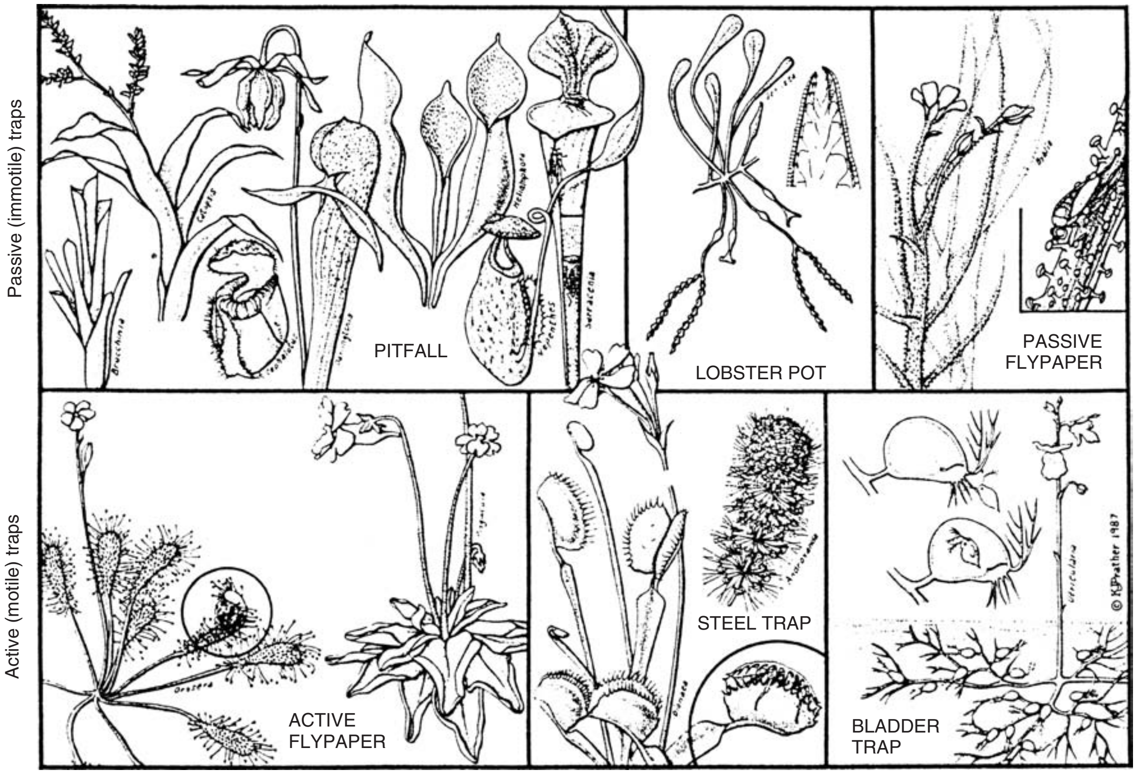

Figure 3.29 Carnivorous plants have evolved on at least six independent occasions as a response to chronic shortages of nitrogen and phosphorus (from Givnish 1988).

These plants have no roots, and produce only a small rosette of linear leaves above ground. Below ground are bundles of hollow subterranean leaves that chemically attract, entrap and then dissolve ciliates (Barthlott et al. 1998). The intensity of the pressure to acquire nitrogen and phosphorus is illustrated by evidence that carnivory seems to have arisen independently at least six times (Figure 3.29) (Givnish 1988).

Parasites

In deeply shaded habitats, there may be no source of energy save for that captured by taller neighbors. Parasitism could provide a plant with resources without necessitating light capture. Over 4500 species of vascular plants in 19 families are parasitic upon other plants (Nickrent 2006) from which they may take water and nutrients, and possibly photosynthates. Many parasitic plants have greatly-reduced leaves and root systems since they do not need to gather resources with these organs (Figure 3.30). Among the known parasitic plants, according to Kuijt (1969), there are no vascular cryptogams, one gymnosperm (*Parasitaxus ustus*) in New Caledonia (its host is also a member of the Podocarpaceae, Farjon 1998), and no monocots: "It is a startling and unexplained fact that the known parasitic vascular plants are limited to the dicotyledons" (p. 3). He suggests that parasitism has evolved independently at least eight times, five times in relatively

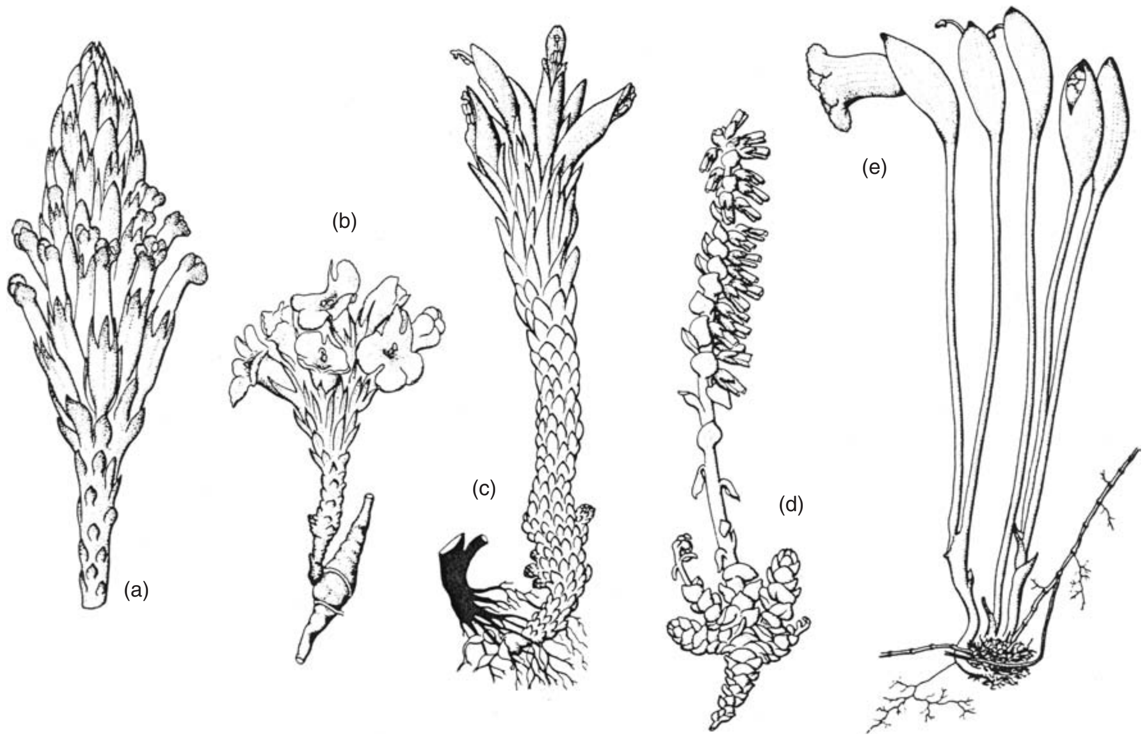

Figure 3.30 The broomrapes (Orobanchaceae) are most common in temperate or Mediterranean climates, and generally absent from tropical regions. These five examples lack chlorophyll and show the typical parasitic growth form with greatly reduced leaves and root systems. Indeed, such plants could be described as little more than parasitic inflorescences. (a) *Harveya squamosa*, slightly less than natural size, (b) *H. purpurea* on root of *Roella ciliata*, (c) *Hyobanche glabrata*, (d) *Lathraea squamaria*, and (e) *Aeginetia japonica* on *Miscanthus sinensis* (from Kuijt 1969).

large groups – Santalales, Scrophulariaceae and Orobanchaceae, Rafflesiaceae and Hydnoraceae, Balanophoraceae, Lennoaceae, and three times in isolated genera – *Cuscuta*, *Cassytha*, and *Krameria*. Evolutionary relationships of parasites are further addressed by Press and Graves 1995, Moreno et al. 1996, and Nickrent 2006.

The occurrence of parasitic plants has been documented for centuries. The large fleshy shoots of the Balanophoraceae appear superficially like a large fungus, but as early as 1729 Micheli reported in *Nova Plantarium Genera* that it was an actual vascular plant parasitic upon other plants. Similarly, the parasitic habit of the Rafflesiaceae was described in 1822 in the *Transactions of the Linnaean Society of London*. In spite of this, when Kuijt produced *The Biology of Parasitic Flowering Plants* in 1969, he was able to begin with the observation that no treatise on parasitic plants was yet available.

There is considerable variation in degree and nature of parasitism. Some species, termed **hemiparasites**, retain most of their photosynthetic ability and apparently take only water and mineral nutrients from hosts (e.g., some members of the Santalaceae, Loranthaceae and Scrophulariaceae). In more extreme cases, termed **holoparasites**, species may have no chlorophyll and be totally dependent upon their hosts for water, minerals, and photosynthetic products. This is the case in some members of the Orobanchaceae, Rafflesiaceae, and Balanophoraceae. Other species of plants, such as the ghostly white Indian pipe (*Montropa uniflora*), may superficially appear to be parasites, with reduced leaves and the absence of chlorophyll. Some of these plants (e.g., *Sarcodes*, *Monotropa*, *Corallorhiza*) instead are associated with fungi that are saprophytic or mycorrhizal. While most parasites attach to the roots of host plants, aerial parasites occur in three families: Cuscutaceae, Lauraceae, and Lornathaceae. The mechanism of parasitism is, however, similar across all groups: contact is made with the host through a **haustorium**, a specialized root that forms a connection between the vascular systems of the host and the parasite.

Although the novelty of this mode of existence is undeniable, its significance in actual plant communities is less clear. There are undoubtedly certain cases of host plants being damaged by parasites; certainly, some parasitic plants are thought to reduce growth of trees in commercial plantations (Musselman and Mann 1978). In most natural communities, it would appear that parasitism has a minor effect upon vegetation, particularly when compared with relatively strong factors such as competition and grazing. However, generalizations are still risky when there have been so few experiments with parasites in natural vegetation. Consider two examples.

Rhinanthus minor is a hemiparasite found in herbaceous vegetation of temperate areas. When it was experimentally removed from four different vegetation types in England, diversity increased in three of them (Watkinson and Gibson 1988). Preferred hosts such as *Koeleria macrantha* increased when the parasite was removed, while neighboring species such as *Festuca rubra* and *Carex arenaria* declined. In the one case where diversity declined, removal of the parasite apparently allowed the favored host plant, *Koeleria*, to increase and suppress neighboring species. *Cuscuta salina* is a parasitic twining plant on *Salicornia virginica* in the salt marshes of California. It damages *S. virginica*, thereby indirectly facilitating growth of two other marsh plants, *Limonium californicum* and *Frankenia salina* (Pennings and Callaway 1996). These presumed facilitative effects, however, vary with elevation.

In summary, parasitism is a distinctive method of resource acquisition often associated with traits including reduced leaves, lowered production of chlorophyll, and haustoria. In some circumstances, parasitic plants can influence the abundance of other plants – either their hosts or neighbors of their hosts. Because of the relative rarity of parasitic plants, however, their significance as factors controlling vegetation will probably always be rather low.

3.8.2 Conservation of scarce resources

Evergreen plants tend to have much lower tissue nutrient concentrations than deciduous plants (Aerts 1996). Evergreen leaves contain 14 percent nitrogen, compared to 22 percent in deciduous leaves. Evergreen leaves contain 1 percent phosphorus, compared to 1.6 percent in deciduous leaves. Thus, from the perspective of the plant, the construction costs of leaves (measured in terms of nutrients invested per unit weight of leaf tissue) is lower for evergreen than for deciduous leaves. Evergreen plants may therefore