row. At the Arboretum, 17 seedlings from six maternal lines were from population SV, and 33 seedlings from 12 maternal lines were from population DM. At Glenlea, nine seedlings from three maternal lines were from population SV, and 30 seedlings from 13 maternal lines were from population DM. Plants were harvested by September 14, 2011.

Phenological variation in common garden populations was measured by noting the first day of nine major stages of growth for all individuals: day planted, seedling emergence, first true leaves, first flower bud, first open flower, open flowers (perianth open, anthers exerted in 75% of flowers), end flowering (perianth closed, anthers withered in 75% of flowers), first seeds, and date of harvest. Plants were checked daily in 2011, and the pattern of growth calculated from 89 plants from 25 maternal lines.

Growing degree days (hereafter GDD) reflect amount of accumulated heat per day and is used to calculate amount of time required for a given species to reach a certain phenological stage. GDD is used in agriculture to predict the co-occurrence of plant and insect life stages as it is more accurate than using calendar date (Miller et al. 2001). In this study, GDD was calculated as:

$$T_{\text{average}} - T_{\text{base}}$$

where T_{average} was the calculated average temperature per day as recorded for Winni-

peg from the Forks weather station on Environment Canada's website (Government of Canada 2017), and T_{base} was the minimum temperature required for plant growth (see Miller et al. 2001). For this study, 5 °C was used as the minimum plant growth temperature based on the minimum temperature used for most cereal crops (Pacific Field Corn Association 2017).

The second (2012) experiment employed split block sampling design to measure genetic effects on plant and seed traits. This design replicates rows of all maternal lines across common garden sites ameliorating micro environmental differences experienced by the plants (Jones and Nachtsheim 2009). A total of 55 maternal lines collected from populations DM ($n = 20$), SV ($n = 13$), and AB ($n = 22$) were planted over three replicates; each row contained seed of one maternal line. This pattern was repeated at both sites. Seed for each maternal line was sampled by volume to maximize number of maternal lines; total number of seeds planted ($n = 30\text{--}1500$) depended on the total seed mass of the maternal line. Samples were soaked in tap water for 24–48 hours then sowed by hand into furrows. Seeds were sown June 9, 12, and 13. Both plots were weeded and watered when necessary. All plants were harvested by September 25, 2012.

Morphological variation for all wild and common garden populations was characterized using total plant size index calculated as plant height \times plant diameter (tip to tip of widest spaced branches) and total seed mass (air dried, in grams). Morphological data were collected for all wild and common garden populations in 2011 and 2012.

Economic Potential

Seed yield was documented in wild *C. berlandieri* populations in Manitoba. We placed nine 1 m² quadrats along the west ditch of Diversion Road leading to Delta Marsh Field Station, 26 km north of

Portage La Prairie, Manitoba in September 2010. Quadrats were placed in areas of high plant density to approximate maximum harvest rate (cf. Seeman and Wilson 1984). Harvesting took place within timed one-minute intervals. Inflorescences were hand stripped into a plastic bag then air-dried immediately after the experiment. Samples were fully air-dried on newspaper in the WIN Herbarium at the University of Manitoba.

To compare Manitoba yields to the Eastern Woodlands, we supplemented our data set with data collected by Smith (1987). Smith (1987:31) used 1 m² areas to document harvest yield in large *C. berlandieri* populations across the Eastern Woodlands. Smith stripped seed from a number of plants, timing the duration of the harvest and weighing the resulting dry mass of the harvested seed. He then calculated harvest yield (kg/ha) and harvest rate (kg/hour) (Smith 1987:34).

Smith (1987) included harvest data from 24 populations from Michigan, Ohio, Pennsylvania, Maryland, South Carolina, Arkansas, and Missouri. Each population was represented by a single estimate (datum). For this analysis, we recognized three sub-regions within the Eastern Woodlands based on general cardinal direction: northeast (Michigan, Ohio and Pennsylvania), east (Maryland and South Carolina), and southwest (Arkansas and Missouri). Manitoba comprises the fourth sub-region, in the Northeastern Plains.

To determine the food value of wild *C. berlandieri* across the Northeastern Plains and Eastern Woodlands regions, bulked seed samples of 200–300 grams from 15 to 35 individual plants per population were sent for nutritional analysis. Since wild populations in Manitoba did not produce an abundance of seed, we used bulked seed samples from populations grown at the Arboretum in 2012. Samples from two Manitoba populations, one from North Dakota, and two from Ohio were

winnowed as close to pure seed as possible and submitted to SGS Lab Services Canada (Burnaby, BC). Samples were tested for main nutritional components, including protein, fat, carbohydrate, dietary fiber, ash, moisture, and energy level. Each sample was tested once for each nutritional component. Protein, fat, carbohydrate, fiber, and ash were calculated by percent dry weight; moisture was calculated by percent fresh weight; energy was calculated in calories/100 grams.

Data Analysis

Any trait that did not meet the assumptions of a normal distribution and homogeneity of variances between groups (population or common garden) was natural-log transformed. Population means \pm one standard error are reported in all figures and tables. Pairwise phenotypic correlations (PROC CORR, Pearsons) between plant and seed traits were estimated within wild and common garden populations. The correlation coefficient and p-value (r , P) are reported for significant relationships. All calculations and tests were run with SAS 9.4 software (SAS Institute 2014).

A series of analyses of variance (PROC GLM) were used to describe sources of variation in the measured traits. Analyses of wild populations tested whether significant differences in traits existed between geographic sub-regions or populations nested within sub-regions; these differences included both direct effects of the environment and underlying genetic differences. In a common garden, the term “population” refers to origin of the seed used. Differences among populations or maternal lines primarily reflected underlying genetic variation because all plants experienced the same general environment. The term “within population”, in parentheses, relates to the statistical model used, i.e., maternal lines were nested within their populations. The terms “common garden” and “repli-

cate” refer to effects of the general and micro-environment, respectively, in which plants were grown.

For all tests, the model statement ($Y = X_1 \dots X_n$) included a dependent variable (Y) reflecting the morphological (plant index, seed mass), phenological (days to first leaf, open flower, seed, harvest), economic (harvest yield, harvest rate, percent chaff), or nutritional (percent protein, fat, carbohydrate, dietary fiber, ash, moisture, energy) trait of interest. Independent explanatory variables ($X_1 \dots X_n$) included various combinations of region, sub-region, and population. Analyses of plants from Manitoba populations grown in the two common gardens included population, common garden, the interaction variable population \times common garden, and nested variables maternal line (within population) and replicate (within common garden).

Results

Population Survey

Although large *C. berlandieri* populations were present in Manitoba, they were not common or widespread. Large populations ($n > 100$ plants) were frequently encountered along field edges, bank edges, and flat flood plain terraces of rivers in the Eastern Woodlands. Despite targeting similar habitats in Manitoba and North Dakota, the primary author was only successful in finding large populations along upper river terraces of major rivers (e.g., the Red and Assiniboine Rivers). Since sizable populations in southern areas were encountered in less search time (Table 1), *C. berlandieri* populations appear to be less frequent in Manitoba than in the Eastern Woodlands and southern areas of Northeastern Plains.

Surveyed populations ranged from large patches of approximately 100 plants covering 30 m² to very large populations containing thousands of plants and extending half a kilometer. Most populations encountered in this study contained a

Table 1. Number of large *Chenopodium berlandieri* populations ($n > 100$ plants) located during search periods in each sub-region (Province or State).

Sub-region	Days searched	Number of Populations	
		River terraces and floodplains	Disturbed roadsides, agricultural fields
Manitoba	15	3	0
North Dakota	3	3	0
Missouri	3	2	2
Ohio	3	2	2

few hundred to a thousand plants, covering around 500 m² (Halwas 2017). In general, population size was smaller in the Northeastern Plains than in the Eastern Woodlands, but single plants and small populations (< 100 plants) were encountered in various disturbed habitats across the study area.

Additionally, pure stands of *C. berlandieri* were rarely encountered in the Northeastern Plains. Most populations contained various colonizing grasses and forbs interspersed with *C. berlandieri* plants. The most common co-occurring species were lambsquarters (*Chenopodium album*), maple-leaved goosefoot (*C. simplex*), knotweed (*Polygonum* sp.), and dock (*Rumex* sp.), along with other weedy agricultural species. Southern populations contained fewer agricultural weedy species compared to northern populations, with co-occurring species including amaranth (*Amaranthus* sp.), foxtail (*Setaria* sp.), and ragweed (*Ambrosia* sp.) (see Halwas 2017:142).

Wild collected populations were analyzed to determine if *C. berlandieri* traits differed significantly among sub-regions (i.e., MB, ND, MO, OH) and populations within regions. Northern populations produced smaller plants with less seed than southern populations (Figure 2), resulting in significant effects of sub-region for both traits (plant size: $F_{3,6} = 5.18$, $P < 0.05$, mean total seed mass: $F_{3,6} = 6.65$, $P < 0.05$). Manitoba populations had the smallest mean plant index

(538 cm²) and total seed mass (1.39 grams). Missouri and Ohio produced plants with mean size indices of 3799 cm² and 4758 cm², and mean seed mass of 14 and 11 grams, respectively (Figure 2). These traits also varied significantly among populations within sub-regions, especially seed mass ($F_{6,373-400} = 13.21$, $P < 0.001$). Two North Dakota populations grouped together; these populations produced taller plants with long, sparse lateral branches (mean plant index 2300 cm²) and produced an average of five grams of seed per population. The third population (ND2) produced shorter plants with narrow lateral branches and grouped with Manitoban populations (Figure 2). Plant size index and mean seed mass were positively and significantly correlated within all wild populations ($r = 0.66-0.94$, all $P < 0.001$), indicating a positive relationship between plant size and seed production similar to that documented between populations.

Common Garden Experiments

Plant Size and Seed Yield

Cultivated wild populations were analyzed to quantify genetic and environmental effects on plant traits. Environment (common garden) had the greatest effect ($F > 117$, $P < 0.0001$) on plant size and seed production by cultivated plants in both years (Figure 3; Table 2). In both years, the Arboretum produced the largest plants (plant size index > 4980 cm²) and highest seed production (mean > 40 grams) for all

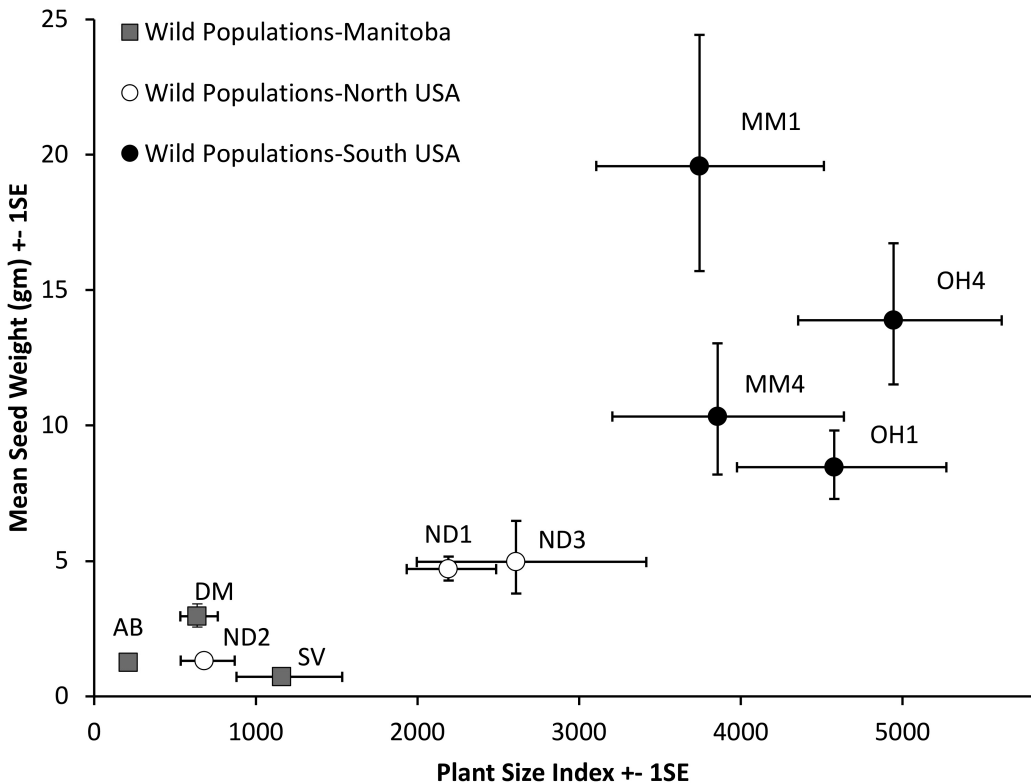


Figure 2. Mean plant size index compared to mean total seed mass for ten wild *Chenopodium berlandieri* populations. Back-transformed data presented.

populations. Plants were similar in height to their wild progenitor population but supported wider or denser lateral branches that produced more inflorescences and individual flowers, resulting in higher total seed mass. In contrast, Glenlea produced plants similar to their progenitor populations in size (plant size index < 455 cm²) and total seed mass (mean < 3 grams) (Figure 3). For each common garden and year, plant size index and total seed mass were positively and significantly correlated within all populations ($r > 0.96$, $P < 0.001$).

Genotype (population and maternal line) also affected plant traits (Table 2). In 2011, plants from SV were larger and higher yielding ($F > 7.4$, $P < 0.01$; Figure 3). In 2012, the population effect depended on common garden (population \times common garden interaction: $F > 4.7$, $P < 0.01$). At

the Arboretum, plant size and seed production values of SV clustered closely to those of DM, but were higher than the production values of AB. At Glenlea production values for all populations were similar (Figure 3).

Phenology

Phenology was documented to explore whether certain plant growth stages could inform cultural choices (Figure 4). Most seeds germinated within ten days or 45 to 69 GDD. Seedlings produced leaves within two weeks of germination (107–138 GDD), began flowering one to two months after germination (359–736 GDD), flowered for approximately two weeks (177 and 299 GDD), and began producing seed 50–110 days after germination (891–1369 GDD). Plants matured from the terminal end; while upper branches were in full flower, the lowest branches were still in

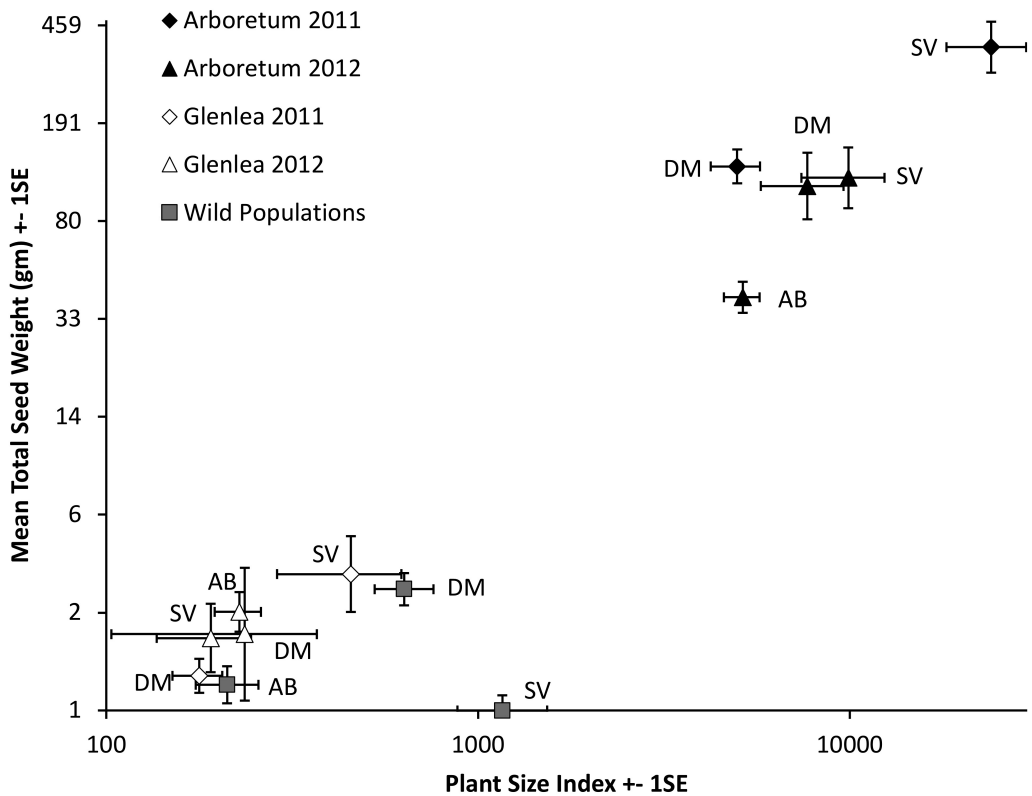


Figure 3. Plant size index compared to mean total seed mass from three wild Manitoban *Chenopodium berlandieri* populations grown at Arboretum and Glenlea common gardens in 2011 and 2012. Back transformed data presented on a logarithmic scale for easier viewing.

Table 2. Analysis of variance for plant traits from three Manitoban populations (AB, DM, SV) grown in Arboretum and Glenlea common gardens in 2011 and 2012. *F*-ratios and associated degrees of freedom for each effect are reported. Significance denoted by **P* < 0.05, ** *P* < 0.01, ****P* < 0.001, not significant (n.s.).

Effect		Plant index	Seed mass
2011			
Population	<i>F</i> _{1,32}	10.41***	7.35**
Common garden	<i>F</i> _{1,61}	423.75***	612.46***
Population × Common garden	<i>F</i> _{1,61}	3.20 n.s.	0.17 n.s.
Maternal line (within Population)	<i>F</i> _{20,62}	4.36***	3.01***
2012			
Population	<i>F</i> _{2,213}	0.74 n.s.	1.50 n.s.
Common garden	<i>F</i> _{1,9-11}	249.31***	116.79***
Population × Common garden	<i>F</i> _{2,213}	4.65**	7.33***
Maternal line (within Population)	<i>F</i> _{33,213}	1.86**	1.75**
Replicate (within Common Garden)	<i>F</i> _{4,213}	2.42*	3.65***

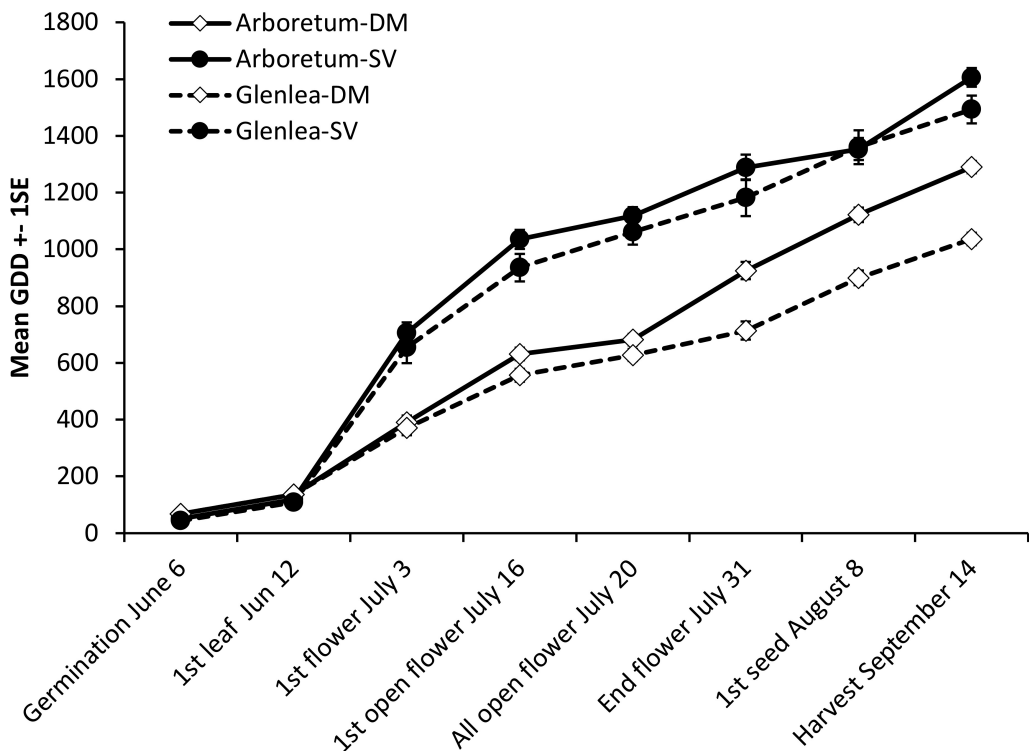


Figure 4. Mean number of growing degree days (GDD) to reach growth stages in *Chenopodium berlandieri* for two Manitoba populations grown at Arboretum and Glenlea common gardens in 2011. Average calendar date is included with each growth stage.

bud. Plants produced mature looking seed in 75% of flowers in approximately three weeks. Plants retained most seed until harvest. Most plants produced by population DM were harvested by mid-August (1022 to 1301 GDD), while the majority of plants produced by population SV were harvested by mid-September (1456 to 1589 GDD). A small amount of unripened seed was present on some of the last individuals harvested in 2011.

Cultivated wild populations were analyzed to quantify genetic and environmental effects on phenology. We present results for analyses of mean GDD; analyses based on calendar day produced very similar results. Significant effects of genotype (population and maternal line) were evident throughout the experiment. In both common gardens, DM reached all stages earlier than SV ($F > 6.99$, $P < 0.05$; Table 3). Initial differences between populations were small but

accumulated over the growing season (Table 3). Environmental (common garden) effects were not apparent until flowering, but were also cumulative and became comparable to population level differences by harvest (Figure 4; Table 3). Growing degree days at harvest were higher for plants grown at the Arboretum than those at Glenlea. Population \times common garden interaction effects became significant once seed production began (Table 3) but decreased in strength by harvest; differences between common gardens were greater for DM than for SV (Figure 4).

Examination of the time to phenological stages (Figure 4; Table 3) revealed that genotype (population) was more influential during vegetative growth ($F = 54.71$, $P > 0.001$), but environment (common garden) affected duration of seed production ($F = 9.46$, $P > 0.01$). Among populations, SV produced leaves significantly longer (mean 544–587

Table 3. Comparison of population, location, and population by location interaction effects on growing degree days (GDD) of a) time to phenological stages and b) time within phenological stage in *Chenopodium berlandieri*. *F*-ratios and associated degrees of freedom per effect are reported. Significance: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

a) Time to stage					
Effect		First leaf	First open flower	First seed	Harvest
Population	$F_{1, 35-50}$	5.06*	46.73***	35.24***	47.35***
Common Garden	$F_{1, 62-64}$	0.60	10.51**	10.83**	46.09***
Population × Common Garden	$F_{1, 62-64}$	0.56	0.21	12.14**	6.74*
Maternal line (within Population)	$F_{20, 62-64}$	1.89*	3.68***	2.45**	3.64***
b) Time within stage					
Effect		Leaf production	Flowering period	Seed production	
Population	$F_{1, 53-71}$	41.69***	0.19	1.22	
Common Garden	$F_{1, 58-64}$	1.03	3.19	9.46**	
Population × Common Garden	$F_{1, 58-64}$	0.14	3.02	3.32	
Maternal line (within Population)	$F_{20, 58-64}$	1.73	1.06	1.00	

GDD, $P > 0.0001$) than DM (mean 234–253 GDD) in both common gardens. Between environments, seed in both populations matured faster at Glenlea (mean 130–137 GDD) compared to the Arboretum (mean 168–252 GDD; Figure 4).

Economic Potential

Analyses of wild collected seed across the Northeastern Plains (this study) and Eastern Woodlands (data from Smith 1987) indicated that sub-region significantly ($F = 24.94$, $P < 0.0001$) influenced quantity of harvested seed per hour, accounting for some variation ($F = 3.84$, $P < 0.02$) in overall yield (Table 4). Yield and harvest rate were lowest in Manitoba (Northeastern Plains) and highest in the Eastern Woodlands (Table 4). Within the Eastern Woodland, sub-regions differed in harvest rates and yields. The northeastern and eastern sub-regions produced significantly more harvested seed per hour (1.12–1.3 kg/hr) compared to the southwestern sub-region (Table 4).

Nutritional Value

Chenopodium berlandieri in Manitoba and the USA were not significantly differ-

ent across most nutritional components, containing approximately 60% carbohydrates, 30% fiber, 20% protein, and less than 10% fat, moisture, and minerals. However significant differences in nutritional components occurred between wild *C. berlandieri* and domesticated quinoa. *Chenopodium berlandieri* was higher in protein ($F_{2, 6} = 10$, $P < 0.01$) and total dietary fiber ($F_{2, 6} = 57.8$, $P < 0.004$), while quinoa was higher in moisture ($F_{2, 5} = 14.7$, $P < 0.01$) and energy levels ($F_{2, 3} = 30.7$, $P < 0.01$). Wild *C. berlandieri* provided around 350 kcal/100 grams compared to 400 kcal/100 grams from quinoa. Wild *C. berlandieri* in Manitoba had slightly higher levels of minerals ($F_{2, 6} = 4.7$, $P > 0.04$) compared to quinoa, but these species were not significantly different in carbohydrate and fat levels.

Discussion

Opportunities and Constraints in Pre-Contact Subsistence Practices

Mixed subsistence strategies incorporate wild native plants and exotic domesticates into highly variable seasonal food procurement and production systems

Table 4. Analysis of variance of harvest yield (kg/ha) and harvest rate (kg/hour) data in four sub-regions across the Northeastern Plains and Eastern Woodlands. Harvest yield and harvest rate data calculated as LS means. Lowercase letters denote significant differences between regions. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, not significant $P > 0.05$.

Sub-Region (Region)	Harvest Yield (kg/ha)	Harvest Rate (kg/hour)
	Mean \pm SE	Mean \pm SE
Northwest (Manitoba, Northeastern Plains)	497 \pm 150.20 a	0.28 \pm 0.07 a
Northeast (Eastern Woodlands)	1287 \pm 201.5 bc	1.12 \pm 0.10 c
East (Eastern Woodlands)	653 \pm 260.2 ab	1.31 \pm 0.13 c
Southwest (Eastern Woodlands)	946 \pm 112.6 bc	0.84 \pm 0.06 b
Sub-Region Effect ($F_{3, 29}$)	3.84*	24.94 ***

(Hamilton and Nicholson 2006:257; Syms and Speirs 2012). Human decisions surrounding daily subsistence are situated within the physical and social environment and are informed by cultural preferences and social goals (Chase 1989; Deur and Turner 2006). The use of a particular species depends on availability and stability of a resource, modes of access, and cultural perceptions that allow species to be recognized and used as foods (Davidson-Hunt et al. 2016). Below we discuss how plant traits and cultural practices may have provided either opportunities or constraints for pre-contact Indigenous people to incorporate *C. berlandieri* into mixed subsistence practices in southern Manitoba.

Seasonal Timing of *C. berlandieri* Leaves and Seed

Traditional ecological and phenological knowledge informed Indigenous peoples about complete life cycles of plant and animal species (Lantz and Turner 2003:280). Therefore, documenting phenology can identify timing of plant availability and illuminate daily and seasonal activities through which pre-contact peoples may have interacted with a species. *Chenopodium berlandieri* phenology varied across Manitoban populations and environments for all growth stages, including leaf production. Leaves of *C. berlandieri* can be eaten fresh or cooked and contain more Vitamin A, fiber, potassium, and magnesium levels

compared to domesticated spinach (*Spinacia oleracea*), beet greens (*Beta vulgaris*), swiss chard (*Beta vulgaris* subsp. *vulgaris*), or broccoli (*Brassica oleracea*) (Kallas 2010:68–69, 79), and more Vitamin C than oranges (*Citrus* sp.) (Zennie and Ogzewalla 1977:79). In modern traditional farming systems in Mexico, *C. berlandieri*, amaranth (*Amaranthus hybridus*), and mustard (*Brassica* sp.) are encouraged in maize fields and harvested for their leaves mid-season (Vieyra-Odilon and Vibrans 2001:427).

Variation in leaf production across populations and environmental conditions indicates young leaves can be produced in Manitoba one to two months after germination. Minimal weeding and watering can increase leaf and branch production in common garden-grown populations. Consistent leaf harvest of young plants also increases leaf production across the summer by thinning populations and encouraging vegetative growth over flower formation (Kallas 2010:73, 75). This suggests wild *Chenopodium* plants grown in pre-contact maize fields could have provided daily nutritious greens that could have been collected by anyone. Older leaves produced when plants begin seed production are also edible but develop a bitter flavor (Kallas 2010).

Variation in *C. berlandieri* seed harvest (June–October) contrasts with our prediction that timing of seed harvest would be uniform (September–October). Seed

maturation appears to have a genetic basis; however, cumulative environmental (common garden) influences can affect harvest times as much as genetic differences. Thus, timing of seed harvest depends on the population to be harvested and location in which it was grown. This situation would have provided pre-contact peoples in Manitoba opportunity to optimize harvest timing in conjunction with wild foods including plums (*Prunus* sp.), chokecherries (*Prunus virginiana*), hazelnuts (*Corylus* sp.), and dock seeds (*Rumex* sp.) (Deck and Shay 1992). If *Chenopodium* was cultivated alongside domesticated maize, beans, and squash, growing seeds from several *Chenopodium* populations together would increase the range of maturation times available at one location. Cultivating plants that mature seed before domesticated crops would space harvest time across these important species. Fairly strong seed retention in wild *Chenopodium* would have also facilitated timely harvest.

Economic Potential of *C. berlandieri* in Manitoba

We show that frequency and yield of wild *C. berlandieri* decreases from southern (Ohio - Eastern Woodlands) to

northern populations (Manitoba - North-eastern Plains). Similarly, *C. berlandieri* populations in Manitoba had lower yields and harvest rates than those documented by Smith (1987) from the Eastern Woodlands. Despite this decrease in availability, wild Manitoban populations still provide comparable yields to other small-seeded species (Table 5). We harvested and cleaned 100 grams of seed, comparable to a serving of quinoa, in 30 minutes, although our rate likely underestimates that of an experienced harvester. Wild *C. berlandieri* seed is also nutritionally comparable to domesticated quinoa (*Chenopodium quinoa*), with higher fiber, protein, and iron but slightly fewer calories per serving. Similar nutrition for wild goosefoot populations and quinoa indicates a high value of wild Manitoba populations and gives incentive for use within a mixed subsistence strategy.

A nutritional constraint to goosefoot seeds is saponin in the pericarp (remnant fruit), testa (seed coat), and embryo (Lopez et al. 2011; Prego et al. 1998). Saponins are water-soluble plant glycosides that deter herbivores, produce a bitter flavor, and can interfere with nutrient absorption (Schlick and Bubenheim 1993). Preliminary data indicated saponin occurrence

Table 5. Harvest yield of native small seed producing species used in mixed subsistence strategies. Domesticated quinoa included for comparison.

Common name	Taxa	Harvest yield kg/ha	Location of study (Reference)
Net seed goosefoot	<i>Chenopodium berlandieri</i>	250–870	Manitoba–Northeastern Plains (this study)
		26–1325	Common garden grown wild seed Manitoba–Northeastern Plains (Halwas 2017)
		300–1800	Eastern Woodlands (Smith 1987)
Lambsquarters	<i>C. album</i>	750–1500	Eastern Woodlands (Asch and Asch 1977)
		276–2854	United Kingdom (Stokes and Rowley-Conwy 2002)
	<i>C. missouriense</i>	450–900	Eastern Woodlands (Seeman and Wilson 1984)
Marshelder	<i>Iva annua</i>	255–620	Eastern Woodlands (Smith 1987)
Amaranth	<i>Amaranthus</i> sp.	204	Eastern Woodlands (Peterson and Munson 1984)
Knotweed	<i>Polygonum</i> sp.	145–1100	Eastern Woodlands (Murray and Sheehan 1984)
Quinoa	<i>C. quinoa</i>	336–2240	Saskatchewan–Canadian Plains (Guenther 2014)

across *C. berlandieri*'s range, including two of three Manitoba populations (Halwas 2017:159). Simple techniques to reduce saponin content to safe levels include freeing the seed from the pericarp and washing the seeds (Lopez et al. 2011). In quinoa, a single dominant gene controls saponin content, and mass selection for "sweet" varieties has been conducted with varying success (Mastebroek et al. 2000). It is possible the differential presence of saponin across Manitoba populations (Halwas 2017:159) may indicate "sweet" and "bitter" varieties.

Availability and Stability of *C. berlandieri* as a Food Source in Manitoba

Our survey indicated that large *C. berlandieri* populations in Manitoba are less frequent than in southern regions. Factors that may affect population frequency include differential flooding and disturbance along major rivers that alter distribution patterns, making populations challenging to locate annually (Smith 2011:839), and the introduction of Eurasian species (e.g., lambsquarters) that out compete native goosefoot species in anthropogenically disturbed soils (discussed in Halwas 2017). However, populations further south often grow in anthropogenically disturbed areas (see Smith 1987) and are still more frequent than in Manitoba.

Chenopodium berlandieri plants from more northern populations were smaller with lower seed yield. This is consistent with research on other species showing decreased age and size at reproduction in more northern populations with shorter growing seasons (Colautti and Barrett 2013). Reduced population size and frequency and smaller yields seems likely to have been present in the past, given evidence that broad climate and vegetation patterns have been relatively stable for the last 1500 years (Shay 1980). These differences would have reduced the availability of wild *C. berlandieri* as a food source in the Northeastern Plains compared to the Eastern

Woodlands, which may have discouraged reliance on *C. berlandieri*. Alternatively, it may have provided incentive for interventions to increase the stability of the resource.

Ameliorating low frequency of wild populations is possible through the use of "low level" cultivation techniques (cf. Smith 2001). Our common garden experiment showed that planting wild *C. berlandieri* seed in tilled soil, followed by light weeding and watering, can lead to substantial increases in plant size and seed production compared to wild populations (Table 5). These basic cultivation techniques are routine for enhancing berry and root crop production by West Coast cultural groups (e.g., Darby 1996; Lepofsky et al. 2006), are used by Baka Pygmy groups to enhance wild yam yields (*Dioscorea* sp.) (Dounias 2001), and to maintain landrace varieties of columnar cacti in Mexico (Casas et al. 2006). Such low-level cultivation of *C. berlandieri* could well have occurred in Manitoba, given cultural exchange with Eastern Woodlands groups that cultivated this species (Flynn 2002), coupled with evidence for cultivation of other crops (Boyd and Surette 2010; Deck and Shay 1992).

Location of common gardens had the strongest influence on seed yield of *C. berlandieri*, despite similar base soil types (Don Flaten, personal communication, 2016; Ehrlich et al. 1953). Plants grown in compacted soil at Glenlea produced comparable yields to wild populations. In contrast, plants grown at the Arboretum experienced regularly tilled and weeded, well-drained riverine soils, and were sheltered from the wind (Don Flaten, personal communication, 2016); their seed yields exceeded those of their progenitor populations by an order of magnitude or more, and also exceeded seed yields from wild populations in the Eastern Woodlands. The latter contrast indicates that local conditions can be more important than overall climate or length of the growing season in determining yield.

The difference between common gardens in Manitoba attests to phenotypic plasticity of local populations and the importance of human management history for crop yield. Plasticity is the ability for an organism to produce different phenotypes in varying environments (Conner and Hartl 2004) and can produce variation in yield and other traits across the landscape. Human management history includes all practices (e.g., tilling, manure) used to modify the soil (Seward 2016). In a manure experiment on annual/perennial crop rotation, tilling solid manure into a clay subsoil over an eight-year period resulted in higher plant biomass across species than application of liquid manure with the same nutritional content (Seward 2016). Given the evidence for cultivation of other crops (cf. Deck and Shay 1992; Lints 2012), well drained, worked soils seem likely to have been available in Manitoba during the pre-contact era. Encouragement of wild species, as is currently practiced in traditional farms (Vieyra-Odilon and Vibrans 2001:427), could have increased size and seed yield of *C. berlandieri*.

Conclusion

Documenting the history of interactions between people, place, and plants can provide information on the type of cultivation practices employed. People modify local environments and regional ecosystems to increase overall productivity, abundance, and/or predictability of resources (Smith 2011:836). Flexibility in plant traits and human behavior can influence which plant populations are harvested, when they are harvested, and how they are incorporated into a seasonal subsistence pattern. Further, documenting underlying genetic and environmental influences on plant and seed traits associated with food resources is important for understanding the evolution of domesticated species. In Manitoba, *C. berlandieri* populations tend to be infrequent on the landscape and produce lower quantities of

seed compared to southern populations in the Northeastern Plains and Eastern Woodlands. The potential to access populations was present and their wide dispersal on the landscape may have incentivized cultivation of populations close to settlements. As our research indicates, low-level cultivation has the potential to make wild *C. berlandieri* in Manitoba a more productive, and likely more reliable, resource.

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