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The roots of carnivorous plants

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Abstract

Carnivorous plants may benefit from animal-derived nutrients to supplement minerals from the soil. Therefore, the role and importance of their roots is a matter of debate. Aquatic carnivorous species lack roots completely, and many hygrophytic and epiphytic carnivorous species only have a weakly developed root system. In xerophytes, however, large, extended and/or deep-reaching roots and sub-soil shoots develop. Roots develop also in carnivorous plants in other habitats that are hostile, due to flooding, salinity or heavy metal occurance. Information about the structure and functioning of roots of carnivorous plants is limited, but this knowledge is essential for a sound understanding of the plants' physiology and ecology. Here we compile and summarise available information on:
(1) The morphology of the roots.
(2) The root functions that are taken over by stems and leaves in species without roots or with poorly developed root systems; anchoring and storage occur by specialized chlorophyll-less stems; water and nutrients are taken up by the trap leaves.
(3) The contribution of the roots to the nutrient supply of the plants; this varies considerably amongst the few investigated species. We compare nutrient uptake by the roots with the acquisition of nutrients via the traps.
(4) The ability of the roots of some carnivorous species to tolerate stressful conditions in their habitats; e.g., lack of oxygen, saline conditions, heavy metals in the soil, heat during bushfires, drought, and flooding.

Introduction to carnivorous plants

Plants benefit in many ways from animals; e.g., animals play a role as pollinators and as dispersers of fruits. However, animals may also contribute to a plant's nutrition by being caught and digested. This phenomenon of carnivory has fascinated the scientific community ever since Darwin drew attention to it (Darwin, 1875). Although carnivorous plants can obtain water and at least some minerals from the soil, they also extract nutrients from captured animals. Carnivorous plants attract their victims by means of scent, colouration and nectar (Lloyd, 1942). They are able to trap and retain their victims, kill them, and digest their soft tissues, and take up at least part of their contents (Juniper et al., 1989; Lloyd, 1942). This whole process is achieved by highly specialized leaves, which have been transformed into various types of traps. Therefore, the leaves may take over functions that are usually restricted to the roots of non-carnivorous plants. The general features of carnivorous plants have been reviewed in detail by Juniper et al. (1989). Five types of traps can be distinguished:

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- *Adhesive traps* produce sticky mucilage that is able to glue little animals to the leaves. Such '*fly-paper*' traps may actively roll over their victims (*Drosera*, *Pinguicula*) or they remain motionless (*Byblis*, *Drosophyllum*).
- In *steel traps*, the leaf forms two lobes, which snap around animals that touch sensitive trigger hairs on the surface of the lobes (*Dionaea*, *Aldrovanda*).
- In *pitcher traps*, leaves have been transformed to a pit that contains a pool of digestive enzymes (*Darlingtonia*, *Nepenthes*, *Sarracenia*, *Cephalotus*, *Heliamphora*). Animals are attracted towards the rim, and glide into the pit along the slippery inner surface, which prohibits escape.
- Even more sophisticated are the *eel traps* that attract prey through a system of claw-like cells and inward-pointing hairs into a bulb where it is digested and absorbed (*Genlisea*).
- The *suction traps* have the form of bladders that arise from leaves. Little animals that touch sensitive hairs near the entrance are sucked into the bladder through a trap door, due to the lower hydrostatic pressure inside, and are then digested (*Utricularia*).

Carnivory has been detected in at least 470 plant species from 9 families and 6 orders of vascular plants (Schlauer, 1986). Carnivory has evolved independently 6 (following the system of Takhtajan, 1969) or seven (Albert et al., 1992) times. Despite their taxonomic diversity, many carnivorous plants have several features in common:

- They are generally tolerant of nutrient-poor soils (Juniper et al., 1989).
- They tend to be poor competitors (Gibson, 1983a; Nash, 1973).
- They tend to prefer sunny habitats (Juniper et al., 1989; Pissarek, 1965; Schnell, 1980)
- Many are calcifuges and tolerate low soil pH (Carow and Fürst, 1990; Juniper et al., 1989; Rychnovska-Soudkova, 1953, 1954).
- Many are tolerant to waterlogging, growing in swamp-like habitats and peat bogs (Schnell, 1976), but others are able to survive severe water stress (Dixon and Pate, 1978; Harshberger, 1925, Lloyd, 1942) and even fires (Carlquist, 1976a; DeBuhr, 1976; Dixon and Pate, 1978; Roberts and Oosting, 1958).
- Since the observations of Nitschke (1860) and Burbidge (1897), it has been a general belief that carnivorous plants only have weakly developed roots or no roots at all. However, a wide variety of root systems can be found. These roots have not lost their ability to absorb minerals from the soil; rather, nutrients obtained from prey can be regarded as an additional source.

In contrast with the great interest in various aspects of their reproduction, nutrition and the morphology of their leaves and traps, information about the roots of carnivorous plants is relatively scarce. Here, we review the few studies that deal with the under-ground organs of carnivorous plants, especially with their roots *sensu stricto*, and describe their morphology and physiology.

The roots of carnivorous plants

In carnivorous species, a wide range of root types occur; schematic drawings of the various roots and under-ground organs of a great variety of carnivorous plants are included in Pietropaolo and Pietropaolo (1986), but quantitative data about size and morphology are found only very rarely in the literature; roots are mainly described as frail, weak or strong. We therefore take over these descriptions in this review. For our own observations, we use the term 'weak' for inconspicuous roots that are much smaller than the above-ground parts of the plant, and 'strong' for roots that are well developed and more than half the size of the shoots.

The roots may function permanently or only during part of the year (Slack, 2000). Some species have deep roots that probably allow continuous water uptake (França, 1925; Menninger, 1965), and others have only poorly developed roots (Nitschke, 1860) or no roots at all (Slack, 2000; Taylor, 1994). The absence of roots does not necessarily mean, however, that the functions of roots are not needed; in some plants, the stem and leaves have replaced their functions, as discussed below.

The radicle

Whereas the root systems of adult carnivorous plants are very diverse, the radicle is quite similar, and only weakly developed in the few species that have been investigated.

In *Drosera*, the radicle is replaced by stem-borne roots soon after germination. Interestingly, it develops extremely long root hairs, which are long lived (Smith, 1931). *Byblis* and *Drosophyllum* have an extensive root system as a mature plant; the radicle, however, is hardly able to anchor the seedling to the substrate, so that even with a total length of 30 mm the plant can be displaced easily (Juniper et al., 1989). Similarly thin is the radicle of *Nepenthes gracilis*. It forms a bunch of long root hairs within the testa, but even so, together with the hairs, the root is too feeble to anchor the seedling or to supply it with sufficient water and nutrients (Green, 1967).

Aquatic carnivorous plants do not have roots

Aquatic carnivorous plants never develop roots. Best known examples are *Aldrovanda* which bears snap traps (Adamec, 2003), *Polypompholyx* and many *Utricularia* species with suction traps, and the closely related *Genlisea* that catches its prey with an eel trap. They grow submerged in water, except for the flowers, which are above the water. Their stem or rhizome floats freely and carries green leaves and traps. They take in the few available minerals through their stems and leaves (Slack, 2000). In *Utricularia*, there are also many terrestrial and epiphytic species that grow in moist soil and in decomposing organic matter from other plants (Taylor, 1994). *Genlisea*, growing in loose sandy soil, is submerged only during part of the year (Slack, 2000). Again in both *Utricularia* and *Genlisea*, no roots are developed. Specialised underground shoots or leaves have replaced their roots.

Roots of hygrophilic carnivorous plants

The moisture of swamps and peat bogs creates a hostile substrate for most plants, because the roots may be poorly aerated (Armstrong, 1979). In addition, organic matter may be mineralised only incompletely, so that the nutrient availability in the substrate is poor. During the decomposition processes, and also due to the action of *Sphagnum* mosses, humic acids are generated which decreases the soil pH down to 3 (Naucke, 1990). Only few plants tolerate these conditions in peat bogs and swamps, and those that survive, for instance through their strategy of carnivory, require specific root adaptations.

Roots of hygrophilic carnivorous plants are usually only short-lived, and they are reduced, frail and thin. Vestigial root systems occur in species of *Drosera* and *Pinguicula* (drawings of these reduced root systems are given by Kutschera et al. (1992), *Dionaea*, all Sarraceniaceae, *Cephalotus* and the carnivorous Bromeliaceae (Figure 1). However, the total of the underground organs (rhizomes with outgrowing roots and tubers) can be quite extensive in some species (Figure 2). In addition, they produce tannic acids and other impregnating substances, like in *Dionaea* (Guttenberg, 1968). However, this feature is not restricted to wetland plants, but occurs also in the dryland plant *Byblis gigiantea* (Lloyd, 1942). There are even examples for well developed deep roots, e.g., in *Triphyophyllum peltatum* (Dioncophyllaceae), which grows in the humid rain forests of West Africa in very poor soils. This species has relatively recently been added to the list of carnivorous plants (Green et al., 1979), and further details about the anatomy and physiology of its roots have not yet been published. In *Drosera rotundifolia*, roots are also used for vegetative propagation. Some of the few roots run parallel to the surface of the soil and form root suckers (Kutschera et al., 1992).

The ecological adaptations to oxygen-deficient soils in some carnivorous plants are reflected in the anatomy of their roots. The cortex may be thin and inconspicuous, with practically no exodermis, as in *Dionaea* (Fraustadt, 1877; Smith, 1931). In contrast, the inner cortex may develop many gas-filled intercellular spaces, which often

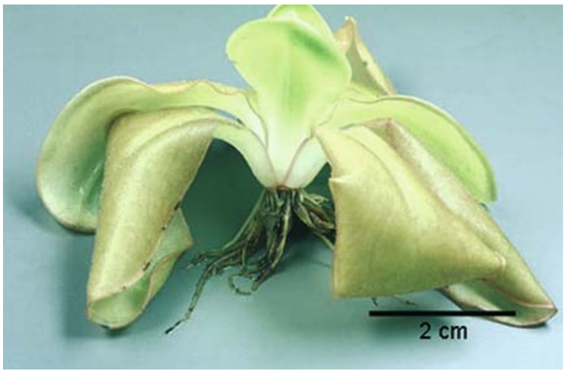

Figure 1. Piguicula moranensis, a tropical plant with large fleshy leaves, has frail and thin roots during its lifetime.

Figure 2. Sarracenia hybrid, although hygrophytic, has extended sub-soil rhizomes from which small roots arise.

collapse to lacunae due to the lysis of cells, and hence allow for the aeration of the tissue (Freidenfelt, 1904; Guttenberg, 1968; Oels, 1879). This is the case in many species of *Drosera, Pinguicula* and *Sarracenia*. *Darlingtonia* has numerous small intercellular spaces around virtually every cortical cell (Figure 3).

The stele of the carnivorous plant roots investigated so far usually is oligarch. In *Dionaea*, the young root has a di- or tetrarch central cylinder; later a multilayered pericambium develops that forms groups of tracheids and phloem elements (Smith, 1931). In *Drosera*, the central cylinder is very similar to that of *Dionaea* in the young roots; in older roots with secondary thickening, however, amphivasal bundles are formed (Guttenberg, 1968).

Root hairs are very prominent in the few species that have been examined. In *Drosera* species, they are extremely long (viz. 15 mm); in *Dionaea* they are up to 1.9 mm long, persistent and so heavily impregnated with cutin that root hairs can be dissolved only in chromic acid (Smith, 1931).

Concerning symbiosis with mycorrhizal fungi, it is a common belief that there is no association with roots of neither hygrophilic nor xeromorophic carnivorous plants (MacDougal, 1899; Peyronel, 1932, reviewed by Juniper et al., 1989). The only exception would be *Roridula*, which forms

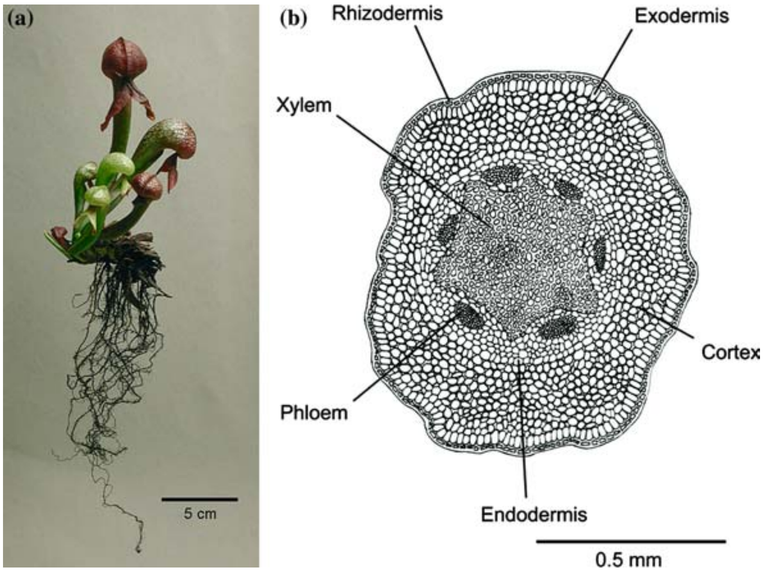

Figure 3. Darlingtonia californica has a relatively large root system that servives fires and heavy metal contaminated soils (a). Transections show the cortex containing numerous small intercellular spaces that encloses the compact hexarch central cylinder with xylem and phloem. Rhizodermis and exodermis are thick walled and heavily impregnated (b).

vesicular arbuscular mycorrhizas (Midgley and Stock, 1998), but this genus nowadays is no longer regarded as carnivorous (Ellis and Midgley, 1996). Recent research showed, however, that such vesicular arbuscular mycorrhiza occurs in *Drosera intermdia* (Fuchs and Haselwandter, 2004).

Roots of dryland carnivorous plants

Carnivorous plants of both moist and arid habitats may develop an extended system of underground organs. This is, however, exceptional, but does occur in *Drosophyllum lusitanicum*, which grows in poor soils derived from sandstone in southern Spain and Portugal, where the summers are hot and dry. During this time, *Drosophyllum* sometimes senesces (Flísek and Pásek, 2000), but more frequently it is found in a turgescent shape, including fresh and sticky mucilage on the traps (Juniper et al., 1989; own unpublished observations). Due to its well developed root system (França, 1925), *Drosophyllum* can survive 5 months without any rainfall, even on southfacing hillsides (Juniper et al., 1989). Water uptake by the roots presumably continues, because the plants have no water storage organs (Juniper et al., 1989). Studies of the root anatomy showed some peculiarities of the endodermis; the primary state of the endodermis is only very short and soon transition into a secondary endodermis is initiated by suberization of the cell walls; no further lignification of the cell walls occurs, but the endodermis remains in this intermediate state throughout the life of the root (Guttenberg, 1968). The rhizodermis, on the other hand, lignifies very soon in young roots (Figure 4).

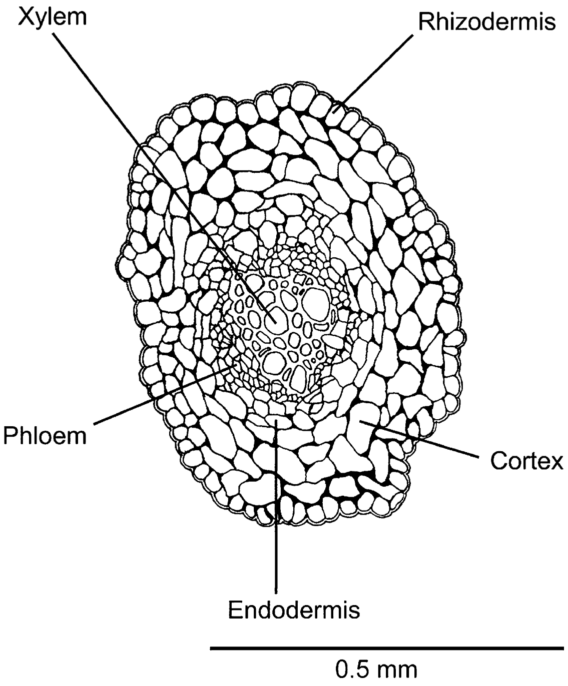

Figure 4. Drosophyllum lusitanicum develops lateral roots with lignified rhizodermis, collenchymal cells in the cortex and a secondary endodermis with heavily suberized cell walls that encloses the diarch central cylinder with xylem and phloem.

The Australian *Byblis* species and *Ibicella lutea* from the southern part of North America are found in dry habitats similar to those of *Drosophyllum*; they also have well developed roots (Juniper et al., 1989). Even more pronounced are the roots of *Nepenthes pervillei* that grows on rocky cliffs; they are described as long and reaching into deep cracks, where they are believed to find moisture and nutrients (Juniper et al., 1989) (Figure 5). Australian dryland *Drosera* species also form extensive root systems. The roots of the recently discovered *Drosera caduca* are contractile, as in many Alliaceae (R. Barrett and M. Barrett, unpublished observation), so that the tubers become drawn into the soil.

Figure 5. Nepenthes hybrid tends to climb but still has long and deep-reaching roots.

Specialized roots occur in tuber-forming *Drosera* species of Australia that are adapted to hot and dry summers; plants die back to a well developed underground stem tuber from which they emerge again when the rainy season begins (Pate and Dixon, 1982). The tuber is covered by leaf scales. From their bases, root-like structures grow downwards; these were termed ‘leaf-rhizoids’ (‘Blattrhizoide’) by Diels (1906). These structures might be reduced roots, because they have several features in common with roots; they grow out of the axis, their apical cells are enforced, and they carry starch grains in the second cell layer behind the tip; the meristem follows only behind. In addition, they produce many outgrowths which were described as ‘hairs’ (Diels, 1906). On the other hand, they have no calyptra which is why Goebel (1923) described them as “dubious roots” (“zweifelhafte Wurzeln”). In addition to the rhizoids, small horizontal roots emerge from the bases of the leaf scales, which enable the stems to be used for the propagation of the plants; they can form a new shoot and produce a tuber (Slack, 2000).

Like in roots of hygrophilic carnivorous plants, also in some dryland species special anatomical features can be found: In *Drosera macrantha* and *D. trinerva* (Oels, 1879), the cortex is developed and even divided into an outer and an inner cortex, which differ considerably; the cells of the outer cortex have thick cell walls, usually without secondary thickening; the parenchymatic cells of the cortex have spiral fibres in their walls similar to the cells of the *velamen radicum* of orchids. These cells can reinforce the exodermis, especially in those cases where the rhizodermis has only fragile cell walls (Freidenfelt, 1904).

Temporary roots

Temperate species of *Drosera* and *Pinguicula* develop roots only during part of the year. In some *Drosera* species, the roots die in autumn, and the winter buds are anchored to the substrate only by the dead remainders (Slack, 2000) (Figure 6). In spring, new leaves and new roots are formed at the same time. In most temperate *Pinguicula* species of the northern hemisphere, the roots die in winter, but the dead parts are completely lost, so that the dormant bud (the hibernaculum) is freely mobile. This can be seen either as a strategy for efficient dispersal or it is a mechanism to avoid damage when the water in the soil freezes and expands (Slack, 2000). As an exception, *P. alpina* has perennial roots (L. Adamec, personal communication).

In the Mexican montane butterworts occuring on limestone, e.g., *Pinguicula gypsicola*, the roots die in winter which is the dry season. The death of the roots is accompanied by a complete change of the shape of the plants; in summer, new roots and broad and sticky carnivorous leaves are formed which both die during the dry season. The leaves are replaced by non-carnivorous and succulent leaves. With the rain in spring, new roots and new carnivorous leaves are formed (Slack, 2000).

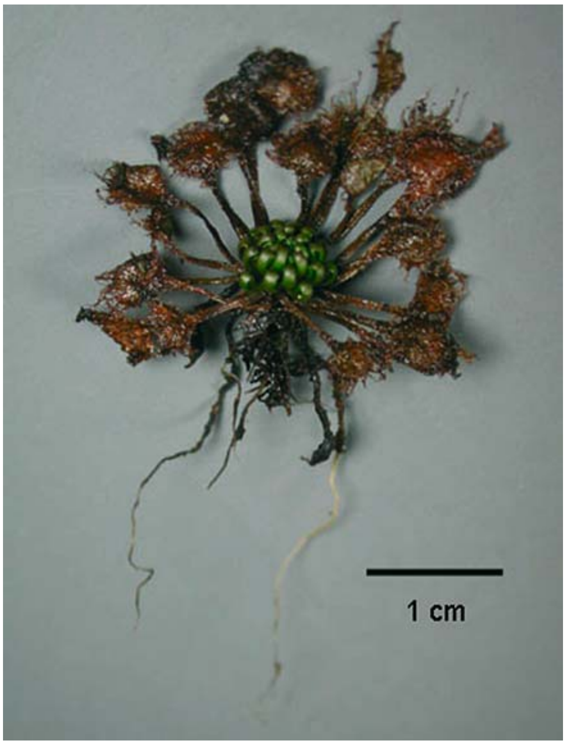

Figure 6. In *Drosera rotundifolia*, only dead roots remain during winter and keep the plants anchored to the substrate.

Physiological traits of the roots of carnivorous plants

Virtually all carnivorous plants are poor competitors (Juniper et al., 1989); therefore they occur in extreme habitats, where the majority of plants cannot grow. The ecological conditions of the habitat require specialized physiological adaptations. Here, only the properties of the roots will be discussed.

The problems of waterlogged habitats were mentioned above. Roots of hygrophytes have adapted to hostile soil conditions of low pH and low oxygen by the development of aerenchyma and/or by the reduction or even lack of roots. In contrast, in the habitat of the Australian *Byblis*, heat, drought and fires occur regularly. The fires destroy all parts of the plant above the ground. The underground organs are protected by the soil, and have been described to endure low-intensity fires (DeBuhr, 1975). Similarly, North American *Dionaea muscipula* (Roberts and Oosting, 1958), *Darlingtonia californica* (R.M. Austin, unpublished data, cited in Juniper et al. (1989); Barbour and Major, (1977)), *Sarracenia* (Plummer, 1963; Plummer and Kethley, 1964), and some *Drosera* species (Pate and Dixon, 1982) survive fires by means of underground organs. Some species, like *Dionaea muscipula* (Schulze et al., 2001), appear to need regular fires, which serve to remove competitors. *Sarracenia flava*, for instance, is outcompeted by wiregrass, *Sporobolus teretifolius*, if the habitat is not burnt regularly (Eleuterius and Jones, 1969; Plummer and Kethley, 1964). The tolerance to low-temperature fires is so widespread amongst carnivorous plants that it is even seen as part of the carnivorous syndrome by Juniper et al. (1989). In peaty soils, the heating during bushfires is restricted to the surface (Heyward, 1938, cited in Roberts and Oosting, 1958), so that underground parts of the plants can survive.

The roots of *Darlingtonia californica* (Figure 3) encounter another kind of stress in addition to fires. They grow only in cool running fresh water; the roots therefore are exposed to temperatures around 10 °C, even during the hottest time of the year, when the air temperature exceeds 25 °C (Juniper et al., 1989). Cultivation experiments show that the roots have an absolute requirement for this low temperature; they die if exposed to temperatures above 10 °C for a prolonged time, and seedlings are even more sensitive (Slack, 2000). The shoot, on the other hand, is not very sensitive to high temperatures (Slack, 2000). The reason for this extraordinary sensitivity of the roots to high temperatures is probably a very low and limited optimal temperature of their ion pumps in root cells (Ziemer, 1973). Similar extreme specializations to a certain temperature are known for many other hygrophytes (Sapper, 1935), but it is unusual for only one organ of the plant.

Heavy metals are another stress factor that is resisted by the root systems of some carnivorous plants. For example, *Darlingtonia californica* (Juniper et al., 1989), *Nepenthes rajah* (Gibson, 1983b), *N. xalisaputrana* (Clarke, 2001), *N. villosa* (Kaul, 1982) and *Stylidium* spp. (Darnowski, 2002; 2003) grow in serpentine habitats. Serpentine soils are rich in Ni, Cr and Mg, which are all toxic for plants when a threshold concentration is exceeded; these soils are also very low in available macronutrients (Kruckerberg, 1954). *Sarracenia purpurea* ssp. *purpurea*, *Drosera rotundifolia* and *Pinguicula* sp. were found growing on ultra basic, heavy metal rich deep mantle rocks (D'Alessi, 2004). In general, plants have developed various strategies to avoid or to tolerate the toxic influence of heavy metals, and in every case the roots play a key role (Greger, 1999; Meharg, in press), but it is not known which strategy is used by carnivorous plants.

Saline soils are tolerated by some carnivorous plants. This is the case for *Dionaea muscipula*, which sometimes grows in brackish, acid swamps (Juniper et al., 1989) and probably also for *Drosophyllum lusitanicum* (Harshberger, 1925). In addition, four species of *Nepenthes*, i.e., *N. albomarginata*, *N. reinwardtiana*, *N. treubiana* and *N. mirabilis* (Juniper et al., 1989), grow at the sea side in spray zones of south-east Asian coasts, where there are no competitors. The distribution pattern of recent *Nepenthes* species indicates that the common ancestor of the genus was a halophyte with a coastal distribution in the Cretaceous period. Only later, descendents also colonized the interior of the land (Speirs, 1981).

It is generally believed that carnivorous plants are calcifuges, and that, for most, Ca is toxic. Exceptions include several Australian *Drosera* species that grow on calcareous sands in alkaline conditions (*D. erythrorhiza* (Dixon and Pate, 1978; Pate and Dixon, 1978), *D. falconeri* Tsang, 1980). Also some *Pinguicula* species (Studnicka, 1981) grow on rocks of calcium sulfate in Mexico (*P. gypsicola,* Taylor and Cheek, 1983), in central Europe (*P. vulgaris* ssp. *bohemica* Hadac, 1977) and *P. alpina* (Adler et al., 1994) and in southern Spain (*P. vallisneriifolia* Diaz-Gonzales et al., 1982). *Nepenthes clipeata* from Borneo (Slack, 1986) is another example of a calcicole. The toxicity of Ca was correlated to the pH value of the soil for *Drosera rotundifolia* by Rychnovska-Soudkova (1953), because it appears that a low pH allows plants to tolerate higher concentrations of Ca. This question deserves, however, additional investigations.

How can carnivorous plants survive without roots?

In a mesomorphic plant, the root fulfills four main functions: anchorage, water uptake, nutrient uptake, and storage of nutrients and photoassimilations. In rootless plants and in plants with only a small root system, these root functions are taken over by other organs, i.e., by the stems and/or by leaves.

The stem takes over the function of roots

In *Utricularia*, roots in the anatomical sense occur neither in aquatic nor in amphibian, terrestrial and epiphytic plants, but the stems usually develop special organs that may accomplish the function of the roots (Taylor, 1994). The stems have adapted in that they anchor the plants to the substrate, probably absorb available minerals and water, and store water and nutrients for times of drought. Four different modifications of the stem have been described (Taylor, 1994), (Figure 7):

- Horizontal stems, so-called stolons, serve for the propagation of the plant.
- Colourless shoots that grow downwards into the soil ('mud shoots', i.e. 'Schlammsprosse' (Adler et al., 1994; Schubert and Went, 1986)). They anchor the plants to the substrate and probably also contribute to their nutrition by taking up minerals. These organs are easily recognised as shoots, because they bear numerous bladders, the traps, similar to the green shoots *sensu stricto*.
- Root-like formations of the stem are so-called 'rhizoids'. They are specialized shoots with limited growth that emerge from the base of the flowering axis, but carry no leaves. They fix the plant within the masses of other floating weeds (Hegi, 1906).
- Stem tubers that form from stolons serve as storage organs to survive drought (in *Utricularia alpina*, *U. menziesii*, *U. inflata*, *U. reniformis*, *U. mannii*, *U. reflexa* and many other species). The tubers are of various morphological origin; in *U. alpina* they consist of huge parenchymatic cells containing an enormous vacuole (our own observations). In terrestrial species, they also serve to anchor the plants. Moreover, they contribute to the propagation of the plant which leads to the formation of large clones (Taylor, 1994).

Figure 7. Utricularia alpina: Morphology of the green and colourless shoots (a). Sub-soil shoots are transformed to tubers and to horizontal and downward-pointing rhizomes that carry traps (b).

Stem tubers are found in some Australian species of *Drosera*, such as *D. erythrorhiza*, *D. zonaria* or *D. hamiltonii* (Slack, 2000). In *D. erythrorhiza* the first tuber is formed under ground at the end of a positive geotropic shoot, the 'dropper', which has its origin in the radicle just above the hypocotyl (Dixon and Pate, 1978; Pate and Dixon, 1978). It is a storage organ and serves as the perennating structure during dry periods and bushfires. With the onset of tuber sprouting, rhizomes emerge from the vertical stem, each terminating in a 'daughter tuber'. They contribute to the clonal propagation of the plant. The tubers

Table 1. Carnivorous plant species, their traps and selected characteristics of their roots[a]

Family	Genus	Number of species	Type of trap	Root system[b]
Sarraceniaceae	*Heliamphora*	5	Pitcher	Weak
	Sarracenia	8	Pitcher	Weak to medium
	Darlingtonia	1	Pitcher	Medium to large
Nepenthaceae	*Nepenthes*	68	Pitcher	Weak to medium
Droseraceae	*Drosophyllum*	1	Fly-paper	Medium to large
	Drosera	110	Fly-paper	Weak and large
	Dionaea	1	Snap trap	Weak, but fleshy
	Aldrovanda	1	Snap trap	None
Roridulaceae	? *Roridula*	2	Fly-paper	Large
Dioncophyllaceae	*Triphyophyllum*	1	Fly-paper	Large
Byblidaceae	? *Byblis*	2	Fly-paper	Large
Cephalotaceae	*Cephalotus*	1	Pitcher	Weak to medium
Lentibulariaceae	*Pinguicula*	52	Fly-paper	Weak
	Utricularia	180	Suction trap	None
	Biovularia	2	Suction trap	None
	Polypompholyx	2	Suction trap	None
	Genlisea	15	Eel trap	None
Martyniaceae	*Ibicella*	1	Fly-paper	Large
Stylidiaceae	? *Stylidium*	136	Fly-paper traps in some species?	Medium
Bromeliaceae	*Brocchinia*	1	Pitcher	Weak
	Catopsis	1	Pitcher	Weak

[a] Based on Schlauer (1986), Juniper et al. (1989), Carow and Fürst (1990), Hartmeyer (1997), Mabberley (2000), Darnowski (2002), and own observations.

[b] Quantitative data are not available. The statements are to be seen in relation to a typical mesophytic plant of a temperate climate. The question marks indicate that for these genera the carnivorous habit is not proven.

are replaced by new ones, which grow inside the old tubers, during each vegetative period, using their stored assimilates for their own growth.

Leaves take over the function of roots

The uptake of water through the leaves was suggested for *Drosophyllum lusitanicum*. The leaves are covered by mucilage-secreting glands from the trap. They are supposed to contribute to the water supply of the plant by absorbing water from fog and humid air (Mazrimas, 1972). A similar suggestion was made for *Pinguicula,* which has specialized glands on the lower surface of the leaves (Lloyd, 1942), but this has never been proven.

The uptake of nutrients from captured prey is principally carried out by the leaves of all carnivorous plants, as it is the leaves that have transformed into traps. They catch and digest their prey, and usually they also absorb the digested substances, although this has not yet been proven for every species, and for some it remains a matter of debate (Juniper et al., 1989; Slack, 2000).

Organic substances of origin other than from animals are also utilized by leaves, as was shown for *Drosera* and *Pinguicula*. *Drosera rotundifolia* as well as some species of *Pinguicula* catch pollen grains with their traps. The pollen is digested (in some species only after the pollen grains have germinated on the trap), and the absorbed nutrients support the growth of the plants considerably (R.M. Austin, 1875, published in Juniper et al., 1989; Harder and Zemlin, 1968). Similarly, the nutrient-rich foliar leachate from the canopy above may feed the leaves, as was suggested by Juniper et al. (1989) for three woodland species of *Drosera*, i.e., *D. schizandra*, *D. prolifera* and *D. adelae*. To possibly more efficiently benefit from the leaching, these plants have developed remarkably broad leaves (Juniper et al., 1989; Lavarack, 1979). In *Heliamphora nutans* large amounts of decaying leaves were found in the pitchers (Studnicka, 2003).

The function of anchorage is achieved by leaf tendrils in many species of *Nepenthes* and in *Triphyophyllum peltatum*. These species are climbers and sometimes even become true epiphytes in later stages of their lives, losing all contact with the soil. Their leaf tendrils fasten them to their supports.

The function of storage of assimilates and water is probably accomplished in *Pinguicula gypsicola* by special leaves that are non-carnivorous but thick and succulent, and occur only during the dry winter before the new carnivorous leaves develop (Slack, 2000).

Traps versus roots: which one takes up what?

The ecological significance of carnivorous nutrition has been discussed ever since carnivory was proven (Darwin, 1875). After 130 years of research, we are aware of a wide range of data concerning the physiological dependence of the plants on their prey, which reaches from almost total dependence to almost total independence. In some groups nutrients can be taken up from the substrate by the roots as well as from animal prey through the traps (e.g., *Pinguicula vulgaris* Aldenius et al., 1983); other species obviously need their prey for sufficient growth (e.g., *Aldrovanda vesiculosa* Adamec, 2000), and some are even suppressed by a nutrient-rich medium (e.g., *Dionea muscipula* Roberts and Oosting, 1958). In general it appears that many, if not all carnivorous plants can survive without animals as prey; many species suffer, however, by reduction of their reproductive organs; they grow more slowly and they lose their vigour (Adamec, 2000; Pringsheim and Pringsheim, 1967; Roberts and Oosting, 1958). In greenhouses, where these experiments have been conducted, this response may be of no significance. In their natural habitat, the carnivorous plants may not be able to tolerate the hostile soil conditions without prey, and hence be unable to compete with the non-carnivorous plants. Only few data about ion uptake in carnivorous plants are available. A comprehensive review of the mineral nutrition of carnivorous plants is given by Adamec (1997).

In some plants, the killed animals may contribute little to their nutrition, as for instance in the South African *Roridula* (Roridulaceae); the killed animals are not digested, the nutrients come either from the soil (Carlquist, 1976b), or through the leaves, but in this case digestion is carried out by bacteria (Midgley and Stock, 1998) or symbiotic hemipterans (Ellis and Midgley, 1996). Because of it lacking digestion, the genus *Roridula* is no longer considered as a carnivorous plant *sensu stricto* (Lloyd, 1942). The West African *Triphyophyllum peltatum* obtains its mineral nutrients also from a well developed root system. In addition, it gets nutrients from animals from sticky trap leaves that are grown during part of the year; *Triphyophyllum* is therefore considered as a ‘part-of-the-time’ carnivorous plant (Green et al., 1979). *Pinguicula gypsicola* and other Mexican butterworts growing on limestone are also carnivorous during part of the year only (Slack, 2000). The same is true for *Drosera caduca* developing insect-trapping lamina in the juvenile growth stages of the leaves. After a few weeks the photosynthetic petiole elongates and broadens considerably (R. Barrett and M. Barrett, unpublished observations).

Darlingtonia californica appears to be quite independent of the nutrient status of the soil. It shows good growth in both nutrient-poor and rich soils, with or without insects, provided its very special temperature requirements (see above) are met (Juniper et al., 1989). *Pinguicula vulgaris* (Aldenius et al., 1983) and *Utricularia uliginosa* (Jobson et al., 2000) can also be cultured on either rich or poor substrates; both species can take up nutrients from the soil. In *Pinguicula vulgaris,* Aldenius et al. (1983) found that maximum size (68 mg average dry mass) is achieved on a nutrient-rich medium, with additional animal feeding. On a rich medium without insect supply, average dry mass was 46 mg. Insect-fed plants on a poor medium reached 33 mg, completely unsupplied control plants were 22 mg. Recent research on *Drosera capillaris*, *D. aliciae* and *D. spathulata* showed that their roots can take up inorganic nutrients like Ni, P, Ca and Mg, but their uptake has to be stimulated by nutrients transported from the leaves, i.e., by successful prey capture (Adamec, 2002).

Some carnivorous plants appear to have a limited capacity for nutrient absorption from the soil, and therefore depend on animals to a greater extent: *Utricularia gibba* (Pringsheim and Pringsheim, 1967) can survive on an inorganic medium, but grows very slowly. Better growth occurs, when beef extract, peptone, glucose and acetate are added to the medium. The same is the case with *Dionaea muscipula* on a nutrient-rich soil: without animals plants produce no new roots, only few flowers, no fertile seeds, and die (Roberts and Oosting, 1958). Therefore, in the natural habitat of *Dionea*, only 8–25% of the total N comes from the soil. The greatest amounts are found in dense vegetation, where the traps work less effectively (Schulze et al., 2001). The closely related *Aldrovanda vesiculosa* is able to survive without animal prey, but shows only poor growth (Adamec, 2000).

The amount of nutrients obtained from either prey or from the soil seems to vary substantially. *Sarracenia leucophylla* can get 60 times more ions from the prey than from the soil (Gibson, 1983b). *Nepenthes mirabilis* gets about 60% of its N from insect prey, whereas in *Cephalotus* it is only 30% (Schulze et al., 1997). In *Drosera rotundifolia* about 50% of the total N is of animal origin (Millett et al., 2003), and in *D. hilaris* 68% (Anderson and Midgley, 2003). The proto-carnivorous *Roridula gorgonias*, which needs symbiotic hemipterans for digestion, even up to 70% of N comes from animals (Anderson and Midgley, 2003).

For another group of plants, applied mineral nutrients (i.e. fertilizers) can be fatal: *Sarracenia alata*, for instance, grows on soil containing sufficient concentrations of N, P and K; it is, however, very sensitive to fertilizer additions, and dies when growing in such nutrient-enriched areas (Eleuterius and Jones, 1969).

Nutrition can also influence the morphology of some carnivorous plants, and the size and number of their traps. In some species of *Sarracenia* (Ellison and Gotelli, 2002) and of *Nepenthes* (Smythies, 1963) more, and more efficient pitchers are produced on a nutrient-poor medium. On a richer medium the leaf bases become flattened and hence more suitable for photosynthesis, whereas the pitchers are reduced.

Another interesting observation is that plants may take up only some specific nutrients through the roots, whereas others come through the leaves from the prey. This is the case for some Australian *Drosera* species that grow in habitats subjected to fires. The soil in this habitat in general is very poor, but enriched in K after a fire. *Drosera* is thought to take up the K^+ by its roots, and the other nutrients from insects (Dixon and Pate, 1978; Pate and Dixon, 1978), but this effect has not been quantified. *Nepenthes pervillei* sends its roots into rock cliffs where the cyanobacterium *Lyngbia* (Oscillatoriaceae) grows. *Lyngbia* fixes atmospheric dinitrogen, which is suggested to be absorbed by the roots, whereas other nutrients may come from animals that are caught in the few functioning traps (Juniper et al., 1989).

Conclusions and future aspects

Roots and root-substituting stems play an important role in the functioning of many carnivorous plant species, yet so far little information is available on their morphology and their physiological traits as well as on possible adaptations to their ecological situation. Much of our knowledge is based on the work of amateur botanists, therefore part of the cited literature is derived from popular journals. Since roots are the 'hidden half' of every plant (Waisel et al., 2002), our understanding of the carnivorous habit can only be improved substantially if we gain further information on the morphology of the roots and their capacity to take up nutrients from the soil as well as to survive the extreme conditions of their habitats.

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