

Joint Effects of Competition, Recruitment Limitation, and Fire Suppression
in an Invaded Oak Savanna Ecosystem

by

Andrew Stewart MacDougall

B.A., University of King's College/Dalhousie University, 1987
M.Sc., York University, 1991

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Abstract

Competition is often assumed to determine relative abundance in plant communities, especially in the absence of disturbance. At the community level, however, the relationship between competitive ability and abundance is rarely tested. Emerging evidence supports an alternative model where species abundance is determined as much or more by differences in dispersal ability. If true, this suggests that factors that restrict dispersal in contemporary landscapes, such as habitat fragmentation, may be more limiting for native species than competition by invasive flora. I tested the relative importance of competition and dispersal in an invaded and fire-suppressed oak savanna in southwestern British Columbia. Dominance by two exotic perennial grasses strongly suggests that competition is restricting the occurrence of native flora, many of which are presently rare. Extreme fragmentation of this savanna (habitat loss > 95%), however, suggests that dispersal may also limit their occurrence. I explored these alternatives using a combination of experimental (field and glasshouse) and biogeographical approaches. My results confirmed the importance of competition for structuring this plant community. Removal of the dominant grasses greatly increased the cover of previously subordinate native forbs. A pair-wise competition experiment revealed that the most abundant species, the invasive perennial grass *Poa pratensis*, dominates by limiting light availability and recruiting by tillering in the light-limited understory. Seed addition experiments, however, also confirmed the importance of recruitment limitation for native species. Despite low light, most native species established and survived in the grass sward. By reducing the dominant grasses and eliminating the litter layer, experimental burning increased the survival of added species but was not a necessary pre-condition for recruitment. For community structure generally, burning transformed the savanna from a grass-dominated system to one dominated by native forbs. However, because forbs are substantially less productive than grasses, litter levels dropped so that fire could not occur continuously over time, which in turn favours recruitment by grasses. Based on these results, I surmise that this system formerly oscillated between domination by grasses and forbs with fire. Long-term fire suppression explains the domination by grasses in many remnant areas presently. In combination, my work revealed that competition and dispersal interact to structure this oak savanna. Disturbance, soil depth, and annual variations in climate also have an impact on the interaction of these two factors.

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Chapter One

Introduction

"It must be remembered that plants, when once established in a suitable climate and soil, soon take possession of the country, and occupy it to almost the complete exclusion of later immigrants. The fact that so many European weeds have overrun New Zealand and temperate North America may seem opposed to this statement, but it is really not so. For in both these cases the native vegetation has first been artificially removed by man and the ground cultivated; and there is no reason to believe that any similar effect would be produced by the scattering of any amount of seed on ground already completely clothed with an indigenous vegetation."

"About this time (1810) large numbers of European, American, and South African plants were imported (to the island of St. Helena) and many of these ran wild and increased so rapidly as to drive out and exterminate much of the relics of the native flora; so now the English broom, gorse, and brambles...and some common American, Cape, and Australian weeds, alone meet the eye of the ordinary visitor. These, in Sir Joseph Hooker's opinion, render it absolutely impossible to restore the native flora which only lingers in a few of the loftiest ridges and most inaccessible precipices and is rarely seen except by some exploring naturalist."

Alfred Russell Wallace *Island Life* (1881)

"We have the apparent double anomaly, that Australia is better suited to some English plants than England is, and that some English plants are better suited to Australia than those Australian were which have given way before English intruders."

Joseph Dalton Hooker *Notes on the Replacement of Species in the Colonies and Elsewhere* (1864) [from Crosby 1986]

Of the many impacts of the colonial era (Crosby 1986), the blurring of the world's biotic boundaries by plant transportation is one of the most significant from the perspective of global biodiversity. Although the mixing of species has occurred throughout geological history (e.g., Stebbins and Major 1965, Vermeiji 1991), it is unlikely that so many of the

world's major biomes have been breached concurrently, and often by many of the same families, genera or species (Elton 1958). Given the association between invasion and the decline of native species, invasion is viewed as one of the major threats to future levels of global diversity (Myers and Bazely 2003). At the same time, our understanding of why invasions have occurred remains in its infancy. The movement of individuals into new habitats or regions is not unique to the transport of plants by humans, and has driven the assembly of many of the world's post-glacial communities (MacArthur 1972, Clark et al. 1998). However, numerous contemporary invasions have not only added to the size of local species pools (Sax and Gaines 2003) but have changed the ways by which many ecosystems function (Vitousek 1986, 1990). What is so paradoxical about this process, as pointed out by Hooker in 1884, is that invaders typically derive from different geo-evolutionary contexts than those that they invade. The ability of invasive¹ species to ignore the long-established adaptive relationship between a species and its habitat seemingly defies the foundational logic of ecological and evolutionary theory.

As intuited by Wallace (above), the key to understanding invasion lies in understanding issues related to competition, dispersal, stability, and disturbance. It is not a coincidence that these same issues are also the foundation of community and ecosystem ecology. The understanding of invasion, therefore, rests in the understanding how communities function and how these principles apply, and interact, to cause or permit invasion (Mack 1986). In many ways, this perspective forms the basis of this thesis. By studying the

¹ Note: the terms "invasive" and "exotic" are used interchangeably in this thesis to describe non-native species that have naturalized, presently occur in large numbers, and may impact community structure (i.e., composition, diversity, and physical stature of the community) or ecosystem function (i.e., changes to the pools and flows of limiting resources). Most non-native species, of course, do not have such impacts.

mechanisms that cause and maintain invasion, there may be considerable insight gained on the ecological functioning of communities in general. This, in turn, will help guide the management and control of invasive species, and the restoration of communities affected by their presence.

A fundamental challenge for understanding invasions is that they typically co-occur with a host of other transformations. Many heavily invaded ecosystems have suffered the effects of habitat loss, the isolation of remnant areas, increased global temperatures and CO₂ levels, eutrophication, or the alteration (increase or decrease) of disturbance regimes. Viewed in this way, it is often difficult to determine if invaders are the primary drivers of ecological change or merely the passengers of more fundamental transformation. Further complicating this issue is our inability to retrace the typically complex series of steps that caused the invasion. Instead, we are confronted with the end-point of years, decades, or even centuries of transformation. Unfortunately, the present-day appearance of a heavily invaded system may suggest one process (e.g., exotic dominance due to competitive superiority) while the underlying cause has actually been another (e.g., exotic dominance due to severe recruitment limitations that influences native species more than exotics) (Fig. 1-1). This theme of "things may not be as they appear" is another primary theme of this thesis. All of the experiments have attempted to test whether the most obvious process is actually causing the current pattern of diversity, or whether alternative yet hidden processes are also at play.

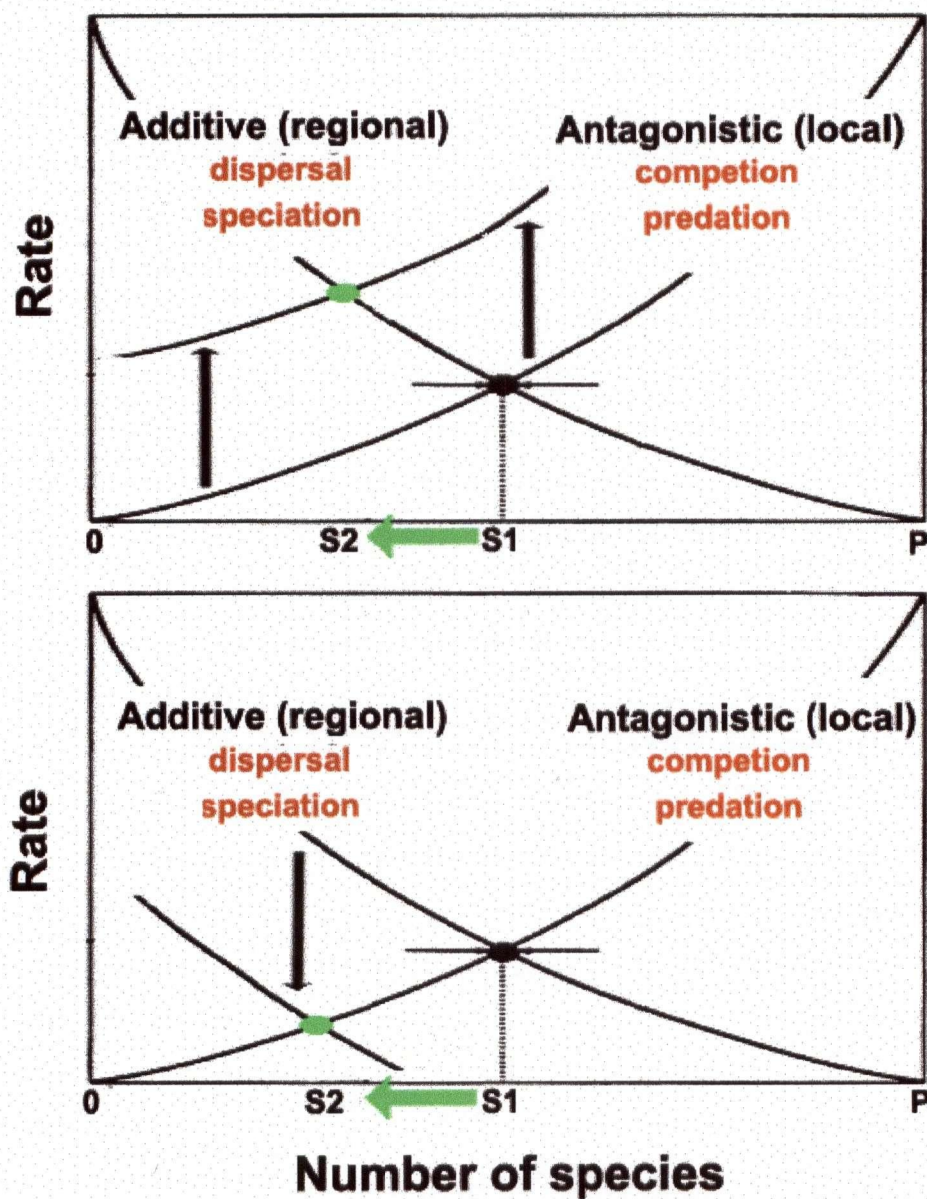


Figure 1-1. Two different interactions between regional “additive” processes and local “antagonistic” processes that can lead to the same result: reduction of species richness. In the top graph, an increase in the rate of species loss caused by competition (for example) with no change in immigration drives richness from S_1 to S_2 . In the bottom graph, a decrease in the rate of immigration with no change in competition results in the identical decrease from S_1 to S_2 . Modified from MacArthur and Wilson (1967).

Are invasive species really that different?: reflections on the competitive ability of invasives

Although Wallace assumed that invasion sometimes depended on the destabilization of the native community, there are many examples that violate this assumption. Numerous invasive species have become established, and subsequently dominated, pristine native communities. This has led to the perspective that invasion is determined by differences in competitive ability between invading and native species. Rather than depending on the de-stabilization of the native community (e.g., over-grazing, cultivation, settlement, fire suppression), invasives are simply better at acquiring limiting resources. But why do such competitive differences exist? Why should species from elsewhere have the ability to sequester the majority of limiting resources compared to the local flora or fauna?

Although the answer is not fully understood (Thebaud and Simberloff 2001, Leger and Rice 2003), research evidence points to at least three possible hypotheses: (i) escape from native pathogens or predators (competitive superiority due to an absence of enemies that were left behind) (Maron and Vila 2001, Keane and Crawly 2002, Wolfe 2002), (ii) evolution in more competitively intense environments (competitive superiority due to the traits that the invader arrived with) (D'Antonio and Vitousek 1992, Byers 2000, Callaway and Aschehoug 2000), or (iii) novel hybridization (Ellstrand and Schierenbeck 2000, Gaskin and Schaal 2002). It is beyond the scope of this thesis to fully test these alternatives. However, more simplified versions of these hypotheses are addressed: are exotic flora really that different in competitive ability, traits, life history, or susceptibility

to disturbance? And how do these differences (or similarities in some cases) relate to current patterns of relative abundance? In exploring this question, Chapin et al. (1996) hypothesized two possibilities based on the degree of trait differences between the invasive species and other members of the community. If invasives are profoundly different, then it is these trait differences that are the primary cause of invasion (e.g., invasive legumes in nutrient poor areas formerly lacking legumes). If the invaders are not that different, the primary cause of invasion will likely be environmental change (e.g., invasive fire-sensitive species in fire-suppressed oak savanna).

Testing whether dominance is caused solely by species traits or by the combination of traits and altered environmental conditions has been difficult. Case studies of invasion typically reveal a complex myriad of past events that have led to the present day levels. A classic example is *Tamarix* spp., one of the most invasive plants (several closely related species) in the United States (Busch and Smith 1993, Cleverly et al. 1997, Deloach et al. 1999, Zavaleta 2000). *Tamarix* profoundly affects ecosystem function in arid environments. It lowers the water table beyond the reach of native species, salinizes the soil due to its ability to excrete salt from its leaves, and increases fire due to its prolific output of leaf litter. However, these effects are also identical to the primary impacts of human activity in this region: lowered water tables due to damming, river diversion, and irrigation; salinization caused by the pumping of ground water, and increased fire due to human land use. Thus we have a dilemma: is *Tamarix* dominant because of its ability to change the ecosystem (i.e., driver), or merely because it tolerates the changes caused primarily by humans (i.e., passenger)? Such intractabilities plague the understanding of

many invasions. The covariance of factors, combined with uncertainty over how invasions have unfolded, leave us struggling to understand the causes of change, and how to reverse their effect. An objective of the experimental work of this project was to examine the impacts of trait differences versus the impacts of environmental change on invasion.

The role of recruitment limitation in invaded systems

If there is one paradigm that characterizes community ecology, it might be that of competitive regulation – ‘two species, one limiting resource, superior competitor eliminates the subordinate’ (e.g., Gause 1934). Such simplistic elegance appealed to mathematical ecologists of the early 20th century who wished to develop first principles of ecological organization rivaling those of physics and chemistry (Kingsland 1995). Since that time, hundreds of studies have documented the occurrence of competition and its role in structuring communities, driving succession, and causing evolutionary character displacement among closely interacting individuals (Keddy 2001).

Although the importance of competition is well recognized, some have argued that its impact has been over-emphasized at the expense of other non-interactive processes, especially immigration, that can also structure communities (Ricklefs 1987, Ricklefs and Schluter 1993). This oversight can be perpetuated because it is relatively easy to measure and model competition. By contrast, the impacts of the so-called “regional” factors (immigration, speciation) are difficult to measure because their influence is revealed only

after years, decades, or millennia. Yet these factors can have profound significance for the formation of contemporary communities (Clark et al. 1998). The debate on the relative role of competition versus regional factors has been coined “MacArthur’s Paradox” (Loreau and Mouquet 1999), after Robert MacArthur who wrote extensively on competition (e.g. MacArthur 1958) but also recognized the importance of immigration in his work with E.O. Wilson (MacArthur and Wilson 1963, 1967). Recently, much research effort has focused on the potential impacts of regional factors on local plant communities (Tilman 1997, Foster 2001, Symstad and Tilman 2001, Foster and Tilman 2003), and has confirmed their significance.

Such arguments are relevant to invasion ecology because the importance of competition for invasion may sometimes be overstated, or may interact with regional factors in ways not fully understood. In invaded communities dominated by one or a few exotic species, differences in relative abundance between the numerically dominant species and the rest of the community are sometimes assumed to directly mirror the relative ability to acquire limiting resources. Regrettably, this is rarely tested. Most studies of the effects of invasion on the decline of native species are correlative rather than causal (Levine et al. 2003), and alternative explanations are rarely eliminated. Davis (2003) has pointed out that competition by invasive species has rarely been demonstrated to be the direct cause of the loss of native species, as opposed to the effects of habitat loss that typically also affects invaded systems. Indeed, reviews by Sax et al. (2002) and Sax and Gaines (2003) indicate that the “one invasive species added, one native species displaced” model may

apply to birds in some cases but never for plants, fish, or insects. Instead, the overwhelming effect of invasion is the increase in the size of the local species pool.

The results of Sax and his collaborators are interesting because they strongly suggest that many communities may be "unsaturated" (*sensu* Srivastava 1999, Loreau 2000). That is to say, rather than community membership being tightly regulated by the battle for limiting resources (i.e., saturation) it may be more limited by the ability of species to arrive and establish. If so: *"then the key to community structure may lie in extrinsic biogeography rather than in intrinsic local processes, making community ecology more of an historical science"* (Cornell and Lawton 1992). In competition-based models of community organization, the significance of immigration is relegated to situations where competition is limited or absent (disturbances, newly created islands, immediate post-glacial landscapes). In immigration-based models, as suggested by the invasive species work of Sax, its significance is much greater. Testing these alternative models of community organization is another theme of this thesis.

Separating the impacts of local and regional processes on communities is more than an academic exercise. Because invasion is viewed as a monumental threat to native diversity (rightly or wrongly), eradication is often viewed as a critical first-step for restoration. However, the validity of this approach rests on whether the invading species are the most limiting factor for native species. If they are, removals can have dramatic positive impacts for restoration (Myers et al. 2000). However, emerging evidence suggests that things are rarely this simple (Myers et al. 2000, Zavaleta et al. 2001). If native plants are

more limited by dispersal due to habitat fragmentation, then the eradication of exotics may have no impact on their recovery. In some cases, exotics have assumed the functional role in the ecosystem that was formerly held by the species that they replaced. Eradication of the exotics, in this context, may have unanticipated consequences, such as the destabilization of food webs or the elimination of resistance to invasion by other functional groups. In grasslands, for example, invasive grasses may resist invasion by woody plants in the same manner that native species did formerly (Wilson 1998). Eliminating these invasive grasses may then hasten conversion to woodland, rather than facilitating recovery of the native grasses. The possibility that invasive species may actually have positive impacts is another of topic of interest in this thesis.

The role of disturbance in invaded systems

All ecosystems are not invaded equally. Many of North America's northern temperate forests, for example, have been largely unaffected by invasion. In contrast, grasslands and savannas have been severely impacted (Grace et al. 2001). In some Californian grasslands, *Bromus tectorum* now comprises 100% of the species cover. *Poa pratensis* and *Dactylis glomerata*, two perennial grasses of primary interest in this thesis, have invaded many mesic grasslands in Canada and the United States (Curtis and Partch 1948, Etter 1951, Towne and Owensby 1984, Schadt and Stubbendieck 1985, Sullivan 1992). Other problematic grassland invaders of North America include: 1) grasses such as *Agropyron cristatum*, *Bromus inermis*, *Bromus japonicus*, *Cynodon dactylon*, and *Imperata cylindrical*; 2) forbs such as *Euphorbia esula* and *Centaurea* spp.; and 3) shrubs

such as *Cytisus scoparius*, *Rhamnus cathartica*, and *Triadica sebifera* (Christian and Wilson 1996, Mooney and Hobbs 2000, Grace et al. 2001). Combined with the effects of habitat loss and over-grazing, grasslands are considered some of the world's most endangered ecosystems (Ricketts et al. 1999).

Grasslands and savanna² are characterized by the dynamic interplay of fire, climate, topography, soil depth, and grazing (Anderson 1990, Knapp et al. 1998, Collins 2000). These factors underlie the evolution of the grassland biome (Axelrod 1985), and presumably many of the species found within. Since the onset of European settlement in North America, this dynamic has been completely reconfigured (i.e., intensive agriculture) or largely eliminated (fire suppression). In areas not converted to an agronomic monoculture, fire suppression is viewed as a major cause of grassland decline (Leach and Givnish 1996) and a contributing factor for invasion (Grace et al. 2001). The re-introduction of fire, therefore, has been proposed as a tool for grassland restoration, including the control of invasives.

A central assumption of this view, however, is that fire will favour natives over exotics. This assumption is rarely tested, however, and may be untrue (Grace et al. 2001). Many grassland invaders have evolved in pyrogenic environments (e.g., the Mediterranean), or are simply unaffected by fire. Fire is also assumed to be a stabilizing factor in grasslands, despite its destructive properties. By offsetting the effects of intense competition (by native and exotic species) and preventing conversion to woodland, repeated fire is

² Note: *grassland* = general term for ecosystems with grass-dominated understories; *savanna* = grass-dominated ecosystems with tree canopy cover from 5-50% (Anderson et al. 1999).

assumed to preserve grassland function. However, this model is spatially dependent (i.e., requires sites elsewhere that are fire-free) and thus operates regionally rather than locally (DeAngelis and Waterhouse 1987, Collins 2000). Unfortunately, grassland ecosystems no longer possess their former regional extent. Instead, remnant areas are small, isolated and contain populations of native plants that are shadows of their former occurrence. Fire, therefore, may behave in completely different ways in these remnants than occurred formerly. The "rush to burn" has thus been questioned (Howe 1994a, 1994b, 1995, Collins et al. 1998). Although the positive impacts of fire for restoration are not debated, considerable research is still required to determine how it interacts with habitat loss, grazing, invasion, and the timing and intensity of its application. Such issues are the focus of Chapter Seven

Invasion in the Quercus garryana savanna

All of the issues described above apply to the fragmented, invaded, and fire-suppressed *Quercus garryana* Lit. (hereafter called Garry Oak) savanna of southwestern British Columbia. This system, therefore, is perfectly suited to test hypotheses on the effect of competition, recruitment limitation, plant invasion, fire, and habitat loss on the structure and function of plant communities. It is one of Canada's most threatened terrestrial ecosystems (Fuchs 2001), now covering only 5% of its former range with remnant areas that are highly isolated and heavily invaded. The co-occurring impacts of invasion and habitat loss present the opportunity to test models of local vs. regional regulation of present-day community structure in this savanna. While the non-native species are

numerically dominant, most do not appear to possess substantial morphological or functional differences from the native species they have replaced. This raises the question of why invasion has occurred, and presents the opportunity for testing the impacts of subtle trait differences, environmental gradients, and disturbance on the interaction between exotic and native species from the four major functional groups of this savanna (annual and perennial grasses and forbs). Finally, this formerly pyrogenic ecosystem has been largely free of fire for at least a century. By experimentally re-introducing fire, the effects of burning on competition, the availability of limiting resources, and invasive species control can also be tested.

These questions are explored using results from four years of experimental work conducted mostly at the Cowichan Garry Oak reserve in the Cowichan Valley of British Columbia. Based on this work, there are three over-arching goals in this thesis: 1) to test hypotheses on the impacts of competition, dispersal, and disturbance on community structure generally; 2) to examine how competition, dispersal, and disturbance influences invasion, and 3) to explore methods for conservation and restoration of this nationally endangered savanna ecosystem. More specifically, the objectives are:

- (i) To test for differences in relative competitive ability among morphologically similar invasive and exotic species.
- (ii) To test for evidence of recruitment limitation of native plant species.
- (iii) To determine the impact of competition, soil depth, and disturbance (fire) on the recruitment of native species.

- (iv) To determine the short- and long-term impacts of dispersal on diversity in remnant areas for native and exotic flora using biogeographical analysis.
- (v) To determine the impact of the dominant invasive species on the structure and function of the oak savanna plant community.
- (vi) To determine the impacts of fire on competitive interactions and successional stability within the oak savanna.
- (vii) To determine the impacts of long-term human activity on the present-day structure of the oak savanna, including invasion.

Organization of the thesis

Several chapters in this thesis are stand-alone papers that have been or will be submitted to journals. To smooth out any discontinuities that this may cause, the objectives of each chapter and how each connects to the overall story of the thesis are outlined below.

Chapter Two provides a brief natural history of the Garry Oak ecosystem. Understanding how this savanna functions rests in part in understanding its biogeographical context. The most pressing questions are: why and how does a xeric oak savanna ecosystem with mostly Californian floristic affinities occur amongst some of the wettest temperate forest of the world? The answers are explained mostly by a unique combination of climatic and topographic factors. These factors determine the seasonal weather patterns, local microclimate, and long-term migration of plant species into this region from the south.

They also explain in part why this ecosystem may be so vulnerable to the effects of contemporary habitat loss, fire suppression, and invasion.

Chapter Three focuses on one specific element of the biogeographical story: the impacts of human activity on ecosystem function. This chapter was co-written with Brenda Beckwith and Carrina Maslovat (both from the University of Victoria). The historical descriptions that served as the basis for this paper are presented in Appendix 2. Although many of North America's ecosystems are assumed to have been "pristine" prior to European colonization, the existence of formerly untrammelled wilderness may be more fiction than fact (Russell 1997, Boyd 1998, Vale 2002, Keeley 2003). Lands surrounding the Strait of Georgia (i.e. southwestern British Columbia) apparently supported the densest concentration of indigenous peoples in North America prior to the influx of old-world diseases in the late 1770s (Harris 1997). The Northern Straits Salish of this region depended greatly on the oak savanna for plant and animal resources, and influenced its composition and structure by burning and the introduction and intensive harvest of numerous plant species (Suttles 1987, Duer 2002). By the 1860s, European settlers began pouring into the region. Many preferentially settled in the savanna region due to the favorable climate and its high agricultural potential. Thousands of domestic livestock were introduced, as were numerous plant species. In combination, the impact of First Nation and European inhabitants has probably influenced the oak savanna for millennia. Determining how and to what degree this influence shaped the savanna is critical for understanding its functioning generally, as well as the underlying causes of invasion and the decline of native species.

Chapter Four addresses two questions: (i) does competition alone explain why morphologically similar exotic and native perennial grasses differ so widely in relative abundance? and (ii) if it does, are these competitive differences determined by the traits of the invaders or by the environmental conditions of the savanna, especially disturbance? Davis et al. (2000) suggested that invasion is contingent on environmental change, either by nutrient enrichment (eutrophication) or by disturbances that free limiting resources. As discussed earlier, the view that invasion depends on disturbance has a long history (Wallace 1881). By implying that native communities will resist invasion unless disturbed, it suggests that invading species may not be profoundly different competitors than the species they replace. Or, that the exotics are superior competitors but only in the context of intensive agriculture-based disturbance to which the exotics are presumably well adapted. These issues are examined using glasshouse and field experiments that compare competitive strategies (“competitive suppression” vs. “competitive tolerance” ability) among four grasses of similar life history. *Poa pratensis* and *Dactylis glomerata* (note: hereafter called *Poa* and *Dactylis*) currently dominate the savanna, while *Bromus carinatus* and *Elymus glaucus*, native perennial species, are relatively uncommon.

Chapter Five tests the relative importance of competition and dispersal for explaining the relative abundance of native and exotic plants in the oak savanna. Because *Poa* and *Dactylis* are so abundant compared to all other species, it suggests that they are limiting these other species competitively. Alternatively, habitat fragmentation may be seriously

restricting the ability of the less-common species to disperse. Their absence may thus be caused by recruitment limitations rather than competition. This is tested experimentally using the addition of seed from 10 forb species of various local abundances (common to rare). If competition regulates abundance, then recruitment success should be extremely low in the dense grass swards of *Poa* and *Dactylis*. If dispersal is most limiting, then recruitment from the added seed should be high regardless of the exotic grasses.

To assess the longer-term implications of this experiment, I conducted a biogeographical analysis comparing the relative abundance of major functional groups between the regional species pool (British Columbia) and site-level pools within remnant areas of the Cowichan Valley on southeastern Vancouver Island. Biogeographical analyses are generally qualitative procedures that are becoming increasingly utilized to test the impacts of regional processes on local communities (Ricklefs 1987, Naeem and Wright 2003). I test whether the relative abundance of species within each functional group at the regional level predicts the relative abundance of species in each site. This can only happen if: 1) membership in each site is determined by a lottery (e.g., if 60% of all species regionally are perennial grasses, then 60% of species per site should be perennial grasses), and 2) that membership is not regulated by competition or site factors (e.g., establishment should not favor species from the competitively superior functional group – perennial grasses). There are two reasons why we would *not* expect full concordance between regional and site-level species pools. First, annual grasses and annual forb species produce prolific quantities of seed that disperse much greater distances compared with most perennial forbs and grasses. If dispersal determines membership in sites, then

these groups should be over-represented. Second, perennial grasses are highly effective competitors in these savannas due to their ability to produce dense layers of foliage and litter. If competition determines membership in sites, then this group should be over-represented compared to the other three. Confirmation of one or the other of these two factors would indicate that regional processes have little importance for site-level dynamics in this savanna.

Chapter Six further examines the relationship between the causes of dominance (by *Poa* and *Dactylis*), and the impact of dominant species on the abundance of other species in the community. Increasing evidence points to the separation of processes causing commonness and rarity in plant communities (e.g., Hubbell 2001). As described above, if native species are more limited by dispersal than competition then the removal of the dominant grasses (*Poa* and *Dactylis*) should have little or no impact on the abundance of subordinate species. We test this with a factorial experiment that includes treatments that reduce the presence of the dominant grasses (mowing) and eliminates them (selective removal). These treatments also give the opportunity to examine the role of the exotic grasses on the suppression of woody plant invasion. Conversion of savanna to woodland has affected many oak savanna remnants in the Pacific Northwest but is hypothesized to be slowed by the presence of a dense grass sward. If the dominant exotic grasses have replaced the functional role of the native grasses, their removal may cause unanticipated increases in woody plants rather than increases in native grasses or forbs.

Chapter Seven examines the impact of fire on the fire-suppressed savanna community. Because of its former importance, fire has been touted as a critical first-step for restoration. It is hypothesized that burning will offset the competitive impacts of the exotic grasses. However, not only may rarer species be unaffected by competition but models of ecological stability predict that repeated fire may be as destabilizing as intense competition (DeAngelis and Waterhouse 1987, Huston 1994, Collins 2000). Re-introducing fire, therefore, may not immediately transform exotic grassland into a species-rich community of native plants. The effects of burning on native species with late summer phenologies (when fire usually occurs) may be especially problematic. Given the small size of remnant areas, fire threatens the persistence of these species including the regional endemic *Sericocarpus rigidus* that is evergreen and flowers in late summer. We test the effects of fire on community stability by monitoring its relative impact on productivity, reproduction, and the abundance of functional groups.

Chapter Eight concludes the thesis by synthesizing the various results of the proceeding chapters

Chapter 2

Brief Natural History of the Garry Oak Savanna

Ecosystem

Introduction

The Garry Oak savanna ecosystem of southwestern British Columbia is part of a prairie and oak savanna vegetation complex that extends south to California via the San Juan Islands and Puget Trough of Washington, and the Willamette Valley of Oregon (Fig. 2-1). Extensive habitat loss and high levels of exotic plant invasion characterize all parts of the range. In British Columbia, the oak savanna is concentrated in southeastern Vancouver Island from Victoria to Comox, and on the southern Gulf Islands. Limited occurrences of Garry Oak and associated ground flora are also known from the lower Fraser Valley and from Savary Island west of Powell River.

The Garry Oak savanna is regionally unique in part because it occurs in close proximity to one of the world's wettest temperate climates. The processes that maintain xeric oak savanna in the Pacific Northwest derive from a combination of topography, soil, fire, and climate (Roemer 1972, Jungen 1985, Fuchs 2001). In British Columbia, it occurs in the rain shadow of the Olympic Mountains and the Vancouver Island Coastal Range. The soils are highly variable in composition and drainage but are generally moderately infertile, glacially derived and well drained. Soils in lower lying areas (<100 m)



Figure 2-1. Major areas of oak savanna occurrence in the Pacific Northwest of North America. The boxed area delineates the ecosystem's distribution on the Saanich Peninsula of southeastern Vancouver Island, as presented in Fig. 3-1.

often contain high amounts of clay and silt deposited as glacio-marine material during the end of the last glacial period. Seasonal variations in Pacific Ocean currents create a sub-Mediterranean climate with wet cool winters and warm dry summers. Prevailing winds are mostly from the southwest in the winter, and from the northwest in the summer. Average annual precipitation on southeastern Vancouver Island range from 50 – 150 cm year⁻¹ (Fig. 2-2). Winter temperatures rarely fall below 0° C.

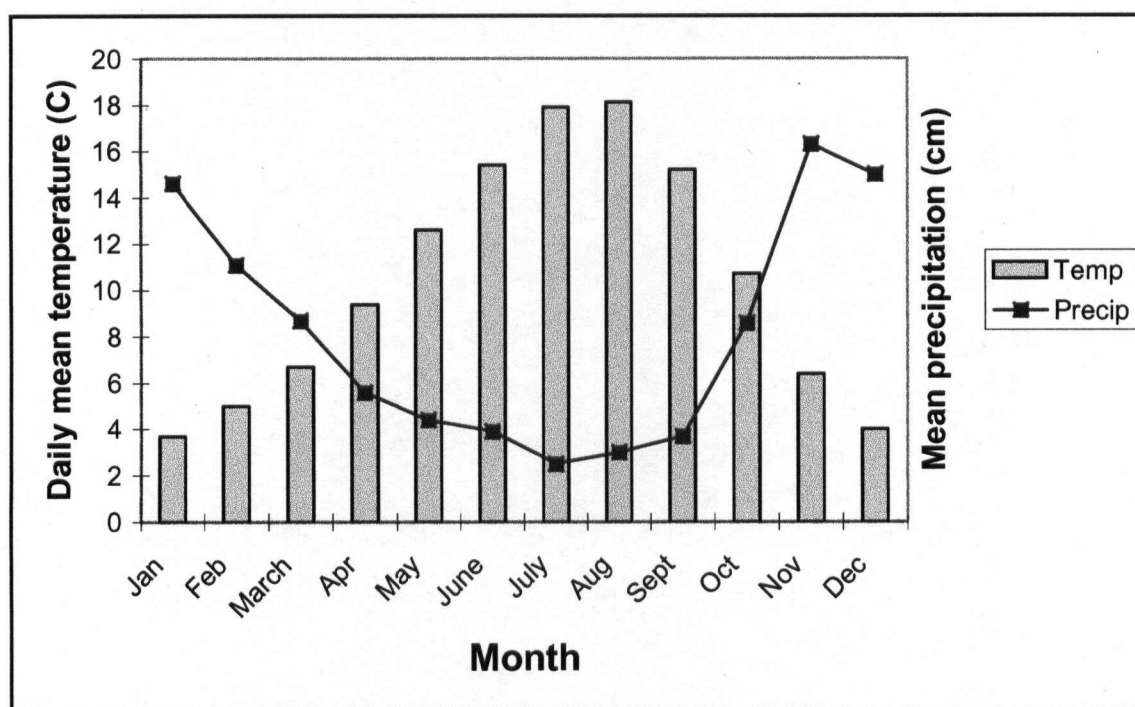


Figure 2-2. Average daily temperatures (C) and mean monthly precipitation (cm) for St. Mary's Lake, Salt Spring Island from 1971-2000. Values on the X-axis apply to both temperature and precipitation. This weather station occurs approximately 8 km to the northeast of my study area. The concentration of rainfall between March-October, the average winter temperatures > 0° C, and the warm average summer temperatures is the typical profile of a Mediterranean climate. Data are from Environment Canada.

Diversity of communities and species

This oak savanna ecosystem possesses high levels of biological diversity compared to most other regions of western Canada, and supports over 100 rare, threatened, and endangered species within a relatively small geographic area (Fuchs 2001). Many of the species of the savanna are associated with xeric climates not typical of the Pacific Northwest, and most are more abundant in regions south of British Columbia. The most visible species is the Garry Oak itself, which is the only oak species native to British Columbia and extends in range to central California (Griffin and Critchfield 1972). Associated with this tree species are close to 700 vascular plant taxa, 150 of which are naturalized non-native species (Fuchs 2001). The most abundant native species include numerous perennial forbs (e.g., *Camassia* spp. (Fig. 2-3), *Ranunculus* spp., *Dodecatheon* spp., and *Lomatium* spp.), annual forbs (e.g., *Plectritis congesta*, *Plagiobothrys* spp., *Montia* spp., *Trifolium* spp.) and perennial grasses (e.g., *Festuca idahoensis*, *Danthonia californica*, *Bromus carinatus*, *Elymus glaucus*, *Koeleria macrantha*, and *Stipa lemmonii*). Appendix 1 provides a full list of oak savanna plant species of the Cowichan Valley on southeastern Vancouver Island. A diverse assemblage of bryophytes and lichens is also supported (Fuchs 2001).

The rarest of the savanna vascular plant species include perennials such as *Tritelia howellii*, *Viola praemorsa*, *Castilleja levisecta*, *Balsamorhiza deltoidea*, and *Seriocarpus*

rigidus (Fig. 2-4). These species are nationally or provincially endangered; the latter three are regional endemics.



Figure 2-3. *Camassia quamash* with the invasive grass *Anthoxanthum odoratum*.

The most abundant exotic flora include perennial warm-season³ grasses (*Poa pratensis*, *Dactylis glomerata*, *Lolium* spp., *Alopecurus pratensis*), the cool-season perennial grass *Anthoxanthum odoratum*, annual grasses (*Aira* spp., *Bromus* spp., *Vulpia bromoides*), annual forbs (*Trifolium* spp., *Myosotis* spp., *Vicia* spp.), and perennial forbs (*Cirsium* spp., *Hypochaeris* spp.).

³ Warm-season = grasses and forbs with summer phenologies (i.e., mostly begins flowering after May); cool-season = grasses and forbs with spring phenologies.

The Garry Oak savanna also supports a number of vertebrate and invertebrate species that are presently regionally uncommon or rare. These include the alligator lizard (*Gerrhonotus coeruleus principis*), sharp-tailed snake (*Contia tenuis*), streaked horned lark (*Eremophila alpestris strigata*), western bluebird (*Sialia mexicana*), Lewis' woodpecker (*Melanerpes lewis*), as well as butterflies such as the propertius duskywing (*Erynnis propertius*) and the moss elfin (*Incisalia mossii*). The island marble butterfly (*Euchloe ausonides*) is considered extirpated from Canada.



Figure 2-4. The regional endemic *Seriocarpus rigidus*.

The floral composition of the oak savanna in British Columbia is not geographically uniform due in part to variations in soil depth, aspect, slope, naturally occurring habitat isolation (e.g., south-facing slopes on isolated mountains), and land use history. Although two intricate vegetation community classification schemes have been derived for the Garry Oak savanna (Roemer 1972, Erickson 1996), for the purposes of this thesis two general categories are recognized: shallow soil savanna (<10-20 cm) and deep soil savanna (> 20 cm). Shallow soil savanna occurs mostly on hilltops and south- and west-facing slopes, escarpments, and hilltops; deep soil savanna is found on low elevation plains of glacial till and marine clays. Deep soil sites (Fig. 2-5) have been more significantly impacted by European agricultural activity and by exotic plant invasion. An estimated 95% of remaining Garry Oak savanna occurs in steeply inclined areas of shallow soil with limited agricultural worth (except possibly grazing).



Figure 2-5 . Soil depth profile near the Cowichan Garry Oak Reserve. A deep layer of semi-previous "finger-shale" underlies approximately 40 cm of clay-based soil.

Fire

A key uncertainty in the functioning of this ecosystem in British Columbia is the importance of fire. This debate mirrors similar speculations on the importance of fire for the origins and long-term maintenance of the prairie biome of central North America (Axelrod 1985). One hypothesis is that burning plays a minor role in maintaining the savanna. Instead, the combination of the rainshadow and the shallow, rapidly drained, and moderately infertile soils are sufficient to maintain the xeric oak savanna assemblage. The alternative hypothesis is that in the absence of repeated fire, this savanna would convert to oak woodland (>50% tree cover) or to Douglas-fir forest with a radically different community of understory plants.

There is evidence to support both hypotheses, and it is most likely that both operate concurrently. For the post-glacial origins of oak savanna in British Columbia, the story is uncontested. Palynological data from Vancouver Island reveal the arrival of oak as early as 8,000-10,000 B.P., peaking around 6,000 B.P. (Mathewes and Huessler 1981, Huessler 1983, Brown and Hebda 1998, Allen et al. 1999) (Fig. 2-6).

This arrival occurred during the warmer conditions of the early- to mid-Holocene. Many or all of the ground flora species may have also arrived at this time, though the pollen record cannot confirm this. Following 4,000 – 3,000 B.P., a cooling climate led to a reduction in oak, and the creation of contemporary West Coast forest dominated by Douglas-fir, and in wetter regions, western red cedar and western hemlock. It is at the

onset of this contemporary period that fire may have been most important for maintaining the savanna. Because of the rarity of lightning strikes on the Pacific coast (Keeley 2002), the origins of these late Holocene fires are presumed to be the result of land use practices by First Nations peoples.

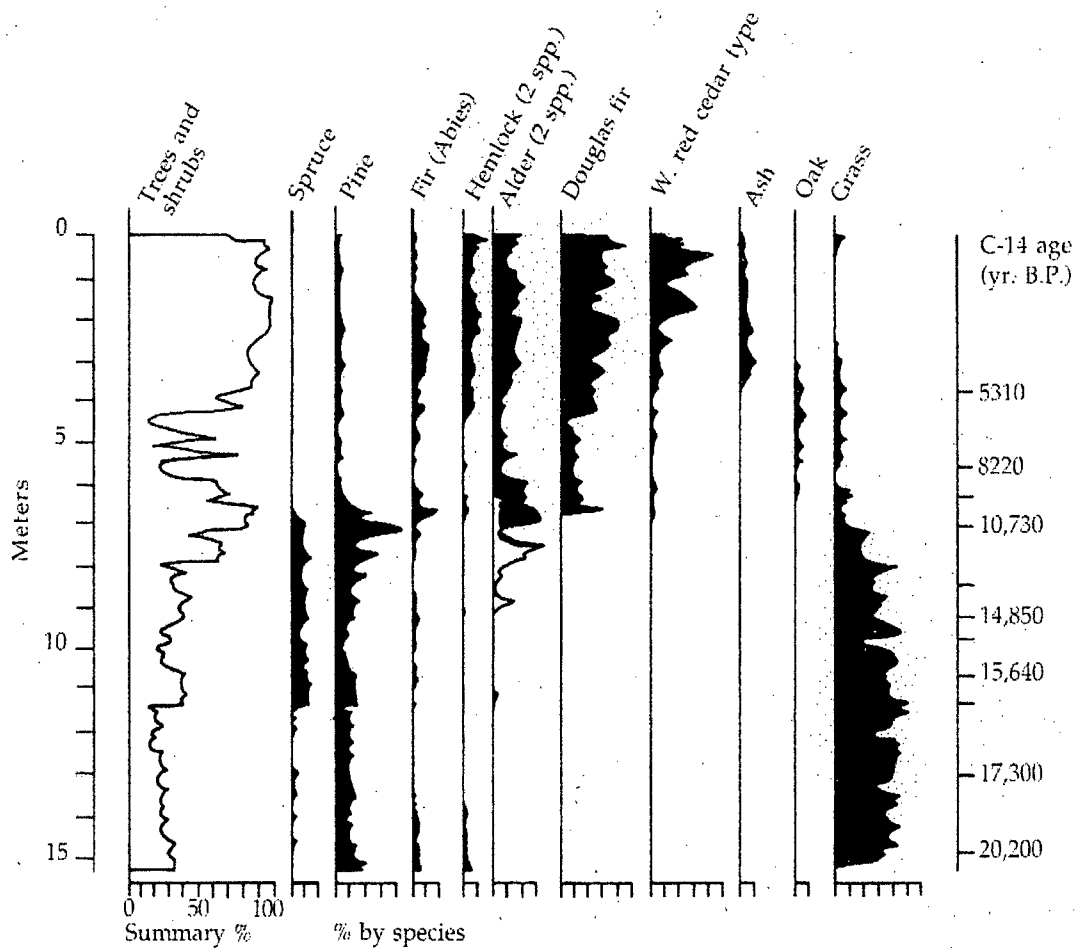


Fig 2-6.. Pollen profile from Washington,, including Garry Oak, for the last 20,000 years. From Krukeberg 1991. Note the maximum occurrence of oak pollen from 9,000-5,000 years before present (B.P.). Ash (*Fraxinus*) is uncommon on Vancouver Island.

The impacts of humans

"Pre-emptions by European settlers (of southeastern Vancouver Island) were often located on former Indian village sites for the simple reason that such places possessed cleared land, fresh water, and safe anchorage. Indeed, the land acts (of the late 1800s) permitted white settlement or commercial activity on most places used by Indians for resource procurement: clam and oyster beds, fishing stations, river courses, camas beds, hunting grounds for deer and waterfowl. Such places had been used for millennia for food procurement..."

Richard Mackie *The Wilderness Profound: Victorian Life on the Gulf of Georgia* (1995)

The Pacific Northwest formerly supported one of the densest concentrations of First Nations peoples in North America (Harris 1997). Large populations developed in this region in part because of the abundance of many plant and animal species that provided food, clothing, and shelter (Suttles 1986). Some of these species were associated partly or entirely with the oak savanna ecosystem, such as black-tailed deer, Roosevelt elk, and plant species such as *Camassia* and *Pteridium aquilinum* (White 1999). The hunting, gathering, and the use of fire to propagate some species (e.g., *Camassia*) not only affected their abundances but probably also had significant impacts on ecosystem function.

If the persistence of the oak savanna depends on fire, then burning by First Nations peoples during the late Holocene may be solely responsible for its presence on the present-day landscape. It is certain that fire was a regular occurrence on southeastern Vancouver Island and adjacent Gulf Islands at the time of European contact (Brown and Hebda 1998). Historical records indicate that the Northern Straits Salish annually burned the savanna to increase *Camassia* production and possibly to improve forage for elk and

deer (Turner 1999). However, it is unclear whether fire is as necessary, or can be supported as frequently, in shallower-soil areas where productivity by plant species is low and succession to forest is less likely to occur. Instead, fire probably interacted with site-level environmental factors to determine whether Garry Oak savanna species were supported at a particular location. On shallow-soil sites, fire may have been unnecessary. As soil depth increases on the lower slopes and till plains, fire becomes more important for preventing conversion to Douglas-fir forest. In the post-settlement era, Douglas-fir invasion of Pacific Northwest prairie has been observed in many areas (Franklin and Dyrness 1988, Krukeberg 1991), including British Columbia. Repeated burning by First Nation peoples would presumably prevent Douglas-fir establishment in deeper-soil areas, as well as limit ground flora biomass accumulation. The question about the importance of fire, and land management activity by First Nations peoples in general, is the focus of the next chapter.

Invasion in the Garry Oak savanna

Invasion of the oak savanna in British Columbia began immediately following the colonization of Vancouver Island in the vicinity of present-day Victoria by the Hudson's Bay Company in the 1840's. Although the area was selected for its arable potential, it is not known how extensively the early settlers modified the land, or how these activities contributed to the present-day declines of native species and to plant invasion. The open conditions of the oak ecosystem may have required little effort to farm, and plant introductions may have been gradual or inadvertent ("passive" model). Alternatively,

there could have been a substantial effort to cultivate the land and establish Eurasian pasture species ("active" model).

The establishment of exotic species was both intentional and accidental, and included birds (e.g., skylark, California quail), animals (rabbits, feral sheep and goats), and many shrubs, trees, grasses and forbs. For plants, many pasture species were introduced repeatedly to improve forage quality in the savanna. Many of these pasture species currently dominate remnant Garry Oak savanna sites (e.g., *Dactylis*, *Poa*, *Holcus lanatus*, *Lolium perenne*, *Anthoxanthum odoratum*, *Bromus sterilis* and other annual brome grasses, *Vicia* spp., *Lathyrus* spp.). The leguminous shrub Scotch broom (*Cytisus scoparius*) was introduced in the mid 1800s as an ornamental, and is most likely the most detrimental invasive species in this ecosystem (Fig. 2-7). As it increases in abundance, Scotch broom shades out ground flora and probably alters soil nutrients (e.g., Peterson and Prasad 1998). Today, native flora typically constitute less than 10% of all species cover in site remnants. In some cases, native species have been completely eliminated. Although the relationship between the increasing abundance of exotic plants and the decline of native species is assumed to be direct, there has been limited research to date that examines whether this is true in the Garry Oak savanna.



Figure 2-7. Invasion by Cytisus scoparius at the Cowichan Garry Oak reserve (top photo – taken in 1999), and results of its manual removal by the Nature Conservancy of Canada (bottom photo – taken in 2003).

Study Area

The experimental work for this thesis was primarily conducted in the Cowichan Garry Oak reserve, located in the Cowichan Valley of southeastern Vancouver Island, British Columbia. The reserve was purchased by the Nature Conservancy of Canada in 1998, in cooperation with numerous local citizens who were concerned that it be protected. It covers approximately 25 ha, of which 15 ha are Garry Oak savanna (the remainder is *Pseudotsuga menziesii* forest or riparian forest with *Acer macrophyllum*, *P. menziesii*, and *Tsuga heterophylla*) (Fig. 2-8). It supports large populations of three rare vascular plant species: *Tritelia howellii*, *Viola praemorsa*, and *Seriocarpus rigidus*.

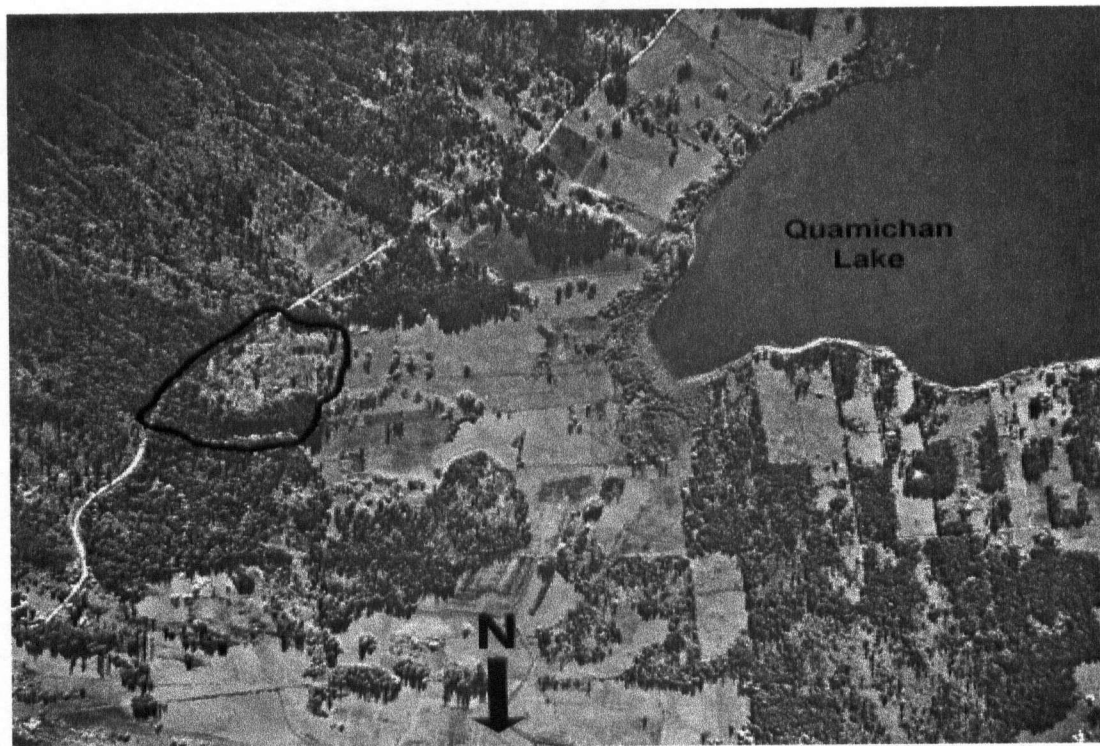


Figure 2-8. The circled area indicates the location of the Cowichan Garry Oak reserve, taken in 1954. Since this photo was taken, there has been considerable infilling by Garry Oak in the southern portion of the reserve, as well as the development of large subdivisions on the east side of Maple Bay Road.

The reserve is one of the largest remaining areas of deep-soil savanna in British Columbia, although it also contains areas with shallower soil (5-20 cm). It is gently sloped (5-15°). Decades of fire suppression have led to the development of a dense, continuous stand of Garry Oak that covers approximately 50% of the total savanna area. The experiments were conducted in two savanna openings on the western side of the reserve, beginning in the summer of 2000.

Chapter Three

Defining Conservation Strategies With Historical Perspectives in the Garry Oak Savanna

Abstract: *The restoration of degraded ecosystems can be constrained by uncertainty over former conditions and the relevance of the past given recent changes. It can be difficult to differentiate among contrasting hypotheses regarding past ecosystem function, and restoration efforts can emphasize species re-establishment without integrating the ecological and cultural processes that once determined their occurrence. As a case study, historical descriptions of an endangered oak savanna in southwestern British Columbia, Canada, were assessed to determine former conditions and assess their validity for defining restoration targets. Twenty-three documents described this ecosystem from 1790-1951. Comparison of early survey records with contemporary occurrences suggests habitat loss > 95%. The identity and former range of most native plant species were poorly described, but accounts of ecosystem structure revealed a diversity of floral communities that has been much simplified. Fire, most likely set by indigenous peoples, interacted with edaphic and topographic factors to create this structural diversity. European settlers intensively modified the ecosystem with grazing, cultivation, and introduced flora. These transformations partly explain the current high levels of plant invasion. Restoration must target the ecosystems' former structural diversity and the ecological and cultural processes that maintained it. Given the recent impacts of fire suppression, habitat loss, and plant invasion, however, land managers must balance the re-establishment of historical processes with their potential negative effects in sites with*

numerous at-risk species. This ecosystem was, and remains, part of a culturally modified landscape, where human activity has maintained unforested areas for millennia but now promotes mostly exotic flora. Although pre-European conditions cannot be fully restored, the historical data provided restoration insights unobtainable from current biological studies emphasizing the end point of long-term ecological change.

Introduction

The importance of melding conservation biology with historical research is recognized but debated (Meine 1999, Egan and Howell 2001). Two issues underlay this debate: (1) uncertainty over how ecosystems functioned formerly and (2) uncertainty whether past ecological processes are relevant given contemporary conditions of habitat loss, invasion, and altered disturbance regimes. At best, historical viewpoints can reveal former patterns and processes that have been obscured or erased (e.g., Blondel and Vigne 1993, Jackson et al. 2001). At worst, they can lead to a preoccupation with issues that have little connection to the current modified landscape (Howe 1994, Kellman 1996).

These problems are especially relevant for restoration ecology. For ecosystems that are degraded and lacking reference sites, there may be no clear indication of what to restore (i.e., the restoration target) or how to maintain them over time (i.e., management). These difficulties often necessitate "looking back" for evidence of the former conditions. However, the effectiveness of this strategy can be limited. Restoration targets in North America, for example, have traditionally focused on pre-European conditions with the

presumption that the landscape was "pristine" at this time. Pre-European conditions, of course, were neither ecologically static nor free from human influence (e.g., Boyd 1999, Keeley 2002, MacDougall 2003). There is also a tendency to overemphasize the obvious former processes, such as fire, which may not have been the most influential factor or may have been coupled with ancillary environmental (e.g., soil depth, topography) and cultural (e.g., cultivation) factors that also require consideration (e.g., Hobbs and Huenneke 1992, Blackburn and Anderson 1993, Beckwith 2002).

Such difficulties suggest an intractable dichotomy: the need to re-establish the historic ecosystem versus the difficulty in defining the ecosystem's parameters based on evidence from the past. Many have suggested that the solution lies in how the data are used (Cairns 1989, Higgs 1997, White and Walker 1997). Rather than defining restoration targets based directly on historical evidence, the implications of retrospective data should be integrated with contemporary ecological, social, and logistical considerations. For example, the reintroduction of fire to highly fragmented grassland may offset woody plant invasion but exacerbate invasion by herbaceous exotics and have unwanted consequences for native flora currently reduced to small and isolated populations (Hobbs and Huenneke 1992). Historical perspectives can also challenge current hypotheses on former ecosystem function. For degraded ecosystems, contrasting opinions often arise regarding the former relative importance of factors such as native grazing, fire, or underlying environmental gradients (e.g., Axelrod 1985, Howe 1994).

A case study is presented on the use of historical information for defining restoration targets in a degraded oak savanna of southwestern British Columbia, Canada. Retrospective data are used to (1) contrast former ecosystem appearance with present conditions, (2) assess current assumptions about past ecosystem functioning, and (3) examine the implications of these findings for restoration in the context of current problems such as fragmentation and species decline.

An analysis of this kind is urgently needed in this ecosystem because there are no unmodified reference sites. There is also no distinctive boundary between a pre-European "pristine" landscape and a post-colonization "disturbed" landscape because this region had such a dense concentration of indigenous peoples prior to the 19th century (Harris 1997). Thus, restoration planning is not simply a matter of defining former species composition and relative abundance. It will require discerning how indigenous peoples affected the ecosystem and how the landscape was subsequently transformed by European settlement. Although we know the end products of European land use (e.g., habitat loss, invasion), the methods employed by early settlers can explain the extent of ecosystem disruption and provide insight into how to counteract the cumulative changes.

Methods

Historical accounts of the exploration, survey, and settlement of southwestern British Columbia during the late eighteenth, nineteenth, and early twentieth centuries were examined for reference to the Garry Oak savanna ecosystem. Documents were identified

from library and archive searches and from anthropological, ethnobotanical, and historical works on the region (e.g., Harris 1997, Boyd 1999).

Each document was scanned for three types of information: (1) distribution, species composition of vascular plants, and general appearance of the ecosystem, including grazing by native ungulates, (2) evidence of fire, including references to the frequency and intensity of burning and to the role of indigenous peoples in initiating and managing the fires, and (3) the timing and method of European settlement, including the introduction of livestock and exotic flora and the degree of ecosystem clearance and cultivation.

Documents were qualitatively assessed to determine the author's purpose, the circumstances of the passage, and the degree of concordance with other accounts. This assessment was done to determine whether biases or inaccuracies could be detected (e.g., Edmonds 2001). Some passages from the 1840s, for example, contain glowing accounts of soil fertility that appear to have been written to entice potential settlers.

Results

Twenty-three documents dating from 1790 to 1951 contained references to oak savanna plant communities in British Columbia. The earliest accounts are limited, having been written by coastal explorers who made few landings on southeastern Vancouver Island (Bodega y Quadra 1792, Menzies 1923, Fidalgo 1971, Vancouver 1984). The most

descriptive accounts are from land surveys conducted before or during the early days of settlement in the mid nineteenth century (e.g., Grant 1857, Wells 1859). During the 1860s, numerous articles were published that describe the general appearance of the land, the local aboriginal peoples, flora and fauna, and settlement prospects. Accounts of the late nineteenth century primarily describe settlement progress and changes to the land. These latter works include ethnographic texts that describe indigenous peoples and their land management practices.

The clarity of the documents varied, especially regarding species identification. Overall, however, the accounts support each other in terms of oak savanna distribution, land appearance, use of fire by indigenous peoples, and the modifications conducted by European settlers. Because European settlement on Vancouver Island greatly increased during the mid-1860s, assessment of oak ecosystem distribution was restricted to observations that preceded this period.

Distribution and vegetation structure

Based on the earliest accounts, the Garry Oak savanna had a restricted distribution and was nested within the more wide-ranging *P. menziesii* forest of Vancouver Island. James Douglas (1842) described the ecosystem as "a perfect Eden in the midst of the dreary wilderness of the north-west coast and so different in its general aspect from the wooded, rugged regions around." This account was shared by several authors, some of whom described its luxuriance as "park-like" compared with the more typical forests of the

Pacific Northwest coast (Fitzgerald 1848, Seemann 1853, Begg 1862, Forbes 1864, McLoughlin 1943).

The regional extent of the *Garry Oak* ecosystem, as described in the mid-1800s, coincides with the present-day range in British Columbia (Fig. 3-1). The ecosystem was described as patchy in distribution and varying in total area, from pocket grasslands of a few hundred hectares to open "prairie" of 8.5 - 13 km² (Grant 1849, Douglas 1842, Verney 1996). The largest tracts were on deep soils. Although some openings were large, the region lacked the extensive continuous prairie of the Willamette Valley of Oregon (Kane 1971) or the Cowlitz and Nisqually regions of western Washington (Douglas 1979). Instead, the larger-sized grasslands were part of a mosaic of community types that included *Garry Oak* and *P. menziesii* woodland (e.g., Grant 1849). Although the contemporary range of this ecosystem matches the former historical range, local occurrences have been greatly reduced (Fig. 3-1).

The stature of the grass- and fern-dominated ground flora varied from extremely short (Anonymous 1849) to over 2 meters (Wells 1859; Richardson 1872; Williams 1977; Douglas 1979), likely depending on soil depth and fire frequency. Many authors described a dichotomy between plant communities in deep and shallow soils and how this distinction shaped patterns of vegetation growth (Douglas 1842, Grant 1849, Forbes 1864, MacFie 1942). Douglas (1979) observed "...two marked varieties of soil on those prairies, that of the best land is a dark vegetable mould varying from 9 - 14 inches in

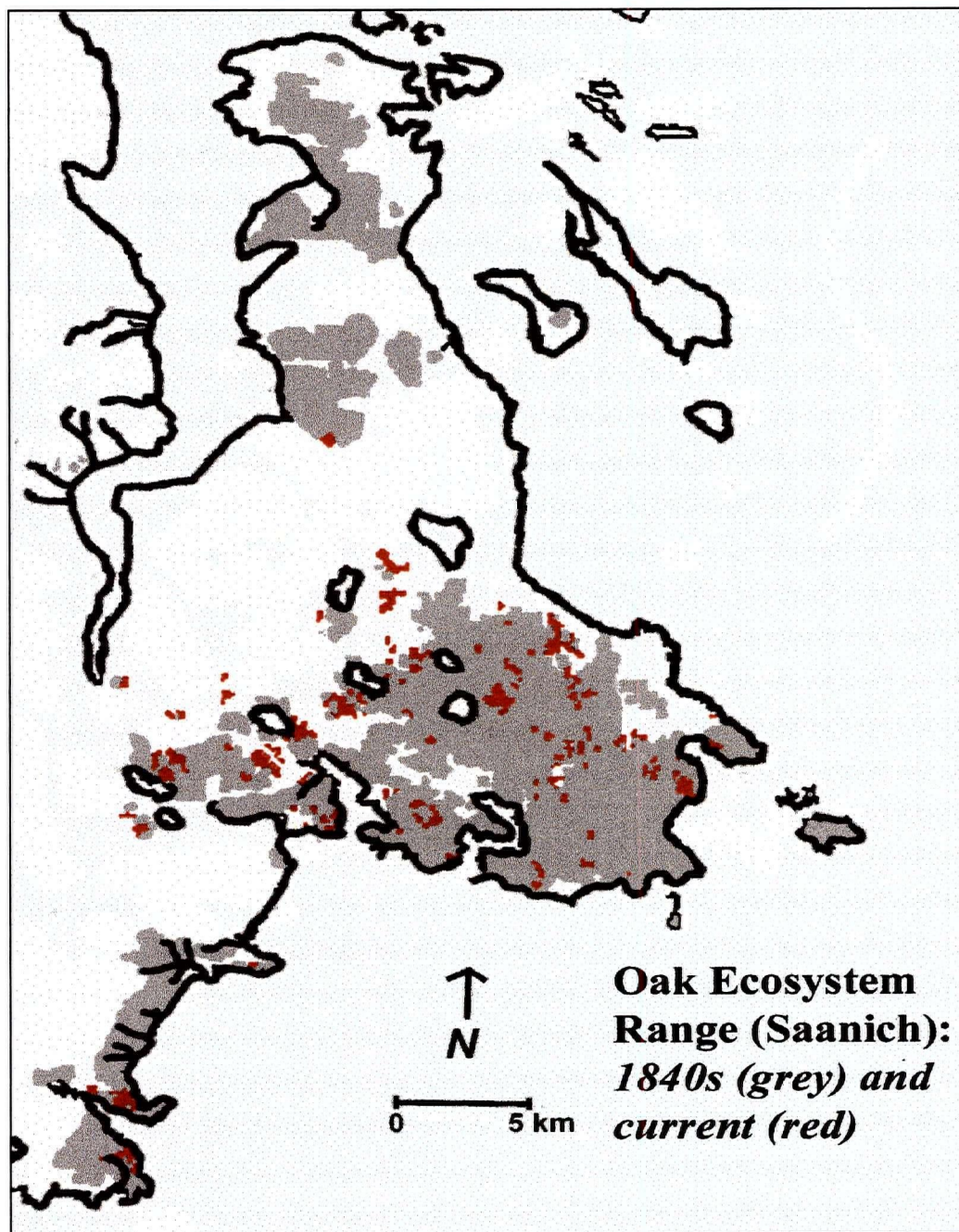


Figure 2. Extent of oak savanna habitat loss on the Saanich Peninsula (Victoria) of southeastern Vancouver Island. The original range is derived from historical records of the mid-nineteenth century, including pre-settlement land surveys. The current range indicates areas that contain Garry Oak and associated native ground flora species. Modified from Lea (2002) and used with permission.

depth...that produces the (greatest) growth of native plants that I have seen in America. The other variety is of inferior value...and...naturally more unproductive.”

Accounts of the former density of native ungulates (*Odocoileus hemionus columbianus*, *Cervus elaphus roosevelti*) and their grazing impact were scarce. Most common were statements such as “the forests were full of wild game” (Ludrin 1928). Vancouver (1984), describing nearby Whidbey Island in Washington, stated, “in these beautiful pastures,...the deer were seen playing about in great numbers.” With these accounts, it is impossible to determine the effect of native ungulates on the oak ecosystem or how their grazing intensity compared with that of domestic livestock introduced in the 1840s. However, it is most likely that pre-Columbian ungulate densities were not sufficiently dense to drive the dynamics of the oak savanna plant community due to climatic factors (e.g., Mack and Thompson 1982), hunting pressure by the Straits Salish, and the former prevalence of cougar and wolves in the region.

Vegetation composition

The most commonly mentioned floral groups were grasses, clover, wildflowers, bracken, wild rose, and various other shrubs (Table 3-1). Individual references to plant species, with the exception of camas, were uncommon and tended to focus on showy species or on species with some economic potential (Table 3-1). These accounts do not provide insight into the ranges or population sizes of these species.

Based on all accounts, large portions of the Garry Oak ecosystem were composed of a patchwork of grasses, grass and forb mixtures, camas swards, bracken fern, and shrubs, with varying densities of oak and sometimes *P. menziesii*. Grass and grass-forb communities were commonly described. From the initial Vancouver Island survey, James Douglas (1842) wrote that "[The soils]...produce [an] abundance of grass and several varieties of red clover on the rich moist bottoms...We saw several acres of clover growing with a luxuriance...more resembling the close sward of a well-managed lea than the produce of an uncultivated waste." In some cases, camas occurred in extensive swards (Hazlitt 1858).

There were multiple references to bracken fern throughout southeastern Vancouver Island (Douglas 1842, Seemann 1853, Wells 1859, Brown 1864, Ludrin 1928, Kane 1971; MacFie 1972). This species is presently infrequent in remnant areas. It was described as occurring in dense thickets and commonly reaching heights greater than 2 meters (Fig. 3-2). Farmers considered bracken fern problematic because its rhizomes produced continuous regrowth. Conversely, it was a favorite food of the indigenous peoples, and they used fire to encourage its occurrence (White 1999).

There were also numerous accounts of wild rose, brambles, blackberries, and briars (Mayne 1967, MacFie 1972, Brown 1989). Given the familiarity of wild rose to European colonists, it was difficult to determine the validity of statements such as "in the spring every plain is covered with the wild rose..." (Mayne 1967). It may have been a species that was overemphasized to attract potential European immigrants. Alternatively, the

wide distribution of wild rose could have been a reflection of resource management by aboriginal residents. Wild rose and other culturally significant native shrubs, ferns, and forbs, thrive with regular disturbance, especially periodic fire (White 1999; Turner 1999).



Fig. 3-2. Two-meter tall bracken fern on the old Cowichan Valley rail line near Duncan. Pictured are Don and Lois MacDougall (summer 2002).

Fire

Between 1843-1865, fires were commonly observed on southeastern Vancouver Island (Grant 1857, Douglas 1979, Verney 1996). This burn frequency suggests a considerably

shorter fire-return interval than the estimated 50-100 years for *P. menziesii* forests of the Pacific Northwest (Agee 1993). The cause of these fires was not always stated, but it was usually implied that indigenous peoples intentionally started them. Lightning strikes were not reported, which is consistent with the rarity of lightning-initiated fires in contemporary oak ecosystems of western North America (e.g., Keeley 2002).

Table 3-1. Native vascular plant species described in the historical documents.^a

Common name (scientific name)	Comment ^b	Location	Reference
Blackberry (<i>Rubus</i> spp.)	widespread; familiar to Europeans	Victoria	Mayne 1967; MacFie 1972; Brown 1989
Blue-eyed mary (<i>Collinsia</i> spp.)	familiar to Europeans	Victoria	Verney 1996
Bracken fern (<i>Pteridium aquilinum</i>)	widespread; familiar to Europeans	Courtenay, Victoria, Duncan	Douglas 1842; Seemann 1853; Wells 1859; Brown 1864; Ludrin 1928; Kane 1971; MacFie 1972
Brambles (<i>Rubus</i> spp. or <i>Ribes</i> spp. ^c)	widespread; familiar to Europeans	Victoria, Duncan	Mayne 1967; MacFie 1972; Brown 1989
Camas (<i>Camassia leichtlinii</i> or <i>Camassia quamash</i>)	showy flower; widespread; indigenous food source	Victoria	Hazlitt 1858; Mayne 1967
Crocus (<i>Olsynium douglasii</i> or	showy flower	Victoria	MacFie 1972

Sisyrinchium spp.^{c)}

Easter lily (<i>Erythronium oregonum</i>)	showy flower	Victoria	MacFie 1972
Blue lupine (<i>Lupinus</i> spp.)	widespread; familiar to Europeans	Victoria	Mayne 1967
Red clover (<i>Trifolium wormskjoldii</i> ^{c)})	widespread along coast	Victoria	Douglas 1979
Sunflower (<i>Balsamorhiza deltoidea</i>)	economic importance (chicken feed)	Victoria	MacFie 1972
Wild rose (<i>Rosa nutkana</i>)	familiar to Europeans	Victoria, Duncan	Mayne 1967; MacFie 1972; Brown 1989

^aCommon names are those mentioned by the original authors. Scientific names follow Douglas et al. (2001). ^bProbable reason why species described. ^cSpecies identity speculative.

Fires were reported for both the Garry Oak ecosystem and for the adjacent coastal *P. menziesii* forest. "Miles of [open grassland] were burnt and smoky, and miles were still burning" (Anonymous 1849). The same author also reported "We ran the Straits the next day...Nothing but forests of (*P. menziesii*). At one part, ten miles of them were on fire...". Although human-initiated burning of *P. menziesii* forest may have occurred for a variety of reasons (e.g., enhancement of plant resources, clearing of underbrush, hunting), it is also possible that these fires were oak ecosystem burns that accidentally escaped, that were part of a multi resource management effort, or were burns that ran unencumbered over the landscape (Brenda Beckwith, unpublished data). Although the authors often

commented on the extensiveness of the fires, it could not be determined if this scale was typical or if these highly visible fires drew more consideration from the observers.

According to ethnographic accounts, local indigenous peoples burned intentionally to promote culturally important resources, especially root foods such as camas (Anonymous 1849, Grant 1857, Suttles 1951, Turner 1999). Camas bulbs were a significant food and trade item among the aboriginal peoples of southwestern British Columbia (Turner 1999, Beckwith 2002). Its harvest occurred on a local and intensive scale, and "...where the camas grew thick, the women had their...plots marked off with stakes...Women dug the bulbs in the spring...Later when it was dry, they burned it over" (Suttles 1951).

The descriptions of the vegetation structure of the oak communities depended on when fire had last occurred, and if indigenous peoples were present in the area. Fitzgerald (1849) reported on the observations of a fellow colonist: "...he walked over a plain of some miles in extent...which had not a blade of grass growing, owing to it having lately been burnt by the Indians, and that a few months afterwards, on going over the same spot, he found the grass up to his middle in height." Similarly, Grant (1849) wrote "There being no natives residing on the spot, the plain has been less burnt over by fire...Consequently, the vegetation deposit not being yearly destroyed..., has accumulated to a much greater depth than it otherwise would have done."

In some cases, the accounts provided valuable information on the frequency and seasonality of fires set by the indigenous people. One author observed "...the fire runs

along at a great pace, and it is the custom here if you are caught to gallop right through it; the grass being short, the flame very little..." (Anonymous 1849). This observation suggests a low-intensity fire that was probably caused by the reduced fuel loads of repeated burning.

Fires were observed during the late summer and early fall (Grant 1857, Hazlitt 1858, Douglas 1979), a period of extended drought in the region due to low rainfall and high temperatures associated with the sub-Mediterranean climate. Europeans disapproved of the burning by the indigenous peoples and sought to eliminate it once their settlements became established (Grant 1849).

European Changes

The European settlers made considerable modifications to the Garry Oak ecosystem during the early colonial period. The most revealing account comes from the late 1850s (MacFie 1972):

"There are open lands...already fit for the plough, and from which a crop may be obtained without any exertion from clearing. But even the richest prairie soil cannot entirely dispense with preparation for ploughing...If fern prevail on the land, it should be ploughed up...All bulbous weeds, such as kamass, should be collected and burned. Fern-land, not required for immediate use, may...be left for hogs to burrow in...The roots of oak descending...vertically into the ground are...not easily eradicate"..

The rate of landscape change by the European settlers was rapid; much of the land was settled or farmed within 30 years. Hundreds of acres of crop fields were established by the late 1840s, and thousands of livestock were introduced. The importation of livestock probably continued throughout the nineteenth century, increasing up to the capacity of the land. Coupled with cultivation and grazing was the intentional introduction of Eurasian pasture flora (e.g., Douglas 1979). Many exotic species, especially grasses, were planted to increase forage quality for domestic livestock and have now become naturalized (Table 3-2).

Settlement had considerable impacts on the indigenous peoples of the region. In 1868, Gilbert Sproat (1987) noted that "...one of the bitterest regrets of the natives is that the encroachment of the whites is rapidly depriving them of their crops of this useful and almost necessary plant [camas]." In admiring the open prairie of the Courtenay region in the 1860s, Mayne (1967) wrote

"The Indians told us that a great many blankets would be wanted for the purchase of this tract, as all the neighbouring tribes resorted there in the summertime to collect berries, shoot deer, ...etc. all of which were found in large quantities. Indeed, they showed some reluctance at taking us over it, feeling sure...that we should desire to possess it when its qualities became known"

Discussion

The historical records provide a detailed perspective on the former structural diversity and dynamic functioning of the Garry oak savanna in southwestern British Columbia.

Although these records are limited by inconsistencies typical of such information, they clarify uncertainties about past ecosystem function, including the role of land management by indigenous peoples, and about the intensity and speed by which this region was transformed by Europeans.

These data also highlight the extent of ecosystem modification by habitat loss, plant invasion, and fire suppression. These changes suggest that the past appearance of this ecosystem cannot serve as the sole blueprint for contemporary restoration activity. Because of habitat fragmentation, for example, it will be impossible to implement the former landscape-wide burning regimes or to re-establish plant populations that match their former regional distribution. Restoration strategies must, therefore, adopt an integrative approach that accounts for the former conditions of the ecosystem, the

Table 3-2. Exotic species introduced to Vancouver Island in the nineteenth century.

Species	Location	Date ^a	Reference
Grasses			
<i>Dactylis glomerata</i> ^b	Victoria,	1860s,	MacFie 1972;
	Courtenay	1890s	Mackie 2000
<i>Lolium multiflorum</i>	Victoria	1860s	MacFie 1972
<i>Lolium perenne</i> ^b	Victoria	1860s	MacFie 1972
<i>Festuca filiformis</i>	Victoria	1860s	MacFie 1972
<i>Festuca trachyphylla</i>	Victoria	1860s	MacFie 1972
<i>Phleum pratense</i> ^b	Victoria,	1840s,	Mayne 1967;
	Courtenay	1860s,	MacFie 1972;
		1890s	Douglas 1979; Mackie 2000

<i>Poa pratensis</i> ^b	Victoria	1860s	MacFie 1972
Forbs			
<i>Trifolium hybridum</i>	Victoria	1860s	MacFie 1972
<i>Lotus corniculatus</i>	Victoria	1860s	MacFie 1972
<i>Onobrychis viciifolia</i>	Victoria	1860s	MacFie 1972
<i>Vicia sativa</i> ^b	Victoria	1860s	MacFie 1972
<i>Trifolium incarnatum</i>	Victoria	1860s	MacFie 1972
<i>Taraxacum officinale</i> ^b	Victoria	1873	Dawson 1989
<i>Medicago sativa</i>	Victoria	1860s	MacFie 1972
<i>Leucanthemum vulgare</i> ^b	Victoria	1870s	Dawson 1989
<i>Trifolium pratense</i>	Victoria	1860s	MacFie 1972
<i>Rumex acetosella</i> ^b	Victoria	1860s,	MacFie 1972;
		1870s	Dawson 1989
<i>Trifolium repens</i> ^b	Victoria,	1847,	Grant 1864;
	Courtenay	1860s,	Mayne 1967;
		1890s	MacFie 1972;
			Douglas 1979;
			Mackie 2000
<i>Barbarea</i> spp.	Victoria	1860s	Grant 1864
Shrubs			
<i>Cytisus scoparius</i> ^b	Victoria	1849	Ludrin 1928

Scientific names follow Douglas et al. (2001). ^aYear or decade of introduction according to the author. ^bCurrently widespread in oak ecosystem remnants.

changes that have most greatly affected its functioning, and the contemporary restrictions that affect the persistence of its native flora.

Former Conditions

The Garry oak ecosystem was formerly a regionally distributed mosaic of vegetation types determined by interactions of topography, soil depth, and fire. Its distribution was naturally patchy, with patch sizes ranging from extensive open prairie to small rock outcrop plant communities. The most significant factor may have been fire occurrence, which prevented conversion to *P. menziesii* forest and maintained structural heterogeneity within the ground flora communities. The significance of recurrent fire in this ecosystem resembles that of many other pyrogenic ecosystems in western North America (e.g., Hanes 1977, Dunn and Ewing 1997) and worldwide (Whelan 1995). The impacts of contemporary fire suppression in the Garry oak ecosystem also resemble those observed in other pyrogenic ecosystems (Leach and Givnish 1996). Remnant areas no longer contain the structural diversity that was described formerly, and are dominated by exotic flora that appear to be competitively superior to other species in these undisturbed settings.

The historical records also confirm that this ecosystem was part of a culturally modified landscape. The exact timing of the onset of aboriginal fire use is unknown but it may extend to the mid-Holocene or earlier (Brown and Hebda 2002). The high frequency of fire described by records lends support to the hypothesis that indigenous burning offset conversion to conifer forest in recent millennia. This is probably most true in deep soil areas, which are less moisture-limited than shallow soil sites (Chapter Six) and prone to infilling by *P. menziesii* in the absence of fire (Tveten 1997). Combined with intensive

harvesting of native plants, and possible plant transplantation (Deur 2002), indigenous land management activities must have dramatically influenced the appearance of this ecosystem as observed by early Europeans. Because few areas probably escaped these impacts, directly or indirectly, the definition of contemporary restoration targets in the wake of their cessation is a primary challenge. Clearly this was not a successional stable or compositionally uniform assemblage of plant species or a "pristine" ecosystem free from the impacts of long-term human activities.

Greatest Ecosystem Changes

The historical records highlight three substantial changes that have affected current ecosystem function: fire suppression, habitat loss, and plant invasion by mostly exotic flora. The relative importance of each of these factors for conservation is unclear, although they interact to limit the occurrence and abundance of native species within the contemporary landscape.

The most significant change may be the suppression of fire. In its absence, dense swards of mostly exotic grasses and shrubs currently dominate remnant sites. In addition to a crowded overstory of living biomass, these swards often contain thick layers of grass litter and are limited in bare soil, ground-level light, and available soil nitrogen (Chapters Five, Six, and Seven). These conditions select against plant functional groups with limited competitive ability. Of the 59 "at-risk" plant taxa in this ecosystem (Fuchs 2001), 31 are small annuals and 20 are short-statured perennial forbs that often perform poorly

in densely vegetated swards (Table 3-3). Although native grasses and bracken fern also formed dense swards (Grant 1857, Hazlitt 1856, Wells 1859), periodic fire would have eliminated litter and opened recruitment sites for subordinate grass and forb species (Maslovat 2001, Dunwiddie 2002). It may also have reduced the local abundance of some of the dominant flora; “competitive” species often have a limited tolerance of repeated biomass loss (Tilman 1988). For the competitively subordinate native species, the elimination of fire has likely contributed to their present-day displacement to mostly shallow-soil locations, where grass and shrub swards can form less densely.

Table 3-3. Habitat associations and functional groups of the 59 at-risk vascular plant species of the Garry oak savanna.

<i>Habitat</i>	<i>No. of species</i>	<i>Functional group</i>	<i>No. of species</i>
vernal pools and seasonally moist soils	29	annual forbs	30
open oak woodlands	11	perennial forbs	20
dry open prairie	10	perennial graminoids	5
rock outcrop	5	ferns	2
closed woodland	2	annual graminoids	1
wet open prairie or wetland	2	shrubs	1
Total	59	Total	59

The effects of fire suppression have been confounded by substantial habitat loss. Although the historical records do not describe the former distribution of native species, their population ranges and among-patch gene flow have almost certainly been greatly reduced. Of the 350 native flora in this ecosystem, many are now uncommon or are

locally abundant but with restricted distributions. This combination of restricted distribution, rarity, limited immigration, and isolated available habitat leads inevitably to species loss (MacArthur & Wilson 1967, Hubbell 2001), which has been observed in other ecosystems experiencing similar circumstances (Leach and Givnish 1996, Laurence et al. 2002). At present, there have only been four confirmed plant extirpations of oak ecosystem flora in British Columbia, but the abundance of many other species has been greatly reduced. Thirty-seven percent of the at-risk plant species occur in vernal habitats (pools, seepage zones) (Table 3-3) that were probably never widespread but now appear to be critically limited. Thus, remnant areas are not only small and isolated but appear to inadequately represent the former habitat heterogeneity of this ecosystem.

European land use has maintained the open condition of southeastern Vancouver Island, preventing the widespread conversion to conifer-dominated forest. However, the species composition of these open areas is now dominated by exotic flora rather than oak ecosystem taxa. The causes of plant invasion in the Garry oak ecosystem are not fully understood, mirroring the lack of consensus on the causes of plant invasion in general (D'Antonio and Vitousek 1992, Williamson 1996). With 151 naturalized exotic plant species, this ecosystem is more heavily invaded than the adjacent forested ecosystems of the Pacific Northwest that have also been intensively disturbed (by forestry). Its relatively high species richness compared with neighboring ecosystems has not conferred resistance to invasion, an outcome observed in species-rich areas in other parts of the world (e.g., Cornell and Lawton 1992, Stohlgren et al. 1999).

What does seem clear from the historical records, however, is that invasion has co-occurred with intensive grazing, cultivation, and the repeated introduction of exotic plants. This implies that invasion by some exotic flora was facilitated by the destabilization of the native plant communities rather than being determined by outright competitive superiority (Elton 1958, Mack 2000). This hypothesis supports the "active" model of plant invasion within this ecosystem, although it is untested and probably does not apply to all exotics. However, if there is a connection between disturbance and invasion, it suggests that reconstructed native plant assemblages could be successfully established if the same combination of intensive perturbation and repeated introductions were employed. This assertion urgently needs testing, and restoration activities planned for this ecosystem (GOERT 2002) will provide the opportunity to do so.

Implications for Conservation

The historical records describe the former widespread spatial and successional heterogeneity of the ground flora communities within this ecosystem. This includes described variations in seasonal phenology associated with the local climate, in vegetation structure caused by fire and other types of indigenous land management, and in habitat caused by topographical and edaphic factors. There was no single plant assemblage or habitat type that defined this ecosystem and that can serve as a principal restoration target.

Because this ecosystem has become regionally and locally simplified by habitat loss and fire suppression, management actions must focus on restoring its former dynamic heterogeneity at both spatial scales. This includes increasing gene flow by expanding the regional distribution of native species, and reintroducing fire or other disturbance (e.g., mowing) to increase structural heterogeneity and to offset the competitive exclusion of subordinate native flora. These measures emphasize active and on-going management. Reserve creation alone is a necessary but insufficient conservation measure because stability promotes the dominance of a small subset of mostly exotic species.

The most obvious first step for restoration, besides habitat acquisition, is the reintroduction of fire. In the context of tallgrass prairie restoration, however, Howe (1994) has cautioned that fire reintroduction may have unwanted consequences if the timing of the burns is not carefully matched with the phenology of the native species. Specifically, repeated burning in a particular season will select against those species that flower or set seed at that time. In the oak savanna, most species formerly escaped the effects of fire because their growing season (March-July) did not coincide with the timing of peak fuel combustibility (August-October) (Table 3-4). Combined with the knowledge that some of the most pernicious invaders are exotic warm season species (*Poa*, *Dactylis*), this implies that late summer or autumn burning will benefit oak ecosystem restoration.

Unfortunately, not all oak ecosystem flora complete their annual life cycle by midsummer or, by implication, are fire tolerant (Table 3-4). This includes many species

from the family Asteraceae, including the endangered regional endemic *Sericocarpus rigidus* Lindl., which is evergreen and flowers in late summer. This reinforces the point that former fire impacts probably varied across the landscape due to combinations of topography, soil depth, and cultural management activities. Areas that remained unburned, or were burned infrequently, may have been important refugia for native warm

Table 3-4. Flowering phenologies for native and exotic species from 13 vascular plant families of the Garry oak savanna ecosystem.

Family	Early (April-May)		Mid summer (June)		Late summer (July-September)	
	<i>native</i>	<i>exotic</i>	<i>native</i>	<i>exotic</i>	<i>native</i> ^a	<i>exotic</i> ^a
Asteraceae	3	3	15	8	22	16
Poaceae	6	17	16	10	5	10
Scrophulariaceae	8	1	6	3	4	0
Apiaceae	8	0	4	0	2	1
Liliaceae	8	4	10	1	1	0
Onagraceae	3	0	4	0	1	0
Fabaceae	15	8	8	8	0	5
Portulacaceae	12	0	0	0	0	0
Ranunculaceae	5	0	6	1	0	0
Caryophyllaceae	5	5	3	2	0	3
Polemoniaceae	4	1	2	0	0	0
Boraginaceae	4	2	2	0	0	0
Saxifragaceae	4	1	3	0	0	0

^aAll species whose flowering times coincide with the primary period of fuel combustibility.

season species. Further, it is apparent that not all exotic flora will be adversely affected by fire (Table 3-4). Numerous introduced species set seed prior to late summer, and some proliferate following fire (Chapter Seven). Thus, if managers reintroduce burning to small isolated remnants, they must account for the native species that are sensitive to fire, and monitor the impacts of fire on exotic species that may flourish in its presence.

Conclusion

These results support two primary conclusions relevant for the restoration of the *Quercus garryana* savanna ecosystem. First, this ecosystem was dynamic and spatially heterogeneous rather than homogeneous, stable and naturally pristine. Second, restorative measures must use a combination of historically based and novel management approaches to recreate this heterogeneity. Managers must sustain or re-establish the complement of historic species and processes (e.g., burning, dispersal) and deal with the realities of contemporary landscapes such as habitat loss and invasion. In cases where fire is impractical or ineffective, for example, alternative or complementary measures such as mowing, mechanical soil disturbance, weeding, and selective thinning may be required. Although some of these actions are intensive and appear contrary to the sensitive status of this endangered ecosystem, they are not without precedent. Intensive cultural activity has shaped this ecosystem for millennia and appears necessary to maintain it into the future.

The relevance of historical data is not unique to the Garry oak savanna. The combined effects of altered disturbance regimes, habitat loss, and shifting cultural practices have led

to conservation challenges in many parts of the world. Retrospective data can clarify issues regarding the former dynamics and subsequent transformation of such systems that might otherwise be irresolvable. This information can also guide the development of restoration objectives, ideally in conjunction with other sources of information on past and current ecosystem function (e.g., archaeobotanical data, population viability analyses). Although past conditions can rarely be fully restored, historical information provides a perspective that is unavailable from current biological studies that focus on the end point of centuries of ecological transformation.

Chapter Four

Relative importance of suppression-based and tolerance-based competition among morphologically similar native and invasive grasses.

Abstract. *Invasive species currently dominate many ecosystems but the competitive strategies underlying this dominance are unclear. Are invasive species generalist competitors, or specialized competitors that only thrive in certain environments? Are they largely associated with post-disturbance plant assemblages, or capable of dominating the end-point of succession? I examined these questions by testing the relative importance of resource acquisition (competitive suppression ability) and the ability to tolerate reduced resource levels (competitive tolerance ability) among four warm-season perennial grass species in an invaded oak savanna. These species are morphologically similar but differ widely in relative abundance. Two species (*Poa pratensis* and *Dactylis glomerata*) are exotic invaders and are dominant. The two native species (*Bromus carinatus* and *Elymus glaucus*) are thought to have been the former dominants. Using glasshouse and field experiments I tested whether the two strategies were maintained with changing resource levels and successional conditions, and the relative roles of the strategies in explaining exotic dominance. The relative importance of suppression- and tolerance-based competition shifted with neighbour density, burning, and planting order. Further, the relative importance of plant traits changed depending on the imposed conditions, and the exotic dominants were only competitively superior under specific circumstances. Competitive suppression was maintained with changing resource levels but was confined*

to post-disturbance conditions. With staggered planting order, individuals that established early were the suppression-based competitive dominants regardless of species, fertility, and neighbour density. Competitive tolerance determined long-term patterns of relative abundance and coexistence, but only under the current conditions of low fertility and limited disturbance in the field. Alteration of these conditions changed the relative abundance of the four grasses, and would likely reconfigure the composition and relative abundance of the entire oak savanna community. Exotic dominance in the oak savanna is largely determined by tolerance-based competitive traits such as low relative growth rate interacting with the long-term absence of disturbance. Dominance is best explained, therefore, by the combination of competitive strategies, resource availability, and disturbance history, rather than any one factor alone.

Introduction

It is often assumed that plant invasion is caused by differences in competitive ability between the invading and the native flora, but the strategies that determine these differences are not fully understood (Herbold and Moyle 1986, Byers 2000). Perspectives on this issue tend to mirror a more general debate in plant ecology: the relative importance of suppression ability (i.e., competitive effect) versus the ability to tolerate low-resource levels (i.e., competitive response) for determining species abundance (Goldberg and Landa 1991, Goldberg and Barton 1992).

The “suppression” hypothesis predicts that invading flora have superior resource acquisition ability due to traits such as fast growth or large size compared to native species. As such, they are inherently better at suppressing other species, they can dominate in a range of environments, and are especially favoured by disturbance where resources are less limiting (e.g., Davis et al. 2000). The “tolerance” hypothesis predicts that exotic flora are more resistant to reduced resource levels in conditions that include intense competition. Tolerance specialists are not associated with disturbance, but may be constrained by trade-offs in their ability to compete for various resources (e.g. light vs. nitrogen) and may be limited to specific environments (Tilman 1988).

Many studies have tested the relative importance of suppression versus tolerance ability for structuring plant communities (e.g., Goldberg and Werner 1983, Goldberg and Landa 1991, Keddy et al. 1994, 2002, Wilson and Tilman 1995). Questions remain, however, concerning which has the greatest impact on community structure (Goldberg 1996), the stability of these relationships along environmental and successional gradients (Keddy 2001), and whether stochastic factors (e.g. establishment order) can influence suppression- versus tolerance-based competition (Gerry and Wilson 1995). In invaded communities, it is unclear whether invasive species are more likely to possess one strategy or the other, the importance of disturbance and environmental heterogeneity for invasion, or if invasion may be more a function of past events than competitive trait differences (e.g., Mack 2000, Mack et al. 2000).

The relative importance of suppression versus tolerance may be determined by trade-offs between the ability to grow rapidly and the ability to recruit within resource-limited understories that develop as plant communities approach equilibrium (Grace 1990; Goldberg 1990, 1996). This has led to several hypotheses on the relative importance of suppression and tolerance competition along environmental and successional axes, and may contribute to understanding the causes of dominance by exotic species:

1. Suppression specialists will be dominant in post-disturbance assemblages in which traits such as maximal growth rate and size will be favoured in competitive interactions (Goldberg 1996, Grime 2001).
2. Because size is a determinant of suppression ability, the order of establishment will influence the outcome of competition following disturbance, and will allow larger, older plants to suppress smaller, younger plants regardless of species (Goldberg and Werner 1983, Goldberg 1996).
3. The influence of suppression-based competition will be transient compared to tolerance-based competition in which the ability to withstand reduced resource levels will determine the final outcome of competition (Goldberg 1996, Tilman and Lehman 2001, Tilman et al. 2001).
4. Short-term suppression ability, determined by larger size and faster growth, will be effective in many environments (e.g., high or low fertility), while longer-term tolerance-based competitive outcomes will be limited to particular combinations of environmental factors (e.g., high fertility and low light) due to trade-offs in the ability to compete for different resources (Tilman 1988, Goldberg 1996).

In this chapter, I test these hypotheses by examining suppression- and tolerance-based competition among four warm-season perennial grass species in an invaded oak savanna. Although these species possess some morphological similarities, they differ greatly in relative abundance. Two of the grasses are invasives that now dominate the ecosystem; the others are hypothesized to have formerly been the native dominants. The mechanisms that have caused the transformation of this savanna are not readily apparent, and I seek to determine the underlying influence of suppression- and tolerance-based competition on current patterns of relative abundance.

Using glasshouse and field experiments, I examined the relative importance of suppression versus tolerance competition in post-disturbance conditions, the traits that determine the competitive outcomes, the influence of order of establishment (i.e., size-asymmetric interactions created by the staggered planting of neighbours) on competitive interactions, the ability of each species to recruit within the established grass sward (i.e., tolerance ability), and the stability of the competitive relationships with changing soil fertility and with experimental burning. The glasshouse study allowed me to isolate the impacts of the various treatments on interactions among the grasses, and the fieldwork served to test the applicability of the glasshouse findings for structuring the natural community.

Methods

Study area and selected species

The field experiment was conducted in the Cowichan Reserve near Duncan, British Columbia (Canada) on Vancouver Island (48°48' N 123° 38' W). This is an 18 ha oak (*Quercus garryana* Lit.) savanna that has never been cultivated or cleared but was periodically grazed by cattle and sheep from the late 1800s to the early 1980s.

The four study species are the most common grasses on the reserve. They have some morphological similarities (Table 1), but presently differ greatly in relative abundance. The two invasive grasses (*Poa pratensis* L. and *Dactylis glomerata* L.) have average cover (based on 160 1 m² plots – see Chapter 6 & 7) values of 47% and 23% respectively. The two native species (*Bromus carinatus* Hook. & Arn. and *Elymus glaucus* Buckl.) are less abundant (6% and 0.4% cover respectively) (hereafter I will use generic names only). All four species are perennial C₃ “warm-season” grasses that flower from June to early August. Both *Poa* and *Dactylis* are highly invasive grasses in many parts of North America (Grace et al. 2001).

Glasshouse experiment

The glasshouse experiment was conducted in an unlit and unheated facility at the University of British Columbia (UBC) in Vancouver, British Columbia (49°03' N 122° 45' W). This experiment assessed suppression ability and tolerance ability among the four species, and how these relationships were altered by soil fertility, the density of neighbours, and staggered planting order. The experiment was an all-possible

Table 4-1. Selected traits of the four perennial grass species. All measured values are from the glasshouse experiment. Maximum height and maximum mass are final means from the target plants grown without neighbours, and with (+) and without (-) fertilizer. "No. of flowering culms" is a combined value over all treatments. Bracketed values = 1 standard error.

Traits	Species							
	Invasive species				Native species			
	<i>Poa pratensis</i>		<i>Dactylis glomerata</i>		<i>Bromus carinatus*</i>		<i>Elymus glaucus</i>	
Growth form	rhizomatous		caespitose		caespitose		caespitose	
Seed mass (mg seed ⁻¹)	0.2		1.4		9.2		4.6	
Emergence time (days)	13.4		10.6		8.2		7.1	
No. of flowering culms	7		24		41		129	
<i>Treatment (+/- fertilizer)</i>	+	-	+	-	+	-	+	-
Max mass (target - g)	18.3	6.8	90.3	19.5	48.3	10.8	39.5	9.3
	(1.51)	(0.42)	(5.51)	(2.4)	(2.85)	(0.35)	(1.46)	(0.62)
Max ht – week 6	4.0	3.1	6.7	6.0	12.0	12.4	14.0	13.9
(target - cm)	(0.13)	(0.08)	(0.11)	(0.11)	(0.25)	(0.17)	(0.21)	(0.17)
Max ht – week 11	25.7	17.7	48.4	38.0	39.9	25.9	33.1	21.6
(target - cm)	(0.44)	(0.45)	(0.85)	(0.97)	(0.6)	(0.49)	(0.57)	(0.46)
Max ht – week 16	35.4	28.1	75.1	48.3	51.5	37.4	52.5	39.5
(target - cm)	(0.67)	(1.31)	(1.49)	(0.85)	(0.91)	(0.99)	(1.0)	(0.95)
Max ht – week 23	102.0	67.8	128.2	79.8	143.1	119.1	172.4	118.6
(target - cm)	(3.72)	(1.89)	(2.33)	(1.51)	(3.61)	(2.61)	(5.6)	(3.5)

*listed as biennial by Pavlik (1995). Listed as biennial or perennial by Douglas et al. (2000). This species grows as a perennial at the study area (MacDougall and Turkington, unpublished).

combinations pair-wise competition study conducted from March to September 2001 (Fig. 4-1). The experiment's duration mimicked that of the growing season of the four species in the field. The plants were started from seed collected in the reserve.

Ten litre pots were used to maximize available rooting volume and were filled with a mixture of peat (45%), sand (45%), and native soil (10%). The native soil was collected from the study area and served as an inoculum in case there were mycorrhizal or microbial associations required by the grasses (Chanway *et al.* 1991; Callaway & Aschehoug 2000). The quality of the potting mixture resembled the quality of the reserve soils, with low pH and limited available N (Potting mixture: pH = 5.2; $\text{NO}_3 = 2.08 \text{ mg kg}^{-1}$ soil; $\text{NH}_4 = 45.07 \text{ mg kg}^{-1}$; Reserve soils: pH = 4.9; $\text{NO}_3 = 4.37 \text{ mg kg}^{-1}$; $\text{NH}_4 = 46.46 \text{ mg kg}^{-1}$). Soil analyses were conducted at the UBC Soil Sciences lab. Nitrate and ammonium were extracted in 1 mol L^{-1} KCL solution.

The experiment was arranged as a split-plot design (Steel & Torrie 1980) with fertility (+/- fertilizer addition) and establishment order (targets and neighbours planted simultaneously, or delayed planting of neighbours) as the main effects, and density (zero [control], four or sixteen neighbours pot^{-1}) and species (four) as the subplot effects. There were three replicates of all treatments. Each pot was planted (from seed) with four target individuals of one of the four grass species. Four targets were used to reduce the effects of size variation among individual target plants (Goldberg and Landa 1991). The total number of pots was 432 (four species X four main effects X nine subplot interactions

[one control pot + eight neighbour treatments (i.e. two densities X four species) per species] X three replicates).



Figure 4-1. Unfertilized (left) and fertilized (right) pots from the glasshouse experiment.

Seeds from all target plants were sown on March 30, 2001. Neighbour plants were simultaneously sown in half of the 432 pots (0 [control], 4, or 16 neighbours pot^{-1}). The remaining 216 pots were sown with neighbors 45 days (May 14) after the target plants were sown. By this time, the target plants had grown to heights averaging between 5-12

cm depending on the species. To achieve the required target and neighbor densities, seeds were over-sown and thinned. Seed germination of all the species was >95%. Once planting was completed, the pots were arranged into twelve blocks (4 main plot combinations X 3 replicates). Half of the blocks were fertilized with a diluted N-P-K (15:5:15, diluted to 100 ppm) water-based solution (ExcelTM by Scott Co.). All pots were watered as needed, which was up to once per day during the summer.

The heights of the target plants were measured four times during the experiment - at 6 weeks (May 14), 11 weeks (June 20), 16 weeks (July 24), and 23 weeks (September 7). This allowed us to chart the changing dynamics of the species interactions from emergence to final harvest (Gibson et al. 1999). Height served as a surrogate for competition because light is an important limiting factor for recruitment and relative abundance in the dense grass swards that currently dominate the reserve (Chapters Six and Seven). I assumed, therefore, that small differences in height would likely have profound impacts of plant interactions in the glasshouse and in the field (e.g., Gaudet and Keddy 1988, Grime 2001).

After 16 weeks, the fertilized pots were encircled with 40 cm-tall wire mesh (5 cm) to prevent plants avoiding within-pot interaction and from interacting with plants in the neighboring pots.

After 23 weeks, all above-ground biomass was harvested over an eight-day period and all target and neighbour individuals separated and counted. The roots of target and

neighbour plants could not be differentiated, so below-ground biomass was not measured. Above-ground biomass was dried for 48 hours at 70° C and weighed.

The competitive influence of the neighbours on the targets, based on final target biomass, was calculated using an index of relative competitive intensity (RCI) (Weigelt and Jolliffe (2003):

$$RCI = \frac{(\ln[\text{control biomass}] - \ln[\text{treatment biomass}])}{\ln[\text{control biomass}]}$$

Treatment biomass was the final mean weight of the target plants grown with neighbours of each species. Control biomass was the final mean weight of each species grown without neighbours. RCI was calculated for monoculture (target and neighbours are the same species) and mixture (target and neighbour are different species) to allow separation of intra- and inter-specific effects (Miller 1996). Values were transformed ($\ln x + 1$) to normalize the data, especially the treatment measures which were highly skewed towards zero (median = 6.4 g plant⁻¹) yet also contained outliers > 110 g plant⁻¹.

Competitive suppression ability of each species x on species y was the mean RCI value with x as the neighbour and y as the target. Competitive tolerance ability was the mean RCI value with x as the target and the other species as neighbours.

I calculated the per-plant competitive interaction (i.e., both suppression and tolerance) of y and x by regressing the density of neighbours (y) on the final biomass of the target (x). I calculated the per-gram competitive influence of y and x by regressing the average final biomass of each neighbour plant (y) on the final biomass of the target (x). Although per-plant and per-gram effects are generally expected to be equivalent (Freckleton & Watkinson 2000), I anticipated that per-plant competitive effects would be significantly greater than per-gram effects if below-ground processes were important; per-gram measures were based only on above-ground biomass.

Treatment effects on final above-ground target biomass (i.e., RCI) were examined using a split-plot ANOVA, with fertilization and planting order as the main effects (Table 4-2). Of particular interest were the higher-order interactions among the four variables, especially the degree to which species/density interactions were shaped by fertility and planting order alone and in combination. Once the significance of these interactions was determined, planned individual comparisons were conducted using Dunnett's test that contrasted the various single treatments with the control (Zar 1999).

The seasonal height data were analysed using repeated-measures ANOVA for the unstaggered treatments only (fertilized and unfertilized). Because the variance-covariance matrices failed the test for sphericity, significance was determined after the probabilities were adjusted using Greenhouse-Geisser and Huynh-Feldt corrections (Zar 1999, Von Ende 2001). Individual contrasts (Tukey's Test) tested the similarity in height among the four species at each period of measurement (May-September) (Zar 1999).

Table 4-2. Summary of split-plot ANOVA for above-ground biomass at final harvest in the glasshouse experiment. Main effects are fertilizer (F) and establishment order (O); sub-plot effects are neighbor density (D), and species (S). Significant effects are shown in bold ($p < 0.05$)

Source	df	Final Biomass	
		F-ratio	p value (<)
<i>Main Effects</i>			
Replication	2	0.46	0.63
F	1	64.7	0.0001
O	1	74.1	0.0001
F*O	1	0.47	0.49
Error	6		
<i>Sub-plot Effects</i>			
S	3	65.7	0.0001
D	8	37.5	0.0001
S*D	24	1.3	0.181
F*S	3	25.1	0.0001
F*D	8	3.6	0.0005
O*S	3	11.4	0.0001
O*D	8	17.2	0.0001
F*S*D	24	1.9	0.0009
O*S*D	24	1.3	0.174
F*O*S	3	3.9	0.01
F*O*D	8	1.6	0.119
F*O*D*S	24	0.84	0.69
Error	280		
TOTAL	431		

To determine the relationship between relative suppression and tolerance ability and trait differences among the grasses, I used step-wise multiple regression analysis (Zar 1999) to determine which trait or traits (Table 4-1) are most strongly associated with the final competitive outcome of the glasshouse experiment. Seed biomass was the average mass per seed based on fifty seeds of each species. Emergence time was determined by averaging the time from planting until germination of fifty seeds for each species. The ratio of "maximum final height plant⁻¹: maximum final biomass plant⁻¹" combines the ability to resist suppression (vertical growth) and to suppress neighbours (lateral growth). All data analyses were performed using JMPIN software (SAS 2001).

Field experiments

Two field experiments were conducted to determine the response of the four grasses to annual burning over three years, and their ability to establish from seed with and without the presence of the grass overstory. Both were conducted in the same 1 m² plots, as part of a larger study examining competition along an experimental disturbance gradient (i.e., Chapters Six and Seven). In the first experiment, three burn treatments were imposed over three years: control (no burning), a fall burn (moderate disturbance), and a summer burn (high disturbance). Percent cover was assessed prior to the first burn in May 2000, and re-assessed in May of 2001 and 2002. Percent cover values were visually estimated following Armesto and Pickett (1985). Percent cover changes by the grasses for each burn regime were examined with a 2-way ANOVA. Planned individual contrasts were conducted with Tukey tests (Zar 1999).

In the second experiment, following commencement of the fall rainy season (October 2001), fifty seeds of each species were planted in 10 cm² subplots within the 1 m² plots. There were four replicates per treatment. The number and height of germinants were measured in December 2001 and April 2002. Final height and percent establishment of each species in each treatment were examined with a 2-way ANOVA. Planned individual contrasts were conducted with Tukey tests.

Results

Competitive suppression and tolerance ability among the four species were influenced significantly by interactions among establishment order, neighbour density, and burning (Table 2). The observed suppression and tolerance hierarchies were not consistent among the treatments or between the glasshouse and field experiments, and the relative importance of various plant traits changed depending on the imposed conditions.

Overall, the exotic dominants (*Poa* and *Dactylis*) were competitively superior only for particular combinations of environmental factors. *Dactylis* was the dominant competitor for both suppression and tolerance in the glasshouse (Fig. 4-2) but was a poor tolerance competitor in the field. *Poa* was the weakest suppression and tolerance competitor of the four species for most of the glasshouse and field treatments, despite being the most abundant species in the study area.

Hypothesis One: Suppression specialists will dominate post-disturbance assemblages.

Glasshouse control conditions

The glasshouse control conditions simulated a post-disturbance environment, with high light availability and no initial competitive interference. Under these conditions, suppression and tolerance hierarchies were identical (*Dactylis*>*Bromus*>*Elymus*>*Poa*).

Dactylis was best able to suppress all target species at both neighbour densities, and was least affected by the competitive effects of the other species. These results did not differ whether I used per-plant ($r^2=0.11$, $p<0.0001$) or per-gram ($r^2=0.13$, $p<0.0001$) measures. For *Dactylis* and *Bromus*, the impacts of intra-specific suppression were significantly greater than the suppressive impacts of *Elymus* and *Poa* (Tukey's Test, $p<0.002$).

Only one trait was significantly associated with both suppression and tolerance ability for the control treatment - mid-season plant height (11 and 16 weeks) ($p<0.039$). Mid-season plant height was also significantly associated with final maximum biomass ($r^2=0.92$, $p=0.008$), although this measure did not significantly predict suppression-based or tolerance-based competitive ability directly ($r^2=0.68$, $p=0.17$).

Two traits, seed mass and emergence time, determined relative growth in the early stages of this experiment (e.g., May plant height) but were not correlated to the final

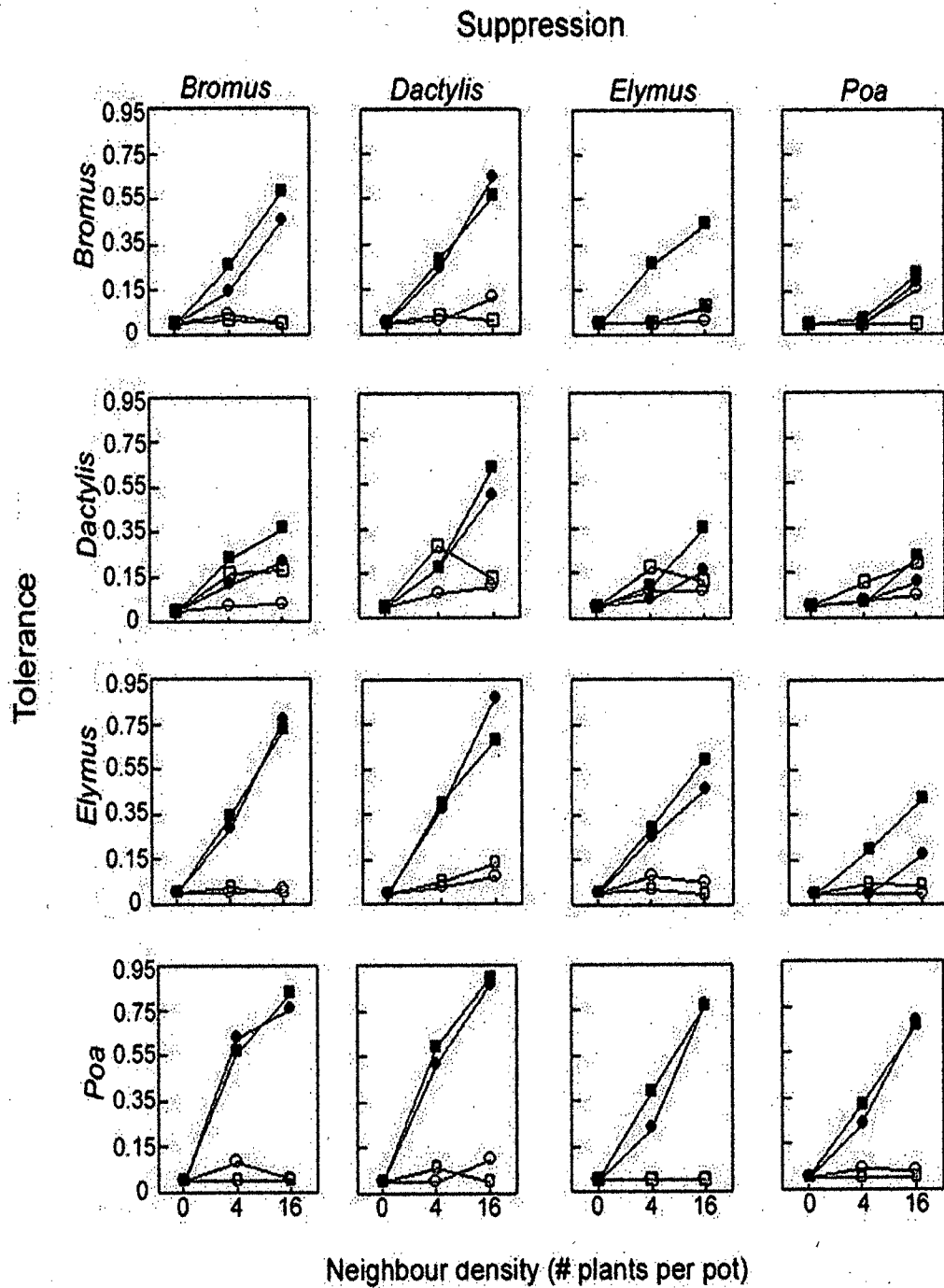


Fig. 4-2.. Per-plant suppression and tolerance for the four glasshouse treatments, based on the calculated competition values. Competition values range from 0 (no competitive influence) to 1 (complete suppression). The greater the positive slope of the interaction, the greater the competitive suppression with increasing neighbour density. Rows indicate "relative tolerance ability", the performance of each species as a target in the presence of the other species as neighbours. Columns indicate "relative suppression ability", the ability of each species as neighbours to reduce the performance of the other species as the target. (●) = fertilized and simultaneous planting of neighbours. (■) = unfertilized and simultaneous planting. (O) = fertilized and delayed planting of neighbours. () = unfertilized and delayed planting of neighbours. For example, in row 1 - column 2 simultaneously planted Dactylis neighbours suppressed Bromus targets with increasing density in both fertilized and unfertilized pots, while delay-planted Dactylis neighbours had no effect on Bromus in either fertility treatment. Standard error bars (n= 3 replicates) are not included for the sake of clarity.

competitive outcome ($p > 0.50$). Large seed mass and rapid emergence, characteristic of the native grasses (Table 4-1), were significantly correlated ($r^2 = 0.86$, $p = 0.042$), determined target height after 6 weeks ($p < 0.03$), and also were significantly associated with final culm production and final maximum height for these species ($p < 0.045$). The initial growth advantage conferred by these traits was temporary; *Bromus* and *Elymus* were overgrown by *Dactylis* by June (week 11) (Fig. 4-3). By contrast, *Poa* had the smallest seed size and was the slowest to emerge and did not overcome this disadvantage for the duration of the glasshouse experiment.

Effects of burning on seedling recruitment

The competitive hierarchies observed for the glasshouse control treatment ($D > B > E > P$) did not match the patterns of relative recruitment success following burning in the field, even though both experiments were initiated from seed, both had limited or no competition from established plants, and both were of similar duration. After 28 weeks in the fall burn plots, *Poa* had significantly lower numbers of surviving seedlings compared to the other grasses, which did not differ significantly (Fig. 4-4a). The summer plots had the highest percentage of bare soil and the lowest level of established vegetation cover, yet there were no significant differences in survival among the four species (Fig. 4-4b). *Poa* had significantly higher survival for this treatment compared to its survival in the control plots ($t = 6.17$; $p = 0.016$) (Fig. 4-4a).

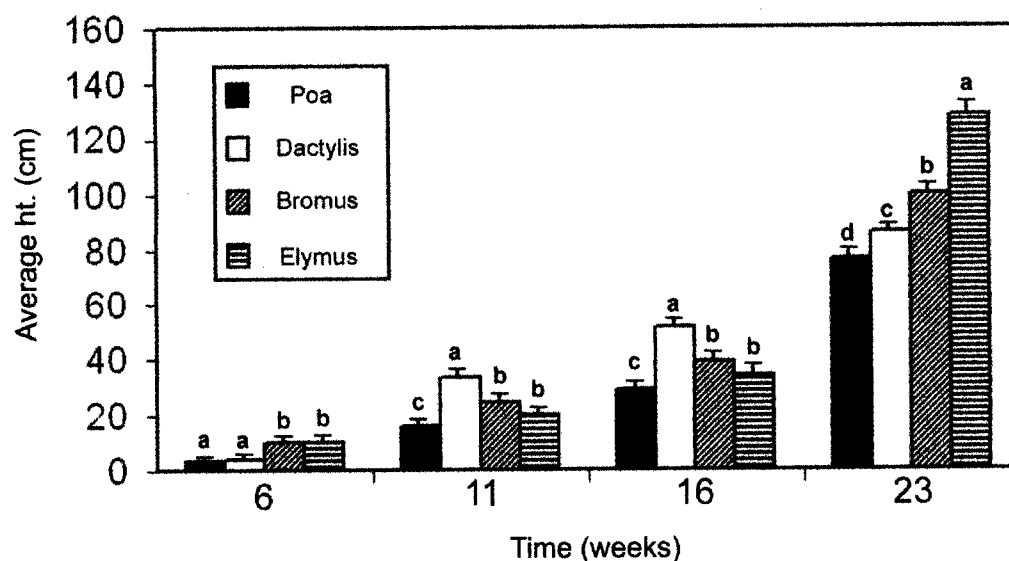


Fig. 4-3. Average maximum seedling height (cm) (bars = 1 SE) at six weeks (May), eleven weeks (June), sixteen weeks (July), and twenty-three weeks (September) for the four grass species in the glasshouse. Bars showing the same letter are not statistically different within each of the four time periods (Tukey's test).

Hypothesis two: The order of establishment will influence the outcome of competition.

Staggered planting altered the observed competitive hierarchy (i.e., D>B>E>P) in the glasshouse for both fertilized and control conditions (Fig. 4-2). Plants that established early were the eventual competitive dominants regardless of species and neighbour density. By the seventh month for each species, the final biomass of target plants grown with neighbours planted six weeks later was not significantly different from final biomass of target plants in the control pots with no neighbours ($p=0.82$).

Height and biomass of neighbour plants were significantly reduced compared to the

neighbour plants that were not stagger-planted ($p < 0.0001$). Average heights of the stagger-planted neighbours did not exceed 20 cm for either fertilized or unfertilized treatments, compared to average heights of the neighbour plants in the unstaggered treatments (101.32 cm [SE = 3.1] and 53.8 cm [SE = 1.9] respectively). Mortality of the stagger-planted neighbours in the fertilized treatment was significantly greater (78% of all plants) than mortality in the unfertilized stagger-planted treatment (19% of all plants) ($t = 6.42$, $p < 0.005$), even though differences in average neighbour height and final competitive impact on target performance were both minimal.

Hypothesis Three: Tolerance ability determines competitive outcomes within undisturbed savanna.

The prediction that the current dominant species (*Poa* and *Dactylis*) would be most capable of regenerating from seed in their own understory was not supported. The two native species (*Bromus* and *Elymus*) had significantly higher levels of seedling survival and final seedling height in the unburned control plots compared to *Dactylis* and *Poa* (Figs. 4-4a & 4-4b). Over time, this result persisted despite the reduction in the number of surviving seedlings of all species. In some control plots, the native species grew tall enough to penetrate the dense overstory of litter and living biomass within the seven month period. The exotic grasses, by contrast, had significantly lower survival rates and average heights after 28 weeks; they were unable to penetrate the litter layer (Figs. 4-4a & 4-4b).

Hypothesis four: Competitive outcomes will be specific to particular combinations of environmental factors.

Fertilization

Fertilization did not alter the competitive hierarchy observed in the control treatment (D>B>E>P). *Dactylis* was the superior competitor for both suppression and tolerance ability (Fig. 4-2). This result occurred despite NO₃ levels 150 times higher in the fertilization treatments (mean = 304.35 mg kg⁻¹) compared to the NO₃ levels in the unfertilized pots, and increased aboveground biomass by an average of 5 times compared to the control treatment. Soil NH₄ levels were not significantly increased by the fertilizer treatments ($t=0.39$, $p=0.64$).

While the competitive hierarchy among the plant species was maintained, the traits that determined this outcome changed. For suppression-based competition, the only trait to vary significantly among the species was the maximum final height:maximum final biomass ratio ($r^2=0.97$, $p=0.014$). Mid-season height (weeks 11 and 16), final maximum height, and final maximum biomass had no significant impact ($p>0.08$). Both *Dactylis* and *Bromus* were able to grow beyond 1 m in height as well as produce dense layers of lateral foliage that suppressed target individuals or reduced the influence of neighbour individuals on its own growth. *Elymus*, by contrast, grew tallest of all species with

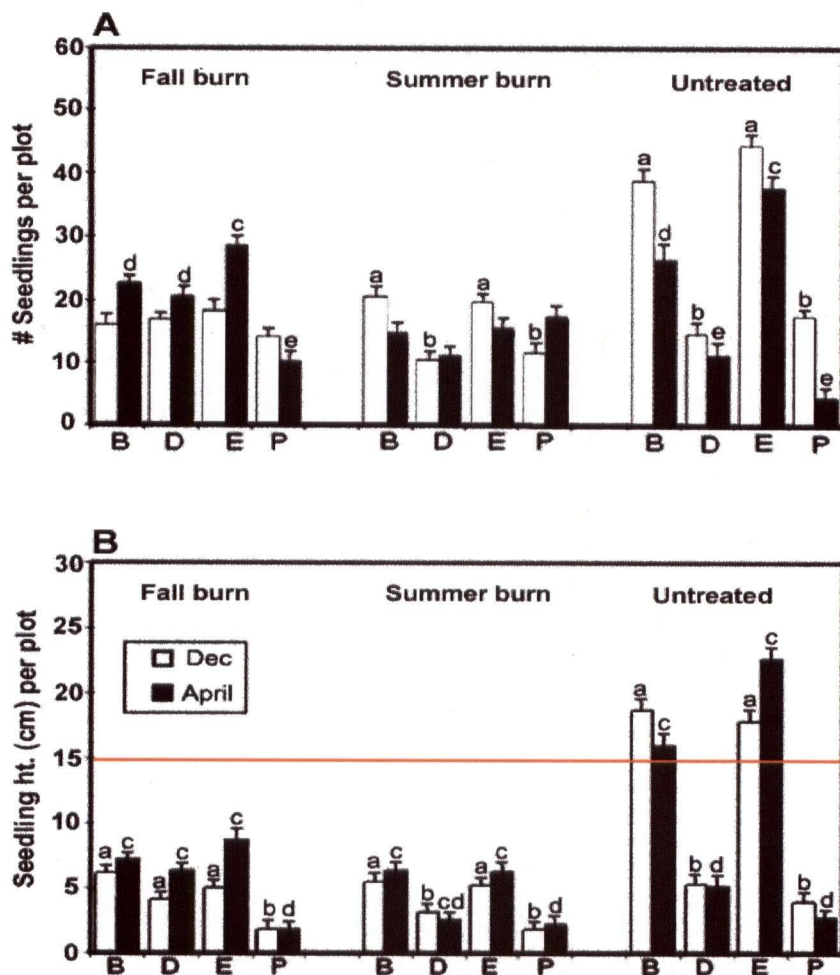


Fig. 4-4. (a) Average number of seedlings plot⁻¹ and (b) average seedling height plot⁻¹ after 12 weeks (December) and 28 weeks (April) for the three field treatments. Bars indicate 1 standard error ($n = 4$). Fifty seeds species⁻¹ were planted in each plot. B = Bromus, D = Dactylis, E = Elymus, P = Poa. Letters indicate statistical relationships among the four species at 12 weeks (a,b) and 28 weeks (c,d,e) within each treatment (Tukey's test, $p < 0.05$). Bars with no letters = no statistically significant differences. Red line indicates approximate height of the litter layer in the control plots.

fertilization but produced little lateral foliage and had limited competitive influence on the other grasses (Fig. 4-5).

The ability to resist suppression by neighbours was significantly associated with a combination of factors: the height:mass ratio ($r^2=0.97$, $p=0.002$) and final maximum height ($r^2=0.91$, $p=0.042$). Because the neighbours surround the target and were prevented from growing laterally due to the wire mesh, target plants that were equal in height or smaller than the neighbours were suppressed.

Seed mass and emergence time were correlated with height in May ($p<0.02$) and maximum final height ($p<0.002$). However, they were not significantly associated with suppression- and tolerance-based competitive ability ($p>0.68$).

Impacts of burning on relative abundance

Burning did not increase the percent cover of any of the grasses; the relative abundance of one or all of these species was significantly reduced depending on burning frequency (Fig. 4-6). For the fall burn, the existing pattern of relative cover was maintained, except *Poa* was reduced significantly (from 45% to 26% average plot cover) compared to control plots ($t = 5.381$; $p = 0.02$). For the summer burn, all of the species decreased

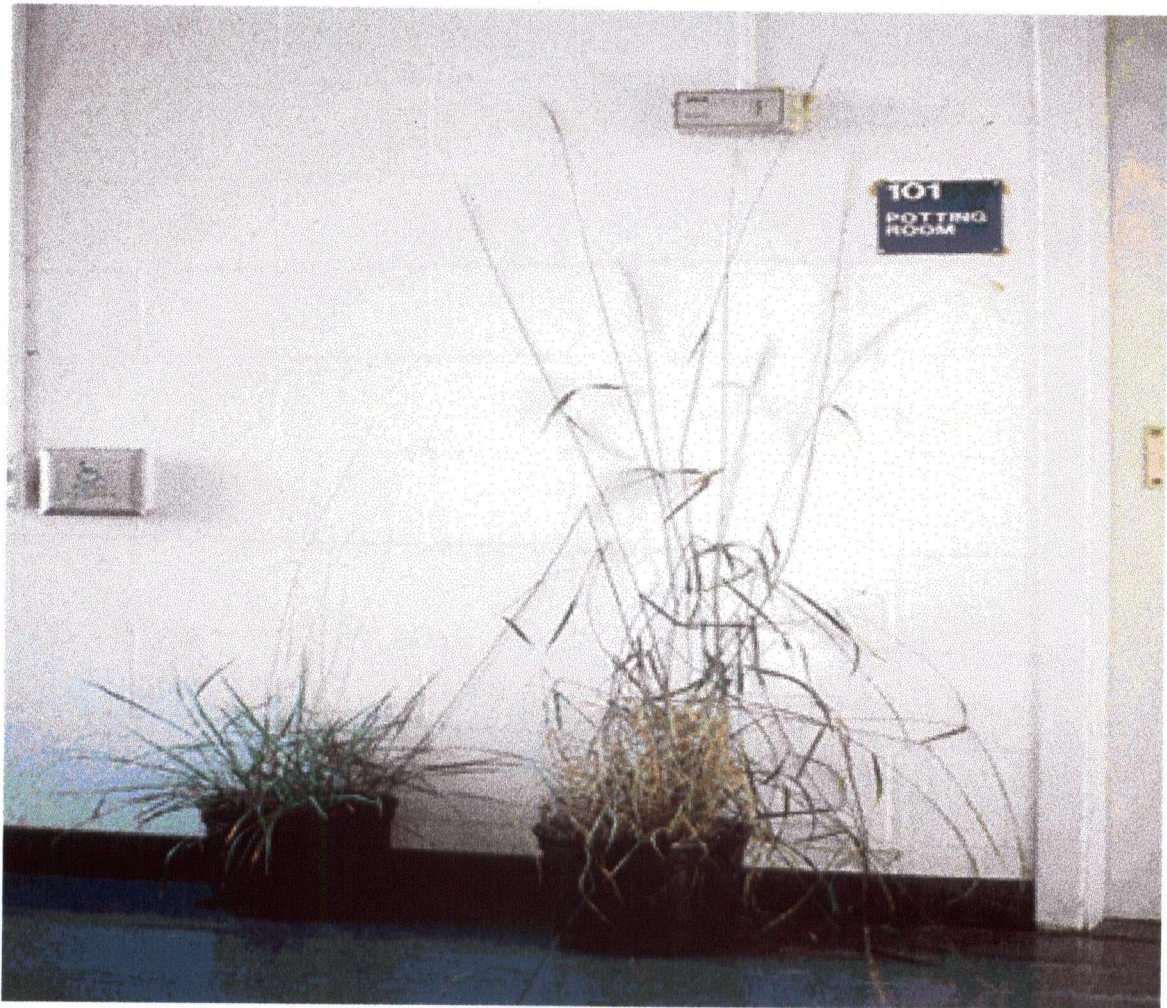


Fig. 4-5. Unfertilized (left) and fertilized *Elymus glaucus* after seven months from the glasshouse experiment.

significantly compared to the control plots (Fig.4-6). *Elymus* was eliminated from all plots, and *Poa* declined significantly (8% average cover) compared to the control plots ($t = 20.621$; $p < 0.0001$).

In the summer burn plots, the four grasses were mostly replaced by a combination of annual forbs (mostly exotic), annual grasses (all exotic), perennial forbs (all native), and the exotic perennial grass *Anthoxanthum odoratum*. The annual species recruited from the

seed bank, while the perennial forbs and *A. odoratum* recruited mostly from dispersal from nearby adults, as well as re-sprouting from individuals that occurred in small numbers prior to disturbance (Chapters Five, Six, and Seven).

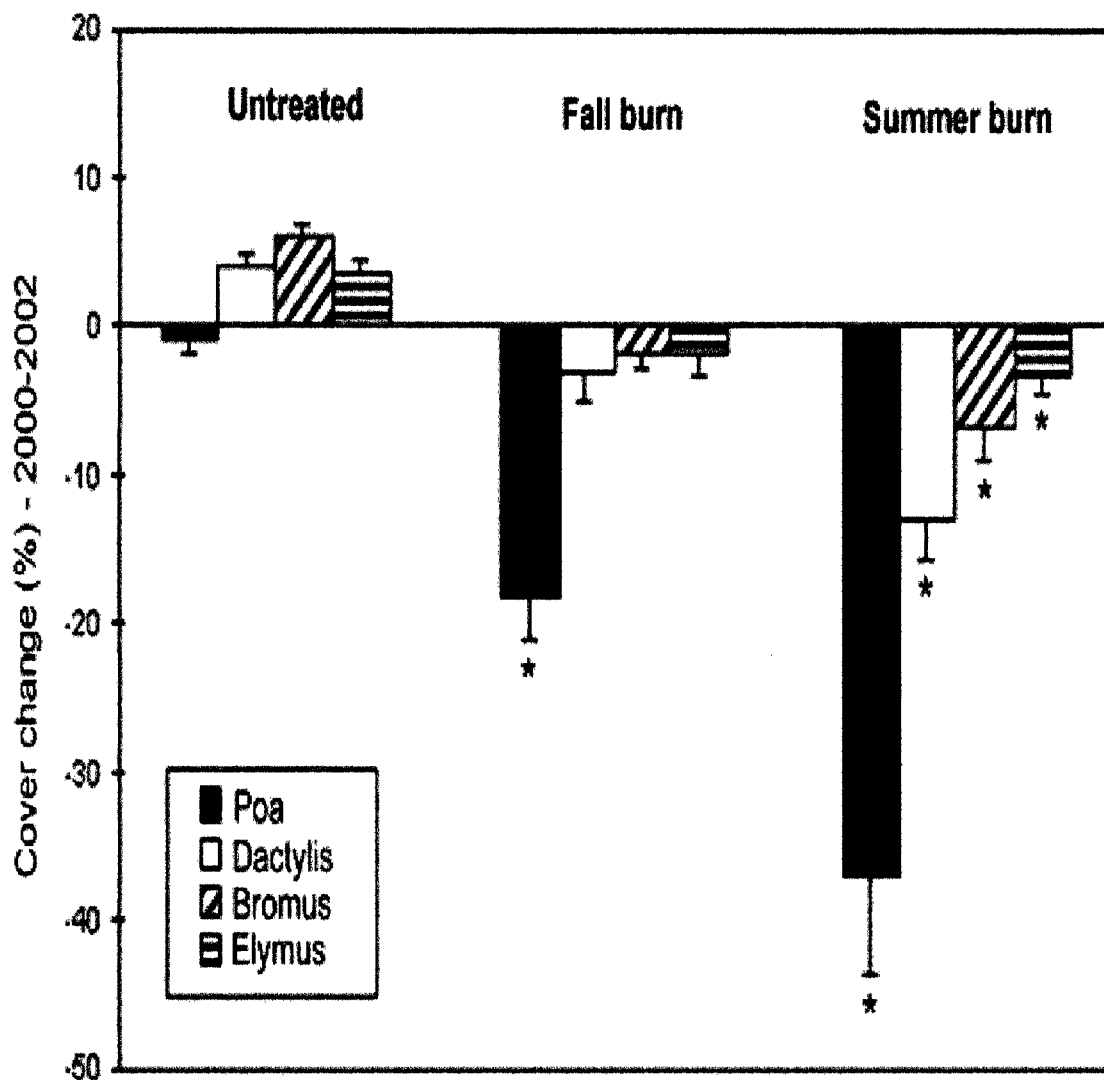


Fig. 4-6. Average change in percent cover (bars indicate 1 standard error, $n = 40$ plots) in control, fall-burn, and summer-burn plots from 2000 (pre-treatment) to 2002. "*" indicates a significant decrease in average cover plot¹ compared to 2000 (Tukey's test, $p < 0.05$). In the summer-burn, *Elymus* was eliminated from all plots.

Discussion

The focus of these experiments was to assess the relative importance of suppression-based and tolerance-based competition among the exotic and native grasses, whether these relationships were maintained with changing environmental conditions and successional phases, and the connection between these strategies and the current patterns of relative abundance in the natural community.

The results indicate that competitive tolerance ability currently determines the patterns of relative abundance for these species in the study area, but is contingent on a particular combination of environmental factors, especially the absence of disturbance. The results also demonstrated the robust but ephemeral status of competitive suppression ability and suggest that deviations from the current environmental regime (i.e., a low-resource low-loss habitat) due to disturbance would shift the relative abundance of these grasses and, most likely, overall community composition, structure, and diversity.

Hypothesis One: Suppression specialists will dominate post-disturbance assemblages.

My results support the hypothesis of numerous authors that suppression specialists dominate post-disturbance plant assemblages (Goldberg and Werner 1983, Grace 1990, Goldberg, 1996, Grime 2001). The traits that determined position within the competitive hierarchy in the glasshouse, under control conditions, were height and growth rate at mid-

season. The robust stature and rapid growth of *Dactylis* led to its suppression of all target species, including itself. But tolerance ability was also relevant. Both suppression and tolerance hierarchies were identical in the control pots, and the ability to resist suppression was as important as being able to suppress neighbouring individuals. In addition, the traits that determined these abilities were almost identical. The positive correlation between suppression and tolerance ability has been predicted for post-disturbance environments where interactions occur among individuals of similar size (Goldberg 1990). By pre-empting available resources, rapidly growing species not only suppress competitors but also are generally indifferent to the competitive influence of their neighbours (i.e., tolerance).

The competitive dominance exhibited by *Dactylis* developed gradually over the first twelve weeks of the glasshouse experiment. Initial seedling emergence favoured the two native species due to their larger seed mass and their ability to break dormancy within a few days of sowing. Many studies have demonstrated the importance of emergence time in determining competitive outcomes within plant communities (Fowler 1984, Bergelson & Perry 1989, Goldberg et al. 2001). For the four species of this study, however, it did not influence final competitive outcome. *Dactylis* was able to overcome the initial size advantages of the two native grasses, over-topping all species by mid-summer. This result highlights the importance of examining the competitive interactions of plants across a range of life history stages, rather than only focusing on the initial or final stages of growth (Gibson et al. 1999; Freckleton & Watkinson 2000).

The ability of *Dactylis* to dominate other species, native or exotic, in post-disturbance conditions suggests why it has become a problematic invasive species in this savanna and elsewhere. Prior to invasion, rapid emergence time by *Elymus* and *Bromus* in this sub-Mediterranean climate was probably an important strategy for maximizing growth before the on-set of the summer moisture deficits, as well as increasing competitive ability following disturbance pulses. However, when competing against similar-sized seedlings of *Dactylis*, the rapid development of *Bromus* and *Elymus* only confers a temporary competitive advantage.

Hypothesis Two: The order of establishment determines the outcome of competition.

Goldberg and Werner (1983) proposed that suppression-based competitive ability may be generally equivalent among plant species, and thus differences in physical size may determine competitive outcomes among individual plants regardless of their species identity. My results demonstrated the influence of establishment order on competition among the four species, thus supporting this hypothesis. In the glasshouse, the 45-day staggered planting altered the suppression- and tolerance-based competitive hierarchies that were observed under control conditions - the larger older target plants dominated regardless of species, density of planting, or fertility level. Even with the slowest emerging species (*Poa* - 13.4 days) planted with the fastest (*Elymus* - 7.1 days), the neighbour plants had no measurable effect on the targets.

Although this suggests the significance of establishment order at the individual level, it is unclear whether these advantages could affect species dominance within the natural community. A number of studies have found establishment order to have a limited impact on the structuring of communities, while others have found the opposite (see Gerry and Wilson 1995). In this ecosystem, it seems unlikely that suppression-based advantages conferred by establishment order could determine longer-term patterns of relative abundance due to the differences in tolerance ability among the four grasses. However, establishment order may be highly significant for the coexistence of subordinate species. It is unlikely that *Dactylis* seed, for example, will always be present when gaps are formed thus allowing individual plants from subordinates to grow large enough to resist subsequent suppression. Such resistance by individual plants has been observed in other heavily invaded Mediterranean regions of western North America (Stromberg & Griffin 1996)

Hypothesis Three: Tolerance ability determines competitive outcomes within undisturbed savanna.

Numerous authors have stated or implied that, over time, tolerance-based competitive ability is more important than suppression-based competitive ability for determining persistence and abundance within plant communities (Goldberg and Werner 1983, Wilson and Tilman 1995, Goldberg 1996, Tilman and Lehman 2001). In the absence of long-term data, I tested this assertion in two ways: (i) by examining whether the competitive differences caused by growth rate and physical size in the glasshouse

experiment match the relative abundance hierarchies in the field, and (ii) by examining the relative tolerance-based competitive abilities of each species within the established grass sward. This latter approach is based on the assumption that to persist, recruiting individuals of the dominant species must be able to tolerate the reduced resource levels that the species imposes on the community (Goldberg 1996).

The discrepancy between the glasshouse results and the relative abundance in the field suggests that suppression-based competition would determine dominance following disturbance, but over time would be replaced by species that could tolerate reduced resources caused by increased crowding. Under glasshouse control conditions, *Poa* was the weakest competitor because of its slow rate of growth and small physical size. However, these same traits, along with larger root:shoot ratios, rhizomatous life form, and the ability to recruit by tillering, should give it a substantial competitive advantage in the absence of subsequent disturbance.

The most significant characteristics favouring *Poa* under low loss conditions (no burning, limited herbivory) is the production of a dense above-ground litter layer and the ability to recruit through this layer by tillering. The other grasses are bunch-type species that do not expand laterally below-ground. The ability of *Poa* to tiller gives it a competitive advantage against most other species of this community that must recruit from seed if they are to persist, including *Dactylis*, *Bromus*, and *Elymus*. Only a small percentage of the eighty species in the study area can recruit consistently within the dense grass sward, and most are exotic pasture species (e.g., *Vicia* spp., *Cerastium* spp.).

In the seed addition experiment, I tested whether the ability of the four grasses to recruit from seed was directly proportional to their relative abundance in the field. This hypothesis was not supported. The exotic grasses had low establishment and survival, suggesting that both recruit rarely from seed in the dense grass understory. The unimportance of seed recruitment by dominant species has been observed in other grasslands (Hartnett and Fay 1998). By contrast, the native grasses were able to establish from seed within the light-limited sward. This ability may be caused by their larger seed mass, which allows the seedlings to penetrate the layer of grass litter and living biomass before their seed reserves are exhausted.

These results have three implications regarding the mechanisms determining persistence and relative abundance of these four grass species. First, it emphasizes the importance of tillering for *Poa* and suggests that *Dactylis* is maintained by periodic disturbance pulses that allow it to recruit and establish. As discussed earlier, *Dactylis* is adept at rapid resource acquisition in post-disturbance competitive environments.

Second, it suggests that the initial penetration by exotic species into this ecosystem required some level of disturbance of the native community. This may have been connected to highly intensive livestock grazing, which began immediately upon European colonization on Vancouver Island, or may have been coupled with the occurrence of fire prior to its suppression in the late 1800s. The intentional introduction

of large amounts of seed in the late 1800s may also have facilitated grass establishment (e.g., Mack 2000).

Third, it indicates that the assumption of former dominance by *Bromus* and *Elymus* may be incorrect. This assumption is based on their current high abundance relative to the other native species at this site. However, their abundance appears to reflect their capabilities of establishing within the exotic sward (i.e., they are capable tolerance competitors from seed). This scenario is consistent with the results of Rabinowitz et al. (1984) where competitive superiority was tied to long-term persistence within the community, but it did not result in high relative abundance.

Hypothesis four: Competitive outcomes will be specific to particular combinations of environmental factors.

I hypothesized that if the relative abundance hierarchy was being maintained by suppression-based competition, then disturbance should maintain or increase this pattern. If driven by tolerance-based competition, then burning should disrupt current resource levels and lead to shifts in abundance. My results demonstrated that the latter assertion is more likely. Burning caused a pronounced transformation in relative abundance among the four species, and in the community in general. With the fall burn, *Poa* was the only species to decrease significantly in percent cover. With the summer burn, all species declined.

The reduction of *Poa* cover with disturbance has been observed elsewhere (Wilson and Tilman 1995, Collins 2000), and is consistent with the view that tolerance competitors are locked into trade-offs that include an inability to respond rapidly to loss (Tilman 1988). The high relative abundance of *Poa* is probably maintained or increased over time in this community following individual-level turnover of other species (e.g., plant senescence) or by in-filling of small gaps by tillering. Turnover caused by frequent and wide-spread disturbances would favour other species.

By contrast, fertilization had no effect on the order of suppression and tolerance competition in the glasshouse experiment. Based on the view that the soils of this ecosystem are infertile, I had hypothesized that abundance was a function of competition for nutrients and that fertilization would eliminate this advantage. This hypothesis was not supported, despite the substantial increase in above-ground biomass of target and neighbour plants.

The primary explanation is that the glasshouse experiment did not adequately simulate the conditions under which these grasses interact in the natural community. With initially high light conditions and competition against individuals of similar size, fertilization merely magnified the advantages of the larger and faster growing species such as *Dactylis*. However, it also appears that soil fertility may not be as limiting in this ecosystem as I had originally assumed. Instead, light limitation seems to have a far more important impact on recruitment and relative abundance as is typical of more productive grasslands (Carson and Pickett 1990, Knapp et al. 1998). I predict, therefore, that

increased fertility in the field would intensify light competition by raising productivity, rather than switching interactions from below-ground to above-ground. My inability to measure root competition prevented us from testing that light is more limiting than nutrients or description of how fertilization affects interactions among roots. However, the concordance of my results at low and high fertility suggests that such measures may be unnecessary (Cahill 2002). Further, fertility increases can cause increases in below-ground competition among grassland plants but this is most likely to occur in unproductive systems where canopies are short and light less limited (Rajaniemi et al. 2003).

Implications for succession

The current pattern of relative abundance for these four grass species in the study area is a result of a combination of events initiated following European settlement in the late 1800s. The study area has been free from intensive disturbance for some time, possibly dating to the 1940s, and sporadic grazing ceased in 1983. It seems likely that this period of stability has contributed to the current dominance of *Poa*.

The other three grasses, however, do not appear to be transient species of early-succession. Instead, they have recruitment strategies that maintain their coexistence. *Dactylis* grows much faster than the other grasses in post-disturbance situations, and is predicted to dominate. At present, disturbances are infrequent, with occasional soil mounding by red-backed voles (*Clethrionomys gapperi* Vigors) or by introduced rabbits

(*Oryctolagus cuniculus* L.). When such openings do occur, *Dactylis* is favoured. *Elymus* and *Bromus* have the ability to recruit within the existing dense grass sward, albeit rarely based on current abundance levels, due to their large seed mass.

The observed competitive strategy of *Poa*, and its dominance in areas of limited disturbance are consistent with successional work on *Poa* by Tilman (1988). He observed *Poa* to be slow-growing, and not associated with immediate post-disturbance assemblages. However, this species was not a successional endpoint but was eventually replaced by other species. This begs the question regarding the future successional status of this oak grassland.

It appears that, in the absence of disturbance, the successional trajectory in the study area could have several possible endpoints: 1) continued dominance by *Poa* due to its ability to suppress recruitment of most other species, 2) invasion and subsequent dominance by different grass species that are better tolerance competitors than *Poa* under existing conditions, or 3) invasion and transformation by species associated with higher fertility, specifically shrubs and trees. The study was too short to indicate the likelihood of any of these scenarios. In some regions of North America, *Poa* can form dense swards that persist for decades (e.g., Curtis 1957). There are slower growing exotic grasses on site (e.g., *Agrostis stolonifera* L.), but all are rare and highly localized. There are also areas where shrubs and trees (exotic and native species) have invaded former grassland. Of particular note is the leguminous shrub *Cytisus scoparius* (L.) Link that has difficulty establishing within the existing grass sward without disturbance (Chapter Six). Once

established, however, it spreads rapidly by altering ground level light availability and possibly by raising levels of available soil nitrogen.

Conclusion

The high abundance of *Poa* implies that it is a robust and aggressive competitor compared to the other taxa of this ecosystem. However, this is only true within a specific environmental context. Underlying its dominance is a particular combination of factors that include its competitive traits; the current conditions of low fertility, low light, and limited loss from fire and herbivory; and a site history that may include initial disturbance and intentional seed introductions.

This finding indicates that there is no single competitive strategy associated with plant invasion in this ecosystem. Invasive species are often assumed to be suppression specialists with rapid seed emergence, high seedling growth rate, and the ability to quickly colonize disturbed areas (e.g., Baker 1965). Although many such species occur in these oak grasslands, including *Dactylis*, it is not the most abundant functional group at present due to limited perturbation. Instead, *Poa* dominates because of its ability to tolerate reduced resource levels under conditions of intense competition. This supports the hypothesis that the relative importance of suppression- and tolerance-based competitive traits can shift in invaded ecosystems over time, a result that also has been reported in lacustrine ecosystems (Kolar and Lodge 2002). Furthermore, it supports the idea that invasibility is best predicted from the combination of life history traits, levels of

limiting resources, and disturbance history, rather than on any one factor alone. The invasive plant species of this community that are fast growing and dominate post-disturbance environments, for example, do not appear to be highly problematic species in the long-term because they compete poorly in late-successional assemblages.

Chapter Five

Impacts of regional-scale processes on local plant diversity

Abstract: *In heavily invaded ecosystems, reduced diversity of native flora is usually attributed to displacement by a small number of competitively dominant species. Because many invaded ecosystems are also highly fragmented, however, it is equally plausible that declining diversity is caused by reduced immigration that prevents native flora from offsetting naturally occurring population turnover. If so, conservation measures that tackle the highly visible problem of invasion may miss the root cause of lowered diversity. I used experimental and biogeographical analyses to determine whether local factors (competition, soil depth) or regional factors (immigration) are currently most limiting for plant diversity in the oak savanna. Seed additions revealed strong evidence of recruitment limitation by native forb species – most were able to establish and survive in dense grass swards. Establishment (# seedlings after two years) was determined by the density of seed added. Survival (% established seedlings/# added seeds) was related to seed mass but only in the control plots – species with the smallest seeds had the lowest survival levels. Burning increased establishment and survival of all species significantly. However, recruitment by native species in burned but unseeded plots was close to nil. Comparison of functional groups between regional and site-level species pools showed no evidence for recruitment limitation for native species at the site level- relative abundance of functional groups regionally predicted relative abundance in sites of the Cowichan Valley. For exotic species, however, site-level pools were over-represented by two functional groups associated with dispersal: annual grasses and forbs. These results*

suggest that regional diversity determines site-level diversity but that this process unfolds slowly due to the limited dispersal ability of perennial species. Although exotic flora dominate remnant patches, many species appear to be “sink” populations maintained by continuous dispersal. By contrast, native flora are dispersal limited and most populations are restricted to areas of shallower soil where competition is low.

Introduction

Ecologists have long debated how species diversity is produced and maintained in communities (Huston 1994, Weiher and Keddy 1999). Given current declines in diversity worldwide, it has never been more important to understand the mechanisms that maintain diversity or cause its reduction. Much work on the regulation of species diversity has focused on the interaction of local and regional processes, debating whether local-scale factors such as competition and environmental variability, or regional-scale factors such as dispersal inefficiencies, are most limiting (Gaines and Roughgarden 1985, Ricklefs 1987, Ricklefs and Schluter 1993, Zobel 1997, Qian and Ricklefs 1999, Partel 2002). This debate is critical because it captures the mechanisms that cause the decline of native species in contemporary landscapes. Local impacts such as invasion and the elimination of pre-colonial disturbance regimes affect diversity by altering competitive interactions in local communities (Grace et al. 2001). Regional impacts such as widespread habitat loss affect diversity by restricting immigration and reducing the size and diversity of species populations (e.g., Leach and Givnish 1996, Drayton and Primack 1996, Hubbell 2001). Understanding whether diversity is locally or regionally regulated, therefore, can also

help predict the relative effects of invasion, habitat loss, or disturbance alterations on species loss and the steps by which these effects could be alleviated.

Although current theory recognizes the relative contribution of local and regional processes for diversity and for conservation, the testing of their relative impacts has been limited (Ricklefs 1987). Most experimental diversity studies are of short duration and focus only on the endpoint of long-term ecological change. The relative contributions of local and regional factors, however, tend to be evident at different spatial and temporal scales that may bias explanations towards shorter-term phenomena or obscure the significance of processes that no longer operate. The impact of rare long-distance plant dispersal, for example, may have limited short-term ecological relevance but may largely explain the assembly of post-glacial plant communities during the Holocene (Clark et al. 1998). In heavily degraded ecosystems, dominance by exotic species may suggest competitive superiority but may actually reflect the impacts of habitat fragmentation on native species and the widespread introduction of exotic seed during the early stages of European settlement. These examples highlight the challenges for discerning the causes of diversity only using experimental methods, and point to a need for integrative studies that investigate local impacts while accounting for the biogeographical context within which they occur (Ricklefs 1987, Ricklefs and Schluter 1993, Losos 1996).

In this study, I combined experimental and biogeographical analyses to test the relative importance of local and regional processes for plant diversity in a degraded oak savanna ecosystem of southwestern British Columbia, Canada. Here I define diversity as the

combination of species richness and relative abundance. Local- and regional-based models can both potentially explain current diversity levels in this savanna. This ecosystem is post-glacial so historical factors underlie its assembly, but the importance of long-term dispersal for explaining contemporary patterns of diversity is unknown. The flora is derived largely from the California Floristic Province (Fig. 5-1) and possesses the high percentage of annuals and perennial forbs that characterize the Californian assemblage (Barbour and Major 1977, Raven and Axelrod 1978). It is unclear, however, whether species pools at finer spatial scales (landscapes, sites) bear this distinctive floristic signature or whether membership is primarily determined by local environmental factors interacting with relative competitive ability. Prior to European colonization in the 1840s, the ecosystem was pyrogenic and organized along a soil depth gradient. Currently, less than 5% of the ecosystem remains, most remnants are shallow-soil sites of limited agricultural value, and fire has been eliminated. Since the onset of colonization, the ecosystem has absorbed 144 exotic plant species but without concomitant losses of native flora (only four extirpations). Although this suggests an absence of competitive-based regulation of plant species diversity (i.e., regional model), all of the native species have reduced ranges and many are precariously rare. Competitive displacement by invaders may account for this reduction, and species loss may be slow to occur but inevitable (i.e., local model).

For the experimental work, I tested for evidence of recruitment limitation, and determined the relative effect of burning, environmental heterogeneity, and species life history differences on site level diversity. For the biogeographical work, I used data on

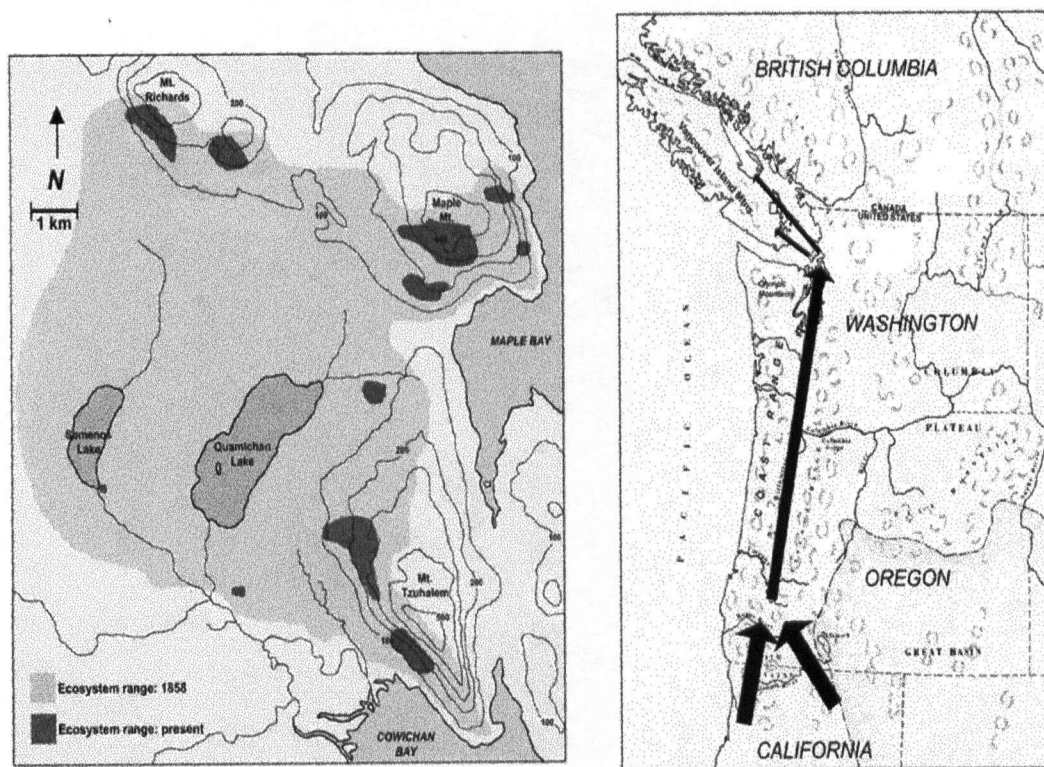


Fig. 5-1. (left) Map of past and present range of the Garry Oak savanna in the Cowichan Valley of southeastern Vancouver Island, and (right) hypothesized migrational route of the oak savanna flora during the Holocene.

the relative abundance of species within the four major functional groups of the savanna at three spatial scales: regional (British Columbia), landscape (Cowichan Valley), and site level pools (remnant savanna of the Cowichan Valley). I test if the site level pools fully sample the regional pool of British Columbia, regardless of differences in site factors or species life history. The alternative hypothesis is that site membership is determined by environmental gradients and relative competitive ability. If so, species from the most competitive functional groups (perennial grasses) should be over-represented at the site level compared to annual forbs and grasses. I also tested for regional and site differences among native and exotic species. Because exotic flora are

probably less dispersal limited than natives, I predict that there will be high similarity between the regional and site pools for this group compared to the native flora.

Methods

Field Experiment

The seed addition experiment was conducted in two large open areas (called Site A and B) of the Cowichan Garry Oak reserve. In May 2000, five 2 X 2 m² (Fig. 5-2) blocks were placed in each opening (5 replicates experiment⁻¹ site⁻¹). At Site A, none of the blocks contained any of the species that were added as seeds. At Site B, the blocks contained low densities of several of the added species (*Camassia quamash*, *Lomatium utriculatum*, and *Ranunculus occidentalis*). Both sites were dominated by *Poa* and *Dactylis*.



Fig. 5-2. Fire plots, prior to seed addition, in the summer of 2000.

Prior to treatment, the blocks were divided into four 0.6 m² plots and each was assessed for species composition, relative species abundance, ground-level light (percent full light, Licor quantum sensor), soil moisture availability (Hydrosense TDR meter), litter biomass (g 0.01 m²), and % bare soil. Light and soil moisture were monitored every two months throughout the experiment. Relative abundance was visually estimated using a 0.6 m² frame divided into 16 segments that was used to guide the visual estimation. For each block, seed bank composition was determined from soil cores (10 cm diameter, 7 cm deep) taken in early July 2000, divided into two layers (the upper 2 cm and lower 5 cm of the core), and cold-stored in plastic bags at 5° C. In October 2000, the core samples were spread over sand-filled trays in a heated greenhouse (Fig. 5-3). For eight months, all seedlings were counted, identified to species, and removed from the trays as they emerged. Unknown species were transplanted to separate pots and grown until they were large enough to recognize. Identification of seedlings to species at this stage aided subsequent seedling identification in the field.



Fig.5-3. Seed bank samples after one month in the glasshouse.

Plots in each block were randomly assigned to one of four treatments: control, burning only, seed addition only, or burning plus seed addition. The burned plots were treated in late July and early October 2000. The method of burning is described in detail in Chapter Seven. An additional 0.25 m was burned around the plots to reduce edge effects. Soil samples from the top 5 cm of each plot were taken before, one week after, and two years after the October burn, extracted with 1 mol L⁻¹ KCL, and analyzed for extractable NO₃ and NH₄ (mg kg⁻¹ soil).

Seeds of ten native forb species were collected from June-August 2000. The species represent a range of life history strategies (Table 5-1) and exhibit different habitat preferences in the Cowichan Valley based on soil depth and canopy cover (Fig. 5-4). Most seed came from the reserve, although limited collection occurred in nearby savanna remnants (< 3 km) to reduce collection pressure on the rarer species. After collection, seeds were air-dried in paper bags at room temperature. In October 2001, seeds of each species were counted, weighed, and added to an all-species mixture that was broadcast over each plot within a 0.6 m² box. Seeds were not stratified (e.g., wetted, cold treatment) prior to broadcasting because all of the added species (or other closely related species) are known to readily germinate in their naturally setting (e.g., Dorner 1998, Keeley 2000). The planting density of each species in the mixture (Table 5-1) was determined by seed availability in the field. Species that produced more seed naturally had more seeds in the mixture. This allowed us to test whether seedling establishment and percent seedling survival were regulated by the density of seed in the mixture (more seed = more survival) or by factors such as seed mass and habitat preference (survival determined by life

history and habitat conditions). Plots that were burned and seeded were covered with 5 cm gauge wire mesh for four months to prevent seed predation by birds.

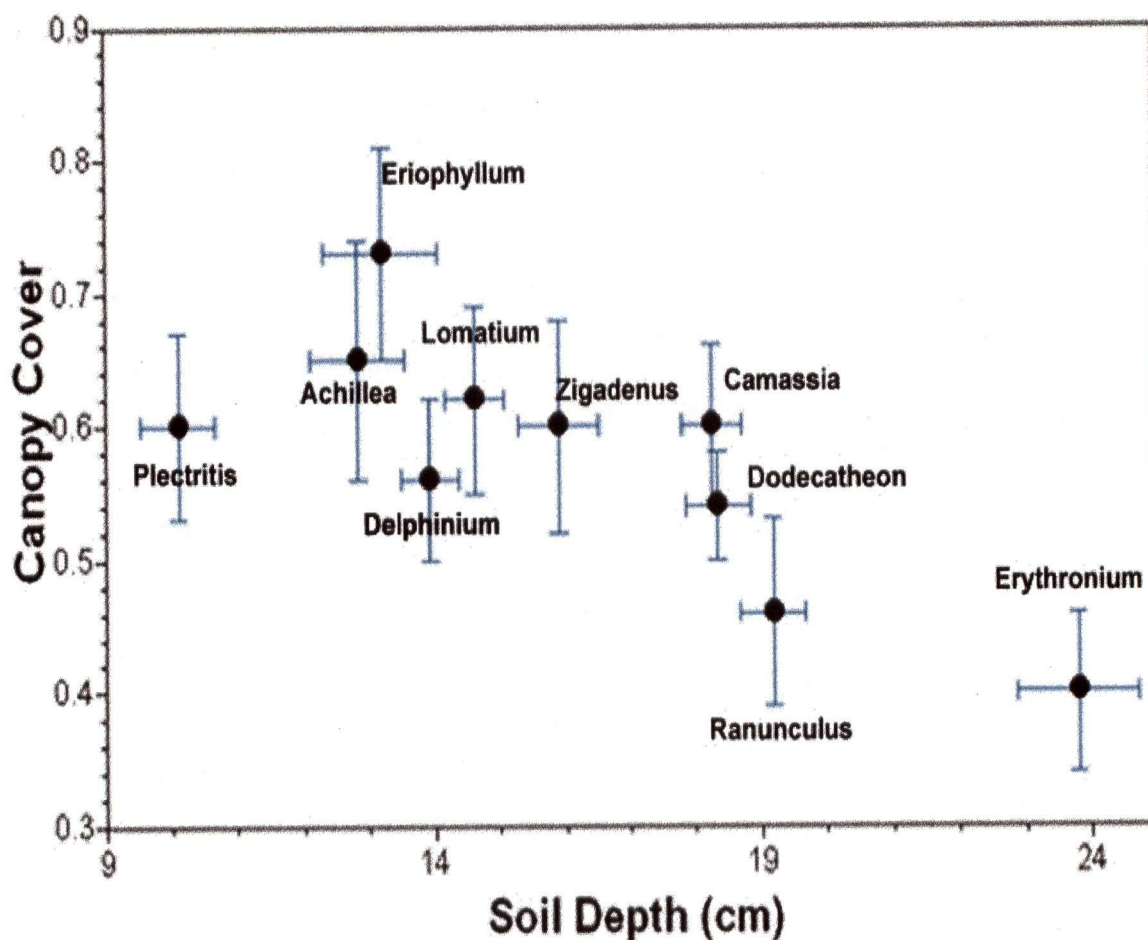


Figure 5-4. Distribution of the ten native forb species used in this chapter across a combined soil depth and canopy cover gradient. Data are from 177 1 m² plots from the six major savanna remnants within the Cowichan Valley (Fig. 5-1).. Soil depth values were determined from four locations in each plot. Canopy cover was measured with a spherical densiometer (Solar Pathfinder©) ranging from full canopy (0) to no canopy (1). Soil depth and canopy cover values for each species were determined by averaging the values for all plots within which each species occurs. Bars = ± 1 SE.

Table 5-1. Summary details for the ten species added as seed*.

Species	Seed mass (mg)	Planting density (plot ⁻¹)	% Cover				Establishment (Control)		Establishment (Burn)		Survival (Control)		Survival (Burn)	
			2000		2002#		A	B	A	B	A	B	A	B
<i>Achillea millefolium</i>	0.13	235	0	0	2	1	0	0	5	0.6	0	0	2.1	0.3
<i>Camassia quamash</i>	4.91	541	0.3	1.6	5	5	28	32.6	56.4	55.6	5.2	6	10.4	10.3
<i>Delphinium menziesii</i>	0.94	65	0	0	2	1	2.2	1	9	9.6	3.4	1.5	13.8	14.8
<i>Dodecatheon hendersonii</i>	1.78	455	0	0.4	6	4	66	39.8	137.4	29.6	14.5	8.7	30.1	6.5
<i>Eriophyllum lanatum</i>	0.53	321	0	0	1	1	1.2	0	5.6	0.2	0.4	0	1.7	0.06
<i>Erythronium oregonum</i>	6.11	121	0.1	0	2	1	12.2	6.8	23.4	13.8	10	5.6	19.3	11.4
<i>Lomatium utriculatum</i>	3.09	239	0	0.7	4	3	19	19.2	69.8	48	7.9	8	29.2	20.1
<i>Plectritis congesta</i>	1.62	222	0	0	4	3	19	9	59.2	43.2	8.6	4.1	26.7	19.5
<i>Ranunculus occidentalis</i>	2.69	273	0	0.1	3	2	12.6	12.4	34.6	27.8	4.6	4.5	12.7	10.2
<i>Zigadenus venenosus</i>	2.71	205	0	0	1	1	8.2	8.2	24.4	19.6	4	4	11.9	9.6

*Seed mass (mg seed⁻¹) is the average from 100 seeds. Planting density is the number of seeds added per 0.6 m² plot. “#” = % cover for burn plots only. “A” = site A (deep soil site); “B” = site B (shallow soil site). Establishment and survival are averages from five plots (per site) for two years after planting. Establishment = average number of seedlings species⁻¹ plot⁻¹. Survival = the percentage of surviving seedlings/number of planted seeds species⁻¹ plot⁻¹ after two years.

After planting, each block was surrounded by 1 m tall wire mesh to prevent herbivory. Although browsing is limited in the reserve (small numbers of European rabbit and black-tailed deer), fencing was used to eliminate all possible herbivore disturbance in case seed survival was extremely low for some species. No evidence of browsing was observed in the blocks during the experiment.

In May 2001 and May 2002, all plots were re-assessed for species composition, relative species abundance (% cover), litter, and percent bare soil. Seedlings of both added and naturally recruiting species were counted. Counting was aided by placing the 16-cell frame over the plot; seedlings were counted one cell at a time. Tillers (mostly *Poa pratensis*) were not counted because their age could not be determined. In May 2001, seedling locations of the added species were marked with colored toothpicks so they could be re-located the following year. Recruitment from seed in untreated plots at both sites was used to quantify the background levels of seed establishment and survival for the added species, in contrast to plots where experimental additions occurred. "Establishment" was the total number of seedlings of the added species in the plots after two years. "Survival" was the ratio of the total number of established seedlings (after two years) to the total number of seeds of each species added per plot.

Using ANOVA, I tested for the main and interactive effects of burning, species, planting density of seeds, site, and blocking on establishment and survival of the added seeds. I was especially interested in the interactions between burning and species, with the assumption that burning would reduce or eliminate the regulation of seed recruitment by

the established grass sward. I was also interested to determine if the response variables differed significantly between sites. *A posteriori* contrasts among the individual species were conducted with Tukey's multiple comparison test. Because there was only one planting density per species, there was collinearity between the variables "density" and "species". As a result, they could not be simultaneously used in the ANOVA (Zar, 1999) so individual ANOVAs were done using one or the other factor. "Density" allowed me to test if total and percent survival varied as the number of seeds increased (irrespective of life history differences among the species such as seed mass, germination time, annual vs. perennial, etc.). "Species" allowed me to test if total and percent survival varied among the ten species for the treatment combinations. Such variation would be presumed to result from species-specific differences in seed mass (i.e., species with larger seed mass would likely have higher survival in the unburned grass sward, as opposed in Chapter Four for the native grasses). All statistical analyses were done using JMP IN (SAS 2001).

Biogeographical Analysis

I tested whether the six major oak savanna remnants of the Cowichan Valley (Fig. 5-1) have sampled the regional species pools proportionally (regional model – more species regionally = more species locally), or whether the sites contain a subset of the regional pool favoring specific functional groups (local model – e.g., over-sampling of perennial grasses, over-sampling of annual species). Site-level and regional species pools of oak savanna flora in British Columbia are easily defined (Fig. 5-5) due to a strong association between the distribution of the member species and the occurrence of a limited set of

environmental factors (soil depth, aspect, slope, canopy cover, elevation). As well, survey work has been relatively extensive in British Columbia including rare flora that are often under-represented in regional databases (Caley and Schluter 1997). The site-level species pools were determined from surveys at the six primary oak savanna remnants of the Cowichan Valley conducted in April-May 2001, combined with other supplemental surveys from the remaining smaller sites in the valley (Fig. 5-1, Appendix 1). The regional pool, defined as all oak savanna plant species of British Columbia, was taken from Fuchs (2001) (see Fig. 2-1). The landscape pool was the total number of species found in the six site pools of the Cowichan Valley combined (listed in Appendix 1).

The analysis focused on the relative proportion of the four main functional groups of the oak savanna: both annual and perennial grasses and forbs. If proportional sampling is occurring, then the relative proportions of the regional pool should be observed in each site (e.g., Caswell and Cohen 1994). Higher relative abundance regionally means a higher probability of being represented within a site-level sample. If directional sampling is occurring, then relative abundance will be shaped by local factors of competition or habitat heterogeneity. I would expect perennial grasses to be numerically dominant (i.e., highest species richness) if local factors are determining diversity because these species are competitively superior in the current context of fire suppression and limited grazing (Chapter Four). If recruitment limitation is most limiting for local species occurrence (e.g., due to habitat fragmentation), then I would expect annual forbs and grasses to be over-sampled at the site level.



Fig. 5-5. The green line indicates the boundaries of an oak savanna remnant on the west-facing slope of Mt. Tzuhalem in the Cowichan Valley, taken in the fall of 2002. The browned area to the right is an Ecological Reserve; the area to the left is a subdivision. Infilling by Douglas-fir sharply delineates the boundaries of the reserve, and the distribution of oak savanna ground flora species. The sharp visual boundaries of most site remnants is matched by a sharp transitional boundary between obligate oak savanna species and non-obligate (and wider ranging) ground flora of the Coastal Douglas-fir ecosystem.

All species were classified into one of four functional groups for both native and exotic species (Appendix 1). Using a 1000-run Monte Carlo simulation, I generated confidence intervals ($\alpha = 0.05$) based on the relative abundance of native or exotic species within

each of four functional groups within the regional pool. Native annual grasses were excluded - the regional pool has eight species but none occur at the landscape and site levels of this study. I then tested whether the relative proportion of these groups in the site and landscape pools fell within the generated intervals using G^2 likelihood ratio chi-square tests (SAS 2001).

Results

Pre-treatment conditions

Only two of the measured environmental variables differed significantly between the sites: late spring understory light and early summer soil moisture (Table 5-2). Although median light levels in April and May were $< 5\%$ of overstory light at both sites, the shallow soil plots had much wider variation; some plots exceeded 10%. The onset of soil moisture reductions caused by summer drought was detected earlier in the shallow soil site; June soil moisture levels were significantly higher at Site A. During the late summer and winter, moisture levels did not differ between Sites A and B. More extensive descriptions of the light, soil moisture, and soil N conditions of the oak savanna ecosystem are presented in Chapters Six and Seven.

Table 5-2. Summary statistics for the deep-soil (Site A) and shallow-soil (Site B) sites prior to burning and seed addition in 2000, and seven (2001) and nineteen (2002) months after burning and seed addition*.

	Bare Soil	Light (%)	Litter (g plot ⁻¹)	Soil Moist.	# species plot ⁻¹	Diversity (1/D)	Poa cover (%)	Seedling recruitment (average # plot ⁻¹) (burned plots only)				
								all species	annuals	perennial grasses	perennial forbs	exotics
2000 (A)	0.48	2.98 ^a	5.45	-	13.0 ^a	3.57 ^{a,*}	68.4 ^{a,*}	71.2 [*]	26.2 ^{a,*}	18.2 ^{a,*}	25.2 ^{a,*}	39.4 ^{a,*}
2000 (B)	0.08	6.51 ^b	4.45	-	20.5 ^b	7.42 ^{b,*}	25.2 ^{b,#}	72.2 [*]	58 ^{b,*}	0.4 ^b	13.6 ^{b,*}	59.8 ^{b,*}
2001 (A)	39.4 ^a	87	0.77	13.06 ^a	24.6 ^a	6.95 ^{a,#}	22.2 ^{a,#}	336.4 ^{a,#}	198 ^{a,#}	4.8 ^{a,#}	43.4 ^{a,#}	161.8 ^{a,#}
2001 (B)	19.2 ^b	89	0.91	10.98 ^b	29.3 ^b	8.76 ^{b,#}	17.2 ^{b,#}	519.2 ^{b,#}	489.6 ^{b,#}	0.2 ^b	9.6 ^{b,#}	484 ^{b,#}
2002 (A)	9.65 ^a	25.1 ^a	1.15	12.5 ^a	23.1 ^a	6.89 ^{a,#}	41.7 [#]	224.6 ^{a,#}	71.4 ^{a,#}	27.2 ^{a,#}	68.8 ^{a,#}	90 ^{a,#}
2002 (B)	6.12 ^b	20.5 ^b	1.03	10.48 ^b	27.2 ^b	8.02 ^{b,#}	19.6	276.4 ^{b,#}	222.2 ^{b,#}	0.8 ^b	18.2 ^{b,#}	227.6 ^{b,#}

* Bare soil is percent cover plot⁻¹. Light is % at ground level compared to light levels above the grass canopy. Soil moisture is % saturation, with 50% as fully saturated; these measures were not taken in 2000. Statistical comparisons for bare soil, light, litter, soil moisture, and # species are within-column and within-year contrasts using Tukey's test ($p < 0.05$) (e.g., 2000A vs 2000B). Statistical comparisons are within-year contrasts (a vs b), and across-year contrasts (* vs #) (e.g., 2000A vs 2001A).

The total number of recruiting seedlings (all species) in the untreated plots (unburned, unseeded) did not differ significantly between sites ($t_{(\alpha=0.05, df = 8)} = 1.99, p = 0.08$), averaging 92 seedlings plot⁻¹ (SE = 13.98, n = 462 total seedlings) at Site A and 203 seedlings plot⁻¹ (SE = 54.02, n = 1017 total seedlings) at Site B (Fig. 5-6). At Site A, 24% of the seedlings were native species but most were not oak savanna obligates (mostly *Sanicula crassicaulis*). *Camas* and *Erythronium* recruited naturally in small numbers (mean = 2.6 and 2.5 seedlings plot⁻¹ respectively). At Site B, seedling recruitment was dominated by two exotic annuals (*Galium aparine*: 44% of all seedlings, and *Lathyrus sphaericus*: 28%). Three oak obligate species (*Camas*, *Lomatium*, *Ranunculus*) recruited naturally, but each averaged < 2 seedlings plot⁻¹ and represented only 1.4% of all seedlings. Relative abundance in the established sward overstory did not predict the relative abundance of recruiting seedlings. Very few seedlings of the two most dominant species (*Poa* and *Dactylis*) were found, and only at Site A (0.4% and 0.8% of total seedlings respectively). *Poa* appeared to recruit almost exclusively by tillering.

Seed bank

Soil cores from Site A contained larger numbers of germinating seed (0.622 seeds/cm³ of soil, n = 4,418 individuals) compared to Site B (0.22 seeds/cm³, n = 2,423), although the average number of species per core sample did not differ significantly (Site A = 13.01 species, Site B = 12.85 species). Most of the germinated seed at both sites were annual

ruderals (Site A=69%, Site B=77.1%). *Poa*, the most abundant overstory species in most plots, was the most abundant perennial grass species in the soil cores (Site A:10% of all

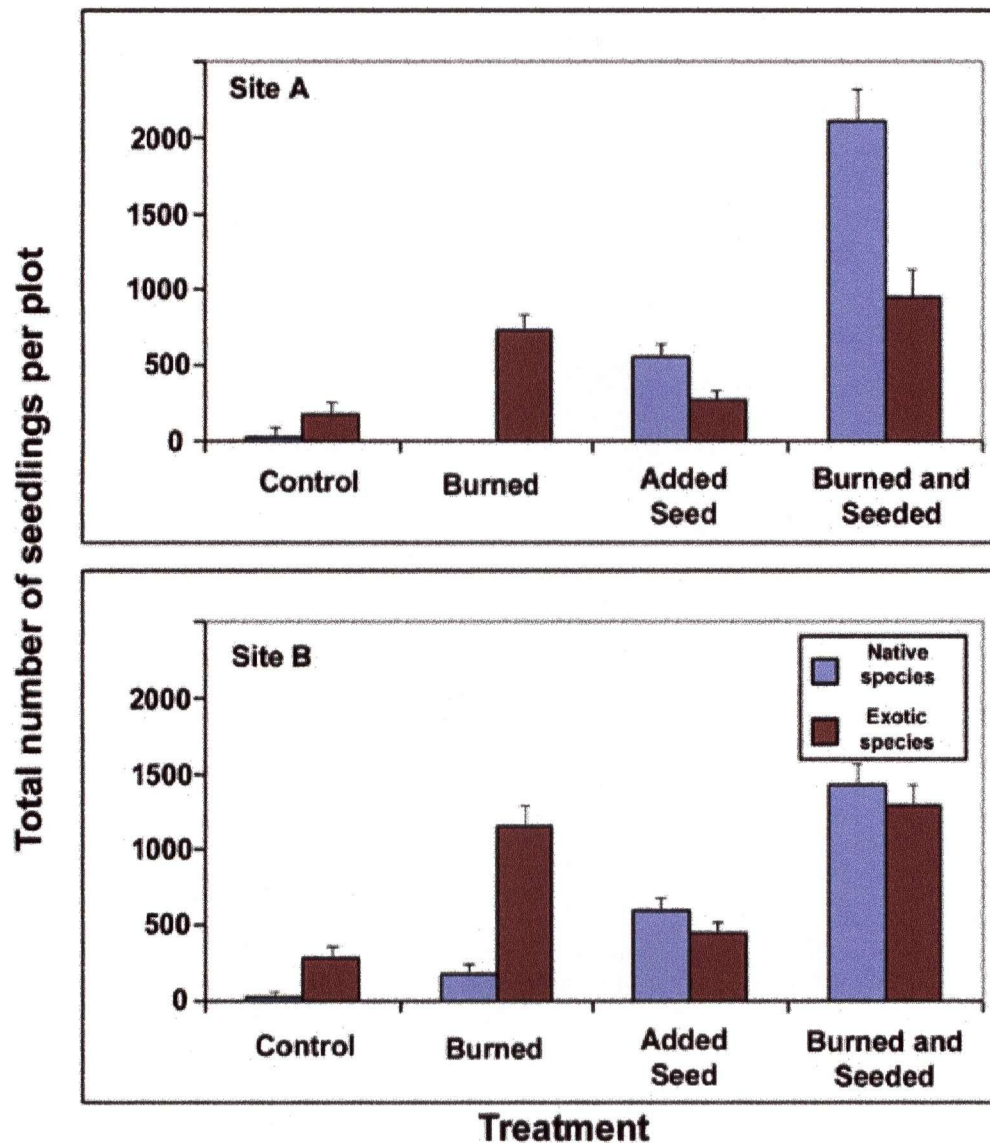


Fig. 5-6. Number of established seedlings in each of the four treatments, two years after the seed additions. Error bars are + 1 SE ($n = 40$ plots; 10 replicates per treatment).

germinating seed, Site B: 7%). *Dactylis* seed was not common (Site A: 0.3%, Site B: 0.4%).

Only 1.8% of all germinated seed, from six species, were oak savanna obligates. At Site A, 92% of these obligate species were graminoids (*Carex inops* and *Bromus carinatus*). At Site B, 63% were perennial forbs (*Camas*, *Lomatium*, and *Ranunculus*). The top 2 cm of the soil core contained over twice the number of germinating seed (1.04 seeds/cm³ of soil) compared to the bottom 5 cm (0.45 seeds/cm³). Most annual ruderal species had significantly higher seed densities in the upper layer ($t_{(\alpha=0.05, df=18)} = 3.62, p = 0.002$). Two species, both exotic, had significantly higher densities in the lower portion of the core: the shrub *Cytisus scoparius* and the perennial forb *Hypochaeris radicata*. Most of the annual ruderal species emerged 1-4 weeks after the soil cores were placed in the greenhouse. All of the native obligate species, except the rapidly germinating grass *Bromus carinatus*, began emerging after 2-4 months.

Recruitment of added seed in unburned plots

All species except *Achillea millefolium* were able to establish from seed in the dense grass sward, regardless of life history or habitat preference and despite low light, limited available N, dense litter, and no bare soil. Establishment was significantly determined by planting density ($r^2=0.46; p=0.009$) - the higher the number of added seeds, the higher the number of established seedlings still surviving after two years (Table 5-3, Fig. 5-7). Although all species were able to establish, not all survived equally well - there were significant differences between the total number of surviving individuals per species (presence/absence), and the percent survival of individuals per species (relative abundance) (Tables 5-1 and 5-4). Survival in the control plots was significantly

associated with differences in seed mass ($r^2=0.24$; $p=0.03$) – species with greater seed mass had greater survival (Fig. 5-7). There was no evidence of density-dependent limitation on seedling recruitment, despite the large quantity of added seed. The total number of non-planted seedlings did not differ significantly between the control and the unburned seed addition plots at either site.

Impacts of burning

Burning transformed the micro-environmental conditions and recruitment dynamics of the plots, although these effects diminished after two years (Table 5-2, Fig. 5-6). Seven months after burning (May 2001), plots still had no litter cover, increased average light levels > 90% full light, higher percentages of bare soil, and higher species richness and diversity. NO_3 and NH_4 levels increased at both sites (Site A= 9.03 and 53.19 mg kg^{-1} respectively, Site B= 27.97 and 50.23 mg kg^{-1}) but were not significantly different from pre-burn levels (Tukey's test). Soil moisture levels were not affected by burning.

Site B had significantly higher numbers of seedlings plot^{-1} compared to Site A (A= 336.4, B = 519.2) ($t_{(\alpha=0.05, df=39)} = 4.67$, $p = 0.0005$). Post-burn recruitment was dominated by species found in high abundance in the seed bank; most seedlings were annual ruderals or, at the deep-soil site, the leguminous exotic shrub *Cytisus scoparius*. Background recruitment by oak obligate⁴ species did not differ between the unseeded burned and

⁴ Ground flora species specifically associated with the Garry Oak savanna (e.g., *Camassia*), as opposed to more wide-ranging species of southwestern British Columbia (e.g., *Sanicula crassicaulis*, *Osmorhiza berteroi*).

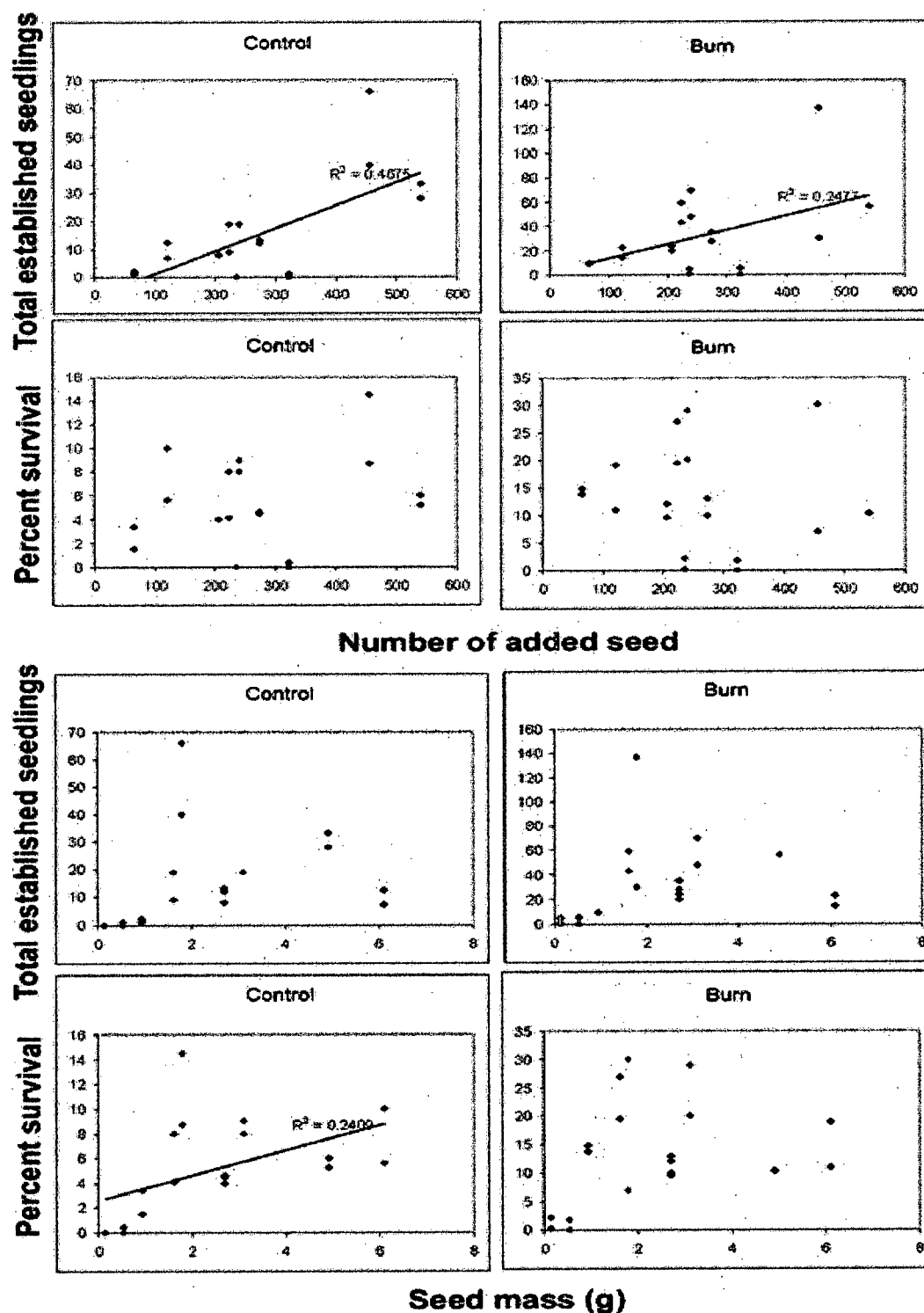


Fig. 5-6. Survival and establishment based on total number of (top) added seed plot⁻¹ and (bottom) average seed mass species⁻¹. Data are pooled from the two sites. Trend line indicates significant relationship.

Table 5-3. Summary of ANOVA results for total seedling establishment. Density refers to the density of added seed per species. Treatment = control versus burning.

Source	df	F	P	R ²
Model	7	18.27	<0.0001	0.40
Error	192			
Total	199			
Effect tests				
Site	1	7.25	<0.008	
Treat	1	32.18	<0.001	
Density	1	47.38	<0.001	
Site * Treat	1	3.52	0.06	
Site * Density	1	2.56	0.11	
Treat * Density	1	11.08	<0.001	
Treat * Site * Density	1	2.50	0.11	

Table 5-4. Summary of ANOVA results for seedling survival.

Source	df	F	P	R ²
Model	39	5.76	<0.0001	0.584
Error	160			
Total	199			
Effect tests				
Species	9	10.76	<0.0001	
Site	1	0.76	0.39	
Treatment	1	0.90	0.34	
Sp * Site	9	0.68	0.72	
Sp * Treat	9	3.16	<0.002	
Site * Treat	1	3.97	<0.05	
Sp * Site * Treat	9	0.76	0.65	

unburned plots although establishment levels were higher at the shallow-soil site after seven months. Six species not observed in pre-treatment plots, all annuals, appeared following fire. Four of these species were native, and three were oak savanna obligate taxa (*Lupinus polycarpus*, *Lotus micranthus*, *Collinsia grandiflora*).

The 80 established species found in the plots prior to the experiment exhibited different degrees of fire sensitivity. The two most dominant species (*Poa* and *Dactylis*) were also the most fire-sensitive; decreasing from 73% to 29.4% plot⁻¹, and 14.9% to 6% plot⁻¹, respectively. At Site B, two native species increased significantly in percent cover (*Camas* + 35%, *Ranunculus* +10% plot⁻¹). Because *Poa* was significantly more abundant at the deep-soil site, post-burn plots at this site had significantly more % bare soil, higher ground-level light levels in spring, higher levels of species richness, and higher seedling recruitment due to the reduction of the dominant species (Table 5-2).

By May 2002, the impacts of burning had diminished. Although the percentage of *Poa* and *Dactylis* cover and the quantity of litter were still significantly lower from pre-treatment levels, ground level light and % bare soil plot⁻¹ were no longer different.

Recruitment by added seed in the burned plots

There were significant impacts of burning and site on the establishment and survival of added seed (Tables 5-3 and 5-4). Most species had higher levels of establishment and survival at the deep-soil site, in association with the higher % bare soil and higher

ground-level light caused by the sensitivity of *Poa* to burning. For establishment, burning significantly increased all species except for *Dodecatheon* at Site B; there was no significant difference between the control and burned plots for this species (Table 5-1). For survival, burning and site interacted significantly due to the higher survival of species in the burned plots of Site A. Burning was most important for survival of the two species with the smallest seed mass - *Achillea* and *Eriophyllum* (Table 5-1).

As with the control plots, establishment in the burned plots was significantly associated with the density of added seed species⁻¹ ($r^2=0.24$; $p=0.026$). Unlike the control plots, however, there was no significant relationship between seed mass and survival ($r^2=0.08$, $p=0.24$).

Biogeographical results

In comparing the relative abundance of species within the four functional groups, there were significant differences between the regional and site-level species pools and between native and exotic flora (Fig. 5-8). For the native species, there was no significant difference between the regional and site pools in sites with both deep and shallow soils (Fig. 5-8; rows A and B). Sites with soil depths < 20 cm had much higher percentages of annual forbs and perennial grasses than the regional pool. For the exotic species, all sites (Fig. 5-8; rows A-F) were significantly different from the regional pool. Each site had significantly higher levels of annual grasses and forbs.

Fig. 5-8. Relative abundance of the four major plant functional groups within the regional (British Columbia), landscape (Cowichan Valley), and site level (A-F) species pools. The left column of graphs are the native species pools (note: landscape and sites A and B statistically similar to regional, based on G^2 likelihood analysis); the right column are the exotic species (# = statistically similar based on G^2 likelihood analysis). The middle column presents the distribution of all sample plots along the gradient of canopy cover and soil depth at each of the six site remnants in the Cowichan Valley. Error bars are derived from a 1000-run Monte Carlo simulation. AG = annual grasses, PG = perennial grasses, AF = annual forbs, PF = perennial forbs.

Discussion

The experimental results demonstrated that the exotic sward could limit but not prevent the establishment of all but one added species, regardless of differences in life history or habitat preference, and despite constraints on resource availability. By contrast, there was strong evidence for recruitment limitation. Naturally occurring recruitment by all native species of this ecosystem, not just those added as seed, was almost zero regardless of the removal of the grass sward by fire. Seedling recruitment significantly increased following fire, but mostly by exotic ruderals from the seed bank.

While establishment was determined primarily by the density of the seed additions (regional regulation), survival was dictated locally by the interaction of site factors and seed mass differences among the species. Larger-seeded species tended to survive better in the deeper soil site with denser litter layers, lower light, and reduced moisture stress in the summer. Recruitment dynamics, therefore, resembled a modified lottery (Turnbull et al. 2000) where more added seed led to more seedling establishment but the probability of success was partially contingent on habitat conditions along with the life history attributes of the species.

Burning significantly increased the subsequent establishment and survival of seedlings from the added seed, but it was not a necessary precondition for recruitment. Seedling survival after burning was significantly greater in the plots of the deep soil site, where

species diversity was lower and levels of exotic dominance high. On one hand, this result was explained by a "diversity" effect where the higher diversity plots on shallow soil were more resistant to recruitment by added seed. Burning these plots caused a proliferation of previously established but uncommon native perennial forbs that lowered light availability and reduced the survival of the added seed. However, the more pronounced cause was differential fire sensitivity among the exotic and native species of this oak savanna. The most dominant species, *Poa*, was highly fire sensitive and decreased by 40% at the deep soil site compared to 5% at the shallow soil site where it was less abundant. High abundance by *Poa* is associated with low plot diversity due to its ability to limit the abundance of other species. Its reduction created higher levels of bare soil, light, and NO_3 , which facilitated seedling survival.

The biogeographical results revealed significant differences in functional group diversity among the regional, landscape, and site levels for native versus exotic flora. For the native plants, I predicted little concordance between the regional pool and the landscape and site pools due to the effects of invasion and reduced dispersal. I found, however, that the regional signature of functional groups was evident at the landscape level and at the site level for remnants that possessed the widest range of soil depth and canopy cover. Four of the sites were mostly unshaded with shallow soils (<20 cm) and had significantly fewer native forbs and more perennial grasses compared to the regional pool. Conversely, the regional signature was not evident at either the landscape or site level for the exotic species. All six sites contained the same functional group profile, with higher percentages of exotic annual grasses and forbs, and lower percentages of exotic perennial forbs.

The results demonstrate that regional processes influence local diversity more than is implied by the current pattern of dominance by a small number of exotic grasses. A balance of dispersal inputs, species-specific habitat preferences, and occasional fire that reduced local competitive pressure determined diversity at the site level. The community appears to be unsaturated, with the capacity to support many more species than presently occur. Current levels of diversity, therefore, are caused as much by reduced immigration as by increased competition due to invasion and fire suppression. While antagonistic competitive interactions probably regulate which species are common or rare, immigration can determine the numbers of species present in this ecosystem irrespective of competition or the life history attributes (e.g., seed mass) of the species.

This regulation of diversity can be depicted as "source-sink" model (Pulliam 1988) where each species has a definable "source" population along the gradient of soil depth and canopy cover (e.g., Fig. 5-4), and numerous additional "sink" populations that are maintained elsewhere by dispersal. Dispersal can thus maintain unexpectedly high levels of species richness across a range of habitats but only if these inputs are continuous. The interaction of local competition and site factors cannot prevent the establishment of incoming propagules but can regulate the relative abundance of species and excludes subordinate flora over time if dispersal inputs are stopped.

This result increases the understanding of the causes of present-day diversity declines, and points toward the combined effects of habitat loss and consequent fragmentation,

population reduction, fire suppression, and invasion on the dynamic between regional and local processes. It also helps determine the conservation strategies required to counteract these changes. European land use activity over the past 150 years has affected diversity in this ecosystem by decreasing regional dispersal (via fragmentation) while intensifying the level of competitive interactions in remnant patches. Habitat loss and fragmentation has substantially reduced total seed output per species because regional populations are so much smaller and dispersal distances for sink establishment are greater. Remnant areas in the Cowichan Valley, for example, are isolated by distances of 3 km or more. Concurrently, fire suppression promotes the dominance of a few exotic grasses that reduce the probability of successful propagule establishment if and when dispersal does occur. Given that dense swards of native grass were reported in unburned areas prior to European settlement (Chapter Three), it is unclear whether the current dominants are competitively superior to their native plant equivalents; evidence from a recent study suggests that they may not be (Chapter Four). These impacts have probably most affected the persistence of "sink" populations within the Cowichan Valley due to the combined effects of dispersal restrictions and increased competition. Native flora may thus be largely restricted to their "source" areas where they are best able to persist based on their life history characteristics (e.g., seed mass, stress tolerance). Because most of the remaining habitat is on shallow-soil, this explains why deeper-soil species have been eliminated or are extremely rare in this ecosystem (Chapter Three).

Results from the biogeographical analysis corroborate the source-sink dynamic detected by the experimental work. The presence of the regional functional group "signature" at

the landscape and the site level within the Cowichan Valley implies a lottery-type model of species accumulation where high relative abundance in the regional pool determines high relative abundance at finer scales. This accumulation is filtered, however, by the soil depth profile of each site and the establishment of permanent source populations may be unsuccessful unless there is the appropriate range of soil depth. The process of species accumulation at finer spatial scales appears to unfold extremely slowly given that the regional pool signature of the invasive species was not detected in the Cowichan Valley after 150 years. Because invasive species are assumed to be less dispersal-limited than native species in contemporary landscapes, it was surprising that the landscape and sites pools did not represent the signature of the regional pool. Instead, the most abundant functional groups were the invasive annuals that are assumed to be less dispersal limited than perennials.

It is also surprising that there was no significantly different impact of soil depth or canopy cover on the invasive species, in contrast to the natives. All six sites possessed the same signature of invasive flora. This suggests that many populations of exotic annuals are "sinks" maintained by continual dispersal that allows them to persist in sub-optimal areas. The proliferation of invasive flora worldwide has often been interpreted as evidence for the competitive superiority of these species. My results, in contrast, indicate that invasion in this ecosystem is maintained by on-going dispersal into a wide range of habitats. If these seed inputs ceased, however, I predict that the distribution of many exotic flora would be reduced to "source" areas as determined by interactions between the life history characteristics of the various species and the patterns of local

environmental variation. The notion that the range of widespread exotic species may eventually become attenuated based on habitat factors has been discussed theoretically (Wilson 1961, Ricklefs and Cox 1974, Sax and Brown 2000) but has been difficult to test. If this is the case in these oak savannas, I surmise that many invasive annuals will eventually become restricted to shallow soil sites and that invasive perennial species will increase in relative abundance within the landscape and site-level pools.

The full impact of regional processes on diversity in this ecosystem would have been difficult to ascertain without the combined approaches used in this study. In this ecosystem, invasion is determined by a combination of regional and local factors that have caused declines in native plant diversity (i.e., relative abundance). Conservation initiatives that target invasion, therefore, may fail because invasion is as much a by-product of habitat fragmentation and fire suppression as it is a cause of reduced native diversity. Conservation measures must embrace an integrative approach, targeting in combination the capture of habitat diversity (and thus "source" habitats), the reintroduction of dispersal to broaden levels of occurrence regionally, and the reintroduction of disturbance to offset competitive intensity and facilitate the establishment of sink populations. The introduction of fire on its own, for example, will fail if it is not coupled with the bridging of dispersal barriers that exist due to habitat fragmentation. The conservation goal in this or any ecosystem is not only the reintroduction of former diversity levels but also the stabilization of re-introduced native assemblages over time. In this ecosystem, this depends on restoring both local and regional processes, an emphasis beyond the scope of traditional conservation measures.

Reserve creation alone, for example, merely promotes ecosystem stability and increases competitive intensity, potentially accelerating the local displacement of native species. Further, the protection of pristine areas may not ensure persistence if populations are "sinks" rather than "sources". This highlights the need to understand the underlying ecological processes that explain the distributions of the species.

An integrative approach for the study of diversity not only clarifies conservation perspectives but also serves to clarify theoretical issues surrounding the maintenance of diversity. Most ecological studies inadvertently target the endpoint of centuries or millennia of ecological change and thus are destined to emphasize the short-term dynamics that are most detectable by these methods. This bias not only limits our ability to understand the processes that maintain diversity but also hampers our capacity to model and predict the consequences.

Chapter Six

Mechanisms and Impacts of Dominance by the Exotic Grasses

Abstract: *The causes of dominance, and the impact of dominant species on community structure, are often attributed to competition. This assumption, however, is rarely tested and alternative non-interactive mechanisms such as immigration and disturbance history can also determine relative abundance. Thus, while numerical dominance may suggest competitive superiority, subordinate species may actually be limited by non-competitive factors. In an oak savanna dominated by two exotic grasses, I examined these issues by experimentally reducing (mowing) or removing (selective weeding) the dominant species, and monitoring the responses of 93 subordinate species. The timing (summer vs. fall) and location (deep and shallow soils) of the treatment applications were varied to determine their impact on the interaction between dominant and subordinate species. A seed addition experiment tested the impact of the dominant species on limiting resources, and how these impacts affected recruitment by the dominant grasses and several less common grass species. My results confirm the importance of competition for limiting the abundance of many community members, although this dominance hierarchy was fully contingent on the absence of disturbance. Numerous subordinate species increased in percent cover following both treatments. The impacts of mowing and weeding on these species were surprisingly similar, and the summer treatments resulted in significantly greater increases in cover compared to the fall treatments. Many species were also severely limited by recruitment, irrespective of the presence of the dominants. As well, the dominant grasses restricted woody plant establishment and, with moderate disturbance, facilitated the survival of juveniles of several native species. The dominant exotic grasses*

have negatively affected the relative abundance of many native species. However, they also have apparently helped to preserve this grassland by slowing conversion to woodland, which eliminates savanna species entirely.

Introduction

Ecologists have long been interested in the questions of why species dominate and how they impact the abundance of other species in the community (Preston 1948, Whittaker 1965, Daubenmire 1968a, McNaughton and Wolf 1970, Tilman 1987, Fox 2002). All dominant species impact the structure of communities by their sheer abundance (e.g., interception of most resources, occupation of most recruitment space) (Smith and Knapp 2003). The degree of impact, however, can differ profoundly depending on the strength of the connection between the mechanisms driving the abundance of the dominant and those causing the rarity of the other species.

In highly interactive (i.e., competitive) communities, dominance is determined by the relative ability of species to attain limiting resources. The dominant species limits the abundance of all others by capturing most of these resources via exploitation, inhibition, or both (Keddy 2001, Amarasekare 2003). The removal of the dominant is predicted to cause substantial changes in community structure as subordinate species gain access to formerly limiting resources. In weakly interactive communities, however, there can be a partial or complete de-coupling of processes limiting common and rare species (e.g., Hubbell 2001). In particular, relative differences in immigration ability or environmental

stochasticity can be strong determinants of rare species abundance, regardless of the mechanisms affecting the dominant (McNaughton 1983, Ricklefs 1987, Collins 2000). Because the effect of these processes tends to unfold more slowly than competition, beyond the temporal resolution of most field experiments, large differences in relative abundance are often attributed to competition but it may not be the sole cause. In communities regulated in this manner, the removal of the dominant is predicted to have little impact on the relative abundance of subordinate flora.

Using a four-year factorial field experiment (i.e., one pre-treatment year [2000] followed by three years of treatment application), I examine the impacts of dominance on the composition and relative abundance of species in an invaded and fragmented oak savanna. There are two dominant species in this savanna: the perennial invasive grasses *Poa* and *Dactylis* that are highly invasive in several regions of North America (Grace et al. 2001). It is unclear, however, whether they limit other species by competition or if non-interactive processes limit the subordinate species in these invaded communities. Both dominants are aggressive exploitation competitors for light and soil resources (e.g., Hensel 1923, Curtis 1959, Zedler and Loucks 1969, Kirsch and Kruse 1973, Sullivan 1992, Choi and Pavlik 1994, Chapter Four), and can potentially alter the functioning of grassland ecosystems due to the enhanced N content of their foliage, especially *Poa* (Wedin and Tilman 1990). Conversely, they have been planted in vast numbers for forage or erosion control in cultivated or often highly fragmented ecosystems (Sullivan 1992, Grace et al. 2001). Their dominance in some areas, therefore, may be caused by site history rather than their interactions or impact on other species in the community.

I examined the impact of *Poa* and *Dactylis* on community structure using a reduction treatment (mowing), a removal treatment (weeding of dominants), and the experimental addition of seeds of various native and exotic grass species. Because the impacts of disturbance on grasses can be highly contingent on site factors and the season of application (e.g., Howe 1994b, 1995, Fowler 2002, Jutila and Grace 2002), I also varied the timing of the treatments (summer vs. fall) and their location (deep-soil vs. shallow-soil). By monitoring treatment responses of 93 subordinate species, I tested whether they were limited by the presence of the dominant grasses, by non-interactive factors relating to dispersal, or some combination of the two. With the seed addition experiment, I examined the relationship between the impact of the dominant grasses on resources, and patterns of recruitment by native and exotic grass species.

Methods

Study area

The experiments were conducted in two grass-dominated sites within the Cowichan Garry Oak reserve in the Cowichan Valley of southwestern British Columbia, Canada (48°48' N 123° 38' W). Both sites had 71 species (N = 95 total species), although Site A was composed of mostly perennial grasses, annual exotic pasture species (*Vicia* spp., *Cerastium* spp.), and native forbs that were non-obligate oak savanna species (*Sanicula crassicaulis*, *Osmorhiza berteroi*). *Poa* and *Dactylis* also dominated Site B but the site had few other perennial grass species and many more native obligate forbs (e.g.,

Camassia quamash, *Dodecatheon hendersonii*, *Ranunculus occidentalis*, *Cerastium arvense*, *Saxifraga integrifolia*). *Camassia quamash* was the only obligate forb species to occur in plots at both sites. The leguminous shrub *Cytisus scoparius* had formerly invaded several sections of the reserve but has been removed (Fig. 2-7). No experiments were conducted on areas formerly dominated by this leguminous shrub, but it was abundant in areas adjacent to Site A. It occurs in large numbers in the seed bank of this site (Chapter Five).

Experimental design and sampling

The experimental layout was a randomized complete block design with no within-block replication. Blocking was used to account for slight differences in slope, soil depth, and relative abundance of the dominant ground flora within each site (Dutilleul 1993) but it had no statistical effect on any of the treatment responses.

In May 2000, ten 4 X 10 m blocks were placed in each site beyond the dripline of the surrounding oak canopy. Plots (1 m²) within each block were randomly assigned to one of six treatments: selective removal of *Poa* and *Dactylis*, mowing, and control applied in July or early October (6 treatments X 2 sites X 10 blocks = 120 plots). There were separate controls for each season. The July treatments had three impacts: (i) the removal of the litter layer, (ii) the elimination of living foliage of *Poa* and *Dactylis* (weeding) or all species (mowing), and (iii) the exposure of the soil surface to increased solar radiation throughout the summer. The October treatments eliminated litter and whatever living

foliage remained by that time of year. The treatments were applied annually from 2000 to 2003. Mowing was conducted with a "whipper-snipper" to ground level, and all cut material was raked and removed. Weeding removed all aboveground biomass of *Poa* and *Dactylis* (Fig. 6-1). Roots and rhizomes were also removed although it was impossible to completely eliminate all of *Poa*'s rhizomes. As a result, this species remained in many weeded plots for the duration of the experiment but at levels typically < 2% cover each year. An explosion of *Cytisus* seedlings from the seed bank followed weeding in several plots at Site A. These *Cytisus* seedlings were removed each year because we were testing the impacts of the dominant exotic grasses on the suppression of non-woody species. An additional 0.25 m buffer zone was weeded or mowed around all plots to reduce edge effects.

Prior to treatment application, all plots were assessed for (i) species richness (number of species plot⁻¹), (ii) rare species richness (species that occurred in <2 plots site⁻¹ [n= 28 species]), (iii) relative species abundance (% cover plot⁻¹), (iv) E_{var} , an index of evenness, (v) Simpson's 1/D, an index of diversity emphasizing the most abundant species in the plot (Magurran 1988), and (vi) levels of light, soil moisture, available soil nitrogen, and organic matter.

Relative abundance of each species was visually estimated (always by me) using a 1-m² frame divided into 20 cells (each 5% of the total plot area) (Armesto and Pickett 1985). Resources were (i) ground-level light (percent full light) during the spring, measured with a Licor



Figure 6-1. Weeding plot in 2000. Flagging tape indicates location of native species, mostly Bromus carinatus and Carex inops. The upper section of the plot, comprised mostly of Poa pratensis has yet to be weeded.

quantum sensor, (ii) soil moisture availability to 12 cm depth (percent volumetric water content; saturation $\cong 50\%$), measured with a Hydrosense TDR meter, (iii) available soil N (mg kg^{-1} soil of NO_3 and NH_4), (iv) % soil OM (g g^{-1} soil), and (v) % bare soil. Available N was obtained from soil samples taken from the top 5 cm in half of the plots ($n = 60$), extracted with 1 mol L^{-1} KCL, and analyzed for extractable NO_3 and NH_4 (mg kg^{-1} soil). The % soil organic matter (OM) was determined by heating 20 g of soil at 400°C for 5 hours and contrasting pre- and post-heating soil weight. Light was measured in spring because this is the period of maximum growth and reproduction by most savanna species. Data on light variations across the entire year are presented in Chapter Seven. Soil

moisture levels were monitored at monthly intervals from March to August, and bimonthly for the other months. Moisture measurements did not begin until November 2000. Percent bare soil plot⁻¹ was visually estimated using the 1 m² frame.

In May of each year from 2001-2003, all measured variables were re-sampled. Exceptions were the measurements of soil NO₃, NH₄, and % soil OM. These were only measured twice: prior to the treatments and three years after the first application of the treatments (August 2002).

Seed of seven perennial grass species was collected in the summer of 2001, air dried in open paper bags, and added to half of all plots in October of that year, just prior to the onset of the winter rainy season. There was no stratification treatment used on the seed prior to planting. Besides *Poa* and *Dactylis*, the selected species represent different relative abundances, phenologies, and habitat preferences (soil depth and canopy cover) within the Cowichan Valley. *Anthoxanthum odoratum* was the third most abundant perennial grass species. This species is also exotic, but flowers earlier (March-May) than *Poa* or *Dactylis* (June-July), and is associated with shallower soil areas. Two native grasses, *Bromus carinatus* and *Elymus glaucus*, tend to co-occur with *Poa* and *Dactylis* but are much less abundant within the Cowichan Valley. *Danthonia californica* and *Festuca roemerii* are native grasses rare to the reserve and currently associated with areas of shallower soil within higher-elevation remnant savanna of the Cowichan Valley. Fifty seeds from each species were added to 15 cm x 15 cm subplots within all plots from two blocks at each site (2 blocks X 2 sites X 6 plots = 24 plots species⁻¹). Germination tests in

moistened and sand-filled petrie plates showed germination >90% for each of the species, with *Danthonia* emerging 4-6 weeks later as reported elsewhere for this species (Maslovat 2002). Percent germination, percent survival, and maximum seedling height were monitored for 37 weeks until the treatments were re-applied.

Statistical analyses

Separate repeated-measures analyses of variance (ANOVA) were used to test the individual and interactive effects of treatment, block, site, year, and season of application on the measured responses (e.g., richness, diversity, species cover) (Potvin et al. 1990, Kuehl 1993) (Table 6-1). A more detailed description of this procedure, and why repeated-measures ANOVA was used instead of MANOVA, is presented in Chapter Seven. Graphs were used to help with the interpretation of the various higher-order interactions, and whether trends were maintained or switched across any of the factors. *A posteriori* contrasts were conducted with Tukey's multiple comparison test ($p < 0.05$). All analyses were conducted on JMPIN (SAS 2000).

Results

Pre-treatment conditions

In the absence of disturbance, the understory environment of the savanna is characterized by low ground-level light and low available nitrogen (Fig. 6-2, see also Fig. 7-1 for light levels). Soil moisture levels fluctuated seasonally following the pattern typical of

Table 6-1. Analysis structure of repeated measures ANOVA for three treatments (mowing, weeding, control), two seasons (summer and fall), two sites (deep- and shallow-soil), conducted over four years (2000-2003). The analysis is conducted as a split-plot design (same design used in Chapter 4) with "year" as the split-effect. Repeated measures ANOVAs were conducted separately for each analyzed response variable (e.g., diversity, percent cover changes by individual species, number of species plot¹). Post-hoc individual comparisons used Tukey's tests ($p < 0.05$).

Source	Number	Degrees of freedom
MAIN EFFECTS		
Site (fixed)	2	1
Block (random)	10	18
Season (fixed)	2	1
Treatment (fixed)	3	2
Site X Season		1
Site X Treatment		2
Season X Treatment		2
Site X Season X Treatment		2
Error 1	17 x 7	119
SPLIT EFFECTS		
Year (fixed)	4	3
Site X Year		3
Season X Year		3
Treatment X Year		6
Season X Treatment X Year		6
Site X Season X Year		3
Site X Treatment X Year		6
Site X Season X Treatment X Year		6
Error 2	8(2[10-1] x [4-1])	432
TOTAL	640-1	639

significant ($F=2.32$, $p=0.135$). Levels of available N averaged 192.8 g kg^{-1} soil plot $^{-1}$ ($SE = 94.4$) at Site A and 108.23 g kg^{-1} soil plot $^{-1}$ ($SE = 35.6$) at Site B.

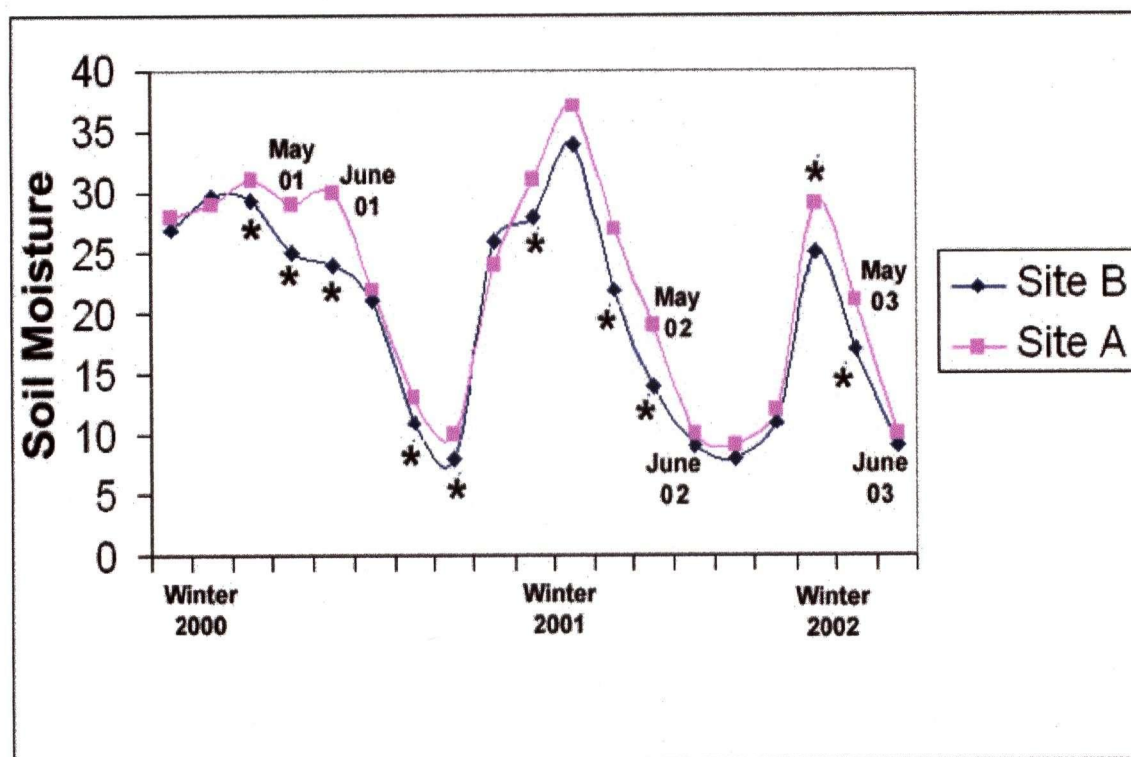


Fig. 6-3. Variations in soil moisture at the deep-soil (A) and shallow-soil (B) sites. “*” indicates significant site differences within the given month. Soil moisture readings of 50% represent full saturation. May and June moisture levels of 2002 and 2003 are significantly lower than in 2001 respectively (Tukey’s test, $p<0.05$).

Bare soil was rarely observed in any plot and at either site, although small amounts of soil mounding by red-backed voles occasionally occurred in the grass understory.

Mowing and weeding impacts on the dominant species

Summer mowing reduced the cover of the two dominant species to levels similar to those observed in both weeding treatments. After three years of summer mowing the average

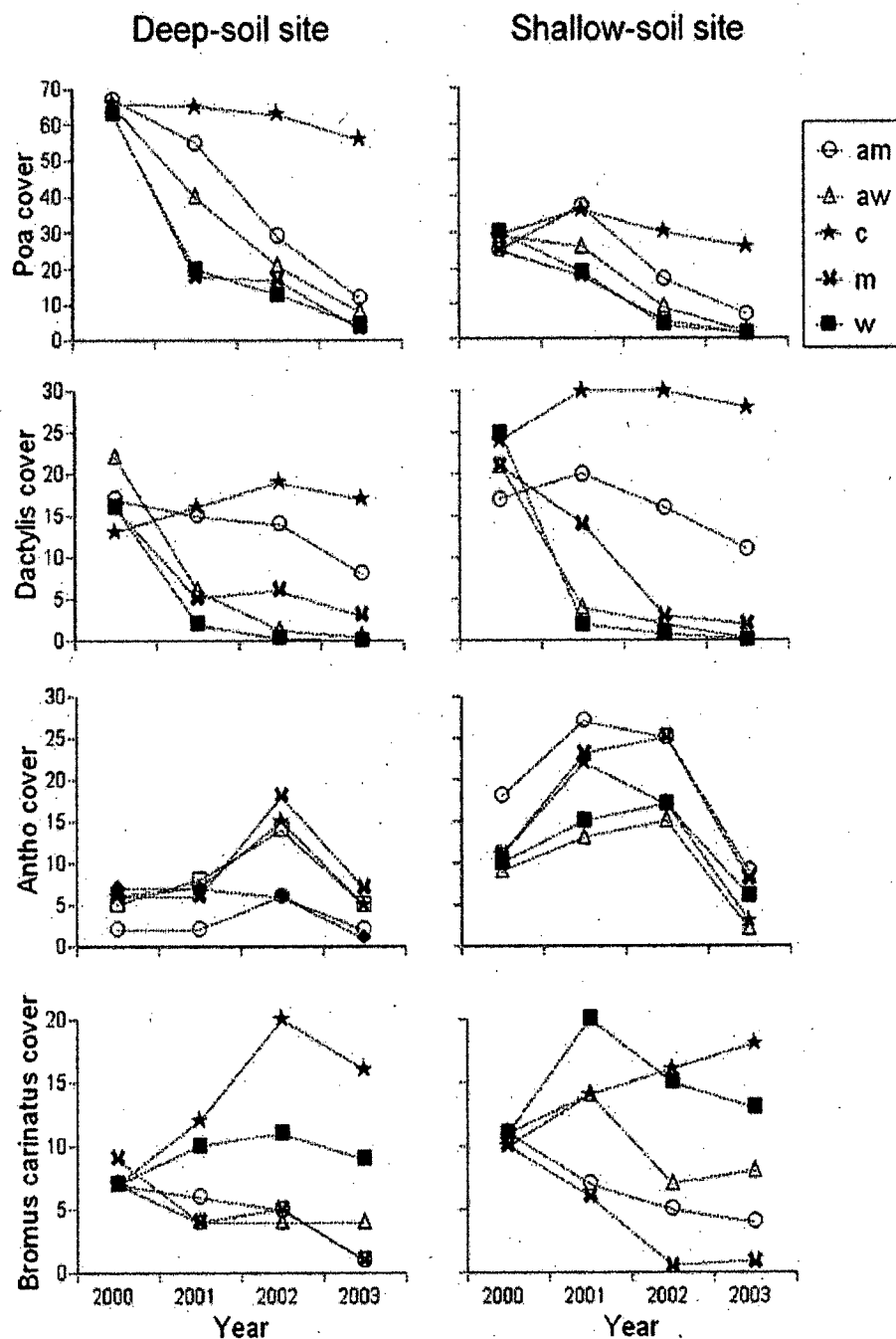


Fig 6-4. Changes in percent cover for the most abundant perennial grasses at the two sites. C = control, M = summer mow, W = summer weed, A = autumn treatment. "Antho" = Anthoxanthum odoratum. For visual simplicity, control values are presented as averages of the summer and autumn control plots.

cover of *Poa* was reduced to $< 2.5\%$ plot⁻¹ at both sites. *Dactylis* also decreased significantly after three years in the summer plots to $< 2.4\%$ at both sites (Tukey's test) (Fig. 6-4).

The impact of fall mowing did not significantly reduce the cover of *Dactylis* at either site. *Poa*, in contrast, was significantly reduced by this treatment, decreasing in average cover plot⁻¹ from 65.4% to 8.0% at Site A and from 25.3% to 8.6% at Site B.

Treatment impacts on subordinate species

Species richness, E_{var} , and Simpson's 1/D increased significantly with mowing and with removals at both sites (Fig. 6-5). The increases in richness and diversity happened immediately after one year (2001) for both disturbances, and these levels were maintained for the remainder of the experiment. These increases were caused mostly by the recruitment of annual ruderals (Fig. 6-6), which occur in high number in the seed bank. Differences in evenness, by contrast, were only detected between the pre-treatment levels (2000) and the final year of the experiment (2003). There was an unexplained increase in evenness within the control plots in 2003 at both sites (Fig. 6-5). The treatments did not affect the number of native species plot⁻¹ (Fig. 6-6) or the number of rare species plot⁻¹.

Treatment responses by the 93 subordinate species of the reserve were widely variable (Note: individual responses of each species not presented for sake of brevity). Some species, such as *Camassia quamash*, increased in percent cover after one year in response to the removal of the dominant grasses (Fig. 6-7) but many others did not immediately respond. Responses fell into six identifiable categories:

- 1) no treatment response until the final year of the experiment (many native forbs) (Figs. 6-5 [forb/grass ratio plot⁻¹] and 6-6 [% native species plot⁻¹])
- 2) an increase after the first round of treatments but declines in subsequent years (e.g., several annual ruderal species [Note: see *Myosotis* panels in Fig. 7-4 as response by this species to burning was identical as its response to mowing and weeding).
- 3) a significant response to the July treatments but not to the October treatments (several perennial grasses and forbs, see *Dactylis* panels in Fig. 6-4)
- 4) significant differences between sites but no response to the treatments (e.g., legumes, Fig. 6-6),
- 5) no significant response to any treatment but fluctuations over the duration of the experiment in concert with annual climatic variations (several forb species),
- 6) significant declines with one or both disturbance treatments. This latter group included several exotic ruderal species commonly associated with mesic pastures (*Cerastium fontanum*, *Galium aparine* (see Fig. 7-4), *Stellaria media* and the native evergreen forb *Cerastium arvense* (see Fig. 7-7), which declined significantly with repeated mowing.

Typically, there were no differences observed between the response of exotic and native species within each of the six response groups. With mowing, most perennial grasses decreased significantly in percent cover including *Bromus* (Fig. 6-4). An exception was *Anthoxanthum*, which increased significantly during two years following the first treatment application but declined to pretreatment levels by the third year (Fig. 6-4). This was not a treatment effect, however, because the control plots followed this same trend. Several native and exotic annuals both increased to similar degrees in the first year following the treatments and then declined subsequently. Overall, there was a maintained significant increase in annual species after three years of treatments (Fig. 6-6) caused by species such as *Valerianella locusta*, *Lathyrus sphaericus*, and *Vicia hirsuta*.

The treatments had no impact on the differences in species composition between the two sites that existed prior to the onset of the treatments. Although there were significant changes in relative abundance, these responses were confined to species that were previously present, rather than facilitating the recruitment of new species.

After three years, the most substantial increases in cover were by native perennial forbs that became the most abundant species in most plots at both sites (Fig. 6-6). Increases in the deep-soil plots were mostly by *Camassia quamash* and *Sanicula crassicaulis* (Fig. 6-8), and in the shallow-soil plots by *Camassia*, *Dodecatheon hendersonii* and *Ranunculus occidentalis*. These changes were greater in response to the July treatments, but were mirrored, albeit at lower levels, in the October plots.

Both treatments caused significant increases in recruitment by woody plants, mostly *Cytisus scoparius* at Site A (Tukey's test). Although mowing and weeding reduced this species each year, its cover by 2003 (composed of hundreds of newly emerged small seedlings) was still significantly greater than its pre-treatment cover in 2000. *Cytisus* cover did not significantly change in the control plots over the four years of the experiment, and seedlings were rarely observed. There were also non-significant increases in recruitment by *Pseudotsuga menziesii* and *Acer macrophyllum*, both native trees, and *Craetagus spp.*, an exotic shrub, at both sites.

Nine previously unobserved species established following the treatments. Most were annual forbs, including several native obligate species of the oak savanna (*Lupinus polycarpus*, *Lotus micranthus*, *Collinsia parviflora*). Most established after the second or third year of application, and most were only observed in one plot (of 120 plots). Some recruited from the seed bank (Chapter Five) while others apparently dispersed from elsewhere in the reserve. Even after three years of treatments, recruitment by perennial forb and grass species was close to nil for both native and exotic species in plots where they were not already established. *Dodecatheon* and *Ranunculus*, two abundant native forbs, established in plots at Site A after the third year of treatment application but did not increase $>2\%$ cover plot^{-1} . Both of these species occurred in small numbers within 10 m of the colonized plots prior to the experiment.

Impact on resources

After three years, the impacts of mowing and weeding on light, available N, soil

moisture, and bare soil were generally the same. Both treatments, not unexpectedly, increased light availability and bare soil. They had no effect on soil N or moisture, which were only affected by site factors (i.e., levels of both resources were significantly higher in plots with deeper soils).

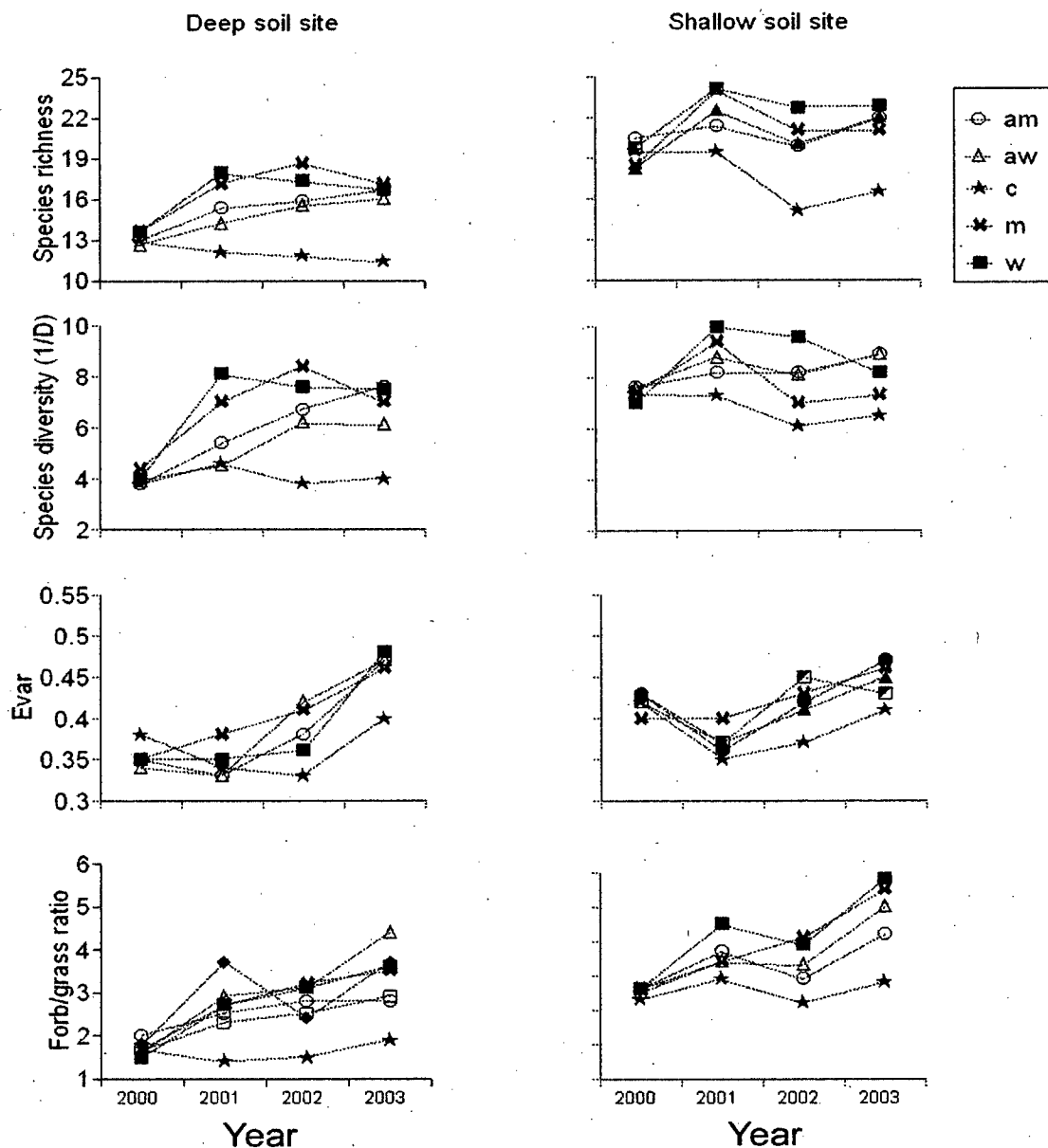


Fig. 6-5. Changes in species richness, species diversity (Simpson's $1/D$), evenness (E_{var}), and forb/grass ratio at the two sites. Forb/grass based on the number of species plot¹.

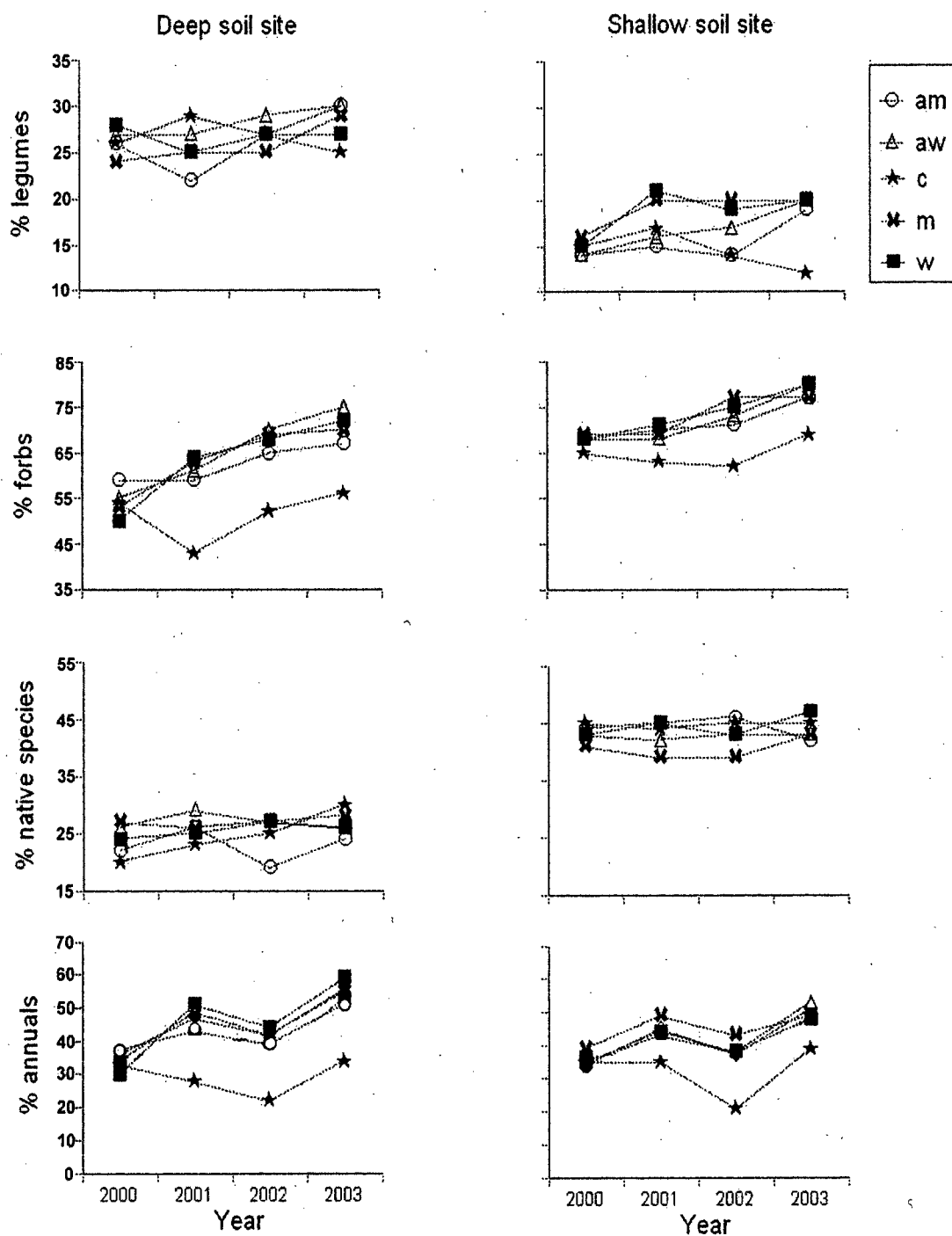


Fig 6-6. Changes in total percent cover of functional groups (legumes, non-leguminous forbs, and non-leguminous annuals) and % native species plot¹ at the two sites.

There were significant treatment differences in light availability caused by the interaction of the season of application, the year of application, and site (i.e., soil depth). After one year, plots that were summer-treated at the deeper-soil site had significantly higher light levels in the spring. This effect was caused by two interacting factors: higher pre-treatment cover of perennial grass at Site A and higher post-treatment cover of perennial forbs at Site B. Because all perennial grasses declined following treatment application, post-treatment light levels were positively correlated with the percentage of pre-treatment grass cover. Because perennial forbs increased significantly after treatment application, post-treatment light levels were negatively correlated with the percentage of pre-treatment forb cover. This effect, however, was no longer evident by 2003 as the percentage forb cover in plots at Site A (mostly *Camassia* or *Sanicula*) increased to levels similar to those at Site B (e.g., Fig. 6-8).

There were also significant differences between the summer and fall mowing treatments in the second and third years. Initially, the two mowing treatments were equally effective at increasing spring light levels. By the second year, however, plots of the summer mowing were significantly brighter and this result was repeated the following year. The difference in light levels between summer and fall were positively correlated with the differences in cover of *Dactylis* cover. This species was not significantly reduced (% cover) by the fall mowing treatment.



Fig. 6-7. Summer weeding plot after three years (May 2003), with high amounts of bare soil and high cover of established and recruiting Camassia quamash.



Fig. 6-8. Summer mow plot after three years (May 2003) at Site A, with high cover of Sanicula crassicaulis (the broad leaved species) and numerous smaller annuals.

Recruitment from added grass seed

For seedling establishment after 12, 28, and 37 weeks, there were significant interactions among species and the timing and type of treatment application (Fig. 6-9). All seven species emerged after 12 weeks in similar numbers in all treatments, except for *Danthonia* that was not evident until 16 weeks (Tukey's test). In the control plots, seedling establishment at 28 and 37 weeks by *Bromus* and *Elymus* was significantly greater than all other species (Tukey's test). *Anthoxanthum* had significantly lower levels for both measures in these plots (Tukey's test). All species but *Anthoxanthum* had moderate to high levels of establishment in the mow and weed plots at 28 weeks but extremely low levels of survival into the summer months when solar exposure was high. Only *Anthoxanthum* was able to survive in relatively large numbers under these conditions. The highest levels of survival for *Poa*, *Dactylis*, *Danthonia*, and *Festuca* were in the autumn treatment plots, a result associated with the cover of *Dactylis* that reduced ground level light intensity during the summer months.

Discussion

The high abundance of *Poa* and *Dactylis*, their impact on light levels and the availability of bare soil, and the rarity of most other flora suggest that this community is strongly regulated by competition. The positive responses of many species to mowing and weeding confirm this conclusion. However, many other species appear to be limited by

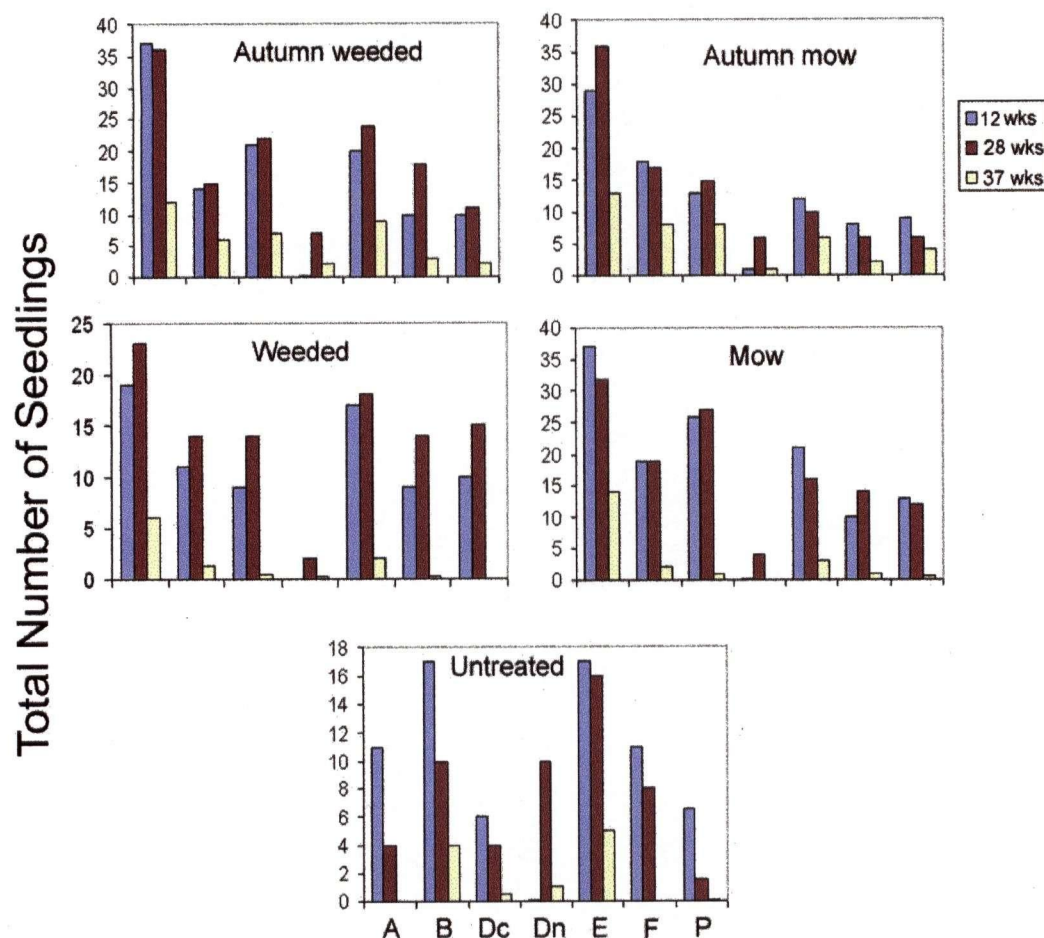


Fig. 6-9. Total number of established seedlings 12, 28, and 37 weeks after seed addition. "A"=Anthoxanthum, "B"=Bromus, "Dc"=Dactylis, "Dn"=Danthonia, "E"=Elymus, "F" =Festuca, "P"= Poa. Data from 168 subplots (15 X 15 cm) from both sites combined.

non-interactive processes relating to dispersal. As well, the dominant grasses appear to have some positive effects on this savanna by suppressing woody plants and facilitating the survival of juveniles following moderate disturbance. Community structure, therefore, is regulated by a combination of inter-active and non-interactive processes rather than one or the other separately.

Competitive impacts of the dominant flora

These data provide considerable evidence for the impact of competition, based on the significant increases in species richness, evenness, diversity, and the growth and reproduction of subordinate flora following the decrease of the dominant grasses. These increases occurred in most plots, at both sites, and were most evident in the summer treatments where the reduction of perennial grasses was most severe. I detected no evidence for alternative non-competitive explanations for these increases. The impacts of mowing and removals, for example, can both cause temporary increases in productivity due to litter feedbacks that could resemble our observed treatment responses (e.g., Berendse 1994). By the fourth year of our study, however, there was little standing foliage remaining and litter was mostly eliminated, yet the increases by the subordinate flora continued. It seems clear, therefore, that asymmetric competitive interactions among the member species in part contribute to the structure and function of this community.

Poa dominates these oak savannas by producing a dense layer of litter and foliage, which limits ground-level light and suppresses many subordinate species. Although some species can recruit from seed under these conditions, levels of success for most species are low and many remain rare. Exotic pasture species such as *Vicia sativa*, *Vicia hirsuta*, *Cerastium fontanum*, and *Galium aparine* are the exception. These species are presumably well adapted to the light-limited conditions of pastures.

The causes of high relative abundance by *Dactylis* are less clear given its inability to recruit within the light-limited understory of the grass sward. As reported in Chapter Four, this species has high relative growth rates compared to morphologically similar grasses of this savanna, which should favour its recruitment when small disturbances occur (e.g., vole mounding). Once established, adult plants are highly tolerant of neighbour competition because of their height (>150 cm) and their production of dense lateral foliage (Chapter Four).

Although the dominant grasses limit the occurrence and growth of other species by competition, they do not appear to be profoundly different from the other warm-season perennial grass species of this savanna. Supporting evidence is demonstrated by the shared sensitivity of these species to repeated mowing. Although the dominant grasses do possess trait differences sufficient to impact recruitment and inter-specific competition (Chapter Four), these trait differences do not extend to the ability to resist repeated disturbance. All perennial warm-season grasses, native and exotic, presently appear to thrive with limited or no disturbance, and co-exist by a range of recruitment strategies relating to differences in seed mass, maturation rate, and tolerance of low light (Chapter Four). This implies that dominance by perennial grasses in the absence of disturbance is not strictly a contemporary phenomenon. Accounts prior to European settlement confirm this, as tall (2 meters) and dense thickets of grass were described in unburned areas (Chapter Three). Thus, exotic dominance is not caused by radically different functional strategies compared to other native and exotic perennial grasses. Instead the various traits of *Poa* and *Dactylis* allow them to dominate in situations where warm-season perennial

grasses would normally be abundant. They dominate in this context because of their combined ability to tolerate the low light (*Poa*) or preferentially regenerate if and when small disturbances occur (*Dactylis*). However, this dominance is fully contingent on the absence of repeated disturbance. As will be discussed in Chapter Seven, repeated disturbance leads to a new hierarchy of relative abundance where warm-season grasses are relatively uncommon.

Evidence for impacts on ecosystem function?

Although *Poa* and *Dactylis* limit other species by competition, it is less clear whether they also affect the functioning of this ecosystem. The alteration of ecosystem function is defined as a species-mediated change in the pools and flow of limiting resources (Vitousek 1986, 1990). A large number of invasive species are known to have these effects. Not only do these species out-compete native flora for limiting resources but they “change the rules of the game” (D’Antonio and Vitousek 1992) by permanently modifying their subsequent availability. The removal of the species, therefore, is not guaranteed to eliminate their impact on the functioning of the system (e.g., elevated N levels in the soil).

Poa and *Dactylis* could have two possible ecosystem effects: increased % soil OM due to increased litter production, or increased soil N due to higher nitrogen concentrations in their foliage (Wedin and Tilman 1990). Our analyses revealed no change in available N or % OM with the removal of the dominant grasses, although this may reflect the limited

number of samples taken, the season when sampling occurred (late summer), or the short duration of the experiment. In other grassland studies, high litter production, as currently occurs in this oak savanna, increases % soil OM (and thus levels of soil carbon), which significantly affects nutrient cycling by its impact on soil microbial activity (Gill and Burke 1999, Knops et al. 2002). Although possible, we suggest that this is unlikely because this savanna was capable of naturally producing high standing biomass prior to invasion (Chapter Three). The key difference between the exotic and native grasses, if one exists, is probably the nitrogen composition of the foliage. This hypothesis remains untested, although the complete absence of un-invaded sites will challenge the ability to distinguish between possible differences in foliage quality and the long-term effects of native versus exotic dominant species on soil processes.

Impacts of recruitment limitation on subordinate flora

In addition to the impacts of competition, there was strong evidence that recruitment limitation severely restricts the distribution of many species within this savanna. In plots where subordinate native taxa were not already established, there was little or no response to the reduction of the dominant grasses. The few species that were able to colonize only did so rarely, and most established 2-3 years after the initial treatment. Conversely, when seeds of locally rare species such as *Danthonia* and *Festuca* were experimentally added they established in large numbers. The low survival by all but one (*Anthoxanthum*) of these grasses in the summer treatment plots was due to the effects of moisture stress, rather than the competitive effects of the dominants (see next section).

Thus, although competition by the dominant grasses exacerbates the dispersal problem (i.e., low establishment by most added grass species in the control plots), it is not sufficient to explain the low abundance of many species.

Although it is unlikely that increased immigration by subordinate species would transform the existing dominance hierarchy, it would increase their relative abundance irrespective of competition by the dominant grasses (as reported in Chapter Five for forbs). The causes of colonization limitation in this ecosystem are unclear. Habitat fragmentation has been severe (Chapter Three), but large populations of native forb species occur in the study area. Many disperse by gravity and thus may be naturally limited in their ability to occupy recruitment sites when they become available. Conversely, recent studies have suggested the importance of ungulates for the longer-distance dispersal of herbaceous ground flora (e.g., Pakeman 2001). Black-tailed deer are common but their movement among savanna remnants is likely restricted. Roosevelt elk, formerly common, no longer occur. Presently, rare and unpredictable dispersal events (storms, rare transport by animals) may be the most important mechanism for establishing new populations for many species (e.g., Clark et al. 1998), if they occur at all. Based on the slow rates of dispersal suggested by this study, it may take considerable periods of time for new populations to establish even within a few hundred meters of existing occurrences. Disturbance would presumably hasten the process by increasing the probability of successful establishment by rare dispersal. However, the rates by which the perennial grasses are reduced or eliminated (several years) is much faster than the rate by which most native flora disperse. Recovery, therefore, will be slow or may be

circumvented by species less limited by dispersal (i.e., other exotics)

Positive effects of the dominant species

There was also strong evidence that the dominant grasses can positively influence the structuring of this community. In moderately disturbed plots, *Dactylis* cover promoted the survival of juvenile grass species during the summer months. In the seed addition experiment, highest survival was in the October treatments that eliminated the litter layer but maintained a cover of living grass foliage. This living cover reduced light penetration to the soil surface in the summer months, presumably reducing heat stress and other related factors. By contrast, the complete removal of litter and living foliage resulted in the high mortality of most species. Even species associated with habitats of shallow soil and high solar exposure (*Danthonia*, *Festuca*) suffered high mortality. Although poor survival of juveniles due to exposure is a common result of removal experiments (D'Antonio et al. 1998), this effect would likely be overshadowed by the naturally occurring limitation in soil moisture during the summer that is characteristic of Mediterranean climates. Native and exotic grass species appear to be equally constrained by these conditions, and survival may be episodic depending on the intensity of the moisture deficit in any given year. Soil moisture in the spring of 2002, for example, appeared to be unusually low, at least compared to levels in 2001. As long as litter levels remain low, a cover of summer grasses facilitates the survival of juvenile grasses and may be especially important in drier years.

Conversion to woodland (predominantly *Pseudotsuga menziesii*) or shrubland (predominantly *Cytisus* or *Symphoricarpos alba*) has occurred in oak savanna ecosystems throughout the Pacific Northwest (Krukeberg 1992, Tveten 1997), in part because of fire suppression. However, the dense swards of grasses appear to greatly slow this conversion to woody plants, as has been observed in grasslands elsewhere (Wilson 1998). In the control plots, newly emerging seedlings of shrubs and trees were occasionally observed but rarely survived. Only oak appeared capable of regenerating consistently, presumably because of the large amounts of nutrients in the acorn. The highest levels of woody plant recruitment were in plots with little or no grass due to the treatments. Although the woody species were eliminated by the re-application of the treatments, less frequent disturbance would hasten the recruitment of woody plants.

The role of the exotic grasses in facilitating juvenile survival and preventing woody plant invasion supports the notion that exotic species may somewhat preserve the functioning of degraded ecosystems, and that eradication may have unanticipated negative results (Myers et al. 2000, Zavalata et al. 2001). In this case, there is a trade-off between the negative impacts of competition on the recruitment of native species, and the positive impacts of their presence for juvenile survival and resisting conversion to woodland. Although the negative impacts are currently more significant, the importance of the positive impacts increases with disturbance. Recruitment appears to be most negatively affected by the litter layer rather than the living foliage, a finding common in many grasslands (Facelli and Pickett 1991, Foster and Gross 1998, Jutila and Grace 2002.). Disturbances in the fall season such as mowing (and burning – see Chapter Seven)

remove this layer but maintain a cover of living foliage, and seedling survival increases for all species measured.

Conclusion

It is critical to understand the causes and consequences of dominance by non-native species because of their apparent ability to displace native flora and alter ecosystem function (Vitousek et al. 1997, Levine and D'Antonio 1999). Although many studies have reported correlations between invasion and the decline of native richness and diversity, few studies have explored the mechanisms underlying these changes (Levine et al. 2003). As demonstrated by this study, exotic dominance can be determined by a complex array of factors relating to competition, recruitment, environmental factors and disturbance, rather than any one factor alone. While extreme differences in relative abundance may suggest competitive displacement, our results reveal that dispersal is also limiting the distribution of many subordinate species. Further, the ability of the invaders to suppress woody plants and facilitate the survival of juvenile grasses in some situations indicates that they may actually maintain this savanna. Conversion of this savanna to woodland is far more detrimental than grass invasion because it eliminates all savanna obligates, including most of the non-native invaders.

These results suggest a dynamic model of restoration for this endangered ecosystem, requiring a balance between the reduction of litter, the maintenance of some herbaceous cover to facilitate juvenile survival, and the simultaneous control of woody plant

invasion. This dynamic model mimics the processes responsible for maintaining grasslands generally (McNaughton 1983, Axelrod 1985, Anderson 1990), where the interacting effects of disturbance, climate, succession, and competition rather than any one factor alone determine stability. These issues will be discussed further in Chapter Seven.

Chapter Seven

The Destabilizing Effects of Fire in a Fire-Dependent Ecosystem

Abstract: *Fire is assumed to stabilize grassland communities by offsetting competitive displacement. Species loss in grassland remnants is often attributed to increased competition due to fire suppression, and this leads to the use of prescribed burning for restoration. However, not only may rare species be unaffected by competition but stability models predict that repeated fire will be as destabilizing as the effects of intense competition. This will be especially true in small remnant areas with spatially restricted populations of native plants. I examined the effects of fire on stability by monitoring its impact on productivity, reproduction, and the abundance of functional groups in the Garry Oak savanna. Four years of summer burning caused a substantial decrease of perennial grasses and a concomitant increase of forbs. Few species were eliminated by repeated fire, and these were warm-season taxa, including the native perennial grass *Elymus glaucus*, which were rare (<5 plots) prior to the start of the experiment. Given the decline in grasses and increase in forbs, we predicted that fire would create a forb-dominated community that was as stable with repeated burning as the grass-dominated community with its long-term absence. Our data did not support this hypothesis. Total production dropped in the savanna, as the increase in forb production was unable to match the former output by the grasses. Due to substantial differences in litter quality and quantity, it is predicted that perennial forb species will be incapable of supporting annual burning over time. Because burning does not completely eliminate the more*

abundant perennial grass species, they would be predicted to increase in response to the decreased occurrence of fire. At the site level, therefore, the savanna community is predicted to oscillate through time between grass- and forb-dominated assemblages. The interaction of soil depth and annual climatic variations are predicted to deflect this oscillation into further unpredictability. Prior to the extensive loss of habitat, the stability of this savanna was probably best defined at the regional level due to the fire-induced variability in forbs and grasses at the site level. Although burning in remnant areas could re-establish this oscillation, many native species no longer have regional distributions and may be highly vulnerable to its effects.

Introduction

Fire has been traditionally viewed as a critical stabilizing factor for many grassland communities (Anderson and Brown 1986). Stability is defined as a lack of statistically detectable change in the composition, physical structure, or any other measurable facet of grassland function (e.g., Collins 2000). Despite its obviously destructive properties, fire can stabilize grasslands by offsetting competitive dominance, preventing conversion to woodland, increasing productivity (or decreasing it in some cases), stimulating seed germination, and eliminating litter (Daubenmire 1968b, Hulbert 1988, Collins and Wallace 1990, Leach and Givnish 1996, Blair 1997). Given its importance, fire suppression is viewed as a critical threat to the persistence of remaining areas of native grassland in North America and elsewhere. As a result, the re-introduction of burning is a

commonly employed technique of grassland restoration (e.g., Curtis and Partch 1948, Whelan 1995, Lesica and Martin 2003).

An inherent assumption of the "fire stability" hypothesis is that the effects of intense competition in unburned grassland are far more detrimental for species persistence than the occurrence of burning. By offsetting the destabilizing impacts of competition on subordinate species, fire thus "stabilizes" the grassland (Anderson and Brown 1986). While intuitively attractive, stability models have clearly demonstrated that the effects of disturbances are as destabilizing for the structure and function of ecological communities as intense competition (Huston 1979, DeAngelis and Waterhouse 1987, Pimm 1991, Wu and Loucks 1995). These effects are especially prevalent at small spatial scales where locally rare species can be quickly eliminated by fire or other types of disturbance. In systems characterized by disturbance, therefore, stability can only be defined at a regional scale where the localized effects of the disturbance are offset by the broader distributions of the species (DeAngelis and Waterhouse 1987). Native grasslands, unfortunately, occupy less than 5% of their former range due to the combined effects of habitat loss, conversion of grassland to woodland, and widespread plant invasion. In this context, the re-introduction of fire is predicted to be highly destabilizing because its negative effects on rare plant populations cannot be balanced by re-colonization from elsewhere. Therefore, fire may actually hasten the loss of species in remnant areas.

We examine the impacts of fire on stability (as defined above as the lack of change) in a highly fragmented and fire-suppressed oak savanna of southwestern British Columbia,

Canada. We focus on the effects of repeated burning on the relative abundance, production and reproduction of the dominant functional groups. Abundance and production are measures of the immediate impact of fire on community-level processes. Reproduction is a measure of the longer-term implications of fire for species persistence. Since widespread burning was eliminated in this savanna more than 150 years ago (Chapter Three), a persistent sward of exotic perennial grasses has formed in many remnant areas. The most dominant grasses (*Poa* and *Dactylis*) restrict the abundance of many native species due to their ability to limit ground-level light and space for recruitment (Chapters Four-Six). With fire, however, grass cover declines significantly (Chapter Four) but it is unclear how fire impacts the production and reproduction of these species and by implication, their stability. It is also unclear how fire impacts the subordinate native forbs. Because these species appear to be light-limited (Chapter Six), fire may cause their proliferation by removing the grass overstory. Alternatively, many of these species are locally uncommon or rare (i.e., averaging $< 2\%$ cover plot⁻¹) and may be susceptible to repeated disturbance. We extrapolate the observed trends from four years of burning in small plots to the longer-term implications of repeated burning at the regional level in this savanna (DeAngelis and Waterhouse 1987).

Methods

Study area

The oak savanna ecosystem of British Columbia, mostly restricted to southeastern

Vancouver Island, is at the northern limit of an oak savanna complex extending south to California (Barbour and Major 1976, Dunn and Ewing 1997, Maret and Wilson 2000, MacDougall et al. 2003). In British Columbia, this savanna is associated with a sub-mediterranean climate and moderately infertile soils of post-glacial origin. Soil depth ranges from < 5 cm to > 100 cm, and influences the distribution of functional groups and species (Erickson 2002). Perennial grasses, shrubs, and trees dominate the deeper-soil sites, while shallower soils have higher percentages of annual and perennial forbs. Over 150 naturalized non-native plant species occur in this savanna along the entire soil-depth gradient (Fuchs 2001).

Average precipitation ranges from 90-100 cm year⁻¹, and occurs mostly from October to March; temperatures in winter rarely drop below 0° C. As with Mediterranean climates in general, there can be considerable annual fluctuations in the quantity and timing of rainfall that are thought to affect production and flowering phenology (e.g., Major 1977). Among the major plant families of this community, 82% of all native species flower from April to early June before the onset of summer moisture deficits (Chapter Three). Many non-native species also flower at this time, but the dominant perennial non-native grasses (*Poa*, *Dactylis*) mostly flower in June and July.

Prior to European settlement in the mid-1800s, fires occurred during the dry season from late July to early October (Chapter Three). This fire regime favors species that complete their annual reproductive cycle by late spring. Charcoal records on southeastern Vancouver Island indicate fire occurrence back to the early Holocene. The negative effect

of late-Holocene climatic cooling on oak savanna distribution was probably offset by the use of fire by Native Americans (Brown and Hebda 1998), especially in areas of deeper soil (Chapters Two and Three).

Pre-colonial levels of grazing by black-tailed deer (*Odocoileus hemionus columbianus*) and Roosevelt elk (*Cervus elaphus roosevelti*) are unknown but were believed to have had limited impact on ecosystem function, especially compared to the impacts of domestic grazing in recent years (Chapter Three). Pocket gophers (*Thomomys* spp.), an important component of oak ecosystem function on the continental mainland (Hobbs and Mooney 1991, Hartway and Steinberg 1997) do not occur in this ecosystem on Vancouver Island.

Experimental design

In May 2000, burn and control plots (1 m^2) were randomly assigned to ten 4 X 10 m blocks in each savanna opening (2 sites X 2 treatments X 10 blocks = 40 plots). Burning was annually applied in a 1.25 m^2 box (Fig. 7-1) in late July from 2000 to 2003. July burns had three impacts: the removal of the litter layer, the elimination of living foliage, and the exposure of the soil surface to increased solar radiation throughout the summer. Because of this last factor, there was no re-growth by the grasses until the onset of the rainy season in the fall. Burning was initiated with a roofing torch, and then re-applied to unburned areas to ensure homogeneity of the application. This allowed us to test the impacts of fire in each plot without the confounding effects of unburned patches on post-

fire vegetation response. An additional 0.25 m buffer was burned around all plots to reduce edge effects.



Figure 7-1. Initiation of burning with a roofing torch – autumn 2003. Photo courtesy of the Cowichan News-Leader (Duncan, British Columbia)

In 2000, the properties of the fire treatment were described by measuring flame height, burn duration, and temperatures at, above (50 cm), and below (5 cm) the soil surface. Temperatures were measured with fire thermocouples (Canadian Forest Service, Victoria) that take readings at one-second intervals for the duration of the burn.

Prior to treatment application (May 2000) and for the three following years (May 2001-2003), relative species abundance (% cover plot⁻¹, n = 95 total species) was visually estimated using the 1 m² frame divided into 20 cells (Chapter Six). The total number of flowering stems plot⁻¹ was counted for the most abundant perennial graminoids and

forbs. The grasses were *Poa*, *Dactylis*, *Anthoxanthum* (all exotic), and *Bromus carinatus*, *Elymus*, and *Carex inops* (all native). The forbs were *Camassia quamash* and *Dodecatheon hendersonii* (both native). In half of the plots at each site, biomass was clipped at different locations in May of each year in 0.01 m² subplots to provide an estimate of production in each plot (g m⁻²). The clipped material was separated into grasses, forbs, and non-arboreal litter (Fig. 7-2).



Figure 7-2. Separated (left to right) litter, grass, and forb (mostly *Camassia*) biomass from a control treatment plot at Site B. Biomass was sampled from a 10 X 10 cm subplot from each 1 m² plot.

Light was measured at ground level at monthly intervals from March to August, and bimonthly for the other months (percent of light measured above the grass canopy of each

plot; Licor quantum sensor). As with the mowing the weeding treatments (Chapter Six), fire had no impact on soil moisture or available NO_3 and NH_4 in the plots at either site.

Statistical analyses

Separate repeated-measures analyses of variance (ANOVA) were used to analyze changes in percent cover of functional groups, reproductive effort, and production caused by burning over the four years of the experiment (Potvin et al. 1990, Kuehl 1993). The independent variables were site, block, year, treatment, and their various interactions (Table 7-1). Because of temporal auto-correlation among plots that are measured repeatedly, the variance:covariance matrices often suffer from sphericity that compromises the validity of the ANOVA analysis (Von Ende 2001). Most of my ANOVA analyses tested significantly for sphericity (Mauchly's test). Therefore, levels of significance in the ANOVA were adjusted using Huynh-Feldt and Greenhouse-Geisser corrections that are more conservative than the unadjusted probabilities but overcome the sphericity problem (Von Ende 2001). In all cases of my analysis, these two corrections were in agreement on significance. An increasingly common alternative form of repeated-measures analysis, multivariate MANOVA (Von Ende 2001), was not used due to the large number of dependent and independent variables that would have made interpretation of the results extremely difficult (Tony Kozak, personal communication). Results of the ANOVA were assessed using *a posteriori* Tukey's multiple comparison tests (significance level = $p < 0.05$). Changes in biomass quantity between May and July were compared with t-tests. Relationships between seasonal light levels and production were

determined using correlation analysis. All analyses were conducted using JMPIN (SAS 2001).

Table 7-1. Summary of repeated measures ANOVA for two treatments (burning, control), one season (summer only), two sites (deep- and shallow-soil), conducted over four years (2000-2003). The analysis is conducted as a split-plot design (same design used in Chapter 4) with "year" as the split-effect. This analysis structure was used separately for each of the analyzed response variables (e.g., diversity, percent cover changes by individual species, number of species plot¹). Individual comparisons were made using Tukey's tests ($p < 0.05$).

Source	Degrees of freedom
MAIN EFFECTS	
Site (fixed)	1
Block (random)	18
Treatment (fixed)	1
Site X Treatment	1
Error 1	39
SPLIT EFFECTS	
Year (fixed)	3
Site X Year	3
Treatment X Year	3
Site X Treatment X Year	3
Error 2	144
TOTAL	159

Results

Fire behavior

Fires mimicked a cool burn typical of grasslands with moderate stature (e.g., Whelan 1995). Flame height was ≤ 1 m and the burns typically lasted < 10 seconds. Thermocouple measures at 50 cm indicated temperature maximums ranging from 133-408° C plot⁻¹ (mean = 263.5 C°; n = 8 plots). Maximum temperatures at the soil surface ranged from 74-213° C (mean = 106.1° C). After 10-15 seconds, temperatures at both heights stabilized to 15° C. Thermocouple measures at 5 cm below the soil surface did not detect any temperature increases due to burning.

Light

Pre-treatment light levels in the grass understory averaged $< 5\%$ of full light at both sites (Fig. 7-3). Deeper-soil plots had significantly lower light, averaging 2.14% (SE = 0.37) compared to 3.56% (SE = 0.36) in plots in shallower-soil plots ($t = 2.93$, $p = 0.005$). These site differences were explained by a negative correlation between total production plot⁻¹ and light ($r^2 = -0.31$, $p < 0.0001$). Throughout the experiment, mean light levels in control plots remained below 10%, with shallow-soil plots being slightly better illuminated in most months (Fig. 7-3). In August, immediately after burning, light levels ranged between 90-97% in most plots

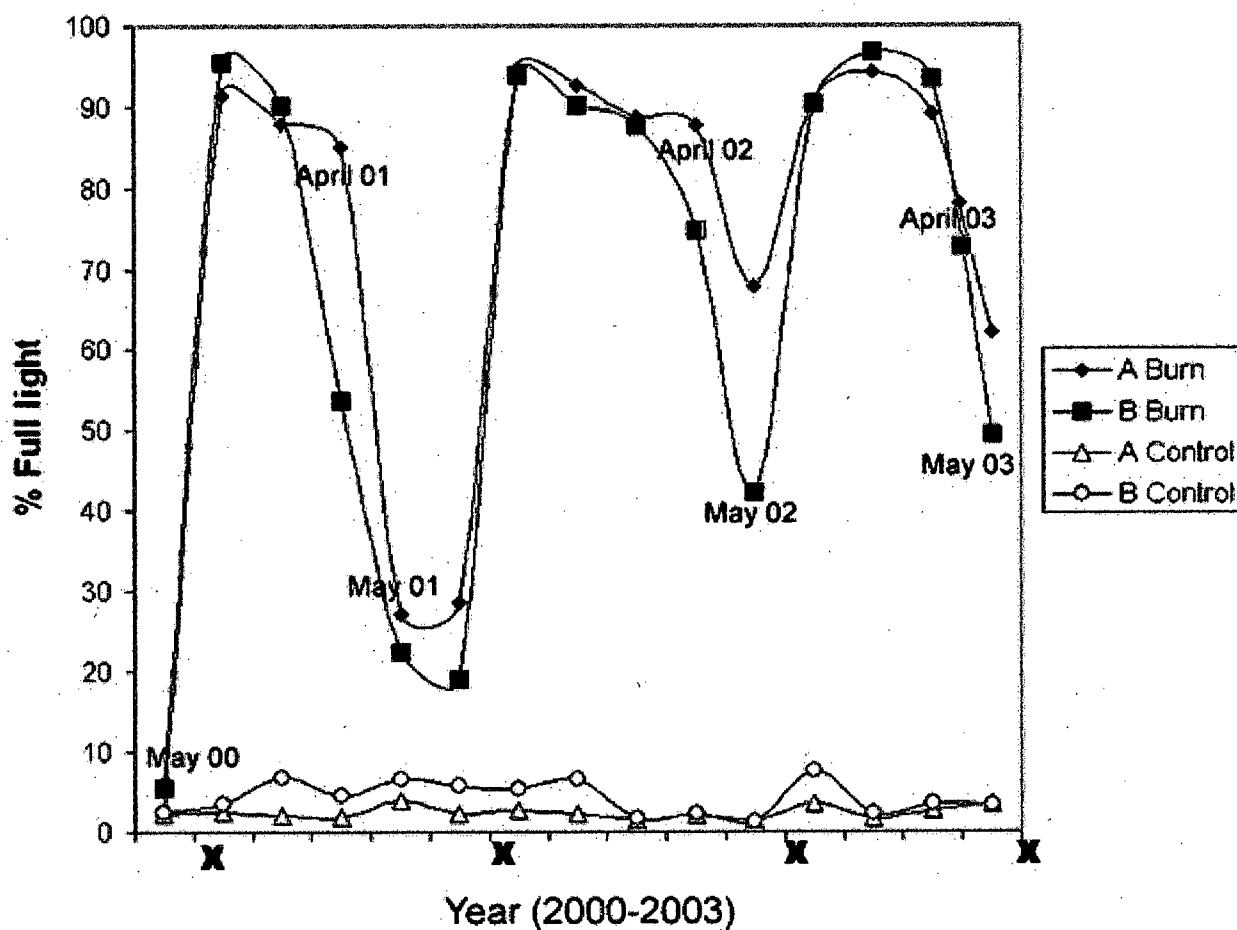


Fig. 7-3. Seasonal variation in ground level light in burned and control plots from 2000-2003. A = plot average at deep-soil site. B = plot average at the shallow-soil site. Burns were applied in late July each year, indicated by the bold "X" on the bottom axis.

and did not differ between sites. Light levels were not 100% because there was slight shading of horizontal light from the standing grass that surrounded each plot. Over the fall and winter months (Oct-Feb) mean light availability remained >85%. Light declined precipitously after March, in response to the increased growth by grasses and forbs at that time (Fig. 7-3).

Among years, spring light levels (April-May) following the first burn (2001) were significantly lower compared to levels following subsequent burns at both sites (Fig. 7-3) (Tukey's test). Average light availability in 2001 ranged from 20-27%, compared to ranges of 40-70% in 2002 and 2003. This result reflected the higher presence of perennial grasses after the first burn compared to the subsequent burns when grass cover < 5% plot⁻¹. Light availability was also inversely correlated with post-burn grass production at both sites ($r^2 = -0.12$, $p < 0.02$).

Between sites, spring light levels were significantly lower at the shallow-soil site in April 2001 and May 2002 but not in April or May of 2003 (Fig. 7-3, Tukey's test). This trend was positively correlated with changes in forb production at both sites following fire ($r^2 = 0.26$, $p < 0.0001$).

Impact on species cover

At both sites, burning caused significant increases in the cover of two functional groups (perennial forbs and annual forbs) and significant declines of one (perennial grasses) (Tukey's test). Burning eliminated two perennial grasses that were rare prior to the treatment: the native *Elymus glaucus* and the exotic *Phleum pratense*. There was no treatment effect on the native perennial sedge *Carex inops* (Fig. 7-4). The percentage of leguminous species plot⁻¹ was also unaffected by fire, although *Cytisus scoparius* and the exotic annual *Trifolium dubium* increased significantly at Site A (Tukey's test).

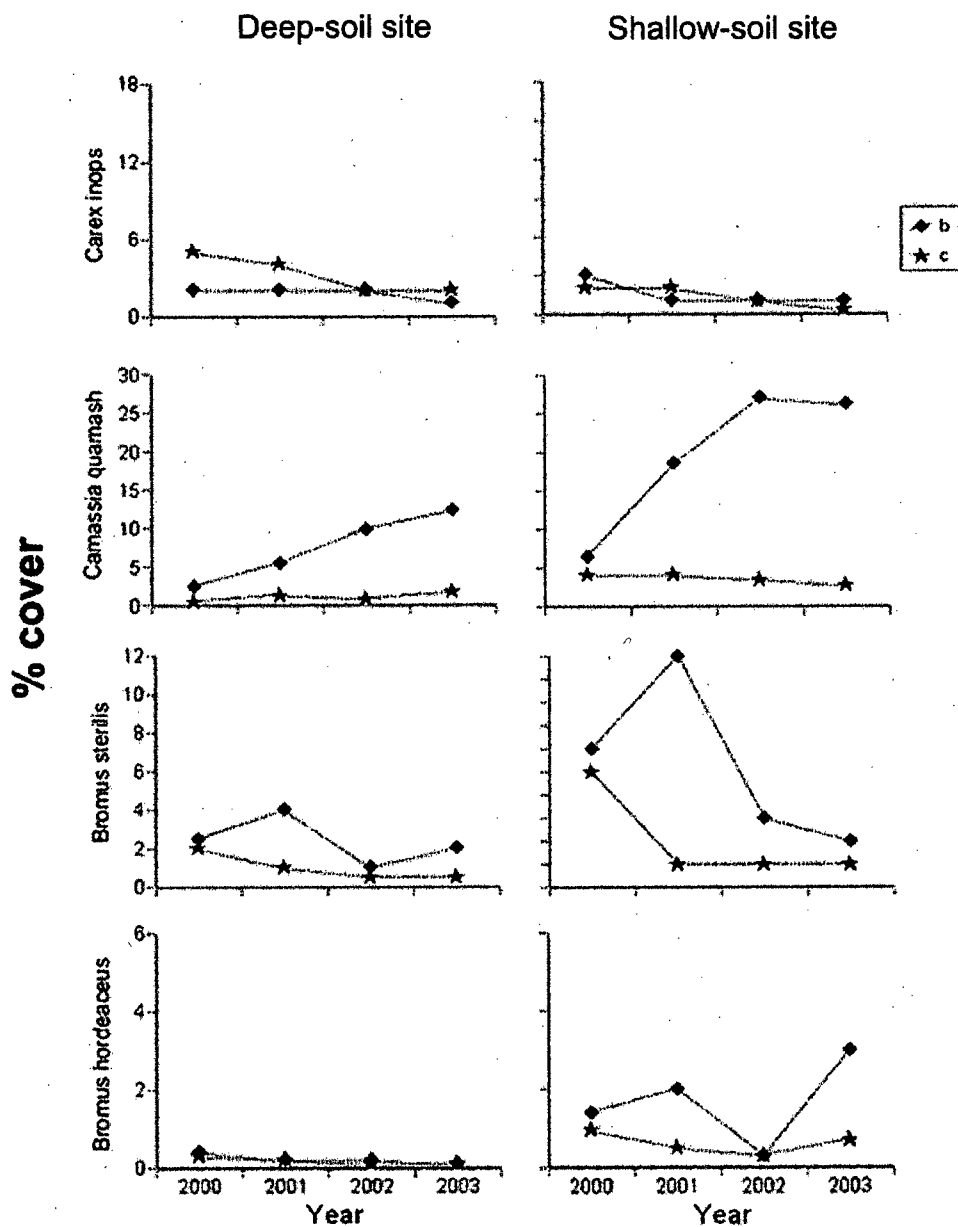


Fig. 7-4. Changes in average percent cover plot⁻¹ for *Carex inops* (native perennial sedge), *Camassia quamash* (native perennial geophyte), and two exotic annual grasses (*Bromus* spp.) with repeated burning. In the legend, b = burn and c = control.

Many annual species were affected positively by repeated burning, with the response by most interacting with site. Annual forbs such as *Valerianella locusta* (Figs. 7-5 and 7-6), *Cardamine oligosperma* (Fig. 7-6) and *Lotus micranthus*, and the annual grass *Bromus hordeaceus* (Fig. 7-4) all increased with fire compared to their average cover in 2000. For some annuals, such as *Myosotis discolor* (Fig. 7-6) and *Bromus sterilis* (Fig. 7-4), this increase was temporary (2001) and their subsequent decline (2002, 2003) was correlated with increasing forb production at both sites by the third year. Annual species that were abundant in control plots dropped significantly with fire (e.g., *Galium aparine* [Fig. 7-6], *Cerastium fontanum*).



Fig. 7-5. Cover of the exotic annual forb *Valerianella locusta* (small white flowers) in a summer burn plot at Site A – May 2002. Likely introduced originally as a medicinal herb, this species is very closely related, and functionally very similar, to the native oak savanna annual *Plectritis congesta*.

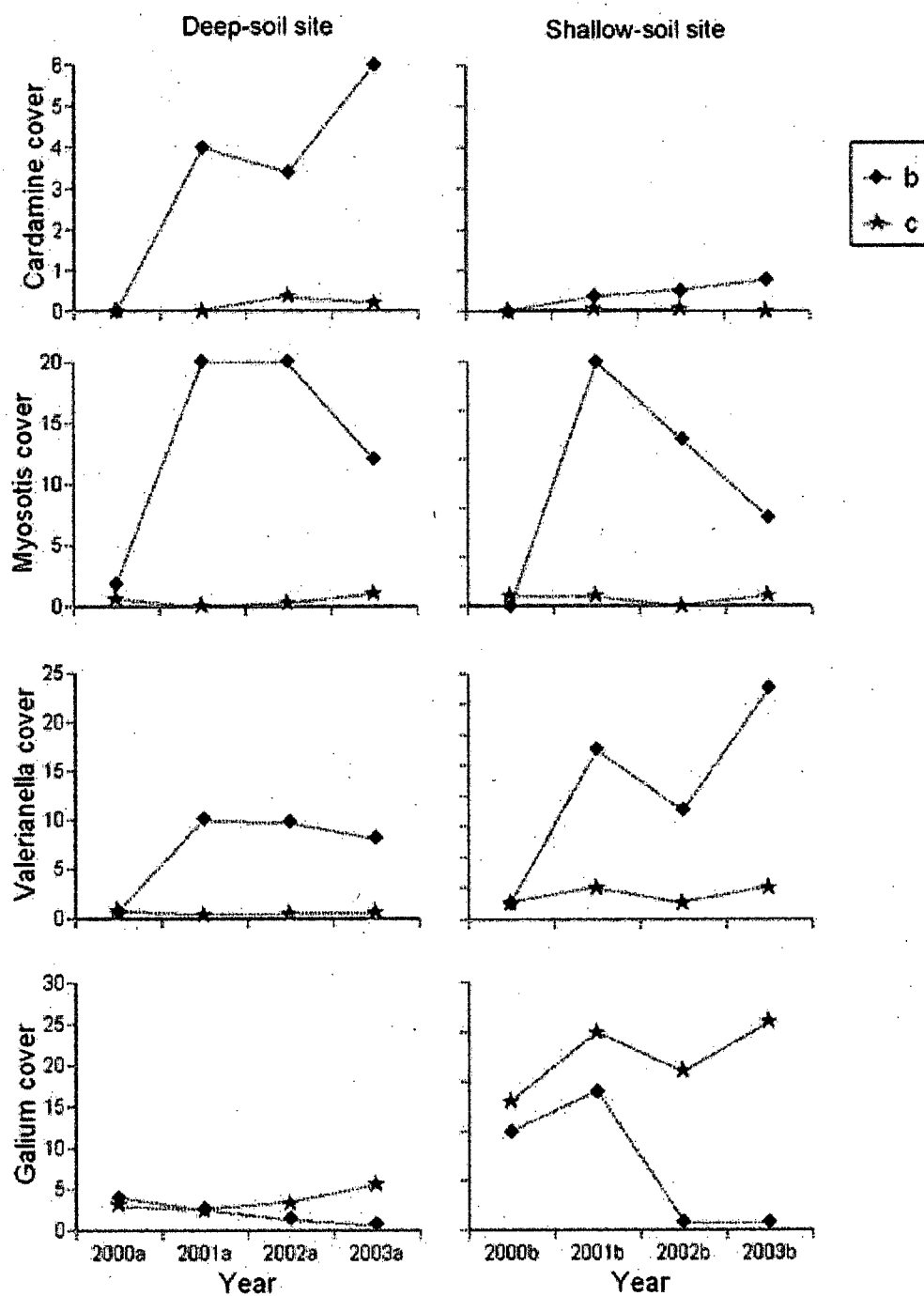


Fig. 7-6. Changes in average percent cover of annual forb species with summer burning from 2000-2003. Cardamine is native to western North America; the remaining species are exotic. In the legend, b = burn and c = control.

Many perennial forb species also increased significantly in percent cover with repeated burning (Tukey's test). Most were native geophyte⁵ species such as *Dodecatheon*, *Ranunculus occidentalis*, *Lomatium utriculatum* (Fig. 7-7), and *Camassia quamash* (Fig. 7-4). One exception was the native evergreen perennial forb *Cerastium arvense* that declined by 50% (Fig. 7-7).

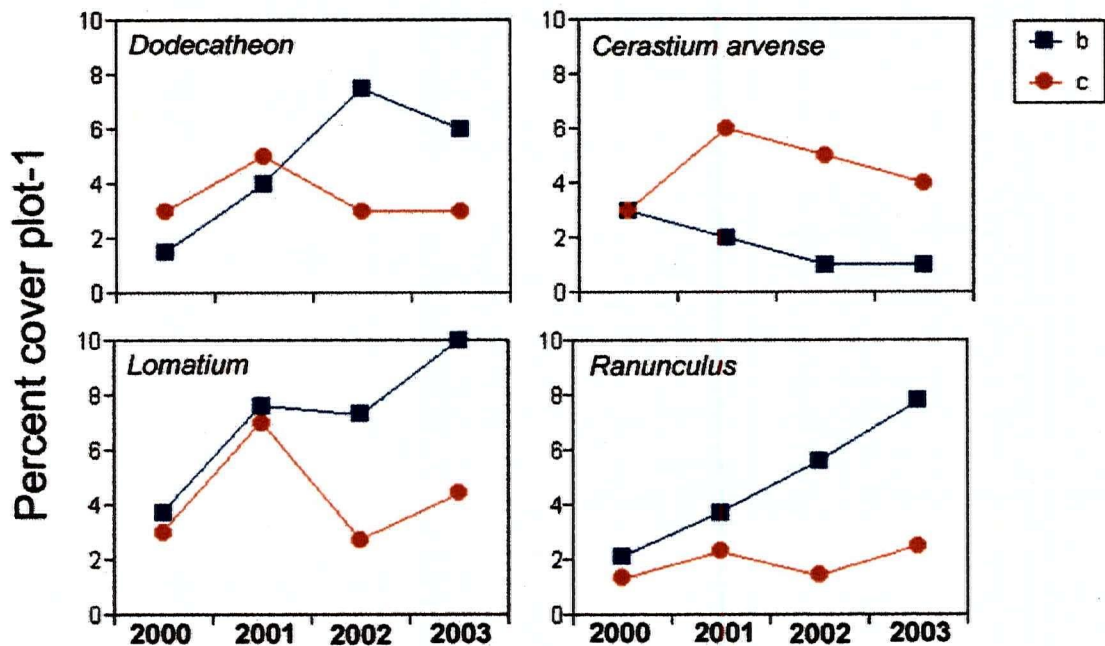


Fig. 7-7. Changes in average percent cover of native perennial forb species with summer burning from 2000-2003. In the legend, b = burn and c = control.

Production

Prior to burning, total production was significantly higher in plots at the deep-soil site (mean = $10.77 \text{ g } 0.01 \text{ m}^2 \text{ year}^{-1}$ [SE = 0.27]) compared to plots of the shallower-soil site

⁵ Geophyte = species that survive unfavourable periods by means of underground storage organs (Allaby 1998)

(mean = $7.82 \text{ g } 0.01 \text{ m}^{-2} \text{ year}^{-1}$ [SE = 0.24]) (Tukey's test) (Fig. 7-8). At both sites, total production was mostly composed of litter and grass foliage. Forb production was significantly higher in the shallow-soil plots ($1.08 \text{ g } 0.01 \text{ m}^{-2} \text{ year}^{-1}$ [SE 0.08]) versus plots from the deeper-soil site ($0.87 \text{ g } 0.01 \text{ m}^{-2} \text{ year}^{-1}$ [SE = 0.06]) (Tukey's test) (Fig. 7-8).

One year after the initial burn (May 2001), total production significantly declined at both sites (Tukey's test) and these decreases were maintained for the rest of the experiment (Fig. 7-8). Burning eliminated the differences in total production between the two sites. The decreased total output was caused by significant declines in grass production and by the near elimination of the litter layer by the third year (Fig. 7-9). In 2001, there were slight but non-significant increases in forb production at both sites. In 2003, these increases had become significant at both sites compared to initial levels in 2000. The increase in forb production, however, could not replace the lost production by the grasses (Fig. 7-8).

Reproduction

Prior to burning in the deep-soil site, *Poa* produced significantly more flowering heads plot^{-1} (mean = 81.4, SE = 11.4) than any other species (Tukey's test) (Fig. 7-10). Numbers of flower heads for *Dactylis*, *Anthoxanthum*, and *Bromus* were not different (means 9-13 heads plot^{-1}). *Camassia* produced an average of 0.6 flower heads plot^{-1} . At the shallow-soil site,

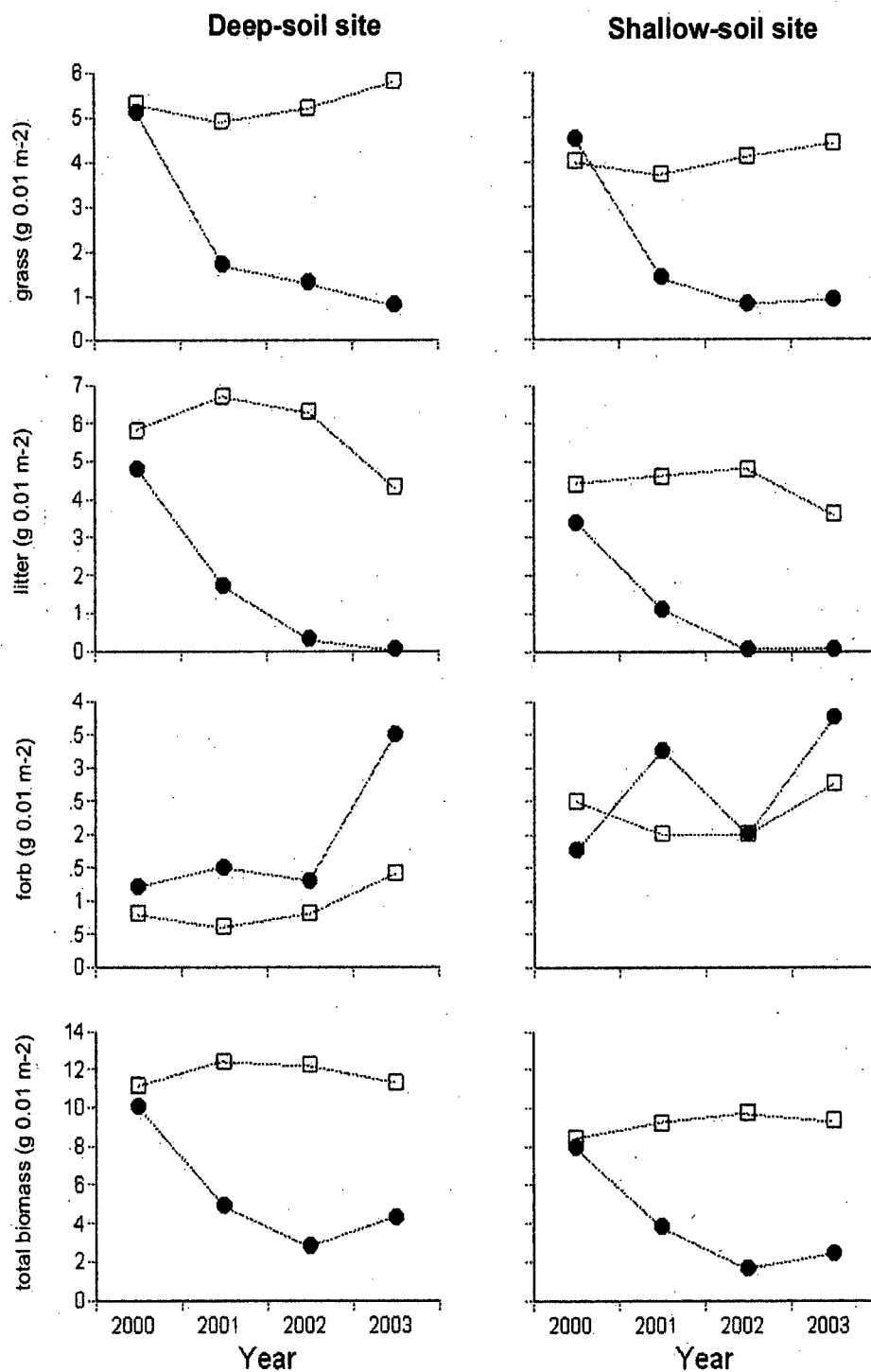


Fig. 7-8. Changes in average total production plot⁻¹ (g 0.01 m⁻²), and average production plot⁻¹ of grasses, forb and litter from 2000 to 2003 in burned and control plots. Solid circles = burn, open squares = control.



Fig 7-9. Contrast in litter cover between control plot (foreground) and a summer burn plot in the winter of 2003.

Poa (mean 26.7, SE = 5.9), *Anthoxanthum* (mean 35.5, SE = 7.2), and *Dactylis* (mean 17.5, SE = 4.5) flowered at similar abundances. *Camassia* averaged 4.7 heads plot⁻¹. *Carex inops* occurred and flowered infrequently in plots at both sites, while *Dodecatheon* only occurred in plots of the shallow-soil site and flowered in small numbers (mean = 0.4 flower heads plot⁻¹).

Burning caused significant decreases in flower-head production by most native and exotic warm-season grasses (*Poa*, *Dactylis* [Fig. 7-10] and *Bromus carinatus*). *Poa* flowering decreased significantly after the first burn, and by 2003 was producing 4.7

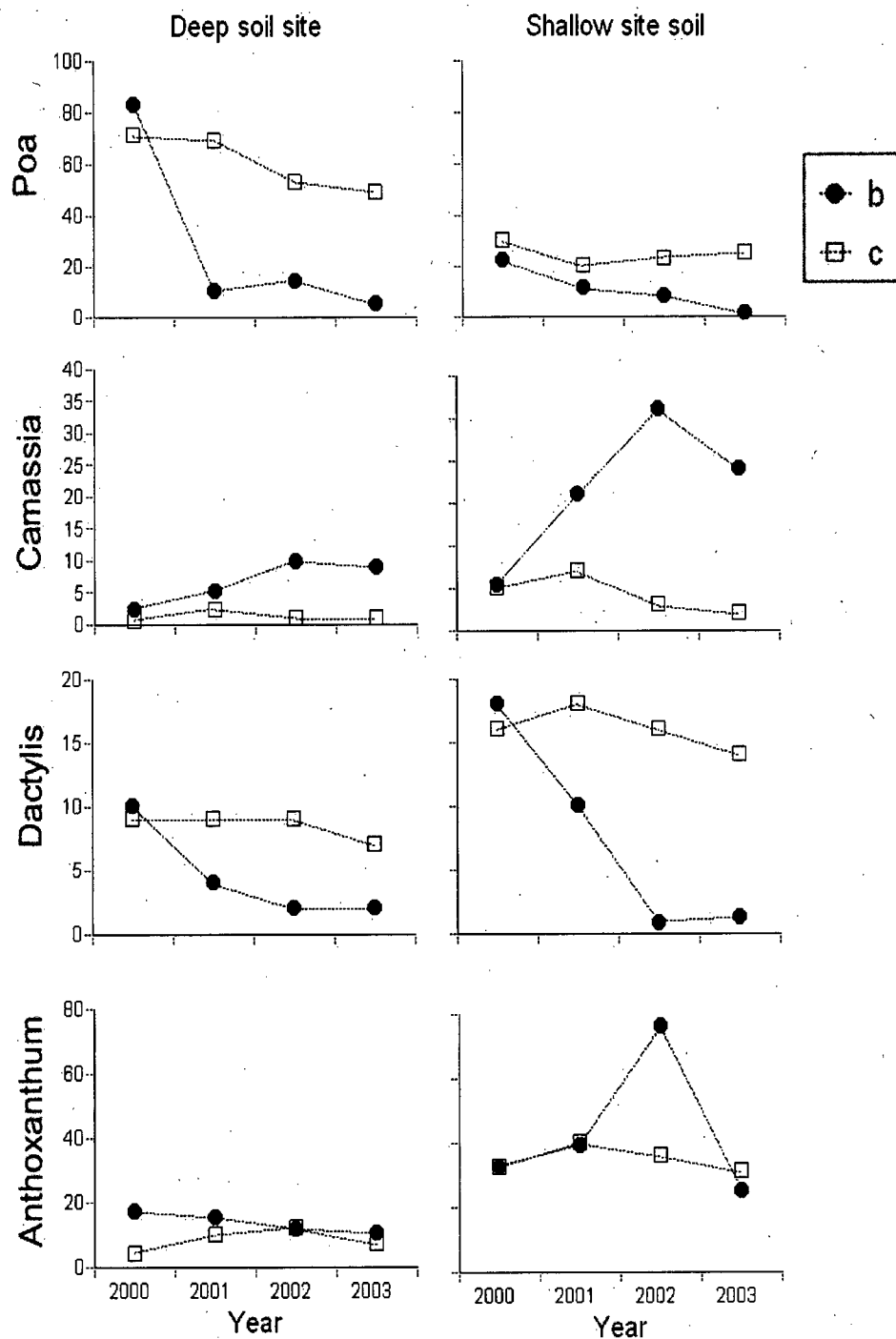


Fig. 7-10. Changes to the average number of flowering heads plot⁻¹ from 2000-2003 in the burned and control plots. In the legend, b = burn and c = control.

heads plot⁻¹ and 1.3 heads plot⁻¹ at the deep- and shallow-soil sites respectively. Flowering by *Dactylis* and *Bromus* did not decrease significantly until after the second burn; by 2003 both species produced < 2 heads plot⁻¹. Flowering by *Anthoxanthum* was unaffected (deep-soil) or varied unpredictably (shallow-soil) with fire (Fig. 7-10). Although *Carex* flowered too infrequently to statistically analyse its response, it produced 90% fewer flowers after three years of burning at the deep-soil site and did not flower at the shallow-soil site.

Burning caused significant increases in flower-head production by *Camassia* at both sites (Fig. 7-10). After three years it produced significantly more heads plot⁻¹ than any other species except *Anthoxanthum* at the shallow-soil site (Tukey's test). At the deep-soil site, its average production of flowering heads plot⁻¹ exceeded the individual averages of all perennial grasses even though it was not in all of the burn plots. *Dodecatheon* did not occur in sufficient number to statistically assess its response to fire, although its average number of heads plot⁻¹ increased from 0.4 to 1.9 at Site B.

Discussion

Predictions for long-term stability

We tested the hypothesis that fire would create a forb-dominated community that was as stable with repeated fire as the grass-dominated community with the long-term absence of fire. The results of this study do not support this hypothesis. While a forb-dominated

community quickly emerges with repeated fire, the limited quality and quantity of its litter suggests it will not be capable of carrying annual fires indefinitely. Because reduced fire will once again favour grasses, local areas must continuously oscillate between grass- and forb-dominated communities over time. We suggest that this non-equilibrium model of community function formerly characterized this system, and is comparable to results from other grassland regions (McNaughton 1983, Sinclair 1995, Knapp et al. 1998, Collins 2000). Because local conditions would continuously fluctuate, the structural parameters of this system were probably best defined from a regional perspective. This regional context no longer exists because of habitat loss and consequent fragmentation. The re-introduction of fire, therefore, may offset the negative effects of biotic feedbacks on native flora within remnant areas but might not stabilize the forb-dominated community that emerges in its wake.

The initial impacts of fire

Repeated burning quickly destabilizes the current savanna community dominated by perennial warm-season grasses. The production and reproductive output of native and exotic grasses declined precipitously, implying that these species would become much less abundant if fire were applied over larger areas. Concurrently, these conditions initially favour the emergence of mostly cool-season forb species. The replacement of grasses by forbs with fire is the opposite response to that typically observed in the published grassland literature. However, these other studies were done in tallgrass prairies (e.g., Turner and Knapp 1996, Knapp et al. 1998) where dormant-season burns

cause the proliferation of C₄ grasses that, in turn, displace forbs by competition. C₄ grasses do not occur in the oak savanna of British Columbia.

The cause of this transition is due to the switch in controlling factors, from severe limitations of light and bare soil to repeated biomass loss during the summer months. Summer fire eliminates all foliage and reproductive structures of the perennial grasses, and this represents a substantial loss of resources. It also eliminates the dense litter layer that favors their recruitment. Most forb species are winter ephemerals, emerging from October to February and finishing their annual cycle by June. Because their growth is restricted to < 8 months of the year, they are mostly unaffected by the fires that occur when they are inactive (summer and early fall). The high percentage of spring-flowering species in this savanna ecosystem, combined with the ability of these species to avoid the harmful effects of fire and summer drought, indicates that these limiting factors have been important for determining community membership in this past. Of the two, the occurrence of fire is probably more limiting because many non-Mediterranean exotics have been able to become established in the absence of fire. The climate is not sufficiently severe to prevent their occurrence (e.g., duration and intensity of summer moisture deficits), although initially there may have been strong selective pressure on these grasses favouring individuals with earlier phenologies.

Annual production and recruitment by perennial forbs is highly dependent on light availability during the late winter and early spring. By eliminating litter and reducing the production of grass foliage, fire greatly increases light levels during this period. Burned

areas remain blackened throughout the winter, which may impact growth due to the warming effect of the sun on the soil surface. High light levels in winter also favour seed recruitment by native forbs. Germination can begin as early as late August or September, depending on the occurrence of heavy rain events during this time (MacDougall and Turkington, unpublished data). In the early years of development, many forb species concentrate the allocation of resources on the formation of belowground root structures. Seedlings thus produce limited foliage, are usually short (<10 cm height), and can be highly susceptible to shading in the late winter and spring. Although most native forb species, including annuals, have some capability of recruiting within the dense grass swards (Chapter Five), recruitment success is significantly higher in burned areas. By mid-summer, seedlings of most species are no longer present aboveground. They escape the impacts of fire, as well as the effects of soil moisture deficits (Chapter Six) and increased solar exposure.

The long-term impacts of fire

Due to substantial differences in litter quality and quantity, perennial forb species are incapable of supporting repeated annual burning. Although production by these species increased significantly after three years of fire, it was not sufficient to replace the combined high levels of foliage and litter production by the grasses. The quantity of litter production was reduced, presumably due to the shorter annual growing period of these species compared to the grasses. The quality of forb foliage also limits their ability to produce a persistent litter layer that that can support fire. Forbs produce foliage with

much less lignin and more water per unit biomass than grasses - their litter quickly dehydrates in the summer and what remains rapidly decomposes in the winter.

Thus, the fire-induced transition from a grass-dominated community to one dominated by forbs cannot persist indefinitely. As the probability of fire decreases, recruitment and survival by warm-season grasses will increase until litter accumulates to sufficient levels to burn once again. Rather than stabilizing the savanna community at the local level, therefore, the continued presence of fire within the landscape will cause its repeated oscillation between forbs and grasses. Formerly, this local cycling would occur repeatedly across the regional extent of the ecosystem, analogous to a river meandering back and forth over time but remaining in the confines of the valley. The spatial and temporal heterogeneity implied by this cycling is consistent with the early historical accounts of this savanna, where fire interacted with soil depth, topography, and cultural activity to create a mosaic of community types across the region (Chapter Three). It also indicates that the regional model of stability observed in other grassland systems (e.g., Collins 2000) applies to the oak savanna of southwestern British Columbia, despite its unique composition and structure (no C_4 grasses, high number of perennial and annual forbs).

Additionally, the impacts and interactions of site factors and annual- and long-term climatic fluctuations on production would deflect these oscillations into further unpredictability (e.g., Knapp and Smith 2001). Because deep soils have higher grass production, presumably due to higher moisture availability, these areas should support

higher-intensity fires and should cycle between grass- and forb-dominated communities more quickly. In the absence of fire regionally, forbs should become limited to shallow soil areas where highly competitive perennial grass species are constrained by moisture availability. Although speculative, this may explain why the diversity of native forbs in the Cowichan Valley is currently highest in areas with soils < 10 cm deep (Appendix 1, Fig. 5-4). Repeated wide-ranging fires should restrict grass distribution, limiting these species to topographic and hydrological refugia (e.g., seepage areas, areas with the deeper soils) where fire may occur less commonly (e.g., Whelan 1995). Although this study was too short to detect the relationship between climate and production, annual variations in the timing and quantity of precipitation are typical of Mediterranean climates and are likely to interact with soil depth in influencing fire. In drier periods, fire will penetrate farther into the refugia of the grasses although production and litter build-up will presumably be decreased somewhat. Wetter years will make areas of shallow-soil "deeper", allowing grasses to invade these areas that serve as competitive refuges for forbs in periods of reduced fire.

Conservation implications

The former temporal and structural heterogeneity of this savanna has been much simplified since the onset of European settlement. Prior to this, regional species co-existence was probably easily maintained. Competitive displacement by dominant species was unlikely because of the interactions among disturbance, life history differences (e.g., forb versus grass), and environmental heterogeneity (soil depth, topography) – there were

always areas of reduced competition. Species loss by environmental stochasticity was unlikely because fire necessarily decreased through time as grasses were replaced by forbs, and because climatic, edaphic, and topographical factors created safe sites where the impacts of fire were limited – there were always areas of reduced disturbance.

The functioning of this ecosystem, however, has been fundamentally changed by habitat loss and the elimination of fire. These changes largely explain the high levels of grass invasion in this system, the occurrence of numerous rare and endangered plant species, and the infilling by tree species in some areas. Although non-interactive factors such as recruitment are known to limit native species (Chapter Five), biotic feedback instabilities may currently pose the greatest long-term risk in remnant areas. The impacts of competition on species loss have recently been questioned in the context of plant invasion (Davis 2003). However, by limiting the relative abundance of native flora, competition directly threatens the persistence of these species or increases their susceptibility to stochastic disturbance events. These risks form the basis for the call for re-introducing fire to these formerly pyrogenic grasslands.

Although fire is likely to reduce the negative effect of biotic feedbacks, the results of this study indicate that burning also has destabilizing impacts on community structure. Of particular concern are those native savanna species that do not complete their annual cycle by early summer. This includes many species from the family Asteraceae and a number of perennial warm-season grasses (Table 3-4). The diversity of flowering phenologies in this community is consistent with the view that this system formerly

possessed both spatial and temporal heterogeneity. Therefore, imposing a regime of repeated burning within habitat remnants of limited size (typically < 10 ha) may be as destabilizing for some species as the current regime of complete fire suppression. The re-introduction of fire must be coupled with attention to the underlying environmental conditions of remnant areas, the phenologies of the species found within, and the likelihood that the annual climatic conditions will affect the performance of the burn. Failure to consider these factors may lead to unanticipated and potentially negative consequences.

This re-enforces the point that small remnant areas may preserve the occurrence of species but not necessarily the processes that formerly maintained them (e.g., Janzen 1986, Kellman 1996). In grasslands and savannas in particular, the processes that determine the structure and function of site-level species assemblages occur and interact at both local and regional scales. Although fire will offset biotic instabilities (i.e., intense competition), the use of fire for conservation purposes must also consider the reduced population range and size of native species and the possibility of unnaturally high fuel levels caused by decades of suppression. Both of these factors may be as un-stabilizing as the long-term absence of fire itself.

Chapter Eight

Conclusions

"(For many invasions) we still have no notion of what happens, except that there is a change"

"Interference (i.e., competition) may lead to the replacement of one species, or part of the populations of one species by another – a demographic event of whose interior causes we may be and usually are ignorant. The snag is that replacement may occur without direct interference...when one species decreases through pure coincidence from independent causes during increase of the other; and interference may occur without replacement, as when two species jostle for nesting sites when there are plenty more around for the loser to occupy."

"The white dead-nettle is a successful (exotic) woodland plant in a rich community of other species. Yet it has been in England for hundreds of years without making the grade here as a woodland plant. But suppose it had done so, would it have replaced some native species or just added one more to the list? This is a recurrent and an insistent question that keeps rising in the mind, and perhaps is the single most important problem lying underneath all the facts of this book"

Charles Elton *The Ecology of Invasions by Animals and Plants* (1958)

Invasion has long been considered paradoxical because it is unclear why species from distant shores should be so successful in unfamiliar habitats. The earliest explanations viewed invaders as weedy species that established in the context of human disturbance. Indeed, many invasive species share a long history with human civilization (Crosby 1986, D'Antonio and Vitousek 1992). However, there are numerous cases where weediness cannot explain invasion. As ecologists have studied this phenomenon more closely, it is becoming increasingly clear that there is a complex range of factors that cause and maintain its occurrence (Myers and Bazely 2003). Further, detailed evaluation of these factors often reveals that invasion is not so paradoxical after all (Levine and D'Antonio

1999, Sax and Brown 2000). Like any ecological system, the underlying processes are intricately connected, occur across a range of spatial scales, and unfold slowly over time. We typically view invasions most closely when they become most problematic. Behind every invasion, however, are often a long series of events and interactions shaped by competition, immigration, disturbance, and other ecological factors. Understanding the causes of invasion, therefore, rests on determining the past interplay of these factors using theoretical and empirical procedures. This approach formed the basis of this project.

Originally, I had planned to study the role of competition in determining the composition, diversity, and distribution of native and exotic plant species in the Garry Oak savanna. Inherent in this objective was the assumption that 1) competition explained the establishment and subsequent dominance of invasive plants, and 2) competition by exotics was the primary limiting factor for the abundance of native species. I envisioned two alternative hypotheses that explained the competitive success of the invaders (e.g., Daehler 2003). First, the “absolute” hypothesis where invaders possessed highly discrete trait differences that allowed them to dominate irrespective of the environmental circumstances. And second, the “contingent” hypothesis where dominance was caused by the myriad of environmental changes that occurred following European settlement. The exotics, therefore, owed their dominance to the destabilizing effects of over-grazing, habitat loss by cultivation and settlement, or the suppression of fire. The experimental work in the glasshouse and field was designed to examine these hypotheses by testing whether the exotics were really that different from various morphologically similar native

species of the oak savanna. I anticipated that by manipulating factors such as fertility and establishment order in the glasshouse, and disturbance frequency and dispersal in the field, I could reject various predictions derived from the two hypotheses. In turn, I would have an understanding of how competition currently determines relative abundance.

Many of my results confirmed the importance of competition. The removal experiment resulted in a proliferation of annual and perennial forbs and grasses that were previously rare or absent. Pair-wise competition work in the glasshouse demonstrated the superior ability of *Dactylis* to compete against other grasses under conditions of initially unlimited resources. The seed addition experiment in the dense grass sward revealed that the native grasses *Bromus* and *Elymus* were effective tolerance competitors due to their ability to regenerate in the light-limited understory. Seed addition work also revealed higher establishment and survival of forbs in burned plots compared to unburned areas.

However, other results did not conform to expectation. Recruitment was found to be limiting, as native species were able to recruit in the grass swards where adult plants currently do not occur. Some species were more limited by soil depth or annual variations in climate than they were by the treatments. Despite being the dominant species growing in the study area, *Poa* was the weakest competitor in the glasshouse under a range of conditions. In the biogeographical analysis, site-level species pools of native plants were found to fully sample the regional pool of native species despite the small area of the remnants, their isolation, and decades of disturbance. Exotic species, by contrast, did not demonstrate this relationship despite their dominance and the presumed frequent

dispersal throughout the region. Thus, while competition is important for structuring this oak savanna, it is clearly not the only factor and perhaps not the primary determinant of the diversity and distribution of species.

Although early ecologists such as Wallace had speculated on the occurrence of invasions, Charles Elton's seminal book *The Ecology of Invasions by Animals and Plants* (1958) was the first to offer a broad array of hypotheses, predictions, and explanations regarding the causes and consequences of invasion. In the chapter *The Balance Between Populations*, Elton speculates at length on the possible role of competition in invasion. While recognizing its importance in many cases, his ultimate conclusion on this matter resembles those of this study – that while “*competition...can be seen by direct observation to be very important...it must be remembered that there are many other forces operating...*” (Elton 1958, p. 123).

Clearly, this statement applies to plant invasion in the Garry Oak savanna ecosystem. Competition is necessary to understand invasion but it is not sufficient to completely explain it. The composition and abundance of exotic and native species are also determined by the dispersal, fire (and its absence), soil depth, annual climatic variations, topographic position, and the long history of human disturbance. Although the strong correlation between the proliferation of exotic plants and the precipitous decline of native species is highly suggestive of competition, the results of my research revealed a more complex and dynamic model of community organization than was originally anticipated.

Competition

My experimental work clarified the mechanisms by which the exotic grasses currently dominate. The primary evidence points towards light as the main limiting resource in this fire-suppressed savanna. Although the soils have been described as infertile (Jungen 1985), the high production suggests that soil fertility is of secondary importance in the areas where this study was conducted. Throughout the year, light at ground level was often as low as the understory of tropical rainforest (i.e., less than 2% full light – MacDougall and Kellman 1992). The most dominant grass species, *Poa*, not only creates these conditions by its copious production of litter, but also easily tolerates them by its continuous regeneration by tillering. Only a few other species can regularly regenerate in this light-limited understory. Not surprisingly, many are weed species of mesic Eurasian pasture such as *Vicia* spp., *Cerastium* spp., *Stellaria media*, and *Lathyrus* spp.

The high abundance of *Dactylis* in the field is harder to explain because it is non-rhizomatous and appears to rarely regenerate from seed in the dense grass understory. However, the glasshouse work clearly demonstrated it to be a classic “competitor” species as described by Grime (2001). Fast growing and physically robust, this species aggressively colonizes disturbances. Once established, it is long-lived and expands slowly by lateral tiller production to produce plants with at least twice the biomass of most other herbaceous species of the savanna. Although *Dactylis* may not regenerate in high numbers due to the sensitivity of its seedlings to low light, it may be expected to

dominate most recruitment opportunities when they occur, and once established, it is not displaced easily by competition from other species.

The results of this study also strongly supported the "contingent" hypothesis for competitive dominance. As predicted by Chapin et al. (1996), when the traits and competitive strategies of interacting species are not widely different then the outcome of competition may readily switch with changing environmental conditions. In the oak savanna, this switch is caused by trade-offs between the ability to tolerate low light, and the ability to tolerate repeated loss of biomass. The exotic perennial grasses were highly sensitive to disturbance, suggesting that their dominance depends on the long-term absence of fire. It was surprising that the responses to the three disturbance treatments (weeding, fire, mowing) were generally indistinguishable. Mowing (and raking) was hypothesized to be the least stressful form of disturbance yet its application in the summer months was as detrimental to the production and flowering of these grasses as their manual removal. Although *Poa* and *Dactylis* both thrive in heavily grazed pastures, the intensity of the treatments I applied, combined with the summer moisture stress of the sub-Mediterranean climate, exceeded their ability to compensate for these losses.

Because the native perennial grasses (*Bromus* and *Elymus*) demonstrated the same sensitivity to disturbance, and because of the significance of establishment order for determining competition in some circumstances (Chapter Four), it further suggests that competitive strategies of *Poa* and *Dactylis* are not profoundly different from the morphologically similar native grasses of this system. They are sufficiently unique,

similarities (Fig. 8-2) but they do not regenerate as quickly or produce nearly the same quantity of seeds to favour their recruitment when small disturbances occasionally occur in this ecosystem.



Fig. 8-2. Dense sward of Dactylis glomerata, Bromus carinatus, and Poa pratensis in the Cowichan Garry Oak reserve (July 2002).

Recruitment

Despite the importance of competition, several key expectations were not validated by the experimental work. Most surprising was the ability of many subordinate forb species to establish and survive in the dense grass sward. Given the low understory light levels and the absence of adult forb plants from most plots, I had predicted that few or no

species would survive except in areas that had been burned. The explanation for this result is not entirely clear, although it is consistent with other recent seed addition studies using similar methods (Primack and Miao 1992, Tilman 1997, Foster 2001, Foster and Tilman 2003) as well as theoretical predictions (Shmida and Ellner 1984, Zobel 1997).

One possibility is that the light environment characterized by my measurements (taken at one point in time at the daily solar maximum) does not accurately reflect the light regime at ground level as experienced by recruiting plants. In shaded forest understories, seedling regeneration often depends on short but intense light pulses (sunflecks) that occur periodically during the day (Percy et al. 1994). Such events would not be fully detected by my measurements and may be sufficient for the survival of young seedlings. The frequency of these events would presumably depend on the quantity of aboveground biomass, aspect and slope, and proximity to tree cover.

Regardless of why regeneration can occur in these swards, this result confirms that recruitment limitation by subordinate species currently limits their presence and relative abundance. While recruitment success depends on site factors, especially soil depth, and increases with fire, the results from this project suggests that many more species per unit area could persist if dispersal were more frequent and occurred at a higher density. As discussed in Chapters Five and Six, the reasons for this limitation are unknown. Although absent from most plots, species such as *Camassia*, *Erythronium*, *Ranunculus*, and *Dodecatheon* occur in large numbers elsewhere in the reserve and likely produce tens of thousands of seeds each year. Based on my results, however, it appears that recruitment

from seed only occurs in close proximity to the parent plants. It is tempting to look towards fragmentation and other contemporary changes (e.g., loss of dispersal agents) as the cause of these dispersal inefficiencies. And this may be so. However, many species appear to be naturally inefficient dispersers (e.g., gravity), suggesting that these landscape changes exacerbate the inability of these species to widely disperse, rather than causing it. This hypothesis urgently requires testing in this ecosystem.

Despite the apparent inability of many ground flora species to disperse long distances, the results from the biogeographical analysis indicate that dispersal has played an important role in the assembly of the oak savanna plant community in the past. Although naturally occurring dispersal by most native perennial forb species was not detected (i.e., in the burned plots with no seed additions), it may simply be operating at frequencies below the temporal resolution of my field study. Combined with my experimental results demonstrating successful recruitment in the grass understory, there is sufficient evidence to suggest that competition cannot fully regulate membership in this savanna if dispersal is frequent. If the savanna community is indeed an "unsaturated" system, this may explain why so few species have disappeared despite the high levels of invasion by exotic flora.

Disturbance

Disturbance is inexorably connected to invasion. It is often presumed to promote invasion by occurring too frequently or by not occurring frequently enough. This latter perspective

often characterizes hypotheses on the proliferation of exotic species in grasslands, leading in turn to use of prescribed burning as a control measure (Grace et al. 2001). There are at least three potential problems with the approach, however. First, the reintroduction of fire does not always control invasive plants in these systems (Grace et al., 2001). Although some invaders are highly sensitive to burning, as demonstrated for *Poa* in this study, many others are not. Second, if fire is applied too extensively it can be as destabilizing for some native species as the effects of long-term fire suppression are for others. Further, the removal of an invader may sometimes facilitate invasion by a more problematic species, as described in Chapter Six for *Cytisus scoparius*. Third, the effects of fire can be strongly influenced by numerous biotic, edaphic, topographic, and climatic factors. Its impacts in any given location, and in any given year, therefore, can be unpredictable. In combination, these problems reveal that the impacts of disturbance on invasion, like those of competition, cannot be understood in isolation. Nor can disturbances such as fire be viewed as a simple tool for the control of invasive species.

Experimental burning in this study confirmed its highly variable effects on oak savanna vegetation, including invasive species. As an agent of control for exotic warm-season perennial grasses, it was effective. This result, however, was largely contingent on the timing of the application with a summer burn being more effective than a fall burn. Further, these burns were also detrimental to native grasses with similar phenologies. Dunwiddie (2002) also observed negative fire effects on native grasses in a long-term burn study on Garry Oak savanna of the San Juan Islands of Washington State. The native perennial grass *Festuca roemerii* declined significantly with fire and took seven

years recover to pre-burn cover levels. It will be difficult, if not impossible, to disentangle the positive effects of fire for controlling exotic grass from its negative effects on phenologically identical native grasses.

The impact of fire was also contingent on the combined effects of soil depth and species composition. The most fire sensitive species were those most abundant on the sites with deeper soil and high productivity – the exotic perennial grasses. As a result, fire at this site resulted in significantly higher levels of light and available bare soil in subsequent years. In some cases, this greatly increased the survival of cool-season forb species added from seed (Chapter Five). In others, it led to extremely high mortality of warm-season grass species due to the combined absence of a protective canopy cover and the low soil moisture levels of the spring of 2002 (compared to the previous year, Fig 6-3).

Although my study was too short to fully quantify the impacts of climatic fluctuations on productivity and fire, it seems likely that variations in annual precipitation could influence both factors (Knapp et al. 1998, Knapp and Smith 2001). A series of wetter years would presumably lead to greater productivity by grasses and the subsequent higher incidence of fire, while long-term periods of drought may produce the opposite effect. It also seems likely that climatic variations could impact the abundance and distribution of invasives. Many of the more abundant grass and forb invaders are non-Mediterranean species with summer phenologies. Although the climatic extremities of the sub-Mediterranean in British Columbia are clearly too weak to limit their establishment within the region, unusually intense years of moisture limitation (e.g., the summer of

2003) may impact their reproduction. Under current predictions of global warming for the Pacific Northwest (Franklin et al. 1991, Hebda 1997), the Mediterranean climate of western North America is predicted to intensify with possibly a longer and drier summer period and a shorter winter period with less precipitation. If this happens, the relative abundance of invasive species in the oak savanna may begin to shift towards those with earlier phenologies. Because the Garry Oak savanna currently supports over 150 exotic species representing a range of functional groups, there are many taxa that fit this profile including some with Mediterranean origins (e.g., *Bromus* spp.).

Given the various biotic and abiotic factors that can interact with the occurrence of fire, its impact on invasive species is not easy to discern. In my study area, burning caused substantial changes to the physical structure (canopy height, bare soil) and relative species abundance of the savanna community due to its impact on *Poa* and *Dactylis*. However, while numerous previously established native perennial forb species proliferated with fire (mostly at Site B), many exotic species also increased significantly. Thus, although fire will reconfigure the composition and diversity of the savanna community it will probably remain dominated by invasives over the long-term. The decreased ability of perennial forbs to support fire as they increase in abundance, combined with the failure of fire to eliminate *Poa* and *Dactylis* completely, suggests that the effects of burning on these currently problematic species will be temporary. Clearly, therefore, fire alone will not be sufficient to restore the savanna to a plant community dominated by native species, if this can occur at all.

Conservation recommendations

The results of this study support several recommendations for the conservation and restoration of this nationally endangered oak savanna ecosystem.

1) Reserve creation alone will probably not protect this ecosystem because a lack of disturbance promotes dominance by *Poa* and *Dactylis*. It may also lead to the subsequent succession to a shrub- and tree-dominated ecosystem within which the current ground flora species (native and exotic) cannot persist. Therefore, while reserve creation is a critical and much-needed first step for protection it must be supplemented with active conservation management of native and exotic species.

2) The re-introduction of prescribed burning could be highly effective for the control of the exotic ground flora that currently dominate most remnant areas. It is likely, however, that while fire will reduce species such as *Poa* and promote some native plant taxa, it will also improve the competitive performance of some of the other 153 exotic taxa that have become naturalized (i.e., no longer require intentional or accidental seed additions by humans to locally persist) within this ecosystem. The positive effects of burning for some native flora, therefore, must be balanced with its potential to increase the occurrence of other problematic invaders.

3) Evidence from this study suggests that the impacts of mowing and raking were as effective as fire at reducing the occurrence of the exotic perennial grasses. Given the

potential dangers of burning, combined with the semi-rural or suburban setting of the Garry Oak savanna at present, a regimen of summer mowing could potentially diminish the need to burn.

4) Although the *type* of disturbance treatment may not matter for the control of exotic perennial grasses the *timing* of its application appears to be critical. These grasses are especially vulnerable to disturbance during the early summer prior to seed set. Although *Poa* did decrease with the fall treatment applications, their effect on this species was less pronounced. *Dactylis* was only weakly affected by mowing or burning in the fall.

5) Because many native species appear to be recruitment-limited, the application of fire or mowing must be supplemented with the addition of seeds or planted seedlings. Failure to do this will perpetuate ruderal species in the seed bank and other regionally abundant exotics such as *Cytisus scoparius* that appear to be less limited by dispersal.

6) The artificial assembly of a native-dominated community through the planting of seedlings (manipulating order of establishment for restoration purposes) may be successful for the lifespan of those individuals, but they may not persist in the long-term. At present, *Poa* is the superior tolerance competitor in this system and unless it can be completely removed, it will likely replace the native flora. The planting of native species (seeds or seedlings) must therefore be accompanied by supplemental measures for the control of exotics.

7) Replicating the former effects of a regional fire regime in a small remnant area may be akin to capturing lightning in a bottle. Large-scale fires are heterogeneous in impact, both spatially and temporally, and this heterogeneity may be impossible to mimic in small areas. That being said, managing for some level of spatial and temporal variability may be essential for the persistence of the diverse array of functional groups and phenologies found within the Garry Oak savanna flora. If applied too widely, the use of fire in small areas can create conditions that are as homogeneous as the current community dominated by *Poa* and *Dactylis*. Not only does this threaten native warm-season plant species, but there is also concern for many resident invertebrate species, especially butterflies. While the life history of invertebrate taxa are incompletely understood in the Garry Oak savanna, the destruction of large areas of standing biomass in the summer could negatively impact their foraging and reproduction.

This latter point indicates that the complexities of this ecosystem do not only apply to the structuring processes of the plant community (i.e., the dynamic interaction of competition, recruitment, and environment examined by this study) but can also extend across trophic levels. The actions of any given conservation measure, therefore, may ripple through the system in ways that are unpredictable or unanticipated. Only by continued research on the ecology of this oak savanna can these complexities be articulated and accounted for in the design of conservation initiatives.

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Appendix 1

Species list of oak savanna species of the Cowichan Valley, British Columbia. Data compiled are plot averages from 177 1 m² plots measured in the seven major savanna remnants of the valley (Cowichan Reserve, Mt. Tzuhalem, Maple Mountain (east and southwest slopes), Mount Richards (east and west peaks), and Cowichan River (Skutz Falls). Note: the Cowichan River site was not used in the analysis for chapter five. Plot frequency = $n/177 \times 100$). Cover = degree of tree canopy cover over each plot; ranging from 0 (full canopy cover) to 1 (no canopy) measured using a spherical densiometer. Soil depth = the average taken from four points steel probe) within each plot. Maximum vegetation height = the height of the tallest plant in each plot. Appendix compiled by Joe Boucher.

Species	Origin			Plot Freq.	Aspect	Elev. (ft)	Cover	Slope	Soil depth (cm)	Max. veg. ht. (cm)
<i>Acer macrophyllum</i> Pursh	Native	perennial	tree/shrub	3.26	157.0	332.33	0.455	20	11.85	67.67
<i>Achillea millefolium</i> L.	Native	perennial	forb	30.43	185.4	703.91	0.56	13.94	13.43	42.67
<i>Aira caryophylla</i> L.	Non-native	annual	grass	34.78	178.4	674.36	0.72	16.15	9.38	40.08
<i>Aira praecox</i> L.	Non-native	annual	grass	21.74	181.6	849.78	0.84	17.05	6.29	31.44
<i>Allium acuminatum</i> Hook.	Native	perennial	forb	4.89	188.8	625.44	0.74	20	9.92	55.33
<i>Allium cernuum</i> Roth var. <i>cernuum</i>	Native	perennial	forb	4.35	196.5	664.50	0.31	10.75	12.25	40.25
<i>Alopecurus pratensis</i> L.	Non-native	perennial	grass	3.26	255.3	114.67	0.5	5	56.75	78.5
<i>Anthoxanthum odoratum</i> L.	Non-native	perennial	grass	36.96	215.2	431.25	0.57	11.58	19.93	52.83
<i>Arctostaphylos uva-ursi</i>	Native	perennial	tree/shrub	2.72	210.8	505.20	0.428	10.6	14.3	52
<i>Aster curtus</i> Cronq.	Native	perennial	forb	0.54	234.0	926.00	0.43	10	25.35	42
<i>Bromus carinatus</i> Hook. &	Native	perennial	grass	11.96	216.9	345.00	0.43	10.86	27.25	60.27

Arn.

<i>Bromus hordeaceus</i> L. ssp. <i>thominii</i>	Non-native	annual	grass	39.67	180.7	648.58	0.73	15.06	11.89	43.72
<i>Bromus sitchensis</i> Trin	Native	perennial	grass	0.54	233.0	456.00	0.81	18	24	46
<i>Bromus sterilis</i> L.	Non-native	annual	grass	13.04	173.9	551.25	0.61	10.5	14.83	44.5
<i>Camassia leichtlinii</i> (Baker) S. Wats. ssp. <i>suksdorfi</i>	Native	perennial	forb	6.52	243.0	204.75	0.365	5.58	48.37	72.17
<i>Camassia quamash</i> (Pursh) Greene	Native	perennial	forb	50.00	198.3	554.46	0.59	12.63	18.23	47.69
<i>Cardamine oligosperma</i> Nutt. var. <i>oligosperma</i>	Native	annual	forb	5.98	179.6	637.27	0.48	15	18.45	52.18
<i>Carex inops</i> Bailey	Native	perennial	grass	38.59	205.2	702.27	0.65	12.19	19.09	41.44
<i>Cerastium arvense</i> L.	Native	perennial	forb	34.24	189.7	689.62	0.64	14.85	12.78	44.05
<i>Cerastium fontanum</i> Baumg. ssp. <i>trivale</i>	Non-native	perennial	forb	1.09	204.5	610.00	0.72	10.5	22.85	43
<i>Cerastium glomeratum</i> Thuill.	Non-native	annual	forb	11.96	173.5	441.18	0.52	13.63	18.27	60.04
<i>Cirsium arvense</i> (L.) Scop. var. <i>horridum</i>	Non-native	perennial	forb	1.63	233.7	151.33	0.47	11.666	47.13	81.67
<i>Cirsium vulgare</i> (Savi) Tenore	Non-native	perennial	forb	1.09	249.0	120.50	0.39	4.5	27.78	70
<i>Clarkia amoena</i> (Lehm.) Nels. & Macbr.	Native	annual	forb	5.43	187.9	857.80	0.90	24.1	7.18	31.7
<i>Claytonia perfoliata</i> Donn ex Willd.	Native	annual	forb	8.70	199.1	490.88	0.46	11.875	21.5	44.4
<i>Claytonia sibirica</i> L.	Native	annual	forb	0.54	270.0	720.00	0.33	3	7.95	43
<i>Clinopodium douglasii</i>	Native	perennial	forb	5.43	178.1	690.50	0.339	8.7	21.89	39.2

(Benth.) Kuntze

<i>Collinsia parviflora</i> Dougl. ex Lindl.	Native	annual	forb	9.78	168.0	710.06	0.61	16.44	9.22	35.22
<i>Collomia heterophylla</i> Hook.	Native	annual	forb	0.54	204.0	512.00	0.53	18	20.5	36
<i>Crataegus monogyna</i> Jacq.	Non-native	perennial	tree/shrub	5.98	254.8	108.36	0.35	5.09	47.45	75.81
<i>Crepis atrabarba</i> (ragweed)	Non-native	perennial	forb	0.54	72.0	351.0	0.43	14	2.33	38
<i>Cynosurus echinatus</i> L.	Non-native	annual	grass	0.54	100.0	893.0	0.42	19	20.28	63
<i>Cystopteris fragilis</i> (L.) Bernh.	Native	perennial	fern	0.54	161.0	971.0	0.26	32	7.95	30
<i>Cytisus scoparius</i> (L.) Link	Non-native	perennial	tree/shrub	41.30	207.9	568.97	0.61	13.	15.21	46.17
<i>Dactylis glomerata</i> L.	Non-native	perennial	grass	21.74	218.4	283.28	0.46	9.425	27.575	68.75
<i>Danthonia californica</i> Boland.	Native	perennial	grass	30.98	168.9	769.07	0.67	14.7	14.75	42.89
<i>Daphne laureola</i> L.	Non-native	perennial	tree/shrub	0.54	223.0	106.00	0.26	3	33	80
<i>Delphinium menziesii</i> DC. ssp. <i>menziesii</i>	Native	perennial	forb	8.15	223.7	582.73	0.633	15.26	12.835	49.86
<i>Dodecatheon hendersonii</i> A. Gray spp. <i>hendersonii</i>	Native	perennial	forb	27.72	201.1	752.45	0.565	11	18.38	37.78
<i>Elymus glaucus</i> Buckl.	Native	perennial	grass	21.20	182.2	768.15	0.54	15.58	15.77	50.76
<i>Eriophyllum lanatum</i> (Pursh) Forbes var. <i>lanatum</i>	Native	perennial	forb	7.07	186.7	739.23	0.73	20	13.24	49.69
<i>Erythronium oregonum</i> Appleg. ssp. <i>oregonum</i>	Native	perennial	forb	13.04	235.3	613.29	0.40	8.375	23.77	47.95
<i>Euphrasia nemorosa</i> (Pers.) Wallr.	Non-native	annual	forb	1.63	194.0	847.33	0.94	20	5.957	38.66
<i>Festuca idahoensis</i> Elmer spp. <i>roemeri</i>	Native	perennial	grass	34.24	188.0	729.25	0.681	16	11.58	41.80

<i>Festuca rubra</i> L.	Native	perennial	grass	0.54	220.0	450.00	0.48	29	14.3	65
<i>Fragaria vesca</i>	Native	perennial	forb	2.72	218.6	502.60	0.34	11	13.92	55.2
<i>Fritillaria affinis</i> (Schult.)	Native	perennial	forb	4.89	218.3	597.22	0.40	9.22	22.43	55.44
Sealy var. <i>affinis</i>										
<i>Galium aparine</i> L.	Non-native	annual	forb	56.52	196.3	575.61	0.52	12.19	20.91	51.97
<i>Geranium bicknellii</i> Britt.	Non-native	annual	forb	10.87	210.5	328.10	0.62	16.65	21.0	61.65
	(?)									
<i>Geranium molle</i> L.	Non-native	annual	forb	25.00	200.8	467.22	0.58	13.23	16.67	53.09
<i>Holcus lanatus</i> L.	Non-native	perennial	grass	2.17	157.8	93.50	0.33	19.5	13.875	77.5
<i>Hypochaeris radicata</i> L.	Non-native	perennial	forb	32.07	180.1	670.32	0.69	15.61	10.72	45.62
<i>Koeleria macrantha</i> (Ledeb.)	Native	perennial	grass	3.26	199.8	574.67	0.78	24	14.65	48.16
J.A. Schult.										
<i>Lactuca muralis</i> (L.) Fresn.	Non-native	annual	forb	1.09	182.5	218.50	0.20	7	41.5	49.5
<i>Lapsana communis</i> L.	Non-native	annual	forb	0.54	269.0	102.00	0.7	2	54	96
<i>Lathyrus nevadensis</i> S. Wats.	Native	perennial	forb	5.98	219.5	726.55	0.33	8.09	22.07	45.09
var. <i>pilosellus</i>										
<i>Lathyrus sphaericus</i> Retz.	Non-native	annual	forb	17.39	234.3	368.75	0.50	7.40	29.45	50.85
(default)										
<i>Leucanthemum vulgare</i> L.	Non-native	perennial	forb	0.54	174.0	1060.00	1	10	5.3	28
<i>Lithophragma parviflorum</i>	Native	perennial	forb	2.72	226.6	621.60	0.44	11.8	21.305	38.6
var. <i>parviflorum</i>										
<i>Lomatium</i> sp.	Native	perennial	forb	0.54	93.0	342.00	0.56	14	7.5	89
<i>Lomatium utriculatum</i> (Nutt.	Native	perennial	forb	45.65	202.4	719.57	0.62	13.39	14.69	39.96
ex T. & G.) Coult. & Rose										
<i>Lonicera ciliosa</i>	Native	perennial	forb	0.54	275.0	515.00	0.31	18	5.8	30

<i>Lotus micranthus</i> Benth.	Native	annual	forb	44.57	188.0	752.33	0.64	13.70	13.54	37.11
<i>Lupinus polycarpus</i> Greene	Native	annual	forb	4.89	204.7	828.56	0.87	17	5.522	24.89
<i>Luzula multiflora</i> ssp. <i>multiflora</i>	Native	perennial	grass	19.02	201.5	640.80	0.53086	12.59	14.57	43.77
<i>Mahonia aquifolium</i> (Pursh) Nutt.	Native	perennial	tree/shrub	15.76	183.0	690.45	0.47345	15.96	14.21	45.65
<i>Melica subulata</i> (Griseb.) Scribn.	Native	perennial	grass	12.50	223.8	680.61	0.31304	9.43	25.78	45.91
<i>Mimulus guttatus</i> DC.	Native	annual	forb	1.63	166.0	193.00	0.79	11	8.83	69.67
<i>Moehringia macrophylla</i> (Hook.) Fenzl.	Native	perennial	forb	1.63	199.3	1006.67	0.27	3.33	30.85	39.33
<i>Montia linearis</i> (Dougl. ex Hook.) Greene	Native	annual	forb	1.09	182.0	539.50	0.565	17	17.9	35
<i>Montia</i> sp.	Native	annual	forb	0.54	264.0	121.00	0.47	6	24.07	55
<i>Myosotis discolor</i> Pers.	Non-native	annual	forb	15.22	172.6	542.32	0.59214	14.39	18.05	49.42
<i>Myosotis</i> sp. (exotic)	Non-native	annual	forb	0.54	180.0	995.00	1	14	6.9	45
<i>Nemophila parviflora</i> Dougl. ex Benth. var. <i>parviflora</i>	Native	annual	forb	9.78	187.6	506.89	0.39111	14.05	23.50	50.16
<i>Orobanche uniflora</i>	Native	annual	forb	1.63	214.3	483.67	0.43	11.67	15.13	51.67
<i>Osmorhiza berteroi</i> DC.	Native	perennial	forb	1.63	265.7	115.67	0.32	6	36.78	75.33
<i>Panicum milliaceum</i> L.	Non-native	annual	grass	1.63	161.0	959.33	0.93	18	6.27	31.3
<i>Pentagramma triangularis</i> (Kaulf.) Yatsk., Windh. & Wollen. ssp. <i>triangularis</i>	Native	perennial	fern	2.17	170.8	696.25	0.75	19.75	16.25	56
<i>Perideridia gairdneri</i> (H. &	Native	perennial	forb	5.43	205.9	684.90	0.49	10.3	25.93	51.2

A.) Mathias

<i>Phlox gracilis</i>	Native	annual	forb	10.87	208.4	667.20	0.75	13.1	9.75	33.1
<i>Piperia elegans</i> (Lindl.) Rydb.	Native	perennial	forb	3.80	201.3	745.71	0.36	7.42	33.25	45.71
<i>Plantago lanceolata</i> L.	Non-native	perennial	forb	5.98	173.3	171.82	0.75	13.81	12.38	71.18
<i>Plectritis congesta</i> (Lindl.)	Native	annual	forb	13.04	179.5	487.29	0.56458	14.16	10.09	45.35

DC.

<i>Plectritis macrocera</i> T. & G.	Native	annual	forb	0.54	161.0	971.00	0.26	32	7.95	30
<i>Poa pratensis</i> L. spp. <i>pratensis</i>	Non-native	perennial	grass	23.91	225.8	321.95	0.48	8.568	31.87	62.43
<i>Polypodium glycyrrhiza</i>	Native	perennial	fern	0.54	214.0	509.00	0.25	1	15.8	81
<i>Polystichum munitum</i>	Native	perennial	fern	0.54	172.0	931.00	0.34	23	12.07	65
<i>Psuedotsuga menziesii</i> (Mirb.)	Non-native	perennial	tree/shrub	8.15	173.5	827.87	0.57	13.06	17.73	34

Franco

<i>Quercus garryana</i> Dougl.	Native	perennial	tree/shrub	4.35	202.5	533.50	0.35	10.375	19.05	54.25
<i>Ranunculus occidentalis</i> Nutt.	Native	perennial	forb	24.46	213.3	687.09	0.54	11.13	19.22	42.26

var. *occidentalis*

<i>Rosa nutkana</i> Presl	Native	perennial	tree/shrub	2.17	236.3	971.50	0.26	5.75	29.02	33
<i>Rubus ursinus</i> Cham. &	Native	perennial	tree/shrub	2.17	157.8	93.50	0.5	19.5	13.87	77.5

Schlecht. ssp. *macropetalus*

<i>Rumex acetosella</i> L.	Non-native	perennial	forb	18.48	182.2	800.91	0.72	14.58	8.18	32.17
<i>Sanicula crassicaulis</i> Poepp.	Native	perennial	forb	23.37	210.4	554.47	0.39	9.744	28.26	49.60

ex DC. var. *crassicaulis*

(default)

<i>Sanicula graveolens</i> Poepp.	Native	perennial	forb	3.80	205.1	933.71	0.51	13.28	19.875	38.71
<i>Saxifraga integrifolia</i> Hook.	Native	perennial	forb	0.54	284.0	183.00	0.77	6	9.5	28
<i>Sedum spathulifolium</i> Hook.	Native	perennial	forb	0.54	88.0	341.00	0.25	9	13	34

<i>Selaginella wallacei</i> Hieron.	Native	perennial	spike-moss	13.04	172.6	715.13	0.74	20.91	7.03	38.02
<i>Sonchus asper</i> (L.) Hill	Non-native	annual	forb	2.17	207.0	509.25	0.87	21	7.825	43
<i>Stellaria media</i> (L.) Vill.	Non-native	annual	forb	2.17	144.0	602.25	0.255	18.5	16.4375	64.25
<i>Stipa lemmonii</i>	Native	perennial	grass	10.33	170.9	826.79	0.86	16.89	8.57	40.63
<i>Symphoricarpos albus</i> (L.)	Native	perennial	tree/shrub	9.78	230.6	612.39	0.38	8.222	25.45	46.61
Blake										
<i>Taraxacum officinale</i> G.H.	Non-native	perennial	forb	3.26	224.0	302.00	0.43	15.33	25.03	66.16
Weber ex Wiggers										
<i>Trifolium dubium</i> Sibth.	Non-native	annual	forb	8.70	214.8	454.19	0.64	15.56	12.75	47.75
<i>Trifolium microdon</i> H. & A.	Non-native	annual	forb	11.96	180.7	805.36	0.80	15.86	10.36	40.5
<i>Trifolium oliganthum</i> Steud.	Native	annual	forb	0.54	240.0	493.00	0.45	10	10.4	58
<i>Trifolium repens</i>	Non-native	perennial	forb	0.54	154.0	967.00	0.52	29	22.1	24
<i>Trifolium variegatum</i> Nutt.	Native	annual	forb	4.35	194.1	699.00	0.65	17.5	17.75	46.75
<i>Trifolium willdenowii</i> Steud.	Native	annual	forb	11.41	176.0	896.43	0.72	15	8.1	34.14
<i>Triteleia hycinthina</i> (Lindl.)	Native	perennial	forb	45.11	192.4	597.12	0.68	12.07	17.16	46.65
Greene										
<i>Valerianella locusta</i> (L.) Latt.	Non-native	annual	forb	14.67	238.8	163.30	0.54	6.77	28.47	62.40
<i>Veronica arvensis</i> L. (default)	Non-native	annual	forb	28.26	195.9	566.06	0.68	15.826	12.46	49.65
<i>Veronica officinalis</i> L.	Non-native	perennial	forb	0.54	88.0	341.00	0.25	9	13	34
<i>Vicia americana</i> Muhl. ex Willd.	Native	perennial	forb	3.26	199.5	565.50	0.31	9.6666	22.57	58.33
<i>Vicia hirsuta</i> (L.) S.F. Gray	Non-native	annual	forb	15.22	224.9	261.64	0.46	8.5714	34.09	59.32
<i>Vicia sativa</i> L.	Non-native	perennial	forb	34.78	220.6	316.97	0.51	10.203	26.96	58.2
<i>Viola praemorsa</i> Dougl ex	Native	perennial	forb	2.17	241.8	115.75	0.28	3.5	36.45	63.75

Lindl. ssp. *praemorsa*

<i>Vulpia bromoides</i> (L.) S.F.	Non-native	annual	grass	23.91	187.2	660.91	0.65	15.818	10.20	36.54
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Gray

<i>Zigadenus venenosus</i> S. Wats.	Native	perennial	forb	20.11	184.2	754.73	0.64	14.07	15.85	42.24
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Appendix 2

Historical descriptions of the *Quercus garryana* ecosystem 1771-1951. These quotes serve as the basis for Chapter Three. They were obtained from the Koerner Library, the Special Collections Library (University of British Columbia), the Duncan Archives, the Surveyor-General Office (Victoria) and the British Columbia Provincial Archives (Victoria).

General Descriptions

John McLoughlin – HBC Fort Vancouver (1831) p286-287. *"In a former part of this letter, I mentioned that Captain McNeill, when cruising in the Beaver had examined the east and southern coast of VI in search of an eligible spot for the erection of a new establishment...(Much of the eastern side of the island to the north has a small extent) of level ground (that is) rocky and barren, thickly wooded with pines (douglas-fir), and without any particular advantage or situation. On reaching the south end of the island, a decided improvement was observed in the appearance of the country. Three good harbours of easy access west of Pt. Gonzalo...The land around these harbours is covered with wood to the extent of a half a mile, interiorly, where the forest is replaced by a more open and beautifully diversefied [sic] country presenting a succession of plains with groves of oaks and pine trees for a distance of 15 to 20 miles...The plains are said to be fertile and covered with the most luxuriant vegetation; but judging from a sample of soil brought here, I think rather light and certainly not the best quality, admitting even this disadvantage, I am persuaded that no part of this sterile and rock bound coast will be found better adapted for the site of the proposed depot or to combine to a higher degree, the desired requisites of a secure harbour, of good pasture, and to a certain extent, of improvable tillage land."*

Vancouver Island (Mayne p393-396..) *"On Vancouver Island, although the quantity of agricultural land is very small in comparison with that in BC, there are many lovely spots for farms...To name all the clear spots on the island would take too much space...I will therefore merely speak of the larger tracts which have been examined and of the system by these, or any portions of them, may be occupied."*

History of Founding of Fort Victoria (In John McLoughlin papers Volume 2 (1838-44) *"(Governor Simpson further angered McLoughlin by proposing) building of a new post at the southern (instead of northern) end of VI, and this he intended by degrees should supercede Fort Vancouver as the HBC headquarters for the entire region. (This was to) see the principal depot moved to some point on the Juan De Fuca Strait, in order that should would not have to cross the dangerous Columbia River bar. (Simpson was concerned over the border uncertainty with the US, thought the VI fort would be of strategic and political importance, and would lay claim of the entire Island for the British)."*

Descriptions of vegetation and soil properties

Flora of the Colonies (MacFie p304): Grasses/Herbs: "Among the grasses may be enumerated white pea, wild bean, ground nut, reed meadow grass, white clover, bent spear grass, wild oat, wild timothy, sweet grass, etc. The fern, so prolific and annoying to the farmer, often reaches the height of from 6-8 feet...[Species List]:...*Glyceria aquatica*, *Poa pratensis*?, *Festuca pratensis*, *Phleum pratense*, *Stipa avenacea*, *Juncus*,..."

General Description of soil/vegetation- July 1858 Victoria (Hazlitt p214-7):"...In some places the spontaneous vegetation testifies to the richness of the soil, such as wild pease or vetches, and wild clover, which I have seen up to my horse's belly, and the most luxuriant growth of underwood, brambles, fern, etc...I visited several farms...no clover, the natural grass [native grass??] supplying sufficient food for the cattle and sheep."

Soil Description (Douglas July 12,1842)"Both kinds (i.e., soils), however, produce abundance of grass and several varieties of red clover grow on the rich moist bottoms. In two places particularly we saw several acres of clover growing with a luxuriance and compactness more resembling the close sward of a well-managed lea than the produce of an uncultivated waste. Being pretty well assured of the capabilities of the soil...we ought to be able to grow any type of grain raised in England. On this point however we cannot speak confidently until we have tried the experiment and tested the climate..."

Landscape (September 1848) – Report in the Times" A few days back a few of us went up Cedar Hill, the highest eminence near...Below us we saw little clear ground, most of it being covered with fir, yew, cedar, and laurel. The oaks are upon the open surfaces. Wherever these grow it was clear from underwood, and we had grass and FERN to gallop along."

Fire (September 1848) – Report in the Times (1849)"Miles of the ground were burnt and smoking and miles were still burning. The Indians burn the country in order to find more easily the roots that they eat. The fire runs along the grass at a great pace and it is the custom here if you are caught to gallop right through it; the grass being short, the flames being little and you are through in a second. All the horses and cattle feeding know it well and make straight for the fire immediately."

Grass / General Description of Vancouver Island (1848): Fitzgerald, J.E. "The general character of VI is mountainous but is extremely varied...In the south there are extensive plains of rich alluvial soil. A gentlemen who had been in the HBC service, once informed the author that he had walked over a plain of some miles in extent, on the south side of the island, which had not a blade of grass growing, owing to it having lately been burnt by the Indians, and that a few months afterwards, on going over the same spot, he found the grass up to his middle in height. Another gentleman informed me that in the NE of the island, after penetrating through an almost impassable forest, he arrived at a beautiful plain, of several miles in extent, covered with high grass, and interspersed with oaks and other trees, having much the appearance of a nobleman's park in this country..."

Resources of these Colonies (Mayne) Fabaceae: Representative of their order are extensively found. The Blue Lupine, Purple Clover, and several varieties of Vetch are

everywhere growing wild as large and strong as any I have seen cultivated in other places. Gramineae: Varieties of nearly every grass which grows in Europe, and many which do not, are found in these colonies: the Wild Oat is as vigorous a plant here as one cultivated at home. I have seen Timothy Grass grown on the Island 8 ft in height."

Cowichan Valley 1862 (Bishop Hills with Captain Verney, in Williams 1977) "Some land I passed over today (in the Cowichan Valley)...rich black soil, grasses 3-4 feet high, fern six feet (tall, and) much open land..."

Species List, Cowichan Valley (MacFie 1865 p48): "Every species of plant grows luxuriantly in Cowichan. In the meadow-lands are the following: white pea, wild bean, wild timothy, wild sun-flower (said to be excellent for fattening poultry) [Balsamorhiza deltoidea], wild oats [Danthonia californica?], wild lily [Lilium columbiana], wild angelica, wild lettuce, brown-leaved rush, ground nut, white clover, reed meadow-grass, bent spear-grass [Bromus spp.], sweet grass, cowslip, crowsfoot, winter cress, partridge berry, and mangold." (p47)...."Besides the staple woods of oak and pine, we have..."

General Description - Victoria (MacFie 1865): "In March, winter gives signs of taking departure, and the warm breath of spring begins to cover the trees with tinted buds and the fields with verdure. Then become visible the star-eyed and delicately blue Collinsia, the chaste Erythronium, the scarlet-blossomed lilies [Lilium columbiana], and the graceful Trillium; the spring grass and young fern show promises of returning life; the unfolding oak leaf and budding wild fruits proclaim that winter is gone...In May, the profusion and fragrance of the wild roses, the wide-spread variegated hues of buttercups and daisies...fill the mind with enchantment unequaled out of Paradise....By the end of June vegetation reaches its annual maturity. Its growth in that and the proceeding month is particularly rapid. Showers are rare during the summer...The protracted dryness of summer often imparts to the soil a parched appearance but it is rather the pasture lands rather than the crops that suffer this influence...The refreshing showers of autumn, however, lasting to the middle of November, clothe the grass a second time with verdure, which it retains until after Christmas."

General Description of Victoria (Verney): "lovely wildflowers of every hue...I cannot believe that any part of the world can show a greater variety and number of wildflowers like this" (May 27, 1862 p43-44)...day after day the cloudless sun pours its rays upon this favored island...each succeeding day finds the forest more green and shows more wildflowers springing into blossom under feet..." (March 30, 1863, p 128)...Almost every day brings out some new wildflower that I have not seen before while some of the earliest ones are already going off" (April 12, 1863 p 130).The wildflowers of every hue are innumerable" (May 9 1863 p137).The spring may be said fairly to have set in now; everything is budding...I have seen one or two specimens of a small blue flower, like a forget-me-not, the young grass too has begun to shoot" (March 27, 1865, p252).

Pocket Grasslands (Verney May 25, 1862 p63)"The forest is in most places pretty thick, but here and there it opens into park like enclosures, and large masses of rock-outcrop bare of all but moss, a little soft turf in the hollows, and the most exquisite wildflowers

among which one recognizes the great abundance calcilaria, the violet, the sweet-briar, and the strawberry..."

Robert Brown (1864): "(At the Saatlam camp site just upriver from Mt. Prevost)...we could have added (to our dinner) trout from the stream, gammas, and wild onions from the woods"

Early Flowers - Forget-Me-Not (Verney March 4 1864, p193): "...the first wildflower, the little forget-me-not, appeared on the 26th of April."

Flora of Vancouver Island - Camas (Hazlitt p 179): "The flora of VI is poor with no new varieties of plants discovered in the country. The open prairie ground, as well as the patches of soil which are met with the clefts of the hills, are principally covered with the camas, a small esculent root about the size of an onion, with a light blue flower, the *Camassia esculenta* of botanists. The camas constitutes a favorite article of food with the savages, and they lay up large quantities of it for winter consumption, burying it in pits in the ground in the same way as they keep potatoes. This root has strong astringent qualities; the savages prepare it for food by digging large holes in the ground, throwing in hot stones, on the top of the stones placing quantities of camas, and covering the whole up with sticks and mats until the root is sufficiently baked. The camas-digging is a great season of reunion for the women of the various tribes, and answers with them to our haymaking or harvest home. Several species of *Campanula* and *Lupinus* are found in the woods and low grounds...Potatoes and dried salmon form the staple food of all natives who can procure them, the camas being by them considered more as a delicacy."

General Description of soil/vegetation- July 1858 Victoria (Hazlitt p214-7): "The character of the soil is favorable to agriculture. It is composed of black vegetable mould of a foot to two feet in depth overlaying a hard yellow clay...In some places the spontaneous vegetation testifies to the richness of the soil, such as wild pease or vetches, and wild clover, which I have seen up to my horse's belly, and the most luxuriant growth of underwood, brambles, fern, etc...I visited several farms...no clover, the natural grass [native grass??] supplying sufficient food for the cattle and sheep...I am told that in September rains fall which renew the face of nature so suddenly that it assumes the garb of spring, with flowers even coming out."

General Description (April 16, 1851) p177 (Fort Vict Letters) "The spring has been remarkably early, the crops look well and the country is covered with verdure and early flowers."

San Juan Island (Mayne traveling in 1858) p39-40. "(On) San Juan...there is more land available for agriculture than of any other of the group...and the HBC established a sheep farm on it some years ago...(The sheep farm) is situated on a beautiful prairie at the SE end of the island...I have never seen wildflowers elsewhere grow with the beauty and luxuriance they possess here...At one time I believe the company had 3000 sheep here."

"Resources of these Colonies" (Mayne) *"There are several kinds of bulbous roots, the commonest is the camass (Scilla esculenta), of which the Indians eat a great deal; it has a slight onion flavour, but is sweet. Rosaceae: Species of this order are very numerous also; in the spring every plain is covered with the Wild Rose and Sweet Brier...Liliaceae: The Camassia esculenta, the Camass of the Indians, is very common: the bulbs, being placed in shallow pits, are covered with a thick layer of dried grass damped with water, a thin layer of earth is placed above it, and a fire is made in the pit. A gradual process of streaming goes on, perhaps for several days, the bulbs when removed are found mellowed, their colour changed to a light brown, and they contain a large portion of saccharine matter. They are then dried and stored for winter food. I pass over the Ferns, Mosses, Lichens, the Fungi, and Seaweeds, with a brief remark that they abound everywhere, the first in quantities somewhat troublesome to the agriculturist."*

Bracken Fern (MacFie 1865): *"(In the Cowichan Valley) fern reaches an extraordinary height of 6 to 8 feet"*

Ferns (MacFie p 196): *"Fern-roots, which teem on the island, afford staple food for the hogs"*

Fern, Camas, and Wappatoo (Kane 148): *"The only other vegetable besides camas and wappatoos that the Indians use, are the roots of fern, which here grow to a very large size"*

Cowichan River Valley River Trip (Brown p51): *"(We crossed Drinkwater's Ranch, the last tangible trace of civilization)...After losing the trail (following the river),...we emerged in an open prairie thickly covered with fern and dotted with clumps of trees...A creek flows through the middle of it..."*

Comox/Courtney Prairies - August 1864 (Brown p111-5): *"Comox...of course as everybody knows is a great agricultural region...We walked on, still over miles of beautiful prairie land visiting several settlers...We traveled for about 2 miles in a westerly direction through open prairies, some of which were preempted but as yet had no houses...Most of the prairies were covered with deep fern (Pteris aquilina) and in other places blackberries..."*

General Description (Bowsfield, HBC Letters 1979) *"In the environs of Camosun the vegetation was the most luxuriant that Douglas had seen anywhere on the continent. The wild clover growing knee-deep and the native grasses and ferns rising to shoulder height provided evidence of a rich productive soil"*

Cowichan Valley 1862 (Bishop Hills with Captain Verney, in Williams 1977 p3) *"Some land I passed over today (in the Cowichan Valley)...rich black soil, grasses 3-4 feet high, fern six feet (tall, and) much open land..."*

Cowichan in the 1860's - Evans 1933 (in Pioneer Women of the Cowichan Valley p23) *"With the advent of the white settlers in the Cowichan district was nearly all heavy"*

timber. There were a few small fern patches which we called prairies but the early settlers did not locate in any of them. Theirs was the tall timber, to hew out clearings to build homes In 1862, the first settlers were guided) up the narrow Indian trail, through the forest and tall bracken”.

Ferns in Comox Prairie (Duncan 1930s, as reported in Mackie 2000) “There was no natural grass in Comox Valley, and the unwooded part was covered with a dense growth of fern, and a tangle of wild rose and berry bushes. The fern grew to a height of five feet, and its roots were a mass of underground ropes, much heavier than those of hops or nettles, making ploughing very difficult, though, as they kept the soil loose and porous, enormous crops of splendid potatoes were raised in early days, and even now it is claimed that Vancouver Island can beat the world in that time”

Fern in the Comox Valley (James Richardson 1872 Geological Survey of Canada.) “The surface of this district, with the exception of single trees and clumps, chiefly of oaks and strips of alder in the bottoms, may be some 12 square miles, the scenery being picturesque and parklike. Its margin is very irregular in shape and it is surrounded by a growth of heavy timber, among the trees of which are the Douglas Spruce, often obtaining two feet (sic) in diameter and 200 hundred feet in height, and in one half of which it is free from branches, and the cedar often equally large. The open country, in its natural state, is mostly covered with a growth of ferns, which sometimes attain a height of ten feet, with stems $\frac{3}{4}$ of an inch in diameter and roots descending to a depth of 3 feet. These roots the native Indians prepare in some peculiar way for winter food, and excavate deep trenches to obtain them. The farmers are under the necessity of grubbing up fern roots before the ground is ready for use, and are often voluntarily assisted by their pigs in this operation, these animals, it is said, relishing the fern root as food.”

Vancouver Island Descriptions (Mayne p393-396.) The Cowichan Valley...(p395-396) was surveyed in 1860, and in the surveyors report will be found the following remarks: “I am firmly persuaded...that (farming returns are as good as any part of America)... The ferns attain a height of six or eight feet, and the grasses all have a vigorous growth. ...

General Description - Victoria (MacFie 1865): “In May,...the profusion and fragrance of the wild roses, the wide-spread variegated hues of buttercups and daisies...fill the mind with enchantment unequalled out of Paradise...”

Flora of the Colonies (MacFie p304): “Oak is abundant in the southern part of VI, though very scarce in BC. The astringent properties of the bark of this tree render it important for tanning purposes.”

Oak -Victoria (Hazlitt p185):“Where ever there is prairie land, two kinds of oak, the *Quercus suber clavigata*, and another similar species somewhat darker in the bark and harder in the quality of the wood, are found; the quality of the wood of both these kinds of oak is hard and tough, and they are excellently adapted to form the knees and timber for vessels; the trees however are small and scrubby, and hide their abashed heads before the towering Coniferae by which they are surrounded .”

Oak Trees – Nisqually vs. Victoria p121 (McLoughlin's Letters from Fort Vancouver)

"The quality of oak at Nisqually is so bad, that I think it is impossible to get the quality of sound timber required, but we may perhaps succeed better...on the south end of VI where I am told the oak is of better quality."

"Resources of these Colonies" (Mayne) Corylaceae: *The Oak is abundant in the southern part of VI; there is none in BC, I am told by Mr. Anderson, of HBC, except a few small specimens on the eastern borders of the Rapids above Fort Yale.*

Soils -Victoria (MacFie 1865 p182-83): *"The character of the soil differs in different districts...On the higher levels is of a poor gravelly description, with a thin layer of vegetable mould, and covered by gigantic timber...these places being saved from absolute sterility by decayed foliage and grasses that have for ages been shed to cover their nakedness. Rich sandy loams are extensively found in the farming sections,...in valleys, ancient lake or river bottoms, and slopes of various dimensions...(It has a) black or dark brown colour (and) is excellently adapted for producing vegetables and every species of cereal.*

Prairie - Victoria (MacFie 1865 p183): *"In a district about 12 miles from Victoria I have seen a single Prairie containing no less than 400 acres of clear land where the alluvial soil, consisting mainly of black loam, was at least a couple of feet thick."*

Oak -Victoria (Hazlitt p185): *"the (oak) trees however are small and scrubby, and hide their abashed heads before the towering Coniferae by which they are surrounded."*
[pocket prairie]

Soil Description (Douglas July 12,1842) *"I observed generally speaking but two marked varieties of soil on these prairies, that of the best land is a dark vegetable mould varying from 9 to 14 inches in depth overlaying a substrate of grayish clayey loam which produces the [greatest?] growth of native plants that I have seen in America. The other variety is of inferior value, and to judge from the less vigorous appearance of the vegetation upon it, naturally more unproductive. Both kinds, however, produce abundance of grass and several varieties of red clover grow on the rich moist bottoms. In two places particularly we saw several acres of clover growing with a luxuriance and compactness more resembling the close sward of a well-managed lea than the produce of an uncultivated waste. Being pretty well assured of the capabilities of the soil...we ought to be able to grow any type of grain raised in England. On this point however we cannot speak confidently until we have tried the experiment and tested the climate..." [i.e. no introductions yet].*

"As the site of a British colony, VI did not appear to have all the splendid qualities Douglas had first discovered while searching seven years earlier for a seaport depot. As the first colonist was later to remark, VI was "little better than a mass of rock, with a few little garden patches as it were, interspersed at intervals along the sea coast". The soil in the immediate vicinity of Fort Victoria was a deep loam, capable of producing excellent wheat, but the surrounding plain was traversed in all directions with beds of

trap and granite (letter from Eden Colville to Pelly, Oct15 1849). Close to Fort Victoria there was insufficient prairie land for the location of the Puget's Sound Agricultural Company's farms. These farms would have to be established near Esquimalt. In the areas outside the reserves of the HBC and AgCo. Douglas now estimated that there was room for only eighty or 100 families since the ridges and high hills rendered unproductive fully one-third of the land between Fort Victoria and Sooke, 25 miles distant Douglas to Barclay Sept13, 1849)."

Distribution and range

Victoria, Saanich, Esquimalt and surrounding areas

Prairie - Victoria (MacFie 1865 p183): *"In a district about 12 miles from Victoria I have seen a single Prairie containing no less than 400 acres of clear land where the alluvial soil, consisting mainly of black loam, was at least a couple of feet thick."*

Prairie - Victoria and Cowichan (MacFie 1865 p184-85): *"The late Surveyor-General states that in the immediate vicinity of Victoria 100,000 acres of valuable farming land exists. In Sooke...there is a moderate proportion of open land within a 5 square mile area...In the Saanich peninsula, which contains an area of 37 square miles, ...there is a high proportion of clear land, combining calcareous and arenaceous properties, together with humus, these soils resting on a clayey but sometimes a gravelly substratum...In Cowichan 45,000 of 57,658 acres are deemed superior in quality"*

Pocket Grasslands (Verney May 25, 1862 p63) *"The forest is in most places pretty thick, but here and there it opens into park like enclosures, and large masses of rock-outcrop bare of all but moss, a little soft turf in the hollows, and the most exquisite wildflowers among which one recognizes the great abundance calcilaria, the violet, the sweet-briar, and the strawberry..."*

General Description of Victoria (Kane April 1847): *"The soil of this locality is good, and wheat is grown in considerable abundance. The interior of the island has not been explored to any extent except by the Indians, who represent it as badly supplied with water in the summer...The appearance of the interior, when seen from the coast, is rocky and mountainous, evidently volcanic; the trees are large and principally pine and oak."*

Description of Open Prairies - Comox to Metchosin and beyond to the west (Hazlitt p163-172): *"...In the neighborhood of Victoria there are altogether seven square miles of open land...There may be about 350 acres of prairie or open land in the neighborhood of Esquimalt harbour...In Metchosin...we have some 620 acres of fine open land; generally speaking however the soil is poor and sandy, and neither produces grasses nor crops with much luxuriance...On the west side of Pedder Bay [Sooke??] is a fine open prairie extending nearly across to Becher Bay. It contains some 700 acres and is interspersed with oak trees; the soil is rich and well-watered...the land is level and consists of a rich black mould, some three feet in depth..."*

Description of Esquimalt (Hazlitt p206): "The whole scenery is of a highland character. The rocky shores, the pine trees running down to the edge of the 'lake', their dark foliage trembling over the glittering surface which reflected them, the surrounding hills, the death-like silence..."

General Description of soil/vegetation- July 1858 Victoria (Hazlitt p214-7): "So far as I wondered, about 10 miles around Victoria, the landscape is dotted with extensive croppings of rock which interfere with the labours of the husbandman...The scenery of the inland country around Victoria is a mixture of English and Scotch. Where the pine prevails you have the good soil broken into patches by the croppings of rocks, producing ferns, rye grass, and some thistles but very few. This is the Scottish side of the picture. Then you come to the oak region; and here you have clumps, open glades, rows, single trees of umbrageous form, presenting an exact copy of the English park scenery. There is no running water...but the meadows and little prairies that lie ensconced within the woods show no signs of suffering from lack of water...the known locations which are well adapted to farming are, first, the district of Saanich, some 17 miles from Victoria,...second Cowichan district..., and third Sooke district in the sw part of the country. The land in all these districts is said to be pretty free from trees, or rather not to be overrun with forest, and to be of good quality and the scenery beautiful."

Initial account of Victoria: James Douglas (July 12, 1842). In Colonization of Vancouver Island [1849]. "At Camosack there is a pleasant and convenient site for the establishment, within fifty yards of the anchorage, on the border of a large tract of clear land which extends eastward to Point Gonzalo at the south end extremity of the island, and about six miles interiorly, being the most picturesque and decidedly the most valuable part of the island that we had the good fortune to discover. The accompanying ground plan shows pretty correctly the distribution of wood, water, and prairie upon the surface...More than 2/3 of this section consists of prairie land, and may be converted either to purposes of tillage or pasture, for which I have seen no part of the Indian country better adapted; the rest of it, with the exception of the ponds of water, is covered with valuable oak and pine timber."

Grass / General Description of Vancouver Island (1848): Fitzgerald, J.E. "The general character of VI is mountainous but is extremely varied...In the south there are extensive plains of rich alluvial soil. A gentlemen who had been in the HBC service, once informed the author that he had walked over a plain of some miles in extent, on the south side of the island, which had not a blade of grass growing, owing to it having lately been burnt by the Indians, and that a few months afterwards, on going over the same spot, he found the grass up to his middle in height. Another gentleman informed me that in the NE of the island, after penetrating through an almost impassable forest, he arrived at a beautiful plain, of several miles in extent, covered with high grass, and interspersed with oaks and other trees, having much the appearance of a nobleman's park in this country..."

General Description (Bowsfield, HBC Letters 1979) "The southern end if the island had a quite different aspect (letter from Charles Ross to George Simpson 1844); this portion was pictured as 'a very Elysium in point of climate and scenery...' 'The place itself

appears a perfect Eden in the midst of the dreary wilderness of the North west coast and so different in its general aspect from the wooded, rugged regions around, that one might be pardoned for supposing it had dropped from the clouds into its present position (Douglas to James Hargrave)."

Vancouver Island Patchy Good Settlement Areas. (Fort Victoria letters) *"As the site of a British colony, VI did not appear to have all the splendid qualities Douglas had first discovered while searching seven years earlier for a seaport depot. As the first colonist was later to remark, VI was "little better than a mass of rock, with a few little garden patches as it were, interspersed at intervals along the sea coast". The soil in the immediate vicinity of Fort Victoria was a deep loam, capable of producing excellent wheat, but the surrounding plain was traversed in all directions with beds of trap and granite (letter from Eden Colville to Pelly, Oct15 1849). Close to Fort Victoria there was insufficient prairie land for the location of the Puget's Sound Agricultural Company's farms. These farms would have to be established near Esquimalt. In the areas outside the reserves of the HBC and AgCo. Douglas now estimated that there was room for only eighty or 100 families since the ridges and high hills rendered unproductive fully one-third of the land between Fort Victoria and Sooke, 25 miles distant Douglas to Barclay Sept13, 1849)."*

General Description – J Douglas 1848 *"VI is the only part of British Oregon which is, at present, susceptible of colonization – it contains some good cultivatable land, in scattered positions, in the Straits of Juan De Fuca, and a much greater extent might soon be reclaimed from the forest by an industrious population"*

Difficulty of Sustenance 1848 (James Douglas) (Fort Victoria Letters) *"A newly opened farm in this country makes no return the first year, the second year it supplies the labourer with food, and the third year it will yield enough for food and clothing, provided there is a market for grain...I am extremely sorry that I cannot make a very favourable report as to the capabilities of this part of the island for the immediate support of an agricultural population (1849)...The land where level and free of stony ridges is generally good, and when properly tilled will produce heavy crops of grain and vegetables; a fact fully established through the experiments made on the company's farm at this post; and the productiveness of the fields cultivated by the natives who grow large quantities of potatoes; in short the soil is of unexceptionable quality, the climate pleasant, and the country healthy...The great want, which will be felt hereafter is the absence of cultivable lands of sufficient extent, for a large agricultural population."*

Description of Victoria/Esquimalt Area (1850) p116 (FVLetters) *"The rough sketch of the Fur Trade and Puget Sound Lands (is enclosed). I still have no correct survey to send. Captain Grant has been employed since the month of May, in making a survey...From the hilly irregular character of the country it is difficult without actual measurements to form a correct idea of the distance from point to point or the extent in acres..."*

Farming Efforts/Description of Land (1850) *"We are using every exertion to raise grain and other farm produce for the supply of this establishment and the posts dependent upon*

it – but it will take some years and large means to accomplish this object. From the character of the country and the quality of the soil, the labour and expense of bringing land into cultivation on Vancouver Island is very much greater than in the Columbia (i.e., Fort Vancouver, Cowlitz River) where the excessive prairies without a bush or stone to check the progress of the plough present a striking contrast to the rocky ridges stony land and bushy glades of this part of the coast” ... (p141) ... plough and brush plough from the United States, which have had repeated trials, being found equally fragile and incapable of breaking up the tough stony land of Vancouver Island...”

The Shelbourne Valley – Victoria Jupp 1975 “Up until 1915 the wide fields of Shelbourne Valley stretched, unbroken, from Gordon Head Road on the east, to Cedar Hill Road in the west. Some few small-holders had indeed established themselves in that part of the valley south of the Cedar Hill Cross Road but, north of this, things were little changed from the Cedar Plains viewed by John Irvine in the 1860’s. Oak trees spotted grassy fields and in summer the spikes of a myriad of wild lupines added mauve and yellow to the peaceful scene. All else was grass. To the northeast the story was very different. Many of the acres once covered with forest had yielded to the axes of the pioneers...It was the need to provide smooth passage to market for (strawberries from the northeast i.e., area presently hosting UVIC) that...brought reality to the long-dreamed “road through the valley...(The survey was done in 1913; the road (Shelbourne Street) went through in 1916). The unrolling of this fully paved road across unmarked country then seemed “one of the wonders of the world”.

General Description of Victoria/Saanich (Mayne 1859) “The northern portion, for about ten miles, contains some of the best agricultural land in Vancouver Island. The coast here, as everywhere else, is fringed with pine; but in the centre it is clear prairie or oak-land, most of it now under cultivation.”

Vancouver Island Descriptions (Mayne p393-396..) “On Vancouver Island, although the quantity of agricultural land is very small in comparison with that in BC, there are many lovely spots for farms...To name all the clear spots on the island would take too much space...I will therefore merely speak of the larger tracts which have been examined and of the system by these, or any portions of them, may be occupied.

The districts of Soke and Metchosin, at the southeast extreme of the island, contain a large quantity of good land, much of which is still unsettled. Of the capabilities of this tract, I cannot do better than quote the evidence of Colonel Grant...He says that the soils produces abundantly...Near Soke River, there are a few patches of open meadowland near the mouth of the river, on which the Indians grow considerable quantities of potatoes...Near the entrance of the harbour, and running from it across a peninsula to the Straits, is a small prairie of 315 acres. The soil in the prairie is a rich, black vegetable mould from three to four deep, with a stiff clay subsoil, resting on sandstone, and the surrounding woodland also consists of very rich soil...”

Immediately round Victoria, and in the Saanitch district, on the peninsula spoken of before, is much good land; but this is now all or nearly all settled and under cultivation.

Cowichan Valley

Prairie - Quamichan and Somenos Lake (MacFie 1865 p186): "...the oak plains around the Somenos and Quamichan Lakes, with a sandy clay sub-soil, are exceedingly well adapted for fruit or garden purposes"

Oak Savanna - St. Peter's Anglican Church at Quamichan as reported by Pastor Reece in 1866 (Williams 1977 p7): "(to the immediate west of St. Peter's church, Mr. Reece described) oak trees standing in all directions in park-like glades with "exuberant herbage" covering the ground"

Cowichan Valley Prairie (Verney May 10 1864, p211): "I have taken advantage of my visit here to visit the interior part of this settlement further from the coast than I have been before; it has been very gratifying to see the abundance of rich open prairie."

Quamichan Village along the Cowichan River (Brown June 9 1864, p46): There is good quantity of good open land here capital soil...About a mile from the village is a small prairie of 20 acres of open land surrounded by woods, soil good dark loam."

Open Park-like Areas along the Cowichan River (Brown p52-4ish): "After making the last portage (of the day) we came to Qualis [below Marie Canyon] a fine open space of ground, backed by pines through the vista of which you could see a beautiful natural park. Passed through fine parklike piece of country. Soil in general stony but suited well for pasturage..."

Quamichan Lake (Cowichan Valley) - Mrs. Philip Jaynes (in Pioneer Women of the Cowichan Valley): "It was so pretty on the lake and around the Stamps Road area. All the Quamichan hillside, where W.P. Jaynes had his farm, was beautiful, covered with oak trees..."

Pocket Prairie on the Nanaimo Trail (Brown August 1864, p99): "Through a wooded country to Drinkwater's farm - a good prairie formed into fields with some under cultivation...A pleasant situation at the base of Mt. Prevost - glen slope with prairies dotted or encircled with clumps of trees...Up at 6 am. Started off traveling through a succession of prairies for 3 miles, then thinly wooded country, then thickly wooded with occasional swamps in hollows until we entered the Chemainus Valley. Passed through fine prairie...(On the Chemainus River (p101)), the timber is pine, red cedar, arbutus, and a few oaks."

Description of Open Prairies - Comox to Metchosin and beyond to the west (Hazlitt p163-172): "...The Cowichan River...flows through a narrow valley containing a good deal of open land, and a considerable portion of available woodland. About three miles up the river there is an extent of some 10 -12 miles, by perhaps half a mile broad on either side of rich open alluvial land; this tract is one of the most extensive uninterrupted tract of available land yet seen on the Island..."

Cowichan Valley – Douglas 1849 p42. *"The Cowetchen Valley is reported by the Indians to be much superior to this part of VI, in respect to extent of cultivatable land, and to the absence of hills and rocky ridges. It is traversed by a considerable river of the same name which discharges into the "Canal de Ario" about 30 miles north of this place...That may hereafter become a desirable place of settlement when the colony gathers strength and a means to push out parties powerful enough to make head against the natives who have never been brought under our influence, have lost nothing of their naturally savage character."*

Cowichan Valley Description – Quamichan and Somenos Lakes (May 1851) *"I received a note yesterday...from Mr. MacKay...He had just entered the Cowichan Valley, which he describes as a stream of some magnitude, discharging as large a body of water as the Cowlitz River. The valley of the river varies from two to three miles in breadth, beyond which the country, on both sides, rises by a succession of acclivities and intervening table lands to a range of hills about ten miles distant. He had discovered two fresh water lakes, surrounded by 'beautiful prairies'. One of these lakes is four miles long by about two miles broad.*

Vancouver Island Descriptions (Mayne p393-396..) *The Cowitchen Valley was surveyed in 1860, and in the surveyors report will be found the following remarks: "I am firmly persuaded...that (farming returns are as good as any part of America)...The climate (lacks the dry of California and the colds of other British North America provinces or eastern US). The loamy soils everywhere possessing a depth of two or three feet, and containing a large proportion of calcareous principle, are especially eligible for fruit-culture; and the oak plains around the Somenos and Quamichan Lakes, with a sandy-clay subsoil are exceedingly well adapted for fruit and garden purposes. Among the native fruits are blackberry, mulberry, raspberry, strawberry, gooseberry, currant, and high-bush cranberry, would require little pains or culture to produce luxuriantly. The varieties of plants are very numerous; a few only were noted growing on the plains or meadow lands, among which are the following: wild pea, wild beans, ground-nut, clover, field-strawberry, wild oat, cut grass, wild timothy, reed meadow-grass, long spear-grass, sweet grass, high ostrich-fern, cowslip, crowfoot, winter cress, partridge berry, wild sunflower, marigold, wild lettuce, nettles, wild Angelica, wild lily, broad-leafed rush, and reed-bush. The ferns attain a height of six or eight feet, and the grasses all have a vigorous growth. ...The following are some of the trees or shrubs: - oak, red or swamp maple..(many others; none interesting or unusual). The whole area surveyed is 57,658 acres, of which 45,000 acres of plain and prairie land may be set down as superior agricultural lands, the remaining portion being woodland, either open or thick."*

"Though I have not perfect confidence in all the details of the gentlemen who was charged with this survey, and who was not one of the regular staff, the general outline may be trusted...The luxuriance of the growth of wild fruits and flowers exceeds that of any country I have ever been in. I do not, of course, mean to compare it with the rank vegetation of the tropics but I assert it is more naturally fertile than any region I have ever visited.

Comox and Courteney

Prairie - Comox (MacFie 1865 p 187): "This district called Comox is said to contain not less than 30 square miles of good farming land....Just above the junction of the Puntluch and Courteney Rivers, on the left bank of the latter, the traveler finds himself in the heart of an immense prairie, extending in a NW direction parallel with the coast for 8-10 miles... This important tract is abundantly watered by the Courtney and some small tributaries....A dense wood surrounds the Prairie.....'It took us a day and a half to walk over this land, though which a plow may be driven from end to end' "

Comox (Verney p 99 - Nov 1862): "I was surprised to see so much clear land...the open land runs in belts stretching for miles..."

Comox/Courtney Prairies - August 1864 (Brown p111-5): "Como of course as everybody knows is a great agricultural region. The prairies are up the river. After paddling up the river...(we saw) a pretty prairie of 100 acres sloping down to the water's edge and bordered with belts and clumps of trees...(visited some settlers, walked over) beautiful rolling prairie through which a stream slowly crawled along...We walked on, still over miles of beautiful prairie land visiting several settlers...We traveled for about 2 miles in a westerly direction through open prairies, some of which were preempted but as yet had no houses...Most of the prairies were covered with deep fern (*Pteris aquilina*) and in other places blackberries..."

General Description - Comox/Courtney Prairies (Brown p120-21): "Comox country was commenced to be settled about (1862) with the aid of Gov. Douglas. The area comprises the prairies...The soil is rich and the surrounding country beautiful. There is none of the extremes of bad soil found in the Cowichan District. (Many vegetable species have been introduced). During our visit hay was being cut in the meadows at the river's mouth for the Victoria market...Sheep none of the settlers have attempted (due to the wolves)...The land is of the richest character with scattered prairies from 500 to 1000 acres, well-watered, and abounding with game...(much hay being cut)..."

Description of Open Prairies - Comox to Metchosin and beyond to the west (Hazlitt p163-172): "...Point Holmes [Comox???], where there are some 10 to 12 miles of open prairie land close to the coast, offering probably a more favorable field for agricultural settlement than any other section of land which has yet to be discovered on the island..."

Courtney-Comox (Mayne 1859): "Landing from the canoe just above the Forks of the Puntluch and Courtney Rivers, and on the left bank of the latter, we found ourselves in the middle of a large prairie, which we discovered continued in a northwesterly direction or parallel with the coast, for eight or ten miles. The Courtney flows nearly through the centre of this, and there are one or two smaller streams, which water the whole abundantly. The ground slopes upwards from the river on both sides, so as to prevent the possibility of overflow to any extent. The whole of this prairie is bounded by dense wood, forming a sheltering coast-fringe on the east, and affording plenty of timber on all sides (except towards the entrance from Baynes Sound) for building, burning, etc. It took us a

day and a half to walk over this land, through which a plough might be driven from end to end...We estimated the clear land here altogether at 7000 or 8000 acres. The Indians told us that a great many blankets would be wanted for the purchase of this tract, as all the neighboring tribes resorted there in the summertime to collect berries, shoot deer, catch fish, etc. all of which were found in large quantities. Indeed they showed some reluctance at taking us over it, feeling sure, no doubt, that we should desire to possess it when its qualities became known."

Nanaimo and Coastal "Oak Openings"

Coastal Grasslands just north of Nanoose Bay - August 18 (Brown p 107): "Hitherto 9 in the vicinity of Nanoose Bay) the forest had come to the water's edge. Now all has changed. Beautiful grassy meadows or what in the north of Scotland are called "links" [pockets!!] skirted the coast for a quarter of a mile in breadth. In some cases intersected with "slues" or inlets of the sea, and in some cases overflows at high water but in some cases intersected by creeks wending their way to the sea. And in some cases scattered with rural lovely looking clumps of pines and quite dry.

Vancouver Island Descriptions (Mayne p393-396..) "(*Nanaimo*, surveyed by Mr. Pearce, estimated them to contain together 43,450 acres...He said the soil is sandy but covered with the most luxuriant vegetation, fern, wild fruit-bushes, and tress among which may be noted the crab-apple and cherry everywhere found...The principal timber is cedar, pine, maple, and poplar, all of which grow to gigantic size [NOTE: no mention of oak or prairie]. Of the Cedar District, which contains 11,000 acres,...[No oak or prairie mentioned]. Of the Delta plains, which contain about 1000 acres, he says:- the southern portion consists of rich vegetable soil, of a great depth, with a subsoil of muddy clay or loam; the northern portion is apparently subject at long intervals to floods, but is, nevertheless, admirably suited for a long stock or grazing farm...bearing a rich long grass, which the Indians annually cut and sell to the settlers at Nanaimo."

Fire

Fire - Victoria (Verney May 25 1862): "I am much charmed by the great beauty of the country: the pines would be very ornamental if it were not for the fires which have at various times passed through these forests. These have killed the trees but left them standing in some places entire, in others but short stumps, and these dead trees and blackened stumps are a great eye-sore..."

Fire- Victoria (Hazlitt p160): "The natives all along the coast have a custom of setting fire to the woods in the summer, which doubtless adds to the density of the fogs and increases the temperature in the atmosphere. I have never seen a drop of rain fall from March till October; the seasons however are uncertain."

Fire (July 24 1848) – Anonymous: Report in the Times (1849). We made Cape Flattery on the 23rd ...Ran up the straits the next day...Nothing but forests of tall pine. At one part

ten miles of them were on fire...We rounded the SE part of the island...and came to anchor close to shore of Esquimalt Bay.."

"No such thing as rain seen or heard during three months; the thermometer at 61 degrees. The sun seems as though you were looking at it through a dark red glass for the forest is on fire but whereabouts we do not know; the air is full of smoke and lots of wood ashes falling on the deck."

Fire (September 1848) – Report in the Times (1849)

"Miles of the ground were burnt and smoking and miles were still burning. The Indians burn the country in order to find more easily the roots that they eat. The fire runs along the grass at a great pace and it is the custom here if you are caught to gallop right through it; the grass being short, the flames being little and you are through in a second. All the horses and cattle feeding know it well and make straight for the fire immediately."

Grass / General Description of Vancouver Island (1848): Fitzgerald, J.E.

"The general character of VI is mountainous but is extremely varied...In the south there are extensive plains of rich alluvial soil. A gentlemen who had been in the HBC service, once informed the author that he had walked over a plain of some miles in extent, on the south side of the island, which had not a blade of grass growing, owing to it having lately been burnt by the Indians, and that a few months afterwards, on going over the same spot, he found the grass up to his middle in height."

First Nations land management

First Nations Plant Use (MacFie p443): "...Their ordinary food, in addition to fish and wild animals, includes potatoes, ground-nuts, acorns, lily-roots, etc."

Fern, Camas, and Wappatoo (Kane 148): "The only other vegetable besides camas and wappatoos that the Indians use, are the roots of fern, which here grow to a very large size"

Camas gathering (Brown, June 9 1864, p46): "Poling [up the Cowichan River] is very hard and dangerous work frequently resulting in the swamping of the canoe. The Indians are few now and busily engaged in obtaining clams, camas, and sea salmon"

Camas - Use and Preparation by the Chinook - Lower Columbia River Gorge (Kane 1858, p127-128): "The only vegetables in use among them are the camas and the wappatoo. The camas is a bulbous root, much resembling the onion in outward appearance, but is more like the potato when cooked and is very good eating. The wappatoo is somewhat similar, but larger and not so dry or delicate in flavor. They [the camas] are found in immense quantities in the plains in the vicinity of Fort Vancouver, and in the spring of the year present a most curious and beautiful appearance, the whole surface [like St. Peter's church??] presenting an uninterrupted sheet of bright ultramarine blue, from the innumerable blossoms of these plants. They are cooked by digging a hole in the ground then putting down a layer of hot stones, covering them with grass, on which the roots are placed, they are then covered with a layer of grass, and on the top

of this they place earth with a small hole perforated through the earth and grass down to the vegetables. Into this water is poured, which, reaching the hot stones, forms sufficient steam to completely cook the roots in a short time, the hole being immediately stopped up on the introduction of the water."

Use of Acorns for Food - Fort Vancouver, Washington (Kane p 128): "*There is another article of food made use of amongst them, which, from its disgusting nature, I should have been tempted to omit, were it not a peculiarly characteristic trait of the Chinook...The whites call it Chinook olives...Prepared as follows. A bushel of acorns are placed in a hole dug...covered over with a thin layer of grass, on top of which is placed about half a foot of earth...Urine is deposited (on this spot and it is left for four or five months before being considered fit for use)".*

Camas Gathering in Victoria (Brown 1864 p 47): "*The whole population (of the village of Somenos) with the exception of about a dozen old women and children were absent gathering clams to dry for winter use and camas in the district around Victoria, particularly a place near Mr. Yale's on the Saanich Road called "Tummas". [same Yale that was at Fort Langley].*

Camas at Point Roberts Prairie (Traditional Indian tale in Brown p188): "*...not far from Point Roberts...The men were off fishing and the women gathering clams on the shore at low tide, seeking gamass or berries,..."*

Cultivation (Douglas 1842): "*We are certain that potatoes thrive and grow to a large size as the Indians have many small fields in cultivation which appear to repay the labour bestowed upon them,..."*

Native hemp p68-69 "*We forward a parcel of hemp manufactured by the natives from a plant which grows abundantly on the rich moist vallies of this island. All the native fishing tackle is made from this material, which possess a remarkable degree of strength and durability...The plant producing it grows to heights of 5 ft. with leaf and stalk very like the common nettle for which it may be readily mistaken..."*

Cultivation Practices (1851) "*The Indians generally are turning their attention to the cultivation of the potato, and to other useful arts..."*

Introduction of plants

HBC Policy – Self-Supporting Forts p xlv (Fort Victoria letters)

"By the will of the HBC, the fur trade would have to be reconciled with settlement and industry; by the determination of the British government, the colony of Vancouver Island would have to be self-supporting."

Planting of non-native species - Vancouver Island (MacFie p194): "*The following are the usual quantities of seed sown per acre...Of vetch 2 and a half bushels per acre". (In an accompanying table, clover is shown to yield 4 tons per acre on Vancouver Island)".*

Sowing Grass (MacFie p198): "To those prepared to embark in farming, having capital sufficient to engage in this pursuit extensively, my advice would be that they should make their green crops subservient mainly to the feed of stock, and lay out as large a portion of their land in timothy grass as much as possible, as returns from hay and cattle are always certain and remunerative".

Planting Clover (MacFie p 203): "Autumn cultivation is not yet common in the colony. Besides wheat, which should be sown in October...there are certain fodder plants that should be put in at the same time. There are clovers - red, Dutch [white], and Alsike. The last-named is the best of the perennial clovers and produces a thick crop of forage. The crimson clover (*T. incarnatum*) forms a rich fodder for cattle in the spring, if cut when in flower. Lucerne (*Medicago sativa*) comes up in spring, a fortnight before clovers or rye-grass. Common bird's-foot trefoil (*Lotus corniculatus*) is highly nutritious, grows on dry elevated pastures, and is consumed avidity by cattle. From the great depth to which its roots penetrate, it is protected against injury from drought, and succeeds in retaining its verdure after the grasses and other plants are burnt up. Common saintfoin (*Onobrychis sativus*) also continues in perfection and ought to form part of all permanent pastures. Common tares or vetch (*Vicia sativa*), hard fescue grass (*Festuca duriscula*), sheep's fescue (*Festuca ovina*) Italian rye (*Lolium italicum*), and common rye grass (*Lolium perenne*)- all of these plants, sown in autumn will produce in spring an early and bulky crop, and should without delay engage the notice of island farmers."

Non-native Grass Introduction (Verney Feb 7 1864, p189): "...I shall sow some grass seed and endeavor to cultivate a lawn on some ground...that has been prepared (though) the earth is too wet to rake or roll at present."

Importation of crop seed - Victoria (Hazlitt p159): "The soil under cultivation is sometimes rich vegetable mould, in other places a clayey loam, and in others somewhat sandy...It produces (wheat, peas, barley, oats, beans, turnips, and potatoes)...I imported all the seeds except for wheat, peas, and potatoes, from Van Diemen Land, through the Sandwich Islands."

Soil Description (Douglas July 12, 1842) "I observed generally speaking but two marked varieties of soil on these prairies...Both kinds, however, produce abundance of grass and several varieties of red clover grow on the rich moist bottoms. In two places particularly we saw several acres of clover growing with a luxuriance and compactness more resembling the close sward of a well-managed lea than the produce of an uncultivated waste. Being pretty well assured of the capabilities of the soil...we ought to be able to grow any type of grain raised in England. On this point however we cannot speak confidently until we have tried the experiment and tested the climate..."

Planting of Timothy and White Clover p xxvi (Fort Victoria letters). "The planting of timothy and white clover was needed at the encampments along the way and at Fort Hope, a post built in 1848 (to improve forage availability for the horses)..."

Grass Seeds (1851) p 171 "I forward...a small requisition for various kinds of grass seeds which I beg be forwarded by the first ship bound for the Island – we entreat that the seeds be fresh and of the best kind – I am informed that seeds put up for abroad are often mixed with inferior and damaged sorts – which would be a serious disappointment in our case. These seeds should be put up in bags of convenient size, packed in tight casks and frequently aired in fine weather only, by a careful person during the voyage to the country. That plan was followed by Mr. Harvey, with the seeds under his care, and succeeded better than any other that has been tried."

Weed Introduction in the Comox Valley (Duncan 1903, in MacKie 2000) "Sown grasses of all kinds, but especially clovers, thrive wonderfully; in fact, white clover is spreading everywhere, covering the roadsides and making itself a kind of nuisance in gardens and hay-fields. I am sorry to say that the weeds of civilization are getting here at last".

Comox Valley Poem (Duncan, 1881, in Mackie 2000) "Now the farmer yokes his oxen and commences to his ploughing, throws the precious seeds in handfuls; Harrows it beneath the surface, In the joyful expectation of a fair and bounteous harvest"

Grass Introduction in the Comox Valley (Duncan 1930, reported in MacKie 2000) "(Forests in the Comox Valley had to be arduously cleared and burnt before crops could be planted). A clearing burnt off in September and sown immediately with timothy [Phleum pratense] and cock's-foot grass (??) among the stumps, will yield so heavily the following summer that the scythe can hardly cut it. If burnt off and not sown it becomes a fearful mass of weeds."

Origins of Clover Accidentally Introduced from England (Kane p144):

"Clover gross plentifully and is supposed to have sprung from accidental seeds which had fallen from the packages of goods brought from England, many of which are made up in hay"

European land management practices

Methods for clearing prairie - Victoria (MacFie p201-02): (A): Prairie: "There are open lands in the colony already fit for the plough, and from which a crop may be obtained without any exertion from clearing. But even the richest prairie soil cannot entirely dispense with preparation for ploughing. Where loose surface stones or small boulders happen to be embedded, they should be first carefully removed. If there be no dense weed or stumps, the land should be broken up, in the first instance, by one or more yokes of oxen, as the farmer may deem necessary. These animals are preferred for strength and steadiness of draught to ordinary horses of the country. If fern prevail on the land [Bracken Fern], it should be ploughed up in the heat of the summer, in order, by exposure of the roots of the rays of the sun, to destroy them. These with all bulbous weeds, such as crocuses [Sisyrinchium], kamass, etc. should be collected and burned. Fern-land, not required for immediate use, may with advantage be left for hogs to burrow in, as they form valuable pioneers. (B) Douglas-fir: "Land covered with pine is not difficult to clear. That tree, being of resinous description, burns freely, and its roots creep close to the

surface. (C) Oak: "The roots of oak descending more vertically into the ground are not so easily eradicated. After clearing, draining and ditching should receive early attention...(in areas where the land is level)".

Cultivation (August 1848) – Report in the Times (1849) In Coughman "(At Fort Victoria) they have cleared a quantity of ground and have some acres of wheat besides vegetables...The people are now kept up late as it is harvest time, and they dare not carry the wheat away in the day, it being so dry that all the grains fall out, so they wait till a little dew has fallen and then go on working until past 12 at night."

Cultivation – Victoria (Douglas 1849) p42 "It will be advisable for both Companies to make improvements soon as possible on their respective sections of land, as the appearance of large unoccupied tracts of land in the country where the extent of prairie is not great may cause discontent among colonists...(Note: explains complaints by early settlers that the best lands were locked up by HBC / Puget Sound Co.)

General Farming Description – winter 1849 p62 "The severe winter of 1848/49 retarded the farm work so much that it was late spring before the seed could be put in the ground...thus short crop of winter wheat this year...The oats on the contrary were the finest ever grown on this farm but owing to the late sowing, 20th of May they ripened only in part. The pease have reproduced remarkably well but the potato crop has in measures failed..."

Sowing (1851) p170 "We are now in the midst of seed time, having sown all the land formerly under cultivation, except for the reserve of grass and hoe crop. The weather continuing favourable for field work we have 100 Indians clearing the brush and trees and bringing new land into cultivation, a process involving much labour, though well repaid by the land reclaimed, which is generally speaking better of better quality than the Prairie soil. The labour is done by contract of 30/ acre. The quantity of grain sown, up to this date, is 301 bushels of wheat, oats, pease, and barley – and we have land prepared for 400 bushels of potatoes."

Weed Introduction in the Comox Valley (Duncan 1903, in MacKie 2000) "Sown grasses of all kinds, but especially clovers, thrive wonderfully; in fact, white clover is spreading everywhere, covering the roadsides and making itself a kind of nuisance in gardens and hay-fields. I am sorry to say that the weeds of civilisation are getting here at last".

Comox Valley (James Richardson 1872 Geological Survey of Canada) "The surface of this district, with the exception of single trees and clumps, chiefly of oaks and strips of alder in the bottoms, may be some 12 square miles, the scenery being picturesque and parklike. Its margin is very irregular in shape and it is surrounded by a growth of heavy timber, among the trees of which are the Douglas Spruce, often obtaining two feet in diameter and 200 hundred feet in height, and in one half of which it is free from branches, and the cedar often equally large. The open country, in its natural state, is mostly covered with a growth of ferns, which sometimes attain a height of ten feet, with stems $\frac{3}{4}$ of an inch in diameter and roots descending to a depth of 3 feet. These roots the

native Indians prepare in some peculiar way for winter food, and excavate deep trenches to obtain them. The farmers are under the necessity of grubbing up fern roots before the ground is ready for use, and are often voluntarily assisted by their pigs in this operation, these animals, it is said, relishing the fern root as food."

Farming Efforts/Description of Land (1850) p132 "*We are using every exertion to raise grain and other farm produce for the supply of this establishment and the posts dependent upon it – but it will take some years and large means to accomplish this object. From the character of the country and the quality of the soil, the labour and expense of bringing land into cultivation on Vancouver Island is very much greater than in the Columbia (i.e., Fort Vancouver, Cowlitz River) where the excessive prairies without a bush or stone to check the progress of the plough present a striking contrast to the rocky ridges stony land and bushy glades of this part of the coast" ... (p141) ... plough and brush plough from the United States, which have had repeated trials, being found equally fragile and incapable of breaking up the tough stony land of Vancouver Island..."*

Introduction of livestock

Grazing - Vancouver Island (MacFie p 195-96): "*Spanish cattle abound on the coast...sheep...horses in almost every variety...oxen...hogs...The small area of VI does not admit of grazing being carried on to so immense a scale as that branch of agriculture in the colonies of the southern hemisphere..."*

Grazing at Fort Nisqually (Kane 1847, p142-143): "*When I visited it [the fort], it had about 6000 sheep and 2000 horned cattle. Its site is beautiful on the banks of the eastern end of Puget Sound. The land is inferior to that in some other parts of the same district, the soil being gravelly; the grass however grows luxuriantly, and the mildness of the climate adapts it well for grazing purposes, as it is never necessary to house the animals."*

Coastal Grasslands just north of Nanoose Bay - August 18 (Brown p 107): "*Wild pasturage of various species grow thickly all over these flats, and when hay is at \$29 a ton...I have no sympathy for men who have not the enterprise to occupy these flats with the thousands of cattle they are capable of supporting. ..Through the middle of one of these flats flowed a river..." [probably Englishman River]*

Time of Cattle Introduction. Fort Victoria. Dispatch from Peter Skene and James Douglas (1846) to George Simpson of HBC, Red River Settlement. "*The farm in Fort Victoria has been considerably enlarged, and upwards of 100 head of cattle and horses carried thither from Puget's Sound (NOTE = Nisqually)...That autumn wild Spanish cattle and workhorses were transported from Fort Nisqually, and in December 5 acres were seeded with wheat. The following year, Finlayson...fashioned crude ploughs and harrows out of oak and broke more land...To avert starvation, Finlayson cleared that land near the harbour to bring to 300 acres the total land under production. The 1847 crop was*

estimated at 1000 bushels of wheat, 400 of pease, 700 oats, and 3000 of potatoes...Two diaries commenced to produce butter in 1847 and a 6-acre orchard was planted.

Early Cultivation practices pLi (Fort Victoria letters) "The fur traders turned out to be 'miserable farmers'. According to Capt Grant *"they ruin the land by paying no attention to the succession of crops and never applying manure and they ruin their stock by no attention to breeding and allowing the majority to run wild in the woods"*.

Cattle/Sheep to Victoria p Lxix (Fort Victoria letters) *"On March 18 1850, the Driver (ship) on Blanshard's requisition, started across the Strait to Fort Nisqually to obtain a cargo of 85 cattle and 800 sheep for the 80 labourers arriving in a few days..."*

Cattle Imports from Nisqually (1851) (Fort Victoria Letters) *"(we sought to import) as many live sheep and cattle for the use of the colony of VI as they could bring."*

San Juan Island (Mayne traveling in 1858) p39-40. *"(On) San Juan...there is more land available for agriculture than of any other of the group...and the HBC established a sheep farm on it some years ago...(The sheep farm) is situated on a beautiful prairie at the SE end of the island...I have never seen wildflowers elsewhere grow with the beauty and luxuriance they possess here...At one time I believe the company had 3000 sheep here."*

Disappearance of Wildflowers in Victoria (Fawcett 1912): *"...Our school and grounds were surrounded by spreading oaks, which covered that part of the city, or country as it was called back then, and it was under these tress that...we ate our lunch...Wildflowers, that are now only found miles away, were found there in profusion*

The pace of cultivation - Victoria (Hazlitt p157): *"(By 1849), there were some eighty acres in cultivation round Victoria."*

Cultivation (August 1848) – Report in the Times (1849) *(At Fort Victoria) they have cleared a quantity of ground and have some acres of wheat besides vegetables...The people are now kept up late as it is harvest time, and they dare not carry the wheat away in the day, it being so dry that all the grains fall out, so they wait till a little dew has fallen and than go on working until past 12 at night."*

Fort Victoria (October 1845) Lts. Warre and Vavasoar *"We visited the HBC post, Fort Victoria,...on the south shore of the island, near the head of the narrow inlet where they have established a fort similar to those already described, a farm of several hundred acres, on which they raise wheat and potatoes..."*

Speed of Cultivation (1851) Richard Blanshard, Governor of VI. *"With the exception of a Canadian who has squatted near Rocky Point, there is not another cultivator on the Island"*.

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Farming August 18 (1851) *"The wheat is still in the field, nearly ready for taking in...Though the summer has been remarkably dry, no rain having fallen since the 9th of May, the crops are fully heavier in grain than last year..."*

General Description of Victoria/Saanich (Mayne 1859) *"The northern portion, for about ten miles, contains some of the best agricultural land in Vancouver Island. The coast here, as everywhere else, is fringed with pine; but in the centre it is clear prairie or oak-land, most of it now under cultivation."*

Random material

Mid-summer dry weather- Cowichan Valley (Verney p 88): *"...from the middle of May the days become warmer and warmer...up to the end of July; then the days become considerably hotter and the sun was quite scorching, burning up the grass"*.

Summer Drought - (Hazlitt p159-60): *"...crops which are not taken in early are apt to be parched up, and run to straw for want of moisture."*

Game (September 1848) – Report in the Times” *The sportsman as yet have met with little to shoot at – a few ducks and partridges early in the morning. They say that as this dry season all the game move inland...we saw a few cranes, humming birds, and squirrels.*”

Birds (Hazlitt p183): *Of small birds there is the Mexican woodpecker [Flicker]...(the woods are generally quiet compared to the lands of the east)...*”

Prairie of the Lower Fraser Valley [Note: disjunct oak ecosystem remnants at Yale and Sumas Mountain, and the description of wide-ranging “prairie” on the Fraser Valley bottomlands in the early 1800s, suggest the possibility that the oak savanna ecosystem occurred more commonly in this region at one time. These quotes below, however, suggest that these prairies were very different than the oak ecosystem of Vancouver Island].

Fraser Valley Prairies (MacFie p 223): *“The broad and fertile plains at Sumas and Chilukweyuk next come into view, which are overflowed by freshets once a year*

Fraser Valley - general description (MacFie p285) *“Five miles above Westminster, on the banks of Pitt River, are meadows clear and of great extent; the only hindrance to their successful cultivation being that they are liable to overflow...‘The banks of the Pitt River (writes Gov. Douglas in 1860) are exceedingly beautiful; extensive meadows sweep gracefully from the very edge of the river toward the distant line of forest and mountain. The rich alluvial soil produces a thick growth of grass, interspersed with the Michaelmas daisy, the wild rose, and scattered groups of willows. This fine district contains 20,000 acres of good arable land, requiring no clearing from timber, and ready for the immediate operations of the plow. Many parts of it, however, are exposed to overflow through periodic inundation of the Fraser...’ ”*

Flooding of Pitt Meadows and Fields Near Langley (Mayne p86). *“In May the waters rise rapidly and continue to do so until the end of June. ..They remain so until the middle of August...During these 6 weeks, the banks being overflowed, the meadows at the entrance, and the extensive plains on the banks of the Pitt River above Langley, are covered for several miles... ”*