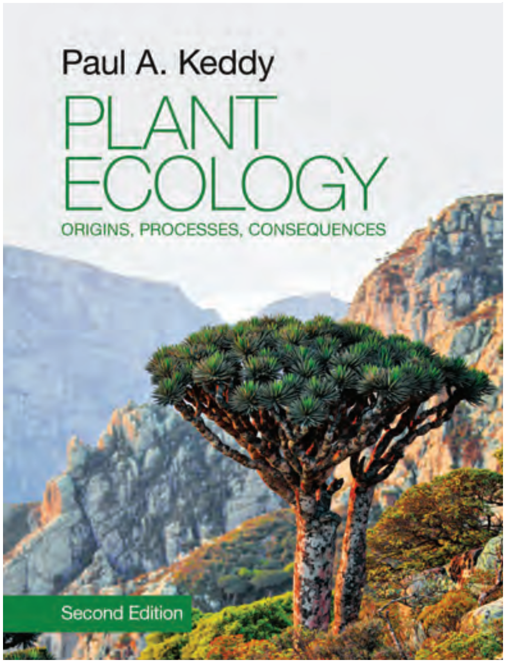

Keddy, P.A. 2017. Plant Ecology: Origins, Processes, Consequences. Cambridge University Press Cambridge, UK. pp. 379-382.

(order from Amazon.ca)

10.2.4 Rock Barrens

Wherever there is shallow soil, it is likely that plants will be under stress. Shallow soil stores less water, thereby increasing the probability, intensity and duration of drought. As well, essential nutrients will be in short supply since the volume of soil available to any plant is a function of soil depth. Consequently, areas with rock near the surface tend to have distinctive vegetation, including plant species tolerant of infertility and drought (McVaugh 1943; Anderson et al. 1999). Since dry vegetation burns easily, recurring fire is also often associated with such conditions. Because the vegetation is slow to regenerate after disturbance, barrens of all kinds are particularly vulnerable to human disturbance.

Rock barrens are common at high latitudes or altitudes where glaciers have removed most of the surface soil. Alvars are a special kind of glaciated rock barren formed over limestone (Figure 10.11). Alvars are globally restricted habitats, being common only in the Baltic areas of northern Europe and in the area north of the Great Lakes (Petterson 1965; Catling and Brownell 1995). Soil depth and vegetation biomass are the primary gradients that produce different vegetation types (Belcher et al. 1992), and in those sites studied to date, below-ground competition exceeds above-ground competition (Belcher et al. 1995). In Europe, grazing has been an important historic factor in alvars, whereas in North America there is evidence that fires were important (Catling and Brownell 1998). Periodic drought may also greatly inhibit invasion by forest, mortality of rates of 60 to 100 percent having been observed in woody plants during one dry summer (Stephenson and Herendeen 1986).

Some rock barrens can be found outside glaciated regions. In the southern Appalachians, outcrops of metamorphic rocks can form smooth domes rising as much as 200 m above the surrounding terrain. Rainfall drains off such domes, and may also carry away organic matter that might otherwise form soil. McVaugh (1943) described a series of such outcrops, and their distinctive flora and vegetation. Amidst expanses of bare rock, small depressions accumulate water and organic matter, and thereby support islands of vegetation. Each depression develops a

FIGURE 10.11 Limestone pavement in an alvar on the south coast of Manitoulin Island. Some of the world's largest alvars occur on this island and on the adjoining Bruce Peninsula. Grasses such as *Sporobolus heterolepis* and *Deschampsia caespitosa* grow in the cracks between the pavement blocks. The distinctive yellow "flowers" (inset) are capitula of *Hymenoxys herbacea* (lakeside daisy, Asteraceae), a species restricted to alvars around the Great Lakes. Each capitulum is about 3 cm in diameter. (Photographs by Ryan Gardner, Misery Bay, Ontario Parks)

series of distinctive vegetation zones. At the very margin are crustose lichens or mosses (*Grimmia* spp.); these give way in turn to fruticose lichens (*Cladonia* spp.) or fern allies (*Selaginella* spp.), then large mosses (*Polytrichum* spp.) and, finally, near the very centre, vascular plants including grasses (*Andropogon* spp., *Panicum* spp.), rushes (*Juncus* spp.) and sedges (*Rhynchospora* spp.). These domes have presumably been isolated from the surrounding forest vegetation for a considerable time since, in the southern United States, at least 12 plant species are endemic to such outcrops (Shure 1999).

In equatorial regions, rock outcrops can have a remarkably rich flora. One of the best examples is the **tepui** (or "inselbergs") of the Guyana highlands in northern South America. Here rock outcrops rise steeply from amidst tropical forest (Figure 10.12). The flora on these outcrops tends to be dominated by four families: Rubiaceae, Melastomataceae, Orchidaceae and Cyperaceae (Prance and Johnson 1991). Many plants have a bizarre growth form

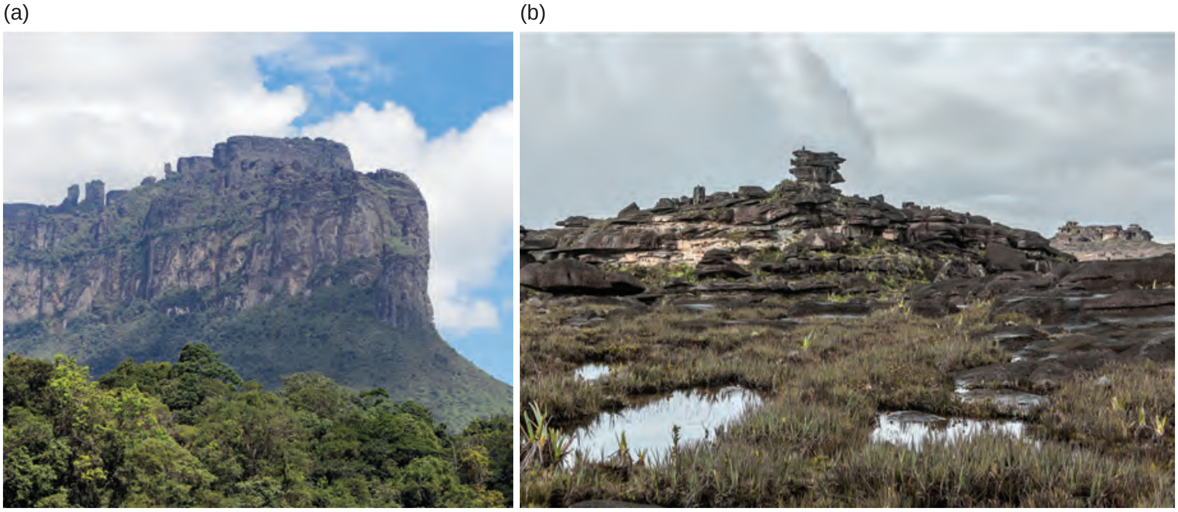

FIGURE 10.12 (a) Tepui are flat-topped sandstone mountains edged with sheer cliffs. Some are surrounded by forest. (b) The tops of tepui have infertile wet barrens and pools with many endemic species including carnivorous plants in the genera *Utriculara*, *Drosera* and *Heliamphora*. (Venezuela, Vadim Petrakov, Shutterstock)

characterized by "thick, sclerophyllous, highly reduced, glossy, waxy or revolute leaves, often crowded into tufts of rosettes or covered by a sericeous, gray, white or brown tomentum. Frequently the stem becomes conspicuously shortened or elongated, simple and virgate producing a weird appearance in the landscape" (Steyermark 1982: p. 205).

Certain rock outcrops impose further constraints upon plant growth through the lack of major nutrients, absence of micronutrients such as calcium, and the presence of higher than normal concentrations of elements such as nickel or chromium. These rocks are collectively known as **serpentine**. They are widespread, with significant outcrops in locations including California, Newfoundland, central Europe, Scandinavia, Russia, Tibet, China, Japan, Brazil, Zimbabwe, New Zealand and Australia (Whittaker 1954a, b; Coleman and Jove 1992). Since the composition of serpentine rocks is quite variable, some suggest the term is of doubtful value, but recurring themes of inadequate soil nutrients and high concentrations of metals seem worthy of recognition. Further, there is now evidence that serpentine rocks have a distinctive geological origin (Coleman and Jove 1992; Roberts 1992). They appear to form when slabs of seabed are lifted onto continental margins instead of being subducted and destroyed along the margins of oceanic plates. Thus the regions of serpentine are associated with the margins of ancient oceans.

Serpentine rocks may have particularly distinctive vegetation when other kinds of stress are superimposed. In northern areas, such as Newfoundland, Roberts (1992) added, stresses include (1) drought, (2) wind, (3) erosion from lack of vegetative cover, and (4) cryoturbation (disturbance by recurring freeze–thaw cycles). Here, serpentine rocks support arctic–alpine plant communities in exposed locations, peatlands and sedge meadows in less exposed sites, and occasionally trees and shrubs in sheltered areas. In tropical areas, leaching may increase the deficiency of nutrients. In equatorial areas such as Brazil (Brooks et al. 1992), such rocks yield sparsely vegetated domes covered in *cerrado* (grasses, shrubs and low trees) giving way to *campo rupestre* (grasses and shrubs).

Serpentine rocks have been studied for many years, in part because they are visually distinct in many landscapes, and tend to have endemic plant species. Simple pot experiments using serpentine soil (Kruckeberg 1954) showed that fertilization with NPK increased the growth of plants in serpentine but only if the plants already possessed the ability to grow on serpentine. Non-serpentine plants did not respond to NPK, which indicates that some other factor was limiting their growth in these soils. Only the serpentine plants could grow on serpentine soil alone, but if calcium was added as gypsum, then both serpentine and non-serpentine plants were able to grow. Such experiments suggest that it is the low calcium level rather than absence of the macronutrients NPK that prevents many plants from growing on serpentine. Of course, increasing the soil pH will also reduce the solubility of possibly toxic metal ions such as nickel and aluminum. This also implies the importance of competition. Serpentine ecotypes cannot spread to sites with normal soils because other plants are better able to exploit these soils. This appears to be another case where stress-tolerant species are competitively excluded to inferior habitats.

10.3 Habitats Where Resources Are Present, Yet Unavailable: Peatlands

In some habitats, the resources are physically present, but stored in a form that plants cannot use. From the perspective of the plant, strain is again induced, but the cause is subtly different. A particularly good example of this is provided by peat bogs (recall Figure 8.24). Here the plants are rooted in a matrix of organic matter, but because of low decay rates the essential elements such as nitrogen and phosphorus remain chemically bound within those partially decayed plant remains. In extreme cases the vegetation depends upon the dilute nutrient solution provided by rain water.

Peatlands are flooded more or less permanently with the water table near the soil surface. Under these conditions decomposition rates are reduced, and organic matter accumulates as peat. Once organic matter has accumulated to a depth of about 10 cm, the plant roots are increasingly isolated from access to the mineral soils beneath the peat. Over time, then, plants become more dependent upon dilute nutrients deposited in rain water (Gorham 1957; van Breemen 1995) and have distributions strongly related to nutrient levels in the groundwater (e.g. Gore 1983; Glaser et al. 1990; Vitt and Chee 1990). Fertilization experiments have shown an array of types of limitation involving nitrogen, phosphorus and potassium (Section 3.4.4).

Adaptation to these infertile conditions requires a variety of unusual plant traits. The most visible is the tendency to sclerophyllous regular type foliage. It is puzzling to see wetland plants showing leaf forms typically found in arid conditions. It appears to be a consequence of low nutrients. Deciduous leaves require conditions of relative fertility, since a plant must continually replace the nitrogen and phosphorus lost in deciduous foliage (Grime 1977, 1979; Chapin 1980; Vitousek 1982). Thus evergreen shrubs in the Ericaceae and evergreen trees in the Pinaceae dominate peatlands. Recall that both of these groups are well known for the use of mycorrhizae in nutrient uptake.

Peatlands are also distinctive in the abundance of bryophytes, and one genus, *Sphagnum* (Figure 10.13), is dominant in bogs. There may be more carbon incorporated in *Sphagnum*, dead and alive, than in any other genus of plant (Clymo and Hayward 1982). The success of *Sphagnum* in dominating large areas has been attributed to at least three characteristics (Clymo and Hayward 1982; van Breemen 1995; Verhoeven and Liefveld 1997). First,