

Domesticating *Chenopodium*:
Applying Genetic Techniques and Archaeological Data to Understanding Pre-contact Plant Use
in Southern Manitoba (AD1000-1500).

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ABSTRACT

Current understanding of pre-contact subsistence economies in southern Manitoba indicates hunter-harvester cultural groups were consuming and potentially cultivating domesticated plants (e.g. maize and beans). These may have originated through long distance trade and/or migration stemming from the adjacent Eastern Woodlands region in eastern North America. Within the Eastern Woodlands, native species (e.g. *Chenopodium berlandieri*) were domesticated for their seed ca. 3500BP. This raises the possibility that cultural groups in southern Manitoba may also have cultivated local native plant species.

This interdisciplinary research explored the potential effects of cultivation on plant and seed traits of *C. berlandieri*. Data were collected to reassess archaeobotanical seed remains from the Lockport (EaLf-1) and Forks (DILg-33:08A) archaeological sites in southern Manitoba to gain a better understanding of pre-contact subsistence strategies.

Ten wild *C. berlandieri* populations surveyed from southern Manitoba to Ohio revealed that populations within each region produced a wide range of plant and seed phenotypes, including varied seed production. Compared to plant phenotypes from parental populations, wild Manitoba seed grown in a cultivated environment increased in total plant size, seed production and exhibited larger seeds with thinner testas. Similarly, percent germination increased for seed produced in a cultivated setting. Seed size and testa thickness were highly heritable and strongly inversely correlated indicating a firm genetic basis for variation in seed traits. Thus low-level cultivation practices created conditions that would have promoted the evolution of the domesticated phenotype (i.e. large seeds with very thin testas).

Archaeological *C. berlandieri* specimens recovered from the Lockport and Forks sites exhibited testa thicknesses nearer the ‘thin’ end of the natural range of variation (0.025-0.035mm) for wild populations in Manitoba. This range of variation in seed traits appears to match ‘weedy’ populations associated with domesticated goosefoot crops from Eastern Woodland sites. ‘Weedy’ populations exposed to cultivated environments apparently developed intermediate seed phenotypes. In Manitoba, archaeological *C. berlandieri* seeds that exhibit relatively thin testas may indicate an intermediate ‘cultivated phenotype’ between wild and domesticated seed morphologies.

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DEDICATION

For Baba and Aunty Pat. All my love, Lima

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PREFACE

My thesis explores the possibility that Late Woodland (ca. AD 1000-1500) cultural groups in southern Manitoba were cultivating local wild populations of *Chenopodium berlandieri* as a stable food resource. The biological effects of harvesting or cultivating wild *Chenopodium berlandieri* populations are not well known. Therefore, understanding the nature and extent of human interaction (selection pressure) on extant populations will provide a baseline for comparison to archaeological seed remains in order to investigate pre-contact plant use. I focus on select aspects of the population structure and seed biology of *C. berlandieri* in southern Manitoba that may have influenced how pre-contact peoples interacted with local plant populations. If cultural groups were cultivating local populations of *C. berlandieri* then it is possible that over time some of these interactions may have generated specific plant phenotypes associated with cultivation. Each chapter explores a point of interaction of the development of people-plant relationships.

In Chapter 1, I outline the theoretical perspective that shaped how I thought about archaeobotanical plant remains and the range of variation in pre-contact subsistence practices. I forward a developmental perspective where specific subsistence practices and overall subsistence economies are generated through practical learning of individuals within their environment. This perspective acknowledges the countless interactions between people, plant populations, and their environments (e.g. local and broad climatic and geographic factors) that generated subsistence economies. Therefore, multiple lines of evidence must be examined to fully understand the complexities of pre-contact subsistence practices.

In Chapter 2, I explore the variation in subsistence practices employed by pre-contact cultural groups in southern Manitoba during the Late Woodland period (AD1000-1500). To fully address the observed variation in the archaeological record, it is necessary to identify the various components of cultural and ecological environments and the opportunities and constraints in which they interacted that generated the plant phenotypes and human activities (material culture) that created the archaeological record.

In Chapter 3, I explore some of the opportunities and constraints generated by *C. berlandieri*'s biology and local ecological conditions. I quantify the range of variation in habitat, potentially important plant phenotypes (e.g. plant size and seed yield), and phenology (seasonality) in extant populations in the Northeastern Plains (southern Manitoba and North Dakota) and the Eastern Woodlands (Missouri and Ohio). Determining the range of variation for plant and seed traits will provide data on phenotypic variation in wild populations available to pre-contact peoples. Exploring the phenology of individual plants will provide data on seed maturation and on when and how people can interact with that plant, and it will help interpretations of the archaeological record (e.g. seasonality).

In Chapter 4, I assess the value of *C. berlandieri*, a member of the genus commonly referred to as goosefoot, as a food resource. Goosefoot seed and leaves are cited as food resources in the ethnobotanical literature and may have been heavily utilized as a food source prior to European contact. To determine the suitability of goosefoot as a stable food resource, a harvest experiment and nutritional analyses of seeds determined the energy return rate via yield, and via protein, carbohydrate, and fat content.

In Chapter 5, I test whether increased seed size and reduced testa (seed coat) thickness are significant traits associated with domestication (cf. Smith 1984; Gremillion 1993). These traits are cited as reducing dormancy factors, enabling quicker germination,

thereby increasing seedling survival rates in domesticated populations of *C. berlandieri* (cf. de Wet and Harlan 1975). It is also possible that extreme climatic conditions in Manitoba may result in stronger selection pressures for certain seed phenotypes. Testing percent germination between Manitoban and Eastern Woodland populations highlights potential differences in natural selection within the wider geographic range.

In Chapter 6, I place the biological information into the archaeological context to gain a better understanding of past plant use by pre-contact groups in southern Manitoba. Palaeoethnobotany, the recovery, analysis, and interpretation of archaeological plant remains, is the foundation for understanding pre-contact human-plant interrelationships. First, I assess the effects of carbonization on morphological features of *C. berlandieri* seeds allowing for the comparison between extant and ancient materials. Second, I quantify the range of variation in seed size and testa thickness of *C. berlandieri* assemblages from two archaeological sites in the Red River Valley, the Lockport site (EaLf-1) and the Forks (DILg-33:08A) site, allowing these assemblages to be placed along the continuum of plant use established by Eastern Woodland assemblages. It is possible that pre-contact people could have affected changes in seed size/seed coat thickness through selection of larger plants in goosefoot populations.

In Chapter 7, I provide a summary of my research discussing the potential for pre-contact cultural groups in southern Manitoba to have influenced seed traits in *C. berlandieri* populations through low-level cultivation techniques.

1. DEVELOPING PEOPLE-PLANT RELATIONSHIPS IN SOUTHERN MANITOBA

1.1 Introduction

Palaeoethnobotany is the study of archaeological cultures through the analysis and interpretation of direct relationships between human populations and the plant world as manifested in the archaeological record (Ford 1979; Hastorf and Popper 1988).

Palaeoethnobotany documents the nature and extent of plant use using people-plant interrelationships as a window into the social aspects of an archaeological culture.

Archaeologists are able to use the material remains of a culture to gain an understanding of how pre-contact people lived, because material remains are the residues of human activities, themselves a product of social, biological, and environmental factors.

One of the most important aspects of palaeoethnobotany is examining subsistence practices. While understanding the ways cultural groups interacted with their environment is necessary for understanding how pre-contact societies lived, cultural groups are no longer defined by discrete subsistence practices. A long held tenant of cultural ecology (e.g. Steward 1995) considered hunter-gatherer groups fully adapted to their environment, exploiting the wild plant resources around them to fulfill their needs. Alternatively, horticultural/agricultural groups modified their environment, cultivating domesticated crops in gardens or fields. It is now known that many pre-contact cultural groups utilized both wild and domesticated food resources. Ford (1985) acknowledged that subsistence practices form a continuum between those groups that gathered wild plant resources to those groups that focused on cultivation of domesticated crops, and that many groups fall in between the two extremes (see below for details). Cultural groups

that fall within the ‘middle ground’ are described as low-level food producers or mixed subsistence economies (Smith 2001).

An evolutionary framework is often used to explore the variation in subsistence economies, investigating why or how some cultural groups maintained a mixed economy while other societies developed domesticated crops and agricultural systems (e.g. Gremillion 1996; Gremillion and Piperno 2009; Kennett and Winterhalder 2006). For instance, Gremillion (1996) explicitly argues that the origin of agricultural systems is a fundamentally evolutionary problem; therefore evolutionary ecology with its “emphasis on the evolution of adaptive behaviours in specific environmental contexts and its systematic methodology” is poised to illuminate the adoption and use of introduced crop species (Gremillion 1996:183).

Relationships between pre-contact people and the plants they used are complex, involving both biological and cultural factors, the study of which requires both biological and social perspectives. People-plant relationships are concomitant, relying on the interaction of human agency, cultural practices and the biological (“adaptive”) properties of plant species. People classify, place value on, and engage with the plant populations they use; they do not just exploit a ready-made resource (*cf.* Chase 1989; Ingold 2000). Recently, researchers studying the origins of agriculture worldwide acknowledge that countless interactions between people, plant populations, climate, and geographic factors resulted in domesticated plants and agricultural systems. As a result, multiple lines of evidence must be examined to fully understand the complexities of pre-contact subsistence practices (Larson *et al.* 2014; Price and Bar-Yosef 2011).

My research focuses on understanding mixed subsistence economies practiced during the Late Woodland period (AD1000-1500) in southern Manitoba. I explore potential effects of selected interactions between pre-contact people and plants used as food resources, using an integrated perspective that merges biological and social theories. I forward a developmental perspective, where people-plant relationships are the outcome of a dynamic ongoing process of interactions between the myriad of components that constitute their environments. The development of these relationships is guided by biological and social interactions, and is historically situated. The remains of this process can be recovered in the archaeological record as artifacts, features, and plant phenotypes represented by archaeobotanical remains. The developmental framework I employ was first laid out by Ingold in what he calls the ‘ecology of life’ (Ingold 2000). An Ingoldian ‘ecology of life’ perspective eliminates the dichotomy between humans as social people governed by socio-cultural rules, and humans as biological organisms governed by natural selection (Ingold 2000). It advocates an organism-in-environment view that organisms (all human and non-human animals, plants and other living taxa) develop in relation to interactions with the biotic and abiotic components of their environment. Organisms are inseparable from their environments. Therefore, humans are not separate entities that move around in the environment without affecting it (Ingold 2000: 16).

1.2 Objectives for a Theoretical Perspective

To set up a developmental perspective, I begin by describing the standard evolutionary perspective, exemplified by the process of domestication as forwarded by Ford (1985) and expanded by Smith (2001), with which I began thinking about people-

plant relationships (Section 1.3.1). This perspective helped me define the hypotheses I tested in my thesis, and was helpful in explaining the biological changes that plant populations go through and the selective pressures associated with instigating those changes. It has not, however, expanded my understanding of the interplay between decisions people made in regards to plants or the numerous interactions plants had with their environment.

A nuanced understanding of evolutionary theory is forwarded by niche construction theory, which I incorporate as a complement to Ingold's (2000) organism-in-environment perspective. Niche construction (Odling-Smee *et al.* 2003), a parallel process of natural selection in which organisms can construct their environments altering some selection pressures they and other organisms are exposed to, provides a way to understand the complexities of plant relationships with their environments (Day *et al.* 2003). From a plants' perspective, humans who interact with them are only one component in a complex environment. The processes of domestication can be viewed as ways that some plant species modified important components of their environments (e.g. through resource use), thereby altering selection pressures, which may have favoured a different set of phenotypes than may have been favoured without the modification (Donohue 2003). I discuss niche construction (Section 1.3.2) and some important aspects of this theory (e.g. phenotypic plasticity) that will be useful for examining the interaction between plant populations and human activities.

I describe the 'ecology of life' and how it provides a rich and nuanced perspective for exploring the ways in which pre-contact people interacted with the plants that made

up their world (Section 1.3.3). I highlight connections to other social theorists (e.g. Bourdieu 1977; Ortner 1989) where appropriate.

Unfortunately many, if not all, of the terms I use to build my theoretical platform have previous definitions and are understood in different ways by different people. To be clear about the terms I am using, I include both the sociocultural definitions and biological translations where possible (see Chapter 8 Glossary, pg. 300). Further, I acknowledge that looking at the entire environment of people and the plants they used and the various interactions that lead to their development is a daunting (somewhat impossible) task. However I believe that even to attempt to examine pre-contact people-plant relationships as the embodiment of interactions over time within their environments can be very informative. I describe in Section 1.3.4 a more integrated theoretical perspective to explore the relationship cultural groups had with plants.

During the Late Woodland period, southern Manitoba was home to numerous cultural groups that relied on various subsistence economies. For instance, there is evidence for wild plant use, domesticated plant use and potential cultivation of wild plant populations (e.g. Johnson 2007; Nickel 2007). It is probable that long-distance trade, migration, and local intra-site cooperation (Hamilton *et al.* 2011; Nicholson *et al.* 2011) spread ideas and practices pertaining to edible plant species between groups. Incorporation of these ideas and practices in new environments may have resulted in new relationships with plants and may explain the diverse archaeobotanical record in Manitoba. I outline in Section 1.4 how my thesis explores some of the potential interactions between native plant species and the people cultivating or caring for them. Interactions may have included both plants and people participating in niche constructing

activities, the results of which may have influenced subsistence strategies identifiable in the archaeobotanical record.

1.3 Toward a Developmental Perspective

1.3.1 Process of domestication

A common perspective in palaeoethnobotany views plant use by humans as a reflection of the relationships between humans and plants (Ford 1985; Harris 1989, 1996, 2007; Rindos 1984, 1989). This relationship is described by the process of domestication, which reflects a continuum of human activities and associated plant phenotypes (Figure 1.1). The type and intensity of human interaction in a plant's lifecycle link human activities with plant phenotypes. Human activities range from gathering wild plant phenotypes to full intensive field agriculture associated with fully domesticated plant forms (Ford 1985). In between exists a range of plant forms and cultivation techniques associated with low-level food production.

I initially focused on the process of domestication to explore people-plant relationships from both conceptual and literal perspectives. This approach describes how selection pressures associated with plant-human interactions alter plant traits over time. Rindos (1984) described the relationship between plants and people as co-evolutionary, emphasizing the importance of the interaction between human activities and plant phenotypes (e.g. morphological/ genetic changes). Human interaction in plant populations result in selection of phenotypic traits that meet human needs (e.g. nutritional, medicinal, ritual). Enhancing the evolutionary fitness of culturally important phenotypes through weeding, watering or removing unwanted phenotypes would be

sufficient to change selection on the plant population. When favoured phenotypes are heritable they will increase in frequency in the plant population. With continued human intervention, these phenotypes will become prevalent in successive generations. Not only does this process cause morphological and genetic changes in plants, but it can influence changes in specific activities or behaviour people employ, e.g. through increased investment of time and effort in the relationship with plants (Ford 1985; Rindos 1984; Harris 1996).

Smith (2001, 2006) built on the continuum of plant forms and human activities highlighting and extending the ‘cultivation zone’ (Figure 1.1), which he associates with ‘middle ground’ (low-level production) societies. He argues that human societies also form a continuum extending from hunter-gatherer groups to fully agricultural groups with the bulk of human societies falling in the middle. This is a promising perspective in palaeoethnobotany because ‘middle ground’ societies use a mixture of subsistence practices including gathering wild plants, cultivation of domesticated crops, and the management of not-wild but not-yet-domesticated plant forms (Smith 2001). This links cultivation techniques utilized by low-level producers with not-wild-but-not-yet-domesticated intermediate plant phenotypes (Smith 2001). It is possible that documenting intermediate plant forms in the archaeobotanical record could help identify ‘middle ground’ societies where other archaeological material is insufficient.

These intermediate plant forms fall in the middle of Ford’s (1985) graph (Figure 1.1) and are associated with a variety of cultivation techniques. While Smith (2006) and others (e.g. Harris 1996) debate where to place boundary markers to categorize the societies within the ‘middle ground’, I argue that boundary placement is not the main

problem with this perspective and is therefore moot. Dividing a continuum will always be arbitrary, and categorizing it nullifies any discussion of a continuum of form for society or human-plant relationships.

The problem with this perspective is that people-plant relationships are viewed in a vacuum. It incorrectly implies that human agency is reduced to a selection pressure on a plant population, while plant phenotypes are “pre-determined by intrinsic environmental parameters” (Rindos 1984:156), reacting only to strong human selection pressure. This creates a one-dimensional linear transition between hunting and gathering and agriculture. Ford’s model implicitly defines a set of progressive stages (Ford 1985: 2-7), while similar models (e.g. Rindos 1984; Harris 1989, 1996) are not deterministic or unidirectional (Harris 2007:20). Even when Rindos acknowledges that humans can modify local environments to increase populations of useful plants, he did not consider interactions between plants and their complete environment as important factors in the evolution of plant phenotypes or populations (Rindos 1984:156).

Investigating subsistence strategies requires multiple lines of evidence (e.g. climate change, population increase, niche construction), rather than a single universal indicator (e.g. Zeder 2009). Recent research focusing on niche construction theory observed that many hunter-gather groups modify their environments and participate in low-level food production (cf. Smith 2001), but very few actually become agriculturalists (Laland and O’Brien 2010: 14). Many pre-contact cultural groups fall into the ‘middle ground’ (Figure 1.1), and focusing only on subsistence economies at the ends of the spectrum ignores the interesting variety of subsistence practices among these ‘middle ground’ economies that utilize both wild and domesticated resources (cf. Harris 2007:30).

1.3.2 Niche Construction theory

A recent advance or updating of standard evolutionary theory in biological and human sciences reinstates the organism as the focus of selection (rather than a Neo-Darwinian focus on the genes or alleles). Niche construction theory provides a complement to earlier evolutionary theory (Odling-Smee *et al.* 2003:2), arguing that organisms develop within their environment, modifying it as much as it modifies them, thereby changing the direction and dynamics of the evolutionary process (Odling-Smee *et al.* 2003: 2; Andersson *et al.* 2014). It introduces feedback into an evolutionary system (Odling-Smee *et al.* 2003:3). For example, “ecosystem engineering” is associated with organisms modifying their own and other’s environments, e.g. beavers build dams across rivers, causing water to back up and flood the surrounding area (Odling-Smee *et al.* 2003). It is also cited as the way humans modified their environments by altering selection pressures on important plant species. Ultimately, these pressures led to domestication of cereal crops and of humans (e.g. Smith 2015; Zeder 2016).

Plants can also construct their environments through direct habitat modification, resource garnering and depletion, or modifying the selective environment that acts directly or indirectly on themselves, their descendants, and other organisms within the environment (Donohue 2003: 79). Phenotypic plasticity is a main avenue through which plants modify their environments in the short term. Commonly, plasticity is the ability for a genotype to alter its phenotype in response to environmental cues (Donohue 2003: 79). More specifically, plasticity is an ability of an organism to react to an environmental input with a change in morphology, physiology, movement or rate of activity (e.g. respiration); it can be active or passive, adaptive or not (West-Eberhard 2003: 34-35). By

responding to environmental cues, plants can alter to some degree the ecological environment they experience, and even the life stage exposed to different environments through morphological and phenological changes (Donohue 2005).

Studies on shade avoidance by *Impatiens capensis* indicated that plants can detect a decrease in the red: far red light spectrum associated with shade conditions and alter their experience of the light environment (i.e. amount of red: far red light) by elongating its stems or flowering early (Donohue 2003:80). The niche construction for *Impatiens* plants was to ameliorate their “poor” light environment by growing out of the shade improving the light environment, or begin flowering earlier, so they can mature fruit prior to canopy closure (Donohue 2003). In this study, plants responded to their light environment through stem elongation, thus altering the light environment they experienced. This resulted in exposure to different selection pressures associated with the new light environment allowing plants to mature later. Plants that remained in the “poor” light environment responded to the environment by maturing earlier, thus a different life stage (e.g. flowering and fruit maturation) experienced the selection pressures associated with the low light environment (Donohue 2005).

Plastic responses to a species environment may also affect another species environment (Donohue 2003). For instance, plasticity in one plant may be a response to an environmental change created by another organism in the environment with which it interacts (Donohue 2003:86). Increase in plant size or seed production may be a plastic response to increased resource availability that may influence other organisms that share the environment (Odling-Smee *et al.* 2003). Larger plant size and higher seed yield may encourage increased human harvesting of plants or plant populations, increasing the

quantity of dispersed seed, thus maximizing the likelihood of the plant population growing the following year. People may maintain plant populations through annual cultivation (e.g. weeding, tilling soil) activities (i.e. ecosystem engineering, Day *et al.* 2003). Activities such as weeding would reduce competition, freeing resources (e.g. light, water, space) for culturally important plants, which may in turn continue to respond plastically to the increased resource availability (Donohue 2003). In this case, maintenance of a plant population through low-level cultivation techniques can maintain genetic diversity by allowing plants with different genotypes but similar plastic responses to increased resource availability to contribute to subsequent generations (Donohue 2003:86).

A type of ecological inheritance, or the extension of niche constructing effects across multiple generations, includes maternal inheritance or effects (Odling-Smee *et al.* 2003). Maternal effects include the influence of a mother's phenotype on her offspring independent of the genetic contribution she makes to the offspring (Roach and Wulff 1987:209). Generally, mothers provision and protect their young. In plants that produce seeds, mothers may supply food reserves for seedlings (e.g. endosperm, perisperm in seed), disperse seeds into suitable habitats (e.g. away from conspecifics where competition would be high), and protect offspring from inclement conditions and predators (e.g. thick seed coat or toxins) (Mousseau and Fox 1998).

Of particular importance to cultural subsistence strategies are those environmental and genetically related maternal effects on seeds. Maternal effects on seed size variation are linked to germination, seedling size, adult plant size and competitive ability of adult plants (Roach and Wulff 1987). Cytoplasmic content from the maternal parent directly

affected seed size in flax; maternal inheritance strongly influenced fatty acid content in maize, oil content in sunflower, and protein in dry beans (Roach and Wulff 1987). A survey of studies on specific environmental conditions experienced by mother plants indicated that day length affected the seed weight in *Chenopodium rubrum* (Cook 1975), while maternal parents exposed to lower temperatures during seed development produced high dormancy levels in the offspring (Roach and Wulff 1987). Dormancy and germination are heavily influenced by maternal inheritance as the seed coat, a main dormancy component, is derived from maternal tissue (Roach and Wulff 1987: 218). For example, seed coat thickness in *Chenopodium bonus-henricus* increased as mothers were exposed to higher elevations. This was linked to a reduction in percent germination because seed coat thickness acted as a physical barrier to dormancy (Dome 1981).

Through the above processes it is clear that organisms and their environments interact and influence each other, creating opportunities and constraints for the expression of new or varied phenotypes and/ or alterations to the selection of environments on established phenotypes. During the process of domestication humans and plants modify selection pressures that act on themselves and other species, thereby influencing evolutionary responses (Laland and O'Brien 2010: 1-2). This makes the evolution of food plants more than just a linear response to human activity. This broader evolutionary perspective dovetails well with the integrated organism-in-environment perspective forwarded by Ingold.

1.3.3 Ecology of Life

The concept of development used by Ingold (2000) as a holistic perspective was originally borrowed from developmental biology, which views life as an ontological process. Organisms are not just a reading of the DNA blueprint, but are the outcome of unique interactions between genes, plus random events of molecular interaction within the cells, occurring over a temporal sequence of environments through which the organism passes during life (Lewontin 2000). Ingold (2000) sees form (e.g. plant phenotypes, human behaviours) revealed through the process of development itself, not from a preconceived image (*cf.* Lewontin 2000). The form and capacities of an organism emerge through development as an ongoing engagement with its environment (Ingold 2000; Lewontin 2000).

Ingold (2000) resituates all living organisms, including humans, plants and animals, into an ongoing and active engagement with their environment, which includes biophysical elements, human and non-human organisms, as well as the interactions between them (e.g. ideas, activities, and decisions). Organisms shape their environment, and in turn are shaped by it (Ingold 2000). Most importantly the environment is relative, in that it exists and takes on meaning according to each organism that perceives and interacts with it (Ingold 2000). This is because organisms engage with the world through their perception of the world.

Based on Gibson's (1979) idea that organisms perceive their world through moving through it, knowledge is gained through a practical engagement with the environment (Ingold 2000:55). While environments are unique to the organism that attends it, they are also shared because aspects of the environment are unchanging or persistent (Mace

2005). Humans and animals (Gibson did not include plants) attend to their environments, perceiving them by using their senses to look, touch, taste, smell, feel, and listen (Gibson 1979). Ingold (2000) argues that plants would be included in this as living organisms, and research on plant interactions indicates that plants do attend to their environment by sensing light, temperature, gravity, and, more recently, through chemical signaling (e.g. Biedrzycki *et al.* 2010; Pollan 2013).

Humans learn through a practical engagement with their environment that is “furnished by the work and presence of others” (Ingold 2000: 4). Practical knowledge is gained by repeatedly performing daily actions, including physical tasks (e.g. washing dishes, collecting raspberries, making a projectile point), and social tasks, i.e. knowing what others mean when they speak to you, knowing what is the appropriate thing to do in a given situation (Bourdieu 1977). Bourdieu (1977) situated daily practice as derived from a pool of knowledge created by an underlying system of structures (*habitus*). Ingold argues that an organism’s form (physical and personality) is generated through the practical experience of living. People learn by doing. Learning is not reliant on an underlying pool of knowledge to provide a set series of acceptable strategies to understand or cope with unforeseen and ever-changing situations (Bourdieu 1977; Dietler and Herbich 1998). Through interacting socially with other people of different generations, backgrounds, and personal histories, people learn to comport themselves in various social situations. Through training and experience conducting practical tasks, individuals learn how to make pottery, sew clothes, write, read, cultivate garden plants, collect wild plants, hunt and husband animals.

Plants need to be viewed as active organisms in their environment. Plant forms are not passive expression of genes but are actively generated through a multitude of interactions of the plant and the abiotic and biotic components of their environment (Ingold 2000: 20). From a biological perspective, a plant's environment includes the soil, climate, weather (temperature, humidity, precipitation, day length), pathogens and insects, plus plants of other species and conspecifics (Comstock and Moll 1963: 293). Ingold expands a plant's environment to include all animals and humans and the interactions between all biotic and abiotic components (Ingold 2000). Essentially plants, like all organisms, grow up within a constantly changing field of relationships (Ingold 2000:4).

Ingold used the tree from a painting called *The Harvesters* (2000: 204) to provide an example of how plants are generated, and in a similar vein, I evoke the image of an old spruce tree growing in a row with other such trees in an old farmyard. Its form was generated within its environment through interactions with the abiotic and biotic components. For instance, the top of the tree may have been split early on from a violent windstorm creating two parallel treetops. Its branches are home to squirrels, and birds, each altering the trunk to create homes. The bark and wood is home to many insects, and woodpeckers have drilled countless holes into the trunk foraging for food. Its roots are exposed near the base, the soil scuffed away, as its trunk was used as a resting place for various dogs, deer, or children playing games. The branches are short on one side, where another spruce had grown more quickly taking up space, light and nutrients, but on the other side, long branches extend outward shading a birdbath placed there many years ago. I could continue, but the point is that the present form of the tree “embodies the entire

history of its development” (Ingold 2000:204). The tree is bound up with the lives of the people that were/are a part of its environment, just as those people’s lives are bound up in the life of the tree (Ingold 2000: 204).

1.3.4 Developing Subsistence Practices

“As hunters and gatherers have explained ... it is essential to ‘look after’ or care for the land, to maintain in good order the relationships it embodies; only then can the land, reciprocally, continue to grow and nurture those who dwell therein” (Ingold 2000:149).

This quote captures the essence of my theoretical perspective, which presents a more integrated way for understanding the relationship cultural groups had with plants. In particular, how did people-plant relationships manifest themselves in the daily physical activities required for people to acknowledge, locate, care for/ harvest plant populations necessary for survival? Is there evidence of these interactions in the archaeological record? To understand these integral relationships it is necessary to understand and explore the interconnectedness between the biological and sociocultural processes that shape them.

The complex web of interactions (i.e. Ingold’s (2000) ‘field of relations’) is visualized in Figure 1.2. This diagram is meant to remind readers of the many and varied factors that could influence human –plant interactions. The list of factors included in the diagram is not exhaustive. The eight nodes identify some of the main factors in the development of people-plant relationships. The lines represent interactions between two nodes, the thickness of the line measures interaction strength. Specific interactions between people and plants used for food initiate intended actions and unintended consequences (cf. Chase 1989), thus creating multiple interaction lines between the wide

variety of factors that affect conditions for growth for both plants and people (Figure 1.2). While all components of an organism's environment are interconnected, the strength of these connections fluctuates over time, and varies with organisms (e.g. plant species and cultural groups) and their environment.

In his visualization of people - plant relationships, Ford (1985) focused on increased direct human involvement (control) in a plant's lifecycle as the main factor influencing plant phenotypes (compare Figure 1.1, x- axis to Figure 1.2, red interaction line). For example, human management of cacti in wild populations increased the frequency of desired fruits (i.e. those with larger, sweet fruits with non-red flesh and thin rinds) by weeding, and discouraging unwanted phenotypes in wild populations (Casas *et al.* 1999). Non-managed wild populations contained low quantities of the desired fruit phenotype with a high proportion of small fruits with low amounts of flesh and thicker rinds (Casas *et al.* 1999).

In reality, these types of studies gloss over the numerous interactions that can contribute to a cascade of effects that ultimately led to the morphological and genetic changes associated with cultivated or domesticated plants (cf. Pickersgill 2007). Phenotypic plasticity may have allowed some plants to take advantage of variation in their environment. The phenotype produced by a plant taking advantage of such an opportunity might be advantageous also from a human perspective and, if heritable, could be selected (indicated by thicker lines between these factors in the network, Figure 1.2).

Recent research on the evolution of teosinte into maize showed that maize-like inflorescence architecture and seed maturation phenotypes were initially generated as plastic responses to environmental stressors (Piperno *et al.* 2014). The domestication of

teosinte into maize probably began during the Holocene transition where CO₂ levels were lower than today (see Piperno *et al.* 2014 for details). Extant teosinte grown in replicated Holocene conditions (lower CO₂ levels) produced plants with female flowers on short lateral branches and a single male tassel at the terminal apex of the plant, much like maize. Seed maturation and fruit architecture was also maize-like (see Piperno *et al.* 2014 for details). Seed collected from these plants and grown the following year produced some offspring with the same inflorescence phenotype (Piperno *et al.* 2014), suggesting Holocene forager-cultivators could have maintained the new phenotype by replanting seeds. This experiment provides evidence for an environmentally induced plastic response (maize-like flower and fruit phenotypes) that altered the selective environment of its fruits. The maize-like fruit phenotypes could have been taken advantage of by human populations in the early Holocene. Early Holocene populations could have collected and replanted seed from maize-like plants maintaining a higher frequency of the favoured phenotype in local populations (Piperno *et al.* 2014).

The above research shows the value of using biological experiments on extant populations to explore archaeological questions. Investigating the interactions between plants and habitat components (e.g. soil, climate, human activities) has the potential to illuminate key aspects about the utility of plant phenotypes relating to food sources for people (e.g. inflorescence architecture, fruits/ seeds). Further, combining variation in archaeobotanical assemblages with knowledge of plant-habitat interactions can provide a better understanding of how pre-contact people made their living.

1.4 Creating opportunities and mitigating constraints: Subsistence strategies in southern Manitoba during the Late Woodland (ca. AD1000-1500)

Late Woodland archaeological research suggests Manitoba contained cultural groups of highly diverse social and cultural backgrounds (Nicholson *et al.* 2011; Hamilton *et al.* 2011; Syms 2015). Research addressing pre-contact subsistence strategies is further complicated by potential migration, diffusion of ideas and technology, and fluid group membership (Hamilton and Nicholson 2006). Previous research indicated cultural groups living across southern Manitoba employed mixed subsistence economies based on hunting and gathering local wild species, as well as modest consumption of domesticated crops (e.g. maize, beans, squash) obtained through trade (Deck and Shay 1992; Quaternary 2010; Boyd *et al.* 2006, 2008, 2014; Boyd and Surette 2010; Syms and Beckwith 2010). (See Chapter 2 for a review of the variation in archaeological subsistence strategies employed across southern Manitoba.)

At issue here is whether Late Woodland groups in southern Manitoba's Red River Valley applied ideas about cultivation practices and/or domestication to edible wild plant populations. Cultivation of native domesticated plants (e.g. chenopods, marshelder, amaranths, dock/knotweeds) was an important subsistence strategy employed by Woodland (1000BC- AD1000) groups in the Eastern Woodland region of North Eastern North America (Smith 2007; Gremillion 1993). Using a developmental perspective, I hypothesize that archaeological cultural groups in the Red River Valley may have cultivated local plant populations to ensure a stable food resource, consistent with earlier processes in the Eastern Woodlands. This strategy may have resulted in intermediate seed phenotypes that would exhibit traits between wild and domesticated morphologies.

My thesis focuses on the relationship between archaeological cultural groups and local native net-seed goosefoot (*Chenopodium berlandieri*) populations as expressed at two archaeological sites, the Forks (DILg-33:08A) and the Lockport (EaLf-1) sites in the Red River Valley (Chapter 6). These people-plant relationships are addressed by exploring phenotypic and genetic components of extant *C. berlandieri* populations to determine plant and seed phenotypes associated with low-level cultivation techniques (Chapters 3-5). Seed phenotypes are then compared to archaeobotanical remains collected from secure culturally affiliated contexts (e.g. sealed hearth or storage pit features).

Chenopodium seeds are ubiquitous in Manitoba archaeobotanical assemblages, and are thought to reflect relationships that existed between *Chenopodium* and cultural groups at the Forks and Lockport sites. Surprisingly, basic biological attributes of local populations are unknown. How local cultural groups may have interacted with these populations is also unexplored. The biological and cultural aspects I describe in the remaining paragraphs form the basis of the mid-level hypotheses developed throughout my thesis.

One foundational component is determining the frequency and size of local *Chenopodium berlandieri* populations. These data have not been compared to similar data from the Eastern Woodlands or adjacent North Dakota where *C. berlandieri* was an important resource. I examine these data in Chapter 3. *Chenopodium* species are an ethnographically known food source for many archaeological cultures and historic aboriginal groups (Arnason *et al.* 1981; Moerman 2010). However, local *C. berlandieri* populations have never been tested for nutritional value or for economic potential (e.g.

harvest yield). I explore both of these aspects in Chapter 4. Previous research on archaeological domesticated *Chenopodium* seeds (Smith 1985; Gremillion 1993) established a benchmark (e.g. testa thickness and seed size) for one extreme on the continuum of plant form and human activities, however, measurement of the wild seed phenotype, the variation in wild phenotypes, or their relationship to the domestication process had never been confirmed (see Chapter 5).

Extant goosefoot populations have been located along the Red River Valley, a known travel route into Manitoba used during pre-contact times. I examine local extant *C. berlandieri* populations to understand how plants interact with their environment, identifying some of the opportunities and constraints pre-contact peoples may have encountered interacting with this species (see Chapters 3-5). Re-examining archaeobotanical data with new insights gained from biological experiments with local plant populations, will illuminate the numerous biological and cultural components necessary to generate people-plant relationships (Chapters 6, 7).

Tables and Figures

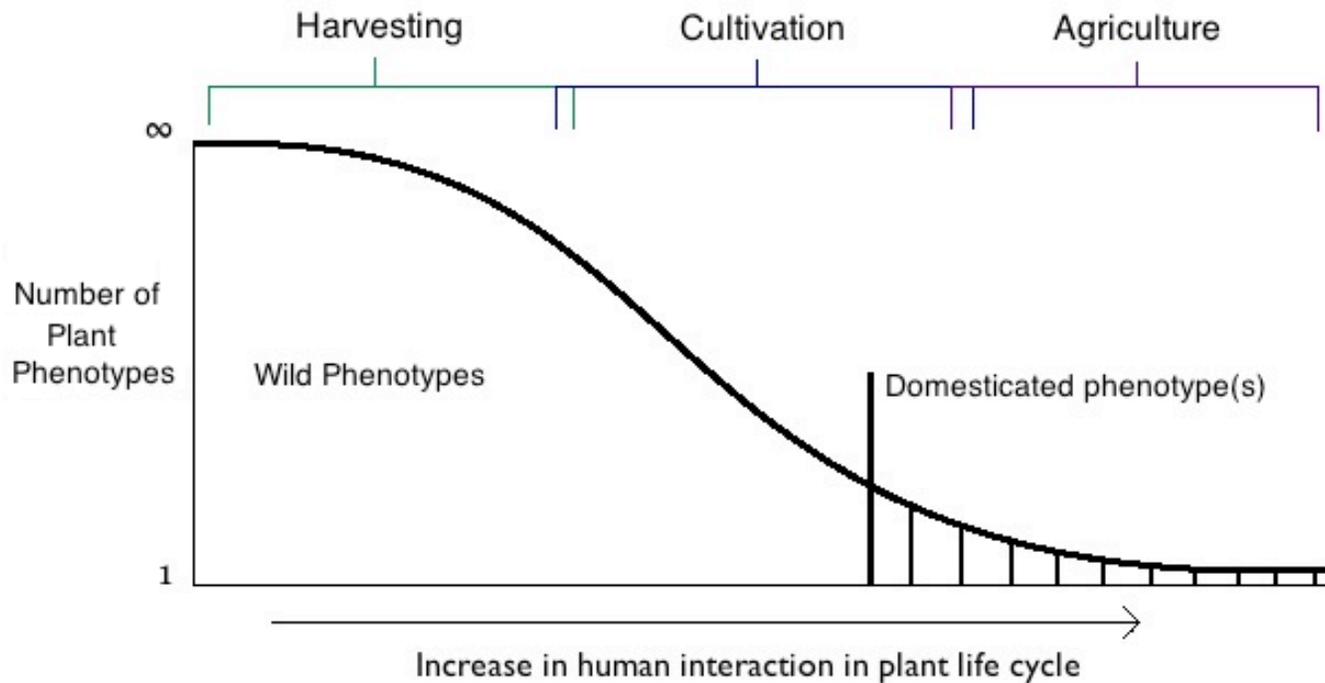


Figure 1.1. Continuum of Plant Forms and Human Activities: Subsistence patterns are shown at the top of the image while the associated plant phenotypes are listed underneath. There is a continuum of subsistence patterns and associated plant forms ranging from gathering wild plant phenotypes to field agriculture of fully domesticated phenotypes. Movement between subsistence patterns and plant phenotypes is commensurate with type and intensity of human interaction (Image adapted from Ford 1985).

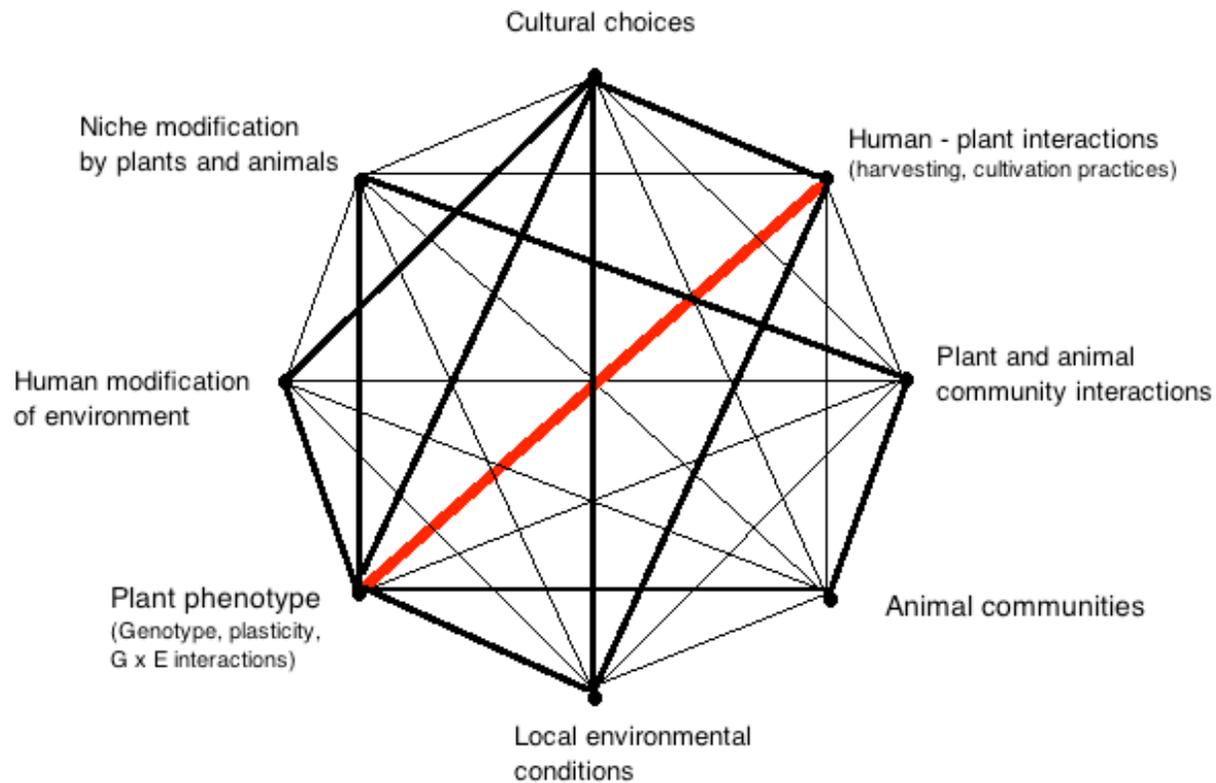


Figure 1.2: Variation in people-plant relationships visualized as a complex web of interactions. Lines represent interactions between components. Thick lines indicate important or highly developed interactions between components while thin lines indicate less intense interactions between components. Ford's (1985) emphasized direct people – plant phenotype interactions (red line, compare to Figure 1.1, x-axis) as more important for altering selective forces on plant phenotypes resulting in a change in morphology or genetic structure.

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2. PRE-CONTACT SUBSISTENCE ECONOMIES IN SOUTHERN MANITOBA: MIXED FOOD PROCUREMENT AND PRODUCTION STRATEGIES

2.1 Introduction

The Late Woodland Period¹ (AD1000-1500) archaeology of southern Manitoba is complex, due in large part, to the topographic and ecological diversity of the region, and the access to resources by various cultural groups. Southern Manitoba is located at the northern edge of the Northeastern Prairies (the most eastern edge of the Great Plains) (Figure 3.1, pg. 131), characterized by broad topographical features and ecological zones that reflect glaciation and postglacial histories (Welsted *et al.* 1997:10). The drainage of glacial Lake Agassiz created lowlands bordered to the east by the Canadian Shield, and the Manitoba Escarpment to the west. These deep clay and silt deposits support prairie grass habitats that grade from tall grass communities in the Red River Valley to mixed grass communities to the west. While northern coniferous forest dominates southeastern Manitoba, and mixed grass Prairie and Aspen Parkland dominates southwestern Manitoba (Welsted *et al.* 1997), numerous rivers, lakes, marshes, and wetlands bisect all ecoregions creating a mosaic of habitats (Smith *et al.* 1998) (Figure 2.1). The intermixing of prairie, deciduous forest, northern coniferous forest and transitional zones provides a wealth of plant and animal species exploited by various cultural groups residing in southern Manitoba or utilizing it to practice all or part of their subsistence economy (Syms 1977; Flynn 2002).

Subsistence economies developed through time as people interacted with the varied abiotic and biotic components of their environments (see Chapter 1; Ingold 2000). Daily

¹ Late Woodland Period used in this chapter is synonymous with the terms Terminal Woodland or Late Pre-contact period used by other researchers.

engagement with local plant and animal communities generated important relationships between people and suites of plants and animals. Interacting with plants at all stages of their lifecycles led to an intimate knowledge of patterns of growth in specific taxa. Experimentation and innovation with different plant species would have allowed new plant species to be incorporated into a subsistence economy (Hastorf 2007). Cultural interactions altered or augmented these relationships through trade or intermarriage (Adair 2004, cited in Ahler 2007; Turner 2005).

Based on general patterns established in adjacent regions, subsistence economies in Manitoba were initially described as one of three general strategies. In a generalized woodland strategy, subsistence was focused on hunting terrestrial mammals, fishing and collecting shellfish, and harvesting local plant taxa (e.g. Buchner 1982; Meyer and Hamilton 1994); Plains bison specialization focused on nearly year-round exploitation of a very narrow range of species (Nicholson 1996:71; Peck 2011); and during the Late Woodland period small-scale maize horticulture associated with Eastern Woodlands and/or Middle Missouri cultural groups was identified (e.g. Gregg 1994; Gibbon 1994). Groups that employed mixed subsistence strategies, combining small-scale maize cultivation with hunting and harvesting local native species were originally identified at Lockport East and West sites (EaLf-1, EaLf-2, respectively) on the Red River, north of Winnipeg (Deck and Shay 1992; McKinley 2001; Flynn 2002). More recently mixed subsistence strategies were identified at sites south of Brandon, Manitoba (Nicholson *et al.* 2011), and at the Forks site (DILg-33:08A), located where the Assiniboine and Red Rivers join in Winnipeg (Quaternary 2010; Lamontagne 2014). This model implies some

degree of commitment to more than one resource strategy, but some flexibility of resource harvest probably occurred (Scott Hamilton pers. comm. 2016).

In the last decade ceramic residue studies (e.g. pollen, phytoliths) have illuminated the wide dispersal and consumption of domesticated crops and a variety of locally harvested or cultivated plant taxa in the diets of many cultural groups living in the Prairie/Parkland and Boreal forest regions of southern Manitoba (Boyd *et al.* 2006b, 2008; Boyd and Surette 2010). This microbotanical evidence is associated with the pottery produced by cultural groups that have not yielded macroscopic (e.g. seeds, tools) evidence of plant consumption (Scott Hamilton pers. comm. 2016). This likely reflects the inadequacy of excavation and analysis methodologies to investigate mixed subsistence practices (Scott Hamilton pers. comm. 2016).

Evidence of mixed subsistence practices in southern Manitoba is also consistent with the growing body of archaeobotanical work conducted in the Great Plains region (Adair 1988, 2003). Syntheses compiled throughout the Plains suggested cultural groups employed a wide variety of subsistence practices including cultivating local plant species (e.g. *Chenopodium*, see Adair 2003: 262). Recovery of microbotanical evidence of mixed subsistence practices (e.g. Boyd *et al.* 2014; Lints 2012) suggests cultural groups in southern Manitoba may have employed a similar range of cultivation techniques, from harvesting and/or cultivating local native plant species, to large scale maize agriculture (Syms *et al.* 2012). This indicates that the sharp binary distinction between hunter-gatherer and farmers is not appropriate (cf. Smith 2001).

2.2 Objectives

From a developmental perspective, subsistence economies developed through cultural groups interacting with various components of their environment. This chapter reviews aspects of habitat composition and cultural interactions to understand the diversity of subsistence practices employed by various cultural groups in southern Manitoba during the Late Woodland Period. This chapter is not exhaustive in description of plant communities, archaeological sites, or recovered materials. Rather, the variation in subsistence strategies represented across southern Manitoba during the Late Woodland period is examined to ask whether some cultural groups in the Red River Valley (e.g. The Lockport East (EaLf-1) and Forks (DILg-33:08A) sites) may have cultivated local wild plant populations as part of their subsistence economy. Sites in the Red River Valley were selected as a case study because they are large stratified sites, contain good depositional integrity, and previous research employed excavation and sampling methodologies to determine subsistence practices within and between levels (Deck and Shay 1992; Flynn 2002; Quaternary 2010).

To this end I first present a summary of the ecological diversity spanning southern Manitoba because many of the pre-contact peoples living there moved across the overlapping ecoregions (Figure 2.1) as part of their annual or seasonal subsistence economies (Syms 1977). Following this, I divide cultural ecology section into southeastern Manitoba, southwestern Manitoba, and the Red River Valley sub-regions as an organizational tool to address this complexity. This in no way implies clear concise 'boxes' in which to place either habitats or cultural groups. There are gradations and 'grey zones' between and within habitats and human communities that provide the variation in cultural and subsistence practices that is the focus of this thesis.

2.3 Ecological Diversity

Despite southern Manitoba being characterized as Prairie, Parkland or Boreal (Figure 2.1), resources in the ecoregions tend to be spatially and temporally (e.g. seasonally, annually) varied, creating a heterogeneous landscape of biodiversity and resource richness dispersed throughout the region (Boyd *et al.* 2006a: 235; Nicholson and Wiseman 2006:231). This varied nature is attributable, in large part, to combinations of climate, landforms, hydrology, underlying geology and soils (Shay 1980; Corkery 1997; Scott 1997). Recent palaeoenvironmental reconstruction studies (e.g. Strong and Hills 2005) support previous palynological work conducted at Lake Manitoba (Teller and Last 1981) and southeastern Manitoba (Richie 1983, cited by Shay *et al.* 1990:76), suggesting that ecoregions have not appreciably changed in the past 1500 years. This suggests that modern community composition and distribution around the Red and Assiniboine River Valleys and adjacent areas broadly resemble pre-contact plant communities (Nicholson *et al.* 2006a: 340; Shay *et al.* 1990:76)). A large caveat to this assumption is acknowledging annual and short-term alterations (e.g. decades) to local habitat composition. Annual climactic conditions interacting with processes of erosion and deposition (e.g. annual river bank flooding) would have created variation in environments pre-contact groups would have encountered.

Most vegetation and climactic reconstructions are based on ethnographic, ethnohistoric, ethnobotanical and historic documentation including 18th and 19th century maps (e.g. Hind's 1858 Red River Settlement map, cited Shay *et al.* 1990) and the Dominion Land Survey sheets (Boyd *et al.* 2006a; Hamilton and Nicholson 1999). A few

ethnobotanical studies were compiled for the Boreal forest (e.g. Marles *et al.* 2000), Prairie/Parkland (e.g. Erichsen-Brown 1969; Johnson *et al.* 1995) and Plains regions (Kindscher 1987, 1992; Wilson [1906] 2014; Zedeno *et al.* 2010). While broad ecological reconstructions indicate the general diversity, it is important to note that ethnographic studies emphasize localized plant resource exploitation within a set distance from the campsite, and ethnobotanical studies emphasize the vast array of important and used plant species from various habitats (Shay 1980:244). Recent discussions combine ecological diversity with pre-contact plant use to characterize habitats within local regions to gain a more accurate inference of exploitable plant resources (Shay 1980; Boyd *et al.* 2006a). For instance, ecological reconstructions combined with local landscape studies define small-scale habitats in the Prairie/Parkland (Nicholson and Wiseman 2006; Nicholson *et al.* 2006a; Hamilton and Nicholson 2006; Boyd *et al.* 2006a), the Red River Valley (e.g. Shay 1980; Shay *et al.* 1990), and the Winnipeg River area (e.g. Syms 2015; Ens 1998).

Habitat descriptions tend to get laden with Latin taxonomic designations can be quite difficult to read. A table of all plant species located in each of the sub-regions with common and Latin names appears in Appendix 2.1. Plant species recovered from archaeological sites appear in Appendix 2.2. Only common names will be cited in the text.

2.3.1 Major ecozones of southern Manitoba

Southern Manitoba can be divided into three main sub-regions: southeastern, southwestern and the Red River Valley, each region dominated by one or two major habitat types. Southeastern Manitoba is dominated by the Boreal Shield ecozone that dips southward along the eastern edge of Lake Winnipeg extending south into the United States and east into northwestern Ontario (Figure 2.2) (Smith *et al.* 1998). The Boreal shield is divided into the Lake Seul Uplands and Lake of the Woods ecoregions (Figure 2.1) (Smith *et al.* 1998). The dominant vegetation is northern coniferous forest that grades into deciduous forests of the Great Lakes- St. Lawrence (Corkery 1997).

Southwestern Manitoba falls within the Prairie Ecozone (Figure 2.2) subdivided into Southwestern Manitoba Uplands, Aspen Parkland and Lake Manitoba Plain ecoregions (Figure 2.1) (Smith *et al.* 1998). This region is described as transitional grassland ecoclimatic zone composed of mixed and short grass prairie, aspen parkland and remnant tall grass prairie sub-regions (Scott 1997).

The Red River meanders through the Red River Plain, which encompasses the most southeastern portion of the Lake Manitoba Plain (Figure 2.1) (Smith *et al.* 1998). Currently, thin strips of aspen parkland and transitional prairie/ boreal forest extend between the Red River Plain and the Lake of the Woods ecoregion to the east (Smith *et al.* 1998). Prior to European settlement, Aspen Parkland and mixed prairie grasses (e.g. fescues) stretched from the Manitoba Escarpment to the Red River Plain, supporting Tall Grass Prairie that extended from the Dakotas creating continuity with diverse habitats (Smith *et al.* 1998; Scott 1997).

While a major habitat type can characterize a region, pockets of these habitats can be found in other ecoregions. For example, northern coniferous forest dominates

southeastern Manitoba, but pockets of coniferous forest are found in the Prairie/Parkland of southwestern Manitoba. The diverse ecozones support six primary habitats: northern coniferous forest, deciduous forests of the Great Lakes- St. Lawrence, Aspen Parkland, Tall Grass prairie, Mixed Grass prairie and forest-grassland transitions that include riverine forests. Localized physiography, soil, climate, hydrology and vegetation create secondary pockets of diversity including wetlands, marshes, bogs and fens, and sand dunes that segment major habitats. While these habitats are not static, but are composed of dynamic plant and animal communities, animal populations traverse habitat boundaries unlike plants. The focus of this section is to describe the primary and secondary habitat types highlighting the floral diversity within them. A short discussion on the importance of natural and anthropogenic disturbance to local diversity will be offered. Following this the major animal species found across southern Manitoba will be briefly covered.

2.3.2 Primary and secondary habitats

Northern coniferous forests are thought to be dense, closed forests dominated by black spruce, tamarack, mosses and sedges. However only poorly drained lowland areas, moderate or rich in nutrients, are dominated by black spruce and tamarack with understories of sedge, willow, and alder (Scott 1997). Upland areas are dominated by jack pine and white spruce, with well-drained lowlands covered in aspen with an understory of hazel, feather mosses and lichens (Scott 1997; Marles *et al.* 2000). Labrador tea and blueberry tend to dominate forest clearing and margins (Marles *et al.* 2000).

Highly localized variability in ecological conditions has been noted throughout this sub-region (e.g. Saylor 1989). For example, the local ecology surrounding the Wanipigow site (EgKx-1) located on Wanipigow Lake (Figure 2.2), includes rocky barren outcrops that drop significantly into low marshy spaces, giving the area an extreme rolling terrain. Upland areas are covered in oak, poplar, aspen, birch and sumac with understories of alder, willow, hazelnut shrubs, grasses and forbs (e.g. wild rose, strawberry) (Saylor 1989; Zoltai 1989). In some south-facing areas, open shallow soils over a bedrock substrate support large prickly-pear cactus populations (Zoltai 1989:69).

Pockets of boreal forest can be found throughout southern Manitoba. For instance, forest groves dominated by white spruce with typical understory species (e.g. bunchberry and twin flower), occur within the Spruce Woods Natural area in the Aspen Parkland of southwestern Manitoba (Scott 1997).

The Lake of the Woods ecoregion contains deciduous forests of the Great Lakes-St. Lawrence dominated by a mixed deciduous and coniferous forest of jack pine, white spruce, black spruce and tamarack, with patches of white cedar in northern areas (Corkery 1997; Smith *et al.* 1998). In the southeastern corner of the province, a broad-leaf deciduous forest habitat is composed of typical boreal species mixed with red pine (Scott 1997). Upland well-drained areas support mixed forests of aspen, balsam poplar, white spruce, burr oak, balsam fir, white birch. Deciduous species increase in abundance to the south and west becoming prominent along the boreal-prairie transition (Scott 1997).

Aspen Parkland is dominated by aspen and balsam poplar, and contains bur oak on elevated ridges. The understory contains various edible berry producing species

including, chokecherry, Saskatoon, red-osier dogwood, gooseberry, sunflower and strawberry. Most of these species were harvested for their fruits or seeds and were important food resources and contained medicinal qualities used to maintain and promote health (Moerman 2010). Aspen Parkland is currently expanding into the Prairie zone, likely due to fire suppression and lack of bison, and is evidenced by an increase in aspen with an understory composed of mainly grass species (Boyd *et al.* 2006a: 240; Scott 1997). In addition, small aspen and balsam poplar groves can be found along the eastern edge of the boreal forest (Scott 1997).

Grassland areas are remnants of once extensive tall and mixed grass and forb prairie. Tall Grass Prairie composed of big blue stem, switch grass, and other grasses and forbs, once dominated the Red River Plain covering more than 6000 km (Reaume 1993). Due to major post-contact agricultural disturbances, wetland drainage, fire suppression, and anthropogenic factors associated with the growth of the city of Winnipeg, less than 1% (2000ha) remains protected in the Tall Grass Prairie Preserve near Tolstoi, Manitoba (Reaume 1993; Shay *et al.* 1990).

Numerous native mesic and short grass species (e.g. needle-and-thread grass, northern wheat grass, blue grama, June grass, little blue stem, sand grass, and sand bluestem) once dominated open rolling hills between aspen groves, riverine gallery forests and oak savanna (Boyd *et al.* 2006a: 243; Nicholson *et al.* 2006a: 338). Forbs include giant ragweed, wild rose, and horsetail; sedges are found in moister areas (Boyd *et al.* 2006a; Scott 1997). Well-drained upland areas contained prairie turnip that was harvested by Plains groups for its starchy root, and was dried and pounded into flour (Kindscher 1987; Kaye and Moodie 1978). Yarrow, found in prairies, meadows, and

open woods was harvested for its flowers and leaves that were dried and steeped for a tea to treat coughing and throat irritations (Kindscher 1992). Yarrow is still dried and sold in health food stores as an herbal tea.

Forest-grassland transitions contain bio-diverse ecological communities (Boyd *et al.* 2006a), as transition zones reflect species composition and community structure similar to forest and grassland habitats, plus unique species characteristic of inter-habitat spaces (Turner *et al.* 2003). Usually berry and nut producing species, such as beaked hazelnut, saskatoon, and chokecherry, grow in these transition areas. These species tend to produce more or higher quality berries, nuts, or other important plant parts compared to old growth stands making these usually narrow zones resource rich and key for harvesting foods and medicines (Turner *et al.* 2003: 440).

Riverine forests bisect all areas of southern Manitoba. Narrow gallery forests found along small rivers and tributaries throughout the Prairie/Parkland are composed of cottonwood, Manitoba maple, green ash, elm, basswood, and willow, plus similar berry and nut producing species (Scott 1997). Along the Assiniboine River, broad leaf forest groves grow on stabilized sand dunes (Scott 1997). Willow, dogwood and alder would have dominated bank edges (Shay *et al.* 1990).

The transition from riverine forests to upland Prairie/Parkland habitats are very rich in edible species including wild cherry, raspberry, false Solomon's Seal, dogwood, gooseberry, snowberry, and grape. Well drained upland forest along the Red River contain oak and aspen with an understory of dogwood and poison ivy shrubs, Virginia creeper, wild hops, and wild grape vines (Shay *et al.* 1990:62, 67). Many herbaceous understory species produced edible seeds including goosefoot, knotweed, and marshelder.

Wood nettle, goldenrod, cinquefoil and ostrich fern were utilized for their stems and leaves. Hazelnuts and sap from the Manitoba maple were also collected (Shay 1980; Marles *et al.* 2000). Many named species also have medicinal uses; for example, cinquefoil roots were used to treat aches, and goldenrod stems and leaves were used to treat kidney and bladder problems (Marles *et al.* 2000).

The current widespread distribution of some common species, such as Manitoba maple, is likely influenced by its ability to rapid grow on disturbed, moist soils and tolerant drought and freezing conditions (Department of Forestry 1963: 258). The elm population, in comparison, has been decimated over the last half century by the Dutch Elm beetle (Nicholson *et al.* 2006b: 328), reducing its distribution and frequency remarkably.

Wetlands and marshes that formed in potholes, lake deltas, lagoons, inter-dunal and lacustrine areas were much more wide spread in the pre-contact period (Boyd *et al.* 2006a: 241). Areas of permanent or semi-permanent lowland marshes were once prevalent extending outward from riverbanks (Shay *et al.* 1990). Wetlands provide surface water sources for animals and humans (Scott 1997). Reeds, cattails, bulrushes, marsh marigold, arrow leaved colt's foot and sedges dominated mineral rich soils. Fowl-meadow grass, reed grass, white top grass, and sedges covered less saturated soils, while aspen and willow dominated wetland fringes (Scott 1997; Boyd *et al.* 2006a). Many of these species were utilized for food and/or medicine. For example cat-tail rhizomes and the inner stem can be eaten fresh in the spring (author's note: inner stems taste faintly like broccoli stems), the mature rhizomes can be cooked like potatoes or dried and pounded into a flour; the mature fluffy seed heads can be dried and used as poultices for burns

(Marles *et al.* 2000: 297). Dried cattail fluff also makes an excellent long lasting wick for oil lamps (K. Brownlee pers. comm. 2011). Common reed stems could be eaten as young spring shoots, while the mature stalks were woven into basketry (Marles *et al.* 2000: 294). Wild onion was found in wet meadows, along banks and shorelines. Their bulbs were boiled to form a syrup to treat coughs and colds. Crushing the plant and soaking it in water created a juice that was antiseptic and sphagnum moss soaked in it was applied to wounds (Johnson *et al.* 1995).

Marshes developed along the southeastern end of Lake Wanipigow, where a number of tributary creeks joined the lake allowing native rice² populations to develop along the southeastern lake edge and along the Wanipigow River (Saylor 1989:5). Native rice was an important food source for many modern, historic and pre-contact Aboriginal communities (Syms 2015).

Fens and bogs, found in low-lying areas in the Boreal shield, also bisect the sandy moraine hills in the southeastern corner of the province and occur in remnant boreal pockets in the Spruce Woods Natural area (Scott 1997). Fens support tamarack, swamp birch, alder, willow, pitcher plants, sundew, sedges and brown mosses, while black spruce, ericaceous shrubs and mosses dominate bogs (Scott 1997; Smith *et al.* 1998).

Sandhills include stabilized and active sand dunes formed from post-glacial deposition and reworked by wind, which created a series of parabolic dunes (Scott 1997). Most dunes are well drained, containing modest surface water resources, although some are underlain by aquifers, which create shallow wetlands surrounded by forest groves protected by sand dunes (Scott Hamilton pers. comm. 2016). Stabilized dunes

² Following Syms (2015) native rice is preferred to wild rice as millennia of harvesting and deliberate planting identifies *Zizania* sp. as domesticated plants.

are covered in forest or mesic/xeric vegetation. Bur oak stands are located on northern dune slopes and interspersed with aspen, numerous grass species, creeping juniper, pincushion cactus, and prickly pear. Other sand habitat (xeric) adapted species including narrow-leaved goosefoot, sand dock, and showy goldenrod are present on more open dunes and likely play an important role in initial dune stabilization (Boyd *et al.* 2006a: 241).

2.3.3 The importance of disturbance

During the middle to late Holocene (7000-500 years ago) vegetation zones stabilized (Brandt *et al.* 2013), resulting in mosaics of forest stands and undergrowth plant communities (Johnson *et al.* 1995). This resulted in heterogeneity across all ecoregions. Heterogeneity is maintained by anthropogenic and natural causes. Fire is a major contributor to the heterogeneous nature of vegetation communities by maintaining successional community stages and promoting fire adapted species, e.g. jack pine (Scott 1997). Pre-contact cultural groups are now known to have maintained and increased diversity in localized areas through deliberate fire regimes (Boyd 2002). For instance, historic accounts by European fur traders of the Anishinaabe people living on Shoal Lake, Ontario in the Rainy River region (Davidson-Hunt 2003) indicate the rich landscape reflected the land management skills of the ancestral Anishinaabe people (Davidson-Hunt 2003:26). The Anishinaabe used prescribed burning techniques (twice annually- spring and fall) to extend the Tall Grass Prairie and maintain open meadows to feed bison and deer herds. Fire regimes were employed in southwestern Manitoba by various pre-contact groups to maintain bison herds (Boyd 2002; Boyd *et al.* 2006a).

Ancestral Anishinaabe people also used elaborate firing to alter southern riparian forest composition, increasing birch, aspen, sugar maple, hazelnut, and berry stands harvested for foods (e.g. maple sugar, hazel nuts, raspberries) and construction materials, e.g. birch bark for canoes (Davidson-Hunt 2003: 26-27).

2.3.4 Animal communities across the southern Manitoba

A wide range of terrestrial and aquatic mammals, birds, fish, reptiles and amphibians are present throughout southern Manitoba that would have been available to pre-contact cultural groups. Distribution and population sizes vary within different ecoregions and at different times (e.g. seasonally, annually). Use of animal species would have been differential based on pre-contact cultural choices, and local population dynamics.

Large ungulates, and other medium to large mammals many cultural groups hunted for meat or fur include bison, moose, caribou, elk, white tailed deer, black bear, wolf, coyote, fox, lynx, wolverine, marten, porcupine, beaver, muskrat, otter, rabbit and hare (Scott 1997). Plains grizzly, cougars, pronghorn antelope, red fox, swift fox, would have been more prevalent in southwestern Manitoba (Nicholson *et al.* 2006a).

Migrant waterfowl would have been abundant. Ducks, geese, loons, pelican, crane, cormorant, and herons would have been present in the wetlands, lakes and rivers. Upland game birds, including sharp tailed grouse and ruffed grouse, were present and are occasionally recovered from archaeological contexts (Nicholson *et al.* 2006a: 338; Playford and Nicholson 2006:411). Hawks, owls, and other raptors, plus various small perching birds were also available and differentially exploited.

Additionally, turtles, frogs, and various mollusks are available (Ens 1998; Scott 1997; Syms 2015). Numerous fish species and freshwater mussels were relied on by cultural groups in southeastern Manitoba and the Red River Valley (Kroker 1993; Syms 2015). While many of the same species were available in the Prairie/Parkland region, it appears cultural groups did not exploit them to any great extent (Nicholson *et al.* 2006a: 338).

Overall, inter-regional similarities would provide familiarity to cultural groups migrating into new areas of southern Manitoba. Intra-regional environment studies indicate great diversity of localized habitats, replete with numerous plant and animal species that would have provided food, medicine, clothing, construction materials and fuel. Localized habitats would have been known and exploited by cultural groups.

2.4 Pre-contact Cultural Diversity: Late Woodland Archaeological Record

The following discussion synthesizes the current understanding of pre-contact history focusing on subsistence economies employed by various cultural complexes across southern Manitoba during the Late Woodland Period (AD800-1500), drawing on the Early/Middle Woodland (2000BC – AD800) where necessary. Various classification systems have been devised to describe and define social groups in the archaeological record (e.g. Midwestern Taxonomic system, McKern 1939 cited in Norris 2012; Culture-history integration, Willey and Phillips 1958, cited in Norris 2102). While these definitions have inherent problems (Meyer *et al.* 2008: 45), complexes are reported as described by the primary authors in the literature. A complex, or archaeological culture denotes the total expression of a group of archaeological sites in a common time frame

(Toom 2004). These groups evidence a shared lifestyle including subsistence and settlement strategies and an overall toolkit (e.g. stone tool, ceramics), reflecting homogeneity within the complex (Syms 1977).

Archaeology and archaeobotanical research in southern Manitoba have not been conducted evenly across the region. Therefore the information compiled on subsistence will necessarily be uneven, with more data available from sub-regions where more recent work has been conducted. For instance, recent archaeological work in the southwestern region (Nicholson and Hamilton 2006), the Forks Site (Quaternary 2010) and Healing Site (Deck and Ward 2007) in the Red River Valley, and the Rivermouth Site (Syms 2015) in southeastern Manitoba provide updated summaries of subsistence patterns in these areas. Recent residue analyses on select ceramic and lithic artifacts from specific sites across the province investigated the incorporation of domesticated crops into local diets (Boyd *et al.* 2006, 2008; Boyd and Surette 2010; Quaternary 2010; Lints 2012; Boyd *et al.* 2014).

There is also a blurring of formal distinctions between cultural groups who practiced different subsistence economies, suggesting a mixture of population migration, diffusion of ideas and technologies, fluid group membership, and ‘hybrid’ group formation (Hamilton and Nicholson 2006:257). Thus identifying and studying variation in subsistence practices is necessary to elucidate pre-contact community dynamics.

2.4.1 Southeastern Manitoba

Southeastern Manitoba is characterized by rivers and lakes used for the transport and transmission of people, ideas and goods (Steinbring 1980). After its initial deglaciation, people moved into the region along the Winnipeg River and its tributaries, moving into the interior drainage system over time (Steinbring 1980). While numerous sites have been located, surveyed and/or excavated (Figure 2.2 contains some of these sites), only a small portion has been analyzed with published accounts (e.g. Buchner 1980; Steinbring 1980; Deck *et al.* 1999; Syms 2015). Few sites have been specifically sampled for the recovery of plant remains (see Figure 2.2 for sites discussed in this chapter) (Deck *et al.* 1999; Syms 2015). Some studies have conducted residue analyses on selected ceramic sherds and lithic tools to investigate plant use (Boyd and Surette 2010; Boyd *et al.* 2014; Lints 2012). Despite the paucity of deliberate archaeobotanical research in southeastern Manitoba, the available information suggests some cultural groups relied on local native plant and animal resources, while other groups had mixed subsistence economies, incorporating domesticated maize, beans, and native rice. Many groups would have traded for domesticated crops, while some groups may have locally cultivated domesticated crops at sites where the micro habitat would have been suitable (Scott Hamilton pers. comm. 2016). Cultural groups appear to have participated in and maintained long-distance trade routes as early as the Middle Woodland.

Subsistence strategies that flourished in the Late Woodland period were developing during the preceding Middle Woodland (700BC – AD1000) period. The Laurel culture represents the best-known Middle Woodland Period occupation in southeastern Manitoba, extending from 100BC- AD800 (Stoltman 1973) and with some localized persistence to AD1000 (Meyer *et al.* 2008; Syms 2015). Laurel culture is

generally regarded as an *in situ* development from the existing Archaic cultures in the boreal forest of western Canada with ceramic influences from pottery producing cultures from Northern Minnesota and eastern cultures around the Great Lakes (Boyd *et al.* 2014). Laurel culture was widely distributed throughout northwestern Ontario, northern Minnesota, into the Winnipeg River drainage system, and central and northern Manitoba, reaching as far as east central Saskatchewan (Meyer *et al.* 2008; Stoltman 1973; Syms 2015). Laurel groups are associated with the initial introduction of ceramics in southeastern Manitoba.³

Laurel cultural groups were associated with a broad boreal forest subsistence economy based on hunting and harvesting local resources, including a variety of terrestrial and aquatic resources, variation depending on season of site occupation or geographic location (Boyd *et al.* 2014). At the Bjorklund site (Figure 2.2) extensive occupation layers and recovered remains of large ungulates (e.g. moose), small fur bearing mammals (e.g. beaver, river otter, muskrat, snowshoe hare), fish (e.g. northern pike, Lake Sturgeon), turtle and birds suggested that Laurel groups returned annually during spring to fall (Buchner 1982). Remains of fish, caribou, beaver and wild raspberry were recovered from the Astwood Site, a potential occupation site for the Tie Creek Petroforms (Buchner and Callaghan 1980; Steinbring 1980). It was identified as a summer fishing camp used during the construction of the petroforms (Steinbring 1980). Fishing and fishing camps in the spring and fall were main subsistence strategies

³ Dave Norris (2012) identified Brainerd ware, an Early/Middle Woodland ceramic type associated with the Elk Lake Culture in Minnesota, in ceramic assemblages in southwestern Manitoba and the Red River Valley. While more work needs to be conducted to determine if Brainerd ware is present in collections from sites in southeastern Manitoba, the presence of Brainerd ware is briefly discussed in later sections.

practiced by many Laurel groups throughout the boreal forest (Boyd and Surette 2010; Boyd *et al.* 2014).

Recent research on ceramic residues indicated that Laurel groups also relied on maize and native rice, as well as other local native plant species (Boyd and Surette 2010; Boyd *et al.* 2014; Zoltai 1989). Mortar and pestles were used for processing plant foods, particularly native rice (Syms 2015). Rice processing features (e.g. rice jigging pits) and macro remains recovered from Laurel occupations at the Wanipigow site (Figure 2.2; discussed in detail below) provide rare artifactual evidence of the importance of native rice (Zoltai 1989; Boyd and Surette 2010). The early date (AD200-500) associated with maize consumption by Laurel groups at The Pas site in northwestern Manitoba (Boyd and Surette 2010), plus evidence of maize, beans and native rice associated with contemporaneous Avonlea occupations (AD300-1000) in west-central Manitoba and central Saskatchewan (Lints 2012) indicate domesticated and native crops were widespread components of Middle Woodland diets. The extensive distribution of maize and beans in subarctic sites, around the same time as it was introduced into southern Ontario, provides evidence of established long distance trade routes and contacts between different cultural groups (Boyd and Surette 2010:128). Future research is required to determine the distribution and nature of domesticated crop use and cultivation of local native plants, including native rice, from other Laurel sites in southeastern Manitoba.

The Late Woodland period is characterized by the appearance of new ceramic technology, i.e. vessels were made inside textile bags (Syms 2015). Various ceramic producing cultural groups constructed numerous wares including Blackduck, Rainy River Composite, Duck Bay Complex, Bird Lake Complex, Winnipeg River Complex, Selkirk

Composite, and Sandy Lake. All wares have been identified from various Late Woodland sites on the Winnipeg River and its drainage system (Figure 2.2) (Peach, Greco and Lenius 2006[2010]). While much work has been done to re-examine ceramic collections to update typologies based on current understanding of ceramic variation (Peach, Greco, Lenius 2006[2010]; Quaternary 2010; Syms 2015), more work remains to be conducted linking subsistence practices to these new groups. Current understanding of Late Woodland subsistence is based on excavations and archaeobotanical research on Blackduck and Rainy River sites (Zoltai 1989; Syms 2015). However, recent residue analyses have increased the knowledge of the other complexes (Boyd and Surette 2010; Boyd *et al.* 2014).

Blackduck is a widespread culture that extends from the Great Lakes region into southeastern Manitoba, and from northern Minnesota northwards throughout much of the central Canadian Shield. Blackduck lasted from AD700 - 1000 within the boreal forest region, evolving into a series of regional cultures grouped into the Rainy River Composite (Lenius and Olynik 1990; Syms 2015). Blackduck sites have also been located in the boreal forest of east-central Saskatchewan (Meyer 1998), and located in the Aspen Parkland, ca. AD700 to AD1300 (Graham 2008; Hamilton, Graham and Nicholson 2007). Blackduck people created distinctive globular vessels with textile impressed exteriors, decorated with cord wrapped object impressions (CWOI), punctates, bosses and vertical combing (Peach, Greco and Lenius 2006[2010]). They are commonly associated with generalized hunting and harvesting in the boreal forest, exploiting terrestrial and aquatic animals including moose, caribou, beaver, muskrat, fish, and local

native plants including native rice (Nicholson 1996:71). However, evidence for mixed subsistence economies has been recovered from various sites (Figure 2.2).

The Wanipigow site, a multi-component occupation site located along the Wanipigow River, near Bissett, Manitoba (Figure 2.2), contained an extensive Blackduck occupation (Saylor 1976, 1977). Faunal and floral remains indicated a reliance on hunting (e.g. moose, beaver, fish) and harvesting local plant resources including knotweed, dock, bunchberry, rose, wild plum/cherry, raspberry, hazelnut, sweetflag, and hairy sarsaparilla, which provided food and medicine (Zoltai 1989:121; Marles *et al.* 2000). Boiling wild sarsaparilla and sweetflag rhizomes together created a solution in which to soak fishnets in order to increase the catch (MacKinnon *et al.* 2009:184).

Cultivation and/or intensive harvesting of native rice and maple-leaved goosefoot also appear to have been important (Saylor 1977; Carmicheal 1977; Zoltai 1989). For instance, large quantities of edible maple-leaved goosefoot seeds were recovered from the Wanipigow Lake areas and the adjacent Cabin Point site (Zoltai 1989). Wanipigow Site also contained the largest quantity of carbonized native rice ever recorded from a pre-contact site, providing the first definitive evidence of pre-contact native rice reliance (Zoltai 1989). In addition, large vessels were recovered that may have been used for storage vessels for plant resources (Carmicheal 1977:62).

Recent residue analysis studies further support mixed subsistence economies in throughout the boreal forest. Analyses indicate the wide spread usage of native rice through the Winnipeg River region (Figure 2.2), and northwestern Ontario (Boyd *et al.* 2014). Maize consumption remained widespread and an important component of the diet, and there is evidence that native rice and maize were cooked together (Boyd and Surette

2010:129). Beans were incorporated to a lesser extent (Boyd and Surette 2010). The widespread distribution of maize and native rice use evidences the long distance trade routes, and contacts between different cultural groups was maintained from Laurel times (Boyd and Surette 2010:128).

Differing perspectives on the end of the Blackduck and transition to subsequent archaeological cultures exist (Scott Hamilton pers. comm. 2016). The perspective presented here is one adhered to by a number of researchers working in southeastern Manitoba (e.g. Syms 2015; Peach, Greco, Lenius 2006[2010]; Quaternary 2010). The cultural designations presented here are taken from the original literature.

Blackduck culture ends around AD1000 in the Rainy River region of northwest Ontario and southeastern Manitoba with the coalescence of the Blackduck with remnant Laurel groups into the Rainy River Coalescent (AD1000-1100), and the subsequent evolution of the Rainy River Composite (AD1200-1400) (Lenius and Olinyk 1990:84). This composite is composed of three temporally and regionally defined complexes: Duck Bay, Bird Lake and Winnipeg River (Lenius and Olinyk 1990; Peach, Greco, and Lenius 2006[2010]). The Selkirk Composite includes the Clearwater Lake Complex centered in the boreal forest regions of Manitoba, but also identified in northwestern Ontario (Peach, Greco, and Lenius 2006[2010]; Boyd *et al.* 2014).

Limited research has been conducted on subsistence patterns associated with these cultural complexes, however the evidence to date indicates some groups relied on native plants and animals, while others incorporated a mixed subsistence economy. Bird Lake groups relied on native animal and plant species at the Eleanor Lake and Margaret Lake sites along the Winnipeg River near Pinawa, Manitoba (Deck, Peach and Ward 1999).

Pin cherry, knotweed, goosefoot, raspberry, wild plum, and rose were harvested around the islands. A variety of terrestrial and aquatic mammals and fish were hunted, and turtle and molluscs collected. Analysis of the fatty acid composition of residues from some Bird Lake ceramics indicates beaver and fish were cooked (Deck, Peach and Ward 1999).

Residue analyses on Winnipeg River and Rainy River ceramics from other sites in the Winnipeg River system (e.g. Bjorklund and Whitemouth Falls sites) indicate that some cultural groups consumed maize and native rice along with native boreal forest resources (Boyd and Surette 2010), while other cultural groups in the Winnipeg River system consumed maize, native rice, and beans (Boyd *et al.* 2014). These subsistence patterns are similar to those expressed by Rainy River Composite groups identified at the Whitefish Lake sites in northwestern Ontario (Boyd *et al.* 2014).

It appears that starting in the Middle Woodland period domesticated maize and beans were traded into the boreal forest of northwestern Ontario that subsequently spread through southeastern Manitoba and into northwestern Manitoba to Laurel groups living at the Pas (Boyd and Surette 2010). The consumption of maize, native rice, and beans throughout southeastern Manitoba during the Late Woodland indicates a continued reliance on mixed subsistence economies from the Middle Woodland period. The prevalence of domesticated crops through the Late Woodland period suggests an increase in the quantity and/or distribution of these crops between cultural groups (Boyd *et al.* 2014).

2.4.2 Southwestern Manitoba

Pre-contact historical developments in the southwestern region of Manitoba are diverse and long abiding, echoing the historical process apparent in southeastern Manitoba. Developments in the Middle and Late Woodland periods (200BC-AD1600) are exemplified by an increasing visibility of Eastern Woodland influences in technology, e.g. introduction of ceramics, and socio-economic aspects, e.g. burial mound ceremonialism, social group organization (Hamilton, Taylor-Hollings, and Norris 2011) through migration, trade, or intermarriage (Nicholson *et al.* 2006[2010]).

The influx of Eastern Woodlands influences include trends that developed within the Mississippi and lower Missouri River valleys and diffused west and north along major rivers and their tributaries. Generally described as the Plains Woodland Tradition, these trends include the introduction of ceramics, coupled with a mixed and/or intensified hunting/harvesting and small-scale cultivation in plots of various sizes. These elements provided a basis for increased sedentism, population growth, and increased social organization (Hamilton, Taylor-Hollings, and Norris 2011).

The Middle Woodland period includes various complexes such as Besant and Sonota, Valley and Avonlea. Subsistence practices range from heavy reliance on communal bison hunting to mixed subsistence economies based on local plant and animal resources and domesticated crops. Discussions of the Besant and Sonota Complexes (2200-1500BP) are contentious; some researchers view these cultures as separate but related entities (Neuman 1975, cited in Peck 2011; Syms 1977), while others view them as regional variants (Hamilton, Taylor-Hollings, and Norris 2011). Both relied heavily on communal bison hunting and were influenced by Eastern Woodland culture via diffusion

of ideas or migration of people (Hamilton, Taylor-Hollings, and Norris 2011:107-109). In the Souris River basin numerous communal bison kill sites, e.g. use of pounds, jumps, corrals and associated midden deposits of butchered bone, coincide with a peak in anthropogenic burning, suggesting Besant/ Sonota used prescribed burning tactics to conduct large-scale bison hunts (Boyd 2002). Sonota groups appeared to have participated in the Hopewellian interaction sphere, a large-scale trade network extending from the Eastern Woodlands (Syms 1977). They constructed burial mounds with Hopewellian style grave goods, e.g. exotic *Olivella* sp. and *Dentalium* sp. shells, obsidian from Wyoming, and copper, and used similar burial treatments, e.g. secondary interments (Neuman 1975, cited in Peck 2011).

Contemporaneous, but poorly understood Middle Woodland cultural groups reflecting the Plains Woodland Tradition, relied on hunting and harvesting riverine resources in restricted river valleys. Valley Complex (2000-1100BP) people hunted small ungulates, aquatic birds, turtles, shellfish, with minimal bison use, and harvested various local plants. Some Valley cultural groups included small-scale cultivation of squash and a native annual marshelder to their subsistence strategy (Hamilton, Taylor-Hollings, and Norris 2011).

The Avonlea Horizon (1750-1150BP) was widely distributed across the Central Canadian Plains, with only a few sites known in Manitoba (Syms 1977; Lints 2012). Avonlea succeeded Besant in the Northern Plains (Peck 2011), but was possibly contemporaneous with terminal Besant occupations (Hamilton, Taylor-Hollings, and Norris 2011). It is possible that the contemporaneous Elk Lake Culture, originally identified in Minnesota, is also present in Manitoba. Based on a recent ceramic analysis,

three Avonlea ceramic types (e.g. Rock Lake net impressed, Truman parallel grooved, and Plain) show affinities to Elk Lake ceramic wares (Norris 2012). The presence of a few solitary sherds from the Avery and United Church Sites in the Tiger Hills (Figure 2.2) region indicates potential Elk Lake occupations as opposed to Avonlea (Norris 2012). More work needs to be conducted on the presence of Elk Lake culture in southwestern Manitoba, and its connection to Avonlea cultural groups and associated resources, before discussions of its subsistence can be undertaken.

Avonlea subsistence economy relied on bison hunting, with communal hunting being commonly observed in Alberta (Peck 2011). A mixed subsistence economy focused on seasonally diverse resources is found in the east. Bison appears to remain the focus of subsistence practices, augmented by other terrestrial mammals, fish and seasonal birds (Hamilton, Taylor-Hollings, and Norris 2011; Lints 2012). Residue analyses of ceramics and grinding stones used for plant processing indicate that both tropical domesticated species and native plants were consumed across sites in south central Saskatchewan and western Manitoba (Lints 2012). Maize, beans and squash, plus native rice, Indian breadroot, Saskatoon, wild plum, chokecherry, oak acorns, cattail, water lily were consumed (Lints 2012: 193). Maize pollen was tentatively identified (Lints 2012: 193), which if confirmed, would indicate maize being grown in the area.

Plant selection indicates regionalization of plant usage. Avonlea groups inhabiting Plains areas in south Saskatchewan relied more on tuber producing plants, while groups living in forest prairie transitional habitats relied more on berry producing species. Presence of tuber producing species and berry producing species in forested and open plains sites, respectively, suggests trade between sites or wide resource collection routes

(Lints 2012). Only the Miniota site contained evidence of maize, beans and squash, while ceramic residue evidence from Saskatchewan sites contain maize and beans or maize only (Lints 2012:242). The widespread consumption of native rice was suggested to be evidence of trade with the contemporary Laurel groups (Boyd *et al.* 2014).

Laurel Composite is not well known from the Parkland or Plains regions of southern Manitoba as it was confined to the southern boreal forest (Syms 1977). Limited evidence from a few sites located within the Prairie/Parkland/ Boreal transition zone (e.g. Miniota, Avery, Montroy, and Paddock sites) indicates Laurel groups maintained a generalist hunting/ harvesting lifestyle with additions of local native rice and imported maize (Boyd *et al.* 2014), and did not extend their subsistence range into the Plains/ Parkland ecoregions (Hamilton, Taylor-Hollings, and Norris 2011; Syms 1977).

During the Late Woodland period southwestern Manitoba was dominated by an influx of people from the boreal forests to the north and east, and a later influx of cultural groups from the Eastern Woodlands that immigrated east along river valleys into the Dakotas and eventually southwestern Manitoba (Nicholson *et al.* 2006[2010]). Subsistence practices continue from the Middle Woodland period. Most cultural groups focus on bison hunting, with immigrant populations adopting partial or full-scale bison hunting strategies (Hamilton *et al.* 2007). Recent residue analyses indicate many groups incorporated domesticated crops (maize, beans, squash) into a locally based subsistence economy with some groups cultivating domesticated crops (Boyd *et al.* 2006; Hamilton, Taylor-Hollings, and Norris 2011; Nicholson *et al.* 2011).

Blackduck cultural groups appeared in the Prairie/ Parkland around AD800 and persisted until AD1400 (Meyer and Hamilton 1994; Anfinson 1979; Nicholson *et al.*

2006[2010]; Hamilton *et al.* 2007). In some cases Blackduck/Duck Bay groups are contemporaneous with later Eastern Woodlands affiliated groups, e.g. Plains Woodland and Plains Village (Hamilton *et al.* 2007:97). Duck Bay Complex, part of the Rainy River Composite, originated in the Manitoba lowlands between Lakes Manitoba and Winnipeg. These groups utilized a seasonal round focused on the highly productive wetland niches of the interlake region and adjacent mixed woods pockets of the boreal forest. This may have eased transitioning to the Prairie/ Parkland habitat, as Blackduck and Duck Bay groups developed full-scale communal bison hunting (Hamilton *et al.* 2007; Nicholson *et al.* 2006a; Nicholson *et al.* 2006[2010]).

Communal bison hunting was practiced at various sites in southwestern Manitoba (Figure 2.2) (Nicholson *et al.* 2006a). Bison were butchered for meat and marrow, and rendered for grease (Tisdale 1978:100; Hamilton *et al.* 1981:109). Inhabitants of the Lovstrom site focused on intensive bison hunting and processing strategy, while the inhabitants of the Hokanson site supplemented bison hunting with small mammals (Playford 2015). Gompf and Hokanson are winter kill sites ((Hamilton *et al.* 2007). An examination of foetal bison bones and comparison to an Aboriginal understanding of seasonality indicated these sites were occupied during January to March, while Hokanson was likely occupied from April to May (Playford 2015:258) with the most persistent occupation occurring at the Stott site.

The Stott site (AD800 to 1250) (Figure 2.2) is a large encampment along the north river terraces of the Assiniboine River Valley best known for Blackduck groups fully adapting a Plains bison specialization lifestyle (Badertscher *et al.* 1987; Hamilton *et al.* 1981; Hamilton *et al.* 2007; Tisdale 1978). While Stott represents a large culturally

homogeneous Blackduck site (Tisdale 1978:3; Hamilton *et al.* 1981:5), contact between Blackduck groups and groups associated with the northeastern Plains and Eastern Woodlands is reflected in exotic lithics materials, such as copper, Knife River Flint, and ceramic vessels decorated with incised lines and trailed lines that are more typical of Plains or Plains Woodland ceramics (Hamilton *et al.* 1981; Tisdale 1978).

Subsistence strategies at the Stott site centered on bison, which comprised 93% of the meat yield for the site (Hamilton *et al.* 1981:14), augmented by canid, beaver, hare or rabbit, black bear, badger, skunk, lynx, birds, and occasional fish/clams (Badertscher *et al.* 1987; Hamilton *et al.* 1981). No archaeobotanical studies (e.g. flotation for carbonized remains or residue analysis) have been undertaken for the Stott site. Even though plant use can only be inferred, it is probable then that occupants of the Stott site utilized an array of plant resources similar to groups at the Wanipigow Site. Inhabitants may have used local native resources such as saskatoon, chokecherry, prairie onion, and wild sarsaparilla (Hamilton *et al.* 1981), but also consumed maize, and possibly beans gained through trade with Plains Woodland groups.

Other Late Woodland cultural complexes supplemented a bison based diet with local animal and plant resources, incorporating domesticated crops in some way into the diet. The Brockington sites (Figure 2.2), located along the Gainsborough Creek Valley, a tributary of the Souris River in the extreme southwestern corner of Manitoba, were occupied by Bird Lake Complex people ca. AD100-1350. Subsistence centered on bison supplemented with local animals and maize, beans and local plant foods (Syms *et al.* 2009: 80). The Williams Complex, a Late Plains Woodland group, occupied the Brockington sites and Snyder sites (Figure 2.2) after ca. AD1450-1650. Similar to the

Bird Lake Complex, they relied heavily on bison, some local game, supplemented by imported maize and beans, and local plant foods (Syms *et al.* 2009: 55; E. Leigh Syms pers comm. 2011).

Through an ongoing process of population migration and diffusion of ideas and technology, influences from the Eastern Woodland tradition spread northward along the eastern Prairie margins into Manitoba (Hamilton and Nicholson 1999:6). This migration phenomenon is loosely associated with Late Woodland, Plains Woodland and Plains Village traditions (Nicholson *et al.* 2006[2010]; Hamilton and Nicholson 1999). Plains Woodland and Plains Village Traditions can be viewed as end points on a continuum of economic and subsistence strategies, where there is a change in degree of horticultural village life rather than a break between Plains Village and Plains Woodland groups (Hamilton and Nicholson 1999:6).

Plains Woodland tradition is associated with generalized woodland foragers with affinities to the Eastern Woodlands developed over time from the Middle Woodland period (Toom 2004; Hamilton and Nicholson 1999). Economically flexible groups heavily utilized both Prairie/ Parkland and Boreal forest regions (Taylor-Hollings 1999). Subsistence at Boreal sites (e.g. Lake of the Woods sites) reflects a generalized hunting and harvesting strategy, with native rice and maize forming important aspects of the diet (Boyd and Surette 2010; Hamilton *et al.* 2011). In Parkland/ Boreal transition zones, groups heavily on bison and native rice with fishing, hunting woodland animals and harvesting prairie and woodland plant species (Hamilton *et al.* 2011). In the heart of the Prairie/ Parkland, Plains Woodland groups relied heavily on bison and lived in wooded riverine locations in close proximity to the prairie for access to bison herds; they

practiced small-scale maize farming, utilized small storage pits, lived in unfortified villages and constructed burial mounds and earth works (Hamilton and Nicholson 2006: 256).

Plains Village Tradition ultimately developed from a continued migration of Eastern Woodland and Mississippian peoples into the Missouri River drainage system South Dakota (Tiffany 2007). Some groups continued moving north and west settling in North Dakota where they developed into the Plains Village Tradition around AD900 (Ahler 2007; Toom 2004; Schneider 2002). Plains Village tradition is associated with a balanced strategy of hunting, harvesting local plant resources, and maize farming. People lived in fortified earth lodge villages, used stone and bone agricultural implements, and collected agricultural surpluses that they stored in many large sub floor storage pits (Hamilton and Nicholson 2006: 256; Gregg 1994:72). It has been suggested that Plains Village groups living in northern areas did not rely heavily on horticultural surpluses, but still grew maize, beans, squash, sunflower and tobacco. These groups relied heavily on bison supplemented with elk, deer, dogs, smaller mammals, and a variety of gathered fruits, nuts, greens, roots and tubers (Gregg 1994:86).

One of the latest manifestations of Plains Village is the Northeastern Plains Village Aggregate identified from eastern North Dakota (Toom 2004). Complexes include Northeastern Plains Village Complex, Cambria Complex, and Scattered Village Complex (Toom 2004; Nicholson *et al.* 2011). Groups within exhibited a Plains Woodland pattern, a mix of Woodland and Plains Village site and settlement organization and subsistence practices (Toom 2004).

In southwestern Manitoba the Vickers Focus is considered to be a part of the Scattered Village Complex defined by an unusual ceramic assemblage with a distinct mixture of ceramic wares including Sandy Lake wares, and a number of lip decorated locally made wares, e.g. finger pinched, tool impressed, punctates, and notched (Nicholson *et al.* 2006[2010]). Sites were placed in sheltered, secluded places with warm silty/sand soils, near larger potholes and small lakes that provided a stable water source, and southern exposures to facilitate maize and bean cultivation (Nicholson 1994:104; Nicholson *et al.* 2011). Vickers Focus groups migrated into southern Manitoba ca. AD 1350-1400 to the Tiger Hills locale (Figure 2.2) establishing a central village at the Lowton site and satellite camps/villages at the Lovstrom, Randall and Big Tiger sites (Nicholson 1994:106; Nicholson *et al.* 2006b Nicholson *et al.* 2008:19).

The central village at Lowton was supported by cultivation of maize, beans and possibly other taxa at satellite villages. Ground penetrating radar scans at Lowton indicates subsurface storage pits, a number of hearths, and boiling pits (Nicholson *et al.* 2008:25). Residue analyses identified maize starch and phytoliths and bean starch from ceramics from the Tiger Hill sites supporting the consumption of maize and possibly beans (Boyd *et al.* 2006b; 2008). Phytoliths only found in the cob portion of maize were also recovered from the ceramic residue. This coupled with the stone and bison scapula hoes and hoe fragments, and grinding stones from surface collections points to local cultivation of domesticated crops (Boyd *et al.* 2008:1137). Bison was still favoured, and a diverse range of animals were exploited, including canid, bear, mustelids, hare/rabbit, and medium to large bird species (Nicholson *et al.* 2006a; 2008). Exotic items including catlinite pipes and sucking tubes, abundant Knife River Flint tools and debitage, obsidian,

and the exotic ceramic wares point to an extensive trade network that flowed through the central village (Nicholson *et al.* 2008:25; Nicholson *et al.* 2011).

Vickers Focus people abruptly left the Tiger Hills, reappearing 50-100 years later at the *Makotchi-Ded Dontipi* locale in the Lauder Sandhills ca. AD1450 (Figure 2.2) (Nicholson *et al.* 2011). Vickers Focus maintained maize cultivation (Boyd *et al.* 2006b: 1136), but at lower level than previously held, increased their bison exploitation, supplementing bison with canid, birds, fox and rabbit (Nicholson *et al.* 2008:25; Nicholson *et al.* 2011; Playford 2015). Carbonized plant remains indicate goosefoot, raspberry, and wild cherry/plum were utilized (Playford 2015).

By AD1600s Vickers Focus people moved further west, occupying Twin Fawns/Schuddemat/Hollow B site (Figure 2.2) in the *Makotchi-Ded Dontipi* locale (Nicholson *et al.* 2006a, 2006b). It appears that Vickers focus people amalgamated into the Mortlach Complex, a Plains bison focused culture identified from Saskatchewan sites (Mokelki 2007). This amalgamation is associated with a new emphasis on local plant foods and other diverse resources including intensified bison exploitation, with a reduction in cultivation, as no horticultural implements have been recovered from these sites (Mokelki 2007:18; Playford and Nicholson 2006; Boyd *et al.* 2006b; 2008). The diversity of animal resources and intensity of bison processing has been linked to season of site occupation rather than a 'bison focused way of life' (Playford 2015:246).

2.4.3 Red River Valley

The Red River Valley is part of the transition zone between the Boreal forest and Prairie/Parkland ecozones, acting as a transportation corridor of people, goods and ideas

linking the Red River Valley and its inhabitants to other regions, as far away as the Gulf of Mexico (Deck and Ward 2007:4). It was also home to many cultural groups who settled key locations along the Red River (e.g. The Forks and Lockport Sites, Figure 2.2) as early as the Archaic period (Buchner 1979; Kroker 1993; Flynn 2002). Documented early occupations along the Red River are few, in part because of the deep sedimentary sequence. However, a Pelican Lake occupation was identified at the Larter Site (Buchner 1979), forming the earliest occupation level at the Lockport site (Buchner 1988; Flynn 2002). Archaic occupations at the Forks (e.g. Hanna, Pelican Lake) indicate that groups used the area as a spring/ summer fishing campsite focused on fish processing, but occupants also utilized other diverse animal resources, mostly fox, beaver and squirrel (MNI 10-15%), with bison, moose, elk and black bear (MNI 5%) also hunted (Kroker 1993: 108). Locally available plants including goosefoot, red osier dogwood and knotweed seeds were harvested (Kroker 1993).

The Middle Woodland period is represented by Laurel occupations and an earlier Brainerd ware/ Elk Lake cultural occupation at the Lockport site (Buchner 1988; Flynn 2002; Norris 2012). These occupations are associated primarily with fishing (MNI 90%), plus some use (MNI 3%) of terrestrial animals, e.g. bison, elk, black bear, wolf, mink, muskrat (Roberts 1992). Residue analyses have not been completed on Middle Woodland or earlier ceramic sherds, so it remains unknown whether the Laurel people at Lockport were involved in the wider trade network that would have supplied them with imported domesticated crops, similar to the Laurel groups at The Pas (Boyd and Surette 2010).

During the Late Woodland Blackduck and Rainy River Composite cultural groups settled along the Red River (Gregg and Hamilton 1994; Lenius and Olinyk 1990). They

employed a mixed subsistence strategy hunting, fishing and harvesting local plant and animal resources, augmented with low quantities of maize, either accessed through trade or locally grown (Boyd *et al.* 2006; Boyd *et al.* 2008). During the final few centuries of the Late Woodland period, farming groups associated with the Northeastern Plain Village Complex from eastern North Dakota moved into the area, e.g. the Lockport Site (Deck and Shay 1992; McKinley 2001; Flynn 2002). At the Lockport Site these people focused on cultivation of maize and beans augmented by fishing, harvesting local plants, and hunting terrestrial animal resources (McKinley 2001; Flynn 2002; Deck and Shay 1992). I will discuss these two subsistence strategies in detail below.

Blackduck groups (ca. AD600-1350), and Rainy River Composite (AD 1200-1400) groups occupied the Lockport and Healing sites (Figure 2.2) (Flynn 2002; Deck and Ward 2007). These Late Woodland groups utilized a range of wild harvested fruit and nut species (e.g. hazelnuts, wild cherry/plum, raspberry) and small seeded annuals (e.g. goosefoot, dock, and knotweed) (Deck and Shay 1992:49; Deck and Ward 2007:23). They relied heavily on fish (e.g. sturgeon, goldeye, pike, sucker, channel catfish, walleye, drumfish; MNI 90%), with some use (MNI 3-8%) of bison, moose, rabbit/hare, beaver, birds, and clams (Roberts 1992; Deck and Ward 2007). These groups at the Healing site appeared to have not participated in the interregional trade networks as all the lithic materials were local (Deck and Ward 2007) as there was no evidence of maize consumption (Boyd *et al.* 2008).

Later manifestations of the Rainy River Composite, including Bird Lake and Winnipeg River groups, occupied the Lockport site slightly before occupying the Healing Site (ca. AD1400-1450) (Deck and Ward 2007; Flynn 2002). Residue analysis indicates

these Rainy River Composite groups were consuming maize and possibly beans at both Lockport and Healing sites (Deck and Ward 2007; Boyd *et al.* 2006, 2008). Surprisingly, no evidence of maize cultivation was recovered at the Healing site (Deck and Ward 2007). Given the proximity and contemporaneity of the maize farming community living at Lockport suggests possible trade of cultigens between the Healing and Lockport sites.

Rainy River Coalescent (Lenius and Olinyk 1990) and Rainy River Composite groups have been identified from recent excavated occupation levels at the Forks site (Figure 2.2) (AD1000 to 1300) (Quaternary 2010:42). During earlier periods (ca. AD1200-1300) a large number of cultural groups collected within Rainy River Composite (e.g. Bird Lake, plus a number of unnamed groups; Syms 2015) heavily utilized the Forks (Quaternary 2010: 208). Based on ceramic style, there are a few vessels indicative of Plains Woodland influences (Quaternary 2010:124). Faunal remains indicate bison, moose, and shellfish species, along with the enormous fish resources available, were harvested. During these periods bison, moose, and elk were the main source of meat (MNI = <2), with rabbit, beaver and muskrat forming secondary sources (MNI <7; Quaternary 2010: 268). Residue analysis indicates bison, pronghorn antelope, fish, duck and possibly beaver were cooked (Quaternary 2010).

Floral residues and pollen from ceramics indicate maize, bean, chenopod/amaranth, wild buckwheat, wild onion, sunflower, pine seeds, oak acorns, chokecherry, saltbush, sumac, beeweed, currant, snowberry, and native rice were cooked in a number of pots (Quaternary 2010: 130). Maize pollen indicates local cultivation in the area when this pot was in use. Residue from a hammerstone/grinding stone indicate wild onion, sunflower seeds, pine nuts, oak acorns, beeweed, and beans were processed in some way;

the same hammerstone/ grindstone was also used to process duck and sturgeon (Quaternary 2010: 147). Firewood was still collected locally, however a change to ash and maple as the first choice, with elm and oak as the second choice, suggests a change in preference or change in forest composition (Quaternary 2010:528).

Later Rainy River Coalescent groups (Lenius and Olinyk 1990) utilized the Forks ca. AD1100, exploiting the abundant fish and shellfish resources, particularly freshwater drum and catfish, as well as some small mammal/ rodent species and a variety of floral resources. Bison, moose and other large ungulates still provided the most meat of all identified species, but their use decreased from earlier periods (MNI one animal each, Quaternary 2010: 167). Rabbit, beaver, and muskrat increased in comparison, (MNI= <15), and provided fur and a secondary source of meat (Quaternary 2010: 167). Residue analysis indicated venison and fish were cooked (Quaternary 2010).

Residue and pollen analyses also indicated a wide range of local plant taxa and particular plant parts were utilized. Members of the goosefoot/amaranth families, grasses, wild onion, saltbush, rose hips, beeweed seed pods, sunflower, and pine nuts were cooked, while carbonized remains indicate hazelnut, wild cherry, raspberry, goosefoot, and nettle were utilized for food and/or medicine (Quaternary 2010: 76). Firewood was collected locally from the riverbottom forest, elm being the most popular choice. Ash and maple were used moderately and poplar/willow and oak were used in smaller quantities (Quaternary 2010: 464). Firewood choice was based on what the fire was used for- heating, cooking, drying/curing hides, smoking meat, firing pottery or warding off insects (Quaternary 2010:536).

The second subsistence pattern incorporated maize cultivation with hunting, fishing, and harvesting local resources has been identified from the Bed B/C stratum at the Lockport site (Deck and Shay 1992). This layer produced a small quantity of carbonized Eastern Complex eight row (Northern Flint) maize kernels and cupules and a possible cultivated bean, plus a wide variety of locally available berry producing (e.g. raspberry, plum, hazelnut), small seed producing plants (e.g. chenopod, knotweed, amaranth), plus other wild taxa. These materials were recovered from the fill of large and small bell shaped storage pits, hearths, and basin-shaped pits (Deck and Shay 1992). People occupying Lockport also relied heavily on fish (e.g. goldeye, walleye, channel catfish; MNI= 90%), bison and other large and medium mammals (e.g. moose, elk, black bear; MNI= 8%), beaver, muskrat, rabbit, and birds (e.g. grouse, pelican, cranes; MNI <2%); shellfish and turtle were also used (Roberts 1992). The Lockport fishery has been in use since pre-contact times, and all pre-contact cultural groups associated with the Lockport site depended on the fishery (Roberts 1992; Flynn 2002).

Pottery residue analysis identified maize phytoliths and starches from kernel and cob plant portions, as well as bean starches, confirming maize and beans were consumed (Boyd *et al.* 2006; 2008). Deformed starch grains identified during residue analysis also indicated maize was milled and boiled prior to consumption (Zarrillo 2008). Recovery of bison scapula bone hoes, (Roberts 1991) and grinding stones (Buchner 1988), and the large and small bell shaped storage pits, indicated maize and beans were grown locally (Deck and Shay 1992; Wilson 2007; Boyd *et al.* 2006, 2008).

Ceramic seriation identified a variety of ceramic wares associated with Bed B/C from Lockport East, reflecting similar assemblages described for the Northeastern Plains

Village Complex (NEPV) sites from eastern North Dakota (Flynn 2002). NEVP groups occupied the Red, James and Sheyenne Rivers region in eastern North and South Dakota (Toom 2004). Occupations appeared suddenly ca. AD1200, displacing many previous Late Woodland forager groups living along the Red River Valley in eastern North Dakota, but coexisting with the Sandy Lake people (Toom 2004:283; Johnson *et al.* 1995). NEPV is related to the Scattered Village Complex that has been linked to Vickers Focus sites in southwestern Manitoba (Nicholson 1996).

NEPV is characterized by semi-sedentary villages, with or without fortifications, mound burial construction with mortuary goods, the dominance of Knife River Flint, and distinctive ceramics (Michlovic and Schneider 1993:118). Cultural groups relied on bison, and small-scale maize cultivation of maize and beans that supplemented a diet of local native plant and animal resources (Flynn 2002:132). At Lockport, mixed subsistence practices combining maize agriculture with locally harvested plant, animal and fish species, coupled with the use of bell shaped storage pits, further reinforce affiliations with the NEPV (Toom 2004).

Some researchers in Manitoba have postulated that, while there are similarities with NEPV, the cultivation occupation at Lockport East (EaLf-1) is a unique Late Plains Woodland group, and should be classified as its own cultural complex (McKinley 2001; Syms *et al.* 2010). The Kenosewun Complex (AD1350-1480), a Cree word meaning “many fishes”, includes the Bed B/C occupation level from Lockport East (EaLf-1) and the Lockport West (EaLf-2) site (McKinley 2001: 272; Syms *et al.* 2010). Traits identified for this complex include village settlements along waterways, use of bell shaped storage pits, and a subsistence economy based on riparian and fish resources,

associated maize cultivation, and possibly other domesticated species, and large ungulates (e.g. bison, moose, elk). The tool kit includes Plains side notch and triangular points, and bone tools (e.g. needles, awls, spatulas) used for ceramic decoration. Ceramics include globular, fabric-impressed vessels, with unevenly smoothed surfaces. Decoration, which is minimal, is primarily on the lip surface. Impressions are made with either a cord wrapped object or bone tool; combinations of both are rare. Rims may also have tabs or castellations, but these are also rare (McKinley 2001: 273-274). Work continues to address the specific cultural affiliations of the cultivation level at the Lockport site, and how it fits into the broader world of the Northeastern Plains during the Late Woodland period (cf. Syms *et al.* 2010).

One way to address cultural affiliation is by investigating subsistence practices, particularly use of local native plants. The Shea site, a well-known NEPV site occupied AD1400-1550, is located along the Maple River, a tributary of the Sheyenne River in North Dakota (Michlovic and Schneider 1993). Groups practiced small-scale maize cultivation to supplement a diet of bison and gathered foods including wild cherry, plum, and goosefoot. Goosefoot comprises a large portion of the recovered plant remains from the Shea site indicating its importance (Michlovich and Schneider 1993: 125,126).

Goosefoot, little barley, and marshelder were domesticated for their seed in the Eastern Woodlands ca. 3500 years ago (Smith 1985). Known as the Eastern Agricultural Complex, these species produced small starchy or oil rich seeds, high in nutritional value, that were harvested similar to cereal crops (e.g. Seeman and Wilson 1984; Pedersen *et al.* 1987; Marles *et al.* 2000). Domesticated goosefoot has been recovered from sites in South Dakota including the Mitchell site (Benn 1974) and the Double Ditch site (Nickel

1977). Sites associated with the Mill Creek culture in northwestern Iowa (AD1100-1250) derived from unfortified Late Woodland farmers from the Missouri Basin moving west and north into the Prairies where they formed nucleated farming villages (Tiffany 2007). Mill Creek sites Chan-Ya-Ta and Brewster (Jones 1993) appeared to have maintained cultivation of native domesticated chenopod, marshelder, little barley, and amaranth along side maize, beans, squash, sunflower, and tobacco (Nickel 1977, 2007; Benn 1974; Jones 1993). The preponderance of chenopod seed and other native species (e.g. knotweed, cherry/plum, grape) recovered from subsequent NEPV Shea site (Michlovic and Schneider 1993) and Mandan village Slant-a-Hook (AD1575-1785; Nickel 2007) suggests this pattern continued into eastern North Dakota. Nickel (2007) that intensification of maize agriculture in core Eastern Woodland groups may have resulted in a reduced reliance on native domesticated plants, and cultivation of Eastern Agricultural species was pushed to peripheral areas such as northwestern Iowa (Jones 1993) and Connecticut (George and Dewar 1999).

It is possible that cultivation of native species, including goosefoot, spread via cultural connections between groups at the Lockport Site and NEPV sites along the Red River Valley in eastern North Dakota. This possibility is supported by large quantities of carbonized goosefoot seed that were recovered from earlier Blackduck/ Rainy River occupations at Lockport (Deck and Shay 1992), Blackduck occupation levels at Wanipigow (Zoltai 1989), and Rainy River Coalescent and Composite occupations at the Forks excavations (Quaternary 2010). A few goosefoot seeds are commonly recovered from most sites, which may indicate its long use as a food resource (Deck and Shay 1992; Quaternary 2010; Zoltai 1989). Upcoming residue studies looking for goosefoot starch

and phytoliths in sites across Manitoba and northwestern Ontario may shed more light on this possible native cultigen (C. Surette pers. comm. 2010). While archaeobotanical research has identified plant species utilized for food from pre-contact sites (e.g. Deck and Shay 1990; Shay *et al* 1990; Kroker *et al.* 1991; Deck and Shay 1992; Shay and Deck 1993; Deck and Shay 1994; Boyd *et al.* 2006; Zoltai 1989), few dedicated palaeoethnobotanical studies have attempted to address larger socio-cultural issues using carbonized seed remains (but see Deck 1989 for assessment of wood use from the Lockport East site).

The remainder of this thesis explores the potential for cultivation of local *Chenopodium berlandieri* populations by cultural groups at the Lockport and Forks sites in the Red River Valley. The first step is identifying the frequency and distribution of *C. berlandieri* populations in the Red River Valley in Manitoba and in North Dakota, and in the center of the Eastern Woodlands, where this species was originally domesticated (chapter 3). Large, numerous populations within the region suggest wide availability, providing more opportunities for human –plant interactions. Second, I include a phenological study of Manitoba populations to identify variation in the timing of seed production. Understanding intra-and inter population variation in seed maturation and harvest availability will provide information on the dependability of this species as a food resource.

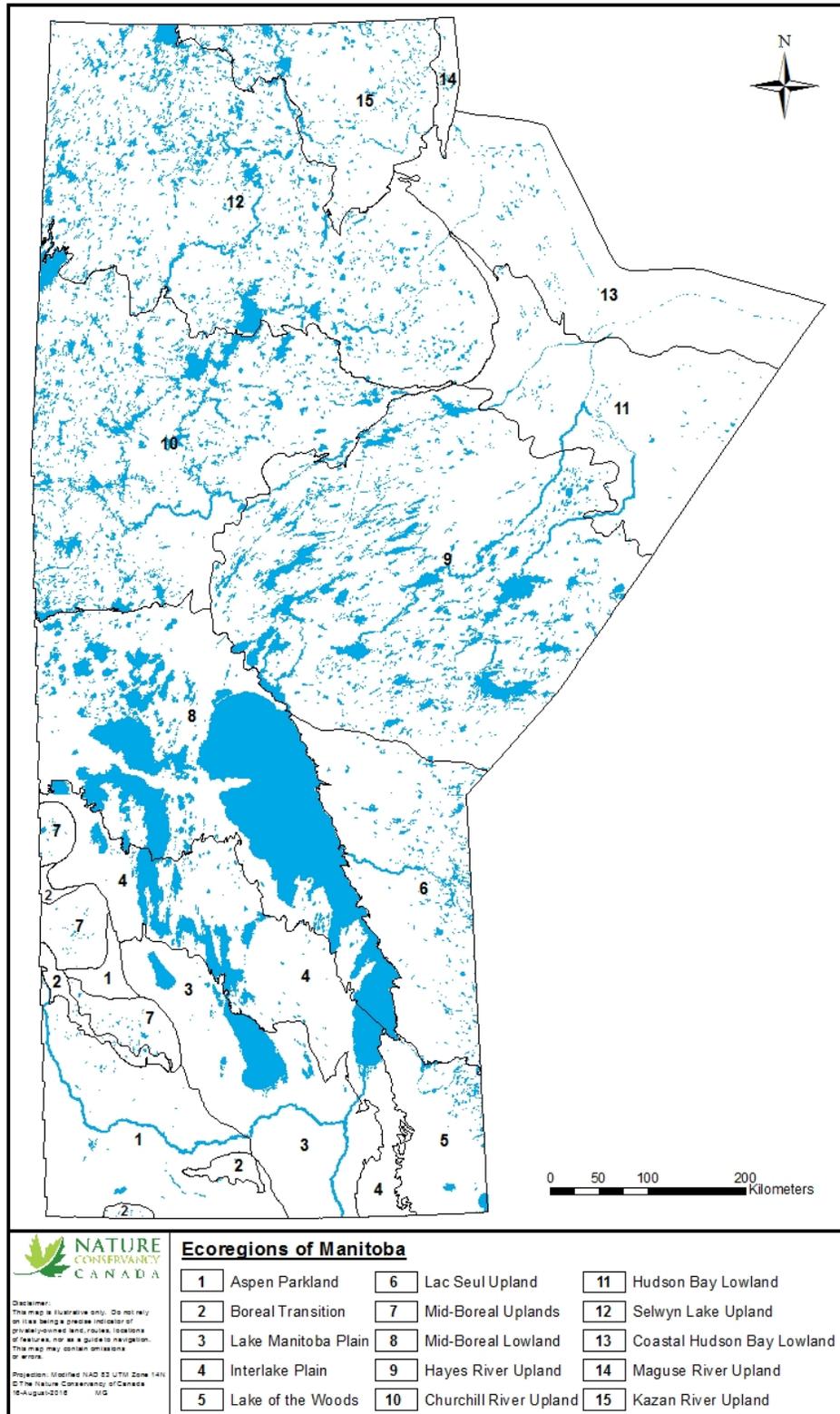


Figure 2.1: Ecozones and subsumed ecological regions of Manitoba showing general habitats pre-contact cultural groups likely experienced.

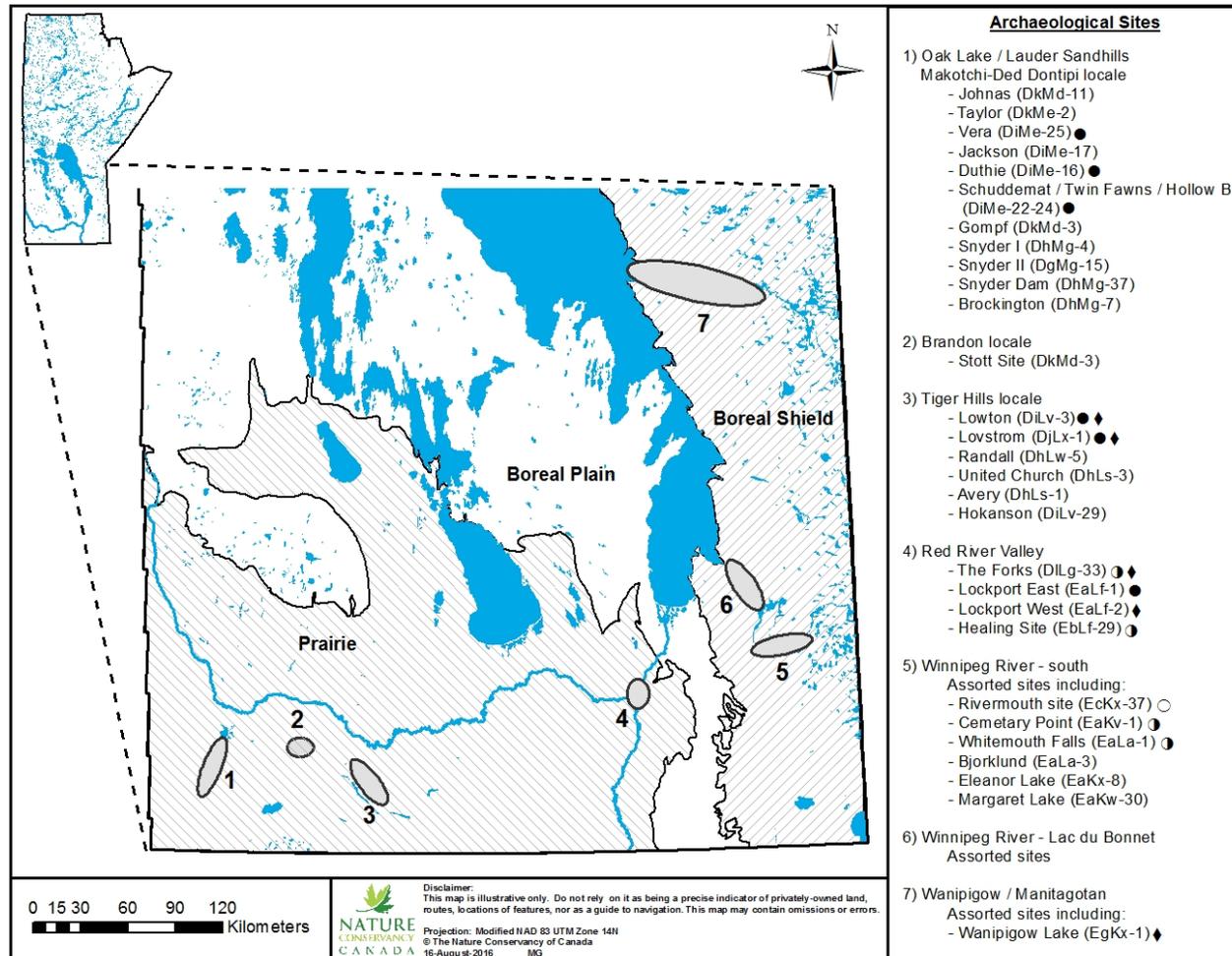


Figure 2.2: The relationship of select Late Woodland (AD1000-1500) archaeological sites to various ecological regions. Sites where evidence of domesticated plants and/or agricultural implements was recovered denoted by filled circles (residue or seed remains), open circles (no botanical evidence), filled diamonds (recovered agricultural implements). Two-tone circles indicate that some cultural levels were associated with botanical remains, while others were not. No symbol indicates sites have not been tested for botanical remains.

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Appendix 2.1

Table of all common names and taxonomic designations of plants mentioned in the text by geographic region and ecoregion.

Region	Common Name	Taxonomic Designation
Ecoregion		
Southeast Manitoba		
Lac Seul Uplands	Alder	<i>Alnus</i> sp.
	Aspen	<i>Populus tremuloides</i>
	Beaked Hazelnut	<i>Corylus conuta</i>
	Black Spruce	<i>Picea mariana</i>
	Blueberry	<i>Vaccinium</i> sp.
	Birch	<i>Betula</i> sp.
	Brown mosses	Amblystegiaceae
	Burr Oak	<i>Quercus macrocarps</i> sp.
	Ericaceous shrubs	Ericaceae
	Feather mosses	<i>Pleurozium</i> sp.
	Jack Pine	<i>Pinus banksiana</i>
	Labrador tea	<i>Ledum groenlandicum</i>
	Lichens	<i>Cladina, Cladonia, Cetraria</i> sp.
	Poplar	<i>Populus</i> sp.
	Prickly-pear cactus	<i>Opuntia fragilis</i>
	Sedge	<i>Carex</i> sp.
	Sphagnum	<i>Sphagnum</i> sp.
	Strawberry	<i>Fragaria virginiana</i>
	Sumac	<i>Rhus</i> sp.
	Tamarack/larch	<i>Larix laricina</i>
	White Spruce	<i>Picea glauca</i>
	Wild rose	<i>Rose</i> sp.
	Willow	<i>Salix</i> sp.
Lake of the Woods	Aspen	<i>Populus tremuloides</i>
	Balsam Fir	<i>Abies balsamea</i>
	Balsam poplar	<i>Populus balsamifera</i>
	Beaked Hazelnut	<i>Corylus conuta</i>
	Black Spruce	<i>Picea mariana</i>
	Blueberry	<i>Vaccinium</i> sp.
	Burr Oak	<i>Quercus macrocarps</i> sp.
	Elm	<i>Ulmus americana</i>
	Green ash	<i>Fraxinus pennsylvanica</i>
	Jack Pine	<i>Pinus banksiana</i>
	Labrador tea	<i>Ledum groenlandicum</i>
	Leather mosses	unknown
	Manitoba Maple/ Box elder	<i>Acer negundo</i>
	Native rice	<i>Zizania</i> sp.
	Paper (white) birch	<i>Betula papyrifera</i>
	Raspberry	<i>Rubus</i> sp.

Appendix 2.1 continued

Region	Common Name	Taxonomic Designation
Ecoregion		
	Red Pine	<i>Pinus resinosa</i>
	Sphagnum	<i>Sphagnum</i> sp.
	Sugar maple	<i>Acer saccharum</i>
	Swamp birch	<i>Betula pumila</i> var. <i>glandulifera</i>
	Tamarack/larch	<i>Larix laricina</i>
	White Cedar	<i>Thuja occidentalis</i>
	White Pine	<i>Pinus strobus</i>
	White Spruce	<i>Picea glauca</i>
Southwestern Manitoba		
Aspen Parkland	Aspen	<i>Populus tremuloides</i>
	Balsam poplar	<i>Populus balsamifera</i>
	Basswood	<i>Tilia americana</i>
	Beaked hazelnut	<i>Corylus cornuta</i>
	Blue grass	<i>Poa</i> sp.
	Buckbrush	<i>Symphocarpos occidentalis</i>
	Burr oak	<i>Quercus macrocarpa</i>
	Chokecherry	<i>Prunus virginiana</i>
	Cottonwood	<i>Populus deltoides</i>
	Green ash	<i>Fraxinus pennsylvanica</i>
	Gooseberry	<i>Ribes</i> sp.
	Red-osier dogwood	<i>Cornus stolonifera</i>
	Manitoba maple/ box elder	<i>Acer negundo</i>
	Saskatoon	<i>Amelanchier alnifolia</i>
	Strawberry	<i>Fragaria virginiana</i>
	Sunflower	<i>Helianthus</i> sp.
	Willow	<i>Salix</i> sp.
Mixed Grass Prairie	Arrow leaved colt's foot	<i>Petasites sagittatus</i>
	Aspen	<i>Populus tremuloides</i>
	Basswood	<i>Tilia americana</i>
	Bulrush	<i>Scirpus</i> sp.
	Bunchberry	<i>Conus canadensis</i>
	Burr oak	<i>Quercus macrocarpa</i>
	Blue grama	<i>Bouteloua gracilis</i>
	Creeping juniper	<i>Juniperus horizontalis</i>
	Cottonwood	<i>Populus delotides</i>
	Elm	<i>Ulnus americana</i>
	Fowl-meadow grass	<i>Poa palustris</i>
	Green ash	<i>Fraxinus pennsylvanica</i>
	Giant ragweed	<i>Ambrosia psilostachya</i>
	Goldenrod	<i>Solidago</i> sp.
	Horsetail	<i>Equisetum hyemale</i>

Appendix 2.1 continued

Region	Common Name	Taxonomic Designation
	Ecoregion	
	June grass	<i>Koeleria gracilis</i>
	Little bluestem	<i>Andropogon scoparius</i>
	Manitoba maple/ box elder	<i>Acer negundo</i>
	Marsh marigold	<i>Caltha palustris</i>
	Narrow leaved cattail	<i>Typha angustifolia</i>
	Narrow-leaved goosefoot	<i>Chenopodium leptophyllum</i>
	Needle-and-thread grass	<i>Stima comata</i>
	Northern wheat grass	<i>Andropyrion smithii</i>
	Pincushion cactus	<i>Coryphantha vivipara</i>
	Prairie turnip	<i>Psoralea esculenta</i>
	Prickly pear cactus	<i>Optunia polyacantha</i>
	Reed	<i>Phragmites australis</i>
	Reed grass	<i>Calamagrostis inexpansa</i>
	Sand bluestem	<i>Andropogon halli</i>
	Sand dock	<i>Rumex venosus</i>
	Sand grass	<i>Calamovilfa longifolia</i>
	Sedges	<i>Carex</i> sp.
	Showy goldenrod	<i>Solidago nemoralis</i>
	Twin flower	<i>Linnaea borealis</i>
	White spruce	<i>Picea glauca</i>
	White top grass	<i>Scolochloa festucacea</i>
	Wild chives	<i>Allium schoenoprasum</i>
	Wild onion	<i>Allium canadense</i>
	Wild rose	<i>Rosa arkansana</i>
	Willow	<i>Salix</i> sp.
	Yarrow	<i>Achillia millefolium</i>
Red River Valley		
Lake Manitoba	Alder	<i>Alnus</i> sp.
Plain	Aspen	<i>Populus tremuloides</i>
	Big bluestem	<i>Andropogon gerardii</i>
	Bulrush	<i>Scirpus</i> sp.
	Burr reed	<i>Sparganium</i> sp.
	Burr oak	<i>Quercus macrocarpa</i>
	Cattail	<i>Typha latifolia</i>
	Chokecherry	<i>Prunus virginiana</i>
	Cinquefoil	<i>Potentillia</i> sp.
	Cottonwood	<i>Populus deltoids</i>
	Elm	<i>Ulnus americana</i>
	False Solomon's Seal	<i>Maianthemum racemosum</i>
	False Virginia creeper	<i>Parthenocissus vitaceae</i>
	Green Ash	<i>Fraxinus pennsylvanica</i>
	Goldenrod	<i>Solidago</i> sp.

Appendix 2.1 continued

Region	Common Name	Taxonomic Designation
Ecoregion		
	Gooseberry	<i>Ribes</i> sp.
	Goosefoot	<i>Chenopodium</i> sp.
	Hazelnut	<i>Corylus</i> sp.
	Knotweed	<i>Polygonum</i> sp.
	Manitoba maple/ Box elder	<i>Acer negundo</i>
	Manna grass	<i>Glyceria</i> sp.
	Maple	<i>Acer</i> sp.
	Marshelder	<i>Iva annua</i>
	Moonseed	<i>Menispermum canadense</i>
	Nettle	<i>Urtica dioica</i>
	Ostrich fern	<i>Matteuccia struthiopteris</i>
	Pin cherry	<i>Prunus pensylvannica</i>
	Poison Ivy	<i>Rhus radicans</i>
	Purslane	<i>Purslane</i> sp.
	Raspberry	<i>Rubus idaeus</i>
	Red-osier dogwood	<i>Corylus stolonifera</i>
	Reed	<i>Phragmites australis</i>
	Reed grass	<i>Calamagrostic inexpansa</i>
	Sedge	<i>Carex</i> sp.
	Snowberry	<i>Symphocarpos</i> sp.
	Switch grass	<i>Panicum virgatum</i>
	Wild hops	<i>Humulus lupulus</i>
	Wild grape	<i>Vitis riparia</i>
	Wild plum	<i>Prunus americana</i>
	Willow	<i>Salix</i> sp.
	White top grass	<i>Scolochloa festucacea</i>

Appendix 2.2

Plant species used for food, medicine, fuel or construction identified from seeds, fruits, charcoal, pollen, phytoliths, and residues recovered from archaeological sites in southern Manitoba. This list is not exhaustive.

Common name	Latin name	Southeastern Manitoba	Red River Valley	Southwestern Manitoba
Amaranth	<i>Amaranthus</i> sp.		X	
Ash	<i>Fraxinus</i> sp.		X	
Beeweed	<i>Cleome</i> sp.		X	
Bunchberry	<i>Cornus canadensis</i>	X		
Cattail	<i>Typha latifolia</i>	X	X	X
Chenopod/ Amaranth	Chenopodiaceae/ Amaranthaceae		X	

Appendix 2.2 continued				
Common name	Latin name	Southeastern Manitoba	Red River Valley	Southwestern Manitoba
Chokecherry	<i>Prunus virginiana</i>	X	X	
Common bean	<i>Phaseolus</i> sp.	X	X	X
Currant	<i>Ribes</i> sp.		X	
Dock	<i>Rumex</i> sp.		X	
Elm	<i>Ulmus americana</i>		X	
Goosefoot	<i>Chenopodium</i> sp.	X	X	X
Hairy sarsaparilla	<i>Aralia hispida</i>	X		
Hazelnut	<i>Corylus</i> sp.	X	X	
Indian breadroot	<i>Psoralea esculenta</i>			X
Knotweed	<i>Polygonum</i> sp.	X	X	
Maize	<i>Zea mays</i>	X	X	X
Maple	<i>Acer</i> sp.		X	
Maple-leaved goosefoot	<i>Chenopodium simplex</i>	X	X	
Marshelder	<i>Iva annua</i>			X
Native rice	<i>Zizania aquatic</i>	X	X	X
Oak (acorns)	<i>Quercus macrocarpa</i>	X	X	X
Pine seeds	<i>Pinus</i> sp.		X	
Poplar	<i>Populus</i> sp.		X	
Raspberry	<i>Rubus</i> sp.	X	X	
Red Osier Dogwood	<i>Corylus stolonifera</i>		X	
Rose	<i>Rosa</i> sp.	X	X	
Saltbush	<i>Atriplex</i> sp.		X	
Saskatoon	<i>Amelanchier alnifolia</i>		X	
Snowberry	<i>Symphocarpos</i> sp.		X	
Squash	<i>Cucurbit</i> sp.			X
Sumac	<i>Rhus</i> sp.		X	
Sunflower	<i>Helianthus</i> sp.		X	
Sweetflag	<i>Acorus calamus</i>	X		
Waterlily	<i>Nymphaea ordata</i>			X
Wild buckwheat	<i>Eriogonum</i> sp.		X	
Wild cherry/plum	<i>Prunus</i> sp.	X	X	X
Wild onion	<i>Allium</i> sp.		X	
Willow	<i>Salix</i> sp.		X	

3. REQUIREMENTS FOR SMALL-SCALE FOOD PRODUCTION:

CHENOPODIUM BERLANDIERI IN PRE-CONTACT SUBSISTENCE STRATEGIES

3.1 Introduction

Over the last 20 years our knowledge of pre-contact subsistence strategies has grown enormously. The strategies and techniques used by North American cultural groups on a daily basis span everything from food procurement techniques (harvesting wild resources) to intensive agriculture (Ford 1985; Deur and Turner 2006; Smith 2001). It is now thought that many pre-contact cultural groups incorporated some form of food production into their subsistence strategy (Boyd *et al.* 2014; Hamilton *et al.* 2011; Nicholson *et al.* 2011; Smith 2006). Small-scale food production combines cultivation techniques with harvesting wild resources (Hamilton and Nicholson 2001; Smith 2001). Cultivation used here describes a range of plant enhancement practices (e.g. watering, weeding, transplanting, burning) to alter both plants and their environments as a means of achieving quantitatively and qualitatively enhanced plant production (Deur and Turner 2006:5). The desired outcome of these practices is an increase in the amount of a desirable plant part(s) and/or to ensure the availability of selected plant populations.

Various types of small-scale food production were practiced throughout North America. For instance, Californian cultures intensively harvested wild plants for seed and broadcast seed on open mud flats along rivers to ensure the availability of important food plants (Anderson 2005). Cultural groups in British Columbia intensified local resources by replanting tubers for the following season's harvest (Turner and Peacock 2006). They used family garden plots in which wild or incipiently domesticated plants were grown (Deur and Turner 2006), and used prescribed fires to enhance berry production (Lepofsky

and Lertzman 2008). Cultural groups in southern Manitoba also used prescribed fires to concentrate bison resources in spring and fall (Boyd 2002). Perhaps the most dramatic result of cultivation is evidenced in the Eastern Woodlands region of North America (e.g. Illinois, Ohio, Tennessee, Kentucky) where ca.3500 years ago a suite of small seed producing native plants, goosefoot (*C. berlandieri* subsp. *jonesianum*), marshelder (*Iva annua* var. *macrocarpa*), sunflower (*Helianthus annuus*), and maygrass (*Phalaris caroliniana*), were domesticated (Smith 2007; Smith and Funk 1985).

It is now recognized that pre-contact cultural groups used different techniques to procure or produce plant foods. Plant management strategies incorporate environmental information, biological traits of plants, cultural preferences and social goals (Chase 1989; Ames 2006; Turner and Peacock 2006). Recent research on plant use by West Coast cultural groups has identified a number of criteria implemented for harvesting important plant species including habitat preference, phenology (growth stage), maturity of plant parts, and size of desired plant parts (Turner and Peacock 2006). Plants are differentially harvested depending on maturation level. Camas (*Camassia*) roots are harvested after seed set, while green shoots of cow-parsnip (*Heracleum lanatum*) are harvested in early spring before flowering (Turner and Peacock 2006). Often intermediate sized roots are harvested, the largest and smallest plants being left to seed the population for the subsequent year (Deur 2006).

Combining the above type of knowledge with archaeobotanical remains recovered from pre-contact sites in Manitoba can broaden understanding of the variation in pre-contact subsistence strategies. Edible native plant species have been recovered from archaeological sites in the Red River Valley of Manitoba, including Lockport –EaLf-1

(Deck and Shay 1992), and The Forks – DILg-33:08A (McCausland 2007; Quaternary 2010; Shay *et al.* 1991). Fruit (wild cherry (*Prunus* sp.)), nut (hazelnut (*Corylus* sp.)), and small seed producing species (goosefoot (*Chenopodium* sp.)) are commonly recovered. In particular, net-seed goosefoot (*Chenopodium berlandieri*) may have been an important food plant for some cultural groups in southern Manitoba.

Net-seed goosefoot was domesticated in the Eastern Woodlands as part of the Eastern Agricultural Complex (Smith 2007). Goosefoot use (cultivation or harvesting) spread into adjacent East coast and Midwest regions (Ahler 2007; George and Dewar 1999; Jones 1993), and by the Late Woodland Period (~AD500-1500) was cultivated by some Northeastern Plains Village cultural groups as part of a mixed subsistence strategy (Ahler 2007; Michlovic and Schneider 1993; Nickel 2007). Recovery of Late Plains Woodland cultural materials and ceramics reflecting Eastern Woodland cultural influences at the Lockport (Flynn 2002; McKinley 2001) and the Forks sites (Quaternary 1997, 2010) indicates cultural connections between Manitoba and southern groups. This connection offers the possibility that local goosefoot populations may have been cultivated for their seed in Manitoba.

Cultivation includes daily and seasonal practices applied to plant populations in order to enhance production (Ford 1985; Harris 1989). In *C. berlandieri*, the result would be a reliable supply of edible seeds and/or young leaves (Moerman 2010). Reliance on this species as a food resource indicates its users could identify and locate plant populations on the landscape, and knew when to harvest desirable plant parts. Furthermore, such use implies people could recognize differences in desired traits

between populations and would define and collect populations based on these traits. It is also probable that they would employ a set of selection criteria when harvesting.

3.2 Objectives

In this chapter I document morphological (plant and seed traits) and phenological (timing of growth) aspects as selection criteria for using wild net-seed goosefoot (*C. berlandieri*) for its edible seed. To gain an understanding of how past peoples may have harvested *C. berlandieri* seeds I focus on the following objectives.

1) I describe habitat, size and abundance of *C. berlandieri* populations in southern Manitoba, and compare these characteristics to other populations in the Northeastern Plains (North Dakota) and the Eastern Woodlands (Missouri, and Ohio). Areas searched are within close proximity to known archaeological sites with cultural ties to Manitoba, and intensively used or domesticated *C. berlandieri*.

2) I describe the phenology of extant *Chenopodium berlandieri* populations to determine how pre-contact cultural groups could have located and used populations throughout the season.

3) I document variation in plant and seed traits within and between populations to assess potentially culturally favoured traits.

3.3 Note on Taxonomy

A basic understanding of the taxonomy of *Chenopodium* is necessary for two main reasons: 1) *Chenopodium* is commonly recovered archaeologically. To understand how cultural groups interacted with their environment and established relationships with

culturally important plant species, the remains need to be correctly identified to species. Much of the archaeobotanical work conducted in Manitoba was completed 20 years ago (e.g., the Lockport site, EaLf-1). Since then, new taxonomic studies have been completed and taxonomic designations have shifted. 2) Introduced Eurasian *C. album* tends to hybridize freely with some native species, particularly *C. berlandieri* (Clemants and Mosyakin 2003). It is possible that extant populations of *C. berlandieri* in Manitoba and surrounding regions may contain hybrids or a mixture of more than one species. Understanding how these species are related and how closely they are related (ease of gene flow between species) could shed light on the process of domestication for some species. The following paragraphs present a brief discussion of the challenges of using *Chenopodium* as a model species.

3.3.1 Revisions to Genus Chenopodium

The genus *Chenopodium* is highly complex, divided into multiple subgenera each with its own sections and subsections (Bassett and Crompton 1982; Welsh, Clemants and Crompton 2003). The culturally important species known from the archaeological record in Manitoba are all located in subgenus *Chenopodium* (Clemants and Mosyakin 2003).

The most important taxonomic changes made to *Chenopodium* is the reorganization of previously identified species. *Chenopodium berlandieri* currently includes six varieties: *C. berlandieri* var. *bushmanum*, *C. berlandieri* var. *boscianum*, *C. berlandieri* var. *macrocalyrium*, and *C. berlandieri* var. *zschackei*. Previously, these were considered separate species (Clemants and Mosyakin 2003). Of these only *C. berlandieri* var. *zschackei* is found in Manitoba, but it grows widely throughout North America. The

other varieties have very limited and specific ranges, mostly in the southern and eastern United States (Clemants and Mosyakin 2003).

Chenopodium berlandieri is also part of “a complex of interfertile New World wild, weedy, and domesticated ecotypes” (Jellen *et al.* 2011: 39). This complex includes weedy *C. berlandieri* and domesticated *C. berlandieri* subsp. *nuttalliae*, domesticated and wild/weedy quinoa (*C. quinoa*) in South America, and *C. hircinum*, a weedy Andean species (Wilson 1990; Jellen *et al.* 2011). Currently all varieties and subspecies of *Chenopodium berlandieri* and quinoa, both ancient and extant, are included within the same subsection denoting their close relationships (Clemants and Mosyakin 2003; Jellen *et al.* 2011).

Lambs-quarters (*Chenopodium album*) is prevalent throughout North America. Earlier floras suggested *C. album* was native (i.e. Wilson *et al.* 1979), which led to its use as a ‘catch all’ in the archaeobotanical literature. Current taxonomic designation by the Flora of North America committee firmly established *C. album* as introduced from Europe, which has been naturalized in North America and is suspected of hybridizing with native *Chenopodium* species (Clemants and Mosyakin 2003). Due to *C. album*’s long history of use as a general term, confusing origins in North America, affinity for hybridization, possible polyploidy, and extensive recent invasions, hundreds of subspecies, varieties, forms and subforms have been identified and recognized by various researchers (Clemants and Mosyakin 2003). The Flora of North America does not formally recognize any of these infraspecific taxa but provides an extensive discussion of the most common groups included in *C. album* sensu lato (Clemants and Mosyakin 2003:297). One such notable species is *C. missouriense*, which is suggested to

be native. It is found in parts of the Eastern Woodlands where it is considered an ubiquitous weed (Clemants and Mosyakins 2003; Smith 2007).

3.3.2 Hybridization and extant *Chenopodium* populations

To further complicate matters, introduced Eurasian *C. album* is said to hybridize quite freely with native species, including *C. berlandieri* (Clemants and Mosyakins 2003). Many populations or patches of *Chenopodium* located in southern Manitoba consist of a mixture of *C. album*, *C. berlandieri*, and in a few instances, *C. simplex*. Of the populations encountered and/or sampled for this research, it is possible that many are actually hybrids of *C. album* and *C. berlandieri*. It is also possible that most extant populations are hybrid swarms and that populations of *C. berlandieri* without any ancestral mixing with *C. album* may not exist. This suggests that various populations of *C. berlandieri* in Manitoba may differ from one another (depending on the quantity of *C. album* within the population), and from populations in other parts of the species range. This possibility must be considered when comparing materials from Manitoba with materials from the wider geographic area.

Clearly distinguishing *C. berlandieri* from *C. album* is essential to identify extant populations to sample for seed phenotyping, germination and heritability studies, and species level identification of *Chenopodium* in Manitoban archaeological assemblages. Morphologically, *C. berlandieri* is difficult to distinguish from *C. album* using stem, leaf, or inflorescence criteria alone. Distinguishing these species is only possible with the achene, a single seeded dry non-dehiscent fruit. In *C. berlandieri* the perianth is strongly

keeled, and the pericarp (remnant ovary wall) that covers the ripe seed, and testa (seed coat) has an aveolate patterning (McGregor 1986).

3.4 Methods

3.4.1 Population search strategy

To place Manitoban populations of *Chenopodium berlandieri* within the context of its wider geographic range, I divided my search between the Northeastern Plains (northern region) and the Eastern Woodlands (southern region). The Northeastern Plains included the Red River Valley of Manitoba and eastern North Dakota. The Eastern Woodlands included eastern Iowa, central Illinois, central Missouri, and southern Ohio. To compare and contrast the habitat and abundance of *Chenopodium berlandieri* populations, my search strategy was initially based on habitat descriptions of various floras, e.g. Flora of Manitoba (Scoggan 1957) and the Flora of North America (1993+), and informal interviews with field botanists and agriculturalists. According to this information, *C. berlandieri* and the closely related *C. album* grow in similar locations: annually disturbed river banks and terraces, along field edges, roadside ditches and disturbed or waste ground, in both sun and shade (Scoggan 1957; Basset and Crompton 1981).

Based on this information, I scouted potential habitat locations in Manitoba throughout July, August and September when *Chenopodium* is fully-grown and easily distinguishable from surrounding species. I investigated all suitable areas by field walking. I spent 10-20 days of the summer months in each of three field seasons searching for populations in Manitoba. I targeted urban areas in the first field season

(2009), the Assiniboine River floodplain and surrounding areas in the following field season (2010) and the Red River Valley/floodplain in the final field season (2011).

I used a similar search strategy to locate *Chenopodium* populations from southeastern North Dakota across to southern Ohio. I had a limited timeframe in which to search, so I targeted areas across this region that were in close proximity to known archaeological sites where *C. berlandieri* was intensively used or domesticated. I focused on the banks and terraces of major rivers and their tributaries. In these areas, I located similar habitats to those in Manitoba where I had located large populations. I spent three weeks at the end of September/beginning of October 2011 focusing 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.

3.4.2 Habitat descriptions and population sampling criteria

Habitats where large populations of *C. berlandieri* were located are described by a series of qualitative factors: location (i.e. in relation to a landmark); size (number of plants or ground coverage in approximate meters squared); canopy (full sun to full shade conditions); soil characteristics (Ehrlich *et al.* 1953; Soils of the Municipality of Richot 2011; USDA-NRCS 2013); slope (elevation of population); and exposure (cardinal direction it was facing). I also recorded associated species and their approximate abundance within or adjacent to the *Chenopodium* population, and the date mature plants were harvested.

Plants were sampled in populations of 50 or more individuals. Transects were placed along the length of the population and individual plants sampled at 1 or 5 meter

intervals, depending on the extent of the population. Between 30 and 60 plants were sampled per population. Individual plants were given a catalogue number (site name, number, year) and 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 tiny mesh size (0.3mm) or paper bags to air dry. Total dry biomass and total 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.

3.4.3 Common garden experiments

Two common garden populations were grown from a subsample of plants (hereafter maternal lines) from three Manitoban populations at two locations, over two years. Seed collected from USA grown plants was not included due to requirements in the Canadian Food Inspection Agency collection permit. The first location 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 to the north and west. The soil is Fort Garry riverine intermixed with Osborne heavy clays (Ehrlich *et al.* 1953), however, soils at this particular location tend to be more silty Fort Gary riverine clays (Don Flaten pers. comm. 2016). These soils were formed from numerous flooding events by the Red River resulting in laminated deposits of fine sandy loam to sandy clay and silty clay (Ehrlich *et al.* 1953). The silt clay mix produced soils that did not dry into a hard surface and the shelter provided by trees and building afforded the plants shelter from wind, rain and sun.

The second location was the Glenlea Agricultural Research Station (hereafter Glenlea). This location is just south of Winnipeg, and is an open field approximately two kilometers west of the Red River. The soil at Glenlea is identified as the Osborne series. These are poorly drained, heavy clays, lying over fine lacustrine clays that developed on flat topography under meadow or swale vegetation. They are highly varied, created by episodes of river flooding by the Red River and long periods of drying that formed deep cracks. During heavy rains, topsoil would wash into these cracks creating deep tongues that intersected underlying soil horizons. This area also contains patches of alkalized and degraded soils due to many years of heavy agricultural use (Ehrlich *et. al.* 1953; Manitoba Agriculture 2011). The lack of shelter from wind, rain and sun, caused the heavy clay soil to dry out quickly, forming a very hard surface.

The focus of each common garden experiment was different. I addressed phenological variation in 2011, and morphological variation in 2012. However, both sets of data were recorded for each year to facilitate generalized comparisons between common garden populations.

The 2011 experiment was designed to characterize the phenology of *C. berlandieri*. A total of 410 seeds from 41 maternal lines from two populations were germinated in the Crop Technology Center (CTC) greenhouse at the University of Manitoba. Ten seeds from 24 maternal lines from the Delta Marsh population (hereafter DM), and ten seeds from 17 maternal lines from the St. Vital population (hereafter SV) were started in 4-inch plastic pots. Ten seeds were planted per pot, and watered every other day, but not fertilized. Seedlings were thinned to a maximum of four per pot, then transplanted at the locations at the 6-8 leaf stage. Seedlings were planted using a random

sampling design. A total of 50 seedlings from 19 maternal lines were planted at the Arboretum and 39 seedlings from 16 maternal lines were planted at Glenlea. At the Arboretum, 17 plants from six maternal lines were from the SV population, and 33 plants from 12 maternal lines were from the DM population. At Glenlea, nine plants from three maternal lines were from the SV population, and 30 plants from 13 maternal lines were from the DM population. Seedlings were planted so there was only one seedling per maternal line per row. Seeds were started in the greenhouse either on June 1 or 2, transplanted around June 15, and harvested by September 14, 2011.

The common garden experiment in 2012 was designed to determine the genetic basis of plant traits. Due to variation in size and seed production of wild goosefoot plants, I maximized the number of maternal lines included in the experiments by sampling all maternal lines with greater than five grams of mature seed.

A split block sampling design was implemented (Anita Babel-Brule pers. comm. 2012). This design replicates rows of all maternal lines tested across the common garden site. In each replicate, all maternal lines (per population) experience all environments within a location, thus reducing environmental effects within populations allowing genetic effects to be measured more clearly (Jones and Nachtsheim 2009). A total of 55 maternal lines collected from the DM population ($n=20$), the SV population ($n=13$), and the Aubigny population (hereafter AB; $n=22$) were planted over three replicates. Each replicate contained 55 rows; each row contained seed of one maternal line. This pattern was replicated at both sites. Seed for each maternal line was sampled by volume; total number of seeds planted ($n=30-1500$) 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 over three days (June 9, 12, and 13) due to rainy weather on June 10 and 11. Both plots were weeded periodically and the plants watered when necessary. All plants were harvested by September 25, 2012.

3.4.4 Repeatability in seed measurements

Chenopodium berlandieri produced thousands of seeds per plant. Mean perisperm diameter was calculated for maternal lines collected from each wild and common garden population. All seeds measured were fresh sectioned by hand. Seeds from each maternal line were soaked in 10ml tap water in sealed plastic vials for 24 hours at room temperature. This softened the testa allowing it to be cut; without soaking, testas shattered during sectioning. After soaking, each seed was sectioned transversely (see Figure 5.1), by holding the seed between thumb and forefinger and slicing with a double-sided razor blade to expose the testa, embryo, perisperm, and other internal features (see Peterson *et al.* 2008 for full sectioning methodology). Seeds were placed cut surface upward on wet filter paper for stability. Perisperm diameter was measured under a dissecting microscope with calibrated measurement program Image Pro Express 4.5 that captured and measured standardized images.

To accurately calculate mean seed traits, a representative number of seeds to measure were identified using a repeatability measure. Repeatability (r) measures the variation in repeated measurements made under identical conditions, meaning the same measurement(s) was made by the same method, same observer, and within a short time frame (Bartlett and Frost 2008). This compartmentalizes total environmental variation for an individual into general environmental variation (V_{EG}) and special environmental

variation (V_{ES}). Special environmental variation is the within individual variation arising from localized developmental circumstances (Falconer and Mackay 1997). For instance, V_{ES} would isolate the variation in seed size or testa thickness within an individual *Chenopodium* plant due to local environmental differences. Further, repeatability is used to identify the accuracy, or bias between multiple measurements using the within subject standard deviation (Falconer and Mackay 1997; Bartlett and Frost 2008). This was used to determine the minimum number of seeds to be measured to maintain accurate trait means. Traits with high repeatability require fewer seeds to be measured, while traits with low repeatability require higher numbers of seeds to be measured (Falconer and Mackay 1997).

I calculated the repeatability of seed diameter and testa thickness in two wild Manitoban populations to be $r = 0.67$, and 0.45 , respectively (15 to 30 individuals, five seeds per individual). These are quite high repeatabilities, and compared to Falconer and Mackay (1997) who graphed the percent gain in accuracy over increase in number of measurements (Falconer and Mackay 1997: 140, Figure 8.3), I determined three to five seeds per individual plant (hereafter maternal lines) collected per population was sufficient to estimate the phenotype for all seed traits measured.

3.4.5 Plant phenotypes and statistical analyses

Morphological variation for all wild and common garden populations was characterized using total plant size index (plant height * plant diameter (tip to tip of widest spaced branches)), total seed mass (air dried, in gm), and seed size (perisperm diameter, in mm). When plant size index was calculated for plants grown in the common

garden, vegetation mass (total above ground biomass minus seed weight) was also measured. Vegetation mass was highly correlated with plant index in both locations and populations ($r = 0.91-0.98$, $P < 0.0001$), thus plant size index will be used. Qualitative traits including stem colour, cauline leaf shape and approximate density of lateral branches were also noted.

Population mean and standard error (PROC MEANS SAS 9.2, 2010) for the plant and seed measurements were calculated. Plant traits (height, diameter, seed mass) were natural log transformed to satisfy assumptions of normality and homogeneity of variances. Mean \pm the standard error are reported in all figures and tables.

To explore geographic variation in plant and seed traits among wild populations, I conducted three analyses of variance (PROC GLM, SAS 9.2, 2010). Dependent variables (Y) were plant index, total seed mass and perisperm diameter. The model statement for each analysis was $Y = \text{sub-region } \text{population}(\text{sub-region})$. Population was analyzed as a random factor using the RANDOM statement, followed by the TEST option. This option invokes a procedure to estimate appropriate expected mean squares and F -tests, given the specified random factors.

To assess factors affecting plant and seed traits in common garden populations, I conducted three analyses of variance (PROC GLM, SAS 9.2, 2010). Dependent variables were plant index, total seed mass and perisperm diameter. The model statement for each analysis of the 2011 data was $Y = \text{location } \text{population } \text{location} * \text{population } \text{maternal line}(\text{population})$. The model statement for each analysis of the 2012 data was $Y = \text{location } \text{population } \text{replicate}(\text{location}) \text{location} * \text{population } \text{maternal line}(\text{population})$. All

factors in the model statements with the exception of location and replicate(location) were considered random.

I also assessed pairwise phenotypic correlations between all plant and seed traits (PROC CORR Pearsons, SAS 9.2, 2010). These were estimated within each wild and common garden population using data from individual plants as data points. The correlation value and p-value (r , P) are reported for significant relationships.

Phenological variation in common garden populations was measured by noting the first day of nine major stages of growth for all individuals. The major stages of growth were 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, but only every three days in 2012. In 2011, the pattern of growth was calculated from 89 plants from 22 maternal lines. The calendar date for each stage was translated into number of days after planting.

Population mean and standard error (PROC MEANS SAS 9.2, 2010) for the number of days to reach each growth stage were calculated. Mean \pm the standard error are reported in all figures and tables.

To assess phenology in 2011 common garden plants, I conducted four analyses of variance (PROC GLM, SAS 9.2, 2010). Dependent variables were the number of days until first leaf, first open flower, first seed and plant harvest. The model statements for each analysis were Y= location population location*population maternal line(population). All factors in the model statement with the exception of location were considered to be random.

3.5 Results

3.5.1 Wild population habitat characteristics

In all areas searched in Manitoba and the Northeastern Plains and Eastern Woodlands, large populations of *C. berlandieri* were located along the well-drained sediments of upper terraces of rivers and creeks, or growing on the annually flooded sediments of river floodplains (Table 3.1). Single plants and small patches of *C. berlandieri* were found growing in naturally and anthropogenically disturbed areas. Large populations of *C. berlandieri* were found growing in naturally disturbed areas only. In Manitoba, two populations (SV, AB) were located along the upper eastern terrace of the Red River. A third population was located along the west bank of the Assiniboine River diversion. Similarly, the North Dakota populations were all located along upper river terraces of the Red and Sheyenne Rivers, while the southern populations from Missouri and Ohio were found in the flat floodplain of the Missouri and Ohio River systems that flood annually (see Figure 3.1 for general locations).

Despite being present in Manitoba, *C. berlandieri* populations were not common or widespread. Frequency of large populations was the most striking difference between *C. berlandieri* populations in Manitoba and areas searched in the USA. In total I located three large populations of *C. berlandieri* in Manitoba in three field seasons. I spent approximately 18 days per field season searching for populations and located a single large population each summer. In contrast, I spent two to three days in any given location looking for *C. berlandieri* populations in the United States. In this limited time I located three large populations in North Dakota, four populations in Missouri and four populations in Ohio. Despite targeting specific habitats in these regions, I was

consistently successful in finding large populations along the upper banks and along floodplains of rivers. Since I was able to locate sizable populations in a relatively short period of time, I surmise that *C. berlandieri* populations are more frequent in these regions of the USA than in Manitoba.

Population size ranged from large patches of approximately 100 plants covering 30m² to very large populations containing thousands of plants and extending half a kilometer (Table 3.1). The majority of population sizes ranged between these extremes, containing a few hundred to a thousand plants and covering around 500m². Population size varied in Manitoba and across its eastern range. In general, northern areas had small, medium and large populations, while southern areas had medium or large populations.

Pure stands of *C. berlandieri* were rarely encountered. Most populations contained various colonizing grasses and forbs interspersed with *C. berlandieri* plants. The most common co-occurring species was *C. album* (Appendix 3.1). Maple-leaved goosefoot (*C. simplex*), knotweed (*Polygonum*), dock (*Rumex*), along with other weedy agricultural species were also commonly noted growing in the stands. There were more agricultural weedy species (e.g. *Cirsium arvense*) noted growing in northern populations compared to southern populations. Co-occurring species in southern areas, particularly Ohio, include amaranth (*Amaranthus*), foxtail (*Setaria*) and ragweed (*Ambrosia*).

I also found differences between where I located individuals or populations of *C. berlandieri* versus *C. album*. I only found sizeable patches of *C. berlandieri* on the upper terraces of the Red and Assiniboine Rivers, in either urban or rural locals. Solitary or small groups of *C. berlandieri* can be found growing with *C. album* in urban settings along roadsides or within construction areas adjacent to river floodplains (e.g.

Assiniboine River). This is likely due to *C. berlandieri* being a native species of grasslands, parklands and boreal forests of the prairie-provinces (Robson 2008:90; Clemants and Mosyakin 2003), and not a cosmopolitan weed like *C. album*.

Most populations grew in full sun; only two populations were located in semi-shade and only one was located under a closed canopy (Table 3.1). *Chenopodium berlandieri* plants exposed to full sun conditions tended to be robust, with many lateral branches, producing high quantities of seed (e.g. DM, OH4). Plants growing in more shaded conditions tended to be more gracile, taller, with fewer lateral branches, and produced less seed (e.g. ND2). Most populations contained tall, robust reddish plants with sparse lateral branches, and numerous inflorescences, ranging from compressed to open panicles. Few populations comprised plants with widely spaced panicles (e.g. ND2). Flowers were clumped into spherical glomerules, and ranged in colour from bright green to green/brown.

3.5.2 Plant size and total seed mass

3.5.2.1 Wild populations

Population of origin significantly influenced plant size (i.e. plant size index) and seed mass (all $P < 0.0001$), while differences among sub-regions (MB, ND, MO, OH) accounted for a small proportion of the variation in plant size and seed mass ($P < 0.04$) (Table 3.2). This means that the differences in plant size and seed production were more related to the population of origin, than geographic sub-region in which the population was located.

Plants were smaller and produced less total seed in northern populations compared to plants in southern populations (Figure 3.2). Manitoba had the smallest mean

plant index (overall mean=538 cm²) and mean total seed mass (overall mean=1.39 grams). Plants from two North Dakota populations tended to be taller with long, sparse lateral branches (mean plant index 2300cm²) and produced an average 5 grams of seed per population. However, the third population (ND2) produced shorter plants with narrow lateral branches, and grouped with Manitoban populations (Figure 3.2). Missouri and Ohio produced plants with mean size indices of 3799cm² and 4758cm², and mean seed mass of 14 and 11 grams, respectively (Figure 3.2). These values differed significantly from both North Dakota and Manitoba. Plant size index and mean seed mass were positively and significantly correlated within all wild populations ($r = 0.66-0.94$, $P < 0.001$) indicating a positive relationship between plant size and seed production.

The DM and SV population estimates for total mean seed mass may be slightly underestimated due to the learning curve associated with harvesting and processing plants. These populations were the first sampled and processed. In order to secure seed samples I harvested plants late August to early September, which may have resulted a slightly lower amount of mature seed on each plant. Regardless, seed mass from these populations was comparable to seed mass from other populations sampled in this study.

3.5.2.2 Common garden populations

Common garden populations were analyzed to determine if population of origin, location and population by location interactions significantly affect plant traits (Table 3.3). The location in which wild collected seed was grown had the greatest effect ($F > 117$, $P < 0.0001$) on plant size and seed production of the common garden populations grown in both years. Population had a significant effect ($F > 7.4$, $P < 0.01$) on plant size and seed

production in common garden populations grown in 2011, but not those grown in 2012. However, strong population by location interactions significantly affected ($F > 4.7$, $P < 0.01$) plant size and seed production of common garden grown populations in 2012, but not in 2011.

Populations grown at the Arboretum produced the largest plants (plant size index $> 4980 \text{ cm}^2$) and highest seed production (mean > 40 grams) for all common garden populations (Figure 3.3; Appendix 3.3). 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. Populations grown Glenlea produced plants similar in size and total seed mass as their progenitor populations (Figure 3.3). These populations also produced the smallest plants (plant size index $< 455 \text{ cm}^2$) and lowest total seed production (mean < 3 grams) in both years (Figure 3.3). The positive relationship between plant size and seed production was consistent across generations within a given population; plant size index and total seed mass were positively and significantly correlated within all common garden populations ($r > 0.96$, $P < 0.001$).

Of the three wild populations grown in common gardens, the SV population produced the largest plants with highest seed mass compared to the other populations (DM and AB) in both years (Figure 3.3). However, plant size and seed production from the SV population at Glenlea was lower in 2012 compared to 2011, clustering closely to the production values of the other two common garden populations (Figure 3.3; Appendix 3.3).

3.5.3 Seed size

3.5.3.1 Wild populations

Significant variation ($F = 168, P < 0.001$) in seed size existed among populations (Table 3.4). Wild populations showed a slightly bimodal distribution for mean seed size (Figure 3.4). Some populations have a larger mean seed size (mean > 1.4mm); others have a smaller mean seed size (mean < 1.3mm). Population significantly influenced seed size ($F = 1.69, P < 0.0001$) whereas geographic sub-region did not influence variation in seed size (Table 3.4). Populations from Manitoba and Ohio exhibit a wider range of inter-population variation, while populations from North Dakota and Missouri show a narrower range variation (Figure 3.4).

Pairwise correlations between seed size, plant size index and total seed mass varied among populations and sub-regions. Seed size was positively and significantly correlated with plant index and total seed mass in Manitoba populations AB ($r = 0.27-0.31, P < 0.05$) and DM ($r = 0.24-0.43, P < 0.05$). These same traits were negatively and significantly correlated in Ohio population OH4 ($r = -0.42-0.47, P < 0.01$).

3.5.3.2 Common garden populations

Population level differences maintained seed size ($F > 46, P < 0.0001$) between Manitoba common garden and wild progenitor populations (Table 3.4; Figure 3.5). In 2011, both DM and SV common garden populations had slightly lower mean seed size (1.24mm and 1.53mm, respectively) compared to their wild populations (1.26mm and 1.61mm, respectively), but slightly larger mean seed size (1.31mm and 1.68mm, respectively) compared to their wild populations in 2012. The single AB common garden

population from 2012 produced seeds with a much larger mean size (1.32mm) compared to its wild population (1.19mm).

Populations experiencing different conditions at the common garden locations significantly ($F > 14$, $P < 0.0004$) influenced seed size. Plants grown at Glenlea produced seeds with a smaller mean size compared to plants grown at the Arboretum for all common garden grown populations (Figure 3.5). In 2011, the DM common garden populations at both locations had significantly smaller mean seed sizes compared to the SV common garden populations (Figure 3.5). In 2012, the DM and AB common garden populations grown at both locations had significantly ($P < 0.0001$) smaller mean seed sizes (mean < 1.35 mm) compared to the SV population (mean > 1.5 mm) grown at both locations (Figure 3.5).

Plant size and total seed mass (plant traits) correlated intermittently with perisperm diameter (seed size) depending on population of origin. Both plant traits were positively and significantly correlated with seed size ($r > 0.21$, $P < 0.001$) in the AB common garden population grown in 2012. Similarly, plant and seed traits were positively and significantly correlated ($r > 0.73$, $P > 0.001$) in the SV common garden grown in 2012.

3.5.4 Phenology in common garden populations

Significant population level effects ($F > 7.12$, $P < 0.01$) were present on all phenology stages of growth tested (Table 3.5). These effects influenced the DM population to mature faster than the SV population (Figure 3.6). Initial differences in mean number of days to each stage were small, but accumulated over the growing season

(Figure 3.6). For instance, differences caused by location were not significant at first leaf, were significant ($P=0.003$) at the start of flowering, and comparable to population level effects by the end of the growing season (Table 3.5). Plants from both populations matured faster at Glenlea compared to the Arboretum (Figure 3.6).

Seeds germinated in one to ten days, produced leaves within two weeks of germination, began flowering one to two months after germination, and produced seed 50-110 days after germination (Figure 3.6; Appendix 3.4). Most flowers (>75%) were open for approximately two weeks. Plants matured from the terminal end; therefore, while the upper branches were in full flower, the lowest branches were still in bud. Plants produced mature looking seed in 75% of flowers in approximately three weeks, and remained on the plant until harvest. Plants were harvested once approximately 75% seed set had been reached. Most plants produced by the DM population were harvested by mid-August (64-80 days after planting), while the majority of plants produced by the SV population were harvested by mid-September (95-103 days after planting). Some of the last individuals harvested in 2011 could have waited another two weeks before harvest.

3.6 Discussion: Incorporating *Chenopodium berlandieri* into daily subsistence practices.

3.6.1 Habitat, population size, and abundance of C. berlandieri populations across geographic range

This chapter considers how southern Manitoba pre-contact cultural groups may have incorporated *C. berlandieri* into daily and seasonal patterns of subsistence. This research focuses on documenting the preferred habitat of *C. berlandieri* populations, and

seasonal growth patterns of useful plant parts. The initial step to incorporating any plant into a subsistence economy is to determine the where populations of *C. berlandieri* grow in southern Manitoba. *Chenopodium berlandieri* has a narrow habitat preference. Large populations (>100 plants) of *C. berlandieri* occur in naturally disturbed areas along riverbanks, either in exposed soil along slumped upper banks, or along upper terraces that had a layer of sediment deposited from spring floods. A number of possible explanations may account for the irregular distribution of large *C. berlandieri* populations. Variation in annual spring flooding, and erosion and deposition of lacustrine soils during these events may unevenly distribute seeds in riverine zones (cf. Smith 2007). Manitoba is at the northern edge of *C. berlandieri*'s natural range (Clemants and Mosyakin 2003:294, Map 29). Marginal populations are less likely to benefit from locally available alleles via gene flow thus adapting to range edges, or be outcompeted by other species (Bridle and Vines 2006). Thus marginal populations may not be able to increase in total population size or frequency on the landscape.

Competition of numerous species adapted to naturally disturbed soils (e.g. *Polygonum* sp., *Rumex* sp., compositae and graminoids) may also account for the low abundance of *C. berlandieri*. It is possible that as a native species with a specific habitat *C. berlandieri* is out competed by other species, specifically by *C. album*. As a naturalized European species and cosmopolitan weed (Voss 1981; Clemants and Mosyakin 2003), *C. album* formed frequent, large populations along field edges, ditches and other disturbed habitats noted by the author during scouting trips. Large populations of *C. berlandieri* may have been more common in the past along the Red River floodplain in Manitoba, but centuries of intensive agricultural use extending right to the

edge of the Red River and other major rivers has eliminated the preferred habitat of annually flooded riverbank terraces, favouring the introduction of *C. album* that now dominates field margins.

Habitat and population characteristics changed from the Northeastern Plains (Manitoba and North Dakota) into the Eastern Woodlands (Missouri and Ohio). Moving south along the Red River, the frequency of moderate to large populations of *C. berlandieri* increased along naturally disturbed riverbanks, while community species mix remained relatively similar.

In the most southern areas searched (Missouri and Ohio), large populations of *C. berlandieri* were more common, and grew in both anthropogenic and naturally disturbed habitats. Individual and small clusters of *C. berlandieri* plants grew along roadways, ditches and campgrounds, abandoned lots, over-grown gardens, and edges of agricultural fields. These observations agree with Smith's (2007) observations of *C. berlandieri* growing throughout the whole of the Eastern Woodlands region. Individual *C. berlandieri* plants were also interspersed throughout populations of *C. missouriense*, a close relative of *C. album* (Clemants and Mosyakin 2003), a situation also noted by Smith (2007). Very large populations of *C. berlandieri* were still restricted to open, flat floodplain areas along major rivers, which in many cases were adjacent to agricultural fields. Floodplains were exposed to annual floods, and tended to have sandy clay soils that were lighter than the heavy clay soils in the northern region. Because large populations were common and *C. berlandieri* grows in almost uniform stands with few competitive species, it would have been easier for cultural groups in the Eastern Woodlands to intensively harvest or cultivate these populations.

The increased frequency of large populations in Ohio, Missouri, and even North Dakota, suggests this resource would have been more prominent on the landscape and potentially more amenable to intensive harvesting and cultivation compared to Manitoba. It is possible that in Manitoba small patches of *C. berlandieri* are the norm, and occasional large populations occur in rare instances of optimal conditions. If large populations were not overly common in the past, and since anthropogenically disturbed ground supports low numbers of *C. berlandieri* plants, using this species as a food resource would require deliberate action by cultural groups. Populations would have been intentionally harvested, and archaeological remains of *C. berlandieri* may be evidence of such use. Even small quantities of seed recovered in secure cultural contexts should be examined as potential cultural remains rather than immediately labelling them as ecological indicators.

3.6.2 *Seasonal variation in seed production in extant C. berlandieri populations*

Defining plant growth patterns can identify timing of use for important plant parts and can illuminate the daily and seasonal activities through which cultural groups interacted with these populations. Cultural groups relied on *C. berlandieri* for its seed and young leaves (Erichsen-Brown 1979; Marles *et al.* 2000; Moerman 2010). Groups that successfully harvested (casually or intensively) or cultivated native *C. berlandieri* populations required knowledge of its lifecycle. While sprouted seeds, young leaves and inflorescences, and mature seed are all edible (MacKinnon *et al.* 2009), archaeological evidence suggests seeds were harvested in southern Manitoba (Deck and Shay 1992;

Quaternary 2010). Therefore, the maturation of seed would be an important stage in the *Chenopodium* lifecycle to pre-contact groups.

It takes *C. berlandieri* approximately four months (June –September/ October) from seedling emergence to final seed harvest. The phenology data indicated that individual populations in Manitoba varied at all stages of growth, but seeds sprouted approximately two weeks after planting. Flowering began in early July and lasted approximately two – three weeks. Seed production varies over the plant, maturing first at the terminal end, moving down the lateral branches. Once the first mature seeds formed, it took two to three weeks for plants establish 75% seed set. It is therefore possible to harvest seed from the terminal end of the plant first and lower/lateral branches at a later date.

Different populations grown at different locations resulted in a range of maturation times for seed. Plants had a longer growing season at the Arboretum location and matured later than plants grown at the Glenlea location. Population level differences resulted in the DM population maturing faster at both locations compared to the SV population, indicating a wide range of harvest dates for mature seeds. This range of availability could have provided opportunities for different cultural groups to select between populations at different times during the growing season.

Chenopodium berlandieri populations in Manitoba overlapped the seed harvest period of other small seeded annuals in the Eastern Woodlands region. Studies on *Polygonum* sp., *Amaranthus* sp., *C. missouriense*, and *Iva annua* populations throughout the Eastern Woodlands region indicated that the bulk of seed was harvestable between late September and late November (Murray and Sheehan 1984; Peterson and Munson

1984; Seeman and Wilson 1984; Smith 2007). Most small seeded annuals harvested by cultural groups in the Eastern Woodlands are available October to December⁴ (Munson 1984). However, variation in *Polygonum* sp. and *C. missouriense* populations resulted in seed produced well into December and in some cases January (Munson 1984; Murray and Sheehan 1984; Seeman and Wilson 1984).

Plants retained mature seed better than the author anticipated. Some seeds brushed off when the author moved past the plants, and some naturally shattered when the perianth ripened enough to expose the seed. However, the amount of seed lost in this manner appeared to be a very small fraction compared to the total amount collected. This compares well to the retention rate of seed in other wild small seeded annuals. Based on the few studies found, *Polygonum* sp. and *C. missouriense* retain seed from four to eight weeks after seed production (Seeman and Wilson 1984). In comparison, *Amaranthus* sp. lost all mature seed in two weeks (Peterson and Munson 1984).

3.6.3 Variation in plant and seed traits in wild *C. berlandieri* populations

Variation in culturally preferred traits between populations would allow people to choose between populations. Based on archaeobotanical material, this species was cultivated for its seed causing the evolution of a thin testa domesticated phenotype in the Eastern Woodlands (Smith and Funk 1985; Gremillion 1993). Variation in total plant size, total seed production, and mean seed size, as visible traits, may have been potential avenues for selection by past cultural groups. Total plant size and total seed production

⁴ I noticed this when I originally drove to Ohio to collect seed at the end of September after I harvested *Chenopodium* plants in Manitoba. From Missouri to Ohio the plants were still flowering and I had to make a return trip at the end of October / beginning of November to harvest these plants.

are highly and significantly correlated, thus past peoples may have targeted populations with large plants because high quantities of seed could be harvested from them.

Plant size and total seed mass tended to increase from northern to southern populations, indicating some influence of geographic region on plant traits. Seed size varies significantly among populations, but is not affected by geographic region. This means that a mixture of populations with various mean seed sizes would have been available throughout the Northeastern Plains and Eastern Woodlands regions. Populations in Manitoba produce smaller plants with low quantities of seed. However, low seed production in the DM and SV populations in Manitoba may be linked to an early harvest date. Seed from these populations grow in a common garden environment (see next section) produced quantities of seed on par or higher than wild southern populations, indicating wild Manitoba populations have the potential for high seed production. Variation between populations in plant and seed traits in Manitoba would have provided choice between *C. berlandieri* populations that pre-contact people would have encountered.

3.6.4: Influence of a common garden setting on plant and seed traits

Location of common garden plots, and their attendant environmental factors, caused the most significant differences in seed production for all common garden grown populations. At both locations, wild seed was planted in tilled soil, lightly weeded, and watered when it was very hot and dry. At the Arboretum location, this management strategy resulted in an increased production of up to a hundred fold. All common garden populations exceeded their progenitor populations in yield, producing 33-500grams of

seed across both years. Ethnographic accounts of West Coast cultural groups identify these cultivation techniques as routine for enhancing berry and root crop production (e.g. Lepofsky et al 2006; Darby 1996; Turner and Peacock 2006). Total seed mass from Arboretum grown plants is more comparable to the average seed production of the southern populations (10-15grams). All populations grown at the Glenlea location produced between one and five grams of seed, comparable to the mean seed production of their progenitor populations.

Location greatly influences plant size and seed production. The Arboretum location is partly sheltered from the wind, and composed of riverine silty clay soil that was well drained, regularly tilled and chemically weeded. The Glenlea location, is open and unprotected from wind, and is also situated on riverine deposits of silt and clay. However, the soils are not well drained and dry into a very hard surface, making this site a less desirable garden location.

Differences between locations also include the human management history of a location (Don Flaten pers. com. 2016). Human management history includes all practices (e.g. tilling regiments, manure treatments) humans use to modify the soil. For instance, different manure treatments with the same level of nutrients used in a long term cropping experiment at the Glenlea Research Station showed increased biomass with the solid manure treatment (Seward 2016). Differences in biomass were generated through interaction between the soil conditions and manure treatment, i.e. human management strategy (Seward 2016).

Few studies have directly quantified differences in yield between cultivated and wild populations, although one study investigated yam yields (Dounias 2001). During

harvest the pre-tuber and terminal end of the yam are left *in situ* to produce two tubers the following year. Compost is used to fill the hole, thus adding nutrients for the next crop (Dounias 2001). Cultivated yams yield 350grams- 4kg per yam pit (includes 2-3 yams) on average, while uncultivated yam pits (includes one yam) yield 280grams per pit (Dounias 2001). An average three-fold increase in yield was calculated when yams were actively cultivated (Dounias 2001). While the cultivation techniques used to manage wild yams differed from than those implemented in this research, the result in both cases was a significant increase in total food production.

Similar research on wild, *in situ* managed and cultivated columnar cacti (*Stenocereus stellatus*) in Mexico explored effects of cultivation on variation in culturally important fruit traits (Casas *et al.* 1999). Casas and colleagues (1999, 2006) reported that indigenous people cultivated populations of cacti in a natural setting or transplanted cacti into home gardens. In natural settings cacti that exhibit preferred traits (e.g. fruit colour, taste) were maintained, undesirable plants eliminated, and desirable plants propagated (branches planted). In home gardens, people protected volunteer seedlings with desirable qualities, and grew landraces received via trade from other people in same village or other villages (Casas *et al.* 2006). These strategies resulted in a significant increase in fruit size, mass of edible fruit pulp, and reduction in density of spines per fruit in cultivated natural and garden populations. For example, mean fruit size increased 23% in managed populations and 30% in cultivated gardens (Casas *et al.* 1999).

In this research, the act of planting wild seed in tilled soil with light weeding and watering resulted in an impressive increase in plant size and seed production compared to plant biomass and seed yield harvested from wild populations. While these differences

were likely due to phenotypic plasticity rather than genetic evolution, the fact that a large increase in total seed production was achieved suggests a potentially profitable resource. Similarities in seed production across years suggest that cultivation of wild *C. berlandieri* populations would make a stable food resource. If cultural groups sought to improve reliability of *C. berlandieri* populations then basic cultivation techniques would enable significant increases in seed production in consecutive years.

In the next chapter, I explore the nutritional value of wild *Chenopodium berlandieri* seed and the potential to harvest sufficient quantities from wild populations to make it economically viable.

Tables and Figures

Table 3.1: Habitat characteristics of wild *Chenopodium berlandieri* populations in Manitoba, North Dakota, Missouri and Ohio.
*Ehrlich *et al.* 1953; Ehrlich *et al.* 1957; USDA- NRCS 2013.

Population		River	Size (N, m ²)	Canopy	*Soil	Slope	Bank	Date of Harvest
MB	AB	Red	~100 (30m ²)	Open	Silty clay	~30° (upper terrace)	West	Sept 1
	DM	Assiniboine	~500 (6000m ²)	Open	Silty clay	~30° to 0° (bank of ditch)	West	Aug-Sept 14
	SV	Red	~500 (210m ²)	Semi- open	Fine clay	~40° to 0° (top of upper terrace)	East	Sept 14-30
ND	ND1	Red	2000+ 20x500 ⁺ m	Open	Silty clay	~30° (upper bank terrace)	East	Sept 20
	ND2	Sheyenne	~100 (50m ²)	Semi- closed	Silty clay	0° (upper terrace)	South east	Sept 20
	ND3	Sheyenne	~800 (750m ²)	Semi- open	Silty clay	0° (top of terrace)	South	Sept 20
MO	MM1	Missouri	~100 (500m ²)	Open	Silt clay loam	0° (top of floodplain bank)	na	Oct 30
	MM4	Missouri	~100 (500m ²)	Open	Silt clay loam	0° (top of floodplain bank)	na	Oct 30
OH	OH1	Scioto	~250 (800m ²)	Open	Silt loam	0° (top of floodplain bank)	na	Nov 5
	OH4	Scioto	5000+ 50x500 ⁺ m	Open	Silt loam	0° (top of floodplain bank)	na	Nov 5

Table 3.2: Sub-region (province and state) and population level effects on plant and seed traits used to characterize ten wild populations of *Chenopodium berlandieri*. Values reported in Table are *F*-ratios and associated degrees of freedom for each effect. Significant denoted by **P*<0.05, ** *P*<0.01, ****P*<0.001, not significant (n.s.).

Effect		Plant Size Index	Total Seed Mass
Sub-region	F _{3, 6}	45.18*	11.42 ***
Population (Sub-region)	F _{6, 400}	6.65*	13.21***

Table 3.3: Analysis of variance for plant traits in different locations for the common garden populations in 2011 and 2012. Values reported in Table are *F*-ratios and associated degrees of freedom for each effect. Significant denoted by **P*<0.05, ** *P*<0.01, ****P*<0.001, not significant (n.s.).

2011		Plant Index	Seed Mass
Effect	F _{1-20, 32-61}		
Population	F _{1, 32}	10.41***	7.35**
Location	F _{1, 61}	423.75***	612.46***
Population*Location	F _{1, 61}	3.20 n.s	0.17 n.s
Maternal line (Population)	F _{20, 62}	4.36***	3.01***
2012			
Effect			
Population	F _{2, 213}	0.74 n.s	1.50 n.s
Location	F _{1, 9-11}	249.31***	116.79***
Population*Location	F _{2, 213}	4.65**	7.33***
Maternal line (Population)	F _{33, 213}	1.86**	1.75**
Replicate (Location)	F _{4, 213}	2.42*	3.65***

Table 3.4: Analysis of variance for perisperm diameter (seed size) of *Chenopodium berlandieri* for ten wild and two common garden populations grown in 2011 and 2012. Common garden populations analyzed for location and year. Values reported in Table are *F*-ratios and associated degrees of freedom for each effect. Significant denoted by **P*<0.05, ** *P*<0.01, ****P*<0.001, not significant (n.s.).

Effect	Wild Populations		Common Garden 2011		Common Garden 2012	
Sub-region	<i>F</i> _{3,6}	1.30 n.s				
Population (Sub-region)	<i>F</i> _{6,400}	168.73***				
Population			<i>F</i> _{1,33}	46.41***	<i>F</i> _{2,212}	127.91***
Location			<i>F</i> _{1,62}	2.62 n.s	<i>F</i> _{33,212}	28.96***
Population*Location			<i>F</i> _{1,62}	14.24***	<i>F</i> _{2,212}	24.33***
Maternal line (Population)			<i>F</i> _{20,62}	4.38***	<i>F</i> _{1,11}	26.10***
Replicate (Location)					<i>F</i> _{4,212}	3.65*

Table 3.5: Analysis of variance for phenological stages for *Chenopodium berlandieri* common garden populations grown in 2011. Common garden grown plants analyzed for population and location. Values reported in Table are *F*-ratios and associated degrees of freedom for each effect. **P*<0.05, ** *P*<0.01, ****P*<0.001, not significant (n.s.).

Effect		First leaf	First open flower	First seed	Harvest
Population	<i>F</i> _{1,36,48}	7.12**	1.88 n.s.	1.36 n.s.	2.08*
Location	<i>F</i> _{1,62-64}	38.49***	9.65**	0.05 n.s.	4.44***
Population*Location	<i>F</i> _{1,62-64}	34.74***	12.15***	12.61***	2.40**
Maternal line (Population)	<i>F</i> _{20,62-64}	46.11***	46.73***	9.94**	3.6***

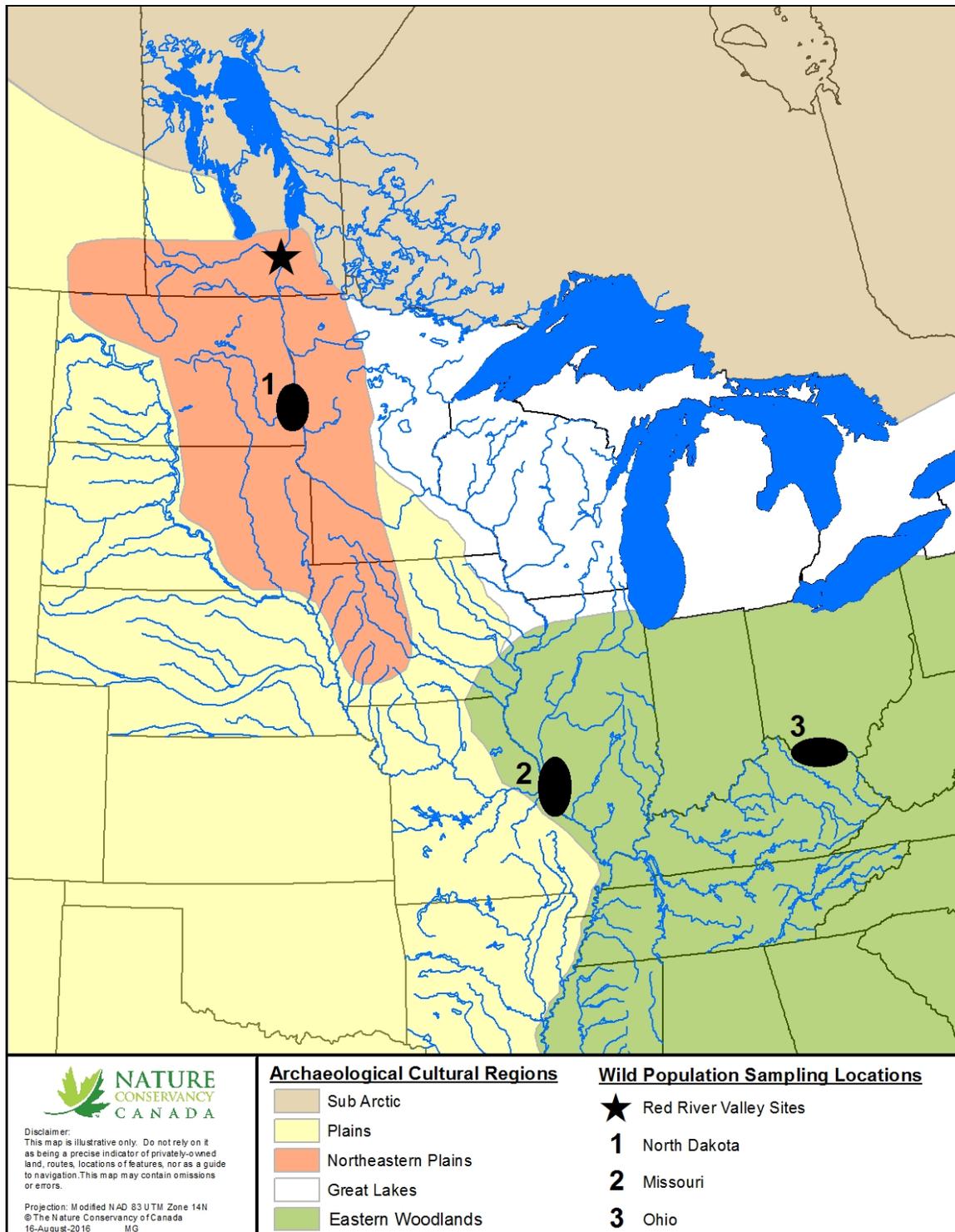


Figure 3.1: Map indicating sampling locations of wild *Chenopodium berlandieri* populations in southern Manitoba, North Dakota, Missouri and Ohio in relation to broad archaeological cultural regions.

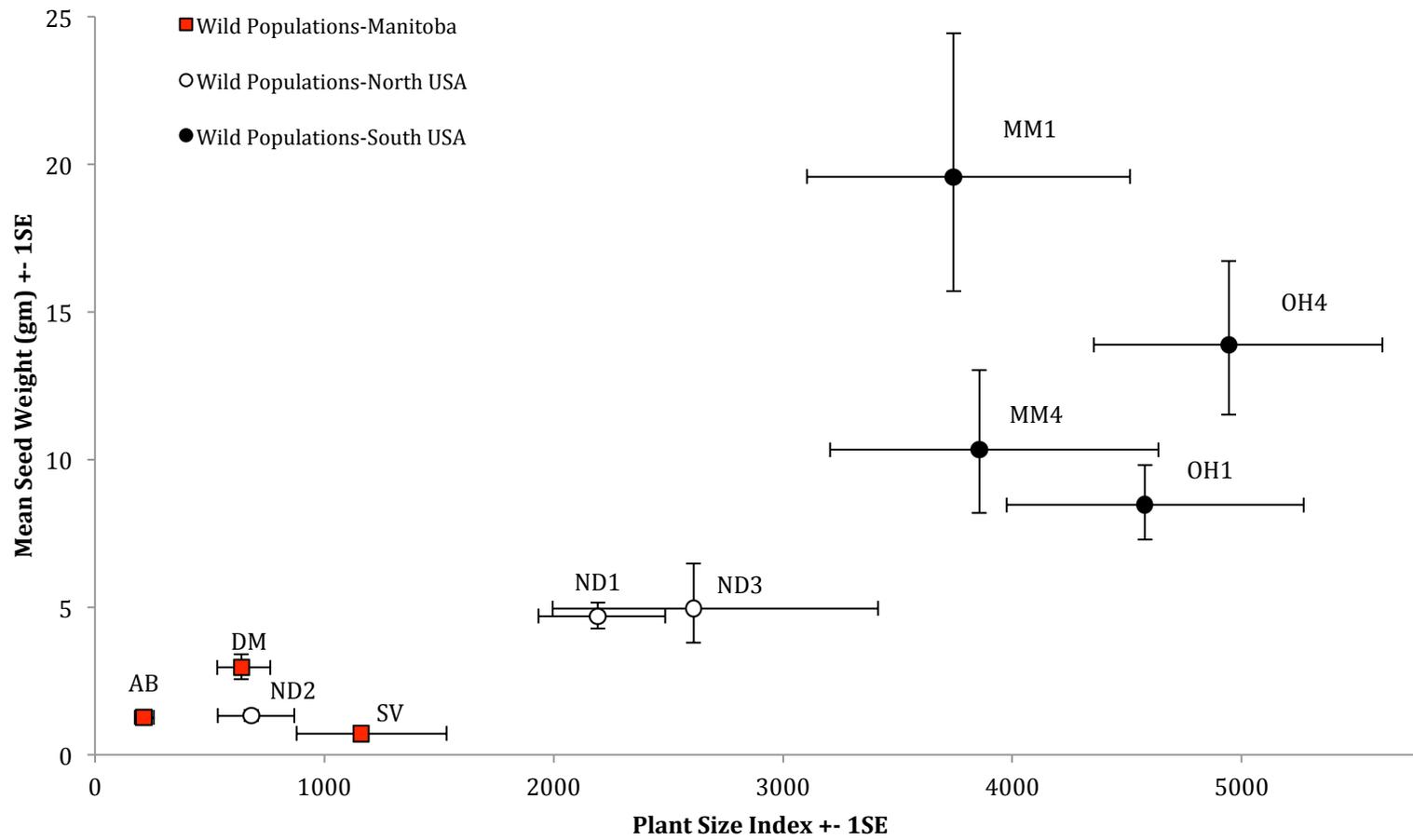


Figure 3.2: Mean plant size index compared to mean total seed mass for ten wild *Chenopodium berlandieri* populations. Back-transformed data presented.

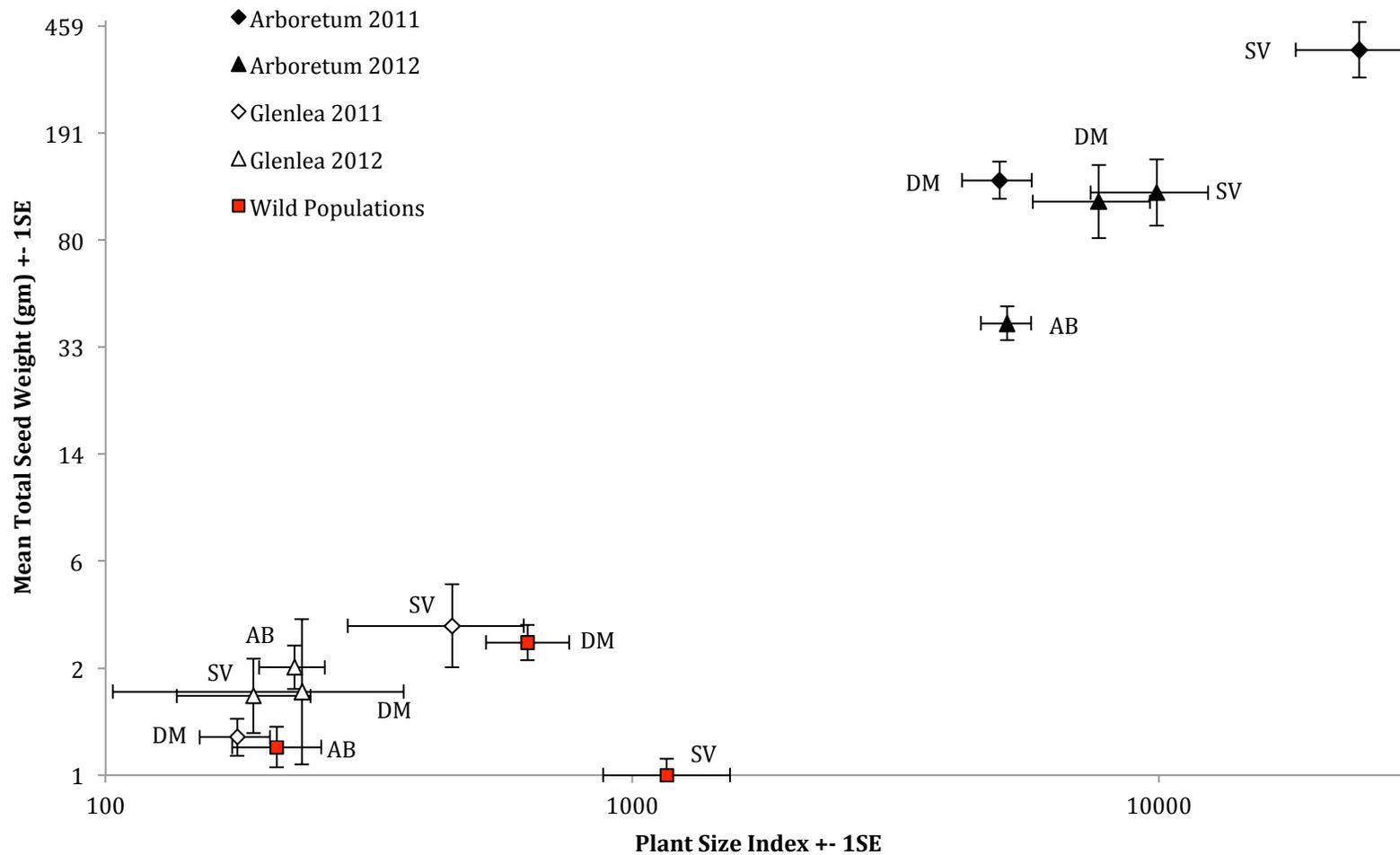


Figure 3.3: Plant size index compared to mean total seed mass from three wild *Chenopodium berlandieri* populations grown in a common garden setting at two locations over two years. DM, and SV populations were grown in 2011. Wild AB, DM, and SV populations were grown in 2012. Back transformed data presented on a logarithmic scale for easier viewing.

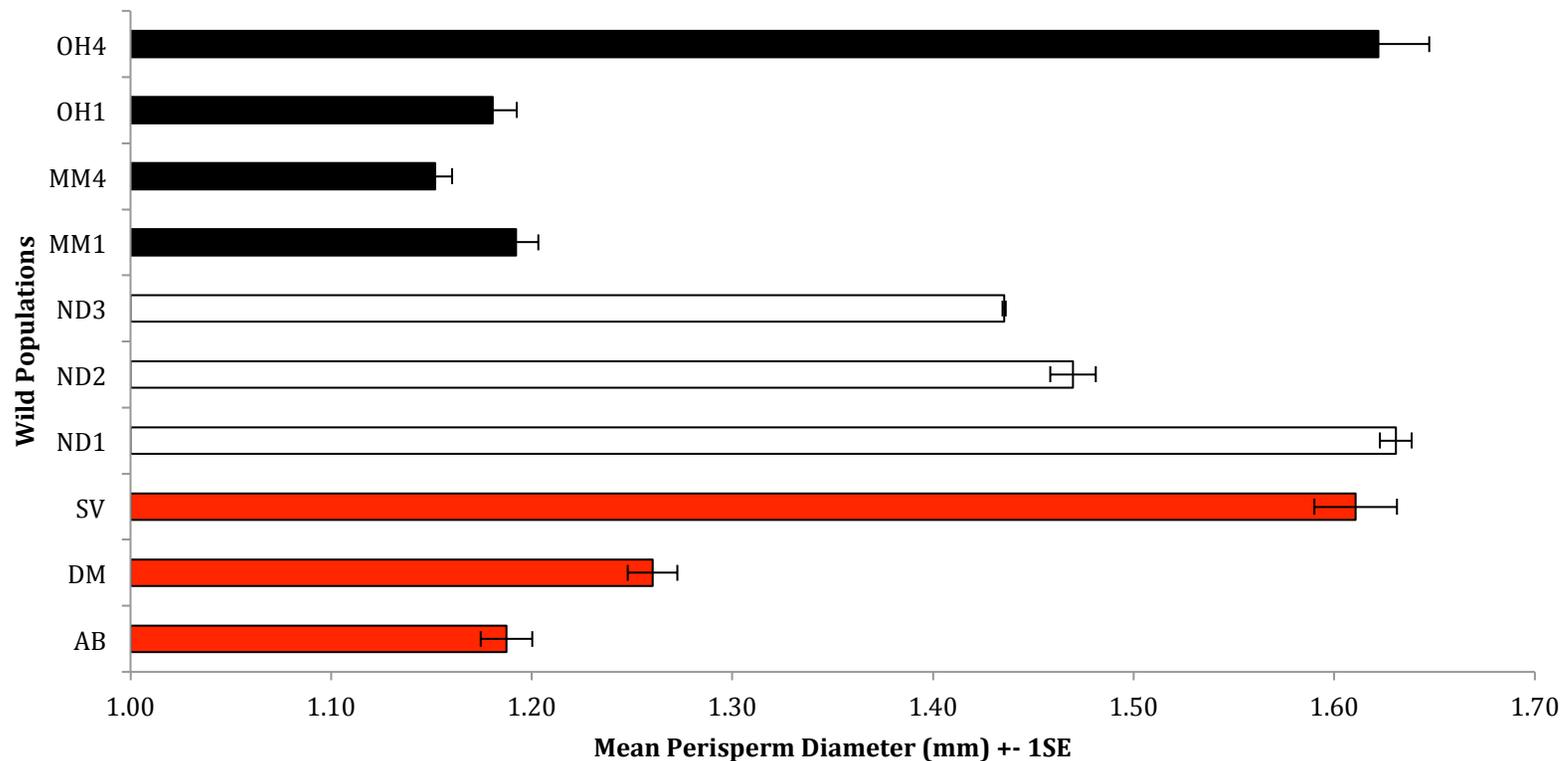


Figure 3.4: Mean perisperm diameter for all wild *Chenopodium berlandieri* populations. Bimodal distribution reflected by some populations exhibiting a small mean seed size (<1.30mm) with other populations exhibiting a larger mean seed size (>1.40mm). Red bars represent Manitoba populations; unfilled bars represent North Dakota populations; filled bars represent southern United States populations Missouri (MM) and Ohio (OH).

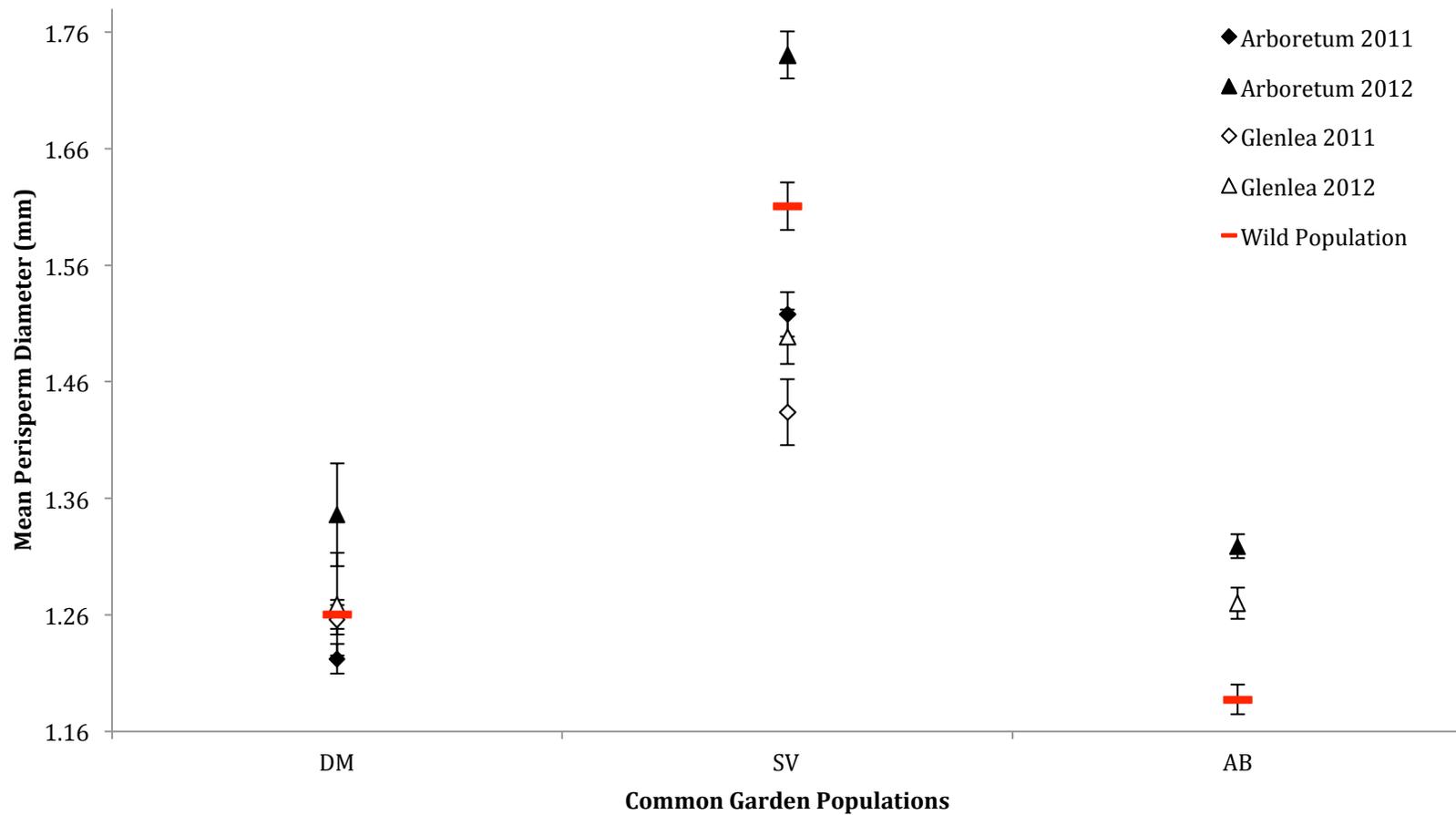


Figure 3.5: Mean perisperm diameter calculated from two years of common garden populations of *Chenopodium berlandieri* from Manitoba. Common garden plants grown from wild AB, DM, and SV populations. Two years of data were collected for DM and SV; only one year of data was collected for AB.

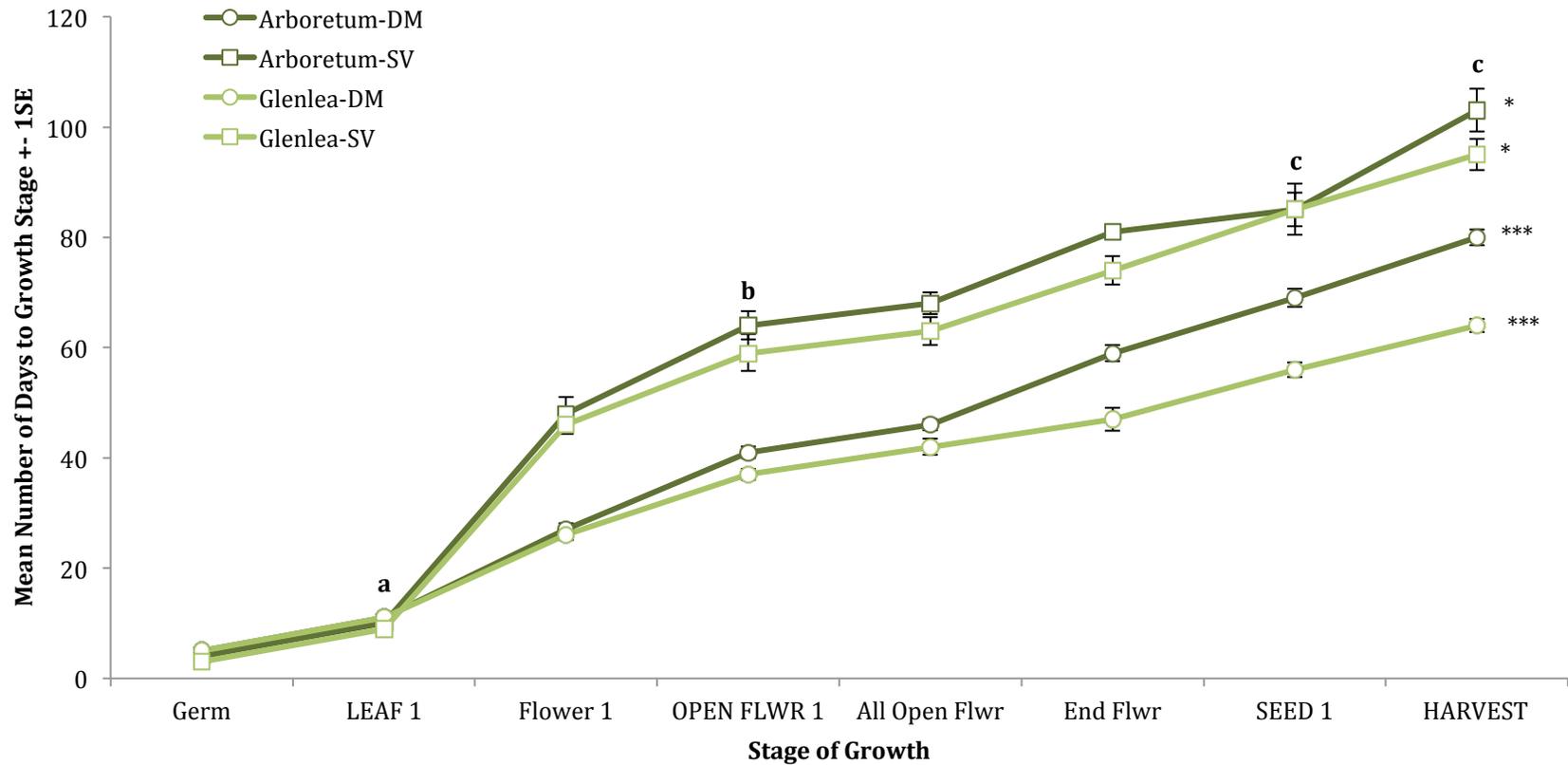


Figure 3.6: Mean number of days to reach each stage in *Chenopodium berlandieri* growth cycle from germination to harvest for two Manitoba populations (DM, SV) grown in two common garden locations (Arboretum, Glenlea). Uppercase indicates that a stage was analyzed statistically. Significant effects at difference stages: population (a), population and location (b), and population, location and population by location interactions (c). Significant differences between least square means for days to harvest: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

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Appendix 3.1

Native and introduced competitive species of *Chenopodium berlandieri* identified from all populations included in this study.

**Chenopodium missouriense* in Eastern Woodlands subsumed under *C. album* (cf. Flora of North America 1997+).

Species	Common name	Status	AB	DM	SV	N1	N2	N3	M1	M4	O1	O4	N
Amaranthaceae													
<i>Amaranthus</i> sp.	Amaranth								x	x	x	x	4
<i>Chenopodium album</i> *	Lambs-quarters	I	x	x	x	x	x	x	x	x	x	x	10
<i>C. capitatum</i>	Strawberry blight	N		x									1
<i>C. rubrum</i>	Red goosefoot	N		x									1
<i>C. simplex</i>	Maple leaved goosefoot	N	x	x			x	x	x	x	x		7
Apocynaceae													
<i>Asclepias</i> sp.	Milkweed	N				x							1
Asteraceae													
<i>Ambrosia</i> sp.	Ragweed	N							x				1
<i>Cirsium arvense</i>	Canada thistle	I	x	x	x	x							4
<i>Helianthus</i> sp.	Sunflower	N					x	x					2
<i>Heliopsis</i> sp.	False dandelion	N				x		x	x	x	x		5
<i>Matricaria discoidea</i>	Pineapple weed	N		x									1
Brassicaceae													
<i>Thlaspi arvense</i>	Shepherd's purse	I	x	x									2
Curcubitaceae													
<i>Echinocystis lobata</i>	Wild cucumber	I			x	x							2
Equisetaceae													
<i>Equisetum arvense</i>	Horsetail	N					x	x					2
Fabaceae													
<i>Melilotus alba</i>	White clover	I		x									1
Poaceae													
	Grasses		x	x	x	x	x	x	x	x	x	x	10
<i>Agropyron repens</i>	Quack grass	I	x	x									2

Appendix 3.1 continued

<i>Echinochloa crusgalli</i>	Barnyard grass	I	x	x								2
<i>Panicum virgatum</i>	Switch grass	I						x				1
<i>Hordeum jubatum</i>	Foxtail barley	N						x	x	x	x	4
<i>Triticum aestivum</i>	Wheat	I		x								1
Polygonaceae												
<i>Polygonum</i> sp.	Knotweed/ Smartweed	N, I	x	x	x	x			x	x		6
<i>Rumex</i> sp.	Dock	N, I		x		x			x	x	x	6
Rosaceae												
<i>Rosa arkansas</i>	Prairie rose	N		x								1
Salicaceae												
<i>Salix</i> sp.	Willow	N				x	x		x	x		5
Total Species			8	15	6	9	5	7	10	9	7	5

Appendix 3.2

Regional mean plant index and total seed mass for wild populations. Mean, upper standard error (USE) and lower standard error (LSE) calculated using SAS. Back-transformed numbers are reported.

Region	Plant Size Index			Total Seed Mass (grams)		
	Mean	USE	LSE	Mean	USE	LSE
Manitoba	538	66	59	1.39	0.14	0.13
North Dakota	1575	189	169	3.13	0.35	0.31
Missouri	3799	661	563	14.23	2.32	2.00
Ohio	4758	775	666	10.84	1.61	1.40

Appendix 3.3

Mean plant index and total seed mass for population by location combinations grown in a common garden setting over two years. Mean, upper standard error (USE) and lower standard error (LSE) calculated using LS Means. Back-transformed numbers are reported for seed mass only.

Year	Soil & Population	Plant Size Index			Total Seed Mass (grams)		
		Mean	USE	LSE	Mean	USE	LSE
2011	Glenlea-DM	178	27.22	23.61	1	0.22	0.19
2011	Glenlea-SV	455	167.00	122.17	3	1.37	0.97
2011	Arboretum-DM	4980	753.99	654.84	130	21.23	18.25
2011	Arboretum-SV	24008	5810.68	4678.32	377	96.62	76.92
2012	Glenlea -AB	228	32.48	28.44	2	0.47	0.39
2012	Glenlea -DM	236	132.64	84.90	2	1.60	0.89
2012	Glenlea -SV	191	54.24	42.24	2	0.68	0.50
2012	Arboretum -AB	5152	567.16	510.91	40	6.01	5.23
2012	Arboretum -DM	7690	1927.77	1541.36	109	37.81	28.07
2012	Arboretum -SV	9903	2493.31	1991.83	117	36.62	27.90

Appendix 3.4

Mean days to selected phenological stages for wild *Chenopodium berlandieri* populations by location combinations grown in a common garden setting. Mean, upper standard error (USE) and lower standard error (LSE) calculated using LS Means. Back-transformed numbers are reported.

Soil type & population	First leaf			First open flower			First mature seed			Harvest		
	Mean	USE	LSE	Mean	USE	LSE	Mean	USE	LSE	Mean	USE	LSE
Glenlea DM	11	0.35	0.34	37	1.01	0.98	56	1.35	1.32	64	1.19	1.17
Glenlea SV	9	0.63	0.59	59	3.46	3.27	85	4.79	4.53	95	2.87	2.79
Arboretum DM	11	0.35	0.34	41	1.09	1.06	69	1.64	1.60	80	1.47	1.44
Arboretum SV	10	0.47	0.45	64	2.61	2.50	85	3.09	2.98	103	3.95	3.79

4.0 ASSESSING THE ECONOMIC POTENTIAL OF *CHENOPODIUM BERLANDIERI* POPULATIONS IN PRE-CONTACT MANITOBA SUBSISTENCE STRATEGIES.

4.1. Introduction

During the Late Pre-contact period (~AD800-1600) numerous cultural groups practiced a range of economic strategies in southern Manitoba. These strategies include generalized hunter-gatherer lifestyles, Plains bison hunting, and small-scale horticulture (Hamilton and Nicholson 2006). However, recent research indicates these strategies were not mutually exclusive. Mixed subsistence strategies emerged from a greater degree of population movement, long distance trade, and occasional hybridization of some cultural groups. Such strategies may have been more common than previously known (Boyd *et al.* 2008; Hamilton and Nicholson 2006; Nicholson *et al.* 2008; Syms 1977).

Information gained from macrobotanical remains (seeds, charcoal), microbotanical remains (pollen, phytoliths, starch granules) and plant residues (C and N isotopes) found on pre-contact ceramics provide new evidence for mixed subsistence strategies. Microbotanical and residue analyses on ceramic sherds from southern Manitoba indicate that cultural groups utilized a wide range of native plant species and tropical domesticated crops (Boyd *et al.* 2006; Boyd *et al.* 2008; Boyd and Surette 2010; Lints 2012; Quaternary 2010).

In southwestern Manitoba, it appears that domesticated maize and beans contributed fairly heavily to the diet of local Late Woodland groups, and it is possible that some communities were growing maize on a small scale (Boyd *et al.* 2006). Some of this evidence might reflect migration of small-scale agricultural groups associated with Late Plains Woodland groups (e.g. Scattered Village Complex, part of the Northeastern

Plains Village Aggregate) from North Dakota into southwestern Manitoba ca. AD1300 (Nicholson *et al.* 2006[2010]; Nicholson *et al.* 2011). Other agricultural groups associated with a Late Plains Woodland tradition (e.g. Northeastern Plains Village Complex, also part of the Northeastern Plains Village Aggregate, Toom 2004) may have migrated to the Lockport site in the Red River valley (Flynn 2002; McKinley 2001; Syms *et al.* 2010). The Kenosewun culture, a Late Plains Woodland group, is associated with small-scale maize agriculture, and harvesting a variety of native wild fruits (e.g. *Prunus virginiana*), nuts (*Corylus americana*), and seeds (e.g. *Chenopodium berlandieri*) (Deck and Shay 1992).

Use of domesticated plants extends through the boreal forest- prairie transition and into the boreal forest. Boyd and colleagues (2014) report that by AD700 maize (*Zea mays*) and native rice (*Zizania* sp.) consumption was widespread, but bean (*Phaseolus vulgaris*) use was limited at sites in the boreal forest region of southern Manitoba and northwestern Ontario. These crops, probably procured through long distance trade, supplemented locally sourced plant and animal resources (Boyd *et al.* 2008). Late Woodland groups (e.g. Blackduck, Rainy River Coalescent ~AD1000-1300) at the Forks site in the Red River valley relied heavily on native tubers (e.g. *Allium* sp.), fruits (e.g. *Symphocarpos* sp.), nuts (e.g. *Quercus* sp.), and seeds/leaves (e.g. Chenopodiaceae, *Cleome* sp., *Helianthus* sp., *Ziziana* sp.), incorporating some maize and beans into the diet (Quaternary 2010).

The microbotanical research described above has broadened our understanding of the quantity, range, and types of native plant species and domesticated crops relied on by various cultural groups. These studies also indicate the importance of native plant species

to the economy, even with the incorporation of domesticated crops to the diet. Numerous studies document the impact of maize and beans on pre-contact subsistence economies (e.g. Hart 2008; Pearsall 2007), and a growing number of studies examine the importance of native domesticates in the Central Plains, Eastern Woodlands and the Northeast (e.g. Adair 1988; George and Dewar 1999; Munson 1984; Smith 2007). Determining the economic potential of native plant species in southern Manitoba is one way to evaluate the quality of these resources and provides information on the potential role of native plant populations in a mixed subsistence economy.

In this chapter I explore the harvest yield potential and nutritional properties of wild *C. berlandieri* populations in Manitoba. *Chenopodium berlandieri* is ubiquitous in archaeobotanical assemblages in southern Manitoba (e.g. Deck and Shay 1992; Boyd *et al.* 2008), and has been recently recovered in microbotanical and residue analyses (Quaternary 2010). Cultural connections tie Manitoba to cultural groups from the Middle Missouri area of North Dakota where wild *C. berlandieri* was intensively harvested and some possible domesticated forms cultivated (Ahler 2007; Nickel 2007). Cultural influences from the Eastern Woodlands also exist, where *C. berlandieri* was domesticated for its seed and widely cultivated for millennia (Boyd *et al.* 2008; Smith 2007). Comparing yields available from native populations and the nutritional quality of the edible seeds from Manitoba with information gained from Eastern Woodland populations will situate this resource in a regional context.

Few harvest yield studies and nutritional analyses exist for *C. berlandieri*. Harvest studies focus on wild populations of *C. berlandieri* from the Eastern Woodlands (Smith 2007), *C. album* from the Midwest (Seeman and Wilson 1984), and *C. album* from the

UK (Stokes and Rowley-Conwy 2002). All studies use timed yield trials, noting duration of harvest (stripping seeds from plants) within 1m² plots. Stokes and Rowley-Conwy (2002) added to the timed trials by deliberately placing their plots over varying densities of plants to test if density of plants affected harvest rate. Conservative estimates of harvest yield for *Chenopodium berlandieri* range from 750 to 1500kg/ha or 0.7 to 1.1 kg cleaned seed per hour (Smith 2007: 177). Both yield and harvest rates are comparable to the lower range of cereal crops (Stokes and Rowley-Conwy 2002). To date, no harvest experiments have been conducted in southern Manitoba.

Nutritional value of wild plant foods provides a definable level of energy recouped from harvesting. Asch and Asch (1985) analyzed seed from two large plants, providing an initial assessment of nutritive value of *C. berlandieri* from the Midwest (Smith 2007). Compared to quinoa (*C. quinoa*), a related domesticate from Central and South America, wild *C. berlandieri* seeds appear to have similar protein and carbohydrate content, with less fat and higher fiber (Asch and Asch 1985, cited in Smith 2007; Abugoch James 2009). The higher fiber content of wild *Chenopodium* is probably due to the thick seed coat (Smith 2007). This suggests that wild populations have similar nutritional qualities compared to domesticated quinoa, and therefore, have similar food value (Asch and Asch 1985, cited in Smith 2007). Unfortunately, no nutritional analyses of wild *C. berlandieri* seed exist for southern Manitoban populations. These populations are approximately 1500km northwest of the area of pre-contact domesticates in Ohio. It is unknown whether wild *Chenopodium* nutritional content remains constant throughout its geographic range. Variation in nutritional level may be a reason for differential use across its range by cultural groups.

The only known drawback of consuming *Chenopodium*, determined from studies of quinoa, is production of saponins. Saponins include a wide range of glycosides, water soluble substances produced as a defense against herbivory (Abugoch James 2009). They are found throughout the plant, including the seed coat, are bitter tasting, and in large quantities, can reduce digestibility (Mastebroek *et al.* 2000). Variation exists for saponin; sweet genotypes have low saponin content (<0.11g/kg), while bitter genotypes have levels exceeding this threshold (Mastebroek *et al.* 2000). While *C. berlandieri* is similar in seed structure (Prego *et al.* 1998) and possibly nutritional analysis (Asch and Asch 1985, cited in Smith 2007), it is unknown whether *C. berlandieri* seeds also include saponin. Determining whether saponins are present in wild *C. berlandieri* populations in Manitoba would provide information on limitations to its use by cultural groups.

4.2 Objectives

Harvest yield and nutritional value are proxy measures of the time and effort necessary to collect and process foods for consumption and the amount of energy gained from such activities. To determine the economic potential of intensively harvesting or cultivating seed from wild *Chenopodium* populations in Manitoba, I focus on four main objectives.

1) To determine the time and effort required to harvest seed in Manitoba, I measured harvest yield (kg/ha) and harvest rate (kg/hour) and compared yields to previous research on wild plants and domesticated crops.

2) To determine the variation in harvest yield and rate across *C. berlandieri*'s eastern geographical range, I compare the yields and rates I calculated (Objective 1) to a

previous harvest experiment Smith (2007) conducted across Northeastern North America. This comparison will indicate if harvest potential remains consistent between the northwestern region (Manitoba) and regions in Northeastern North America.

3) To determine the nutritional value of wild *C. berlandieri*, I had the nutritional value of seed collected from wild populations in the Northeastern Plains (Manitoba and North Dakota) and Eastern Woodlands (Ohio) analyzed for carbohydrate, protein, fats, moisture, ash, fibre, and calories (energy). Comparing these results to nutritional analyses previously conducted on a wild *C. berlandieri* population from Illinois (Asch and Asch 1985) will reveal if nutritional level varies geographically.

4) Comparing nutritional value of wild *C. berlandieri* with quinoa (*C. quinoa*), will reveal if wild *C. berlandieri* has comparable nutritional levels to this highly nutritious (FOA 2015), and closely related domesticated. If wild *Chenopodium* seeds have comparable nutritional value, wild populations would have provided a valuable food resource for pre-contact cultural groups.

5) To determine if saponin is present in wild *C. berlandieri* populations, samples of seed from populations located in Manitoba, North Dakota, Missouri and Ohio (sub-regions) were tested. Initial testing for the presence of saponins will indicate potential limitations to pre-contact use.

4.3 Methods

4.3.1 Harvest experiment

I designed a harvest experiment to determine seed yield potential from *C. berlandieri* populations in Manitoba. The experiment took place in mid September 2010

along the west ditch of Diversion Road (co-ordinates 50.147921°, -98.383520°) leading to Delta Marsh Field Station, 26km north of Portage La Prairie, Manitoba. Portions of the ditch experience annual flooding from the diverted Assiniboine River, and in June I located a large population (800+ plants) of *C. berlandieri*.

Based on previous harvesting experiments (*cf.* Seeman and Wilson 1984; Smith 2007) nine 1m² units were deliberately placed in areas of high plant density to approximate a maximum harvest rate. Stem bases (total number of plants) were counted and terminal inflorescences approximated, providing density of inflorescences per plot. Harvesting took place within timed one-minute intervals. Inflorescences were stripped by hand into a garbage bag tied to the waist. I, and two assistants, harvested three units each for a total sample of nine units.

Stripped inflorescences were left in the opened plastic garbage bags to air dry in one of the buildings at the Delta Marsh Field Station immediately after the experiment. This decreased the possibility of mould forming in the bags. Harvested fruit samples were taken to the WIN Herbarium at the University of Manitoba where each sample was transferred to newspaper and fully air-dried. Each sample was carefully turned once or twice a day until completely dry. Samples were then placed in labeled paper bags for long-term storage in the herbarium.

Samples were screened through 6mm and 4 mm mesh to remove leaves, stem fragments and other debris leaving mature fruits⁵ surrounded by the perianth. These are considered unwinnowed samples. Unwinnowed samples were weighed on a Denver Instrument XP-1500 scale in grams.

⁵ An achene, or single seeded fruit encased in a thin pericarp (ovary wall). Harvested fruits tend to retain the perianth (fused sepals). Most authors use the terms seed and fruit interchangeably.

4.3.1.1 Chaff

Five seed samples were processed to collect chaff data, in addition to the chaff data collected from the harvest experiment (n= 9 samples). Two seed samples were from Manitoba grown common garden populations DM and SV. Three samples were from wild harvested USA populations, ND3 from North Dakota, and OH1 OH4 from Ohio.

Winnowing followed procedures described by Smith (2007). The first attempt consisted of placing the sample in a fine nylon mesh bag (0.3mm) and rubbing to remove the perianth, leaf, stem and other vegetative fragments. Samples were then tumbled down a flat sheet of the same mesh fabric in the hopes that the chaff would stick (*cf.* Smith 2007). Unfortunately the majority of perianth material was not removed by this method, and static electricity caused the fruits to stick to the fabric. Sieving through 2mm and 1mm nested screens did not separate the chaff from the fruits. This process also took almost an hour to complete, and it was deemed it too inefficient to continue processing the remainder of the samples in this way. (This sample was not included in the harvest rate or chaff analyses; see Sample 4 Table 5.1).

The remaining samples were poured onto an old cotton tea towel and vigorously rubbed between the hands, which removed much of the perianth from the fruit. At this point, 2mm and 1mm nested screens were used to remove stem, leaf and other vegetative fragments from the sample. At this stage the sample was considered winnowed and it was weighed. The time it took to process was also recorded. This process was more efficient than the initial attempt, and was used to process the remaining samples. To eliminate variation in processing, only the author processed seed samples.

4.3.1.2 Bruce D. Smith's (2007) harvest experiment

The data from my harvest experiment was supplemented with harvest data collected by Bruce Smith in 1987 from a series of harvest experiments conducted throughout the Eastern Woodlands region (Smith 2007). Smith conducted opportunistic harvest experiments in large populations during a field survey trip for *C. berlandieri*. When large populations were encountered, Smith stripped seed from a number of plants timing the duration of the harvest and weighing the resulting dry mass of the harvested seed (methods similar to those described above). He then calculated harvest yield (kg/ha) and harvest rate (kg/hour). In order to make direct comparisons with Smith's harvest data, only the data he collected using 1x1 meter test plots were used to supplement the harvest data from this experiment (Smith 2007:168, Table 7.2).

Smith's (2007) data included harvest yields and rates from 24 populations from Michigan, Ohio, Pennsylvania, Maryland, South Carolina, Arkansas, and Missouri. Each population was represented by a single estimate (datum). These were divided into four regions: northeast (Michigan, Ohio and Pennsylvania), east (Maryland and South Carolina), and southwest (Arkansas and Missouri). Each state (i.e. sub-region) is an average of one to three populations, except Missouri, which is an average of 16 populations (Smith 2007). State means were then averaged to obtain a regional mean and standard error.

I calculated sub-regional (e.g. Province, State) and regional (e.g. northwest) means and standard errors (PROC MEANS SAS 9.2, 2010) for the harvest yield (kg/ha), harvest rate (kg/hr) and percent chaff removed from seed. Traits were normally distributed (PROC UNIVARIATE SAS 9.2, 2010), satisfying assumptions of normality

and homogeneity of variances. Mean \pm the standard error are reported in all figures and tables.

To explore geographic variation in harvest yield, seed cleaning time, and percentage of chaff produced among sub-regions, I conducted three analyses of variance (PROC GLM, SAS 9.2, 2010). Dependent variables (Y) were mean harvest yield, mean harvest rate, and percentage of chaff produced. The model statement for each analysis was $Y = \text{region}$. Region was analyzed as a random effect.

4.3.2 Nutritional value and toxic limitation of C. berlandieri

To determine the food value of wild *C. berlandieri* across the Northeastern Plains and Eastern Woodlands regions, five seed samples, two from Manitoba, one from North Dakota, and two from Ohio, were sent for nutritional analysis.

Samples from each population consisted of a bulked seed sample of 200-300 grams from 15 to 35 individual plants per population. Wild populations in Manitoba did not produce an abundance of seed. To form suitable samples, individuals grown in a common garden setting from harvested wild individuals were sampled. Seed from 15-20 individuals from descendent populations was consolidated.

Samples sent for nutritional analysis were winnowed as close to pure seed as possible. Samples were first screened through 4mm and 2mm geological sieves to remove large leaf and stem fragments. This resulted in fruit with attached perianth, and small leaf and stem fragments. Winnowing consisted of removing all chaff, perianth and remaining debris, excluding the pericarp. This was accomplished by first briskly rubbing the fruits between rough leather glove-clad hands small quantities at a time, which

removed some perianths and broke down larger chaff fragments. This was then abraded against 0.5mm mesh in a geological sieve to help remove adherent perianths and to break down unwanted vegetative material. Small quantities of sample were thus worked through until clean seed remained in the sieve. Samples were weighed before and after processing and the percent chaff per sample calculated. While each sample was not directly timed, general duration was noted. The rough leather increased the amount of chaff removed compared to rubbing seed between cotton cloth. Winnowed samples consisted of pure fruit (pericarp adherent), although the Manitoba samples contained more tiny chaff fragments in the winnowed state than the other samples.

Samples of each area were submitted to SGS Lab Services Canada (Burnaby, BC) and tested for the main nutritional components protein, fat, carbohydrate, dietary fiber, ash, moisture, energy level, and essential mineral composition (Sodium, Iron, Calcium, Magnesium, Potassium, Zinc, Copper, Selenium and Manganese), plus Vitamin A/ Beta Carotene, and Vitamin C. Each sample was tested once for each nutritional component. Specific methodologies for each type of analysis are available from SGS Canada (Wilson pers. comm. 2015). Protein, fat, carbohydrate, fibre and ash were calculated by percent dry weight; moisture was calculated by percent fresh weight; energy was calculated in calories/ 100grams; vitamin A, and Beta Carotene were calculated as RE/100g; vitamin C and minerals were calculated as parts per million (ppm).

4.3.2.1 Quinoa nutritional analysis comparisons

To better understand the value of wild *C. berlandieri* seed, the values of protein, fat, carbohydrate, dietary fiber, ash, moisture, and calories were compared to published

values from domesticated quinoa. The same nutritional components from six primary studies on domesticated quinoa were sourced for comparison (White *et al.* 1955; Ruales and Nair 1992, 1994; Schlick and Bubenheim 1993; Koziol 1992; Wright *et al.* 2002; DeBruin 1963).

To assess differences in nutritional value between wild *C. berlandieri* collected in Manitoba and the USA, and domesticated quinoa, I conducted seven analyses of variance (PROC GLM, SAS 9.2, 2010). Dependent variables were percent of protein, fat, carbohydrate, dietary fiber, ash, and moisture, and energy level (calories). The model statement for each analysis was Y = group; the three groups were quinoa, *C. berlandieri* from Manitoba, and *C. berlandieri* from the USA. All factors in the model were considered fixed.

4.3.2.2 Saponins

Dried seed samples were also tested for presence/ absence of saponin. Nine wild and common garden populations were tested. Two additional Manitoba samples (DM and SV populations) of cleaned bulked seed were also tested. Three maternal lines per population were randomly sampled, and one gram of dried unwinnowed seed (seed with pericarp and perianth attached) was placed in a plastic 50ml graduated test tube with five milliliters of water. The test tube was capped and agitated for 10 seconds using a Vortex-Genie, speed 7. The presence of a white foamy layer indicated the presence of saponins in the fruit (Wright *et al.* 2002). A relative measure of saponins was based on amount and persistence of foam produced. Three levels were identified: no foam, little foam (less than 5ml) and lots of foam (more than 5ml). Foam that persisted longer than 10 minutes

indicated the presence of saponins (Abbas *et al.* 2012).

4.4 Results

4.4.1 Manitoba harvest experiment

In the harvest experiment conducted in Manitoba, an average 65g of fruit was gathered within a one-minute time frame (Appendix 4.1). This amount appeared to be surprisingly high to the author, as only a fraction of the fruit available per one m² plot was harvested. Wind affected the amount of fruit collected by either blowing fruit from the hand during harvest or blowing the harvest collection bag around, making it hard to get the fruit into the bag. When inflorescences were placed inside the bag prior to stripping, most of fruit landed in the bag. However, this slowed the harvester and reduced the amount of inflorescences stripped within the one-minute time frame.

4.4.2 Harvest yield and rate in the Northeastern Plains and Eastern Woodlands regions

Harvest yield and harvest rate data collected in this experiment and Smith's (2007) experiment varied across the Northeastern Plains and Eastern Woodlands (Table 4.1). Sub-regional effects accounted for some of the variation in yield and harvest rate. Analysis of variance indicated that sub-region significantly ($F=24.94$, $P<0.0001$) influenced harvest rate, but only slightly influenced ($F=3.84$, $P<0.02$) harvest yield (Table 4.2).

Yield and harvest rate were lowest in the northwestern sub-region (hereafter Manitoba) (Table 4.1). Yield ranged between 254 and 870 kg/ha (mean=497.32kg/ha), and a mean 0.2kg of cleaned seed was produced in an hour (Figure 4.1). The northeastern

sub-region produced the highest and most variable yields of all locations Smith (2007) sampled in the Eastern Woodlands, and compared to the harvest data from this experiment (Figure 4.1). Yields ranged from 680 – 2850kg/ha (mean =1287.4 kg/ha), and harvest rates averaged 1.6kg/hour (Figure 4.1). The wide variation in harvest yield in the northeastern data is likely due to the small number of samples (n=2) that met the requirements for inclusion in this analysis, and these two samples were quite different. One sample included the seed from one very large plant, while the other sample comprised bulked seed from 10 smaller plants (Smith 2007).

Manitoba produced significantly lower harvest yields than the northeastern and southwestern sub-regions, and less cleaned seed per hour compared to all other sub-regions (Table 4.2; Figure 4.1). Within the Eastern Woodland, the northeastern sub-region produced the largest yields (1290kg/ha) but not significantly larger than other sub-regions (Table 4.2). The northeastern and eastern sub-regions produced the largest quantity of cleaned seed per hour (1.12-1.3kg/hr). These rates were significantly higher than harvest rates from southwestern sub-region (Table 4.2).

4.4.3 Chaff

Analysis of variance indicated that the area where wild populations originated did not significantly affect quantity of chaff produced by any of the populations tested ($F < 4.5$, $P > 0.06$). Northern wild populations (mean =18.3) produced similar amounts of chaff to southern populations (mean =27.5). Common garden populations from Manitoba produced the highest quantities of chaff compared to all wild populations (Figure 4.4).

4.4.4 Nutritional analysis and toxic limitations

Chenopodium berlandieri in Manitoba was not significantly different in any nutritional component compared to *C. berlandieri* populations from the USA (Figure 4.3). Analysis of variance indicated significant differences ($F>10$, $P<0.004$) in nutritional components between wild *C. berlandieri* and domesticated quinoa (Table 4.3).

Chenopodium berlandieri was significantly higher in protein and total dietary fibre compared to quinoa, while quinoa was significantly higher in moisture and energy levels (Figure 4.3). Wild *C. berlandieri* in Manitoba had slightly higher levels of ash ($F= 4.7$, $P>0.04$) compared to quinoa, but these species were not significantly different in carbohydrate and fat levels.

4.4.4.1 Saponin tests

Saponins were present in all populations tested, and in all but three maternal lines tested (Table 4.4). Saponin was present in all USA maternal lines, however the amount of foam produced differed by maternal line and population. Two thirds (61%) of maternal lines produced more than 5ml of persistent foam, while the remainder produced less than 5ml of persistent foam. The USA populations produced larger quantities of foam, and had more persistent foam than the Manitoba populations. Of the Manitoba samples tested, 33% of maternal lines produced no foam, and 67% of maternal lines produced less than 5ml of foam, which readily broke down to a thin film that remained as long as the foam produced by USA populations. However, foam produced by the cleaned seed samples from Manitoba produced similar levels of persistent foam as the USA populations. The

results of this test suggested different saponin levels across maternal lines that require further testing.

4.5 Discussion

4.5.1 Cultivation potential of wild C. berlandieri seed

The harvest experiment indicated that a surprising amount of *C. berlandieri* fruit could be harvested and processed (200g cleaned seed per hour) with minimal effort from populations in Manitoba. This amount (200g) is equivalent to two serving sizes suggested for quinoa per the nutritional information on Safeway™ brand quinoa. Harvesting wild seed invariably led to seed loss, contributing to the seed bank, and potentially the next generation. Seed dispersion is a natural occurrence of wild *C. berlandieri*. However, pre-contact cultural groups may have deliberately dispersed the seeds from preferred plants. Combined with local plant management in natural habitats (cf. Casas *et al.* 2006), this could have led to an increase in plants with preferred phenotypes. Harvesting plants could have supported population regeneration creating a stable food source that could be visited annually.

Harvest yield from wild Manitoba populations is significantly lower than yields produced in wild Eastern Woodland populations (Smith 2007), and domesticated quinoa (Guenther 2014). Wild *C. berlandieri* populations in Manitoba produced 250-870kg/ha of winnowed seed, which is at the low end of the range (300-1800 kg/ha) produced in the Midwest and Southeast regions (Smith 2007). Smith (2007) suggests refining harvest yield to account for the thick testa, which domesticated forms lack. Smith calculated that testas accounted for approximately 30% of seed weight. Reduction of harvest yield from

his experiment by 30% (750-1500kg/ha to 525-1050kg/ha) resulted in a seed production rate comparable to quinoa harvest yield, e.g. 500-1000 kg/ha (Smith 2007:176, references therein). This yield is supported by modern quinoa harvests in Saskatchewan that range 336-2240 kg/ha, averaging 1120 kg/ha (Guenther 2014).

Additionally, total mean seed produced from seed harvested from wild Manitoba populations (DM, SV, AB, described in Chapter 3), were quite low (1-8 kg/ha) compared to the harvest experiment. Yields calculated from the common garden populations grown at two locations described in Chapter 3, averaged 26.15 kg/ha at Glenlea and 1325.32 kg/ha at the Arboretum. Reducing this range by 30% to account for the thick testa (cf. Smith 2007), yields ranged between 18.31- 927.72kg/ha from the common garden populations. The high end of this range is comparable to the mean quinoa production in Saskatchewan (Guenther 2014). This demonstrates the wide range of harvest yields obtainable from wild populations and the plasticity in seed production, which may have been influenced by common garden environment and cultivation techniques (e.g. weeding, watering, tilling the soil). This extends the possibility for cultural groups to influence seed production, suggesting high cultivation potential of wild *Chenopodium* populations.

Moderate to high yields were produced in wild populations of *C. berlandieri* in Illinois (750-1500kg/ha, Asch and Asch 1977), in *C. album* (276 and 2854 kg/ha, Stokes and Rowley-Conwy 1984), and in *C. missouriense* (450-900 kg/ha, Seeman and Wilson 1984). Smith (2007) and Stokes and Rowly-Conwy (2002) suggest wild populations of *C. berlandieri*, *C. album*, and *C. missouriensis* would produce yields closer to the high end of the range expressed across small seed producing species. In these studies plants were

located in large populations (10,000 plus plants), which could be exploited over a longer season. For example, one of the large populations of *C. missouriensis*, located in an abandoned garden in Indiana, was harvested on several occasions from September to December due to *C. missouriensis* retaining its fruit on the plant (Seeman and Wilson 1984).

Low to moderate yields were obtained from other small seeded annuals including *Iva annua* (255-620kg/ha, Smith 2007), *Polygonum* species (145-1100kg/ha; Murray and Sheehan 1984), and *Amaranthus* species (204kg/ha, Peterson and Munson 1984). It should be acknowledged that in these studies yields at the high end of the range represent calculated maximum yields in the most optimal conditions (*cf.* Murray and Sheehan 1984).

Overall yields in Manitoba are moderate compared to the Eastern Woodlands and domesticated quinoa, but the time required to clean wild seed from Manitoba may have limited the potential for cultivating large populations of *Chenopodium*. The harvest rate is low, 0.18-0.63kg clean seed per hour, compared to 0.75-1.5kg clean seed per hour from the Eastern Woodlands. Only Smith's (2007) experiment on wild *C. berlandieri* calculated harvest rate. None of the above mentioned harvest experiments for other small seeded annuals calculated the time it took to clean the seed.

Harvest rate may be influenced by the amount of chaff (dried flower parts) retained on the seed. Although Manitoba samples did not produce significantly more chaff compared to the Eastern Woodlands samples (Figure 4.2), *C. berlandieri* fruits and perianth fragments were difficult to separate with any methods used. From Smith's description fruits were readily removed from their perianths and clean fruit with only a

low quantity of chaff were recovered (Smith Pers. comm. 2011). However, partially processed fruit would be compact enough to store easily. This is similar to a harvesting experiment on *C. album*, where stem, leaves and other large contaminants were extracted from the collected samples leaving the fruit in perianth as the final storable/edible product (Stokes and Rowley-Conwy 2002). It is probable that prior to consumption *C. berlandieri* could be winnowed in a light breeze (*cf.* Seeman and Wilson 1984) or mixed with water to float off the chaff.

4.5.2 Nutritional value of Manitoba *Chenopodium berlandieri*

This study indicated that wild *Chenopodium berlandieri* populations have similar nutritional values to domesticated quinoa in terms of protein, carbohydrate, fat, moisture and ash or mineral content. This supports the previous study by Asch and Asch (1985). Asch and Asch calculated protein, fat, carbohydrates, and fibre levels for seed from two plants collected in Illinois (1985 cited in Smith 2007:179), which were similar to levels reported for domesticated quinoa (Figure 4.3; Appendix 4.2) (DeBruin 1963; Koziol 1992; Ruales and Nair 1992, 1994; Schlick and Bubenheim 1993; White *et al.* 1955; Wright *et al.* 2002). However, statistical analysis indicates quinoa was significantly higher in carbohydrates and calories, while wild *C. berlandieri* was significantly higher in protein and total dietary fibre. The process of domestication resulted in a reduced testa thickness and increase in perisperm diameter, the main nutritive tissue for seedling development in *C. berlandieri* (Smith 1985:166). The perisperm contains high carbohydrate levels, while the embryo and endosperm tissue, a 1-2 cell thick lining surrounding the radicle, are protein rich (Prego *et al.* 1998). Thick seed coats in wild

seeds probably contribute to the higher fibre content calculated for wild populations. Similar values for the main nutritional components between Manitoban and USA populations suggest wild Manitoba populations of *C. berlandieri* would have provided a similar level of nutrition as populations cultivated or domesticated in the Eastern Woodlands.

It has been suggested that *C. berlandieri* has a similar amino acid pattern to quinoa (Smith 2007:179) although amino acid profiles for Manitoba samples were not obtained in this research. Quinoa contains high quantities of lysine and methionine, two important amino acids necessary for protein building and human nutrition (Schlick and Bubenheim 1993). Quinoa's rich lysine content makes it a complete protein, and lack of gluten makes it ideal for celiac sufferers (Abugoch James 2009). If wild Manitoba *Chenopodium* contains a similar amino acid profile, then wild *Chenopodium* would be an important vegetable protein source. This situation would increase its potential for intensive harvesting or cultivation.

Chenopodium berlandieri has comparable nutritional profiles to other important North American domesticated crops, maize, beans, squash, and sunflower (see Appendix 4.3). It has similar levels of moisture and ash/ mineral content as the other domesticates, as well as similar levels of carbohydrates as maize and beans, but double the carbohydrate count of pumpkin and sunflower (Bressani *et al.* 1953; Cancelon 1971; Enyisi *et al.* 2014; Lazos 1986; Sotelo *et al.* 1995). *Chenopodium berlandieri* shares similar fat content with maize, but contains around a quarter of the fat in sunflower (Lazos 1986; Wan *et al.* 1979). Wild *C. berlandieri* has vastly higher fibre content than

all other domesticates (Ardabili *et al.* 2011; Ingale and Shrivastava 2011; Lazos 1986; Wan *et al.* 1979).

Similar nutritional profile of wild *Chenopodium* to quinoa would allow it to be a valuable addition to pre-contact diets. Since wild *Chenopodium* is so similar to quinoa, it is probable that the serving size designated for quinoa would provide a suitable comparison. Using the nutritional facts provided on commercial quinoa, one cup uncooked results in three cups of cooked quinoa; and a half cup (100g) uncooked is suggested as a serving size for quinoa. This provides 5% fat, 13% carbohydrates, 20% fibre and 15% iron of an adult's daily intake. Wild *Chenopodium* has higher fibre and protein levels, but lower total carbohydrates, which would alter the percent daily intake for these nutritional components. Wild *Chenopodium* seed would have been an important inclusion into a pre-contact diet that may have included some imported domesticates and a range of wild plant foods.

The only limitation to wild *Chenopodium* is the saponin contained in its pericarp (remnant fruit), testa (seed coat) and embryo (Lopez *et al.* 2011; Prego *et al.* 1998). Saponins are plant glycosides that produce a bitter flavour and can interfere with digestive enzymes preventing the absorption of nutrients (Schlick and Bubenheim 1993). Some quinoa studies note that freeing the seed from the pericarp or washing the seeds in water prior to consumption is necessary to remove saponins (Lopez *et al.* 2011). The presence/absence test conducted in this study indicated that wild *C. berlandieri* also contains saponins in the fruit, seed, or potentially in the chaff, as unwinnowed fruits were tested. Other parts of the *C. berlandieri* plant, especially leaves, contain levels of saponin (Mastebroek *et al.* 2000). This finding should be confirmed with further testing. Wild *C.*

berlandieri also showed variation in saponin levels between maternal lines, suggesting that some maternal lines may contain low or no saponins similar to some varieties of quinoa. Previous studies have indicated there are “bitter” and “sweet” varieties of quinoa, containing more or less than 0.11% saponin, respectively (Lopez *et al.* 2011). A single dominant gene controls saponin content in *C. quinoa*, and mass selection for “sweet” varieties has been conducted with varying success, as quinoa has an outcrossing breeding system (Mastebroek *et al.* 2000). Further research will elucidate the extent of “bitter” and “sweet” lines in wild *C. berlandieri*.

Based on the above research, the economic potential of intensively harvesting or cultivating seed from wild *Chenopodium* populations in Manitoba is high. Wild populations produce moderate amounts of seed that can be cleaned for use with low to moderate effort. It is possible that the low frequency of wild populations on the landscape (see Chapter 3) may have limited its probability of domestication, compared to the high seed yields and high frequency of large populations in the Eastern Woodlands. Seed from wild *C. berlandieri* in Manitoba contains similar nutritional value as wild populations from the Eastern Woodlands region where it was domesticated, but contained higher protein and fibre levels than domesticated quinoa. Further, wild populations in Manitoba showed varied saponin content between maternal lines, suggesting the possibility of “bitter” and “sweet” varieties, similar to quinoa. While saponin content requires additional testing, all lines of evidence suggest that local *C. berlandieri* seed was a viable and nutritious wild resource, and indicates the potential of this species to be incorporated into small-scale food production systems.

Tables and Figures

Table 4.1: Harvest yield (kg/ha) and harvest rate (kg/hour) data calculated for eight locations in four regions across the Northeastern Plains and Eastern Woodlands. Mean and standard error for each region and location are presented. Data from the northwestern region (Manitoba) collected from this study. All other data collected by Smith (2007), see Methods for details.

Region	Location	Harvest Yield		Harvest Rate	
		Mean	SE	Mean	SE
Northeastern Plains					
	Northwest (Manitoba)	497	81.77	0.28	0.06
Eastern Woodlands					
	Northeast	1287	418.57	1.31	0.15
	Michigan (MI)	741	177.50	1.02	0.33
	Ohio (OH)	1767	1087.50	1.31	0.30
	Pennsylvania (PA)	1423	.	0.95	.
	East	653	153.11	1.31	0.15
	Maryland (MD)	735	224.50	1.23	0.21
	South Carolina (SC)	490	.	0.95	.
	Southwest	946	85.68	0.84	0.05
	Arkansas (AR)	1045	111.88		
	Missouri (MO)	923	102.86	0.84	0.06

Table 4.2: Analysis of variance of harvest yield (kg/ha) and harvest rate (kg/hour) data in four regions across the Northeastern Plains and Eastern Woodlands. LS Means calculated from 33 populations from GLM reported. Lowercase letters denote significant differences between regions. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, not significant $P > 0.05$.

Effect	Harvest Yield	Harvest Rate
Region	$F_{3, 29}$	24.94 ***
Region	Mean +- SE	Mean +-SE
Northwest (Manitoba)	497 +-150.2 a	0.28 +-0.07 b
Northeast	1287 +-201.5 bc	1.12 +-0.1 a
East	653 +-260.2 ac	1.31 +-0.13 a
Southwest	946 +-112.6 bc	0.84 +-0.06 c

Table 4.3: Analysis of variance of main components of nutritional value comparing wild *C. berlandieri* in Manitoba (n=2) with wild *C. berlandieri* from the USA (n=3) and domesticated quinoa (n=6). Protein, carbohydrate, fat, total dietary fibre and ash content expressed as percent dry weight. Moisture is expressed as percent fresh weight, and energy is expressed in calories per 100grams. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, not significant $P > 0.05$.

Component	Wild versus Domesticate
	$F_{2, 49}$
Protein	10.00**
Carbohydrate	3.76 n.s.
Fat	0.68 n.s.
Total Dietary Fibre	57.57***
Ash	4.71*
Moisture	14.67**
Energy	30.68**

Table 4.4: Presence/ absence of saponins in fruits and surrounding perianth of *Chenopodium berlandieri* from populations in Manitoba, North Dakota, Missouri and Ohio. Three maternal lines per population were tested. Samples of fruit (perianth removed) from two Manitoba populations (DM and SV) were tested to determine if saponin was present in cleaned seed. Presence (X) scored by amount (0ml, <5ml, 10ml +) of foam produced and maintained after one hour.

Region	Population	0ml	<5ml	10ml +
Manitoba				
	AB Arboretum 2011	X	XX	
	DM Arboretum 2012		XXX	
	SV Arboretum 2012	XX	X	
	DM- seed only			X
	SV- seed only			X
North Dakota				
	ND1		XXX	
	ND2			XXX
	ND3		XX	X
Missouri				
	(MM1)			XXX
	MM4		X	XX
Ohio				
	(OH4)		X	XX

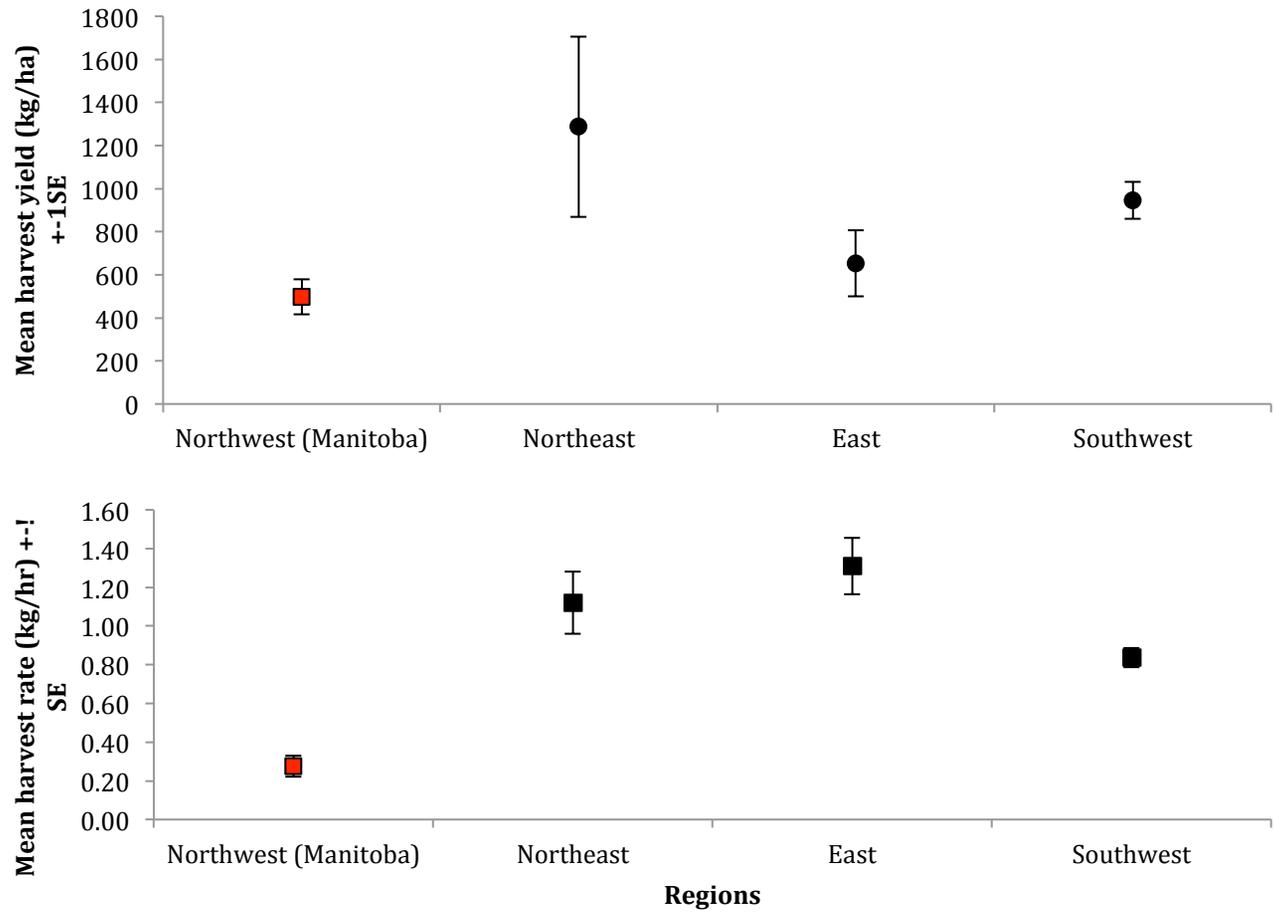


Figure 4.1: Mean yield (kg/ha) and mean harvest rate (kg/hr) from wild *Chenopodium berlandieri* populations in four regions. Harvested locations (see Table 4.1) are averaged within region. Manitoba data (Northeastern Plains) collected in this study. Smith (2007) collected all other sub-regional data in the Eastern Woodlands.

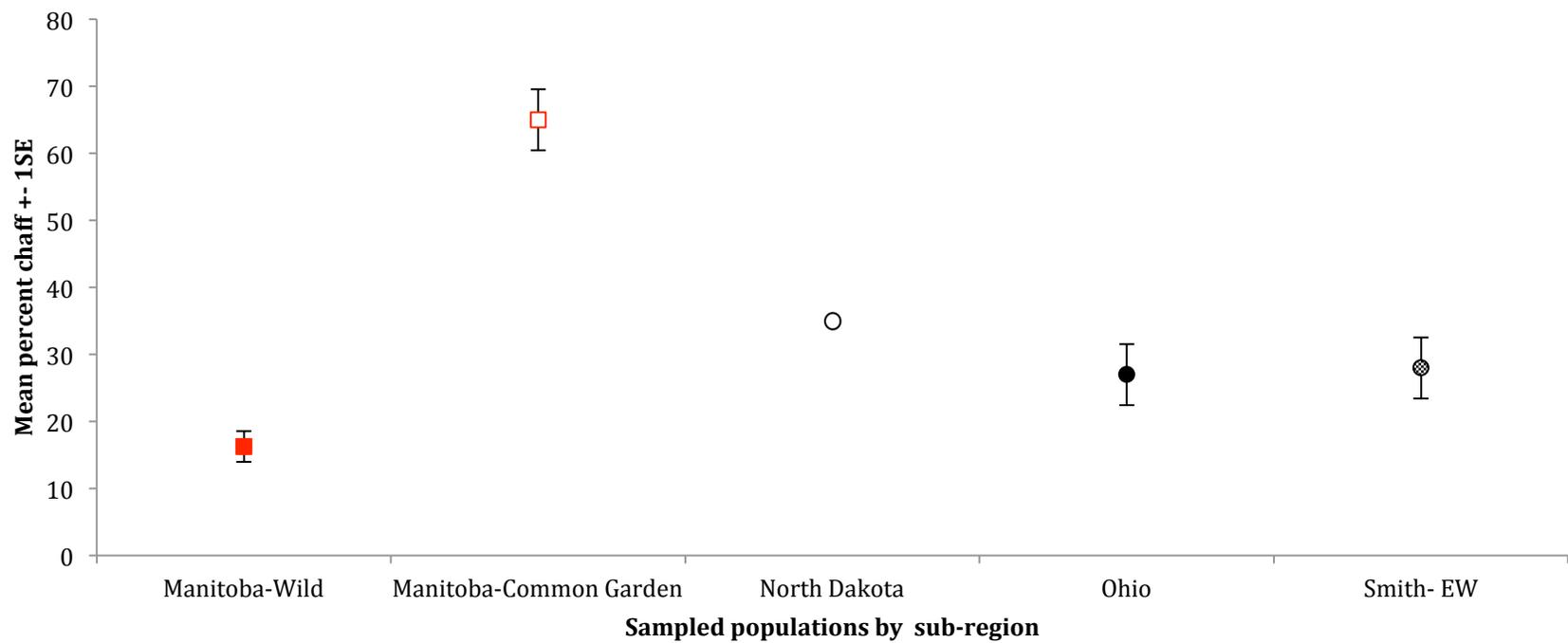


Figure 4.2: Mean percent chaff processed from wild and common garden populations of *Chenopodium berlandieri*. Data from this study from three sub-regions: Manitoba includes a wild population (DM-MB, n=8) and a common garden population (CG-MB, n=2); populations from North Dakota (ND, n=1) and Ohio (OH, n=2). Eastern Woodland data (Smith-EW, n=2) are from Smith's (2007) harvest experiment.

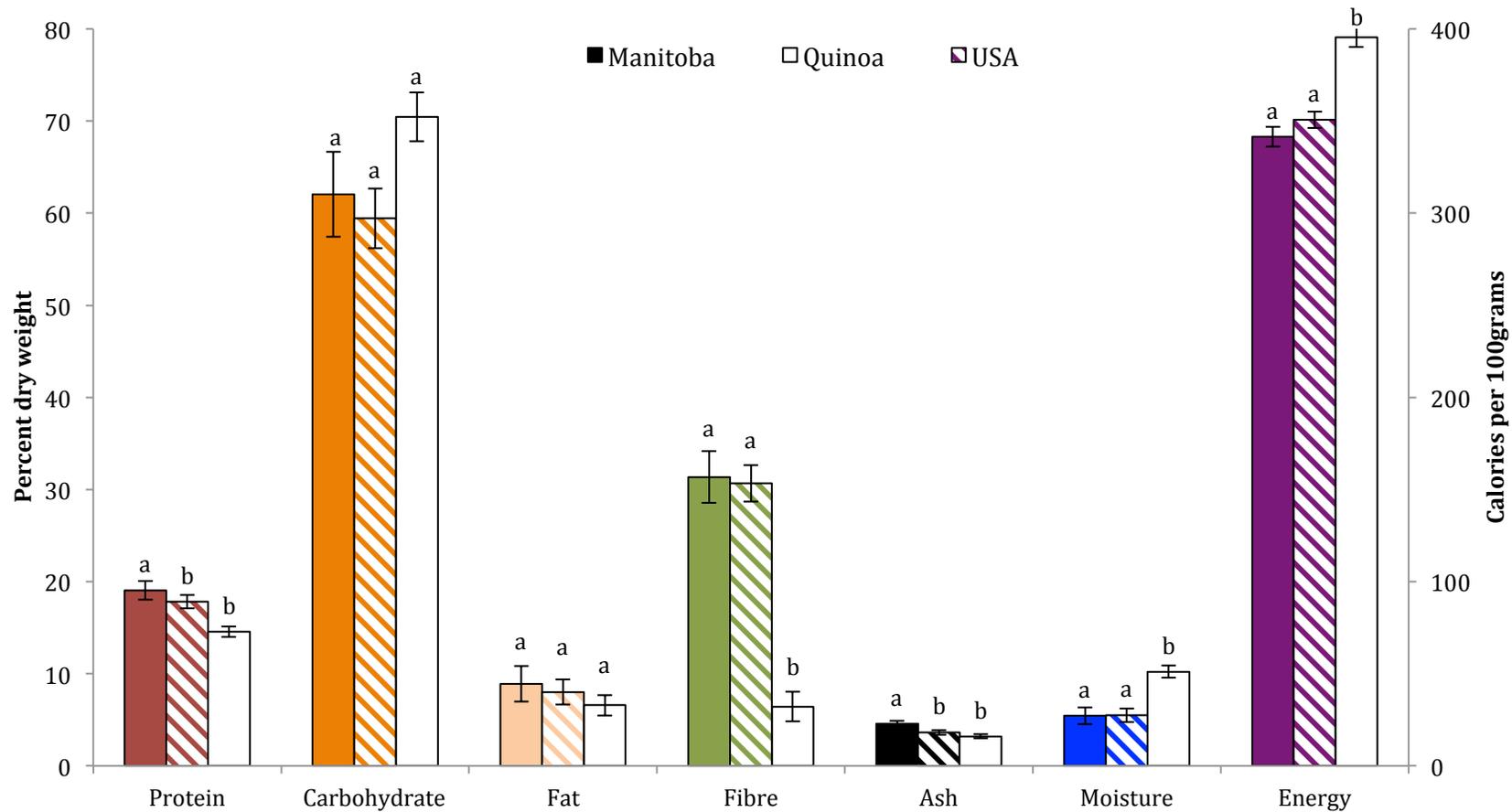


Figure 4.3: Mean quantity of main nutritional components of wild *C. berlandieri* seeds from Manitoba and USA populations and quinoa (*C. quinoa*) seeds. Protein, carbohydrate, fat, fibre, and ash expressed as percent dry weight; moisture is expressed as percent fresh weight and energy is expressed as calories/100grams. Lower case letters denote significant differences between nutritional components. Stars represent significant differences based on analysis of variance, see text for details. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, not significant $P > 0.05$.

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Appendix 4.1

Harvest yield information for nine one-meter square plots of *Chenopodium berlandieri* collected from a wild population near Delta Marsh Field Station, 2010. Each plot harvested in a one-minute timeframe. * first sample processed, not included in means; see Methods for details. Mean and standard error for harvest yield and rate calculated in SAS (2010).

	SAMPLE	1	2	3	4	5	6	7	8	9	Mean	SE
Harvester		MP	JP	SH	MP	SH	JP	MP	JP	SH		
No. Inflorescences/m²		100	50	100	160	120	180	120	140	180	127.8	
No. Inflorescences harvested		14	18	21	20	15	22	19	25	17	19	
Percent Inflorescences stripped		14	36	21	12.5	12.5	12.2	15.8	17.9	9.4	16.8	
Harvested weight (g)/ m²/ minute		51.6	65.1	57.85	40	54.7	75.8	82.2	101.1	64.3	65.1	
Processing time (minutes)		3	9	11	60*	14	14	16	16	11	11.8	
Cleaning rate (g/minute)		17.2	7.23	5.26	0.67	3.91	5.41	5.14	6.32	5.85	6.33	
Harvest Yield (kg/ha)		422	544.5	474	253.5	440.5	639.5	714.5	870	543	497.3	81.77
Harvest Rate (kg/hour)		0.633	0.327	0.237	0.001	0.176	0.256	0.252	0.307	0.296	0.28	0.055

Appendix 4.2

Nutritional analysis results for five *Chenopodium berlandieri* seed samples from various populations from the Northeastern Plains and Eastern Woodlands.

Component	Population	SO1	SO4	DM	SV	ND3
		<i>C. berlandieri</i>				
Moisture	%	5.6	5.5	5.5	5.4	5.4
crude ash	%	3.1	3.3	4.5	4.6	4.6
Crude protein	%	17.7	18.8	18.5	19.6	15.7
Carbohydrates	%	63.5	62.7	62.5	61.6	64
Total dietary fibre	%	30.5	28.9	34.5	28.2	35.3
Fat	%	10.1	9.8	9.1	8.7	10.3
Energy1	Cal/100g	355	356	336	347	341
Energy2	kJ/100g	1484	1490	1407	1452	1426
Vitamin A						
(Retinol)	IU/100G	<20	<20	21.3	<20	<20
Beta Carotene	IU/100G	35.3	35.1	66.3	92.3	42.5

Vit A (as RE)	RE/100g	<20	<20	<20	<20	<20
Population	SO1	SO4	DM	SV	ND3	
Component		<i>C. berlandieri</i>				
Beta Carotene	RE/100g	<20	<20	<20	<20	<20
Vitamin C (ascorbic acid)	mg/100g	<2.0	<2.0	<2.0	<2.0	<2.0
Fructose	g/100g	<0.2	<0.2	<0.2	0.4	<0.2
Glucose	g/100g	<0.2	<0.2	<0.2	0.7	<0.2
Sucrose	g/100g	1	1.7	2.5	2.7	1.8
Maltose	g/100g	<0.2	<0.2	<0.2	<0.2	<0.2
Total sugar	g/100g	1	1.7	2.5	3.7	1.8
Lactose	g/100g	<0.2	<0.2	<0.2	<0.2	<0.2
Phosphorous	ppm	3733	4931	3805	3984	4157
Sodium	ppm	<10	<10	<10	<10	<10
Calcium	ppm	2141	1589	2275	2111	2926
Magnesium	ppm	2897.8	3133.3	4673.7	4651.4	3312.9
Manganese	ppm	47.6	71.9	52.5	73.6	132.7
Appendix 4.1 continued						
Population	SO1	SO4	DM	SV	ND3	
Component		<i>C. berlandieri</i>				
Potassium	ppm	10751	12607	15454	15207	16697
Zinc	ppm	30	46	24	26	34
Copper	ppm	5.8	8.5	11.5	10.1	7.8
Iron	ppm	48	58	448	264	62
Selenium	ppm	0.5	0.6	0.2	0.2	0.8

Appendix 4.3

Nutritional analysis results for *Chenopodium berlandieri* and quinoa (*C. quinoa*) seed collated from a literature search.

Component	Unit	Asch and Asch	White et al	Ruales &	Schlick &	Koziol	Wright et	DeBruin
		1985	1955	Nair 1992-94	Bubenheim	1992	al 2002	1963
		<i>C. berlandieri</i>	quinoa	quinoa	quinoa	quinoa	quinoa	quinoa
Moisture	%	.	.	.	12.6	9.6	8.2	10.5
crude ash	%	3.5	3.4	3.4	3.4	3.8	2.9	2.4
Crude protein	%	19.12	12.5	14.1	13.8	16.5	16.1	14.5
Carbohydrates	%	47.55	72.5	72.5	58.7	69	75.8	74.3
Total dietary fibre	%	28.01	5.6	13.3	4.1	3.8	9.6	2.1
Fat	%	1.82	6	9.7	5	6.3	5.3	7.15
Energy1	Cal/100g	.	.	392	.	399	.	.
Vit A	RE/100g	.	.	0.2	.	<6	.	.
Beta Carotene	RE/100g
Vitamin C	mg/100g	.	.	16.4	.	4	.	0
Phosphorous	ppm	.	.	5350mg/100g	.	3837mg/kg	.	355mg/100g
Sodium	ppm	.	.	22	.	122	.	11
Calcium	ppm	.	.	874	.	1487	.	85
Magnesium	ppm	.	.	2620	.	2496	.	220
Manganese	ppm	.	.	33	.	100	.	2.7
Potassium	ppm	.	.	1201	.	9267	.	845
Zinc	ppm	.	.	36	.	44	.	2.4
Copper	ppm	.	.	10	.	51	.	8.2ppm
Iron	ppm	.	.	81	.	132	.	8mg/100g

Appendix 4.4

Nutritional analysis results for main domesticated crops collated from a literature search.

Component	Unit	Bressani <i>et al.</i> 1953	Enyisi <i>et al.</i> 2014	Sotelo <i>et al.</i> 1995	Sotelo <i>et al.</i> 1995	Ardabili <i>et al.</i> 2011	Lazos 1986	Wan <i>et al.</i> 1979	Ingale <i>et al.</i> 2011
		<i>Maize</i>	<i>Maize/ maize products</i>	<i>Wild beans</i>	<i>Common beans</i>	<i>Pumpkin</i>	<i>Pumpkin and melon</i>	<i>Sunflower kernels Oil v seed</i>	<i>Sunflower seed</i>
Moisture	%	.	11.6-20	.	.	5.2	5.4	.	3.6-4.6
Crude ash	%	1.08-1.85	1.1-2.95	5.15	4.15	2.49	4.65	3-3.9/ 1.65	~4.8
Crude protein	%	6.8-12	4.5-9.9	25.5	21.7	25.4	32.3	27-30/ 29-34	~25
Carbohydrates	%	.	44.6-69.6	61.6	68.1	25.19	.	.	27-34
Total dietary fibre	%	1-1.8	2.1-26.7	7.1	5.0	5.34	12.1	2-2.7/ 2-4	12.1
Fat	%	3.8-7.6	2.2-4.4	0.56	0.89	41.59	45.4	49-55/ 53-56	45.4
Energy1	Cal/ 100g	343-512

5. DEVELOPING ‘CULTIVATION’ PHENOTYPES:

THE PROCESS OF DOMESTICATION FOR *CHENOPODIUM BERLANDIERI*

5.1 Introduction

Recent residue analyses on ceramics recovered from the Boreal forest and Boreal-Prairie interface in Canada documented the widespread presence of domesticated maize (*Zea mays*) and beans (*Phaseolus*), plus the remains of a variety of native plant species including wild onion (*Allium*), beeweed (*Cleome*), sunflower (*Helianthus*), cocklebur (*Xanthium*), cattail (*Typha*), wild plum/cherry (*Prunus*), saskatoon (*Amelanchier*), and bur oak (*Quercus*) (Boyd and Surette 2010; Lints 2012; Quaternary 2010). This research has documented the use, and potential cultivation, of domesticated crops hundreds of years prior to European arrival. This and other recent research (e.g. Syms and Beckwith 2010), also suggested that cultivation of non-domesticated plant populations should be regarded as a common subsistence practice (Syms 2015). Cultivation is no longer only associated with the harvesting, storing, and subsequent planting of stored seed of domesticated crops. It involves both wild and fully domesticated plants, and all plant phenotypes that fall in between (Ford 1985; Harris 1996; Smith 2001). Termed “low level food production” (see Smith 2001), cultivation includes activities of varying human involvement such as intensive harvesting, broad scale sowing of seed, weeding, watering, tilling the soil around native plants, pruning and burning shrubs to increase fruit production, selective harvesting and replanting, fertilization and building gardens (Anderson 2005; Deur and Turner 2006; Smith 2001).

Domestication is a cumulative process initiated by selection pressures from human activities on certain culturally important wild plant phenotypes that led to genetic

changes in wild plant populations over time (de Wet and Harlan 1975). However, the cumulative process involves more than the application of singular, strong human selection forces to plant phenotypes. Recent research on the agricultural origins of cereal crops acknowledges that this process is long lasting, and sustained over many millennia (Fuller *et al.* 2012; Denham *et al.* 2007). Other research suggests that even minimal human interaction with a plant's life cycle, such as harvesting, impacts plant populations and can invoke phenotypic change. On the Northwest Coast aboriginal cultural groups collected aquatic perennial species such as cinquefoil (*Potentilla*) that produce edible roots. During the harvest, very large and very small tubers were left for the next year's harvest. Over time this type of interaction created large uniform populations (Turner and Peacock 2006). Cultural groups in Mexico altered the proportion of favourable phenotypes (e.g. larger fruit size, sweeter fruit flesh, non-red coloured flesh) within wild populations of columnar cacti (*Stenocereus stellatus*) through selective harvesting and vegetative propagation (Casas *et al.* 1999). Management of wild populations *in situ*, regarded as incipient domestication, was critical for maintaining genetic and morphological diversity in this species of cactus (Casas *et al.* 1999; 2006).

People – plant relationships developed through daily interactions with people creating and maintaining habitats that sustained diversity of culturally important plant species (Anderson 2005; also see Chapter 1 section 1.3.2). Interactions are continuous, multifaceted, thereby altering both plants and humans over successive generations (Ingold 2000). This process generated specific phenotypes in food plants, and behaviours or activities through which people interacted with these plant populations. These relationships can be viewed as a continuum from wild to fully domesticated phenotypes,

and non-intensive to fully controlling human activities (e.g. harvesting to modern agricultural practices) (see Ford 1985; Harris 1996). But what are the phenotypic and genetic effects of utilizing a plant species for food? How did daily harvesting or other cultivation practices affect plant phenotypes, particularly plant parts used for food? Recognizing domestication as a diachronic process provides a way to explore how various components interacted to influence plant phenotypes, particularly those recovered from the archaeological record (Ford 1985; Gremillion 1993; Harris 1996; Smith 2001). Acknowledging the various interactions of people and plants in the environment will provide new avenues to explore these interactions. One avenue is using the process of domestication to “work backward” exploring variation in plant phenotypes and the type/ strength of human selection pressure that may be associated with these changes within a given environment.

5.1.1 The process of domestication: genetic and environmental aspects

The accumulation of phenotypic changes deriving from domestication processes is known as the Domestication Syndrome. It comprises a suite of traits distinguishing domestic plants from their wild counterparts (Harlan *et al.* 1973; Pickersgill 2007). In seed crops, phenotypic traits desirable to humans include increase in number or size of plant parts, the loss of fruit/seed dispersal, loss of seed dormancy, and change in plant growth habit (Pickersgill 2007). Each characteristic is accompanied by one or more adaptive plant traits visible in modern domesticated crops. For example, control of seed dormancy traditionally invokes increased seedling competition from standardized planting of stored seeds in prepared seedbeds (Harlan *et al.* 1973; Smith 1984). This

change in selection pressure favours seeds that can germinate quickly, thereby out-competing their neighbours for water, nutrients and sunlight. This pressure could also be found where people were cultivating natural plant populations (e.g. weeding, tillage). Uniform germination of seeds can affect maturation and harvest uniformity and timing. Therefore, the loss of germination inhibitors, e.g. chemical, physical or physiological (Baskin and Baskin 1998) is necessary to rapidly establish a population prior to serious competition from other species (Pickersgill 2007). Selection for increased seed size would lead to better competitive ability, due to an increase in food reserves (endosperm or perisperm), and a reduction or loss of dormancy, most notably associated with a reduction in seed coat (testa) thickness (Harlan *et al.* 1973; Bouwmeester and Karsen 1993).

A number of factors are important for understanding the process of domestication. First, traits associated with domestication may be controlled by one to many genes. Quantitative traits are continuous, controlled by many genes with small effects, and the effects of individual genes can be difficult to distinguish (Sleper and Poehlman 2006). Total phenotypic variation is comprised of genetic variation, environmental variation, and genetic by environmental (GxE) interactions. Since domestication relies on the accumulation of genetic changes over time, it is necessary to separate genetic variation from environmental variation and GxE interactions, although all three factors need to be considered to gain a full understanding of the complexity of phenotypic variation in any given trait.

For evolution of traits to occur, phenotypes need to be heritable. Heritability (H^2) refers to the proportion of genetic variation passed from parent to offspring (Falconer

1989). If parents are inbred, (i.e. they fertilize themselves), the heritability estimate is calculated from both parents. Since the proportion of genetic variation differs between individuals, knowing both parents provides a more accurate estimate of heritability (Conner and Hartl 2004:131). The actual breeding system of *C. berlandieri* is unknown, but it is likely that this species out crosses (Wilson and Manhart 1993). If these plants are wholly outcrossing, then genetic variation from only the maternal line is known. Heritability is calculated from the maternal line, and can be doubled to estimate heritability of the trait from both parents. However, it is important to note that the estimates may also be inflated due to maternal effects, i.e. influence on offspring through provisioning of seeds or eggs (Conner and Hartl 2004:120).

Selection acts on organisms that are made up of interconnected traits, e.g. genetic, physiological, or developmental (Conner and Hartl 2004:151). Phenotypic and genetic correlations refer to traits that vary together, i.e. selection on one trait results in changes to another trait (Conner and Hartl 2004:151). Phenotypic correlations measure the amount two traits vary in relation to each other; genetic correlations measure the amount of variation exhibited by two traits affected by the same genes (pleiotropy) or pairs of closely linked traits (linkage disequilibrium) (Falconer 1989; Conner and Hartl 2004). Genetic correlations are vital for understanding the effects of selection, i.e. how changes to one trait could cause simultaneous changes to other characters, and for understanding how natural selection affects populations, i.e. the relationship between genetic traits and fitness values (Falconer 1989). For instance, a recent study exploring the relationship between domestication traits in a wild emmer wheat and domesticated durum wheat cultivar indicated strong positive genetic correlations between seed weight (size), kernel

number and grain yield (Peleg *et al.* 2011). These traits were controlled by genes on multiple chromosomes, some genes exhibiting pleiotropic effects. Selection of this suite of traits resulted in increased seed size and improved grain yield (Peleg *et al.* 2011).

It is possible that human selection pressures influencing domestication traits may be out weighed by environmental factors, including phenotypic plasticity and climactic variation across geographic regions. Plasticity is the ability for an organism (genotype) to produce different phenotypes, e.g. morphological form, growth rate, or resource allocation, in varying environments (Conner and Hartl 2004; West-Eberhard 2003:34; Schlichting 1986). Plasticity is a trait under genetic control, with some environmental responses being adaptive, while others are not (Schlichting 1986:668). Traits can be differentially plastic depending on the environment (Scheiner 1993:37). Plastic responses can be viewed as “immediate” responses by plants to changing environmental conditions. Selection may act on the ability of a plant to respond to environmental change, i.e. the plasticity trait, without acting on the response itself (Pigliucci 2001). Few studies explore the “immediacy” of environmental responses of traits associated with domestication to cultivation practices. A study of evolution of growth forms in wild and domesticated manioc indicates that cultivation reduced the strength, elasticity and stiffness of branches in both the shrub and vine forms of manioc (Menard *et al.* 2013). While plasticity of growth form was maintained, i.e. plants developed as shrubs or vines, reallocation of starches from the stems to the edible tubers reduced the mechanical strength of the stems. It was also possible that human selection during manioc’s domestication (prior to European contact) selected for brittle stems, as they would have been easier to section for planting in swidden (i.e. slash and burn) agricultural fields

(Menard *et al.* 2013). This suggests that plasticity of growth form allowed farmers to grow the desired shrub form in open swidden fields, while maintaining the plant's ability to grow as vines in closed environments. Potential selection for brittle stems allowed farmers to cultivate manioc, with a potential unintended consequence of reducing stem strength even further by selecting for larger, starchier tubers.

Climactic factors associated with increasing latitude have been linked to a decrease in seed size (e.g. mass) creating a north-south gradient (Moles *et al.* 2007). Moles and colleagues (2007) collected seed mass data for nearly 12,000 species around the globe to analyze variation in seed mass by latitude. Their findings indicate a 5.5 fold increase in seed size around the tropics, with a relatively consistent decrease in seed size into northern latitudes; northern species exhibit predominantly smaller seeds compared to southern species (Moles *et al.* 2007:112). Where seed traits may be correlated (e.g. seed size and testa thickness), this latitudinal trend may affect multiple traits. This may mean that northern climates (e.g. Manitoba) may favour species that produce smaller seeds and potentially thicker testas as a way to deal with cold winter climates. This same selection pressure may not be as strong in species in southern regions (e.g. Ohio) where winter temperatures are milder. Thus natural selection for seed traits may outweigh human selection pressures.

5.1.2 *The process of domestication in target species: Chenopodium berlandieri*

In this chapter I focus on *Chenopodium berlandieri*, a native annual utilized for its edible seeds (Arnason *et al.* 1981), the seeds of which are commonly recovered from Manitoba archaeological sites (Deck and Shay 1992). *Chenopodium berlandieri* was

domesticated for its seed ca. 3800 years ago in the Eastern Woodlands (Smith and Yarnell 2009). Domesticated seeds have thin seed coats and are lighter in colour (Smith and Funk 1985:446-447; Smith and Yarnell 2009: 6564). In *C. berlandieri*, it is assumed that humans selected for increased seed size (perisperm diameter) and a reduced testa (seed coat) thickness (Figure 5.1). Testa reduction is cited as the significant trait associated with the domestication of *C. berlandieri* as it is assumed to be linked to dormancy, germination and uniformity of seedling growth (Smith 1984:166; Gremillion 1993).

The testa is viewed as a physical barrier contributing to seed dormancy. Previous research on *C. album*, a close relative of *C. berlandieri*, suggests that seed dormancy is related to testa thickness and testa colour (Bouwmeester and Karssen 1993). Seeds with thinner testas were brown in colour and had shorter dormancy periods than black seeds with thicker testas (Karssen 1968, 1970, 1976). Further, ancient domesticated *C. berlandieri* and a modern relative quinoa (*C. quinoa*), have thin testas (<0.02mm) (Bruno 2006; Gremillion 1993). If seed colour is strongly correlated with testa thickness, then seed colour may provide a visual trait that people could have selected for, while being linked to the trait selection pressure acted on.

However, *Chenopodium berlandieri* has never been tested to see if a reduction in testa thickness actually improves its ability to germinate, and by extension reduces this species dormancy. If testa thickness in *Chenopodium berlandieri* seeds is a physical barrier restricting germination, then seeds with reduced testa thickness will have a higher chance of germination than seeds with thicker testas. Seeds that have increased nutritive tissue and/or loss of dormancy factors should germinate quickly. Therefore larger seeds

with thinner testas may also have higher percent germinations than small seeds with thicker testas. Additionally, if testa thickness is associated with colour (Pickersgill 2007), then seeds with thinner testas will be lighter in colour (e.g. red or tan), while seeds with thick testas will be darker in colour (e.g. black or red black).

Evolution of seed phenotypes in general requires suitable variation in seed traits on which human selection pressures can work to be present. Seed traits need to be heritable for human selection to affect the trait over generations. In addition, seed traits associated with domesticated phenotypes (i.e. increased seed size and reduced testa thickness) need to be linked to the process of domestication, in this case, percent germination.

5.2 Objectives

The primary goals of this chapter are to explore whether seed traits (seed size and testa thickness) are the traits involved in the process of domestication of *C. berlandieri*, and determine if selection pressures associated with human harvesting or cultivation of *C. berlandieri* populations resulted in changes to these seed traits. To investigate what effects low-level cultivation have on seed phenotypes in wild populations of *C.*

berlandieri I propose the following objectives.

- 1) I will determine the range of phenotypic variation in seed traits (perisperm diameter, testa thickness, and testa colour) in wild populations in the Northeastern Plains and Eastern Woodlands.

- 2) I will estimate what influence garden location (i.e. environment) and genotype has on phenotypic variation in seed traits in common garden populations. Common

garden experiments will replicate selection pressures associated with some cultivation practices, e.g. planting stored seed, weeding, watering, tilled soil, plus abiotic (e.g. soil condition) and biotic (e.g. reduced inter species competition) factors to provide data on the strength of human influence on seed traits. Testing the effect of garden location on seed traits will indicate levels of phenotypic plasticity in these traits.

3) I will calculate the heritability and genetic correlation of seed size and testa thickness to provide a measure of genotypic influence on seed phenotypes. If seed traits in *C. berlandieri* correlate in a similar fashion to its domesticated relative quinoa, I hypothesize that larger seeds will have thinner testas and be lighter in colour.

4) I will employ a short cold treatment to test whether testa thickness affects percent germination in relation to seed phenotypes in wild populations. The same treatment will be used to determine the influence of garden location and genotype on percent germination of seeds collected from common garden grown plants.

5) I will employ a long cold treatment to test whether seeds from cold adapted populations will germinate in higher percentages compared to seeds from non-cold adapted populations. I hypothesize that geographic area of origin affects percent germination and seed phenotypes: seeds from northern climates will germinate in higher percentages than seeds from southern climates. Further, seeds that germinate after the long cold treatment will have thicker testas compared to seeds that germinate after the short cold treatment.

6) I will test whether seeds with larger perisperm diameter and/or thinner testas germinate before small/ thick testa seeds. I hypothesize that larger seeds with thinner testas will germinate earlier than small seeds with thick testas.

5.3 Methods

5.3.1 Repeatability in seed measurements

Chenopodium berlandieri produces hundreds of thousands of seeds per plant. To accurately calculate mean seed traits, a representative number of seeds to measure was identified using a repeatability measure. The details are presented in Chapter 3, Section 3.4.1, but the calculations revealed that between three to five seeds per individual plant were sufficient to estimate plant phenotypes for all seed traits measured.

5.3.2 Phenotypic variation in seed traits in wild populations

To estimate the range of variation in seed traits across the Northeastern Plains (Manitoba and North Dakota) and Eastern Woodlands (Missouri and Ohio) regions I sampled 10 wild populations in 2010 and 2011. Populations were located within four sub-regions: Manitoba, North Dakota, Missouri and Ohio. Areas searched were in close proximity to archaeological sites where wild or domesticated *Chenopodium berlandieri* was harvested or cultivated. I sampled three wild populations in the Red River Valley of southern Manitoba, three populations in eastern North Dakota, two populations near St. Louis, Missouri and two populations in southern Ohio. Between 30 and 72 plants per population were sampled, i.e. stripped of all seed. Chapter 3 discusses the search (Sections 3.4.1) and sampling (Section 3.4.2) strategies in detail.

Mean perisperm diameter and testa thickness and seed colour were determined for maternal lines collected from each wild population. Three to five seeds per maternal line were randomly selected and fresh sectioned by hand (see Chapter 3 Section 3.4.5 for full sectioning methodology; Figure 5.1 for seed orientation during sectioning).

Perisperm diameter and testa thickness were measured under a dissecting microscope with calibrated measurement program Image Pro Express 4.5 that captured and measured standardized images. Each seed was scored visually for colour: black (1), red black (2), red (3), red tan (4), or tan (5). This range of seed colours was previously identified by various researchers (Asch and Asch 1977; Bruno 2006; Smith 2007).

I calculated population mean and standard error (PROC MEANS SAS 9.2, 2010) for the seed size (perisperm diameter and testa thickness), percent germination, and seed colour. Median seed colour was calculated for each maternal line then averaged for a population mean. Mean \pm the standard error is reported in all figures and tables. The distributions of perisperm diameter and testa thickness for all wild and common garden populations were normal (PROC UNIVARIATE SAS 9.2, 2010).

To explore geographic variation in seed traits I conducted three analyses of variance (PROC GLM, SAS 9.2, 2010). Dependent variables (Y) were perisperm diameter, testa thickness or mean seed colour. The model statement used in each analysis was $Y = \text{sub-region} + \text{population}(\text{sub-region})$. Population was considered to be random.

Pairwise correlations between the three seed traits were also estimated within and across populations (PROC CORR Pearsons, SAS 9.2, 2010). These were estimated within populations using data from individual plants. Correlations were estimated among populations using population trait means. The correlation co-efficient and p-value (r , P) were reported for significant relationships.

5.3.3 Influence of environment and genotype on seed phenotypes: common garden populations

Two common garden populations were grown from a subsample of individual plants (hereafter maternal lines) from three Manitoban populations at two locations, over two years. Each year the focus of the common garden experiment was different. I focused on phenological variation in 2011 (see Chapter 3 for methodology and results, Sections 3.4.4 and 3.5, respectively), and variation in seed morphology and genetic basis of seed traits in 2012 (methodology discussed in Chapter 3, Section 3.4.4). However, seed morphology data were recorded for each year to allow generalized comparisons between common garden populations per year.

To assess factors affecting seed traits in common garden populations, I conducted three analyses of variance (PROC GLM, SAS 9.2, 2010). Dependent variables (Y) were perisperm diameter, testa thickness or mean seed colour. The model statement used for each analysis was $Y = \text{location} \text{ population} \text{ replicate}(\text{location}) \text{ location} * \text{population} \text{ maternal-line}(\text{population})$. All factors in this statement with the exception of location and replicate were considered to be random.

I conducted three mother - offspring regressions (PROC REG, SAS9.2, 2010) to estimate the narrow-sense heritability (h^2) of perisperm diameter and testa thickness for populations grown in the common garden in 2012. Mothers were the wild plants used to establish maternal lines. Offspring phenotypes were estimated for each maternal line by averaging individual plants across common garden replicates. Heritability was calculated separately for each population and location.

The genetic correlation (r_A) between perisperm diameter and testa thickness was estimated using the covariance between the parental (wild) mean perisperm diameter and offspring (common garden 2012) mean testa thickness (Falconer and Mackay 1996: 316, equation 19.3). The standard error was also derived from genetic covariances and heritability (see Falconer and Mackay 1996: 316, Equation 19.4). Genetic correlation for seed colour was incalculable because seed colour was invariant among maternal plants. Maternal-family correlations for pairs of seed traits (perisperm diameter, testa thickness, and seed colour) were estimated for each combination of population and common garden location. Mean phenotype for offspring maternal lines were calculated by averaging individual plants across common garden replicates. Only significant relationships were reported.

5.3.4 Percent germination in relation to seed phenotypes

In 2012, I conducted two germination experiments to examine the relationship between seed phenotypes and percent of germinated seed. The first experiment was designed to determine whether testa thickness was a physical barrier to germination, i.e. whether perisperm diameter and testa thickness affected percent germination of seeds, and to explore the relationship between seed colour and testa thickness. Seeds underwent a short cold treatment, as chilling simulates an over winter period which is necessary to break dormancy in many *Chenopodium* species (Williams and Harper 1965; Chu *et al.* 1978). The second experiment was designed to test whether seeds from cold adapted populations will germinate in higher percentages compared to seeds from non-cold

adapted populations. Seeds were exposed to long cold conditions to determine if geographic area of origin affects percent germination and seed phenotypes.

Based on the range of variation in wild populations and common garden populations, I chose 8 to 14 plants per population that spanned the range of variation for seed size and testa thickness (see Appendix 5.1 for details). Wild populations had been sampled in 2010 (Manitoba populations DM and SV) and 2011 (Manitoba population AB, and all USA populations). Seed was stored dry in paper bags until sampled for the germination experiment. Seed from each plant formed a maternal line for the experiment. At the time of the long cold germination experiment (Autumn 2012), only two common garden populations (DM and SV grown in 2011) were included. The third common garden population (AB) was not processed in time to be included. The short cold germination experiment was conducted after the long cold experiment had started. Enough AB maternal lines had been processed for it to be included in the short cold experiment. Of the common garden populations, 10 maternal lines were sampled from the DM population, and four maternal lines sampled from the SV population.

Maternal lines were sampled by volume of unwinnowed seed. Unwinnowed seed was the mature fruit surrounded by the dried perianth (see Chapter 3 for full details). The seed was winnowed and placed dry in labeled plastic vials. Maternal lines were sampled with a half teaspoon (2.5mL). Number of seeds per sample was counted for all maternal lines from Manitoba and North Dakota populations because there were few winnowed seeds per 2.5mL sample. For all other populations/maternal lines, winnowed seed number per 2.5mL sample was very high, and therefore total number of seeds per

maternal line was estimated. Estimates were based on two previously counted 2.5mL samples from each wild population.

5.3.4.1 Short cold treatment

Seed samples from all sampled populations underwent a short cold treatment prior to germination. Samples contained air-dried seed and were stored dry at $5^{\circ}\text{C} \pm 1^{\circ}\text{C}$ for four weeks (Williams and Harper 1965:143; Bouwmeester and Karssen 1993). After chilling, seeds were soaked in distilled water for 48 hours at the same temperature. Each sample was spread on one layer of Whatman filter paper in a sterile standard sized plastic petri dish moistened with two to five milliliters of distilled water. Seeds in each sample were evenly spaced to decrease potential moulding.

The germination experiment was run for 16 days. All maternal lines were randomized on two shelves using a random number table. Samples were placed in an incubation chamber under dark conditions, and a temperature setting of 18h at 30°C , 6h at $20^{\circ}\text{C} \pm 1^{\circ}\text{C}$, RH 70%. Petri dishes were checked every four days (sampling days 4, 8, 12, 16) for germinated seeds. Seeds were considered fully germinated once the radical penetrated the fruit wall (Karssen 1968).

During the first check, all seeds of each colour were counted to determine percent of each seed colour. During each sampling day, germinated seeds of each colour were counted and removed from the petri dish and placed in labeled vials for subsequent metric analysis. Non-germinated or incomplete germinated seeds (i.e. split testas without radical emergence) were quantified as a group (*cf.* Karssen 1968). Final percent

germination was calculated for each maternal line and seed colour within maternal line at the end of the trial.

A subsample of germinated seeds from each sampling day for each population was sectioned and the perisperm diameter and testa thickness measured and seed colour qualified (Appendix 5.1). Seeds were fresh sectioned following the above-mentioned protocol. A maximum of three seeds per collection date per maternal line were sectioned.

5.3.4.2 Long cold treatment

The same methodology, populations, maternal lines and size of seed sample per maternal line as described above were repeated in the long cold treatment germination experiment to provide comparable results. Number of maternal lines varied slightly; between 13 and 18 lines were included per population. The long chilling procedure was as follows: dried winnowed seed samples from each population were sewn in a small mesh (0.3mm) bags and buried in a flowerbed approximately 2-3cm below the surface on October 31, 2012. The bags were removed from the flowerbed on May 7, 2013 approximately two weeks after the snow melted and night time temperatures were 0°C or higher. In total, seeds were cold chilled for six months at a range of below 0°C temperatures (Table 5.1).

Initially, these seeds were going to be plated on petri dishes and germinated in the incubator, the percent germination being sampled every four days as in the short cold treatment experiment. However, the seeds had germinated in the bags prior to removal from the flowerbed. For the long cold treatment experiment, the total percent of seed colours, the total percent of germinated seed per colour, and percent germination were

calculated. A subsample of seeds from each seed colour and maternal line was measured for perisperm diameter, testa thickness, and seed colour. All were quantified in the same manner described for the short cold treatment.

5.3.4.3 Analyses of cold treatment experiments

Percent germination for each maternal line was estimated by dividing the number of germinated seeds by the total number of seeds. The effect of cold treatment on percent germination was assessed using the difference in percent germinations between treatments for each maternal line. Paired *t*-tests (PROC UNIVARIATE, SAS 9.2, 2010) were conducted to determine if there was a statistically significant difference in percent germination between the short and long cold treatments within each wild and common garden population.

To assess how germination success was influenced by population and seed traits, I used general linear models (PROC GENMOD, SAS 2010) with a binomial distribution and a logit link function. Germination was analyzed as successes divided by number of trials (germinated seeds / total seeds) for each maternal line (mother). I conducted two separate analyses because the two covariates (testa thickness and perisperm diameter) were correlated therefore violated assumptions of independence. The model statement for testa thickness was $\text{germinated/total} = \text{population} \text{ testa thickness}$. The model statement for perisperm diameter was $\text{germinated/total} = \text{population} \text{ perisperm diameter}$. Separate analyses were conducted for short and long cold treatments.

Similar analyses were conducted to assess whether seeds from the common gardens differed in germination. The germination data for the common garden were

unbalanced because mothers grown at the Arboretum originated from two wild populations (DM, SV) whereas mothers grown at Glenlea originated from only DM. The available combinations of location and population of origin were included as a categorical “group” effect in the model. The model statement for each analysis was $\text{germinated/total} = \text{group}$ testa thickness and $\text{germinated/total} = \text{group}$ perisperm diameter.

Results from the short cold treatment experiment were used to assess whether seeds with thin testas germinated earlier than seeds with thick testas. Repeated measures analysis with germination day as the repeated factor was used (PROC REPEATED, SAS 9.2, 2010). Dependent variables (Y) were perisperm diameter and testa thickness across four sampling days (4, 8, 12, 16). The model statement was $Y_4 \ Y_8 \ Y_{12} \ Y_{16} = \text{sub-region} \ \text{population}(\text{sub-region})$. All factors in the model statement with the exception of sub-region were considered random.

5.4 Results

5.4.1 Phenotypic variation in seed traits: wild populations

Analysis of variance indicated moderately strong ($F > 11$) and significant ($P < 0.0001$) differences between populations for all seed traits tested but no differences between sub-regions (Table 5.2). Variation in perisperm diameter was slightly bimodal, approximately half the populations having mean perisperm diameters greater than 1.4mm, and the other half having mean perisperm diameter less than 1.3mm (Figure 5.7A). The range of variation for testa thickness appeared to be a continuous distribution spanning 0.025mm to just over 0.047mm (Figure 5.7B). Populations from Missouri

clustered together while populations from Manitoba, North Dakota, and Ohio showed partial or no clustering (Figure 5.2A). The SV and OH4 populations had much larger seed size (mean =1.60mm) and slightly thinner mean testas (mean = 0.03mm) than the other populations from Manitoba and Ohio, respectively. The ND1 population also exhibited a larger seed size (mean = 1.62mm) but a slightly thicker testa (mean =0.035mm) than the other two ND populations (Figure 5.2A).

Mean seed colour varied by population (Figure 5.2B) but black (colour score =1) and red-black (colour score =2) seeds were most prevalent. Black seeds comprised the highest percentage of seed colours per population, ranging from 44 to 92%. These populations also contained low quantities of red, red-tan and tan coloured seeds, comprising 30% or less of the total sample. Even ND1, which exhibited red-black seeds (Colour score = 2.25), had higher proportions of black coloured seeds. The SV population was the only exception, having only 29% black seed, with 70% of seeds comprised of the other colours (Appendix 5.2).

Seed traits were generally correlated in the expected direction, both across and within wild populations, i.e. seeds with thick testas tended to be darker with smaller perisperms than seeds with thin testas. Decreased testa thickness corresponded to lighter seed colour across populations ($r = -0.67$, $P < 0.05$; Figure 5.2B), as well as within nine of the ten populations surveyed (all significant $r < -0.25$, $P < 0.05$). Similarly, seeds with thin testas corresponded to increased seed size across populations ($r = -0.69$, $P < 0.05$, Figure 5.2A), although this relationship was only significant within two populations from Manitoba and Ohio, SV ($r < -0.42$, $P < 0.02$) and OH4 ($r < -0.58$, $P < 0.0003$), respectively. Finally, increased perisperm diameter corresponded to lighter seed colour

within two populations, North Dakota 2 ($r > 0.33$, $P < 0.03$) and Ohio 1 ($r > 0.45$, $P < 0.006$) but this relationship was not significant across populations or within the remaining populations.

5.4.2 Influence of environment and genotype on seed traits: common garden populations

5.4.2.1 Phenotypic variation in seed traits

Seeds produced by common garden plants had on average thinner mean testas and larger mean perisperms compared to their wild parental populations. These seeds were also slightly lighter in colour compared to wild progenitor populations (Figure 5.3). Analysis of variance indicated that the effects associated with population and the location in which plants were grown (hereafter location) were highly significant for mean perisperm diameter and mean testa thickness (Table 5.3). They were only moderately significant for mean seed colour. Differences between populations depended on location, as indicated by significant population by location interactions (Table 5.3).

The response of seed traits from three wild populations grown at two locations was visualized (Figure 5.3). Differences among wild populations and rank order of population means were generally retained in plants grown at the Arboretum. The SV population had the largest perisperms with the thinnest and lightest testas. The AB and DM populations were similar to one another with smaller perisperm, thicker testas, and mostly black seeds. At Glenlea, differences among populations decreased or disappeared (Figure 5.3).

Common garden population seed phenotypes were correlated in the same direction as in the wild progenitor populations (Table 5.4), i.e. seeds with thick testas

tended to be darker with smaller perisperms than seeds with thin testas. In Arboretum grown plants, decreased testa thickness corresponded to larger seeds ($r < -0.78$, $P < 0.0001$), and lighter colours ($r < -0.71$, $P < 0.001$) within AB and DM populations. Additionally, increased perisperm diameter correlated with lighter seed colour within the AB and DM populations ($r > 0.52$, $P < 0.007$). While SV population exhibited similar direction of correspondence between traits the results were not significant due to low sample numbers of maternal families ($n = 5$).

In Glenlea grown plants, seed traits correlated in similar strength and direction as described above, however results were not significant due to low sample numbers of maternal families (e.g. SV population, $n = 5$). Despite low sampling, decreased testa thickness corresponded to lighter seed colour in the AB and SV populations ($r < -0.6$, $P < 0.003$). Similarly, increased perisperm diameter corresponded with lighter seed colour ($r = 0.98$, $P = 0.02$) in the DM population.

5.4.2.2 Heritability and genetic correlations in seed traits

Regression of offspring means on maternal phenotype indicated perisperm diameter and testa thickness were moderate to highly heritable (Table 5.5). Only the AB population provided significant results, due to low sample number of maternal families for most traits tested. Perisperm diameter heritability was high ($h^2 = 0.99 \pm 0.128$, $P < 0.0001$) while testa thickness was moderate ($h^2 = 0.37 \pm 0.156$, $P = 0.03$). Only perisperm diameter from the AB population had a high and significant ($h^2 = 0.78 \pm 0.157$, $P = 0.0002$) heritability at Glenlea. It is important to note that reported h^2 values might

need to be doubled if *C. berlandieri* is proved to be wholly outcrossing (see section 5.1.1, this chapter).

The genetic correlation between perisperm diameter and testa thickness was similar in direction, strength and significance to phenotypic correlations previously discussed. Perisperm diameter had a strong negative relationship with testa thickness in the AB population. The estimated r_A was -0.699 with a standard error of 0.08. An error value of 0.08 was calculated regardless whether the heritability values for each trait were doubled (assuming out crossing) or not (assuming selfing).

5.4.3 Percent germination in wild and common garden populations: overview

Percent germination resulting from both cold treatment experiments ranged widely across populations and cold treatments (1-37%) but was low (less than 15%) for many of the wild populations (Table 5.6). No significant differences were detected between percent germinations for either chilling experiment for Manitoba or Missouri populations (Figure 5.4). Percent germinations from North Dakota populations were significantly higher after the long cold treatment (>25%) compared to the short cold treatment (<10%). The reverse was true for Ohio populations; a decrease in percent germination from 25% to <15% was noted (Figure 5.4).

Percent of germinated seeds produced by common garden grown plants significantly increased across both cold treatments compared to percent germination of wild Manitoba populations (Figure 5.5). Analysis of the proportion of germinated seeds indicated a significant difference in percent germination between the wild populations and their common garden grown offspring in both cold treatment experiments. The DM

and SV populations had significantly higher percent germination (Walde $\chi^2 > 49$, $P < 0.0001$) at both locations compared to their wild progenitor populations (Table 5.7). A Student's t-test indicated that no significant differences existed between the proportion of germinated seeds from common garden plants grown at different locations (DM-Arboretum: $t = 1.25$, $P = 0.26$; DM-Glenlea: $t = -0.03$, $P = 0.97$; SV-Arboretum: $t = -1.29$, $P = 0.33$).

A note about the SV population grown at the Glenlea: this population was calculated from a single maternal line (SV2109). This maternal line comprised the only individual that produced germinated seeds in both experiments and for this reason the SV Glenlea population was removed from the remainder of the analyses.

5.4.4 Percent germination and seed phenotypes

Two trends were noted in the data. First, populations with thick testas tended to have low percent germination regardless of stratification treatment. The AB and DM populations from Manitoba and the Missouri populations all had mean testa values greater than 0.039mm (Figure 5.8). After the long cold treatment, the proportion of germinated seeds in these populations surpassed percent germination reached after the short cold treatment, but the differences were not significant. For instance, after the short cold treatment the DM population had 1% percent germination, which rose to 11% after the long cold treatment (Figure 5.8).

Second, the SV population, which exhibited a relatively thin mean testa, increased in percent germination from 11% to 19% after the long cold treatment. This trend was not significant but a similar increase in percent germination after the long

chilling period was also exhibited by the North Dakota populations, and was significant. North Dakota populations exhibited a range of thinner testas (mean: 0.033 – 0.036mm), and had some of the lowest quantities of germinated seeds (mean <9%) after the short cold treatment. After the long cold treatment the trend reversed, and percent germination from North Dakota populations increased above 25%. The opposite trend was exhibited by the Ohio populations, which had relatively thin testas (mean: 0.032 – 0.036mm), and produced the highest percent germinations (mean >20%) after the short stratification treatment. After long stratification, percent germinations from Ohio populations decreased to less than 20%. Percent germination from the Ohio 4 population in particular dropped from 28% to 10% (Figure 5.4).

Analysis of the proportion of germinated seed produced by individual plants accounted for population of origin, perisperm diameter and testa thickness when testing for significant influences on germination. The results indicated that population significantly affected percent germination in both the short and long chilling experiments (Table 5.4). Testa thickness had a significant and strongly negative influence on percent germination in both chilling experiments (short chilling: estimate -34 ± 2.49 , $P < 0.0001$, long chilling: estimate -44 , $P < 0.0001$) indicating that as mean testa thickness decreased, percent germination increased. Perisperm diameter had a smaller effect on percent germination in the short cold treatment experiment (estimate 0.24 ± 0.11 , $P = 0.03$), and a small but highly significant effect in the long cold treatment experiment (estimate 1.55 ± 0.12 , $P < 0.0001$) indicating that as seed size increased so did percent germination.

5.4.5 Germination day effect on seed traits

The repeated measures analysis indicated that testa thickness exhibited some influence ($F=3.13$, $P=0.03$) on the day seeds germinated, but perisperm diameter did not (Table 5.8). The effect of germination day for both seed traits was consistent across populations and sub-regions. Across the germination experiment, the number of maternal lines with germinated seed reduced from 86 to 28 (Table 5.9). Seeds with thinner testa germinated earlier in the experiment compared to seeds with thicker testas (Table 5.9). Seeds that germinated four days after ‘planting’ had mean testa thickness of 0.021mm, while seeds that germinated 12 days after planting had mean thickness of 0.026mm. Larger seeds germinated earlier in the germination experiment compared to smaller seeds (Table 5.9). Perisperm diameter of seeds that germinated four days after planting averaged 1.48mm, while seeds that germinated 12 days after planting averaged 1.39mm in perisperm diameter. In both seed traits, seeds that germinated 16 days after planting reflected the opposite trend: mean testa thickness was quite reduced (mean= 0.025mm) and perisperm diameter increased slightly (mean= 1.40mm) (Table 5.9).

5.4.6 Phenotypes of germinated seeds

In both experiments, germinated seeds from all wild populations were slightly larger with noticeably thinner testas compared to their respective progenitor populations. Analysis of variance indicated that population remains a very strong and significant factor ($F > 6.5$, $P < 0.0001$) influencing germinated seed size, testa thickness and seed colour (Appendix 5.4). The distribution of germinated seed phenotypes overlapped the distribution of phenotypes from all combined populations (Figure 5.7A). Perisperm diameter from germinated seeds from both experiments maintained the bimodal

distribution exhibited by seed size across all populations measured, albeit less dramatically (Figure 5.7A).

The distribution of testa thickness of germinated seeds from all populations in both chilling experiments fell over the thin end of the distribution of testa thicknesses for all populations measured (Figure 5.7B). This means that the seeds that germinated expressed a range of thin testas. Germinated seeds had thinner testas (mean $<0.022\text{mm}$) compared to the mean testa thickness for all populations (*cf.* vertical arrow in Figure 5.B; mean $>0.031\text{mm}$). Of the germinated seeds, the DM population from Manitoba exhibited significantly thicker seeds (mean 0.032mm , $P=0.006$) compared to germinated seeds from all other populations. Germinated seeds from the SV population from Manitoba, the Ohio populations and the Missouri 4 population had the thinnest testas (mean $<0.020\text{mm}$, $P<0.031$).

Of all seeds measured from either cold treatment experiment, the thinnest testas (mean $<0.010\text{mm}$) were measured on small seeds (mean $<1.0\text{mm}$) that were red-tan or tan coloured. These seeds were more apparent during the short chilling experiment, likely because seed samples were larger and were spread out on white filter paper in larger petri dishes, increasing their visibility. It is possible that these seeds represent one extreme in seed phenotype variation that was not well represented in all population subsamples. It is also possible these seeds were immature, thus their very small size and thin testa would be reflective of development. While these seeds did exhibit the hallmarks of germination (radicle protruding through the testa) it is not known whether this phenotype would have produced viable seedlings.

Dark coloured seeds (black and red-black) comprise the majority (~90%) of seed colour expressed in all wild and common garden populations, with lighter seed colours (red to tan) forming less than 10% (Figure 5.8). Distribution of seed colour of germinated seeds from the long cold chilling experiment resembled the total distribution. Most seed that germinated were black in colour, with almost equal proportions of red-black and red coloured seeds germinating. The lightest seed colours (red-tan and tan) barely registered. In contrast, germinated seeds from the short chilling experiment expressed almost equal amounts of all seed colours expressed (Figure 5.8).

Across populations, Manitoba populations (DM and AB) produced some of the darkest coloured germinated seeds, exhibiting little variation in germinated seed colour after either cold treatment (Appendix 5.2). All other wild populations exhibited a wide range of seed colours in the germinated seeds after the short treatment, but less variation in seed colour after the long cold treatment. Populations from the Eastern Woodlands region (Missouri and Ohio) maintained the widest range of seed colour in the germinated seeds after both experiments (Appendix 5.2).

Seed colour of germinated seeds from the common garden populations followed a similar pattern as the wild populations: germinated mean colour was lighter after the short cold treatment and darker after the long cold treatment. An exception was the SV population, which had lighter seeds after the long cold treatment. The SV population also exhibited a lighter mean seed colour at the Arboretum, compared to Glenlea. The DM population produced black coloured germinated seeds at both locations.

5.5 Discussion: The Process of Domestication in *Chenopodium berlandieri*

What is the potential for pre-contact cultural groups in Manitoba to alter seed phenotypes of wild *C. berlandieri* populations through use of the seeds as food? In this chapter I began to address whether selection pressures associated with harvesting and other low-level cultivation practices (e.g. intensive harvesting, weeding, watering, tilling) could alter seed phenotypes in wild populations. To answer this question I first examined three fundamental assumptions: first, were the seed phenotypes associated with domesticated *C. berlandieri* (Smith and Funk 1985) limited to the Eastern Woodlands region or were they present in wild *C. berlandieri* populations in Manitoba? Second, were the seed traits linked to the domesticated phenotype (i.e. reduced testa thickness, increased seed size and lighter seed colour) actually associated with germination? Most importantly, was testa thickness a physical barrier to dormancy, the reduction of which allowed for increased germination?

The second set of assumptions was written as fact by previous researchers (e.g. Ford 1985; Rindos 1984; Smith 1985; Gremillion 1993) who assumed the domestication of *C. berlandieri* followed a similar process to the domestication of cereals (de Wet and Harlan 1975; Pickersgill 2007). It was suggested that planting stored seed would lead to seedling competition, those seeds that germinated first would out compete conspecifics and other species (de Wet and Harlan 1975). Seeds that germinated first would have thinner testas, decreasing the physical barrier to dormancy, and be larger, providing more food reserves to aid the initial growth of the embryonic plants (Smith 2007:113). The assumption was that deliberate storage and subsequent replanting of seed initiated a series of morphological changes including decreased testa thickness, and an increase in

overall seed size (Smith 1985:165-166). This pattern ultimately led to a domesticated phenotype *C. berlandieri* ssp. *jonesianum* (Smith and Funk 1985), which was documented from a number of archaeological sites in the Eastern Woodlands region (e.g. Fritz 1984; Smith 1985; Smith and Yarnell 2009).

After discussing the validity of these assumptions, I turn to exploring the effects of low-level cultivation practices on seed phenotypes. What are some of the effects of growing seed collected from wild plant populations in a common garden setting, with tilled soil, weeding and watering plants being the main sources of selection pressure? Would these effects increase the frequency of the preferred phenotype (large, light coloured seeds with thin testas) in successive plantings of stored seed? Here I examine the influence of genotype (population and maternal family) and environment on variation in seed traits grown in a common garden environment.

5.5.1 Variation in seed phenotypes across the geographic range

The domesticated seed phenotype of *Chenopodium berlandieri* documented in the Eastern Woodlands was a thin testa phenotype, red-black in colour exhibiting a range of seed sizes (e.g. Ash Cave, OH seed size 1.3mm -2.2mm, mean testa thickness =0.015mm, Smith 2007:121-122; Russel Cave, AB seed size 1.0mm – 1.8mm, mean testa thickness = 0.011, Smith 1985:166; Salts Cave, KY, seed size > 1.4mm, testa thickness <0.021mm, Gremillion 1993: 501). The populations sampled in this study expressed a range of seed phenotypes from small, black to red-black seeds with thicker testas to larger, red-black to red seeds with thinner testas. Half of the populations surveyed exhibited larger seeds (mean>1.40mm) and thinner testas (mean<0.035).

Populations surveyed also tended to be conservative in seed size and testa thickness, exhibiting low variation around the mean (see Figure 5.2A). Populations with relatively thin testas were distributed throughout in the Red River Valley in Manitoba and the Northeastern Plains, and areas of the Eastern Woodlands. The distribution of this phenotype is probably due to population of origin having a large impact on the seed phenotypes expressed within a given population, without similar influence on a broader geographic scale. This means that each population exhibited a unique seed phenotype and the populations with large, lighter coloured seeds (i.e. red-black or red versus black) with thinner testas could have been available in southern Manitoba.

Combinations of seed phenotypes also depend on the degree of correlation between seed size and testa thickness. This research indicated that seed traits were strongly and significantly correlated indicating a close association between seed size, colour and testa thickness. As seed size increased, testa thickness decreased, and seed colour lightened. However, this was dependent on the population in question. Studies examining correlations between seed size and testa thickness are absent from the literature. However, researchers examined genetic and phenotypic correlations between seed length, width, thickness and trait indices for improvement of African yam bean (*Sphenostylis stenocarpa*) crops (Adewale *et al.* 2010). High positive phenotypic and genetic correlations for seed length x length/width index and seed length x length/thickness index indicated that an increase in seed length would result in an overall increase in seed width and thickness (Adewale *et al.* 2010:113). Similarly, improvement on seed yield in the Asian legume green gram (*Vigna radiata*) could be achieved through selection of one or more corresponding traits (e.g. plant height, pod/plant, pod length)

that were strongly genetically and phenotypically correlated with seed yield (Chakraborty *et al.* 2011).

Most populations of *C. berlandieri* in this study expressed a strong correlation between testa thickness and seed colour, indicating that reducing the testa mean in a given population will result in lighter seed colour. Only two populations, SV in Manitoba and OH4 in Ohio, showed a strong negative correlation between seed size and testa thickness. In these populations an increase in perisperm diameter would result in reduced testa thickness. This suggests that smaller seeds can have thinner testas and be lighter in colour, and it may be possible to select for this seed phenotype.

5.5.2 Seed traits, germination, and domestication

In this chapter I have consciously conflated germination and dormancy, although they are very different processes (Bewley 1997). Germination is the process by which seeds imbibe water to initiate metabolic processes culminating in the emergence of the radicle, while dormancy is the failure of a viable intact seed to complete any portion of germination under ideal conditions (Bewley 1997: 1055). Physical barriers to germination such as coat enhanced dormancy (Bewley 1997), as is the suggested state for *Chenopodium berlandieri* (Smith 2007), is not the only factor in breaking seed dormancy and completing seed germination (Baskin and Baskin 2014). There are chemical and metabolic factors that affect the breakdown of the testa and the growth of the radicle through the testa wall (Baskin and Baskin 2014; Karssen 1976). Combinations of giberellic acid and light induced germination in dormant *C. album* seeds (i.e. black coloured), while either giberellic acid or light was able to induce germination in non-

dormant (i.e. light coloured) forms (Karssen 1976). Additionally, the conditions in which maternal parents produce seeds can affect seed traits. In *C. polyspermum* and *C. amaranticolor*, mothers that grew in long day conditions produced seeds with thick testas that had low germination rates (Baskin and Baskin 1998). In most wild populations I tested, percent germination was low, but the maximum number of germinated seeds did increase for populations with thinner mean testas. Statistical analysis indicated that percent germination was significantly increased by a reduction in testa thickness, suggesting that coat enhanced dormancy is a major factor in the dormancy of *C. berlandieri*.

Seeds that germinated were larger with thinner testas compared to overall seed means calculated for wild populations. A reduction in testa thickness was strongly associated with an increase in percent germination for all populations tested. In Manitoba, a reduction in testa from ~0.031mm to 0.020mm increased percent germination from 1% to 18%. Similar patterns of seed size and testa thickness were noted in wild, semi-cultivated and cultivated forms of lablab bean (*Lablab purpureus*), a tropical legume. Wild forms had significantly thicker testas, a generally small seed size and reduced variation in seed size compared to semi-cultivated and cultivated forms that exhibited thinner testas and larger seed size (Maass and Usongo 2007).

Reduced testa thickness and increased seed size corresponded to a significant increase in percent germination across cold treatments. Chilling is necessary to break some dormancy factors in many species and may be required by species adapted to northern climates (Baskin and Baskin 2014). For the long cold treatment seeds were stored outside over 2012-2013 winter to release dormancy (see Section 5.4.3). Increased

percent germination was apparent in Manitoba, but was especially visible in North Dakota populations (Figure 5.4). As hypothesized, seeds with thin testas tended to germinate first. The increase in percent germination between short and long chilling periods suggests *C. berlandieri* plants from Manitoba and North Dakota require a long cold chilling period to release some dormancy factors. This may suggest that to cultivate *C. berlandieri* in Manitoba and the Northeastern Plains seed would have been sown in the fall to allow the long chilling period necessary to break dormancy.

Testa thickness also influenced the number of days to seedling emergence, i.e. seeds with thin testas sprouted in the first four to eight days after planting. In a study on the lablab bean day to seedling emergence varied between wild and cultivated forms. Most cultivated seeds germinated within the first four days after planting. Only half of planted wild seeds germinated after 10 days (Maass and Usongo 2007). The lag in germination for wild forms was due to hardseededness, (i.e. presence of a thick testa), a germination inhibitor, which was circumvented by scarring the testa. Scarring of hardseeded specimens increased germination 58-93% (Maass and Usongo 2007). Increased seed mass also strongly corresponded to seedling emergence with increased planting depth in five species of domesticated beans (Kluyver *et al.* 2013). Seeds with greater mass (i.e. larger nutritive stores for the seedling embryo) were able to have seedlings emerge from lower depths, a trait linked to the domestication of many species of bean (Kluyver *et al.* 2013).

In *Chenopodium*, seed colour and its relation to testa thickness may also be related to different types of dormancy. In *C. bonus-henricus*, seed produced at higher elevations had thick testa with increased levels of polyphenols compared to seeds

produced at lower levels. These dark, thick-coated seeds were linked to reduced germination because the thick seed coat acted as a physical barrier to dormancy (Dome 1981; Baskin and Baskin 1998). In *C. album* darker coloured seeds with thicker testas exhibited long-term dormancy allowing seeds to survive in the seed bank for years or decades, while lighter coloured seeds were able to germinate quickly taking advantage of current conditions (Karssen 1970).

Long versus short dormancy may have been reflected in the percent germination of two Manitoba populations. The AB and DM populations exhibited the lowest percent germination, some of the thickest testas (mean >0.04mm; Figure 5.2), with the least amount of variation in seed colour (e.g. black or red-black, see Appendix 5.2) measured from all wild populations included in this study. These very dark, thick testa seeds may have been associated with long-term dormancy, which would explain the low percent germinations after both stratification experiments (e.g. percent germinations increased from 1-3%, see Figure 5.4). It is also possible that low germination exhibited in these populations is due to seed age. These populations were the first to be harvested in 2010, and the seed was subsequently stored for two years in dry conditions, which may have initiated long-term dormancy (cf. Karssen 1970).

5.5.3 Effects of low-level cultivation on seed phenotypes

The assumption that selection of important seed phenotypes resulted in domestication is predicated on the genetic presence of variation for relevant traits. Genotypes with a selective advantage will produce more offspring and become more common. Increased presence of the preferred phenotype, coupled with increased human

interaction in the plant's lifecycle, could have sustained this phenotype in populations. Generations of selection would eventually result in a genetically and morphologically altered population (Rindos 1984:138-139). For the last century the Illinois Long-term Selection Experiment has been breeding different populations of maize through selection of high and low oil and protein (Moose *et al.* 2004). Researchers selected the top 12 to 24 ranking ears (assaying maize kernels to determine ranking) to forward the next generation. Through over 100 cycles of annual selection, researchers increased oil content from 4.7% to 22% and protein levels from 11% to 32% in Burr's White open pollinated variety (Moose *et al.* 2004).

The variation in seed phenotypes (and plant phenotypes, see Chapter 3) present in southern Manitoba would have provided suitable resources for people to utilize. Seed phenotypes were retained in the first generation of seed grown in the common garden environments (see discussion below). In the few populations tested, perisperm and testa thickness were moderate to highly heritable, with perisperm diameter having a slightly higher heritability than testa thickness, but since these traits were highly correlated, it is probable that they are passed on together. Larger seeds with thinner testas are present in populations in Manitoba, and seeds with thinner testas also germinated before seeds with thicker testas. These data suggest that Manitoban populations of *C. berlandieri* could potentially be altered through a similar mass selection regime as the Illinois Long-term Selection study on maize (Moose *et al.* 2004).

Seed phenotypes from different populations were also influenced by environmental factors present at the location in which they were grown (i.e. GxE interactions). Large interaction effects on seed traits (size, testa thickness, and colour)

indicated plasticity played a role in ultimate seed phenotype. Overall, growing wild collected seed in a common garden setting (tilled soil, weeded and watered) resulted in larger seeds with thinner testas and lighter seed colours. Between the different locations, populations tended to produce larger, thinner testa seeds at the Arboretum location versus the Glenlea location.

Environmental variation incorporates various factors including climate, soil conditions and the human management history of the plot (Don Flaten pers. com. 2016; see Chapter 3 discussion for full details). Different management strategies affected biomass and seed mass production in common garden grown plants in this research (see Chapter 3), as well as in other annual and perennial crops (Seward 2016). Plants grown at the Arboretum produced higher seed mass, and produced larger seeds with thinner testas, and variation in seed colours compared to plants grown at the Glenlea location and plants collected from the wild progenitor populations. Seed and plant phenotypes (small plants with smaller, thick walled seeds) were more similar between the Glenlea grown plants and the wild collected plants. While it may be difficult to determine the pre-contact management history of landscapes, environmental factors, including the process of land management, impacts plant and seed phenotypes should be considered for a fuller understanding of plant domestication.

Common garden grown plants also had higher percent germination after both cold treatments compared to the wild populations. This may represent a plastic response to improved environmental conditions, suggesting that one can increase percent germination through low-level cultivation. This would increase the total population of plant and seed phenotypes from which to select. Further, seed grown in the common

garden environment (i.e. 2012) had been originally harvested from their respective wild populations up to two years prior (i.e. 2010, 2011) to the common garden experiment and subsequent germination experiments. It is possible seed age-related effects might have reduced percent germination, though long-term seed dormancy is known for the genus (*C. album*, Karssen 1970) and dormancy has evolved in the majority of plants to combat environmental variation (Baskin and Baskin 2014; Finch-Savage *et al.* 2006). There were no significant differences in percent germination between any common garden grown populations across cold treatments, suggesting that cold winters did not adversely affect percent germination.

5.5.4 Potential for pre-contact cultivation and domestication

Chenopodium berlandieri populations in southern Manitoba show a number of characters similar to populations within the range of where the species was domesticated (e.g. Ohio), and North Dakota where local populations were intensively cultivated (Ahler 2007). This research supports the hypothesis that selection for increased seed size and decreased testa thickness is a key process in the domestication of *C. berlandieri* seed. Cycles of selection of culturally important seed phenotypes can be achieved through mass harvesting. For instance, the largest seeds are close to 2mm in diameter and variation in seed colour is discernable. In all wild populations, black seeds were the most frequent, but the full range of seed colours was present at low frequencies (Figure 5.8).

This research has shown that subsequent sowing of stored seed in prepared beds resulted in a plastic response to seed phenotype with high genetic variation underlying its seed traits: most populations showed an increase in seed size with a reduction in testa

thickness. The overall percent germination of common garden grown plants significantly increased as well. Larger, lighter coloured seeds with thinner testas would germinate first, which, if protected, could grow into a more or less uniform population. The strong correlation between seed size and testa thickness, and high heritability of these of these traits translates into this seed phenotype being passed into the following generation. Harvesting, storing, and subsequent planting of higher frequencies of this seed phenotype would continue to increase the frequency of this phenotype over future generations.

Applying the information gained from this research, I present a short thought experiment. Please bear in mind that these responses to selection do not account for any other factors, such as change in the selection differential or heritability in subsequent generations, and should be read with caution.

The Breeder's equation is a formula that calculates the response to selection of a given trait (R) based on the heritability (h^2) of the trait in question and the strength of selection (S).

$$R = S \cdot h^2$$

The strength of selection (also referred to as the selection differential) is the mean of the proportion of the population selected for the next generation compared to the population mean (Freeman and Herron 2007; Adewale *et al.* 2010). To calculate S from my research I used only those maternal lines that were included in both germination experiments. This was to see if there was a change in response to selection based on increased percent germination for northern populations. The population mean was calculated from the means of all maternal lines included in the germination experiments. A weighted mean for the maternal lines selected for the next generation was calculated by multiplying the

mean of each plant by its proportion of germinated seeds. The selection differential was difference between the weighted mean of these maternal lines and the population mean. The selection differential in these calculations represents those seed phenotypes that exhibited varying fitness levels (because some maternal lines did not have any germinated seeds). The heritability calculated for the AB population from Manitoba was applied to all populations.

I calculated the response to selection for seed size (perisperm diameter) and testa thickness for the SV population from Manitoba and the ND1 population from North Dakota. These populations were selected because sufficient variation in germination was present to calculate suitable strength of selection (S).

The response to selection calculated from both germination experiments was quite similar. Responses for seed size and testa thickness in the SV population in Manitoba were quite high. Seed size was calculated to increase 0.25-0.26mm after one generation. This means that the mean seed size would increase from 1.63mm to 1.88mm after one generation! Seed size would increase to over 2mm the second generation, which is similar to the range of seed sizes associated with domesticated seed samples from Ash Cave that included some specimens over 2mm (Smith 2007: 142). Similarly, testa thickness was calculated to decrease between 0.0025mm and 0.002mm after one year of selection. This seems small but at this rate of decrease it would only take 11 generations to virtually eliminate the testa. The domesticated testa thickness is considered to be less than 0.02mm (Gremillion 1993). Calculations based on the long stratification experiment indicated the testa would reduce to the domesticated phenotype

after 29 generations. Because these two calculations are quite variable, it is likely that a real-world response to selection would fall somewhere in between.

The North Dakota population calculations present a more conservative response to selection, using long cold treatment data sets to calculate S . Response to selection for seed size is still quite high ($R=0.017\text{mm}$), increasing the mean perisperm diameter from 1.63mm to 1.64mm after one year of selection. After 25 generations, the mean seed size would increase to just over 2mm. The response to selection for testa thickness was not as high, at -0.00043mm . It would take 50 generations for the testa thickness to reduce from 0.037mm to 0.016mm, which would place it within the range of domesticated *C. berlandieri*.

5.5.5 Potential blocks to pre-contact cultivation and domestication

While it is possible that some populations in Manitoba may have undergone this process, there are a few biological differences that may impede the process of domestication of *C. berlandieri* in southern Manitoba. First, the wild AB and DM populations in Manitoba exhibited small dark coloured seeds with thicker testas. Depending on the relative frequency of populations with this seed phenotype that would have been present in the pre-contact period (see Chapter 3 for discussion of populations structure and frequency), and the relationship between this phenotype and long term dormancy, mass selection for seed traits may not have resulted in larger seeds with thinner testas similarly to the Illinois Long-Term Selection Experiment (Moose *et al.* 2004). Further, genetic correlation between seed size and testa thickness, and heritability of seed traits were only estimated for a single population (AB population). The power

was too low (small sample size) to determine significance for these estimates for the DM and SV populations. In addition, percent germinations in wild AB and DM populations were very low (<5%) compared to all other wild populations. The sampling design used in the germination experiment lacked the strength to properly test for differences in percent germination by population and location for the common garden accessions. Despite low sample sizes in the germination experiment, common garden populations seed traits followed the trends set by germinated seeds from the wild populations. Percent germination was high, seed size increased and testa thickness decreased and seed traits were heritable. Future research needs to determine what influence human selection pressures apply to common garden grown populations across generations.

Tables and Figures

Table 5.1: Mean air temperature and precipitation for the months seed samples were chilled in the long cold treatment germination experiment. Means calculated by Environment Canada (www.weather.gc.ca). Precipitation includes snow and rain.

	November	December	January	February	March	April
Mean Temperature (°C)	-6.4	-14.7	-17.4	-14.3	-9.2	-1.6
Mean Precipitation (mm)	22.4	24.4	21.0	5.0	11.7	38.2

Table 5.2: Analysis of variance for perisperm diameter, testa thickness and percent seed colour of *Chenopodium berlandieri* from ten wild populations from Manitoba and North Dakota, Missouri and Ohio (sub-regions). Values reported in Table are *F*-ratios and associated degrees of freedom for each effect. Significance denoted by * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, n.s. $P > 0.05$).

Effect		Perisperm diameter	Testa thickness	Seed colour
Sub-region	$F_{3,6}$	1.30 n.s	168.73***	0.51 n.s
Population (sub-region)	$F_{6,400}$	0.86 n.s	30.54***	28.86***

Table 5.3: Analysis of variance for perisperm diameter, testa thickness and mean seed colour for three common garden populations of *Chenopodium berlandieri* grown in 2012 at two locations. Values reported in Table are *F*-ratios and associated degrees of freedom for each effect. Significant denoted by * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, n.s. $P > 0.05$).

		Perisperm diameter	Testa thickness	Mean seed colour
Population	$F_{2,211-212}$	127.91***	9.38***	3.86*
Maternal line (Population)	$F_{33,211-212}$	26.10***	2.77***	3.42***
Location	$F_{1,11-20}$	28.96***	24.00***	5.12*
Replicate (Location)	$F_{4,211-212}$	2.65*	1.37 n.s	2.15 n.s
Population * Location	$F_{2,211-212}$	24.33***	6.59**	11.51***

Table 5.4: Phenotypic and genetic correlations between perisperm diameter, testa thickness and seed colour for wild and common garden *Chenopodium berlandieri* populations from Manitoba, North Dakota, Missouri and Ohio (sub-regions). Common garden means calculated from parent-offspring maternal family means. Genetic correlation calculated using family means in parents and offspring from the AB population grown at the Arboretum. Significance denoted by * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, n.s. $P > 0.05$).

	N	Testa x Perisperm	Testa x Colour	Perisperm x Colour
Across wild populations		-0.69*	-0.67*	0.59 n.s.
Within wild populations				
Manitoba - AB	58	-0.02 n.s.	-0.28*	0.08 n.s.
Manitoba - DM	68	0.07 n.s.	-0.25*	0.03 n.s.
Manitoba - SV	31	-0.42*	-0.58***	0.07 n.s.
North Dakota - ND1	40	-0.14 n.s.	-0.52***	0.14 n.s.
North Dakota - ND2	44	-0.15 n.s.	-0.56***	0.33*
North Dakota - ND3	40	0.14 n.s.	-0.58***	0.09 n.s.
Missouri - MM1	32	-0.06 n.s.	0.20 n.s.	-0.07 n.s.
Missouri - MM4	27	0.018 n.s.	-0.69***	-0.21 n.s.
Ohio - OH1	35	-0.02 n.s.	-0.68***	0.45**
Ohio - OH4	35	-0.58***	-0.48**	0.14 n.s.
Within common garden populations				
Arboretum - AB	115	-0.62***	-0.71***	0.72***
Arboretum - DM	17	-0.58*	-0.83***	0.63**
Arboretum - SV	39	-0.65***	-0.84***	0.52**
Glenlea - AB	57	-0.27*	-0.69***	0.41**
Glenlea - DM	5	-0.24 n.s.	-0.79 n.s.	-0.76 n.s.
Glenlea - SV	22	0.10 n.s.	-0.60**	-0.10 n.s.
Genetic (AB at Arboretum)		-0.70 (0.08)	Not estimated	Not estimated

Table 5.5: Heritability (H^2) of perisperm diameter and testa thickness calculated for Manitoba *Chenopodium berlandieri* populations grown at the Arboretum location. Heritability was calculated by regression of family means in offspring on parental phenotype for each trait. Significant heritability calculated for the AB population is also reported.

Population	N	Perisperm	Testa thickness
AB	19	0.99***	0.37*
DM	10	0.58	0.15
SV	5	1.12	0.05
AB- Glenlea	16	0.78***	n.s.

Table 5.6: Analysis of the proportion of germinated seed from the short and long cold treatment experiments for ten wild *Chenopodium berlandieri* populations. Overall differences between populations and comparisons between selected sub-regions reported. Effect of testa and perisperm diameter on proportion of germinated seeds from each cold treatment experiment also reported. ★ Estimated with different model because it correlated strongly with testa thickness. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, n.s. $P > 0.05$.

	Short Cold Treatment		Long Cold Treatment	
	DF	Wald Chi square	DF	Wald Chi Square
Population differences	9	2410***	8	4630***
Sub-region differences				
Ohio vs Manitoba	4	243**	3	1792***
Ohio vs SV	2	79***	1	664***
North Dakota vs Manitoba	5	19**	4	1156***
Testa	1	189**	1	364***
Perisperm ★	1	4.6*	1	161***

Table 5.7: Analysis of proportion of germinated seed from the short and long cold treatment experiments for *Chenopodium berlandieri* plants grown in common gardens. Group reflects different population and location combinations (e.g. AB grown at the Arboretum). Common garden populations were compared against their wild progenitor populations to determine differences in percent germination in a single progeny generation. Significance denoted by * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

Effect	Short Cold Treatment		Long Cold Treatment	
	DF	Wald Chi square	DF	Wald Chi Square
Group	4	179***	4	369***
Wild DM vs. DM Arboretum DM Glenlea	2	49***	2	133***
Wild SV vs. SV Arboretum	1	73***	1	59***

Table 5.8: Analysis of perisperm diameter and testa thickness of germinated seeds from ten wild and two common garden populations of *Chenopodium berlandieri* across four sampling days in the short cold treatment germination experiment. Repeated measures test on perisperm diameter and testa thickness explored whether seed size and seed coat thickness changed across sampling day (day 4, 8, 12, 16) in the germination experiment. Effect of population and sub-region on seed traits also tested. Significance denoted by * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, n.s. $P > 0.05$.

Effect		Mean perisperm	Mean testa thickness
Sampling day	$F_{3, 48}$	1.10 n.s.	3.13*
Population (Sub-region)	$F_{9, 48}$	1.73 n.s.	1.28 n.s.
Sub-region	$F_{14, 48}$	0.64 n.s.	1.34 n.s.

Table 5.9: Germinated seed means (testa thickness and perisperm diameter) from the short cold treatment germination experiment. Trait means for each sampling day averaged all germinated seed measurements across ten wild and two common garden populations of *Chenopodium berlandieri* included in germination experiment. LS Means calculated from 25 maternal families used in the repeated measures analysis from four sampling days (day 4, 8, 12, 16) reported. For comparison, means of testa thickness and perisperm diameter for all maternal lines with germinated seeds (n variable) sampled from the short cold treatment test (PROC MEANS, SAS 2010) are reported.

Testa thickness	All Replicated Maternal Lines			All Maternal lines in short cold germination experiment		
	N	LS Means	SE	N	Mean	SE
Sampling Day 4	25	0.021	0.002	86	0.020	0.001
Sampling Day 8	25	0.023	0.002	54	0.022	0.001
Sampling Day 12	25	0.026	0.016	52	0.027	0.001
Sampling Day 16	25	0.025	0.002	28	0.024	0.002
Perisperm Diameter						
	N	LS Means	SE	N	Mean	SE
Sampling Day 4	25	1.48	0.049	86	1.49	0.028
Sampling Day 8	25	1.41	0.048	54	1.46	0.033
Sampling Day 12	25	1.39	0.049	52	1.43	0.035
Sampling Day 16	25	1.40	0.049	28	1.43	0.046

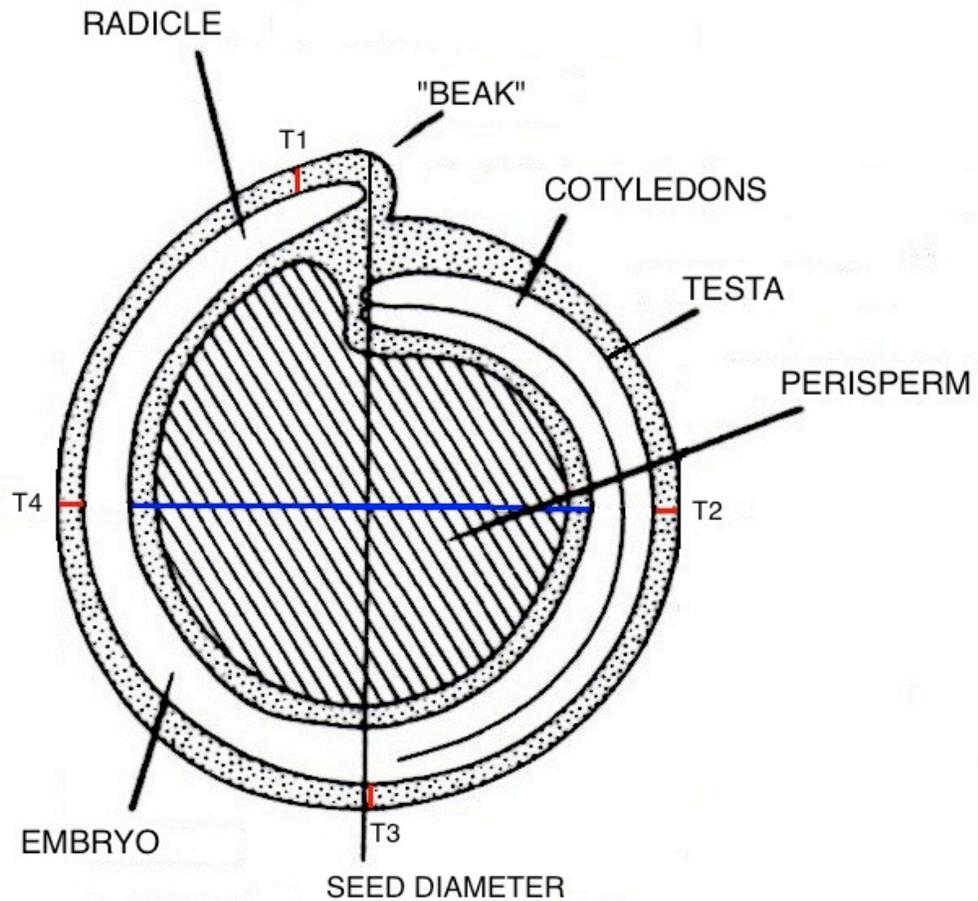


Figure 5.1: Cross section of a *Chenopodium* seed. Main seed components are labeled. Measurements were taken on total seed diameter, perisperm diameter, and testa thickness. To account for variation in testa thickness, four measurements (T1, T2, T3 T4) around circumference of seed (red lines) were averaged. Perisperm diameter (blue line) measured as seed diameter – (T2 + T4). Image adapted from Smith 2007: Figure 5.3, pg. 112).

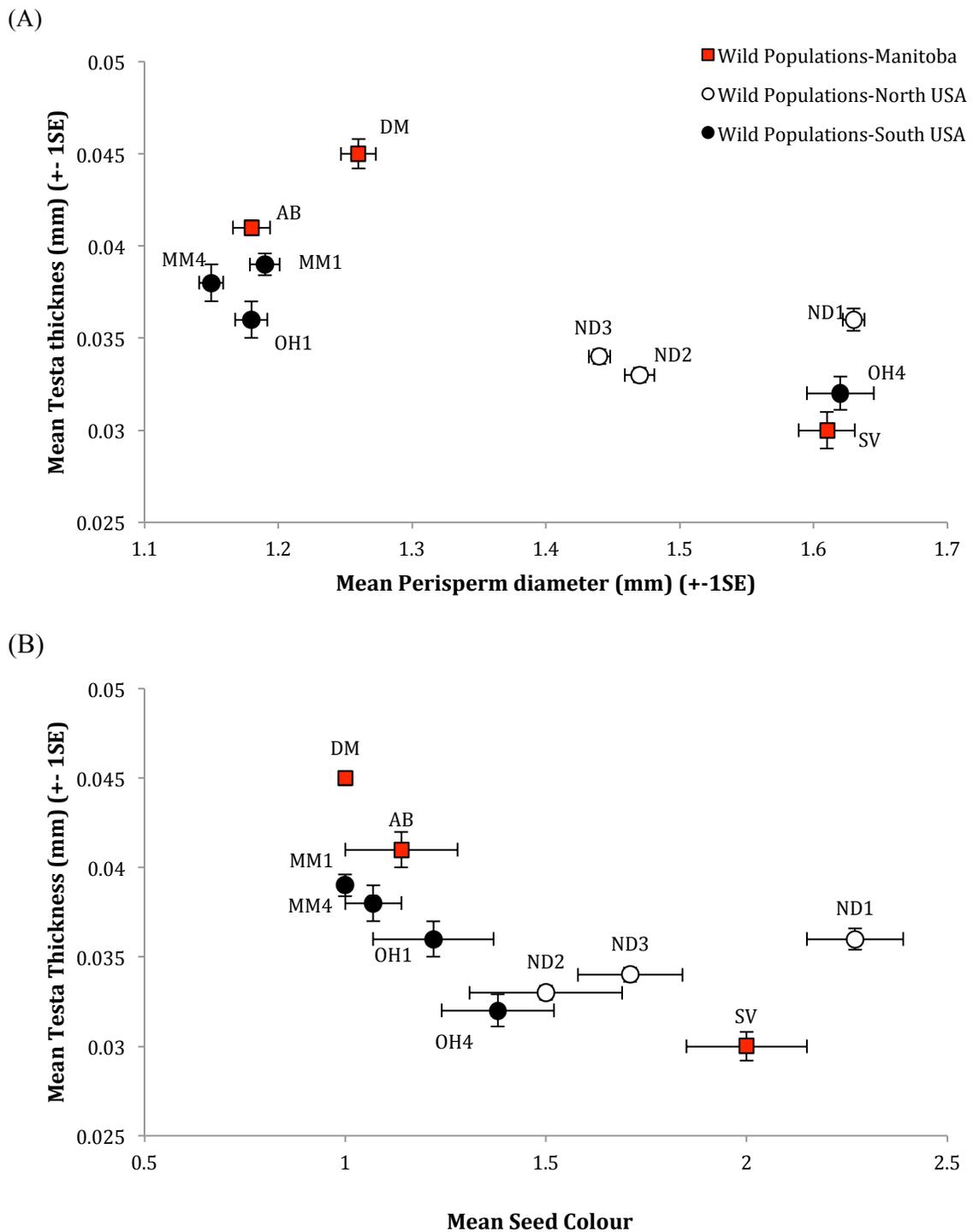


Figure 5.2: Mean seed traits for wild populations of *Chenopodium berlandieri* from Manitoba and North Dakota (northern sub-region), Missouri and Ohio (southern sub-region). (A) Mean perisperm diameter and mean testa thickness for wild populations. (B) Mean seed colour plotted against mean testa thickness for all wild populations. Colour designations: black=1, red-black=2.

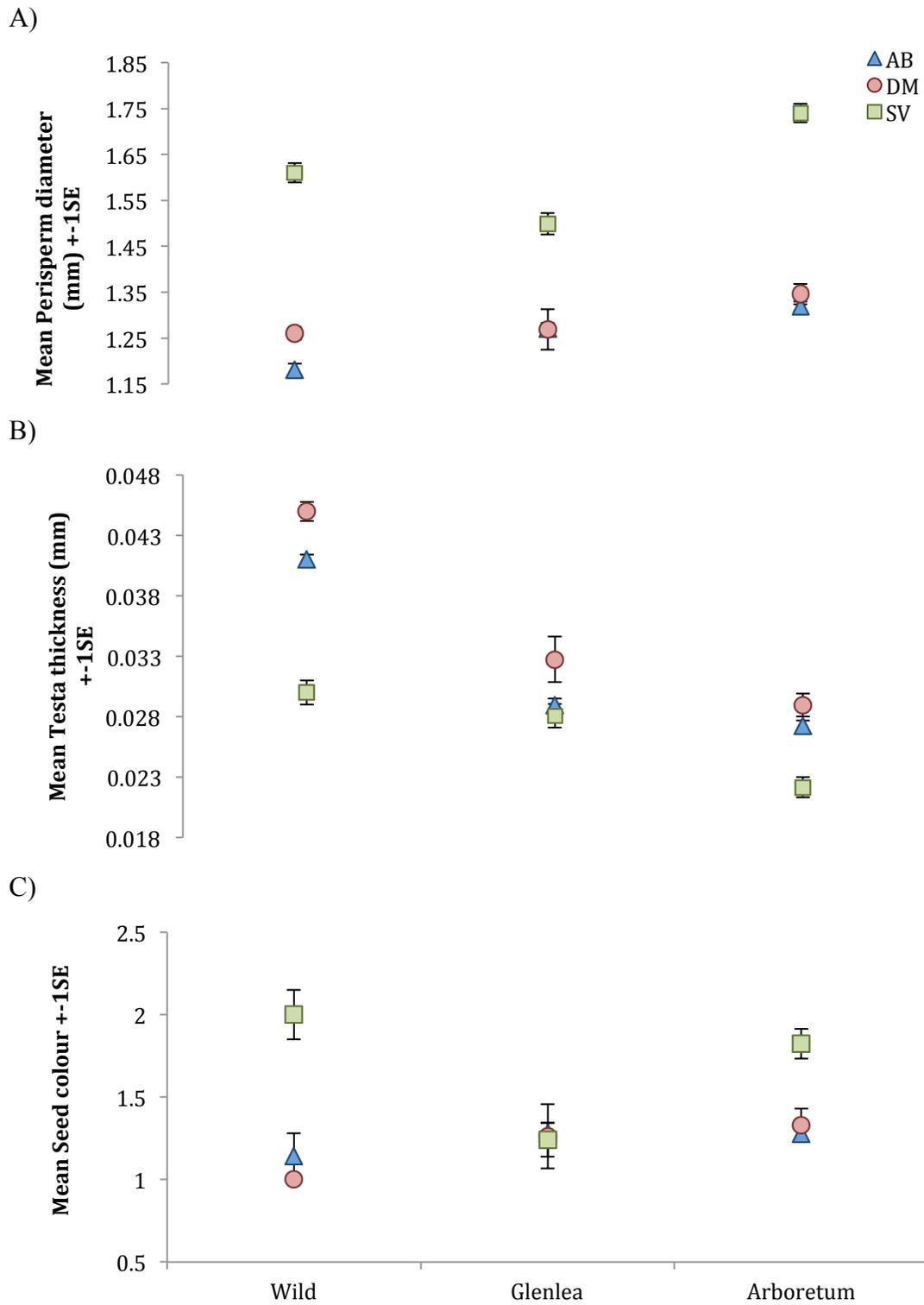


Figure 5.3: Genotype-environment interactions for perisperm diameter (A), testa thickness (B), and seed colour (C) in wild and common garden populations of *Chenopodium berlandieri*. Means graphed by population across location: wild, Glenlea, Arboretum. Colour designations: black=1, red-black=2. Error bars indicate \pm 1 S.E.

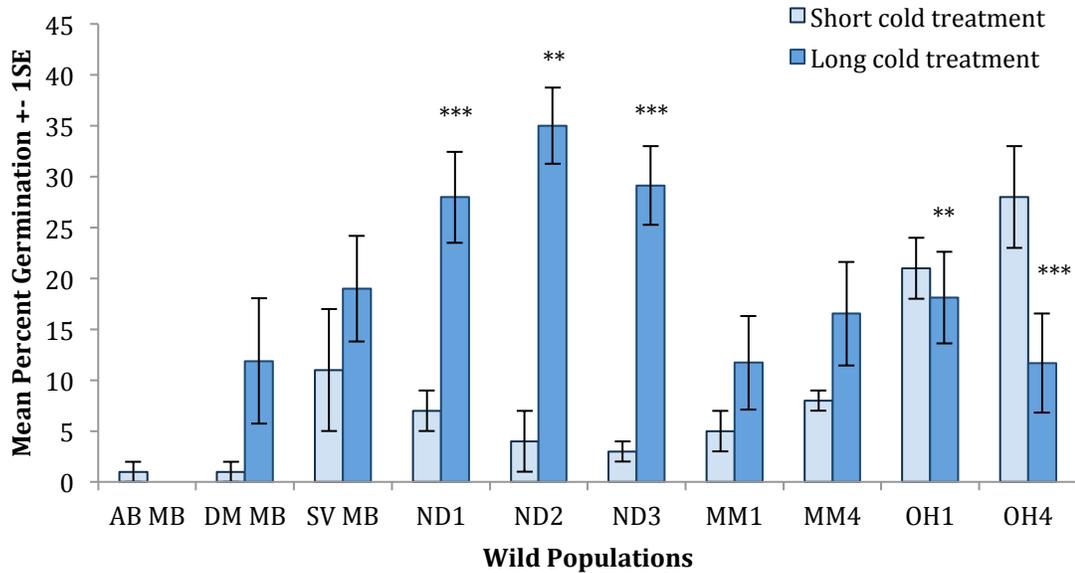


Figure 5.4: Comparison between mean percent germination calculated for the short and long cold treatments across wild *Chenopodium berlandieri* populations. Significant differences in percent germination between the two experiments are ** $P < 0.01$, *** $P < 0.001$.

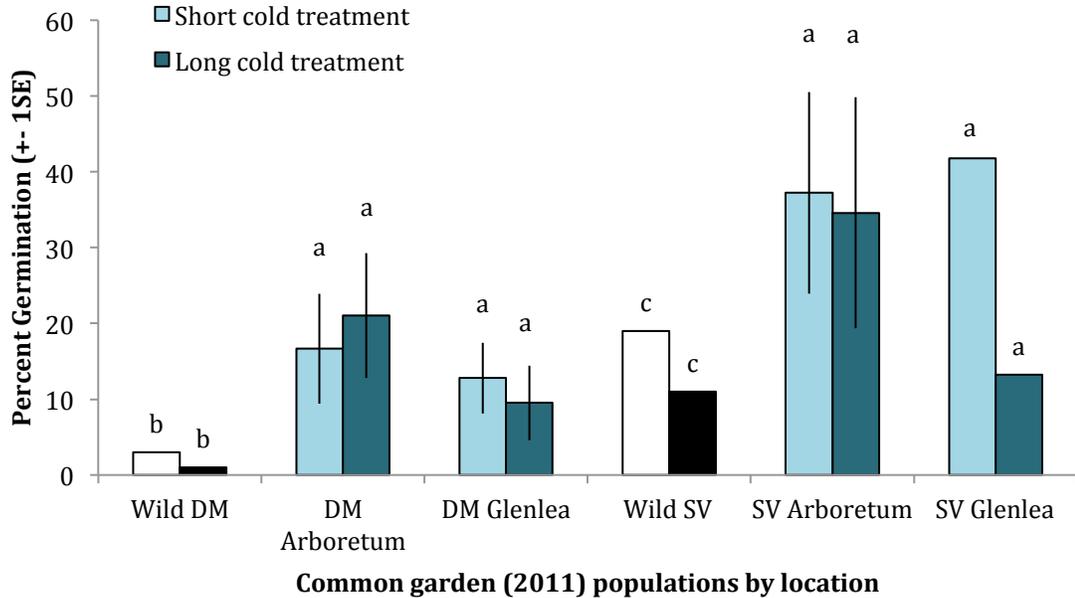


Figure 5.5: Percent germination of common garden *C. berlandieri* populations by location for the short and long cold treatment experiments. Mean and standard error (+/- 1 SE) reported. A single maternal line (same maternal line for both short and long stratification) represents the SV population grown at Glenlea (error bars not included). All other common garden populations had 14 maternal lines. a, b, c denote significant differences in percent germinations between population*location combination.

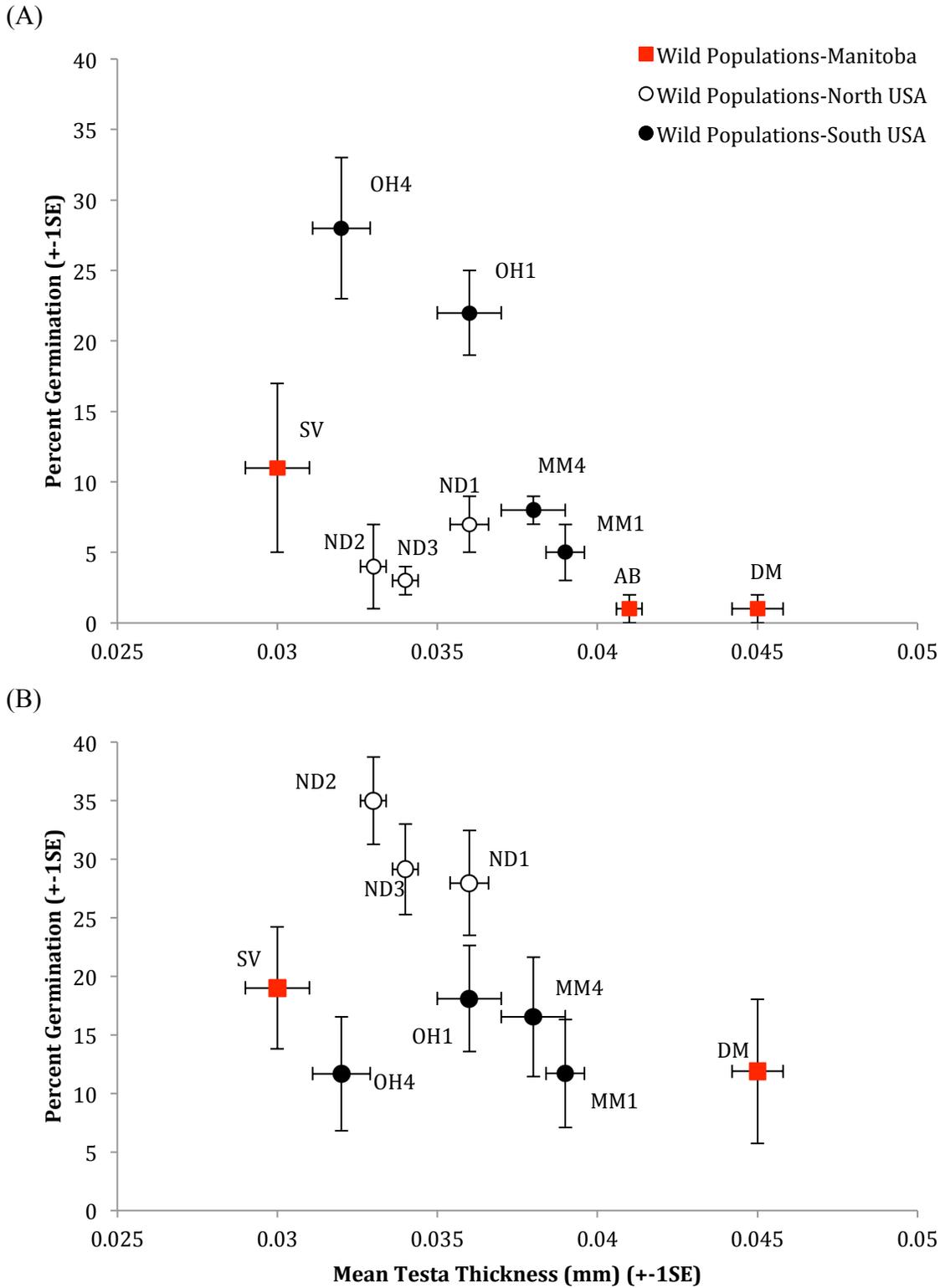


Figure 5.6: Interaction between mean percent germination and testa thickness (mean $\pm 1SE$) for all wild populations of *Chenopodium berlandieri* from (A) short cold chilling experiment, and (B) long cold chilling experiment.

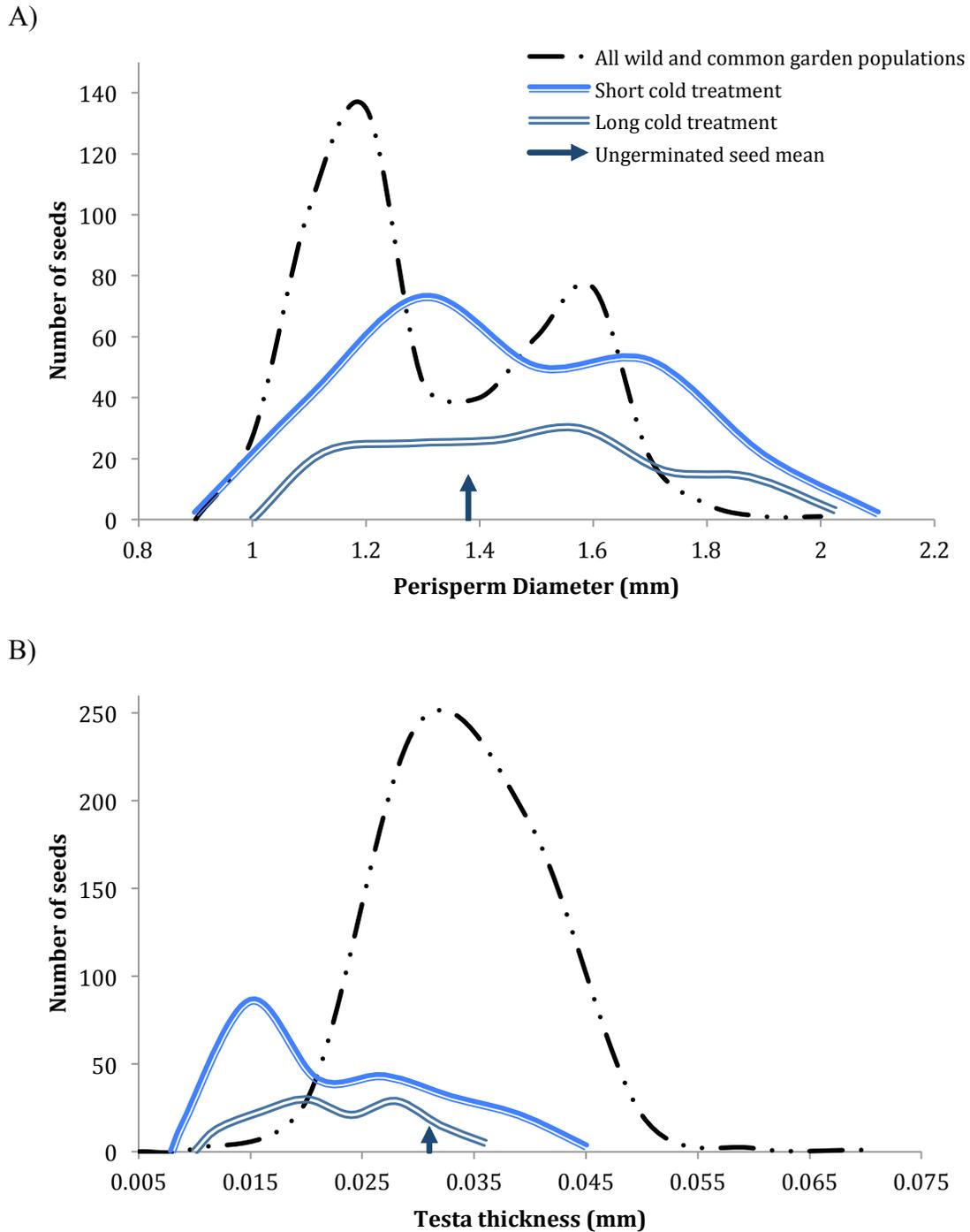


Figure 5.7: Distribution of perisperm diameter (A) and testa thickness (B) for germinated *C. berlandieri* seeds from short and long cold treatment experiments plotted against distribution of the respective seed traits for all wild populations. Vertical arrows represent mean perisperm diameter and testa thickness of ungerminated seeds from both germination experiments (perisperm diameter ~ 1.39 mm; mean testa thickness ~ 0.031 mm). Distributions used 0.12 mm (perisperm) and 0.01 mm (testa) intervals for bins and smoothed lines.

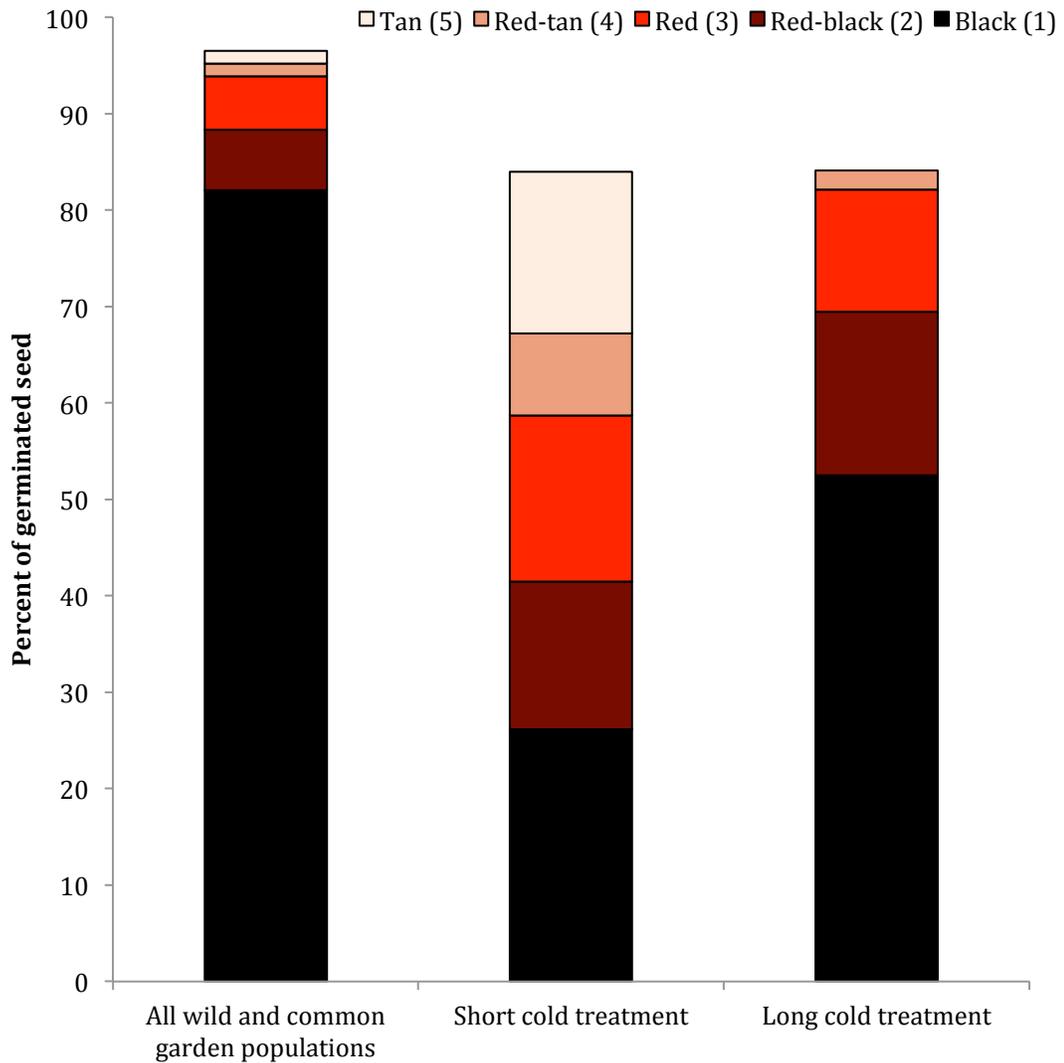


Figure 5.8: Percent of germinated seeds per colour category from the short and long cold treatment germination experiments for all wild and common garden populations of *Chenopodium berlandieri*. The total percent of germinated seed per colour category is reported for comparison. Germinated seed in each seed colour category calculated as a proportion of germinated seeds per colour divided by total germinated seed.

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Appendix 5.1

Summary of total *Chenopodium berlandieri* populations, maternal lines, and seeds measured in short and long cold treatment germination experiments. Total seeds approximated from a sub sample of four maternal lines counted per population and multiplied by total number of maternal lines included.

Population	Short cold treatment				Long cold treatment			
	SS-Maternal lines	Number of germinated lines	Total seeds	Total germinated seeds	LS-Maternal lines	Germinated lines	Total seeds	Total germinated seeds
DM	14	3	350	5	18	8	936	36
SV	14	6	350	86	17	15	1251	237
AB	14	4	350	35	-	-	-	-
ND1	15	12	3600	251	14	14	3370	1177
ND2	8	5	3600	128	14	14	4989	1786
ND3	14	10	5040	137	14	14	4612	1428
MM1	8	8	10,800	558	15	12	20,100	1151
MM4	14	13	27,300	2079	13	12	20,540	1880
OH1	9	7	9900	1864	14	14	15,540	1750
OH4	13	10	4550	1476	14	14	5000	683

Appendix 5.2

Analysis of variance for perisperm diameter, testa thickness and mean seed colour of germinated seeds from ten wild *Chenopodium berlandieri* populations included in the short and long cold treatment germination experiments. Values reported in Table are *F*-ratios and associated degrees of freedom for each effect. Significance denoted by **P*<0.05, ** *P*<0.01, ****P*<0.001, n.s. *P*>0.05).

		Perisperm diameter	Testa thickness	Mean colour of germinated seeds
Short Stratification				
Sub-region	<i>F</i> _{3,6}	3.14 n.s.	0.29 n.s.	0.23 n.s.
Population (Sub-region)	<i>F</i> _{6,111-193}	23.16***	8.50***	7.51***
Long Stratification				
Sub-region	<i>F</i> _{3,5}	1.22 n.s.	1.95 n.s.	0.45 n.s.
Population (Sub-region)	<i>F</i> _{5,140}	44.96***	6.54***	13.15***

Appendix 5.3

Analysis of variance for perisperm diameter, testa thickness and mean seed colour of *Chenopodium berlandieri* plants grown in common garden populations included in the short and long cold treatment germination experiments. Values reported in Table are *F*-ratios and associated degrees of freedom for each effect. Significance denoted by **P*<0.05, ** *P*<0.01, ****P*<0.001, n.s. *P*>0.05).

		Perisperm diameter	Testa thickness	Mean seed colour	Mean germinated seed colour
Short cold treatment					
Population	<i>F</i> _{1,33}	66.61***	18.24***	3.42 n.s.	0.00 n.s.
Location	<i>F</i> _{1,62}	1.72 n.s.	4.26*	1.87 n.s.	0.10 n.s.
Population * Location	<i>F</i> _{1,62}	-	-	0.66 n.s.	5.20*
Long cold treatment					
Population	<i>F</i> _{1,10}	67.70***	7.40*	3.50 n.s.	5.71*
Location	<i>F</i> _{1,10}	0.766 n.s.	1.08 n.s.	0.13 n.s.	0.09 n.s.
Population * Location	<i>F</i> _{1,10}	1.58 n.s.	6.15*	8.64*	0.00 n.s.

6.0 THE NATURE OF PEOPLE-PLANT RELATIONSHIPS IN SOUTHERN MANITOBA: POTENTIAL CULTIVATION OF *CHENOPODIUM BERLANDIERI*

6.1 Introduction

In the last decade, knowledge about the types of subsistence economies practiced by pre-contact cultural groups in West-Central Canada has grown significantly. Residue analysis on ceramic sherds and lithic tools from numerous Middle and Late Woodland sites across Boreal, Aspen Parkland, and Prairie regions indicate that many indigenous groups combined native plant use with native cultigens (e.g. native rice, *Zizania palustris*, *Z. aquatica*) and domesticated maize (*Zea mays*), bean (*Phaseolus vulgaris*), and squash (*Cucurbita* sp.) (Boyd and Surette 2010; Boyd *et al.* 2014). Consumption of domesticates increased during the Late Woodland period (AD1000-1500), becoming widespread throughout the Prairies and Boreal forest. Consumption and probable cultivation of crops was especially frequent in southwestern Manitoba and the Red River Valley region (Boyd *et al.* 2006; 2008; Boyd and Surette 2010). Small-scale horticulture may have been practiced at some sites in the Boreal forest (Boyd *et al.* 2014).

Residue studies have also illuminated regional variation in people-plant relationships as expressed through subsistence economies reported in the Boreal forest, Aspen Parkland, and Canadian Prairie regions. This regionalization of plant use (through procurement or production, *cf.* Smith 2001) is dependent on diverse factors including the ecology and biology of plants, cultural choices and cultural interactions. Increased frequency and intensity of imported crop consumption and cultivation in the Prairie region reflects, on one level, more suitable conditions compared to cultivation over the Boreal forest (Boyd *et al.* 2014). Boreal soils are thin and acidic compared to the thick

humic soils of prairie that supports modern agriculture. Specifically, the adoption of beans may have been limited to lower latitudes because sprouting bean plants are more susceptible to cold weather; the colder subarctic climate would limit their cultivation while the cold tolerant maize varieties would have grown successfully (Boyd *et al.* 2014; Deck and Shay 1992).

Cultural choices and interactions also influenced subsistence practices. Avonlea groups (AD300-1100) living in the Aspen Parkland employed a mixed subsistence strategy incorporating maize, beans, native rice and native berries, tubers and other food types (Lints 2012). These people lived far from native rice sites, so they would have traded for native rice, probably with contemporaneous Laurel groups (BC150-AD1100) (Lints 2012). Contemporaneous cultural groups living near Whitefish Lake, northwestern Ontario employed a subsistence economy focused on cultivating native, harvesting local native plants and incorporating imported or locally grown maize (Boyd *et al.* 2014). Boyd and colleagues suggest native rice filled the protein rich plant food requirement that beans tend to fill, therefore adding beans to the diet was not necessary. Maize was adopted because it would have supplied a storable carbohydrate source (Boyd *et al.* 2014), and cold tolerant varieties of maize would have been available (Schneider 2002).

People-plant relationships develop over time, through individuals pragmatically engaging with their environment (Ingold 2000). The environment in a developmental perspective (see Chapter 1) includes all aspects that compose an individual's world, within which each individual acts and interacts (Ingold 2000). Environments include abiotic conditions such as large-scale climatic conditions, geology, hydrology, and landscape, to local microclimate and soil conditions. Biological aspects include all

organisms- people, plants, animals, fungi, bacteria, and viruses, plus all interactions between these components. The main interactions include cultural interactions (e.g. intrafamilial to intercommunity), biological interactions (e.g. genetic, genetic x environment) and interactions between people and culturally important plant species (e.g. cultivation). A developmental perspective incorporates biological theoretical perspectives such as niche construction theory, in that all organisms shape their environment as much as their environment shapes them (Odling-Smee *et al.* 2003), which provides opportunities and constraints for growth and change.

From a developmental perspective, the recovery of tropical and native domesticated crop residues in the Canadian Prairies and Boreal forest indicate that different cultural groups were establishing various relationships with plant species. Trade, migration and/or the diffusion of ideas appeared to have generated mixed subsistence patterns. These subsistence economies may represent previously unknown strategies that employed various mixtures of native plant harvesting, cultivation of native plants, and domesticated crops (Boyd *et al.* 2014; Lints 2012).

Mixed economies, once thought lost to the “archaeological grey zone” (Harris 2007; Smith 2001), are being investigated through new applications of old techniques, such as pollen and phytolith analyses (Boyd *et al.* 2006, 2008; Gremillion and Piperno 2009; Gremillion *et al.* 2014), residue analyses (e.g., Raviele and Lovis 2014), and application of expanded theoretical perspectives on people-plant relationships. Perspectives include niche construction theory that investigates the role of human-constructed areas and ‘domesticated landscapes’ in domestication and the development of agriculture (Terrell *et al.* 2003; Crawford 2014). Other researchers focus on the process

of domestication that alters morphological traits and their underlying genetic structure, and how this process can enlighten the ‘how, when and where’ of people-plant relationships (e.g., Zeder *et al.* 2006).

My research applies the process of domestication to *Chenopodium berlandieri*, a native annual, small-seed producing species, ubiquitously recovered in Late Woodland period archaeological sites in southern Manitoba, which was used for its seed by pre-contact cultural groups (Arnason *et al.* 1981; Moerman 2010). At issue here is whether the characteristics in archaeologically recovered seeds might substantively address whether pre-contact people were gathering wild resources or cultivating *C. berlandieri* populations.

6.2 Archaeological Site and Target Species Selection

Two depositionally stratified archaeological sites in the Red River Valley region yield evidence of occupation reflecting different lifestyles and subsistence strategies. They are the Forks site (DILg-33:08A), located at the junction of the Red and Assiniboine Rivers in downtown Winnipeg, and the Lockport site (EaLf-1), located on the Red River 30km north of Winnipeg. These sites are some of the few excavations that employed appropriate methodologies to recover seed data to address subsistence questions. Extensive sampling and flotation for the recovery of floral remains produced evidence of the use of various native and domesticated plants.

First, the cultural affiliations reported at these sites are summarized. The cultural chronology of Manitoba has undergone and is currently undergoing refinement and, in some cases, restructuring. Current knowledge of which pre-contact peoples lived and

utilized resource areas in southern Manitoba indicate varied cultural affiliations and political economies based on ceramic stylistic attributes, subsistence ecology, settlement patterns, and other cultural information. Many and varied Late Woodland groups (e.g. Blackduck, Rainy River Composite, Duck Bay, Selkirk) utilized these sites at different times and in different ways. Clearly attributing cultural affiliation to specific plant remains is quite difficult, and in many cases, generalized cultural designation will have to be used.

6.2.1 The Lockport site (EaLf-1)

The Lockport Site, occupied ~1500BC -AD1450 (MacNeish 1958; Buchner 1988) contain evidence of occupation by several pre-contact cultures. Subsistence strategies of two general cultural affiliations associated with the Late Woodland period (AD1000-1500) are presented. The first broad group of people has ancestral ties to both the Boreal forest and Canadian Prairies regions and likely developed *in situ*. Potential contributors to Late Woodland cultural groups include Blackduck, Rainy River Composite, Duck Bay, and Selkirk groups (Flynn 2002; Deck and Shay 1992). These groups are associated with a hunter-gatherer lifestyle that focused on harvesting native plants, hunting and fishing, but they also consumed some maize (Boyd et al. 2006). Utilized native plant species used include raspberry (*Rubus* sp.), strawberry (*Fragaria virginiana*), rose (*Rosa* sp.), amaranth (*Amaranthus* sp.), dock (*Rumex* sp.), and knotweed (*Polygonum* sp.). Goosefoot (*Chenopodium* sp.) was the most frequent recovery (Deck and Shay 1992).

The other broad cultural group represents a migration of Late Plains Woodland maize cultivators (Flynn 2002; Deck and Shay 1992), likely related to Northeastern

Plains Village variant groups (Flynn 2002) who occupied the headwaters of the Mississippi and Red Rivers from Iowa, western Minnesota and eastern North Dakota and practiced a mixed farming-harvesting economy (Hamilton pers. comm. 2016). The multi-component Lockport site is the first known maize cultivation site in Manitoba with definitive macro plant remains and residue evidence. Small quantities of carbonized kernels and cupules of the Eastern eight-row maize variety were recovered along with native plant resources, including berries (e.g. *Prunus* -wild cherry), small seeded annuals (e.g. Goosefoot), and medicinal plants (e.g. *Mentha* -mint) (Boyd and Surette 2010; Deck and Shay 1992). Residue analysis recovered evidence of maize starch and phytoliths associated with kernels and cobs, and starch of domesticated bean (*Phaseolus vulgaris*) (Boyd *et al.* 2008). Phytolith and starch evidence of maize cobs is associated with local farming rather than trade, while evidence of domesticated bean starch only suggests this crop was traded in (Boyd *et al.* 2006, 2008). Analysis of the maize starch grains identified a high incidence of crushed and deformed grains indicating it was first milled then boiled (Zarrillo 2008).

The presence of maize, bison scapula hoes, grinding stones, hearths, and bell-shaped storage facilities, and a relatively late date are associated with the Late Plains Woodland Kenosewun Complex (McKinley 2001), who are linked to Northeastern Plains Village variant groups (Deck and Shay 1992; Flynn 2002; Schneider 2002). Since no large garden plots, fortifications or semi-subterranean house structures were identified, it was originally suggested that maize was adopted on a small scale and grown in small to moderate sized garden plots, supplementing intensive native plant harvesting, bison hunting, and the Lockport rapids fishery (Hamilton *et al.* 2006). Recent calculations of

the scale of farming that occurred at the Lockport site, based on the size and number of bell shaped storage pits associated with maize cultivation, indicate that it is probable these groups were cultivating maize on a large scale, e.g. 1-4 acre fields (Syms and Speirs 2012). The suggestion that local ancient populations were farming maize and other domesticates on a larger scale is controversial because pre-contact farming in southern Manitoba was previously envisioned as supplemental, i.e. gardening or horticulture (Flynn 2002; Nicholson *et al.* 2011). This controversy forwards the need for constant rethinking and reanalysis of archaeobotanical and archaeological materials as new methodologies and more detailed analyses become readily available (Scott Hamilton pers. comm. 2016).

6.2.2 *The Forks site (DILg-33:08A)*

People have been living at the junction of the Red and Assiniboine Rivers (hereafter, the Forks) for millennia (Shay *et al.* 1991). Archaeological excavations at the Forks over the past 30 years indicated widespread evidence of historic buildings and work areas, and pre-contact habitation and processing sites associated with ceramic and pre-ceramic producing groups (Kroker 1989; Kroker *et al.* 1991; Shay *et al.* 1991). This research focuses on the Late Woodland period (AD1000-1500).

Mixed subsistence patterns associated with Late Woodland groups (e.g. Rainy River Composite, Bird Lake), and Late Plains Woodland groups were identified from the 2008 mitigation excavation for the basement of the Canadian Museum for Human Rights (Quaternary 2010). Differential sample processing between occupation levels resulted in the majority of the archaeobotanical remains recovered from Level 1 (AD1280), with

fewer recoveries from Level 2 (AD1260), Levels 2a and 2b (ca.1200), and Levels 3 and 3a (ca. AD1100) (Quaternary 2010). Additional soil processing is required to accurately document differences in plant use between cultural periods.

Botanical analyses from ceramic sherds and soil samples collected from Level 1 and Level 2 Complex (see Quaternary 2010 for descriptions of stratigraphy) indicate that site occupants consumed native plants and domesticates. Food species determined through macro plant remains analysis (Appendix 6.3) indicate hazelnuts, wild cherries, raspberries, goosefoot seeds, and nettle were consumed. Residue analyses further indicate that wild onion (*Allium* sp.), pine seeds (*Pinus* sp.), sunflower (*Helianthus* sp.) seeds and leaves, chokecherries (*Prunus virginiana*), saltbush (*Atriplex* sp.) seeds, maize, beans, and wild rice (*Zizania aquatic*) were consumed (Scott-Cummings *et al.* 2009 cited in Quaternary 2010). Lipid analysis indicated that bison, duck, antelope, beaver and fish were cooked with various combinations of these plants (Scott-Cummings *et al.* 2009 cited in Quaternary 2010).

Connections between Late Woodland and Late Plains Woodland cultural groups and groups are evident in the ceramic styles indicative of Plains or Eastern Woodland influences identified in all cultural levels (see Chapters 4-12 in Quaternary 2010). Residue analysis on a ceramic sherd from the Level 2 Complex (AD1260) indicated use of small-flowered marshelder (*Iva axillaris*). This is a species of the western Prairies, native to Manitoba. The root was used as a medicine to treat stomachaches, cramps, colds, or the leaves made into a tea to wash sores (Foster and Hobbs 2002). The presence of pronghorn cooked in the same vessel (Scott-Cummings *et al.* 2009 cited in Quaternary 2010) may suggest Plains or Parkland connections. However, the historic range of

antelope extended to the edge of the Tall Grass Prairie, relict areas of which remain in southeastern Manitoba (Nature Conservancy Canada n.d.). Therefore, pre-contact cultural groups would have been living within hunting distance of antelope populations.

Sherds from all levels tested contained pollen from pine, alder (*Alnus* sp.), sunflower, chen-am (*Chenopodium/ Amaranthus* sp.), wild buckwheat (*Eriogonum* sp.), and maize (Scott-Cummings *et al.* 2009 cited in Quaternary 2010). Much of the pollen recovered indicated the condition of the local environment (Scott-Cummings *et al.* 2009 cited in Quaternary 2010). However, a number of these genera include species harvested or cultivated for food. Maize pollen suggests plants may have been grown in the area, as pollen it typically only present when plants are flowering. Bison scapula hoe fragments and a possible squash knife were also recovered, further supporting the potential for maize horticulture in the area (Quaternary 2010). If domesticated maize was being grown in the area, it is possible that the sunflower and *Chenopodium* pollen may suggest these plants were cultivated.

6.2.3 Chenopodium berlandieri: target species

Net-seed goosefoot (*Chenopodium berlandieri*) is the target species used in this research to explore whether pre-contact groups were harvesting wild resources or cultivating domesticated plants. Net-seed goosefoot was selected because it is a native annual that produces many small edible seeds. It was one of the suite of domesticated native annuals identified in the Eastern Woodlands region (Asch and Asch 1977; Smith 1985; Smith and Funk 1985; Gremillion 1993), used widely prior to the adoption of maize and other domesticated plants (Smith 2007; Jones 1993; George and Dewar 1999),

and is related to domesticated quinoa (*Chenopodium quinoa*) (Wilson 1980; Bhargava *et al.* 2007). Cultural connections between southern Manitoba and the Eastern Woodland region (Hamilton and Nicholson 2006) suggest that subsistence strategies (e.g. incorporation of imported domesticates) may have spread into the Red River Valley from the south (Ahler 2007; Boyd *et al.* 2008), or from the east through the Boreal forest/ Great Lakes region (Boyd *et al.* 2014).

To understand if pre-contact plant relationships reflect harvest-based interactions, or cultivation of local native plant populations, archaeobotanical⁶ analysis and interpretation of subsistence practices must be undertaken. Recovery of macro plant remains (e.g. fruits, seeds, charcoal) through collection and processing of soil samples is predicated upon preservation of organic materials and understanding the taphonomic processes that led to their preservation and recovery.

6.3 Preservation of *Chenopodium*: Carbonization

In Manitoba carbonization is currently the most common preservation mode for archaeobotanical remains (Minnis 1981). Understanding the taphonomic record, the processes by which materials are deposited, moved and altered during and after deposition (Minnis 1981; Mischeck 1987), provides a more complete interpretation of archaeological remains. The carbonization process transforms organic matter into inorganic carbon and may distort the morphology of the organic material. Burial in the soil will also alter the state of preservation through changes in soil moisture, impacting

⁶ Ford (1979) distinguishes between archaeobotany as the recovery and analysis of plant remains from archaeological contexts and palaeoethnobotany as the interpretation of human-plant interrelationships from archaeological plant data. While I agree with Ford's use of the terms, I use archaeobotany and palaeoethnobotany interchangeably here.

roots, abrasion of the surface of seeds during redeposition, recovery through screening and/or flotation and other such mechanisms (Hubbard and al Azm 1990). Therefore it is important to understand the effects carbonization has on seed morphology and recovery of seed remains.

Previous carbonization experiments (e.g. Boardman and Jones 1990; Wilson 1984; Wright 2003) tested small batches of seeds from a number of cereal crops and associated weed species (including *C. berlandieri*) under a number of temperature regimes, time periods and environments. Boardman and Jones (1990) and Wilson (1984) tested European cereal crops and associated weed seeds, the majority of recovered materials tending to be from kiln heating, which produces different conditions than open fires used by cultural groups in southern Manitoba. Wright (2003) carbonized seeds from native plant species commonly recovered in archaeological sites in northeastern North America. The time, temperature and environmental settings from previous research are used in this study to determine how carbonization affects seed traits of locally sourced *C. berlandieri*.

6.4 Objectives

The range of *Chenopodium berlandieri* seed phenotypes associated with different cultural groups from Lockport and the Forks sites can provide information about potential effects of cultivation. Phenotypic variation in archaeological *C. berlandieri* seeds will be compared to the range of seed phenotypes documented from wild populations (Chapter 5) and the previously documented domesticated phenotype, *C. berlandieri* ssp. *jonsianum* (Smith and Funk 1985; Gremillion 1993). If archaeological seed phenotypes are similar to the domesticated phenotype, then it is possible selection pressures attributable to

cultivation activities affected these populations. The following research focuses on three main objectives in this chapter.

1) To determine the effects of heat over time on morphological seed traits of *Chenopodium*, I will quantify the effects of time, temperature, and environmental context on the conditions of preservation and distortion to seed morphology, and seed phenotypes (seed size and testa thickness). These data will allow me to analyze the condition of archaeological seeds and understand how the taphonomic process of carbonization affects seed morphology and size.

2) I will document the range of variation in archaeological *C. berlandieri* seed phenotypes by measuring the dimensions of seeds associated with Late Woodland groups from Lockport and The Forks and the Kenosewun maize cultivating group(s) from Lockport. Differences in archaeological seed phenotypes across cultural groups may indicate different relationships with *C. berlandieri* populations.

3) I will compare seed size and testa thickness of archaeological *C. berlandieri* seeds with carbonized samples from extant Manitoba populations, and the domesticated phenotype identified from Eastern Woodland assemblages to determine if the archaeological seed phenotypes are more similar to the wild or domesticated phenotype. Archaeological seed means will be corrected for effects of carbonization and compared with extant wild population means from the Northeastern Prairies and the Eastern Woodlands to determine any patterns.

6.5 Methods

6.5.1 Carbonization

This experiment was designed to quantify the distortion and changes in the state of preservation to the external morphology, shape, and measurements of Manitoba sourced *C. berlandieri* fruits/seeds exposed to a set of temperatures and soil conditions. This experiment was conducted in a low temperature drying oven with a maximum temperature of 250°C and a Thermolyne muffle furnace able to reach 1200°C. Seed collected from two Manitoban populations (two plants per population, 10 seeds per plant per treatment) were carbonized under three combinations of time and temperature (hereafter temperature), and four soil conditions. Seeds were exposed to 100°C (~210°F) and 250°C (~450°F) for 20 hours, representing temperature environments at the edges of a campfire. Seeds exposed to 400°C (~620°F) for four hours represent temperature environments closer to the center of a fire (*cf.* Boardman and Jones 1990; Wilson 1984; Wright 2003).

Four conditions were used: dry oxidized, dry reduced, wet oxidized and wet reduced, representing different soil conditions in/around an open fire (Wilson 1984). The oxidized condition represents soil environments where seed/fruits landed in or around an open-air fire and did not become covered with ash. The reduced condition represents soil environments where seed/fruits fell in or around a fire and were buried in ash reducing the oxygen and therefore ‘burnability’ of the plant material. For oxidized conditions, each replicate was placed in a dry ceramic crucible; another crucible was carefully stacked on top (like stacked juice glasses) to act as a lid. For the reduced conditions, crucibles were half filled with sand, seeds placed on top, then covered with a thin layer of sand. In

addition, seeds/fruits could have been carbonized fresh (higher water content), dried for storage, or were in the process of being prepared for human use (i.e. soaked in a pot). All seed samples had been dried and stored for at least one year. To reproduce a partially prepared state (i.e. wet conditions), seeds/fruits were soaked for 48 hours in distilled water prior to the experiment.

6.5.2 *Qualifying and quantifying preservation and distortion*

Carbonization produces varying states of preservation to individual seeds in the same treatment. Some authors suggest that the poorest state of preservation that covers the highest proportion of the seed should be described, as the worst degradation is representative of the taphonomic history (Hubbard and Al Azm 1990). While this is true, the purpose of this experiment was to gain an understanding of how carbonization affected the morphological features of *C. berlandieri*. For this reason, the overall preservation of the seed was described, specifically noting the distortion of the features necessary for species identification (e.g. damage to testa patterning).

Seeds were visually assessed through a dissecting microscope and quantified using modified classification (Table 6.1) based on carbonization experiments with cereal grains and weed seeds of agricultural fields (Boardman and Jones 1990; Hubbard and Al Azm 1990; Wilson 1984). The classes and descriptions for preservation and distortion listed are largely self-explanatory. However, distortion class 2 needs a brief explanation. In *Chenopodium*, seeds are lenticular or rounded lenticular in longitudinal profile (Figure 6.1). This shape accommodates the central perisperm and the embryo encircling it. During carbonization, the perisperm expands sometimes fusing with the embryo. The

pressure forces the testa to split transversally along the margin of the seed. This appears to be a natural suture as germinated seeds also split along this same trajectory. In some cases the expanded perisperm will squeeze through the split testa forming a bubble like projection (Figure 6.1). This is referred to as the perisperm exudate (Hubbard and Al Azm 1990).

6.5.3 Measurements of experimental carbonized seeds

All seeds were measured for each temperature interval prior to the experiment using an ocular scale (Appendix 6.1). Only seed diameter was measured per seed as measuring testa thickness requires the seed to be bisected. Mean testa thickness per maternal line, which was previously calculated (see Chapter 5), was used as the testa thickness for extant *C. berlandieri* samples included in this experiment.

Carbonized seeds were measured for total seed diameter and testa thickness under a dissecting microscope with calibrated measurement program (Image Pro Express 4.5) that captured and measured standardized images. Testa thickness was measured at a maximum of four places in transverse section when testa was visible (see Figure 5.1). No seeds were intentionally broken to access testa measurements. Attempts to break carbonized seeds to access the testa resulted in shattered seeds. Therefore some seeds could not be measured. The pre- and post-carbonization data for seed diameter and testa thickness for each temperature setting and soil condition tested is found in Appendix 6.1. Mean and standard error were calculated (PROC MEANS SAS 9.2, 2010) for each population per temperature and treatment set.

To characterize the distortion and preservation of morphological traits I conducted two analyses of variance (PROC GLM SAS 9.2, 2010). The dependent variable (Y) for each analysis was distortion and preservation class. Models were of the format: Y = population temperature condition. Both temperature and soil condition were considered to be fixed. Population was considered to be a random factor. To assess whether carbonization significantly altered seed size, I conducted two analyses of variance (PROC GLM SAS 9.2, 2010). Dependent variables were seed diameter or testa thickness. The model statement in each analysis was Y = population temperature condition. Both temperature and soil condition were considered to be fixed. Population was considered to be a random factor.

6.5.4 Metric analysis of archaeological Chenopodium

To document differences in archaeological seed phenotypes between cultural groups, *Chenopodium berlandieri* seeds associated with food storage and processing features and contexts from the Lockport and the Forks sites were measured for seed size and testa thickness. Seeds were analyzed by associated cultural affiliation: Late Woodland cultural groups from the Lockport site (ca. AD1000), Late Woodland cultural groups from the Forks site (ca. AD1200-1300), and the Kenosewun maize cultivating group(s) from the Lockport Site (AD1200-1400). The Late Woodland groups from the Lockport site were associated with late Blackduck and transitional Rainy River Composite (Flynn 2002:402), while Late Woodland groups from the Forks were associated with the Rainy River Composite (Quaternary 2010).

Based on initial interpretive reports (Deck and Shay 1992; Wilson 2007) and discussions with Dr. C.T. Shay, one of the principal investigators, I selected samples collected from hearth features, organic layers and several unidentified features linked to either the Kenosewun maize cultivation occupation layer or the Late Woodland occupation at the Lockport site (Table 6.2).

At the Forks site, soil samples were selected from a number of different features (e.g. hearths, living floors) in order to gain a general understanding of plant use in Level 1, with fewer samples processed from Level 2 Complex and Level 3 Complex for comparison. The bulk of samples processed were from Levels 1 and 2 dating to AD1260-1280 (Quaternary 2010). Since these samples cluster so closely in date, they will be discussed together.

The majority of the Forks samples selected for this study were processed from hearth features and areas adjacent to hearth features, with fewer samples processed from living floors (i.e. the ground surface of the associated cultural period excavated), organic layers and unidentified features (Table 6.2).

All carbonized *C. berlandieri* seeds were sampled and the measureable seeds included in the analysis. However, the actual number of measureable seeds per cultural group was low (Table 6.3). Measureable seeds were complete enough to measure diameter, and collect at least one testa thickness measurement. Testa pattern and margin shape (cross-section) was noted if discernable (Smith 1984; Gremillion 1993). Archaeological seeds were scored for distortion and preservation using the criteria listed in Table 6.1. Mode of preservation and distortion class for each cultural affiliation per archaeological site was calculated. Mean and standard error for seed size and testa

thickness were calculated (PROC MEANS SAS 9.2, 2010) for each cultural affiliation per archaeological site.

To assess whether archaeological seeds associated with different cultural groups exhibited varying states of preservation, I conducted two analyses of variance (PROC GLM SAS 9.2, 2010). Dependent variables were the preservation and distortion class. The model statement for each analysis was $Y = \text{cultural-affiliation}$, where affiliation was Late Woodland at Lockport, maize cultivation at Lockport or Late Woodland at the Forks, and was considered to be fixed.

To document whether archaeological cultural groups were associated with different seed phenotypes, I conducted two analyses of variance (PROC GLM SAS 9.2, 2010). Dependent variables were the perisperm diameter and testa thickness. The model statement for each analysis was $Y = \text{cultural-affiliation}$, where affiliation was Late Woodland at Lockport, maize cultivation at Lockport or Late Woodland at the Forks, and was considered to be fixed.

6.5.5 Comparison of archaeological materials to wild and domesticated seed sizes

To assess whether *C. berlandieri* phenotypes differed across Late Woodland cultural groups, I compared the archaeological seed phenotypes associated Late Woodland groups described above to extant seed phenotypes from Manitoba, and the domesticated seed phenotype measured by Gremillion (1993: 499, 501) from archaeological sites in Kentucky and Tennessee. Based on my surveys (Chapters 3 and 5), extant Manitoba populations span the range of wild seed phenotypes represented measured in the Northeastern Prairies and Eastern Woodlands.

The archaeological seeds measured from Manitoba sites were carbonized, while the domesticated seeds, recovered from dry caves and rockshelters, were preserved by desiccation (Gremillion 1993:498). However, two samples included in Gremillion's study were carbonized. Based on a carbonization experiment (Smith 2007:121) in which seed size reduced less than 5%, she concluded that the carbonized seeds and desiccated archaeological seeds selected for her research did not have to be corrected for the effects of carbonization and were therefore directly comparable to extant seed phenotypes (Gremillion 1993:498). To correct for the effects of shrinkage due to carbonization in the Manitoban archaeological seed phenotypes, a conversion factor was calculated using the pre and post carbonization seed phenotypes from the experiment I conducted (see Section 6.5.3).

Archaeological seed phenotypes from Manitoba, extant *C. berlandieri* seed phenotypes from Manitoba, and the domesticated seed phenotype *C. berlandieri* ssp. *jonesianum*, were graphed to visually assess differences in seed size and testa thickness. Mean and standard error for the archaeological specimens and extant wild populations from Manitoba were calculated in SAS (PROC MEANS SAS 9.2, 2010). Summary statistics for *C. berlandieri* ssp. *jonesianum* were obtained from Gremillion (1993:499, 501). These data were not formally analyzed due to limited information about source populations for the archaeological data, and the fact that individual seed measurements were only available for seeds from Manitoba.

6.6 Results

6.6.1 Preservation and distortion effects after carbonization

Distortion varied by soil condition over all as well as condition by temperature (Figure 6.2). Analysis of variance indicated only temperature significantly ($F=14.5$, $P<0.05$) affected preservation and distortion levels (Table 6.4). This means that the temperature of the fire to which seeds were exposed had greater effect on the level of distortion and preservation of the seeds than the soil conditions they were in during exposure.

Seeds carbonized at 400°C for four hours had a higher level of distortion than at lower temperatures, and overall poorer preservation of the testa for all soil conditions (Figure 6.2). Seeds split transversely, and in many, the perisperm had exuded between the two halves of the testa. The pericarp of most seeds was preserved at least in part, and the testa pattern was faintly visible. Seeds became more fragile after exposure to this temperature, with flakes of testa and pericarp sloughing off with minimal contact by the tweezers. A few seeds were charred beyond recognition and disintegrated when touched.

Seeds carbonized at 250°C after 20 hours, had varying levels of distortion for overall size and morphological features of the seeds (Figure 6.2). Seeds were relatively well preserved, the testa of most seeds remained intact, the pericarp preserved in full or fragmented, and the testa pattern remained at least partially visible. In many seeds, carbonization caused the perisperm to expand creating a ‘puffed’ up appearance, usually leading to the seed splitting transversely. In some seeds, the edges where the seed had split open were slightly warped.

Seeds did not carbonize at all at 100°C, even after 20 hours. There was also no difference between the treatments at this temperature. All seeds remained uncarbonized and perfectly preserved. Because these seeds had not been morphologically altered, they were excluded from all analyses. No further assessment was made of exposure to low heat for a long period affected the perisperm or embryo.

6.6.2 Effect of carbonization on seed metrics

Overall carbonization reduced seed diameter and testa thickness. Analysis of variance indicated that population of origin and temperature has significant ($P<0.05$) effects on both seed traits (Table 6.4). In all soil conditions and temperature settings tested, seed diameter reduced less than testa thickness (Figure 6.3). Seed diameter was reduced on average 20% (13-24%) while testa thickness was reduced on average 30% (9-45%). Seed diameter reduced on average 0.20mm at 250°C 0.24mm at 400°C in the DM population. Seeds reduced slightly more in the SV populations under both temperatures (0.25 at 250°C and 0.27mm at 400°C).

In a general comparison, there was little difference between the mean reduction of testa thickness between the 250°C and 400°C within a population, but there was a difference between populations (Figure 6.3). It appeared that carbonization reduced the testa thickness of seeds from the DM population more than seeds from the SV population. In the DM population, the mean testa reduction for seeds carbonized at 250°C and 400°C was 0.017 and 0.016mm, respectively. The means of the same treatments for the SV population were 0.007 and 0.009mm, respectively.

6.6.3 Preservation and metric analysis of archaeological seeds

Chenopodium berlandieri seeds recovered from all examined samples were relatively well preserved (mode=2/3), but exhibited moderate to high level of distortion (mode =3/4) (Table 6.3). Analysis of variance indicated that seeds recovered from contexts at the Forks site were significantly better preserved ($F=15.82$, $P<0.0001$) than seeds recovered from the Lockport contexts but exhibited similar levels of distortion (Table 6.5). Seeds from the Forks contexts were recovered whole, with intact testas that were moderately cracked or warped. Testa patterning was partially, or faintly, visible on most specimens. Only a few specimens had missing or incomplete testas, or were too carbonized to take measurements. No seeds exhibited exudate perisperm material.

Seeds associated with the Late Woodland and Kenosewun maize cultivation occupation levels at the Lockport site exhibited similar levels of distortion (mean= 3.0 - 3.1) and preservation (3.8 – 3.9), which were not significantly different (Table 6.5). Distortion and preservation levels were moderate to high, meaning most seeds were broken, testas were partial or missing, with remaining testas cracked, warped or fragmented. A few specimens exhibited exudate perisperm material. Additionally, 16 carbonized *Chenopodium* ‘embryos’ (embryo fused to the perisperm during carbonization) were recovered from Late Woodland features at Lockport, but a few ($n=8$) were recovered from the Kenosewun maize cultivating contexts. Some fragments of testa were recovered with the Kenosewun maize cultivation specimens, so it is probable they had testas when deposited on site and the testas broke apart by taphonomic processes.

Analysis of variance indicated that *Chenopodium* seed associated with the Kenosewun maize cultivation occupation was significantly ($F=4.95$, $P=0.013$) smaller in

diameter than the seeds associated with either Late Woodland occupation from the Lockport and Forks sites (Table 6.5). There was no significant difference in testa thickness between any of the cultural groups (Table 6.5). Correcting for shrinkage due to carbonization, seeds would have been on average 20% larger with 30% thicker testas. Seeds associated with all cultural affiliations would have ranged from 1.41-1.56mm in diameter with testas 0.029 to 0.034mm thick. Both seed diameter and testa thickness fell within the total range of variation (Figure 6.5) measured for these traits from extant populations from the Northeastern Plains and Eastern Woodlands (see Chapter 5).

6.6.4 Comparison of archaeological Chenopodium in Manitoba and the domesticated phenotype from the Eastern Woodlands

Differences between extant wild *Chenopodium berlandieri* populations in Manitoba, archaeological *Chenopodium* specimens from the Lockport and the Forks sites, and the domesticated phenotype, *C. berlandieri* ssp. *jonesianum*, from the Eastern Woodlands region could not be statistically analyzed because only seed means for the domesticated phenotype were available (see Gremillion 1993). This means that the statistical power necessary to make meaningful comparisons was not present. A visual assessment of the mean seed diameters and testa thicknesses is provided (Figure 6.4). Two of the three domesticated goosefoot populations are clearly distinct from the other populations exhibiting a greatly reduced testa and overall larger seed size. The cultigens also exhibited little variation around means for testa thickness, but high variation around seed diameter indicating seed size was quite variable, while testa thickness was not. The archaeological specimens from the Forks and Lockport sites clustered closely with the

‘weedy’ morph (Figure 6.4). These populations also exhibited sizeable fluctuations around mean seed size and testa thickness, but the ‘weedy’ morphs appeared to have greater variation around seed size than the archaeological seed means from Lockport and the Forks. In comparison, the two wild extant populations from Manitoba had low variation around the means for both seed traits. The SV population clustered quite closely to the archaeological specimens from Manitoba and the weedy morph, while the DM population exhibited the smallest seeds with the thickest testas of all populations included (Figure 6.4).

6.7 Discussion

Both cultural and biological processes influence how a cultural group interacts with their environment. The relationship between plant species and cultural groups is built on cultural choices and beliefs, specific biological properties of a plant, and their interactions. To gain a better understanding of the relationship people had with the plants they used for food, archaeological *Chenopodium berlandieri* seed remains preserved through carbonization were examined. Specimens collected from food processing and storage features associated with three different cultural groups were analyzed in three ways. Information derived from the carbonization process was used to re-examine the archaeobotanical remains to better understand how these remains were preserved at the archaeological sites (e.g. effects of temperature), what types of activities potentially generated these remains (e.g. wet versus dry conditions), and details about the seed phenotypes represented in the archaeological record. A metric analysis of seed size and testa thickness provided data to address whether specimens associated with Late

Woodland or Kenosewun maize cultivation groups were wild, cultivated or domesticated phenotypes. Finally, the biological information gained through this thesis provides a wider context to examine *C. berlandieri* use and the potential for cultivation by various cultural groups in the Red River Valley.

6.7.1 Preservation by carbonization of C. berlandieri seeds

Analyzing the impact of temperature and context (wet or dry and oxidized or reduced conditions) on preservation of goosefoot seeds revealed that only temperature significantly affected preservation and distortion levels. Moisture content and soil condition were not significant factors affecting preservation and distortion levels, although they are important for categorizing how carbonization altered seed morphology. Future research may reveal that different durations of exposure across a series of temperatures may affect distortion and preservation levels.

Seeds recovered from the Forks were better preserved than seeds recovered from any contexts from the Lockport site. At the Forks, seeds associated with Late Woodland groups recovered from samples collected near hearth features were observed to exhibit preservation and distortion patterns similar to seeds carbonized under reduced conditions. These seeds appear to have been buried in ash or sediment and protected from direct heat from the fire. Carbonization experiments that compared gross morphological changes found that small seeds carbonized under reduced conditions preserved better than those in oxidized conditions (Wilson 1984; Wright 2003). Further, fruits/seeds with durable exteriors, or seed coats, fully carbonized when buried 5cm under a fire. The same

fruits/seeds were partially carbonized or only dehydrated when buried 10 cm under a fire or buried in the periphery of the campfire (Sievers and Wadley 2008).

At the Lockport site, seeds associated with both cultural occupations recovered from hearth samples were poorly preserved. The seeds were broken, warped and too carbonized to measure. In an open fire carbonization experiment, Sievers and Wadley (2008) found that a variety of fruits and seeds exposed directly to heat and flame at the center of the fire did not survive. The level of distortion exhibited by the Lockport specimens suggests a few possible scenarios. It is possible that *C. berlandieri* seed fell through the fire and was buried in ash or was buried adjacent to a hearth but much closer than the seeds recovered at the Forks. It may be that due to the multiple uses of many of the hearths at Lockport (Wilson 2007), *C. berlandieri* seeds were subjected to multiple firings and this caused the high levels of distortion. Multiple firing of different fruits/seeds is a potential avenue for future research.

Carbonization reduced seed diameter and testa thickness on average 20% and 30%, respectively. These findings were consistent with previous carbonization experiments (e.g. Wright 2003). Strong influence from population of origin indicated that seeds from different populations retained differences in seed sizes after carbonization. The wild DM population from Manitoba had a small mean seed size ($1.26\text{mm} \pm 0.012$), while the SV population had a large mean seed size ($1.61\text{mm} \pm 0.021$). The corresponding carbonized means from the DM population ranged between $0.96\text{mm} \pm 0.01$ and $1.10\text{mm} \pm 0.03$ across tested soil conditions (Appendix 6.1). The range of carbonized seed means for the SV population was $1.32\text{mm} \pm 0.01$ and $1.39\text{mm} \pm 0.04$ (Appendix 6.1). Population of origin accounted for much of the variation in testa

thickness. However, using testa thickness of carbonized seeds to differentiate populations does not provide as clear a distinction as using seed size (Appendix 6.1).

6.7.2 Pre-contact *C. berlandieri* in Manitoba: wild, cultivated or domesticated?

To definitively demonstrate that archaeological *C. berlandieri* seeds were domesticated, they need to exhibit the same range of characteristics described from the domesticated sub population *C. berlandieri* subsp. *jonesianum* identified from sites in the Eastern Woodlands (Smith and Funk 1985). Most importantly domesticated seeds had a testa thickness less than 0.020mm (Smith and Funk 1985). The domesticated phenotype measured from samples of desiccated and carbonized seed recovered from Salts Cave, KY and Big Bone Cave, TN ranged in mean testa thicknesses from 0.011mm to 0.021mm, respectively (Gremillion 1993:499). Mean testa thicknesses of 0.011mm and 0.015mm were obtained from seed samples from Russell Cave (n=425; Smith 2007:121) and Ash Cave (n=1000; Smith 2007:142), respectively. Wild populations have mean testa thicknesses of greater than 0.030mm (cf. Chapter 6 of this thesis; Smith 1984). Domesticated seeds had a truncate margin, rectanguloid in cross section, and smooth testa compared to its wild relatives that exhibited biconvex to rounded seed margins and reticulate-alveolate testa patterning (Smith and Funk 1985; Gremillion 1993:499). While seed size of the domesticate fell within the range of variation for wild conspecifics (Smith and Funk 1985), it was assumed that frequency of relatively larger seeds would increase compared to the distribution of seed sizes of wild seeds. The increase in seed size was assumed to accommodate the increased perisperm and embryo associated with a change

in selection pressure due to planting in prepared seedbeds (Harlan et al. 1973; Smith 1984).

Archaeological specimens recovered from all three contexts examined in this study exhibited a range of characteristics more consistent to those described for wild populations in Manitoba. Due to the effects of carbonization it was difficult to determine an accurate margin shape, but the few seeds that were not warped or ‘puffed up’ had round or biconvex margins. Occasionally, half of the testa would dislodge from the archaeological specimens. Dislodging of half the testa was also noted during a carbonization experiment on wild and domesticated archaeological *Chenopodium* seeds (Jones 1993). Wild seeds with thick testas split open around the horizontal margin (like a clam shell opening), and many of the testas become dislodged from the rest of the seed (Jones 1993). Testas were less often lost from domesticated specimens because carbonization led to the perisperm to puff up and adhere to the testa (Jones 1993). Jones (1993) suggested that rounded-truncate margin shape and thin testa of the domesticated phenotype influenced morphological differences in distortion after carbonization.

A large proportion of the specimens recovered from hearth features associated with Late Woodland cultural groups from the Lockport site appeared to be fused embryo and perisperm (hereafter embryo). No testa fragments adhered to the embryos, but there were small testa fragments in the same vial. The embryo specimens also exhibited rounded-rectangular cross sections, but it was impossible to determine whether this margin shape was due to the overall shape of the testa or effect of the carbonization process.

The archaeological seed remains exhibited differences in seed size across archaeological contexts (Figure 6.4). *Chenopodium berlandieri* specimens associated with the Late Woodland groups at Lockport had a large mean seed size (corrected mean $1.58\text{mm} \pm 0.027$), and narrow range of variation around the mean. This indicated that people in these groups focused on one or more population(s) with large mean seed size. Specimens associated with the maize cultivation groups at Lockport had a small mean seed size (corrected mean $1.42\text{mm} \pm 0.037$), also with a narrow range of variation around the mean. This suggested people belonging to the maize cultivation occupation utilized one or more population(s) with a smaller mean seed size. Seeds associated with Late Woodland groups at the Forks exhibited a small mean seed size (corrected mean $1.47\text{mm} \pm 0.047$), but seed size was more variable. The range of seed sizes at the Forks suggests that two or more population(s) with different mean seed sizes were represented in these seed remains.

Testa thickness of the archaeological specimens also fell within the range of extant wild populations, but interestingly fell toward the thin end of the unimodal distribution curve for extant Manitoba populations. Testa thickness was normally distributed in extant populations. Seeds collected from extant Manitoba populations ranged in testa thickness from 0.019- 0.069mm with an average testa thickness around 0.040mm thick. Archaeological testa thickness (corrected for carbonization effects) ranged from 0.029mm to 0.034mm. The Kenosewun maize cultivation occupation was associated with seeds exhibiting the thinnest testas (0.029mm), while the Late Woodland occupation from Lockport was associated with the thickest testas (mean = 0.034mm).

While the archaeological seeds did not display the hallmarks of the domesticated phenotype, these specimens potentially display morphological indicators associated with cultivated populations. The reader is reminded that the number of measured seeds for all archaeological cultural groups was low. Therefore the following paragraphs discuss an interesting observation that identifies an avenue for future research.

High frequencies of moderately large seeds with relatively thin testas were associated with domesticated phenotypes at a number of locations in the Eastern Woodlands (Figure 6.4). A cache of desiccated and carbonized seeds recovered from dry rock shelters in Kentucky and Tennessee contained domesticated and ‘weedy morphs’⁷ (Gremillion 1993). The weedy morphs exhibited a range of mean seed sizes ($1.24\text{mm} \pm 0.17$ to $1.52\text{mm} \pm 0.12$), but all exhibited relatively mean thin testas ($0.031\text{mm} \pm 0.008$ to $0.035\text{mm} \pm 0.0085$) with relatively low variation around the mean (Gremillion 1993: 499-501). Cultigens exhibited either a small mean seed size (mean= $1.46\text{mm} \pm 0.14$) or a large mean seed size (1.83 ± 0.09). Again, all populations exhibited very thin testas ($0.011\text{mm} \pm 0.0055$ to $0.0212\text{mm} \pm 0.0047$) with low variation around the mean (Gremillion 1993).

A deposit of carbonized domesticated and ‘weedy’ chenopod seeds from Marble Bluff rockshelter, Missouri showed similar characteristics for both phenotypes. The ‘weedy morphs’ exhibited a range of seed sizes (1.1- 2.0mm) and relatively thin testas (0.025mm), with biconvex- rounded margins (Fritz 1997). These measurements were not corrected for shrinkage due to the carbonization process (Gayle Fritz, pers. comm. 2017). Applying the correction factor calculated in this research, these specimens are similar in

⁷ ‘Weedy’ species have specific growth habits, and life history traits. Many ‘weedy’ or non-domesticated plants were tolerated or encouraged to grow with cultivated crops as they were edible, had medicinal properties, or used as animal fodder (Vieyra-Odilon and Vibrans 2001).

size, testa thickness and margin shape as those measured from the Lockport and Forks sites, and those measured in Gremillion's research in Kentucky and Tennessee.

Both Fritz (1997:62) and Gremillion (1993:502) identified these deposits as evidence of crop-weed complexes, where wild or non-domesticated ('weedy') goosefoot populations grew near or within cultivated domesticated crops. They suggest that the non-domesticated population would have experienced similar selection pressures from cultivation on seed size and testa thickness as the domesticated population. It is possible, then, that a high frequency of archaeological seeds with thinner testas (mean $\sim 0.030\text{mm}$) with low variation around the mean, regardless of the range in seed size, could be considered morphological indicators of cultivation. An addendum to this would be archaeological seeds should be recovered in secure, datable archaeological contexts.

Tables and Figures

Table 6.1: Classes of preservation and distortion to carbonized *Chenopodium berlandieri* seeds.

Class	Preservation	Class	Distortion
1	Perfect/ uncarbonized	0	None/ uncarbonized
2	Carbonized; testa intact; no cracking, warping	0.5	Seed intact, not split, but missing a fragment of testa providing a view of the perisperm
3	Testa intact, cracked or warped; pericarp mostly intact but fragmented; pericarp/testa pattern at least partially visible	1	Seed split transversally along margin
		2	Seed split as above, testa halves open wide enough to see perisperm; perisperm \pm exudate
4	Testa incomplete, fragmented, cracked warped; pericarp fragmented; pericarp/testa pattern partly to faintly visible	3	Seed split as above, only half testa with perisperm remaining; perisperm \pm exudate
		4	Embryo on its own, testa non adherent
5	Testa missing or highly fragmented; perisperm present; pericarp/testa pattern faintly visible or eroded	5	Only half of the testa present without embryo
		6	Testa and perisperm highly fragmented; destroyed

Table 6.2: Archaeological contexts sampled and number of archaeological soil samples selected for *Chenopodium* seed from the Lockport and the Forks sites, Manitoba.

Site and Cultural group	Date	Sample Number	Feature type	<i>Chenopodium</i> seeds
Lockport Maize cultivation occupation	ca. AD 1450	3	Hearth	4 seeds
		1	Organic layer	4 embryo
		1	Unidentified feature	3 embryo
Late Woodland (Late Blackduck/ Rainy River Composite)	ca. AD1200- 1300	2	Hearth	1 embryo
		2	Hearth	8 seeds
The Forks Late Woodland (Rainy River Composite)	AD1260-1280	1	Unidentified feature	15 embryo
		2	Hearth	1 embryo
		2	Adjacent to hearth	6 seeds
		2	Adjacent to hearth	7 seeds
		1	Living floor	1 seed

Table 6.3: Seed trait measurements (in mm) and preservation and distortion levels of the archaeological *Chenopodium berlandieri* seeds recovered from various features associated with different cultural groups living at the Lockport and Forks sites, Manitoba.

Archaeological Site and Cultural Affiliation	Date	N	Seed diameter ±SE	N	Testa thickness ±SE	Distortion/ Preservation Class
Lockport						
Maize cultivation	AD1450	12	1.18 ±0.032	5	0.022 ±0.003	4/3
Late Woodland	AD1200-1300	32	1.32 ±0.022	22	0.026 ±0.001	4/3
The Forks						
Late Woodland	AD1260-1280	13	1.22 ±0.036	12	0.024 ±0.001	3/2

Table 6.4: Analyses of variance of A) preservation and distortion classes, and B) seed size and testa thickness from seeds included in the carbonization experiment. Seeds from two populations were exposed to three temperatures (100C, 250C, 400C) and four conditions (wet and dry oxidized, wet and dry reduced). Values reported in Table are *F*-ratios and associated degrees of freedom for each effect. Significance denoted by * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, n.s. $P > 0.05$).

Effect		Preservation	Distortion	Perisperm diameter	Testa thickness
A)					
Population	$F_{1, 41}$	1.83 n.s.	0.88 n.s.		
Temperature	$F_{2, 41}$	28.06***	95.6***		
Condition	$F_{3, 41}$	1.44 n.s.	1.47 n.s.		
B)					
Population	$F_{1, 39-41}$			634.2***	37.1***
Temperature	$F_{2, 39-41}$			160.5***	57.0***
Condition	$F_{3, 39-41}$			1.5 n.s.	0.34 n.s.

Table 6.5: Analyses of variance of A) preservation and distortion classes, and B) seed size and testa thickness of carbonized archaeological seeds associated with Late Woodland groups and Maize cultivation groups at the Lockport site, and Late Woodland groups at the Forks site. Mean seed traits \pm SE calculated from Least Squares Means. Values reported in Table are *F*-ratios and associated degrees of freedom for each effect. Significance denoted by * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, n.s. $P > 0.05$).

Effect		Preservation	Distortion	Perisperm diameter	Testa thickness
A) Cultural affiliation	<i>F</i> _{2, 44}	15.8***	0.22 n.s.		
B) Cultural affiliation	<i>F</i> _{2, 21-34}			634.2***	37.1***
Cultural affiliation					
Late Woodland at Lockport				1.32 \pm 0.024a	0.026 \pm 0.001a
Maize cultivation at Lockport				1.18 \pm 0.047b	0.022 \pm 0.002a
Late Woodland at the Forks				1.22 \pm 0.031b	0.024 \pm 0.002a

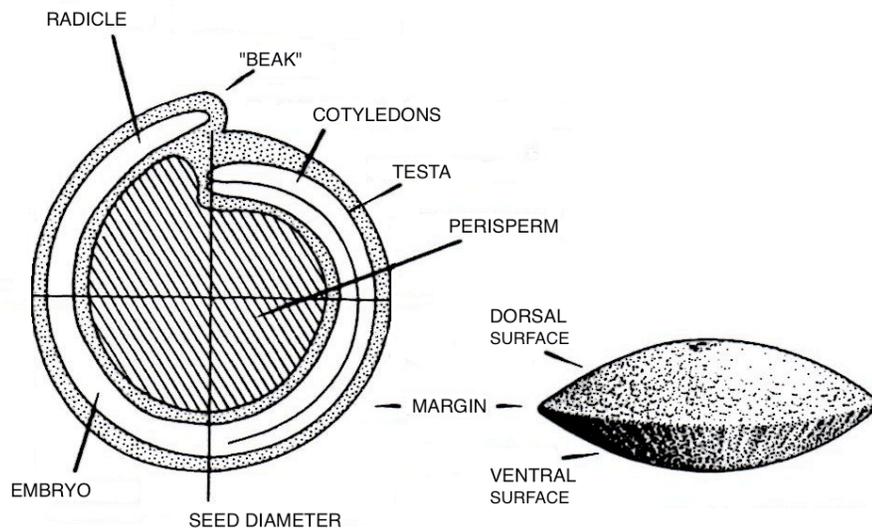


Figure 6.1: Left panel: Line drawing of *Chenopodium* seed: testa (seed wall), embryo (composed of radicle and cotyledons), and perisperm (nutritive tissue) and seed margin shown in x.s.; dorsal and ventral surfaces and seed margin shown in l.s. (adapted from Figure 6.7 in Smith 2007). Right panel: transverse view of a carbonized seed that has split along the seed margin with the perisperm exudate (photo by Halwas 2013).

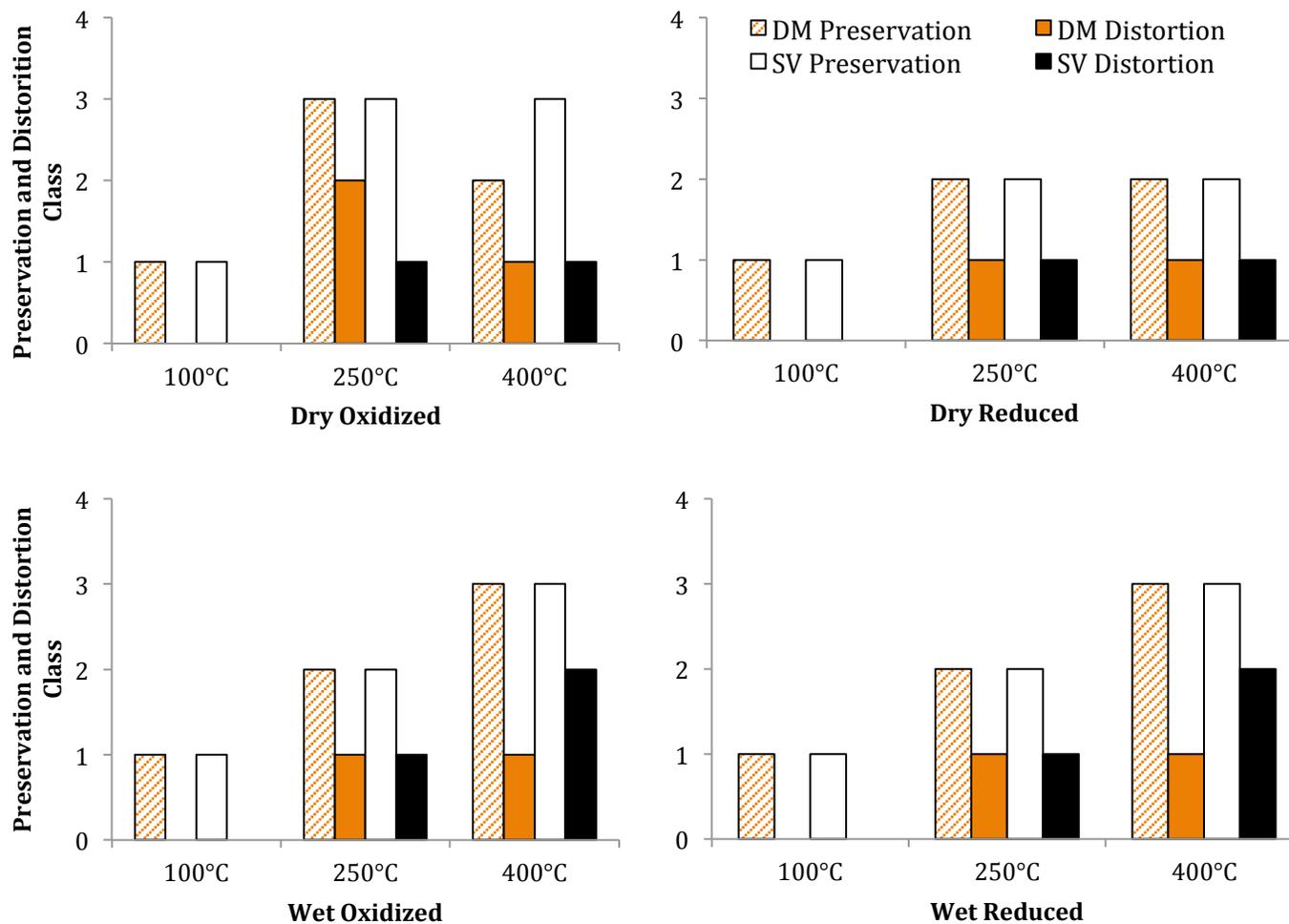


Figure 6.2: Preservation and distortion class of *Chenopodium berlandieri* seeds carbonized at three temperatures (100°C, 250°C, 400°C) and four conditions (Wet and Dry Oxidized, and Wet and Dry Reduced). Blank spaces represent data points at the '0' class. See text for details.

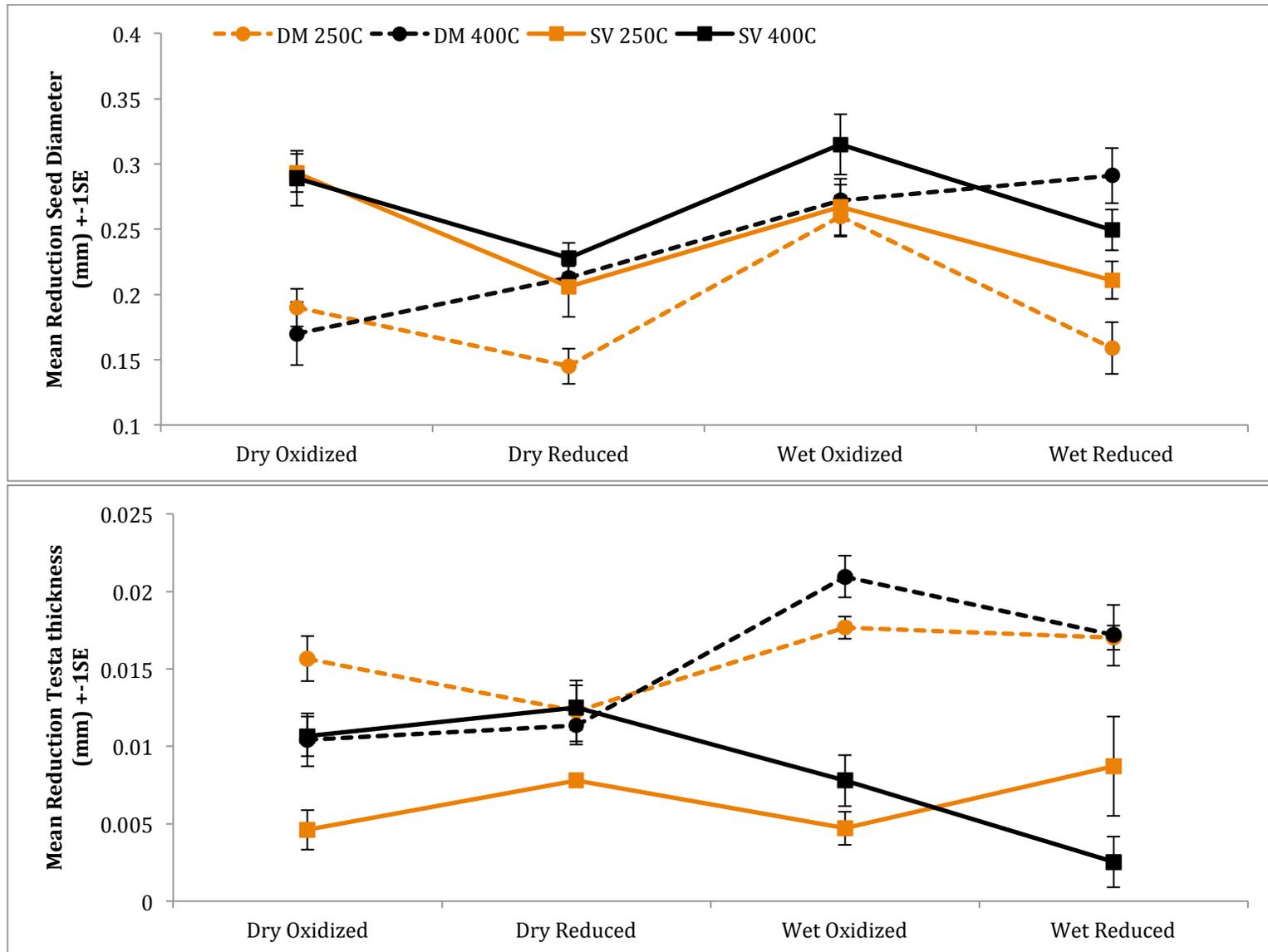


Figure 6.3: Mean reduction in seed diameter (top) and mean testa thickness (bottom) of *C. berlandieri* during carbonization by condition. Conditions are divided into temperature setting (250°C and 400°C) by population (DM and SV).

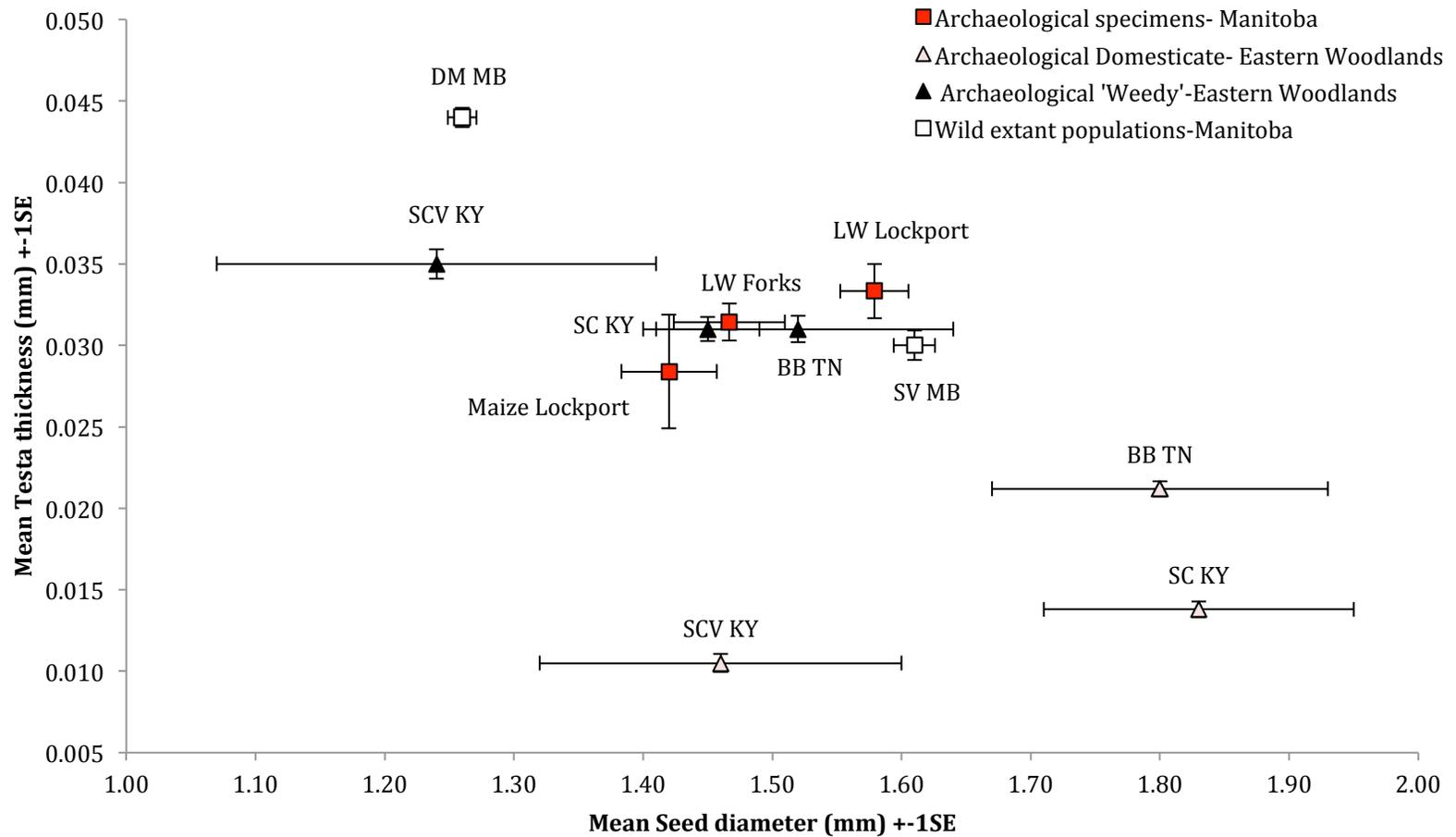


Figure 6.4: Mean seed diameter and testa thickness of archaeological *Chenopodium berlandieri* seeds two Late Woodland occupations (Lockport and the Forks sites) and the maize cultivation occupation (Lockport site) Archaeological seeds corrected for carbonization effects (see text for details). The means of the domesticated phenotype and an associated 'weedy' morph recovered from two archaeological sites in the Eastern Woodlands (Salts Cave and Salts Cave Vestibule, Kentucky, and Big Bone Cave, Tennessee) (Gremillion 1993) are included for comparison.

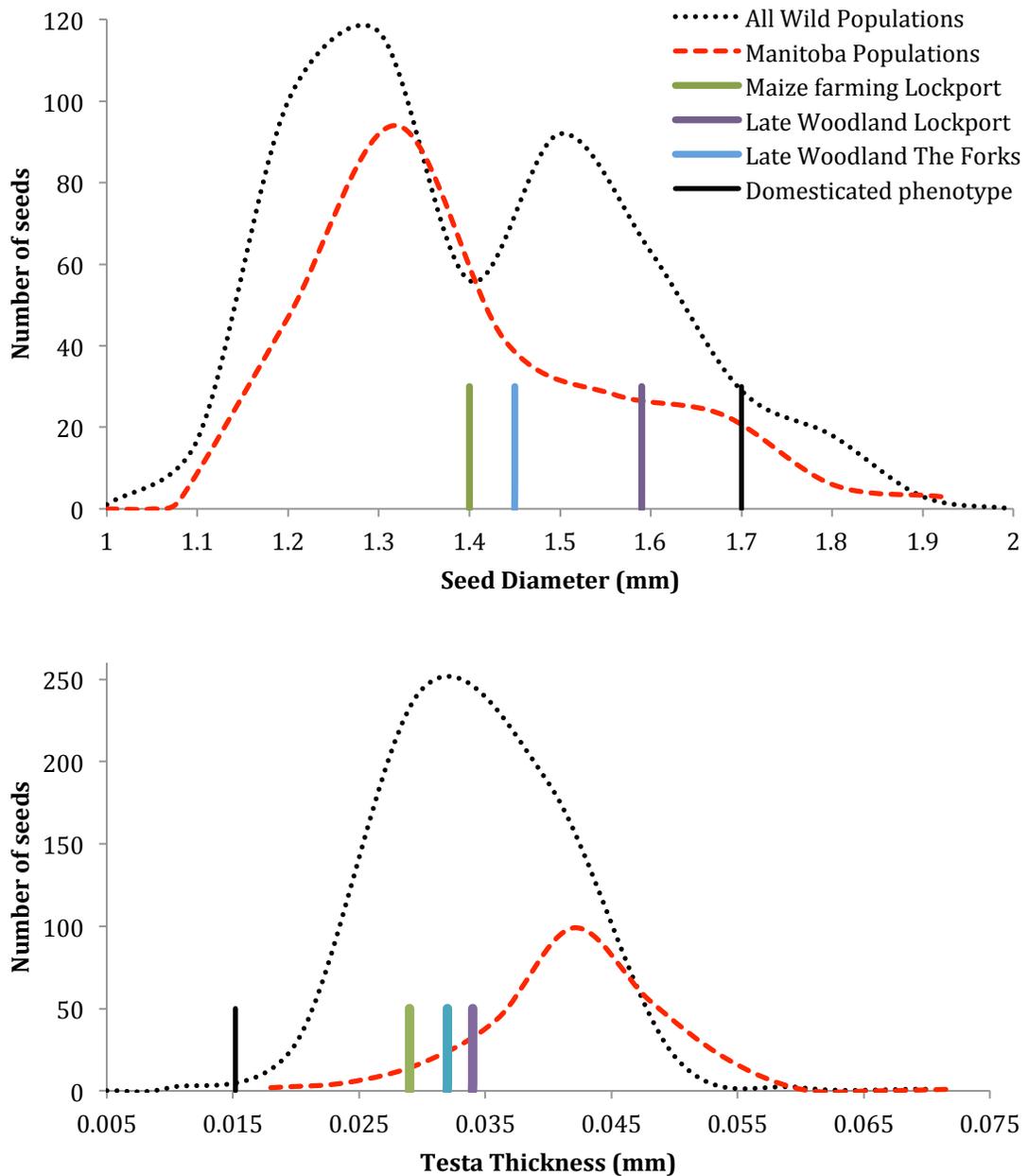


Figure 6.5: Mean seed diameter (top panel) and mean testa thickness (bottom panel) of archaeological *Chenopodium berlandieri* seeds corrected for carbonization effects (see text for details) superimposed on distribution of wild seed traits. Seed phenotype associated with two Late Woodland occupations (Lockport and the Forks sites) and the maize cultivation occupation (Lockport site) is compared to the domesticated phenotype (Gremillion 1993). Distribution of seed traits calculated from wild Manitoba populations, and wild populations across the Northeastern Prairies and Eastern Woodlands (see Chapter 5) indicated Manitoba seed traits are representative of *C. berlandieri* wider geographical range.

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Appendix 6.1

Mean diameter and testa thickness for uncarbonized and carbonized for *C. berlandieri* seeds from each treatment and time/temperature setting in the carbonization experiment. Experimental mean seed diameter for *C. berlandieri* was calculated from 40 seeds from two maternal lines from two wild Manitoba populations per time/temperature setting prior to the experiment. Mean testa equates to population mean for maternal lines used in experiment. Seeds from the 100°C set did not carbonize; only uncarbonized measurements are recorded. *no standard error calculated by SAS.

Time/ Temperature	Population		Treatments							
			Dry Oxidized		Dry Reduced		Wet Oxidized		Wet Reduced	
			Diameter	Testa	Diameter	Testa	Diameter	Testa	Diameter	Testa
20h@ 100°C	DM	U	1.23 ±0.06	0.047	1.22 ±0.03	0.047	1.23 ±0.02	0.047	1.23*	0.047
		C
	SV	U	1.64 ±0.005	0.034	1.62 ±0.02	0.034	1.65*	0.034	1.65 ±0.03	0.034
		C
20h@ 250°C	DM	U	1.22 ±0.01	0.047	1.25 ±0.03	0.047	1.27 ±0.04	0.047	1.23 ±0.02	0.047
		C	1.03 ±0.04	0.032 ±0.004	1.09 ±0.03	0.031*	1.01 ±0.06	0.03 ±0.004	1.10 ±0.03	0.031 ±0.004
	SV	U	1.65 ±0.03	0.034	1.61 ±0.005	0.034	1.61 ±0.04	0.034	1.62 ±0.02	0.034
		C	1.35 ±0.03	0.029 ± 0.002	1.40*	0.031*	1.34 ±0.02	0.029 ±0.004	1.35 ±0.01	0.022 ±0.002
4h@ 400°C	DM	U	1.27 ±0.02	0.047	1.27 ±0.02	0.047	1.23 ±0.005	0.047	1.25 ±0.02	0.047
		C	1.10 ±0.03	0.036 ±0.0005	1.06 ±0.03	0.036 ±0.0005	0.96 ±0.005	0.026 ±0.003	0.96 ±0.005	0.029 ±0.0005
	SV	U	1.64 ±0.01	0.034	1.62 ±0.02	0.034	1.64 ±0.03	0.034	1.63 ±0.06	0.034
		C	1.35 ±0.01	0.024 ±0.005	1.39 ±0.04	0.023 ±0.002	1.32 ±0.01	0.027 ±0.003	1.38 ±0.05	0.031 ±0.002

Appendix 6.2

Carbonized seed specimens recovered from soil samples collected during the excavation at the Forks (DILG-33:08A) for the Canadian Museum of Human Rights, Winnipeg, Manitoba in 2008. Only levels and features with identified archaeobotanical materials included.

Species	Common Name	Hearth				Near Hearth		Floor
		Level 1	2	2B	3	1	2	1
<i>Atriplex</i> sp.	Orach	2						
cf <i>Arenaria</i> sp.	Possible Sandwort	1						
cf Asteraceae	Possible Aster Family	1						
cf Caryophyllaceae	Possible Pink Family					1		
<i>Chenopodium</i> cf <i>berlandieri</i>	Pitseed goosefoot	7		1	1		2	
<i>Chenopodium</i> cf <i>hybridum</i>	Maple leaved goosefoot	1						
<i>Chenopodium</i> sp	Goosefoot	2	2			22	8.5	1
cf Cyperaceae	Possible Sedge Family		1			1		1
<i>Fragaria virginiana</i>	Strawberry	4						
<i>Galium</i> cf <i>boreale</i>	Possible Northern Bedstraw	5	16				2.5	
Poaceae	Grass Family	3	8			5		23
cf Poaceae	Possible Grass Family	2						
Poaceae rachis	Grass chaff							1
cf Lamiaceae	Possible Mint Family		1					
cf <i>Mentha</i>	Possible Mint						1	
Polygonaceae	Knotweed Family							1
cf Polygonaceae	Possible Knotweed Family		1	1		1		
<i>Polygonum</i> cf <i>aviculare</i>	Possible Smartweed							1
cf Rosaceae	Possible Rose Family		2					
<i>Rubus</i> sp.	Raspberry		4		1			
<i>Rumex</i> cf <i>occidentalis</i>	Possible Dock							1
<i>Rumex</i> sp.	Dock	1						
cf <i>Rumex</i> sp.	Possible Western Dock							1
cf <i>Physalis</i> sp	Possible Ground Cherry					1		
<i>Urtica dioica</i>	Nettle	1	8			1		
cf <i>Urtica dioica</i>	Possible Nettle		1		1			

Appendix 6.2 continued		Hearth				Near Hearth		Floor	
Species	Common Name	Level 1	2	2B	3	1	2	1	
Type 1 (<i>Urtica</i> -like)	Unknown nettle like		151					2	
Fruit stone frag		1							
Unidentified		4	17	2		12	3.5	15	
Total Charred Seeds		362.5	35	212	4	3	44	17.5	47

**CHAPTER 7: COMBINING BIOLOGICAL AND ARCHAEOLOGICAL DATA:
EXPANDING OUR UNDERSTANDING OF PEOPLE – PLANT RELATIONSHIPS IN THE
RED RIVER VALLEY OF SOUTHERN MANITOBA**

The interaction between cultural groups and different plant species within their environment may have established relationships with culturally important plant species reflective of low-level cultivation. Low-level cultivation is a characteristic of mixed subsistence practices, which include cultivation of both tropical cultigens, and domesticated and non-domesticated native plants (e.g. Nickel 2007; Jones 1993). Archaeological and botanical evidence (e.g. seeds, pollen, phytoliths, starch) indicates mixed subsistence practices, mixing domesticated maize, native rice, and beans with local native plant (e.g. goosefoot, wild cherry, hazelnut, beeweed, sunflower) and animal resources was widespread during the Late Woodland period in southern Manitoba (e.g. Boyd *et al.* 2014; Hamilton, *et al.* 2011; Quaternary 2010; see Chapter 2 for full details). Based on cultural connections between southern Manitoba and the Eastern Woodlands where native *Chenopodium berlandieri* was domesticated for its seed (Smith 1985), the possibility exists that some Late Woodland cultural groups in the Red River Valley incorporated cultivation of native *Chenopodium berlandieri* seed into local mixed subsistence economies.

To explore this possibility I investigated whether wild *C. berlandieri* populations in Manitoba would provide a stable food source for pre-contact people. I examined aspects of population size and location, seed biology (e.g. seed size and testa thickness), seasonal availability, harvestable yield, and nutritional value to determine if local populations of *C. berlandieri* constituted a viable food resource. I further explored aspects of the process

of domestication to understand the links between seed traits and cultivated environments, and investigated the ability for people to cause change in seed morphology through harvesting or low level cultivation techniques. Finally I investigated whether archaeological evidence supported the possibility that pre-contact cultural groups in the Red River Valley of southern Manitoba were cultivating local populations of *Chenopodium berlandieri*.

The results of this research indicates that local wild *C. berlandieri* populations would have made a suitable food resource for pre-contact people living in the Red River Valley in southern Manitoba. Local populations of wild *C. berlandieri* grow along major rivers, including the Red and Assiniboine, and their tributaries. Extensive populations are currently infrequent on the landscape, but may have been more widespread prior to European contact and the ensuing development of intensive agriculture near waterways. Despite the alternative possibility that population density was low, *C. berlandieri*'s preferred habitat along major and minor rivers would have made this species visible to pre-contact people moving into and through the Red River Valley.

Population of origin influences plant size, seed weight (yield), and seed traits (e.g. seed size and testa thickness), while influences from broader geographic regions were lacking. This means that populations varied in plant biomass, total seed production and seed traits across the Northeastern Plains and the Eastern Woodland regions. Populations composed of large plants that produced high quantities of seed could be found throughout these regions. Seed traits are conserved within population, indicating populations that produce smaller seeds (<1.3mm) with thicker testas (>0.040mm), and populations that produce larger seeds (>1.4mm) with thinner testas (<0.035mm) are also

available across these regions. All patterns in population size, location, plant biomass, total seed production, and seed traits indicate that specific wild populations would have particular plant and seed traits that could have been targeted by pre-contact cultural groups, thus representing choice available to pre-contact people.

Variation in harvestable seed yield also exists across wild *C. berlandieri* populations, with mature seed harvestable from mid-August to late October. However, all wild Manitoba populations included in this research exhibited similar levels of nutrition. Wild Manitoba populations produced moderate seed yields (mean ~500kg/ha), which produced enough cleaned seed (mean=30g) for a meal in an hour. These returns were comparable to the low end of yield range for domesticated quinoa and other small-seeded annual plants (e.g. *Amaranthus* sp.; Peterson and Munson 1984). Nutritional analysis indicated that wild *C. berlandieri* is similar to domesticated quinoa, a close relative, in carbohydrate, fat, and mineral content, and significantly higher in protein and dietary fibre. Quinoa was significantly higher in overall calories (see Chapter 4). This suggests that wild harvested goosefoot seeds would have been an economically viable resource, and a nutritional component to the diet.

My research indicated the high potential for cultivating wild populations of *C. berlandieri* in the Red River Valley. Growing harvested seed in cultivated environments, be it prepared garden plots or worked mudflats (e.g. Californian cultural groups, Anderson 2005), has always been associated with the domestication of *C. berlandieri*. The effects of cultivation on plant and seed traits in this research were immediately apparent. Growing wild harvested seed from different populations in tilled soil with light weeding and watering increased overall plant size and seed production a hundred-fold in

at the Arboretum common garden location! This reflected a plastic response to plant biomass and total seed production- plants increased in height and number of lateral branches that resulted in an increased number of inflorescences, therefore increased overall yields. Growing wild seed in a cultivated environment also altered seed phenotypes, slightly increasing seed size, and slightly decreasing testa thickness.

Much of the variation in seed phenotypes was due to the interaction between population and the location in which plants were grown, which includes the human management history of the common garden location. At the Arboretum location, soils were regularly tilled and chemically weeded, and the field was relatively sheltered. In comparison, the Glenlea location was open, irregularly tilled and weeded, with poorly drained soils that dried into a hardpan. Plants grown at the Arboretum produced larger plants with higher total seed mass across populations and years. These results support the assertion that in *C. berlandieri*, plants grown in cultivated soils exhibit plastic responses in plant and seed traits that can be the basis for selection by ancient cultural groups. Modified selection pressures from maintained cultivated soils might also maintain the plasticity expressed by seed and plant traits. If the genetic underpinnings of plasticity were also passed between generations, this would forward the process of domestication for this species.

Evolution of the domesticated phenotype in response to cultivation requires that seed size and testa thickness influence percent germination, and that variation in seed traits has a genetic basis. Across germination experiments, seed size had a small influence on proportion of germinated seed, but seeds with thinner testas sprouted in significantly higher percentages, and significantly earlier than seeds with thick testas.

Furthermore, both seed size and testa thickness are heritable (H^2 : 0.99 and 0.37, respectively), and strongly genetically correlated ($r_A = 0.69 \pm 0.08$). This means that a large proportion of the genetic variation for these traits is passed on to subsequent generations. Genetic correlations indicate the effects of selection, i.e. selection for one trait will cause simultaneous changes to another character. In this case, selection for a reduced testa will cause an increase in seed size. These data support the hypothesis that testa thickness is a physical barrier to dormancy as research indicated that larger seeds with thinner testas tended to germinate in higher numbers and sooner than smaller seeds with thick testas.

Common garden population produced higher percent germination compared to their wild progenitors, and the seeds that germinated had thinner mean testas compared to the progenitors. This means that cultivation practices can increase the number of seeds that germinate, and, of those, the seeds that germinate first tend to have thinner testas. This would give plants with thin testas a competitive edge, allowing them to grow larger quicker than later germinating seeds. Tending these early seedlings to full grown plants then collecting and planting stored seed, or deliberately scattering seed while harvesting to provide for next year, would increase the frequency of plants with thinner testas and early germination. Over time these seed traits and their ability to germinate earlier would become fixed in the population. This indicates that people interacting with wild populations could impact the genetic underpinnings of seed traits, thus affecting genetic change over time.

To understand if pre-contact plant relationships could have reflected cultivation of local native plant populations, carbonized *C. berlandieri* seeds recovered from the

Lockport and Forks sites were measured for seed size and testa thickness and compared to extant Manitoba populations. From the Lockport site, *C. berlandieri* seeds were associated with two different cultural groups: Late Woodland groups that focused on local resources use with some consumption of imported maize, and migrant cultural group(s) who focused on maize agriculture with local resource use. At the Forks site, *C. berlandieri* seeds were associated with Late Woodland groups that focused on local resources use with some consumption of imported maize. After accounting for the effects of carbonization (e.g. shrinkage and distortion of morphological features), the archaeological seeds associated with each cultural group displayed different patterns. Late Woodland groups from Lockport were utilizing one or more populations of *C. berlandieri* that exhibited a large mean seed size and relatively thin testa (Mean= 1.56mm and mean=0.034mm), compared to the agricultural groups from the same site. People associated with maize agriculture appeared to have focused on one or more *C. berlandieri* populations with a smaller mean seed size, also exhibiting a relatively thin testa (mean=1.41mm and mean =0.029mm, respectively). Late Woodland groups from the Forks utilized a range of populations with different seed sizes. Results suggest that people with different cultural affiliations were selecting *C. berlandieri* populations with different seed traits.

It is possible that cultural groups at both sites were cultivating local wild populations. The archaeological seed phenotypes associated with all three cultural groups also fell toward the thinner end of the unimodal distribution for testa thickness for extant Manitoba populations. The range of testa thicknesses exhibited by the archaeological seeds is similar to the range of testa thicknesses measured from ‘weedy’ seeds associated

with domesticated *C. berlandieri* seeds from archaeological deposits in some Eastern Woodland sites (Gremillion 1993). Gremillion (1993) suggested that an intermediate seed phenotype associated with the ‘weedy’ *C. berlandieri* populations was generated through interaction between the domesticated crop and wild populations growing along field edges. This research lends support to this hypothesis in that wild seed grown in cultivated environments decreased in testa thickness and the genetic variation appears to be sufficient to allow for evolution of modified testa thickness in subsequent generations.

Under the umbrella of a developmental perspective, it is possible that within the context of mixed subsistence economies and blurred cultural lines, some people living in southern Manitoba developed a particular relationship with local *C. berlandieri* populations that may have incorporated cultivation practices. Over time, continued interaction between people and *C. berlandieri* populations appears to have generated conditions that resulted in a morphological change to seed phenotypes (e.g. decreased testa thickness). Interactions between people, plants, and local environmental conditions are integral in generating new opportunities for knowledgeable agents to act. It is possible that the changes in plant and seed traits from initial interactions between people and *C. berlandieri* may have set the conditions for increased interaction by local cultural groups with local goosefoot populations solidifying a relationship that incorporated cultivation practices.

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8.0 ANNOTATED GLOSSARY OF TERMS

8.1: Definitions

Cultivation: (here synonymous with management) includes all techniques or activities used to influence the structure or productivity of individual plants, whole communities or entire landscapes (Lepofsky and Lertzman 2008:131; Terrell *et al.* 2003). Individual plants or plant populations also range from wild to fully domesticated (see below). Techniques range along a continuum from foraging or harvesting activities with minimal or incidental impacts, to tilling soil, weeding, watering, fertilizing, pruning, burning communities or landscapes, and intensive gardening, to deliberate selection and breeding programs leading to domestication (Turner and Peacock 2006:103; Harris 2007:25; Smith 2001).

Development: the process through which organisms generate form, function, learning and skills through active engagement with their environment (see Organism-in-environment) (Ingold 2000). In evolutionary developmental biology theory, development refers to how organisms change over time. Development includes all phenotypic change (e.g. morphological, behavioural, and physiological characteristics) throughout an organism's lifetime derived from ontogenic responses to an organism's environment (West-Eberhard 2003: 32; Davis and Wund 2016: 430).

Domesticate: traditionally, a plant or animal population that has been more or less permanently modified morphologically or genetically, though conscious or unconscious human interactions via selection, harvesting and subsequent planting of stored seed (Terrell *et al.* 2003: 325; Ford 1985). Wild or non-domesticated plants exhibit none or few of the morphological or genetic characteristics as domesticated plants (Smith 2001). However, merely quantifying or qualifying the suite of domestication traits (Harlan *et al.* 1973; Pickersgill 2007) for certain plant species may not be suitable for understanding people-plant interactions (e.g. Jones and Brown 2007).

Domestication: is a dynamic process in which human intervene in the lifecycle of plant and animals resulting in biological and behavioural changes in plants and animals and concomitant changes in human behaviour (Harris 1996:442; Ford 1985). In the strictest sense human interaction in the lifecycle of plants (and animals) alters genetic traits over time, causing morphological changes in plants and animals, and concomitant changes in human behaviour (Ford 1985; Harris 1996:442, 2007; Rindos 1984:138). In plants this tends to result in plants that are unable to reproduce without human help (Ford 1985). Other researchers view domestication as a symbiotic or co-evolutionary relationship between plant and people that was beneficial to both organisms altering traits in both species (Rindos 1984:99), however, not all people-plant interactions that may have resulted in domestication are symbiotic (e.g. parasitism, see Ingold 1980, cited in Harris 1996:440).

Environment: is relative, unique to each organism and cannot be divided from the organism that inhabits it. It can be viewed as one all encompassing system containing all aspects of an organism's world including biophysical components (e.g. geology, soils, temperature, precipitation), human and non-human organisms, and all interactions between them (Ingold 2000; Odling-Smee *et al.* 2003). The environment is continually being generated through the organism's interactions and living within it, therefore environments are continuously generated. This incorporates the idea of ecological and evolutionary niches (see below), but differs from a human ecology definition of environment. Human ecology views social environments composed of people, technology, cultural and social values, norms and choices as separate from but intrinsically linked to the ecological environment complete with all non-human biological organisms and abiotic components of the physical world (Martens 2001).

Fruit: is a mature, ripened ovary in angiosperm plants, which contains seeds and any adjacent parts that fuse with it during maturation (Raven *et al.* 2005: G-9). The pericarp, or ovary wall that develops into the fruit can be soft and fleshy, leathery,

hard, thin and paper-like, adherent to the seed or easily removed (Pearsall 2000: 140).

Genotype: is the specific complement of genes in an organism.

Niche: an ecological and evolutionary niche presented in niche construction theory, considers a niche the “sum of all the environmental factors acting on the organism”, thus defining the niche in time and space (Hutchinson 1944, cited in Odling-Smee *et al.* 2003:38). Niches are associated with species, including all resources necessary for its survival utilized over time and space (Schoener 2009: 5).

Niche construction theory: describes the process through which organisms can modify their own and other organisms’ environment, through metabolic changes, activities and choices. The system includes feedback and changes extend to both physical and selective environments. An organism’s selective environment includes all the selective forces acting on it (Odling-Smee *et al.* 2003).

Organism-in-environment: describes the indivisible totality of organisms developing through interactions with and within their environment (Ingold 2000: 19). Organisms and environments are not two components that are brought together to interact along the edges as described by human ecology (*cf.* Martens 2001, Chapter 1 Figures), they are one complex and dynamic system. In this system form emerges through the life process creating both organism and environment (Ingold 2000: 19).

People-Plant relationships: the myriad of ways humans have “intervened in the ecology of plants to obtain food (and other products), to which many plant species and populations have responded opportunistically, increasing their biological fitness as a result” (Harris 1996: 444). People-plant relationships are concomitant involving complex biological and socio-cultural factors (e.g. plant phenotypes, soils, climate, human agency, cultural choices).

Phenotype: the physical manifestation (i.e. composition of traits) of a plant generated through development of a genotype within its environment. Phenotypes are trait specific (e.g. height or Vitamin C content). The phenotype of these traits could include tall or short plants, high or low Vitamin C levels.

Phytoliths: are opal silicate bodies produced in and between cell walls and tissues of many plant species. Monosilicic acid from groundwater is drawn up through the plant and deposited in epidermal and other cells in stems, leaves, roots, and inflorescences forming cell shapes that are diagnostic to plant species and that survive after the organic tissue has been burned or decayed away (Pearsall 2000: 356).

Plasticity: is the ability for an organism to react to an environmental input with a change in morphology, physiology, movement or rate of activity (e.g. respiration), it can be active or passive, adaptive or not (West-Eberhard 2003: 34-35). Typically it relates to one genotype (or genetically identical organisms) being able to develop different phenotypes based on different environmental conditions (Davis and Wund 2016: 430).

Pollen: is the male reproductive part of an angiosperm, composed of the microgametophyte (the gamete producing generation) surrounded by a tough exterior wall (exine) and thin inner layer (intine) (Pearsall 2000: 251; Raven *et al.* 2005: G-18).

Procurement and Production: in recent classification systems of human food acquisition, the human activities and associated plant phenotypes are placed along a continuum from procurement of wild plant foods, to wild plant food production, with varying levels of cultivation, to crop production with domesticated cultivars (Harris 1996; Smith 2001). Procurement replaces foraging or collecting of wild or non-domesticated (see Smith 2001 for discussion) plants and is a more accurate term for what hunter-gatherers do (see Ingold 1996 for arguments) as procuring

relates to obtaining through care, effort or management. Procurement ascribes care, sophistication, and knowledge to the resource-getting abilities of hunter-gather groups (Bird-David 1992, cited in Ingold 1996: 149).

Residues: the remains of foods cooked ceramic vessels, plants or animals processed with various stone tools (e.g. grinding stones, or chipped stone blades), or soil samples collected from archaeological contexts where food was prepared or stored, that contain microscopic remains of pollen, phytoliths, starches or chemical signatures that can be extracted and identified (Boyd *et al.* 2008; Pearsall 2015; Syms 2015, and references therein).

Seeds: are the reproductive structures of a plant that contain the plant embryo, usually surrounded by nutritive tissue, encased in a protective seed coat (Pearsall 2000:133; Raven *et al.* 2005: 432, G-21).

Starch: molecules consist of polymers of six-carbon sugar D-glucose. Glucose is formed from two polymers, amylose (a linear polymer) and amylopectin (a larger branched polymer). Starch granules are formed through accretion of layers of these polymers starting at the hilum; the ratio of amylose to amylopectin affects granule morphology and functionality in foods (Pearsall 2015: 342). Starch is the major form of stored energy in higher plants. Starch is stored in the seeds (e.g. cereal grains, grass seeds), tubers, roots and stems (e.g. potato, tapioca), fruits (e.g. green bananas, apples) and leaves (e.g. tobacco) (Jane 2007:4-9). See Pearsall (2015) Chapter 6 on starch for further details.

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