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Climatic Influences on Weeds and their Herbivores: Biological Control of St. John's Wort in British Columbia

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Abstract

The biological control of St. John's wort (*Hypericum perforatum*) in British Columbia is an example of climatic limitations of successful weed control. In some areas of British Columbia complete control of St. John's wort has not been achieved despite the presence of an apparent abundance of the biological control agents, chrysomelid beetles. Areas of successful control have climates similar to the native Mediterranean habitat of *Chrysolina quadrigemina*, characterized by warm, dry summers. Areas where the weed persists in large stands have moister, colder weather, and the dominant beetle species is *C. hyperici*. Results of field and laboratory studies were used to demonstrate ways in which temperature may determine beetle species composition, reproduction, and feeding activity. Greenhouse and field studies demonstrate the beneficial effect of moisture on St. John's wort seed germination and recovery from herbivory.

Effets du Climat sur les Plantes Nuisibles et les Herbivores: Lutte Biologique Contre le Millepertuis Perforé

Si le climat peut gravement perturber la reproduction et l'alimentation des insectes utilisés comme agents biologiques, lemauvais temps peut aussi nuire à la croissance des plantes et à leur capacité de récupération après les attaques des herbivores et limiter leur aire de propagation. La théorie relative à la lutte biologique reconnaît généralement l'importance du climat pour le succès de l'établissement des insectes, mais les effets du temps sur les mauvaises herbes peuvent aussi influer sur la lutte biologique. La lutte biologique contre le millepertuis perforé en Colombie-Britannique est un exemple des contraintes imposées par le climat à l'élimination des plantes nuisibles. Dans certaines régions de la Colombie-Britannique, les millepertuis perforés n'ont pas été entièrement éliminés en dépit de l'abondance apparente des coléoptères. La lutte a été efficace dans les régions dont le climat est similaire à celui de l'habitat de *Chrysolina quadrigemina*, espèce originaire des zones méditerranéennes où les étés sont chauds et secs. De vastes touffes de plantes nuisibles persistent dans les régions humides et plus froides, où l'espèce dominante est *C. hyperici*. Les résultats des études sur le terrain et en laboratoire ont servi à montrer comment la température peut influer sur la composition, la reproduction et l'alimentation des espèces de coléoptères. Les études en serre et sur le terrain mettent en évidence les effets de l'humidité sur la capacité de récupération du millepertuis perforé attaqué par les herbivores et sur sa reproduction.

Introduction

While climate may severely constrain insect control agent reproduction and feeding activity, poor weather may also reduce plants' capacities to grow and recover from herbivory, and may limit propagation. Biological control theory traditionally recognizes the importance of climate for the successful establishment of insects (DeBach 1964), but the weather's effect on weeds may also influence biocontrol (see references in Harris 1980).

For example, variations in the density of the weed, tansy ragwort (*Senecio jacobaea* L.; Compositae) can be related to climatic factors (Dempster and Lakhani 1979). In a study of the relationship of tansy ragwort and the cinnabar moth, *Tyria jacobaeae* L. (Lepidoptera: Arctiidae), Cox and McEvoy (1983) demonstrated that moisture availability can limit plant compensatory growth after defoliation.

The noxious range weed, St. John's wort, *Hypericum perforatum* L. (Clusiaceae), has been limited to economically acceptable levels over millions of acres in North America (DeBach 1964). However, it remains a problem in parts of Canada, United States, and Australia where summer rainfall is common (Delfosse and Cullen 1981; Harris and Maw 1984), even though some of those areas experience periodic defoliation by chrysomelid beetles (Delfosse and Cullen 1981; Williams, Myers, and Edwards, unpubl. data). We have examined the system of *Hypericum* and the chrysomelid beetles introduced as control agents in diverse habitats of British Columbia to examine the influence of temperature and rainfall on populations of weeds and their control agents.

Table 1. Habitat differences of the Okanagan and East Kootenay Valleys of British Columbia (means ± s.e.).

Parameter	Okanagan	E. Kootenay
Temperature (°C)	Mean max./mean min.	Mean max./mean min.
Sept.–Feb. (fall–winter)	7.5 ± 1.2/–1.0 ± 0.8	4.9 ± 1.3/–5.1 ± 1.0
Mar.–Aug. (spring–summer)	19.0 ± 1.0/6.6 ± 0.8	17.7 ± 1.1/4.2 ± 0.8
Rainfall (mm)		
Sept.–Feb.	121.8 ± 19.1	184.4 ± 33.1
Mar.–Aug.	146.9 ± 15.5	322.8 ±5.8
Snowfall (cm/yr)	79.5 ± 15.1	167.4 ± 16.9
Soil type	Fertile alluvial	Glacial gravel
St. John's wort phenology	Plants senesce during summer	Many remain green during summer
Control	Complete	Ineffective

Unsuccessful weed control in new habitats may be a result of: (1) inadequate herbivore performance; or (2) superior performance of the plant under the new environmental conditions. In the case of persistant St. John's wort in the East Kootenay of British Columbia, the beetles appear to have established populations and consume considerable amounts of the weed (in some springs they consume almost all of the spring rosette growth, Williams, Myers, and Edwards, unpubl. data). Therefore, the purpose of this study was to examine the hypothesis that weather in the E. Kootenay might improve St. John's wort growth and reproduction.

Materials and Methods

Study Sites

Chrysolina quadrigemina (Suffr.) and *C. hyperici* (Forst.) (Coleoptera: Chrysomelidae) successfully controlled outbreaks of St. John's wort in California and Australia and were introduced to control the weed in British Columbia in the 1950s (DeBach 1964). The weed occurs across the Province from Vancouver to the E. Kootenay Valley of southeastern B.C. In the mid-1900s St. John's wort presented a serious problem in the Okanagan and Kettle Valley rangelands of southern B.C. (DeBach 1964). Although it took 7–10 years for the beetle populations to become established, the weed was reduced to acceptable levels in many parts of B.C. Two areas were chosen for study: the Okanagan Valley as a site of successful control, and the E. Kootenay Valley as a site of ineffective control. The E. Kootenay and Okanagan habitats differ considerably in temperature, precipitation, and soil types (Table 1), and in the E. Kootenay the beetles have established populations but the weed persists in relatively pure stands (Harris and Maw 1984; Williams, Myers, and Edwards, unpubl. data).

Seed Germination

To examine the effect of rainfall patterns on seed germination of St. John's wort, seeds were collected from plants around Vancouver (on the University of British Columbia campus) in June 1984. Seeds from several plants were combined to control for interplant variations. Fifteen plastic petri dishes (1.5 cm deep) were filled with potting soil and 200 seeds/dish were planted just below the soil surface. Five dishes each were used in three treatments: (1) WET — soil kept constantly moist; (2) WET ONCE – soil watered once, initially, then allowed to dry; and (3) DRY — soil remained dry. Petri dish lids were replaced and the dishes were kept in a controlled temperature chamber at 20°C, 10 hr daylength, to mimic field conditions for germination. The dishes were checked daily until the first cotyledons showed above the soil. New seedlings were counted periodically thereafter (Table 2) and all seedlings were removed after they were counted.

Table 2. Germination of St. John's wort (*Hypericum perforatum* L.) seeds under several moisture conditions. Numbers represent mean cumulative numbers of seeds (± s.e.) germinating in three treatments (with five replicates of 200 seeds each).

Day of Experiment	Treatment		
	Wet	Wet Once	Dry
7	32.0 ± 4.1[1]	0[2]	0[2]
14	47.0 ± 5.9	0	0
16	59.8 ± 8.6	0	0
18	73.4 ± 9.8	2.2 ± 1.0[1]	0
21	—	—	0[1]
25	83.8 ± 11.1	5.2 ± 0.9	1.4 ± 1.4
30	87.0 ± 9.5	5.8 ± 0.8	2.2 ± 1.5

[1]Begin experimental protocol: soil kept wet.
[2]Begin experimental protocol: soil allowed to dry between waterings.

Defoliation Experiment

A field experiment was conducted to determine the effect of herbivory on young shoot growth of St. John's wort. Seventy St. John's wort (mean shoot length = 45.1 ± 2.9 cm) were transplanted into the U.B.C. field laboratory on campus from an undeveloped area about 2 km away. The plants were watered regularly and allowed to establish for 3 wks after transplantation. At that time, all of the plants were completely defoliated (all green shoots were removed). Thirty-five of the plants were designated as the experimental group. Biweekly for the next 6 wks, shoot length/plant was measured and the experimental plants were defoliated again. The mean total shoot length produced/plant during the experiment for the treatment and control groups was compared using a t-test.

Field Studies

Observations were made and data collected at the Okanagan and E. Kootenay study sites in 1981, 1982, and 1983 (Williams, Myers, and Edwards, unpubl. data). Temperature and precipitation information used in this study was collected by Environment Canada at weather stations at the Kelowna Pollution Control Center (near the Okanagan site) and at Elko (near the E. Kootenay site).

Results

Rainfall

In the E. Kootenay during the summer months, rainfall occurs more regularly and in greater amounts than in the Okanagan (Table 2). Thus, because of its lower summer rainfall, the Okanagan climate resembles a classic Mediterranean habitat more closely than that of the E. Kootenay. That resemblance to the native climate of St. John's wort is also reflected in the summer senescence of St. John's wort in the Okanagan (Edwards 1982).

Table 3. Monthly mean precipitation (mm ± s.e.) in British Columbia. Data were compiled from 1975–81.

Month	Okanagan	E. Kootenay
Apr.	25.7 ± 7.3	123.1 ± 52.2
May	32.2 ± 4.8	73.0 ± 10.4
June	26.7 ± 3.3	77.2 ± 10.0
July	19.0 ± 2.5	63.7 ± 14.8
Aug.	40.3 ± 8.4	61.7 ± 12.0
Sept.	21.4 ± 7.8	31.6 ± 5.2

Seed Germination

When exposed to continually wet conditions, 16±2% of the seeds germinated after 7 d. When seeds in the WET ONCE treatment failed to germinate after 7 d, the protocol was altered to wetting the soil shortly after it dried out (about 3-day intervals). No seeds had germinated after 7 d more, so the soil was watered and kept moist to determine seed survival. Four days later (day 18 of the experiment) cotyledons appeared, but comparing the numbers of seedlings appearing after watering in the WET ONCE and the WET treatment, mortality in the former appeared to have been high (Table 3). No seeds germinated in the DRY treatment after 7 d either, and the protocol for them was shifted to 'wet when dry' (as described above). No seeds had germinated after 14 d more, and the soil was watered and kept moist to determine the relative seed survival. Four days later, seeds began to germinate (on day 25 of the experiment), and after 30 d mortality in that treatment appeared to be even greater than in the other treatments. In summary, St. John's wort seeds seem to require 7 d of continuous moisture, or slightly less after periodic watering. Periodic watering appeared to decrease survival, perhaps due to desiccation of very young seedlings.

Defoliation Experiment

The total shoot length produced by plants that were defoliated once only and by plants defoliated repeatedly was not significantly different. The 'control' plants produced

31.4±3.7 cm and the 'defoliated' plants produced 25.0±3.7 cm new growth ($t = 1.21$, $P>0.1$). An unexpectedly heavy amount of rain fell on Vancouver during the time of the experiment. In fact, rainfall on the U.B.C. field site during the experiment was within the range of rain that falls on the E. Kootenay at the same time of year (77.5 mm at U.B.C. *vs.* 63.7±14.8 mm at Elko, 1975–81). Thus, the result that compensatory growth of shoots after defoliation was equivalent to shoot growth of control plants suggests that the relatively abundant rainfall of the E. Kootenay may allow equally robust recovery from herbivory.

Discussion

The moist summer climate of the E. Kootenay appears to permit greater reproductive output of St. John's wort by enhancing germination, and may improve the ability of plants to recover from herbivory. In their native habitats *C. quadrigemina* and *C. hyperici* feed and reproduce in fall, winter, and spring. In Mediterranean climates the winter and early spring defoliation by adults and larvae is followed by the annual summer drought and has been regarded as crucial to successful St. John's wort control (Clark and Clark 1952). However, the severe winter weather of B.C. constrains beetle activity and temporally limits herbivore pressure on the weed populations.

In California and Australia, *C. quadrigemina* begin to mate and oviposit soon after they emerge from aestivation in early autumn. In contrast, mating and oviposition by *C. hyperici* in the autumn is delayed by as much as 4 months (Holloway and Huffaker 1951; Clark 1953; Harris 1962). The phenological difference between the species limits *C. hyperici* exposure to harsh autumn and winter temperatures and appears to confer a substantial advantage to *C. hyperici* in terms of survival and reproductive output (Williams, unpubl. data). In this system, as in any other, selection acts to improve the survival of individuals. The apparent selective advantage of *C. hyperici* in the E. Kootenay seems to be manifested in the beetle species composition there, where *C. hyperici* predominates (75% of the beetles in spring). While the delayed activity of *C. hyperici* improves their survival, the relatively short period of feeding limits the herbivore pressure on St. John's wort and, thus, reduces the level of biological control achieved.

Several studies have examined herbivory and discussed how insect predation on seeds (Louda 1982) and plant parts (see references in Derizo 1984) may limit plant populations. However, the influence of weather on the interactions of herbivores and their host plants, and successful control of weeds, such as St. John's wort and tansy ragwort (Myers 1980; Cox and McEvoy 1983), is crucial. In eastern B.C., and perhaps other moist areas, the St. John's wort plants appear to have an ecological advantage over their herbivores, due to their ability to tolerate habitat differences. I propose that the successful control of St. John's wort by *Chrysolina* around the world has resulted, in large part, from the herbivore acting in concert with summer water stress characteristic of a Mediterranean climate. When that stress is relieved, as it is in eastern B.C., herbivory by *Chrysolina* is not sufficient to limit St. John's wort populations. In such systems, biological control may be improved by augmenting the pressures on the plant imposed by other control agents, or with improved competition by native plants (Harris 1980).

In conclusion, the impact of herbivory on plant population dynamics must be evaluated in the context of other features of the plants' environment in order to improve the predictability of the outcomes of biological control strategies.

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