Restoration Strategies for Propagation of *Camassia quamash* on the Weippe Prairie

A Thesis
Presented in Partial Fulfillment of the Requirements for the
Degree of Master of Science
with a
Major in Natural Resources
in the
College of Natural Resources
University of Idaho
by
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August 2020

Authorization to Submit Thesis

This thesis of Kathryn Matthews, submitted for the degree of Master of Science with a Major in Natural Resources and titled "**Restoration Strategies for Propagation of *Camassia quamash* on the Weippe Prairie**," has been reviewed in final form. Permission, as indicated by the signatures and dates below, is now granted to submit final copies to the College of Graduate Studies for approval.

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Abstract

Camassia quamash (camas) is a plant that is well-known throughout its native habitat in the Pacific Northwest of the United States, despite the growing decline of its preferred habitat type across the region. This plant requires specific site conditions to ensure a successful growing season. Its habitats, often referred to as camas prairies, were important traditional harvest sites for many indigenous cultures. In the 19th century federal land policies removed many tribes and first nations from their ancestral homelands and transferred ownership of those lands to early Euro-American settlers. Ultimately, these land uses proved particularly destructive to wetland prairies, including camas prairies. The decline of wetland areas across North America has resulted in significant loss of a habitat type that provides valuable ecosystem functions, while also reducing and degrading culturally significant landscapes. Camas' cultural and ecological significance make it an ideal species to focus on for wetland restoration projects. Weippe Prairie, a well-recognized traditional harvest area used by the Nez Perce people within the Palouse Bioregion, of north-central Idaho, provides an ideal site to both study and restore camas prairie habitat. This study identified site characteristics and evaluated different restoration techniques to aid in creating a restoration protocol that can be used to rehabilitate camas prairies across the Pacific Northwest.

Acknowledgements

I would like to express my sincere gratitude to those who supported me throughout this work. To my major professor, Dr. Mark Kimsey, for providing valuable assistance and guidance throughout the process. To Dr. Anthony S. Davis, for encouraging this work through our camas connections and providing me the opportunity to study camas at the University of Idaho. To Dr. Paul McDaniel, for showing me how interesting and important soils are. To the staff at Nez Perce National Historical Park and Upper Columbia Basin Network Inventory and Monitoring Program, without whom this project would not be possible. Jason Lyon, Beth Erdey, Heidi Tamm, Jeff Lonneker, Devin Stucki, Kristine Leir, and Mary James- thank you for support, assistance, and encouragement. To Bridget McNassar and Don Regan, for their help ensuring I would have camas propagules to work with. To staff at the US Forest Service Rocky Mountain Research Station, Dr. Kas Dumroese and Joanne Tirocke, for providing me lab space, patience, and expertise in the soil lab. To Cecilia O’Leary, for your unwavering support. And finally, to the many people who assisted me with field work, who worked tirelessly through rain, snow, and sunshine with enthusiasm.

Dedication

To my mom, for everything.

Table of Contents

List of Tables

List of Figures

Chapter 1:

Need for wetland restoration

Wetlands perform crucial ecological functions by acting as sources and sinks for a variety of chemical, biological and genetic resources; they provide habitat to a distinctive array of specialized plants and animals; and play a critical role in the health of other connected ecosystems, making them some of the most significant ecosystems in the world (Cowardin et al. 2005; Dahl 1990; Mitsch & Gosselink 2015). Consequently, reduction or degradation of wetland ecosystems can negatively affect overall landscape ecosystem function and quality (Mitsch & Gosselink 2015).

During the period of 1780 to 1980, the continental United States lost approximately 53% of its wetlands (Dahl 1990; Mitsch & Gosselink 2015). These acres of wetlands were and continue to be lost by altering the landscape primarily through draining and/or ditching operations. These modifications ultimately alter the hydrology for alternative land uses such as agriculture, mining operations, and other uses attributed to urbanization (Mitsch & Gosselink 2015). The most common factor for wetland loss is ascribed to agricultural conversion (Dahl 1990; Mitsch & Gosselink 2015). Approximately 56% of wetlands in Idaho have been converted to other uses following Euro-American settlement (Dahl 1990). In the Palouse Bioregion, an area encompassing a portion of eastern Washington to northern Idaho, 97% of wetlands have been lost (Black et al. 1998). A study of the Palouse Bioregion’s wetlands estimates approximately 13% of the region was previously considered to be camas prairies (Black et al. 1998; Servheen et al. 2002).

Camas Prairies

In the northwestern United States, seasonally wet-prairie ecosystems are an important wetland type that were once widely distributed across the region prior to Euro-American settlement (Servheen et al. 2002). Wet-prairie ecosystems dominated by camas species (*Camassia* sp.) and associated wet-prairie vegetation (i.e. *Carex* spp., *Equisetum* spp., *Juncus* spp., etc.), are called camas prairies or meadows; hereafter referred to as camas prairies (Thoms 1989; Servheen et al. 2002). Early botanists and explorers of the region, such as John Leiberg described that before Euro-American settlement, "Every meadow was a camas field," and when describing a camas prairie in northcentral Idaho, "The plant was so plentiful in many places…more than one-half of the total herbaceous vegetation…was comprised of this one species" (Leiberg 1897). These thriving camas prairies overlapped with the territories of many indigenous tribes and first nations throughout the Pacific Northwest region (Thoms 1989). Prairies, such as Weippe Prairie, provided traditional harvest areas for common camas (*Camassia quamash* (Pursh) Greene) (Spinden 1964; Thoms 1989; Gritzner 1994).

For the Nez Perce, a Native American people from the Inland Northwest, USA, camas was once a major component of their diet and still is a vital component of Nez Perce culture (Spinden 1964; Stevens et al. 2001). The dietary and cultural importance of camas was due to its abundance across the region, providing a sustained and reliable food source (Marshall 1999; Deur 2002). Reliance on this important food fostered management practices by indigenous people that encouraged and cultivated productive camas prairie habitat (Gritzner 1994; Turner & Peacock 2005). Horticultural activities such as burning, weeding, and selective harvesting resulted in high camas yields (Marshall 1999; Beckwith 2004).

Despite the importance of camas prairies to Native people across the region, camas started to be seen as a weed instead of a staple with the influx of Euro-American settlers moving into the area (Leiberg 1897; Thoms 1989). The privatization of land following tribal resettlement by the US government was particularly destructive to wetland prairies (Black et al. 1998; Servheen et al. 2002). These highly productive areas were recognized by Euro-American settlers as ideal for the application of Euro-American agriculture (Taft & Haig 2003).

The change in land use from activities associated with facilitating high camas yields, to land conversion that better suited Euro-American agricultural practices, has led to the decline of an important wetland ecosystem type making it one of the most endangered habitats in North America (Turner & Kuhnlein 1983; Taft & Haig 2003). With the privatization of land and introduction of intensive Euro-American agriculture, the traditional habitats of these camas wet-prairie ecosystems were dramatically changed. Efforts were made to dry the wet meadow systems. Intentionally reducing seasonally wet areas to promote forage and cereal crops also promoted conditions that proliferate non-native species invasions. (Black et al. 1998; Servheen et al. 2002). Detrimental disturbances, such as tilling, grazing, and mowing can lead to soil compaction which has negative effects on camas prairies (Mastrogiuseppe 2000; Stevens et al. 2001; Beckwith 2004).

Species Description

Camassia quamash is the major vegetative component of the camas prairie plant community in the inland northwest (Gould 1942; Servheen et al. 2002). *C. quamash* is one of six species having eight subspecies, within the *Camassia* genus, in the subfamily Agavoideae, within the Asparagaceae family (Chase et al. 2009). *C. quamash* is also known as common camas, small camas, camas lily, and blue camas; hereafter it will be referred to as camas.

Camas is a geophyte with a raceme of showy liliaceous flowers ranging in color from white, to light blue to deep purple and has a whorl of bright green, waxy linear leaves (Gould 1942). Native to North America and found in the western portion of the continent, its geographic range lies between northern California and Vancouver Island, and eastward to Montana and northern Utah reaching into Alberta and British Columbia, Canada with an elevational range of ≤ 3300m (Gould 1942; Stevens et al. 2001). The distribution of camas is the result of natural dispersal processes that are significantly affected by past glaciation and geographical barriers (Tomimatsu et al. 2009). According to pollen data, camas has been present in the Pacific Northwest more than 70,000 years and is widely distributed among seasonally wet habitats (Thoms 1989).

Ecology

Camas is a facultative wetland species, occurring primarily in wetland environments with seasonal wet periods (Gould 1942). Usually found in large colonies, these camas dominated wetland areas are often referred to as camas prairies (Maclay 1928; Gould 1942). Camas prefers soil that is saturated at or near the soil surface during the early portion of the growing season, and dry during the summer (Maclay 1928; Thoms 1989). Camas needs well-defined cold/warm and wet/dry periods (Thoms 1989). Soil that is too moist during the dry period can have negative effects on flowering and seed dispersal and can lead to rotting bulbs (Beckwith 2004). Extremely hot or dry environments will not promote camas growth however, camas is tolerant of cold temperatures, but growth may be affected if conditions are cold throughout the growing season (Beckwith 2004).

Soils associated with camas prairies tend to be derived from basalt parent material and have high silt and clay contents with a loamy texture (Maclay 1928). Camas preferences for soil pH range from acidic to slightly alkaline. Relationships between pH levels, flower color, and bulb size have been detected (Beckwith 2004). More basic soils were found to promote a blue flower with a larger bulb, while more acidic soils produce a purple flower with a smaller bulb (Kramer 2000). Soils are generally soft and wet during the growing season, hardening and drying out in the summer (Maclay 1928).

Increased camas production has been attributed to harvesting camas (Thoms 1989; Marshall 1999). Wetland soils are typically anaerobic affecting available oxygen. Digging camas tills the soil, introducing oxygen to the system and encouraging nutrient cycling (Marshall 1999; Kramer 2000). Digging practices also reduce intraspecific competition and open areas up, which can positively influence camas populations (Thoms 1989; Anderson 1997; Kramer 2000).

Camas reproduces primarily through seed, and, less commonly, by offset bulblets (Thoms 1989). Contractile roots allow the camas bulb to position itself to the proper depth within the soil profile (Kawa & De Hertogh 2010). Seedling establishment can be negatively affected if sown too deep, or inhibited by litter (Kramer 2000; Beckwith 2004). It can take up to 3-5 years for camas to produce a flower from seed (Thoms 1989; Beckwith 2004).

Leaves start to emerge in late winter. Blooming time occurs in the early spring producing large showy flowers. Flowers senesce by mid to late summer, producing up to 35 capsules which dehisce allowing up to 36 small black seeds to emerge from each. The plant goes into a dormancy period after seeds have matured into late fall (Thoms 1989; Stevens et al. 2001).

Camas provides important resources for a diverse group of insects that utilize pollen, nectar, as well as vegetative portions of the plant (Stevens et al. 2001; Parachnowitsch & Elle 2005). The list of observed insects includes, European honeybees, bumble bees, mason bees, butterflies, hover flies, beetles and lady beetles (Schultz 2002; Stevens et al. 2000). Deer, elk, and moose will eat camas; and gophers will eat and stash camas which can aid in bulb dispersal (Thoms 1989).

Cultural Significance

Camas has been noted as the most important root food for many indigenous groups across the Northwestern US and southwestern Canada (Gould 1942; Turner & Kuhnlein 1983; Thoms 1989). Among the Nez Perce, camas constituted a substantial portion of their diet and was frequently an item of trade (Harbinger 1964). Camas harvested across the Nez Perce homeland was known for its large size, superior taste, and great quantities (Mastrogiuseppe 2000). The stable and ubiquitous nature of camas allowed for gathering, processing, and storing large quantities of this staple making it an important winter food for the Nez Perce and other indigenous people across the region.

Cooked camas is high in protein, having more than beef liver, beans or potatoes (Scrimsher 1967; Thoms 1989). Across its range camas bulbs were harvested during the late spring, late summer, and early fall depending on the phenological and climactic conditions of the specific areas in which it was found (Marshall 1999). Among the Nez Perce camas was generally harvested in the late summer and early fall using a tool uniquely designed for digging into soft grounds (Harbinger 1964). This digging stick, known by the Nez Perce as a *tủuk̉es* was customarily created using a strong wood such as yew (*Taxus brevifolia*) or oceanspray (*Holodiscus discolor*) and could be slightly curved to straight (Spinden 1964). The handle was fashioned out of wood, antler, bone or stone (Mastrogiuseppe 2000). The *tủuk̉es* is pushed into the ground by applying pressure to the handle and then pulled in a sideways or downward motion to pry up a clump of soil or sod, revealing camas bulbs underneath (Harbinger 1964; Spinden 1964). Among the Nez Perce not all camas bulbs were harvested (Scrimsher 1967). Only larger bulbs were taken, as the smaller ones were left in the soil for future harvests and proliferation of the population (Anderson 1997).

Once the bulbs were harvested, they were generally prepared for consumption and long-term storage through cooking in earthen ovens. Cooking camas was a multi-day affair and required constant tending. For these reasons large quantities of bulbs were often cooked at one time. Among the Nez Perce large pits reaching a meter or two across and nearly a meter deep are excavated into the ground. The pit is lined with specifically selected rocks and wood. The wood is then burned to heat the rocks. Various types of vegetation is used to cover the hot rocks. The outer husk of the bulbs are all removed and then placed in the pit layered with vegetation. Water is poured over the top to create steam. Another layer of rock is added and the completed earthen oven is topped with a thin covering of soil. A fire is started on top of the pit and maintained at a constant temperature for up to three days.

Once cooking is completed the bulbs are removed from the pit. The constant heat and slow cooking of the bulb changes the color of the bulb from an uncooked white to a rich dark brown to black. This process also breaks down inulin found within the bulb to easily digestible fructose. In its uncooked form, almost half the bulb is composed of the complex carbohydrate inulin (Turner & Kuhnlein 1983). Inulin cannot be digested raw, however after it transforms to fructose through the slow cooking process the bulb is now easily digestible and highly nutritious (Konlande & Robson 1972).

Roasted camas can be dried and stored or crushed into other food stuff such as porridge, bread, or cakes (Scrimsher 1967). For the Nez Perce, processed and stored camas was an essential component of the winter diet. It was also traditionally used as travel food, for trade, in fests and celebrations, flavor for other foods, or as a treat or special food (Harbinger 1964; Gritzner 1994; Mastrogiuseppe 2000).

Cultural Keystone Species and Cultural Keystone Landscape

Camas is a *cultural keystone species*; meaning it is important not only to the ecological community which it is an integral part of, but also for its cultural value to the indigenous people who once depended on it (Garibaldi & Turner 2004). Camas has a rich history of co-evolving with a myriad of indigenous groups encouraging cultural ties to many different tribes and first nations across western North America. It was particularly important due to its edibility and abundance, and its carbohydrate rich bulb continues to be harvested, cooked, and eaten today. Historically, camas harvests were an opportunity for indigenous peoples to trade and interact, both within and between different indigenous groups.

Cultural landscapes are areas in which there has been a long-standing, close relationship between cultures and their surrounding environments. These areas, also known as *cultural keystone landscapes or places*, are culturally significant in part due to the presence of cultural keystone species (Gomes 2012). A key component of a cultural keystone place is the role a culture plays in utilizing and manipulating the landscape, often in a way that benefits the biotic, including human, community (Gomes 2012).

The Weippe Prairie in north-central Idaho is a cultural keystone place due to its importance as a communal gathering place for both the Nez Perce as well as other indigenous peoples in the region. Harvesting camas was often a social event where families and bands of Nez

Perce would gather to dig, cook, and process large quantities of camas. During these times activities such as socializing, trading, storytelling, arranging marriages, playing games, gambling, and a host of other activities common to group gatherings occurred (Harbinger 1964; Gritzner 1994; Mastrogiuseppe 2000). These activities were often conducted in concert with the camas harvest due to the incredible densities of camas found in these gathering areas.

In his 1989 study Thoms attempts to quantify the number of camas/ m^2 in terms of historical density levels in a highly functioning camas prairie. In his work with the Salish-Kootney people in the Flathead Valley of Montana, he identified a density of approximately 300 plants/m^2 for a “typically productive” camas prairie. He further states that this number is based on observations within a moderately dense camas population and that “exceptionally productive” camas prairies would likely be much higher. In her research across southwestern British Columbia, Beckwith (2004) has found actual camas counts in exceptionally productive areas are closer to 1700-2100 plants/m^2. She also points out that Thoms’ numbers do not account for seedlings or small camas plants. Based on the historical accounts and Nez Perce traditional knowledge of the area it is very likely the Weippe Prairie is consistent with having areas of “exceptionally productive” camas populations that may have reached or even exceeded 800 plants per m^2.

Significance of the Weippe Prairie as a Study Site

In September 1805, members of the Lewis and Clark expedition made their way out of the Bitterroot Mountains onto the Weippe Prairie. It was here that the first contact was made between the Lewis and Clark Corps of Discovery and the Nez Perce Tribe (Spinden 1964). Nez Perce were harvesting camas when the expedition arrived at the Weippe Prairie. Nez Perce aided members of the expedition by providing food to the starving group (Gould 1942). Weippe Prairie was also the location of the type collection for the *Camassia* genus (Gould 1942). This collection was made by Lewis and Clark in 1806 on their return trip through the area (Gould 1942).

During the late 1800's, Euro-American agriculture was introduced to the Weippe Prairie by settlers (Harbinger 1964; Franklin & McCoy 2012). This resulted in much of the prairie being divided up into individual farms. The settlers rapidly began a transformation of the once-productive wetland prairie to further their pursuits of grazing, farming, and haying. Chief among these were altering the hydrological condition of the prairie through ditching and channeling to remove the water from the system. These changes were made to the land to better suit farmers' needs in supporting economically viable forage and cereal crop species.

The majority of the Weippe Prairie remains in private ownership today and still supports the agricultural pursuits of its owners. With the creation of Nez Perce National Historical Park in 1965, the Weippe Prairie was included as a component of the Park. Later in 2003, 274 acres of property on Weippe Prairie were acquired by the National Park Service (NPS) as the Weippe Prairie unit of Nez Perce National Historical Park. These designations were due in large part to the cultural significance of camas to the Nez Perce People, its association with Lewis and Clark, and the natural significance of camas as an important wetland species. Consequently, the NPS has identified the historical landscape associated with camas and the preservation and conservation of the camas prairie habitat to be of the utmost importance in maintaining the significance and character of the site (Rodhouse et al. 2007). Furthermore, camas has been recognized as a "vital sign" of the site and its distribution and abundance is actively monitored by the NPS and used as an indicator of the health of the ecosystem and condition of the site.

The use of cultural keystone species for restoration projects are ideal because they become more meaningful, as the impact is not just towards developing a more resilient ecosystem, but also benefits the cultural identity of the indigenous tribes who have associations and relationships with the species in question (Garibaldi & Turner 2004). These relationships also provide an opportunity to integrate Traditional Ecological Knowledge (TEK) with current restoration techniques (Garibaldi & Turner 2004). TEK is defined as, "a cumulative body of knowledge, practice, belief, evolving by adaptive processes and handed down through generations by cultural transmission, about the relationship of living beings (including humans) with one another and with their environment" (Berkes et al. 2000). This is plainly evident for the Nez Perce who through reliance on camas as a food source have developed and adapted a variety of management techniques to encourage and promote the health of camas prairie ecosystems. This longstanding relationship provides valuable knowledge which could aid in the identification and success of establishing best management practices for healthy camas prairie habitats.

Why Restore?

Restoring camas prairies provides an opportunity for recovery of important natural and cultural landscapes. Re-introducing the historically productive ecosystems associated with camas prairies that are currently distorted by non-native plants and reduced hydroperiods will serve in both restoring the functionality of these ecosystems as well as restoring lands that are culturally significant to many indigenous groups. These efforts will further help restore the cultural bond between a group of people and the resources, places, and cultural experiences that have on many occasions been completely removed from a particular landscape. This is especially true with the Weippe Prairie where thousands of years of Nez Perce use and management of the site have been severed for nearly 140 years.

One of the key aspects allowing for restoration of the camas prairies is the incredible abundance of camas within those systems. However, there is also a companion suite of species known to occur with camas in these complex systems (Servheen et al. 2002). Additionally, the response of camas populations to changes in habitat conditions make it a good indicator species for understanding the general ecological conditions of wet prairie ecosystems (Rodhouse & Stucki 2015). Using camas as a driver for the restoration process in rehabilitating camas prairies will facilitate site conditions needed by the suite of companion wet-prairie species associated with them. Creation of a restoration protocol is needed to move towards more successful camas prairie restoration projects.

Chapter 2:

Introduction

Wetlands are important ecosystems that perform a variety of important ecological functions. One such function is providing habitat to plants, like camas, which are specifically adapted for site conditions associated with wetland ecosystems. Camas prairies are a specific type of wetland found in the Pacific Northwest that were once prevalent across the region but are now considered one of the most endangered ecosystems in North America (Lincoln et al. 2018). These areas were particularly appealing to Euro-American settlers focused on agricultural pursuits. The introduction of Euro-American agriculture significantly reduced land previously attributed to wetland ecosystems.

Human intervention on the Pacific Northwest land once worked to establish camas habitat by maintaining camas prairies, to encourage the growth of a staple food source and to promote and sustain a healthy camas prairie ecosystem. Indigenous people used management practices such as fire, weeding, and selective harvesting to cultivate the land and encourage camas populations, thereby sustaining the camas prairies. Euro-American agricultural practices did not prioritize camas growth, but rather worked to improve land drainage to encourage the growth of primarily introduced crops and forage species. These efforts altered the Pacific Northwest landscape, shifting them away from the naturally occurring camas prairie towards an agronomic grassland. The introduction and rapid spread of Euro-American agriculture brought with it the introduction of intensive land management practices including altering the hydrology, introducing pasture grasses and other non-native species, and altering soil chemistry and characteristics through the introduction of heavy equipment, chemicals, and grazing operations (Servheen et al. 2002; Lincoln et al. 2018).

The Euro-American alteration to the hydrology was primarily accomplished through draining and/or ditching operations. This effort reduced the presence of water on these fertile lands, allowing the camas prairies to be replaced with haying and grazing operations. The loss of naturally occurring flood pulses in conjunction with reduced hydroperiods led to changes in soil characteristics, and greatly altered vegetation structure and composition (Middleton 2000). These changes to hydrology characteristics eliminated camas seedling dispersal and recruitment by allowing litter to accumulate, which changed the frequency and type of soil disturbance that in turn reduced bare soil availability available for new plants (Xiong & Nilsson 1999; Middleton 2000; Thogmartin et al. 2009)

In addition to changes in hydrology of camas prairies, Euro-Americans also introduced non-native species to these areas. They plowed over the naturally occurring wet-prairie vegetation associated with many camas prairies to encourage pasture grasses for haying and grazing operations. European pasture grasses can be especially problematic, often forming dense stands with thick sod and litter layers that can impede native species from establishing and negatively affect pollinator species (Bosy & Reader 1995; Stanley et al. 2008; Davis 2015). Site preparation and maintenance for pasture grasses allow non-native species such as reed canary grass (*Phalaris arundinacea*) and timothy (*Phleum pretense*) to proliferate (Thoms 1989; Servheen et al. 2002). Invasive perennial grasses are one of the biggest risks to prairies, affecting vegetation and wildlife composition and diversity, community structure, soil properties, and litter accumulation (Stanley et al. 2008).

Finally, Euro-American agriculture practices also altered the soil characteristics and chemistry of camas prairies. Soil characteristics, including bulk densities, organic matter content, and pH were also impacted by the introduction of Euro-agricultural methods. Euro-American operations included intensive land use such as plowing, tilling, applying chemicals, and introducing livestock. These new activities led to soil compaction, contamination of ground-water and soils, and erosion (Black et al. 1998).

Restoration to a functioning wet-prairie ecosystem can facilitate a return to a culturally significant landscape by reestablishing 1) functional nutrient cycling, 2) a return to historic camas densities and associated plant communities, 3) wildlife refugia, and 4) a seed source for native plant populations in a fragmented, agriculturally dominated landscape.

Camas as a Restoration Tool

Camas possesses several traits that make it an ideal species for use in restoration projects. These characteristics include seed viability and its use as a food source. Camas populations can also be used as indicator species for ecological conditions of wet prairie ecosystems because they respond to changes in habitat conditions (Rodhouse & Stucki 2015). Finally, established camas prairies promote and facilitate the growth of other native species.

This widely distributed, hardy, long-lived species has a 30-year seed viability. Camas bulbs can go into dormancy and weather unfavorable conditions until favorable conditions for growth are present again. It provides a valuable food source to a variety of wildlife and is appealing to insects, ultimately benefiting local pollination systems. Insects that benefit include an endangered butterfly and potentially a rare bumble bee (Schultz 2002; Parachnowitsch & Elle 2005; Davis 2015). Accordingly, these traits make camas a good species for promotion of wildlife habitat and provision of refugia in agricultural areas.

When camas prairies are established, they also provide habitat for a diverse group of native species beyond the dominant camas plants (Servheen et al. 2002). Using camas to drive camas prairie restoration and rehabilitation processes will facilitate site conditions needed by other wet-prairie species that prefer camas prairie habitat. Camas populations can also be used as an indicator species for ecological conditions of wet prairie ecosystems because they respond to changes in habitat conditions (Rodhouse & Stucki 2015).

State of Knowledge

A considerable body of research has been conducted on the cultural significance, traditional use and management, physiology, phylogeny, taxonomic history, cytology, species descriptions, and phylogeography of the *Camassia* genus. The works referenced here should be explored further for more detailed information regarding their specific inquiries. The focus of this research is looking specifically at *Camassia quamash* and its use in restoring camas prairies.

While ethnobotanical, taxonomic investigations, and botanical research have been explored, more scientific research is needed that focuses on the ecological and environmental conditions necessary for the successful adaptation of camas as a restoration tool for rehabilitating camas prairie ecosystems. Artificial environments such as nurseries and gardens have been used for most camas studies, and there are a growing number of projects in Garry oak (*Quercus garryana*) ecosystems and coastal areas. However, there are currently no published studies conducted in a natural setting that identify protocols specific for camas restoration. Further investigation is needed to explore the use of camas as a restoration tool. This research is needed to develop a restoration protocol that will successfully rehabilitate camas populations as well as the species composition, biodiversity, and system functionality that are associated with camas prairie habitats. Identifying the specific habitat criteria that camas requires and evaluating different restoration techniques is a restoration protocol tool for camas that can be applied to camas prairies across the inland Northwest, USA.

Objectives

The goal of this study is to develop a protocol for successful restoration of camas prairie habitat via identifying ideal camas plant growth conditions at the Weippe Prairie. The land use history of the Weippe Prairie, ecological importance of camas wetlands, and the commitment by the NPS to restore this wetland prairie ecosystem make this an ideal research location for identifying camas restoration strategies. The study site represents a unique opportunity to examine differences in site variability among a population of camas, allowing us to identify the range of conditions conducive to supporting healthy camas plants. Therefore, the objectives of this study are twofold: i) identify the preferred site characteristics associated with high camas densities and ii) compare six restoration methods to identify the most successful regeneration method.

Hypotheses

Our hypotheses for this restoration study are: i) soil physical properties differ between areas of low and high camas densities, ii) fall seeding is superior to spring seeding for camas germination rates, iii) outplanting bulbs provides higher camas germination success than sowing seed, and iv) planting bulb depth (shallow vs deep) does not significantly affect germination success.

Methods and Materials

Site Description

The Weippe Prairie is a palustrine wetland meadow located in north-central Idaho. The entire area encompasses over 450 km^2. It is located approximately 900-950 m above sea level and is stream fed by Jim Ford Creek. The study site for this research is located approximately 10 km from the town of Weippe, ID and is comprised of a combination of previously divided agricultural parcels totaling 110 ha. It is bisected and bordered by county roads and Jim Ford Creek and surrounded by agricultural land. The topography and soil characteristics of the surrounding area maintain many small ponds in addition to Jim Ford Creek, which drains into the nearby Clearwater River. The study site is relatively flat with a total gradient of less than a meter. Average annual precipitation is approximately 104 cm with average temperatures ranging from 17 to -4 degrees C in the summer and winter, respectively (Erixson & Cogan 2012).

The study site was managed for livestock grazing and haying production lasting approximately 100 years, until shortly after the NPS acquired the final parcel in 2003. Agricultural developments affected the hydrology and vegetation of the site (Rodhouse & Stucki 2015). Drainage ditches from agricultural applications have artificially removed surface waters from the prairie, causing the seasonally wet meadow to dry out prematurely, altering the historic hydrology across the site. The introduction of European pasture grasses changed the vegetation community from the historical wetland community to dry upland grass prairie community. A vegetation survey was completed in 2009 for the study site (Erixson & Cogan 2012). Dominant species noted were smooth brome grass (*Bromus inermis*), timothy (*Phleum pratense*), red top (*Agrostis gigantea*), and meadow foxtail (*Alopecurus pratensis*). These Eurasian grasses are all associated with hay production. Invasive species were also identified onsite, which included, orange hawkweed (*Hieracium aurantiacum*), oxeye daisy (*Leucanthemum vulgare*), Canada thistle (*Cirsium arvense*), and reed canarygrass (*Phalaris arundinaceae*).

Initially, the Park took a passive management approach recording observations on camas presence and density throughout the site. By 2008, agricultural operations were removed from the entire site. The NPS began a monitoring program to determine the camas density and distribution across the site in 2005. These monitoring efforts found that average camas densities ranged from 4.5 to 48.7 plants/m^2 in 2005 (Rodhouse & Stucki 2015). Across the site there was variability in camas density, where some highly productive microsites were identified with camas densities of more than 100 plants/m^2. These areas were less than 2 ha on average and were not consistently distributed (Personal communication Jason Lyon 2016). Since monitoring began in 2005, there was an increase in camas densities during 2007-2011 across the study site. However, overall trends in camas density suggest that population densities may be returning to those densities observed in 2005 (Rodhouse & Stucki 2015).

There are two National Resource Conservation Service (NRCS) soil survey map units represented across the study site, Gramil-Lewhand complex and Lewhand-Burntcreek complex and the soil was classified as either an Vitrandic Hapludalf or a Vitrandic Fragiudalf (Soil Survey Staff et al. 2019). A hydrological analysis completed in 2009 and soil analysis completed in 2014 determined that there is a very slow permeable fragipan or clay layer located 45-75 cm below the soil surface. This layer, as well as the drainage of Jim Ford creek, creates the hydrology that influences the site habitat suitability. The site is saturated at or near soil surface for four to seven months out of the year in the wettest areas; however, pooling does not occur continuously across the site (Noon & Smillie 2009; McDaniel & Falen 2010, 2014). This saturation is caused by a combination of low- relief topography, subsoils that have hydrologically restrictive subsoil horizons, and perched water tables working dynamically together in conjunction with channelization that was implemented across the site for agricultural pursuits. The upper horizons of the soil consist mostly of sandy clay loam, silty clay, and clay textures. A soil survey suggested that the soil's seasonal saturation of four to seven months of wetness was related to its ability to support camas presence (McDaniel & Falen 2010, 2014).

Plot Location and Microsite Identification

The site was stratified into low and high camas density areas, where five plots were then installed across each stratum to represent the average camas density condition (Figure 2.1). Individual plot locations were determined by camas presence. High density areas were identified as having a high number of camas stalks from last season's flowers, lower elevation, prolonged surface pooling, and by relatively low concentrations of non-native vegetation. Low density areas were identified as having a small number of camas stalks present, higher elevation, shorter duration surface pooling, and by high concentrations of non-native vegetation. Plot locations were installed based on camas density (low, high) and visual observation of similar vegetation presence. This ensured that each plot location had the potential to grow camas and would therefore help to delineate key differences between camas preferences.

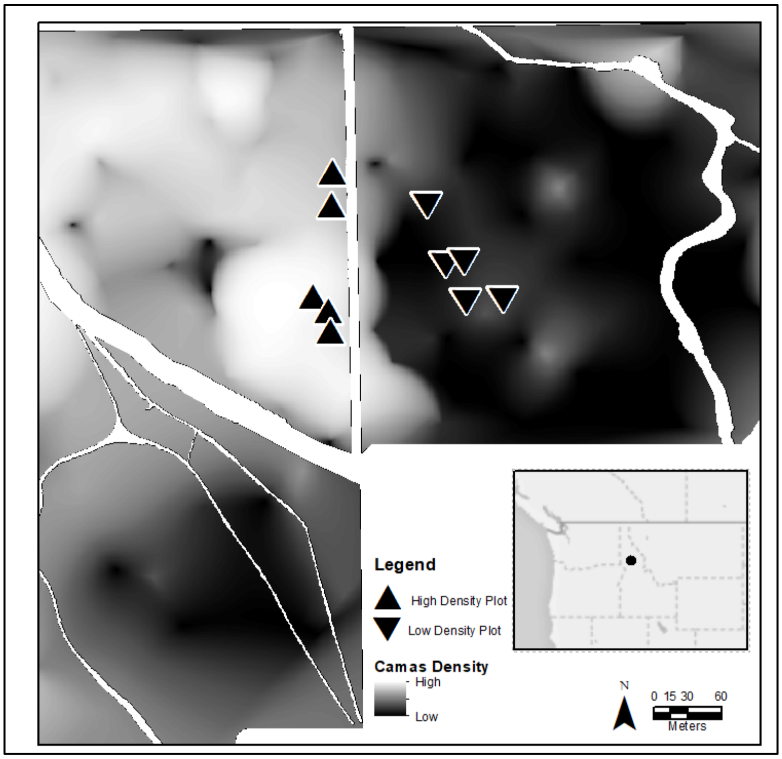

Figure 2.1 Map of Weippe Prairie study site with high and low population density plot locations (black triangles), within high and low density populations (density levels indicated by greyscale gradient across the study site), located on the Weippe Prairie National Historical Park site, in north-central Idaho, USA.

Seed Collection and Processing

Camas seeds were collected July 2016 for fall/spring seeding treatments and growing bulbs for outplanting treatments. Seed pods were collected and dried in paper bags. Collections were made from the high- and low-density macrosites and kept separate. Each collection consisted of seeds taken from between 10-17 individual plants in the immediate area (20m² area). Ten collections were made from different areas identified as high density and low density, respectively.

Seeds were processed through a seed aspirator at the US Forest Service Rocky Mountain Research Center (Moscow, ID) in August 2016 to remove debris and unviable seeds. Seeds were weighed September 2016. Three samples of 100 seeds each were taken from each collection, resulting in significant seed weight differential between the low and high camas population density areas. This information was used to determine the average number of seeds per collection as well as compare weights between collections. Collections with the highest weights from the high camas population density areas were combined into one high camas population density collection. Seeds with the highest weights from the low camas population density areas were combined into a single low camas population density collection.

Plot Installation

Ten macroplot locations were established in the study site. Five macroplots were installed in high camas population density areas and five in low camas population density areas. Within each macroplot (7 m^2), nine microplots of either 25 cm^2 (four microplots), 1m^2 (four microplots), or 90 cm^2 (one microplot) were installed for treatment applications (Figure 2.2).

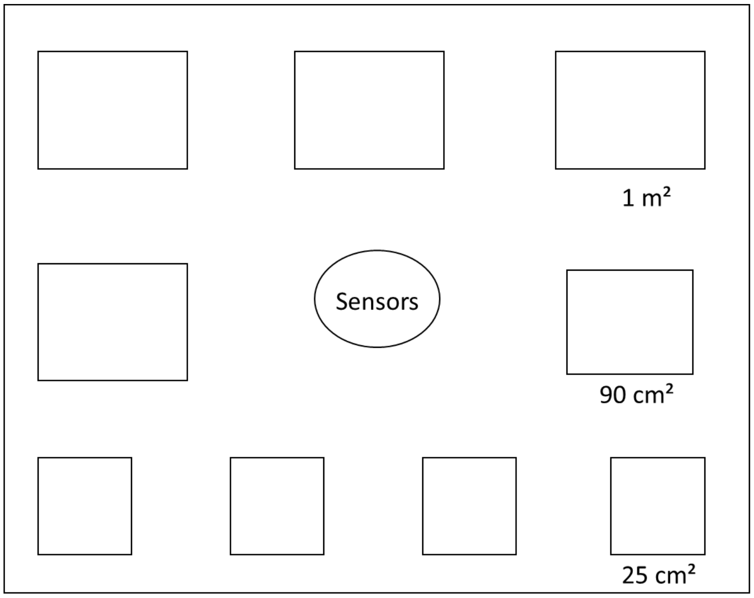

Figure 2.2 Diagram of macroplot (7 m^2) with all associated microplots: 25 cm^2 (four microplots), 1m^2 (four microplots), or 90 cm^2 (one microplot), and sensor locations.

Plot Preparation

The existing vegetation and sod layer at all microplots were removed by hand scraping prior to treatment installation to eliminate confounding planted seed/bulbs with existing native populations already in the soil. In addition, native bulbs were removed from the top of the soil to further eliminate treatment contamination. This was completed by sifting soil through a 6.35 mm hardwire mesh screen. Sifted/cleaned soil was added back to the microplot it came from for treatment installation. Every attempt was made to "clean" the soil of naturally occurring propagules, however due to the discrete size of seeds, seedlings, and young bulbs, it was not possible to remove all naturally occurring propagules.

Vegetation Monitoring

Plant specimens were collected across the site and keyed out using *The Flora of the Pacific Northwest* (Hitchcock & Cronquist 2018) at the Stillinger Herbarium at the University of Idaho to assist in describing vegetation community differences between plot locations. Monitoring surveys based on the phenology of the camas populations did not overlap with grass flowering times, making identification to the species level of grasses within plots difficult. Attempts were made to return to plot locations to record presence/absence of grass species however, due to the difference in phenological timing these surveys were insufficient to identify vegetation differences between plots at the species level to create a more comprehensive species list for each macrosite. To alleviate this issue, species were grouped by vegetation type (graminoid, forb, or shrub) to determine if there was a significant difference in the vegetation structure and type diversity between high- and low-camas population density areas. This vegetation survey was completed May 2019 using the FIREMON Fire Effects Monitoring and Inventory System to record vegetation presence based on percent cover (Lutes et al. 2006).

Soil-Site Property Monitoring and Analysis

Em5b Data Collections System dataloggers (Decagon/ Meter Devices, Pullman, WA) were used with soil moisture (Model EC-5, Decagon/ Meter Devices, Pullman, WA) and temperature sensors (Model RT-1. Decagon/ Meter Devices, Pullman, WA) installed at 15 and 45 cm below the soil surface, but above the fragipan layer in six of the ten macroplots, with recordings at every three hours. A weather station was also installed in a central location between all ten macroplots to capture ambient temperature (Model RT-1 Decagon/ Meter Devices, Pullman, WA.) and precipitation (RAINEW 111 Tipping Bucket Wired Rain Gauge, Rainwise Inc, Trenton, ME.).

Soil samples were collected at each plot monitored for soil moisture and temperature. Soil cores were collected using a slide hammer soil sampler at depths of 15 and 45 cm and analyzed for bulk density, wilting point/field capacity, organic matter content, texture, percent sand, silt, and clay, and pH. Bulk density samples were airdried and weighed at the Silviculture lab in the University of Idaho. Organic matter content was determined using the Loss-on-ignition method (Carter 1993). Soil water holding capacity was assessed using the pressure method to determine the wilting point (-1.5 MPa) and field capacity (-0.033 MPa) (Soil Survey Staff 2014). Samples assessed for bulk density, pH, and texture used the methodology described in the Kellogg Soil Survey Laboratory Methods Manual (Soil Survey Staff 2014).

Treatments

There are a total of six treatments in our experimental setup, all of which are described in the sections below. Each of the six treatments were in a microplot associated with each microplot, all of which were replicated at both the high and low camas population density areas. (Table 2.1)

Seeding

There were two seeding treatments, Fall (Treatment 1) and Spring (Treatment 2). In both the Fall and Spring seeding treatments, thirty-six seeds were sown less than 1 cm below the soil surface in each of the plots. Fall seeds were sown directly into treatment plots. Seeds used for the Spring seeding treatment went through a cold stratification process to stimulate germination, as camas requires a cold period to break seed dormancy before sowing (Russell 2011).

Bulb Outplanting

Bulbs were grown from seeds collected in Summer 2016. Seeds were sent to the Oxbow Native Plant Nursery, in Carnation WA for production. First year bulbs (Treatment 3) were grown for one year before outplanting; second year bulbs (Treatment 4) were grown for two years before outplanting. Bulbs for each treatment were collected from the Oxbow Native Plant Nursery a month before treatment installation at the study site and were planted 12-15 cm below the soil surface. Planting depth plots (Treatment 5) were prepared as described for Treatment 4, the only difference being planting depth was 2 cm below the soil surface.

Disturbance Only

Disturbance only plots were paired with each of the above-mentioned treatment types (Treatments 1-5). Installation occurred as described per each specific treatment, without the addition of plant propagules (seed/bulb).

Table 2.1 Treatment descriptions identifying number assigned to each treatment type, treatment name, plot size, propagule type applied, and the monitoring dates for each treatment type. Each treatment was present at each macroplot location.

Treatment #	**Treatment Name**	**Seeded/planted Date**	**Plot Size**	**Propagule Type (Sowing/Planting depth)**	**Monitoring Date**
1	Fall seeding	October 2016	25 cm²	Seed (<1 cm)	Spring/Summer 2017, Spring 2018, Spring 2019
2	Spring seeding	May 2017	25 cm²	Seed (<1 cm)	Spring 2018, Spring 2019
3	One Year bulbs	November 2017	1 m²	Bulb (12-15 cm)	Spring 2018, Spring 2019
4	Two Year bulbs	November 2018	1 m²	Bulb (12-15 cm)	Spring 2019
5	Planting	November 2018	90 cm²	Bulb (<2 cm)	Spring 2019
6	Disturbance	October 2016; May 2017; November 2017, November 2018	25 cm²; 1 m²	None (sod removal and soil aeration only)	Spring/Summer 2017, Spring 2018, Spring 2019

Treatment Monitoring and Data Collection

Monitoring treatment plots required counting the number of camas germinating in each plot. Germination counts were made each spring for the duration of the study, distinguishing between seedlings (single leaf), vegetative (2 + leaves), and sexually reproductive individuals (flowers). Total germination counts for each treatment type and year were recorded and summarized along with the associated site characteristics. Germination count was determined by taking the number of camas plants that germinated in a plot per season. Continuous visits to the sites throughout the spring and summer recognized an increase in vegetation recruitment within plots. Additional vegetation clearing was not performed to reduce any inconsistent effects on the camas treatments within plots.

Data Analysis

To determine key site characteristic and soil property differences between high and low camas density population areas, we looked at the correlation between site characteristics and camas density. Site characteristics included soil bulk density, texture, percent sand, silt, and clay, organic matter content, pH, and soil moisture and temperature. Site characteristics associated with discriminating between low and high camas population densities were assessed in a two-step process. First, site characteristics correlated with camas density were identified by calculating Pearson's correlation coefficients using PROC CORR in SAS 9.4 (SAS Institute Inc. 2015) using a significance level of 0.1. Second, the site characteristic means and associated standard errors for significantly correlated variables were generated by estimation in a linear model using PROC GLM and least square means using the LSMEANS statement and an alpha of 0.1. Least square means are an estimation approach that groups means after controlling for a covariate (in this case, by density class- low or high).

We then looked at the germination success of different treatments within high and low camas population density areas to assess the hypotheses regarding germination success based on differences in restoration treatment methods. Mean germination count was used as the metric to compare restoration success across treatments. Treatment means were compared within, but not across, a camas population density class. Germination counts between treatments within a camas density class were compared using analysis of variance (ANOVA). This comparison of treatment success was done using PROC GLM with least square means (LSMEANS) in SAS 9.4 at a significance level of 0.1. The Tukey-Kramer adjustment for multiple comparisons was employed to account for the small sample size of observations and uneven samples sizes between treatments.

Results

Relationships Between Camas Density Populations and Soil-Site Characteristics

High density camas areas are associated with lowest site elevation (i.e., high water accumulation zones, p=0.0031) and forb-dominated vegetation communities (p<.0001). Low camas density areas were associated with water shedding zones and were dominated by graminoid vegetation (p=0.0001) (Figures 2.3a, b). Soil textures were similar across the landscape. Observations trended more towards silt content in the upper 15 cm (p=0.0877) of the soil horizon but overall, there was no significant difference in the sand and clay percentages between high and low camas density sites (Figures 2.4a, b, c).

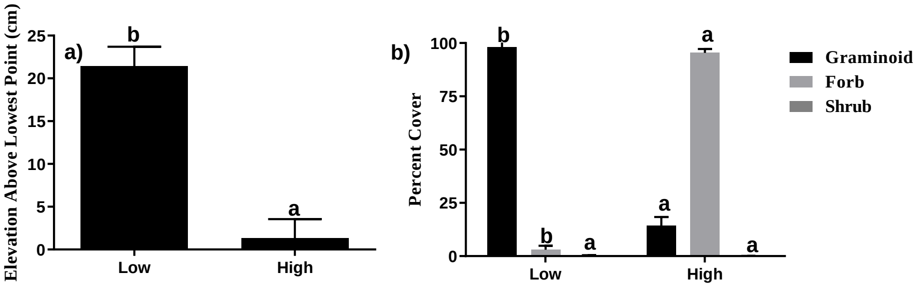

Figure 2.3 Plot elevation range between low and high camas population density areas relative to lowest elevation point within study (a), and vegetation community structure (b). Different letters indicate significant differences at an alpha level of 0.1.

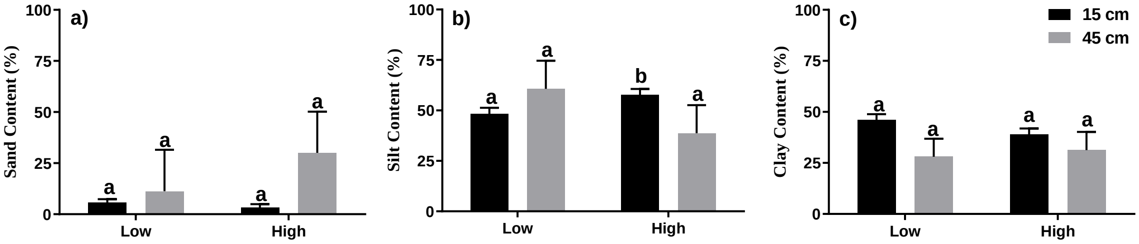

Figure 2.4 Percent sand (a), silt (b) and clay (c) differences between low and high camas population density areas. Different letters indicate significant differences at an alpha level of 0.1.

Organic matter content (15 cm) was significantly lower in the high camas density areas (p<.0001) (Figure 2.5b). Soil water retention observations at -1.5 MPa and -.033 MPa, were inconclusive in defining differences in camas densities across the study site and were therefore removed from analysis. Soil pH and bulk density characteristics collected across the study area were not found to be significant (p>0.1), regardless of density location (Figures 2.5a, c).

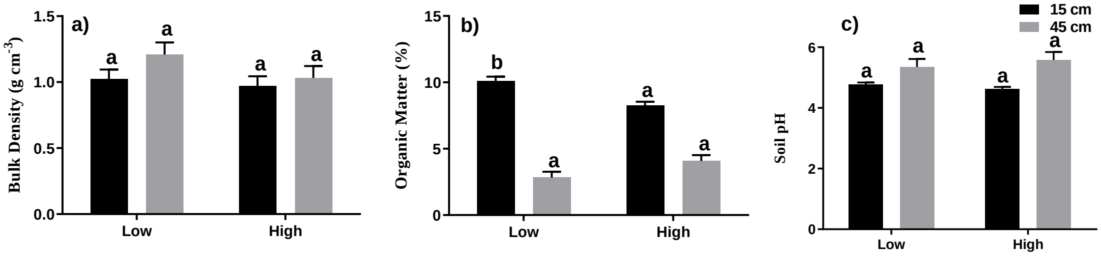

Figure 2.5 Differences in mean soil bulk density (a), mean organic matter content (b), and mean soil pH (c) between low and high camas density populations. Different letters indicate significant differences at an alpha level of 0.1.

Soil moisture and temperature monitoring showed a clear distinction between cold/warm and wet/dry periods across camas population densities throughout the duration of the study. These periods, hereafter referred to as climatic periods, are the number of days between soil moisture inflection points at both the 15 and 45 cm depths over the year across the two different camas population density areas. Four different climatic periods were identified and classified: Spring dry down (SDD), Summer dry period (SDP), Fall wet-up (FWU), and Winter wet period (WWP) (Table 2.2).

Table 2.2 Descriptions of climatic periods with average calendar timelines identified through sensor monitoring with minimum, median, and maximum number of days for the duration of each period for both the high and low camas population density areas.

Climatic Period type†	Description	General Timeline (approx.)	Duration					
			High			Low		
			Min	Med	Max	Min	Med	Max
SDD	Ponded water evaporates/ moves off site	Starts mid-May; Ends early July	32	44	89	25	36	58
SDP	No surface water/ soil water content at annual low point	Starts early July; Ends late September	24	68	81	37	67	101
FWU	Soil moisture recharge begins	Starts early October; Ends early January	2	5	58	11	72.5	99
WWP	Ponding/soil saturation period	Starts early January; Ends late June	204	233	251	181	206.5	228

†SDD=Spring dry down; SDP=Summer dry period; FWU=Fall wet-up; WWP=Winter wet period

Camas population density areas were associated with significantly different soil moisture and/or temperatures within varying climatic periods. During the spring dry down (SDD) period, higher camas population density areas were associated with higher volumetric water content at the soil surface (15 cm) (p=0.0692) in addition to wetter (p=0.0042) and warmer soil temperatures [2.3°C higher] (p<.0001) at the 45 cm depth, relative to low camas population density areas for a longer period of time [16 days longer] (p=0.434) (Figures 2.6a, b, c, d). Higher soil volumetric water content during the summer dry period (SDP) was also associated with high population density areas at the 45 cm soil depth (p=0.0566) (Figure 2.7a), in addition to warmer soil temperatures at 15 cm depths [2.5°C higher] (p=0.0049) (Figure 2.7b). Temperatures were higher by almost 1.5° C (p=0.0882) in high camas population density areas and took a significantly shorter number of days [47 days less] (p=0.0108) for soils to become wet during the fall wet up (FWU) period at 45 cm (Figures 2.8a, b). Furthermore, a longer winter wet period (WWP) [26 days longer] (p=0.0297) with higher soil temperatures at 45 cm [1.2 °C higher] (p=0.0619) was associated with high population density areas, relative to low camas population density areas (Figures 2.9a, b, c.).

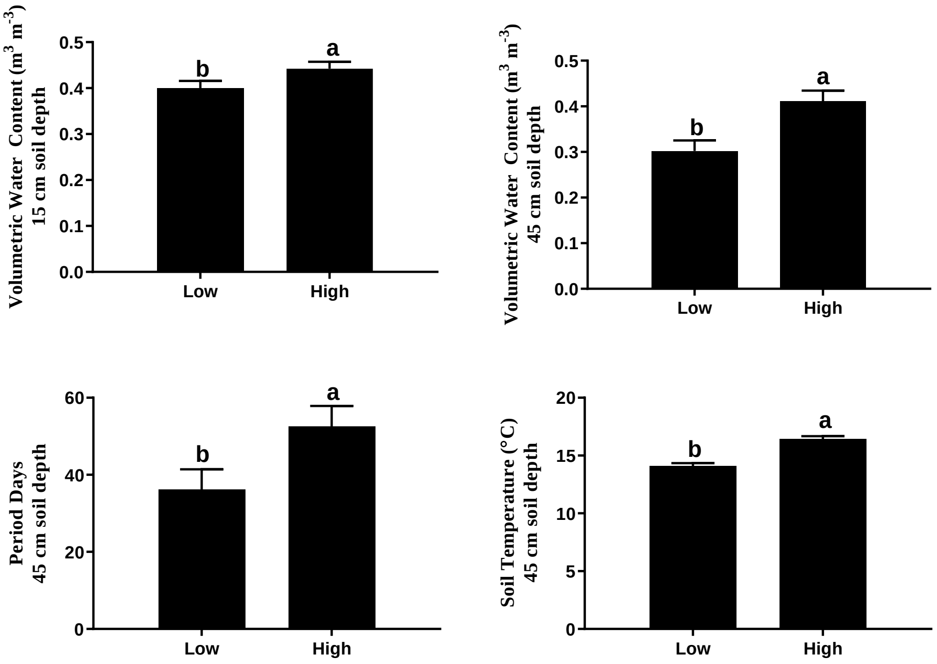

Figure 2.6 Significant differences between mean soil volumetric water content at 15 cm soil depth (a), soil volumetric water content at 45 cm soil depth (b), the duration of the climatic period (c), and soil temperature at 45 cm soil depth between the low and high camas population density areas during the spring dry down (SDD) climatic period. Different letters indicate significant differences at an alpha level of 0.1.

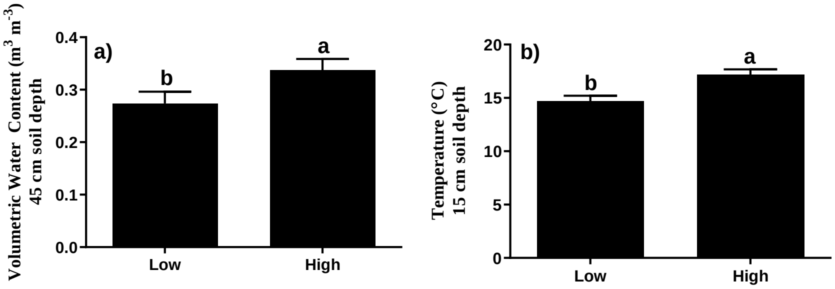

Figure 2.7 Significant differences between mean soil volumetric water content at 45 cm soil depth (a), soil temperature at 15 cm soil depth (b) between the low and high camas population density areas during the summer dry (SDP) climatic period. Different letters indicate significant differences at an alpha level of 0.1.

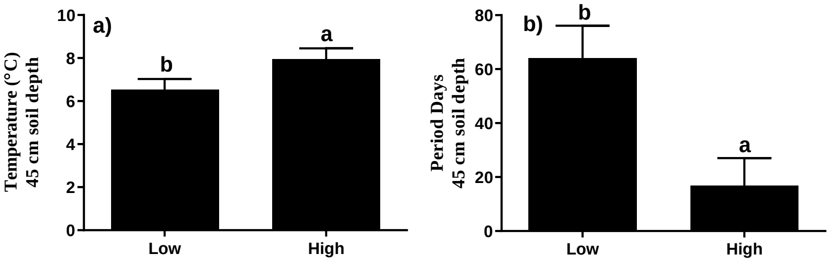

Figure 2.8 Significant differences between mean soil temperature at 45 cm soil depth (a), and the mean duration (number of days) of the climatic period at 45 cm soil depth (b) between the low and high camas population density areas during the fall wet up (FWU) climatic period. Different letters indicate significant differences at an alpha level of 0.1.

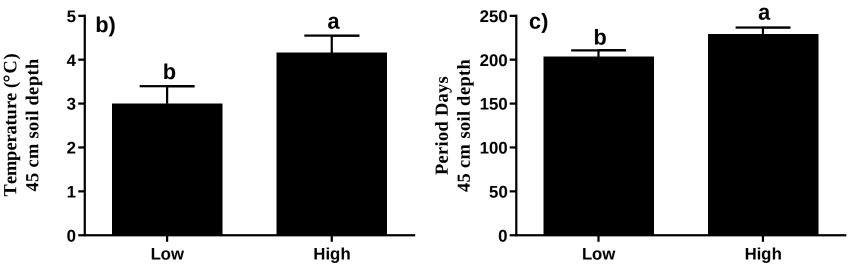

Figure 2.9 Significant differences between mean soil temperature at 45 cm soil depth (a), and the mean duration (number of days) of the climatic period (b) between the low and high camas population density areas during the winter wet (WWP) climatic period. Different letters indicate significant differences at an alpha level of 0.1.

Restoration Treatment Outcomes by Population Density Class

In the low population density areas, all bulb treatments (Treatment 3 p<.001; Treatment 4 p=0.0010; Treatment 5 p=0.0003) and fall seeding (Treatment 1 p=0.0015) were significantly more successful compared to all other treatment methods. While one-year old bulb treatments has the most regeneration, there was no significant difference between one-year bulb, two-year bulb (p=0.3624), planting bulb treatments (p=0.9617), and fall seeding treatments (p=0.3114) (Figure 2.10a).

Multiple years of each treatment were tracked to determine if there was a delayed impact on treatment. Primary treatment effects often showed no significant impact in the first year, but after a period of 2 or 3 years, a significant impact on restoration was seen. High camas population density areas had significant regeneration with disturbance only treatments (Treatment 6 p<.001), bulb outplanting (Treatment 3 p<.001; Treatment 4 p=0.0006) and spring seeding (Treatment 2 p=0.0038). Treatments that had the greatest significance in camas regeneration were the one-year bulb, disturbance efforts, and the two-year bulb treatments, respectively. No significant difference between the disturbance treatment, one-year bulb (p=0.9734) and two-year bulb (p=0.9991) treatments was detected. Fall seeding was the least successful treatment over the monitoring period and was not determined to be significantly different than spring seeding (p=0.9659) (Figure 2.10b).

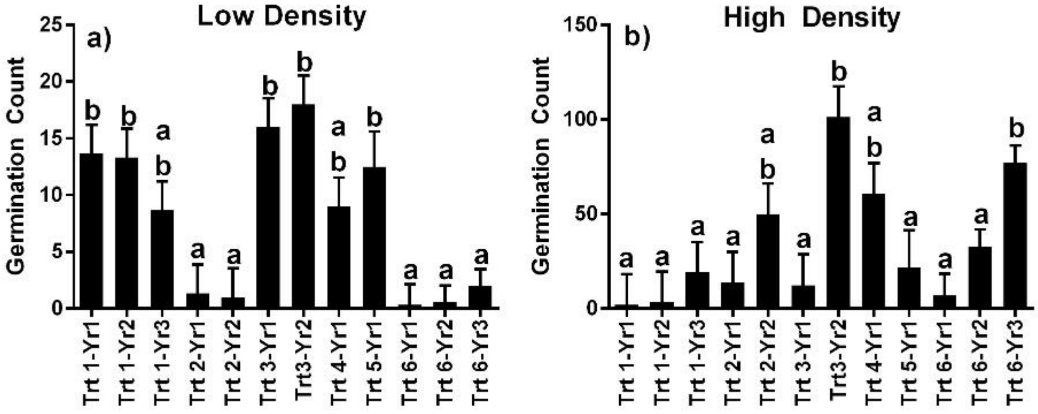

Figure 2.10 Germination count by treatment type in the low camas population density area (a), and high camas population density area (b). Different letters indicate significant treatment differences at an alpha level of 0.1.

No significant difference in germination counts was detected between bulbs outplanted at both the deeper planting (Treatment 4) and shallow planting (Treatment 5) in either the low density areas (p=0.9990) or high- population density areas (p=0.9235) (Figures 2.10.a, b).

Discussion

While we did not detect significant differences in soil physical properties, like soil bulk density, soil pH, texture, or water retention capabilities, we were able to identify differences between sites associated with low- and high-density camas populations. This causes us to reject our first hypothesis that soil properties differ between low- and high-density camas sites. Soils did differ, but due primarily to landscape position and vegetative cover, not inherent soil physical properties as measured. Camas densities are defined by differences in elevation, vegetation structure, organic matter content, soil temperature, and soil moisture. Overall, high-density camas plots were associated with lower elevation, less sod-forming grasses, lower organic matter content, higher soil temperatures, and higher soil moisture. This agrees with Thoms' study who reported the it was a combination of ideal site factors, not just one specific characteristic, that are important to camas' distribution and success (Thoms 1989). Outplanting bulbs and fall seeding treatments had the highest germination success. Furthermore, aerating the soil and removing the sod layer to create ideal site conditions for restoration. This treatment decreases competition with camas germination and increases available habitat space is an important component of camas restoration. These findings address our last three hypotheses, suggesting that fall seeding and outplanting bulbs are more successful in terms of germination and that depth does not make a difference in success. All these identified characteristics can help us to promote camas prairie restoration.

This study supported National Park Service staff observations that areas with high camas population densities were lower in elevation and therefore more susceptible to water accumulation than low camas population density areas. This difference in camas density is likely due to the actual elevation of sites, and with the potential for water accumulation in these areas due to the presence of ditches at certain elevations. Lower elevation areas are less affected by ditches, because at these sites the diches are often eroding and failing across the old agricultural site. The ditches are most likely failing because they are lower in elevation and are therefore wetter for longer. Low camas population density areas are more affected by ditches that remain on the site and are still functional. These functioning ditches can remove enough water to reduce the amount and length of soil wetness in those areas and negatively affect camas populations.

Vegetation structure was highly correlated with the population density area type. Low camas population density areas were dominated by graminoid species, contributing to the litter and sod layers present in these areas. High camas population density areas had less sod forming grasses present to inhibit camas germination (Bosy & Reader 1995). Noticeable differences were observed during plot installation noting that the low camas population density plots had a thick sod layer, while high camas population density areas took little effort to reach bare ground for treatment installation.

In this study, areas with a lower organic matter content were associated with high camas population density areas. This is likely the result of the existing vegetation community characteristics addressed above. Observations during site visits identified graminoid cover in the low camas population density areas consists mostly of non-native grasses. This creates a sod layer and leads to accumulated litter, causing increased organic matter content, which negatively affects camas germination. This study shows that site selection and preparation should include reduction and/or elimination of nonnative sod-forming grasses.

Soil temperature was identified as a significant site characteristic when assessing camas population density areas. The influence of temperature on geophytes generally states that temperature is critical to growth and development of bulbs (Khodorova & Boitel-Conti 2013). Most bulbous plants need to go through a “warm-cold-warm” temperature cycle throughout the year for successful growth and reproduction. This study identifies a range of soil temperatures associated with successful camas germination that fit the “warm-cold-warm” temperature cycle as well as the range across the high and low camas population density areas. This range identifies soil temperatures throughout the year that camas is capable of growing in. Soil temperature averages were higher in high camas density areas by 2°C during SDD, 3°C during SDP, 4°C during FWU and 1°C during WWP. While camas was able to germinate in both low and high camas population density areas, the observed differences in soil temperature suggest warmer temperatures during the warm-cold-warm cycles are more conducive to supporting camas regeneration.

Differences in soil temperatures identified between the two camas population densities are primarily a function of the vegetation community present. High camas population density areas had a less persistent vegetative cover (i.e., sod-forming grasses) and more volumetric water content within the soil, reducing litter presence, and affecting soil insulation. This suggests that management target sod-forming non-native grass species for removal and increase water accumulation where possible to aid in restoring the camas prairie ecosystems.

Soil moisture was also identified as a significant site characteristic relating to camas population density areas and agrees with Gould's findings relating to the importance of soil moisture, especially during the growing season (Gould 1942). High camas population density areas were significantly wetter for almost one month longer than low camas population density areas. This can be attributed to the importance of water during the storage period for geophytes, associated with the WWP identified in this study (Khodorova & Boitel-Conti 2013). These site characteristics are likely critical to the germination period required by camas seeds. This difference between density areas in length of soil saturation duration is likely the result of altered site hydrology. Restoring the naturally occurring hydroperiod would benefit areas that have been altered.

Overall, we found that hydrology and vegetative community are the driving forces for camas population differences. Restoring the naturally occurring hydrology to the site would promote native species to establish as well as reduce non-native sod-forming grasses which are less adapted to wetland prairie habitats (Schook et al. 2019). Reduction in non-native sod-forming grasses would reduce competition, prevent those species from inhibiting camas germination, and would therefore encourage camas densities to increase in such areas. Areas where camas is present and consists of a reproductive population, provide approximately 7.5 months of wet soil within 45 cm of the soil surface, warmer soil temperatures, and limited competition with non-native plants will likely have site characteristics to support a functioning camas prairie habitat.

Comparisons between treatments were difficult due to the large number of highly viable seed a single camas plant can produce. Plots in the high camas population density areas were surrounded by dense stands of reproductive camas, making contamination of treatment plots by native population propagules probable. This study shows the value of having a robust seed source available within the project area. Areas can be minimally altered to promote camas density where camas is an existing component of the vegetative community, as these areas likely possess many of the ideal characteristics to support a camas population. Work presented here identifies that encouraging soil disturbance by creating bare ground through sod removal and through soil aeration in areas with a native seed bank present, can aid camas establishment by creating more available habitat for seedlings and removing competitors. This disturbance treatment provides a significant positive biological impact, with a relatively low amount of input.

Areas with low or no native camas populations would benefit from outplanting bulbs regardless of bulb size and/or a fall seeding application in addition to a disturbance treatment. There was no significant difference between the germination success of all bulb treatments and fall seeding treatments. This implies that reducing competition and aerating the soil are crucial components to creating site conditions necessary for camas germination, which is supported by the work presented by Thoms in 1989. Once these site conditions are met, both propagule types (seeds and bulbs) are good treatments to use for restoration projects. Fall seeding treatments require less resources compared to the methods needed to produce bulbs and is therefore preferred over outplanting in projects where project resources are limited and/or time to reach maturity is less of a concern. Once these site conditions are met, germination from either bulb or fall seed treatments will have high germination success. Disturbance alone will not be effective unless a propagule source is added to the soil. Spring seeding was not significant and therefore not a viable restoration strategy.

Planting recommendations for bulbs suggest depths of 1-15 cm, depending on the size and maturity of the bulb (Stevens et al. 2001). A study looking at outplanting with camas bulbs in British Columbia noted that the actions associated with harvesting could benefit the smaller bulbs by “redistributing” them to their preferred depth sooner, which could result in faster bulb development (Beckwith 2004). This presented an opportunity to test an idea grounded in traditional ecological knowledge: the more camas is harvested, the more it grows (Anderson 1997). Harvesting methods would traditionally redistribute camas propagules throughout the soil profile by disturbing soil and through intentional bulb selection which led to transplanting unwanted bulbs (Beckwith 2004). Through this study, we saw no evidence to support that the germination was affected by bulb depth in the first year. From this we can conclude that bulbs require little effort for outplanting methods, however, planting bulbs deeper can simulate selective harvesting methods and provide plants the opportunity to reach maturity faster. Continuing to track germination counts and monitoring maturation timing between the flower development in each camas population density area would benefit the restoration protocol by identifying any delayed treatment results past three years as well as inform reproductive timetables in a natural setting between treatment types, specifically fall seeding and outplanting bulbs at different depths.

Conclusions

Camas is an ideal plant to use for restoration because it is extremely successful at native recruitment and it is useful as an ecosystem indicator for a functioning camas prairie system. Camas relies on habitat conditions that provide soils that contain more soil moisture and are saturated at or near the soil surface for longer periods of time, with limited competition from non-native sod-forming grasses. If camas propagules are present or added to the site, the probability for germination is high, provided the right site conditions are present.

Creating proper site conditions requires aerating the soil and creating bare spots for seedling establishment, encouraging adequate hydrology that create wet soils for 7.5 months of the year at or near the soil surface, and provide warmer soil temperatures and reducing competition from non-native plants. If a native population is no longer present at the site, it is important to focus on establishing a flowering and reproductive population of camas. Investing in creating islands of reproductive camas that can be encouraged to naturally expand across a project area and will benefit camas populations. This study showed that by creating bare ground near flowering camas individuals, self-seeding can increase the number of camas germinating in an area. Creating corridors of bare ground between islands to connect camas prairie habitat can connect fragmented habitats providing refugia for flora and fauna associated with camas prairies.

The disturbance created by aerating the soil, breaking up the sod layer, removing accumulated litter, and creating bare ground allowed this study to test restoration methods that have similar effects to known traditional horticultural techniques. Traditional ecological knowledge (TEK) provides background information about the history of an ecosystem and how it was managed in ways that can be incorporated in future management plans. Management plans should look to TEK to incorporate information learned over time, such as increased camas production and its association with selective harvesting. Further investigations into the role of fire and weeding provide additional tools that can provide insight into additional management techniques, such as prescribed burns, mowing, and invasive species treatments needed to restore and maintain productive camas prairie habitat. When combined with TEK and additional research into historic site conditions, management plans can be developed to guide site specific restoration for other similar locations.

In this work, we have successfully identified characteristics that define low- and high-population density camas sites, as well as significantly more successful restoration techniques for camas populations. We suggest that future work continue to track camas plant success. Germination information can continue to be gathered over time to determine if any treatments are more significant after these initial two/three years. Further studies could also assist in determining time frames needed to incorporate different management techniques and the appropriate times for application. Continued monitoring for reduced camas germination and/or densities will allow us to identify the timeframe that we can detect long term trends in camas populations and employ whatever management techniques are available in response to long-term trends (i.e. fire, litter/sod reduction, herbicide applications, mowing, etc.). This will allow for adaptive management processes into a restoration protocol that can be applied for long-term management of camas prairies similar to the Weippe Prairie, across the Northwest, USA.

Management Implications

1. Identify if there is camas present in the restoration area. If so, site conditions are likely to provide appropriate hydrology necessary for camas germination. If no camas is present, the appropriate site conditions need to be created for successful germination. Ideal conditions would provide 7.5 months of high volumetric water content near or at the soil surface. This would likely be done through filling ditches and altering hydrology.
2. If a camas population exists on the site, aerate the soil and create bare ground. Methods for establishing bare ground include, removing sod and litter layers, reducing invasive species presence though herbicide or manual techniques, prescribed fire, and/or mowing. If a population does not exist on the site, in addition to aerating and creating bare ground, camas propagules will need to be included in restoration methods. Outplanting bulbs and/or a fall seeding application are the best methods for camas regeneration. If time and resources are limited, investing in bulbs to reach maturity faster may be appropriate. More long-term projects can focus on fall seeding to reduce costs associated with bulb production.

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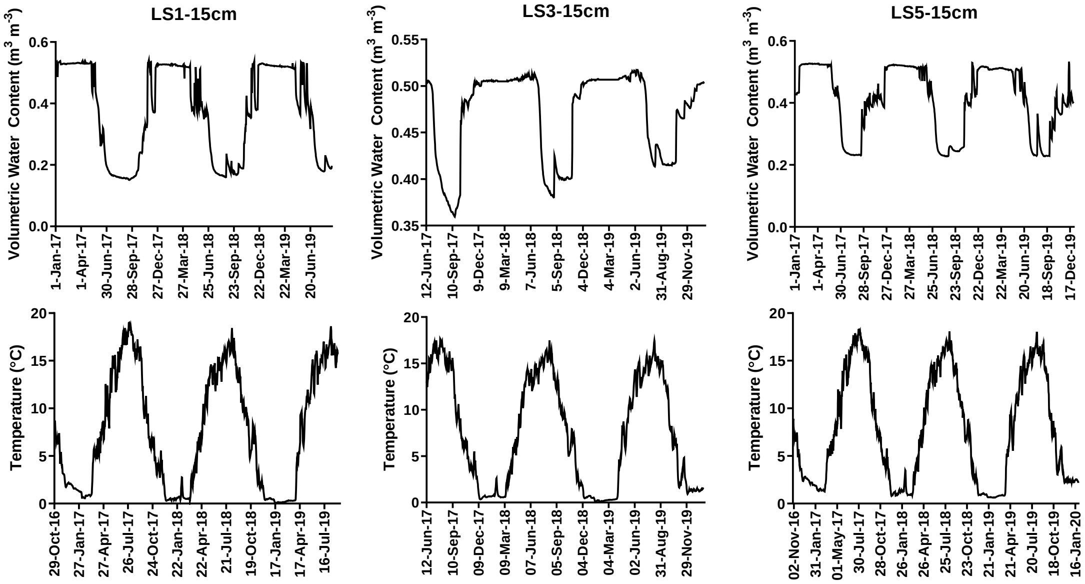
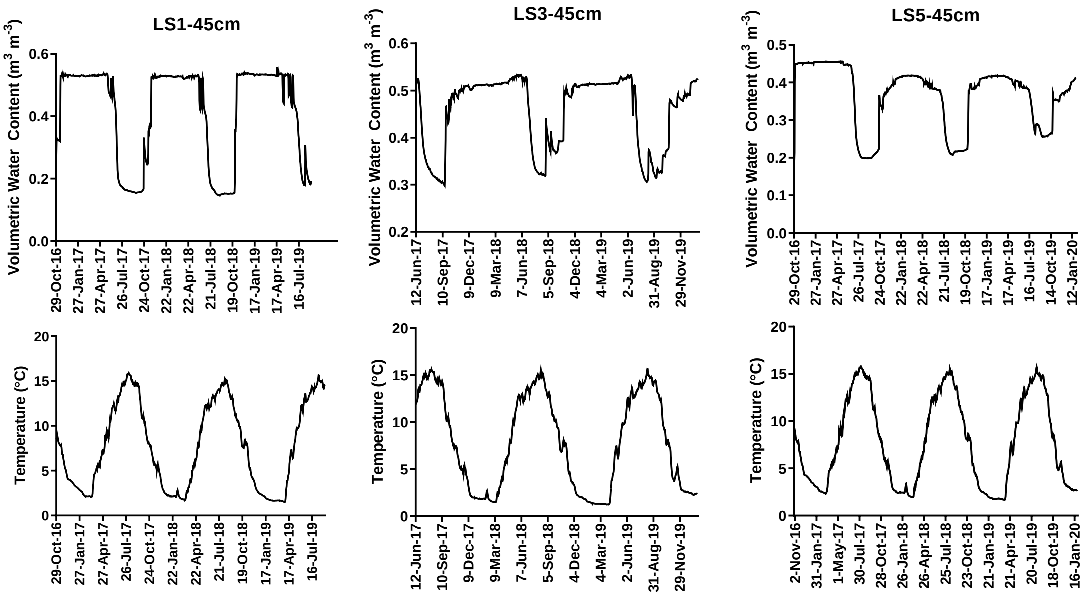
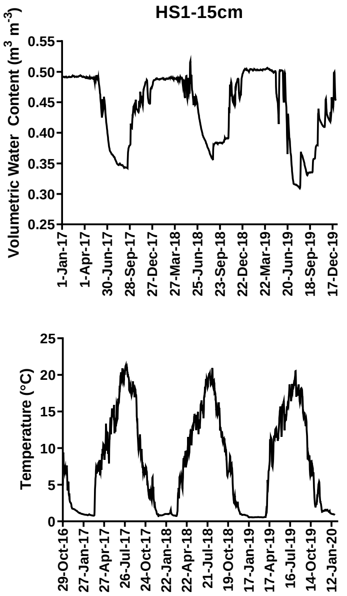
Appendix A: Soil Moisture and Temperature Sensor Data






HS1-15cm
Volumetric Water Content (m^3 m^{-3})
0.55
0.50
0.45
0.40
0.35
0.30
0.25
1-Jan-17
1-Apr-17
30-Jun-17
28-Sep-17
27-Dec-17
27-Mar-18
25-Jun-18
23-Sep-18
22-Dec-18
22-Mar-19
20-Jun-19
18-Sep-19
17-Dec-19
Temperature (°C)
25
20
15
10
5
0
29-Oct-16
27-Jan-17
27-Apr-17
26-Jul-17
24-Oct-17
22-Jan-18
22-Apr-18
21-Jul-18
19-Oct-18
17-Jan-19
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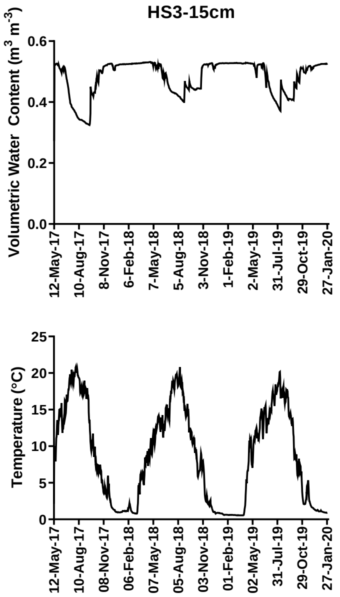
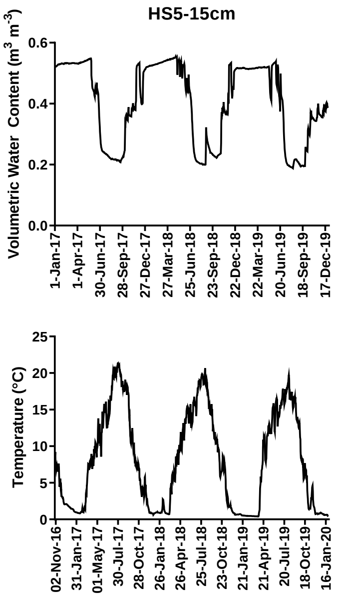
16-Jul-19
14-Oct-19
12-Jan-20


HS3-15cm
Volumetric Water Content (m^3 m^{-3})
0.6
0.4
0.2
0.0
12-May-17
10-Aug-17
8-Nov-17
6-Feb-18
7-May-18
5-Aug-18
3-Nov-18
1-Feb-19
2-May-19
31-Jul-19
29-Oct-19
27-Jan-20
Temperature (°C)
25
20
15
10
5
0
12-May-17
10-Aug-17
08-Nov-17
06-Feb-18
07-May-18
05-Aug-18
03-Nov-18
01-Feb-19
02-May-19
31-Jul-19
29-Oct-19
27-Jan-20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Volumetric Water Content (m^3 m^{-3})
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0.4
0.2
0.0
1-Jan-17
1-Apr-17
30-Jun-17
28-Sep-17
27-Dec-17
27-Mar-18
25-Jun-18
23-Sep-18
22-Dec-18
22-Mar-19
20-Jun-19
18-Sep-19
17-Dec-19
Temperature (°C)
25
20
15
10
5
0
02-Nov-16
31-Jan-17
01-May-17
30-Jul-17
28-Oct-17
26-Jan-18
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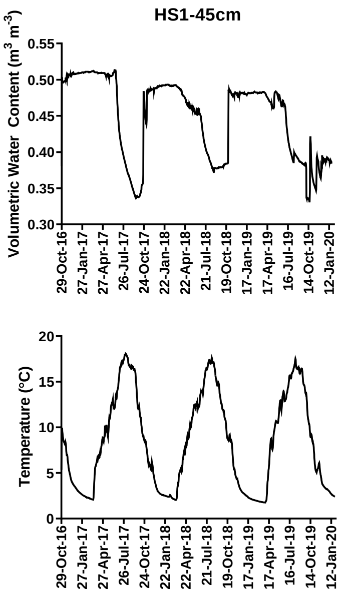
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0.50
0.45
0.40
0.35
0.30
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27-Jan-17
27-Apr-17
26-Jul-17
24-Oct-17
22-Jan-18
22-Apr-18
21-Jul-18
19-Oct-18
17-Jan-19
17-Apr-19
16-Jul-19
14-Oct-19
12-Jan-20
Temperature (°C)
20
15
10
5
0
29-Oct-16
27-Jan-17
27-Apr-17
26-Jul-17
24-Oct-17
22-Jan-18
22-Apr-18
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19-Oct-18
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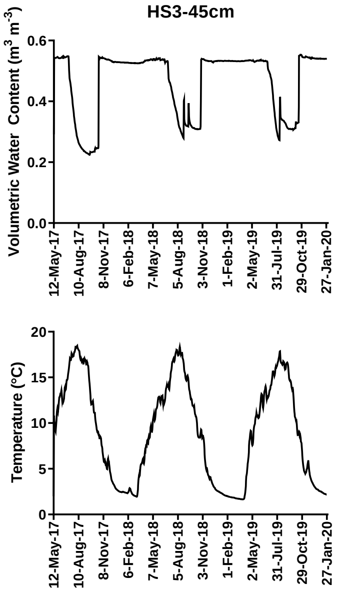
12-Jan-20


HS3-45cm
Volumetric Water Content (m^3 m^{-3})
0.6
0.4
0.2
0.0
12-May-17
10-Aug-17
8-Nov-17
6-Feb-18
7-May-18
5-Aug-18
3-Nov-18
1-Feb-19
2-May-19
31-Jul-19
29-Oct-19
27-Jan-20
Temperature (°C)
20
15
10
5
0
12-May-17
10-Aug-17
8-Nov-17
6-Feb-18
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3-Nov-18
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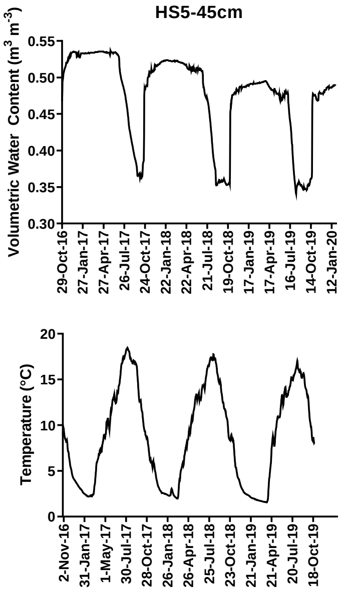
HS5-45cm
Volumetric Water Content (m^3 m^{-3})
0.55
0.50
0.45
0.40
0.35
0.30
29-Oct-16
27-Jan-17
27-Apr-17
26-Jul-17
24-Oct-17
22-Jan-18
22-Apr-18
21-Jul-18
19-Oct-18
17-Jan-19
17-Apr-19
16-Jul-19
14-Oct-19
12-Jan-20
Temperature (°C)
20
15
10
5
0
2-Nov-16
31-Jan-17
1-May-17
30-Jul-17
28-Oct-17
26-Jan-18
26-Apr-18
25-Jul-18
23-Oct-18
21-Jan-19
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