Rosaceae—Rose family

Rubus L.

blackberry, raspberry

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Growth habit, occurrence and use. *Rubus* is a large and complex genus with 12 subgenera. The 2 largest subgenera and those most important in North America are *Eubatus* (blackberries) and *Idaeobatus* (raspberries). There are about 200 species in *Ideobatus* and perhaps as many as 1,000 or more in *Eubatus* (Fernald 1950; Jennings 1988). There are 3 other subgenera—*Chamaemorus* (cloudberries), *Cyclatis* (Arctic berries), and *Anoplobatus* (flowering raspberries)—that include 1 or more North American species. Blackberries are distinguished from raspberries by the presence of a core or torus filling the center of the berry when it is removed from the plant; the ripe fruits of raspberries have no core and are shaped like a thimble when removed from the plant. Most species are native to the cool, temperate regions of the Northern Hemisphere; a few are found in the tropics and the Southern Hemisphere (Jennings 1988). The occurrence, general uses, and growth form of some species common in North America are listed in tables 1 and 2.

Although more than 1 species may occur on a given site within a specific geographic area, each species has a specific site-type on which it achieves best development. For example, in Wisconsin there are 6 *Rubus* spp. (Curtis 1959). Allegheny blackberry, trailing raspberry (*R. pubescens* Raf.), and red raspberry are the most widespread and occur together on some sites, but the maximum presence for each is in southern dry, northern wet-mesic, and boreal forests, respectively. The other 3 species—swamp dewberry, blackcap raspberry, and thimbleberry—attain maximum presence in northern dry, southern dry-mesic, and boreal forest types, respectively (Curtis 1959). Most species occur on relatively similar sites throughout their ranges. However, thimbleberry occurs on very different sites over its natural range. For example, in western Oregon it occurs in areas generally free of frost, whereas in Wisconsin and northern Michigan, maximum presence is in areas receiving significant amounts of snow and having prolonged winter air-temperatures well below freezing. Species distribution for various geographic regions can be found in works by Hickman (1993), MacKinnon and others (1992), Meades and Moores (1994), USDA Forest Service (1993), and Viereck and Little (1972), as well as in other regional flora and site classification manuals.

Rubus spp. are a major fruit crop in the north temperate zone in Europe and North America; this is their dominant use. Because the primary product is a fruit, there has been a large amount of research focusing on factors limiting fruit production, and thus directly and indirectly seed production. In this chapter, we can only briefly summarize the available literature; a more complete discussion can be found in Ourecky (1978), Moore and Janick (1983), and Jennings (1988). Jennings (1988) provides a very thorough discussion of *Rubus* breeding and cultivation.

The many growth forms of the various species, and the wide range of site conditions on which they occur, make the species useful in reclamation, revegetation, and erosion control projects. Because of the stout spines on some species, dense stands make good barriers to restricted areas as well as providing cover and food for many animal species. Stems and leaves are browsed by a large number of animals. Palatability varies among species and seasons of the year and by site conditions for a species. The fruits are eaten by animals ranging in size from insects to birds to small mammals to the Alaska brown bear (*Ursus middendorfii*). Fruit and bark of the roots and stems have medicinal properties and were used by Native Americans to cure a variety of ailments (Coladonato 1990a & b; Krochmal and others 1969; MacKinnon and others 1992; Meeker and others 1993; Snow and Snow 1988; Tirmenstein 1990a−f). Salmonberry was introduced in Great Britain and has become a weed problem in lowland forests and plantations (Paterson 1996).

Rubus spp. native to North America and some naturalized exotic species can be found at all stages of forest succession (table 1). The most impressive communities in terms of sheer abundance and site domination are found after major disturbances such as forest harvesting and fire and on abandoned agricultural land and along roadsides, where light, water, and nutrients are readily available. These stands originate from soil seedbanks, with subsequent clonal development (as in the case of red raspberry in north temperate and boreal forests) or from vegetative reproduction (as in salmonberry in the coastal forests of the Pacific Northwest) (Lautenschlager 1991; Ruth 1970; Tappeiner and others 1991; Whitney 1978, 1982, 1986; Zasada and others 1992, 1994) (figures 1 and 2). Dense stands can prevent or greatly delay establishment of trees and other species (Tappeiner and others 1991; Lautenschlager 1990). Trailing raspberry in north temperate forests, cloudberry and nagoonberry in boreal forests and tundra, and 5-leaf bramble (*R. pedatus* Sm.) in coastal forests of the Pacific Northwest and Alaska are perennials with a low or trailing growth form and are present in understory plant communities in mature and old growth forests (Coladonato M 1990a & b; Graber and Thompson 1978; Tappeiner and Alaback 1989; Mackinnon and others 1992; Maxwell 1990; Maxwell and others 1993; Meeker and others 1993; Meidinger and Pojar 1991; Piroznikov 1983; Tirmenstein 1990a−f; Viereck and Little 1972; Viereck and others 1992; Whitney 1978).

Rubus spp. collectively have one of the most versatile systems for reproduction, colonization, and species maintenance among woody plants. In addition to sexual reproduction, asexual reproduction (apomixis) is well-developed in most species. Asexual reproduction also includes all forms of vegetative reproduction and agamospory (formation of seeds without sexual reproduction) (Grant 1981; Richards 1986). These various modes of reproduction affect the frequency and distribution of genotypes in natural populations; sexually reproducing species have more genotypes than those where apomixis is common (Nybom and Schaal 1990).

Although a detailed description of all aspects of vegetative reproduction is beyond our scope, a general knowledge of these characteristics is necessary to understand spatial and temporal variation in fruit and seed production. There are 3 basic types of clone development, each producing ramets with different life expectancies and flowering potential. These are layering, development from roots or rhizomes, and basal sprouting (figures 1 and 2). The longevity of ramets within a clone varies from 1 growing season to 15 years or more, depending on the species and site conditions (Jennings 1988; Rantala 1976; Ryynanen 1973; Suzuki 1987, 1989, 1990; Tappeiner and others 1991, 2001; Whitney 1978, 1982, 1986; Zasada and others 1992, 1994). Salmonberry has relatively long-lived ramets developing from rhizomes, whereas red raspberry ramets are biennial and produced from a spreading root system. Even in red raspberry, however, ramets may be produced by basal sprouting from one point on the root system, giving that physical position a life-span of more than 2 years (figure 1). Yet another pattern is that of cloudberry, an herbaceous, perennial species with a well-developed rhizome system from which leaves and flowers are produced annually (Jennings 1988; Rantala 1976; Rynnanen 1973). Clonal expansion in other species, for example trailing raspberry and Himalaya blackberry, occurs by layering at the tip or other nodes (Jennings 1988; Whitney 1978, 1986) (figure 1).

Although most species are deciduous, several are evergreen—for example, cutleaf blackberry, Himalaya blackberry, both exotic species that have become naturalized in the western United States. Stems of some species lack spines or bristles whereas others are very well-armed. Dense thickets of Himalaya blackberry and Allegheny blackberry can be very difficult and painful (!) to walk through. The density of spines for a given species can vary with site conditions (Zasada 1996) and the genes controlling spine production are known (Jennings 1988).

Humans have a mixed relationship with *Rubus* spp. On the one hand, they provide a highly edible and nutritious fruit in cultivation and in native plant communities. On the other hand, they can be competitors for growing space, often retarding or (in the extreme case) preventing the establishment of commercially valuable trees. In this case, significant measures are taken to reduce their density and biomass. An understanding of seed production, seed longevity, germination, and seedling establishment is necessary for benefitting from all of the values of these plants while minimizing their development on sites where their presence may prevent achieving management goals.

Geographic races. The genetics of *Rubus* is complex because of the presence of sexual and asexual reproduction. This appears to be particularly true in the Eubatus subgenus, where hybrids with varying degrees of sterility are produced sexually. Sterility is to a significant degree dependent on ploidy levels and these range from 2 to 7x (x = 7). Once produced, these hybrids reproduce asexually by vegetative reproduction and agamospermy. The subgenus *Ideobatus* is predominantly diploid and sexual reproduction is most common. Crossability among species within both subgenera has been studied (Brainerd and Peitersen 1920; Grant 1981; Jennings 1988; Peitersen 1921).

Flowering and fruiting. Most *Rubus* species are monoecious, but there are dioecious species—for example, cloudberry (Agren and others 1986) and other Arctic spp. (Jennings 1988). Flowering occurs during the spring or summer and rarely in the fall (table 2). Flowers normally have 5 sepals and petals. Size of the flowers varies with subgenus, and *Anoplobatus* flowers generally are the largest.

Pollination by insects is common, and pollinators have been identified for some species—for example, cloudberry (Hippa and Koponen (1976), salmonberry (Barber 1976), and red raspberry (Whitney 1978). *Rubus* flowers produce large quantities of nectar, thus attracting insects (Jennings 1988). In blackberries, self-pollination is often adequate to provide the stimulus necessary for asexual seed production, but a mixture of self-pollination and crosspollination often occurs. Fertilization occurs about 1 day after pollination (Jennings 1988; Nybom 1985, 1986, 1988; Ourecky 1975).

Pollen can be collected and stored for use at a later time. Maintenance of viability during storage varies with temperature and humidity, and species (Otterbacher and others 1983; Ourecky 1975; Perry and Moore 1985). Perry and Moore (1985) concluded that pollen should be collected every few days to assure that pollen is fresh for crossing and that if pollen must be stored, then subfreezing temperatures (!5 to !40 EC) and low humidities provided the best conditions. Nybom (1985) described methods for assessing pollen viability in subgenus Rubus.

A raspberry or blackberry fruit is an aggregate of small, usually succulent drupelets (figure 3), that each contain a single hard-pitted pyrene or nutlet (figure 4). [The words “nutlet” and “seed” can be used interchangeably, but we have used seed.] Each drupelet is a complete fruit, a miniature version of a cherry or plum (which are drupe-type fruits). Each aggregate fruit is the product of 1 flower and the number of drupelets per aggregate varies with species, pollination success, and environmental conditions (figure 3; table 4). Ripening occurs 30 to 36 days and 40 to 70 days after pollination in raspberries and blackberries, respectively. Drupelets within an aggregate fruit ripen uniformly, but there can be considerable variation among fruits. Three phases of development are recognized: rapid fruit growth following pollination, slow growth as the seed develops, and a final period of rapid growth before the fruit is fully mature (Jennings 1988). In natural populations, the interaction between microclimate and genetic variation in flowering and fruit ripening usually spreads the timing of aggregate maturation over a period of several weeks or more.

The breeding system in *Rubus* is often described as versatile because seeds are formed sexually and asexually. The relative importance of these two types of seeds varies within and among subgenera and species and may differ within a plant depending on the pollen source. In the *Ideobatus* group, seeds are normally formed sexually. In *Eubatus* species, seeds are produced sexually and asexually (Jennings 1975; Nybom 1985, 1986, 1988). In most cases, pollen is required to produce seed asexually, but the embryo is not produced by the fusion of male and female gametes (pseudogamy). Parthenogenesis (seed formation without pollination) occurs in some species. Seeds of both sexual and asexual origin may be present in the same fruit (Jennings 1975; Nybom 1985, 1986, 1988).

The abscission layer that develops as the fruit ripens differs in raspberries and blackberries. Fruits may drop from the plant or be removed by various animal species. The number of drupelets or entire aggregates removed at any one time depends on the size of the fruit and the size and eating habits of the animal (Snow and Snow 1988). Seeds are usually deposited with other materials in the feces. In large animals like the grizzly bear (*Ursus horribilis*), there maybe 50,000 to 100,000 salmonberry seeds in one pile of feces. Seeds may be secondarily consumed or moved from the feces piles by small rodents and birds. Brunner and others (1976), Jordano (1984), Gervais (1996), and Traveset and Willson (1997, 1998) discuss other aspects related to selection and dispersal of *Rubus* seeds by animals. The amount of fruit removed has been found to vary from near 100 to 40% and will depend on habitat type and type of animal feeding on the fruits (Jordano 1982; Snow and Snow 1988). In British Columbia, forest silvicultural practices are being altered in coastal riparian areas to provide for adequate fruit production by salmonberry and other species that are important food sources for grizzly bear

(McLennan and Johnson 1993).

Although fruit consumption is often viewed as a loss of seeds, in *Rubus* spp. consumption of seeds is important to the reproductive biology of the plant. Several examples are described below. Dispersal of seeds away from parent plants depends on animals. The distribution of seeds in space and time depends on the size and eating habits of the animal (for example, bears deposit large quantities of seeds in one place, whereas small birds deposit only a few seeds at a time), and the movement habits of the animal following feeding. Seeds that pass through the digestive tract of animals receive varying degrees of scarification (for example, salmonberry seeds in bear feces may have had the fleshy fruit wall completely removed or be little affected as evidenced by the presence of complete fruit aggregates) and as a result have potentially different germination patterns. Deposition in feces of differing composition and chemistry affects the germination substrate, and physical and chemical environment available for seedling establishment. If animals are feeding simultaneously on fruits of different plants, fecal deposits may affect competitive and other interactions between *Rubus* spp. and other genera.

Good seedcrops occur nearly every year. Environmental factors affect the amount of flowering and fruit production. In northern Wisconsin, red raspberry crop failures may occur in clearcut areas as a result of severe frosts in mid- to late June, whereas in adjacent areas with 50 to 75% canopy cover, frost may have little effect (Zasada 1996). There are a host of fungi, bacteria, viruses, and insects that affect fruit production in domesticated cultivars and varieties (Jennings 1988; Mason and others 1981; Ourecky 1975).

Flowering occurs on perennial stems (salmonberry), biennial canes (red raspberry), and flower buds produced annually from rhizomes (cloudberry) (figures 1 and 2). Because of the importance of biennial caned species for fruit production, considerable information exists (Jennings 1988; Ourecky 1975; Whitney 1978; Zasada 1996). Briefly, the first-year vegetative canes in red raspberry are termed "primocanes." During the second growing season, they flower ("florocanes"), produce a fruit crop, and die. Within a natural stand of red raspberry, primocanes usually outnumber florocanes by a factor of 2 or more (Whitney 1978, 1982, 1986; Zasada 1996). Primocanes do produce flowers on occasion, and this trait has been developed into a fall-producing cultivar (Prive and others 1993a & b).

The rate of node production is about constant in primocanes. Node density, and thus density of potential flower buds, is determined by the rate of internode elongation. Flower bud initiation occurs at about the time that canes become dormant and may continue in the spring after a period of dormancy. Nodes can have primary, secondary, and tertiary flower buds; the secondary and tertiary buds develop if the primary bud is damaged or dies (Hudson 1959; Jennings 1988).

In florocanes, there is little or no height growth. Fruiting laterals develop from the nodes. The number and distribution of fruiting laterals is dependent on genotype, node position, and microclimate. Fruit production per lateral may vary from 10 to 100 in domestic cultivars of raspberry and blackberry (Jennings 1988).

Primocanes and florocanes may compete for resources, and fruiting may be reduced on individual florocanes. Similarly, in the absence of florocanes more primocanes are produced. Clones vary considerably in the effects of this interaction on fruiting (Crandall and others 1974; Waister and others 1977). Vegetative characteristics of salmonberry and red raspberry stems are affected by light and other resource availability in forest stands where they commonly grow

(Lautenschlager 1990; Tappeiner and others 1991; Zasada 1996).

Collection of fruits. During the maturation process, fruits change from green to their characteristic color (table 2). Although all species have a characteristic fruit color when ripe, there can be variation among genotypes. For example, in salmonberry, there are 2 mature fruit color polymorphisms—red and orange. The orange form is generally more common in the southern (that is, Oregon) part of the range, and the red form in the northern (southeastern Alaska) part of the range, although clones with red and orange fruits intermingle in both areas (Gervais 1996). The red fruit form passes through an orange stage on the path to maturation (Gervais 1996; Traveset and Willson 1998), but at maturity there is a distinct and easily observed difference in color. The amount of variation in fruit color may also vary among sites and geographic areas. Thus, to use fruit color as an index of maturity, one needs to know the color variation that occurs in a species. Although fruits are usually collected when they are fully ripe, Ourecky (1975) suggested that fully developed green fruits contain well-developed seeds and could be picked in that condition. Another index of ripeness is the ease with which fruits can be picked as a result of the development of the abscission layer. Fruits in natural populations will be available for picking over a period of several weeks to a months because of the variation in maturation due to the effect of genotype and microclimate on flowering and fruit development. Because of the importance of fruits as animal food, it may be important to closely monitor an area in order to collect adequate quantities before animals take them (Snow and Snow 1988). For salmonberry, it has been shown that the red-fruited form may be preferred to the orange-fruited type in some cases and may vary by species of birds and mammals (Traveset and Willson 1998).

Rubus fruits are usually picked by hand, but machines have been developed to mechanically harvest commercial crops (Ourecky 1975). They can also be picked after they have dropped from the plant. The number of seeds per fruit varies considerably among species (table 4). Within a species, seeds per fruit may also vary by a factor of 2 or more depending on microclimate, pollination, and genetic variability. Seed weight also varies considerably among and within species (table 4). For example, in *R. ulmifolius* Schott., the individual seed weight with the highest frequency was 2 to 2.5 mg, whereas weights ranged from 1 to 5 mg (Jordano 1984).

Extraction and storage of seeds. Seeds may be extracted by macerating the fruits in water then floating off or screening out the pulp and empty seeds (Brinkman 1974). Because of the high strength of the endocarp (figure 5), maceration does not damage the seeds (Rose 1919). Small lots of fruit may be covered with water and macerated in a blender until the pulp and fiber are separated (Morrow and others 1954). Additional water is then added, the sound seeds allowed to settle, and the pulp and empty seeds decanted. Several changes of water will yield cleaner seeds. Seed yield data are presented in tables 4 and 5.

The cleaned seeds should be dried before storage. Clark and Moore (1993) reported that seeds from raspberry cultivars germinated well after storage for 26 years at 4 to 5 EC.

Rubus seeds can be present in the forest floor of many forest types in North America (Barber 1976; Graber and Thompson 1978; Granstrom 1982; Maxwell 1990; McGee 1988; Moore and Wein 1977; Peterson and Carson 1996; Piroznikov 1983; Quick 1956; Ruth 1970; Whitney 1978; Yokohama and Suzuki 1986; Zasada 1996) long after the species has disappeared from the site. The longevity of seeds in the forest floor is believed to be on the order of decades to a century or more, indicating that seeds can be stored for long periods of times under seasonally alternating temperature and moisture conditions.

Understanding longevity of seeds in the forest floor is complicated for at least 2 reasons. First, Graber and Thompson (1978) found that 6,000 to 7,000 viable *Rubus* seeds/ha (2,400 to 2,800/ac) were deposited annually in northern hardwood forests in New England, making it difficult to determine the age of the seed population. Second, few controlled experiments have been conducted to demonstrate seed longevity in the soil; Granstom (1987) reported that artificially buried seeds remain viable for at least 5 years.

Germination. Raspberry and blackberry seeds are described as having deep dormancy caused by one or more of the following: impermeable seedcoat (endocarp), mechanical resistance of the seedcoat to growth, chemical inhibitors in the seedcoat and endocarp and the presence of a dormant embryo (Jennings 1988; Nybom 1980; Ourecky 1975). Under natural conditions, dormancy is broken by a combination of factors, including exposure to freeze-thaw cycles, diurnal and annual changes in temperature, cycles of wetting and drying of the seedcoat, passage thru the digestive system of animals, and activity of fungi and insects on the seedcoat. A given cohort of seeds germinates over a period of 2 to 3 or more years under field conditions, with some seeds apparently lying dormant for decades. The germination pattern will vary by species, microclimate, and condition of seeds when dispersed, among other factors (Barnes 1985; Dale and Jarvis 1983; Krefting and Roe 1949; Maxwell 1990; Nybom 1980; Tappeiner and Zasada 1993). It is commonly believed that passage through the digestive tract of an animal speeds germination. However, the importance of this treatment appears to be dependent on the species and the type of animal passing the seeds (Barber 1976; Lautenschlager 1990).

There may be an interaction between the way in which seeds are handled and dried and the type of dormancy seeds exhibit. For example, Dale and Jarvis (1983) indicate that raspberry seeds that do not undergo a prolonged period of drying germinate better that those that are dried. Rantala (1976), however, indicates that some species may germinate better after prolonged drying. The point is that dormancy may be manageable to some degree for some species during the handling process. Depth of dormancy may also be affected by the temperature at which fruits develop (Dale and Jarvis 1983).

The list of treatments used to improve overall germination and rate of germination is comprehensive to say the least. These have included the following by themselves or in various combinations: chemical scarification with sulfuric acid or sodium hypochlorite (either used alone or both sequentially); mechanical scarification by removing part of the endocarp, seedcoat, and endosperm; hormone treatment (gibberellic acid); warm temperature incubation; immersion in boiling water; cold stratification; incubation in oxygenated water; treatment with nitrate; and recovery of seeds from feces of various animals (Barber 1976, 1978; Brinkman 1974; Campbell and others 1988; Dale and Jarvis 1983; Galletta and others 1989; Jennings 1988; Ke and others 1985; Lautenschlager 1990; Lundergan and Carlisi 1984; Maxwell 1990; Moore and others 1974a & b; Nesme 1985; Nybom 1980; Ourecky 1975; Rantala 1976; Rose 1919; Scott and Ink 1957; Traveset and Willson 1998; Warr and others 1979). In spite of the efforts to improve the uniformity of germination, results are highly variable within and among species and no standard method seems to be available for germination of species in the genus.

Some form of sulfuric acid treatment followed by cold stratification is a common treatment prior to germination. Sulfuric acid significantly changes the structure and thickness of the endocarp and the weight of the seed (Lautenschlager 1990; Moore and others 1974b). Some important considerations for acid treatment mentioned in the above references are listed below:

- The seed surface should be dry, otherwise the reaction between water and acid will result in temperatures lethal to the embryo.
- Raspberry seeds should be treated for no more than 15 to 20 minutes, whereas blackberry seeds require up to an several hours. Seeds should be stirred frequently during treatment.
- It may be necessary to immerse the container with seeds and acid in an ice bath to keep the temperature at safe levels for the embryo.
- Seeds should be thoroughly washed following treatment to remove acid. Although some seeds will germinate with acid treatment alone (which essentially removes the seedcoat as a barrier) (Nesme 1985), a 60- to 120-day period of cold stratification seems to improve germination for some species.

Various concentrations of sodium or calcium hypochlorite can be used as an alternative to sulfuric acid (Campbell and others 1988; Galletta and others 1989). Sometimes calcium hydroxide is used in combination with the hypochlorite. Hypochlorites also significantly alter the endocarp but do not carbonize it as does sulfuric acid. Duration of the treatment is several days as opposed to minutes or several hours for sulfuric acid. Solutions of 12 to 15% appeared to work best for raspberry but were not as effective with blackberries (Galletta and others 1989). Seeds should be thoroughly washed after treatment.

Plant breeders often excise embryos or "nick" the endocarp of individual seeds to improve germination when seed supply is limited or when seeds from particularly valuable controlled crosses are being grown (Ke and others 1985; Nesme 1985; Warr and others 1979). This is generally not possible for large seedlots.

The effectiveness of the cold stratification treatment depends on the stratification temperature and the length of stratification (Rantala 1976). The optimum temperature may differ among species. Cloudberry, for example, seems to germinate better following stratification at 1 EC than at 4 EC. Rantala (1976) and Barber (1976) have demonstrated the value of stratifying seeds for 6 months or more for cloudberry and salmonberry, respectively.

Seed quality can be can be estimated from cutting tests and x-radiography (Nesme 1985). Seeds that sink when placed in water contained what appeared to be viable embryos, and a general separation of high from low-quality seeds is possible in this way (Lautenschlager 1990; Nybom 1980).

Germination following the above described treatments that attempt to alter the condition of the seedcoat and eliminate inhibitors or other conditions by cold stratification is highly variable among species and within species. In table 6 are listed a few examples of the variation in germination that may be encountered in seeds collected from natural populations and from varieties produced for fruit production. Generally, treatments that mechanically remove the endocarp improve germination above the values in table 6. Rate of germination is generally slow; in tests conducted out-of-doors and allowed to run for a year or more, germination will commonly occur over at least 1 or 2 growing seasons for many species (Barnes 1985; Nybom 1980; Tappeiner and Zasada 1993; Traveset and Willson 1997, 1998). Graber and Thompson (1978) concluded that seeds are most likely to germinate after being in the soil at least 5 years. It seems safe to conclude that many of the tests that are conducted do not stratify seeds long enough to remove the impediment to germination. Brinkman (1974) provides general germination information for several other species.

The examples shown in table 6 were generally conducted in a constant temperature environment. For some species, diurnally fluctuating temperatures result in better germination than constant temperatures (Campbell and others 1988).

Light appears to improve germination in many species (Nybom 1980; Ourecky 1975). However, some species (for example, red raspberry, cloudberry, and salmonberry) do not require light to germinate (Warr and others 1979; Lautenschlager 1990).

Germination is epigeal (figure 6). Cotyledons are normally 2, but Nybom (1980) observed that seedlings with more than 2 cotyledons were fairly common and that treatments increasing germination increased cotyledon number. Polyembryony has been reported in cloudberry (Rantala 1976).

Nursery practice. The best germination usually follows sowing of scarified seeds in the late summer or early fall (Wroblowna 1949), although spring-sowing scarified and stratified seeds is also recommended (Heit 1967). Seeds should be sown in drills and covered with 3 to 5 mm (⅛ to ⅜ in) of soil (Brinkman 1974). Mulching over winter reduces drying and soil-freezing (Hill and Beattie 1956).

Barnes (1985) recommends the following schedule for production of *R. deliciosus* Torr. from seed: gather seeds in late summer, clean and store them at near freezing; sow from October–December in unfertilized sand beds and cover with sand; wet down and firm soil over seeds; once seeds have germinated and reached a height of 5 to 7 cm (2 to 3 in) transplant to deep 15 cm (6 in) pots to promote both lateral and vertical root development. Fall-sowing produces better results than spring-sowing of stratified seeds. Seeds germinate over several growing seasons and the beds are usually not resown for at least 2 seasons in order to get better return of seedlings from sown seeds.

Ourecky (1975) found that full-sized green fruits can be collected cleaned, treated, and sown. Moist vermiculite and finely shredded sphagnum are both good planting media. Seeds should not be covered with more than 2 to 8 mm (1/10 to 3/10 in) of the medium. As soon as the second true leaf appears (figure 6), seedlings can be transplanted to individual containers.

Vegetative propagation—by tip-layering, rooting suckers, and crown division and by taking leaf-bud and stem cuttings—is used to increase availability of desirable varieties (Ourecky 1975). Salmonberry can be established in coastal Oregon under field conditions with little post-planting care from crowns or rhizome cuttings if planted in the winter during the wet season (Maxwell 1990).

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Figure 1—*Rubus,* blackberry, raspberry: general structure of ramets in populations with different growth habits: First, species in which clone development occurs in the soil by development of root (for example, red raspberry) or rhizome (for example, salmonberry) systems (**A**, which is red raspberry, a biennial cane species). Then, species in which clones expand by layering of above ground stems (for example, trailing raspberry) (**B**). **KEY: a** = primocanes, **b** = florocanes, **c** = dead canes, **d** = part of stem or root system that is either dead or non-flowering. (Drawings are based on observations by Whitney (1982, 1986), Suzuki (1987, 1989, 1990), and the authors.)

Figure 2—*Rubus,* blackberry, raspberry: red raspberry clone showing distribution of ramets (**circles**) as they were in a clone excavated on an upland site in central Alaska. This plant was about 5-years-old and originated from seed. Red raspberry clones develop by expansion of the root system. Salmonberry, thimbleberry, cloudberry, and other species may develop clones with similar ramet distribution, but clone expansion occurs by the growth of rhizomes. Ramet longevity in these latter species is also different.

Figure 3—*Rubus,* blackberry, raspberry: fruits, H 2.

Figure 4—*Rubus,* blackberry, raspberry: nutlets (seeds), H 12.

Figure 5—*Rubus canadensis,* smooth blackberry: longitudinal section of a seed, H 36.

Figure 6—*Rubus occidentalis,* blackcap raspberry: seedling development at 1, 13, 22, and 36 days after germination.

Table 1—*Rubus,* blackberry, raspberry: nomenclature and occurrence

Scientific name & synonym(s)	Common names	Occurence
SUBGENUS: *Eubatus* (blackberries)		
***R. allegheniensis* Porter**	**Allegheny blackberry**, sow-teat blackberry	New Brunswick to Minnesota, S to Missouri, Arkansas, E to North Carolina
***R. canadensis* L.** *R. millspaughii* Britt. *R. randii* (Bailey) Rydb. *R. amabilis* Blanchard	**smooth blackberry**, thornless blackberry, mountain blackberry	Newfoundland to Ontario & Minnesota, S to Tennessee & Georgia
***R. hispidus* L.** *R. obovalis* Michx. *R. sempervirens* Bigel.	**swamp dewberry**, running blackberry	Prince Edward Island to Ontario, S to Wisconsin, E to Maryland & mtns of North Carolina
***R. laciniatus* Willd.** *R. fruticosus* var. *laciniatus* West. *R. vulgaris* Weihe & Nees	**cutleaf blackberry**, evergreen blackberry	Old-World origin; escaped from cultivation in Massachusetts to Michigan & S; also W of Cascade Mtns from British Columbia to California
***R. procerus* P.J. Müll. & Boulay**	**Himalaya blackberry**	Europe; naturalized from Delaware to Virginia, S British Columbia to California W of Cascade Mtns
***R. ursinus* Cham. & Schlect**. *R. macropetalus* Dougl. ex Hook	**trailing blackberry**, Pacific blackberry	British Columbia to California & Idaho
SUBGENUS: *Idaeobatus* (raspberries)		
***R. idaeus* L.**	**red raspberry**	Present in all states but SE US, Texas, & Oklahoma & all provinces of Canada
***R. occidentalis* L.**	**blackcap raspberry**, black raspberry, thimbleberry	New Brunswick to Minnesota, S to Colorado, E to Georgia
***R. spectabilis* Pursh** *R. stenopetalus* Cham.	**salmonberry**	SE Alaska to Idaho & California; becoming naturalized in Great Britain
SUBGENUS: *Chamaemorus* (cloudberry)		
***R. chamaemorus* L.**	**cloudberry**, bake-apple	Alaska, New England, & all Canada
SUBGENUS: *Anoplobatus* (flowering raspberries)		
***R. odoratus* L.** *Rubacer odoratus* (L.) Rydb.	**fragrant thimbleberry,** flowering raspberry, purple-flowering raspberry	S Quebec to Ontario S to Michigan & E to Georgia
***R. parviflorus* Nutt.**	**thimbleberry**, western thimbleberry	SE Alaska to California, New Mexico, Dakotas to N Great Lakes area
SUBGENUS: *Cyclatis* (Arctic berries)		
***R. arcticus* L.**	**nangoon berry,** arctic	North America from Alaska to Labrador &

	bramble, wineberry	Newfoundland; also Minnesota

Sources: Brinkman (1974), Curtis (1959), Fernald (1950), Hickman (1993), Jennings (1988), MacKinnon and others (1992), Viereck and Little (1972).

Table 2—*Rubus,* blackberry, raspberry: height or length at maturity and fruit ripeness criteria

Species	Growth habit	Height or length at maturity (m)	Year first cultivated	Fruit ripeness criteria: Preripe	Fruit ripeness criteria: Ripe
SUBGENUS: *Eubatus*					
R. allegheniensis	Shrub	1.8	1905	Red, hard	Black-purple
R. canadensis	Shrub	2.8	1727	Red, hard	Black, soft
R. hispidus	Vine	1.8–2.5	—	Red, hard	Reddish purple to black
R. laciniatus	Vine	2.8–4.6	1770	Dull red	Black, sweet, shining
R. procerus	Vine	6.2–9.2	1890	Red, hard	Black, soft
R. ursinus	Vine	4.6–6.2	—	Red, hard	Black, shining, soft
SUBGENUS: *Idaeobatus*					
R. idaeus	Shrub	2.2	—	Pink, hard	Red, sweet
R. occidentalis	Shrub	1.5–2.2	1696	Bright red, hard	Purple-black, soft
R. spectabilis	Shrub	2.8–4.6	1827	Pink, hard	Orange or red, soft
SUBGENUS: *Chamaemorus*					
R. chamaemorus	Perennial forb, below-ground rhizome	0.1–0.2	—	Red, hard	Orange, soft
SUBGENUS: *Anoplobatus*					
R. odoratus	Shrub	1.8	1635	Pink, hard	Red, soft
R. parviflorus	Shrub	0.5–2.5	—	Pink, hard	Red, soft

Sources: Brinkman (1974), Fernald (1950), Jennings (1988), MacKinnon and others (1992), Viereck and Little (1972).

Table 3—*Rubus,* blackberry, raspberry: phenology of flowering and fruiting

Species	Location	Flowering dates	Fruit ripening dates	Seed dispersal dates
SUBGENUS: *Eubatus*				
R. allegheniensis	—	May–July	Aug–Sept	Aug–Sept
R. canadensis	—	June–July	July–Sept	July–Sept
R. laciniatus	NE US	June–Aug	July–Oct	Sept–Oct
R. hispidus	—	June–early Sept	Mid-Aug–Oct	Aug–Oct
R. procerus	Washington	June–Aug	Aug–Sept	—
R. ursinus	Pacific Coast	June–July	Aug–Sept	Oct–Nov
SUBGENUS: *Idaeobatus*				
R. idaeus	Rangewide	Late May–July	Late June–Oct	July–Oct
R. occidentalis	—	Apr–June	June–Aug	June–Aug
R. spectabilis	Alaska	May–June	June–Aug	June–Aug
	Oregon–Washington	Apr–May	May–July	June–July
SUBGENUS: *Chamaemorus*				
R. chamaemorus	Boreal North America	June–July	July–Aug	Aug–Sept
SUBGENUS: *Anoplobatus*				
R. odoratus	—	June–Sept	July–Sept	July–Sept
R. parviflorus	Pacific Northwest	May–June	June–July	July–Aug

Sources: Barber (1976), Brinkman (1974), Coladonato (1990a), Hippa and Koponen (1976), Viereck and Little (1972), Whitney (1978).

Table 4—*Rubus,* blackberry, raspberry: fruit weight and number of seeds/fruit

Species	Fresh fruit wt (g)	Seeds/fruit Avg	Seeds/fruit Range	Source
R. spectabilis	—	62	28–128	W Oregon
	—			40 17–65 SE Alaska
R. parviflorus spp. *strigosus*	—	190	127–246	W Oregon
R. idaeus ssp. *strigosus*	1.3 (0.8–2.4)	36	28–47	British Columbia & N Alberta
R. idaeus ssp. *vulgatus*				
General (N = 8 cv)	—	63	27–103	Norway
Restricted pollination	—	13	—	Norway
Open-pollination	—	32	—	Norway
R. arcticus	0.37–1.09	25	10–35	Finland
R. chamaemorus				
Full light	—	11	7–13	Sweden
Shade	—	14	10–16	Sweden
Hand-pollination	—	11	—	Sweden
Open-pollination	—	8	—	Sweden
No defoliation	—	8	—	Sweden
50% defoliation	—	8	—	Sweden
General	2.5	18	—	Finland
General	—	10	3–18	Alaska
Rubus subgen. *Eubatus*	1.2–6.8	56	27–83	Arkansas

Sources: Ågren (1989), Moore and others (1974a), Nybom (1986), Rantala (1976), Redalen (1977), Ryynänen (1973), Staniforth and Sidhu (1984), Suzuki (1990), Van Adrichem (1972), Willson (1996), Whitney (1978), Zasada (1996).

Table 5—*Rubus,* blackberry, raspberry: seed yield data

Species	Place collected	Seed wt/fruit wt g/kg	Seed wt/fruit wt lb/100 lb	Thousands of seeds/wt Range /kg	Range /lb	Average /kg	Average /lb
SUBGENUS: *Eubatus*							
R. allegheniensis	—	40	4	370–724	168–329	574	262
R. canadensis	—	40	4	458–495	208–225	476	216
R. hispidus		—	—	282–513	128–233	408	185
R. laciniatus	Washington	7	0.7	—	—	301	137
R. procerus	—	—	—	—	—	323	147
R. ursinus	Washington	58	5.8	—	—	845	384
Rubus (general European)*	Sweden	—	—	359–869	163–395	480	219
SUBGENUS: *Ideobatus*							
R. idaeus	Minnesota	30	3	667–845	303–384	722	328
	British Columbia/ Alberta	46	4.6	469–794	213–397	632	288
R. occidentalis	Minnesota	30–80	3-8	629–845	286–384	735	334
R. spectabilis	Oregon 1	—	—	251–528	115–240	354	162
	Oregon 2	—	—	189–321	87–146	240	109
	Oregon 3	—	—	270–45	123–157	316	144
	Oregon 4	—	—	216–298	98–135	265	120
	Alaska	—	—	—	—	315	143
SUBGENUS: *Chamaemorus*							
R. chamaemorus	Sweden/Finland	59	(5.9)	—	—	122	56
	Alaska	—	—	80–101	37–45	90	40
SUBGENUS: *Anoplobatus*							
R. odoratus	Pennsylvania	—	—	—	—	1,085	493
R. parviflorus	Oregon	—	—	357–806	162–367	611	278
	Washington	—	—	719–1201	327–546	20	418
SUBGENUS: *Cyclatis*							
R. arcticus	Sweden/Finland	76	(7.6)	—	—	980	446

Sources: Brinkman (1974), Lautenschlager (1990), Nybom (1980), Rantala (1976), Zasada (1996).
* Seeds of 20 species in Sweden.

Table 6—*Rubus,* blackberry, raspberry: germination results

Species or variety & source	Germination temp (EC)	Total germination (%)	Time to 50% germination
*R. idaeus**	10	69 (18–94)	28 days
	20	93 (84–96)	6 days
	30	60 (40–88)	33 days
R. idaeus† 'Glen Cova'			
No stratification	—	48	—
Stratification	—	53	—
R. idaeus‡			
Bear feces			
Acid scarification	21	6	—
No scarification	21	0	—
Coyote feces			
Acid scarification	21	10	—
No scarification	21	0	—
Fresh seed			
Acid scarification	21	8	—
No scar.ification	21	0	—
R. spectabilis§			
Fresh seeds			
Acid scarification	21–28	0	—
Scarification & 2-mon stratification	21–28	0	—
Scarification & 4-mon stratification	21–28	62	—
Scarification & 6-mon stratification	21–28	81	—
Bird feces			
No stratification	21–28	0	—
4-mon stratification	21–28	25	—
6-mon stratification	21–28	73	—
Coyote feces			
6-mon stratification	21–28	6	—
*R. chamemorus*2			
3–5-mon stratification	Variable	<1	—
6–9-mon stratification	Variable	3–10	—
10–13-mon stratification	Variable	30–31	—

Sources: Barber (1996), Dale and Jarvis (1983), Lautenschlager (1990, in press), Lundergan and Carlisr (1984); Moore and others (1974); Nesme (1985), Rantala (1976).

* Seeds were treated as follows: surface sterilized in 1% sodium hypochlorite (NaClO) for 10 minutes, nicked to expose radicle; soaked for 3 min in 1% NaClO, and incubated in the dark for 1 year.

† Seeds were extracted and air-dried, treated for 20 minutes with sulfuric acid and 7 days with calcium hypochlorite; stratified at 5 EC or unstratified. Fruits were collected 43 days after anthesis. Seeds were from fruits collected earlier or later differed in germination response.

‡ Seeds were from natural populations in Maine; they were stratified for 2 to 6 months after acid treatment; tests were conducted for 30 days.

§ Fresh seeds from Washington state populations; stratified at 2 to 5 EC.

2 Seeds stratified at 1 EC and germinated monthly in a mist propagation chamber.