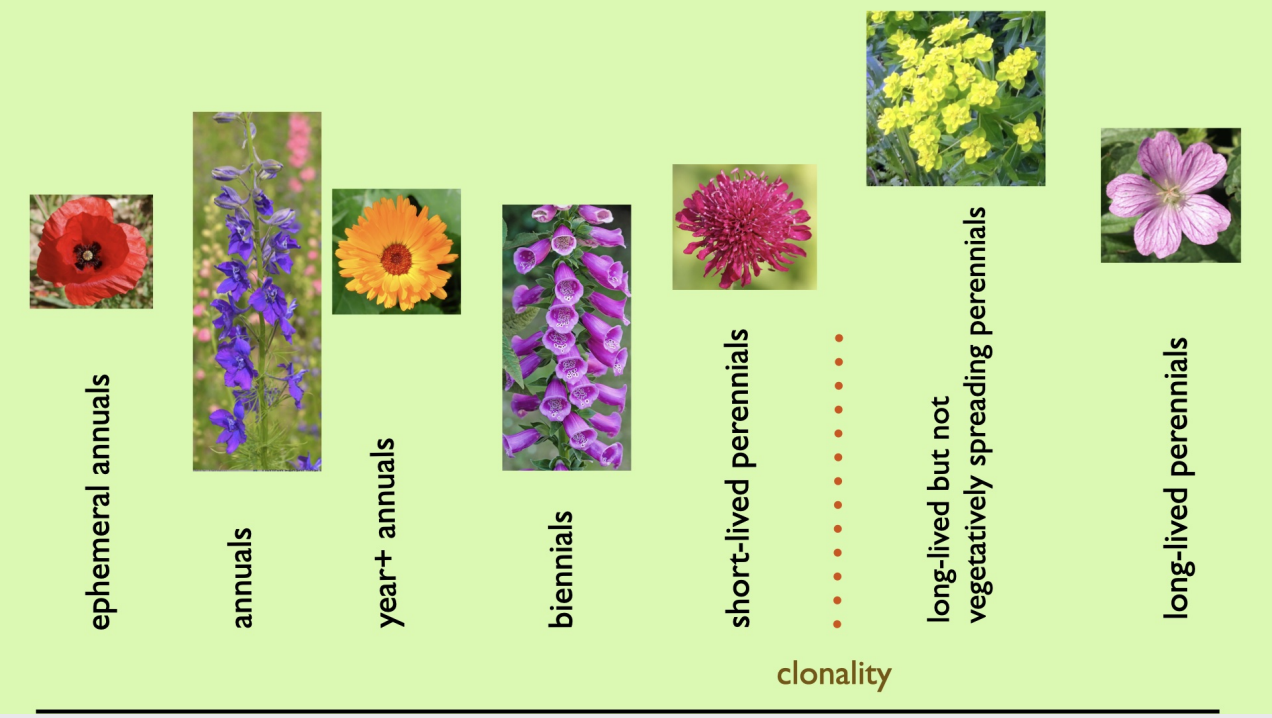
Perennial longevity

Conventional horticultural language makes a distinction between three categories: annuals, biennials and perennials. Reality is far more complicated! And as so often in nature, longevity is best understood to be on a gradient – between species whose individuals only survive a few months to those which can live for …. as long as conditions allow, potentially for ever!



In this diagram, moving from left to right, from the shortest to the longest lifespan, we start with ephemeral annuals.

1.1 Longevity and Succession

Longevity is closely linked to succession – early succession environments are largely made up of short-lived species, while mature late succession environments will be composed largely of long-lived ones, from the trees down to the herbaceous ground layer. The ruderals (pioneers) of early succession environments are of course short-lived.

It is worth briefly pointing out that late succession environments will be dominated by long-lived trees, typically species of *Quercus, Fagus, Fraxinus, Tilia* (and in North America, *Carya* and certain *Acer*). Short-lived trees (e.g. *Betula, Prunus*, many *Pinus*) typically dominate young regenerating woodland, i.e. early succession woodland but alongside slower-growing late succession species, so typically we may see seedlings of *Betula* alongside a few *Quercus* – come back in 100 years in your time machine and there will only be *Quercus*.

It is interesting to look at root mass when we consider the longevity of herbaceous plants. Typically annuals have a low ratio of root to above-ground growth, and long-lived perennials a higher ratio. All annual roots have to do is provide a flow of water and nutrients to the foliage, flowers and developing seed pods. Annuals with taller stems may have a long taproot for stabilisation purposes. We see this taproot developed more in biennials, and some short-lived perennials.

Cerinthe major, one of many annuals with a very limited root system, illustrating the basic architecture of non-clonal herbaceous plants, with one shoot-root point of connection.

When we get down on hands and knees to look at the base of an annual plant, we typically see a stem diving down into the ground and no sign of any growth that indicates that the plant may grown again next year.

Biennials often develop a sturdy tap root to store nutrients over the winter, essential for the rapid growth of a tall stem, this also requires a deep root to stabilise it, which the tap root can do. Carrots and parsnips are typical of biennial roots; many members of the *Apiaceae* adopt this strategy. Tap roots are also to be found amongst those members of the

Many annuals grow to a very definite genetically-determined lifespan – flower, seed and die. No amount of good cultivation will lengthen their lifespan. *Papaver rhoeas* is a good example. Another is the well-known weed *Cardamine hirsuta*. Then there are other annuals where good cultivation, i.e. plentiful water and nutrients, may allow a somewhat longer flowering season, e.g. *Nigella* and *Delphinium consolida*. Finally there are those that can carry on growing and flowering into a second year. Typical of these are some plants from Mediterranean habitats where the winter is not too cold and spring offers the opportunity for renewed growth, flowering and of course seed production. *Calendula offcinalis* and *Eschscholzia californica* can both germinate in autumn, flower next spring/summer, and then if the summer is not so hot and dry as to kill them they can renew growth in the autumn, survive through the winter and even go into a third year. They will look a mess but their endurance has to be admired!

Short-lived perennials is a category which is unfortunately not generally recognised. These have a genetic predisposition to survive for only a few years, very often three to five, flowering each year but even in ideal conditions will then die. Typically, they are like annuals and biennials and produce considerable quantities of seed which germinates quickly and often extensively. So, if an unfamiliar plant is producing a lot of seed and a lot of seedlings are appearing, then it could well be short-lived. Like annuals and biennials there will be one point of connection between roots and shoots.

Short-lived perennials, biennials and annuals are nearly always rhizophytes.

A four-year old *Aquilegia vulgaris*. Multiple primary roots emerge from a unified basal, from which several shoots, each potentially supporting a flower stem, emerge.

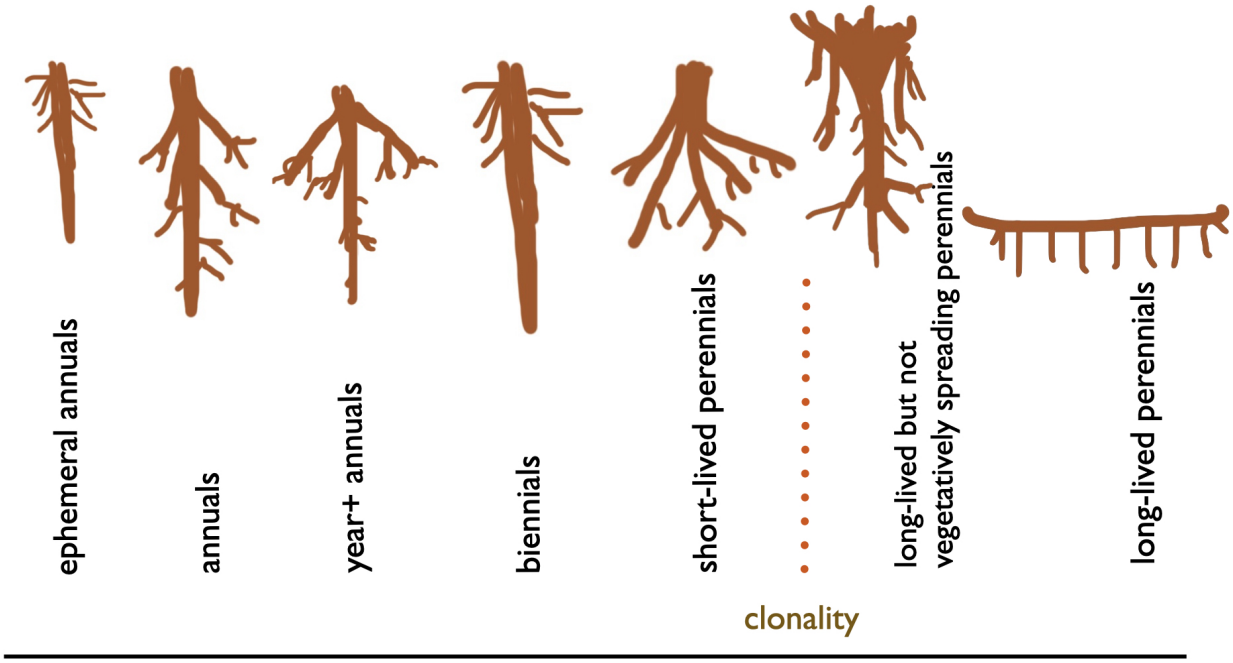
1.2 Long-lived perennials

Truly perennial perennials will be able to produce enough vegetative growth to be able to ensure that they will be able to clone themselves and/or build up such massive underground structures that their longevity is assured.

Clonality refers to the ability of plant to produce genetically-identical copies of itself, i.e. clones, through vegetative, i.e. non-sexual, reproduction.

Some rhizophytes are clonal - if the central tap root decays and is replaced by a number of surviving plants formed from its outer parts. Rhizocaulophytes are technically clonal in that they are produce potential new plants around their perimeters, each with their own tap root/s. However in many cases species of plants with these underground structures do not clone themselves, or only do so after long periods of time, as their crowns are very stable and do not break up easily.

Caulophytes with no tap roots and with rhizomes, are completely different! Rhizomes - adapted stems - easily able to produce new shoots and new roots, and frequently branching, enable caulophytes to spread successfully, and often quickly, and with the capacity to readily produce clones. Rhizomatous growth may theoretically enable a plant to live for ever!



Root and other underground structures typically get larger with longer-lived plants. Biennials and short-lived perennials typically have either large or branching tap roots, but as rhizophytes they have a limited ability to expand sideways and so propagate themselves vegetatively. Rhizocaulophytes, including many long-lived but not vegetatively spreading perennials typically have a large crown with multiple roots. Caulophytes are truly long-lived perennials with their branching rhizomes.

It is difficult to make hard and fast categories but if there is one distinction which is relatively clear, it is the division between clonal and non-clonal herbaceous plants. Non-clonal plants do not have the physical resources and/or the genetic traits, to enable them to develop structures which enable them to create independent plants. Clonal plants do, even if sometimes this may be quite rare.

One final point about rhizomatous plants and longevity. Rhizomes vary greatly in their longevity. Short-lived rhizomes that rapidly lose connection with the parent plant are very vulnerable, as they have few resources to draw on as they spread into a new environment. This means that a plant that is theoretically long-lived can in reality die out quite quickly. Much will depend on the soil and on other conditions which affect the survival rates of the young plants.

1.4 'Conservative' plants

A somewhat unfortunate term for a useful concept in nature conservation but also for planting design. This does not 'true blue' (English joke) or a member of CPAC (US joke) but refers to the 'Co-efficient of Conservatism', which is an assessment of how likely a species is to be lost owing to habitat destruction. Very weedy ruderals which pop up anywhere are = 0, whereas slow-growing species such as trilliums, baptisias, *Sporobolus heterolepis* grass or *Veronicastrum virginicum* are = 10. These appear only very slowly in restored habitats, and in plantings they can be very slow and sometimes difficult, to establish, but once they do get going, they tend to be quite resilient and long-lived, largely owing to extensive root systems.

The concept of the conservative plant is a useful one for us, as it focuses attention on the difficulty/slowness of establishment for some species, but also on their longevity.

Reference:

<https://botany.one/2018/09/ecology-of-floristic-quality-assessment-testing-for-correlations-between-coefficients-of-conservatism-species-traits-and-mycorrhizal-responsiveness/>
<https://en.wikipedia.org/wiki/Floristic_Quality_Assessment>

Conservative plants

These:

- are slow to establish, sometimes taking several years to reach flowering size from seed,
- build up a considerable, and often deep, root mass,
- are often difficult to transplant, often failing or taking several years to re-establish, particularly problematic are those indicated with T
- are notably long-lived,
- do not spread vegetatively, or do so very slowly (there are exceptions – as some are root spreaders - RS)
- are vulnerable to competition or predation (or being trodden on!), in the first 2-3 years after planting, at least from small plants,
- the majority are rhizocaulophytes, but for caulophytes where rhizomatous spread is extensive, this is only after many years

Acanthus - RS
Actaea
Amsonia
Anemone hupehensis, x hybrida group - RS
Aralia
Aruncus
Astilbe
Astilboides
Baptisia - T
Boehmeria
Clematis – herbaceous species
Convallaria
Datisca
Dictamnus - T
Eupatorium, Eutrochium
Gentiana - T
Gillenia
Heliopsis helianthoides
Helleborus
Hemerocallis
Inula
Iris

Jeffersonia
Macleaya – M. microcarpa is RS
Mertensia
Paeonia – T
Platycodon grandiflorum
Podophyllum
Polygonatum
Pulsatilla - T
Rheum
Rodgersia
Silphium - T
Trillium - T
Trollius
Veratrum - T

1.5 Short-lived species in planting design

Short-lived perennials will need to reproduce by seed, which will need space in which to germinate and grow. Dense plantings dominated by vegetatively-spreading perennials will clearly not present many opportunities for this. More open plant mixes on less fertile substrates will present many more opportunities for seeding. Indeed these species will tend to play a more important part in natural environments on drier and less fertile soils.

Disturbance clears vegetation and therefore creates seeding opportunities. So having short-lived seeding species in planting situations where disturbance is likely (such as public plantings) is important, as these can help a 'self-repair' process. Otherwise deliberate thinning or removal of existing plants may be needed. On fertile soils this clearly creates an opportunity for weeds as well as desired species to germinate and grow too. Much will depend on the seed bank or what weed species are likely to blow in on the wind.

Short-lived self-seeders tend to have a different architecture to longer-lived perennials. Tending to grow in more physically open environments they are more likely to have a large proportion of leaf surface areas lower down – the rosette of leaves, all within 30cms of the ground is a very common pattern. Longer-lived perennials in denser plant communities are more likely to have more leaf surface area higher up, as they will be surrounded by competitors all fighting for a space in the light. Combining the two will result in the former being suppressed – rosette-formers and upright perennials simply do not mix.

A well-known problem with self-seeders is that they seed too much and become their own weed problem. This puts many gardeners and designers off using them. The opposite problem is that desired species do not seed enough to maintain their presence in the planting. A major problem here is that the success of self-seeding is highly variable and we do not have much idea of the factors that direct the level of successful seeding. Indeed some practitioners who collaborated on a book even referred to the Black Box – we know what goes in and what comes out but we do not know how the two are connected.

Planting at Sichtungsgarten Hermannshof, Weinheim, Germany. Dominated by long-lived perennials but with a minority element of the biennials *Verbascum bombyciferum* (yellow) and *Salvia turkestanica* (silver-white) and short-lived perennial *Knautia macedonica* (deep red, far left). The location of these will change from year to year

1 *Cultivating Chaos: How to Enrich Landscapes with Self-Seeding Plants* Jonas Reif, Christian Kress, and Jürgen Becker. Timber Press, 2015.