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The Reproductive Ecology of Broadleaved Trees and Shrubs: An Overview

by

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College of Forestry
Forest Research Laboratory
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THE REPRODUCTIVE ECOLOGY OF BROADLEAVED TREES AND SHRUBS: AN OVERVIEW

Broadleaved trees and shrubs play an integral role in both managed and unmanaged forests. They affect nearly all ecosystem processes and functions. For example, they provide food and cover for wildlife, they help stabilize slopes and slow erosion, they cycle nutrients within the system—in different forms, at different times, and in different amounts than do conifers—and some fix nitrogen, something no conifer can do. In addition, broadleaved trees and shrubs provide humans with a variety of special forest products and values. Some, like salal and Oregon-grape, are used commercially in floral arrangements. Others, like cascara buckthorn, contain chemical compounds with special medicinal properties. Still others, like huckleberries and blackberries, have significant food value, while many, like the maples, cause our forests to burst with color each fall. And all species contribute to the biological diversity of our forest ecosystems. On the other hand, broadleaved trees and shrubs compete directly and intensely with each other and with conifers, particularly after timber harvest when forests are regenerating. Often it is this last role, that of a competitor, that draws the most attention.

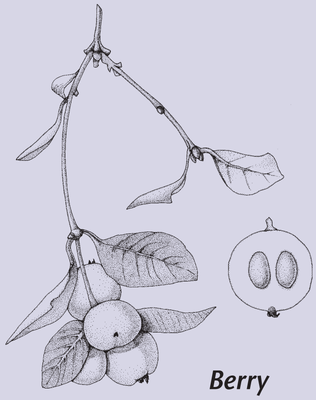
Understanding these roles will help resource managers address the many different species, uses, and values that are intertwined in a forest ecosystem. By understanding how broadleaved trees and shrubs reproduce, managers can better predict how these species will respond to management activities. Being able to predict responses will enhance the ability of managers to create different habitats, forest structures, and plant communities aimed at accomplishing a variety of objectives. For example, when scenic value along a forest road is of interest, managers can encourage the development of vine maple, adding beauty and structure to the forest, especially during the fall when leaves change color. Understanding how vine maple reproduces is critical for achieving this objective. Likewise, if red alder is desired for improvement of nitrogen availability, land managers need to understand its reproductive requirements in order to effectively encourage its establishment.

Most broadleaved trees and shrubs have the ability to reproduce in two ways: sexually (by seed) and asexually (vegetatively)—although different species vary dramatically in the extent to which they rely on each method.

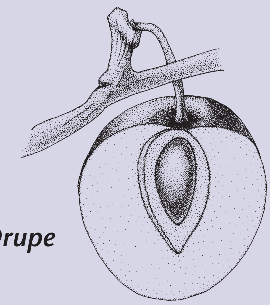
Sexual Reproduction

In developing from seed to maturity, plants pass through a series of stages. This paper discusses six: seed production, seed dispersal, overwintering and long-term storage of seeds, seed germination, early seedling survival, and plant establishment and later growth.

Seed Production

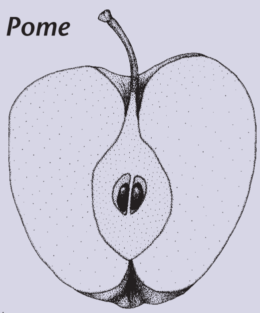


Berry



Drupe

Pome



Aggregate

Legume

Seeds are produced following pollination and fertilization of the female flower. The success of these two processes (measured by the number of viable seeds produced) is dependent on the age and vigor of the parent plant, as well as environmental factors such as weather. Age is important because a plant must be sexually mature before it can produce seeds. However, the age of sexual maturity differs dramatically among plant species. Oaks, for example, become sexually mature around age 40, while alders mature around age 10. The vigor of a parent plant is directly dependent upon the environment in which it grows. For example, a harsh environment might produce a tree or shrub with poor vigor. This often results in a poor seed crop because so much of the plant's resources are tied up in processes related to survival. However, some plants respond to a harsh environment in the opposite manner, producing a heavy seed crop in order to generate viable offspring. Environmental factors such as weather are also important to the reproductive process. For example, cool, damp weather at the time pollen is shed plays a tremendous role in pollination because it limits dispersal by wind and restricts the activity of pollinating insects.

Seeds of broadleaved trees and shrubs are borne within fruits that come in a variety of shapes and sizes. In the Pacific Northwest, the following types are especially common.

Fleshy Fruits (those in which the seeds are enclosed inside a soft, fleshy ovary):

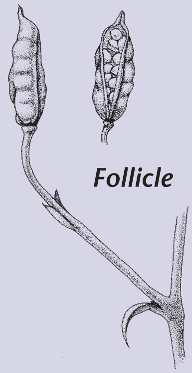
- **Berry**: Multiple seeds loosely arranged inside a fleshy fruit. The fruits of salal, huckleberries, elders, snowberries, and Oregon-grapes are all berries.
- **Drupe/drupelet**: Hard, usually single, seeds surrounded by a fleshy covering. The fruits of cherries, plums, Indian-plum, devilsclub, California-laurel, and cascara buckthorn are all drupes. Drupelets are merely small drupes; the fruits of blackberries are actually aggregates of drupelets.
- **Pome**: Multiple seeds borne inside papery capsules, surrounded by a fleshy fruit. The fruits of apples, pears, hawthorns, mountain-ashes, and serviceberries are pomes.
- **Aggregate:** Multiple seeds, with each seed borne inside its own fleshy covering. The fruits of raspberries, blackberries, and magnolias are aggregate fruits.

Dry Fruits (those in which the seeds are enclosed inside a dry, often papery, ovary):

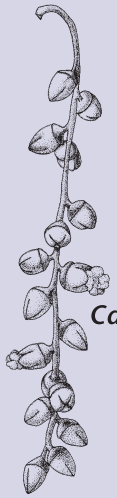
Dry fruits are further categorized by whether their outer covering splits open at maturity to release its seeds (dehiscent), or does not split open (indehiscent).

Dehiscent (splitting open along predetermined lines at maturity):

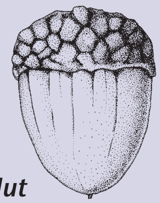
- **Legume or pod**: A multiple-seeded fruit that develops from a single carpel. When mature, the carpel splits open along two predeter-



Follicle

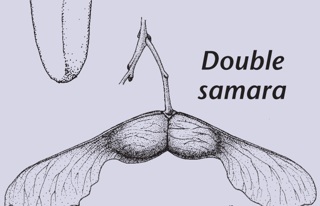


Capsules

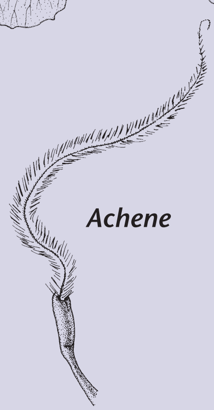


Nut

Samara



Double samara



Achene

mined sutures, often explosively expelling its seeds. The fruits of Scotch broom, gorse, locusts, and honeylocusts are legumes.

- **Follicle**: A multiple-seeded fruit that develops from a single carpel. When mature, the carpel splits open along one side. The fruits of ocean spray, ninebark, spirea, and milkweed are follicles.
- **Capsule**: A multiple-seeded fruit that develops from two or more fused carpels. When mature, the carpels open in various ways. The fruits of rhododendrons, mockorange, willows, cottonwoods, boxwood, and *Ceanothus* species are capsules.

Indehiscent (not splitting along predetermined lines at maturity):

- **Nut/nutlet**: A single-seeded fruit with a hard outer shell. The fruits of California hazel, tanoak, golden chinkapin, and all oaks are nuts. Acorns are nuts capped by scaly or bristly caps (involucres). Nutlets are merely small nuts that may be winged, as in the alders and birches, or unwinged.
- **Samara**: Dry, single-seeded fruit with a prominent wing. The fruits of ashes are single samaras; the fruits of maples are typically double samaras.
- **Achene**: Dry, one-seeded fruit that is not winged but may have a feathery or hairy tail. The fruits of bitterbrush, sagebrushes, rabbitbrush, and mountain-mahoganies are achenes.

Seed Dispersal

Once mature, seeds are dispersed in a variety of ways. Although it is common to focus on what happens from the time seeds leave their parent until they reach the ground (primary dispersal), redistribution after they land (secondary dispersal) often determines the resources available to them for germination and early growth. The most common dispersal mechanisms for seeds are gravity, wind, water, and animals, often working in conjunction with one another.

- **Gravity**: Gravity plays a role in the dispersal of all seeds, but it is especially important for those that are heavy and unwinged, like acorns and other large nuts. Although gravity's role is often thought of in conjunction with primary dispersal, it is also an important secondary dispersal mechanism, especially on steep slopes.
- **Wind**: Wind is especially important for the primary dispersal of winged and plumed fruits such as samaras and achenes, carrying them far from their parents. It is also an important secondary dispersal mechanism, redistributing seeds and some dry fruits after they hit the ground.
- **Water**: Water is typically a secondary dispersal mechanism, carrying seeds away from their primary landing spot to new locations. The cottony tufts of willows, cottonwoods, and aspens are all redistributed by water, as are the samaras of ashes and maples and the winged nutlets of some alders.
- **Animals**: Animals are important primary and secondary dispersers for both fleshy and dry fruits. Birds and many small mammals have the ability to collect seeds either directly from the parent plant or

after they hit the ground. Once gathered, the seeds may be swallowed immediately or stored for later consumption. When swallowed, some seeds are destroyed by the digestive process, but others pass through the animal's system intact and may be deposited far from where they were gathered. If stored, many seeds are never rediscovered by their hiders, leaving them free to germinate when conditions are right. Large fruits like acorns, hazel nuts, and walnuts are commonly stored, but so are small seeds like those of manzanita and *Ceanothus*.

Seed Overwintering and Long-term Storage

Following dispersal, most seeds require a "storage" or "dormant" period in order to undergo physiological changes or overcome physical barriers such as the seed coat before they can germinate. The length of this storage period is determined by interactions among internal factors controlling the seed's dormancy and external biotic and abiotic factors. Duration of dormancy can be short or long depending on the species. For example, cottonwood and willow seeds have a short storage period and must germinate within several weeks of dispersal, or they will die. Bigleaf maple and salal seeds remain dormant over winter and germinate in the spring. Vine maple seeds remain dormant for up to 3 or 4 years, while the seeds of salmonberry and some species of *Ceanothus* may remain dormant for decades or even centuries. Each strategy has significant implications for forest managers. A brief storage period allows a species to occupy a site rapidly after seeds are dispersed. A long storage period may permit a plant to re-colonize a site long after the original parent plant has died. Seeds stored in the soil for long periods of time are known as a "seed bank." These stored seeds are "waiting" for a disturbance or for the right environmental conditions to occur before they will germinate.

Storage is a dynamic and risky period in a seed's life. While some seeds are lost to predation from animals and fungi, new ones are continually added from plants in the surrounding area, a process commonly called "seed rain." Predation from animals tends to have a greater impact on large-seeded species such as oaks and tanoaks, because they are more easily collected and provide more nutrients than the small seeds of species such as alder. Pathogens also take a tremendous toll on seeds during the storage period. For example, damping-off fungi often impact seeds and seedlings of species such as red alder and *Ceanothus*. These fungi result in death of new seedlings and root rot in older ones.

Seed Germination

In order to germinate, seeds must undergo specific physiological changes during their storage period. To overcome dormancy, all seeds need water. In addition, some may need one or more of the following stimuli:

- **Light**: For example, red alder seeds need exposure to infrared light before they will germinate.
- **Heat**: Some species of *Ceanothus* need exposure to intense heat to break their seed coats. As a result, *Ceanothus* seeds often germinate abundantly following wildfire or prescribed burns.
- **Cold period**: Seeds of California hazel and bigleaf maple require a cold storage period lasting 2 to 6 months before germination will occur.
- **Scarification**: Either mechanical (scraping or scratching of the seed coat) or chemical (chemical breakdown of the seed coat). In a laboratory, soaking dogwood seeds in sulfuric acid accelerates germination; mechanically removing or cracking the hard wall around the seed aids germination of California-laurel. Outside the lab, animals play a significant role in scarification by passing seeds through their digestive tracts. Trampling by hooves also plays an important role in the germination of some species.

Early Seedling Survival

Following germination, seedlings are fragile and are susceptible to a variety of damaging agents. For example, pathogens, insects, birds, competition from other vegetation, litterfall, frost heaving, soil temperature extremes, drought, and other environmental variables all work against a new seedling's chances for survival. Vital to early survival is a "safe" growing site for the seedling. A safe site is one that has a hospitable microclimate (the right mixture of light, temperature, moisture, nutrients, etc.) and tolerable levels of predation by pathogens, insects, and other predators. The size of the seedling immediately after germination helps determine how "safe" a site must be. For tiny seedlings that germinate from tiny seeds (like western hemlock, red alder, Pacific madrone, redwood, and salal), a safe site is much more critical than for big, hearty seedlings that germinate from large seeds (like bigleaf maple, oaks, and tanoak). Some environmental factors, such as soil surface temperature, may play a critical role in the survival of seedlings during several days or weeks of their early development, yet never again be important to the plant's growth.

Plant Establishment and Later Growth

After a seed has germinated and the seedling has survived the early period of growth, the seedling's response is determined by whether its environment is "right" for it. The right environment is one that meets all of the seedling's requirements, allowing it to grow to maturity and reproduce. If, however, the seedling's requirements are not met, one of two things can happen: 1) the seedling may persist in the understory for a long time, delaying maturity and creating a "bank" of seedlings that remain until the overstory is disturbed and they become free to grow, or 2) the seedling may die. Once created, seedling banks are quite dynamic, with seedlings constantly being gained and lost. Tanoak, bigleaf maple, and huckleberries are Pacific Northwest species noted for their ability to create seedling banks.

The concept of tolerance is helpful in understanding what constitutes the “right” environment for seedlings, although the term is used in various ways. A plant can be tolerant or intolerant of a whole host of environmental conditions—for example, shade, heat, drought, moisture, predation, browsing, and crushing, to name but a few. Although we often label a plant as tolerant or intolerant of a single environmental factor, this is almost always an oversimplification and may lead to false understanding. For example, although we commonly describe plants as being tolerant or intolerant of shade, we now know that shade-tolerant plants must also tolerate intense competition from neighboring plants, predation by insects and disease, browsing by animals, mechanical crushing, and drought, among other things. For the purpose of our discussion, a shade-tolerant seedling is one that can withstand reasonably high levels of shade, moisture stress, and predation, and one that competes well for nutrients—in essence, one that can survive typical understory conditions.

As a seedling becomes firmly established on a site, it develops the ability to withstand damage and to reproduce, either sexually or vegetatively. If damaged, a plant may respond in several ways: it may die, it may repair itself, or it may propagate itself, often vegetatively. After 5 or 10 years, plants are commonly ready to begin regenerating—through seed production (although in some species this may take several decades) and vegetatively, through rhizomes, layering, sprouting, or suckering.

Summary: Sexual Reproduction

Plants produce vast numbers of seeds throughout their lives, although smaller-seeded species produce far more than larger-seeded species. In any given year, hundreds of thousands of seeds, if not millions, are produced and dispersed per acre of forest, depending, of course, on the species, age, and vigor of the plants involved. During storage, germination, and early survival, hazards such as predators, pathogens, and inhospitable environments destroy innumerable seeds and seedlings, removing them from the pool of plants that might eventually reach maturity. Although precise numbers do not exist (and they would vary dramatically by seed size and physical environment), it is not unreasonable to say that only about 10 of every 100,000 seeds produced (0.01 percent) actually live long enough to become established plants—and of those, only a small fraction live long enough to produce seeds of their own. Seed size and type determine the amount and form of predation (*e.g.*, animals, insects, diseases). Larger seeds are preyed upon by birds and small mammals, while smaller seeds are especially susceptible to insects and pathogens. As a seedling increases in size, it may, under the right environment, be free to grow and eventually reproduce.

It is important to remember that all broadleaved trees and shrubs are capable of reproducing by seed—but that some are much better at it than others. Each species has a different strategy, or set of adaptations, that enables it to reproduce and grow under different conditions.

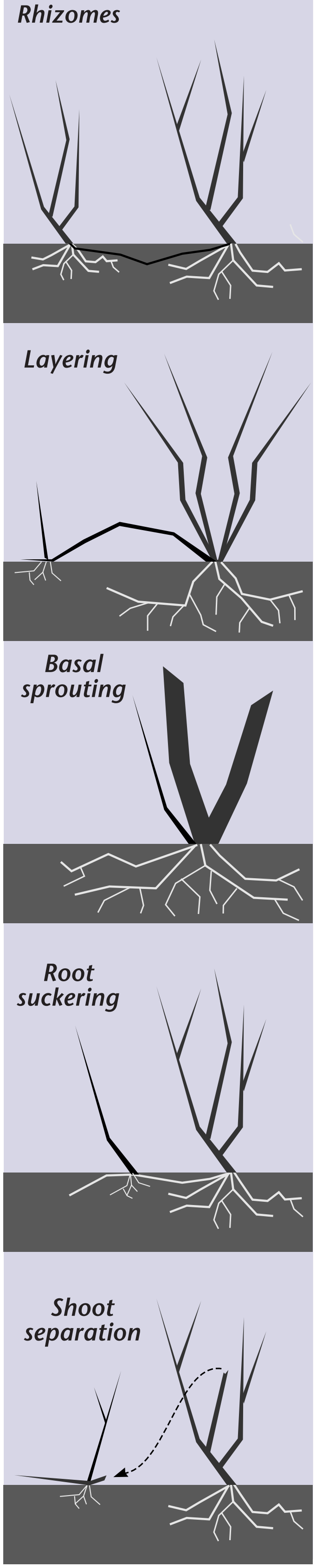
Light-seeded species such as red alder are able to quickly occupy newly created openings, not only because their seeds travel long distances, but also because each tree produces a tremendous amount of seed in a given year. Members of the *Ceanothus* genus use a slightly different strategy. They produce numerous tiny seeds that are cached or buried and can be stored in the forest floor for decades or even centuries, remaining viable until a disturbance stimulates them to germinate. Heavy seeds, such as those of oaks, tanoak, and chinkapin, are often dispersed short distances from the parent tree and are well prepared to withstand the rigors of growth in the understory because of the energy stored in their seeds. Land managers must understand the processes involved in sexual reproduction in order to predict how seed-producing plants will respond when an opening is created or a site is disturbed.

Vegetative Reproduction

In addition to reproducing by seeds, most broadleaved plants have the potential to propagate vegetatively. Sometimes new members arise directly from the base of the "parent" plant, as in basal sprouting, and sometimes they arise at quite a distance, as with root suckers and rhizomes. In each case, resources from the parent (called an ortet) are used to support the "offspring" (called a ramet). Over time, ramets are often separated from the ortet, becoming independent plants that are genetically identical to their parent. Collectively, an ortet and its ramets are called a clone. Some scientists call this process vegetative reproduction; others prefer to call it vegetative propagation, reserving the term "reproduction" for events involving sex. Regardless of what the vegetative process is called, it allows plants to rapidly occupy new territory, capturing available water, light, and nutrients. In plants that reproduce vegetatively, sexual reproduction is still important for moving species long distances and for maintaining genetic diversity within the plant population.

As plants capable of vegetative reproduction grow, they often produce a surplus of buds (sometimes called a bud bank) that have the potential to develop into new shoots or roots. These buds may be stored above or below ground—on stems, at the root collar, along underground stems (rhizomes), or along roots. In addition, buds may develop along existing stems, branches, or roots following some form of disturbance; these are called adventitious buds and can also give rise to new plants. Together, bud banks and adventitious buds result in the formation of new shoots and new plants. Five common methods of vegetative reproduction are rhizomes, layering, basal sprouting, root suckering, and shoot separation. Some species have the capacity to reproduce using several of these methods, while others are limited to one.

Mechanisms for Vegetative Reproduction



- **Rhizomes**: Rhizomes are stems that grow horizontally either partially or totally below the ground's surface. Like all stems, they produce buds that have the potential to give rise to new stems and leaves. In the case of rhizomes, most of these buds remain dormant, but some develop into new above-ground plants. The new aerial stems and the roots that develop to support them (collectively called ramets) have the potential to become independent ortets. Ramets and ortets are genetically identical to one another. Rhizomes, and the stems and roots that arise from them, are capable of forming a network of plant biomass so dense that the establishment of other species may be inhibited. Salmonberry, thimbleberry, salal, and Oregon-grape are several Pacific Northwest species that reproduce by rhizomes.
- **Layering**: Layering occurs when adventitious roots form along stems or branches that come into contact with the soil for long periods of time. After roots have become established, latent buds that have been stored along the branch or adventitious buds that form following root development may develop into new aerial stems. Over time, these new stems may become separated from the parent plant and grow independently. Layering enables a single plant to occupy and dominate a large area over time. Vine maple often spreads via layering.
- **Basal sprouting**: Basal sprouting occurs when a plant sends up new shoots (called sprouts) from buds located either at the base of the stem or on below-ground burls. Sprouting most commonly occurs when the original stem is killed, injured, or disturbed. Sprout clump size depends on the size and age of the parent plant. A large parent is capable of producing a tremendous clump of sprouts, while a small parent may produce only a small clump. Some species that commonly basal sprout are capable of producing sprouts even if the parent plant appears to be healthy and undisturbed. This sprouting ability allows a plant to maintain itself on a site under a wide range of conditions. Tanoak, bigleaf maple, California black oak, and Pacific madrone are several Pacific Northwest species that sprout profusely from their bases. The location of a species within its range may also influence its ability to sprout. Some species that sprout near the centers of their ranges will not sprout near their extremes; the pattern for other species is just the opposite.
- **Root suckering**: Root suckering occurs when the roots of a parent plant are capable of producing buds that sprout into new shoots. Almost any type of disturbance to the root system, from heavy machinery to animal hooves, can trigger a suckering response; suckering also occurs in the absence of apparent disturbance. Quaking aspen is the Pacific Northwest species best known for root suckering, although it also occurs in cottonwoods and locusts.
- **Shoot separation from the parent plant**: Some shoots have the ability to sprout new roots and shoots when severed from the parent plant. Humans take advantage of this attribute by taking "cuttings" and stimulating them to produce new roots and shoots; however, small branches can also become separated from the parent plant through damaging agents such as wind, flood, or animals. These

separated shoots, when carried away from the parent plant by wind or water and deposited in a new area, can then become established if environmental conditions are favorable. Black cottonwood is one Pacific Northwest species that utilizes this strategy. In fact, its ability to abscise short, leafy shoots may help it colonize sand and gravel beds along streams.

Factors Affecting Vegetative Reproduction

Nearly all broadleaved trees and shrubs have the ability to reproduce vegetatively. In sexual reproduction, age and vigor of the parent plant are primary influences on seed production. In vegetative reproduction, primary influences are the species involved, the vigor of the plants, and the type of disturbance that occurs.

Most plants that reproduce vegetatively first produce a "bud bank"—buds stored along their rhizomes, roots, stems, or branches. Bud banks located on rhizomes and roots continuously expand as the rhizomes and roots extend laterally; buds stored on stems, burls, or root collars increase in number as the plant grows. In addition, the plant must have enough vigor (energy) to respond to disturbance. And finally, the plant must be stimulated to respond, either through disturbance to the plant or to its immediate environment. If these conditions are met, the plant may respond by producing several to several dozen new stems per plant, which may translate into tens or hundreds of thousands of new plants per acre, depending on plant density.

Even in the absence of disturbance, some vegetative reproduction is likely to take place (*e.g.*, shoots from rhizomes will continue to be produced; layering will occur). In addition, as older above-ground stems senesce and die, buds in the bud bank may be released and sprouting may occur. As the forest canopy closes, sprouting plants may die back and revert to smaller forms with smaller bud banks, waiting until an opening occurs to sprout again.

Summary: Vegetative Reproduction

Plants have the ability to reproduce vegetatively in a variety of ways—for example, through rhizomes, layering, basal sprouting, root suckering, and shoot separation from the parent plant. These mechanisms may occur with or without disturbance to the parent. However, disturbance typically increases the development and release of stored and adventitious buds, stimulating vegetative reproduction. The tremendous potential that some broadleaved trees and shrubs have for reproducing vegetatively should cause land managers to carefully assess the potential impacts of a management activity such as thinning or clearcutting on plants that are visible above ground, as well as on those that may exist below ground.

Associated Literature

A number of papers describing the reproductive ecology of individual broadleaved trees and shrubs are listed in the "Associated Literature" section that accompanies this educational package.

Additional Notes

Educational Package

This leaflet is part of a larger educational program on the reproductive ecology of Pacific Northwest broadleaved trees and shrubs. The complete program consists of two audio-visual components—a videotape on the reproductive ecology of broadleaved trees and shrubs and a series of slide-tapes on shrub identification—and four printed components: 1) an overview of plant reproduction, 2) a series of leaflets on PNW trees and shrubs, 3) a glossary of relevant terms, and 4) a list of associated literature. To obtain the complete educational package, contact: Forestry Media Center, College of Forestry, Oregon State University, Corvallis, OR 97331, (503) 737-4702. To obtain only the printed documents, contact: Forestry Publications Office, Forest Research Laboratory, Oregon State University, Corvallis, OR 97331-7401.

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