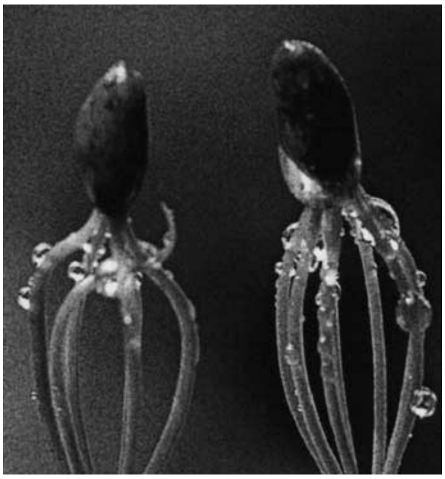
Part I

Introduction



Chapter 1

Why seedlings?

Mary Allessio Leck, Robert L. Simpson, and V. Thomas Parker

> It was, as it were, a little green star with many rays, half an inch in diameter, lifted an inch and a half above the ground on a slender stem. What a feeble beginning for so long-lived a tree! By the next year it will be a star of greater magnitude, and in a few years, if not disturbed, these seedlings will alter the face of Nature here.
>
> *Henry D. Thoreau (1993), writing in approximately 1862 about Pinus rigida (Pinaceae).*

1.1 Seedlings as part of a plant's life cycle

The seedling, the young spermatophyte plant following germination, is but one stage in the continuum of a seed plant's life cycle. For ecological purposes, discussion on the life cycle (illustrated in Fig. 1.1) focuses on the processes involved in replacing the adult and/or colonizing new habitats. A reproductive adult plant produces seeds that, once dispersed, become part of the seed bank (Parker *et al.*, 1989; Simpson *et al.*, 1989). Then, following germination, a seedling faces unpredictable environments and is limited by its particular genetic constraints. However, if successful, it survives to adulthood and reproduction.

Seedlings are highly vulnerable, subject to varied abiotic and biotic factors that affect growth and establishment. Their adversities, although variable in severity – depending on habitat and seedling form – include drought, flooding, herbivory, and lack of resources, such as mycorrhizal associates and light. The probability of a seed producing a successful, established plant is usually quite small (e.g. Simpson *et al.*, 1985; Leck & Simpson, 1994; Bazzaz, 1996; Kitajima,

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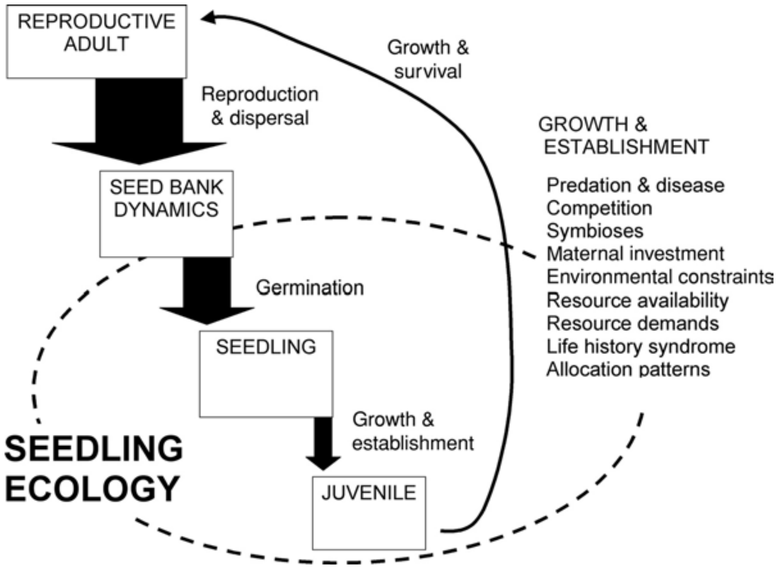

Fig. 1.1 Seed plant life cycle continuum. Shown are factors influencing seedling growth and establishment. The change in thickness of arrows from stage to stage suggests amount of attrition. The dotted line encompasses seedling ecology and indicates the scope of this book.

2007). The seedling stage, therefore, is a bottleneck, and selection pressure is assumed to be high (e.g. Grubb, 1977; Harper, 1977; Fenner & Thompson, 2005; Kitajima, 2007). The successful survival of some seedlings of every species is, ultimately, critical because it underlies the development and sustainability of plant communities.

For an individual plant, changes occur in morphological detail as well as in its reproductive ability, as it passes from "seed, to seedling, juvenile, immature, virginile, reproductive (young), mature (old), subsenile, and senile" stages (Bell, 1991, p. 324). Duration of a particular stage varies with species. Seeds of *Salix* spp. (Salicaceae), for example, germinate within 12–24 hours of dispersal (Young & Young, 1992). Those of other species [e.g. *Verbascum* sp. (Scrophulariaceae)] persist in the soil for more than a century (Telewski & Zeevart, 2002). Similarly, some seedlings, such as those of desert annuals that produce seeds within a few weeks of germination, are not seedlings for long. Conifer seedlings of forests of British Columbia (Canada), in contrast, may be held in the seedling stage for more than 150 years – until light conditions are suitable for continued development (Antos *et al.*, 2005).

Sometimes stages are skipped. For some viviparous species, such as mangroves (e.g. *Bruguiera* spp. Rhizophoraceae; Burger, 1972) and seagrasses (*Thalassia* spp. Hydrocharitaceae; Sculthorpe, 1967), embryo development is continuous and it is not held inactive and dormant within the seed (see Chapter 2). In other cases, plants may proceed directly from seedling to flowering stage. *Chenopodium rubrum* (Chenopodiaceae), *Pharbitis (Ipomoea) nil* (Convolvulaceae), and *Xanthium strumarium* (Asteraceae) have photoperiod sensitive cotyledons, flowering as seedlings following short-day inductive photoperiods; *C. rubrum* produces flowers within six days of initiation of imbibition (Downs & Hellmers, 1975). This precocious behavior is also seen in certain wetland species, including *Lindernia dubia* (Scrophulariaceae) (Leck, pers.

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obs.), *Limosella australis* (Scrophulariaceae), and *Myriophyllum variifolium* (Haloragidaceae) (Brock, pers. comm.), that flower within weeks of germination during soil seed-bank experiments. These examples illustrate the plasticity found among plants in the seedling stage of their life cycles.

To become a seedling, the seed must first germinate, often distinguished by the protrusion of the radicle through the seed coat (see Chapter 2). Depending on the species, this process is regulated by dormancy mechanisms interacting with availability of water, quantity and quality of light, (alternating) temperature, levels of oxygen, and/or, in some cases, an external supply of nutrients (see Baskin & Baskin, 1998; Fenner & Thompson, 2005). In a community context, germination is a facet of seed-bank dynamics that are important because what happens to seed banks influences seedlings (Parker *et al.*, 1989; Simpson *et al.*, 1989). Seed banks may be transient or persistent. The relative transience or persistence is related in some habitats to disturbance regime and to seed size, with transient seed-bank species having larger seeds (e.g. Grime, 1989; Leck & Brock, 2000; but see Leishman & Westoby, 1998). Seeds of transient species are present in the soil for <1 year, short-term persistent for >1 year but <5 years, and long-term persistent for >5 years (Fenner & Thompson, 2005). Maintenance of seed banks can involve various mechanisms, including physical, physiological, morphological, and morphophysiological dormancy, and the dormancy level can cycle between dormant and nondormant states (e.g. Baskin & Baskin, 1998). In temperate areas, the larger-seeded transient seed-bank species may germinate at low temperatures (5 °C) and do not require light; their earlier spring germination means that they are in place before later (and smaller) germinators appear (Thompson & Grime, 1979; Leck & Simpson, 1993). Seedling establishment, generally considered to be the process during which a germinated seed achieves independence from maternal reserves (e.g. Fenner & Thompson, 2005), is favored by early germination at least in systems where the environment is predictable. Moreover, seedling establishment requirements of small-seeded persistent species would appear to be different from seedlings of large-seeded transient seed-bank species.

Successful negotiation of stages may vary with species. For example, in tidal freshwater wetland annuals, 91% of *Polygonum punctatum* (Polygonaceae) seeds overwintered to germinate and grow to seedlinghood but less than 1% of *Ambrosia trifida* (Asteraceae) did so (Leck & Simpson, 1994). Survivorship of seedlings varied with species and with location relative to a tidal stream channel (Parker & Leck, 1985). In this tidal freshwater wetland with predictable hydrology and dominated by both annuals and perennials, the later germinating perennials, like *Typha latifolia* (Typhaceae), were not observed to survive in study plots (Parker & Leck, 1985; Leck *et al.*, 1989b; Leck & Simpson, 1995).

Some components of the life cycle are discrete. For example, the seed is an entity, comprised of an embryo, typically with maternally supplied nutrient reserves, within a maternally derived seed coat (e.g.

Baskin & Baskin, 1998). In contrast, the seedling may be more arbitrarily delimited. Although the seedling stage has a defined start when the radicle emerges from the seed coat, its end point is along a growth continuum and is more difficult to recognize (Chapter 2). Furthermore, when a seedling is a seedling may depend on the focus of the viewer. The morphologist considers morphological changes, whereas the physiologist emphasizes the attainment of independence from seed reserves. However, in the case of orchids and parasites, dependence is transferred from maternal resources, if present, to hosts or to mycorrhizal fungi. Thus, it is likely that no one definition, except possibly – *the young spermatophyte plant, following germination* – covers all seedlings.

1.2 Vulnerabilities and bottlenecks

At each stage of its life cycle, the plant's success is limited by an assortment of intrinsic and extrinsic factors that are to some degree driven by chance. Because of their small size, seedlings have greater susceptibility to resource limitations and other factors that affect establishment and growth (Fig. 1.1). In addition to resource limitations related to size, seedlings may be vulnerable because of low levels of morphological and physiological defenses. Cotyledons of *Toxicodendron pubescens* (Anacardiaceae) suffer herbivory whereas its leaves do not (Miller & Miller, 2005). However, in the case of *Quercus alba*, sprouting causes seeds that are favored by squirrels (*Sciurus carolinensis*) to become less digestible and, under some circumstances, squirrels bite out the embryo, preventing these changes (Steele & Koprowski, 2001). Seeds may present physical barriers that limit granivory; for example, the burs of *Xanthium strumarium* (Asteraceae) are never eaten (N. Good, pers. comm.).

Vulnerability can vary with habitat. As a generalization, dormancy-breaking mechanisms have evolved to increase the probability that germination occurs in a safe site – when and where the likelihood of survival is greatest (e.g. Grubb, 1977; Harper, 1977; Baskin & Baskin, 1998; Fenner & Thompson, 2005). Although a species actually may be able to germinate or live in a range of habitats, it may not find all habitats equally suitable because primary stresses vary. For example, shade-adapted seedlings can slowly acclimate to sunny locations, but survive best inside a forest despite being subject to high levels of herbivory and pathogens; in large gaps, establishment is prevented by competition with fast growing species (see Chapter 8). *Impatiens capensis* (Balsaminaceae) in temperate woodland habitats is more susceptible to white-tailed deer (*Odocoileus virginianus*) herbivory than when growing in a tidal freshwater wetland (Leck, Parker, & Simpson, pers. obs.). Moreover, although germination may occur over a wider range of conditions (along an inundation gradient in a tidal channel), establishment conditions may be narrower (Parker & Leck, 1985; Leck & Simpson, 1994).

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Vulnerability varies with phylogeny within a given habitat. Some taxa are more susceptible to an environmental constraint than others. Seedlings of maples (*Acer* spp. Aceraceae) succumb to frost heaving to a greater extent than seedlings of *Carya tomentosa* (Juglandaceae) in successional old fields (New Jersey, USA) (Myster, 1993). Similarly, small seedlings of *Bidens laevis* (Asteraceae), a tidal freshwater wetland dominant, have less predictable establishment than the co-occurring, larger seedlings of *Impatiens capensis* or *Polygonum arifolium* (Leck & Simpson, 1995). In temperate old fields, early spring germinants of *Ambrosia trifida* and *Polygonum* species can tolerate low night temperatures, whereas seedlings of *Abutilon theophrastii* (Malvaceae) and *Ipomoea* cannot; variation in burial depth, resultings in varied emergence time, reduces the intensity of selection (Bazzaz, 1996).

Regardless of the cause of vulnerability, small size, limitation in ability to acclimate, habitat suitability, phylogeny, or other constraints, the seedling stage faces hurdles that are exacerbated by stochastic events. Collectively, these contribute to the significance of the seedling stage as a bottleneck in a species' life history. Selection at the seedling stage may produce seedling specialists or generalists. Examples of specialists are the bulb- and corm-forming seedlings of Australian desert perennials (Pate & Dixon, 1982). These specialized seedlings have the ability, because they possess contractile roots and hypocotyls, to place the apical growing point and a storage bulb, corm, or rhizome well below the soil surface, where they can avoid drought and heat during their first growth season. Another group of specialists are diminutive, woody, microstilt Australian perennials that produce heavily lignified, adventitious stilt roots, which allow the plant to survive desiccation and reduce prolonged soil surface heat stress (Pate, 1989). *Ambrosia trifida*, an example of generalist seedlings, can be found in tidal freshwater marshes or as weeds in agricultural fields. Communities may or may not have high seedling competitive ability, depending on the intensity of competition (Lamb & Cahill, 2006). Seedlings may also be conservative or opportunistic in their use of resources (see Chapter 8) or fugitive or stress tolerators (Shipley *et al.*, 1989).

1.3 Making it: filters, safe sites, and establishment

The idea of the seedling serving as a bottleneck in a species' life history necessitates considering how the individual survives from the seed bank to establishment and, ultimately, to an adult (Fig. 1.2). A location that assures seedling success and that has all the necessary resources for survival may be termed a *safe site* (e.g. Harper, 1977; Fenner & Thompson, 2005). Safe site requirements vary with species, genotype, and time with functionality related to all the factors that influence establishment and growth (Fig. 1.2).

In a particular habitat, the safe-site filters can vary spatially and temporally, resulting in zonation or in cyclic changes in vegetation.

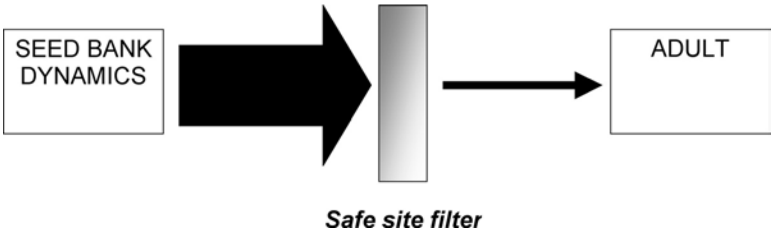

Fig. 1.2 The importance of safe site filters affecting seedling populations. The thickness of the arrows suggests the impact of the filter(s) on seedling establishment to adult.

In wetlands, for example, water (inundation) can sort species across depth gradients or produce different communities, depending on drawdown/flooding patterns determined by rainfall (e.g. van der Valk, 1981; Leck & Brock, 2000). In a desert, small-scale habitat differences, such as those caused by porcupine digging or a nurse tree (see Chapter 15), can provide safe sites not available nearby.

The array of factors that can result in a seedling's failure to achieve establishment may act together or separately, and are environmental filters (Fig. 1.2). These factors may be abiotic (light, temperature, drought) and/or biotic in nature (competition, availability of microbial symbionts), and may have varying spatial or temporal impact. Seedling attrition may be huge. Moreover, the behavior of the seedling following germination can be intimately tied to seed characteristics, including dispersibility, size, and dormancy. These characteristics are controlled by genetic as well as by environmental factors during development, maturation, and storage (Gutterman, 1993). Individual traits, such as seed mass, can influence susceptibility of seedlings to drought, depth of burial from which seedlings may emerge, range of microsites suitable for seedling establishment (via gap detection mechanisms; e.g. Dalling, 2005), and tolerances to herbivory (Hoshizaki *et al.*, 1997). Agents of burial, whether biotic (e.g. dung beetles; Andresen & Feer, 2005) or abiotic (e.g. soil cracks; Harper, 1977; Bonnis & Lepart, 1994), influence seed position in the soil. In addition to seed dormancy mechanisms (e.g. Baskin & Baskin, 1998), exogenous influences, such as availability of a dispersal vector or disturbance, that place the seed and, thus, the seedling in a position where chances for survival are optimal, cannot be underestimated.

1.4 Seedlings: a primer

Seedling organs include the *radicle* (or primary root), *cotyledons* (seed leaves), stem, leaves, buds, and surface appendages, such as hairs (Lubbock, 1892; Burger, 1972; de Vogel, 1980). Seed plants include gymnosperms with two to many cotyledons, dicots that typically possess two cotyledons, and monocots with one structure designated as a cotyledon (Fig. 1.3). In each group, major seedling distinctions are based on the position of the cotyledons during germination. When the cotyledons rise above the soil surface, the seedling has *epigeal* germination, and if the cotyledons remain at or below the soil surface,

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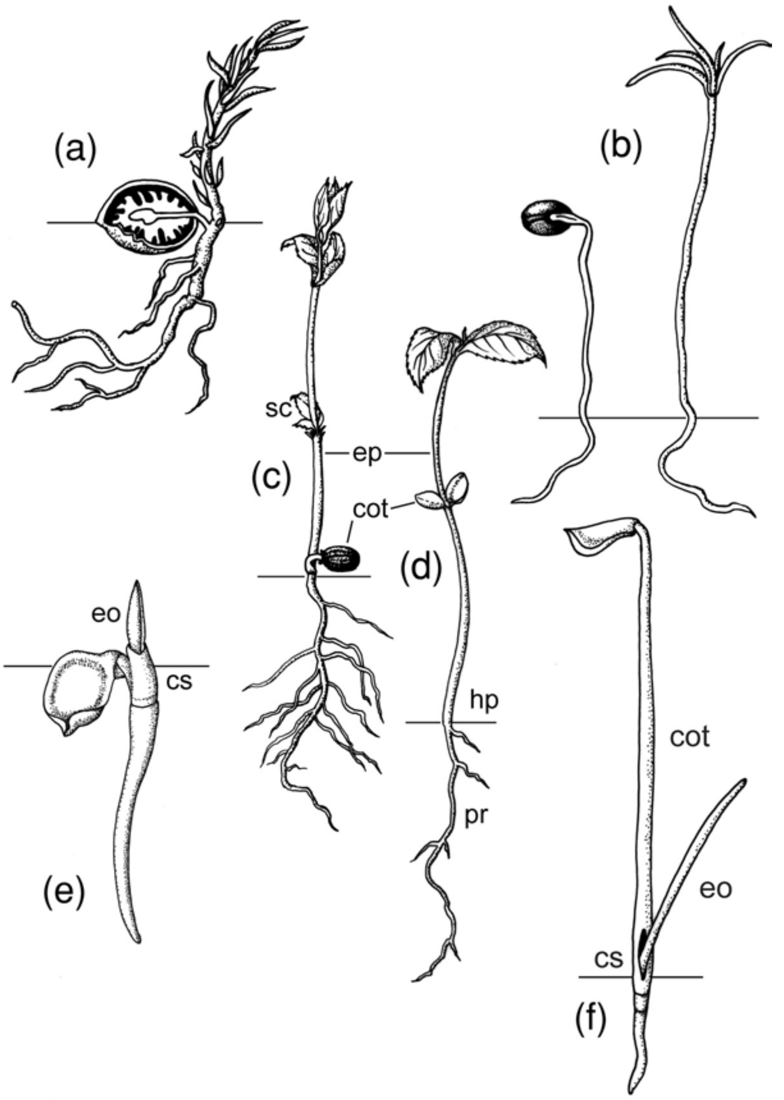

Fig. 1.3 Representative seedlings of gymnosperms, dicots, and monocots illustrating hypogeal and epigeal germination types. Gymnosperms are (a) *Torreya myristica* (hypogeal), with part of the seed removed revealing endosperm and one of two cotyledons, and (b) *Taxus baccata* (epigeal) (Taxaceae); dicots are (c) *Prunus americana* (hypogeal) and (d) *P. virginiana* (epigeal) (Rosaceae); and monocots are (e) *Asphodelus lusitanicus* (hypogeal) and (f) *A. tenuifolius* (epigeal) (Asphodelaceae). Not drawn to scale. Abbreviations: cot – cotyledon, cs – cotyledonary sheath, eo – eophyll (the expanded blade part of the cotyledon), ep – epicotyl, hp – hypocotyl, sc – scale leaf, pr – primary root or radicle. Redrawn by A. Hoffenberg: (a) from Chick (1903), (b) Rudolf (1974), (c, d) Grisez (1974), and (e, f) from Tillich (2000) with permission from CSIRO.

germination is *hypogeal*. As the seedling grows, the stem above the cotyledonary node is the *epicotyl* and that below, the *hypocotyl*. The hypocotyl is usually distinct in the embryo of epigeal seedlings; in hypogeal seedlings, it is poorly developed and does not elongate during germination (de Vogel, 1980).

Overall, most gymnosperms and dicots are epigeal and most monocots are hypogeal. Hypogeal germination was once considered advanced (Eames, 1961), but both types can be found within the same taxon (Fig. 1.3). Although this brief description suggests that the seedling form is relatively stereotyped, a particular part, such as the cotyledon, can vary considerably in form and function in both dicots (Fig. 1.4) and monocots (Fig. 1.5). Efforts to correlate structure and function provide other levels of classification (e.g. Garwood, 1996). The greatest number of functional types may be found among tropical

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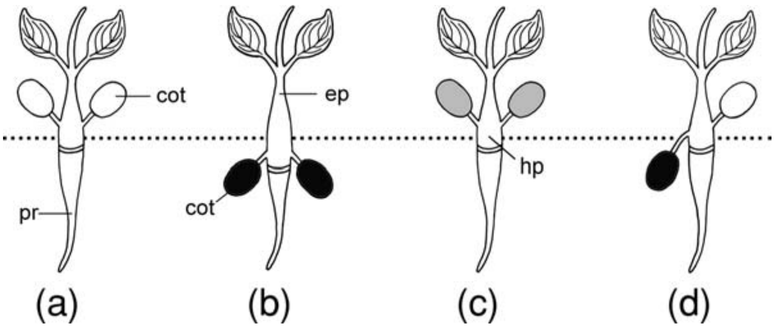

Fig. 1.4 Dicot seedlings showing cotyledon types: (a) photosynthetic, (b) storage, (c) haustorial (see legend Fig. 1.5), and (d) mixed form where only one cotyledon is photosynthetic. The double line indicates the collet, the transition zone between stem and root. Abbreviations: cot – cotyledon, ep – epicotyl, hp – hypocotyl, pr – primary root or radicle. Redrawn by A. Hoffenberg with permission from Bell (1991), copyright Oxford University Press.

woody dicots (Garwood, 1996) and monocots (e.g. palms; Tomlinson & Estler, 1973; Bell, 1991). Focus has been on function and position of cotyledons, but primary roots may vary in site of origin, architecture, and persistence (Tillich, 2000).

1.5 What seedlings can tell us

Observations from particular environments have relevance across other habitats. For example, Titus and Hoover (1991) observed that in submerged plants, potential challenges to seedling establishment, as well as lack of understanding of the physiology and demography of seed banks and germination, severely limit the predictability of sexual reproductive success in the field. They also note that small seedling size, rapid growth, sparse seed banks, and unfavorable conditions for germination and establishment all contribute to the lack of quantitative data. Garwood (1996) also laments the lack of information about seedlings in reports on germination and other aspects of species biology in tropical environments.

During the past decade, work with *Arabidopsis* (Brassicaceae) mutants has greatly improved understanding of seedling development and physiology (e.g. Leyser & Day, 2003; Achard *et al.*, 2006). Insights have relevance to understanding seedling establishment. For example, *Arabidopsis* studies help explain the basis of etiolation (stem growth in darkness), which raises the cotyledons to the soil surface (Leyser & Day, 2003). Furthermore, understanding seedling requirements may improve the chances for success of restoration projects. In sedge- (Cyperaceae) dominated created wetlands, seedlings may not establish even when high-quality commercial seeds are planted or following transplantation of healthy seedlings (van der Valk *et al.*, 1999). Soil amendments, such as organic matter, are necessary to improve soil moisture and permit establishment (see Chapter 17).

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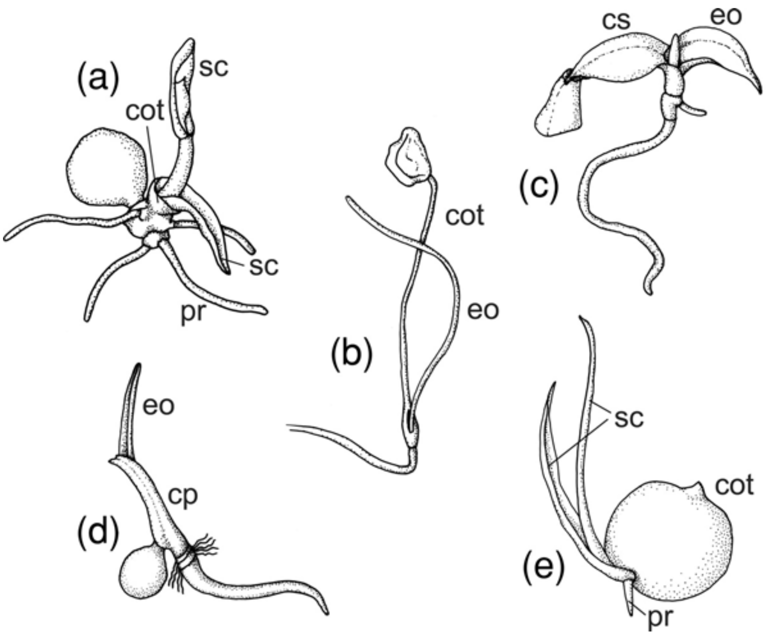

Fig. 1.5 Monocot seedling types distinguished by Tillich (2000): (a) compact cotyledon, characterized by a low sheath and a completely haustorial hyperphyll* that is completely imbedded in the seed and not visible (*Bomarea edulis* Alstroemeriaceae); (b) cotyledon with photosynthetic assimilating, elongated, and upright hyperphyll that raises the seed above the soil surface (*Albuca fastigiata* Hyacinthaceae); (c) cotyledon with wide assimilating sheath (*Pitcairnia corallina* Bromeliaceae); (d) cotyledon with a long coleoptile (*Hypoxis hygrometrica* Hypoxidaceae); and (e) storage cotyledon where, due to absence of endosperm, the hyperphyll has storage function (transient seed coat removed) (*Orontium aquaticum* Araceae). Not drawn to scale.

Abbreviations: cot – cotyledon, cp – coleoptile, cs – cotyledonary sheath, eo – eophyll, sc – cataphyll, pr – primary root or radicle.

*Definitions: *Cataphylls* – first leaves following the cotyledon, sometimes called scale leaves; *coleoptile* – an elongated tubular extension of the sheath above the insertion of the hyperphyll; *eophyll* – first, expanded photosynthetic leaf; *haustorium* – in monocots the leaf blade (or end) of the first leaf, found within the seed, and in gymnosperms and dicots the undifferentiated, colorless suctorial organ that acts as an absorptive organ, transferring nutrients from the endosperm to the growing embryo and developing seedling; *hyperphyll* – part of the cotyledon connecting the haustorium to the sheath, also called the cotyledonary petiole (this may be short in admotive, adjacent germination and long in remote germination); *primary root* – the first root also called the radicle. Redrawn by A. Hoffenberg with permission from Tillich (2000), copyright CSIRO.

Despite numerous studies, literature on seedlings is diffuse and, often, information about seedling ecology is lacking even in species accounts. Also, other stages of the life cycle contribute to seedling success (e.g. Howard & Goldberg, 2001; Chapter 10), including dispersal and maternal investment to seeds. Thus, improved understanding of the roles of seedlings is challenging. Yet, an understanding of plant life cycles underpins the pursuit of knowledge in botanical, ecological, environmental, and agricultural disciplines.