The biology of Canadian weeds. 102. *Gaultheria shallon* Pursh.

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Fraser, L., Turkington, R. and Chanway, C. P. 1993. **The biology of Canadian weeds. 102. *Gaultheria shallon* Pursh.** Can. J. Plant Sci. **73**: 1233–1247. *Gaultheria shallon* Pursh., salal (Ericaceae), is a densely growing perennial evergreen shrub occurring only from the panhandle of Alaska along the entire coast of British Columbia to southern California; it is of native origin. Salal grows on a wide range of soil types and textures, and is abundant in open habitats near the coast particularly on rocky knolls and along bluffs. It is a persistent, pervasive woody perennial and is a serious competitor with coniferous species. The plant produces numerous seeds but the most significant and effective form of colonization is through vegetative spread. Several herbicides are recommended for control of the the weed but it is both resistant and resilient to many herbicides. This contribution summarizes the known biological data for this species.

Key words: *Gaultheria shallon*, salal, evergreen shrub, weed biology, competition

Fraser, L., Turkington, R. et Chanway, C. P. 1993. **Biologie des mauvaises herbes du Canada. 102. *Gaultheria shallon* Pursh.** Can. J. Plant Sci. **73**: 1233–1247. *Gaultheria shallon* Pursh., le salal (Ericacées), est un arbrisseau pérenne, touffu, à feuilles persistantes, que l'on ne retrouve, dans son habitat d'origine, que sur la côte du Pacifique, de la bande côtière sud (le "Manche-de-poêle") de l'Alaska à la Colombie-Britannique et jusqu'au sud de la Californie. Il pousse sur un vaste assortiment de types et de textures de sols. Il est abondant dans les habitats ouverts près de la côte, en particulier sur les buttes rocheuses et le long des escarpements. C'est une vivace ligneuses, persistante et envahissante, qui crée une grosse concurrence aux conifères. La production grainière est abondante, mais la plante se propage surtout par voie végétative. Plusieurs herbicides sont recommandés, mais la plante résiste à de nombreuses préparations. Le mémoire récapitule les données biologiques connues concernant cette espèce.

Mots clés: *Gaultheria shallon*, salal, arbrisseau à feuilles persistantes, biologie des mauvaises herbes, concurrence

1. Name

Gaultheria shallon Pursh. — **salal** (Scoggan 1978), **shallon** (Conners 1967), **lemon leaves** (Anonymous 1970); **wintergreen** genus, Ericaceae, Heath or Heather Family, (Hitchcock and Cronquist 1973), Éricacées.

2. Description and Account of Variation

(a) A sparse to densely growing perennial, evergreen shrub (Fig. 1) ranging from nearly prostrate to erect. *Gaultheria shallon* forms an extensive shallow root system with very fine roots (0.1-2.0 mm in diameter) and rhizomatous-like structures spreading from a central point. Stem 0.5–2.5 m high, creeping to upright, smooth, but may become scored with age. Twigs green when young, pilose to hirsute, and often glandular. Mature twigs red or brown. Buds 1.0–1.5 cm long, usually green but sometimes tinged red, ovoid and acute-tipped. Leaves alternate and petiolate; persistent, leathery and shiny; ovate to ovate-elliptic, 3-10 cm × 3-5 cm, sharply serrulate; margins often finely toothed. Petioles 2-4 mm long. Flowers 5–15 in terminal and sub-terminal bracteate racemes that appear one-sided because pedicels are deflexed; racemes usually 5–12 cm long. Bracts reddish,

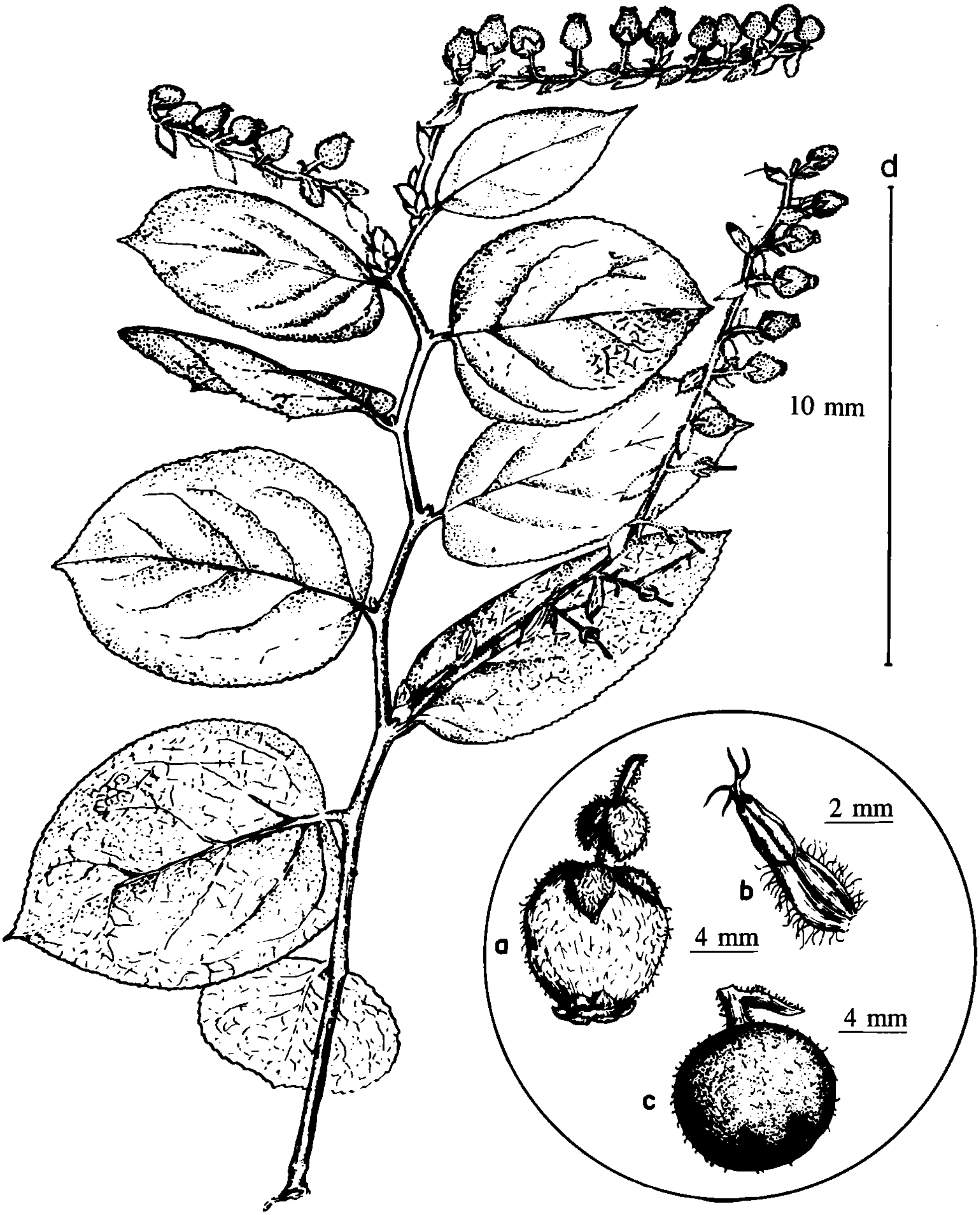

Fig. 1. *Gaultheria shallon* Pursh. (a) single flower (b) stamen (c) fruit (d) mature plant.

6–10 cm long and prominent. Calyx lobes triangular to lanceolate, glandular-pilose and red in color, usually 1/3 to 1/2 length of corolla, but often increasing in size with age. Corolla white or pinkish, urn-shaped, with five short recurved lobes, glandular, and sticky, 6–11 mm. Stamens 10; filaments basally expanded; anthers with four slender apical awns, opening by terminal pores; superior ovary, multiple seeds. Fruit a depressed capsule 6–10 mm thick, purplish-black, berry-like because of the thickening of the calyx at its base, fleshy, pubescent (Szczawinski 1962; Hitchcock and Cronquist 1973). The chromosome base number is 11; the chromosome somatic number is 88 (Taylor and MacBryde 1977).

(b) The most distinguishing feature of salal is its large leaves which are ovate, shiny green and leathery. Leaves live for approximately 2-4 yr but can persist for as long as 6 yr (Koch 1983; Haeussler and Coates 1986). Another distinguishing feature is the hairy, dark purplish fruits. Fruits persist for several months after maturation (between August and October); eventually they dry up and drop off in December. However, some fruits can remain on the plant considerably longer. *Gaultheria miqueliana* Takeda is similar to salal but is found only in east Asia, and the westernmost Aleutian Islands (Scoggan 1978). *Gaultheria miqueliana* racemes with rarely over six flowers, these to about 5 mm, and with white fruit. *Gaultheria shallon* racemes are many-flowered, up to 8 mm long, and purplish black fruit.

(c) Variability of morphology has been reported for *G. shallon* in the size and shape of leaf, stem and rhizome. However, no subspecies or varieties have been described (Hitchcock and Cronquist 1973). The presence of altitudinal ecotypes is possible but not probable (Pojar 1974).

3. Economic Importance

(a) *Detrimental* — *Gaultheria shallon* is a persistent and pervasive plant and is considered a serious competitor with coniferous species, particularly Douglas-fir (*Pseudotsuga menziesii*) on semi-xeric sites in low-elevation coastal British Columbia (Tan et al. 1977; Stanek et al. 1979; Price et al. 1986). On wetter sites. *G. shallon* competes with young planted seedlings of western red cedar (*Thuja plicata*), western hemlock (*Tsuga heterophylla*), Pacific silver fir (*Abies amabilis*) and Sitka spruce (*Picea sitchensis*) following clear-cut logging (Germain 1985; Weetman et al. 1990; Messier 1991). Harmful effects from salal on their neighbours vary from reduced growth to chlorosis of the needles and mortality of tree seedlings. Considering that in coastal British Columbia salal is dominant in at least 10 000 ha of cedar-hemlock forests (Barker et al. 1987; Weetman et al. 1990), and slightly fewer hectares of Douglas-fir forests (Nuszdorfer et al. 1991), the economic loss to the forest industry is potentially very high. Presently, the added expenditure of site preparation and management on salal-dominated sites is substantial (C. Fox, personal communication). In addition, salal can grow so rapidly that most plantable sites may become occupied and nearly impossible to clear manually.

(b) *Beneficial* — Salal forms a very large rooting system with many fine roots and associated microorganisms (mycorrhizae and rhizophere bacteria) in only a few years following clearcutting. Therefore, salal maintains nutrients in the system that would otherwise have been leached and lost. Furthermore, the roots may act to reduce soil erosion on recently disturbed sites and contribute to the organic matter content of the soil (Sabhasri 1961). The leaves of salal also contribute to the organic matter content of the soil, as well as cycling nutrients back into the soil. When salal is abundant, the leaf litter is very large and may serve as a mulch, thus reducing evapotranspiration. This trait is particularly useful in dry habitats. *Gaultheria shallon* has also been recommended for coastal sand dune stabilization (Brown and Hafenrichter 1962).

The young leaves, twigs and berries of salal are an important food source for many animals, in particular, for black-tailed deer, which is the major big game species of the Pacific Northwest (McTaggart-Cowan 1945; Singleton 1976; Crouch 1979; Jones and Bunnell 1984; Chambers 1988). Other animals which feed on salal include ruffed grouse, blue grouse and other birds (Martin et al. 1951; King 1969; Zwickel and Bendell 1972; Viereck and Little 1972; King and Bendell 1982), black bears, Roosevelt elk (Bailey

1966; Singleton 1976), mountain beaver (Banfield 1974), and small mammals (e.g. red squirrel (Dimock et al. 1974). Sheep will also eat young, tender salal leaves which has recently led to their introduction into salal-dominated areas.

Salal is a very attractive plant used by landscapers and florists. Florists use the leaves as a foliage supplement (trade name "lemon leaves") for cut flower arrangements (Anonymous 1970). Salal is also grown commercially in greenhouses. In 1980 salal had an annual retail value of approximately $2 million in BC (Hunt 1980).

Salal berries are nutritious and plentiful and were known to be a staple food source for the native peoples of British Columbia (Turner 1975). The berry was prepared many ways but the main form was as a dried fruit for winter food. As well, native Indians smoked the leaves with kinnikinnick (*Arctostaphylos uva-ursi*) and used it for medicinal purposes (Gunther 1945).

4. Geographical Distribution

Gaultheria shallon occus from the panhandle of Alaska (56°N) along the entire British Columbia coast continuing to southern California (34.5°N) (Fig. 2). All recorded populations in BC occur west of the Coast Mountains except for a single isolated population along the east shore of southern Kootenay Lake (Szczawinski 1962; Calder and Taylor 1968). *Gaultheria shallon* has

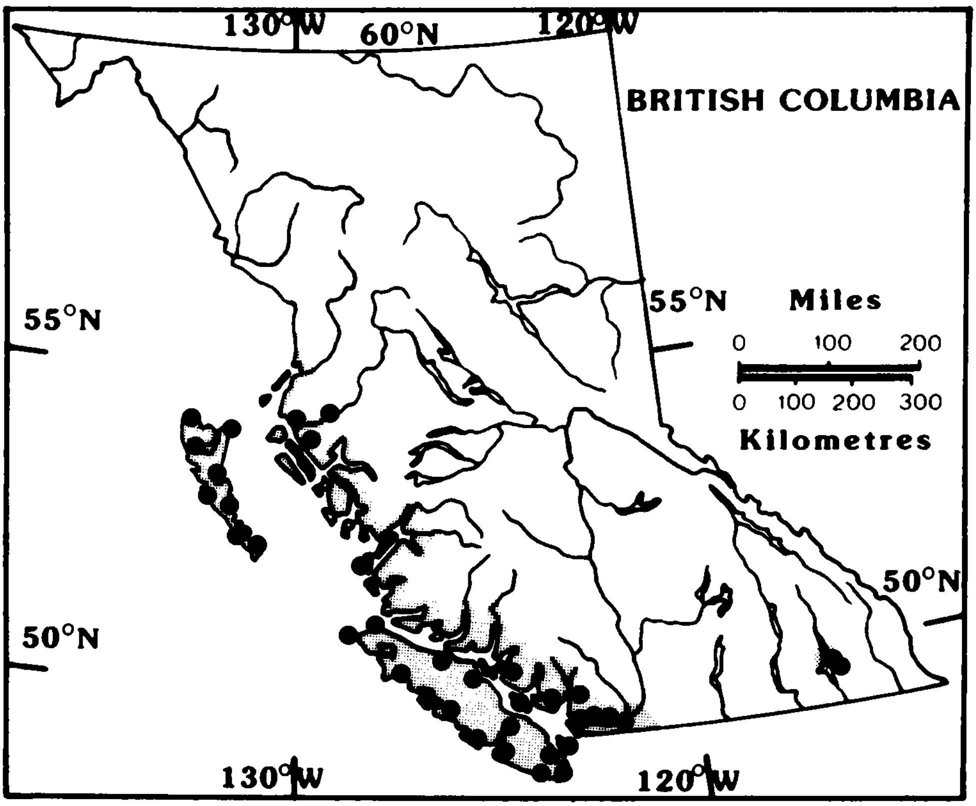

Fig. 2. The distribution of *Gaultheria shallon* in British Columbia (adapted from Szczawinski (1962), Haeussler et al. (1990), and Hultén (1968). The shaded area indicates the general distribution, while the individual points represent the locations where herbarium samples were collected.

been introduced to England, but is found nowhere else in the world.

Gaultheria shallon is found mainly at lower elevations. In its southern range it can be found up to approximately 800 m (Lyons 1952), in the north salal rarely exceeds 100-200 m elevation.

5. Habitat

(a) *Climatic requirements* — Salal is restricted to a humid to perhumid coastal climate with mild temperatures, little snow, and unfrozen soils in winter. It is abundant on open habitats near the coast particularly on rocky knolls and along bluffs (Calder and Taylor 1968), where it can withstand gale force winds. Salal is sensitive to frost (Paul Bavis, personal communication). Sabhasri (1961) observed that a short period of freezing temperature in the middle of May killed nearly all germinants. Although salal can grow under dense forest canopies in 0.3% full sunlight, the vigour, growth rate and flowering of salal increases as the light intensity increases (Sabhasri 1961; Stanek et al. 1979; Koch 1983; Messier et al. 1989; Bunnell 1990; Messier 1993). However, best growth is in partial shade rather than in full sunlight (Anonymous 1970; Dimock et al. 1974; Koch 1983).

Characteristic of many trees, shrubs, and herbaceous plants salal leaf morphology differs dramatically under different light intensities. Sun leaves develop in bright light, whereas shade leaves develop under low light levels. Sun leaves characteristically have prostrate stems and small, thick blades. Shade leaves are found on taller, more erect plants with larger but thinner blades. Smith (1991) found that sun leaves had a mean specific leaf area less than 90 cm^2 g^{-1}; and shade leaves were greater than 90 cm^2 g^{-1}. At 1.8% full sunlight (80% canopy cover), leaves were almost three times larger in area than they were in a clearing (Messier et al. 1989). Under deep shade (0.3% full sunlight), Messier et al. (1989) reported that leaves were similar in size to those in the clearing, but only half the dry weight. Smith (1991) reported that sun leaves of salal require at least 10% full photosynthetically active radiation (PAR), less than 10% of PAR will result in the formation of shade leaves.

(b) *Substratum* - *Gaultheria shallon* grows on a wide range of soil types and textures including peat, glacial till, sand dunes, and shallow rocky soils. It is most commonly found on Podzols, often with deep mor humus forms, but is also found on Folisolic, Brunisolic and organic soils (Klinka et al. 1979). Moist sandy or peaty soil is the best medium for cultivation. It does not grow well in alkaline soil conditions (Anonymous 1970). Salal exhibits vigorous upright growth in shaded conditions, good soil and plenty of moisture (Anonymous 1970). However, if the soil is poor salal often produces a low mat-forming habit. Salal can often be found growing in old stumps and decaying wood, and will also grow epiphytically on living trees in extremely humid climates (Anonymous 1970). Sabhasri (1961) has demonstrated that salal can survive and grow on soils of low fertility, but the addition of nutrients produces a definite growth response.

(c) *Communities in which the species occurs* — Using the biogeoclimatic classification for British Columbia (Krajina 1965), *G. shallon* occurs predominantly in the Coastal Western Hemlock and the Douglas-fir zones, i.e. lowland coniferous coastal forests. In the Douglas-fir zone, the species with which salal usually grows are *Pseudotsuga menziesii* var. *menziesii, Abies amabilis, Thuja plicata, Mahonia nervosa, Vaccinium parvifolium, Rosa gymnocarpa, Pteridium aquilinum, Rubus ursinus, Symphoricarpos mollis, Kinbergia oregana, Hylocomium splendens* and *Phytidiadelphus triquetrus* (Nuszdorfer et al. 1991). The species with which salal usually grows in the Coastal Western Hemlock zone are shown (Table 1).

6. History

Gaultheria shallon is of native origin throughout its present range. Salal is the Coastal Indian name for the plant. When David Douglas landed in Oregon in 1825, Haskin (1934; cited in Szczawinski 1962) reported

Table 1. Zonal vegetation of subzones of the Coastal Western Hemlock biogeoclimatic zone (adapted from Pojar et al. (1991)). vh, very wet hypermaritime; xm, very dry maritime; dm, dry maritime; mm, moist maritime; vm, very wet maritime. *Gaultheria shallon* is not present in the wh (wet hypermaritime), wm (wet maritime), ds (dry submaritime), ms (moist submaritime), and ws (wet submaritime) subzones. Percent cover classes, a — 0.1-1%, b — 2-5%, c — 6-10%, d — 11-25%, e — 26-99%

Botanical name	vh	xm	dm	mm	vm	Common name
Gaultheria shallon	**e**	**e**	**b**	**d**	**d**	**salal**
Abies amabilis	–	–	–	d	d	amabilis fir
Acer circinatum	–	–	b	–	–	vine maple
Achlys triphylla	–	b	–	b	–	vanilla-leaf
Blechnum spicatum	c	–	–	–	c	deer fern
Chamaecyparis nootkatensis	d	–	–	b	–	yellow-cedar
Chimaphila umbellata	–	a	–	a	–	prince's pine
Coptis aspleniifolia	a	–	–	–	–	fern-leaved goldthread
Cornus canadensis	b	–	–	b	b	bunchberry
Hylocominm spledens	d	d	c	b	b	step moss
Listera cordata	a	a	–	a	a	heart-leaved twayblade
Mahonia nervosa	–	c	–	a	–	dull Oregon grape
Maianthemum dilatatum	a	–	–	–	–	false lily-of-the-valley
Menziesia ferruginea	b	–	a	a	b	false azalea
Picea sitchensis	b	–	–	–	–	Sitka spruce
Plagiothecium undulatum	a	a	d	a	b	flat moss
Polystichum munitum	–	b	b	–	–	sword fern
Pseudotsuga menziesii	–	e	e	d	–	Douglas fir
Pteridium aquilinum	–	b	b	–	–	bracken fern
Rhytidiadelphus loreus	e	b	b	d	d	lanky moss
Rubus pedatus	–	–	–	a	–	five-leaved bramble
Rubus ursinus	–	a	a	–	–	trailing blackberry
Scapania bolanderi	b	–	–	–	–	
Thuja plicata	d	c	d	d	c	western redcedar
Tiarella trifoliata	–	–	–	a	–	three-leaved foamflower
Tsuga heterophylla	d	d	e	e	e	western hemlock
Vaccinium alaskaense	b	–	a	d	d	Alaskan blueberry
Vaccinium ovalifolium	a	–	–	a	b	oval-leafed blueberry

that "he was so impressed by the sight of salal he could scarcely see anything else. Throughout all his journey in the west, the salal was one of Douglas' favorites and he held great hopes of introducing it into England, and making of it a cultivated fruit."

7. Growth and Development

(a) *Morphology — Gaultheria shallon* has slow initial growth for approximately the first 2 yr, but once it is established it spreads vegetatively very rapidly by means of rhizomes (Messier 1991). The length and complexity of the rhizomes of an individual salal plant in an area dominated by salal has not been determined but Koch (1983) found new shoots up to 2 m from the parent plant. Bunnell (1990) observed a strong tendency for daughter shoots to be clumped around the mother shoot under sparse canopies, whereas daughter shoots were farther away from the oldest shoots under closed canopies. Salal accumulates considerable biomass in a growing season, but mainly through the expansion of rhizomes leading to the production of new shoots, not through significant increase in the height of pre-existing shoots (Sabhasri 1961).

Salal's ability to respond to a continuum of understory light conditions by producing either sun leaves or shade laves (Messier et al. 1989; Smith 1991) is important to its survival. Under dense stands salal can persist by forming shade leaves; in clearings or in openings of otherwise dense stands, salal forms sun leaves. Another important adaptive characteristic to capture light is stem elongation which responds to high red light levels

(Sabhasri 1961; Vales 1986) occurring in dense stands (Messier et al. 1989).

Leaves of *G. shallon* have a thin epicuticular layer that consists mostly of triterpenes, and always contains ursolic acid; this material also had traces of external flavonoid agylcones, namely galangin-3-methyl ether (Wollenweber and Kohorst 1984). Salasoo (1981, 1988) determined the patterns of alkane distribution in the epicuticular wax of *G. shallon* and detected rimuene. The wax was 28% hydrocarbon.

The pollen tetrad diameter of *Gaultheria shallon* has been calculated by Hebda (1978) from a sample size of 100 tetrads collected in Burns Bog, Delta, BC. The mean tetrad diameter is 46.97 μm, with a range of 41–53 μm and a standard deviation of 2.50. Hebda (1978) postulated that small tetrads (41–44.5 μm) indicate growth of salal in dry conditions, intermediate tetrads (44.6–49.5 μm) imply dry to intermediate habitats or fire, and large tetrads (49.6-53 μm) reflect wet sites.

(b) *Perennation* — Individual shoots may survive for 10–15 yr, but leaves are rarely older than 4 yr before senescence (Haeussler and Coates 1986). Shoots will bear leaves only during the first few years (Koch 1983). Rhizomes have the potential to continue reproducing vegetatively if there is sufficient light through the forest overstory (gaps and sunflecks) for shoot growth. Bunnell (1990) found extensive mats of salal rhizomes in conifer stands between 80 and 110 yr old, even when aboveground salal densities were low. During winter, salal is virtually dormant and is very sensitive to frozen soils and frost (Sabhasri 1961).

(c) *Physiological data* — Salal is at least a moderately shade-tolerant species (Sabhasri 1961; Koch 1983) but its photosynthetic and respiration characteristics are consistent with a shade-intolerant plant species (Sabhasri 1961). For an actively growing plant it was found that at low light intensities (6.06 μmol m^{-2} s^{-1}) respiration was greater than photosynthesis. Photosynthetic activity and seedling growth significantly increased with increased light intensities up to the maximum level tested (24.24 μmol m^{-2} s^{-1}) (Sabhasri 1961). Maximum growth occurs under red light (Sabhasri 1961). Bunnell (1990) reported that the cost of flowering was shared across connected shoots of a plant, showing there is physiological integration between ramets.

(d) *Phenology* — The maximal growth of salal (roots, rhizomes, shoots and leaves) is between late April and August, peaking in early June. Vegetative buds burst in early April (Sabhasri 1961). Flowering can occur anytime between March and July depending on the area (Dimock et al. 1974). In Alaska, flowering occurs between March and June (Viereck and Little 1972). Near Vancouver, BC, Pojar (1974) reported flowering between 12 June and 4 July. In Washington state, flowering begins in the 3rd week of June. Fruits ripen between August and October and remain on the stem until December (Dimock et al. 1974).

(e) *Mycorrhizae* — Largent et al. (1980) reported that *G. shallon* can be associated with three different kinds of mycorrhizae: arbutoid, ericoid, and ectomycorrhizae. Three different fungal species have been identified, one is *Oidiodendron griseum* Robak and the taxonomic position of the other two species are being studied (Xiao and Berch 1992). This is the first report of O. griseum as an ericoid mycorrhizal fungus of *Gaultheria*.

8. Reproduction

(a) *Floral biology* — *Gaultheria shallon* flowers are pollinated by insects, primarily bumblebees and flies (Pojar 1974). The fruit is a many-seeded capsule, and each inflorescence has 5-15 capsules. However, Bunnell (1990) found that salal will flower only when two conditions are met: on vigorous stems greater than 4 yr old, and at a mean crown completeness (a measure of forest canopy closure) less than 30%. Hebda (1982) found that *Gaultheria shallon* contributed less than 2% of the pollen and spore rain in areas dominated by salal, indicating how little salal flowers.

(b) *Seed production and dispersal* — The fruits of salal remain on the stem until December and those seeds remaining are viable for up to 1 yr following ripening (Dimock et al. 1974). Fruits have an average of 126 seeds each. When conditions are suitable for flowering, heavy crops of fruit are produced on a regular basis (Haeussler et al. 1990). Seeds are dispersed mainly by the animals which feed upon the fruit: black-tailed deer, Roosevelt elk, mountain beaver, ruffed grouse, blue grouse, and other small mammals and birds (Halverson 1986).

(c) *Viability of seeds and germination* — Seeds can remain viable for several years in cold, dry storage, but the viability of seeds under natural conditions is generally much reduced (Dimock et al. 1974), Sabhasri (1961) stored seeds at 4.4°C for 1 yr and found a decline in germination from 31 to 21%. Seeds do not require chilling (Haeussler et al. 1990) or stratification (McKeever 1938) to induce germination. Successful germination requires moist, acidic sites under partial shade (Dimock et al. 1974) and light for 8 h or more per day is essential (McKeever 1938). In Washington, germination rates of 27–35% from fresh seed under lighted conditions were reported (Sabhasri 1961; Dimock et al. 1974). In British Columbia, Messier (personal communication) obtained germination rates of approximately 60% under the same conditions.

Despite the large quantity of seeds produced and the many seeds which germinate, seedling survival is very low (Haeussler et al. 1990). Sabhasri (1961) found that in Western Washington, seedling establishment is most successful in the understory of young Douglas-fir stands.

(d) *Vegetative reproduction* — The most significant and effective form of colonization is through vegetative spread, both in open habitats and in deep shade. Once salal is present on a site, further expansion is almost exclusively by vegetative means (Sabhasri 1961; Koch 1983; McGee 1988; Messier 1991) including layering and suckering from roots and stem bases. However, among the 54 naturally growing plants that Bunnell (1990) examined, no evidence of stem layering was found; rhizomes were the only means of producing new shoots. Bunnell (1990) forced stems into the organic mat and examined them 1 yr later to find that they had grown adventitious roots, and concluded that layering must also occur naturally. He found, while monitoring the colonization of salal, that 85% of the space occupied by salal after 9 yr of growth was occupied during the first 3 yr. Bunnell also observed that the vegetative reproduction of ramets was negatively associated with age ($r^2 = 0.95$) and that no new shoots were produced after an individual ramet reached 9 yr of age. Seed production may be significant in the initial colonization of a newly disturbed area (e.g. windthrow, clearcut), but considering that a plant must be at least 4 yr old before it will flower, and that most colonization of an area occurs within the first 3 yr, the vast majority of colonization occurs through vegetative spread. Bunnell (1990) found no seed production, only vegetative spread, at a mean crown completeness greater than 30%.

9. Hybrids

Gaultheria shallon does not naturally hybridize with any other species (Pojar 1974). However, an artificial hybrid between *G. shallon* and *Pernettya mucronata* has been produced in England (Dimock et al. 1974).

10. Population Dynamics

The rate of increase of salal populations depends largely on the stage of succession of the area. Messier (1991) proposed a general growth model based on the work of Messier (1991), Messier and Kimmins (1991), Messier et al. (1989), Vogt et al. (1987), and Vales (1986) (Fig. 3) of the development of salal over a 60-yr period following a major disturbance (e.g. clear-cutting and slashburning) of old-growth western red cedar and western hemlock forests on northern Vancouver Island. The development of the live fine-root, leaf, stem and rhizome biomass of salal has three different stages. Stage one is between

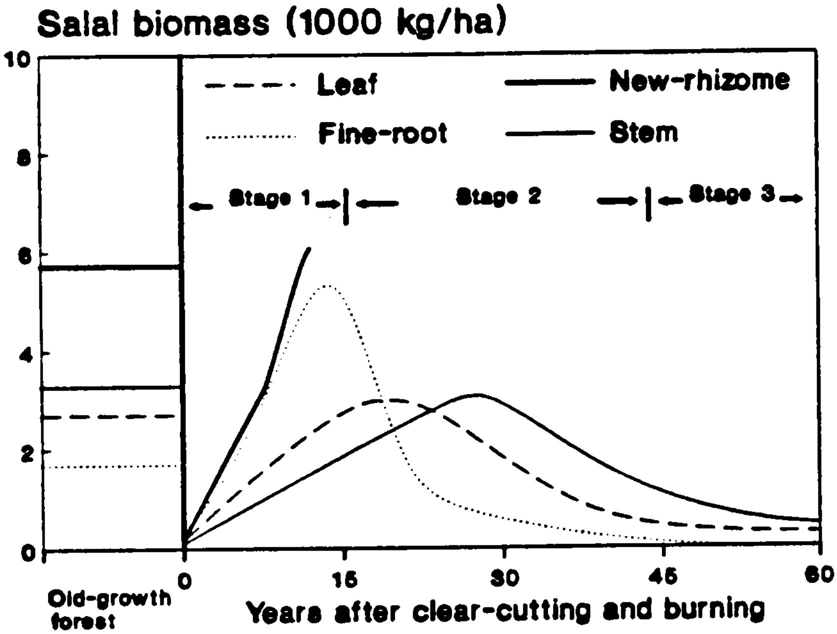

Fig. 3. Hypothetical development of fine-root, leaf, stem and rhizome abundance of *Gaultheria shallon* over a 60-yr period following the clear-cutting and burning of old-growth forests of western redcedar and western hemlock on northern Vancouver Island (taken from Messier (1991)).

1 and 15 yr and is characterized by a rapid growth rate of rhizomes and fine-roots, in particular, between 8 and 15 yr. Stage two, approximately between 16 and 45 yr, begins with a rapid decline in salal live fine-root biomass followed by a more gradual decrease in leaf and stem biomass. The decline of the population is caused by shading due to an increase in the overstory tree canopy. There are no data for rhizome biomass in the 10- to 60-yr period, but it is believed to be high (Messier 1991). The final stage, occurring from 46 yr until the next major disturbance, is the virtual exclusion of salal by the dense overstory canopy. However, it is not completely excluded and can quickly re-establish following a disturbance.

Much research effort has been focused on the competitive interactions of salal and coniferous tree species in low-elevation coastal British Columbia forests (Tan et al. 1978; Black et al. 1980; Price et al. 1986; Weetman et al. 1989a; Klinka et al. 1989; Bunnell et al. 1990; Messier et al. 1990; Messier 1991). The competitive influence of salal on the seedlings of Douglas-fir, western hemlock, and Sitka spruce is believed to be much stronger than on western red cedar and lodgepole pine (Bunnell et al. 1990). Competition is most severe during the early stages of stand development (Long 1977) but may continue through the rotation, in particular, if the canopy is open enough to allow a well-developed understory of salal to persist (Stanek et al. 1979).

Young stands of Douglas-fir on sub-xeric sites are limited by soil water potential (Tan et al. 1977). At low values of soil water potential, the reduction in stomatal conductance is greater for Douglas-fir than for salal, indicating that salal transpiration would account for a higher proportion of total stand transpiration (Tan et al. 1978). Price et al. (1986), found that the removal of the salal understory of thinned 32-yr-old Douglas-fir significantly increased rates of photosynthesis and tree growth due to an increase in the soil water potential. Other researchers have proposed that salal may be competing for nutrients in the Douglas-fir forests (Stanek et al. 1979; Haeussler and Coates 1986).

There is evidence to suggest that salal may also be competitive in moist ecosystems (Weetman et al. 1989b; Messier 1991). Two hypotheses have been proposed to account for this. First, is the resource exploitation hypothesis. Weetman et al. (1989a,b) have shown that on northern Vancouver Island western red cedar and western hemlock cutovers that are dominated with salal are nutrient deficient. Germain (1985) and Messier (1991) found that salal can have an impact on the nutrient budget for conifers. *Gaultheria shallon* forms three symbiotic fungal associations: ericoid-, arbutoid- and ecto-mycorrhizae (Largent et al. 1980), whereas western red cedar and western hemlock only form one fungal association each: endomycorrhizae and ectomycorrhizae, respectively. Therefore, *G. shallon* might be more efficient at extracting nutrients such as nitrogen and phosphorus at low pH, and accessing nutrients in complex organic forms (Xiao, Cade-Menum and Berch, personal communication). Parke et al. (1983) suggest that dense salal can lower soil temperatures causing reduced conifer growth by inhibiting root growth and mycorrhizal infection. The second hypothesis involves the possible allelopathic properties of salal. Del Moral and Cates (1971) did not find convincing evidence for allelopathy in salal, but Rose et al. (1983) have shown that allelochemicals in salal litter may inhibit seedling growth. It has been suggested that salal may have an allelopathic effect through the production of tannins and phenolic acids (de Montigny, personal communication).

Gaultheria shallon can be classified as a stress-tolerator with a low R (the level of resource below which the population is unable to maintain itself) (Messier 1991). Evidence that salal has a low R is its ability to maintain a higher stomatal conductance than Douglas-fir under a low soil water potential (Tan et al. 1978).

11. Response to Herbicides and Other Chemicals

In general salal is both resistant and resilient to many herbicides. The most successful herbicide in controlling salal is triclopyr ester (Garlon). Applying triclopyr ester at 4 kg a.i. ha^{-1} reduced salal cover by 78% (Barker 1988). Combining diesel with triclopyr ester effectively controlled salal for three seasons in a Douglas-fir salal ecosystem on the southeast coast of Vancouver Island (Dunsworth 1986). In an experiment conducted in a dry cedar–hemlock ecosystem, 4 kg a.i. ha^{-1} triclopyr ester in diesel oil at 100 L ha^{-1} in early spring or late summer reduced salal cover by 60-90%. When using mineral oil as the carrier instead of diesel oil, salal cover was reduced by only 40% (Haeussler et al. 1990).

Stewart (1974b) tested 10 herbicides mixed in diesel-oil carriers. Salal plants were sprayed on 1 April, when flower buds were swelling and vegetative buds were dormant. Silvex, dichlorprop, 2,4,5-T, and dicamba produced at least 80% topkill and a 50% reduction in salal cover with silvex showing the best control. Salal is resistant to these same herbicides when applied in water, or applied later in the growing season (Gratkowski 1970; Stewart 1974a).

Other herbicides which are less effective but have been reported to cause slight damage to salal are glyphosate and 2,4-D (Conard and Emmingham 1984). Results from hexazinone applications are variable; Newton and Knight (1981) and Boateng and Herring (1990) found it to be ineffective at controlling salal. However, Wellman and Harrison (1987) reported that an April ground application of 2 kg a.i. ha^{-1}granular hexazinone resulted in control of salal. Two years after herbicide application, salal biomass on the treated areas was about half that on the untreated areas.

In all of the herbicidal tests to control salal, little is known about how the below-ground plant portion responds. D'Anjou (cited by Haeussler et al (1990)) showed that although aboveground parts of salal were well controlled by triclopyr ester, living roots (dry weight basis) still comprised 89% of that in untreated controls, indicating that roots continue to survive despite substantial foliar control.

12. Responses to other Human Manipulations

Several studies have reported that salal will rapidly increase in cover and vigour following the removal or reduction of the forest canopy (Sabhasri 1961; Long and Turner 1975; Long 1977; Stanek et al. 1979; Black et al. 1980; Koch 1983; Gholz et al. 1985; Price et al. 1986; Vales and Bunnell 1988; Messier et al. 1989). Messier (1991) found that salal re-establishes relatively quickly below ground following clear-cut logging and slashburning, but the aboveground portion does not grow as rapidly and may take many years to become dominant.

Prescribed burning and logging can increase the growth of salal if the burn is light. Fire stimulates resprouting from roots and stem bases (Sabhasri 1961). Only severe burns that penetrate sufficiently deep to kill the roots can reduce salal cover. Vihanek (1985) reported that on dry sites on eastern Vancouver Island high severity burns decreased salal cover by 80% compared to adjacent unburned areas; whereas low to moderate burns decreased cover by only 40%.

Fertilizer application, particularly nitrogen-rich fertilizer, increases both above and below-ground growth of salal (Sabhasri 1961; Anonymous 1970). However, in forest stands, applications of fertilizer that result in an increased tree canopy density may cause a decline in the vigour and cover of the salal understory due to shading (Long an Turner 1975; Stanek et al. 1979).

Salal readily forms new plants from cuttings of the stem and roots (Sabhasri 1961), so it can be expected that any form of soil disturbance that causes mechanical damage to the plant, but that does not physically remove it from the site, will stimulate resprouting. However, it has been reported by Muller (1989, cited in Haeussler et al. (1990)) that heavy scarification on areas on southern Vancouver Island has resulted in very slow reinvasion of salal. Based on trials on southern Vancouver Island, B. Green (personal communication) has speculated that heavy soil scarification (i.e. removing the organic layer) on dry sites causes mortality of salal rhizomes due to desiccation.

Table 2. The percentage of total number of leaves infected by commonly observed fungal taxa on 1240 leaf discs of *Gaultheria shallon* Pursh. (adapted from Petrini et al. (1980)).

Acremonium sp.	2.4
Geniculosporium sp.	8.4
Leptothyrium berberidis Cooke et Massee	3.6
Nodulisporium sp.	2.4
Pezicula sp.	6.4
Phialophora spp.	7.2
Phomopsis sp.	4.8
Phyllosticta pyrolae Ellis et Everh.	34.7
Phyllosticta vaccinii Earle	5.6
Ramularia sp.	4.8
Septogloeum sp.	4.4
Sigmoidea sp.	1.2
Xylaria hypoxylon (L. ex Fr.) Grev. anamorph	2.0

13. Responses to Parasites

Salal is infected by numerous fungal parasites. The most common and serious is the leaf spot fungus (*Mycosphaerella gaultheriae*) (Conners 1967; Haeussler et al. 1990). In a study conducted in western Oregon, Petrini et al. (1982) isolated 13 different species of endophytic fungi (Table 2). The most frequent was *Phyllosticta pyrolae* Ellis et Everh. which occurred on 34.7% of the observed leaves. They found that the frequency of endophyte infections diminishes with decreasing habitat moisture. Furthermore, rates of overall infection were higher in samples taken from densely wooded sites than in samples taken from more open sites. Other fungi reported on salal are *Asterella gaultheriae, Bulgaria melastoma, Lachnella gaultheriae, Leptosphaeria gaultheriae, Phacidium gaultheriae, Phyllosticta gaultheriae,* and *Poria ferrea* (Conners 1967). Linderman and Zeitoun (1977) found *Phytophthora cinnamomi* Rands, a very widespread fungus, occurring on nursery-grown salal. Apothecia of *Valdensinia heterodoxa* Peyr. (Sclerotiniaceae), have been found on fallen *G. shallon* leaves

(Redhead 1974). Salal is known to have at least one higher plant parasite, *Boschniakia hookeri* Walp. (Olsen and Olsen 1981; Kuijt and Toth 1985), a perennial root parasite. It is not known to what degree the parasite actually damages salal.

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