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Light management important factor for partridge berry

Factors essential for plant life include adequate levels of light, moisture, mineral nutrients, and temperature; though the list is small, each is crucial for survival. This article is a contemplation of how one of these critical factors, light, impacts the biology of our 2012 Wildflower of the Year, Mitchella repens, partridge berry. Aside from issues of reproductive biology, ecological literature on partridge berry is meager. Consequently most of what follows is derived from general works on woodland ecology, perusal of which provides sufficient insight about the biology of Mitchella to inspire ideas worthy of further study.

Partridge berry plants are creeping evergreen perennials that inhabit the forest floor. They are among the smallest botanical components of their habitat, closer in size and scale to woodland mosses than to most other herbaceous perennials of the eastern deciduous forest. Relative to the trees that dominate, and thereby create, their habitat, partridge berry plants are miniscule. Each aspect of the photobiology of partridge berry discussed here is linked in one way or another to the size differential between it and the giants that loom above the forest floor.

Leaf litter and light. One fact of life on the forest floor is that tree leaves fall. Whereas leaf fall in a tropical rainforest might be likened to a steady drizzle, in temperate deciduous forests it is more like a hard, steady, rain that lasts for a few weeks every autumn. Loosely packed, crinkly, dry leaves of broad-leaved trees can accumulate to depths of several inches. Leaf fall is important to forest ecology. Leaf litter is gradually broken down, contributing organic matter and minerals to forest soils. And just like mulch in a garden, a layer of leaf litter insulates forest soil against rapid temperature fluctuations and it helps retain soil moisture. But, of course, another reason that

Spotlight on partridge berry

Illustration by

Nicky Staunton

gardeners use mulch is to discourage weed seeds from sprouting or to smother weeds outright—and by analogy, here we see two challenges facing b small woodland herbs: How do little seedlings get established under a layer of natural leaf litter? And how do mature plants keep their leaves above the annual autumnal avalanche of tree leaves? Of course, these challenges are not unique to partridge berry. Seedlings of all woodland herbs face the same problem as do adults of similar species with perennial leaves held near ground level; for example, rattlesnake orchids (Goodyera), snakeroot (Sanicula), and pipsissewa (Chimaphila) face the same challenge.

Several ecological studies have examined the smothering effects of leaf litter on forest herbs. Sydes and Grime (1981) found that shoot biomass of herbaceous perennials decreases with increasing depth of leaf litter in English woodlands; further, they found that topography matters: small hollows in the forest floor contain the greatest depths of leaf litter and are nearly devoid of herbaceous vegetation. An experiment conducted in central New York (Beatty and Sholes 1988) explored the dynamics of litter in pits formed by root masses lifted during treefalls. Leaf litter was removed from experimental pits and wire cages were installed to exclude incoming new leaf fall; after three years, litter-excluded pits showed enhanced germination and establishment of herbaceous perennials. A 16year study was conducted in a Polish forest (Dzwonko and Gawronski 2002); 5- X 5-meter plots were raked clear of leaves every fall and compared with adjacent controls. As might be expected, litter removal greatly enhanced seedling establishment and species diversity of herbaceous plants. There was, however, a downside to regular

removal of leaf litter: soil of raked plots showed significantly lower levels of mineral nutrients than naturally mulched plots.

A somewhat cursory search of the literature yielded no published studies linking partridge berry, leaf litter, and seedling establishment. One can infer with some confidence, however, that partridge berry seedlings must become established preferentially in forest locations with minimal amounts of leaf litter. Seldom is the forest floor a monotonously uniform habitat. Much like snow drifts in winter, the redistribution of fallen leaves must be influenced by slope aspect relative to prevailing wind direction, micro-relief of pits and mounds, and the swirls and eddies formed as wind encounters standing large trees, fallen logs, and large rocks, to mention just a few possibilities. It seems reasonable to hypothesize that partridge berry plants will be found only in forest floor microhabitats with shallow or minimal leaf litter-here, seedlings can become established and adults can avoid death by smothering. Testing this hypothesis should be straightforward.

Photosynthesis. For plants, of course, smothering with leaf litter is really a matter of light deprivation. When light levels are so dim that photosynthesis cannot make enough organic matter to support the metabolic demands of living cells, the plant declines. The same leaves that drop from forest trees in the fall also cast shade during the summer growing season, making the forest floor a relatively dark environment and imposing severe limitations for plant life.

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Leaf litter

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It is perhaps not surprising, therefore, that woodland herbs exhibit a variety of adaptations to the challenge of dim light in shady forests. Some plants are simply shade-adapted; they grow slowly by eking out a slim margin of photosynthetic gain above and beyond levels necessary to maintain on-

going life processes. Two categories of plants opt to go dormant when the forest canopy is fully developed: wintergreen species like crane fly (Tipularia) and putty root (Aplectrum) orchids are leafy and photosynthetic through the relatively unshaded winter season, forming their flowers and fruits in summer; and spring ephemerals, like bloodroot (Sanguinaria), spring beauty (Claytonia), compress all active growth and reproduction into the few short weeks between late winter and mid-spring spring canopy closure. In contrast, partridge berry and some other familiar woodland herbs, like rattlesnake plantain (Goodyera) and pipsissewa (Chimaphila),

are evergreen. The biochemistry and physiology of evergreen leaves must be exquisitely versatile and adaptable in order to maintain living biomass during the dim but warm days of summer and the bright but cold days of winter.

Summer shade and sunflecks. Plant ecologists point out that, in most forests, the herb layer is not uniformly shady during summer—sunflecks, bright spots of sunshine, usually penetrate the canopy. Sunflecks on the forest floor are highly variable both spatially and temporally because the sun's angle changes continually through the day, because canopy branches jostle about in response to wind, because trees grow larger every year, and because, periodically, storms

bring down some branches and, sometimes, whole trees. The forest canopy is a dynamic place. In terms of duration, sunflecks can range from a few seconds to an hour or more; in terms of size, they range from centimeters to pools of light a few meters in diameter; and the time interval between successive sunflecks at a given spot can be on the order of seconds to hours (Chazdon and Pearcy 1991). It should also be noted



Partridge berry leaves, stem, and a berry struggle to rise above the leaf litter on the forest floor. (Photo by Richard Moss)

that the light of sunflecks is quantitatively and qualitatively different from the ambient light of forest floor shade. The light of sunflecks can be equivalent to full sunlight in terms of intensity (photon flux density) and spectral composition (wavelengths or colors of light). Forest shade is not only dimmer than full sunlight but, having passed through canopy foliage, the balance of wavelengths that make up the biologically active light spectrum is also altered. Although all wavelengths are affected, forest shade light is characterized as having a decreased ratio of red to far-red wavelengths, which is significant because red wavelengths are absorbed by chlorophyll and far-red wavelengths are not. Photosynthetic responses

to ambient shade versus sunfleck light have been studied for only a few forest floor plants, but some intriguing differences have been noted. For example, there is a time lag (induction period) between the start of a sunfleck and attainment of maximum photosynthetic rate; the duration of this induction period varies from species to species and is also affected by amount of time since the occurrence of the pre-

vious bright light episode. It has been shown that sunfleck-driven photosynthesis can be responsible for 35 to 65 percent of the plant's total daily carbon gain (Chazdon and Pearcy 1991). The dynamics of sunflecks and photosynthesis in partridge berry is completely unstudied. Who knows what further insights wait to be discovered?

Winter season photosynthesis. In deciduous woodlands, the forest floor is not always a dark environment. Between leaf fall in autumn and canopy closure in spring, inhabitants of the forest floor experience full, direct, sunshine, but this favorable light regime comes with seasonally cool to down-

right cold temperatures. On mild days of late fall and early spring, photosynthesis is likely to be optimum for evergreen plants like partridge berry. But what about winter? As it turns out, summer and winter photosynthesis for a few populations of Mitchella growing in Maine has been studied in some detail (Burkle and Logan 2003). Remarkably, in a deciduous forest, full-sun winter photosynthesis on a very cold day (-11 C at midday) was reported at roughly one-third the rate measured on a balmy summer day (24 C at midday) in the shade of broadleaf trees. (Presumably, leaf temperature at ground level must have been above the freezing point!) Perhaps even more remarkable, in a population growing in the per-

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petual shade of evergreen trees, the same cold day photosynthetic rate exceeded the warm summer rate! Although the investigators did not report measurements of light levels impinging on the plants in their study, they attributed these remarkably high rates of winter photosynthesis to the high albedo (reflectance) of snow cover flooding the plants with light.

Clearly, the evergreen habit and winter photosynthesis must confer an advantage for partridge berry in terms of maintaining a positive carbon balance necessary for growth and reproduction. However, the photosynthetic

machinery of evergreen plants carries a liability. Cold temperatures generally slow down enzyme-driven biochemical reactions, of which there are many that take place in photosynthesis. However, the physics of light absorption by pigment molecules is largely unaffected by temperature. Thus, evergreen plants can absorb light energy far in excess of their ability to use it in the enzymatic reactions of photosynthesis. This can be dangerous; excess highly energized pigment molecules can wreak havoc on other components of the chloroplast. There is, however, a safety valve; several different xanthophyll molecules exist in the chloroplast and function to dissipate this unused

energy as heat. In the same study cited previously, Burkle and Logan (2003) also studied xanthophylls, noting significant increases in total xanthophyll pools of partridge berry in winter relative to summer. Thus, by adjusting the pigment complement of its chloroplasts, partridge berry is able to take advantage of winter sunshine for photosynthesis without suffering the ill effects of too much light on bright winter days.

The take-home lesson is clear. As is often the case, success in life is a combination of luck and inner strengths. For partridge berries, tiny jewel-like herbs living at the feet of towering forest trees, eking out a life depends on the luck of

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