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Terrestrial Plant Ecology

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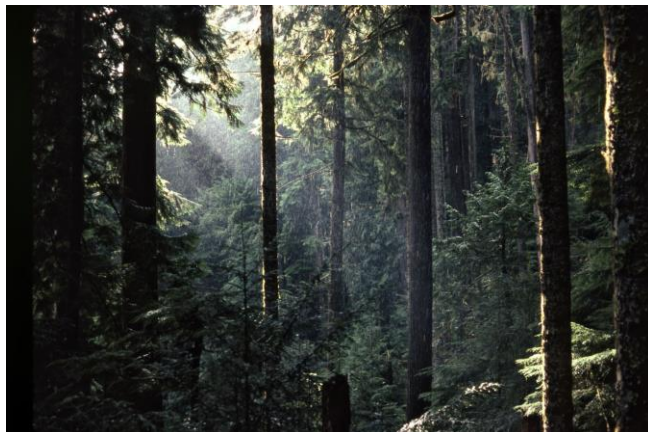
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RESEARCH HISTORY AND INTERESTS:

I have been conducting studies of various aspects of terrestrial plant ecology for over 40 years. My focus has been on the dynamics of forest stands and their constituent species in Northwestern North America. However, I have diverse interests under the broad umbrella of terrestrial plant ecology. I consider myself both a community and population ecologist. Just as high species diversity can make a region more interesting, a diversity of research topics can make life more interesting. I have worked on topics ranging from forest succession following volcanic disturbance to gender-specific reproductive differences in dioecious plants.



MAJOR AREAS OF RESEARCH:

Volcanic disturbance and forest

succession: My first work was on forest succession in the Rocky Mountains. I then moved on to considering population dynamics of a tree species in the Cascade Mountains, but life is unpredictable. I didn't plan to study volcanic disturbance. The study plan did not include having my initial Ph.D. project blown up by a volcano. However, "disasters" can often be turned into opportunities. Thus after the 1980 eruption of Mount St. Helens, I ended up studying the effects of tephra (volcanic ash) deposits on forest understories. In collaboration with Don Zobel at Oregon State University, I have maintained permanent plots at Mount St. Helens for 4 decades, and we have published a long series of papers on post-disturbance changes in the understory of old-growth forests impacted by tephra deposits. Now we are collaborating with Dylan Fischer at The Evergreen State College who will continue this long-term study. This work led to a substantial increase in understanding of how forest understory plants respond to disturbance and subsequently expand over 40 years. Survival of plants during the tephra disturbance was critical and clonal growth was very important in subsequent expansion of plant cover. We found that in

some situations the forest understory may be deflected toward a system substantially different than the one that existed prior to disturbance.



Mount St. Helens – summer 1980



Herb-rich, old-growth forest buried with tephra – summer 1980



Understory trees destroyed by tephra that fell on a snowpack



Plants saved by erosion of the tephra



The same old-growth forest as above, 20 years later

Clonal growth and population ecology of forest understory plants:

The work at Mount St. Helens caused me to consider understory herbs in new ways. Clonal growth was pivotal to responses to the tephra disturbance and is a key feature of most forest understory plants. Thus I started conducting studies of below-ground structures and clonal spread. Excavating rhizome systems provides a new perspective on the growth of plants – very different from our typical aboveground view – and is also great fun (like unraveling a mystery). I have intermittently continued studying the below-ground growth patterns and clonal spread of forest understory species, which has been very rewarding work. Most species spread via rhizomes, but some spread via stolons, which can result in rapid expansion. Most “plants” (ramets) in the forest understory actually result from clonal growth and not directly from seed. The work on clonal growth has contributed nicely to understanding of the population dynamics of herbaceous forest plants.

Dynamics of old-growth subalpine

forests: Although I have spent much of my career studying the effects of disturbance, I am fascinated by the idea that some forests appear to undergo very limited directional change over substantial periods of time. Starting about 25 years ago, I initiated a series of studies with Roberta Parish (now retired from the BC Ministry of Forests) on the dynamics of old-growth forests. We obtained nearly complete age structures for five old-growth subalpine forests in southern British Columbia, three in the Interior and two on the Coast. Two of the Interior stands started from a stand-initiating disturbance, but the other three stands showed no



Clintonia uniflora – grew through tephra via long rhizomes



Chimaphila umbellata – a species with an exceptionally large system of persistent rhizomes and attached aerial shoots

evidence of an initial disturbance and appear very close to “steady-state” forests. Most surprisingly we found extremely old trees in what appeared to be typical forests on the Coast. In a stand on northern Vancouver Island, all four species present had individuals over 900 years in age.

More recently we have used the growth ring data from these stands to examine relationships with climate variation and assess how these forests are likely to respond to changes in the CO₂ concentration of the atmosphere. It appears that at least some old forests are unlikely to increase in growth in response to increasing CO₂ concentration of the atmosphere. However, they store large amounts of carbon and are

thus an important storage reservoir of carbon. Collectively this work has increased understanding of the dynamics of old forests and their growth, both historically and potentially in the future.



Ancient forest at Mt. Elphinstone, coastal British Columbia



Very old (594 years) but only 16 cm diameter *Abies amabilis* at Mt. Cain, Vancouver Island

Tree seedling banks: Our studies of old forests contributed to the realization that seedling banks (advanced regeneration) were important in the dynamics of these forests. Thus we specifically focused some effort on determining age structure and growth of small trees in the seedling bank. Individuals can grow exceedingly slowly and persist for very long periods at a small size. For example, *Abies amabilis* in the understory can be 100 years old when only a meter tall. However, when the canopy opens up, these small individuals can increase in growth. In addition, seedling banks (advanced regeneration) are a major source of new canopy trees following disturbance by bark beetles, a topic I have studied in relation to the recent, major bark beetle outbreak in British Columbia. I would like to pursue further work on seedling banks as these appear to be of major importance to the population dynamics of shade-tolerant tree species and stand development following some disturbances.



Seedling bank *Abies amabilis*

Ecology of stress-tolerant subalpine

conifers: I have a long-standing interest in subalpine trees of harsh environments. In graduate school I started work on yellow-cedar (*Callitropsis (Chamaecyparis) nootkatensis*) but lost a field site to a volcano and thus switched projects! However, I subsequently considered this species when we studied age structure of ancient subalpine forests. I have also studied whitebark pine (*Pinus albicaulis*) with Elizabeth Campbell of the Pacific Forestry Centre. This is an especially interesting species of major importance in timberline forests, but is declining dramatically for a number of reasons, including disease and bark beetles. Long-lived, stress-tolerant species of cold environments are fascinating and warrant much more study to fully understand their population dynamics.



Whitebark pine (*Pinus albicaulis*)

Sex ratios and reproductive allocation in dioecious plants: Dioecious plants often have biased sex ratios and very unequal reproductive allocation between genders; however, the reasons for and consequences of these characteristics are inadequately understood. Gerry Allen (my spouse) and I conducted a series of studies on the reproductive biology of the dioecious, monotypic shrub *Oemleria cerasiformis* (osoberry). Much of this work was conducted on the University of Victoria campus, and thus very efficient. This series of studies resulted in a better understanding of sex ratios and consequences of differential reproduction allocation between genders in this species. I am interested in pursuing further studies of reproductive allocation – a key topic for understanding population biology.

Population ecology and prolonged dormancy of rare plants: The demography and population dynamics of rare species need to be carefully studied in order to understand how to most effectively protect these species. Former students Mike Miller and Allan Hawryzki studied two rare species with the interesting life history characteristic of prolonged dormancy, the situation where plants fail to appear aboveground for one or more years. This feature appears to be common attribute among herbaceous perennial plants, and has a variety of important implications for the population dynamics and persistence of species with this characteristic.

Tree invasion and restoration of

mountain meadows: Encroachment of woody plants into grasslands is a world-wide phenomenon of major conservation concern. I have been working with Charlie Halpern of the University of Washington on this topic. Our model system for this study is a montane meadow complex in the Oregon Cascades with extensive tree invasion (Bunchgrass Ridge; project website: <http://depts.washington.edu/bgridge/>). We examined patterns of tree invasion and initiated a large, long-term meadow restoration study. A thorough examination of the age and size structure of trees encroaching on meadows has yielded a detailed history of the timing, spatial distribution, and mechanisms of tree invasion. The large-scale restoration study involved tree removal with and without burning. Early results indicate pronounced increases in meadow species, but we also found that the system may not fully converge on the composition of natural

reference meadows. This long-term experiment is planned to be ongoing for many years and will yield further understanding of the effectiveness of restoration treatments, as the plots are re-measured periodically over the next couple of decades.



Bunchgrass Ridge meadows

GRADUATE STUDENTS:

I have no funding available for graduate students. However, I would be glad to talk to prospective students about possible projects. I am also glad to be on graduate student committees where my expertise can be of use.

UNDERGRADUATE STUDENTS:

An Honours project can be a very rewarding experience for undergraduate students. I encourage students to consider this option and would be glad to discuss possibilities with students interested in this program. My experience supervising Honours projects has been very positive.

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I have contributed to two popular plant guides as one of the authors. I primarily contributed to general ecological and range information, and to a lesser extent, editing and advising on species to include, key construction, and species descriptions.

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