Camas (*Camassia leichtlinii* (Baker) S. Watson, *C. quamash* (Pursh) Greene) functional trait responses to urban pressures in Greater Victoria

by

Erin Rolleman
B.Sc., University of Victoria, 2021

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Supervisory Committee

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Abstract

Coastal oak meadows are fragmented across an increasingly urbanized landscape in Greater Victoria with implications for great and common camas (qʷɬəɬ/KŁO,EL/*Camassia leichtlinii* and *C. quamash*) success. Both camas species are ecologically and culturally important across this region. Research into plant response to urbanization has largely examined how urban pressures shape plant community composition and structure, but how these pressures influence individual plant fitness remains unclear. To improve our understanding, Chapter Two of this thesis examined the response of common camas growth and reproduction to urban pressures in oak meadows across Greater Victoria. An urban-rural gradient was defined across the landscape and environmental conditions and camas growth and reproductive traits were measured. Urbanization was associated with increased trampling and soil compaction, and decreased soil depth, canopy cover, and soil phosphorus and reduced common camas growth and reproduction. Chapter Three examined the capacity of great camas (a slow-growing geophyte) to express phenotypic plasticity in response to three urban pressures (soil compaction, canopy cover, and grazing) within a single growing season in a greenhouse experiment and examined how these pressures affected resource allocation back into the bulbs. Great camas bulbs were divided into a cross-treatment design and growth and storage organ traits were measured. Great camas exhibited a limited capacity to respond to pressures within a single growing season with growth most strongly correlated to pre-season bulb mass. Bulb resources were not affected by urban pressures, but nearly all bulbs lost mass over the season. The shortened growing season and abnormally warm temperatures during the spring growth phase were highlighted as important drivers impacting great camas growth, reproduction, and development. These results can inform local and regional planning to support more successful urban camas populations into the future.

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Acknowledgements

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To conclude, I would like to thank my friends and family who have been firmly rooted in my court since day one. I am deeply grateful for your love and encouragement. To my parents, my first teachers, thank you for spending so much time with my sisters and me outdoors, and for supporting my curiosity in the natural world. A special thank you to my husband, Adam, for providing unfaltering support and being steadfast through the changing seasons – I would not be where I am today without you by my side.

Chapter 1: General introduction

1.1 The ecological effects of urbanization and examining plant response

Urban expansion and densification are processes that are increasing around the world. The United Nations predicts that by the year 2050, 68% of the global population will reside in cities (2019). The widespread conversion of natural areas into highly developed regions to support growing and migrating human populations has impacts on ecosystems within, surrounding, and at times great distances from urban areas (Grimm, Faeth, et al., 2008). The altered environmental conditions associated with urban land use are extensive and can include the loss and/or degradation of natural areas, altered local hydrology (due to vast expanses of impermeable surfaces), modified nutrient cycling, increased introductions of invasive species, air and water pollution, among others (Grimm, Faeth, et al., 2008; Kowarik, 2011; Parris, 2016; Pickett et al., 2001). The modified environmental conditions associated with urbanization are often complex and interact across multiple spatial and temporal scales (Grimm, Foster, et al., 2008). Urban plant communities are understood to be affected by these changes in their environment directly through modified site conditions (e.g., increased soil temperature) and indirectly through altered habitat availability and spatial configuration (Albrecht & Haider, 2013; Vallet et al., 2010). Combined, these effects can benefit some plant species in urban spaces while locally extirpating others (Albrecht & Haider, 2013).

Most urban green spaces, whether remnant ecosystems or human-designed, represent novel ecosystems, where altered habitat conditions, disturbance regimes, and non-native species introductions interact to produce new species assemblages with no historical reference (Lepczyk et al., 2017; Ossola et al., 2017).There is a common belief that these novel ecosystems, existing within the concrete jungle of cities, are dominated by non-native species (Lepczyk et al., 2017). However, in truth, urban areas can support a large diversity of species (both native and non-native), including endemic native species and others of conservation concern (Aronson et al., 2014; Lepczyk et al., 2017; Ossola et al., 2017). Existing research has firmly established how urban plant community composition and structure is shaped by urban land use (Albrecht & Haider, 2013; Knapp et al., 2009; Williams et al., 2015), whereby altered environmental conditions and disturbance regimes associated with urban land use act as filters, selecting plant species with particular attributes or functional traits (Kalusová et al., 2017; Knapp et al., 2009; Palma et al., 2017; Vallet et al., 2010; Williams et al., 2015). For example, researchers have found that urban environments (within a largely European context) consistently favour plant species that are taller (Palma et al., 2017; Thompson & McCarthy, 2008; Williams et al., 2015), have greater seed mass (Palma et al., 2017; Williams et al., 2015) and a shorter lifespan (Vallet et al., 2010), and are tolerant of drought, alkaline substrates, and high soil fertility (Kalusová et al., 2017; Thompson & McCarthy, 2008; Vallet et al., 2008; Williams et al., 2015). This understanding of the environment filtering for specific plant traits enables the prediction of species frequency and distribution across an urban-rural gradient (Knapp et al., 2009; Vallet et al., 2010). What remains unclear is how individual plants of a single species vary in their response to these changes in their environment, with implications for plant success and persistence in urban areas. Only a handful of studies globally have examined how individuals within a species vary in their response to the complex, often interacting environmental pressures associated with urbanization (Borowy & Swan, 2020; Cochard et al., 2019; Pisman et al., 2020; Zhu & Xu, 2021). The results of these studies indicate that urban conditions impose strong filtering effects on individual plants within a species. For example, Zhu and Xu (2021) found that certain leaf traits of *Euonymus japonicus* increase or decrease in response to greater urban atmospheric particulate matter in China. Pisman et al. (2020) observed that urban populations of *Taraxacum officinale* in Belgium exhibited reduced early seed production following herbivory compared to rural populations. Investigating plant functional trait responses to urban pressures on individuals within a species can enable us to better understand how these species may fare in the face of increasing urbanization into the future.

Plant functional traits are a useful framework for examining the attributes of plants and the patterns of their response to different environmental pressures (Kattge et al., 2020; Pérez-Harguindeguy et al., 2013; Williams et al., 2005). Plant traits are the morphological, physiological, and phenological characteristics of plants that impact growth, reproduction, and survival (Violle et al., 2007). Plant traits influence the success of individuals and determine how plants respond to environmental variables and affect ecosystem processes (Kattge et al., 2020). Plant traits vary more among species (interspecific trait variation) than within species (intraspecific trait variation); however, intraspecific variation is not negligible and has the capacity to contribute to a significant proportion of trait variation in plant communities (Siefert et al., 2015; Westerband et al., 2021). Understanding how trait values vary between individuals across an urban-rural gradient can provide information on individual reproductive and fitness response (and potential adaptability) to urbanization (Pisman et al., 2020; Weston et al., 2021).

This thesis aims to contribute to improving our understanding of individual plant response to urban environmental conditions by examining the functional trait responses of common camas

(*Camassia quamash*) and great camas (*Camassia leichtlinii*) to urbanization in Greater Victoria, BC. The two *Camassia* spp. are of immense ecological and cultural importance to local Indigenous peoples (Beckwith, 2004; Garibaldi & Turner, 2004) and are commonly found in coastal oak meadows in BC, an ecosystem that is fragmented across an increasingly urbanized landscape (GOERT, 2011). Examining the response of these two species to urban pressures provides an opportunity to better understand how the survival and success of these valued species may be impacted by urbanization, and how they may respond to increasing urbanization into the future.

1.2 Thesis objectives

This thesis seeks to explore how camas may be responding to urbanization in Greater Victoria and whether there are patterns in the response that enable predictions of how camas may respond to increasing urbanization into the future. Chapter Two examines how common camas growth and reproductive traits are impacted by increasing urbanization in oak meadows across Greater Victoria through a field-based study. There were two questions guiding this work: (1) *is urbanization associated with key modified environmental conditions in oak meadows in Greater Victoria?* and (2) *how are common camas individuals responding to these altered conditions?* An urban-rural gradient was defined across the landscape and environmental conditions and camas growth and reproductive traits were measured in oak meadows across this gradient. Chapter Three investigates the trait plasticity of great camas to three key pressures present in urban oak meadows in Greater Victoria (grazing, canopy cover, and soil compaction) in a greenhouse experiment. Great camas bulbs were divided into a cross-treatment design and their growth and storage organ traits were measured after one season of growth.

This thesis provides novel insight into how urbanization may be altering site conditions in oak meadows across Greater Victoria, how camas may be responding to these altered conditions, and the degree of trait plasticity camas can exhibit in response to three key pressures. Results will contribute to local and regional planning to target key urban pressures and support more successful urban camas populations into the future. More broadly, this research will contribute to global efforts that aim to better understand how plant species may respond to urbanization, a pressure that is largely increasing in vulnerable ecosystems worldwide.

1.3 Coastal oak meadows in BC

Coastal oak meadows are unique ecosystems comprised of distinct flora, sometimes referred to as Garry oak prairies or oak savannahs (Figure 1). These meadows burst into a colourful array of purples, pinks and yellows each spring, and are home to an incredible diversity of species with over 100 provincially listed species at risk found in these ecosystems (GOERT, 2011). Oak meadows range from California to British Columbia, with southeastern Vancouver Island and the Gulf Islands representing the northern most extent. Sheltered between the Vancouver Island and Olympic mountain ranges, this region in BC is characterized by a Mediterranean climate with mild, wet winters and warm, dry summers (Barlow et al., 2021; GOERT, 2011). Coastal oak meadow plant species thrive under these conditions of plentiful spring rain followed by seasonal summer drought (Beckwith, 2004; MacDougall et al., 2004).

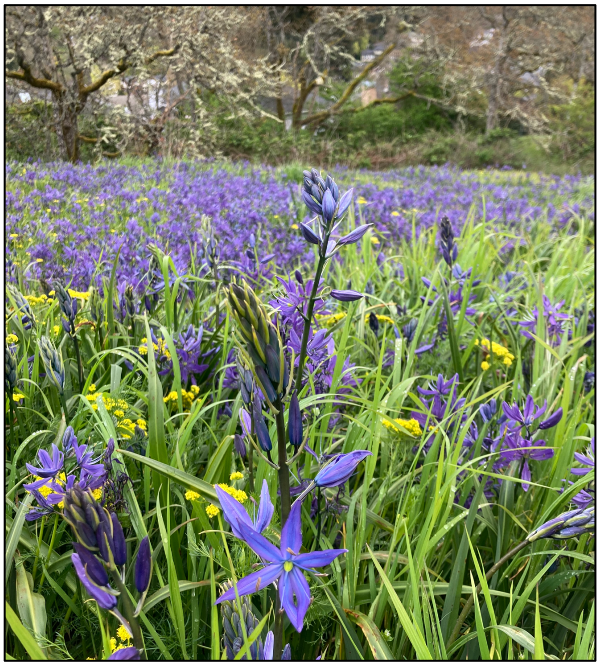


Figure 1. A coastal oak meadow in Greater Victoria, BC featuring a great camas (*Camassia leichtlinii*) individual in the foreground.

Prior to European colonization, coastal oak meadows covered large swathes of land across southeastern Vancouver Island and the Gulf Islands (MacDougall et al., 2004). Indigenous stewardship practices centered around cultivating food, medicine, and other culturally important species led to coastal oak meadows thriving across this region. With the arrival of settlers and the dispossession of Indigenous peoples from their lands, oak meadows were converted into agricultural and residential areas (MacDougall et al., 2004). The meadows were targeted for settlement and agriculture because in the eyes of the European settlers they appeared as open, cleared tracts of park-like land absent of human occupation or cultivation (Deur, 2002; MacDougall, 2008). In stark contrast to this assumption, however, was the reality that these meadows had been actively stewarded by local First Nations for millennia to sustain a highly productive food system (Beckwith, 2004; Turner & Kuhnlein, 1983). Fire stewardship, soil building, weeding, tilling, and rock removal, among other practices over centuries, sustained the presence of these vast meadows and prevented the encroachment of what would otherwise be late succession Douglas-fir forests (Turner, 1999; Turner & Kuhnlein, 1983). As a result of the loss of First Nations stewardship, as well as further habitat degradation from human disturbance (including extensive urban development), habitat fragmentation, exotic species invasions, and overgrazing, coastal oak meadows today are among the most endangered ecosystems in Canada (Clements, 2013; Dunwiddie & Bakker, 2011; GOERT, 2011). The distribution of coastal oak meadows, particularly on southern Vancouver Island, is limited to small, fragmented patches across an increasingly urbanized landscape (GOERT, 2011).

1.4 *Camassia* spp. (camas) ecology and cultural significance

Common camas (*Camassia quamash* (Pursh) Greene) and great camas (*Camassia leichtlinii* (Baker) S. Watson) are the two most prevalent species in the North American genus *Camassia* in BC (POWO, 2023). Colloquially referred to as ‘camas’ (qʷłəł in lək̓ʷəŋiʔnəŋ́ and KŁO,EL in SENCOŦEN), these two species turn coastal oak meadows across Coast Salish territories into an undulating sea of purple and blue flowers every spring. Attracting an array of pollinators, these meadows become abuzz with insects seeking out camas nectar (Rammell et al., 2019). In the Asparagaceae family, camas are bulbous geophytes, perennial plants with an underground storage structure (Hitchcock & Cronquist, 2018). They are slow growing species that take many years to reach maturity and flower (Carney et al., 2021; Proctor, 2013). As the bulbs grow, they move deeper into the soil and once the bulb reaches a certain size and soil depth, the plant will flower (Beckwith, 2004). Both species exhibit a range in mature bulb size that is influenced by location and site conditions. Camas reproduce both from seed and asexually through bulb division (Beckwith, 2004; Carney et al., 2021). Each flower that matures into a capsule produces several shiny black seeds (15-36 seeds on average per capsule) (Hitchcock & Cronquist, 2018; Thoms, 1989).

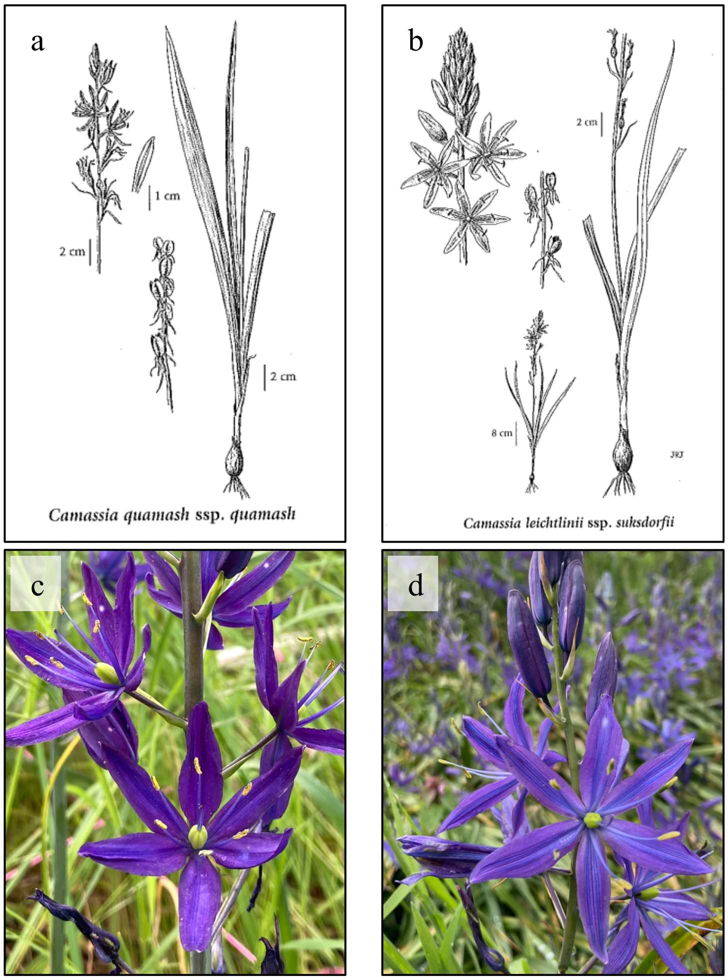


Figure 2. (a) and (b) botanical illustrations of common and great camas bulb, leaf, flower, and seed capsule morphology (Hitchcock et al., 1969), (c) common camas (*Camassia quamash*), and (d) great camas (*Camassia leichtlinii*).

The two camas species are visually similar but can be differentiated based on flower morphology (Figure 2). Great camas has six tepals that spread radially around the ovary; common camas has five of the six tepals curving upward with the sixth pointing downward (Beckwith, 2004). As the tepals begin to wither on great camas plants, they twist around the ovary, whereas on common camas plants, the tepals wither outward from the ovary. On Coast Salish territories, common camas tends to bloom shortly before great camas from early April to early May, with great camas blooming late April to late May (Hitchcock & Cronquist, 2018). Despite both species being present in coastal oak meadows across BC, great camas is less common in oak meadows across other regions and is restricted to the west side of the Cascade Mountain range (Figure 3) (Hitchcock & Cronquist, 2018). Common camas extends into the interior and is widely abundant in oak meadows from California to BC. Both species exhibit variability across their ranges, including in their ecological traits, with two subspecies of great camas and six subspecies of common camas present in the Pacific Northwest (Hitchcock & Cronquist, 2018). Common camas, being more abundant in the study area, was selected as the species of focus for the field-based research in Chapter Two. Great camas is of equal importance regionally but is less abundant locally, thus, great camas was assessed in a controlled greenhouse experiment in Chapter Three.

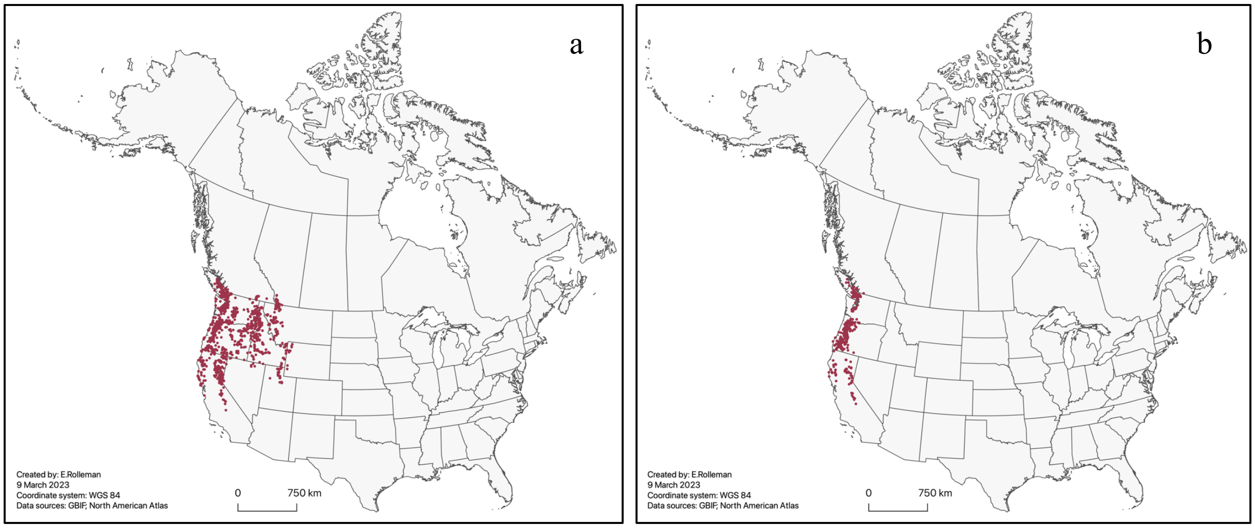


Figure 3. Range of (a) common camas (*Camassia quamash*), and (b) great camas (*Camassia leichtlinii*) (GBIF.org, 2023a, 2023b).

Both species of camas were extensively cultivated across Coast Salish territories prior to European colonization (Garibaldi & Turner, 2004; GOERT, 2011; Proctor, 2013). Camas bulbs were a dietary staple providing a key source of carbohydrate and vegetable protein in an otherwise largely animal-based diet (Gritzner, 1994; Turner & Kuhnlein, 1983). The bulbs are usually prepared by steaming or roasting in earth ovens, where hot temperatures for sustained periods of time convert the complex carbohydrates into easier to digest forms (Carney et al., 2021; Turner & Kuhnlein, 1983). Evidence of camas consumption dates back over 8000 years in the Pacific Northwest (Carney et al., 2021; Kramer, 2000), and trade moved these bulbs extensively around the region (Lutz, 2008). Sophisticated land management practices regulated camas production in family-run plots, and cultivation practices based on extensive knowledge of camas and its habitat enabled tremendous bulb harvests (Beckwith, 2004; Gritzner, 1994; Lyons & Ritchie, 2017; Turner, 1999). Today camas is still cultivated and harvested by local First Nations (Penn, 2006), but a mere fraction of pre-colonization camas habitat exists.

The remaining oak meadows in this region have become important sites of eco-cultural revitalization centered on camas. Local First Nations are engaging in a resurgence of cultural practices within the qʷɬəɬ/KŁO,EL food system to revitalize stewardship practices and regenerate community roles and responsibilities (Corntassel & Bryce, 2012). The same forces that threaten the biodiversity of coastal oak meadows also threaten Indigenous peoples' relationships with their homelands and the health and well-being of their communities (Corntassel & Bryce, 2012). Through land-based learning, youth education, and broader public education (e.g., community pit cooks and invasive species removals), local First Nations are reinstating traditional roles and practicing everyday acts of resurgence within coastal oak meadows.

1.5 Positionality

I am a white settler and second generation Canadian. My maternal grandparents, Anne and Richard Lloyd, immigrated to Canada from England in the 1950's and settled in Powell River on the traditional territory of the Tla'amin First Nation. My paternal grandparents, Trudy and Dick Rolleman, immigrated separately to Canada from Holland in the 1930's and settled in Matsqui, on the traditional territory of the Stó:lō Nation. I grew up on Sinixt, Ktunaxa, and Syilx traditional territories (Nelson, BC) and moved to lək̓ʷəŋən and W̱SÁNEĆ territories in 2016. My relationship to the land, conservation, and ecological restoration are inextricably linked to my identity. My biases have been shaped by this identity and limit how I perceive and act in the world. The academic field of ecology remains largely dominated by white settler scholars, like me, who operate within the sphere of western science. Collaboration with Indigenous partners in ecological research is on the rise, but this approach remains the exception to the norm. I hoped to step outside of this, but I fell short of engaging in a collaborative project with First Nation partners. Restricted by rigid academic timelines that do not align with the slow nature of meaningful relationship-building, I was unable to form a partnership. We went ahead and studied a deeply cultural species outside the sphere of collaboration in the hope we could produce useful information to support thriving camas populations. It is paramount to acknowledge the deep ecological knowledge local Indigenous peoples have of coastal oak meadows, and explicitly state that this perspective is missing from this work. It is my hope that despite this, this work proves beneficial for land stewards, Indigenous and settler, who aim to support healthy camas populations across Coast Salish territories into the future.

Chapter 2: Common camas (*Camassia quamash*) response across an urban-rural gradient in coastal oak meadows in Greater Victoria

2.1 Abstract

Coastal oak meadows are fragmented across an increasingly urbanized landscape in Greater Victoria with implications for common camas (qʷłəł/KȽO,EL/*Camassia quamash*) fitness. Common camas, frequently present in coastal oak meadows, is an ecologically important cultural keystone species that forms the foundation of one of the most important Indigenous food systems in the region. Previous research has examined how the pressures associated with urbanization shape plant community composition and structure, but how these pressures influence individual plant fitness remains unclear. To improve our understanding, we assessed environmental conditions and common camas growth and reproductive traits across an urban-rural gradient in Greater Victoria. We found that urbanization on this landscape alters several key environmental variables (namely increased trampling and soil compaction, and decreased soil depth, canopy cover, and soil phosphorus) and that common camas is responding to these altered conditions with a reduction in growth and reproductive trait values. By targeting the identified pressures, management can work towards supporting more successful urban camas populations into the future.

2.2 Introduction

In 2022, 55% of the global population resided in urban areas and the United Nations (2019) predicts that this percentage will increase to 68% by 2050. In Canada, population growth in urban centers is outpacing nation-wide growth, urban areas are becoming more densely populated, and urban sprawl continues to expand into surrounding rural areas (Statistics Canada, 2022). Urbanization is associated with a range of altered environmental conditions, including the loss and/or degradation of natural areas, altered local hydrology (due to vast expanses of impermeable surfaces), modified nutrient cycling, increased introductions of invasive species, air and water pollution, among others (Grimm, Faeth, et al., 2008; Kowarik, 2011; Parris, 2016; Pickett et al., 2001). Urban land use can have direct effects on plant communities by altering site conditions (e.g., soil temperature) and indirect effects through modifying habitat availability and spatial configuration (Albrecht & Haider, 2013; Vallet et al., 2010). It is well understood that these direct and indirect effects of urbanization shape plant community composition and structure (Albrecht & Haider, 2013; Knapp et al., 2009; Williams et al., 2015).

Altered environmental conditions and disturbance regimes associated with urban land use act as filters that control community composition through the selection of plants with a particular set of attributes or functional traits (Knapp et al., 2009; Palma et al., 2017; Vallet et al., 2010; Williams et al., 2015). Plant functional traits are a useful framework for examining the attributes of plants and the patterns of their response to different environmental pressures (Kattge et al., 2020; Pérez-Harguindeguy et al., 2013; Williams et al., 2005). Urban areas tend to favour the same set of plant traits, often leading to biotic homogenization whereby species and functional diversity decrease (Ruas et al., 2022; K. Thompson & McCarthy, 2008). This understanding of the environment filtering for specific plant traits enables the prediction of species frequency and distribution across an urban-rural gradient, particularly of interest for species not well adapted to urban environments (Knapp et al., 2009; Vallet et al., 2010). However, how individual plants of a single species vary in their response to these changes in their environment remains unclear, with implications for plant success and persistence in urban areas.

Intraspecific trait variation is the trait variation within a species (Violle et al., 2012). It varies less than the trait variation among species (interspecific trait variation), but it is not negligible and has the capacity to contribute to a significant proportion of trait variation in plant communities (Siefert et al., 2015; Westerband et al., 2021). Only a handful of studies globally have examined how individuals within a species vary in their response to the complex, often interacting environmental pressures associated with urbanization (Borowy & Swan, 2020; Cochard et al., 2019; Pisman et al., 2020; Zhu & Xu, 2021). Exploring variation in traits in individual species across an urban-rural gradient will provide insight into the drivers of reproductive and fitness response (and potential adaptability) of these species to urbanization (Pisman et al., 2020; Weston et al., 2021). This is particularly important for ecologically and culturally important species that only exist in largely urban areas.

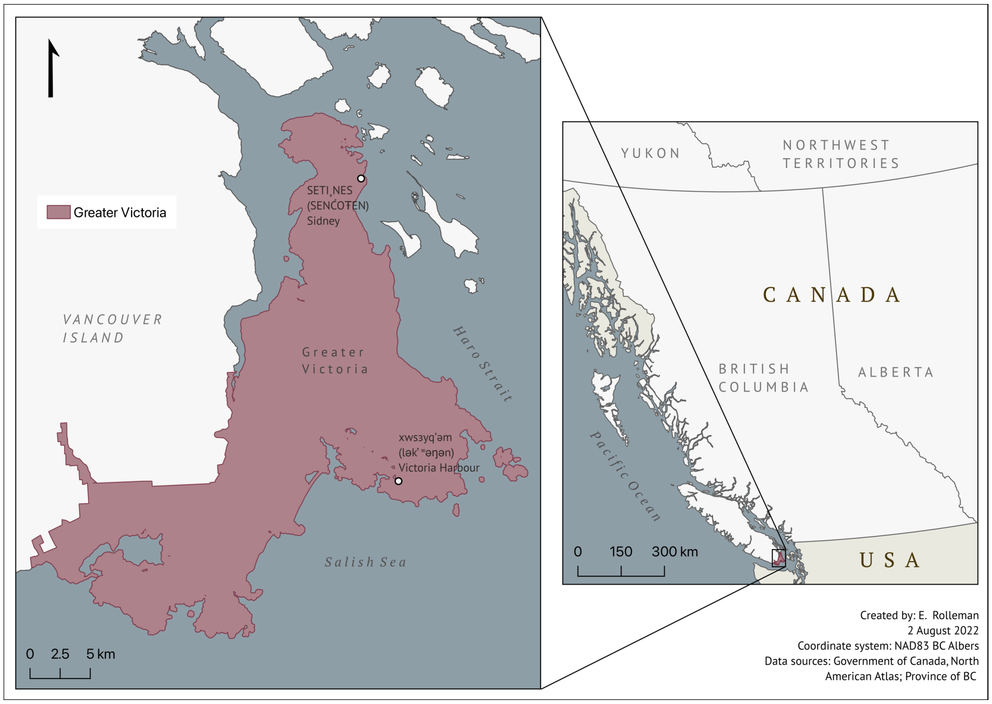
The objective of this study was to address this knowledge gap by investigating how common camas (qʷɬəɬ in lək̓ʷəŋiʔnəŋ́ and KȽO,EL in SENCOŦEN, *Camassia quamash*) is responding to increasing urbanization in Greater Victoria. Common camas is an ecologically important cultural keystone species (Beckwith, 2004; Garibaldi & Turner, 2004; Gritzner, 1994; Proctor, 2013) that exists almost entirely in urban areas across its Canadian range (GOERT, 2011). Present in oak meadows from northern California to southern British Columbia, common camas is a perennial forb species in the Asparagaceae family with an inflorescence of striking blue-purple flowers that bloom into a showy floral display in oak meadows each spring (Hitchcock & Cronquist, 2018). Across Coast Salish territories, camas was, and continues to be, actively stewarded by Coast Salish First Nations and is a significant component of their traditional foods system (Proctor, 2013; Turner & Kuhnlein, 1983). Prior to European colonization and the dispossession of Indigenous peoples from their lands, camas was extensively cultivated across this region (Beckwith, 2004; Garibaldi & Turner, 2004; Proctor, 2013). Today, the distribution of common camas in this region, particularly on southern Vancouver Island, is limited to small, fragmented oak meadows across an increasingly urbanized landscape (GOERT, 2011). Understanding that this region is experiencing some of the greatest urban population growth in the country (Statistics Canada, 2022), it is paramount to understand how this species is responding to the pressures associated with urbanization to support its success and persistence into the future.

To assess how common camas growth and reproduction is impacted by increasing urbanization in the Greater Victoria region, this study was twofold. First, we sought to examine whether urbanization is associated with shifts in the environmental conditions found in remnant oak meadows in Greater Victoria. Second, we sought to investigate how common camas individuals are responding to these altered conditions. An improved understanding of how urbanization affects local site conditions in oak meadows across Greater Victoria, and how common camas individuals may be responding to these altered conditions, will contribute to local and regional planning and initiatives that seek to target specific urban pressures and support more successful urban camas populations into the future. At a broader scale, examining how individual plants respond to environmental change can contribute to global efforts that aim to better understand how plant species may respond to urbanization, a pressure that is largely increasing in vulnerable ecosystems worldwide.

2.3 Methods

2.3.1 Study area

The project area is within the traditional territory of the lək̓ʷəŋən, W̱SÁNEĆ, MÁLEXEȽ, Sc’ianew, and T’Sou-ke peoples. Located on the southern tip of Vancouver Island, off the west coast of British Columbia, Canada (Figure 4), this region experiences a Mediterranean climate characterized by mild, wet winters and warm, dry summers (GOERT, 2011). In the rain shadow of the Olympic and Vancouver Island mountain ranges, this region is the driest part of the Coastal Douglas fir biogeoclimatic zone and supports coastal oak meadow ecosystems (Barlow et al., 2021; GOERT, 2011). Ranging from northern California to southwestern BC, oak meadows in Canada represent the northernmost extent of these ecosystems, with most of their Canadian range limited to southeastern Vancouver Island and the southern Gulf Islands (GOERT, 2011).



Created by: E. Rolleman
2 August 2022
Coordinate system: NAD83 BC Albers
Data sources: Government of Canada, North American Atlas; Province of BC

Figure 4. A map of the Greater Victoria region on Vancouver Island, British Columbia.

Coastal oak meadows are unique ecosystems with distinct flora, often containing Garry oak (*Quercus garryana*) trees, and are frequently associated with Garry oak woodlands, grasslands, vernal wetlands, coastal bluffs, and rocky outcrops (Fairbarns, n.d.; GOERT, 2011). These ecosystems are among the most endangered ecosystems in Canada, largely due to habitat degradation from human disturbance, habitat fragmentation, exotic species invasions, overgrazing, fire suppression, and the loss of First Nations stewardship (Clements, 2013; Dunwiddie & Bakker, 2011; GOERT, 2011). Indigenous stewardship of these ecosystems to cultivate food, medicine, and other culturally important species led to these ecosystems thriving across much of the Greater Victoria region pre-European colonization (MacDougall et al., 2004). With colonization and the dispossession of Indigenous peoples from their traditional territories, these systems of stewardship were disrupted, and large swaths of oak meadows were converted to agriculture or residential areas. The meadows were targeted for settlement and agriculture because in the eyes of the European settlers they appeared as open, cleared tracts of park-like land absent of human occupation or cultivation (Deur, 2002; MacDougall, 2008). In stark contrast to this assumption, however, was the reality that these meadows had been actively stewarded by local First Nations for millennia to sustain a highly productive food system (Beckwith, 2004; Turner & Kuhnlein, 1983). Fire stewardship, soil building, weeding, tilling, and rock removal, among other practices over centuries, sustained the presence of these vast meadows and prevented the encroachment of what would otherwise be late succession Douglas-fir forests (Turner, 1999; Turner & Kuhnlein, 1983). Ongoing habitat loss and degradation has led to the remaining patches of oak meadows being fragmented across an increasingly urbanized landscape, with implications for species migration, dispersal, and persistence (Evju et al., 2015; GOERT, 2011).

2.3.2 Ecology and history of camas

Common camas (*Camassia quamash* (Pursh) Greene) is one of the six species in the North American genus *Camassia* (POWO, 2023) (Figure 5). Common camas is the most widespread of the five species across the Pacific Northwest and can be found from northern California to southern British Columbia. Common camas is a bulbous geophyte, a perennial plant with an underground storage structure (Hitchcock & Cronquist, 2018). In early spring, long basal leaves emerge from the underground bulbs. A few weeks later, a terminal raceme blooms with pale to deep blue-purple flowers, putting on a showy display across oak meadows from early April to early May, and attracting a diversity of pollinator insects (Hitchcock & Cronquist, 2018; Rammell et al., 2019). Each flower that matures into a capsule produces several shiny black seeds (Hitchcock & Cronquist, 2018). From seed, common camas have a lengthy maturation period that can take 5 or more years for the seeds to grow into mature, flowering plants (Carney et al., 2021; Proctor, 2013). Common camas reproduce both from seed and asexually through bulb division (Beckwith, 2004; Carney et al., 2021). The resources stored in their bulbs can also enable camas plants to remain dormant during the growing season in response to harsh environmental pressures such as drought or resource limitations (Beckwith, 2004).

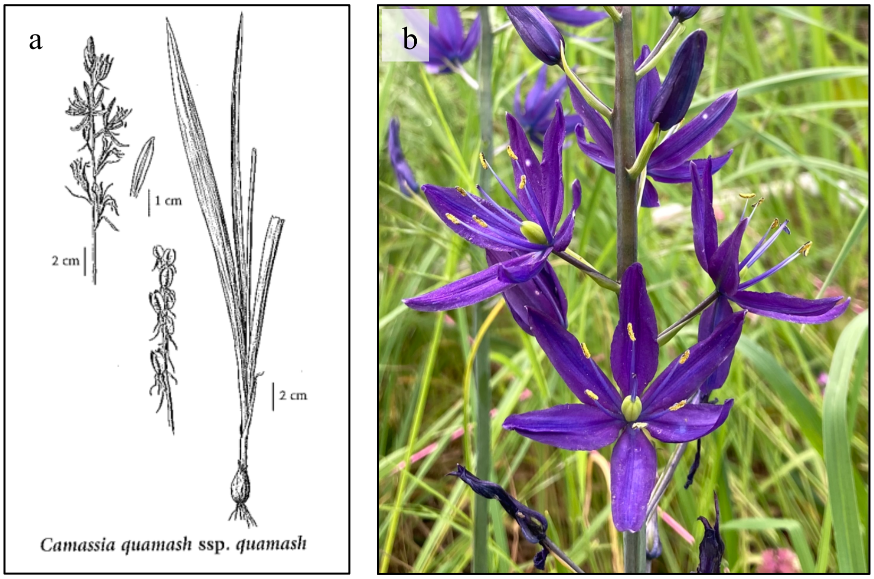


Figure 5. (a) Botanical illustration of common camas bulb, leaf, flower, and seed capsule morphology (Hitchcock et al., 1969) and (b) common camas *(Camassia quamash).*

Common camas and great camas (*Camassia leichtlini*) (another species of camas frequently present in coastal oak meadows) were extensively cultivated across Coast Salish territories prior to European colonization (Garibaldi & Turner, 2004; GOERT, 2011; Proctor, 2013). Camas bulbs were a dietary staple providing a key source of carbohydrate and vegetable protein in an otherwise largely animal-based diet (Gritzner, 1994; Turner & Kuhnlein, 1983). The bulbs are usually prepared by steaming or roasting in earth ovens, where hot temperatures for sustained periods of time convert the complex carbohydrates into easier to digest forms (Carney et al., 2021; Turner & Kuhnlein, 1983). Evidence of camas consumption dates back over 8000 years in the Pacific Northwest (Carney et al., 2021; Kramer, 2000), and trade moved these bulbs extensively around the region (Lutz, 2008). Sophisticated land management practices regulated camas production in family-run plots, and cultivation practices based on extensive knowledge of camas and its habitat enabled tremendous bulb harvests (Beckwith, 2004; Gritzner, 1994; Lyons

& Ritchie, 2017; Turner, 1999). Today camas is still cultivated and harvested by local First Nations (Penn, 2006), but a mere fraction of pre-colonization camas habitat exists.

The remaining oak meadows in this region have become important sites of eco-cultural revitalization centered on camas. Local First Nations are engaging in a resurgence of cultural practices within the qʷłəł/KŁO,EL food system to revitalize stewardship practices and regenerate community roles and responsibilities (Corntassel & Bryce, 2012). The same forces that threaten the biodiversity of coastal oak meadows also threaten Indigenous peoples’ relationships with their homelands and the health and well-being of their communities (Corntassel & Bryce, 2012). Through land-based learning, youth education, and broader public education (e.g., community pit cooks and invasive species removals), local First Nations are reinstating traditional roles and practicing everyday acts of resurgence within coastal oak meadows.

2.3.3 Sample site selection

We characterized the urban-rural gradient across Greater Victoria using a 1m^2 land cover classification raster layer obtained from Habitat Acquisition Trust (prepared by Caslys Consulting Ltd., 2013) for the study area based on aerial imagery from 2011. Using a preliminary dataset previously developed which combines the best-known oak meadow distributions in the region (Appendix A), 100m buffers were drawn around each oak meadow patch and used to calculate the number of 1m^2 pixels of each land cover type surrounding each oak meadow (Figure 6). The number of urban land cover pixels (defined as all impervious surfaces including buildings and roads) per 100m buffer was converted to a percentage to generate a gradient across the landscape. All oak meadow patches surrounded by > 60% urban land cover were less than 13km^2 in size, so all meadow patches larger than

$13km^2$ were removed from the analysis to control for habitat patch size. The number of study sites was further reduced to twelve sites by restricting the scope to four municipalities (the Capital Regional District, City of Langford, City of Victoria, and District of Saanich). The twelve study sites were reviewed by archaeologist Dr. Darcy Mathews to ensure the study sites did not conflict with any recorded archeological sites. See Figure 6 for a map of the twelve sites where field data were collected.

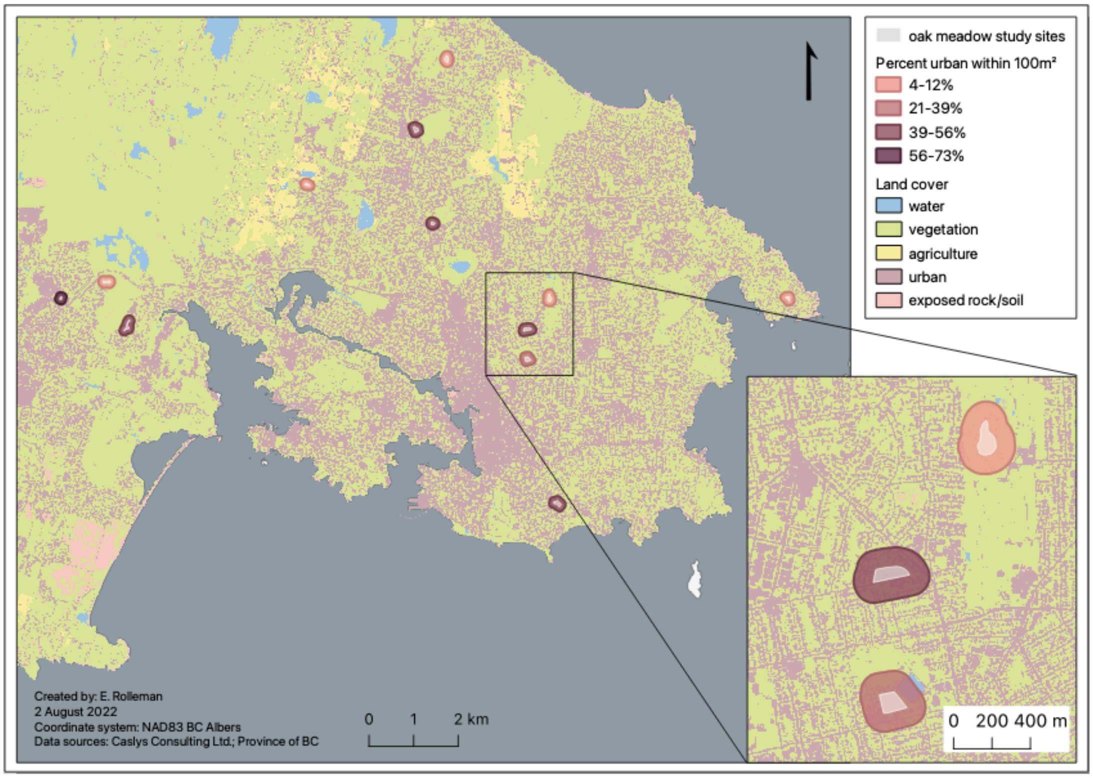


Figure 6. A map of the twelve oak meadow study sites ranging from 4-73% urban land cover in the surrounding $100m^2$.

Within the twelve study sites, a stratified-random sampling design was implemented to select four $1m^2$ data collection plots. Data collection was limited to four plots at each site due to the seasonal constraints of a short blooming window for common camas. Each study site was divided into four equal area quadrants and ten points were randomly located within each and labelled 1-10. In the field, data were collected at one point location per quadrant, starting at the point labelled 1. If there were not five common camas individuals in bloom at point 1, data were collected at point 2, and so on. If five common camas individuals were not present at any of the ten point locations in a quadrant, a location within the quadrant was visually selected. If that was not possible due to a lack of five blooming camas individuals within 1m^2, a location within one of the other three quadrants was selected that was not spatially proximate to the other data collection plots at the site.

2.3.4 Data collection

Data were collected at two scales, at the 1m^2 plot-level and at the individual plant-level, and occurred in two phases. The first phase took place April 20 - May 12, 2022 when common camas was in peak bloom, and the second phase took place July 4 - 11, 2022 when the camas had gone to seed (Table 1).

Table 1. Definitions of all measurements, at what scale they were measured, and during which phase (phase 1 being April 20 - May 12, 2022, and phase 2 July 4 – 11, 2022).

Measurement	Definition (units)	Method of measurement	Scale	Date
Disturbance	The percentage of the plot affected by trampling (flattened foliage) and/or herbivory (%)	Visual estimation	Plot	April/ May
Canopy cover	The percentage of ground covered by the vertical projection of surrounding vegetation (%)	Spherical densiometer	Plot	April/ May
Soil pH	(0 – 14 from acidic to alkaline)	Soil sample tested at the Province of BC's Analytical Laboratory	Plot	July
Soil compaction	The extent and depth of subsurface compaction (kg/cm^2)	Penetrometer	Plot	July
Soil nutrient content	The amount of total carbon, nitrogen, and sulphur (%), and available phosphorus (mg/kg) present in the soil	Soil sample tested at the Province of BC's Analytical Laboratory	Plot	July

Soil depth	The vertical distance from the soil surface to bedrock, parent material, or other physical barrier to plant root growth (cm)	Metal skewer and ruler	Plot	July
Species composition and cover	The plant species present and the estimated percentage cover of each (%)	Visual estimation	Plot	April/ May
Camas abundance	The number of *Camassia quamash* in bloom, and the number *Camassia quamash/leichtlinii* in bud or lacking an inflorescence (count)		Plot	April/ May
Height (Hmax)	Distance between base of a plant at the soil surface and highest photosynthetic tissues (cm)	Ruler	Plant	April/ May
Specific leaf area (SLA)	The ratio of fresh leaf area to dry leaf mass (mm^2/mg)	WinFOLIA	Plant	April/ May
Longest leaf	Length of the longest leaf per individual (cm)	Ruler	Plant	April/ May
Leaf count	Number of leaves per individual (count)		Plant	April/ May
Flower count	Number of flowers per inflorescence (count)		Plant	April/ May
Capsule count	Number of fruit capsules per individual (count)		Plant	July
Seed mass	The average air-dried mass of one seed per individual (mg)	High precision scale	Plant	July
Seed count	Number of seeds produced per individual and average number of seeds per capsule (count)		Plant	July

Plot-level measurements were recorded in each of the $1m^2$ data collection plots. Canopy cover readings using a spherical densiometer were taken from the four compass directions and averaged for a more accurate estimate. Soil compaction (using a handheld penetrometer) and soil depth were measured five times in each quadrat (once in each corner and once at the center) and averaged. One soil core was taken per plot using a 1-inch diameter soil auger, and the sample was air-dried and sieved to <2mm before being sent to the BC Analytical Laboratory for nutrient and pH testing. Forb species in each plot were identified using *Flora of the Pacific Northwest* (Hitchcock & Cronquist, 2018) and the abundance of each species was estimated using seven cover classes: A <1%, B 1-5%, C 6-25%, D 26-50%, E 51-75%, F 76-95%, G >95%

(Daubenmire, 1959). Graminoids were not identified to family due to the challenges of identification pre-bloom. Camas abundance was calculated by counting the number of camas plants in bloom, bud, or neither (juvenile plants lacking an inflorescence or adult plants whose inflorescence was absent) per quadrat. Differentiating *Camassia quamash* from *Camassia leichtlinii* is easiest when in bloom (based on the symmetry of their petal arrangement); therefore, the number of camas plants in bud and the number lacking an inflorescence may include *Camassia leichtlinii* individuals. Slope, aspect, and elevation were similar across the gradient and therefore were excluded from the site condition assessment.

Plant trait data were collected from five common camas plants in each of the $1m^2$ data collection plots using a stratified random sampling design. The common camas plants selected for measurement were all in peak bloom to control for differences in phenology and to confirm species identification. The plant traits selected relate to the competitive vigor and reproductive capacity of plants (Borowy & Swan, 2020; Pérez-Harguindeguy et al., 2013).

Two leaves were collected from the five selected plants per $1m^2$ quadrat. The outer leaves were more often affected by herbivory and the inner leaves were often smaller than the outer, therefore, one outer and one inner leaf were collected. When possible, leaves not affected by herbivory were collected. The leaves were cut as close to the soil surface as possible and stored in sealed plastic bags with damp paper towel. A breath was added into the bags to enhance CO_2 concentration and air humidity, which minimizes transpiration and water loss (Pérez-Harguindeguy et al., 2013). Samples were stored in a cooler until scanned for leaf area later in the same day using a flatbed scanner and WinFOLIA software (Regent Instruments Canada Inc., 2020). Both leaves were scanned at the same time for a total leaf area measurement. Some leaves were curled, wilted, or affected by herbivory. We quantified the magnitude of this error by estimating the percent of leaf that was curled or wilted and thus not captured in the area measurement. The herbivory error was recorded as one, both, or neither sample leaves chewed. Once scanned, the leaves were placed in a drying oven at 70°C for 72 hours and weighed for dry mass. Specific leaf area (SLA) was calculated by dividing fresh leaf area by dry leaf mass.

Due to the inability to count fruit capsules and collect seeds across all sites at the same time, some stems had desiccated capsules and/or seeds missing when sampled. This error was estimated by visually assessing whether seeds were likely missing to dispersion (yes or no), and another error estimate captured whether herbivory of the inflorescence since the previous measurements (flower count) was likely (yes or no).

2.3.5 Statistical analysis

2.3.5.1 Plot-level analysis

An analysis of plot-level measurements was conducted to examine how urbanization in Greater Victoria is altering local site conditions. All analyses were performed using R statistical software (version 4.2.1, R Core Team, 2022). An analysis of plot-level measurements was performed by fitting a linear regression between each plot-level measurement (the response) and the percent of urban land cover in the surrounding 100m^2 (the predictor). The disturbance measurement was separated into its two component parts, trampling and herbivory. In each model, sample size was n = 48 (one value per plot, with four plots in each of the twelve sites), and study site was included as a random effect in all models to account for non-independence in observations within each study site (Zuur et al., 2009).

To determine whether each response variable should be fit with a linear mixed model (LMM) or a generalized linear mixed model (GLMM), the normality of each response variable was assessed. If the data satisfied the assumptions of a normal (Gaussian) distribution, a LMM was fit using the lmer() function from the *lme4* package (Bates et al., 2015) in R. If positive skew was present in the histogram of residuals, the response was log-transformed, and normality assessed. If the log-transformed data satisfied the assumptions of a Gaussian distribution, a LMM was fit using the log-transformed data. Otherwise, a GLMM was fit using the glmmTMB() function from the *glmmTMB* package (Brooks et al., 2017) in R, with the family of distribution selected based on an understanding of the general characteristics of each distribution and the best fit (via model checking). Response variables fit with a LMM include canopy cover, soil compaction (log-transformed), soil depth (log-transformed), soil phosphorus (log-transformed), soil carbon, and soil sulphur. Response variables fit with a GLMM with a beta distribution (logit link function) include soil nitrogen and soil pH. Response variables fit with a GLMM with a beta distribution (logit link function) and zero-inflation term include trampling (23% zeros), herbivory (29% zeros), and graminoid cover (2% zeros). For each response, residuals were plotted against fitted values, a histogram of residuals was visually examined, the normality of a quantile-quantile plot was assessed, and a Shapiro-Wilk test was run (a p-value ≥ 0.05 satisfies a normal distribution). All models were checked and validated using the *performance* package (Lüdecke et al., 2021) and the *DHARMa* package (Hartig, 2022) in R (Appendix B.1.2).

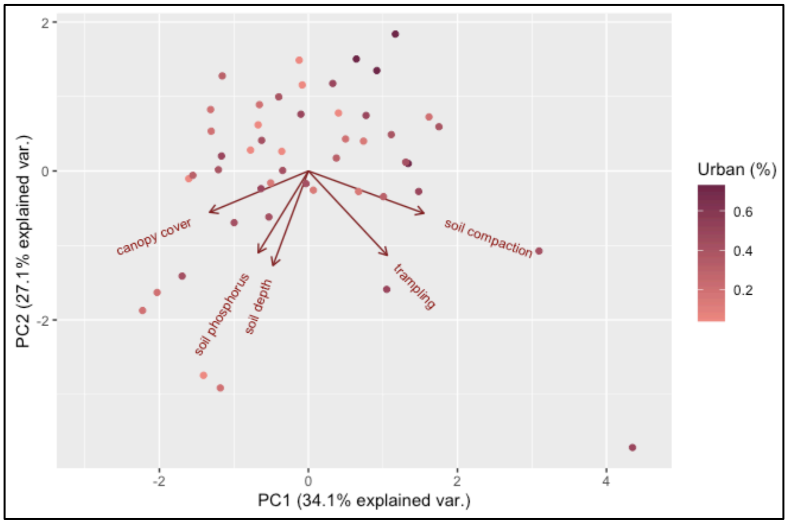
2.3.5.2 Individual plant-level analysis

An analysis of individual plant-level measurements was performed to investigate how individual common camas plants are responding to the local site parameters associated with urbanization on this landscape. Table 2 outlines the plant-level response variables and the associated sample size. Longest leaf was the only trait not included in the statistical analysis as herbivory was so prevalent across the landscape that this measurement did not provide useful information on plant growth or resource allocation. Five individuals were measured per plot (48 plots total, n = 240); however, by the second phase of data collection some of the previously measured individuals were no longer present, likely due to herbivory or human disturbance, resulting in smaller sample sizes.

Table 2. Definitions of individual plant level response variables including units and the corresponding sample size.

Response variable	Definition (units)	Sample size
Foliar biomass	(Dry mass of two leaves / 2) * number of leaves per individual (g)	240
Specific leaf area (SLA)	Area of two leaves / dry mass of two leaves per individual (mm^2/mg)	240
Stem height	Distance from soil surface to highest photosynthetic tissues (cm)	240
Number of flowers per inflorescence	Number of flowers per inflorescence (count)	240
Ratio of flowers to capsules	Number of capsules / number of flowers per individual (%)	203
Average number of seeds per capsule	Number of seeds / number of capsules per individual (count)	153
Average mass of a single seed	Mass of seeds / number of seeds per individual (g)	153

To further examine how each trait was responding to the pressures associated with urbanization on this landscape, a Principal Component Analysis (PCA) of the local site parameters associated with urbanization was performed, and the resulting components were used as the predictors (fixed effects) in a linear mixed model for each response trait. A PCA enabled a reduction in the number of fixed effects included in each mixed model. The inputs for the PCA were the variables most closely related to the urbanization gradient in the plot-level analysis, and included trampling, canopy cover, soil compaction, soil depth, and soil phosphorus. Graminoid cover and herbivory had a weak relationship to the percent of urban land cover in the surrounding 100m^2 and therefore were not included in the PCA. The first two principal components (PC1 [34.15%], PC2 [27.12%]) explained 61% of the variance and thus were the two components selected to be included in the linear mixed models (henceforth referred to as 'urbanization stress index (USI) 1' and 'urbanization stress index (USI) 2'). USI 1 is largely associated with an increase in soil compaction and trampling, and a decrease in canopy cover (Figure 7). USI 2 is largely associated with a decrease in soil depth, trampling, and soil phosphorus (Figure 7).



Input variables	USI 1 (PC1)	USI 2 (PC2)
Trampling	0.43	-0.52
Canopy cover	-0.54	-0.26
Soil compaction	0.64	-0.26
Soil depth	-0.20	-0.58
Soil phosphorus	-0.28	-0.51
Variance explained	**34.2%**	**27.1%**

Figure 7. The first two principal components in the PCA ordination plot explain 61% of the variance. Principal component 1 is associated with increased trampling and soil compaction, and decreased canopy cover, soil depth, and soil phosphorus. Principal component 2 is associated with decreased trampling, canopy cover, soil compaction, soil depth, and soil phosphorus.

A linear mixed model was run for each of the seven plant trait measurements outlined in Table 2. The response variable was the plant trait measurement, the three predictors (fixed effects) were USI 1, USI 2, and herbivory, and the random effect was a nested random effect of plot within study site to account for non-independence in observations within each of the four plots within each study site (Zuur et al., 2009). The ratio of flowers to capsules model had a study site random effect near equal to zero and the conditional r-squared could not be computed, therefore, the model was run with plot as the only random effect. The model outputs were the same as those from the model that included study site as a random effect. To determine whether each response variable should be fit with a LMM or a GLMM, the same model structure fitting process was used as outlined in the plot-level analysis. Response variables fit with a LMM include specific leaf area, foliar biomass (log-transformed), stem height (log-transformed), and flower count (log-transformed). Response variables fit with a GLMM include the ratio of flowers to capsules (beta distribution (logit link function) and zero-inflation term), the average number of seeds per capsule (tweedie distribution), and the average mass of a single seed (tweedie distribution).

Certain plant trait measurements had errors associated with them. The errors were plotted against the model residuals to determine whether any pattern existed. If there was a pattern, the model was run including the error variable(s) as fixed effect(s) and the significance examined. If the errors as fixed effects returned a p-value of <0.05, the error variable(s) were left in the model. All models were checked and validated using the same methods as applied to previous models (Appendix B.2.1). To check the validity of the PCA axes, the model results were also compared to models using percent of urban land cover as the urbanization fixed effect (Appendix B.2.2).

The individual plant level mixed models were visualized using the ggpredict() function from the *ggeffects* package (Lüdecke, 2018). The *ggeffects* package computes estimated predicted values for the response by holding the non-focal variables constant (Lüdecke, 2018). Specifying the ggpredict() function as either “fixed” or “random” returns the same population-level predictions, however, “fixed” returns confidence intervals and “random” returns prediction intervals (taking into consideration the uncertainty in the variance parameters (the mean random effect variance)), therefore the visualizations were specified as “fixed” to return confidence intervals.

2.4 Results

2.4.1 Plot-level

None of the plot-level measurements indicated a significant relationship to the percent of urban land cover in the surrounding 100m^2 (Figure 8). There was a change in these local site parameters across the landscape (except for soil carbon, sulphur, and pH) however, they were not strongly associated to urbanization as defined for this study. The two variables with the strongest relationship to urbanization were soil compaction (p-value = 0.096) and trampling (p-value = 0.079).

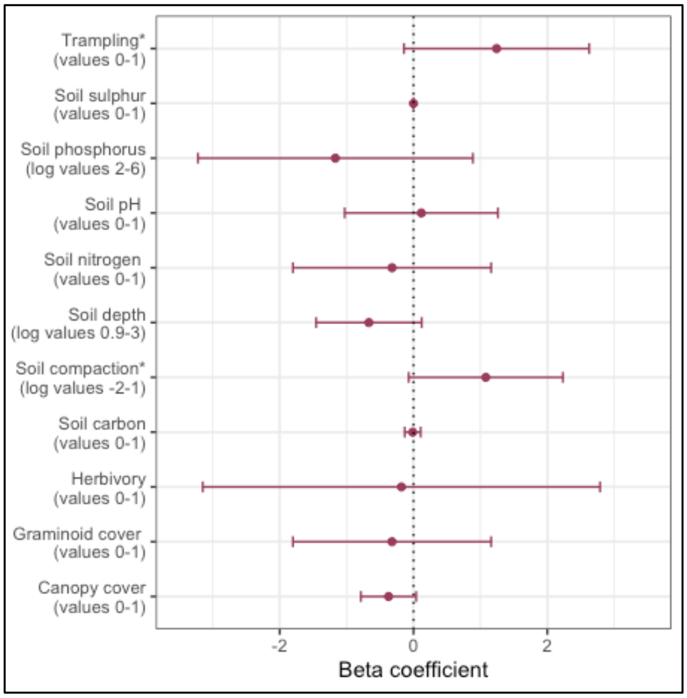


Figure 8. Urbanization had a weak to absent relationship with the environmental variables measured in each quadrat as indicated in the beta coefficient plot where all 95% confidence intervals cross zero. A positive coefficient indicates an increase in the plot-level measurement with greater urbanization and a negative coefficient indicates a decrease. Response variables with an asterisk were significant at the alpha = 0.1 level.

2.4.2 Individual plant-level

An increase in trampling and soil compaction, and a decrease in canopy cover, soil depth, and soil phosphorus were correlated with a shift towards lower growth and reproductive trait values in common camas (Figure 9). A positive correlation indicates an increase in the trait value as the site parameter measurement increases, and a negative correlation indicates a decrease in the trait value as the site parameter measurement increases.

	trampling	canopy cover	soil compaction	soil depth	soil phosphorus
foliar biomass	0.082	0.379	-0.318	0.374	0.41
sla	-0.05	0.262	-0.154	-0.11	-0.183
stem height	0.027	0.546	-0.476	0.424	0.272
flower count	0.044	0.274	-0.292	0.326	0.263
flowers to capsules	0.059	-0.178	0.049	-0.106	0.103
seeds per capsule	-0.094	0.024	-0.196	0.016	-0.107
seed mass	-0.112	0.253	-0.31	0.01	0.094

Figure 9. A table of Pearson correlation coefficients between the seven plant trait measurements and the five key site parameters.

Six out of the seven plant trait responses were significantly related to one or both urbanization stress indexes (a p-value <0.05) (Table 3). Seeds per capsule was the only response variable that was not significantly related to either urbanization stress index. Foliar biomass, specific leaf area, plant height, flower count, and seed mass all decreased with USI 1. The ratio of capsules per flowers increased with USI 1; however, this trait was strongly driven by measurements at two urban sites and was significantly influenced by the error associated with herbivory. Foliar biomass and plant height decreased with USI 2. The three response variables with errors associated (specific leaf area, capsules per flowers, and seeds per capsule), all displayed significant relationships with the error measurements. Herbivory was not significantly related to any of the plant trait responses on this landscape.

Table 3. Summary of the plant-level mixed-effects models. β is the beta coefficient, and CI is the confidence interval. Predictors with a significant relationship to the response variable are in bold (p-value < 0. 05). The marginal r-squared considers only the variance of the fixed effects, while the conditional r-squared takes both the fixed and random effects into account (Nakagawa & Schielzeth, 2013).

Response	Sample size	Predictor	Distribution	β	95 % CI	p-value	Marginal/ conditional R^2
Foliar biomass	240	**USI 1**	gaussian, log transformed	**-0.23**	**[-0.33, -0.14]**	**<0.001**	0.26/ 0.58
		USI 2		**-0.16**	**[-0.27, -0.05]**	**0.006**	
		herbivory		0.24	[-0.20, 0.68]	0.293	
SLA	240	**USI 1**	gaussian	**-0.11**	**[-0.21, -0.02]**	**0.020**	0.19/ 0.51
		USI 2		0.06	[-0.05, 0.17]	0.279	
		herbivory		0.01	[-0.49, 0.51]	0.959	
		curled leaf (y/n)		**-1.19**	**[-1.99, -0.39]**	**0.004**	
		leaf chewed (y/n)		**0.28**	**[0.15, 0.41]**	**<0.001**	
Height	240	**USI 1**	gaussian, log transformed	**-0.14**	**[-0.18, -0.10]**	**<0.001**	0.38/ 0.63
		USI 2		**-0.05**	**[-0.09, 0.00]**	**0.049**	
		herbivory		0.09	[-0.09, 0.27]	0.328	
Flower count	240	**USI 1**	gaussian, log transformed	**-0.14**	**[-0.21, -0.07]**	**<0.001**	0.15/ 0.41
		USI 2		-0.05	[-0.13, 0.03]	0.203	
		herbivory		0.06	[-0.26, 0.38]	0.715	
Capsules per flowers	203	**USI 1**	beta (logit link function), zero inflation term	**0.24**	**[0.10, 0.38]**	**0.001**	0.38/ 0.90
		USI 2		-0.13	[-0.29, 0.03]	0.106	
		herbivory		-0.42	[-1.07, 0.24]	0.210	
		herbivory likely (y/n)		**-0.56**	**[-0.94, -0.18]**	**0.004**	
Seeds per capsule	153	USI 1	tweedie	-0.05	[-0.17, 0.06]	0.352	0.08/ 0.38
		USI 2		0.09	[-0.03, 0.21]	0.147	
		herbivory		0.16	[-0.30, 0.63]	0.488	
		seeds missing (y/n)		**-0.22**	**[-0.43, -0.01]**	**0.042**	
Seed mass	153	**USI 1**	tweedie	**-0.12**	**[-0.19, -0.06]**	**<0.001**	0.16/ 0.37
		USI 2		0.01	[-0.06, 0.09]	0.701	
		herbivory		0.20	[-0.07, 0.48]	0.151	

Along the urbanization stress gradient (as depicted by USI 1), foliar biomass was predicted to decrease on average 80% from 1.27g [CI 0.96, 1.68] to 0.25g [CI 0.16, 0.38], specific leaf area 20% from 4.1mm^2/mg [CI 3.81, 4.38] to 3.3mm^2/mg [CI 2.84, 3.75], plant height 63% from 67.05cm [CI 59.84, 75.14] to 25.15cm [CI 21.08, 30.00], flower count 63% from 16.34 flowers [CI 13.41, 19.90] to 6.01 flowers [CI 4.35, 8.30], and seed mass 58% from 8.15g per thousand seeds [CI 6.84, 9.70] to 3.45g per thousand seeds [CI 2.55, 4.66] (Figure 10). The ratio of flowers to capsules was predicted to increase on average 125% from 32% of flowers producing capsules [CI 0.24, 0.41] to 72% producing capsules [CI 0.57, 0.83] (Figure 10).

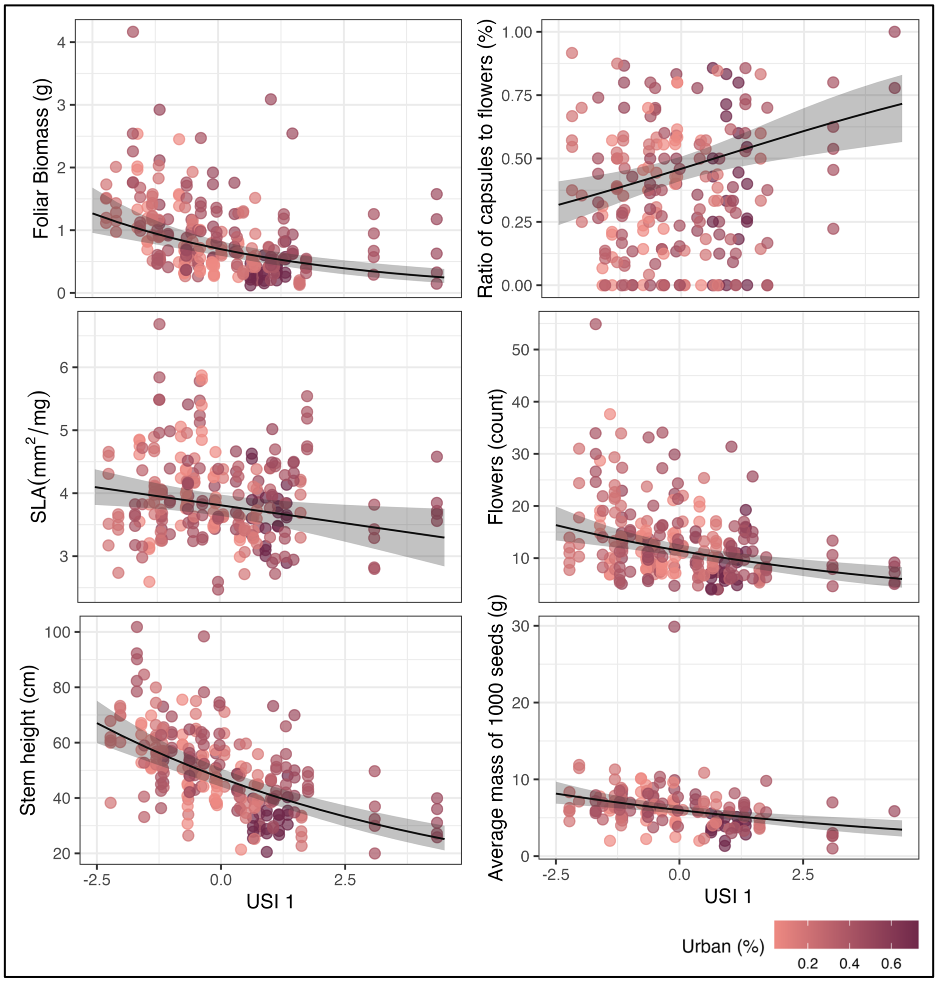


Figure 10. Assuming a linear relationship, foliar biomass, specific leaf area, stem height, flower count, and the average mass of 1000 seeds were predicted to decrease with an increase in USI 1.

The ratio of capsules to flowers was predicted to increase. Greater urban stress as defined by USI 1 is indicated by increasing values along the x-axis.

Along the urbanization stress gradient (as depicted by USI 2), foliar biomass was predicted to decrease on average 62% from 1.34g [0.84, 2.15] to 0.51g [0.39, 0.67] and plant height was predicted to decrease on average 24% from 56.65cm [46.87, 68.46] to 43.14cm [38.56, 48.27] (Figure 11).

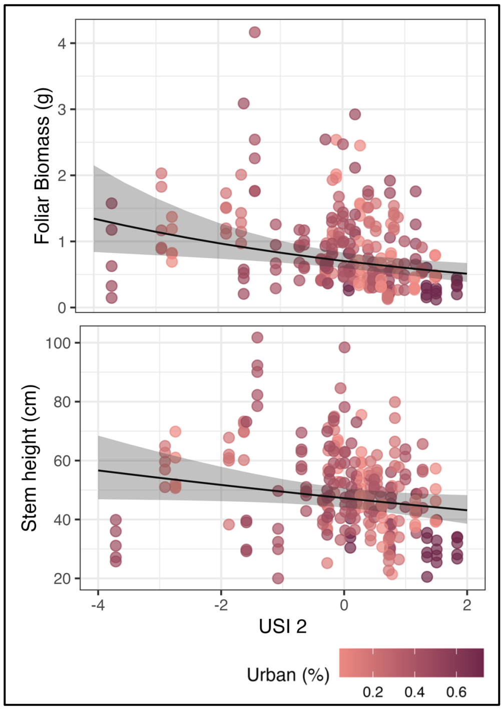


Figure 11. Assuming a linear relationship, foliar biomass and stem height were predicted to decrease with an increase in USI 2. Greater urban stress as defined by USI 2 is indicated by increasing values along the x-axis.

2.5 Discussion

Common camas growth and reproductive trait values exhibit a decrease in urban oak meadows in Greater Victoria, indicating that common camas individuals have decreased fitness in highly urbanized environments. Urbanization does not have consistent effects on the local environment on this landscape but does seem weakly related to key variables, namely trampling, soil compaction, canopy cover, soil depth, and soil phosphorus (Appendix B.1.1). These key variables are not strongly related to urbanization on their own, however, when combined into two axes (via the PCA) they explain a large proportion of the variation across the gradient and drive trait responses in common camas individuals.

The weak relationship between the environmental variables measured and the percent of urban land cover in the surrounding $100m^2$ may be due to the oversimplified way the urban-rural gradient was defined and the absence of a temporal perspective (Foster et al., 2003; Ramalho & Hobbs, 2012). Urban growth and intensification are not linear processes but instead occur in patchy and complex spatial patterns across the landscape, resulting in natural areas transitioning to urban areas at different rates, with implications for the state and processes of remnant ecosystems (Ramalho & Hobbs, 2012). Interacting with the patchy growth and intensification of cities is the lagged ecological responses to urbanization, whereby the impact on the environment is not immediate and the biotic responses being currently observed can be masked by ongoing fragmentation and environmental change that is not yet reflected in the ecosystem (Ramalho & Hobbs, 2012). The oak meadows across Greater Victoria were urbanized at different times and have unique land-use legacies that are likely still influencing the plant communities that exist (Armstrong et al., 2021; Perring et al., 2016). Land-use legacies associated with agriculture have been observed to affect urban remnant soils (through soil inputs, grazing, and tilling) (Foster et al., 2003; Ramalho & Hobbs, 2012) and Indigenous land-use legacies have been observed to influence present-day soils and leave unique genetic signatures in extant plant communities resulting from millennia of habitat modification (Armstrong et al., 2021; Lowther, 2022; McCune et al., 2013). The elevated soil phosphorus levels present in some of the rural oak meadows on this landscape may be the result of Indigenous habitation and/or an agricultural past. To strengthen the relationship between local site conditions and urbanization on this landscape, how the urban-rural gradient was defined could be improved upon by incorporating a temporal perspective that integrates the time since each oak meadow was urbanized and the land-use legacies that may continue to influence each patch.

Several past studies show that across the urban-rural gradient, urban soils are more compacted than rural soils, with implications for plant establishment and growth (Bassett et al., 2005; Bejarano et al., 2010; Mariotti et al., 2020). Common camas appears to be responding to increased compaction in this region with a reduction in foliar biomass and plant height, with implications for resource acquisition, competitive vigor, and fecundity (Borowy & Swan, 2020; Pérez-Harguindeguy et al., 2013; Weiher et al., 1999). Compacted soils physically impede root growth and seedling establishment, and alter the oxygen, water, and nutrients available to plants (Alameda & Villar, 2012; Kuss & Graefe, 1985; Mariotti et al., 2020). In the case of geophytes, soil compaction can also impede bulb development (Beckwith, 2004). In response to soil compaction, plants have been observed to exhibit reduced above- and belowground growth traits, including decreased aboveground biomass and plant height (Alameda & Villar, 2012; Mariotti et al., 2020). Soil compaction in urban meadows is likely a consequence of the absence of Indigenous cultivation practices as well as the result of the high number of visitors to these parks. Indigenous harvesting and stewardship practices in the qʷɬəɬ/KȽO,EL food system involved regularly digging up camas bulbs and tilling the soil (Beckwith, 2004; Turner & Kuhnlein, 1983). These practices frequently aerated the soil, and in turn facilitated camas growth and development (Beckwith, 2004).

Urban meadows exhibited a more open canopy on this landscape, potentially benefitting common camas populations despite their growth appearing greater in the more shaded, rural sites. Plant species that thrive in open habitats (such as common camas) may allocate more resources into acquiring sunlight when partially shaded, resulting in greater aboveground growth (e.g., increased plant height and aboveground biomass); however, this often occurs at the cost of decreased flowering and fruiting (Arenas-Corraliza et al., 2021; Kutschera & Briggs, 2013). Thus, individuals growing under partial canopy may appear to have more vegetative competitive vigor, but if shaded over the long term, these species can be replaced with more shade-tolerant species (GOERT, 2011; McCune et al., 2013). The common camas populations observed on this landscape appeared to be experiencing this phenomenon where individuals exhibited increased height, specific leaf area, and foliar biomass in the more shaded, rural meadows, but greater seedling production as evidenced by increased abundance in the more open canopy, urban meadows (Appendix C). The increased canopy cover observed in rural areas may be associated with the ongoing encroachment of conifers and other woody species into coastal oak meadows from surrounding forested areas (GOERT, 2011; Gedalof et al., 2006; McCune et al., 2013). Coastal oak meadows are a fire-dependent system and have been shaped by the Indigenous stewardship practice of controlled burning (Turner, 1999). Prior to European settlement and the suppression of fire, low-intensity fires maintained the open canopy habitat necessary for the shade-intolerant species of coastal oak meadows to thrive (Gedalof et al., 2006; Turner, 1999).

Herbivory (grazing) was hypothesized to stimulate a response in camas growth and reproduction across the urban-rural gradient, however, no response was detected potentially because the observed grazing pressure across this landscape was universally so high (Appendix B.1.1). This region is characterized by high ungulate densities, primarily of black-tailed deer (*Odocoileus hemionus*) (MacDougall, 2008). Over the past 100 years, black-tailed deer abundance has increased dramatically due to habitat fragmentation, declines in hunting pressure, and the eradication of predators (Gonzales & Arcese, 2008; MacDougall, 2008). This grazing pressure on the landscape was expected to stimulate a reduction in common camas growth and reproduction based on literature that associates the herbivory of plants, especially during the early growing season, with reduced plant fitness (Gonzales & Arcese, 2008; Hawkes & Sullivan, 2001; Stephan et al., 2017; K. A. Thompson & Johnson, 2016). However, common camas traits on this landscape show no detectable response to herbivory. Geophytes have been observed to be resilient to frequent, severe summer defoliation owing to the resources stored in their underground storage organs (Schmiedel et al., 2021); however, carry-over effects into the next growing season have been reflected in reduced aboveground biomass and inflorescence production (Morris, 2021). Restricted to one field season, it is unknown how common camas individuals may be responding year after year to the persistent, heavy grazing pressure on this landscape; they may be exhibiting tolerance or be universally struggling.

The overall reduction in growth and reproductive trait values in common camas in urban oak meadows indicates a potential reduction in overall fitness, with implications for the future success and persistence of this species in urban spaces (Borowy & Swan, 2020; Pérez-Harguindeguy et al., 2013). It is important to note that the findings of this study likely affirm what First Nation land stewards have long understood about what conditions support thriving camas populations. The knowledge of how different site conditions (e.g., aerated soil, open canopy) influence common camas growth and reproduction is reflected in the Indigenous land management practices that led to tremendous camas productivity in this region (Lyons & Ritchie, 2017; Proctor, 2013; Turner, 1999; Turner & Kuhnlein, 1983). Heading into an increasingly urbanized future with environmental impacts some of which we cannot predict co-led management with Indigenous partners could be vital to supporting the persistence and success of camas on this landscape.

2.6 Conclusion

Our results clearly illustrate that common camas is responding to a handful of key variables frequently associated with urbanization, namely increased trampling and soil compaction, and decreased canopy cover, soil depth, and soil phosphorus. To support remnant urban camas populations, management and planning initiatives should target these key pressures specifically. Trampling, soil compaction and canopy cover are all conditions that can be managed at small or large scales. Delineating formal trail networks through oak meadow parklands could help reduce trampling, and aerating the soil through weeding, invasive species removal, and local Nations harvesting camas bulbs would likely increase camas fitness. The removal of shrubs and other woody species encroaching into oak meadows could prove effective at reducing canopy cover and encouraging camas abundance. Meaningfully involving descendant Indigenous communities in the restoration of these ecosystems would provide benefits that extend beyond the ecological. As important sites of eco-cultural revitalization, these meadows provide opportunities for reinstating traditional roles and practices, and for Indigenous youth to learn alongside their knowledge holders and scientists (Corntassel & Bryce, 2012). Understanding that Coast Salish stewardship practices have never been static, past practices can be adapted to assist in addressing present-day challenges (Grenz, 2020).

Further research to build upon this work could examine how common camas populations respond to the restoration actions outlined or extend the analysis to camas populations in other geographical regions. As urbanization continues to shape ecosystems and plant communities around the world, it is critical that we understand how individual plants respond to these pressures to support the persistence of ecologically and culturally important plant species across urban landscapes for generations to come.

Chapter 3: Great camas (*Camassia leichtlinii*) trait plasticity in response to soil compaction, canopy cover, and grazing

3.1 Abstract

It is well understood that plants have the capacity to respond to conditions in their environment through variations in the traits they express, and these response traits vary among and within species. Within-species trait variation in response to the environment is termed phenotypic plasticity. It remains unclear whether spring geophyte species, slow-growing perennial species with underground storage organs, can express phenotypic plasticity within a single growing season in response to different pressures in their environment. To investigate this uncertainty in greater detail, we examined the phenotypic plasticity of growth traits in a spring geophyte species, great camas (*Camassia leichtlinii*), in response to soil compaction, canopy cover, and grazing in a greenhouse experiment over one season. We also examined how the different pressures affected resource allocation back into the bulbs with implications for subsequent seasons of growth. Our results indicated a limited capacity for great camas to exhibit trait plasticity within one growing season with growth traits most strongly correlated to pre-season bulb mass. Bulb resources were also not affected by the different pressures; however, 92% of bulbs in the experiment lost mass with those that produced the most foliar biomass exhibiting the biggest loss. The shortened growing season and abnormally warm temperatures during the spring growth phase were observed as important drivers impacting great camas growth, reproduction, and development. These results highlight the necessity for coastal oak meadow management to address not only urban pressures threatening camas populations, but also the potential impacts of climate change in the face of a warming future.

3.2 Introduction

Ecosystems around the world experience highly contrasting environmental conditions; from deserts to tropical rainforests to tundra, and plants exhibit different attributes, or traits, that enable them to establish, persist, and reproduce in these different environments (Albert et al., 2011; Garnier et al., 2016; Violle et al., 2007). The varying trait values that different plant species express can be partially explained by evolutionary ancestry (genetic differences) but are also largely influenced by abiotic and biotic conditions (Garnier et al., 2016). Biotic (e.g., competition, predation) and abiotic (e.g., climate, resource availability, disturbance) conditions act as filters that control community composition through the selection of plants with a particular set of attributes or functional traits (Kalusová et al., 2017; Lavorel & Garnier, 2002; Violle et al., 2007). When environmental conditions change, plants can respond with variation in some of their trait values (Lavorel & Garnier, 2002). These responses to environmental factors can vary among species and within individuals of the same species (Lavorel & Garnier, 2002; Westerband et al., 2021). Response trait variation within a species is also termed phenotypic plasticity (Bradshaw, 1965; Violle et al., 2012).

Phenotypic plasticity is the change in form or function expressed by a single genotype in response to environmental factors (Bradshaw, 1965; Gratani, 2014; Violle et al., 2012). Plants are often highly plastic in their responses, with individuals varying by orders of magnitude in size, growth rates, allocation to different organs, reproduction, and chemical constituency in response to a wide variety of environmental conditions (Callaway et al., 2003). This plasticity in phenotype can be permanent within a generation, relatively fixed for a growing season, or dynamic across short time scales (Callaway et al., 2003), and can differ among traits within a single plant. A better understanding of phenotypic plasticity will provide vital insight into discerning a species' capacity to persist across rapidly changing landscapes (Gratani, 2014; Henn et al., 2018; Nicotra et al., 2010; Westerband et al., 2021). In ecosystems around the world, environmental conditions are rapidly changing due to a variety of forces including climate change, habitat destruction, pollution, invasive species, among others (Bellard et al., 2022). The rapid rate at which environmental conditions are changing might exceed the rate of adaptation through evolutionary processes in long-lived plant species, with phenotypic plasticity potentially playing an important role in persistence (Gratani, 2014; Henn et al., 2018; Nicotra et al., 2010). Trait plasticity in response to changes in the environment is often assumed to be adaptive but it may also be neutral, non-adaptive, or maladaptive (Ghalambor et al., 2007; Gratani, 2014). Examining phenotypic plasticity within a species to specific environmental pressures can improve our understanding of its capacity to respond to rapidly changing conditions, whether the responses are adaptive or not, and can improve our predictions of responses to similar pressures into the future (Henn et al., 2018; Westerband et al., 2021).

Geophytes, perennial plant species with an underground storage organ, provide an interesting case study for understanding phenotypic plasticity. Geophytes are long-lived species that invest significant resources into their belowground organs (Khodorova & Boitel-Conti, 2013; Werger & Huber, 2006). Each spring, during the vegetative growth phase, bulbous spring geophytes acquire carbon through photosynthesis and transport it into the bulbs as an energy reserve for the following season of growth (Khodorova & Boitel-Conti, 2013). Environmental conditions that impact vegetative growth, such as grazing, could therefore affect not only current-season growth, but also growth in subsequent seasons by affecting resource allocation back into the bulb

(Beckwith, 2004; Werger & Huber, 2006). It remains unclear whether bulbous geophytes are capable of exhibiting trait plasticity within a single growing season. The objective of this study was to address this knowledge gap and investigate the trait plasticity of a geophyte species, great camas *(Camassia leichtlinii*), over one growing season.

Great camas is a perennial forb species in the Asparagaceae family that is present in oak meadows from northern California to southern BC east of the Cascade Mountains (Hitchcock & Cronquist, 2018). Great camas, like common camas (*Camassia quamash*), is an ecologically important cultural keystone species (Beckwith, 2004; Garibaldi & Turner, 2004; Gritzner, 1994; Proctor, 2013). Across Coast Salish territories, camas was, and continues to be, actively stewarded by Coast Salish First Nations and is a significant component of their traditional foods system (Proctor, 2013; Turner & Kuhnlein, 1983). Prior to European colonization and the dispossession of Indigenous peoples from their lands, camas was extensively cultivated across this region (Beckwith, 2004; Garibaldi & Turner, 2004; Proctor, 2013). Today, the distribution of camas in this region, particularly on southern Vancouver Island, is limited to small, fragmented oak meadows across an increasingly urbanized landscape (GOERT, 2011).

Urbanization rapidly changes landscapes and alters environmental conditions within and surrounding urban centers (Grimm, Faeth, et al., 2008; Weston et al., 2021). Altered environmental conditions associated with urban land use can have positive effects (e.g., increased nutrient availability) and negative impacts (e.g., reduced habitat availability) on urban plant populations (Albrecht & Haider, 2013; Vallet et al., 2010). The Greater Victoria region on Vancouver Island is experiencing some of the greatest urban population growth in the country

(Statistics Canada, 2022), but the ecological effects of this urbanization and its impacts on urban plant populations remains unclear. Examining great camas trait plasticity in response to pressures associated with local urbanization in Greater Victoria, therefore, provides a spatially and temporally relevant case study. Three factors associated with local urbanization were selected for examination in this study: soil compaction, canopy cover, and grazing (Figure 12).

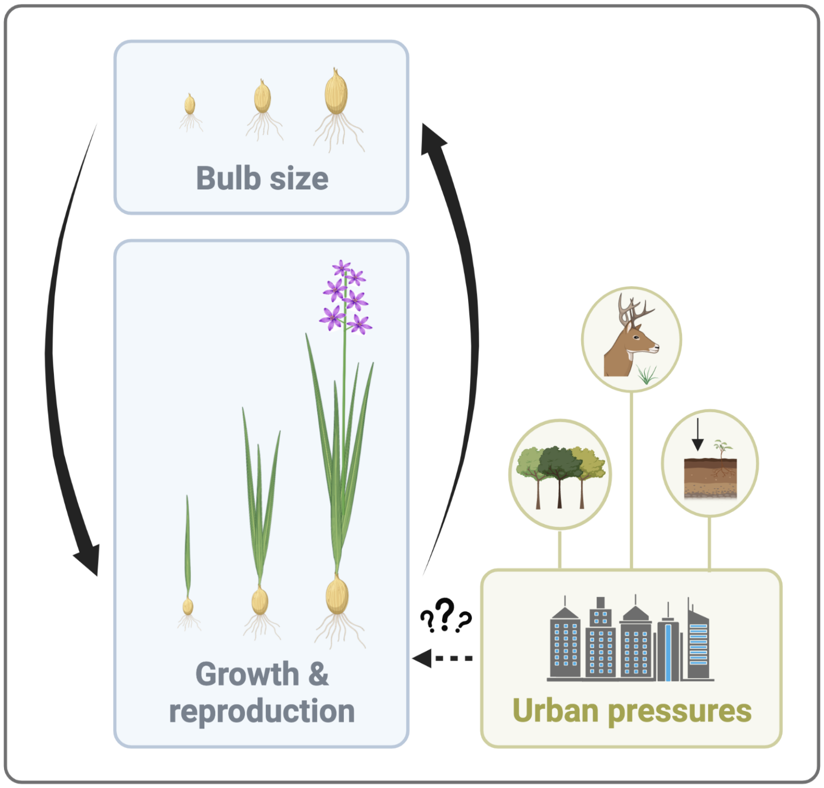


Figure 12. Great camas bulb size influences aboveground growth and reproduction, but it remains unclear whether camas can exhibit growth trait plasticity in response to different environmental pressures within one growing season, with potential implications for resource allocation back into the bulbs.

To investigate great camas trait plasticity in response to soil compaction, canopy cover, and grazing, this study took place in a controlled greenhouse experiment and was guided by the following questions: 1) does great camas exhibit plasticity in its vegetative growth traits in response to soil compaction, canopy cover, and/or grazing within one growing season? and 2) does soil compaction, canopy cover, and/or grazing impact resource allocation back into the bulbs (with potential implications for subsequent seasons of growth)? This research will contribute to supporting more successful urban camas populations across an increasingly urbanized landscape, and more broadly, to efforts to better understand the response of slow-growing geophytes to changing environmental conditions.

3.3 Methods

3.3.1 Great camas ecology

Great camas (*Camassia leichtlinii* (Baker) S. Watson) is one of the six species in the North American genus *Camassia* and can be found from southern BC to California (POWO, 2023). Great camas is frequently found on southeast Vancouver Island and the Gulf Islands, although less widespread in BC than the other prevalent camas species, common camas (*Camassia quamash*) (Hitchcock & Cronquist, 2018). Great camas is a bulbous geophyte, a perennial plant with an underground storage structure (Figure 13) (Hitchcock & Cronquist, 2018). Come springtime on Coast Salish territories, long basal leaves emerge from underground bulbs. As the leaves capture sunlight and acquire resources, a terminal raceme emerges and blooms with pale to deep blue-violet (occasionally creamy white) flowers from late April to late May (Hitchcock & Cronquist, 2018). This showy floral display attracts an array of pollinator insects and along with common camas, creates a beautiful sea of purple across coastal oak meadows. Reproducing both sexually and asexually through bulb division, each flower that matures into a capsule produces several shiny black seeds that have a lengthy maturation period of five or more years (Beckwith, 2004; Carney et al., 2021).

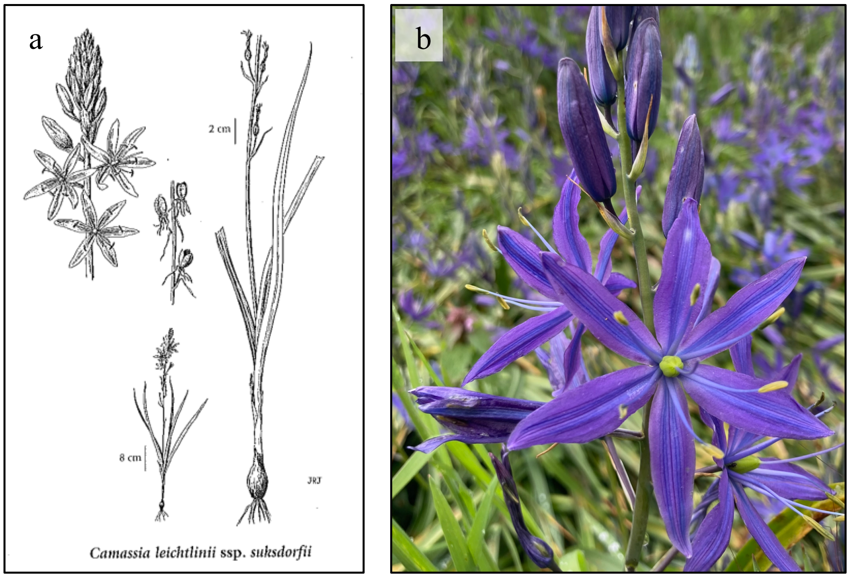


Figure 13. (a) Botanical illustration of great camas bulb, leaf, flower, and seed capsule morphology (Hitchcock et al., 1969) and (b) great camas (*Camassia leichtlinii*).

Great camas bulbs are usually solitary and have black or brown tunics (Beckwith, 2004). They range in shape and size depending on age, growing conditions, and location (Figure 14). Juvenile camas bulbs can take several years to reach optimal depth and maturity for reproduction, and over this time they can exhibit a variety of shapes including an elongated form that likely facilities the downward movement of the bulb as it increases in age (Beckwith, 2004). Each year, the bulb develops new scales from a terminal bud. The bulb is composed of two developmental sections: the mother bulb and the developing daughter bulb (Beckwith, 2004; Maclay, 1928; Thoms, 1989) (Figure 14). The older scales of the mother bulb envelope the developing scales of the daughter bulb in the early spring. As spring progresses, the daughter bulb uses carbohydrates stored in the mother bulb and increases in size while the mother bulb decreases in size and beings to shrivel. The development of an immature daughter bulb occurs in the weeks after seed set and this new bulb becomes next year’s mother bulb (Beckwith, 2004; Maclay, 1928; Thoms, 1989). The resources stored in the bulbs can enable camas plants to remain dormant during the growing season or abort growth if conditions are suboptimal, for example, in the case of drought or resource limitations (Beckwith, 2004).

Figure 14. (a) Great camas (*Camassia leichtlinii*) bulbs range in size and shape and (b) consist of two developmental phases: the mother bulb and the daughter bulb.

3.3.2 Study design

Seventy-five adult great camas bulbs were salvaged from a development site in Langford, BC in June 2022, and a further sixty purchased from a local supplier in July 2022 for a total of 135 bulbs. All bulbs were of reproductive age, having bloomed and developed fruiting capsules in the 2022 growing season. Immediately after acquiring, the bulbs were planted in Black Earth soil (a humus-rich potting soil) and left outdoors in Victoria, BC. In September 2022, the bulbs were moved into cold storage where they were kept at 5° C with no light or moisture for four months. On January 10, 2023, the bulbs were measured, weighed, and replanted 10cm deep into 1.6L tree pots with 968g of Black Earth soil. The bulbs ranged from 5.2 - 13.1mm in circumference and 2.3 - 37.1g in weight. On January 11, 2023, all the bulbs were moved into a greenhouse where they were exposed to twelve hours of sunlight every day for the duration of the experiment and all pots were watered regularly to ensure similar soil moisture content between treatments. The average ambient air temperature in the greenhouse was 21°C for each month of the experiment from January to April 2023 (average lows of 20°C and average highs of 23°C). To shorten the growing season, the greenhouse air temperature was higher than what is typical during the camas growing season in Greater Victoria (average lows of 1-11°C and average highs of 9-22°C from February to July) (Environment Canada, 2023).

The 135 bulbs were separated into the two source populations and then randomly divided into a cross-treatment design with eight treatments; each treatment had nine bulbs from the salvage site and seven bulbs from the local provider (Table 4). The extra seven bulbs were randomly distributed among Treatments 1-7. For this study, the focus was on three locally important environmental factors associated with urbanization in Greater Victoria: soil compaction, canopy cover, and grazing. Increased soil compaction can physically impede root growth and seedling establishment of plants, and alter the oxygen, water, and nutrients available to plants, resulting in reduced above- and belowground growth (Alameda & Villar, 2012; Kuss & Graefe, 1985; Mariotti et al., 2020). The soil in the soil compaction treatments in this experiment was compacted in two layers using a 10lb sliding drop hammer (based on a modified version of the Proctor method) into a concrete mold. Soil was filled to 10cm from the top of the pot and compacted with fifteen drops from the hammer. The bulb was then placed in the pot and the remainder of the soil added. Five more drops from the hammer compacted the soil to an approximate surface compaction of 1.5 kg/cm^2.

Table 4. The eight treatments in the cross-treatment design.

	Treatment							
	1	2	3	4	5	6	7	8
Grazing	√			√	√		√	
Canopy cover		√		√		√	√	
Soil compaction			√		√	√	√	

Increased canopy cover, which tends to reduce plant exposure to sunlight and therefore capacity to undergo photosynthesis, can initiate highly variable responses in plants, with some responding with a reduction in growth and competitive vigor and others exhibiting increased aboveground growth to compete for limited light resources (Arenas-Corraliza et al., 2021; Kutschera & Briggs, 2013). The canopy cover treatment in this experiment shaded all pots in Treatments 2, 4, 6 and 7, using garden shade fabric that was rated to block 50% of incoming light.

Lastly, consistent herbivore grazing on vegetative and reproductive structures is frequently correlated with reduced overall plant fitness (Gonzales & Arcese, 2008; Hawkes & Sullivan, 2001; Stephan et al., 2017; Thompson & Johnson, 2016). Grazing in this experiment was performed twice during the growing season using shears to trim 50% of the leaves present. The method of grazing was designed to mimic how deer graze camas plants in the field. The first round took place from February 6-17, 2023, in the order of days since emergence, and the second from March 17-29, 2023, in the same order. The longest leaf was measured, and all leaves were cut at the height of half that length.

3.3.3 Data collection

Plant trait data were collected on individuals in the order they emerged, occurring from March 8 – April 5, 2023. The traits selected for measurement have been observed as variable and likely to respond to the three factors simulated in the experiment (Alameda & Villar, 2012; Arenas-Corraliza et al., 2021; Hawkes & Sullivan, 2001; Kutschera & Briggs, 2013; Mariotti et al., 2020; Stephan et al., 2017) and are important for understanding plant fitness (Borowy & Swan, 2020; Pérez-Harguindeguy et al., 2013). I also intended to measure reproductive traits; however, only a few of the plants that emerged produced an inflorescence and bloomed (11%). The plants that bloomed were recorded and the flowers hand-pollinated (with pollen from the same individual), but the sample size was too small to analyze reproductive traits.

To measure leaf traits, the two outermost leaves were collected from each individual. The leaves were cut as close to the soil surface as possible and stored in sealed plastic bags with damp paper towel. A breath was added into the bags to enhance CO_2 concentration and air humidity, which minimizes transpiration and water loss (Pérez-Harguindeguy et al., 2013). Samples were stored in a fridge until scanned for leaf area later the same day using WinFOLIA software (Regent Instruments Canada Inc., 2020). Both leaves were scanned at the same time for a total leaf area measurement. Once scanned, the leaves were placed in a drying oven at 70°C for 72 hours and weighed for dry mass. Specific leaf area (SLA) was calculated by dividing fresh leaf area by dry leaf mass. Foliar biomass was calculated by dividing leaf dry mass in half (for the average dry mass of one leaf) and multiplied by the number of leaves per plant.

The plants were not watered after March 24, 2023 to encourage senescence and dormancy. On April 24, 2023, the plants were moved into a growth chamber set to 27°C with grow lights illuminating the chamber eight hours per day (with the shade cloth still covering the plants in the canopy cover treatment). On May 3, 2023, once the aboveground vegetation had fully died back, the bulbs were dug up and measured and weighed.

3.3.4 Statistical analysis

All analyses were performed using R statistical software (version 4.2.1, R Core Team, 2022). The analysis of great camas vegetative growth traits was performed by fitting a linear regression between each growth trait (the response) and canopy cover, soil compaction, grazing, and pre-season bulb mass (the predictors). There were three questions guiding model structure: 1) what is the individual effect of canopy cover, soil compaction, and grazing on vegetative response traits? 2) what is the combined effect of the three factors (the eight treatments) on vegetative response traits? and 3) how does the effect of bulb mass interact with canopy cover, soil compaction, and grazing to affect vegetative response traits (e.g., are larger bulbs more resilient to environmental stressors)? (Table 5). These three model structures were run for each response trait and outputs from the Akaike Information Criterion corrected for small samples sizes (AICc) using the *AICcmodavg* package in R (Mazerolle, 2023) were compared. Any models with < 2 delta AICc were considered to have the highest support.

Table 5. The three different model structures run for each great camas vegetative growth trait response variable.

Model	Model structure
1. individual effect	~ bulb_mass + compaction + canopy + graze
2. combined effect	~ bulb_mass + treatment_type*

3. bulb mass interaction	~ bulb_mass + compaction + canopy + graze + (bulb_mass*compaction) + (bulb_mass*canopy) + (bulb_mass*graze)

*treatment_type has eight levels (the eight treatments): control, canopy cover, compaction, grazing, canopy cover/grazing, canopy cover/compaction, compaction/grazing, and canopy cover/compaction/grazing.

Bulb origin was not included as a random effect (to account for the non-independence in observations from the same source population) as there are only two 'levels' or groups (bulbs were either from the salvage site or the local producer) and random effects require at least five levels to achieve robust estimates of variance (Harrison et al., 2018). Bulb origin was also not included as a fixed effect because it was highly correlated with pre-season bulb mass. Out of the 135 bulbs planted, 116 emerged (86%) for a sample size of n=116, however, over the growing season some plants withered partially or entirely, leading to smaller sample sizes for the leaf trait models.

The analysis of great camas resource allocation back into the bulbs was performed by fitting a linear regression between the relative change in bulb mass over the season (the response variable) and canopy cover, soil compaction, grazing, and foliar biomass (the predictors). Relative change in bulb circumference was highly correlated with relative change in bulb mass, thus, bulb mass alone was used in subsequent analysis. There were two questions guiding the structure of the bulb resource allocation model: 1) what is the individual effect of canopy cover, soil compaction, and grazing on the relative change in bulb mass over the season? and 2) what is the combined effect of the three factors (the eight treatments) on the relative change in bulb mass over the season? (Table 5). The AICc outputs were compared, and the top model selected for data visualization. The sample size was n=134 as one bulb had broken down and was no longer present for the post-season bulb measurements. See Table 6 for all response variables and associated sample sizes.

Table 6. Definitions of response variables including units and sample size.

Response variable	Definition (units)	Sample size
Longest leaf	Length of the longest leaf per individual (cm)	111
Foliar biomass	(Dry mass of two leaves / 2) * number of leaves per individual (g)	102
Specific leaf area (SLA)	Area of two leaves / dry mass of two leaves per individual (mm^2/mg)	102
Bulb mass relative change	(Post-season – pre-season bulb mass) / pre-season bulb mass (%)	134

All analyses employed a linear model (LM) using the lm() function in R. For each response, residuals were plotted against fitted values, a histogram of residuals was visually examined, the normality of a quantile-quantile plot was assessed, and a Shapiro-Wilk test was run (a p-value ≥ 0.05 satisfies a normal distribution) to assess if the data satisfied the assumptions of a normal (Gaussian) distribution. All response variables satisfied the assumptions of a Gaussian distribution except specific leaf area which exhibited positive skew in the histogram of residuals. The specific leaf area response variable was log-transformed to meet the assumptions of a Gaussian distribution. All models were further checked and validated using the *performance* package (Lüdecke et al., 2021) and the *DHARMa* package (Hartig, 2022) in R (Appendix D.2). While interpreting the models, beta estimates were considered significantly different form zero if the 95% confidence interval did not overlap zero. The models were visualized using the ggpredict() function from the *ggeffects* package (Lüdecke, 2018).

3.4 Results

The model structure selected for further analysis and data visualization for each response trait is highlighted in Table 7. The top model was selected for all response variables. For longest leaf, the three different model structures were within <2 delta AICc of each other, however, the model structures including interactions did not provide additional information that the top model did not capture.

Table 7. AICc table of the vegetative growth trait and bulb resource allocation linear mixed models. *k* is the number of parameters and $AICc_w$ is the AICc weight. The model structure selected for further analysis and data visualization is in bold (Table 8).

Response	Model structure	*k*	AICc	ΔAICc	$AICc_w$
Longest leaf	**no interaction**	**6**	**727.87**	**0.00**	**0.42**
	interaction between treatments	10	728.39	0.52	0.32
	interaction between pre-season bulb mass and treatment	9	728.80	0.93	0.26
Foliar biomass	**interaction between pre-season bulb mass and treatment**	**9**	**-36.94**	**0.00**	**1.00**
	interaction between treatments	10	-14.94	22.04	0.00
	no interaction	6	-12.90	24.04	0.00
SLA	**no interaction**	**6**	**-143.75**	**0.00**	**0.90**
	interaction between pre-season bulb mass and treatment	9	-138.85	4.90	0.08
	interaction between treatments	10	-135.86	7.89	0.02
Relative change in bulb mass	**no interaction**	**6**	**-37.17**	**0.00**	**0.92**
	interaction between treatments	10	-30.95	6.22	0.04

Longest leaf was negatively related to grazing and positively related to pre-season bulb mass. Foliar biomass was positively related to pre-season bulb mass and the interaction between pre-season bulb mass and canopy cover, and negatively related to the interaction between pre-season bulb mass and grazing. Specific leaf area was positively related to canopy cover and negatively related to pre-season bulb mass (Table 8 and Appendix D.1).

Table 8. Summary of the growth trait and bulb allocation models using the top model structure outlined in Table 7. β is the beta coefficient, and CI is the confidence interval. Predictors with a significant relationship to the response variable are in bold (p-value < 0. 05).

Response	Sample size	Predictor	Distribution	β	95 % CI	p-value	Adjusted R^2
Longest leaf	111	**pre-bulb mass**	gaussian	**0.57**	**[0.44, 0.70]**	**<0.001**	0.62
		grazed		**-12.23**	**[-14.55, -9.92]**	**<0.001**	
		canopy cover		1.28	[-1.03, 3.60]	0.279	
		soil compaction		-0.25	[-2.60, 2.09]	0.833	
Foliar biomass	102	**pre-bulb mass**	gaussian	**0.05**	**[0.04, 0.06]**	**<0.001**	0.85
		grazed		0.03	[-0.11, 0.18]	0.670	
		canopy cover		-0.14	[-0.28, 0.01]	0.065	
		soil compaction		-0.07	[-0.22, 0.07]	0.341	
		pre-bulb mass*graze		**-0.02**	**[-0.03, -0.01]**	**<0.001**	
		pre-bulb mass*canopy		**0.01**	**[0.00, 0.02]**	**0.023**	
		pre-bulb mass*compaction		0.00	[-0.01, 0.01]	0.717	
Specific leaf area	102	**pre-bulb mass**	gaussian, log transformed	**-0.01**	**[-0.01, -0.01]**	**<0.001**	0.46
		grazed		0.00	[-0.04, 0.05]	0.891	
		canopy cover		**0.07**	**[0.03, 0.12]**	**0.003**	
		soil compaction		-0.04	[-0.08, 0.01]	0.118	
Bulb mass relative change	134	grazed	gaussian	-0.05	[-0.12, 0.02]	0.178	0.08
		canopy cover		-0.06	[-0.13, 0.01]	0.116	
		soil compaction		-0.02	[-0.09, 0.05]	0.603	
		foliar biomass		**-0.12**	**[-0.20, -0.05]**	**0.001**	

All vegetative growth traits were significantly related to pre-season bulb mass. With an increase in pre-season bulb mass, longest leaf was predicted to increase on average 134% from 17.02 cm [CI 14.24, 19.80] to 39.84 cm [CI 35.59, 44.08], and foliar biomass 4,260% from -0.05 g [CI -0.19, 0.09] to 2.08 g [CI 1.84, 2.35]. Specific leaf area was predicted to decrease on average 36% from 2.88 mm2/mg [CI 2.72, 3.03] to 1.84 mm2/mg [CI 1.70, 1.99] (Figure 15). Relative change in bulb mass over the season was significantly related to foliar biomass with the relative change in bulb mass predicted to decrease on average 89% from -35% [CI -0.42, -0.27] to -66% [CI -0.82, -0.49] with an increase in foliar biomass.

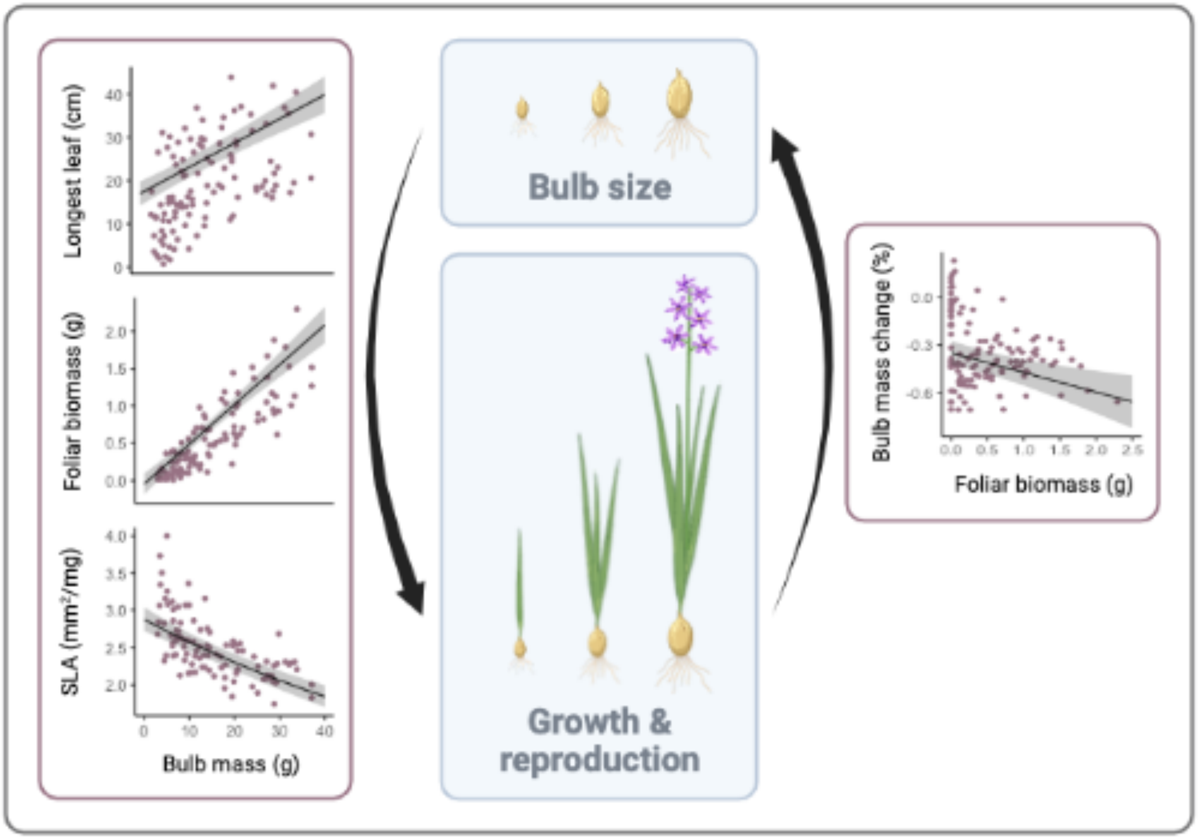


Figure 15. Great camas growth traits are strongly correlated to pre-season bulb mass with longest leaf and foliar biomass increasing with greater pre-season bulb mass and specific leaf area decreasing. Great camas vegetative growth strongly impacted resources allocated back into the bulbs, with relative change in bulb mass decreasing with greater foliar biomass.

3.5 Discussion

The marginal amount of plasticity observed in this study is likely a consequence of environmental conditions in the present growing season being largely manifested in future growing seasons in spring geophyte species (Werger & Huber, 2006). Great camas, like other spring geophytes, make optimal use of the short growing season by developing belowground storage organs and preforming their leaves and reproductive structures in the previous growing season, enabling them to emerge quickly and complete sexual reproduction before surviving relatively unfavourable conditions in a dormant state (Beckwith, 2004; Werger & Huber, 2006).

The preformation of plant structures assists camas in coping with predictable seasonality but may limit its capacity to respond to different environmental pressures on short time scales. Thus, phenotypic plasticity within a single growing season in great camas may be limited to highly plastic structural traits, such as SLA, that are not as constrained by organ preformation (e.g., number of leaves) (Werger & Huber, 2006).

In this study, specific leaf area and foliar biomass were the two growth traits that exhibited a response to the treatments, to canopy cover and to the interaction between pre-season bulb mass and canopy cover, respectively (Appendix D.1). Specific leaf area (SLA) increased in response to canopy cover and is a largely plastic growth trait that has been observed to readily respond to changes in light conditions (Borowy & Swan, 2020; Liu et al., 2016; Mondal et al., 1986). An increase in SLA suggests that shade-grown leaves had less volume, a response commonly observed across plant species including geophytes (Liu et al., 2016; Mondal et al., 1986; Popović et al., 2016; Wein et al., 1988). Foliar biomass responded to the interaction between pre-season bulb mass and canopy cover with plants with larger bulbs producing more foliar biomass under canopy cover than those with smaller bulbs. Greater bulb mass infers more resources stored in the bulbs and therefore capacity to invest in aboveground growth (Khodorova & Boitel-Conti, 2013; Rees, 1969), providing a competitive advantage for plants with larger bulbs in limited light environments. The interaction between pre-season bulb mass and canopy cover indicates that bulb size has the potential to buffer, or intensify, the effects of urban pressures on great camas vegetative growth. Foliar biomass also appeared to respond to the interaction between pre-season bulb mass and grazing, however, this was a consequence of the method in which the leaves were grazed (all leaves cut to half the length of the longest leaf), and longest leaf appeared to decrease in response to grazing but this was due to the leaves being measured after the first round of grazing occurred.

The importance of past growing seasons on spring geophyte growth and reproduction is further evidenced in this study by the observation that great camas growth traits were strongly related to pre-season bulb mass. It is well-established in the literature that bulbous geophyte growth traits are strongly related to bulb size (Khodorova & Boitel-Conti, 2013; Rees, 1969; Werger & Huber, 2006). Beckwith (2004) found this to be true of *Camassia* spp. where great camas (*C. leichtlinii*) bulb mass was significantly related to aboveground traits (leaf number, flower number, and flowering stalk height). Larger bulbs have more stored resources and increased capacity to invest in aboveground growth (Khodorova & Boitel-Conti, 2013; Rees, 1969). In our study, longest leaf and foliar biomass increased with greater pre-season bulb mass, and specific leaf area decreased. Reduced specific leaf area with greater pre-season bulb mass suggests that the leaves growing from larger bulbs have more volume than those from smaller bulbs.

Across treatments, nearly all (92%) of the bulbs lost mass from the start to the end of the growing season, likely due to forcing the growing season into a shorter window, high temperatures early in the vegetative growth phase, stress associated with transplanting, or another unknown source of stress for the plants. Over half of the bulbs in the experiment lost 4g - 22g of mass over the season (an average decrease of 5.4g), with potentially severe impacts for subsequent seasons of growth and plant fitness. Under normal growing conditions, bulbous geophytes tend to gain bulb mass after each season (Khodorova & Boitel-Conti, 2013). During active aboveground growth in the spring, bulb species accumulate carbohydrates through photosynthesis and transport them towards their bulbs, leading to bulb enlargement (Khodorova & Boitel-Conti, 2013). Beckwith (2004) observed that camas bulbs on average increase in size and weight over time but not at a steady rate. Forcing the growing season into a narrow window may not have given the plants enough time to capture resources during their growth phase and reallocate carbohydrates into the bulbs. Fortanier (1971) found that tulips forced to grow on a 6-month cycle were 10-20% smaller than bulbs forced to grow on an 8-month cycle. Warmer temperatures during the spring aboveground growth phase have also been noted to reduce bulb size in spring geophytes (Bertrand & Lapointe, 2023; Gandin et al., 2011; Khodorova & Boitel-Conti, 2013). Warmer temperatures improve photosynthetic activities, but the leaves senesce (die back in anticipation of dormancy) earlier, preventing the bulb from reaching a larger size (Bertrand & Lapointe, 2023; Khodorova & Boitel-Conti, 2013). Warmer temperatures can also increase photosynthetic activities so much that they exceed the capacity for the plants to transport assimilated carbohydrates in their tissues into their bulbs resulting in no net gain in bulb mass (Gandin et al., 2011; Khodorova & Boitel-Conti, 2013). The average ambient air temperature in the greenhouse was warmer than the typical climate conditions of the Greater Victoria region during the camas growing season, and on January 28, 2023, a heat valve broke in the greenhouse and the camas plants were subjected to high temperatures (daily maximums of 26-30°C) for 3 days. This was during their early vegetative growth phase which in a natural setting is characterized by cool air and soil temperatures (Beckwith, 2004; Davis & Davis, 2021). These warmer temperatures likely affected the capacity of the camas plants to reallocate carbohydrates into their bulbs by increasing photosynthetic activity to the point of exceeding resource allocation into the bulbs and by triggering early senesce. The removal of two leaves per plant for the leaf trait measurements may have confounded this further by reducing resource capture capacity and therefore resources available to be transported into the bulbs.

Despite the treatments not explaining the relative change in bulb mass over the season, foliar biomass was strongly related to the change in bulb mass. Plants with greater foliar biomass had the greatest loss of bulb mass over the season. The connection between aboveground biomass and underground storage organ size are well understood, with larger bulbs producing more aboveground biomass, and greater aboveground biomass resulting in increased carbon fixation capacity, often leading to more resources transported back to the bulb resulting in bulb enlargement (Beckwith, 2004; Khodorova & Boitel-Conti, 2013; Lapointe, 2001). The camas plants in this experiment that produced the most foliar biomass also experienced the most relative loss in bulb mass, likely due to these plants having expended the most resources into aboveground growth without being able to replenish them during a short growing season; a likely result of the warm temperatures triggering senesce and affecting carbohydrate accumulation (Bertrand & Lapointe, 2023; Gandin et al., 2011; Khodorova & Boitel-Conti, 2013).

The short growing season, high early season temperatures, and stress associated with transplanting may have also impacted inflorescence development. The intent of this study was to investigate reproductive traits as well as growth traits, however, only 11% of plants (of those that emerged) in the experiment bloomed. An additional 14% produced a visible inflorescence but were aborted before maturation. The abortion of inflorescences and low rates of flowering in geophytes has been associated with transplanting stress and adverse environmental conditions including warm temperatures and drought (Beckwith, 2004; Khodorova & Boitel-Conti, 2013).

By aborting inflorescences under unfavourable growing conditions, camas can hold onto resources in the bulb that would otherwise be expended and not replenished (Beckwith, 2004). Exploratory results with the thirty-four plants that produced an inflorescence in this study confirmed this; on average, individuals that aborted their inflorescence lost less mass over the season than those that bloomed (Figure 16).

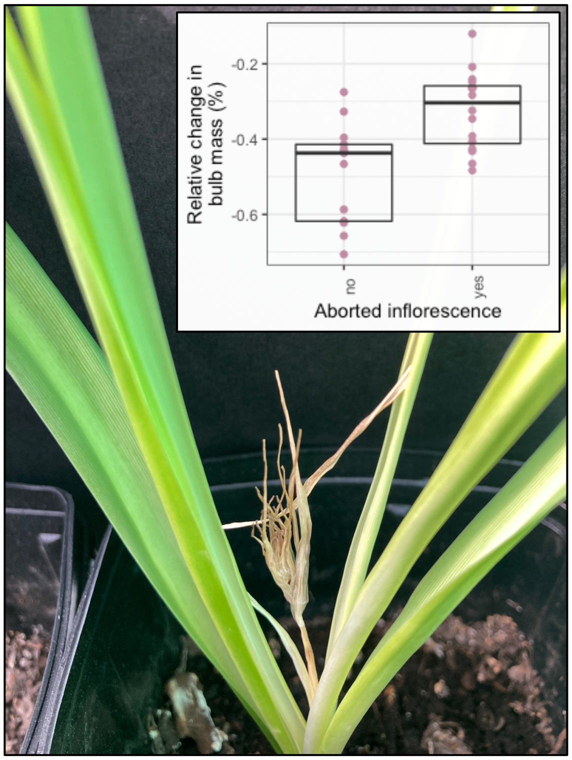


Figure 16. Out of the great camas plants that produced an inflorescence, those that aborted their inflorescence lost significantly less bulb mass on average than those that bloomed.

The results of this study suggest that camas may be increasingly susceptible to the effects of warming air temperatures. Understanding that camas populations exist across an increasingly urbanized landscape in Greater Victoria, urban pressures may be compounded by warming temperatures, with potential implications for camas fitness and persistence in this region. Temperature plays a predominant role in controlling growth and flowering in bulb species (Khodorova & Boitel-Conti, 2013). In the face of climate change and an increased likelihood of extreme heat events in BC (Rodenhuis et al., 2009), camas may become increasingly exposed to higher-than-normal temperatures during the spring vegetative growth phase, affecting growth, reproduction, and bulb development with potentially severe implications for the success of camas populations into the future. This study has shown that warmer temperatures may not only narrow the optimal window for growth and reduce resources stored in bulbs but can also severely affect seed production by triggering plants to abort their inflorescence. Phenotypic plasticity within the same season could play an important in role in camas adapting to extreme heat events as they occur on an unpredictable season-by-season basis (Gratani, 2014; Henn et al., 2018; Nicotra et al., 2010). In this study, great camas reproductive structures were largely aborted, saving resources that would otherwise be expended and not replenished, but aboveground growth was not as quick to respond with the plants continuing to invest in aboveground growth following the high temperatures. Further research into how great camas responds to warm temperatures during the spring growth phase would provide a better understanding of great camas phenotypic plasticity in response to temperature and provide insight into the role phenotypic plasticity may play in camas persistence across this warming landscape. Addressing the effects of climate change alongside urbanization may be essential to supporting successful urban camas populations across this landscape into the future.

3.6 Conclusion

This study highlights the limited capacity of a geophyte species to respond to environmental conditions within a single growing season. In many geophytes, phenotypic plasticity is likely constrained by organ preformation and the carry-over effect of resources from one season to the next (Werger & Huber, 2006). Some plasticity may be possible in certain leaf structural traits, such as specific leaf area, but further observational studies are required.

The limited capacity of great camas to exhibit trait plasticity in response to different pressures within one growing season suggests that camas is less adaptable to rapidly changing environmental conditions, such as those associated with urbanization. On the other hand, the capacity of geophytes to store resources may enable camas to buffer against unfavourable growing conditions in a particular year by remaining dormant or relying on previously stored reserves (Beckwith, 2004; Werger & Huber, 2006). Research that examines camas response to pressures associated with urbanization in a controlled environment over multiple growing seasons would provide better insight into how camas growth, reproduction, and bulb development are impacted by changing environmental conditions.

This study indicates that temperature may be just as important as urbanization when trying to understand camas success and persistence on this landscape in Greater Victoria. The negative effects of temperature on great camas growth, reproduction, and bulb development highlight the need for further research into the effects of warm temperatures during spring vegetative growth. This research would provide important insight into how camas may fair in the face of a changing climate and an increase in the likelihood of extreme heat events in BC (Rodenhuis et al., 2009). Adapting management strategies to consider how a changing climate, alongside the effects of urbanization, may impact urban camas populations would help support the persistence of successful camas populations across Greater Victoria for generations to come.

Chapter 4: General conclusion

4.1 Overview of results

The objective of my thesis was to examine the functional trait responses of common camas (*Camassia quamash*) and great camas (*Camassia leichtlinii*) to urban pressures in Greater Victoria, BC. I did this by examining whether urbanization is associated with key modified environmental conditions in Greater Victoria (Chapter Two), assessing how common camas individuals may be responding to these altered conditions (Chapter Two), and investigating whether great camas exhibits phenotypic plasticity in response to three selected urban pressures within a single growing season (Chapter Three).

In Chapter Two, an urban-rural gradient was defined across the Greater Victoria region with oak meadows ranging from 4-73% urban land cover in the surrounding $100m^2$. Environmental conditions and common camas growth and reproductive traits were measured across this gradient, and I found that urbanization in Greater Victoria is most strongly associated with increased soil compaction and trampling, and decreased soil depth, canopy cover, and soil phosphorus. These five pressures were weakly associated with the urban-rural gradient, but when combined using a PCA into two urbanization stress indexes (USIs), they explained a large proportion of the variance across the gradient. My analysis showed that common camas responded to urban stress, as defined by the two USIs, with an overall reduction in growth and reproductive trait values. My results demonstrate that the effects of urbanization on this landscape are complex, but that management and planning initiatives could be tailored to address key pressures associated with urbanization, such as increased soil compaction and canopy cover, to support more successful urban camas populations into the future.

In Chapter Three, I examined the phenotypic plasticity of great camas growth traits in response to soil compaction, canopy cover, and grazing in a greenhouse experiment over one growing season and investigated how these pressures impacted resource allocation back into the bulbs. This experiment highlighted the limited capacity of great camas to exhibit growth trait plasticity in response to pressures in a single growing season. Growth traits were most strongly correlated with pre-season bulb mass, a phenomenon well described in the literature (Khodorova & Boitel-Conti, 2013; Rees, 1969; Werger & Huber, 2006). Resource allocation into the bulbs was also not strongly influenced by the different pressures but nearly all (92%) of bulbs exhibited a reduction in bulb mass over the season, likely in part due to forcing a shorter growing season and the warm temperatures during the spring growth phase. Furthermore, only 25% produced an inflorescence (14% of which aborted the inflorescence before maturity), which also may have been due to the shorter growing season and warm temperatures. My results demonstrate that climate change effects (namely the increased likelihood of extreme heat events in BC (Rodenhuis et al., 2009)) may prove just as important as pressures associated with urbanization when trying to understand camas success on this landscape.

Overall, this thesis provides novel insight into altered environmental conditions associated with urbanization in coastal oak meadows in Greater Victoria, and how camas are responding to these pressures with implications for the success of urban camas populations into the future. Compounded with urbanization are the effects associated with climate change on this landscape. Planning and management of coastal oak meadows, therefore, must be adaptive to the rapidly changing environmental conditions associated with urbanization and climate change. Meaningfully engaging descendent Indigenous communities in the restoration of these ecosystems will provide immense ecological and cultural benefits. Understanding that Coast Salish stewardship practices have never been static, past practices can be adapted to assist in addressing present-day challenges (Grenz, 2020), including the complexity that urbanization and climate change pose. This research, more broadly, contributes to global efforts aimed at understanding plant functional trait responses within a species to urbanization, and the capacity of spring geophytes to exhibit phenotypic plasticity within a single growing season.

4.2 Limitations and future research opportunities

My research has made an important contribution to our understanding of how *Camassia* spp. are, or are not, responding to different pressures associated with urbanization in coastal oak meadows in Greater Victoria. There are limitations, however, that are inherent in my research project that provide opportunities for future research. In Chapter Two, I defined the urban-rural gradient using a $1m^2$ land cover data set from Caslys Consulting Ltd. (2013). This dataset is outdated but was the best available high-resolution land cover dataset at the time. Pixels within buffer zones were corrected for recent development, but an updated source would provide a better estimate of urban land cover. Future studies that aim to examine plant response across an urban-rural gradient would also benefit from incorporating additional data layers into the gradient, for example, approximate time since conversion to urban land cover, proximity to agriculture, an estimate of park visitation, among others that capture the patchy spatial and temporal development of cities. Limited by time, I developed the best gradient I could with the data available.

Time constraints were also a limiting factor in the number of replicates used in Chapter Two. Camas is characterized by a short growing season and the maximum number of replicates possible was four plots per site (with one person collecting data). Implementing a similar research project with more replicates would bolster results, particularly if they extended beyond one field season to account for seasonal climate variations from year to year that can contribute to trait measurement errors.

In Chapter Three, great camas plants were grown in a controlled greenhouse environment to shorten the growing season to fit within a limited time frame. There are different challenges associated with growing plants in a greenhouse, including accurately replicating day length, temperature, and humidity, which in a natural setting fluctuate daily. The heat valve that broke in the greenhouse also strongly impacted my experiment. It is possible that phenotypic plasticity in great camas growth traits was not observed because the plants were responding to the warmer temperatures by initiating senesce and did not have the chance to respond to the different pressures. Further research into camas phenotypic plasticity would be beneficial in an outdoor setting under typical climate conditions and day length cycles.

The bulbs in Chapter Three were from two different source populations, one from a natural setting and the other from a home garden. Beckwith (2004) highlighted how bulb characteristics can differ between plants grown in horticultural environments and natural settings. Without financial limitations, bulbs could be acquired from one source, reducing bulb variation at the outset of the experiment.

Both camas species are slow-growing, long-lived perennials that would benefit from observation in both field and greenhouse environments over multiple growing seasons. Examining the response of camas growth, reproduction, and bulb development to different pressures over multiple years would provide insight into how plastic camas growth traits may be across seasons. Research spanning multiple growing seasons could also examine the interactions between urban pressures and bulb development in a field setting. The findings in Chapter Three highlighted the strong relationship between bulb size and aboveground growth and reproduction, thus, a better understanding of how urban pressures influence bulb development may provide insight into some of the biggest drivers of camas fitness.

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Appendix A: Southern Vancouver Island oak meadow ecosystem distribution mapping

A.1 Methods

The three primary data sources used to develop the preliminary map (the BC the Sensitive Ecosystem Inventory (SEI), Lea’s (2006) Garry oak ecosystems map, and Lilley’s (2007) remnant oak savanna map) were compiled and processed using QGIS 3.4. All polygons that overlapped between Lea’s (2006) dataset and the SEI were included in the final map with corrections made for recent development. Additional SEI polygons were included to capture associated ecosystems, such as coastal bluffs and herbaceous rocky outcrops, that may not have Garry oak trees present but support meadow communities. Additional polygons were delineated based on indicator species occurrences (accessed from the Global Biodiversity Information Facility (GBIF)) (Table 9) and visually estimated locations that were field checked.

Table 9. Coastal oak meadow indicator species used to delineate polygons.

Scientific name	Common name
Allium acuminatum	Hooker’s onion
Camassia leichtlinii	Great camas
Camassia quamash	Common camas
Eriophyllum lanatum	Common woolly sunflower
Fritillaria affinis	Chocolate lily
Lomatium nudicaule	Pestle lomatium
Lomatium utriculatum	Common lomatium; Springgold
Olsynium douglasii	Satin flower
Triteleia hyacinthina	White brodiaea

A.2 Results

Figure 17 depicts a preliminary spatial distribution of Garry oak and associated ecosystems, including coastal oak meadows, on southern Vancouver Island. This dataset is incomplete and requires further field checking and the inclusion of private property.

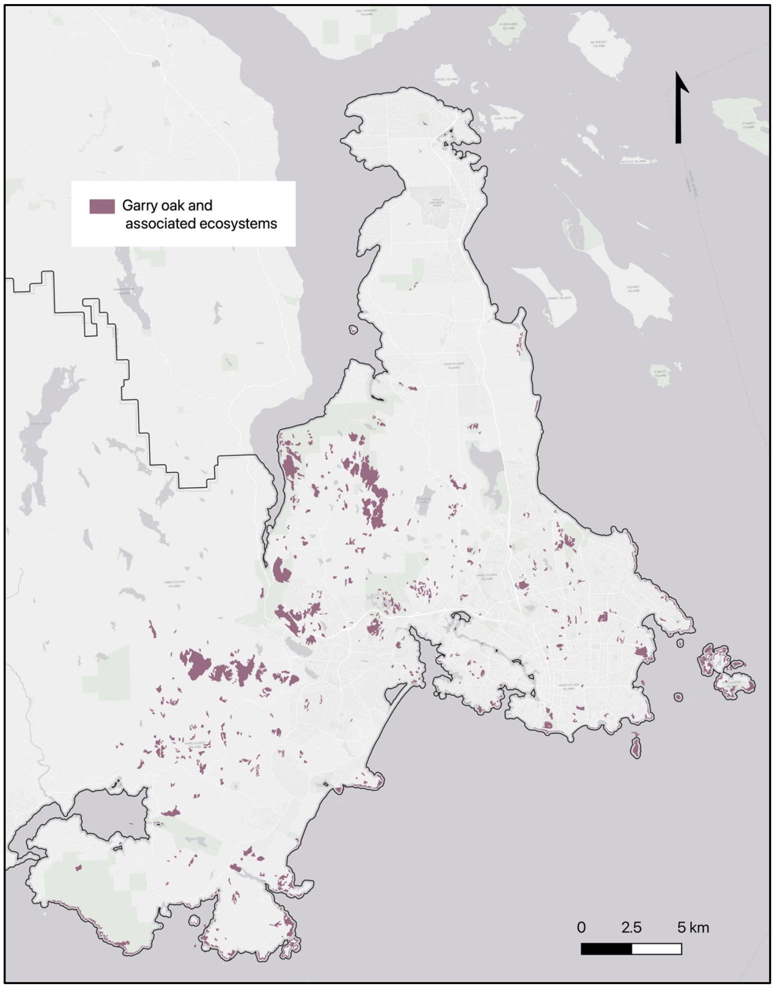

Figure 17. A preliminary map of the distribution of Garry oak and associated ecosystems on southern Vancouver Island.

Appendix B: Chapter 2 supplementary results

B.1 Plot-level outcomes

B.1.1 Plot-level parameter predictions across the urban-rural gradient

Trampling, canopy cover, soil compaction, soil depth, and soil phosphorus exhibited the strongest relationship with the percent of urban land cover in the surrounding $100m^2$ (Figure 18, Table 10). Trampling and soil compaction increased, whereas canopy cover, soil depth, and soil phosphorus decreased. Over the rural-to-urban gradient, trampling was predicted to increase 100% from 11% [CI 0.07, 0.17] to 22% [CI 0.13, 0.34] and soil compaction 110% from 0.49kg/cm2 [CI 0.33, 0.73] to 1.03kg/cm2 [CI 0.61, 1.75]. Canopy cover was predicted to decrease 50% from 52% [CI 0.38, 0.66] to 26% [CI 0.08, 0.45], soil depth 37% from 9.97cm [CI 7.61, 13.07] to 6.3cm [CI 4.39, 9.03], and soil phosphorus 56% from 70.81mg/kg [CI 35.16, 142.59] to 31.5mg/kg [CI 12.43, 80.64].

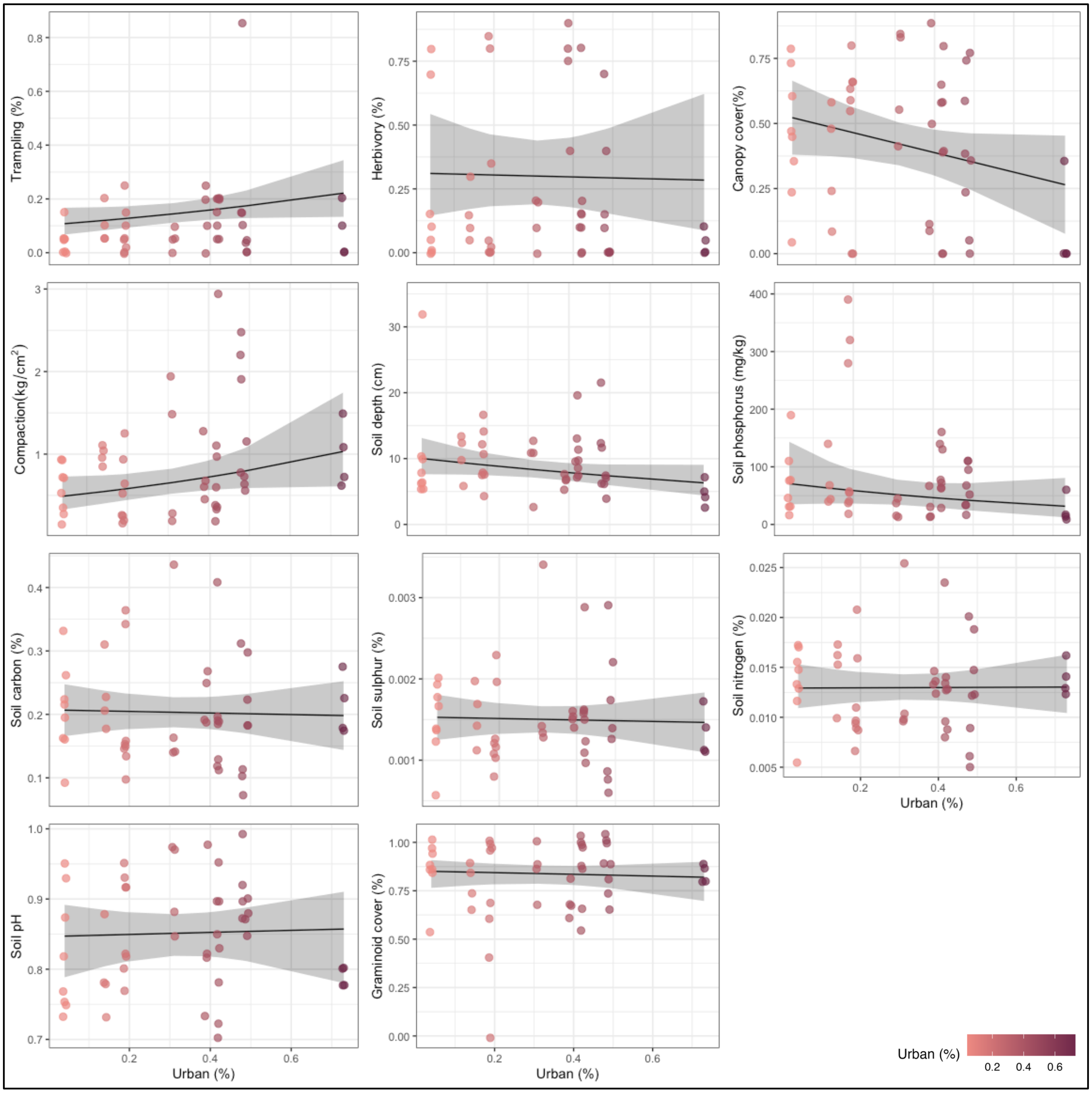

Figure 18. Linear mixed model predictions of plot-level parameter values across the urban-rural gradient.

Table 10. Plot-level mixed-effect model distributions. Response variables with a significant relationship to the percent of urban land cover at the alpha = 0.1 level are indicated in bold.

Response	Distribution	p-value
Trampling	**Beta (logit link function), zero inflation**	**0.079**
Herbivory	Beta (logit link function), zero inflation	0.905
Canopy cover	Gaussian	0.107
Graminoid cover	Beta (logit link function), zero inflation	0.670
Soil compaction	**Gaussian, log transformed**	**0.096**
Soil depth	Gaussian, log transformed	0.129
Soil phosphorus	Gaussian, log transformed	0.292
Soil carbon	Gaussian	0.840
Soil nitrogen	Beta (logit link function)	0.965
Soil sulphur	Gaussian	0.827
Soil pH	Beta (logit link function)	0.842

B.1.2 Plot-level model validation

All plot-level mixed effects models were validated using the *performance* package (Lüdecke et al., 2021) and the *DHARMa* package (Hartig, 2022) in R. The *performance* package provides utilities for computing indices of model quality and goodness of fit, and assessing mixed models for overdispersion, zero-inflation, convergence, and singularity (Lüdecke et al., 2021). The check_model() function was used to visually investigate the homogeneity of variance, the collinearity, the normality of residuals, and the normality of random effects of each model. The *DHARMa* package uses a simulation-based approach to create scaled quantile residuals for mixed models (Hartig, 2022), and the simulateResiduals() function was used to simulate model residuals and further examine model fit (Figure 19).

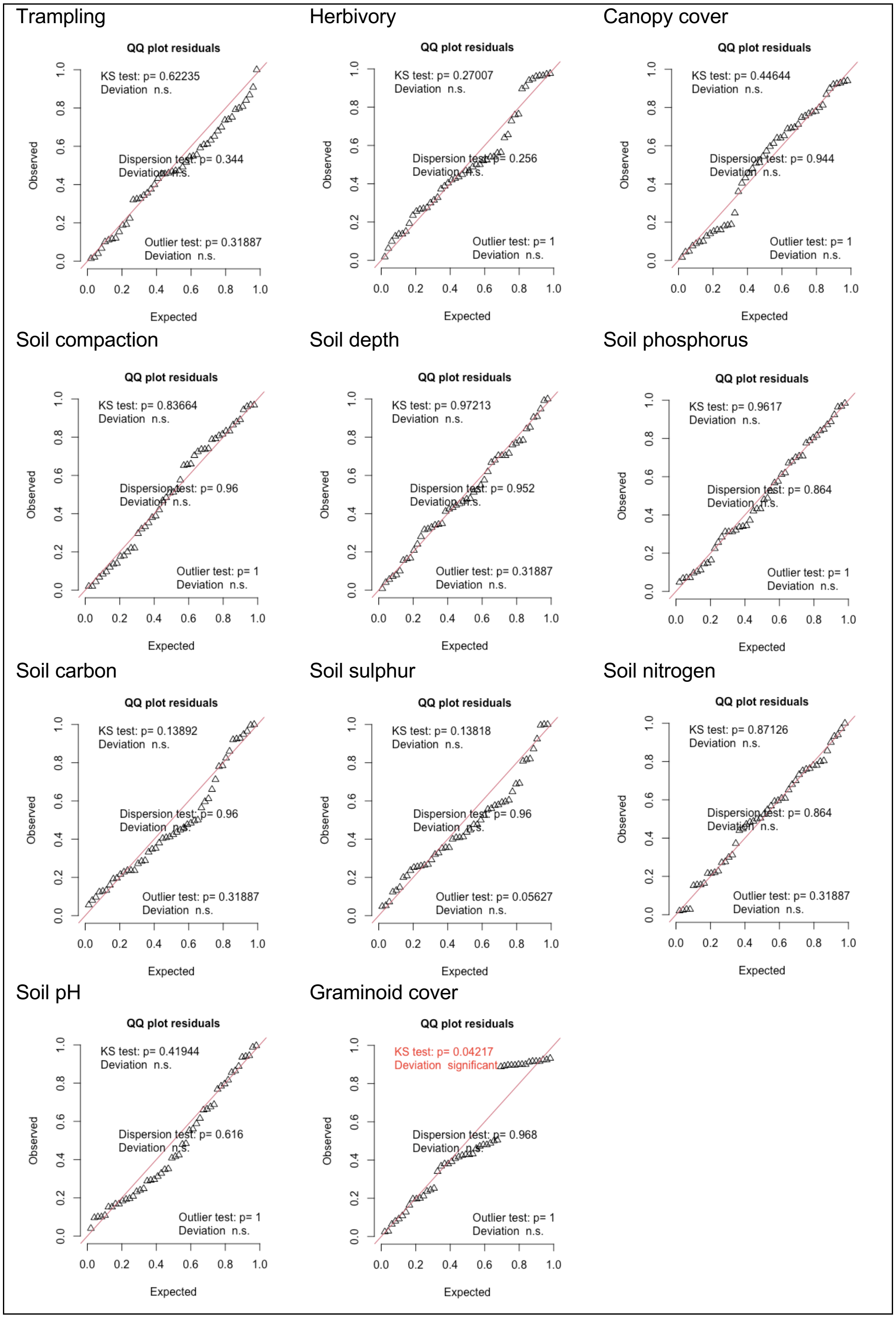

Figure 19. DHARMa quantile-quantile plot residuals for the eleven plot-level mixed effect models.

]

B.2 Plant-level outcomes

B.2.1 Plant-level model validation

The seven plant-level mixed effect models were validated using the same methods as applied to previous models (Figure 20).

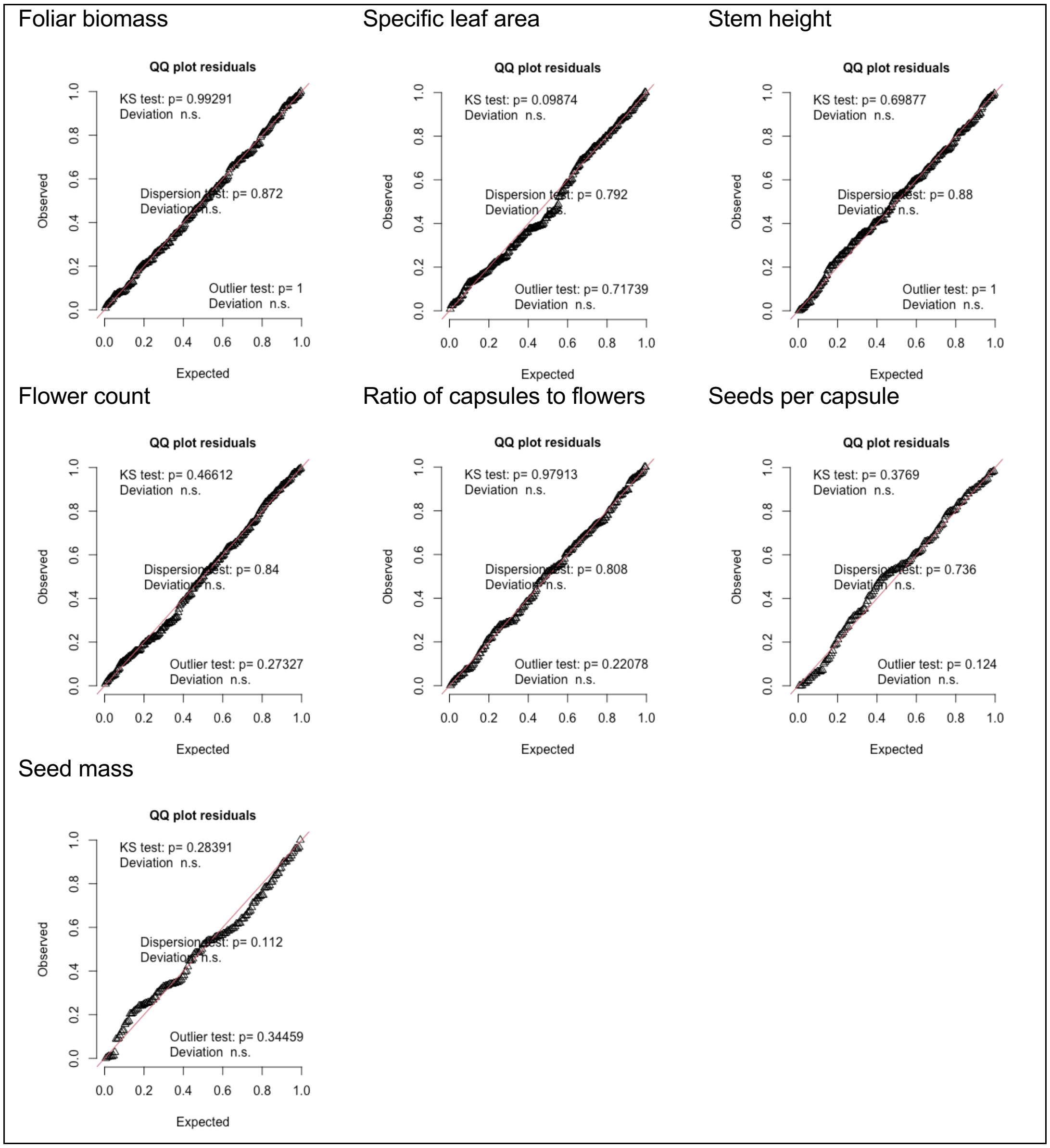

Figure 20. DHARMa quantile-quantile plot residuals for the plant trait mixed effect models.

B.2.2 Common camas trait response predictions across the urban-rural gradient

To validate the two Principal Component Analysis (PCA) axes used as predictors (fixed effects) in the linear mixed effect models that examined the common camas trait responses to urbanization, the models were run again with the percent of urban land cover in the surrounding 100m^2 as a predictor in place of the two urbanization stress indexes (Figure 21). The response variable was the plant trait measurement, the two predictors (fixed effects) were the percent of urban land cover in the surrounding 100m^2 and herbivory, and the random effect was a nested random effect of plot within study site to account for non-independence in observations within each of the four plots within each study site (Zuur et al., 2009). The same model structure fitting process was used as outlined in the plant-level analysis and the same distributions fit these models as did the ones with the PCA axes as predictors. Response variables fit with a LMM include specific leaf area, foliar biomass (log-transformed), stem height (log-transformed), and flower count (log-transformed). Response variables fit with a GLMM include the ratio of flowers to capsules (beta distribution (logit link function) and zero-inflation term), the average number of seeds per capsule (tweedie distribution), and the average mass of a single seed (tweedie distribution).

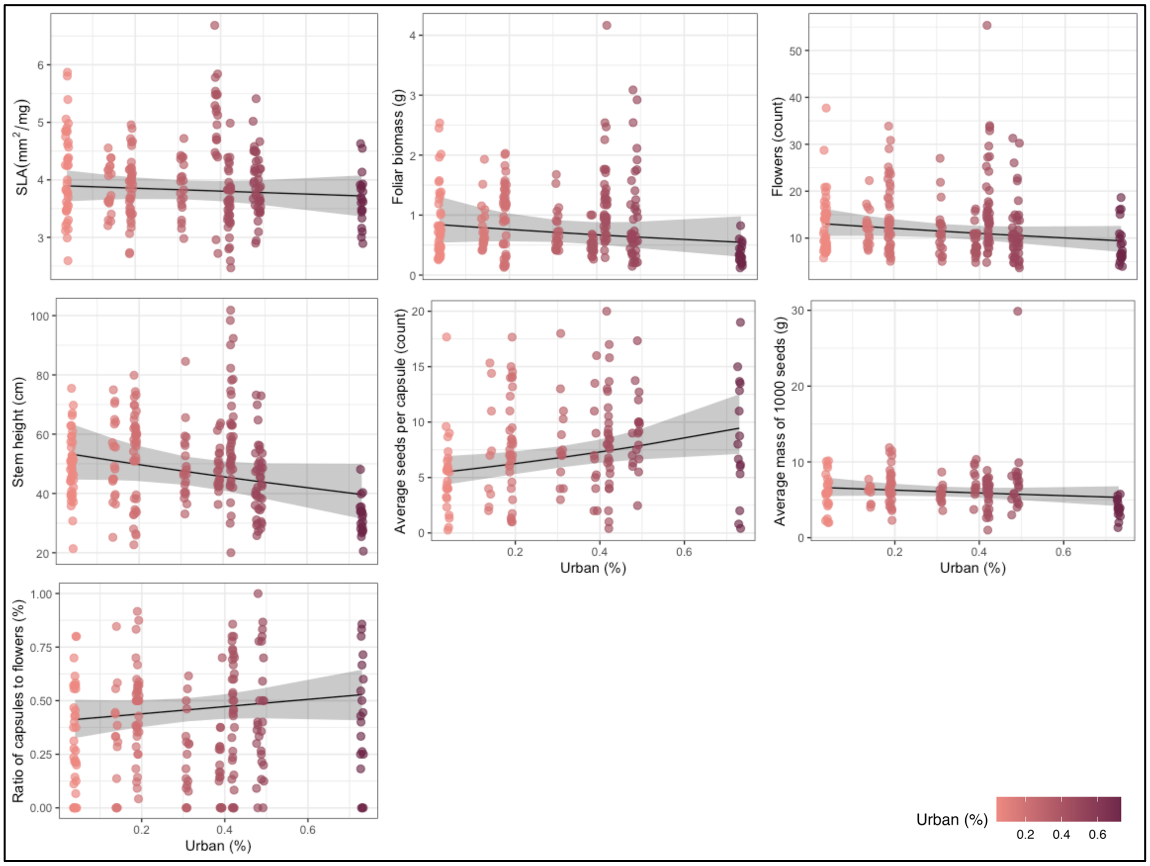

Figure 21. Linear mixed model predictions of common camas trait values across the urban-rural gradient.

The predicted relationships between the seven camas growth and reproductive traits were similar between the two sets of models (those with the PCA axes as predictors and those with urban land cover as the predictor), albeit not identical. All the trait measurements except the average number of seeds per capsule exhibited the same trend (decreased or increased with urbanization). The average number of seeds per capsule did not have a significant relationship with either urbanization stress index in the model with the PCA axes as predictors, however, this trait did have a significant relationship (p-value <0.05) in the model with the percent of urban land cover as the predictor. Despite this discrepancy between the two sets of models, the similarity in the relationships of the other traits provides the basis for utilizing the PCA axes as predictors in the liner mixed effect models used to predict common camas trait responses to urbanization.

Appendix C: Chapter 2 common camas abundance analysis

C.1 Methods

Common camas abundance was recorded as the number of camas plants in bloom, bud, or neither (juvenile plants lacking an inflorescence or adult plants whose inflorescence was absent) per quadrat. An exploratory analysis (Figure 22) examined the abundance of common camas (separated into the different life stages) across the urban-rural gradient.

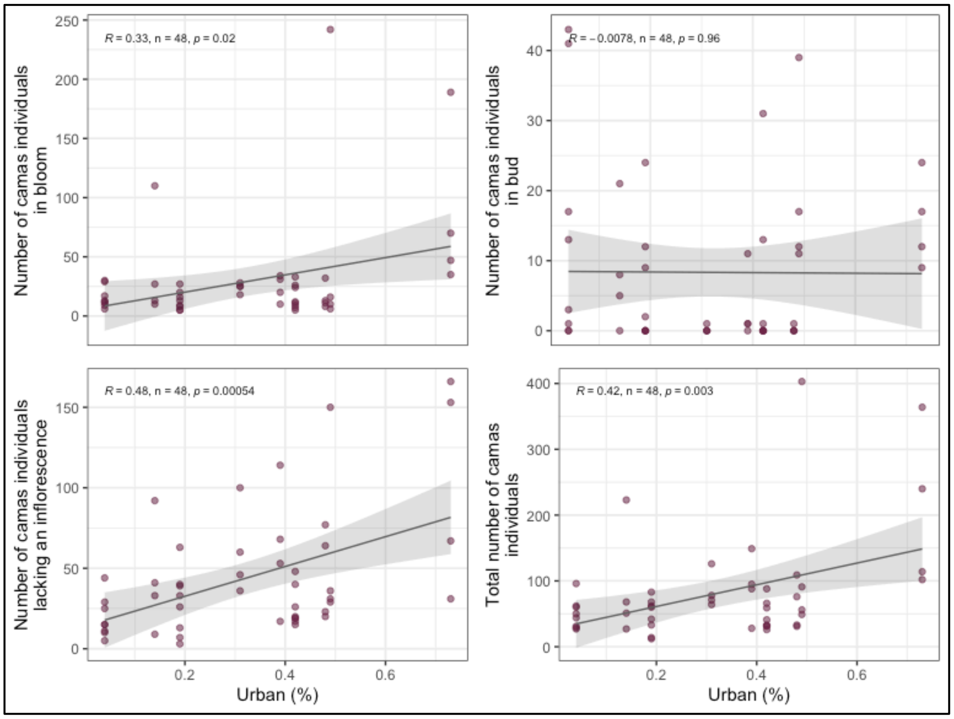

Figure 22. Exploratory linear regressions between common camas abundance and the percent of urban land cover in the surrounding $100m^2$.

A linear mixed model was run to further examine total common camas abundance across the urban-rural gradient. The response variable was the total number of camas individuals (in all life stages), the three predictors (fixed effects) were USI 1, USI 2, and herbivory, and the study site was included as a random effect to account for non-independence in observations within each study site (Zuur et al., 2009). The model was fit using a Gaussian distribution (with the response variable log-transformed) based on the same model structure fitting process as outlined in the plot-level analysis.

C.2 Results

Total common camas abundance was significantly related to both urbanization stress indexes (a p-value <0.05) (Table 11 and Figure 23). Along the urbanization stress gradient, common camas abundance was predicted to increase on average 34% from 3.66 individuals [CI 3.23, 4.09] to 4.89 individuals [CI 4.5, 4.89] (USI 1), and increase on average 32% from 3.38 individuals [CI 2.66, 4.1] to 4.46 individuals [CI 4.06, 4.87] (USI 2).

Table 11. Summary of the camas abundance mixed-effects model. β is the beta coefficient, and CI is the confidence interval. Predictors with a significant relationship to the response variable are in bold (p-value < 0.05).

Response	Sample size	Predictor	Distribution	β	95 % CI	p-value
Total camas abundance	48	**USI 1**	gaussian, log transformed	**0.18**	**[0.03, 0.32]**	**0.025**
		USI 2		**0.18**	**[0.01, 0.35]**	**0.048**
		herbivory		-0.67	[-1.37, 0.02]	0.065

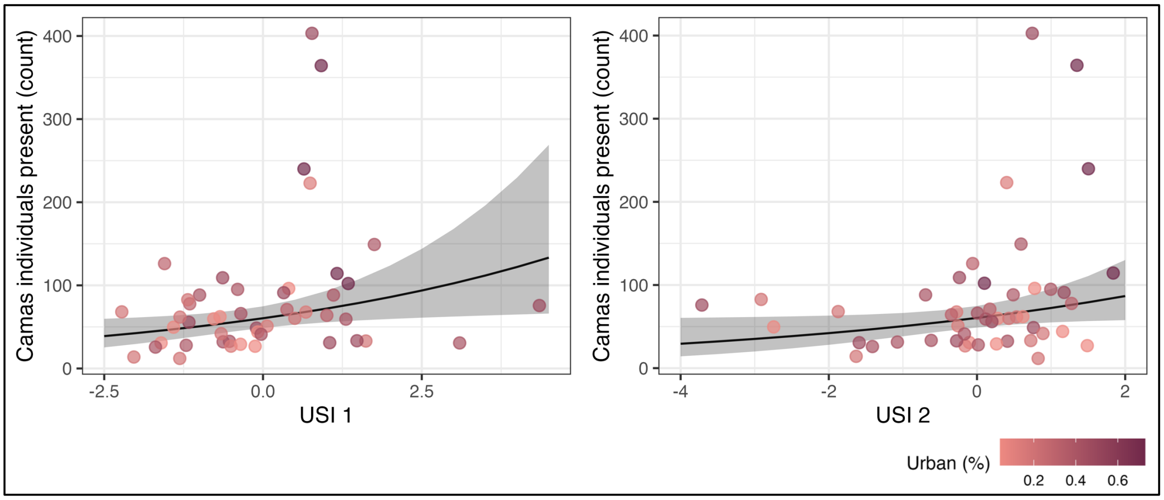

Figure 23. Assuming a linear relationship, total camas abundance was predicted to increase with both urbanization stress indexes. Greater urban stress as defined by USI 1 and USI 2 is indicated by increasing values along the x-axis.

Appendix D: Chapter 3 supplementary results

D.1 Model outcomes

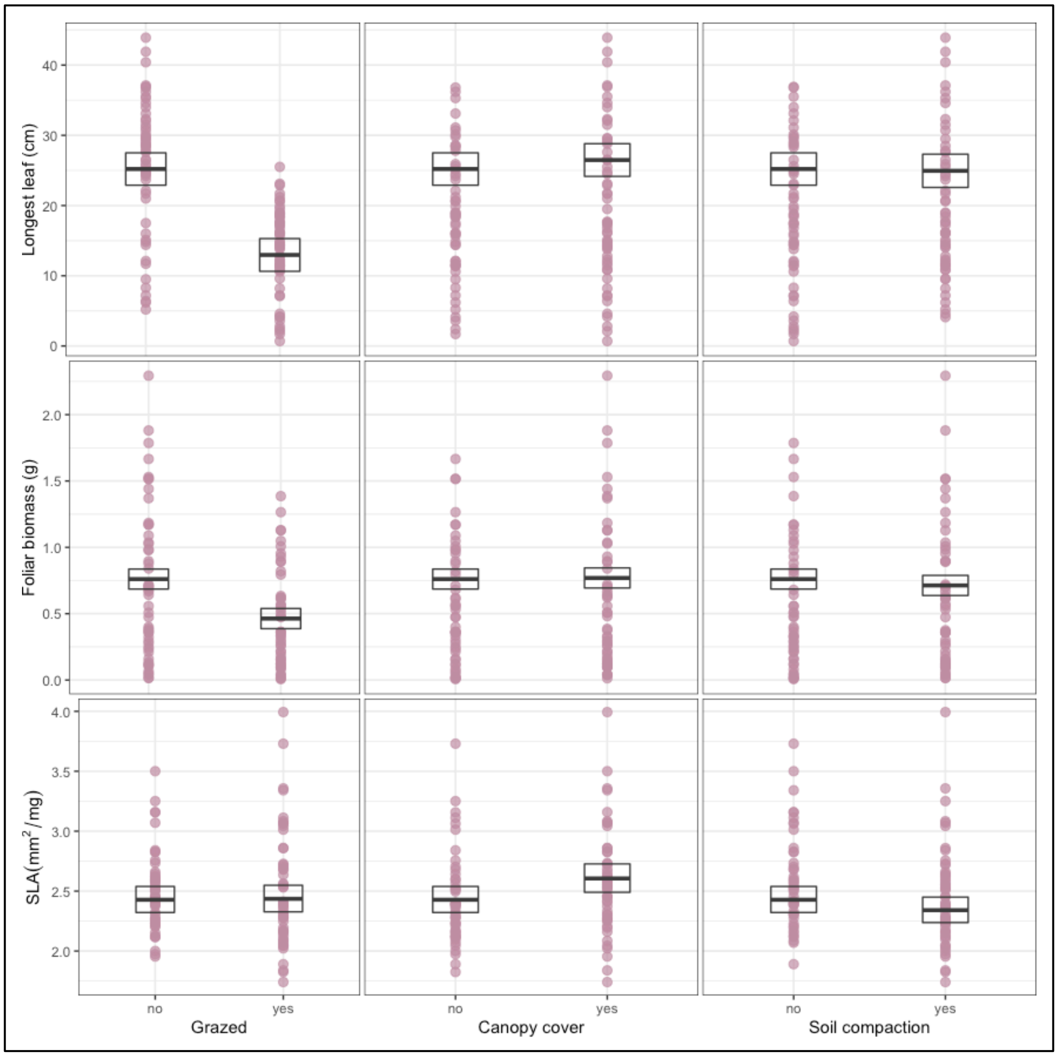

Figure 24. Great camas growth trait model predictions in response to the three pressures. Longest leaf and foliar biomass were predicted to decrease with grazing and specific leaf area was predicted to increase with canopy cover.

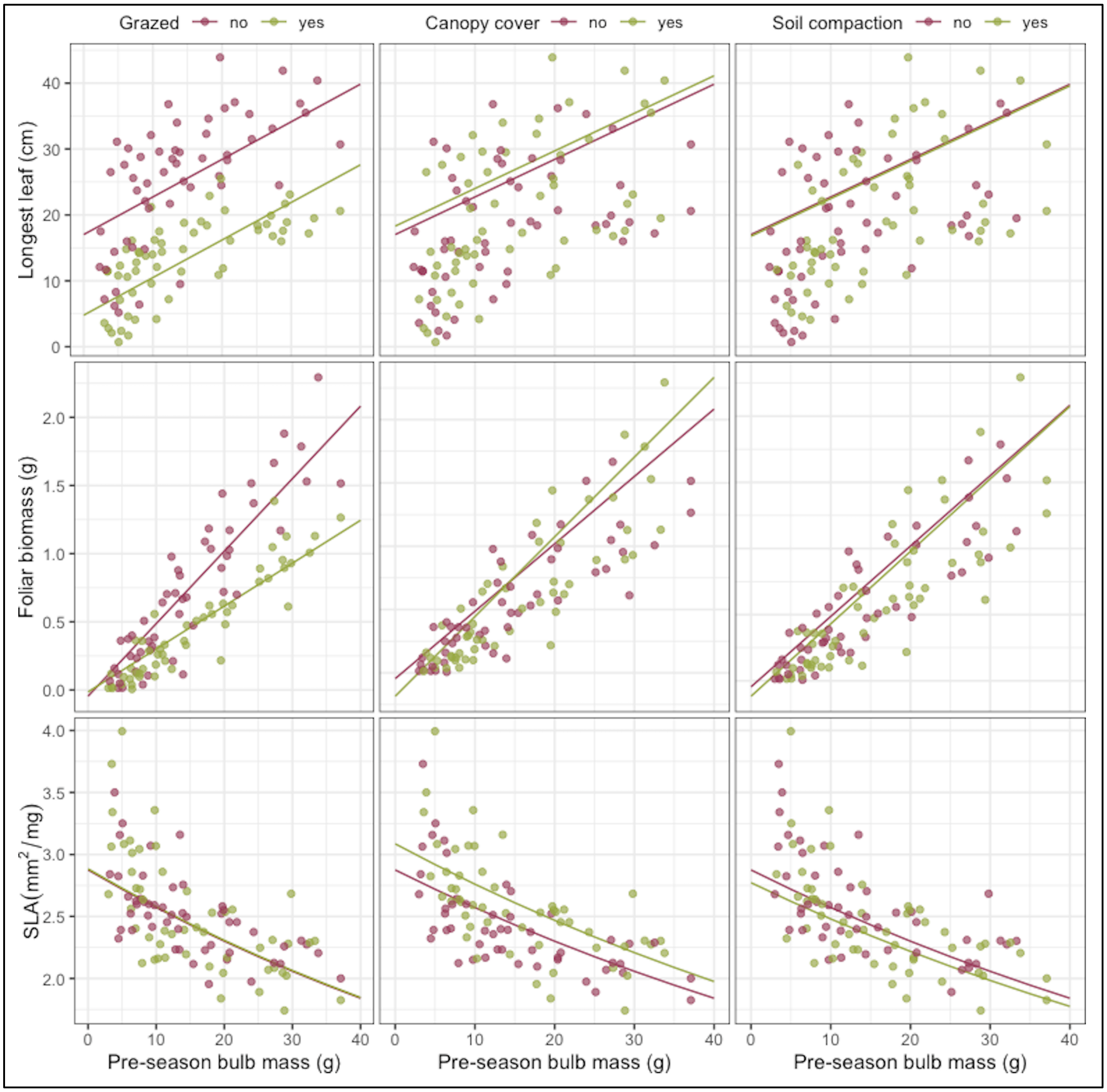

Figure 25. Great camas growth trait model predictions in response to pre-season bulb mass and the three pressures. Longest leaf was predicted to increase with pre-season bulb mass and decrease with grazing. Foliar biomass was predicted to increase with pre-season bulb mass and the interaction between pre-season bulb mass and canopy cover and decrease with the interaction between pre-season bulb mass and grazing. Specific leaf area was predicted to decrease with pre-season bulb mass and increase with canopy cover.

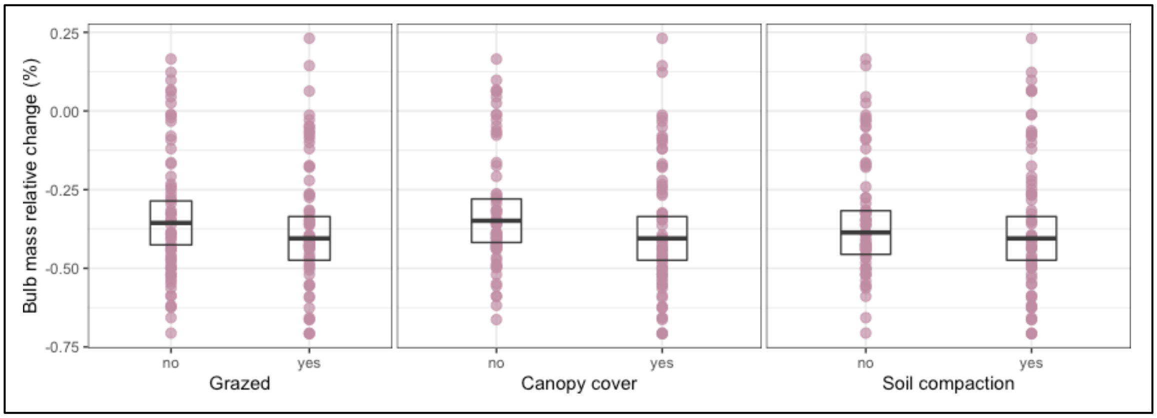

Figure 26. No significant relationships were observed between the three pressures and the relative change in bulb mass over one season.

D.2 Model validation

All models were validated using the *performance* package (Lüdecke et al., 2021) and the *DHARMa* package (Hartig, 2022) in R. The *performance* package provides utilities for computing indices of model quality and goodness of fit, and assessing mixed models for overdispersion, zero-inflation, convergence, and singularity (Lüdecke et al., 2021). The check_model() function was used to visually investigate the homogeneity of variance, the collinearity, and the normality of residuals of each model. The *DHARMa* package uses a simulation-based approach to create scaled quantile residuals for mixed models (Hartig, 2022), and the simulateResiduals() function was used to simulate model residuals and further examine model fit (Figure 26).

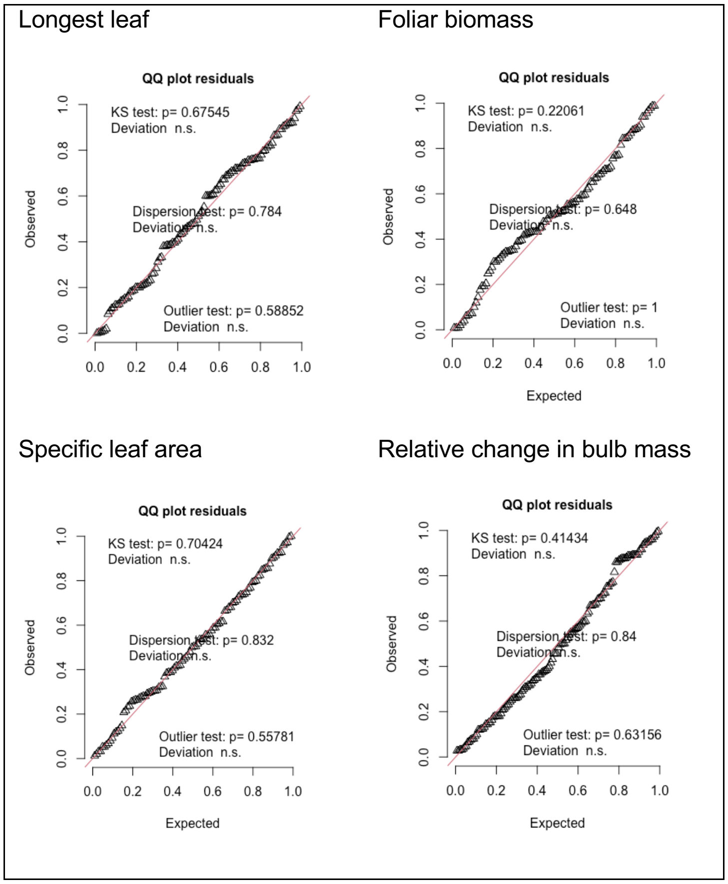

Figure 27. DHARMa quantile-quantile plot residuals for the three vegetative growth trait models and the relative change in bulb mass model.

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