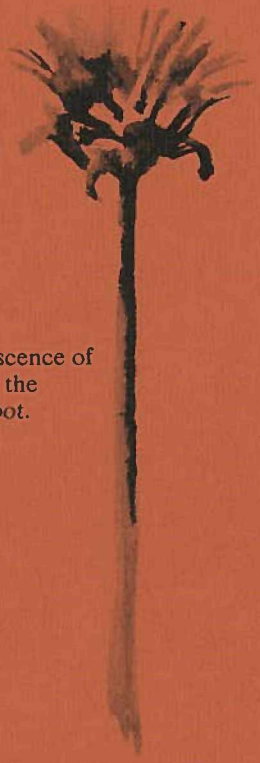
DAVIDSONIA

VOLUME 5 *NUMBER 3* *Fall 1974*

Cover

Fruiting branch of *Rhus glabra*, Smooth Sumac. Leaf coloration in the fall can be quite spectacular.



A dried fruiting inflorescence of *Balsamorhiza sagittata*, the Arrow-leaved Balsamroot.

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Heterostyly

FRED R. GANDERS

Since ancient times man has been fascinated by the multitude of colours and forms exhibited by flowers. Flowers, however, are not primarily for human edification; they are the reproductive organs of the plant. They reflect the amazing diversity of floral structure evolved to attract pollinators and promote cross-fertilization.

One of the most intriguing pollination systems, at least to me, is heterostyly. In a heterostylous species, such as many of the primroses, two kinds of plants occur which differ in the structure of their flowers. Half the plants produce flowers with a long style and short stamens. These are called long-styled or "pin" flowers. The other plants produce flowers with a short style and long stamens, referred to as short-styled or "thrum" flowers. Stigmas in pin flowers correspond in position to the anthers in thrum flowers, whereas pin anthers correspond in position with thrum stigmas. Thus the stigmas and anthers are reciprocally positioned in flowers of the two forms.

The terms "pin" and "thrum" have a quaint derivation. Many years ago English florists referred to long-styled primroses, which displayed the globular stigma at the mouth of the corolla tube, as pin-eyed. Short-styled flowers which displayed the anthers were called thrum-eyed. Thrum was a term for the ends of weaver's threads, and the cluster of anthers apparently reminded some primrose-growing weavers, or weaving primrose growers, of such threads.

The first recorded observation of heterostyly was made by the Flemish herbalist Clusius in 1583. However, it was not until the mid 19th Century when the German botanist Hildebrand, who coined the term heterostyly, and Charles Darwin began experimenting with heterostylous plants that the remarkable nature of this floral dimorphism was discovered.

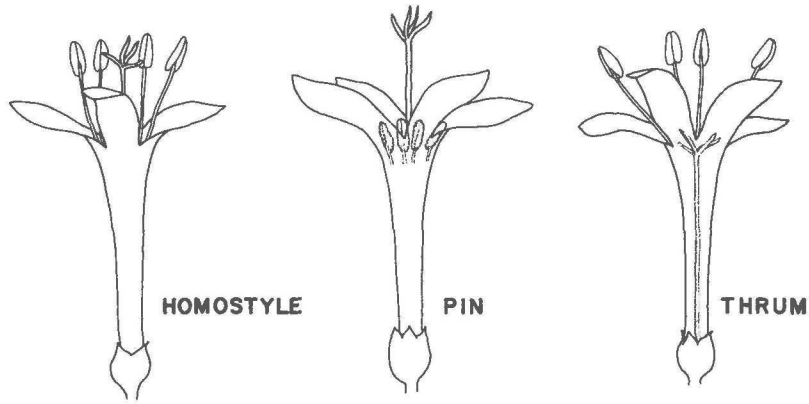


FIGURE 1. The three flower types that may be found in heterostylous plants, i.e., *Mitchella repens*.

Darwin carefully self-pollinated the pin and thrum forms of the primrose, as well as making crosses between plants of the same form and crosses between plants of opposite form. Self-pollination and pollination within a form failed to produce seed, but pollination between pins and thrums were fully fertile. Darwin termed these fertile pollinations between the forms legitimate, and those within a form illegitimate. He concluded that heterostyly was a system to ensure cross-fertilization between pins and thrums.

Darwin microscopically examined a moth and two kinds of bumblebees that his son caught visiting primroses, and found that most of the pin pollen had adhered to the tips of the insects' proboscises and most thrum pollen to the bases of their proboscises.

He concluded that the difference in another position between pins and thrums caused their pollen to be deposited on different parts of pollinating insects. He suggested that the part of a pollinator carrying pin pollen would then be most likely to come in contact with a thrum stigma, and vice versa, because of the reciprocal positions of the floral organs. This would ensure that legitimate pollination took place.

Since Darwin's time, much has been learned about heterostyly, particularly about the genetics controlling the floral dimorphism and the genetic control of legitimate and illegitimate pollinations.

When a plant produces functional ovules and pollen but is physiologically incapable of self-fertilization, it is said to be self-incompatible. Self-incompatibility in heterostylous plants is controlled by a complex gene with two alleles (alternative character states, like blue eyes or brown eyes in humans). This gene also controls the morphology of the flowers, determining whether stamens are long or short, and so on. Therefore all pin plants have the same self-incompatibility gene and pollinations between any pin plants are self-incompatible. The exact physiological mechanism of incompatibility is poorly understood, but when pin pollen is deposited on a pin stigma, it fails to grow a pollen tube, or the pollen tube stops growing in the style, and never reaches the ovary where the fertilization of ovules occurs. Thrum pollen on a pin stigma is not inhibited in this way because thrum plants have a different self-incompatibility allele.

Darwin's hypothesis that the difference in flower structure between pin and thrum promotes legitimate pollination has been tested only recently. In some heterostylous species, pin and thrum pollen grains differ in size or shape, so they can be distinguished under the microscope. I have collected stigmas from natural populations of several heterostylous species, counted the number of pin and thrum pollen grains on each type of stigma, and compared these numbers with what would have been expected if pollination had been random and the floral dimorphism made no difference. The details are too tedious to recount here, but the results showed that while heterostyly works far from perfectly, it does significantly increase the proportion of legitimate pollinations.

Heterostylous flowers often show other differences between pin and thrum, besides stamen and style length and pollen size or shape. In some, such as buckwheat, thrum flowers are larger than pin flowers. The corolla may be shaped differently in pins and thrums. Darwin noted that in the British cowslip, "Village children notice this difference, as they can best make necklaces by threading and slipping the corollas of the long-styled flowers into one another." Whether pin form cowslip necklaces are still in vogue in English villages I don't know.

More than 500 heterostylous species are known, scattered in more than 20 families of flowering plants. Since these families are not closely related, heterostyly must have evolved several times, a remarkable example of the independent convergent evolution of a complex pollination system. Heterostylous plants are found in all sorts of habitats, from the arctic to tropical rainforests, alpine regions, deserts, bogs, seashores, and even floating on water. The floating water hyacinth, *Eichhornia crassipes,* which is such a pest in subtropical and tropical waterways, is heterostylous.

British Columbia is rather poor in native heterostylous species. The bogbean, *Menyanthes trifoliata,* and related *Fauria crista-galli* are heterostylous inhabitants of bogs and lakes. Our only other heterostylous species is *Primula mistassinica* of the Rockies, although there are unconfirmed reports of heterostyly in *Cryptantha leucophaea* and species of *Douglasia.*

Heterostylous plants are not of much economic importance. Buckwheat, *Fagopyrum esculentum,* is heterostylous, and curiously, it is the only species that exhibits heterostyly in the large family Polygonaceae. The drug quinine is derived from heterostylous tropical trees of the genus *Cinchona,* and the illicit drug cocaine comes from *Erythroxylon coca,* also heterostylous.

FIGURE 2. Pin and thrum flowers of *Lithospermum californicum.*

Heterostylous garden ornamentals include *Forsythia* and most cultivated primroses. The primrose, in fact, has become the "classic" heterostylous plant and has received more study than any other. The partridgeberry, *Mitchella repens,* a heterostylous native of eastern Canada and the United States, is sometimes grown as a terrarium plant. Heterostylous species of *Oxalis* are grown as house plants and heterostylous species of *Lithospermum, Lythrum, Linum, Limonium,* and *Pulmonaria* are occasionally cultivated. *Lythrum salicaria,* purple loosestrife, is sometimes found in wet areas in British Columbia, having been introduced originally from Europe. Several years ago it was heavily promoted as a "new" garden flower.

Lythrum and *Oxalis* deserve special mention. They have an unusual kind of heterostyly called tristyly, in which there are three forms of flowers instead of just two. There is a long-styled form, with mid-length and short stamens, a mid-styled form, with long and short stamens, and a short-styled form, with long and mid stamens. The genetics and legitimate pollination relationships become quite complicated, but basically any one form can be fertilized by the other two.

One interesting aspect of heterostyly is that sometimes it breaks down. Due to rare recombinations within the heterostyly gene, a form is produced that has the long style length of a pin and the long stamens of the thrum form (or conversely, the short style of a thrum and short stamens of a pin). Such plants are called homostyles. In most homostyles the pollen from long stamens behaves like thrum pollen so it can legitimately pollinate the long pin-like style, and the plants are therefore self-compatible. Since the anthers and stigma are at the same level in the flowers, self-pollination is likely. If these plants arise in an environment where self-pollination is advantageous, the homostyles may increase or completely replace the heterostylous plants. It has been shown experimentally that some homostylous *Primula* species originated in this way, and the homostylous wild primroses in British Columbia, *Primula incana, P. stricta,* and *P. egaliksensis,* presumably did so too. Because these homostylous primroses are self-pollinating and do not need to attract insects, it is not surprising that their flowers are relatively inconspicuous.

Despite one hundred years of investigation, much remains to be learned about heterostyly. Because of the unique features of this pollination system, heterostylous plants will continue to be useful in the study of pollination biology, plant genetics, and evolution. I suspect they will also continue to be fascinating to naturalists, gardeners, and others who like flowers.

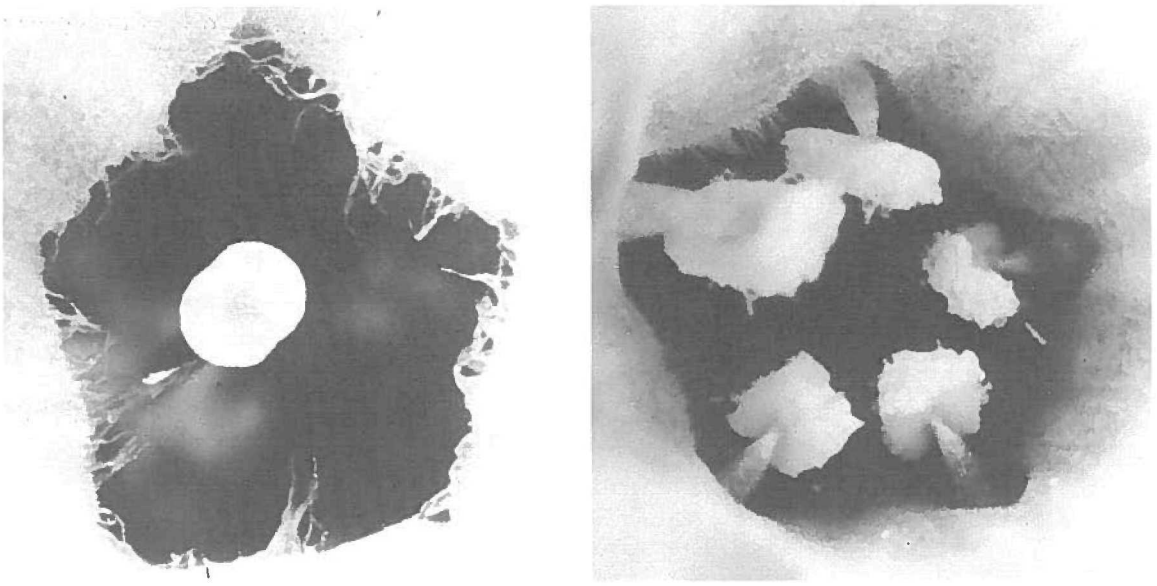


FIGURE 3. Deep throats of pin and thrum flowers of *Amsinckia spectabilis* var. *microcarpa,* as they might appear to a visiting bee about to insert its tongue. In the pin form (left) the anthers are low in the corolla tube (not visible in the photograph), and in the thrum form (right) the stigma is low in the corolla tube. Thus the tip of a bee's tongue is most likely to pick up pin pollen and deposit it on thrum stigmas, while the face would contact thrum pollen and pin stigmas.

FIGURE 4. Thrum, homostyle, and pin flowers in the partridgeberry, *Mitchella repens.* Homostyles usually result from genetic recombination within the heterostyly gene, combining the style length of the pin form with the stamen length of the thrum form.

New Garden Areas

ROY L. TAYLOR

This past summer the Botanical Garden was expanded by the addition of some 30 acres of campus land to the existing areas currently under its management. The new acres are located at the tip of the Point Grey peninsula and comprise landscaped and natural forested areas of the Graham House School of Social Work, Cecil Green Park, extended facilities of the Department of Anthropology, the new Museum of Anthropology, and the former President's residence. The area comprises a strip of land running along the brow of the cliffs at the northwestern tip of Point Grey and is separated from the rest of the campus by Northwest Marine Drive.

The assignment of the area to the Botanical Garden was the result of an agreement by the University with the Provincial Government and the Vancouver Board of Parks and Recreation that the area would be maintained as a park-like setting for the use of the University and the surrounding community. The new area contains a number of academic facilities with gardens and natural plantings that are particularly important as education displays for the Museum and Botanical Garden. The Botanical Garden will be responsible for the planning and management of the landscaped plantings and natural areas. Development of these will enhance the use of the area by both the University and local communities.

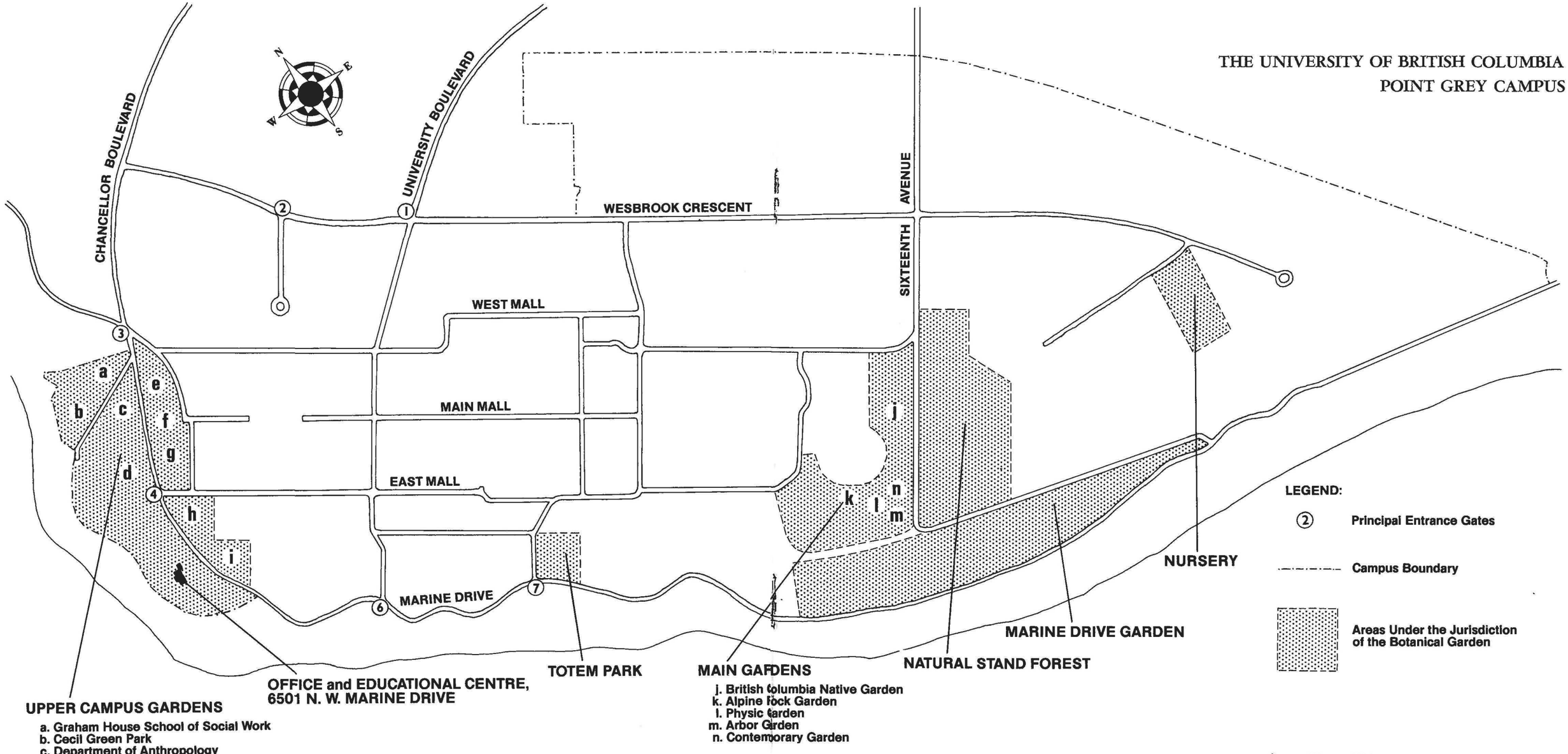
The foreshore area of the Point Grey peninsula is under the jurisdiction of the Greater Vancouver Regional District and managed as a recreational area by the Vancouver Board of Parks and Recreation. Much of the peninsula is bounded by cliffs that rise sharply to more than 300 feet above the sea. One of the immediate concerns for the area is the continuing erosion of the cliffs through natural and man-made causes. The University, Provincial Government and the Vancouver Board of Parks and Recreation are co-operating in a search for ways to abate the erosion and stabilize the cliffs against further erosion. The Botanical Garden is initiating a research program on the types of vegetation suitable for assisting the stabilization program.

July 1 saw the start of the renovation and development of the new area. The Botanical Garden is working closely with the architects of the new Museum to develop plant collections that will enhance the establishment of representative Indian villages within the landscaped areas of the Museum complex. Particular attention is being focused on those plants of ethnobotanical interest to the native peoples of the Pacific Northwest. The Gardens around the former President's residence will be used as demonstration units for the continuing education programs offered by the Botanical Garden and will provide resource material for academic classes.

The office and educational centre for the Botanical Garden is now established in the former President's residence. The move to these new facilities will allow us to provide expanded service to both the public and the University. In addition, the Botanical Garden will be in a position to develop a closer liaison with the Alumni of the University as we are now responsible for the maintenance and development of the garden components at Cecil Green Park, the home of the Alumni Association.

A map of the campus at UBC showing the areas under the jurisdiction of the Botanical Garden is shown on pages 30 and 31.

THE UNIVERSITY OF BRITISH COLUMBIA
POINT GREY CAMPUS



UPPER CAMPUS GARDENS

a. Graham House School of Social Work
b. Cecil Green Park
c. Department of Anthropology
d. Museum of Anthropology
e. Triangle Garden
f. Rose Garden
g. Faculty Club and Graduate Centre
h. International House and Panhellenic House
i. Nitobe Memorial Garden

MAIN GARDENS

j. British Columbia Native Garden
k. Alpine Rock Garden
l. Physic Garden
m. Arbor Garden
n. Contemporary Garden

Rhus glabra L.

SMOOTH SUMAC, SCARLET SUMAC
Member of the Family Anacardiacae

Natural Distribution

Rhus glabra occurs from southern British Columbia south on the east side of the Cascade Mountains through Oregon and Nevada to Mexico, east to New England, and south to Florida. It has a very wide distribution and is found throughout the contiguous United States. In British Columbia the species occurs in the southern Dry Interior at lower elevations from Princeton through Keremeos, the Nicola Valley, Lillooet and Grand Forks.

Habitat

Rhus glabra is found in poor, dry, often sandy soils in sunny situations, e.g., old fields, roadsides, margins of woods, and power line right-of-ways. In British Columbia it is often found in Ponderosa Pine and Douglas Fir forests. According to Krajina (1959) it forms part of the edaphic climax vegetation in the Ponderosa Pine — Bunchgrass Bioclimatic Zone.

Description

An erect, stout, usually sparsely branched shrub, or occasionally a small tree, (0.5-)1-3(-6) m tall. Branches stout, often crooked and twisted, glabrous or sparsely to densely pubescent near the inflorescence. Contains a resinous or milky, often acrid but apparently innocuous juice. Characteristically occurs in thickets because of its tendency to reproduce vegetatively by suckers.

Root system shallow with very long and robust roots.

Bark smooth, reddish brown.

Twigs stout, pubescent, 3-sided, light reddish-brown at first, becoming smooth and grayish-brown with age. Leaf scars C-shaped, more or less raised and nearly encircling buds. Lenticels scattered on older stems. Pith extensive, continuous, often pink or brown.

Buds moderate or rather small, solitary, sessile, round-ovoid, hairy and indistinctly scaly or with 3 or 4 evident scales; end-bud often lacking.

Leaves deciduous, alternate, 3-4 dm long, compound, odd-pinnate with (7-)11-29(-31) leaflets, with a characteristic "plume-like" appearance from a distance. Leaflets narrowly ovate to elliptic, subrevolute to serrate or rarely subentire-margined, (2.5-)5-12 cm long, with apex acuminate; leaves deep to light green and smooth above, paler and somewhat glaucescent beneath, becoming intense red or orange-yellow in autumn. Lateral leaflets subsessile, 6-12 cm long, 1.5-3 cm broad, base rounded or cuneate if leaflet sessile, lateral petiolules about 1 mm long. Terminal petiolule 0.2 cm long, rachis segments about 3 cm long, and petioles 8-11 cm long, thick and exstipulate.

Flowers April to July depending on the range. Inflorescence a dense terminal thyrus, (0.5-)2.0(-4.5) dm long and about 7 cm broad. Bracts linear-lanceolate, deciduous, 1 mm long and 0.4 mm broad, pointed at apex, pubescent or glabrous on outer surface and glabrous within, ciliate with simple hairs, and 1 per flower. Flowers many but inconspicuous, regular, petiolulate and mostly imperfect; the plant polygamo-dioecious. Calyx lobes (3-)4-6(-7), persistent, ovate to narrowly ovate, somewhat acute at apex, 1-2 mm long and 1 mm broad, very sparsely pilose on outer surface and pilose on inner surface. Petals equal in number to sepals, (0.5)1-2mm long and 1mm broad, shorter in pistillate than in staminate flowers, narrowly ovate, acute and curved inward at tip, yellowish or greenish to white, short-pilose on outer surface and long-pilose on inner, imbricated in bud, spreading in anthesis, deciduous. Stamens 5, alternate with petals inserted at base of annular lobed fleshy disk at base of corolla; filaments same length as sepals; anthers lanceolate, 1.5 mm long and 0.8 mm broad, pistillate flowers with 5-10 staminal vestiges. Style short, 3-parted to just below stigma; stigmas 3. Ovary superior, 1-celled; ovule 1, basal.

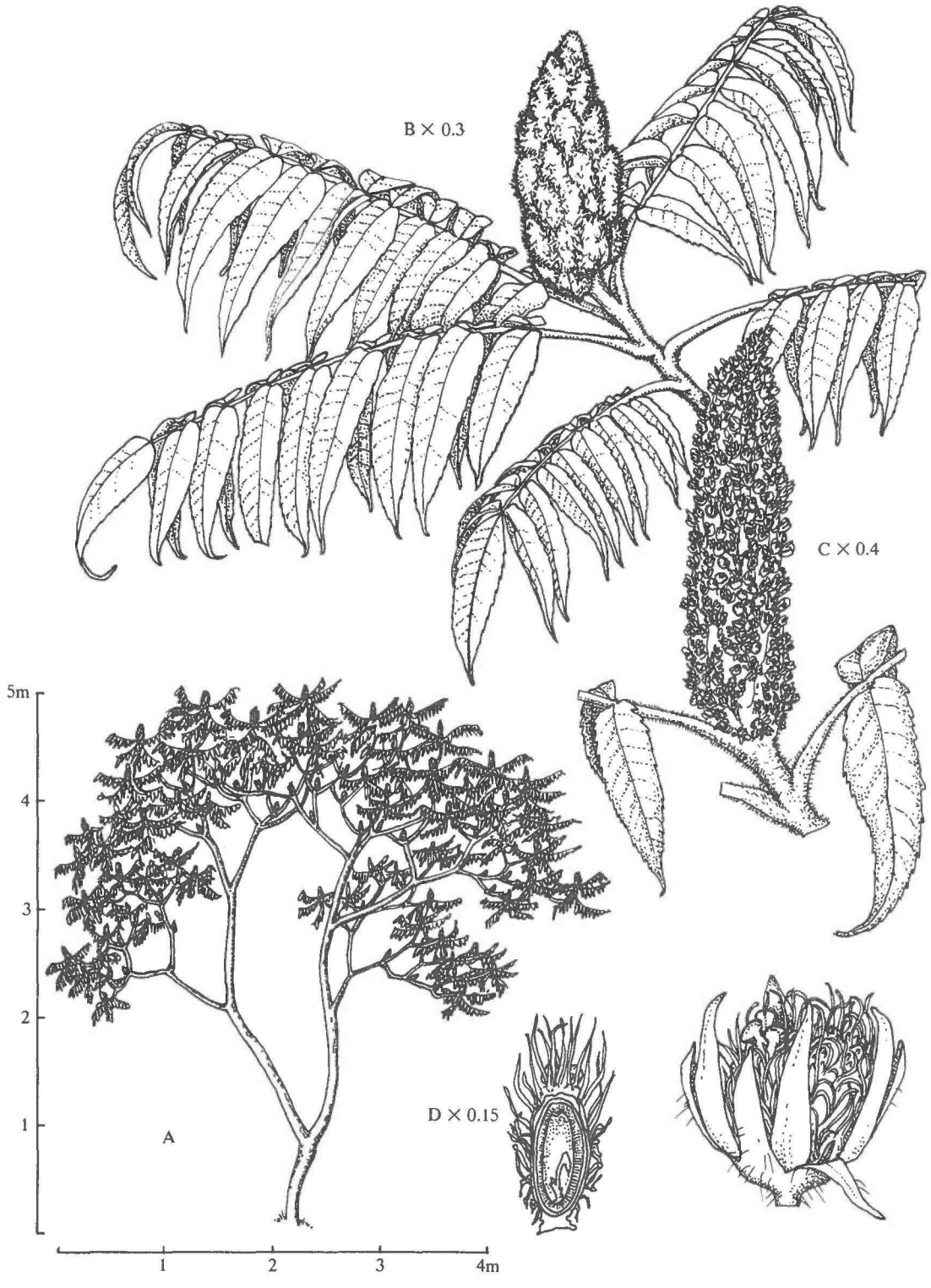


FIGURE 5. *Rhus glabra*. A. Habit of mature shrub, B. fruiting inflorescence, C. flo glandular hairs, E. single flower with vestigial stamen exhibited above reflexed

Fruit a dry berry-like drupe, 4-5 mm long and about as broad, somewhat flattened, red, densely reddish-hairy, very glandular. Seed solitary, 2.5-3 mm long, 2-2.5 mm broad, smooth, slightly larger at one end, testa bony. Fruits may form a conspicuous conical mass near top of shrub, and ripen in August to September depending on the range.

Propagation

Easily propagated by seeds sown in late autumn or stratified for 5 months at greenhouse temperatures, then for 3 months at 40°F before sowing. If germination does not occur after several months, provide a second cold period. Root cuttings have been successful when taken in autumn or early spring, cut into 5-10 cm lengths and inserted in shallow trenches. Shrubs also sucker readily.

Transplantation

Transplanting is most successful when plants are young. Older specimens do not transplant well, owing to the extensive root system.

Conditions for Cultivation

The shrub is fast-growing, taking only 1-4 years to assume a mature role in the landscape. The recommended hardiness zone in Canada is 2b (Sherk & Buckley, 1968). *Rhus glabra* thrives in any type of soil and will survive extreme heat and cold, but it does best on rather poor, dry, sandy soil in a sunny situation. No regular pruning is necessary, although the shrub will make a handsome foliage plant if pruned to the ground each year or every other year in February.

Landscape Value

Smooth Sumac is often used as an ornamental plant because of the attractive foliage with its brilliant autumn coloration — it is one of the most brilliantly colored native plants. The reddish fruits are also attractive and often remain on the plant all winter when the bare crooked branches make fine silhouettes. It is best suited for naturalizing in a large garden, especially in a mass planting on a hillside where it can be seen to good advantage and the suckering habit presents no problem. The shrub is also attractive when planted among evergreens which show off the fall foilage to best effect. It may also be used as a screen planting at a summer cottage.

Availability

Rhus glabra is available from a few nurseries in Canada, mainly in the east, but nurseries in British Columbia should be able to obtain it.

Varieties and Ornamental Cultivars

Rhus glabra is considerd a polymorphic species with many variations, e.g., color of leaves, glaucescence, number of leaflets, and form. These variations are apparently quite independent of one another and occur throughout much of the range of the species.

Two rather marked varieties do occur: *Rhus glabra* var. *laciniata* Carriere (f. *laciniata* (Carriere) Robinson or 'laciniata') and *Rhus glabra* var. *borealis* Britton. The laciniate-leaved variety, found in Pennsylvania, Delaware and Indiana, is a stoutly-branched glabrous shrub with leaves bipinnately compound and with 19-29 pinnae, each pinna with 3-11 leaflets; lateral leaflets lanceolate, 3-5 cm long and 0.6-1 cm broad, entire, serrate of laciniate; terminal leaflet laciniate. The general effect of the leaves is fern-like, but they are inclined to revert to type. The more northern variety, var. *borealis,* found in Ontario, Michigan and Minnesota, has slender, sparsely pilose branches; leaflets are few, small and serrate, and the fruit is covered with glandular hairs about 0.5 mm long. It has been suggested that this may be a hybrid of *R. typhina* and *R. glabra,* in which case it should be known as *R.* × *borealis* (Britt.) Greene. *Rhus* × *pulvinata* Greene, another hybrid of the same parentage with soft felt-like leaflets, is found in the eastern part of the continent as far west as southern Ontario and Michigan and south to Indiana and Virginia.

Other Uses

The Indians of North America have long used *Rhus glabra* in many ways — the fruit was used to make a cooling drink in summer or cooked with maple syrup to give a hot drink in the winter. The Iroquois ate newly grown sumac sprouts raw as a salad and alterative. It has been suggested that all parts are suitable for medicinal purposes, and an infusion of *R. glabra* was once listed in the Pharmacopoeia of the United States. The Fraser River Lillooet Indians of British Columbia used some parts of the shrub to remove warts, whereas the Thompson Indians drank a decoction of the stems as a cure for syphilis. It was said to be powerful medicine, but dangerous if made too strong or taken in too large a dose. All parts can be used for dyeing wool or cotton; the leaves and young shoots contain large amounts of tannin, producing a tan to dark brown color, whereas the ripe berries will give a yellowish-tan or gray color depending on the mordant used. The eastern Northern American Indians boiled a mixture of the central pith of the stems and bloodroot to give an orange color for dyeing rush or woven bark mats and other materials.

It has also been suggested that the shrub may be of economic value as a ground cover to protect land from erosion, allowing revegetation of denuded areas. Smooth Sumac also has a value in wildlife management, as the 'fruits' and shoots supply food during late winter and early spring to deer and many game birds.

Diseases and Problems of Cultivation

The shrubby sumacs are known to be weak-wooded, breaking easily in heavy snow and ice storms. *Rhus glabra* tends to produce suckers particularly when the roots are disturbed by soil cultivation, and these may become a nuisance in lawns and mixed plantings unless the shrub can be located in an area where suckering does not impede growth of other plant materials.

Only one fungal disease apparently affects *Rhus glabra* in the wild in British Columbia — *Coryneum* sp. causes leaf spot (Toms, 1964). No information is available on insect diseases in the province.

The genus name *Rhus* is the ancient classical Greek name of Sicilian sumac, *Rhus coriaria* L., a native of the Mediterranean region. It may be derived from *rhous,* reddish, referring to the color of the fruit and perhaps to the brilliant autumn fall foilage. The specific name *glabra* means glabrous or without hairs. The common name Sumac or Sumach is from the Syriac *summaq,* 'red', referring to red dye obtained from the Mediterranean shrub.

The type locality of the species is eastern North America. The plant was first published in K. Bauhin's 'Prodromus' in 1620, although it was wrongly reported as coming from Brazil, and it was later named by Linnaeus. It was introduced into England in or about 1726 when it was grown by a nurseryman Christopher Grey at Fulham, although the earliest known date of cultivation in western gardens was about 1620.

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Botanical Garden News and Notes

University Recognition of Gardeners as a Trades Group — For a number of years the Botanical Garden has been concerned that the gardeners on the Campus should be a recognized trades group. The initial step was taken during 1973, when Mr. Ken Wilson of the Botanical Garden staff was appointed by the Personnel Department as chairman of a review and recommendations committee to establish the guidelines for the recognition of the trades status. During the late summer, approval was given by both the Canadian Union of Public Employees (C.U.P.E.) and the University for recognition of gardening as a trade at the University. Review of staff was undertaken, leading to reclassification of members of the staff involved. Of particular importance to the Botanical Garden was the establishment of two new employee categories, namely Horticulturist 1 and 2. These positions provide for the development and employment of highly trained specialists in horticulture, a necessary prerequisite for successful development of a Botanical Garden. The Garden is proud to have played a leading role in the recognition of the skill and knowledge required of plantsmen on the staff of the University.

Initiation of an Apprenticeship Program — The Botanical Garden commenced this fall the development of a specialized apprenticeship training program to augment the existing Department of Labour Program in the Province of British Columbia. The program is under the direction of the Supervisor of Operations. A course outline for use by apprentices was published in co-operation with the Department of Physical Plant and five members of the current Botanical Garden staff are participating in the program. The first graduates of the program are anticipated in the summer of 1976.

Staff Member Part of Expedition to Peru — Mr. A. James MacPhail participated in a special expedition to Peru by members of the American Rock Garden Society and the Alpine Garden Club of British Columbia. A total of four weeks were spent in Peru and Equador and many alpine regions were explored. A large number of unusual and interesting plants were returned to Canada for incorporation into both private and public collections. Many of these plants will find their way into the new Alpine Rock Garden at UBC.

Educational Program Initiated for Senior Citizens — A special program developed in co-operation with the Centre for Continuing Education and the President's Office was initiated during the summer. Six courses, each one week long, were given to a total of 120 senior students. Special attention was devoted to the care and development of plant materials of particular interest to the senior citizen and to the small urban home-, apartment-or townhouse-dweller. The program was put on for the senior students without cost and proved to be a great success.

CLIMATOLOGICAL SUMMARY*

Data *1974*	*July*	*August*	*September*
Mean temperature	58.30°F	62.35°F	61.35°F
Highest temperature	77.0°F	81.0°F	81.0°F
Lowest temperature	47.0°F	48.0°F	45.0°F
Grass minimum temperature	36.0°F	38.0°F	32.0°F
Total rainfall/No. days with rainfall	3.72"/11	0.16"/3	1.68"/3
Total snowfall/No. days with snowfall	0	0	0
Total hours bright sunshine/possible	241.6/482.5	290.6/439.0	243.6/372.2
Max. wind speed for 1 hour/direction	12/NW & SE	10/N, E & SE	16/N
Mean mileage of wind at 3'	73.4	69.6	70.8
Mean mileage of wind at 40'	99.1	97.1	99.9

**Site: The University of British Columbia, Vancouver, B.C., Canada*
Position: lat. 49° 15'29"N; long. 123° 14'58"W. Elevation: 342.6'

A fruiting inflorescence of *Achillea millefolium*, Common Yarrow.

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Mrs. Rosamund Pojar (Research Assistant)

Eriogonum niveum, the Snow Umbrellaplant, an intriguing plant of the dry Interior that provides a delicate pink hue to the sagebrush hillsides. The perianth segments are thin and papery and the plant itself is white-pubescent, hence the common name.

DAVIDSONIA

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