Exotics are probably the results of escapes from lakes such as Cow Lake that have been stocked in the past. *R. balteatus* and *C. rhotheus* were taken only above the falls. However, their apparent disrupted distribution is probably the result of sampling error since they are known from other nearby locations below the falls in the Clearwater and Snake Rivers (Maughan, 1976).

The major differences in species composition above and below the falls appeared to be the absence of *C. beldingi* above the falls. *C. beldingi* is the most abundant cottid in the lower Clearwater River and tributaries near the mouth of the Clearwater (Maughan, 1976) and presumably also the lower Snake River. Over much of the Clearwater, *C. rhotheus*, *C. beldingi*, and *C. bairdi* occur sympatrically (Maughan, 1976). Therefore, the absence of *C. beldingi* above the falls probably does not involve competitive exclusion or habitat change.

There is evidence that differences below the species level occur upstream and downstream of the falls. *C. columbianus* above the falls has been designated as a separate subspecies from populations below the falls (Smith, 1966), as has *R. balteatus* above and below the falls (Schultz, 1936). The form of *C. rhotheus* above Palouse Falls does not appear to be the typical *C. rhotheus* described by Smith (1882) and may represent a separate form (Bond, pers. comm.). The form of *C. bairdi* found in the Palouse drainage is not the form described as *C. hubbsi* (Bailey and Dimick, 1949) but is similar to that described as *C. punctulatus*. *C. bairdi* of the *hubbsi* form is the only *bairdi* form found in the Clearwater drainage to the south (Maughan, 1972).

The exclusion of *C. beldingi* and *C. bairdi* of the *hubbsi* form from above the falls would seem to indicate that the Palouse River and its tributaries were subjected to multiple invasions of cottid species and forms from centers of endemism; *C. beldingi* and *C. bairdi* of the *hubbsi* form are more recent invaders than *C. bairdi* ssp. and *C. rhotheus* ssp. Existing populations and distribution resulted from competition, elimination, or integration of these invaders with prior resident species and forms.

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Golden Chinquapin (Chrysolepis chrysophylla) in Washingt State: A Species at the Northern Limit of Its Range

Abstract

Golden chinquapin (*Chrysolepis chrysophylla*), an evergreen tree (Fagaceae), reaches its r limit in Washington as small outlier populations. Some Hood Canal colonies were defol an ascomycetous fungus in 1976 and may not survive. A small colony also occurs at th eastern edge of the Big Lava Beds, just north of the Columbia River. Small population duced vitality of some individuals, and human activity may adversely affect the fate of the in Washington.

Introduction

The occurrence of a species at the limits of its natural range has a particular fasc for the evolutionary biologist. Peripheral populations are likely to have different resources and environmental tolerances than those of populations in the heart species' range. When such an outlier is a spectacular evergreen tree, the interest status is enhanced. The distribution of the golden chinquapin (*Chrysolepis chrys.* (Dougl.) Hjelmqvist) is one such case.

Only two small colonies of golden chinquapin are known to occur in Washi one in Skamania County near the Columbia River and the other 320 km to the west in Mason County above Hood Canal. Just south of the Columbia River in n Oregon, it takes on a more continuous distribution in the Mount Hood area and ward through western Oregon to its southern limit in cismontane northern Califo

It is the purpose of this paper to report on the status of the outlier populati chinquapin in Washington. As a result of the efforts of members of the Wash Native Plant Society and others, a current account of the tree in its few isolated s can be given.

There are only two species of *Chrysolepis*, both native to western North A The other species, *C. sempervirens* (Kell.) Hjelmqvist, is a shrub of the mount California and southern Oregon. Until 1948, the western North American chinq had been retained in *Castanopsis*, a genus now reserved for old world, mainly t species. It was on the basis of features of the bur fruit and the inflorescence that H qvist (1948) established the genus *Chrysolepis* to embrace our two chinquapin s

Chrysolepis chrysophylla is an evergreen member of the Fagaceae (Oak Fa of arborescent shrub habit, or a tree to 45 m in height (Figs. 1, 2). It reaches i growth form as a tree in low elevation, cismontane valleys of northwestern Cal and southwestern Oregon. At higher elevations or in more xeric habitats, specime shrubs, not more than 5-10 m tall. It can occur in a variety of woody plant commu mostly with conifers like Douglas-fir and coast redwood. Nowhere is it commo rarely does it occur in pure stands.

1. Foliage and staminate flowers of *Chrysolepis chrysophylla*. Figure 2. Habit of tree, University of Washington campus. Figure 3. Defoliated tree, Jorsted Creek, Mason County, Washington. Figure 4. Close-up of defoliated branches. (Figures 1 and 2 by W. Marten; figures 3 and 4 by Sigurd Olsen).

For many years the only known locality of golden chinquapin in Washington along the Columbia River at Moffatt's Spring (now Bonneville Hot Springs, *ca.* 2 NW of North Bonneville) in Skamania County. The single collection was mad 1904 by M. W. Gorman (cited in Piper, 1906). Attempts by the present author others to relocate the Bonneville Hot Springs locality have failed. Activities conne with the human settlement of the area and with the construction of Bonneville] are likely to have caused its disappearance. Other collections since 1904 have beer stricted to the country adjacent to the Big Lava Beds in Skamania County (*ca.* 48 north of the Gorman locality) and to the disjunct locality west of Hood Canal in M County.

The Hood Canal Station

The Washington Environmental Atlas (Anon., 1975) shows three localities in Ma County; near Shelton, at Lake Cushman, and near Eldon. We have confirmed the oc rence of chinquapin in the lower reaches of the drainages of Jorsted Creek and Hamma Hamma River, both near Eldon. On 19 June 1976, members of the Washing Native Plant Society explored the second growth forest bordering the Jorsted Cr road. Specimens of golden chinquapin were located in section 32 (T24N, R3W3, about 2 km along Forest Service Road 248A, from Benchmark 998 ft (704.19 northwestward. All were nearly completely defoliated, indicating a pathological c dition (Figs. 3, 4). I comment on the probable causes and consequence of this def ation below.

The field party then continued northwest to enter the drainage of the Ham Hamma River and proceeded east, back down the river road to U.S. Highway 101. Ab 2 km west of the highway we found a single specimen of chinquapin, a fine tree o 15 m tall, showing no sign of defoliation.

A single specimen was also discovered just off U.S. Highway 101, between roadway and nearby Hood Canal, 2.5 km south of Jorsted Creek. It is a vigorous, healt tree, 6 to 8 m tall, with several erect boles from the root crown. One of the trunks h been cut and removed. It is possible that this specimen was transplanted to this priv beach property from nearby natural colonies.

In April of 1977, several of us reconnoitered a colony newly discovered by J Messmer, a Washington Native Plant Society member. The site is west and within sig of Highway 101. The habitat is a Douglas-fir and hemlock forest on a high bench a adjacent broken terrain, situated about 100 m above the level of the highway. It can reached by a private road leading west from milepost 322, *ca.* 1.6 km south of Jorst Creek. This is the largest of the known Hood Canal colonies. Here there are seve large trees with boles clear of branches 6-8 m upward to the dense, rounded crow Nearby we estimated that there were 150 to 200 smaller trees and saplings back of t high promontory, in open woods (recently thinned by selective logging). On t gravelly slide just below the bench where the largest specimens are growing, there a several bushy chinquapins, presumably seeded there from the mature specimens u slope. The latter produce fruits in fair quantity; beneath the trees we found the spe burs of the previous year's fruit crops.

The finest single specimen of chinquapin in the Puget Sound area is on the nor side of Kitsap Lake, just northwest of Bremerton in Kitsap County. It is 60 cm i liameter with twin trunks, reaching heights of *ca.* 15 m. The tree is on private property ıear a dwelling. Though its origin and history could not be determined, it most likely vas planted by former owners many years ago. The general vicinity is rather densely ɔuilt up with suburban residences. This single specimen is *ca.* 32 km east of Hood Canal; no intervening colonies have ever been sighted on Kitsap Peninsula. Chinquapins ɔlanted on the grounds of private residences have been observed in the vicinity of the Hood Canal natural colonies.

The chinquapins of the Hood Canal area are few in number, occur in isolated colɔnies, and are in habitats where the forest vegetation is frequently altered by human ıctivity. Moreover, the colonies in the upper Jorsted drainage are undoubtedly severely weakened by the defoliation we witnessed in 1976. The unseasonable loss of leaves is associated with a leaf spot caused by a fungus. Leaves on the ground and the few remaining on the trees all had a dense pattern of black pustules. Thus far the leaf spot symptom appears to be restricted to one colony, though it is only about 5 km west of the healthy grove of chinquapins just above Hood Canal. University of Washington mycologists have tentatively identified the pathogen as a species of *Didymella* (or *Venturia*), an ascomycete.

The Hood Canal stands of chinquapin occur with second-growth Douglas-fir forests of varying age classes and density. The chinquapin appears to be most compatible with Douglas-fir in relatively xeric sites, where the conifer stands are either open or young enough as not to shade the chinquapin. We observed at the milepost 322 site that the best trees were standing in the open, away from Douglas-fir. Also, the recent selective logging had left many spindly saplings of *Chrysolepis* that had evidently been shaded by the 40-60 year old Douglas-fir formerly present. It is our judgment that the fortuitous thinning of conifers at this locality will improve the growth and longevity of the younger chinquapins.

The Big Lava Beds Colony

South central Skamania County, Washington, contains one of the state's most spectacular geologic phenomena: 16,000 acres of land were covered by a Quaternary (450-4000 years B.P.; Hammond *et al.*, 1976) flow of lava leaving a lunar landscape of jumbled, jagged rock, not over 10 m higher (usually only 1-2 m) than the surrounding flat to sloping terrain. Since the flow, the contorted topography of the flow has been thinly colonized by elements of the adjacent flora and by a few exceptional species. A partial checklist of the lava bed's flora is given in the appendix to this paper.

When Don Jole reported in the June 1976 number of *Pacific Search* that he had sighted chinquapin in the Big Lava Beds country, we were anxious to investigate the find. After one failed attempt, in September of 1977 Mareen Kruckeberg and I made a careful search of the southeastern perimeter of the Big Lava Beds, and found several chinquapins in a healthy state. The trees are infrequent and local in flat forested terrain to the south of the lava beds proper. The approximate location of the trees is within section 29 (R9E, T4N); access is along U.S. Forest Service Road N501, *ca.* 2 km west of Forest Service Road N604. The chinquapins here are in both dense Douglas-fir regrowth and in older, more open stands of mixed conifers and hardwoods. The best specimens are in the latter habitat where the forest is composed of Douglas-fir, western hemlock, western white pine, grand fir, western yew, Pacific dogwood, vine maple, and

a rich variety of shrubs and herbaceous species. Individuals are widely spaced community, doing best in clearings within the forest. They average 5-15 m i and tend to have two to several boles per individual. The foliage showed no necrosis or fungal infection. The area is about 40 km north of the Columbia R the site of the 1904 collection at Bonneville Hot Springs.

Records of the growth of planted chinquapin have been kept at the Win Arboretum (Anon., 1959), located about 20 km due west of the Big Lava B Fourteen trees were planted in 1913, of which ten were surviving in 1956; t reached a height of 13.8 m,* showing the best growth of any hardwood specie collection. "The trees (in 1956) are tall and straight, of excellent vigor, and ı bear fruit. They have produced a large number of natural seedlings througł arboretum." A more intensive search in the Wind River drainage is likely tı other stands of chinquapin, though none are now around the Wind River Arł nor did we find any along the route from the Big Lava Beds to the Wind Riveı

State of the Outlier Colonies of Golden Chinquapin

A species at the limits of its range can be expected to have attributes not to b in the more centrally situated populations. Features likely to differ include ve vigor, growth-form (habit), size of populations, reproductive capacity, age-clas bution of individuals, and biotic interactions (pests, competitors, pollinators, c agents, etc.). Further, it would be expected that habitat features such as local regimes, topography, and substrates could differ from outlier status to the centeı range.

Taking the Hood Canal populations as the northernmost native populat chinquapin, we have found isolated specimens here that match in vigor those in r Oregon where the tree is more widespread. However, the one grove we reloc: Jorsted Creek is markedly reduced in vigor due to the defoliation, presumably by a fungus pathogen. Trees of the Big Lava Bed locality showed no sign of attack and the individuals are as healthy as those in localities where the species quent and more continuous in distribution (e.g., the Mt. Hood area of Cla County, Oregon).

Golden chinquapin is shade intolerant, at least in the northern sector of its It can easily be overtopped in growth by conifers, especially Douglas-fir. As me earlier, the Hood Canal population above milepost 322 (U.S. Highway 101) shov effects of conifer shading. Saplings and small trees of chinquapin that were clos rounded by Douglas-fir and western hemlock were spindly and leafless nearly t tips. Selective logging of the site may improve the chances of survival of thes On a nearby open promontory, the chinquapins have sturdy boles and ampl crowns. Following fire and/or logging, golden chinquapin can compete well for with the conifer regrowth. But given the more rapid growth rate of the conif chinquapin is sure to become suppressed in growth beneath the canopy of do needle-leaved evergreens. This adverse response of an evergreen hardwood to s has also been noted in the case of *Arctostaphylos columbiana* (Kruckeberg, 1977

Reproduction of chinquapin has been commented on by several authors (D

*Douglas-fir can be expected to grow 25.6 m tall in the same length of time.

1826; Jepson, 1910, Schopmeyer, 1974, Vandersal, 1939). It is said to fruit sparingly, and to set few seed with low germinability (14-59 percent). Seed stored at 41°F can remain viable up to five years (Schopmeyer, 1974). None of the authors comment on the occurrence of seedlings in the California and Oregon populations. We have not discovered seedlings or small saplings in the native groves of Washington, unlike the abundant reproduction of plantings at the Wind River Arboretum. It is not known if golden chinquapin, a monoecious species, is self-compatible. If it were, and if seed from selfed parents were less vigorous, then single isolated trees or small groves might have a lowered reproductive output.

Natural vegetative propagation by layering or suckering may possibly occur. Sucker growth could account for the clump or thicket-forming nature of certain specimens. Intentional coppicing to induce sucker growth has not been reported. Neither is it known if golden chinquapin can crown-sprout after fire. We must conclude, therefore, that the reproductive capacity of chinquapin is low and that the prospects for maintaining even small populations at the periphery of the range are not good. In the absence of natural or man-made disturbance, the isolated stands of chinquapin in Washington may not persist indefinitely.

Although such human activities as clearcut logging, burning, land development, etc. probably would eliminate the Washington colonies, other kinds of human interference in chinquapin habitats may be beneficial. Selective logging or pre-commercial thinning of associated conifers and deciduous hardwoods (maple, alder, and cottonwood) prevent suppression of the slower growing chinquapin, and provide a suitable seed bed and nursery for chinquapin progeny. The Washington Native Plant Society will encourage custodians of forest land to manage chinquapin habitats in Washington so as to preserve the existing trees and to foster their reproduction.

Our field studies of golden chinquapin might be expected to give some clues as to the causes for both the isolated Washington colonies and for the northward termination of the species' range. Yet some of the small isolated populations seem just as healthy as those in the core portions of the species' range, while one population appears in danger of extinction; size of population, then, is not the limiting factor.

Physical factors in the environment are not perceptibly different between northern Oregon and the outlier habitats in west central Washington. Regional climates from the Columbia River and northern Oregon to Puget Sound are not appreciably different, especially when one considers local climatic regimes, some of which would closely match those in chinquapin habitats further south. It is possible that occasional occurrences of extremes in climate could limit the ability of the peripheral isolates to persist or to expand their ranges northward. Mason (1936) has argued for this interpretation, using the example of coast redwood and the growth-deterring conditions of an extreme year (1932). Perhaps we are obliged to resort to the suitably vague biogeographic law that species are limited in their distributions by limits in their physiological tolerance to environmental factors (Cain, 1944). But we are still left to wonder which particular set of environmental attributes (and at what intensities) is operating to determine the limits to distribution.

Unique and even capricious episodes of dispersal no doubt have placed outliers of a species well beyond its usual range. Two modern authors (Brockman, 1958; Scheffer, 1961) have seized upon one such explanation, first hinted at by David Douglas in 1826.

Douglas found chinquapin seeds in the crop of a band-tailed pigeon he had s 320 km from the nearest source of the tree. Could the Washington plants h from such a chance dispersal? The same explanation has been invoked to ac the very local occurrence of *Pinus ponderosa* on the Fort Lewis prairies, the c tion of ponderosa pine west of the Cascades in Washington.

If the geologist's aphorism is reversed to read "the past is a key to the pre are led to a paleoecological basis for present chinquapin distribution. Wolfe lists chinquapin as one of many woody plants that were present in the early an Miocene flora of the Pacific Northwest. Not only did it persist through the Pl but Wolf suggests that it could have evolved from a summer-wet Mixed M forest species to become adapted to the more xeric summer-dry conditions of Pleistocene, especially during the warm (Hypsithermal) interval between 5 3000 years B.P. In this view, chinquapin may be interpreted as a relictual s present, persisting locally from a time when it could have been both more c and further north in its distribution.

Appendix

Partial list of the plants of the Big Lava Beds, Skamania County, Washington.

Trees
- Abies lasiocarpa (northern sector)
- Pseudotsuga menziesii
- Pinus contorta
- P. monticola

Shrubs
- Acer circinatum
- Arctostaphylos columbiana
- A. nevadensis
- Garrya fremontii
- Holodiscus discolor
- Juniperus communis
- Pachystima myrsinites
- Rhamnus purshiana
- Vaccinium parvifolium

Herbs
- Apocynum androsaemifolium
- Cheilanthes gracillima
- Comandra umbellata
- Cryptogramma crispa
- Goodyera oblongifolia
- Penstemon fruticosus
- P. rupicola
- Polystichum munitum
- Xerophyllum tenax
- Woodsia oregana

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If the geologist's aphorism is reversed to read "the past is a key to the present," we are led to a paleoecological basis for present chinquapin distribution. Wolfe (1969) lists chinquapin as one of many woody plants that were present in the early and middle Miocene flora of the Pacific Northwest. Not only did it persist through the Pleistocene, but Wolf suggests that it could have evolved from a summer-wet Mixed Mesophyte forest species to become adapted to the more xeric summer-dry conditions of the post-Pleistocene, especially during the warm (Hypsithermal) interval between 5000 and 3000 years B.P. In this view, chinquapin may be interpreted as a relictual species at present, persisting locally from a time when it could have been both more continuous and further north in its distribution.

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Phenological Relationships of Spiraea betulifolia Pall. and Apocynum androsaemifolium L.

Abstract

The phenology of two widespread understory species was examined at three elevations during seasons, 1972 and 1973. Occurrence of several identified phenological phases related well to accumulated temperature at the site but poorly to calendar date or soil moisture content. Phenol cal phases of transplant stock from high to low elevation and the reverse followed native pl at the site in the case of *Spiraea*, but were seemingly insensitive to local control in the high to transplants of *Apocynum*.

Introduction

Forest and range sites, especially in the mountainous terrain of western North Amer can range in local climate from desert to alpine within short distances. Climatic measu ments at all locations would be difficult. A chronology of the stages of native plant velopment (phenological phase) may be helpful in comparing climatic regimes : their seasonal progression, especially at harsh sites. Such a chronology should l eventually to a more informed selection of management techniques.

The main requirements for precision in site evaluation by this method are sensitivity of the phenological phase to climate and the ability to determine some p sumably causal relationship between phenological phase and the climatic factors. though some phases of plant development may be controlled by a single factor, the pl in general responds to a composite of external and internal controls. Due to simplic and to past successes, a thermal index is often used in describing the phenological lationship. Wang (1960, 1972) presents an interesting historical account of devel ment of phenological observations and the thermal index and evaluates performance this approach.

To determine the utility of phenology in evaluating climate at remote forest si the relationship between phenological phase of two common understory plant spec and thermal and soil moisture regimes at three elevations was examined. The elevatic selected encompass the major portion of the elevational range of distribution of the t species.

Methods

Spiraea betulifolia Pall. (birchleaf spirea) and *Apocynum androsaemifolium* L. (spre ing dogbane) were selected for evaluation in this study. *Spiraea* is a rhizomatous sh