Plant Survival Strategies – Competitive, Stress Tolerant and Ruderal (CSR theory)

1.0 This is a theory that attempts to summarise how plants grow, survive and reproduce. It was developed in the 1970s by J. Philip Grime, at the University of Sheffield. Although originally devised as a way of understanding how plants grow in nature, it has become important as a way of helping us make plant selections for designed environments.

CSR theory, as it is often known, proposes that there are three basic strategies for plant survival: competitive, stress tolerant and ruderal. It is important to realise that these are strategies, not categories, as most plants combine them to some extent. It can only be used as a general guide to grouping plants. However it can do much to help us understand plant growth and competition over time, and to develop appropriate management strategies.

To summarise:

- **competitors** are good at making the most of resources, and compete with each other in high resource environments;
- **stress-tolerators** are good at surviving and growing in resource poor environments;
- **ruderals** are pioneer plants, which grow rapidly from seed wherever and whenever opportunities allow; they are inevitably short-lived.

Before we go on, there are two other terms which should bring in here:

- **generalists** are plants that will survive in a wide variety of environments, tolerating a range of different conditions, although not necessarily very extreme ones. Many competitors and ruderals are generalists;
- **specialists** are adapted to thrive in particular conditions, within a fairly narrow range of environmental variables; stress tolerators are mostly specialists.

1.1 Resources

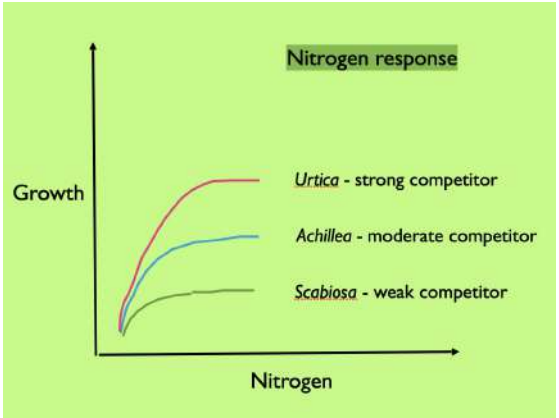
When we talk about resources, ecologists mean three things:

- **light**, vital for powering photosynthesis,
- **nutrients**, i.e. mineral nutrients: NPK etc., vital for building plant tissues,
- **water**.

2 Competitive plants

These are species which are good at utilising resources. Plants vary greatly in their ability to use resources, so for example if we feed different plant species with fertiliser, we find that some will grow a lot whereas many make very little new growth. There is a

Farmers like ryegrass (*Lolium perenne*) as it has good nutrient response – pour on the nitrogen and it grows and grows. Feed the stress-tolerant grass *Festuca glauca*, and it will not grow much more.



Nitrogen response – many plant species only grow more, with more nutrients, up to a certain point, beyond this there is no increase in growth .

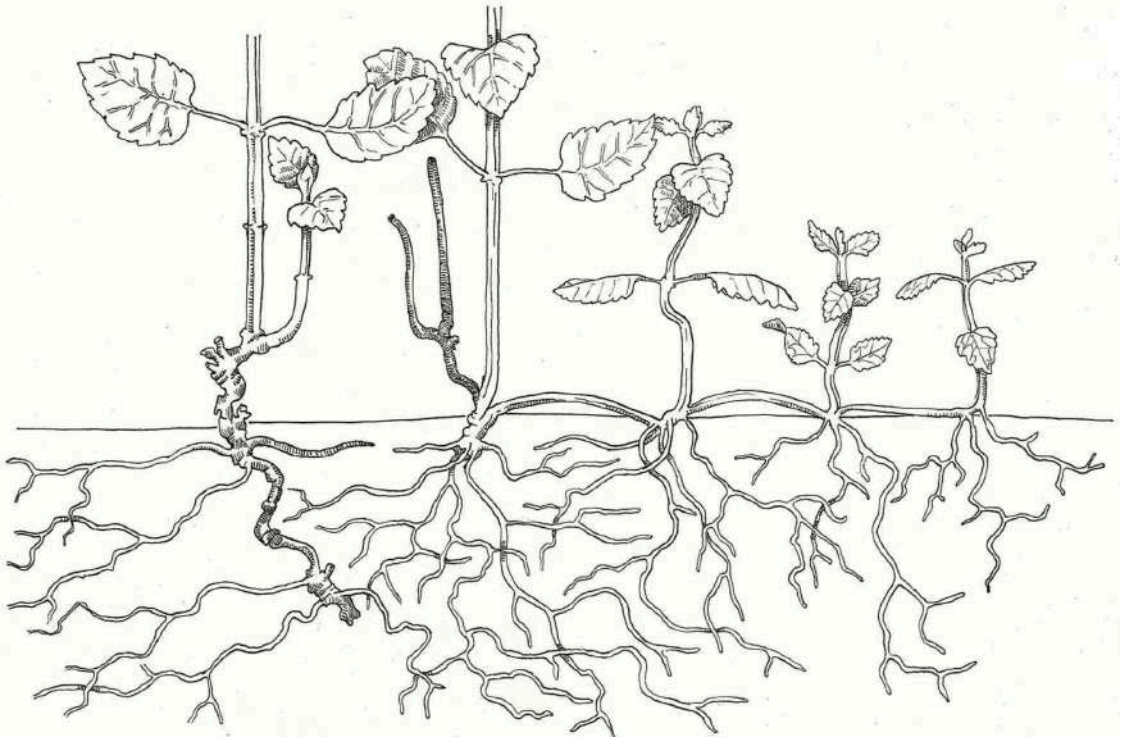
The more effectively a plant can use resources the more quickly it can grow. And the faster it can grow, the more effectively it can get bigger than other plants around it, enabling it to have better access to light, nutrients and moister than others. In a resource-rich environment, plants are all trying to grab what resources they can, in order to survive and overwhelm others. It is a fight! In very resource-rich environments, such as eutrophic (high nutrient) water bodies one species often dominates, e.g. reed, *Phragmites australis.* Such monocultures are rare in nature, and in this case are the result of one species being able to dominate at the expense of others as it is the one that is the most able to utilise resources.

Common high resource environments include wet meadows and river floodplains. Grasslands on neutral or calcareous rocks are often on soils rich in nutrients. In the mountains, tall-herb floras flourish in places where ground water rich in dissolved minerals flows underground. In all of these there is plenty of all three resources: light, nutrients and water.

Looking at the vegetation in these area we notice its lush, luxuriant quality. Leaves are bright green, packed with chlorophyll. Stems are tall. Many plants are actually quite soft and are easily pushed aside or trodden underfoot. Growth is very obviously rapid. In a resource rich environment it is more important to make some growth rather than none – so if leaves or stems are weak, sappy, or short-lived it does not matter too much as it is easy and quick to grow more. Most leaves are in any case, quite short-lived. Plant forms are dominated by the need to get to the light and by doing so, to dominate neighbouring plants – a plant in the light casts its neighbours into shadow. Not surprisingly many are tall. Others may try to dominate through having wide leaves that overshadow others at a lower level.

Inula species competing effectively with the notorious weed *Aegopodium podagraria*, Ebert Park, Ludwigshafen, Germany. The aegopodium spreads through rhizomes and adventitious shoots from its roots, but the Inula has large low-level leaves which overshadow it, and it grows considerably taller.

A key feature of many competitive perennials is that as well as trying to grow tall, they try to spread, to project themselves sideways. Rhizomes that can branch and clone the plant can deny space to competitors and enable the plant to exploit new resources – water and nutrients through the roots, light through the leaves. Some plants have **stolons**, above ground stems which root at their nodes, spreading the plant.



Galeobdolon luteum, sometimes grown as a garden plant but also invasive in North America – spreading through stolons, above ground. *Una Scherer*

Let's look at three extreme competitors to get an idea of how form follows environment.

- *Urtica dioica*, the familiar and much-hated Stinging Nettle, grows tall, up to 2m! if there is enough nitrogen and phosphorus in the soil. It spreads rapidly through a rhizome that sits just below the soil surface. It out-competes almost everything herbaceous.
- *Petasites japonicus* 'Giganteus'. Occasionally seen as an escape from once-grand gardens, the enormous leaves are clearly effective at stifling the growth of much beneath them, the rhizomes spreading it rapidly in damp ground.
- *Persicaria amplexicaulis*. A deservedly-popular garden plant, the approach of this competitor is more subtle; its rhizomes spread it quite slowly but its branching stems create an interlocking mesh of growth. Both combine to deny space to anything else.

Persicaria amplexicaulis, spreading through branching rhizomes and with a dense canopy of interlocking branching stems.

Geranium endressii, illustrating a long-lived branching rhizome. The oldest part (3 years) is on the right.

Lythrum salicaria, relatively late flowering as is often the case with species from resource-rich wetland habitats. This does not spread vegetatively however, but instead puts its energies into upright growth to get ahead of the competition.

By now it should be obvious that competitive perennials put a lot of their energy into vegetative growth. To produce flowers may be a waste of energy, and to do so before establishing a strong mass of growth a foolish commitment. Many competitors flower late, from late summer into autumn, as with North American prairie perennials and many species of wet habitats.

2.1 Perennials with guerrilla tendencies

Most of the perennials we grow tend to form clumps which expand outwards forming a steadily expanding circle. This is known as **phalanx** spread. Some however tend out new shoots from underground in a more unpredictable fashion, with odd shoots appearing some way from the parent plant. Conventional gardeners have usually been negative about this, as the plant seems to be making its own decisions as to where it wants to grow. A more positive way of looking at them is to see plants like this as potential gap-fillers; conventional horticulture with big gaps between plants is an open opportunity for them to spread rapidly, dense ecologically-based plantings offer fewer opportunities for them to spread into – competition keeps them confined.

Plants with this characteristic are essentially engaged in an insurance policy, not set on world domination. Many are species from unstable or rapidly-changing habitats, such as river banks or grassland-scrub combinations, and need to project new growth as far away from the parent as possible. Some of the most dramatic spreaders; *Euphorbia cyparissias* is an example, are not in fact spreading through rhizomes but through **adventitious shoots** from their roots.

In a dense planting these guerrilla spreaders can only occupy gaps, they are not a threat to other species, especially those that form strong clumps. However many practitioners do not like to plant these species at the same time as everything else but to introduce them at a later date, so that the bulk of the planting is fully established and their opportunities for spread are limited.

Two perennials with guerrilla tendencies: silver *Artemisia ludoviciana* and *Euphorbia cyparissias* (yellow flowers) forming an attractive interweaving with other perennials.

Euphorbia cyparissias has a tap root with emerging adventitious shoots (soboles) – 1, and lateral roots – 2, also with shoots.

Ajania pacifica – an example of a hybrid phalanx-guerrilla spreading strategy, a dense phalanx of rhizomes with a few outlying guerrillas (circled).

A more clearly guerrilla-spreading plant – rhizomatous *Euphorbia amygdaloides* var. *robbiae*.

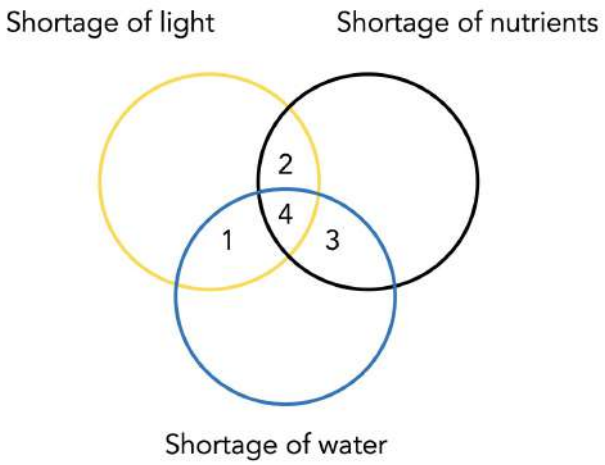
3. Stress-tolerant plants

Where resources are lacking, ecologists talk about stress. There are many different reasons for this and consequently an overview of stress-tolerant plants reveals a much more complicated picture. Plants in stressful environments are fundamentally concerned with gathering and conserving resources.

Whereas all high resource environments point to a single meeting point – high levels of everything, low resource environments offer many different possibilities. Stress, which is fundamentally about factors that limit the ability of plants to access nutrients, may be due to many different reasons. Soil chemistry for example may limit the access plants have to certain nutrients, as with very acidic or alkaline soils. Waterlogging may create difficult

Shortage of light, of nutrients and of water, all create their particular problems for plants, and in environments where this is the case, we will see different species and different plant communities grow.

Where shortages overlap, stress is accentuated, and the vegetation will be different again. Two sets of stress, as in 1,2,3, greatly limit the species which will thrive, while in 4, we have a combination of all three, the location which as any gardener knows, is the most difficult to find plants for. 1 – dry shade, is difficult enough.



Consequently there are many different categories of stress-tolerant plants. Many stress-tolerators are specialists, able to flourish only in very particular environments, usually ones which other plants could not cope with.

For our purposes two sets of full sunlight stressful environments which are worth looking at: very acidic soils and very alkaline ones. In the case of the latter, shallow soils over limestone which are also often dry.

The range of generalist – tending to competitive, perennials and ornamental grasses we grow do not flourish on very acidic soils. Plant selection here needs to work with a specialist selection, overwhelmingly sub-shrubs of the *Ericaceae* family, ferns, certain grasses and sedges (*Carex* spp.). The selection of European natives is limited and historically gardeners have looked to other floras, especially those of Asia, for additional species.

Whereas the line between an acidic garden flora and an 'average' one is quite distinct, it is less so with the potential ornamental flora of shallow calcareous soils, and indeed many typical species of this habitat are very good in 'ordinary' growing conditions. Europe's calcareous soils have a very rich and ornamental flora and consequently conditions created by alkaline building rubble which approximate to those of dry limestone meadows are not a challenge but an opportunity!

3.1 General characteristics of stress-tolerant plants

Despite what has just been said, there is a general convergence in the characteristics of plants from stressful environments. Common characteristics include:

- slow growth, resulting in small, dense plants, often low-growing,
- small leaf size, with various adaptations to reduce water loss, such as hairy or waxy leaf coatings, inrolled leaf margins,
- being evergreen helps to conserve resources – as dropping leaves in autumn risks loses those resources altogether.

3.2 Shade

Lack of light reduces the ability of plants to photosynthesise. Different plants respond to this in different ways. If the soil does not dry out in the summer and is reasonably fertile, most perennials do not suffer that much in some light shade, although there may be a problem with taller species leaning out towards the light. Grasses however are impacted much more severely. Most ornamental grasses need full sunlight. However the impact on turf and wild grasses can be turned to our advantage, since they are the major competitors of perennials in many situations. Woodland gardens where there is a wide variation in the levels of shade but always enough to suppress grasses can be very rewarding places to grow a wide range of woodland edge and shade-loving perennials. Inter-plant competition and weed growth are reduced and a high-diversity planting with little need for management is possible.

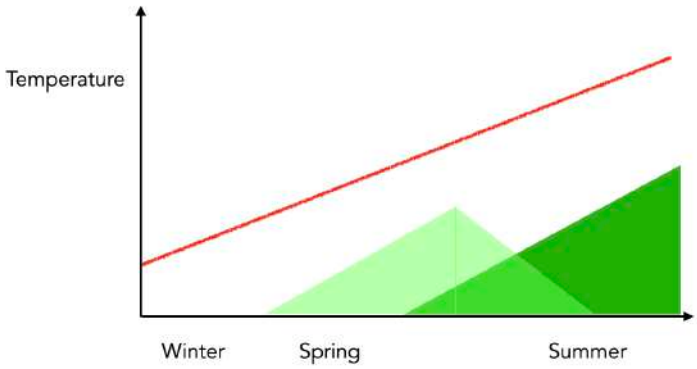
Moist shade, or at least where the soil does not dry out, can be a very rewarding environment, as there is a wide variety of high quality foliage plants which will thrive: *Hydrangea, Hosta, Polygonatum*, ferns. As the soil becomes drier, which is usually accompanied by a reduced level of available nutrients, the range of species reduces and becomes less luxuriant. Dry shade is the most problematic of all, as the range of species is particularly low, and dull dark evergreen foliage the norm.

Lush growth in shade with summer-long moisture: *Hosta* spp, *Anemone x hybrida*, *Aruncus dioicius* and *Polygonatum* spp. Sichtungsgarten Hermannshof.

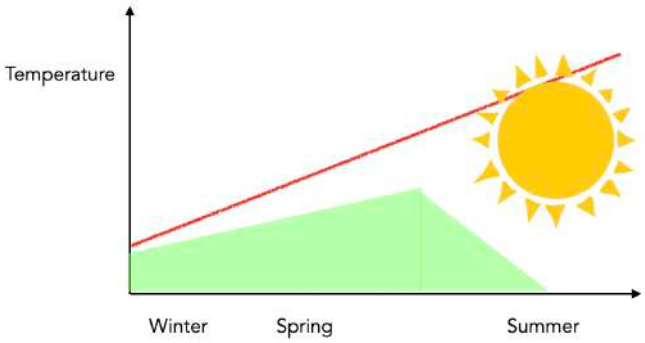
3.3 Stress-avoiders

So far, we have been talking about species that face up to stress, but there is another strategy, to avoid it. Stress-avoiders are those plants that behave as competitors when in active growth, but when hard times arrive, they retreat – generally underground and survive as specialised storage organs. Spring bulbs (and those classified as corms and tubers – collectively known as **geophytes**) survive winter underground, emerge in spring before the trees have their leaves and before most herbaceous perennial growth has started. They are able to grow rapidly at low temperatures and exploit a narrow window of opportunity to flower, seed and put away nutrients underground before decreasing light, and soil moisture and nutrient levels make life difficult.

'Bulbs', i.e. geophytes have long been popular with gardeners for their almost instant impact. For long-term planting design their great use is that they are able to create a second layer of planting – for spring, which takes advantage of the fact that they are at their maximum period of growth while perennials are just starting.



Bulbs and some early-season perennials exploit the window of opportunity between the cold and the growth of taller perennials and the development of a leaf canopy on woody plants. Light green = perennial growth; dark green = woody plants.



Stress avoidance is a common strategy for bulbs and perennials in Mediterranean climates where there is growth through the winter and a retreat into dormancy by mid-summer. Annuals do the same here, their 'dormancy' being the more total one of surviving as seeds.

4. Ruderals

Ruderals are pioneer plants, short-lived and temporary residents of wherever there is somewhere for their seed to germinate and grow. Some ruderals also have a competitive character too, some of these can be fearsome weeds, others like *Eschscholzia*, give us colour for months. Most are generalists, able to take advantage of the site conditions prevailing where they germinate.

As explained earlier, we are discussing not just annuals and biennials but short-lived perennials too. These latter are often valued as garden plants, but there is generally little understanding of their lifespans. Being short-lived, they have a biological imperative to produce seed in order to keep the species alive, so they tend to have showy flowers and often for longer than clonal perennials which do not have this same imperative to produce seed. Not surprisingly they are attractive and we tend to like to grow them. However they cannot be relied upon to be permanent elements of a planting.

As already noted the annual lifecyle is one ideally suited to Mediterranean climates where winter rainfall encourages growth, albeit at low temperatures, but summer heat and drought discourage growth. Survival as seed can be seen as another form of dormancy – emphasising a key point of the ruderal lifecycle, that the survival of genes is more important than that of individual plants.

4.1 Short-lived perennials

We have already noted the possibilities of short-lived plants. Perennials with a lifespan of three to five years can be a major component of a planting but only if they are able to regenerate from seed. Their capacity to do so varies enormously however, as it is very dependent on different soil and other environmental conditions; and species vary greatly in their responses to these conditions. Self-seeding then is unpredictable! The best we can do is to be aware of, and document, the behaviour of the plants we grow. The ideal perhaps is *Aquilegia vulgaris*, which in most gardens does reliably self-seed, but almost never to excess. It also illustrates an important characteristic of short-lived perennials – that they are uncompetitive. They have a narrow profile which enables them to fit in amongst other plants without overshadowing them, and they will not of course

sideways. Others such as *Knautia macedonica*, may have stems that sprawl sideways but only from a single location, and so have a limited capacity to compete.

Established plantings with a dense canopy of vegetation, the top layer of soil dominated by the crowns and rhizomes of long-lived perennials is not a good environment for shorter-lived perennials to spread their seed in, as seedlings will have little place in which to grow. Inevitably then, the role of short-lived perennials in such plantings is limited. If however existing plants die or are damaged, opportunities for their seedlings may arise.

Knautia macedonica, tap root and side shoots but without any sign of them developing their own root systems – so non-clonal.

A tight clump often indicate a non-clonal plant – all the growth coming from one central crown, and peeling back the outer foliage, no sign of any shoots rooting