An investigation into the performance of species in ecologically based ornamental herbaceous vegetation, with particular reference to competition in productive environments.

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7

AN ANALYSIS OF PLANT TRAITS AND CHARACTERISTICS – POSSIBILITIES FOR DEVELOPING A SYSTEM OF CATEGORISATION FOR HERBACEOUS PLANTS

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7.1 INTRODUCTION

Very little work has been done on systematically trying to classify herbaceous plants on the basis of their morphological and phenological characteristics. Raunkaier's (Griffiths 1992) classification of plants based on growth forms was a start, but there is no real clear boundary between his division of chamaephyte and hemicryptophyte, or between hemicryptophyte and cryptophyte or cryptophyte and geophyte – instead there is a gradient, running broadly between geophytes and chamaephytes. Klimes et al. (1997) developed a scheme for the classification of clonal plants – but this was based on an attempt to classify types of clonality rather than an attempt at creating categories based on the whole plant. Horticultural terms tend to be extremely vague, and even ecologists do not appear to have a defined set of terms.

The majority of herbaceous plants used in EBPS can be regarded as hemicryptophytes. Their morphology is clearly different, and a cursory examination will result in the recognition of several broad categories. This morphology can be regarded as important, and a meaningful, coherent and clear classification system for it potentially important for the following reasons:

- Morphology has a role to play in design aesthetics
- It often has a functional characteristics, e.g. plant suitability as ground cover
- It impacts on the development of effective horticultural management regimes
- It is often recognised that plant communities are composed of a number of distinct growth forms, or guilds (e.g. Goldberg and Werner 1993, Boutin and Keddy 1993, Keddy et al. 1998), the interaction of which contributes to community stability and diversity

Morphology is closely related to phenology, with a clear linkage between certain growth forms and period of active growth. It is the intention here to consider the two together as much as possible.

It is regarded as vitally important for the effective use of herbaceous plants, in both conventional horticulture and EBPS that a coherent system of categorisation be developed. This would have the effect of enabling practitioners to articulate more clearly plant specification for particular aesthetic and functional purposes. It is also vital for the attempt to predict plant competitive ability from morphology (and phenology).

7.1.1 AIMS

- To develop a series of categories which describe those morphological and phenological characteristics of herbaceous perennials which are relevant to horticultural management and planting design. Gradations in the categories to be recognisable to render them quantifiable.
- To clarify distinctions between characters which are genetically determined traits and characteristics which are the result of gene x environment interaction, and thus of growing conditions.
- To produce a system of categorising herbaceous plants based on morphology and phenology which would assist practitioners in horticulture and landscape design to select plants for visual effect, functionality and for the development of simple and coherent management regimes.
- To develop a categorisation system which relates primarily and clearly to identifying those characters of morphology and phenology which would appear to enhance competition.

7.2 SELECTION AND MEASUREMENT OF PLANT CHARACTERS

7.2.1 Traits and characteristics

Measuring traits which may be favourable to enhancing competitive ability, Boutin and Keddy (1993) undertook research to see how far it was possible to classify vegetation (in this case wetland) into 'guilds', or assemblages of species of similar functional type, using the measurement and analysis of plant traits, specifically those concerned with nutrient uptake, competition and reaction to disturbance or stress. Since different guilds occupy space and use resources differently, they allow (or to be more precise the reality which they describe allows) a multitude of species to share a given environment. Achieving and maintaining diversity in landscape plantings is one of the goals of EBPS, and hence the guild concept is one, which is potentially useful in this field. Boutin and Keddy suggest that a guild-based rather than a species-based approach might be useful in conservation biology, and a promising approach for predictive work.

Boutin and Keddy's research is based on screening for traits measured on pot-grown plants. This basic concept is adapted in this study, but applied to established plants in the open ground; with the emphasis is on the systematic collection and classification of observational data. As McIntyre et al. (1999) and Weiher (1999), note, the direct measurement of physiological traits is often impractical; instead they suggest the use of structural-functional traits, as advocated by Box (1996) - physical traits which represent underlying physiological traits. Weiher et al. (1999) agree, and address the issue of the 'need for a common language of plant traits', noting several problem areas, amongst these are several with which an attempt is made to tackle here, notably capacity for vegetative spread and plasticity. It is these structural-functional traits which are considered here.

One distinction needs to be stressed - between *traits*, i.e. genetically determined morphological and phenological features, and *characteristics*, i.e. features of plant growth which are the result of gene-environment (GE) interactions (Chahal & Gosal 2002). The former are of course genetically determined, the latter are not, but given that the species under consideration tend to perform well and consistently (in horticultural terms) in a wide range of environmental conditions, characters are considered which reflect traits.

A wide range of morphological and phenological characters can be seen as *representing* traits if they are seen as being *relative* to each other. All plants under study were grown in similar conditions, approximating to the optimum for the vast majority of herbaceous plants used in horticulture and in EBPS, so a comparison of characteristics has a validity, with the proviso that they are to be seen as relative to each other, and as typical of the taxon, in near-optimum horticultural conditions

Table 7.1 illustrates this relative relationship between characteristics (or gene x environment interaction) in different taxa when plants are grown in the same environment.

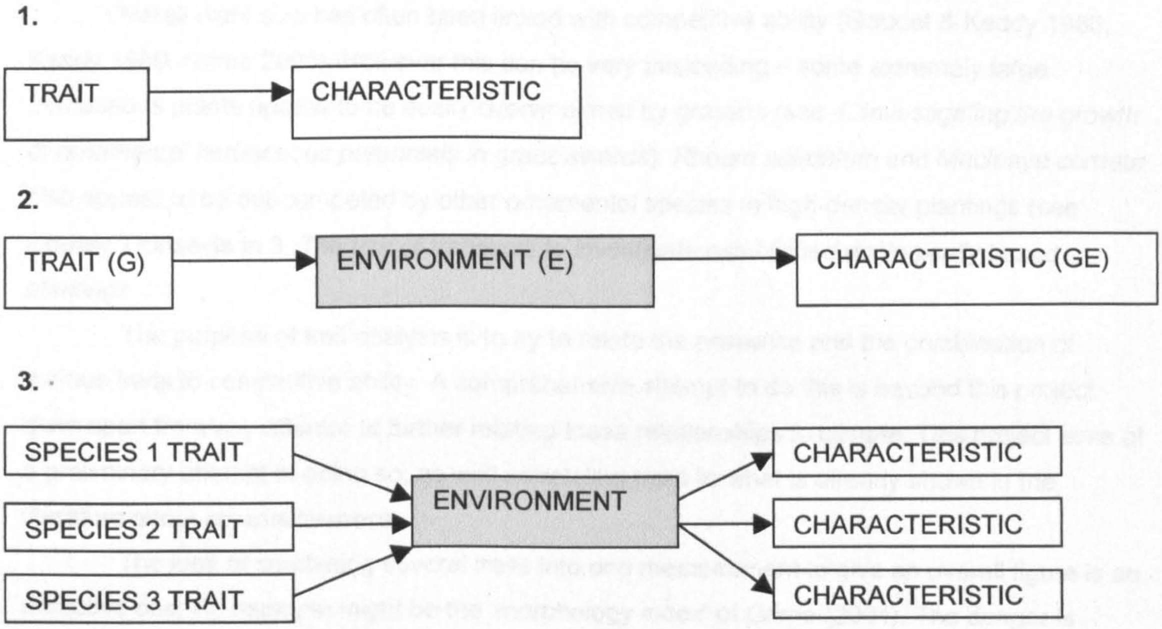


Fig.7.1

Traits and characteristics

Whilst characteristics are the results of the environment acting on genetic traits, they may or may reflect underlying traits to a greater or lesser degree.

1. In some cases, a characteristic may be measured which does not change, or changes only minimally, for the species in question from one environment to another, e.g. specific leaf area, or dry matter content. These are almost entirely characteristics which measure physiologically processes. Their measurement is also generally too involved for practitioners to concern themselves with.
2. A morphological characteristic is generally too much the result of environment acting on genetic traits for it to be used to accurately measure traits.
3. However, within the parameters of similar growing conditions, environment will act equally on traits, so resulting characteristics will be relative to each other, and therefore enable comparisons between species to be made.

Traits, or characteristics, chosen need to be comparable across all species under study. Choosing such traits can be difficult because of the problems in choosing structures, which can be meaningfully compared. The emphasis here is very much on choosing traits which can be measured across a wide range of species. In some cases, only one or two species under study may exhibit a particular trait – this however may itself be significant, see 7.2.2 *Choosing species to measure*. That only a very limited number of species may show a particular trait in itself suggests that that particular trait reduces the aesthetic or practical value of a species for EBPS.

Overall plant size has often been linked with competitive ability (Gaudet & Keddy 1988, Keddy 1989, Grime 2001). However this can be very misleading – some extremely large herbaceous plants appear to be easily overwhelmed by grasses (see *4. Investigating the growth of ornamental herbaceous perennials in grass swards*). *Rheum palmatum* and *Macleaya cordata* also appear to be out-competed by other ornamental species in high-density plantings (see Cowley Transects in 3. *The use of transects to investigate established ecologically based plantings*

The purpose of trait analysis is to try to relate the presence and the combination of various traits to competitive ability. A comprehensive attempt to do this is beyond this project, quite apart from any attempt at further relating these relationships to climate. This project aims at a preliminary attempt at doing so, as well as relating traits to what is already shown in the literature about competitiveness.

The idea of combining several traits into one measurement to give an overall figure is an attractive one. An example might be the 'morphology index' of Grime (2001). The danger is though of considerable oversimplification - this example does not distinguish between the spread of the clump as a whole and that of the foliage. It may be possible to produce such an index, but it should arguably be 'richer' i.e. draws upon a wider range of characteristics, and with a clear indication as to what a combination of these characteristics actually means or indicates.

A number of traits have been considered by other workers, but were here rejected: individual weights, shoot weights, lifespan, specific leaf area.

1) Individual weights

In determining which traits can be measured for comparison purposes, it is undeniably difficult to find some, which can meaningfully be compared. Comparing the dry weights of individuals is one obvious route, but is rejected; the first problem is with defining the individual. Weiher et al. regard the fundamental unit as the ramet, but recognise that there is a problem with tussock-forming graminoids, where the tussock acts as a functional unit in terms of spatial occupation (Weiher et al. 1999Trials which measure plants grown from seed at least have the virtue that they are measuring what can undeniably be called individuals. However, since herbaceous species vary considerably in the speed with which they develop from seed, it cannot be said that a trial conducted with plants anything less than three years old is measuring like with like. This particularly affects slow-developing species like *Baptisia australis* or *Helleborus x hybridus.*

2) Shoot weights

The problems presented in defining individuals also arise in defining individual shoots or ramets. Some herbaceous species are clearly clonal, i.e. each visible shoot could become an individual plant, and a good proportion do in the course of 'normal' events in the wild or the garden, whereas others are much more tightly bound, and generally do not separate from the parent, although they can be by the nurseryman practising division, e.g. *Knautia macedonica*. Furthermore, with many clonal species, a considerable number of shoots are produced, so that for much of the growing season there is a multiplicity of shoot sizes. Some will develop into new and separate plants, others will not, in particular there may differences in how they react to the environment (Watson et al. 1997) and in some cases, where shoot production is particularly high (e.g. *Persicaria bistorta* and *Phlomis russeliana*) it is possible that many of these shoots could be described as 'insurance policy' ramets; they are there to allow the plant to regenerate after a destructive event such as grazing. In other words there is no clear equivalence between these shoots. It is noted that apical and axilliary meristems, for example, may behave differently in different conditions, the latter tending to be more sensitive to good growing conditions, and to be highly responsive to local conditions (Watson et al. 1997).

Whilst the concept of measuring shoot weights of all species considered is rejected, its potential for making comparisons within sub-groups is recognised, in particular those species which develop upright flower-bearing stems, where there is no disputing the equivalence of these structures.

3) Assessing life span

Weiher et al. (1999) discuss the difficulty of describing the lifespan of clonal perennials which are effectively immortal and suggest the simple annual/biennial/perennial categories.This however repeats the inaccuracy in describing lifespan found in horticultural literature, where no distinction is made between short-lived perennials (generally ruderals), those which do not spread clonally, but which are relatively long-lived, and clonal spreaders. Hansen and Stahl (1993) at least discuss longevity although they do not relate it to plant lifestyle and do not offer any systematic listings, only examples.

Because of the lack of systematic data covering the species under discussion, mention is made of lifespan only if it known to be particularly short. The vast majority of species considered are potentially very long-lived perennials, given suitable circumstances (i.e., space to expand and a lack of competition) most could live more or less indefinitely. Where lifespan is short, but the plants are not biennial or monocarpic, it is observed that ramet formation either never happens or integration with the parent is so total that ramet lifespan is limited too; individual plants are seen to have a definite lifespan, becoming senescent and dying – *Tanacetum parthenium* being an example. There is a possible category of species which appear to be long lived (for at least five years) but which do not form clear ramets, e.g. *Aquilegia vulgaris, Salvia nemorosa*). It is not known, and no data is known to exist, on just how long-lived these species are.

4) Specific Leaf Area (SLA)

SLA is described by McIntyre et al. (1999), as being a 'core trait', correlated with leaf life-span, photosynthetic capacity and leaf N content, Weiher et al. (1999) note its relationship to growth rate, and a flexible response to spatially patchy resource availability.

Van der Werf et al. (1998), in a study of changes in floral diversity on agricultural land, found that differences in growth rate are mainly accounted for by differences in leaf area ratio, through differences in SLA, with species from fertile soils having higher SLA. Poorter and Remkes (1990) found in a study comparing fast- and slow-growing species, that there was a high correlation between SLA and growth rate. Weiher et al. (1999) found that species with high SLA could respond readily and flexibly to spatial irregularly distributed resources.

SLA data was a by-product of the CSR analysis, and is considered for those species where a CSR ordination was carried out. Its measurement however requires a procedure which many practitioners would regard as too involved, so in the spirit of developing methodologies as 'practitioner -friendly' as possible was not developed more extensively.

7.2.2 Choosing species to measures

Species exhibiting a wide range of different morphologies and phenologies were chosen, concentrating on those which are important in the author's work with EBPS, with a strong and definite bias towards those which are generally grown in the environment most important in public EBPS – full sun, relatively high fertility, and mesic. A number of genera particularly important for EBPS were selected for the measurement of traits across several species. Most of the species included are well established in cultivation, mostly non-native; also included were a small number of species new to cultivation, but which show potential for use in EBPS A particular limitation has been on the choice of species of North American or Eurasian origin. The vast majority of ornamental herbaceous perennials are from these regions. Southern hemisphere species were excluded from the monthly measurements partly because they have such a low role to play in EBPS – this in itself is perhaps partly due to issues of 'visual ecology', i.e., visual inappropriateness in some of the locales where EBPS is used (Kingsbury 2006). Two, a crocosmia and a kniphofia, were however included in the *Perennial Data Table* (7 Appendix.1).

The range of traits shown by the species chosen may be considerably different to the range exhibited by perennial species in general, or indeed from that of cultivated perennials in general.

7.2.3 Choosing individuals for study

Weiher et al. (1999) suggest that 'well-grown' individuals should be chosen for study . The vast majority of those looked at were the same individuals selected for the CSR ordination (see 2. *The CSR model of plant functional types)*. In most cases these were growing in conditions and at densities that allowed them to develop in a way, which can be regarded as typical for EBPS, i.e. at higher densities than would be normal in botanical or domestic gardens, but still at much lower densities than would be found in nature. Given that all plants, with many herbaceous plants in particular, exhibit considerable plasticity in their growth, measurements of morphology were made of plants which were growing in situations were optimal growth was to be expected, and which were not unduly hemmed in by neighbours.

Specimens were selected which were known, from several years of experience of cultivation to be average. In most cases some three separate clumps of each species could be examined.

7.2.4 Traits and characteristics assessed from data collection

The decision was taken to measure a number of traits and characteristics monthly during the growing season (March to September), with a limited number of further measurements during the rest of the year – during which a minority of the species studied where showing some signs of growth or photosynthetic activity, and a number of one-off measurements. The traits and characteristics measured are discussed here. Details of the measurements are given in the following methodology section.

A number of workers have found that the intuitive notion that plant size is related to competition, (Gaudet & Keddy 1988, Keddy 1989) to be supported by evidence. Size is related however to a number of measures, of which total mass gives the clearest all-round indication, and is clearly linked to competitive ability (Gaudet & Keddy 1988, Keddy et. al. 2002). The two basic dimensions of canopy height and lateral spread are the easiest to measure, and which both relate to the physical occupation of space by a plant. Lateral spread is effectively made up of two morphologically different and separate groups of traits: 1) leaf spread – which enhances the ability to capture light and to shade competitors, and (more properly characteristic) 2) ramet spread, which controls the size of the clump. One study, of wetland species, however showed that competitive ability is not necessarily strongly linked to canopy diameter or area (Gaudet & Keddy 1988); 63% of competitive ability could be explained by plant biomass, and the remainder by plant height, canopy diameter and area, and leaf shape.

In addition to measures related to plant size discussed in greater detail below, other aspects of foliage morphology, characteristics of phenology, and ramet morphology and production were also measured.

7.2.4.1 Phenological characteristics

Commencement of growth at the beginning of the year is taken as a key variable, as it is the beginning of the annual process whereby a plant begins to compete during the growing season. Grime (2001)has shown how early emergence in high-resource environments enables species to establish dominance early, but *only* if this trait is combined with large size – small vernal and evergreens species may be suppressed; he also shows how species with late emergence can also establish dominance – through an alternative strategy – litter accumulation. This is measured by **Time of emergence.**

Leaves covering the ground during winter can be expected to play some role in competition: reducing light for emergent seedlings or ramets which may emerge in species able to grow at lower temperatures. True evergreens are generally more 'efficient' at using resources than non-evergreens, but amongst hemicryptophytes are limited to woodland habitats (Aerts 1995). Hemicryptophytes in maritime climates vary enormously in their response to winter light and temperature. True evergreens are generally species with a low growth rate and stress-tolerant character (Grime 2001), and not generally competitive; however there are also species which are able to photosynthesise and grow at low temperatures and light levels - many of the key elements in British grass communities are able to do this, (Rodwell 1992) and not surprisingly not only dominate such communities but also frequently appear as weeds in horticultural situations. Ornamental species in EBPS may reasonably be expected to compete better if they too are able to grow at low temperatures. Conversely they may be expected not to compete effectively if they start to grow when species around them are already in active growth. The presence of winter foliage and a characterisation of the differences between true and opportunist evergreen character is measured by **Wintergreen character.**

Considerable variation can be observed in the morphology of shoots as they emerge; this is recorded, as it can possibly be related to climate regime and to the ability of a species to compete with other plants emerging at the same time, or which have emerged previously. Grime 2001 links emergent shoot morphology to the ability to penetrate, or to be unable to penetrate, accumulated leaf litter. Shoot morphology is measured by **Character of emerging shoots.** Ability to produce growth after the main season of spring growth illustrates a potential ability to continue to compete during the growing season through plasticity of growth (Grime 1994, 2001) and in particular for clonal species to occupy new territory during periods when active growth is possible (Luken 1990, Hutchings 1997). This is measured by **Later-season basal growth.**

Some species have the ability to produce new growth either after flowering, or to continue to produce branching tip growth, with or without flowers, recorded as **Later-season tip growth.** On the other hand, early dormancy effectively means that a plant is leaving the struggle for supremacy earlier than potential competitors. This may be a key part of an 'avoidance strategy' enabling it to co-exist with more effective competitors, an example of 'niche diversity (Hutchings

1997). Data is recorded as **Time of Dormancy.** Persistent litter creates an aureole around a plant, which reduces the ability of competitors to penetrate close to the plant base (Grime 2001). A detailed measurement of litter accumulation (as in the morphology index of Grime 2001) was rejected, owing to problems in making accurate measurements of the litter accumulation of the majority of subject species, due to the relatively crowded conditions in which they are grown. In any case the litter of the vast majority of ornamental herbaceous plants decays quickly and is not likely to affect competition with neighbours. A basic qualitative measurement of litter persistence is included as **Persistent litter.**

Starting time of flowering is not a characteristic which can be directly related to competition; nevertheless it is included as it may throw some light on habitat-competition relationships, or linkages between nature of competitive ability and region of origin.

7.2.4.2 Foliage Morphology

Givnish (1982), Gaudet and Keddy (1988), Grime (2001) all give evidence that increased height enables a plant to establish dominance and enhances its competitive ability. Canopy height is an obvious and easy character to measure. Maximum vegetative (i.e., canopy) height is the most widely recognised, and is regarded as the most effective measure of plant height; more so than maximum height, as many species produces tall inflorescences, whose height does not reflect photosynthetic ability or ability to suppress neighbours. This is supported by Rösch et al. (1997) who found that maximum vegetative height x maximum diameter was a better indicator of competitive effect than maximum total height x maximum diameter. Data is recorded by Canopy height.

Foliage size and character can be expected to have a major impact on competition. Gaudet & Keddy (1988) suggest that there is only a weak correlation between leaf length and competitive ability. However the study in question was of wetland vegetation which included several species vertically held linear foliage, a foliage type not found much amongst ornamental forbs. Consequently a measure termed **Leaf Stretch** is used to record how effectively a leaf projects shade onto the area beneath it. Gaudet & Keddy (1988) found that leaf shape, as measured by length: width provided some explanation for competitive ability, with wider leaves conferring competitive ability. Keddy et al. (2002) found that such leaves were advantageous where competitive performance was important, but that longer and narrow foliage was more advantageous in stressed environments. **Leaf shape** is the measure used here .

Plant architecture presents a complex and varied set of characteristics, which are difficult to simplify, but which at first sight appear to be correlated with habitat, and therefore possibly to effective competition within that habitat. Givnish (1987) notes a strong relationship between phenology and leaf/stem relations, in particular the link between an 'umbrella' leaf shape with extensive petiole support to reduce self-shading, characteristic of earlier-emerging species of partly-shaded habitats and upright-growing species with small, expendable, leaves on species which reach maximum height in late summer – typical of open, high-resource habitats. **Leaf/stem relationship** is a measure used here in any attempt to categorise plant architecture through a classification of a key indicator.

Certain monocot species, which are noted competitors, have a notably different leaf orientation to other herbaceous species. Lauenroth and Aguilera (1998) note the disadvantage of grasses with vertically oriented leaves – these are easily shaded. However it must be assumed that they maximise photosynthetic area at height, especially if height can be maintained above competitors early in the growing season. **Leaf orientation** records orientation.

In semi-natural meadow conditions, some species, e.g. *Geranium phaeum, Alchemilla mollis* can be observed with growth which is intermingled with, and partly supported by, neighbouring species; in garden conditions where competition is reduced, more extensive growth can be observed to collapse after flowering, resulting in shading or physically suppressing competition. **Angle of flower-bearing stems** is used here to record this characteristic. Characteristic of some species are ramets which may grow into one of two distinct mature forms, one with a flowering stem and the other without – as distinct from those species where every ramet produced in spring produces flowers. The former are defined as **Bimorphic shoots**.

Some data collected was consolidated or processed. One result was a measure of **Growth rate,** is widely accepted as being a trait that contributes to competitive ability (Grime 2001) – it can of course proceed in any direction. Lateral growth rate is indirectly measured by, and in effect subsumed by the measure of basal cover, discussed above. Growth rate expressed upwards is widely understood to be a measure of how effectively a plant can intercept light and prevent others from doing so. It is however, by no means an important factor in all environments – Rösch et al. (1997), did not find it significant in their study of dry habitat species. Grime (2001) discusses growth rate as contributing to morphological plasticity and therefore the ability to maximise light interception.

7.2.4.3 Basal cover – developing a combined measure of shading (GC+SE)

Experience with growing ornamental forbs in a grass sward (see 4. *Investigating the growth of ornamental herbaceous perennials in grass sward*) strongly suggests that degree of basal cover is a characteristic fundamentally linked to effective competition. Unlike height this is not so straightforward to measure. Grime (2001) and (Coomes & Grubb 2000) does however point out that effective shading beneath a plant does not necessarily indicate that this is the dominant factor in competition, or in achieving dominance over neighbours, as dense canopies often co-incide with extensive root systems able to effectively extract moisture and nutrients from a wide area.

However the level of basal cover is highly dependent on a number of factors, not only the local availability of light, nutrient and moisture which is also going to affect overall size and height, but also the presence and density of neighbours. Growing plants in isolation would enable the maximum basal cover to be observed, and completely eliminate 'neighbour effect' – this however would require more than a year to establish and considerable space. The decision to opt for the study of established plants growing in existing plantings was taken in order to maximise the number of species. However, the crucial phase in basal cover is early in the growing season as plants are establishing their zones of control and resource exploitation, when inter-plant contact is minimal.

Given the importance of neighbour effect as plants develop through the growing season, measures of basal cover cannot be treated as simple gene x environment (GE), but GE plus neighbour influence. The use of measures of basal cover cannot then be regarded as characters which indicate underlying traits as with other aspects of plant growth being discussed here. Instead they will be treated as characteristics, which are dependent, possibly highly dependent, on context. Leaf shape, size (measured here as degree of 'leaf stretch') and leaf-stem architecture are more likely to be indicative of underlying traits conducive to an *intrinsic* ability to suppress neighbours than simply measuring basal cover, quite probably in conjunction with other characters such as overall size and/or height. Discussion of the impact of basal cover on competitive ability will be treated here as being heavily contextualised by the fact of cultivation in a southwest British climate zone, and in relatively dense horticultural plantings.

Accurate measurement of basal cover is difficult, and time-consuming. There seems to be no generally accepted standard of measuring basal cover; there is also no obvious clear-cut characteristic to measure, as is the case with height. The calculation of canopy area by measuring the standard area for an ellipse (Keddy et al. 2002) is rejected as too time-consuming. Greig-Smith (1983) proposes two measures:

Cover - the proportion of the ground defined by a perpendicular projection on to it of aerial parts of the plant,

Basal area – proportion of ground surface occupied by a plant.

Rather than take a small number of accurate measurements, a larger number of easily taken measurements, based on a visual assessment, are taken which together give an idea of a plant's occupation of surface area.

. Here, *basal cover* will be used to describe the effective coverage a plant manages to achieve over the ground around it. Basal cover can, and usually does, vary considerably through the season. Measurements were taken throughout the growing season to qualitatively assess the amount of cover, but concentrating on traits which create significant areas of shade around the subject. The view is taken that the shading effect created by the foliage of most species being looked at is not particularly significant, compared to a limited number of species with a very clearly effective shading ability. Basal cover is measured from April to July, the period of maximum growth, when the ability to shade ground can be assumed to be the most important, because this is the period in which weedy competitor vegetation is growing most strongly in border/EBPS situations in the UK and when competition between species in planting schemes is most intense.

Two aspects of basal cover will be considered here:

1. **Ground Coverage (GC)**.

The effectiveness with which a plant is able to create shade over its basal clump. - which could be seen as playing an important role in competitive response, as the more effective the surface was covered the less likely it was that a competitor could infiltrate or overshadow the plant base. This is based on Greig-Smith (1983) who uses the term *basal area*.

2. **Shading Effectiveness (SE)**.

The ability to project foliage beyond the circumference of the plant's basal clump and so create project a shaded zone outwards. This is similar to *cover* in Greig-Smith (1983).

Total annual GC+SE.

By the addition of GC and SE it is possible to arrive at a measure of how effectively a plant creates shade both around and above its core. A cumulative total of monthly measurements is a way of combining a measurement of growth and effective coverage since the beginning of the growing season. Since the growing season in the maritime British climate begins very early, there is a very noticeable differential response to this by plant species (particularly by non-native ones). A cumulative figure from the beginning of the growing season up to a particular month would represent its dominance of space up to that time; a cumulative figure to the end of the growing season would represent its dominance of space through the whole growing season. This latter will be referred to as **total annual GC+SE**, abbreviated to **GC+SE**.

In addition, the extent to which the lowest leaves were very close (within 50mm) of the soil surface was measured, a trait which could effectively suppress at least seedling competition around the subject (Presence of bulk of leaf lamina of lowest leaves within 5cms of soil surface).

7.2.4.4 Nature of ramets/spreading ability

Weiher et al. (1999) consider that there is no simple measure of clonality (Weiher et al.1999). Boutin & Keddy (1993) note that within their analysis of plant guilds, there is a clear distinction between clonally-spreading species and those which only form discrete clumps. They found that clonal species had a massive belowground structure, a consequently a high below- to above-ground ratio, whereas non-clonal species had a more shallow and smaller belowground structure. This study was however based on wetland species, and it cannot necessarily be expected that this generalisation be extended to other environments. Klimes et al. (1997)have produced a system of categorisation of clonality, but their categories are based on major distinctions of morphology; an analysis of how clonality operates within plant communities would require a categorisation and analysis of the phenomenon which provided a more detailed level distinction between characteristics.

A clonal plant is defined by Van Groenendael et al. (1987) as being a plant 'capable of naturally producing potentially independent offspring by means of vegetative growth', each potentially independent unit being a ramet. However as noted above (7.2.1 *Traits and characteristics*) there is a grey area. It is proposed here, that as far as possible, the key distinction is made between naturally splitting away to form new *independent* plants and not doing so, i.e. clonal and non-clonal. Species that form shoots from a central rootstock, which do not appear to form separate new plants will not be regarded as clonal.

It is argued that any meaningful categorisation of clump size needs to take into account the long-term development of clumps, in particular whether they have the capacity to continually expand, potentially *ad infinitum*. It is important to distinguish between species which have large clumps simply because they are large plants, but which do not appear to continually expand, e.g. *Cephalaria gigantea*, and those with much smaller clumps after a similar number of years, but which have the capacity to form continually expanding mats of growth, such as *Liriope muscari*. There appears to be a trade-off in clonal hemicryptophytes between the ability to spread (involving longer and more frequently produced ramets) and the ability to occupy a smaller space over a long period of time (shorter ramets, closely integrated, and considerable diversion of resources to roots), (Schmid & Bazzaz 1987); this could be interpreted as a competitive-ruderal as opposed to a competitive-stress tolerator division (Grime 2001).

The reality is that it is very hard to draw hard and fast conclusions about eventual capacity for spread, partly because in the case of species which form clumps slowly, specimens may not have been in place long enough without disturbance to be able to assess whether this is the case. Plants in gardens are in effect constantly disturbed by a variety of horticultural operations or by 're-design' of plantings every few years. In addition record-keeping is almost never detailed enough over a long period to be useful. In the wild, plants are growing so densely that capacity to spread is limited and very difficult to evaluate.

Further distinctions are based on how effectively a plant spreads its ramets, basically a question of measuring distances between ramets, the pattern of spread, and the rate. Rate is difficult to measure meaningfully for a variety of reasons:

i) Rate of production appears to vary considerably with growing conditions. Experience suggests that it increases with increasing soil fertility. Neighbour competition may considerably reduce rate.

ii) There is often considerable ambiguity over what a meaningful ramet is - see above. Many species with a high rate of production appear to produce many shoots, but of which only some develop fully, the rest staying very small, and possibly present as an insurance policy to allow rapid recovery if fully developed shoots are damaged. This is an area in which further research is needed, with mapping of ramets over several years.

iii) Ramet production may in some cases appears to be linked to plant age. Salisbury suggests that length of ramets is (Salisbury 1929).

iv) A meaningful study of ramet production would involve the assessment of multiple plants, which could be very time-consuming.

It is possible that many species have small resting buds or areas of tissue, which can form ramets. The number or quantity of such material is not at all easy to assess – the result is that it is never certain how many ramets there are when a test subject is planted.

Schmid 1985, Schmid and Harper 1985 describe species with a guerrilla habit as aggressive at low densities of neighbouring plants but liable to be suppressed at higher, and visa versa for phalanx species. In most EBPS, with the development of a closed vegetation canopy over time, it might therefore be expected that guerrilla species would be reduced. Here an attempt is made to develop a more nuanced version of the guerrilla/phalanx model with the measure **Pattern of Spread.**

Alpert and Stuefer (1997) considers that the ecological significance of clonality is most evident when the spacing between ramets is greater than the diameter of the ramets i.e. when wide vegetative spread becomes a possibility. This is measured here by **Distance between Ramets. Rate of ramet or shoot production, approximate number after 3 years** is a measure which may be expected to vary between different locations, with nutrient, moisture and light levels playing a part in influencing this variation. It may itself be a measure of how much competition a plant is receiving. Of all the traits recorded here, it is possibly the least accurate, and is an area where further research under controlled conditions over several years would be very valuable.

Clonal species vary in the degree to which material persists in the same location from one year to another. A tendency or previous year's ramets to die out could be expected to weaken competitive ability by providing an opening for competitor seedlings or ramets - Grime (2001) describes such behaviour as 'ruderal perennial'. This is recorded as **Persistence of living basal material.**

Measurements were taken of established plant clumps, to measure total spread, clearly a good way of assessing competitive effect, and recorded as **Size of clump after five years.** Clump size can vary considerably depending on a wide range of factors and the measurement of a limited number of clumps in one location can only be expected to give an idea of average spread for a very particular set of conditions.

7.3 METHODOLOGY

7.3.1 Outline

Some 96 spp. were measured from December 2004 to September 2005 (leaving out January), with a variety of plant characteristics being evaluated. Additional data was collected from one-off evaluations. Measurements of height and tendencies towards lateral shading were also consolidated to produce measurements of growth rate and accumulated basal cover.

Much of this data was summarised and used to assemble the *Perennial data table* (7. Appendix 1), which included a small number of additional species which were not measured monthly, bringing the total to 108. This table is regarded as the main summary of data collected during this part of the study.

7.3.2 Monthly measurements

The monthly data measurements collected are shown in *Characters measured monthly table* (7. Appendix 2). Those shown in light grey were given a simple yes (=1) or no (=0), those in dark grey were given a category on an ascending scale, those unshaded were measured in mm. and then grouped into categories on an ascending scale.

The detailed data collected is given in *Monthly data* (7.Appendix 3). Each month for which data was collected is in an Excel file and explanatory notes of the nature of the data collected in an accompanying Word document.

7.3.2.1 Measurements of basal cover

A key set of data concerns details of the GC and SE measurements used to assess basal cover. They are outlined here, followed by a discussion of how they were consolidated.

Ground coverage by growth (GC) - approx. % of ground covered by current season's growth (and last year's if evergreen) within the limit of the area covered by the clump, as estimated by a visual inspection from directly above. In the case of species whose ramets split off to form separate clumps, density is understand as being that of each sub-clump.

This assessment was carried out from March to July (see above).

1 - <10%
2 - 10-25%
3 - 25-50%
4 - 50-75%
5 - 75-100%

Shading effectiveness (SE)

Data was collected as **Shade zone,** but then summarised as **Shading effectiveness**.

Shade zone was defined as an area around base of clump which is completely overshadowed by foliage growth of subject:

0 – coverage absent

1 - coverage complete but by narrow linear foliage, liable to be blown to one side by wind, or very partial through pinnate, or very deeply toothed foliage or by sparse larger leaf cover, or by relatively sparse procumbent stems.

2 – coverage complete at a height less than 15cms above ground level by foliage angled upwards, so light can penetrate sideways

3 – coverage complete by foliage which tends to arch over, frequently touching the ground at the tips, so creating effective overshadowing

These measures are given for three concentric zones around the crown of the plant:

0-100mm
100-200mm
200-300mm

This measure is designed to highlight those species which can be seen to clearly form an 'exclusion zone' for possible competitors around their base. Effectively excluded are species, which have:

- Large leaves distributed discontinuously around the base of the plant
- Leaves which are angled upwards so that light can penetrate to the area around the base of the plant

This assessment was carried out from March to July.

The shade zone data was then simplified to produce the **Shading effectiveness** measure so that for each month where measurements are taken:

0 – shading absent or not particularly pronounced

1 – effective shading to 100mm beyond base of plant (as 3 above) or less effective (as 2 above) to 200mm or beyond.

2 - effective shading to 200mm beyond base of plant (as 3 above) or less effective (as 2 above) to 300mm or beyond.

3 - effective shading to 300mm beyond base of plant (as 3 above)

4 - effective shading to beyond 300mm beyond base of plant (as 3 above)

The values for basal cover discussed above for each month can be totalled, to give a cumulative annual total, or totalled to give a cumulative total up to each month.

Measures of basal cover

Measurements of basal cover are summarised in *Degree of Basal Cover* (7. Appendix 5). This illustrates the following:

Ground coverage (GC) cumulative total to July
Shading effectiveness (SE) - cumulative total to July
Sum of GC and SE in April
Cumulative GC + SE to June
Leaf proximity to soil surface - annual total
Sum of ground coverage and shading effectiveness to July (GC + SE)
Distance '/' ramets + Canopy Height
Distance '/' ramets + canopy height + (GC+SE)
Sum of GC and SE and Spread after 5 yrs

ESTIMATED COMPETITIVE ABILITY (ECA) (SEE 8. ASSOCIATING PLANT CHARACTERISTICS AND TRAITS...WITH COMPETITION...).

7.3.2.2 Growth rate and height

A number of treatments of growth rate and height are made and detailed in *Height Summaries*, (7.Appendix 4):

1. **Rate of growth in height, derived from monthly max. height measurements:**
    a. **from March to June**
    b. **from March to September**

Herbaceous canopy in terms of ground coverage is largely complete by June in the British climate, so a. is probably a more realistic measure of competitive ability. Measurement of b. would highlight tall growing, largely prairie species but not necessarily competitive in t 4erms of ability to dominate ground.

The above two growth rates are summarised as follows:

0 = minus growth to 0, minus growth can refer to any of the following:

- loss of canopy height through senescence of canopy foliage borne on short-lived flowering stems, e.g. *Brunnera macrophylla*
- Collapse of stems, or at least the lower part, *e.g. Centaurea montana*
- Early dormancy, e.g. Papaver *orientale*

1 = 1 – 49 mm
2 = 50- 99 mm
3 = 100- 199 mm
4 = 200- 299 mm
5 = 300 – 399 mm
6 = >399 mm

2. Number of months taken to maximum height, starting from March

This is arguably a better measure than either the above as it establishes an overall figure for rate of growth.

3. Number of month's height is maintained at least 75% of maximum

This can be seen as a measure of the ability of a plant to dominate space during the growing season.

7.4 RESULTS - THE PERENNIAL DATA TABLE

(7.6.1 Appendix 1)

This summarises both consolidated monthly data and data from the once-only measurements:

Summary:

a. Phenological
 - Time of emergence
 - Nature of wintergreen character
 - Character of emerging shoots
 - Time of dormancy
 - Presence of later season basal growth
 - Presence of later season tip growth
 - Persistent leaf litter thatch around plant
 - Start time of flowering

b. Foliage morphology
 - Canopy height
 - Leaf stretch
 - Leaf shape, *see below*
 - Leaf/stem relationship
 - Bimorphic shoot production, *see below*
 - Angle of flower-bearing stems

c. nature of ramets/spreading ability
 - Pattern of Spread
 - Distance between ramets
 - Rate of ramet or shoot production,
 - Persistence of living basal material
 - Size of clump after 5 years

7.4.1 Detail of contents of Perennial Data Chart

a. phenological characteristics

Time of emergence

Strong growth emerging in:

1 – effectively evergreen

2 - February

3 – March

4 – April

5 – May

6 - June

Wintergreen character

0 – always dormant during winter

1 – some basal shoots produced during autumn may over winter in mild winters

2 – leaves generally alive in winter, but deteriorating

3 – large quantity of last year's foliage, and/or basal shoots in active growth during all but the coldest weather

4- full healthy set of foliage, leaves living for at least one year, i.e. true evergreen

Character of emerging shoots

1 - Flowering stem with leaves develops rapidly, larger basal leaves emerge later

2 - First leaves to emerge are basal or lower stem leaves which function as basal leaves, or all leaves emerge from base

3 - Shoot with no leaves or greatly reduced leaves at first. Leaves develop higher up stem later.

4 - Shoot emerges with small stem leaves, no leaves which persist as basal leaves for more than a few weeks or are clearly differentiated from stem leaves

5 – Basal leaves emerge first, and die or become senescent on emergence of flowering stem with reduced leaf complement

Time of Dormancy

0 – at least some leaves overwinter

1 – dormancy complete mid-summer

2 - definite deterioration mid-summer, growth may be replaced by new

3 – autumn dormancy

Later-season basal growth

0 – no additional growth produced after spring emergence

1 – some tendency to produce new basal growth, after June

2 – pronounced tendency to produce strong new basal growth, after June, but without flowering

3 - pronounced tendency to produce strong new basal growth, after June, with second set of flowers, with new growth largely or entirely replacing spring growth

Later-season tip growth

0 – none observed

1 – some production of distinct new shoots after flowering, often with foliage reduced in size, but generally without flowers, from existing growth

2 - constant production of new shoots throughout flowering season, bearing both leaves (generally reduced in size) and flowers

3 – pattern of growth during flowering season involves constant branching with production of both flowers and foliage, generally reduced in size

Persistent litter

0 – little persistent litter observed during winter

1- persistent litter to end of winter

Starting time of flowering

1 – February or earlier

2 – March/April

3 – May/June

4 – July/August

5 – September/October

b. Foliage morphology

Canopy height

1 - 0 - 99 mm
2 - 100 - 299 mm
3 - 300 - 599 mm
4 - 600 - 999 mm
5 - 1000 -1499 mm
6 – 1500- 1999 mm
7 - 2000 – 2999 mm
8 – 3000 mm plus

Measured to uppermost leaves, although these were ignored if very small.
In the case of species where stems are typically procumbent height is measured to top of functional canopy and is not therefore equivalent to length of stem.

Leaf Stretch

0 - effectively 0
1 - 0 - 49 mm
2 - 50 - 149 mm
3 - 150 - 299 mm
4 - > 300 mm

This measures projection of a leaf onto the ground. The length of leaf which is effectively more or less horizontal, i.e., is involved in casting shade beneath it, from base of petiole to tip. Angled leaves are thus not measured directly from base to petiole to tip but only their horizontal projection.

Leaf shape

1 - fine – narrow grassy or sword like or other predominantly linear foliage
2 – pinnate, trifoliate, or very deeply toothed or divided
3 – palmate, or approximately as wide as long, but deeply divided
4 – entire and broad, i.e. ovate, cordate, broadly lanceolate, if toothed or divided, divisions not deep
5 – entire, but narrow or fine

Leaf/stem relationship

1 – all leaves truly basal, leaf and petiole merge imperceptibly, broader photosynthetic surface developing immediately above ground level

2. - Leaves basal, or at least stem is virtually non-existent and at ground level but leaf petiole serves as a stem, leaves being held well above ground,

3 – leaves carried on very short, generally horizontal above ground stems, often thick and woody looking in appearance

4 - leaves all attached to stem, however lowest leaves often appear to be basal owing to short internodal distances (pseudobasal leaves), lower leaves which are clearly stem leaves are of similar size, those on upper part of stem reduced, often greatly so, general appearance is of basal leaves predominating

5 – as above, but with pseudobasal leaves in a clear minority, leaves further up stem predominant in number, and not reduced in size

6 - more or less equal division between basal and stem leaves in total area, i.e. stem leaves, at least lower ones, not significantly smaller, and sometimes more numerous

7 - all leaves clearly stem leaves, widely spaced up stem, except for very lowest leaves, lower leaves the largest, getting progressively smaller further up stem

8 – all leaves stem leavers, <5 leaves per stem, more or less similar size

9 - all leaves attached to stem, those in middle section of stem generally significantly larger,

10 – all leaves stem leaves, numerous, relatively even distribution up stem, and +/- even sized, except very close to base and inflorescence,

11 – stem leaves attached to persistent procumbent stems

12 – leaves attached to woody or semi-woody above ground growth which persists over the winter, leaves more or less equal size

Leaf orientation

1 – horizontal, or tending towards it

2 - vertical

Bimorphic shoot production

1 – approx. equal numbers of flowering and non-flowering shoots

2 - non-flowering shoots clearly outnumber flowering

3 – flowering shoots clearly outnumber non-flowering,

4 - every shoot produced in spring which matures produces a flowering stem

5 – chamaephyte, with flowers produced on previous year's stems

Angle of flower-bearing stems

1 – Erect

2 - Erect tendency, but to arch

3 - Initially erect, frequently falling to the horizontal, or initially horizontal, arching upright.

4 - Largely procumbent

Pattern of Spread

0 - short-lived, not spreading vegetatively

1 – tight clump, with shoots which do not clearly function as ramets, or ramets present but so few that spread is minimal, or very close integration to parent so independent capacity in doubt

2 - tight clump, definite ramets, spreading only very slowly

3 – more open phalanx clump, at least at outer edges, more strongly spreading

4 - very strongly spreading, capable of forming mats, phalanx

5 - clump with underground guerrilla phalanx

6 - sparse clump, underground spread

7 - rooting from stems above ground surface

See fig. 7.2 for illustration.

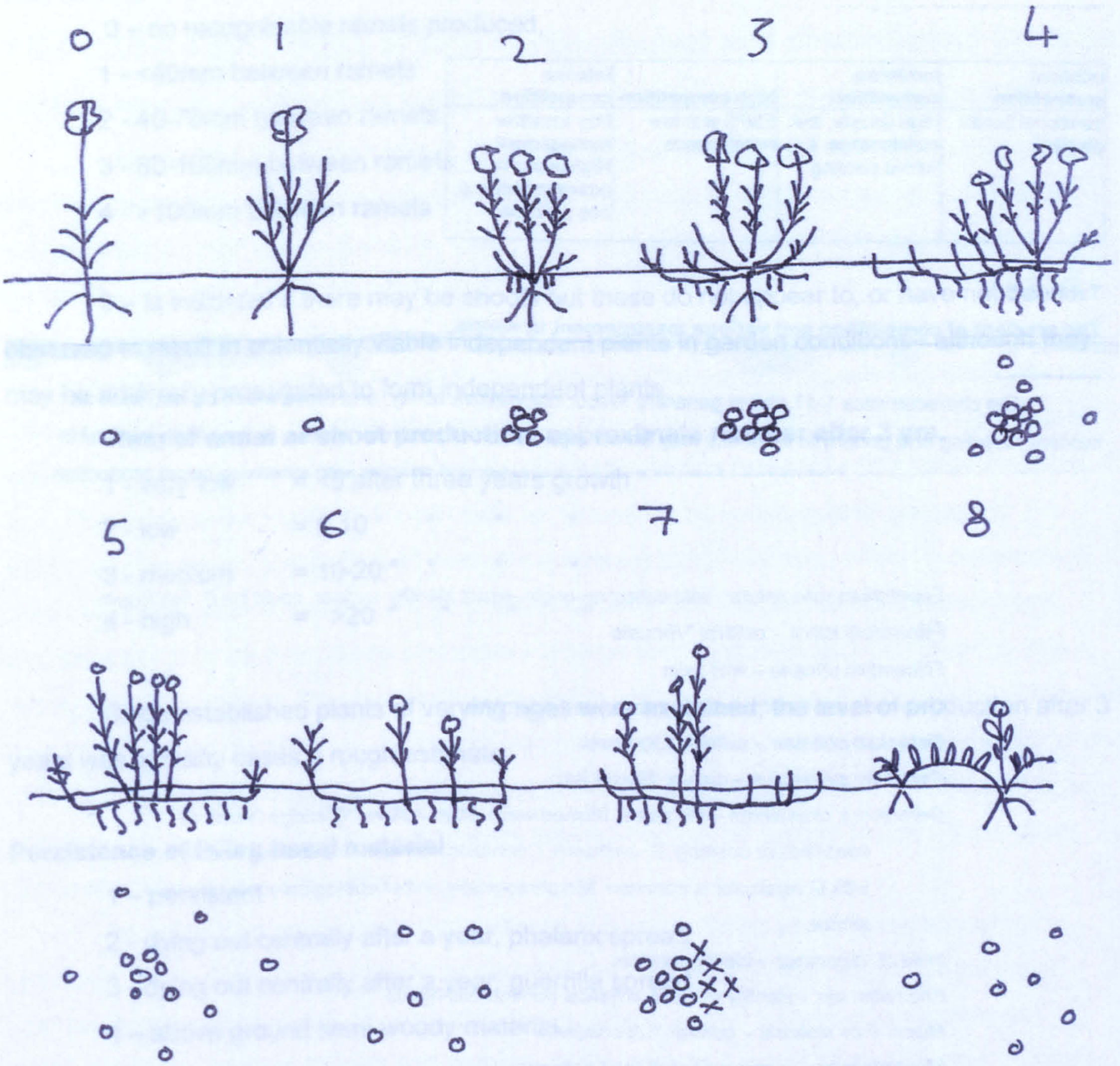


Fig. 7.2

Pattern of spread categories

Each category is represented by a cross section and a plan view of ramets, where one circle is a live ramet, and a cross a dead ramet.

Distance between ramets

0 – no recognisable ramets produced,
1 - <40mm between ramets
2 - 40-79mm between ramets
3 - 80-100mm between ramets
4 - >100mm between ramets

0 – is indicated if there may be shoots but these do not appear to, or have not been observed to result in potentially viable independent plants in garden conditions– although they may be artificially propagated to form independent plants.

Rate of ramet or shoot production, approximate number after 3 yrs.

1 - very low = <5 after three years growth
2 - low = 5-10 " " " "
3 - medium = 10-20 " " " "
4 - high = >20 " " " "

Since established plants of varying ages were examined, the level of production after 3 years was in many cases a rough estimate

Persistence of living basal material

1 – persistent
2 - dying out centrally after a year, phalanx spread
3 - dying out centrally after a year, guerrilla spread
4 – above ground semi-woody material

Size of clump after five years

1- < 100mm
2- 101-200mm
3- 201-300mm
4- 301-500mm
5- 501-1000mm
6- 1001-2000mm
7- >2001mm

Data here is based on measurements of clumps at least five years old, and in most cases of more than one location.

7.5 DISCUSSION OF ANALYSIS OF CHARACTERS

7.5.1 Introduction: Categorising morphological and phenological traits as a route towards developing meaningful categories for herbaceous plants

The fact that there has been so little attempt in either the plant ecology or horticultural literature to produce a comprehensive system of categories for herbaceous plants is strongly suggestive of the difficulty in doing so. Given the subconscious human skill at recognising categories, for example the morphological boundaries for plant and animal species (Diamond 1997), the difficulty of seeing obvious clear-cut morphological categories for herbaceous plants also suggest that there may in fact not be any. Simple observation suggests that there are some clear-cut strategies, e.g. tall species with more or less equal sized leaves more or less equally spaced; there are many species which would fall between this category and another clear-cut one. There are also a number of what could be referred to as 'cross-cutting' categories. For example the category just described contains species which whilst very similar in architecture from just above ground level up, are very different below this line, e.g. some form very tight clumps with tightly packed ramets and others emerge from long underground rhizomes to in a widely scattered pattern. One possibility is to create a hierarchical tree of sub-dividing categories. This is very inelegant however. An honest part of a solution would be to recognise the complexity of herbaceous plant morphology, one derived from the fact that the herbaceous lifecycle is an adaptive solution to a wide range of habitats, and accept that no system is going to be either comprehensive or truly descriptive.

An alternative approach to classification is proposed, one which takes account of gradients as an alternative to clearly demarcated boundaries. It is also suggested that one species may be represented on more than one gradient, so that instead of categories the morphology of a species may be represented, potentially, as a series of co-ordinates. A similar model might be the Ellenberg numbers used to describe the ecological preferences of central-European plants (Ellenberg 1974).

It might also be possible to identify two key gradients and produce a grid, which would recognise the contributing elements of two gradients and clarify the possible existence of more or less discrete groups, which may not be otherwise apparent. This approach has already been used successfully to elucidate a complex area of planting design philosophies and techniques, where there are often no clear divisions between practices (Kingsbury 2003a).

Plant morphology has to recognise a number of different aspects:

- Plant architecture – the arrangement of leaves and stems in space – essentially through the expression of genetically-determined traits, but recognising that this architecture may be more or less plastic.
- The morphology of vegetative spread.

It is also recognised that there is a very close relationship between two temporal aspects of herbaceous plants and the morphological:

- Plant lifespan – with the exception of one species (*Tanacetum parthenium*), all the plants examined are known to have lifespans of at least around 5 years. However the morphology of some species, combined with what is known (largely through anecdotal evidence) of plant lifespans, suggests that there is a relationship between lifespan and morphology.
- Morphological differences appear to be linked with different phenologies; the approach here is to consider morphology separately from phenology but accept that in any final analysis, there may well be re-enforcing categories.

7.5.2 Phenology and growth cycle groups

The length of time a plant has foliage healthy enough to photosynthesise is a reflection of its ability to create resources to survive and to compete.

Herbaceous plants exhibit a wide range of growth cycles through the year. The intention here is to try to divide the species studied into meaningful and coherent growth cycle categories. Growth cycle categories would be useful for horticultural managers as the presence or absence of plant growth is fundamental to aesthetic issues, timing management, and co-ordination with non-herbaceous vegetation. There may well also be a link between growth cycle categories and competitive ability.

Distinctions between groups are somewhat arbitrary. In all cases there is no clear distinction between one group and another. An example is the fact that a great many herbaceous plants produce at least some degree of secondary set of growth later in the season, after the main flush of spring (primary) growth. There are great variations however, in the degree to which how much secondary growth is produced and the degree to which it replaces primary – it is reasonable to suppose that weather conditions play a major role, although there may also be genetic variation within species.

The *Growth Phenology table* (7. Appendix 6) illustrates the existence of healthy functioning growth for the species under study, for 2004, an 'average' British Isles summer, i.e. without prolonged drought or excessive rain.

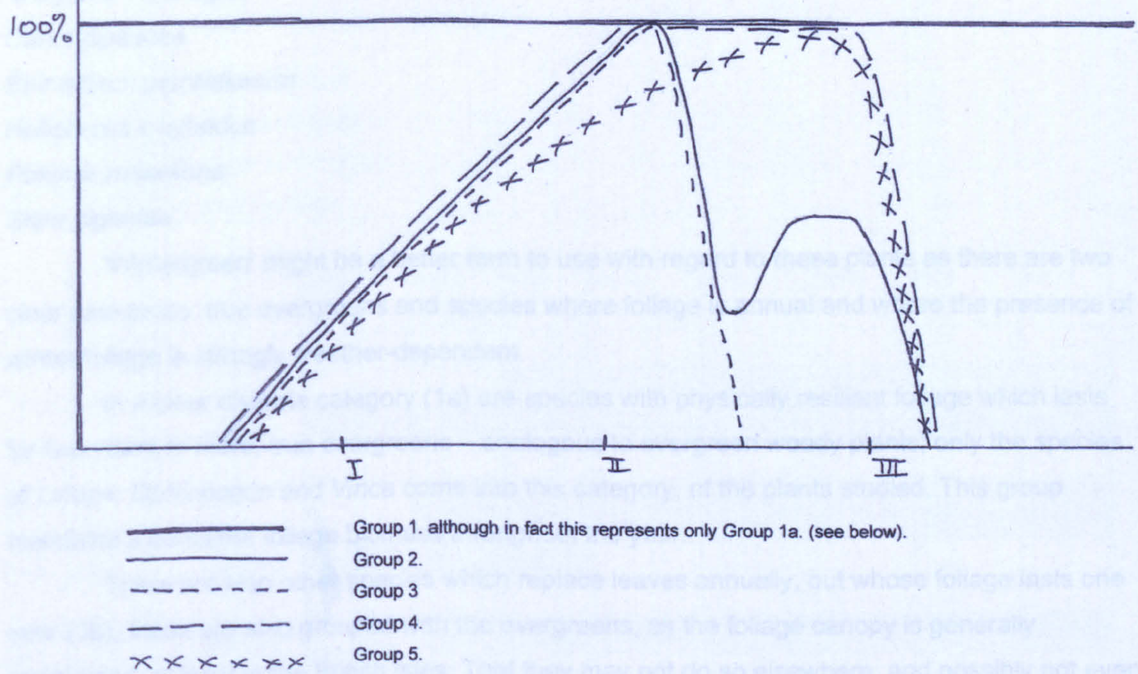
This table illustrates the following characteristics:

- Predominantly healthy current season's growth (primary growth).
- Secondary growth, occurring later in the growing season, entirely replacing first growth: usually over a period of months, making exact point of replacement indicated somewhat arbitrary.

For February:

- Current season's growth or healthy last season's foliage, i.e. evergreen/wintergreen:
- Some limited over wintered foliage:

From this table, and supporting data from Monthly *data* (7.Appendix 3.) the following groups are proposed, which serve to describe relatively clearly defined categories of the production, maintenance and senescence of growth in the range of ornamental herbaceous perennials under study in north-west Europe. Annual cycles of growth are summarised in graph 7.1.



Graph 7.1 Outline phenology of Growth Cycle Groups

This graph represents in a simplified format the outline features of the phenological characteristics of foliage production of the five groups defined here – in the climate of the British Isles.

X axis represents the year, starting and ending with mid-winter, I = spring equinox, II = mid-summer, III = autumn equinox

Y axis represents the percentage of the maximum foliage biomass present as healthy and functioning.

7.5.2.1 Group 1. Wintergreen/evergreen species, i.e. extensive foliage usually present during the winter

1 a. True evergreens

Liriope muscari
Ophiopogon bodinieri
Vinca minor

1 b. Semi-evergreens

Bergenia 'Abendglut'
Carex dipsacea
Epimedium perraldianum
Helleborus x hybridus
Phlomis russeliana
Stipa gigantea

'Wintergreen' might be a better term to use with regard to these plants as there are two clear categories: true evergreens and species where foliage is annual and where the presence of winter foliage is strongly weather-dependent.

In a clear discrete category (1a) are species with physically resilient foliage which lasts for two years or more, true evergreens – analogous to evergreen woody plants; only the species of *Liriope, Ophiopogon* and *Vinca* come into this category, of the plants studied. This group maintains a complete foliage biomass throughout the year.

There are also other species which replace leaves annually, but whose foliage lasts one year (1b), these are also grouped with the evergreens, as the foliage canopy is generally maintained, at least in the British Isles. That they may not do so elsewhere, and possibly not even in their region of origin, indicates a trait favourable to a phenological plasticity which may render them particularly fit in ecological terms to benefit from the long growing season and mild winters of the British Isles; *Phlomis russeliana* is not evergreen in The Netherlands (Oudolf, personal communication 2008) and given that its region of origin (Turkey) has a notably continental climate, it must be assumed that it is deciduous there. Such species clearly must have many of the advantages of the true evergreens, i.e. ability to photosynthesise in winter thus exploiting a phenological niche (Grubb 1986), but perhaps without some of the disadvantages of the evergreen strategy: greater leaf construction costs, a correlation with lower rates of photosynthesis (Aerts 1995).

It should be pointed out that the latter group, unlike the former, because it replaces annual foliage in spring, will not maintain a complete foliage biomass throughout the year – there will be a period in spring when old leaves are senescent and young ones still immature, when total foliage biomass will be less than 100%. This could be referred to as the foliage replacement period. This group are sometimes referred to as semi-evergreens, the standard British definition of "retaining most or some of its foliage throughout the year" (Huxley 1992) serving to describe the phenomenon in a superficial way. In any given year, the degree to which the plant maintains foliage through the winter can be expected to depend on the severity of the winter.

Differences between the true evergreens and those species which maintain inherently shorter-lived foliage, whose lifespan is partially dependent on weather conditions is illustrated in table 7.1.

Table 7.1

The two categories of wintergreen species.

▤ young foliage
▥ mature foliage
■ senescent foliage
▦ dead foliage

		late winter	**early spring**	**late spring**	**early summer**	**late summer**	**early autumn**	**late autumn**	**early winter**
1a. e.g. liriope	*year one*			▤	▤	▥	▥	▥	▥
	year two	▥	▥	▥	▥	▥	▥	■	■
1b. e.g. helleborus	*year one*		▤	▤	▥	▥	▥	▥	▥
mild winter	*year two*	▥	▥	■					
cold winter	*year one*		▤	▤	▥	▥	▥	▥	■
	year two	▦							

The Group 1a species have leaves which last for more than one year.

Group 1b. have leaves which survive the winter in mild winter climates and are therefore functionally evergreen in such climates.

7.5.2.2 Group 2. Very strong tendency to substantial later season basal growth, at least partly replacing spring growth.

Centaurea montana
Cirsium rivulare
Geranium asphodeloides
Geranium endressii, G. x oxonianum
Nepeta x faassenii
Persicaria bistorta 'Superba'
Salvia nemorosa
Symphytum caucasicum

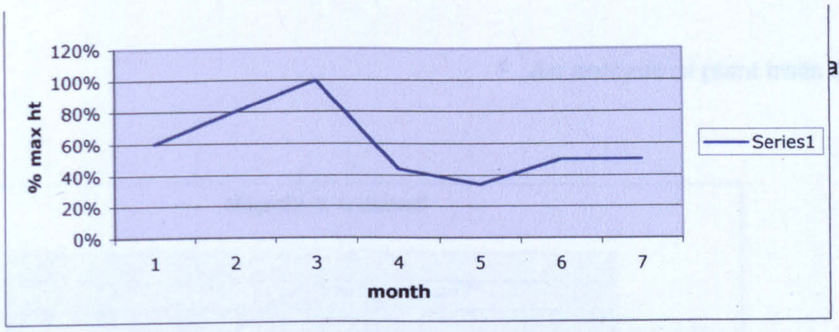
Plants can dominate space through height, but also through the production of new basal shoots through the growing season after the main flush of spring growth – there is a gradient between species that show a strong tendency to do this and those which never seem to. There is a small but distinct group of plants that, at least in the British Isles, grow a second set of foliage and flowers during the summer, which matures in the autumn, either completely replacing or largely replacing the set grown in the spring, which tends to fall around the plant as litter. Both the new growth and the litter production seem to offer a considerable competitive advantage in border or EBPS situations. Two of the species which do this, *Centaurea montana* and the *Geranium endressii* group have been observed naturalised in a closed canopy of semi-natural grass-dominated vegetation in Britain (multiple author observation for both species) illustrating considerable competitive ability. *Persicaria bistorta* 'Superba' is a (possibly tetraploid) form of a common central and north European native meadow species.

Nepeta x faassenii is also included in this group because although its spring foliage does not become entirely senescent, a very strong production of mid-summer growth does partly replace it. *Salvia nemorosa* behaves similarly. It is worth noting that the *Geranium endressii* group and *Centaurea nervosa* are occasionally seen successfully established in native vegetation

In the case of the two geranium species, and the cirsium, the survival of the secondary growth through mild winters, makes the plants *de facto* wintergreen.

Some of these species are from southern European or maritime regions where there is long growing season, but it is not possible to make any generalisation. It is reasonable to assume that the volume of growth is related to moisture availability.

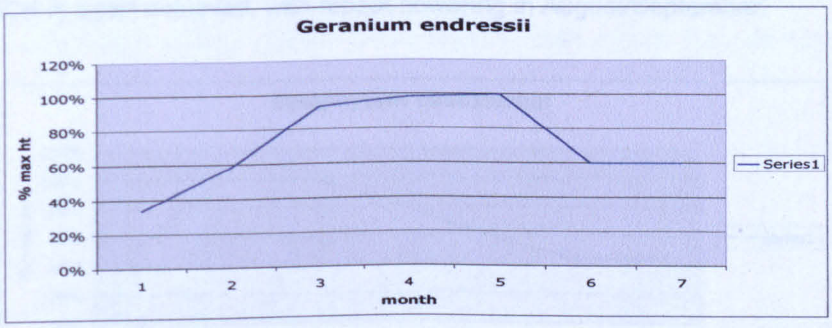
Graphs of several species show the percentage of the Maximum Canopy Height (MCH) achieved Feb to Sept, during 2004, and indicate the range of behaviours of species in this group.



Graph 7.2

Growth phenology of *Centaurea montana*, percentage of maximum canopy height achieved in each month of the growing season. **(1 = March, 2 = April, 3 = May, 4 = June, 5 = July, 6 = August, 7 = September.)**

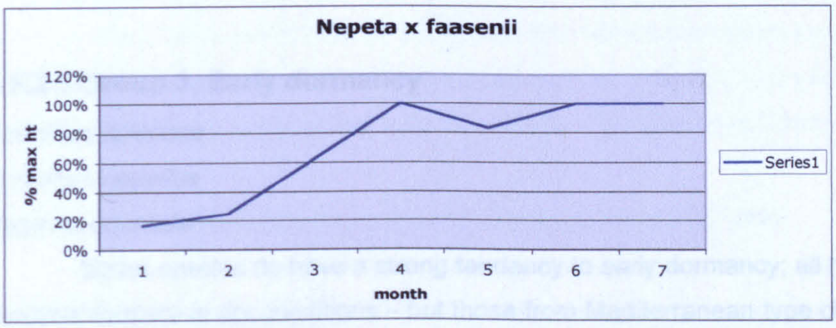
Centaurea montana – over half MCH achieved by March, flowering in May/June followed by rapid collapse and senescence of flowering stems which carry all of the primary growth foliage. Rapid production of secondary growth to a maximum height in August. Repeat flowering is occasionally observed, including the year of study.



Graph 7.3

Growth phenology of *Geranium endressii*, percentage of maximum canopy height achieved in each month of the growing season. **(1 = March, 2 = April, 3 = May, 4 = June, 5 = July, 6 = August, 7 = September.)**

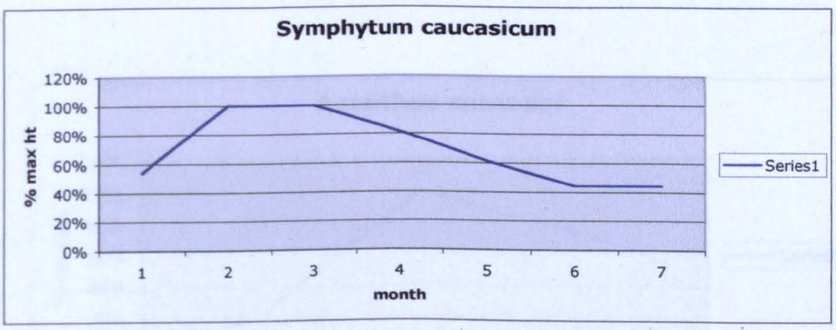
Geranium endressii (and *G. x oxonianum*) typically reach MCH at flowering time in June/July, after which primary growth collapses and slowly becomes senescent. Secondary growth starts in August, flowering September-October, but never reaching the same height.



Graph 7.4

Growth phenology of *Nepeta x faassenii*, percentage of maximum canopy height achieved in each month of the growing season. (1 = March, 2 = April, 3 = May, 4 = June, 5 = July, 6 = August, 7 = September.)

Nepeta x faassenii has a partial collapse of primary growth after flowering in June, production of primary growth never really ceases; it also never completely senesces; by August, MCH is again achieved, with repeat flowering in August/September.



Graph 7.5

Growth phenology of *Symphytum caucasicum*, percentage of maximum canopy height achieved in each month of the growing season. (1 = March, 2 = April, 3 = May, 4 = June, 5 = July, 6 = August, 7 = September.)

Symphytum caucasicum achieves MCH in April, flowering over the next two months; during this time production of new flowering shoots is continuous, so that there is a succession - in comparison to nearly all other species studied which produced flowers from distinct tranches of flowering stems (*Nepeta x faassenii* also had a tendency to do this). Flowering stems tended to rapidly collapse and senesce after flowering, and from June onwards, they reduced in canopy height. By August all had collapsed, leaving only large pseudobasal leaves.

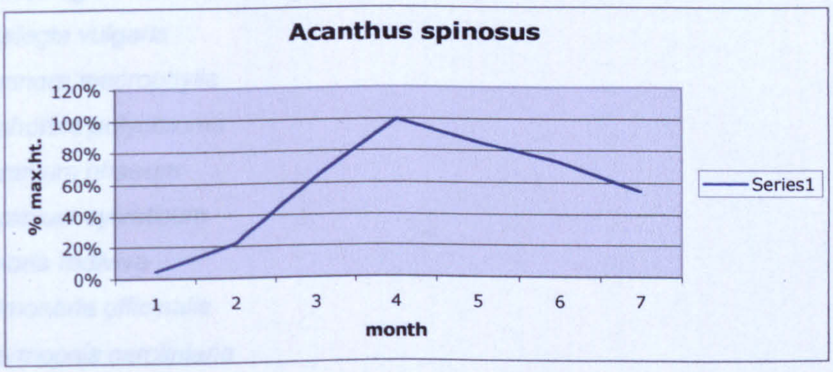
7.5.2.3 Group 3. Early dormancy

Acanthus spinosus

Aconitum napellus

Papaver orientale

Some species do have a strong tendency to early dormancy; all herbaceous species will become dormant in dry conditions – but those from Mediterranean-type climates or other environments where summer drought is a regular occurrence are particularly liable to be able to go into dormancy without deleterious effects. Whereas many such species are able to continue to maintain healthy foliage and even to produce new growth in conditions where moisture supplies are good (e.g. *Salvia nemorosa*, a species of dry meadows which often becomes dormant in summer in the wild (Adler et al. 1994), others inevitably die back, e.g. *Papaver orientale*. It is suggested that species which have a strong tendency to become dormant, at least in drier British summers, are given a distinct category (Group 3), as they are unable to compete during a time when other species may still be able to do so for several more months. Some, such as *Papaver orientale* never produce growth later season growth, others, such as Acanthus, usually do.



Graph 7.6

Growth phenology of *Acanthus spinosus*, percentage of maximum canopy height achieved in each month of the growing season. (1 = March, 2 = April, 3 = May, 4 = June, 5 = July, 6 = August, 7 = September.)

Acanthus spinosus indicates the continuum between Groups 2 and 3. MCH is achieved with flowering in June/July. In dry situations it can then become dormant, but in this study, flowering shoots and their large arching leaves only slowly deteriorated and were partially replaced by smaller and lower leaves on new shoots emerging at the base. It is suggested that the response of species such as this, with an ability to respond to soil moisture by avoiding it through dormancy if dry or further growth if not, is a potentially valuable one for places with uncertain moisture supplies. *Salvia nemorosa* illustrates a continuum too – usually new basal growth produced during summer flowers in September in Britain, even though dormancy is frequent in its native environment – for this reason it is included in Group 2.

7.5.2.4 Group 4. Maximum canopy height achieved by July

There is not only a continuum between species which produce secondary growth with new shoots from the base, or in the case of caespitose grasses, with the production of new leaves; there is a continuum of when species stop growing a taller canopy. This is closely linked to flowering time. Given that maximum light intensity is reached on June 21, there would appear to be a fundamental difference between species that reach maximum height around, or before this date and those that do not. It is suggested that the former respond to primarily to light and secondly to temperature, but that the latter respond primarily to temperature. It is proposed that two further groups are created, which recognise this distinction between species which stop growing in the month and a half after midsummer's day and those which carry on growing.

If flowering times are taken account of, it is possible to distinguish sub-groups.

Group 4a.
Flowering no later than May
Aquilegia vulgaris
Brunnera macrophylla
Euphorbia polychroma
Geranium phaeum
Geranium sylvaticum
Lunaria rediviva
Pulmonaria officinalis
Thermopsis caroliniana

All, except the thermopsis, are European/west Eurasian, specis of woodland, woodland edge or meadow habitats (see *Appendix 1. Habitat and Region of Origin*).

Group 4b.
Mid-summer flowering
Where flowering either begins no later than July, soon after the time of maximum light intensity.

Achillea millefolium
Aconogonon 'Johanniswolke'
Alchemilla mollis

Anaphalis triplinervis
Artemesia lactiflora
Aruncus dioicus
Calamagrostis x 'Karl Foerster'
Calamintha grandiflora
Campanula latifolia
Cephalaria gigantea
Cirsium canum
Clematis heraclifolia
Dianthus carthusianorum
Eryngium bourgatii
Euphorbia schillingii
Filipendula rubra 'Venusta'
Filipendula ulmaria
Geranium pratense
Geranium sanguineum
Geranium 'Johnson's Blue'
Geranium 'Rozanne'
Hemerocallis 'Golden Chimes'
Heuchera micrantha
Hosta fortunei
Inula cf. racemosa
Iris sibirica
Lysimachia punctata
Lythrum salicaria
Macleaya cordata
Persicaria amplexicaule
Stipa calamagrostis
Tanacetum macrophyllum
Tanacetum parthenium
Thalictrum aquilegifolium
Veronicastrum virginicum

All, except *Filipendula rubra*, the veronicastrum, and the heuchera are European or Asian, with moist and montane habitats predominating.

Group 4c.

Late summer flowering

Where flowering begins, well after the peak of maximum light intensity.

Aconitum arctuatum

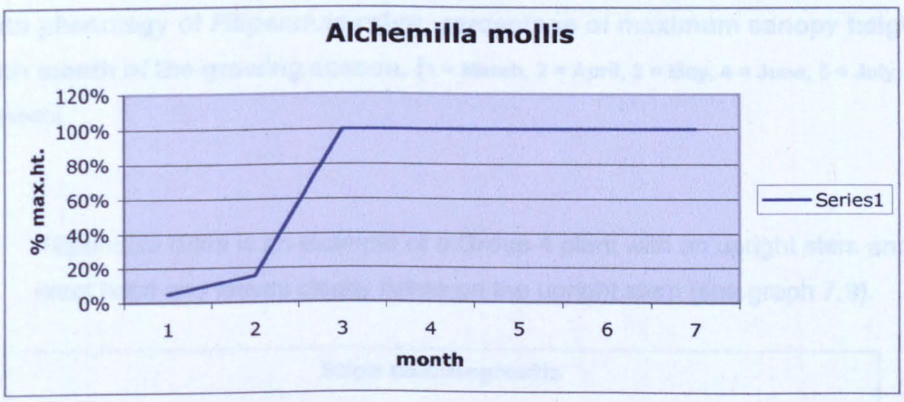
Aster cordifolius

Aster puniceus

Chelone obliqua

Rudbeckia fulgida var. deamii

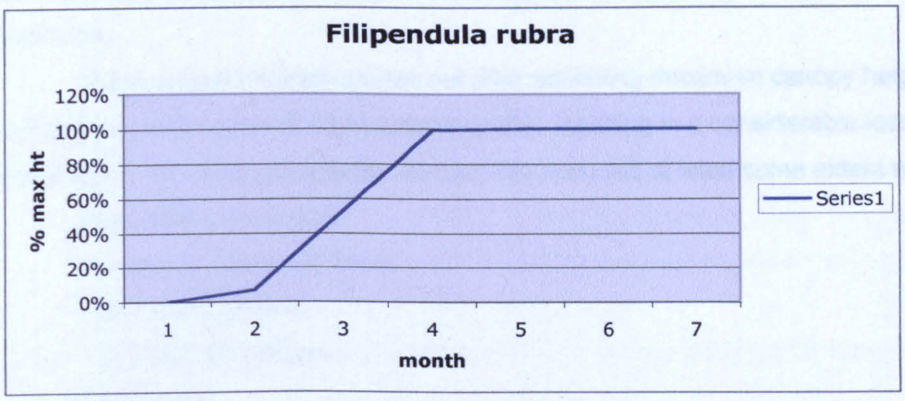
Sanguisorba tenuifolia



Graph 7.7

Growth phenology of *Alchemilla mollis,* percentage of maximum canopy height achieved in each month of the growing season. (1 = March, 2 = April, 3 = May, 4 = June, 5 = July, 6 = August, 7 = September.)

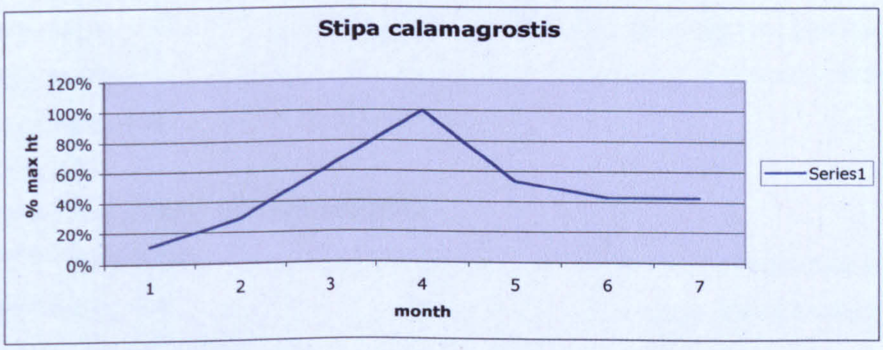
Alchemilla mollis is an example of a Group 4 species with basal or pseudobasal leaves which achieve MCH at the approximate same time as flowering and which is maintained after flowering (see graph 7.8).



Graph 7.8

Growth phenology of *Filipendula rubra,* percentage of maximum canopy height achieved in each month of the growing season. (1 = March, 2 = April, 3 = May, 4 = June, 5 = July, 6 = August, 7 = September.)

Filipendula rubra is an example of a Group 4 plant with an upright stem and strongly erect habit and leaves clearly borne on the upright stem (see graph 7.9).



Graph 7.9

Growth phenology of *Stipa calamagrostis,* percentage of maximum canopy height achieved in each month of the growing season. (1 = March, 2 = April, 3 = May, 4 = June, 5 = July, 6 = August, 7 = September.)

Not all Group 4 plants maintain height – physical collapse resulting from stem weakness or lack of support from neighbours can happen. Senescence of stem leaves associated with early summer flowering stems can also result in canopy height loss, e.g. with many geraniums.

In some cases foliage arches out after achieving maximum canopy height – this is strongly so in the case of *Stipa calamagrostis,* resulting in a considerable loss in height (see graph 7.10). Amongst species studied this occurred at least some extent with:

Euphorbia polychroma
Geranium 'Johnsons' Blue'
Geranium pratense
Geranium sylvaticum
Iris sibirica
Persicaria bistorta
Thermopsis caroliniana

It should be noted that all of these species flower in May or June.

7.5.2.5 Group 5. Maximum height achieved later than July

Amsonia orientalis
Anemone x hybrida
Aster novi-belgii
Aster umbellatus
Astrantia major
Baptisia australis
Echinaea purpurea
Echinops ritro
Eupatorium maculatum subsp.*purpureum*
Euphorbia cyparissus
Euphorbia palustris
Helianthus 'Lemon Queen'
Knautia macedonica
Leucanthemella serotina
Lysimachia ciliata
Lysimachia clethroides
Miscanthus sinensis
Molinia caerulea subsp. *arundinacea*
Monarda hybs.
Origanum laevigatum
Phlox paniculata
Rudbeckia 'Juligold'

Sedum spectabile
Solidago rugosa
Stipa arundinacea
Vernonia crinita

A variety of habitats is represented, although some e.g. *Astrantia major*, are woodland edge, none are true woodland species, and nearly all from open habitats. One additional factor does stand out – the number of species of North American origin.

A limited number of other species continue to make canopy growth after flowering:

Baptisia australis
Clematis heracleifolia
Euphorbia cyparissus
Euphorbia palustris
Euphorbia polychroma
Euphorbia schillingii
Lunaria rediviva
Thermopsis caroliniana
Vinca minor

However this tendency is not necessarily linked to increasing height – it may instead result in greater bushiness through side-shoot production or in the case of vinca, trailing stems. The tendency of the *Euphorbia* species studied to do this, including two species from very different habitats: the dry meadow *E.cyparissias* and the wetland *E.palustris*, indicates that this tendency is probably a genetically determined trait.

7.5.3 Morphology and architecture

Spearman Rank Order Correlations were used to highlight areas of association between the variables studied, although it is recognised that in some cases the quantification of plant characters which are inherently not varying in mathematical intensity (as does e.g. height), but exist through the creation of categories on a spectrum (e.g. leaf/stem relationship, which is a gradient from domination by true basal leaves through to presence only of stem leaves), makes mathematical correlation difficult. In any case correlation does not shed any light on cause and effect.

Correlations are shown in the table: *Investigation of correlations assessed in the perennial data* (7.Appendix 7)

Where r_s was greater than 0.5, or less than –0.5 the relationship was examined in detail.

Whilst Spearman Rank Order correlations were used to highlight some possible linkages between traits characters, the emphasis has been on analysing what is termed leaf-stem relationship, the most visible and easily recognisable characteristic for the practitioner, as well as rate and mechanism of vegetative spread.

The following plant characters showed a Spearman Rank Order correlation of > 0.5 or < -0.5:

Time of emergence and wintergreen character, $r_s = -0.58$. This would be expected, as both these characters are discussing aspects of the same property.

Bi-morphic shoot production and leaf/stem relationship, $r_s = 0.51$.

Discussed below.

Character of emerging shoots and Leaf/Stem Relationship, $r_s = 0.53$.

Discussed below.

Leaf stretch and leaf/stem relationship, $r_s = -0.53$.

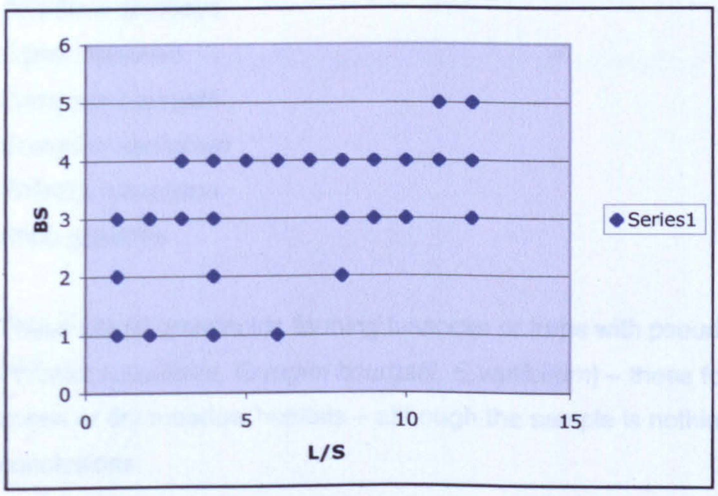
Discussed below.

Pattern of spread and time of flowering, $r_s = 0.68$ and

Pattern of spread and distribution of ramets. $r_s = 0.58$.

As with distinct correlations between the character 'Size of clump after 5 years', and other assessments of rate and pattern of spread, these are essentially measurements of aspects of the same property.

7.5.3.1 Relationship between bimorphic stems and leaf-stem relationship. (for explanation and discussion of these terms see 3.7 The Perennial Data Table)



Graph 7.10

Leaf/stem relationship (L/S) plotted against Bimorphic shoot production (BS) for species studied.: correlation, r_s= 0.51

BS 1 - *more or less equal number of flowering and non-flowering stems –*

Achillea millefolium

Alchemilla mollis

Astrantia major

Brunnera macrophylla

Cirsium rivulare

Helleborus x hybridus

Iris sibirica

Kniphofia var.

Liriope muscari

Ophiopogon bodinieri

Papaver orientale

Persicaria bistorta

Pulmonaria officianalis

Symphytum caucasicum

Trachystemon orientalis

Monocots or where pseudobasal leaves predominate e.g. *Achillea millefolium* or where petiole serves as a stem, e.g. *Helleborus x hybridus.*

BS 2 - *where non-flowering stems outnumber flowering stems –*

Acanthus spinosus
Carex dipsacea
Eryngium bourgatii
Eryngium varifolium
Phlomis russeliana
Stipa gigantea

These are all graminoids forming tussocks or forbs with pseudobasal leaves (*Acanthus spinosus, Phlomis russeliana, Eryngim bourgatii, E.varifolium*) – these forbs from Mediterranean climate zones or dry meadow habitats – although the sample is nothing like wide enough to draw any conclusions.

BS 3 - *where flowering stems outnumber non-flowering* – no clear pattern

BS 4 - *where every shoot which emerges in spring produces flowers –*

These comprise 69 out of the 106 species studied.

Dominant are species with stems with more or less similarly sized foliage, – leaf-stem relationship categories 7-11 accounts for 51 species.

Leaf-stem relationship groups 3 and 4, where pseudobasal leaves predominate, comprise a bergenia, a cirsium and all of the geraniums studied (apart from 'Rozanne', see below).

Leaf-stem relationship group 5&6, an intermediate category between species where pseudobasal leaves clearly dominate and species with erect stems and more evenly distributed leaves:

Echinops ritro
Filipendula rubra 'Venusta'

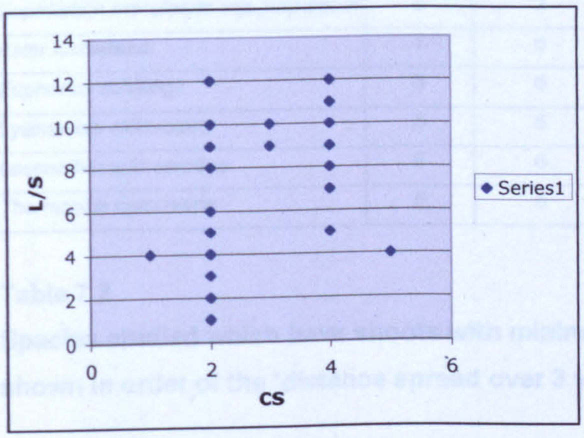
This habit is characteristic of filipendula. *Persicaria amplexicaule* and *Geranium* 'Rozanne' are special cases (see belows).

BS 5 – *chamaephytes –*

Clematis heracleifolia
Vinca minor

There is an ambiguous category of what are technically chamaephytes, but which are generally treated by horticulturalists as herbaceous perennials, possibly because the woody growth formed is weak, and the plants are treated as herbaceous in cultivation.

7.5.3.2 Relationship between character of emerging shoots and leaf-stem relationship.



Graph 7.11
Character of emerging shoots (CES) plotted against Leaf/stem relationship (L/S) for the species studied. Correlation: r_s=0.53

Emerging shoots with minimal leaves (i.e. category CS 4) most usually found in species with spp, in leaf-stem relationship category 7-12 species.

Particularly distinctive are those species (category CS 3) where leaves are minimal. It may be surmised that this is an adaptation to the effective penetration of leaf litter, or to gain height before expending energy on lamina development. Grime (2001) suggests that effective shoot thrust is linked to the ability of some slower growing species to survive in competitive environments – shoot thrust, with a minimum of photosynthetic area is dependent upon the mobilisation of stored resources. It is interesting to note that of the species studied with this characteristic, all are from productive habitats and have a strongly upright habit. Their ability to spread through ramet production however varies greatly (see table 7.2).

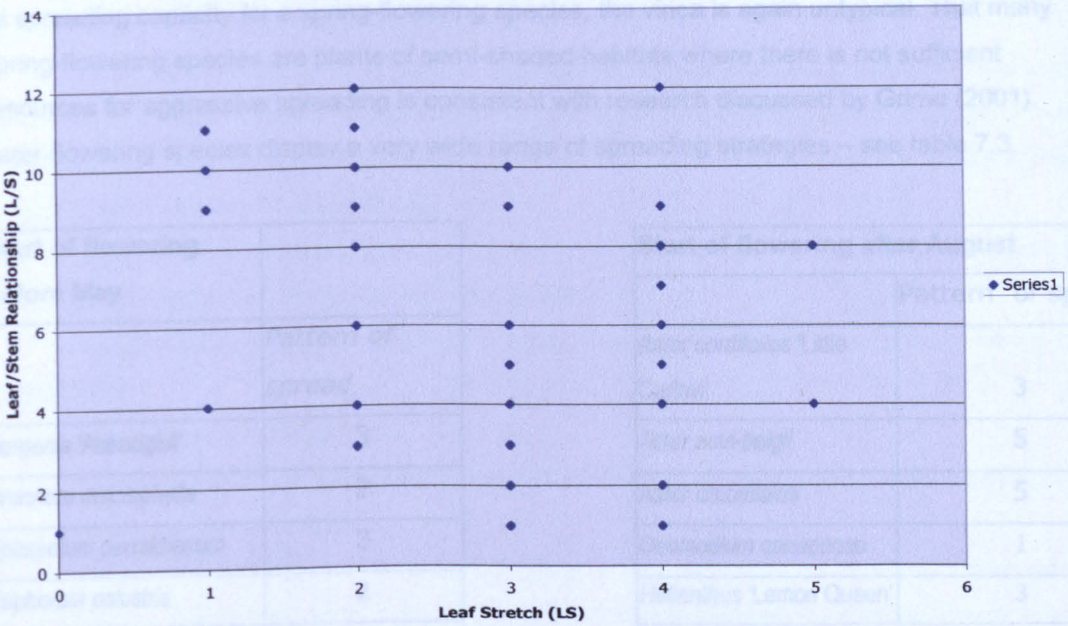
	Canopy height	Pattern of spread	Distance + rate of spread
Amsonia orientalis	3	2	3
Baptisia australis	5	2	3
Lythrum salicaria	5	1	3
Eupatorium maculatum ssp.purpureum	8	2	4
Aster umbellatus	7	5	6
Euphorbia schillingii	5	6	6
Lysimachia clethroides	5	5	6
Leucanthemella serotina	6	6	7
Thermopsis caroliniana	5	5	8

Table 7.2

Species studied which have shoots with minimal foliage on emergence (category CS3) shown in order of the 'distance spread over 3 years + rate of spread'.

None of the category CS3 plants exhibit later-season basal growth, although three show later-season tip growth (*Baptisia australis*, *Euphorbia schillingii*, *Thermopsis caroliniana*) and one a complex pattern of repeated branching of flowering stems (*Lythrum salicaria*). It is noted that canopy heights tend to be high. One is effectively non-clonal (*Lythrum salicaria*, but highly effective at recruitment through seed), several are notably slow to establish and form dense, slowly but effectively spreading clumps (*Amsonia orientalis*, *Baptisia australis* and eupatorium; the remainder spread more rapidly. Two species (out of 12 studied) included are in the highest category of distance between ramets – they have a very different production of ramets, that of *Euphorbia schillingii* being exceptionally low, and that of *Thermopsis caroliniana* being in the highest category.

7.5.3.3 Relationship between a measure of leaf stretch (LS) and leaf/stem relationship (L/S).



Graph 7.12

Leaf Stretch (LS) and plotted leaf/stem relationship (L/S) for the species studied, Correlation: $r_s = -0.53$

Leaf stretch is a measure of the downward projection of a leaf onto the ground, so effectively a measure of the 'reach' of a plant.

There seems to be a weak tendency for leaves with greater projection from the core of the plant to be carried near the base of the plant. It is noted that category 10, that of (usually numerous) more or less equal size stem leaves, a very common architectural form for later flowering plants is limited in this measure of leaf projection. Very far projecting leaves though can be supported by a variety of different leaf-stem architectures – in reality large leaves are always on the lower part of the stem; Givnish (1982 and 1987) discusses this in terms of basic engineering principles and in terms of the architecture of species of productive habitats needing leaves which can be readily discarded and replaced by new ones, higher up the stem – small leaves with little supporting structure are thus an economical model.

7.5.3.4 Pattern of spread and time of flowering

r_s = 0.68.

There is no particular linkage which stands out here. Spring flowering species studied do have a strong tendency towards tight clumps (PS 3 or less); the symphytum here is exceptional in its spreading capacity for a spring-flowering species, the vinca is again untypical. That many spring-flowering species are plants of semi-shaded habitats where there is not sufficient resources for aggressive spreading is consistent with research discussed by Grime (2001). Later-flowering species display a very wide range of spreading strategies – see table 7.3.

Start of flowering before May	
	Pattern of spread
Bergenia 'Abendglut'	3
Brunnera macrophylla	2
Epimedium perraldianum	3
Euphorbia palustris	2
Euphorbia polychroma	2
Helleborus x hybridus	2
Lunaria rediviva	2
Pulmonaria officianalis	2
Symphytum caucasicum	5
Vinca minor	7

Start of flowering after August	
	Pattern of spread
Aster cordifolius 'Little Carlow'	3
Aster novi-belgii	5
Aster umbellatus	5
Desmodium canadense	1
Helianthus 'Lemon Queen'	3
Leucanthemella serotina	6
Liriope muscari	3
Molinia caerulea subsp. arundinacea	2
Panicum virgatum	2
Rudbeckia 'Juligold'	3
Solidago rugosa	3
Stipa arundinacea	2
Vernonia crinita	2

Table 7.3

Pattern of spread of spring-flowering and late summer flowering species studied

7.5.3.5 Categories based on leaf-stem relationship (L/S)

The leaf-stem relationship is crucial to herbaceous plant morphology. It is also crucial to the linked issues of aesthetics and functionality which governs plant selection in horticulture. This relationship determines whether or not it may be selected for its strong visual structure, or instead used as an amorphous 'filler plant' (Kingsbury and Oudolf 1999), and whether it may be used as *en masse* as a weed suppressor (Thomas 1970).

During the course of the 2005 growing season, samples of plants included in the study were drawn, in order to clarify and illustrate the nature of the leaf-stem relationship, with a view to supporting the set of categories developed to define this relationship. These are shown in *Plant Architecture Diagrams*, (7.Appendix 9).

Species were chosen to represent either examples of clear categories, or to explore leaf-stem relationships where there was no clear category.

Diagrams are highly schematic, and whilst drawn to scale, leaf orientation shown is highly approximate.

The following is noted:

- There are few clear categories; instead there seems to be a rough gradient between the following two extremes:
    - A large number of species in ornamental horticulture have an erect stem and large number of more or less equally spaced leaves, decreasing in size only slightly as they go up the stem
    - A large number of large leaves at the base, densely packed, with few, more widely spaced and very much smaller ones further up the stem; many monocarpic species not included in this study illustrate this type most clearly, e.g. *Digitalis purpurea*.

  Clearly any categorisation is inevitably of a rather arbitrary character.
- In the majority of dicot species all leaves emerge from a flowering stem; only a minority produce non-flowering stems
- Dicot species do not really have 'basal' leaves, rather there is a stem with very closely-packed leaves just above ground level; 'pseudobasal' leaves might be a more accurate distinction, the monocots examined do produce leaves, which might be more accurately described as truly basal.
- A minority of species have growth which emerges from a semi-woody and persistent above ground stem, e.g. *Dianthus carthusianorum*.
- A minority of species have stems which branch, often producing two stems at the foot of an inflorescence-bearing stem

It must be assumed that the growth patterns of some species must be very fluid, the potentially very long petiole lengths of some species examined (e.g. *Astrantia major* and geranium species) indicate that growth is very plastic and responsive to the growing conditions, this plasticity indicates that leaf-stem relationships are potentially flexible in some species – making categorisation increasingly problematic.

Here an attempt will be made to analyse the leaf-stem relationship in terms of its relationship to phenology and to other morphological characteristics and traits, with the intention of assessing how an understanding of the relationship may contribute to a meaningful characterisation of herbaceous plants.

The leaf/stem relationship categories used in the *Perennial Data Table* (Appendix 7.1) can be simplified into 4 broader categories:

I Basal leaves

1 – all leaves truly basal, leaf and petiole merge imperceptibly, broader photosynthetic surface developing immediately above ground level

2. - Leaves basal, or at least stem is virtually non-existent and at ground level but leaf petiole serves as a stem, leaves being held well above ground,

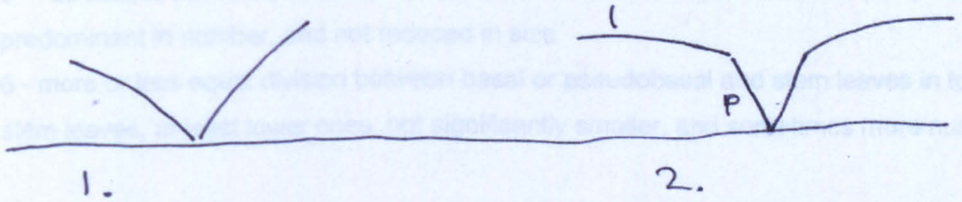


Fig.7.3

Effectively basal leaves. In (1) there is no petiole, e.g. hemerocallis. In (2) petiole (p) emerges at ground level, lamina (l) held above ground level, e.g. helleborus.

II Effectively basal or emergence very close to ground

3 – leaves carried on very short, generally horizontal, aboveground stems, which are often thick and woody looking in appearance

4 - leaves all attached to stem, however lowest leaves often appear to be basal owing to short internodal distances (pseudobasal leaves), lower leaves which are clearly stem leaves are of similar size, those on upper part of stem reduced, often greatly so, general appearance is of basal/pseudobasal leaves predominating

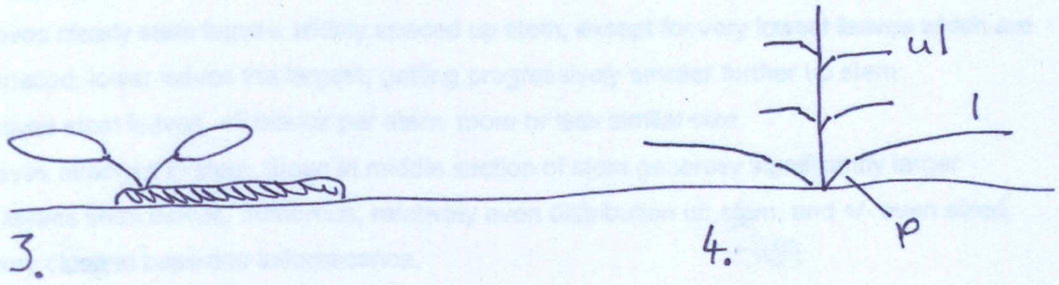


Fig. 7.4

Leaves emerging very close to ground. In (3) leaves emerge from a thick stem at ground level, e.g. bergenia. In (4) the vast majority of the plant leaf lamina area (l) is held on a petiole (p) which emerges so close to the ground as to be effectively basal, on a stem which supports small upper leaves (ul), e.g. brunnera.

III Division between pseudobasal and stem leaves

5 – as above, but with pseudobasal leaves in a clear minority, leaves further up stem predominant in number, and not reduced in size

6 - more or less equal division between basal or pseudobasal and stem leaves in total area, i.e. stem leaves, at least lower ones, not significantly smaller, and sometimes more numerous

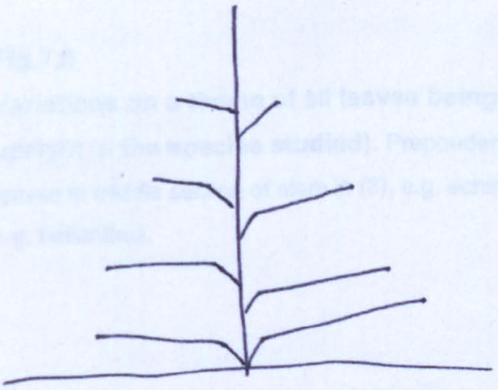


Fig.7.5

Presence of both pseudobasal and clear stem leaves. Both with significant surface area, e.g. filipendula (6).

IV Stem leaves

7 - all leaves clearly stem leaves, widely spaced up stem, except for very lowest leaves which are closely spaced, lower leaves the largest, getting progressively smaller further up stem

8 – all leaves stem leaves, <5 leaves per stem, more or less similar size

9 - all leaves attached to stem, those in middle section of stem generally significantly larger

10 – all leaves stem leaves, numerous, relatively even distribution up stem, and +/- even sized, except very close to base and inflorescence,

11 – stem leaves attached to persistent procumbent stems *

12 – leaves attached to woody or semi-woody above ground growth which persists over the winter, leaves more or less equal size

* clearly the fact of procumbency needs to be recognised in any further analysis

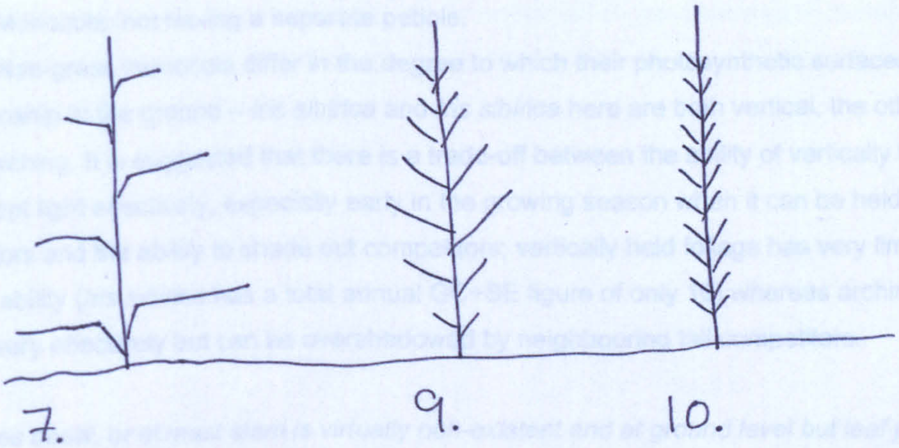


Fig.7.6

Variations on a theme of all leaves being stem leaves on stems (which are generally upright in the species studied). Preponderance of surface area low down in (7), e.g. macleaya, larger leaves in middle section of stem in (8), e.g. echinaea, all leaves more or less equal, and numerous, in (9), e.g. helianthus.

L/S I - Basal leaves

1 – all leaves truly basal, leaf and petiole merge imperceptibly, broader photosynthetic surface developing immediately above ground level

Carex dipsacea

Hemerocallis 'Golden Chimes'
Iris sibirica
Kniphofia var.
Liriope muscari
Ophiopogon bodinieri

Monocots, not having a separate petiole.

Non-grass monocots differ in the degree to which their photosynthetic surfaces are held in relationship to the ground – *Iris sibirica* and *Iris sibirica* here are both vertical, the others more or less arching. It is suggested that there is a trade-off between the ability of vertically held foliage to intercept light effectively, especially early in the growing season when it can be held above competitors and the ability to shade out competitors; vertically held foliage has very limited shading ability (*Iris sibirica* has a total annual GC+SE figure of only 10) whereas arching foliage shades very effectively but can be overshadowed by neighbouring tall competitors.

2. - leaves basal, or at least stem is virtually non-existent and at ground level but leaf petiole serves as a stem, leaves being held well above ground,

Epimedium perraldianum
Helleborus x hybridus
Hosta fortunei
Trachystemon orientalis

These are all species which are typically grown in shade in cultivation. Givnish 1987 supports the link between this morphology and shade – and early emergence.

L/S II - Effectively basal or emergence very close to ground

3 – leaves carried on very short, generally horizontal, aboveground stems, which are often thick and woody looking in appearance

Bergenia 'Abendglut'
Heuchera micrantha

Few species in cultivation have this distinctive habit. Both bergenia species and *Heuchera micrantha* are known to occur frequently on rocks (see *Appendix 1 habitats*). The horizontal stem habit may be an adaptation to such environments.

4 - leaves all attached to stem, however lowest leaves often appear to be basal owing to short internodal distances (pseudobasal leaves), lower leaves which are clearly stem leaves are of similar size, those on upper part of stem reduced, often greatly so, general appearance is of basal/pseudobasal leaves predominating.

Group L/S II.4.	growth cycle group	start of flowering	angle of flower bearing stems
Acanthus spinosus *	3	3	1
Achillea millefolium, *	4c	3	1
Anemone x hybrida *	5	4	1
Aquilegia vulgaris *	4a	3	1
Brunnera macrophylla	4a	2	1
Cephalaria gigantea *	4b	3	1
Cirsium canum	4b	3	1
Cirsium rivulare	2	3	1
Eryngium bourgatii	4b	3	1
Eryngium varifolium		3	1
Geranium pratense	4b	3	1
Geranium sylvaticum	4a	3	1
Inula cf. racemosa *	4b	4	1
Persicaria bistorta	2	3	1
Phlomis russeliana *	1	3	1
Thalictrum aquilegifolium	4b	3	1
stems tending away from vertical			
Alchemilla mollis *	4b	3	3
Geranium asphodeloides	2	3	3
Geranium 'Johnsons Blue'	4b	3	2
Geranium phaeum *	4a	3	2
Geranium renardii		3	2
Geranium sanguineum	4b	3	3
Geranium x oxonianum	2	3	3
Papaver orientale *	3	3	2
Pulmonaria officinalis *	4a	2	2
Symphytum caucasicum *	2	2	2

* = see Plant Architecture Drawings, 7.Appendix 9

Table 7.4

Species studied which have a preponderance of pseudobasal leaves listed with their Growth Cycle Group, and measures of Start time of flowering and Angle of flower bearing stems (see 7. Appendix 1. The Perennial Data Table).

Pseudobasal or lower stem leaves strongly appear to form the majority of the photosynthetic area, and live for several months, generally deteriorating after flowering, often being replaced by smaller leaves higher up the flowering stem or by leaves on new basal shoots.

Species in this group (see table 7.4) nearly all flower or start to flower before mid-summer. Although in a superficial visual inspection there is a great deal of variation, a breakdown of characteristics reveals distinct patterns. One of the key differences is between species with flower stems which form strongly vertical flower stems and those where flower stems are presented at a number of angles, or arch or bend. Within the vertical group, the main visual difference is between tall species (e.g. t*Thalictrum aquilegifolium*h) and shorter ones, the latter having a higher proportion of leaf area to flower stem, therefore creating a very different impression – however the underlying architecture is the same. The non-vertical group do tend to have a similar superficial impression, that of low clumps dominated by pseudobasal leaves. None of this latter group start flowering after mid-summer's day.

L/S III - Division between pseudobasal and stem leaves

5 – pseudobasal leaves present and visually striking but in a clear minority, leaves further up stem predominant in number, and not reduced in size as above, but with pseudobasal leaves in a clear minority, leaves further up stem predominant in number, and not reduced in size

Geranium 'Rozanne'
Persicaria amplexicaule (see Plant Architecture Drawings, (7.Appendix 9)

Geranium 'Rozanne' is atypical, being procumbent, unlike either of its parents. Its habit is very useful in planting design owing to its ground-covering and weed-suppressing abilities.

Persicaria amplexicaule has an unusual morphology for ornamental perennials, having large leaves dominating the middle section of the multiply branched stem. Stems are highly variable in the degree of branching and the size and number of leaves supported. Stems are also angled out from the base of the plant. The result is the occupation of considerable space.

10 – more or less equal division between basal or pseudobasal and stem leaves in total area, i.e. stem leaves, at least lower ones, not significantly smaller, and sometimes more numerous

Astrantia major *
Echinops ritro *
Filipendula rubra 'Venusta'
Filipendula ulmaria *

10 = See Plant Architecture Drawings, (7. Appendix 9)

These species have leaves arranged around an upright stem. Growth of *Astrantia major* appears to be particularly plastic, as stems are often densely packed, and there appears to be a high level of tolerance of competing neighbouring vegetation (author observation: Elmtree Cottage, and various locations, Austria).

L/S IV – Stem leaves dominant

10 – all leaves clearly stem leaves, widely spaced up stem, except for very lowest leaves which are closely spaced, lower leaves the largest, getting progressively smaller further up stem

Macleaya cordata
See Plant Architecture Drawings, (7.Appendix 9)

8 – all leaves stem leavers, <5 leaves per stem, more or less similar size

Calamagrostis x acutiflora 'Karl Foerster'
Miscanthus sinensis
Molinia caerulea subsp. *arundinacea*
Panicum virgatum
Stipa arundinacea
Stipa calamagrostis *
Stipa gigantea

10 = see Plant Architecture Drawings, (7.Appendix 9)

All are grasses, although varying from definitely caespitose to more strongly clump-forming (panicum, miscanthus, calamagrostis).

9 – all leaves clearly attached to stem, those in middle section of stem generally significantly larger

10 – all leaves stem leaves, numerous, relatively even distribution up stem, and +/- even sized,
except very close to base and inflorescence,

Arguably the differences between these two groups are only a matter of degree. They are therefore combined. Essentially, photosynthetic area in the form of the total leaf lamina area is distributed up the stem, with a tendency to even distribution. It is also noted that the lifespan of lower leaves is often very short (Givnish 1982, 1987).

Group L/S IV, 9 & 10	**growth cycle group**	**start of flowering**	**angle of flower bearing stems**
Stems distinctly upright			
Aconitum arctuatum	4c	4	1
Aconitum napellus	3	3	1
Amsonia orientalis	5	3	1
Anaphalis triplinervis	4b	4	1
Artemesia lactiflora	4b	4	1
Aster novi-belgii (P)	5	5	1
Aster puniceus (P)	4c	4	1
Aster umbellatus (P)	5	5	1
Campanula latifolia	4b	3	1
Chelone obliqua	4c	4	1
Desmodium canadense (P)		5	1
Echinaea purpurea (P)	5	4	1
Eupatorium maculatum ssp.purpureum (P)	5	4	1
Euphorbia cyparissus	5	3	1
Euphorbia schillingii	4b	3	1
Helianthus 'Lemon Queen' *(P)*	5	5	1
Leucanthemella serotina	5	5	1
Lysimachia punctatum	4b	3	1
Lythrum salicaria	4b	4	1
Monarda hybs. *(P)*	5	4	1
Phlox paniculata	5	4	1
Rudbeckia fulgida var. deamii (P)	4b	4	1
Rudbeckia 'Juligold' *(P)*	4c	5	1
Sanguisorba tenuifolia	4c	4	1
Senecio tanguticus		4	1
Solidago rugosa (P)	5	5	1
Tanacetum parthenium	4b	3	1
Thermopsis caroliniana (P)	4a	3	1
Vernonia crinita (P)	5	5	1
Veronicastrum virginicum (P)	4b	3	1

Table 7.5

Members of L/S groups 9 and 10, where stems strongly tend to be upright, with growth cycle group, start time of flowering and angle of flowering stems.

Group L/S IV, 9 & 10	**growth cycle**	**start of flowering**	**angle of flower bearing stems**
stems tending away from vertical			
Aconogonon 'Johanneswolke'	4b	3	2
Aruncus dioicus	4b	3	2
Aster cordifolius 'Little Carlow'	4c	5	2
Baptisia australis	5	3	2
Calamintha grandiflora	4b	4	4
Centaurea montana	2	3	2
Euphorbia palustris	5	2	2
Euphorbia polychroma	4a	2	4
Knautia macedonica	5	3	3
Lunaria rediviva	4a	2	2
Lysimachia ciliata	5	4	3
Lysimachia clethroides	5	4	2
Nepeta x faassenii	2	3	4
Origanum laevigatum	5	4	3
Salvia nemorosa	2	3	3
Salvia verticillata		4	2
Sedum spectabile	5	4	2
Tanacetum macrophyllum	4b	3	2

Table 7.6

Members of L/S groups IV 9 and 10, where stems tend away from the vertical with growth

There is a wide range of variation here. Species with distinctly vertical stems do have a common architecture, although as with Group II.4 above this can be disguised by differences in height and density of clumps. There is also a wide variation in the degree of branching, which affects the immediate appearance. Species with less strongly vertical stems may differ for a variety of reasons: in some cases, simple crowding may result in arching stems, as when a large number of stems is produced from a dense central clump as in the aconogonon and the aruncus. There is a tendency for the second group to be shorter.

There is a wide range of flowering times, unlike Group II.4 (see table 7.5 and 7.6). It is noted however that of the North American tallgrass prairie (or at least open productive habitat species) there is a strong tendency towards uniformity of morphology – notably very upright tall stems.

*11 – stem leaves attached to persistent procumbent stems **

Persicaria affinis
Veronica incana
Vinca minor

Obligate procumbency is typical of rocky environments (Ellenberg 1988) and can often be observed amongst woodland floor species. No further consideration will be made of it, as it is of little relevance to the more productive environments under discussion.

12 – leaves attached to woody or semi-woody above ground growth which persists over the winter, leaves more or less equal size

Clematis heracleifolia
Dianthus carthusianorum
Teucrium hircanicum

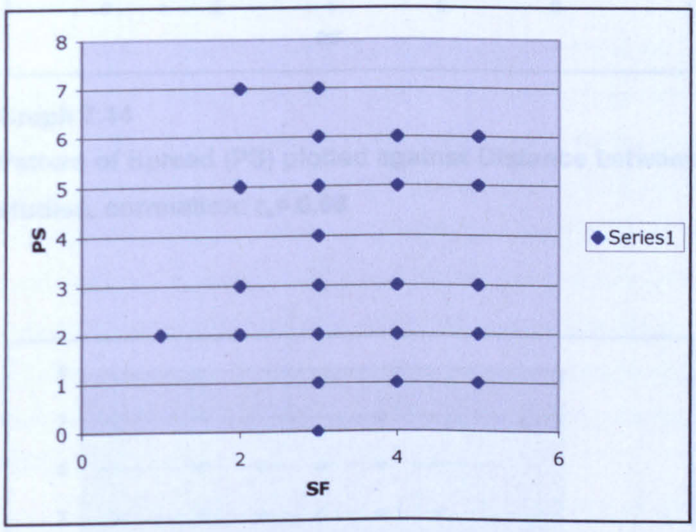
Chamaephytes to some extent, the woody growth of dianthus being only weakly so and limited in extent, and that of the teucrium over wintering only in mild winters. Such species could be more usefully seen as being at one end of a continuum which continues on to sub-shrubs such as *Lavandula* and many *Salvia* species rather than as true herbaceous plants, especially since the majority are species of low productivity or water-stressed habitats, and have little relevance to the more productive environments which are the focus here.

7.5.4 Mechanisms and rate of vegetative spread

It has already been noted how problematic it is to study vegetative spread. There is potentially a huge amount of variation between environments –illustrated by the appearance of *Euphorbia palustris* in cultivation and in the wild. In cultivation it forms a bushy clump, with multiple and multiply branched stems, and an apparently non-clonal, almost woody, base. In Cerknica, Slovenia, on the floor of a winter-flooded lake, it has been observed in two forms. One is as single stems amongst grasses, ranunculus and trifolium species. The other is as large clumps, more than 2 m^2, dominating neighbouring vegetation; it is not clear if these are groups of seedlings or clonal in origin.

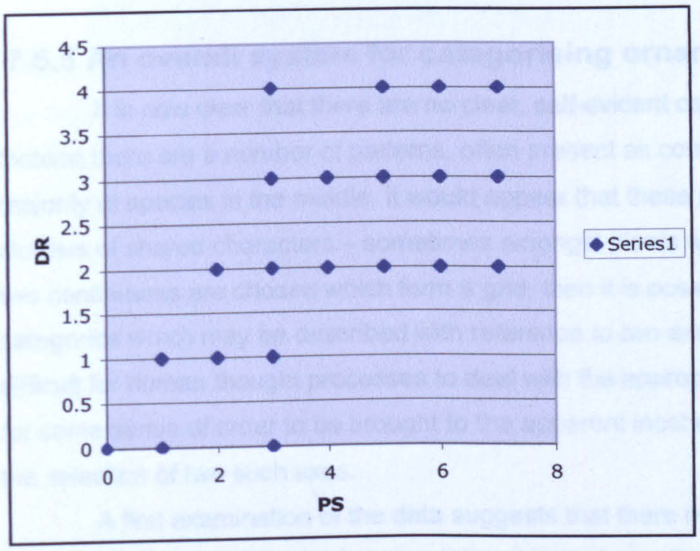
Vegetative spread may occur only sporadically and at a low rate in natural/semi-natural vegetation, and be important when opportunities arise for spread and recruitment. What is arguably important is *potential* for vegetative spread, which the near-optimum, low competition conditions of cultivation, is a good place in which to evaluate.

Pattern of spread (PS), distance between ramets (DR), rate of ramet production (RRP) and size of clump after 3 years (SC) are all clearly inter-related. They do not however amount to the same thing. *Pattern of spread* is an attempt at nuancing the continuum between non-clonal growth and guerrilla spread. Inter-ramet distance does vary greatly, but the ability of a species with far-flung ramets to spread may be compromised by a slow rate of production. RRP was the most difficult and unreliable to measure; instead a measure of outcome was also used – *size of clump after 3 years*.



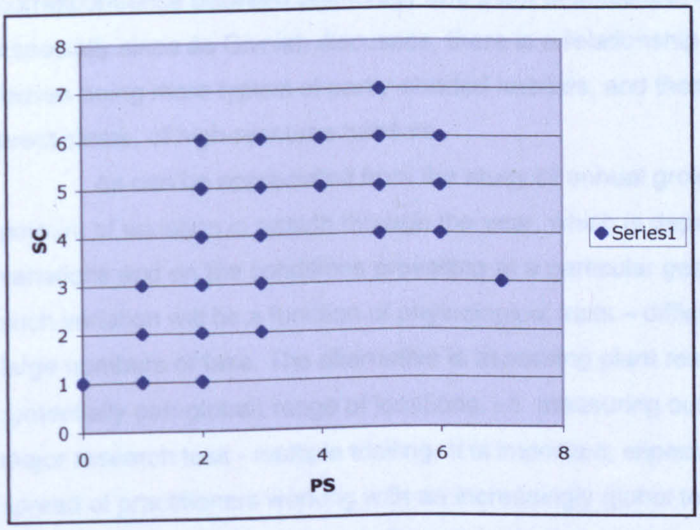
Graph 7.13
Start time of flowering (SF) plotted against Pattern of Spread (PS) for species studied, correlation: r_s= 0.68

There appears to be a tendency for early-flowering species to form clumps with spreading ramets, but not strongly spreading. Greater spreading ability would appear to be more likely to be found amongst later-flowering species. Of plants with an underground guerrilla vanguard spread, 21 out of 23 start to flower May or afterwards, with 13 after mid-summer. Of those with strong phalanx spread, 10 out of 17 started flowering before mid-summer. This suggests that there may be a tendency for phalanx spread to be more typical for earlier-flowering ornamental perennials.



Graph 7.14

Pattern of Spread (PS) plotted against Distance between ramets (DR) for the species studies, correlation: r_s= 0.68



Graph 7.15

Pattern of Spread (PS) plotted against Size of clump aftter 5 years (SC) for the species studied, correlation: r_s= 0.62

Correlations support the idea that increasing inter-ramet distance and a pattern of spread which favours spreading ramets further away from the parent plant favours spread. However, it is not a clear relationship, as rate of ramet production inevitably affects rate of spread. The relative success of guerrilla versus phalanx spread is also likely to vary between different environments.

7.5.5 An overall system for categorising ornamental herbaceous perennials

It is now clear that there are no clear, self-evident categories for herbaceous perennials. Instead there are a number of patterns, often present as continuums between extremes, with the majority of species in the middle. It would appear that these continuums intersect, creating clusters of shared characters – sometimes amongst plants with close taxonomic relationships. If two continuums are chosen which form a grid, then it is possible to generate a set of meaningful categories which may be described with reference to two axes. More axes, and it becomes very difficult for human thought processes to deal with the appropriate conceptualisation. It is possible for some sense of order to be brought to the apparent incoherence of herbaceous plants through the selection of two such axes.

A first examination of the data suggests that there is a link between plant architecture – as expressed here by the leaf-stem relationship and growth cycles – that lower-growing species with visually dominant pseudobasal leaves make earlier growth than species with upright stems carrying smaller foliage at height. This has been noted by Givnish (1982 and 1987), who notes the relationship with habitat, with height and upright stems being more characteristic of productive open habitats. It would make sense to assume that since there appears to be a measure of correspondence between phenology and plant architecture, that one be taken as one axis, especially since as Givnish discusses, there is a relationship with habitat, with species with basal leaves being more typical of partly-shaded habitats, and those with predominantly stem leaves on erect stems, of high-resource habitats.

As can be appreciated from the study of annual growth cycles, there is an enormous amount of variation in growth through the year, which is dependent upon year-to-year climate variations and on the conditions prevailing at a particular geographic location. Plant response to such variation will be a function of physiological traits – difficult to measure, and impractical for large numbers of taxa. The alternative is assessing plant response to conditions in a wide (potentially pan-global) range of locations, i.e. measuring outcomes, but again this requires a major research task - multiple trialling. It is important, especially given the wide geographical spread of practitioners working with an increasingly global temperate zone horticultural flora, thatgeneralisations are not made from the experience of one location. Hence the use of plant phenology as one axis of a system of categorisation is deeply problematic.

Plant architecture is the expression of genetically determined traits, whereas other measures of morphology which play a major part in plant selection by practitioners and in competition are inevitably more affected by gene x environment interactions, e.g. height and density of canopy cover. It is therefore proposed that *leaf-stem relationship,* as an expression of architecture, as an expression in turn of genetically driven traits, be taken as one axis.

Vegetative spread is a key issue, though complex to measure, and much affected by gene x environment interaction. Given its importance and the fact that the expression of genetic traits conducive to vegetative spread is enhanced under the conditions of cultivation, it would seem an obvious second axis. *Pattern of spread* is chosen as the decisive figure of assessment, as although not continuous or quantified, it does relate to both means of spread and a rough assessment of spreading ability. Furthermore, the importance of the word *pattern* must be stressed, as *pattern of spread* describes a genetically-driven architecture or morphology (and also to some extent phenology) of spread – rate and extent will be the result of GE interaction, but the underlying pattern will be more fundamental, and therefore more appropriate for use in an attempt at systematising data as here.

See *Perennial Category Grid*

PERENNIAL CATEGORY GRID

Creating a grid for categorising herbaceous perennials based on measurements of 'pattern of spread' and 'leaf-stem relationship'

G = graminoid

Leaf/Stem Relationship	Pattern of Spread						
	0 Short-lived	**1 No ramets**	**2 Very tight clumps of ramets**	**3 Vigorous phalanx spread of ramets**	**4 Strongly spreading phalanx**	**5 Clump with distinct guerrilla vanguard**	**6 Widely scattered guerrilla ramets**
I (1-2) Basal leaves			Carex dipsacea G Helleborus x hybridus Hemerocallis 'Golden Chimes' Kniphofia var.	Epimedium perraldianum Hosta fortunei Iris sibirica Liriope muscari	Trachystemon orientalis	Crocosmia 'Lucifer' Ophiopogon bodinieri	Cirsium canum Inula cf. Racemosa
II (3-4) Basal /pseudobasal leaves predominate		Aquilegia vulgaris Thalictrum aquilegifolium	Brunnera macrophylla Cephalaria gigantea Eryngium bourgatii Eryngium varifolium Geranium asphodeloides Geranium pratense Geranium sylvaticum Heuchera micrantha Papaver orientale Phlomis russelliana Pulmonaria officianalis	Acanthus spinosus Achillea millefolium Alchemilla mollis Anemone x hybrida Bergenia 'Abendglut' Geranium phaeum Geranium renardii Geranium sanguineum Geranium x oxonianum Geranium 'Johnsons Blue'		Cirsium rivulare Persicaria bistorta Symphytum caucasicum	
III (5-6) Greater importance of stem leaves			Astrantia major Echinops ritro Geranium 'Rozanne'		Filipendula ulmaria	Persicaria amplexicaule	Filipendula rubra 'Venusta'
IV (7-12) Stem leaves only	Tanacetum parthenium	Clematis heracleifolia Desmodium canadense Knautia macedonica Lythrum salicaria Salvia nemorosa Salvia verticillata	Aconogonon 'Johanneswolke' Amsonia orientalis Anaphalis triplinervis Artemesia lactiflora Aruncus dioicus Aster puniceus Baptisia australis Calamintha grandiflora Campanula latifolia Centaurea montana Dianthus carthusianorum Echinaea purpurea Eupatorium maculatum ssp.purpureum Euphorbia palustris Euphorbia polychroma Lunaria rediviva Miscanthus sinensis G Molinia caerulea G Nepeta x faassenii Origanum laevigatum Panicum virgatum G Sanguisorba tenuifolia Sedum spectabile Solidago rugosa Stipa arundinacea G Stipa calamagrostis G Stipa gigantea G Vernonia crinita Veronicastrum virginicum	Aconitum arctuatum Aconitum napellus Aster cordifolius Calamagrostis x acutiflora G Helianthus 'Lemon Queen' Rudbeckia fulgida var. deamii Rudbeckia 'Juligold' Teucrium hircanicum	Tanacetum macrophyllum	Aster novi-belgii Aster umbellatus Chelone obliqua Euphorbia cyparissus Lysimachia ciliata Lysimachia clethroides Lysimachia punctatum Macleaya cordata Phlox paniculata Senecio tanguticus Thermopsis caroliniana	Euphorbia schillingii Leucanthemella serotina Monarda hybs.

7.5.5.1 Creating groups based on Pattern of Spread (PS) and Leaf-Stem Relationship (L/S).

For the purposes of simplification, Leaf /Stem (L?S) Group 7.IV is not included in the *Perennial Category Chart* as all three members: *Persicaria affinis*, *Veronica incana* and *Vinca minor* are very untypical, being procumbent. Species with a short lifespan (<3 yrs) – PS 0, which are not the focus for this study might also be excluded (*Tanacetum parthenium*).

An assessment of how useful such a grid system of categorisation is for ornamental perennials can only be made over a long period of time; in particular its use and assessment by practitioners, particularly in climate zones or habitats other than that to be found in southern Britain; its application to other species would also be an important test. Its limitations must also be realised; it is not in any sense a guide to cultivation or selection. Instead it is a tool, to bring some order to a disordered field; by focusing practitioner attention to the key issues of plant architecture and pattern of vegetative spread it might make the task of selection for plant function and visual appearance within planting design an easier task. However, it is hoped that since the two axes used to describe the grid are the key factors in describing plant architecture, that there will be some predictive power in relation to competitive ability; at the least there is now a more coherent framework with which to analyse the relationship between competitive performance and morphology.

Assessing the value and coherence of the grid requires a reading of it in relation to practitioner experience – by its very nature often unrecorded and intuitive. Reading the grid also facilitates a macro-view of the research, and highlights mistakes and inaccuracies.

An initial examination of the grid leads to:

- The importance of stressing that each category is on a continuum, so inevitably boundaries are fuzzy,
- Some re-evaluation of gradings given for pattern of spread – perhaps inevitable in a system which relied heavily on visual assessment rather than accurate measurement. The following were re-assigned, from PS 2 to PS 3:

  Aster cordifolius 'Little Carlow'
  Calamagrostis x acutiflora 'Karl Foerster'
  Epimedium perraldianum
  Geranium 'Johnson's Blue'
  Iris sibirica
  Liriope muscari
  Rudbeckia 'Juligold'
  Solidago rugosa
- PS 2 is much the dominant category – reflecting either the bias of the author's work or horticulture generally towards species with a particular robust, but limited

spreading capability. Given the number of other criteria looked at, there is considerable scope for further sub-division if required. One possible option is the removal of graminoids (indicated by G) from the grid altogether – they are a highly distinct group morphologically and are recognised as distinct by the horticulture and landscape industry; given similar architecture, their most important morphological character as it relates to cultivation is the continuum which reaches from caespitose character to tillering (or similar means of extensive vegetative spread (Grounds 1989).

GCG 1						
	1	**2**	**3**	**4**	**5**	**6**
I		xx	xx		x	
II			x			
III						
IV		x				
GCG 2						
	1	**2**	**3**	**4**	**5**	**6**
I						
II			x		xxx	
III						
IV	x	xx				
GCG 3						
	1	**2**	**3**	**4**	**5**	**6**
I						
II		xxx	x			
III						
IV			x			
GCG 4a						
	1	**2**	**3**	**4**	**5**	**6**
II	x	xxx	x			
III						
IV		xx			x	

GCG 4b						
	1	**2**	**3**	**4**	**5**	**6**
I		x	xx			xx
II	x	xxxx	xx			
III		x		x	x	x
IV	xx	xxxxxxxxx	xx	x	xx	x
GCG 4c						
	1	**2**	**3**	**4**	**5**	**6**
I						
II			x			
III						
IV		x	xxx		x	
GCG 5						
	1	**2**	**3**	**4**	**5**	**6**
I						
II			x			
III		xx				
IV	x	xxxxxxxxxxxx			xxxxx	xx

Table 7.7

The Pattern of Spread (categories 1-6) Leaf-stem Relationship (L/S categories I-IV) grid for each Growth Cycle Group (GCG).

x = one species studied

For definitions of Pattern of Spread used here see: *7.2.4.4 Nature of ramets/spreading ability*

Growth Cycle Groups see: *7.5.2 Phenology and growth cycle groups*

Leaf Stem Relationship used here see: *7.5.3.5 Categories based on leaf-stem relationship (L/S)*

A comparison of the overlap between Growth Cycle Groups (GCG) and the grid based on Pattern of Spread and Leaf-Stem Relationship shown in table 7.7 confirms the previous discussion. Of the species studied, there is strong tendency for species which have wintergreen foliage (GCG 1) or which can make early growth followed by repeat growth later in the summer (GCG 2) to have architecture dominated by basal/pseudobasal leaves (L/S I and II) and those which continue growth, and to flower, after mid-summer (GCG 5), to have an architecture dominated by upright stems and a more even distribution of leaves (L/S IV). Summer-flowering species in GCG 4 and 5 are also more likely to spread in guerrilla fashion, as is indicated by the higher numbers of species given Pattern of Spread ratings of 5 or 6..

Whilst the *Perennial Category Grid* illustrates that herbaceous plants cannot be divided up into discrete 'types', it, along with other evidence gathered in this study, suggests that certain distinct combinations of traits may be found, across taxonomic boundaries. It is also suggested that another gradient be recognised, related to resource conservation as opposed to extensive resource foraging.

7.5.5.2 'Geophyte/Caespitose-type tendency' in forbs and the resource conservation strategy

The caespitose grass habit is well established in the literature (e.g. Briske & Derner 1988). It is suggested by de Kroon and Bobink (1997) in a study of Molinia *caerulea* that tussock-forming graminoids are able to 'store' nitrogen through a cycle of deposition of litter, re-mineralization, and re-absorption through the roots, beneath their dense tussocks – which are practically impenetrable to other species . Briske and Derner term the tussock strategy a 'Consolidator strategy' whereby grasses effectively monopolise resources within their immediate environment, and that resource accumulation may be more important as a mechanism of resource monopolisation *vis a vis* competing vegetation than as a mechanism to increase availability of nutrients to ramets. This strategy is clearly very successful in many stressful habitats, e.g. moorland and steppe, but also in highly productive prairie habitats (Wedin & Tilman 1990, Blair et al. 1998); perhaps it occurs in *either* stress-prone habitats or productive ones with a short-growing season. It is perhaps not a competitive strategy *per se* but appears to be essentially one of securing persistence. It is noted that this strategy is inherently prone to disruption, at least where nitrogen availability is high, as the 'locking-up' strategy is thus undermined (Wedin & Tilman 1990).

It has been suggested here that it might be useful to consider this habit as one end of a continuum in grass/graminoid behaviour. Caespitose species dominate space through the existence of a physically tough and tightly-packed mass of ramets which is difficult for other species to penetrate and aids their development of a zone around them dominated by their shade-creating foliage and their roots.

Geophytes also rely on storage of nutrients, but this is done within bodies below ground level. Stored nutrients enable the plants to conserve resources. It is suggested that both the caespitose and the geophyte strategies both involve conserving resources in or very close to the plant; a characteristic linked closely to a lack of mobility in the plant, as would be observed amongst more competitive and rapidly-growing species.

It is also suggested that some forbs also display similar behaviours. Above (7.5.3.2 *Relationship between character of emerging shoots and leaf-stem relationship*), it was noted that some herbaceous species rely on stored resources in order to make a substantial amount of early-season shoot growth as a survival strategy in competitive environments. In the opinion of some who have grown *Baptisia australis* (Cullina 2000, Gerritsen & Oudolf 2003) this plant shows a character which indicates that it could belong to this group – it is slow to establish but very long-lived and well able to survive competition. Such species may share certain characteristics with both caespitose grasses and geophytes: considerable investment in stored resources, rapid growth on emergence, but slow rate of establishment – a reflection of the investment in underground resources which enables long-term survival.

It is suggested that several species in Group PS 2 – L/S IV of the Perennial Grid display this behaviour, and that a caespitose habit and/or a geophyte habit be recognised as one extreme of a continuum of clonal forbs; one further step along the continuum might be species such as *Baptisia australis* with a caespitose-type habit. Several species in this group have one or more of the following characteristics, which make them very distinct from species that readily form clumps from ramets which may be easily separated:

- Woody rootstock - *Aruncus dioicus* "difficult to divide owing to woody rootstock" (Jelitto & Schacht 1990), *Euphorbia palustris and* Eupatorium *maculatum are* similar.
- Exceptionally dense production of shoots from a small clump - *Artemisia lactiflora, Anaphalis triplinervis* (see Illustration A1.). These species are however not noted as having reputations for being long-lived and resilient in neglected locations - *Euphorbia palustris* and *Eupatorium maculatum* (Gerritsen & Oudolf 2003, Jelitto & Schacht 1990), Also *Amsonia* species. It is noted that this is not due to competitive ability but to ability to survive competition, i.e. competitive response not effect.
- *Iris sibirica* has a character which is both reminiscent of caespitose grasses (a tight mass of ramets), and of geophytes (an extensive system of thick roots) and a character unlike either of them – the non-persistence of ramets from year to year, resulting in the plant slowly moving its location.

Further investigation into this group would need to focus on root architecture and storage capabilities. It is noted that all hemi-cryptophytes store resources below ground in specially adapted tissues (or in litter and soil dominated by the plant) to a greater or lesser extent. The recognition of a spectrum of nutrient storage options from 'very conservative' to 'minimal' would be a valuable contribution to understanding herbaceous perennials. Distinct positions on this gradient are illustrated in fig. 7.6. That resourse conservation strategies are perhaps most realistically studied in the wild is indicated by the much greater integration of species in the wild, suggesting that it is less easy to monopolise resources – see fig. 7.7.

The opposite end to the geophyte/caespitose tendency is a highly mobile resource-foraging strategy. The monarda taxon studied is an extreme example; any species with a guerrilla strategy such as the lysimachia species studied could also be placed on this end of the spectrum – which could perhaps be described as 'discontinuous spreaders'.

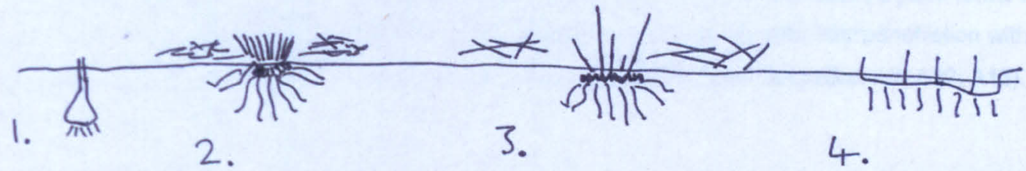


Fig.7.6

Resource conservation strategies

Plants are shown dormant.

Geophytes (1) effectively store resources within plant tissues, and only rarely dominate space.

Caespitose grasses (2) store resources in leaf litter and in soil around the plant; a combination of growth habit, efficient foraging and dense leaf litter reduce competition around them, so enabling them to monopolise resources.

Many phalanx-spreading clump-forming forbs (3) store resources in roots, which may store a greater or lesser quantity. Resources stored in leaf litter and surrounding soil are far more likely to be shared with neighbours, depending on a variety of factors, such as density of litter and foraging efficiency of roots. *Iris sibirica* (see 5.2.1 *Examining the relationship between plant characters and ECA through mean values*) is one which does all these very effectively.

Forbs with a more fugitive character, in particular those with a guerrilla spread (4) may store resources in roots, but their dispersed character means that there is only limited recycling from litter or monopolisation of soil nutrients.

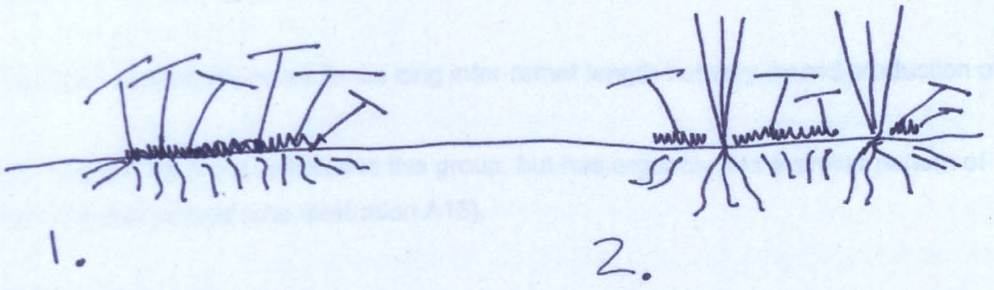


Fig.7.7

Resource conservation strategies in the wild and the garden

The growth of perennials in garden or other horticulturally managed situations often gives a false impression of their ability to monopolise space and resources, lending support to the idea that only study of plants in the wild can reveal reliable data about this aspect of their performance. In (1) in cultivation, a plant forms a dense clump, completely dominating space, (see illustration A8) in (2) in the wild, interpenetration with other species (often graminoids) occurs, so space and resources are shared (see illustration A9, A12, A13).

Potential in EBPS

The potential for some in this group in EBPS is considerable, with the proviso that slow establishment may cause problems. Once established, the ability of these species to survive and cope with competition long-term would make them very useful.

7.3.5.3 'Discontinuous spreaders'

A number of species spread outwards somewhat erratically and discontinuously. They are not a cohesive group, but all can be regarded as having a strategy of more aggressive resource foraging:

Monarda hybrids form annual shoots, which tend to move outwards from the original point of planting. The shoots are highly dependent on the absence of competition. Possibly for this reason they are recommended only for highly managed borders by Hansen & Stahl (1993).

Inula cf.racemosa spreads slowly and steadily but not predictably. Its thick roots, persistence of clump core and almost woody clump suggests that it is perhaps best included in with conservative strategy species such as geophyte/caespitose tendency.

Cirsium canum, Filipendula rubra 'Venusta', *Leucanthemella serotina*, all form clumps at varying speeds, but in somewhat unpredictable directions. It is noted that on older plants (5 years plus, not included in this study) that clump cores tend to deteriorate.

Euphorbia schillingii is noted for its long inter-ramet length but very limited production of ramets.

Phlox paniculata is not included in this group, but has arguably has a similar pattern of discontinuous spread (see illustration A16).

Potential in EBPS

Those discontinuous spreaders which are able to spread in conditions where there is competition from neighbours have potential – their spreading ability suggests long-term reliability, quite apart from the longevity of the clump core in some. Discontinuous spreading is less likely to suppress neighbours, therefore enhancing potential for high-diversity plantings; none of these species have been noted as suppressing neighbours in any of the locations studied.

7.3.5.4 Aggressive spreaders

Species with a reputation for such a strong spread that they are sometimes regarded as dysfunctionally invasive in horticultural contexts are to be found in Pattern of Spread groups 4-6 – i.e., where inter-ramet distance is long. 'Invasiveness' is a highly subjective concept however. Of the species which are regarded as potentially problem species, in the garden literature (e.g. Carter et al. 2007, Thomas 1976, Gerritsen & Oudolf 2000, 2003, Rice 2006): e.g. *Euphorbia cyparissias, Macleaya cordata, Leucanthemella serotina, Symphytum caucasicum, Lysimachia punctata, L. clethroides, Thermopsis caroliniana, Trachystemon orientalis*), these do not appear in only one of the Perennial Grid boxes, but are scattered across at least five; data collection on more plants would probably increase this number. It almost goes without being spelled out, that aggressive spread is highly dependent upon certain ecological conditions being present; in addition it is the result of several traits, not just long inter-ramet distance, but rate of ramet production, and ramet lifespan.

What sets these species apart from the 'discontinuous spreaders' is that they continue to hold ground they have occupied, and should therefore not be regarded as the end of the spectrum which began with the conservative geophyte and caespitose strategists.

Potential in EBPS

These species are invaluable for quick establishment and occupation of larger areas of ground where weed take-over is the alternative. They might also be worth trying in areas where vigorous grasses and other species will, because of low-level management strategies, be expected to dominate.

7.3.5.5 'Opportunist spreaders'

Possibly a construct of the research, but an intriguing group made visible by the grid is Group PS 5 – L/S II: *Cirsium rivulare, Persiciaria bistorta, Symphytum caucasicum.* All are plants which either thrive in moist, productive environments or are known to inhabit them. All form substantial clumps and are able to make growth over a long season – here they are termed 'opportunist spreaders' as they seem to be particularly able to react quickly and flexibly to good growing conditions: moisture in late summer or early or late year warmth, in contrast to many other species which seem to be more restricted, or programmed, in the times at which they make active growth. However, they are very different in their ability to spread: the cirsium appears to spread somewhat erratically (Gerritsen 2003), the persicaria to be a strong spreader but not invasive (see 4.1 in *3.The use of transects to investigate established ecologically-based plantings*), the symphytum to be extremely invasive (author observation, Cowley Manor, and other locations).

Indeed, perhaps the best way to understand this group is to see the ability to respond to good growing conditions as a trait which cuts across the resource conservation – foraging gradient just described.

Potential in EBPS

The ability of these species to form large clumps makes them attractive for EBPS, although in some cases invasiveness could be an issue. Most importantly though, their ability to respond to good growing conditions in climates which offer a long growing season, and with good overall, but occasionally erratic water supply, makes them ideal for maritime climates such as north west Europe. Their usefulness in climates with short growing seasons is likely to be less so, as their advantages in being able to react to good growing conditions with growth would be limited.

7.3.5.6 An alternative grid for understanding herbaceous perennials

Discussion of the groups tentatively identified above suggests an alternative grid:

X-axis:

Resource conservation <<<<<<<<<<<<<<<<<<>>>>>>>>>>>>>>> Extensive resource foraging
geophytes, caespitose habit....phalanx clump formers...,..aggressive spreaders.....discontinuous spreaders

Y-axis

Decreased ability to respond to beneficial growing conditions
V
V
V
V
V
V
Increased capacity to respond to beneficial growing conditions

It is noted that the x-axis bears a close resemblance to the *Pattern of Spread* measure in the *Perennial Category Grid*, but instead is based on ecological and physiological criteria. What is missing are the species which do not have functioning ramets – these could possibly be located to the left of the geophytes; this however awaits the outcome of future research.

It is suggested that the above grid, based on an understanding of plant ecological and physiological functioning rather than morphology and phenology, and therefore requiring more in-depth research, may be alternative model for future research. What might be particularly valuable for practitioners is a better understanding of the y-axis: response to temperature, light and resource availability by different ornamental herbaceous taxa – this is fundamentally important in plant specification for different climate zones.

7.3.5.7 An alternative system for describing plant character

The system developed by Ellenberg for describing the most important parts of a species' distribution in relation to a range of habitat descriptor variables is a possible model for describing the key phenological and morphological characters under consideration. Just as the Ellenberg numbers (Ellenberg 1974) allow the reader to get a quick summary of the species/habitat/distribution relation, so might a similar system for horticultural and landscape practitioners with regard to characters essential for plant architecture and performance through the year. Characters are chosen which are easy to assess, which present a more or less clear gradient, and which are relevant to plant performance and competition (see next section).

Growth Cycle Group

1. Truly evergreen species, i.e. leaves living for at least one year
2. Very strong tendency to substantial later season basal growth, at least partly replacing spring growth.
3. Early dormancy
4. Maximum canopy height achieved by July
    - 4a. Flowering no later than May
    - 4b. Mid-summer flowering
    - 4c. Late summer flowering
5. Maximum height achieved later than July

Start time of flowering

1. Late winter/early spring, i.e. directly temperatures begin to rise.
2. Spring, simultaneously with expansion of new foliage.
3. Late spring to early summer, i.e. around the time when light levels at the highest.
4. Post mid-summer's day.
5. Late summer to autumn, i.e. towards end of growing season, when foliage growth has reached its maximum extent.

The value of including this information in a brief summary of plant characters, when it is largely duplicated (by the previous) should be justified – but since flowering time is of crucial importance to practitioners and is not entirely described by the previous figure, this does seem appropriate.

Maximum Canopy Height

1 - 0 - 99 mm
2 - 100 - 299 mm
3 - 300 - 599 mm
4 - 600 - 999 mm
5 - 1000 -1499 mm
6 – 1500- 1999 mm
7 - 2000 – 2999 mm
8 – 3000 mm plus

Leaf-stem relationship (illustrated in fig.7.2 in 7.4.1 *Detail of contents of Perennial Data Chart*)

I Basal leaves
II Effectively basal (pseudobasal) or emergence very close to ground
III Division between pseudobasal and stem leaves
IV Stem leaves

Pattern of spread (illustrated in fig.7.7 below)

0 - short-lived, not spreading vegetatively, i.e. non-clonal
1 – very tight clump, with shoots which do not clearly function as ramets, or ramets present but so few that spread is minimal, or with a caespitose habit or similar
2 - tight clump, definite ramets, phalanx
3 – clump, with guerrilla outliers
4 - clump with underground guerrilla ramets
5- clump with very widely spread guerrilla ramets
6 - sparse clump, underground spread, limited ramet production
7 – non-persistent growth, with clump breaking up on the side previously occupied
8 - rooting from stems above ground surface

Rate of spread

0 – non-clonal
1 – spread effectively minimal, tight clump
2 – spread slow, with slow rate of ramet production and limited inter-ramet distance
3 – spread moderate
4 – spread fast, with higher rate of ramet production and/or inter-ramet distance clearly visible
5 – spread very fast, owing to high rate of ramet production and with inter-ramet clearly wide

It may be objected that this measure partly duplicates the previous. However pattern and rate of spread are distinct, and do not necessarily co-incide. It may also be objected that the measure could be made quantitative – which indeed it could, but rate of spread is undoubtedly very dependent upon climate; too much precision would inevitably refer only to the climate zone in which any measurements were taken.

Projection onto ground surface

Where GC+SE to July is equal to:

1 – 0-9
2 - 10-14
3 - 15-19
4 - 20-24
5 - 25-30+

GC+SE to July is chosen as the most appropriate way to measure a plant character which is, admittedly, difficult to measure, given that it is highly dependent upon growing conditions and the nature, and in particular the density, of neighbouring vegetation. Essentially the 0 to 30 scale represents a gradient of increasing ability to shade the ground immediately below and around the basal clump, and reflects two factors: the lateral extent of foliage and the early production of such foliage.

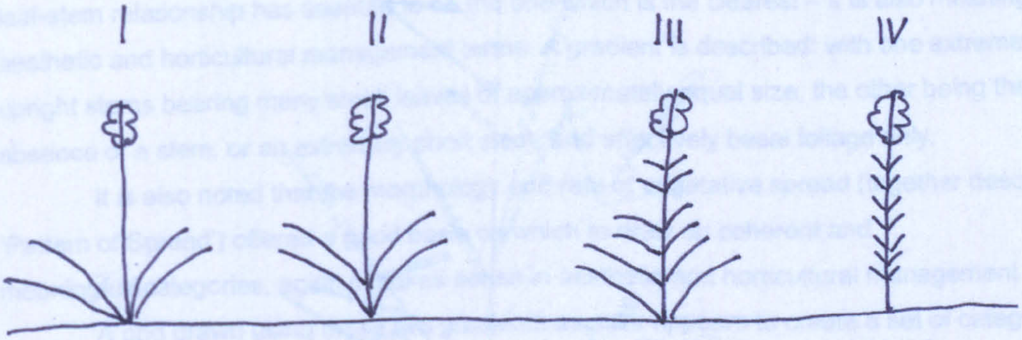


Fig. 7.7
Summary of simplified Leaf-stem relationship categories I to IV.

7.6 CONCLUSIONS

Two approaches to categorisation were made, one based on relatively distinct phenological differences in the species studied, the other on an understanding of the spectra of morphological differences shown.

7.6.1 Phenology-based categories - Growth Cycle Groups.

The following groups were described. However it should be noted that these are highly dependent upon growing conditions, and may only apply to the relatively maritime climates of northwest Europe.

Group 1. Truly evergreen species, i.e. leaves living for at least one year
and summarises the growth cycle groups discussed below:
Group 2. Very strong tendency to substantial later season basal growth, at least partly replacing spring growth.
Group 3. Early dormancy
Group 4. Maximum canopy height achieved by July
Group 4a. Flowering no later than May
Group 4b. Mid-summer flowering
Group 4c. Late summer flowering
Group 5. Maximum height achieved later than July

7.6.2 Morphology-based categories

In attempting to describe coherent and meaningful categories based on morphology, the leaf-stem relationship has seemed to be the one which is the clearest – it is also meaningful in aesthetic and horticultural management terms. A gradient is described: with one extreme being upright stems bearing many small leaves of approximately equal size, the other being the absence of a stem, or an extremely short stem, and effectively basal foliage only.

It is also noted that the morphology and rate of vegetative spread (together described as 'Pattern of Spread') offered a good basis on which to draw up coherent and meaningful6categories, again it makes sense in aesthetic and horticultural management terms.

A grid drawn using these two gradients as axes appears to create a set of categories that is also coherent and meaningful; there appears to be some synergistic relationship with the phenology-based categories; the grid also appears to describe some relatively discrete and distinctive categories that deserve further investigation. However a variety of other morphological distinctions may cut across the grid.

7.7 APPENDICES

7.7.1 Appendix 1 Perennial Data Table.xls	(on CD)
7.7.2 Appendix 2 Characters measured monthly.xls	*(on CD)*
7.7.3 Appendix 3. Monthly data (Folder)	*(on CD)*
7.7.4 Appendix 4 Height summaries.xls	*(on CD)*
7.7.5 Appendix 5 Degree of Basal Cover.xls	*(on CD)*
7.7.6 Appendix 6 Growth Phenology.xls	*(on CD)*
7.7.7 Appendix 7 Investigation of correlations.xls	*(on CD)*

7.7.1 Appendix 9 Plant Architecture Diagrams

A set of schematic diagrams was drawn during 2005 in order to elucidate plant architecture, specifically the relationships between the following characteristics:

Plant height
Leaf number
Positioning of leaves of different sizes on stem
Proportion of leaf lamina to petiole
Branching and positioning of growth tips
Leaf senescence

Drawings were generally made at the commencement of flowering, with stems of a good average condition, relatively unaffected by neighbour competition. Inflorescences are shown only very schematically and crudely – simply to indicate position. Scale varies and is indicated for each species.

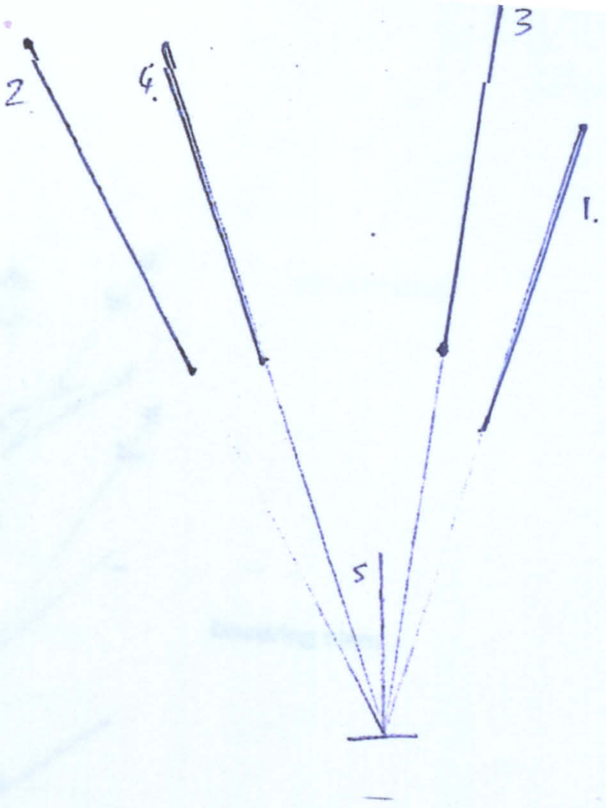
ABBREVIATIONS

○	flowers or flower buds, schematic representation.
	buds, undeveloped shoots
	green – leaf lamina black – petiole
1. 2. 3. etc.	leaves numbered in order of emergence

Acanthus spinosus

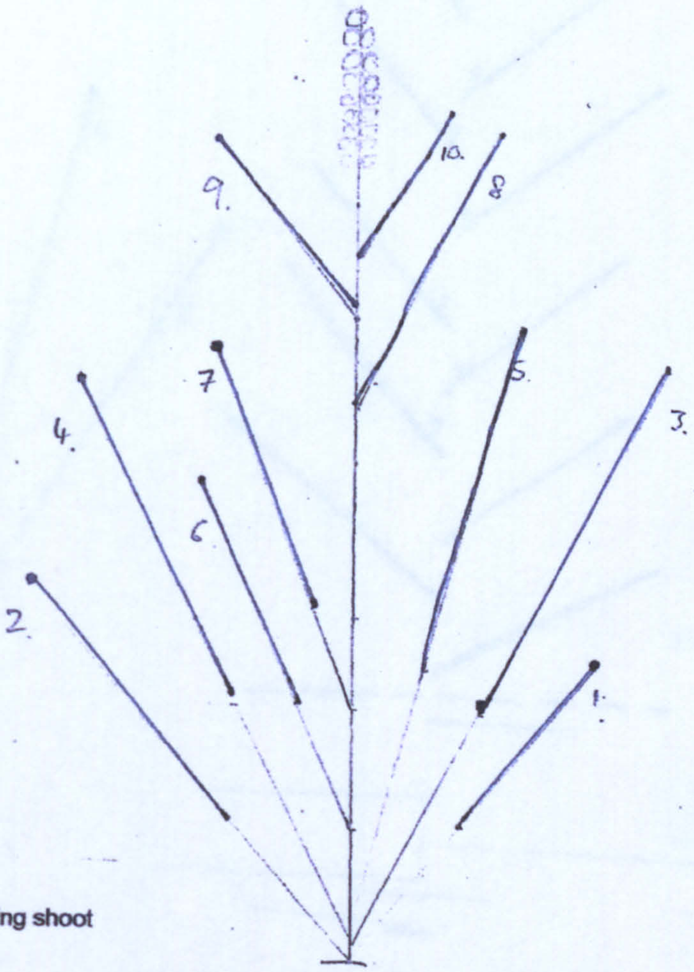
3.July.2005

1:10



non-flowering shoot

4, 5 – immature

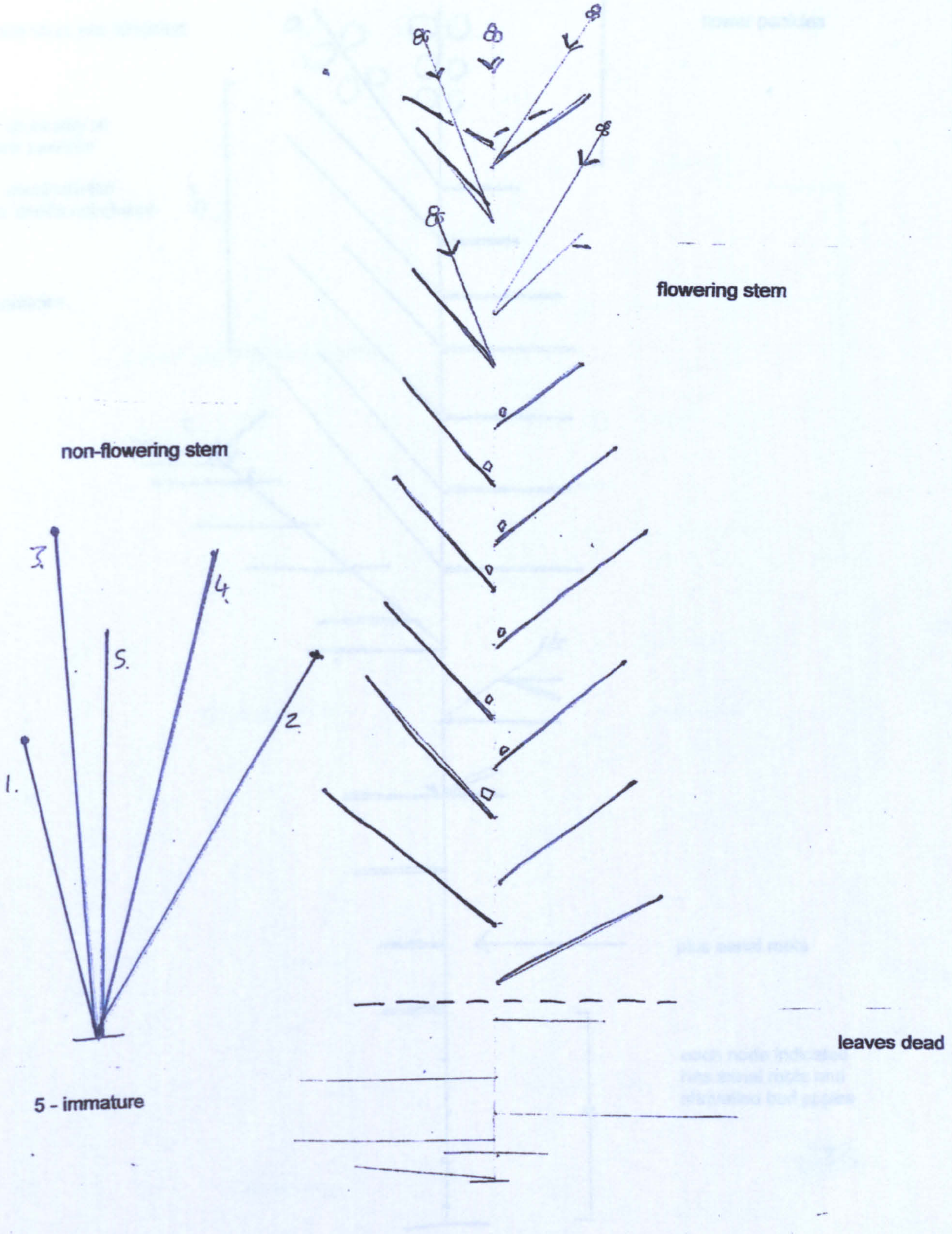


flowering shoot

Achillea millefolium

2.July.2005

1:4



ACONOGONON 'JOHANNESWOLKE'

18.June.2005

1:10

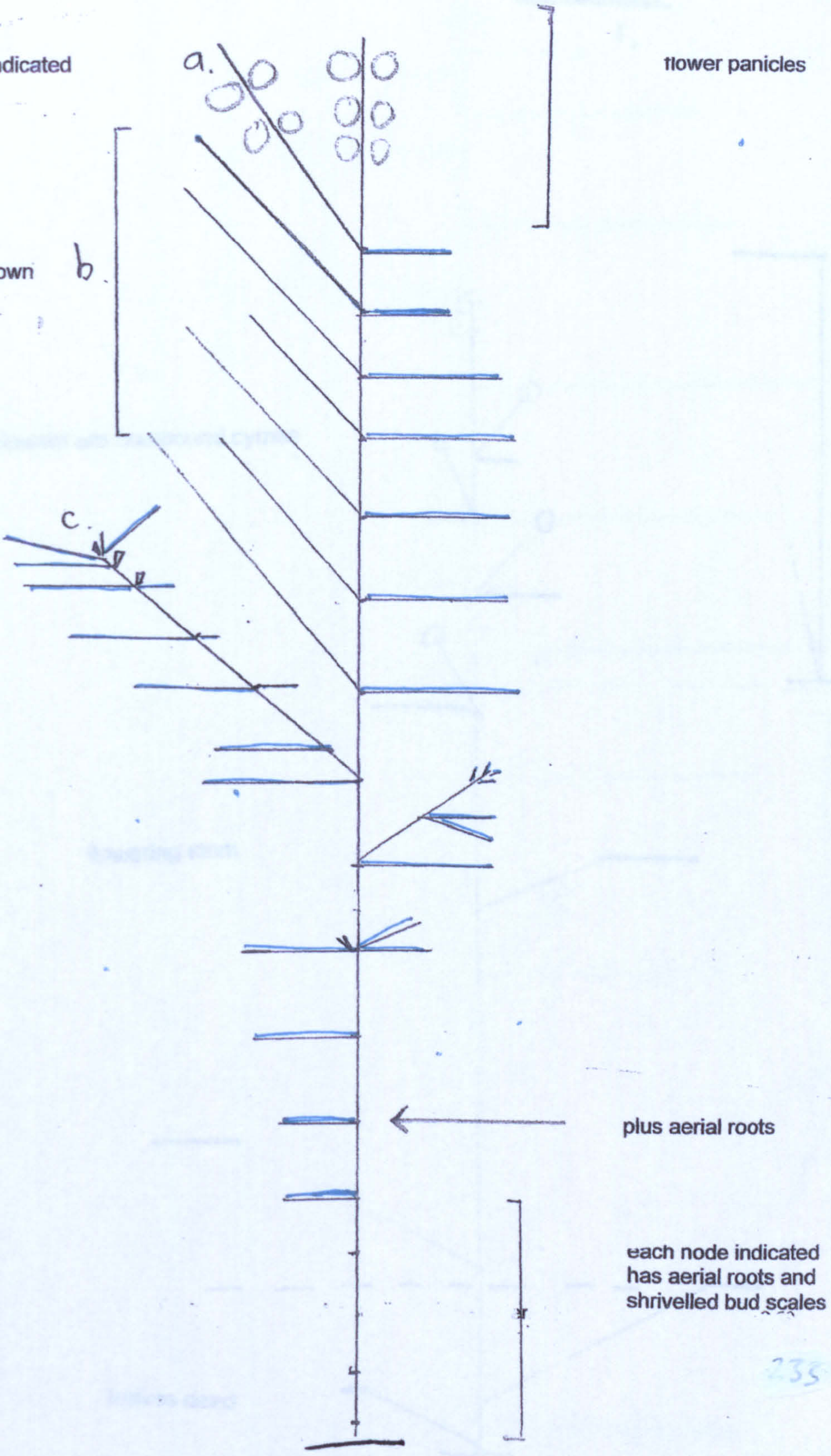
petioles short, not indicated

a. shoot with all flower panicles

b. shoots similar to c. details not shown

c.

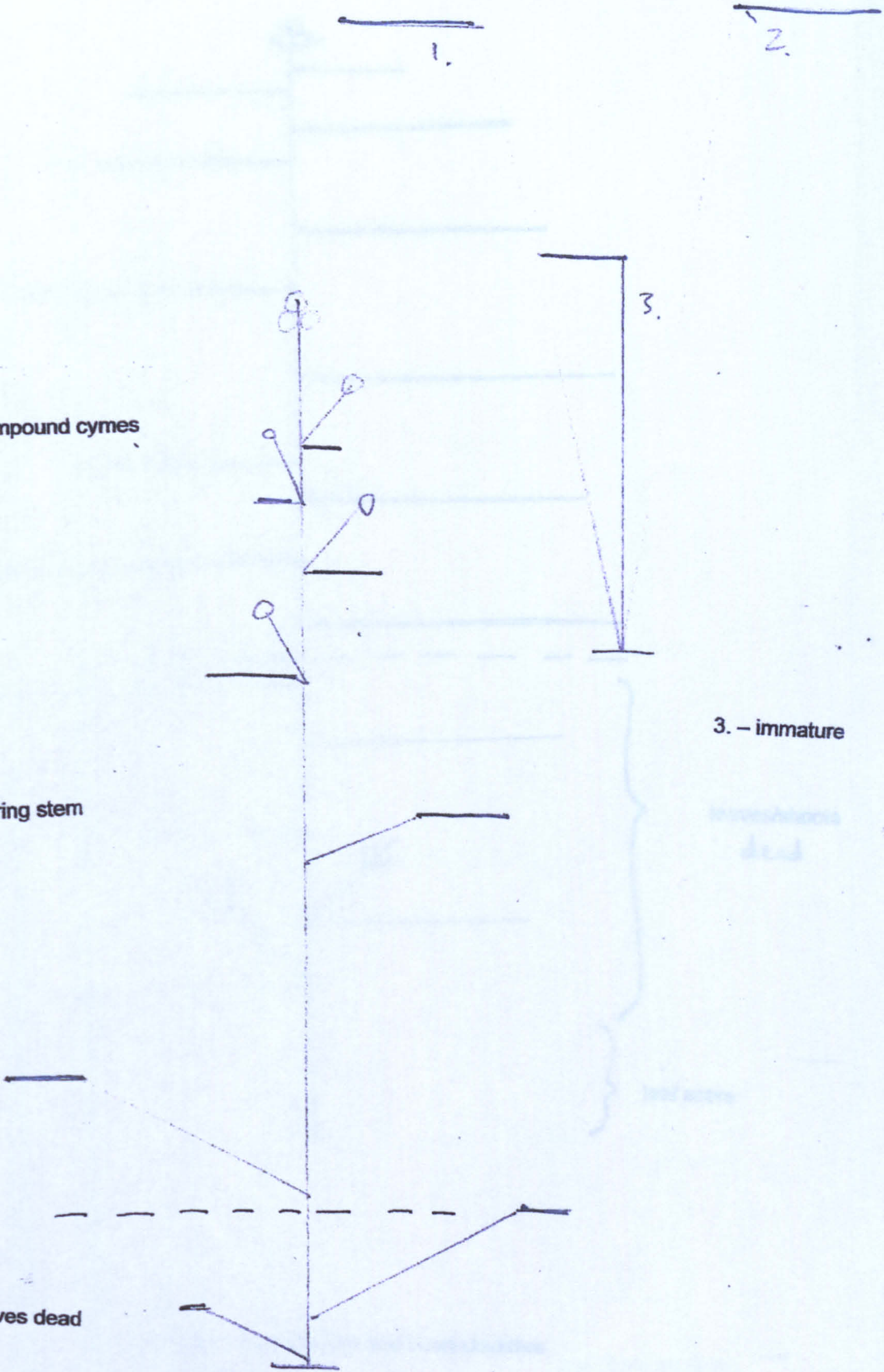
flower panicles



Alchemilla mollis

2.July.2005

1:4



non-flowering stem

flowers are compound cymes

flowering stem

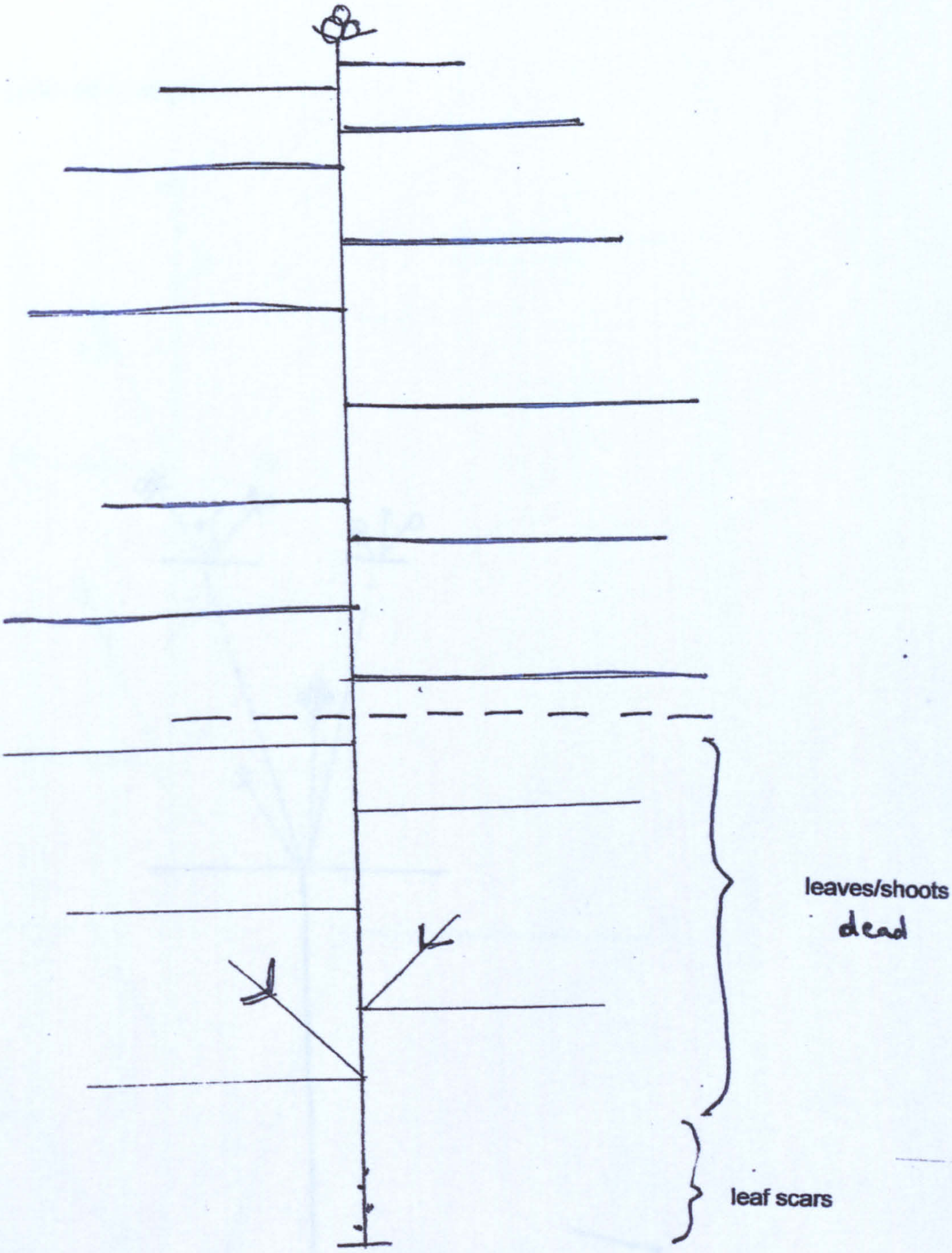
3. – immature

leaves dead

Anaphalis triplinervis

19.July.2005

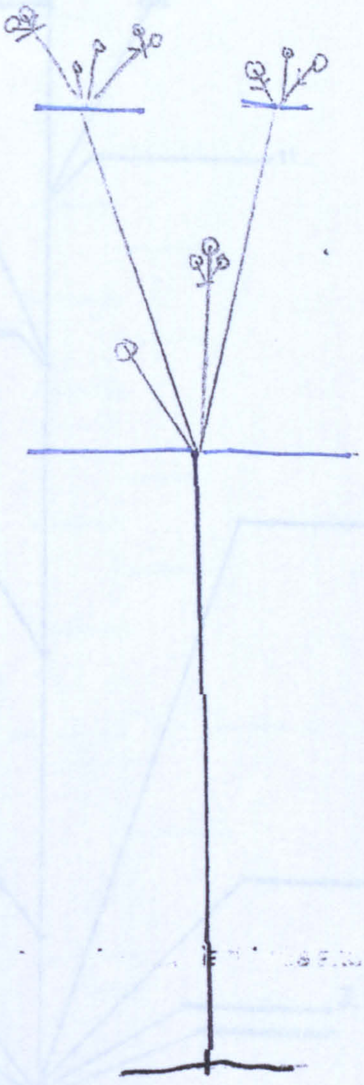
1:2



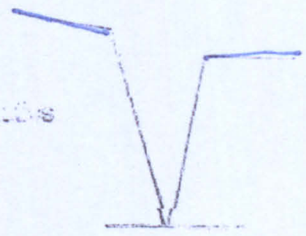
Anemone x hybrida

25.Aug.2005

1:10



flowering stem



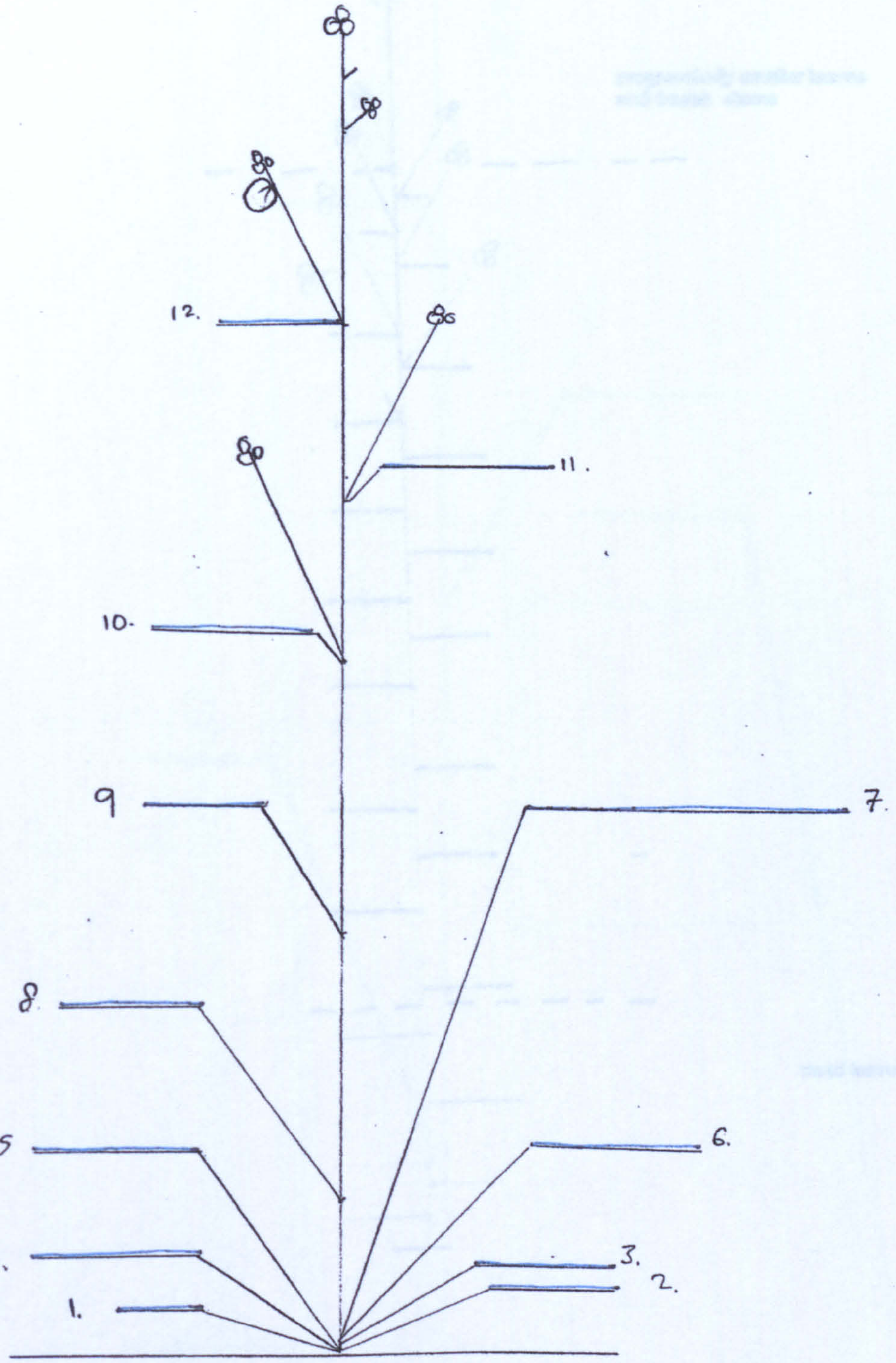
non-flowering stem

AQUILEGIA VULGARIS

5.May.2005

1:4

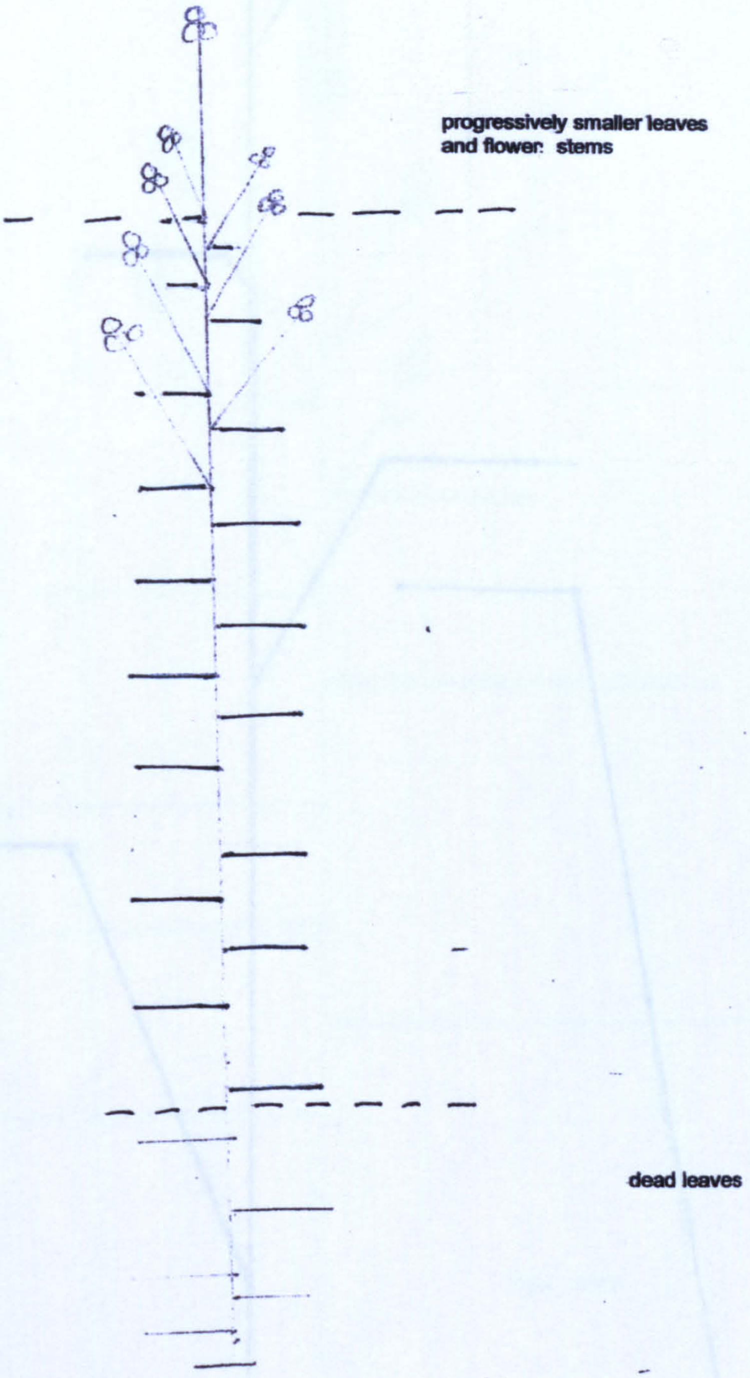
leaves numbered in order of emergence



Artemesia lactiflora

2.July.2005

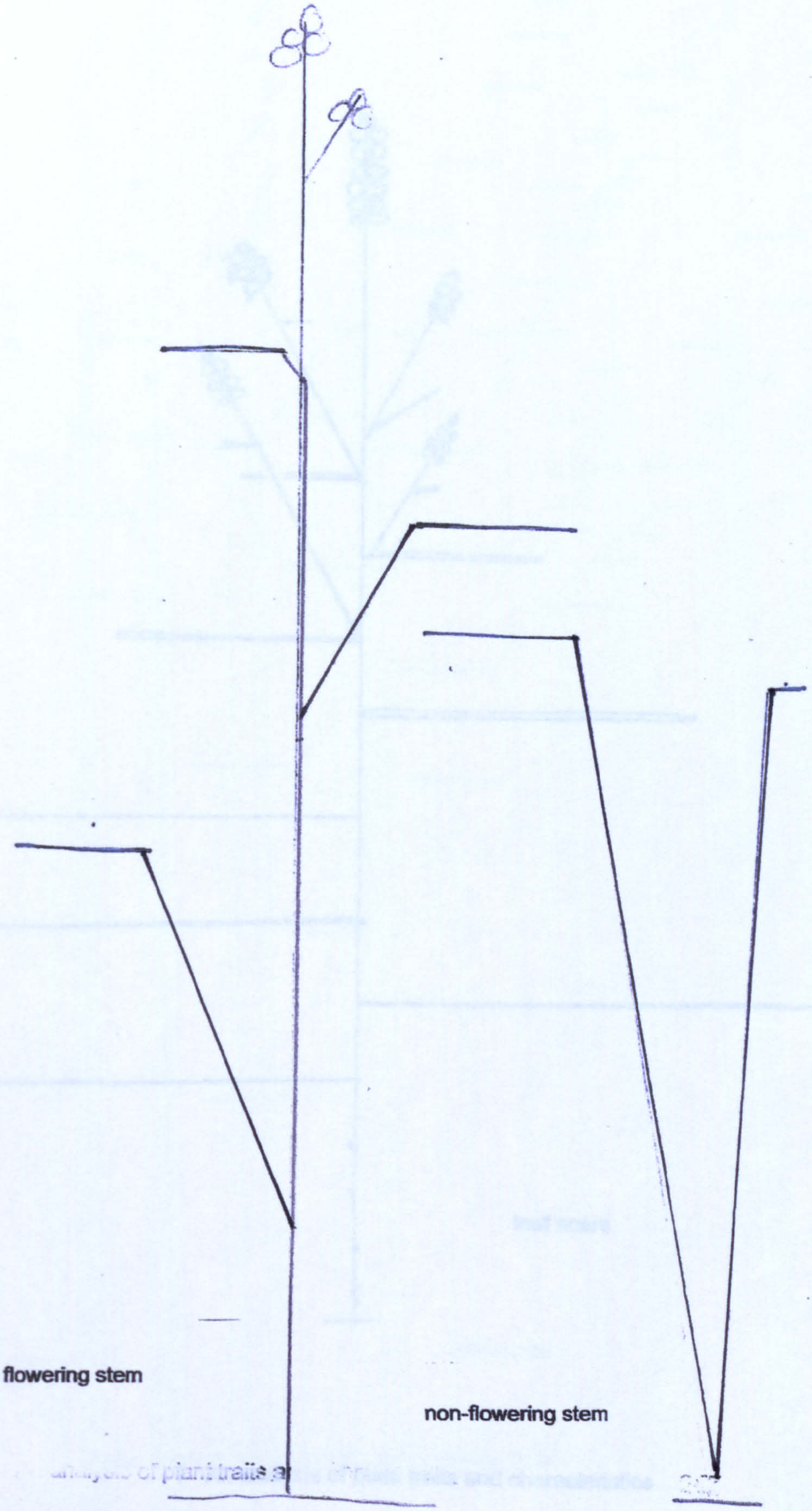
1:10



Astrantia major

1.July.2005

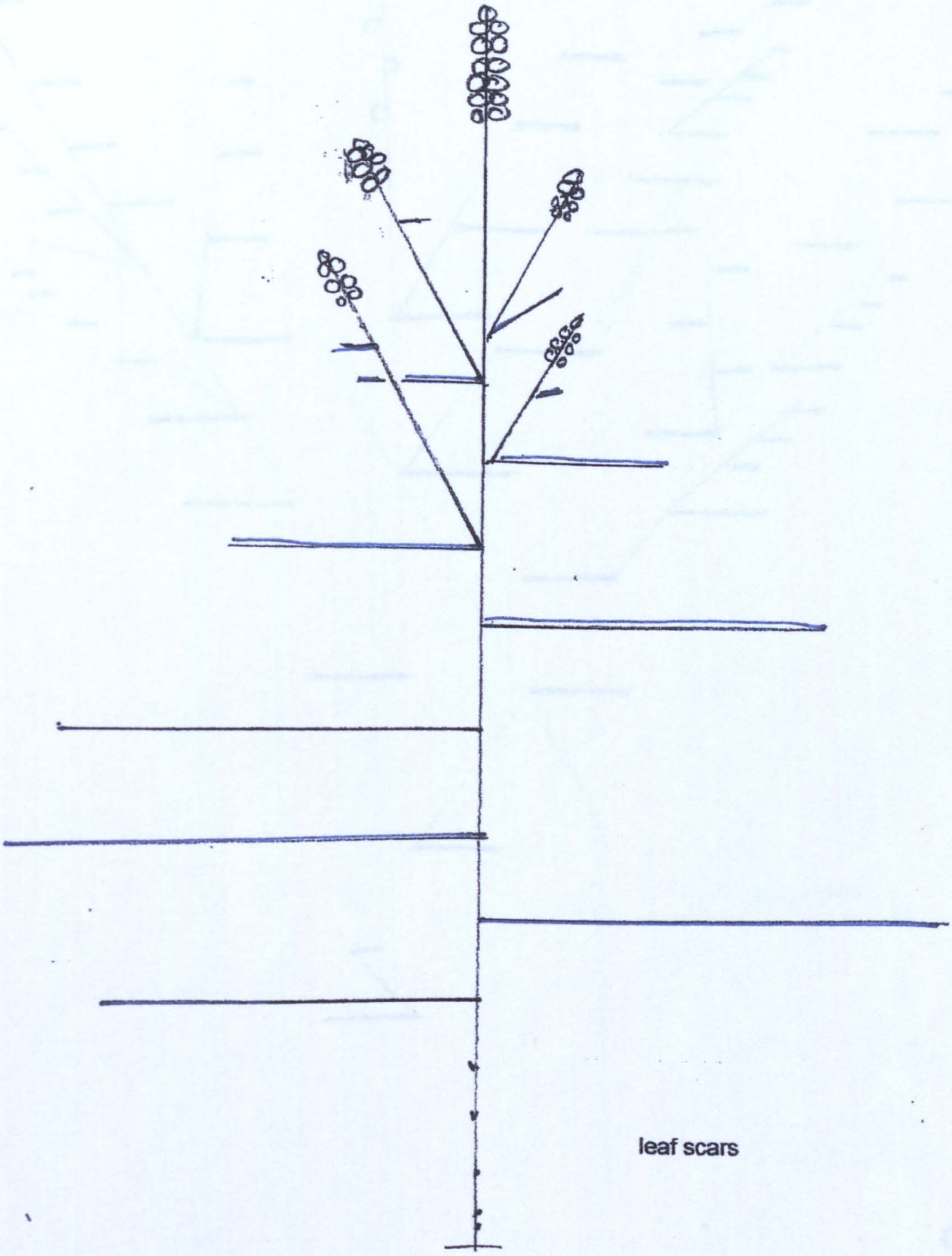
1:4



Aruncus dioicus

3.July.2005

1:10



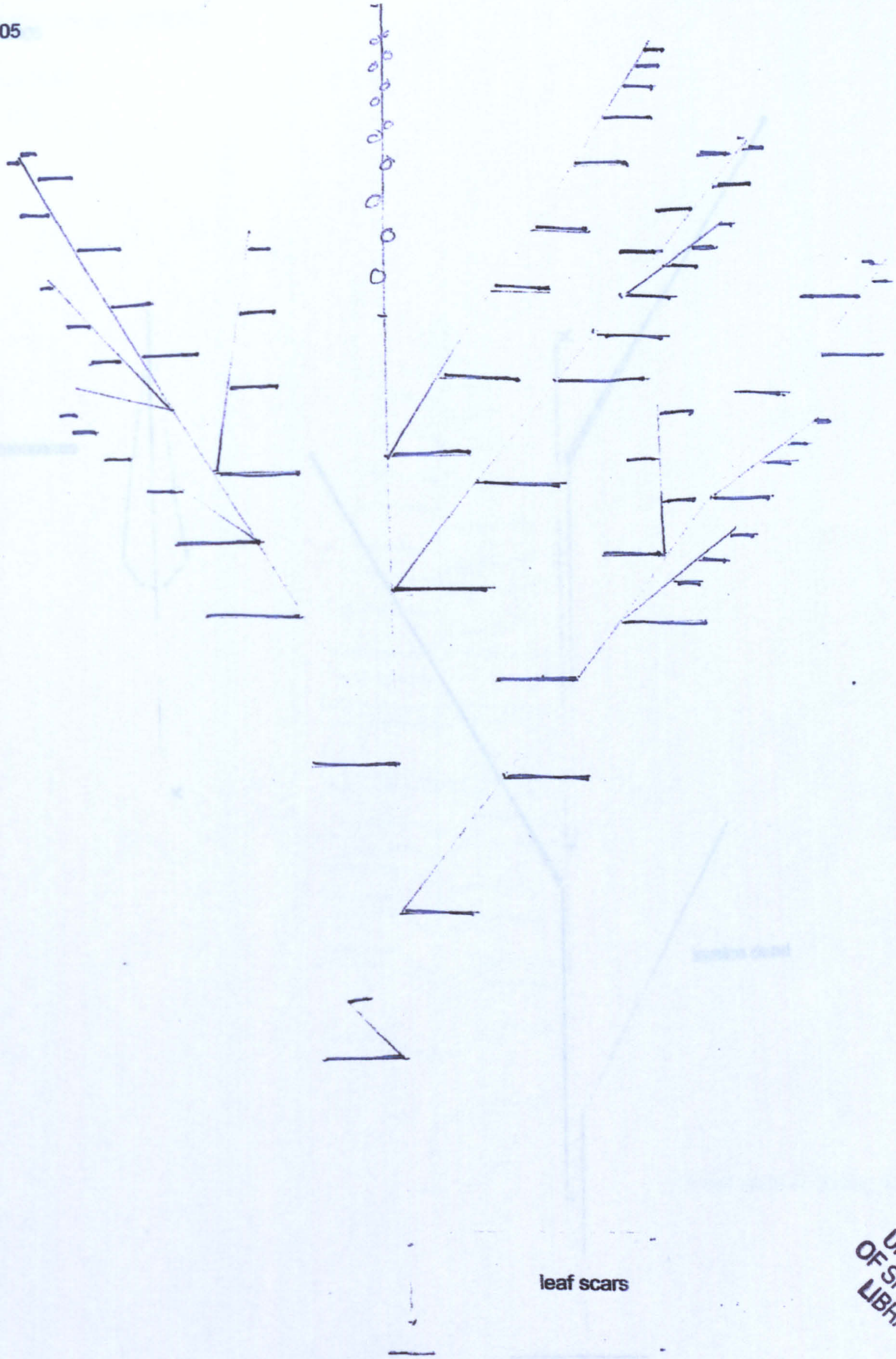
leaf scars

7 An analysis of plant traits and characteristics

Baptisia australis

19.July.2005

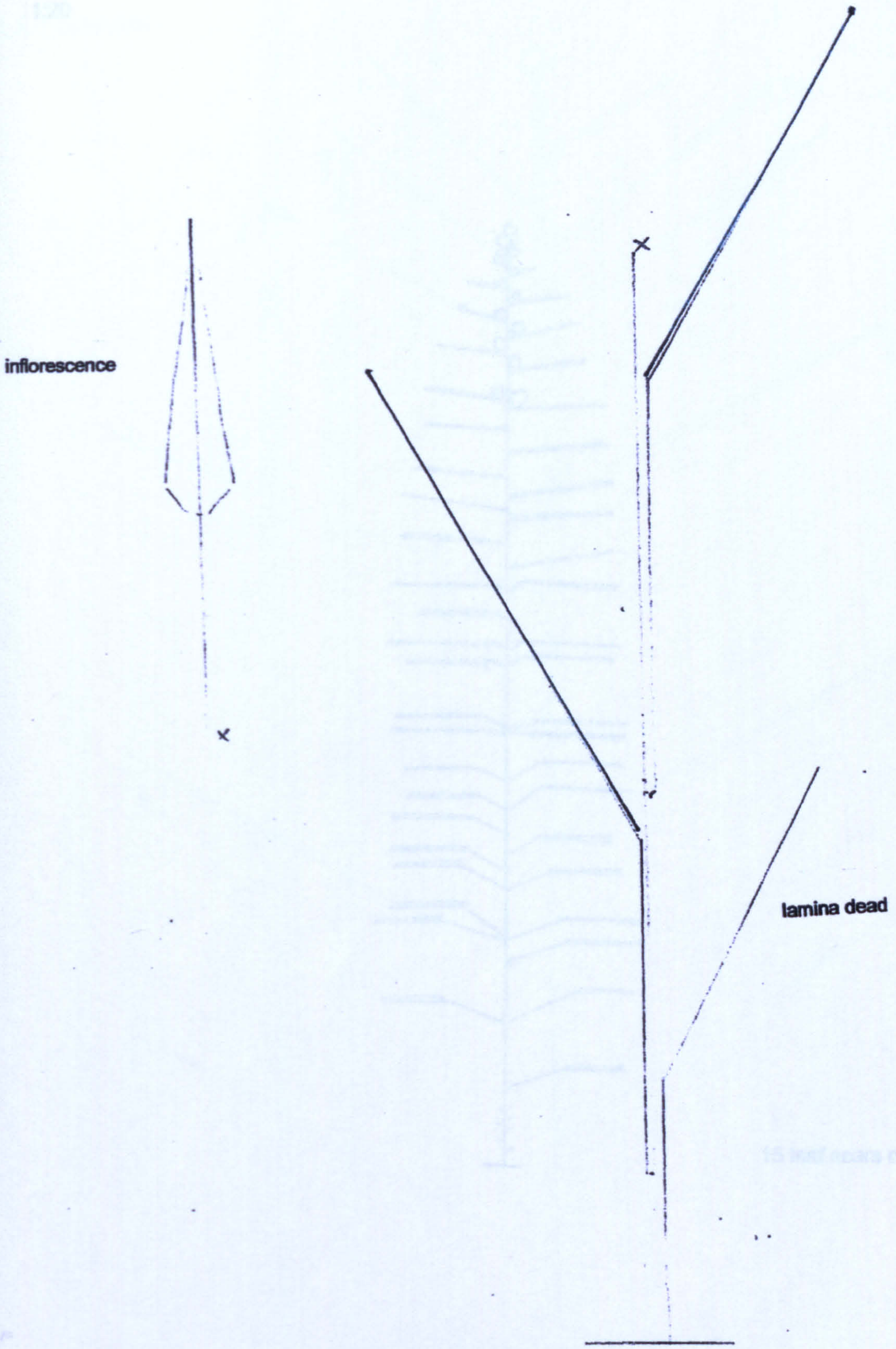
1:4



Calamagrostis x acutiflora

1.July.2005

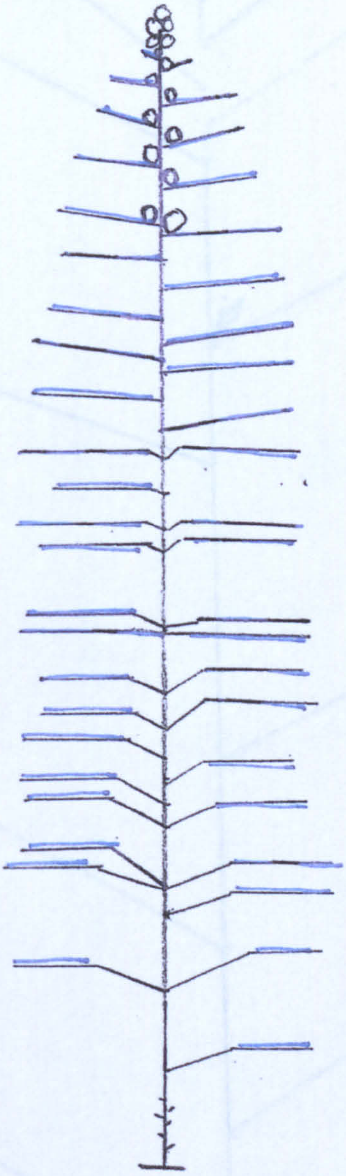
1:5



Campanula latifolia

2.July.2005

1:20



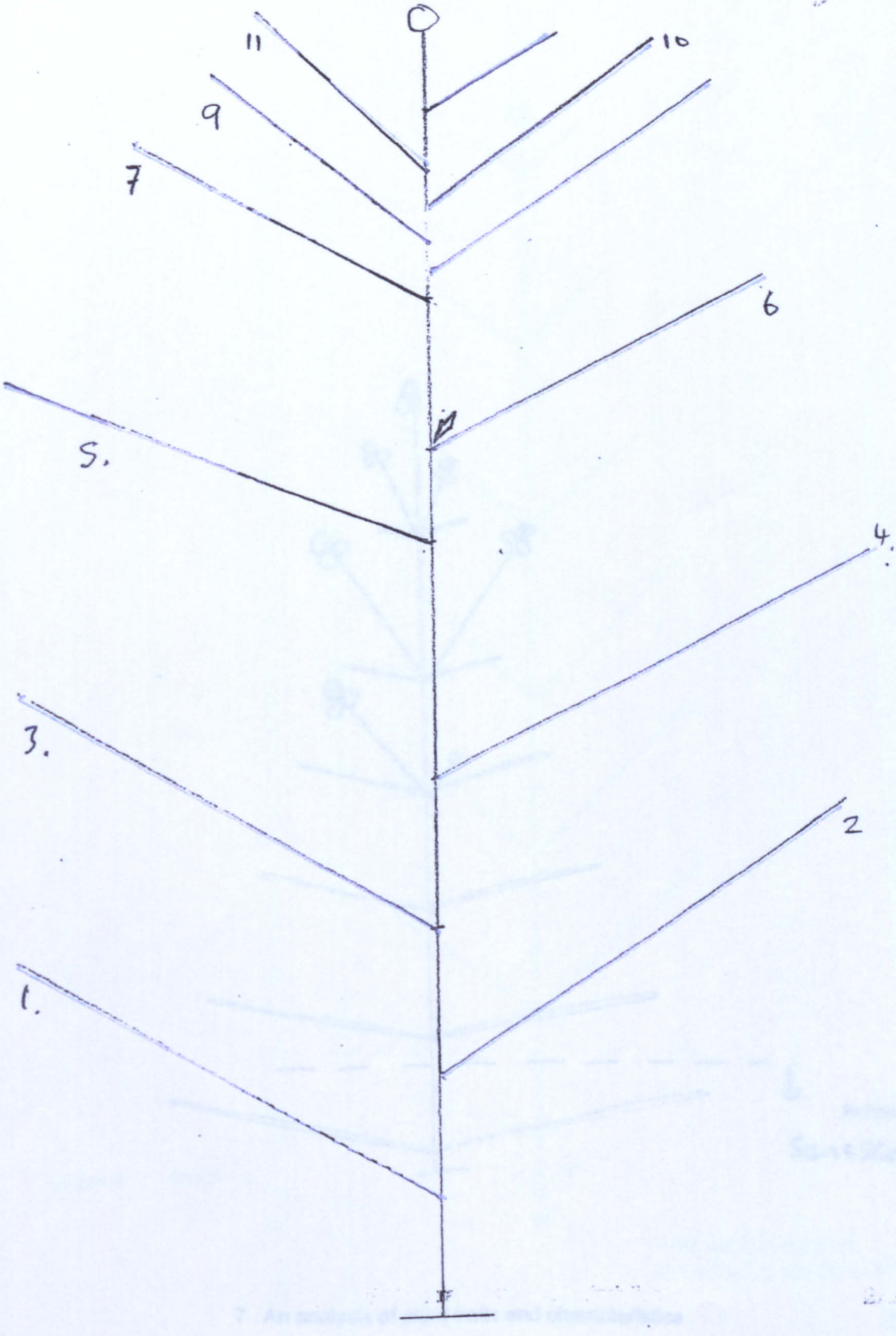
15 leaf scars on lowest 130mm

CENTAUREA MONTANA

20.June.2005

1:4

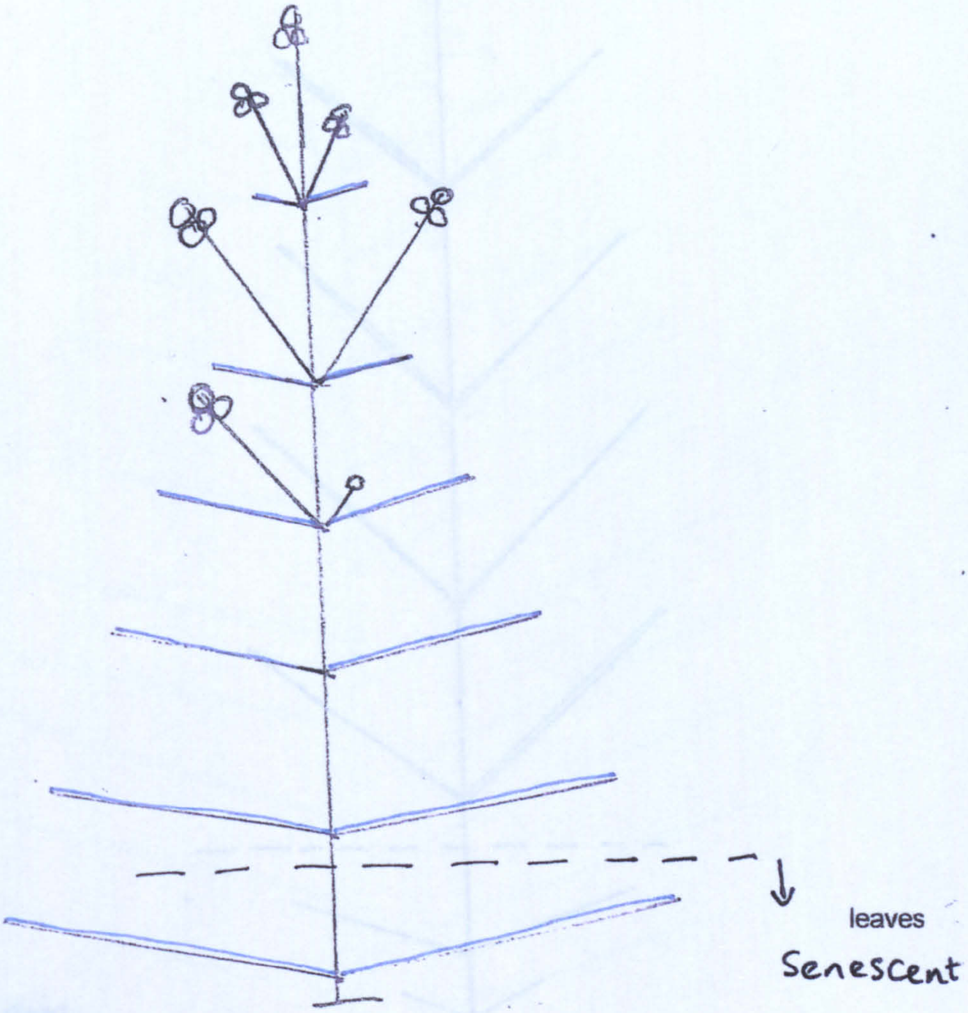
leaves 1,2,3 shrivelled



Cephalaria gigantea

2.July.2005

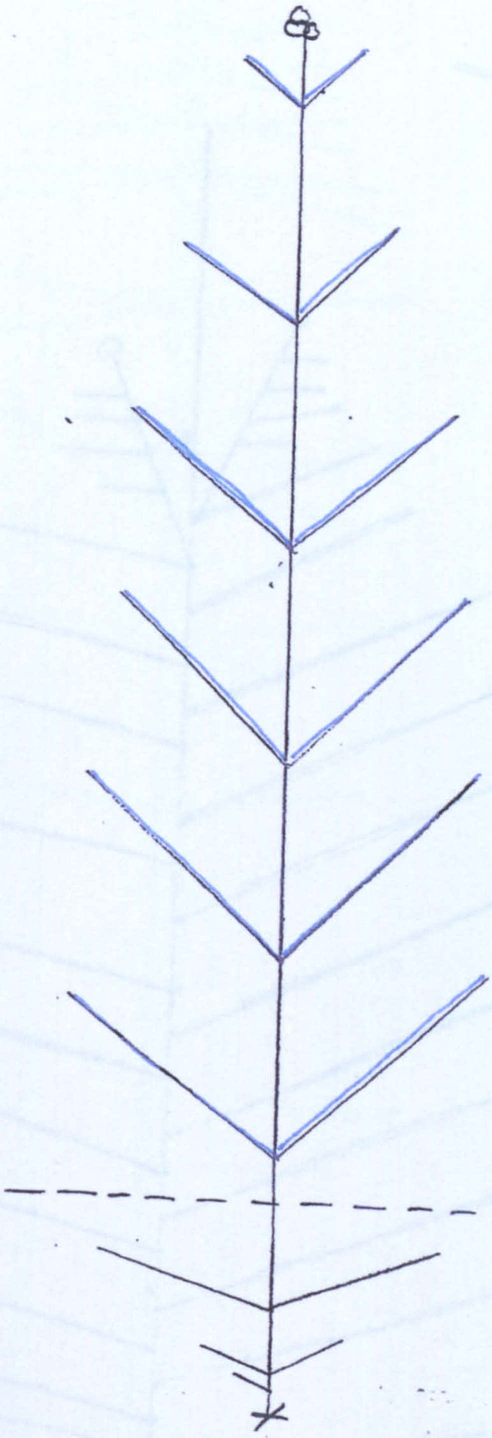
1:20



Dianthus carthusianorum

2.July.2005

1:4



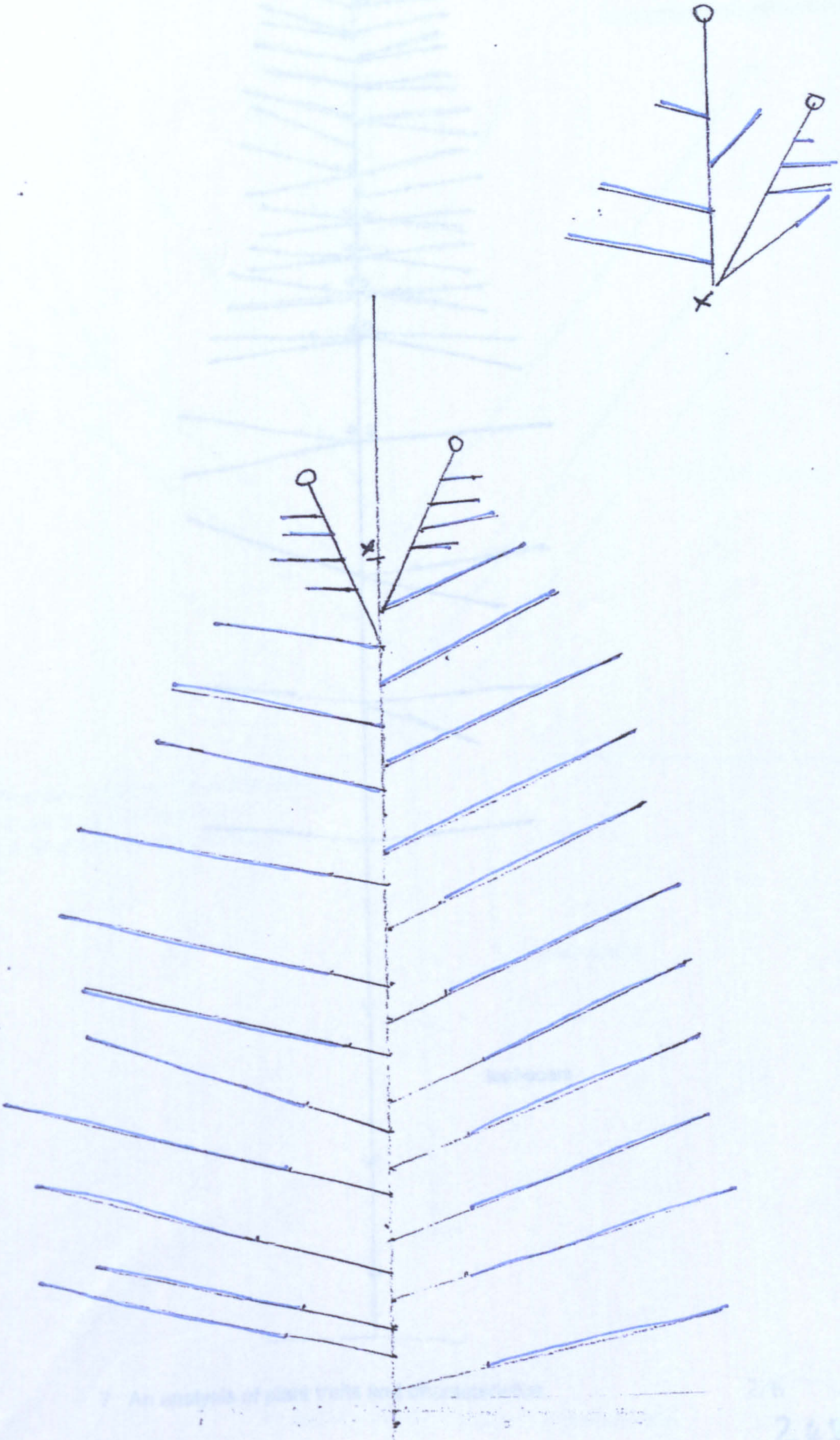
leaves dead

base emerging from
persistent stem 30-50mm above grou

Echinops ritro

11.Aug.2005

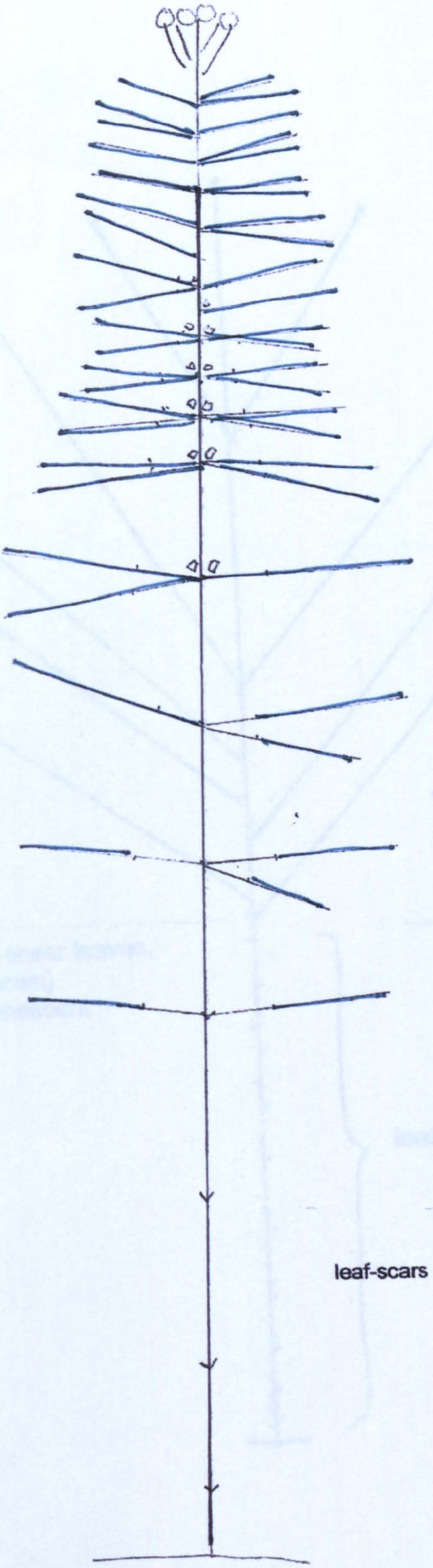
1:10



Eupatorium maculatum

27.Aug.2005

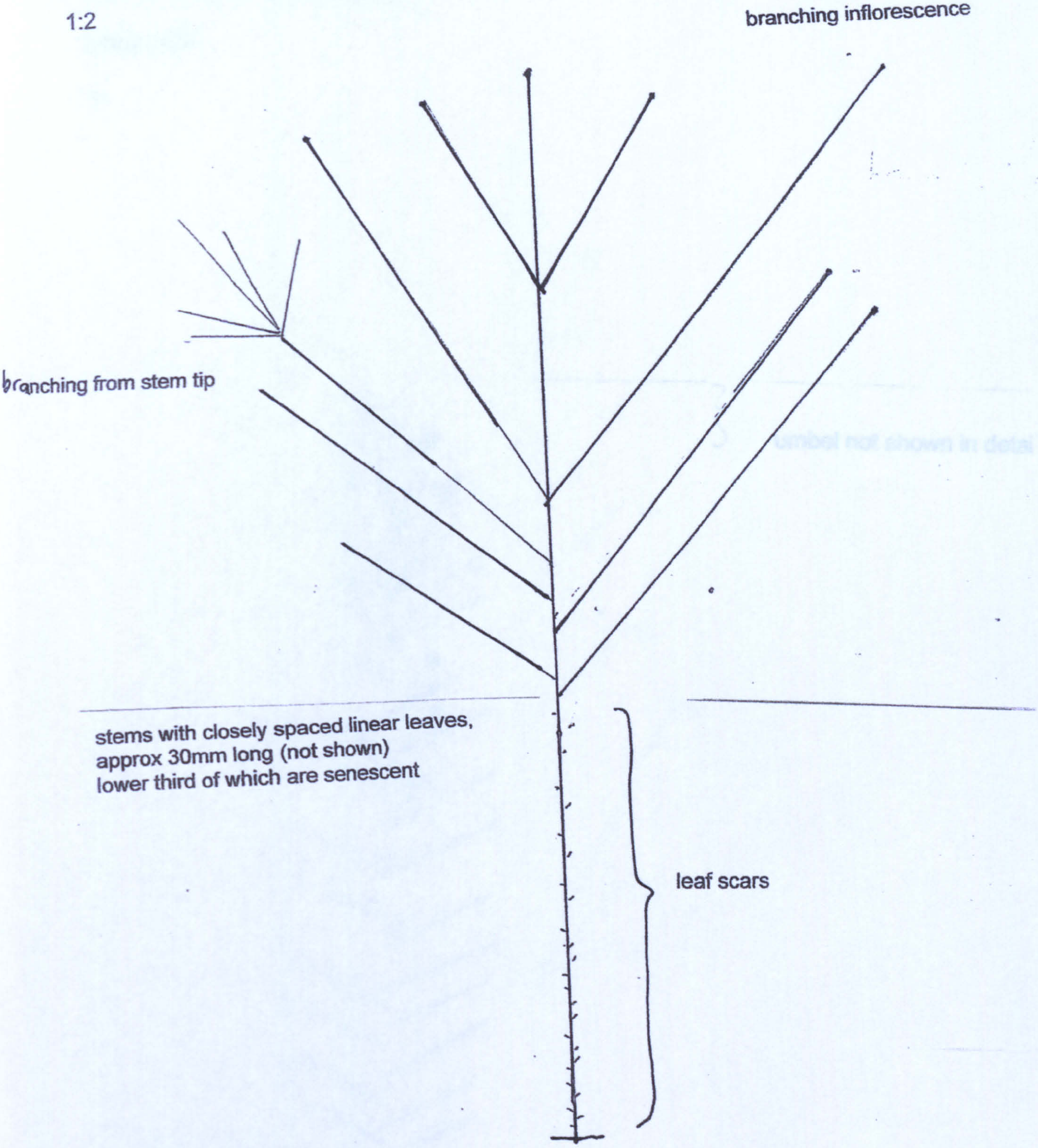
1:5



Euphorbia cyparissias

19.July.2005

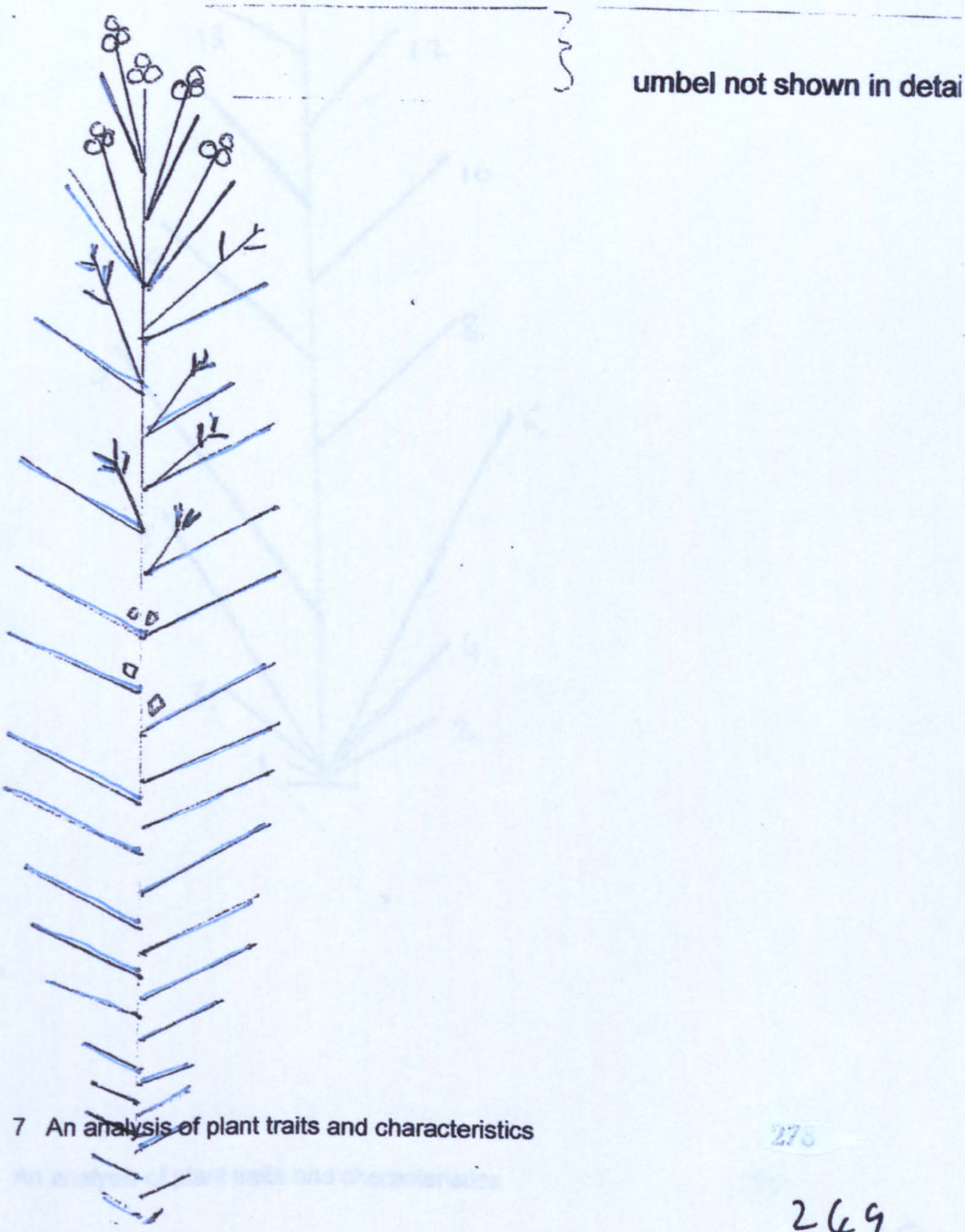
1:2



EUPHORBIA PALUSTRIS

5.May.2005

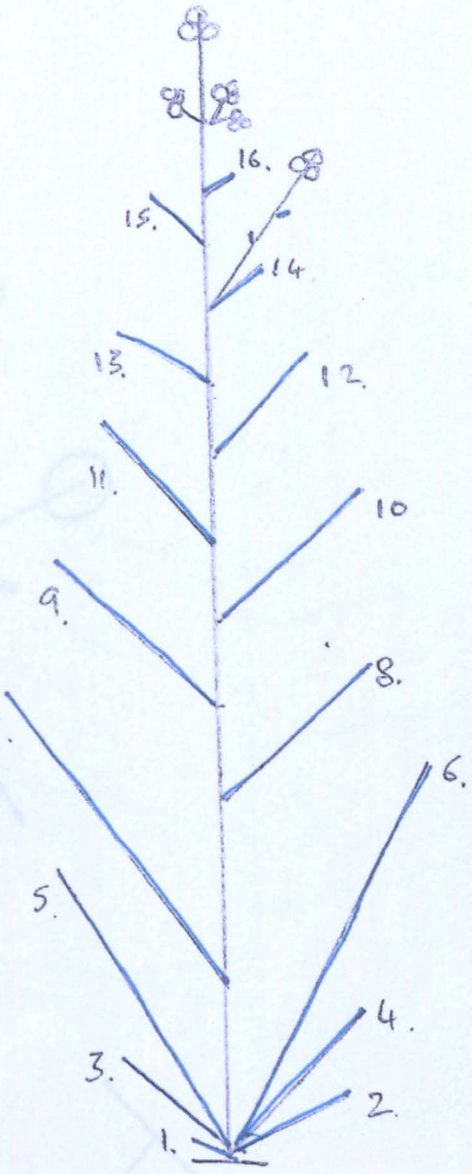
1:4



Filipendula ulmaria

2.July.2005

1:10

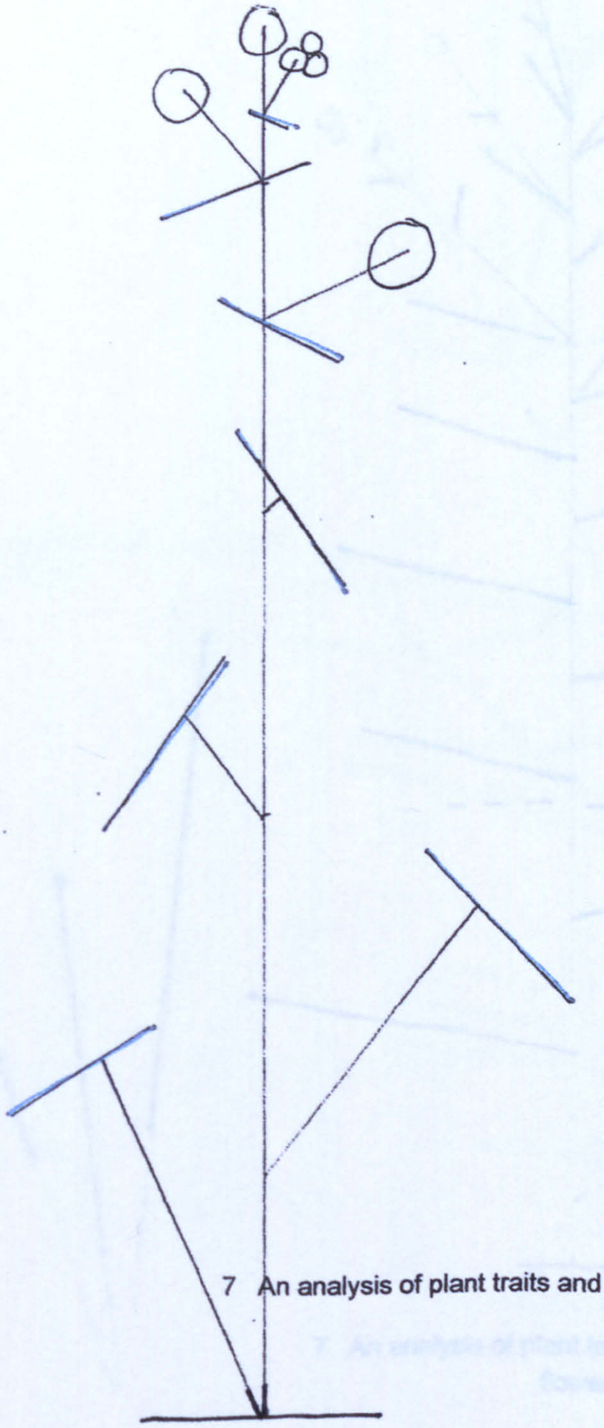


leaves 1-5 dead,
6-8 senescent

GERANIUM PHAEUM ‘LILY LOVELL

5.May.2005

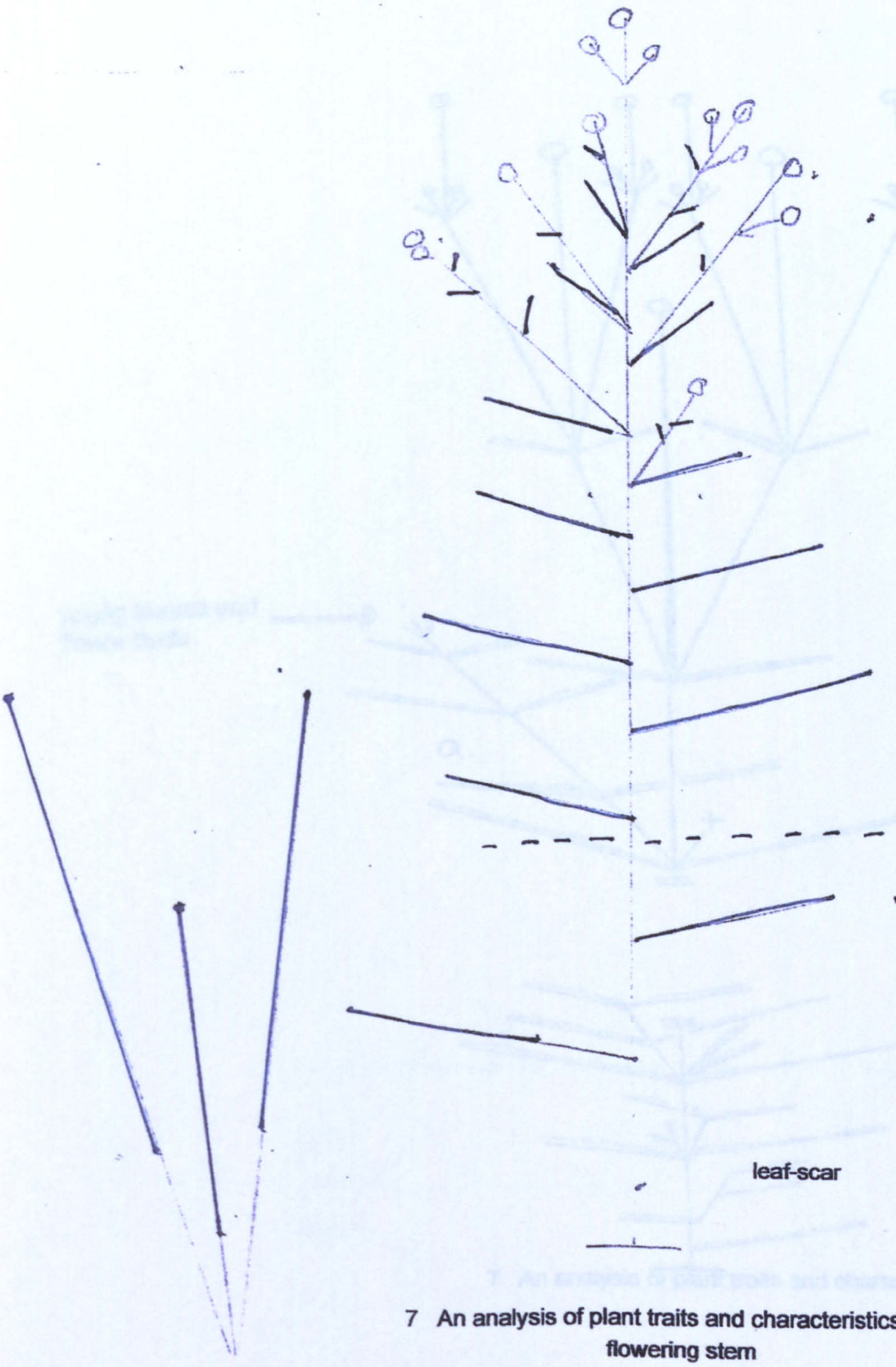
1:4



Inula cf. magnifica

25.Aug.2005

1:10

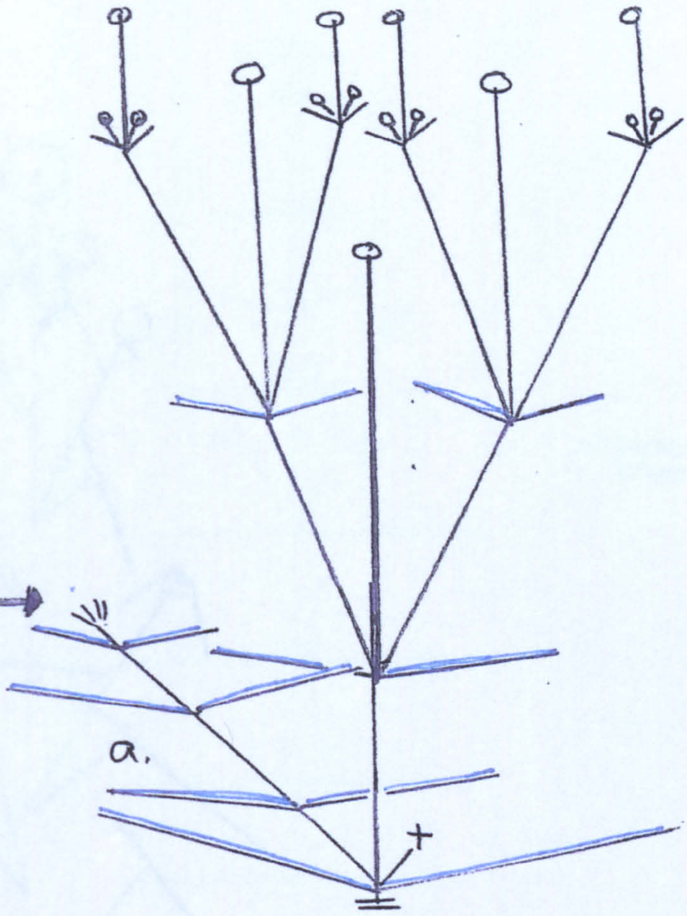


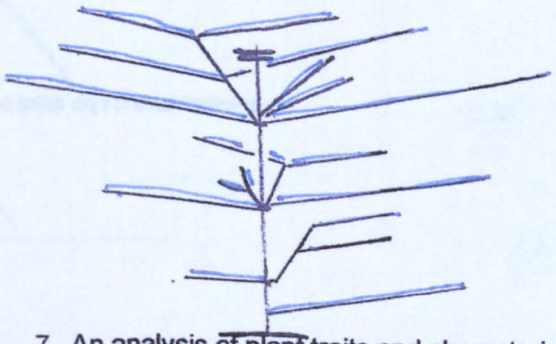
7 An analysis of plant traits and characteristics
flowering stem

KNAUTIA MACEDONICA

20.June.2005

1:4

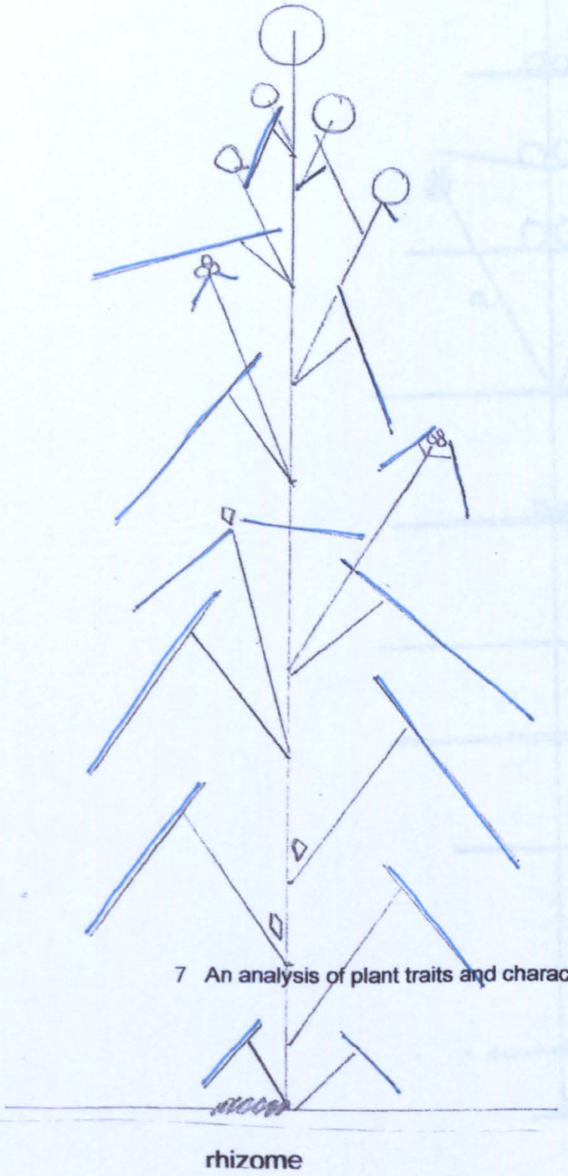




LUNARIA REDIVIVA

5.May.2005

1:4



7 An analysis of plant traits and characteristics

254

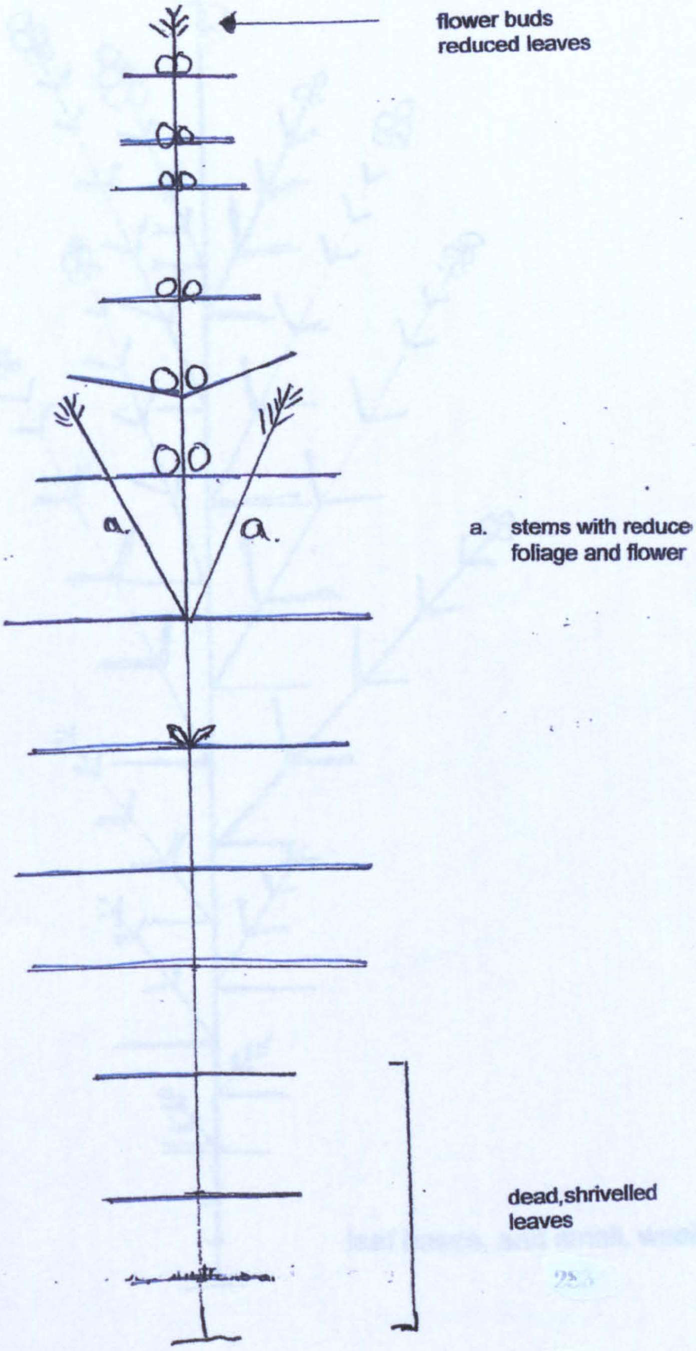
LYSIMACHIA PUNCTATA

18.June.2005

1:4

each pair of leaves indicated represents 4 leaves

petioles short, not indicated

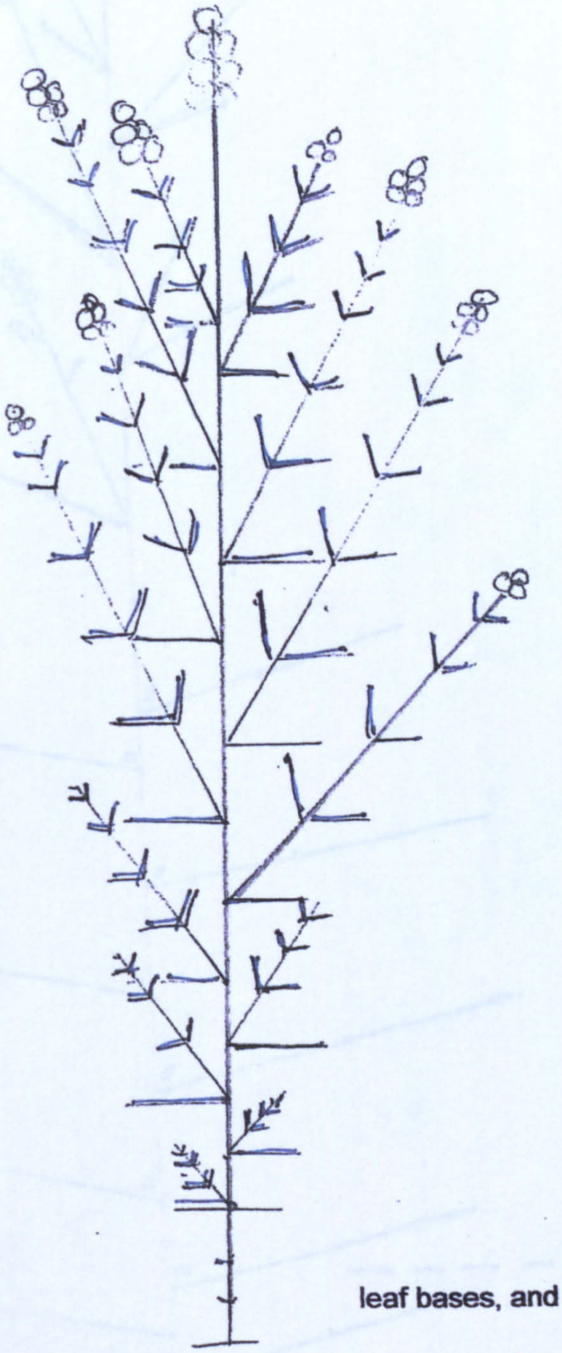


Lythrum salicaria

19.July.2005

1:10

stems shown as alternate, are in fact opposite, only half being shown

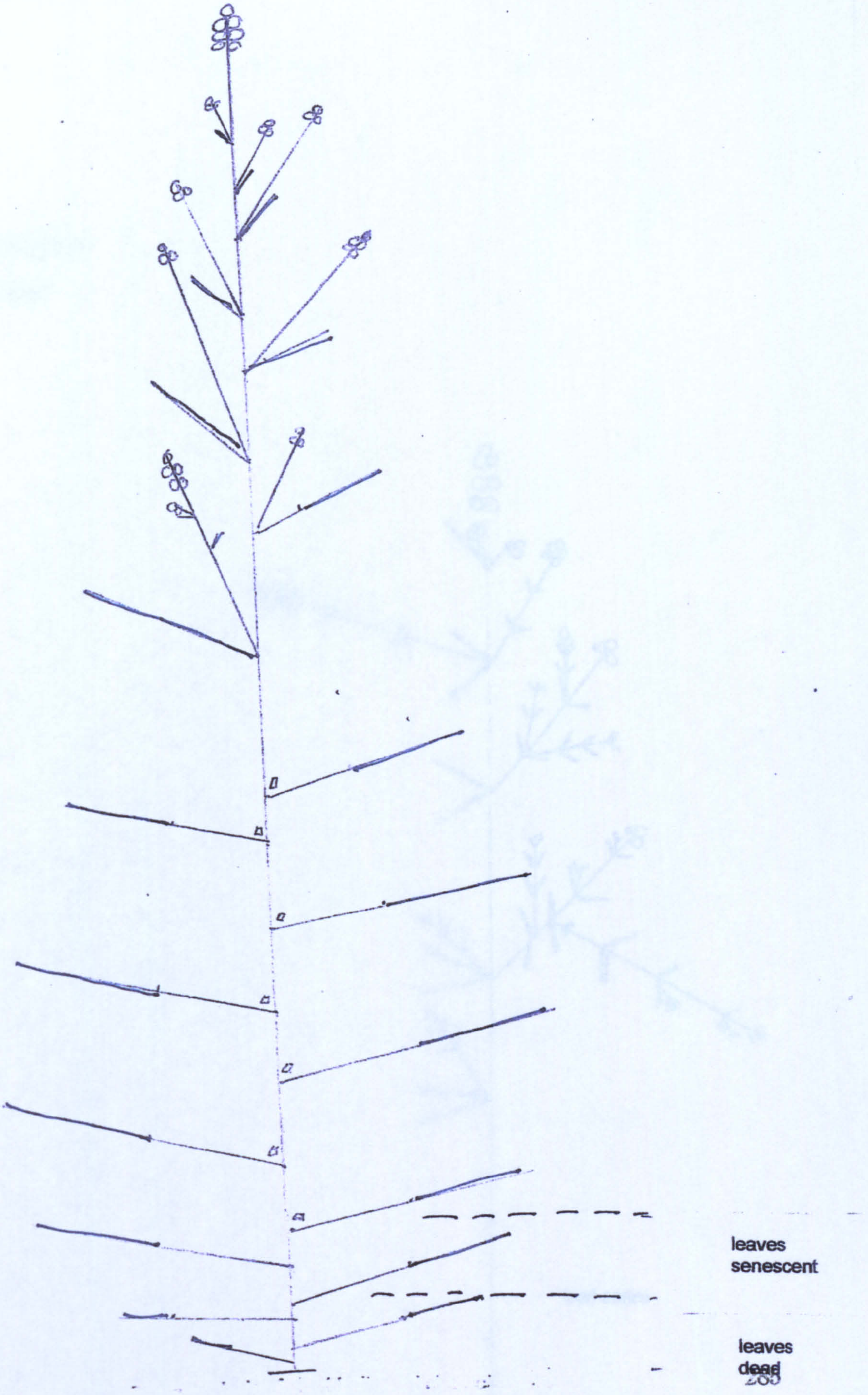


leaf bases, and small, weak stems

Macleaya cordata

3.July.2005

1:10



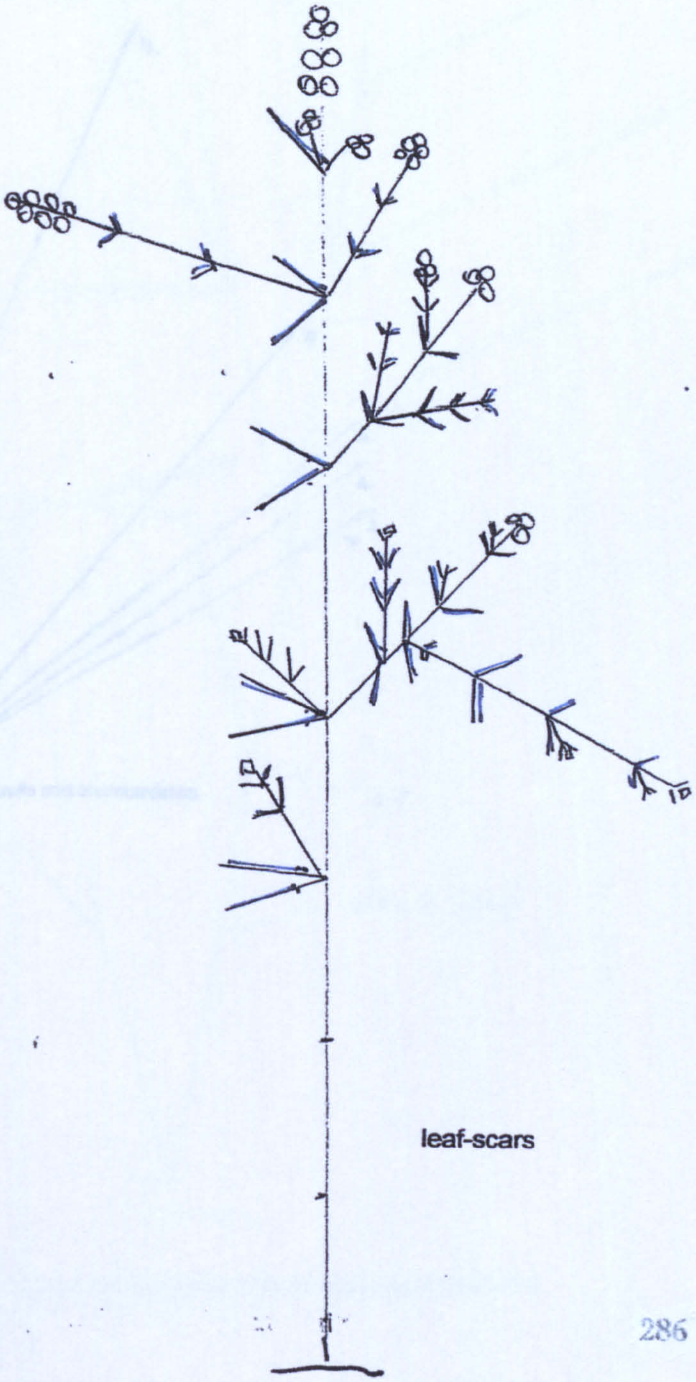
Nepeta x faassenii

13.Aug.2005

1:4

note – stem is actually procumbent

- stems very variable

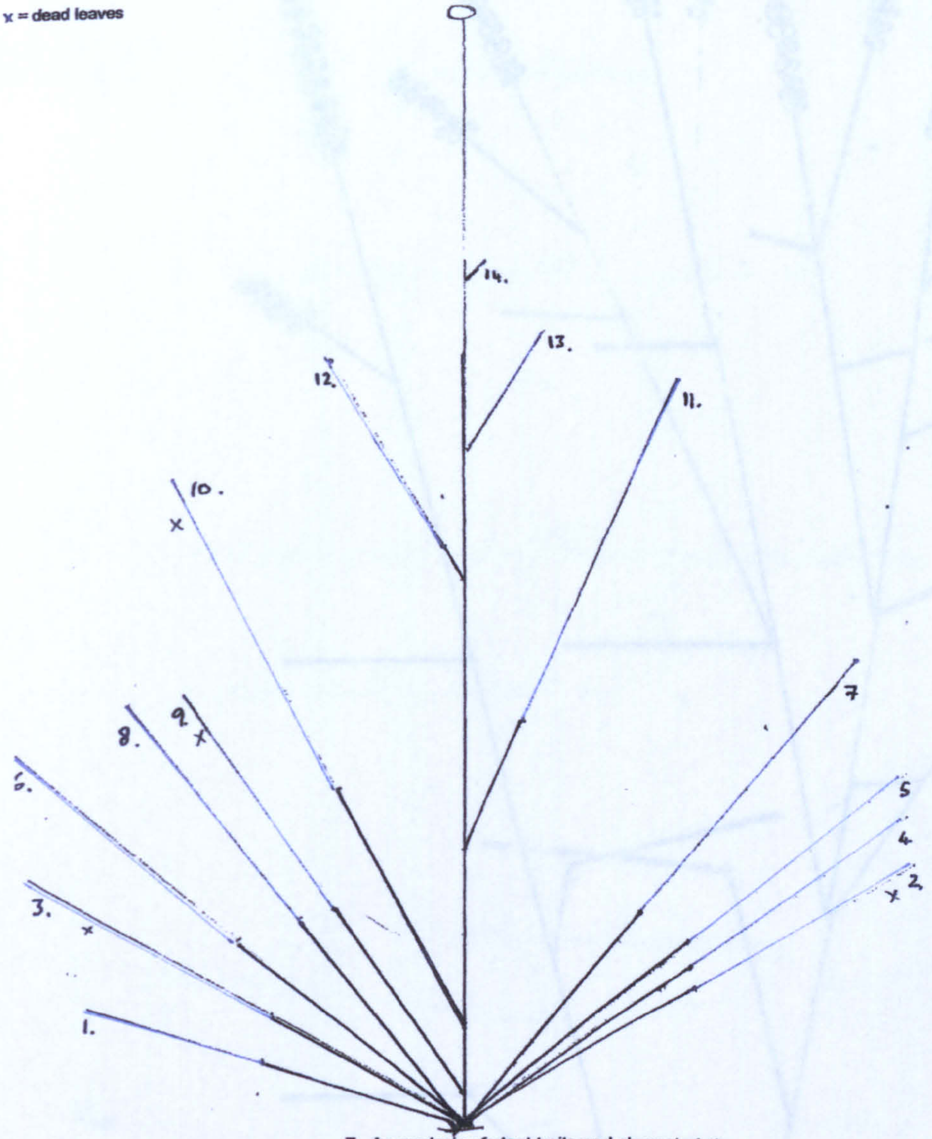


PAPAVER ORIENTALE (OF HORT)

20.June.2005

1:4

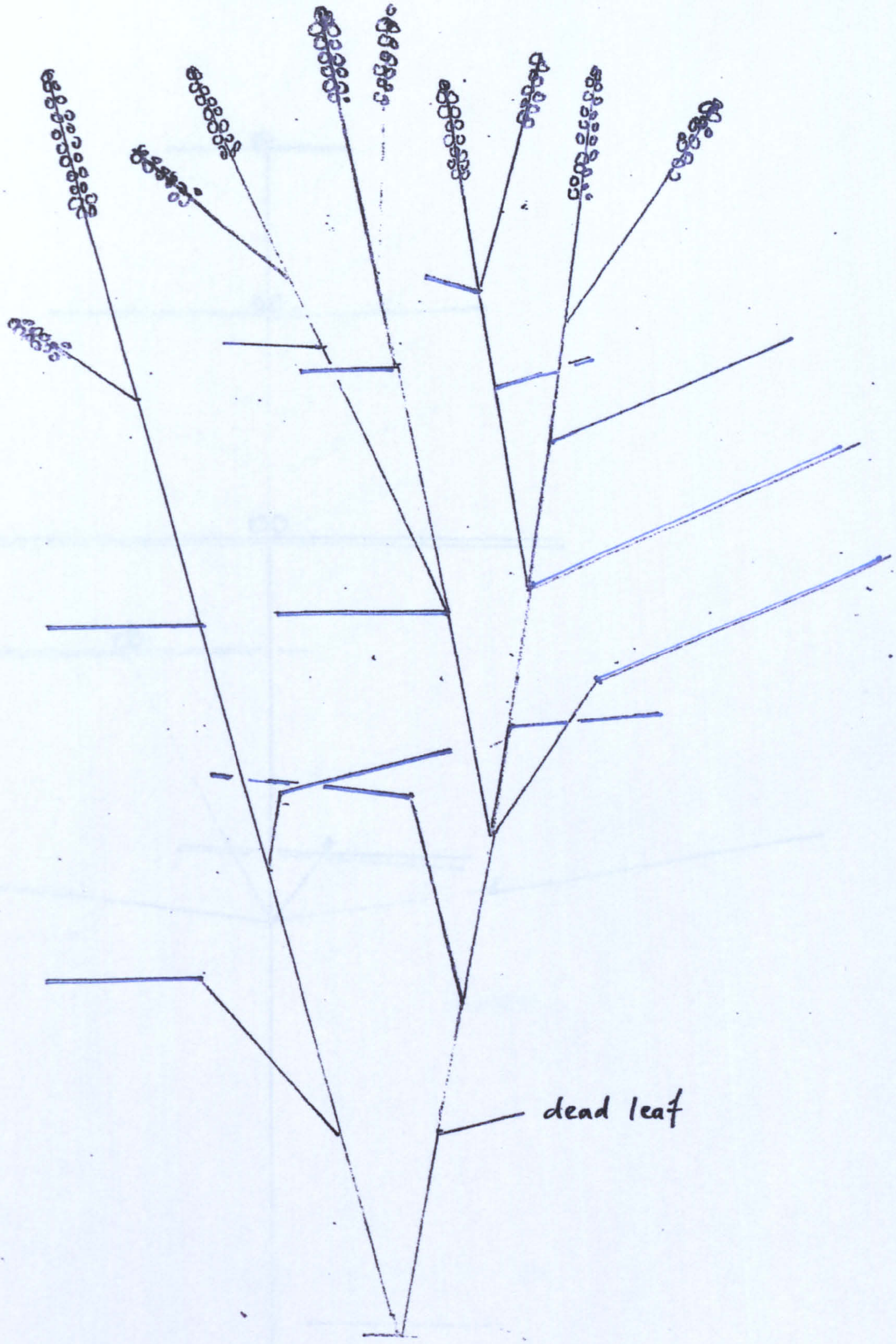
x = dead leaves



PERSICARIA AMPLEXICAULE

14. Aug. 2007

1:4



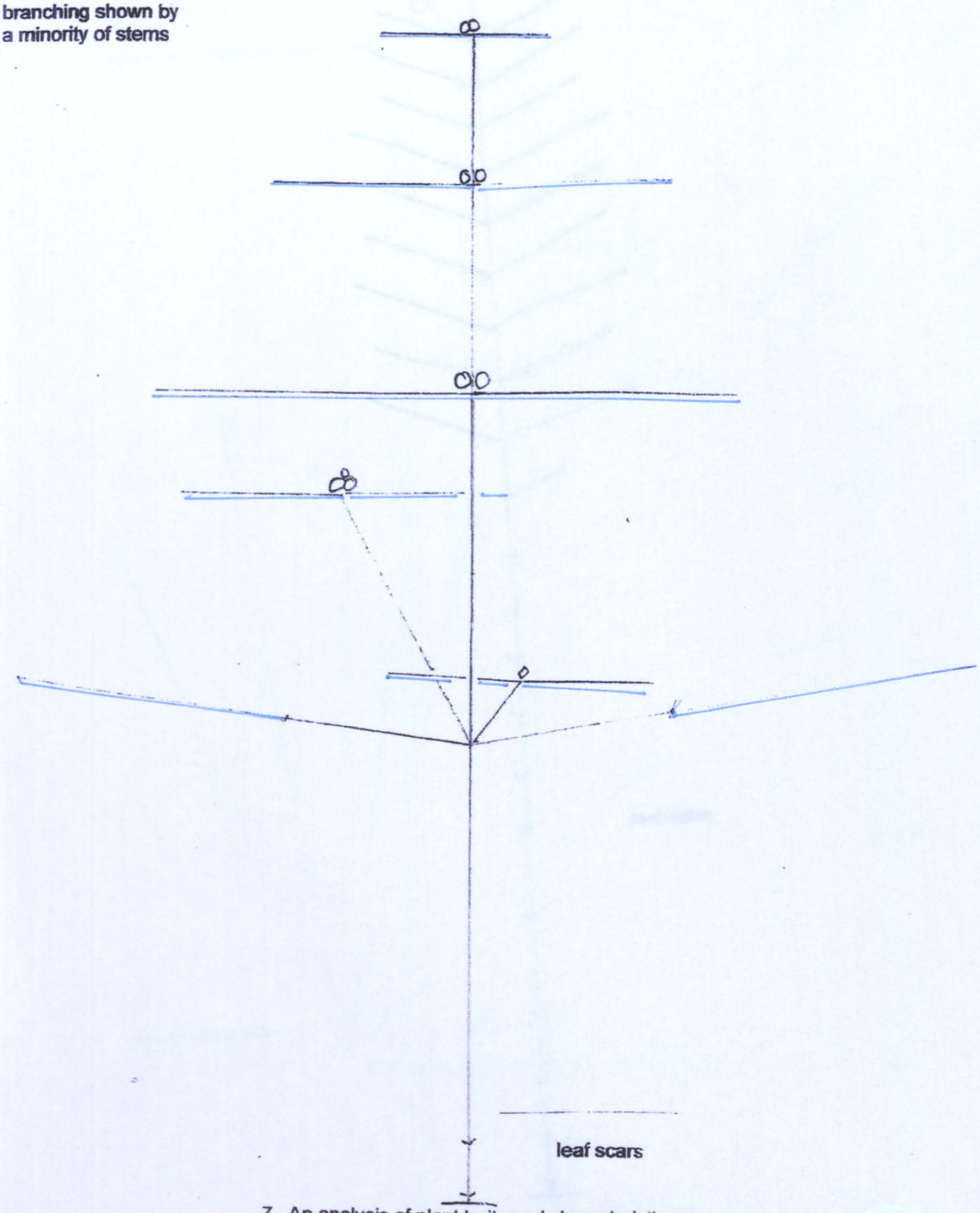
Phlomis russelliana

11.Aug.2005

1:4

branching shown by
a minority of stems

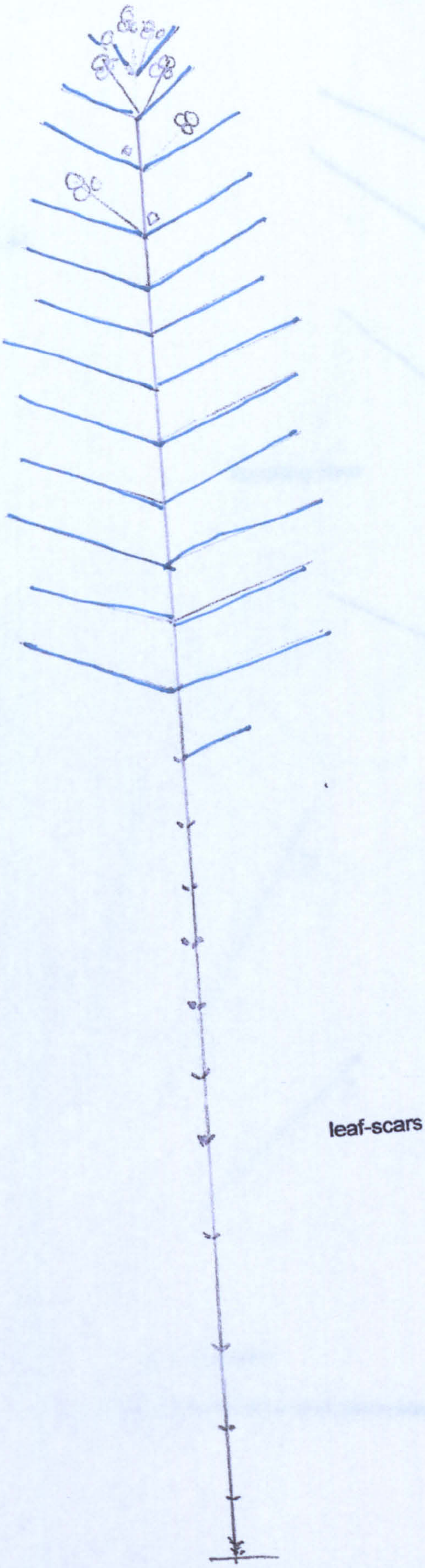
flowering stem only shown



Phlox paniculata

11.Aug.2005

1:5



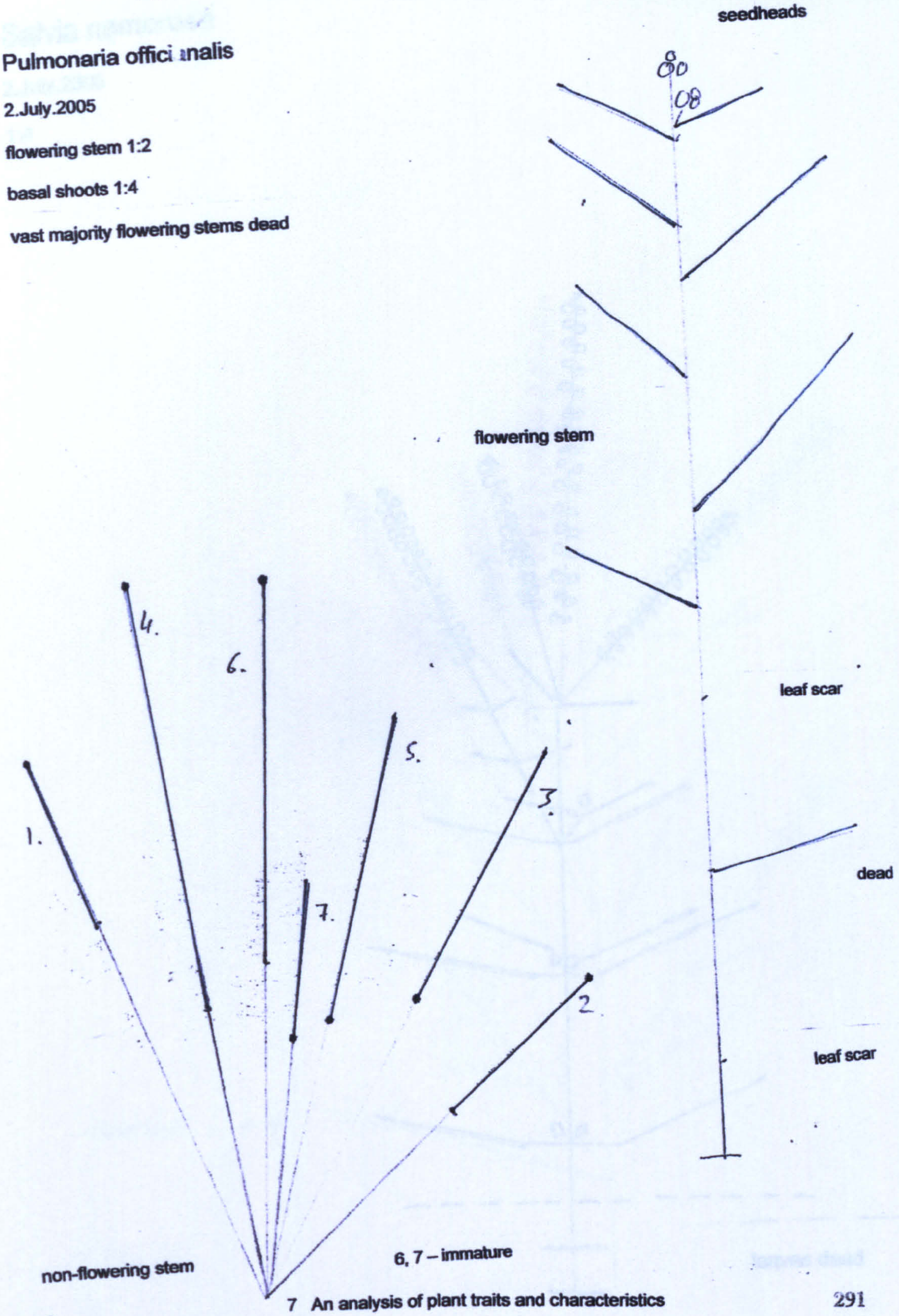
Pulmonaria officinalis

2.July.2005

flowering stem 1:2

basal shoots 1:4

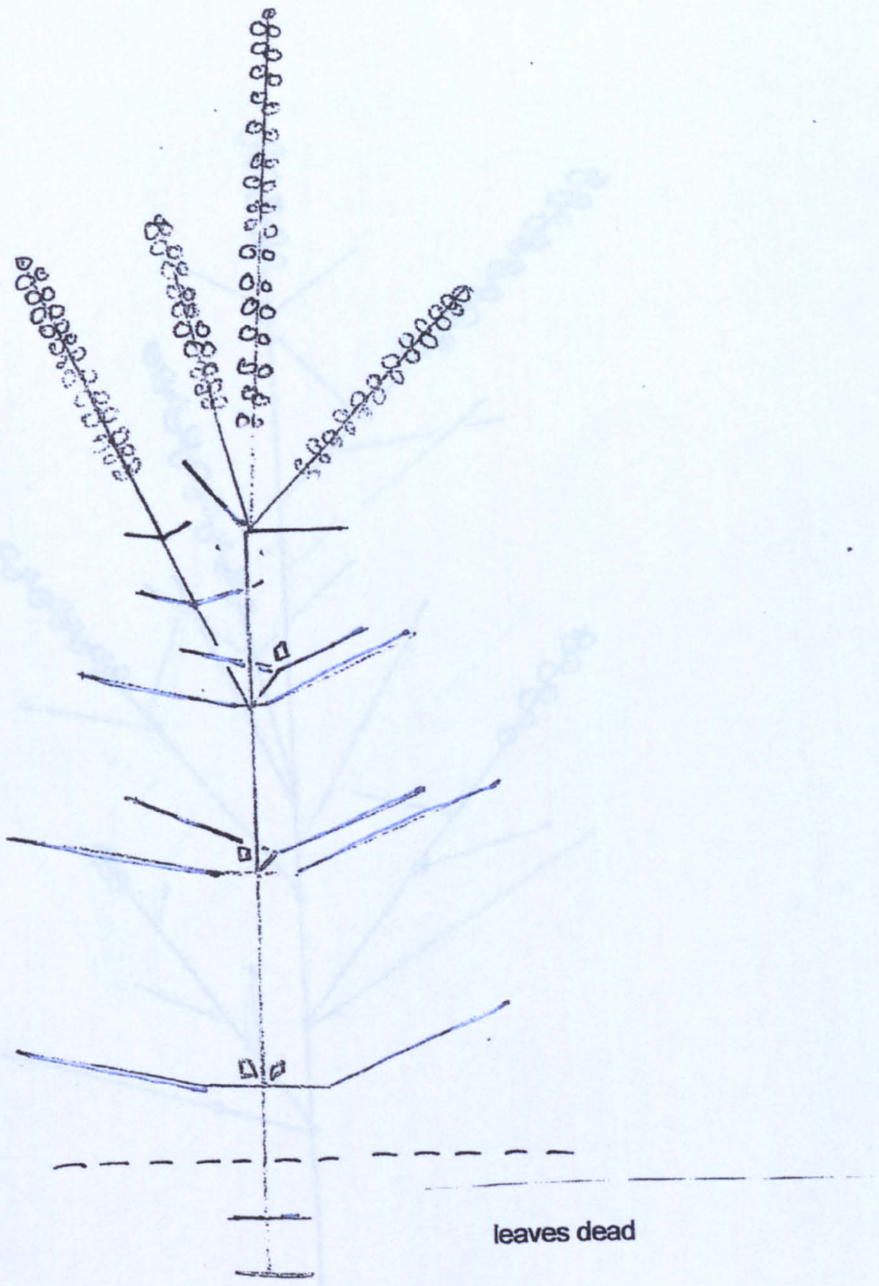
vast majority flowering stems dead



Salvia nemorosa

2.July.2005

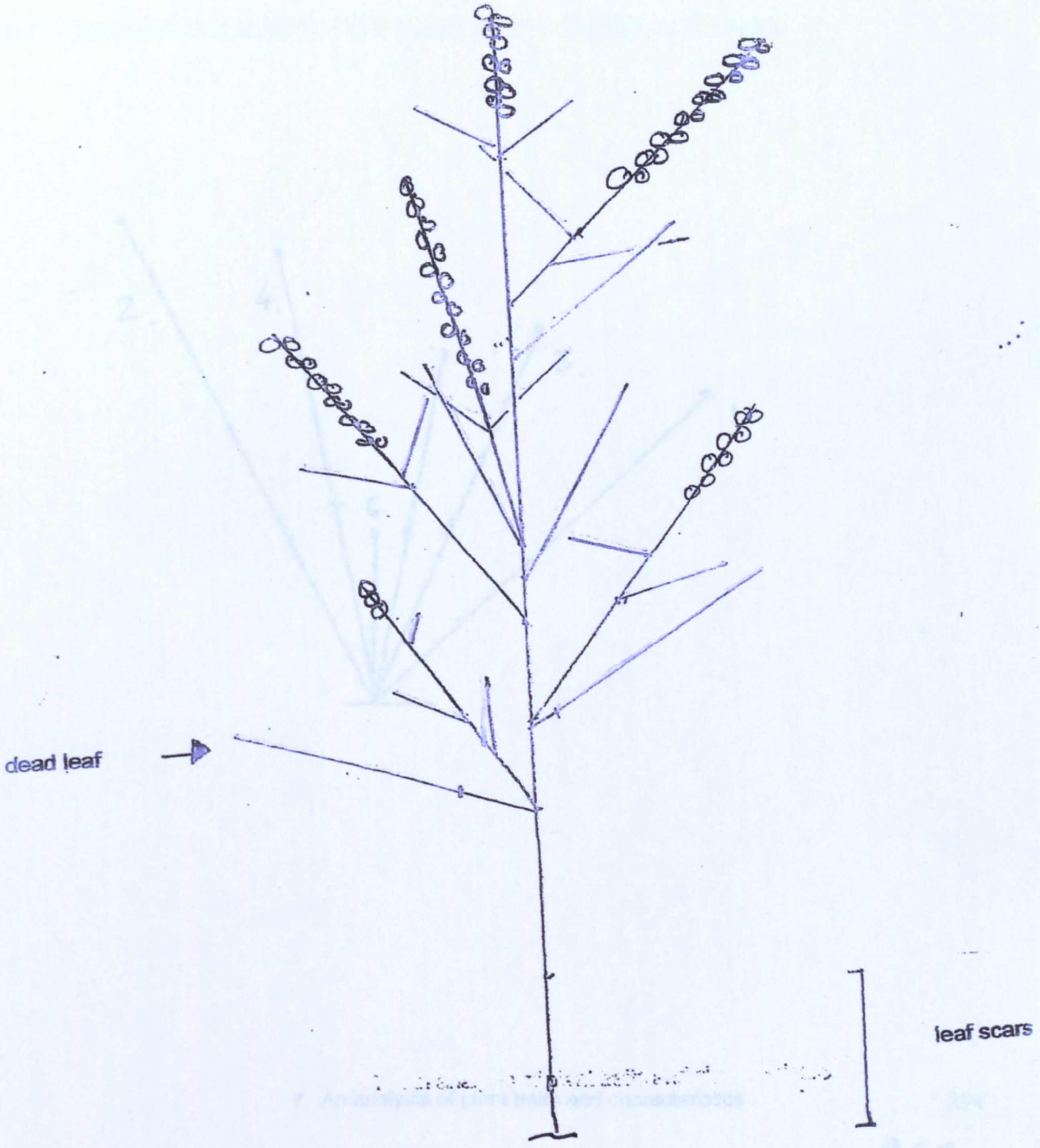
1:4



SYMPHYTUM CAUCASICUM
flowering stem

20.June.2005

1:5

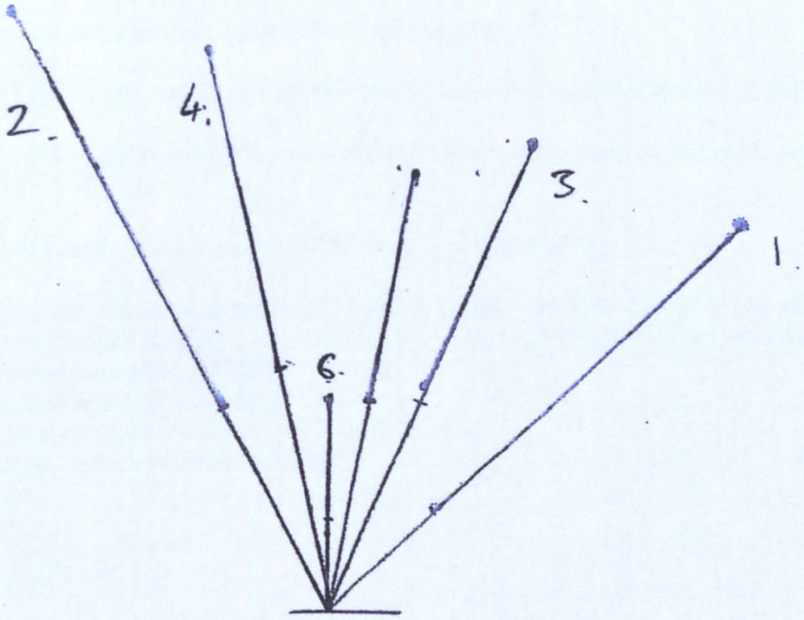


SYMPHYTUM CAUCASICUM
basal leaves

20.June.2005

1:5

leaves numbered in order of emergence



8.

AN INVESTIGATION INTO THE RELATIONSHIP BETWEEN HERBACEOUS PLANT TRAITS AND CHARACTERISTICS AND COMPETITIVENESS

AN INVESTIGATION INTO THE RELATIONSHIP BETWEEN HERBACEOUS PLANT TRAITS AND CHARACTERISTICS AND COMPETITIVENESS

8.1 PLANT CHARACTERISTICS AND TRAITS AND COMPETITION AS INDICATED BY ESTIMATED COMPETITIVE ABILITY (ECA)

8.1.1 Developing a meaningful single-figure measure of competitive ability

Grime's 'morphology index' (Grime 2001) to indicate competitive potential is based on the importance to competitive ability of various plant traits. If there is at least some experimental or other empirical evidence of the impact that these traits make on competition, then this kind of index may be useful as a way of combining and simplifying a number of measurements and may be compared to a quantified measure of what we know about plant performance. To produce the index, the quantifiers of certain characteristics may need to be multiplied to represent their relative importance; clearly such measures are based on subjective assessments of an objective reality – however the key issue here is that any such index is not an absolute measure but a relative one, i.e. species may be assessed relative to each other. In addition such an index may be varied with regard to the characteristics that are used.

$M = (a + b + c) / 2$
where
a is the estimated maximum height of leaf canopy
b is the lateral spread
c is the estimated maximum accumulation of persistent litter

This measure is not used here. Height cannot be regarded as fundamentally important in EBPS; the poor performance of some tall species in the informal assessment of species performance in rough grass (see 4. Investigating the growth of ornamental herbaceous perennials in grass swards) indicated that some scepticism over the importance of height may be needed. Experience also indicates that many low or medium height plants can be very invasive, e.g. *Euphorbia cyparissias* (Carter et al. 2007). Accumulation of persistent litter, whilst quite possibly a definite factor in the competitive effect of some species is difficult to measure in cultivated situations, as so much is removed during routine maintenance.

The intention here is to develop a system of assessing competition which can be used to make associations with the plant phenological and morphological traits and characteristics discussed in the previous section of this study. Measuring plant competitive performance over a range of species would involve a long series of trials. The alternative is to develop a measure at one remove, i.e. based on practitioner assessment according to a set of criteria. The attempt at doing so here should be seen as a trial run for a more extensive study involving multiple practitioners.

8.1.2 Aims

- To develop a basic system of assessment of competitive abilty based on practitioner experience.
- To attempt to relate morphology and phenology to competitive performance in horticulture and in particular in EBPS.

8.2. ESTIMATED COMPETITIVE ABILITY (ECA)

It is possible to give a figure to the species under study to indicate an estimated figure for their competitive ability based on the observer's experience in growing the plants. Such an estimated, and *inevitably subjective*, figure might have little validity for a scientific plant ecologist, but it does have a number of points in its favour: that it provides a measure of empirically gained (albeit it subjectively evaluated) experience against which more objectively gained figures may be compared, and that it reflects and sums up the situation for a *defined geographical region*. At this stage in the research in the field, where there is so little experimentally-gained empirical evidence as to competitive ability and dominance, such a measure will at least perform the function of providing a basic means against which to test the evaluation of plant characters, which could then be used as a starting point for future work. A suggestion that it is possible to rank ornamental herbaceous species in this way is made in Hitchmough 1995.

Furthermore, there is so little systematic assessment of plant performance in cultivation, that any attempt at assessing it could be regarded as valuable. Conventional horticultural practice in trialling has been orientated towards selecting plants of high standard, and for cultivation in the conditions of conventional horticulture, e.g. the Royal Horticultural Society trials (RHS 2007, 2008). Commercial trialling is similar, and is not in the public domain. Much information regarding plant performance is not only subjective, but entirely anecdotal in character; it could be argued that *any* attempt at producing a quantifiable system of categorising this anecdotal and subjective knowledge has value.

The figures given here are based on two methods of assessment:

1. The experience of growing the plant in competition with others in densely-planted mixed border situations – which of course may not the 'natural' or the 'optimum' habitat for the plant, although the situations considered are broadly within the range of conditions for which the plant is considered suited (Burrows 1990, Crawley 1997b). The locations include Elmtree Cottage, Cowley Manor, several parks and public space plantings in Bristol.
2. Familiarity with the majority of the species observed in a wide variety of gardens and parks in southern Britain, The Netherlands and Germany, usually gained through multiple observations at different seasons over a ten-year period.

ECA is primarily a measure of a 1 to 5 gradient that reflects three factors: the ability to survive competition (competitive response), the ability to overwhelm neighbours (competitive effect). It should also be noted that the experience upon which this estimate is made varies considerably between species; clearly the more experience of a species across a range of habitats, the more valuable this measure is. It should be noted that seeding ability is excluded, as this clearly involves a completely different range of issues. It is to be stressed that ECA is an evaluation based not on an estimate of competitive process or ability, for example ability to spread in ideal conditions (i.e., with no neighbours), but *outcomes* in real-life horticultural situations.

In making these evaluations, the following factors have been taken into consideration:

- Degree of spread of clumps in the presence of neighbouring species– factors indicating a high (4 or 5) evaluation would be large clumps, clear and successful guerrilla spread, especially over a wide area, through or past neighbouring plant clumps.
- Degree of apparent suppression of neighbouring species – high values for high levels of suppression
- Ability to survive high competition, particularly with grass, or robust weedy native perennials, or very robust ornamental perennials
- Age of clumps/individual plants – factors indicating a low (1 or 2) evaluation might include a poor survival rate in mixed plantings, or apparent easy suppression by neighbours, or failure to increase clump size or number of healthy shoots or plant size, in proximity to other species.

The proposed ECA gradient:

1 – very readily overwhelmed by stronger neighbours

2 – readily overwhelmed, but with some ability to survive competition

3 – moderately robust, with ability to survive competition, but not to expand except in conditions with *no competition* – only to 'hold their ground'

4 – moderately spreading, ability to suppress or infiltrate neighbours

5 – characteristically aggressively spreading, suppressing or heavily infiltrating neighbours

The evaluation tended to adopt the middle position, 3, unless there were good reasons for a higher or a lower figure; this was intended to minimise the effect of a highly subjective evaluation method being too swayed by possibly untypical examples.

It might be possible to produce separate figures for each of the factors mentioned above – indeed such figures could be readily developed over time by practitioners in the field, if a set of descriptive indicators could be agreed, and be developed as a check-list. This could form the basis of a reduction in the subjectivity of this method, and thus be a basis for further research.

ECA evaluations are given in the *Perennial Data Table* (see 7.4 *Results - the perennial data table*).

8.2.1 Relationships between ECA and plant characters

Plant characters shown on the *Perennial Data Table* , and a number of other characters reached during the monthly measurements were tested for correlations with ECA through a Spearman Rank test. The same cautions should be noted regarding the use of this test for seeking correlations of categories rather than pure quantities, as noted previously (see 7.5.3 *Morphology and Architecture*). Table 8.1 gives a summary of the stronger correlations.

Characters measured	**correlation with ECA**
Size of clump after 5 years	0.55
Distance '/' ramets + Canopy Height	0.47
Distance between ramets	0.37
Pattern of Spread	0.34
Canopy height	0.33
Rate of ramet or shoot production, approx. no. after 3 yrs.	0.27
Distance between ramets + rate/ramet production	0.24
Shading effectiveness (SE) - cumulative total toJuly	0.22
Sum of ground coverage and shading effectiveness to July(GC + SE)	0.19
Specific Leaf Area SLA (1)	0.17
Ground coverage (GC) cumulative total to July	0.13
Cumulative GC + SE to June	0.12
(1) Where SLA was not measured for the CSR ordination it was obtained from Kleyer et al. n.d.	

Table 8.1
Correlations (Spearman rank) between Estimated Competitive Ability and characters measured where r_s = >0.10.

The strongest correlation (with size of clump) is rejected, as it essentially a circular reference, as size of clump was one of the criteria used for ECA.

It is noted that measurements of ground shading by plants (such as GC and SE) show very weak correlations. Higher correlations are shown by measures of height and of traits that lend themselves to rapid expansion of clumps. The highest correlation, but not strong at $r_s = 0.47$ is 'distance between ramets' plus 'canopy height'. In view of the fact that this is the sum of two of the variables measured, and it is one that is easily measured, it is suggested that this is taken as a key indicator which *suggests* that a species will compete well in EBPS. It will not necessarily do so, and more importantly must *not* be taken as an exclusive indicator of potential competitive performance. There is consistency here with the choice of *Pattern of Spread* and *Leaf/Stem Relationship* being taken as key gradients in the *Perennial Category Grid* table (see . 7.5.5.1 *Creating groups based*...), as *Distance between ramets* and *Pattern of Spread* are clearly closely related; height is related to *Leaf/Stem Relationship* too – nearly all tall perennials studied have stems with stem leaves predominant.

Given the relationship between competitiveness and an ability to maintain a high growth rate (Grime 2001) this measure (as column *Growth rate, March to June and March to September* in *Height summaries* – see 7. Appendix 4) was correlated with ECA. Given that Grime 2001 also indicates that shading of the ground by foliage during the time when growing conditions are at their best is an important factor in competitiveness, the measure *Number of months height is maintained at least 75% of maximum* (see Table 7.3) was also tested.

Traits were tested for correlations with ECA through a Spearman Rank test. They were also analysed through the following procedure – the mean ECA value of the species within each trait category was found, and compared to the overall ECA mean for all species tested (which is 3.3).

8.2.1.1 Growth rate

Growth rate – March to June. r_s= -0.01

Growth rate – March to September. r_s= -0.14

Species which maintain evergreen or wintergreen foliage and therefore effectively constant height are excluded.

There appears to be no competitive advantage to a having a high growth rate. Those species with the highest rates, which can be as much as 30mm per day in June (*Aconogonon* 'Johanneswolke', *Eupatorium maculatum*) are not especially aggressive competitors – on the contrary they have very little spreading power and average and less than average, respectively, shading potential (GC+SE).

Some species that make very early growth appear to show a decline from March to September, for different reasons, which does not make them poor competitors:

- *Brunnera macrophylla* – senescence of early-season flowering spikes which also carry foliage. The majority of the foliage is carried at a lower level.
- *Centaurea montana* – lodging of flowering stems. This is observed to happen in such a way that the plant tends to 'cartwheel' i.e., with stems radiating out from the base, their lower parts at ground level, the upper parts upright. This effectively crushes and shades out neighbours.
- *Stipa gigantea* – an evergreen species whose young foliage is upright, becoming arching as it matures. Although linear it is very dense, resulting in effective shading (GC+SE - 24).

8.2.2.2 Number of months height is maintained at least 75% of maximum. r_s=0.01

Species which maintain evergreen or wintergreen foliage and therefore effectively constant height are excluded

Maintaining a foliage canopy near maximum density does not appear to contribute to competitiveness. Indeed three of the highest ECA category species maintain this level of canopy cover for only three months:

Centaurea montana – as noted above, this species habit of lodging and overshadowing neighbours can be expected to make up for its failure to maintain maximum canopy height. In addition its ability to produce a second set of growth in the centre of a zone made up of its lodged stems from June onwards can be interpreted as an effective competitive strategy.

Persicaria bistorta 'Superba' – As with *Brunnera macrophylla*, there are effectively two levels of canopy operational: an upper one of foliage attached to the flowering stem, which tends to senescence from June on, and a lower one of more densely ground-covering foliage, which is refreshed by new basal growth throughout the summer.

Thermopsis caroliniana – although this species tends to lodge, and not replace early season growth with later-season new growth, its ability to send out very long runners and emerge early in the year can be seen as possibly outweighing a mid-season loss of canopy height.

8.2.2 Examining the relationship between plant characters and ECA through mean values

Characters measured were also analysed through the following procedure – the mean ECA value of the species within each trait category was found, and compared to the overall ECA mean for all species tested (which is 3.2). Results are shown in *Mean ECA Rating* (table 7.10).

Wintergreen character

The 'always winter dormant' category has the highest mean ECA score (4.2), suggesting that being winter dormancy is linked to competitive advantage; this is consistent with Grime's work on competitive species which suggests that there is a link between high foliage turnover, rapid growth and competitiveness (Grime 2001). However category 3, where foliage which lives for less than one year but which tends to stay healthy and where there is some active growth during mild weather, includes among a limited number of examples (4), two taxa with very noticeably competitive tendencies: *Geranium x oxonianum* and *Phlomis russeliana*.

Being wintergreen (trait category 1) confers no major competitive advantage over winter dormancy, but appears to be linked to an ability to persist; of wintergreen species only *Achillea millefolium* is noted as being strongly spreading.

Time of emergence

All species that frequently show strongly competitive behaviour emerge February to April. Species emerging after April only show average persistence ability rather than ability to strongly compete.

Character of emerging shoots

There is no clear relationship between this characteristic and competitive behaviour. The sole occupant of category 5, where basal leaves are relatively short-lived, is the exceptionally aggressive *Symphytum caucasicum*, where it should be noted that basal leaves are produced in rapid succession over many months. Category 3, where emerging stems are notable for their high ratio of stem to leaf, should be noted for their, at least average, competitive ability. This strategy, which could be interpreted as: a) enabling a plant to achieve maximum height over competitors before expending reserves on foliage and b) penetrating an overhead canopy of competitor foliage or litter.

Time of dormancy

All categories show more or less average ECA, with the somewhat surprising exception of category 1 (dormancy complete mid summer), occupied by two species which make early growth and persist well (*Papaver orientale* and *Pulmonaria officianalis*) and two which likewise make early growth and are notably aggressive (*Symphytum caucasicum* and *Centaurea montana*). The latter may also produce a second set of growth later in the summer during favourable seasons.

Of species that become summer dormant, only one, *Aconitum napellus*, is noted as being less persistent in competition, which could be related to its slow rate of spread.

Later-season basal growth

There is no clear pattern here, with both relatively high mean ECA amongst both those with no late tendency to basal growth and those with a pronounced tendency to do so. Species with ECA scores of <2 may be included in either.

A tendency to produce later-season basal growth may have distinct advantages in situations where vegetation is mown in mid-growth season, e.g. a meadow regime. This is supported by experience with *Geranium x oxonianum* (author observation, Cowley Manor, 1997-2000).

Later-season tip growth

Likewise, this does not seem to convey any particular competitive advantage. Theoretically however, given the competitive advantage that height does seem to confer, the increase in height which post-flowering time tip growth leads to could expect to be advantageous. Fundamentally, this characteristic must reflect an underlying trait, similar to the trait for the production of later-season basal growth – species with this trait may expect to be also suitable for meadow regimes; it is noted that *Euphorbia cyparissias* is a common component of meadows in central Europe (Klotz et al. 2002).

Growth Cycle Groups

There appears to be no clear relationship whatsoever between ECA and Growth Cycle Groups.

Persistent thatch/litter

Despite Grime's work (Grime 2001) suggesting that persistent litter is notably linked to competitive ability, there is no apparent link here. However as noted before, litter does tend to get removed during maintenance operations. However observation of geranium taxa suggests that litter surrounding the plant does play a role in limiting the growth of neighbouring species, particularly when this is linked to the collapse of long flowering stems on neighbouring plants; the persistence of litter over winter may also lead to the suppression of seedlings germinating around the plant. The quantity and persistence of litter of *Iris sibirica* is noted, both in the garden and in the wild (personal observation – three locations in Slovenia, June 2005, June 2007). (See illustration A14).

ECA scores are average for species noted for persistent litter. There is no obvious relationship with height. All are plants of woodland edge habitats or meadow, most with a clump-forming habit. It is perhaps worth noting that none of the prairie species studied have persistent litter.

Canopy height

There is a weak correlation between ECA and height (r_s=0.33). Species below the 300-599mm category have a lower ECA than average.

Canopy height category	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**
ECA scores								
no. spp. <3	0	3	10	3	1	1	0	0
no. spp. >3	0	0	5	8	6	9	4	0

Table 8.2

Scores of Estimated Competitive Ability above and below ECA 3 according to canopy height categories

Table 8.2 indicates a clear relationship between canopy height and estimated competitive ability.Species below the 600-999mm category (category 4) include a greater number of less competitive and a smaller number of more strongly competitive species. Category 4 and above (ie. taller than 600mm) include a greater number of more competitive and a lower number of the less competitive species.

It is worth noting that of the species with the highest ECA scores, two (*Euphorbia cyparissias* and *Persicaria bistorta*) are in the 600-999mm category, i.e. are not particularly tall.

Leaf Stretch

Although there is no clear correlation there is some relationship. Of species with an ECA of less than 3, only 5 have a leaf stretch greater than 149mm, whereas of species with an ECA of greater than 3, 18 have. However the number of species with ECA scores lower and higher than 3 is almost equal for species with a leaf stretch below 150mm. From this we may surmise that leaves with greater stretch confer a competitive advantage, but that low leaf stretch is not a disadvantage, as is clearly indicated by *Iris sibirica* and *Crocosmia* 'Lucifer', which have no effective leaf stretch, as the leaves are orientated vertically. *Crocosmia* taxa in cultivation in particular are strongly competitive, able to compete and spread in a grass sward (personal observation Elmtree Cottage, variety locations Cornwall). This particular taxon is a notably tall and vigorous hybrid; however it is well established that lower-growing members of the genus have frequently naturalised in a variety of habitats in southwest England.

Leaf Shape

At first there appears no clear relationship between ECA and leaf shape. However looking at species with a leaf stretch of greater than 150mm, all three of the species with an ECA of 2 have leaf shape 1 (narrowly linear). Of the 13 species with a leaf stretch of greater than 150mm and ECA of 4 or 5, seven have leaf shape 4 – entire and broad, including all 3 of the species with an ECA of 5.

We can suppose that possession of large entire leaves offer a competitive advantage as they enable a plant to suppress competition through shading, but that they are by no means necessary.

Leaf Shape	**1**	**2**	**3**	**4**	**5**
% with ECA of 4 or 5	21%	28%	23%	36%	33%

Leaf Shape	**1**	**2**	**3**	**4**	**5**
% with ECA of 1 or 2	28%	5%	38%	5%	10%

Table 8.3

Relationship between leaf shape and Estimated Competitive Ability.

From the figures shown in table 8.3 it would appear that species in categories 2 (pinnate, trifoliate or deeply divided) and 4 (entire) are more likely to be competitive but that species in category 5 (entire but narrow) may not be disadvantaged by having narrow leaves. The markedly less competitive nature of those in category 1 (fine, grassy) may be more to do with associated characteristics than the leaf shape *per se*, as this group includes several carex and stipa species noted for a tight, only very slowly spreading tussock habit.

Leaf/stem relationship

There seems to be some relationship between competitive ability and leaf/stem relationships. Many of the species with higher ECA have prominent basal/pseudobasal leaves (categories L/S groups 4,5,6) or have large numbers of relatively evenly sized and spaced stem leaves (category L/S 10). However, a cursory examination of the relationship between this particular morphological gradient (see above: 4.5 *An overall system for categorising ornamental herbaceous perennials*) does suggest a definite link between morphology and competitive ability in particular habitats, which could have major implications for plant selection in different climate zones and/or habitats. This is supported by Givnish (1982 and 1987).

Angle of flower-bearing stems

No clear pattern emerges, yet further investigation should reveal the role that the tendency of the flowering stems of some species to procumbency could play in competition. Two types are noted: those which start off erect and then fall out sideways, as in *Knautia macedonica* and *Geranium endressii*, and those which start out growing almost horizontally, such as *Nepeta x faassenii*. Observation suggests that the tendency of geranium flowering stems to fall outwards can play a significant role in suppressing competition (see 2.1 in *4. Investigating the growth of ornamental herbaceous perennials in grass swards*); stem size and weight could be expected to play a part here - observation suggests that the smaller stems of knautia is notably less successful at establishing domination in borders, and those of the much smaller *Calamintha* *grandiflora* still less so again.

Stems that become procumbent very rapidly, such as those of many nepeta species and hybrids appear to form a highly effective shading effect immediately around the plant. Further experimental work on the density of this shading could reasonably be expected to show that there is a relationship between density of growth (and hence shading) and competitive ability.

It should be noted here that this characteristic is highly dependent upon environment; species such as those discussed tend to fall sideways in cultivation, whereas in natural habitats they would either be supported by surrounding vegetation; in any case they could be expected to have shorter and less top-heavy growth in the wild where nutrient resources would generally be less available than in cultivation. 'Stem strength' may be regarded as the underlying trait – one whose expression is closely related to nutrient availability.

Pattern of spread

A weak correlation (r_s=0.34) indicates that there is a relationship between competitive ability and pattern of spread; ECA values are lower for species with growth that does not spread or spreads through ramet production only slowly. Species with fast-developing clumps that are physically able to spread outwards quickly, either through phalanx or guerrilla means, tend to be strongly competitive.

Distance between ramets

A weak correlation (r_s=0.37) indicates that there is a relationship between competitive ability and the distance between ramets. It is clear that long distances between ramets is a measure of a plant's ability to project propagules far from the parent plant, improving foraging ability and so dominate space (Herben & Hara 1997).

Rate of ramet production

A weak correlation (r_s=0.27) indicates that there is a relationship between this trait and competitive ability. Indeed from categories 1 to 4 there is a constant rise in mean ECA scores. However certain species have a high rate of ramet production within very tight clumps, e.g. the grass *Panicum virgatum* and the forb *Anaphalis triplinervis*, which do not translate into speed of spread – the caespitose or tussock strategy clearly serves another strategy.

Distance between ramets *plus* rate of ramet production

There is only a weak correlation (r_s=0.24) between this measure and ECA; however of the species with the highest scores (7 and 8), the ECA has a mean of 3.8, and most of the highest ECA scoring species are included within these scores. The implication is that, comparing the correlations of this and the previous trait, rate of production counts for little in enhancing competitive ability; in this regard it is informative to note those species which produce a very large number of ramets, but very densely packed, as in caespitose grasses, or of the forbs studied here: *Artemisia lactiflora* and *Anaphalis triplinervis*.

Persistence of living basal material

Species whose previous year's growth does not survive into the next year do not form a solid clump – and their competitive ability can be compromised. Monarda species do this, and not surprisingly have a relatively low ECA score. *Iris sibirica* however manages to maintain very tight clumps, with a dead centre; its competitiveness does not appear to suffer.

Species which develop semi-woody material, with new growth growing from this rather than at ground level do not have much spreading ability. Few species of this character were looked at here; none competes strongly and some can be notoriously short-lived in gardens because of their habit of 'growing out of the ground' and not forming regenerating clumps, e.g. heucheras. Both heuchera and bergenia are noted as being found naturally in rocky habitats, as do certain other species with this habit.

8.2.3 Competitive ability as estimated by ECA and basal cover

See table *Degree of Basal Cover* 7. Appendix 5

Here an attempt will be made to explore the relationship between the measure of ground cover and shading effectiveness (GC + SE) and ability to spread, with competitive ability as estimated by ECA.

GC and SE do appear to be linked: for species with a GC score of >15, there is a correlation of $r_s=0.81$, and for those where there is an SE score of >0 there is a correlation of $r_s=0.76$.

This is to be expected, as the ability to ensure good coverage of the ground occupied by the plant clump and the ability to create shade around it might be expected to be associated, both the result of leaf morphology.

There is no clear correlation between GC+SE and ECA - $r_s = 0.19$, and as can be seen from table 8.4, which would seem to indicate that *Distance between Ramets* might be a better predictor of competitiveness, with mean inter-ramet rising with higher ECA ratings.

ECA	**Mean of distance between ramets**	**Mean total GC+SE to July**
2	1	15
3	1.5	17
4	2	17
5	3	17

Table 8.4
Relationship between and means of istance between ramets and means of GC+SE to July for each of the categories of Estimated Competitive Ability. Note: ECA 1 is excluded as the sample size is so small.

Given the way in which ECA is estimated this is to be expected; the ECA figures are estimated for planting situations which may be denser and involve more inter-species competition than the comparatively-widely spaced planting of a conventional border, but which are kept clear of the majority of seriously competitive perennial weeds, and which are still considerably less dense than how plants would grow in the wild or in competition with turf grasses in a grass sward. The results of the Cowley trial (see 2.1 in *4. Investigating the growth of ornamental herbaceous perennials in grass swards)* did indicate that in situations where competition was more severe, such as a grass sward, GC+SE might be a useful guide to ability to persist, and possibly also to ability to spread at the expense of neighbouring species.

It is clear that GC+SE by itself is no indicator of competitive ability as indicated for the situations described by ECA.

Whilst species with higher GC+SE values do not necessarily have higher ECA, those with higher ECA are more likely to have higher GC+SE values.

Of the 22 species where annual total SE >0, all have an ECA of at least 3, indicating that the ability to maintain coverage over the clump is strongly indicative of competitive ability, or at least the ability to persist.

Of the 58 species where annual total GC >15, 52 have an ECA of at least 3. Of the 6 which do not:

- *Stipa arundinacea* and *S.calamagrostis* have clumps where very fine foliage does not maintain good coverage over the clump in the earlier part of the year. The clump of *S.calamagrostis* is notably sparse throughout the year. *S.arundinacea* has a very tight clump with good shading effectiveness late in the year when its seedhead heavy foliage causes the plant to droop over neighbouring plants – it has little observed ability to compete with other vigorously growing species however, possibly a consequence of slow growth in the early part of the growing season. Observations of 5 plants in a grass sward at Elmtree Cottage (2000) showed that they were out competed by native turf grasses within one year.
- *Heuchera micrantha, Origanum laevigatum, Saliva nemorosa* are relatively short in stature and do not form spreading clumps; it is noted that they are also from less resource-rich environments than most of the other species.
- *Monarda* hybrid has a non-persistent habit.

If listed in order of GC + SE, all species in the highest quartile have an ECA of at least 3, of 24 species: seven are ECA 4 and four ECA 5.

8.3 ANALYSING THE RELATIONSHIP BETWEEN COMPETITIVE ABILITY AS INDICATED BY ECA AND THE MORPHOLOGY OF BASAL COVER AND VEGETATIVE SPREAD

Here, plants studied are grouped according to whether they are assessed as having high competitiveness (ECA = 4 or 5), medium (ECA = 3) or low (ECA – 1 or 2). The groups are then sub-divided according to their level of basal cover, as measured by GC+SE and their spread after 5 years. Outstanding common characters or anomalies are then discussed for each group.

The groups discussed are:

(i) ECA = 4 or 5, High GC + SE (>19), strongly spreading, spread after 5 yrs, > 3
(ii) ECA = 4 or 5, High GC + SE (>19), strongly spreading, spread after 5 yrs, > 3
(iii) ECA = 4 or 5. Lower GC + SE (<20), strongly spreading - spread after 5 years >3
(iv) ECA = 4 or 5. Spread after 5 years <3.
(v) ECA = 3, GC+SE > 19 and a spread after 5 years > 2.
(vi) ECA = 3. GC+SE > 19 and a spread after 5 years > 2.
(vii) ECA = 3. GC+SE <20, spread after 5 years of >2.
(viii) ECA = 3. GC+SE <20, spread after 5 years of <3
(ix) ECA – 1 or 2.

8.2.4.1 Estimated Competitive Ability = 4 or 5

(i)

High GC + SE (>19), strongly spreading, spread after 5 yrs, > 3:

Aconitum arcuatum B
Anemone x hybrida A
Persicaria amplexicaule B
Persicaria bistorta A
Symphytum caucasicum A
Tanacetum macrophyllum B

All emerge in early spring (March), only one wintergreen, tendency to later-season basal growth, broad foliage, even if pinnate or divided, foliage can be predominantly basal or stem leaves, pattern of spread variable, from dense clumps to somewhat looser, tendency for ramets to be distant and be rapidly produced.

There are two distinct groups visible:

A - clump-formers – where foliage tends to be basal/pseudobasal, or at least where leaves are predominantly lower down the stem, and where there is effective foliage shading of the base and its vicinity by broad foliage; spread is overwhelmingly phalanx, although occasional guerrillas are observed.

B - erect-growers – where strongly upright stems produce are more or less evenly distributed leaves over most of their height, where there is less tendency towards effective coverage of the base by foliage; the degree of sideways spread through ramets may vary considerably – being either guerrilla or phalanx.

It will now be indicated here if a species falls more or less clearly into one or other of these categories.

(ii)

High GC + SE (>19), not necessarily strongly spreading:

Centaurea montana B
Echinops ritro B
Geranium phaeum A
Geranium x oxonianum A

All emerge in early spring (February-March), tendency to later-season basal growth, foliage can be predominantly basal or stem leaves, pattern of spread is for dense clumps varying considerably in speed of spread.

All here are clearly group A or B, except for *Echinops ritro*, which early in the season looks A, but as the stem matures appears to be B; since stem leaves do predominate for most of the growing season it will be classed as B.

(iii)

Lower GC + SE (<20), strongly spreading - spread after 5 years >3:

Achillea millefolium A, p
Aster cordifolius B, p
Aster novi-belgii B, g
Aster umbellatus B, g
Euphorbia cyparissus B, g
Filipendula rubra B, p
Filipendula ulmaria B, p
Helianthus 'Lemon Queen' B,p
Iris sibirica, p
Leucanthemella serotina B, g
Lysimachia ciliata 'Firecracker' B, g
Lysimachia punctatum B, g
Phlox paniculata B, p
Rudbeckia fulgida var. deamii B, p
Thermopsis caroliniana B, g

Time of emergence early to mid spring (generally March – April), thirteen out of fifteen have foliage dominated by a large number of stem leaves (leaf/stem relationship categories 6, 9 or 10), putting them in group B. Only one is a clear category A, and one, *Iris sibirica*, stands out as an anomaly, with a radically different morphology.

In looking further at category B plants, two sub-categories may be recognised:

a) Phalanx spreading, where the clump is always tight – indicated by *p*.

b) Guerrilla spreading, where the clump is preceded by a outer zone of scattered ramets, indicated by *g*.

(iv)

Four remaining species are classed as ECA 4, but are not so strongly spreading, two with high GC + SE (=19): *Alchemilla mollis* (A), *Geranium* 'Johnson's Blue' (A), two lower (*Miscanthus sinensis* and *Rudbeckia* 'Juligold' (B). Both emerge by March.

It is noted that there is a strong tendency for species to have high foliage canopy (average category of 5.0).

Of species rated as ECA 4, GC is mostly 10 or above, the exceptions being *Achillea millefolium*, whose wintergreen foliage and spreading habit may give it alternative advantages, and *Aconitum arctuatum*, which is able to make rapid growth in spring and so possibly keep ahead of competition; in some respects it has similarities with the crocosmia discussed above: its height, growth rate and the presence of substantial tubers – it could almost be described as a geophyte. *Rudbeckia* 'Juligold', with its GC of 4, stands out as an anomaly; it is however one of several species of North American prairie origin which make impressive rates of growth between June and September – it stands amongst the top three for growth-rates during this period. Its competitive ability can perhaps be best explained as a combination of physiology and distance between ramets.

There is a tendency amongst species rated as ECA 4 to have high levels of ramet production, although the distance between ramets tends to be very variable.

8.2.4.2 Estimated Competitive Ability = 3

GC+SE > 19 and a spread after 5 years > 2.

(v)

Acanthus spinosus A
Aruncus dioicus B
Bergenia 'Abendglut', A
Cephalaria gigantea A
Echinacea purpurea B
Epimedium sp. A
Euphorbia palustris B
Geranium asphodeloides A
Geranium sylvaticum A

Hemerocallis 'Golden Chimes'
Hosta fortunei A
Lunaria rediviva B
Nepeta x faassenii B
Stipa gigantea
Vinca minor B

There is a variety of morphology, including:

- linear foliage (*Hemerocallis* 'Golden Chimes'),
- basal foliage with a petiole serving as a stem (*Epimedium sp.* and *Hosta fortunei*) – these can be grouped with category A species,
- where leaves are attached to a low semi-woody stem (*Bergenia 'Abendglut'*), clearly A
- where basal/pseudobasal leaves predominate (*Acanthus spinosus, Cephalaria gigantea, Geranium asphodeloides, G. sylvaticum*), A
- grasses with stem leaves (*Stipa gigantea*)
- where stem leaves predominate (*Aruncus dioicus, Echinacea purpurea, Euphorbia palustris, Lunaria rediviva, Nepeta x faassenii, Vinca minor*), B. It is noted that all of these have a spread pattern of 2, i.e. a tight clump, except for the *Vinca minor*, which indeed displays this pattern, but then spreads through the rooting of its prostrate stems.

It is suggested that this particularity of *Vinca minor* can be recognised through the phalanx-guerrilla distinction introduced above.

(vi)

GC+SE > 19 and a spread after 5 years > 2.

Campanula latifolia, B
Geranium 'Rozanne', *B*
Helleborus x hybridus A

All these have a tight clump, but with varying leaf-stem relationships.

The campanula is similar to many other species with an erect stem and numerous stem leaves.

Species of *Helleborus* is similar to those of *Epimedium* and *Hosta*, in that it's the petiole can be seen as functioning as a stem.

Geranium 'Rozanne' would fit in with list (v) above, apart from its tendency to maintain an extremely tight, non-spreading clump, and its predominance of stem leaves would put it in category B; this characteristic, plus its combination of prostrate stems and tight clump make it similar to *Nepeta x faassenii* in its competitive strategy.

(vii)

GC+SE <20, spread after 5 years of >2.

Aconogonon 'Johanneswolke' *B*
Amsonia orientalis B
Aster puniceus B
Astrantia major B
Baptisia australis, B
Brunnera macrophylla A
Calamagrostis x acutiflora 'Karl Foerster'
Chelone obliqua B
Cirsium canum A
Cirsium rivulare A
Eupatorium maculatum ssp.purpureum B
Euphorbia polychroma B
Euphorbia schillingii B
Geranium pratense A
Inula cf. racemosa A
Lysimachia clethroides B
Lythrum salicaria B
Macleaya microcarpa B
Molinia caerulea 'Transparent'
Ophiopogon bodinieri
Pulmonaria officianalis A
Sanguisorba tenuifolia B
Solidago rugosa 'Feuerwerke' B
Vernonia crinita B
Veronicastrum virginicum B

A variety of morphology includes:

- Linear foliage, strong guerrilla spread (*Ophiopogon bodinieri*)
- Basal or pseudobasal foliage predominant (*Brunnera macrophylla*, *Cirsium canum and C. rivulare*, *Geranium pratense*, *Inula cf. racemosa*, *Pulmonaria officianalis*), A
- Stem leaves of varying sizes tending to predominate (*Aconogonon* 'Johanneswolke', *Astrantia major*, *Lythrum salicaria*, *Macleaya microcarpa*, *Sanguisorba tenuifolia*) B

Grasses with stem leaves (*Calamagrostis x acutiflora* 'Karl Foerster', *Molinia caerulea 'Transparent'*

- Where numerous even size leaves are found up an erect stem, the remainder, B

As with (v) above, there is a strong tendency for the species to form a tight clump, with only 8 out of 25 species showing a tendency to spread more strongly.

(viii)

GC+SE <20, spread after 5 years of <3

Aquilegia vulgaris A
Calamintha grandiflora B
Clematis heracleifolia
Geranium sanguineum A
Knautia macedonica B
Liriope muscari,
Papaver orientale A
Sedum spectabile B
Tanacetum parthenium B
Thalictrum aquilegifolium A

Morphologies include:

- Linear foliage, (liriope)
- Clear dominance of basal/pseudobasal leaves (the *Aquilegia vulgaris*, *Geranium sanguineum*, *Papaver orientale*, *Thalictrum aquilegifolium*) A; however two of these, *Aquilegia vulgaris* and *Thalictrum aquilegifolium*, which are closely-related genera, are unlike other category A plants, in that they exhibit a substantial minority of distinct stem leaves and a high proportion of stem to leaf; they are amongst the few herbaceous plants with tall stems to flower in early summer.
- Stem leaves dominant, although the overall impact is very different: the *Calamintha grandiflora* is similar to *Nepeta x faassenii* in its combination of stems tending to the prostrate and stem leaves, the *Knautia macedonica* with its larger leaves distributed lower down a short stem appears to be similar to category A plants in the density of foliage near ground level, the sedum is much more comparable to erect-growing category B plants.
- Woody stemmed, the *Clematis heracleifolia*.

Apart from the geranium and the *Clematis heracleifolia*, all show either a tight clump or a clump without clear ramets (*Aquilegia vulgaris* and *Thalictrum aquilegifolium*). *Clematis heracleifolia* is something of an oddity, as it is essentially a chamaephyte, although its stems are weak and horticulturally is generally cut back annually as if it were herbaceous.

Of species rated as ECA 3, there is a tendency to have an average GC, be strongly spreading, with a tendency towards a wide distance between ramets. The level of ramet production in some cases can be low; two species stand out: *Cirsiuim canum* and *Euphorbia schillingii*. The *Cirsium* species however makes early growth in the year, which may give it an advantage; it also is in the highest category of leaf lamina proximity to soil surface. *Euphorbia schillingii*, of all the species in the study has one of the lowest levels of ramet production, which is combined with a considerable distance between ramets, a habit which is combined with an ability to maintain a steady rate of growth through the growing season.

Aconitum napellus, an ECA 2, species also appears to be an anomaly. There may be some inaccuracies in measurement, particularly of rate of ramet production – in addition to which rates of clump spreading seem to be highly variable between individual plants in the same planting area. However this species is noted for its tendency to become summer dormant, and appears to be easily out-competed in dense vegetation. This is possibly related to its origin as a sub-alpine tall-herb flora species (Adler et al. 1994), which has a high early-season growth rate, which renders it vulnerable to competition in situations where there is a longer growing season than in its natural habitat. It is also notably variable (Jelitto & Schacht 1990); strains in cultivation may vary in their degree of summer dormancy, which although noted by practitioners (e.g. Pasley-Tyler 2007) is not mentioned in garden literature.

8.2.4.3 Estimated Competitive Ability = 1 or 2

Aconitum napellus B
Anaphalis triplinervis B
Artemesia lactiflora 'Rosenschleier' *B*
Carex dipsacea
Dianthus carthusianorum B
Eryngium bourgatii A
Heuchera micrantha A
Monarda hybs. B
Origanum laevigatum B
Salvia nemorosa B
Stipa arundinacea
Stipa calamagrostis

- All form a tight clump apart from the monarda, which forms what are effectively annual ramets, resulting in a very sparse clump, as Grime discusses for *Ranunculus repens* (Grime 2001).
- Rate of ramet production varies; in cases where it is high (e.g. the anaphalis) this happens within the context of a very tight clump.

- Spread after five years is not necessarily low: *Monarda hybs* forms a sparse clump, aconitum has been discussed above, while *Stipa calamagrostis* forms a distinctly open clump, with relatively low GC+SE
- GC+SE is lower than average (an average of 15 as compared to 17 for all species considered), but this is hardly significant.
- Considering leaf/stem relationships, a range is shown, but it is worth noting that only two have predominantly basal foliage: the *Heuchera micrantha*, which is somewhat untypical in having a semi-woody stem and the eryngium.
- Height is somewhat lower than average; category 3.9 (300-599mm) compared with an average of category 4.0 (600-999mm) for all species considered.
- The majority are from environments which tend to be less productive

8.2.4.5 Morphology and competitiveness

There is no indication that groups A and B have any correlation with competitiveness. However the relationship between this basic morphological division, phenology and habitat has been noted several times already, particularly in relationship to Givnish's work (Givnish 1982, 1987).

It is noted that the following are factors that indicate a tendency towards competitive ability as suggested by ECA:

- Higher GC+SE values, indicated visually by bulkier leaf architecture or production of plentiful foliage necessary for high GC+SE values
- Greater canopy height
- An ability to spread ramets widely
- Early season growth, and to some extent, an ability to produce new growth from the base later in the year

It is stressed that these are sufficient but not necessary factors.

Less competitive species generally have less biomass.

Any one of these three factors *may* suggest a tendency towards greater competitiveness. It is also suggested that combination with a high growth rate would increase a tendency towards competitiveness.

However it is also noted that having one of the three factors by itself does not always indicate competitive ability.

8.2.4.6 Monocots

Monocotyledons are in a definite minority amongst herbaceous plants; they also present strikingly different morphologies.

Poaceae and Cyperaceae

Carex dipsacea
Calamagrostis x acutiflora 'Karl Foerster'
Miscanthus sinensis
Molinia caerulea subsp. *arundinacea*
Stipa arundinacea
Stipa calamagrostis
Stipa gigantea

In addition *Panicum virgatum* was considered in the *Perennial Data Table* (see 7. *Appendix 1 Perennial Data Table).*

All species considered are clump forming as opposed to turf forming (except *Calamagrostis x acutiflora* 'Karl Foerster'), as is the case with the majority of ornamental grasses (Grounds 1969). Casual observation points to a huge range in competitive ability: wintergreen *Stipa gigantea* is observed to be very persistent in herbaceous borders, whilst *Panicum virgatum*, which emerges late, is observed to be easily out-competed.

It is difficult to draw conclusions from a small sample of species, but the following points can be noted. GC +SE tends to be low; a reflection of narrow leaves that cannot cast much shade, and indeed an observation frequently made is that native turf-forming grasses are able to smother the crowns of many of these species with ease. At one extreme the wintergreen crown of *Stipa gigantea* ensures effective year round shading (GC+SE of 20) whilst the sparse growth from the crown of *Stipa calamagrostis* and the late emergence of new growth of *Stipa arundinacea* ensure a low GC +SE (12 and 11 respectively), and indeed the later are noted as being easily out-competed (ECA is 2).

Nearly all graminoid ornamentals are tussock-formers, and have a tendency towards a caespitose habit.

non-*Poacea/Cyperaceae*

Two additional Southern Hemisphere species were considered in the *Perennial Data Table.*

Crocosmia 'Lucifer'
Hemerocallis 'Golden Chimes'
Kniphofia cv.
Iris sibirica
Liriope muscari
Ophiopogon bodinieri

The *Hemerocallis* 'Golden Chimes' and the *Kniphofia* cv.qualitatively assessed only), a moderately high rate or ramet production; their genera also have a reputation for ease of naturalisation amongst native grass-dominated flora (*Hemerocallis* taxa in Bavaria (Simon 1994), *Kniphofia* taxa in Cornwall (personal observation). Whilst their morphology is very different, an approximation could be made to geranium in terms of their competitiveness and crude overall form.

Liriope and *Ophiopogon* species are woodland plants (Phillips and Rix 1991) and are typical of many plants of such habitats, in being low-level, evergreen, and slowly spreading. Their tolerance of full sunlight (at least in northern Europe) and of competition ensures their use widespread use in horticulture – in this way they are unlike many other woodland species. As woodland species, it is not surprising that their characteristics may be markedly different to other species considered.

Crocosmia 'Lucifer' and *Iris sibirica* stand out as interesting anomalies. Both have vertical foliage that casts minimal shade (Iris sibirica has a GC+SE of only 10, the *Crocosmia* would be similar). *Crocosmia* taxa are widely known to naturalise in the maritime west of the British Isles in a variety of native vegetations, whilst the *Iris sibirica* is noted for its longevity and resilience in herbaceous borders. Whilst the *Crocosmia* taxa form dense clumps, *Iris sibirica* has ramets which live for two years, orientated so that the plant forms a circle, with living tissue on the outside and a dead hole in the centre. Observations at Cowley (3.The use of transects to investigate established ecologically-based plantings) suggest that whilst seedlings are able to germinate and grow in the centre of the *Iris sibirica* plant, ramets of other species are unable to penetrate the ring. Maximum canopy height is achieved within two months of March, and so it can be assumed that this must give it considerable advantage over later-growing or slower competitors.

Additionally, both these species may illustrate the relevance of roots – an area not considered here, or indeed in many studies (Casper et al. 2003); *Crocosmia* taxa, as noted previously, can be classed as geophytes, and can achieve considerable growth early in the year (although it flowers relatively late), whilst *Iris sibirica* is observed to have very thick roots which may be able to store considerable quantity of nutrients and a very extensive network of finer roots. Observations in the natural habitat of the *Iris sibirica* (personal observation Slovenia 2005, 2007) point to an ability to form large and persistent stands. In the wild the very dense mat of persistent litter around the plants is also a feature which points to not only the probably suppression of neighbours but also monopoly nutrient recycling.

8.3 CONCLUSIONS

It is difficult to draw many clear conclusions about which morphological and phenological traits are firmly linked to competitiveness. A prominent example is the A – B morphology distinction just discussed in relation to competitiveness, describes a spectrum of traits, yet owing to the interplay of other factors, it does not relate clearly to competitive ability.

8.3.1 Estimated Competitive Ability

It is proposed that a measure of Estimated Competitive Ability (ECA) be used in order to try to utilise practitioner experience of ornamental plants competitive performance; the use of category-based qualitative judgements is a route towards a crudely quantifiable measure.

8.3.2 Factors which indicate competitive ability

Ability to achieve high biomass indicates competitive ability. However this is made up of several elements

The following stand out as factors that may indicate competitive ability, *especially if combined*:

- The ability to produce an extensive network of ramets with long inter-ramet distances, distributing daughter plants over a wide area, with the proviso that older growth persists; relating this to the distinction between phalanx and guerrilla strategies (Crawley 1997a), this may or not take the form of a guerrilla tendency, the key issue being that space eventually becomes occupied by a dense mass of shoots, as opposed to a guerrilla tendency which occupies space and moves on, as in some monarda species – which can be seen as a ruderal rather than competitive strategy – Grime (2001) describes such a strategy as 'ruderal-perennial. The ability to produce a network of ramets too may be readily assessed visually, either from the pattern of growth, supported by digging around the plant to ascertain the presence of connecting underground structures. A tendency to spread through extensive ramet growth tends to be visible on plants from the second year from seed on, and is generally visible in pot-grown plants.
- Greater canopy height.
- Production of foliage of a shape sufficient to effectively shade out competition around and over the base of the plant, and/or its production in sufficient quantity, and its presence for most of the growing season. It should be noted however that this is not combined with long inter-ramet distance or extensive ramet production in any of the species studied – it is suggested that there is a trade-off between these two characteristics.
- An early season start to growth – in other words, an ability to start growth at relatively low temperatures.

'Distance between ramets' and 'Canopy Height' are indicated as the factors measured in the research that are the strongest predictors or competitive ability.

A variety of other traits may confer competitive advantages, but the level of advantage is quite probably heavily dependent upon the nature of the environment, both in terms of abiotic conditions and the density and species composition of neighbouring species. In particular there are indications that a combination of possession of vertical foliage and roots with a high level of winter nutrient storage (linked to an ability to rapidly mobilise these stored resources) may be a 'minority' competitive strategy.

9.

DISCUSSION, CONCLUSIONS AND FUTURE RESEARCH

DISCUSSION, CONCLUSIONS AND FUTURE RESEARCH

9.1 DISCUSSION

9.1.1 Traits and characteristics favourable to competition

A central part of this study is the relationship between genetically determined traits, and characteristics – i.e. the result of gene x environment interaction. Since the former are largely physiological and therefore difficult or time-consuming to measure, it is recognised that the measurement of morphological and phenological characteristics which reflect traits are the next best alternative (McIntyre et al. 1999, Weiher 1999, Box 1996). For our purposes, which are geared towards easy to recognise indications for practitioners, it is suggested that many characteristics reflect traits which may be described as 'a tendency towards' developing a particular morphological or phenological characteristic, the degree to which the trait is expressed being very dependent on prevailing conditions. It needs to be recognised what these conditions are.

A variety of characteristics have emerged during the course of this study as being pertinent, pertinence being defined by:

- The level of clear variation within them amongst the species studied
- Their importance for the functionality, aesthetics and management of horticultural schemes and EBPS
- Their importance for competition in EBPS.

It should be noted that 'characteristic' is a term that has been defined relatively tightly on the basis of a limited number of morphological or phenological features wherever possible.

The characteristics (or more correctly bundles of characteristics) listed below are indicated in this research to appear to favour competition (1-7), or effective competitive response or which confer an ability to survive long-term (8-9), in EBPS in northwest Europe. 10-11 are included, although they are outside the scope of this research, as they have been strongly indicated by other research as potentially being important for species survival (e.g. ruderals: Grime 2001, Pfälzner-Thomsen1995, molluscs: Hitchmough 2003, Hitchmough & de Fleur 2006)

7 – 11 have not been looked at in any detail in this study, but their importance for future research is regarded as very high.

The broad nature of the underlying traits is suggested in italics.

1. **Extensive ramet production**, initially guerrilla-led, but followed by persistence of growth
   - *Tendency for large number of new growth points to be produced leading to potential high rate of ramet production*
   - *Morphology of ramets*

2. **Effective basal cover** and consequent shading of both neighbours (competitive effect) and protection of base of plant from neighbour competition (competitive response) through dense foliage
    - *Foliage shape, tending to be broad*
    - *Position of foliage, lower on stem*
    - *Quantity of foliage*

3. **High biomass** as a combination of canopy height and ability to project growth laterally.
    - *Morphology, physiological ability to mobilise resources*
4. **Early growth** - an ability to produce new shoot growth at relatively low temperature and light levels
    - *Physiological response to temperature and possibly light*
5. **Phenological plasticity** - a strong tendency to produce new shoot growth later than time of primary production of new growth in spring - when conditions are favourable
    - *Physiological responses to growing conditions*
6. **Morphological plasticity** (see below) – the ability to adapt plant shape in response to spatial competition.
    - *Morphology of plant habit, stem strength*
7. **Root competition** - ability to forage for resources through extensive root growth laterally, or vertically
8. **Nutrient recycling** - ability to recycle, and thus to monopolise, nutrients through monopolisation of space by foliage and roots (as in caespitose grasses)
    - *Morphology and physiology of plant habit*
9. **Nutrient storage** - ability to rapidly mobilise nutrients from large quantity of stored resources (as in species with a geophyte type habit)
    - *Morphology and phenology of physiology and habit*
    - *Morphology and physiology of roots*
10. **Ruderality** - ability to produce large quantities of readily germinating seed
    - *Morphology and physiology of reproduction*
11. **Low mollusc palatability**
    - *Morphology (e.g. leaf hairs) and production of secondary metabolites that discourage grazing.*

9.1.2 Expression of characteristics

Categorising the conditions which effect the expression of traits as characteristics into a hierarchy of importance and relevance for particular conditions is the prelude to assessing the expression of the underlying traits for a particular locality.

It is suggested that a hierarchy of conditions which affect expression of traits amongst ornamental herbaceous vegetation might look like this:

1. **'Macro' factors** – climatic factors which affect the entire region, notably: length of growing season, minimum winter temperature, moisture availability during growing season.
2. **Microclimatic factors** – the impact that aspect etc. has in modifying the above for the particular planting locality.
3. i) **Soil conditions** – notably moisture and nutrient availability. These are often modified by conventional horticultural practice.
   ii) **Light conditions**. These may be modified or may change as surrounding woody vegetation or built structures change.
4. **Competition** from neighbouring species within the planting scheme.

It should be readily appreciated that the conditions become more localised from 1 to 4 and that they can be more easily changed from 1. to 4, i.e. the practitioner has more influence over them.

9.1.3 Differences between expression of traits as morphological characteristics in the wild, in EBPS and in conventional horticulture

Given the relationship between fundamental and realised niches, it could be argued that many plant species in the wild are growing in conditions which are far from ideal – many species are to be found not because they do well in the habitat in which they are found but only because their competitors are less able to survive (Ellenberg 1988). Given the nature of competition, which in densely packed habitats such as hay meadows and prairies, may be intense, plant morphology may also be quite different between the wild and cultivation. In particular the relationship between plant form and shoot or ramet distribution does appear to differ considerably in some species, which may well relate to differing potential for expression of competitive ability. In some cases, where plants in cultivation build up clumps with multiple basally derived shoots, this is observed much less frequently in nature, e.g. *Euphorbia palustris* in mature wet meadow vegetation often only occurs as single stems (personal observation, Slovenia, 2005) (illustration A6, fig. 9.1). From this is might be argued that the expression of traits as characteristics in the wild may not only be very different to that in cultivation but also give less indication of the potential of the plant to express certain characteristics. For example, the trait of the *Euphorbia* species just mentioned to produce multiple stems from the base is indicated better in cultivation than in the wild. However as noted earlier (see 7.5.4 *An analysis of plant traits and characteristics*) plants in the wild will give a truer picture of how a species will perform in conditions of intense competition. Resolving this paradox and clarifying what we can learn from plants in the wild, it is suggested that the following applies – that observation in the wild emphasises competitive response whilst competitive effect is highlighted in cultivation.

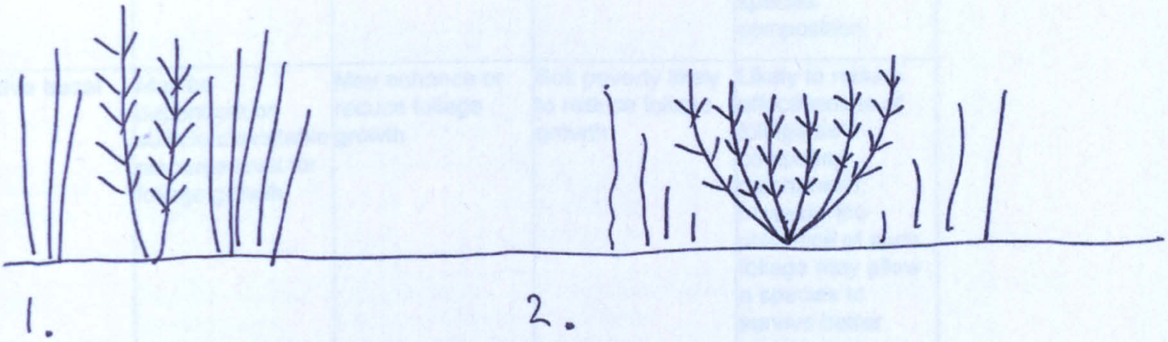


Fig. 9.1

Eupborbia palustris in the wild and in cultivation illustrating competitive response and effect.

(1) In the wild, the plant is at least as tall as the dense neighbouring vegetation, illustrating an effective response to competition.

(2) In cultivation relative lack of competition enables it to produce more shoots, which because of their outward-leaning tendency are able to shade neighbouring plants, thus increasing competition effect. In EBPS at low to medium plant densities, such as in open border situations (see 2.3.4., 1. *Introduction*) this will be of advantage to this species, but as densities increase and approach that of natural habitats, expression of the ability to produce more shoots will be expected to decline because of increased competition for resources, which in turn will reduce the ability of the plant to shade out neighbours.

Morphologies which are apparent in cultivation which might appear to enhance competitive ability in the border may not do so in EBPS - or in the wild; and of course vica versa. Outcomes, of population density etc. may also be very different, as competition between many different species will give different results to competition between only a few species (as in much EBPS) or none (as in the conventional herbaceous border).

Table 9.1 considers how the four factor-categories outline above under 9.1.2 *Expresssion of characteristics*... might be expected to influence the bundles of characteristics 1-11 outlined above under 9.1.1 *Traits and Characteristics.* The likelihood of the impact of competition has drawn largely on Grime 2001.

	Macro factors	**Microclimatic factors**	**Soil conditions**	**Competition – (presence of)**
Extensive ramet production	Possibly reduced production in climates with short growing season	May enhance or reduce ramet production	Soil poverty likely to greatly reduce ramet production	Likely to reduce rate and extent of ramet production, resulting in intermingled rather than monocultural species composition
Effective basal cover	May be dependent on sufficient available resource level for foliage growth	May enhance or reduce foliage growth	Soil poverty likely to reduce foliage growth	Likely to reduce effectiveness of foliage as a competing mechanism, however the presence of such foliage may allow a species to survive better
High biomass	Will be reduced where growing season is short (1)	May enhance or reduce biomass production	Soil poverty likely to reduce biomass '(2)	Likely to substantially reduce biomass
Early growth	Only possible in climates where winter temperature permits growth	May enhance or reduce foliage growth	Soil poverty likely to reduce quantity of early growth	Competing species will also have shading impact if also early; root competition may reduce advantage
Phenological plasticity	Only an advantage in unpredictable or long growing season climates	May enhance or reduce level of growth	Soil poverty likely to reduce advantage	Likely to reduce effectiveness of foliage as a competing mechanism, especially if other phonologically plastic species present
Morphological plasticity	No obvious relationship	No obvious relationship	Soil poverty likely to reduce growth and therefore advantage	Likely to reduce effectiveness of foliage as a competing mechanism. May be effective if combined with persistent litter

	Macro factors	**Microclimatic factors**	**Soil conditions**	**Competition - presence of**
Nutrient recycling	Only an advantage where climatic conditions reduce likelihood of effective resource foraging	May enhance or reduce biomass production	Soil poverty may increase advantage	Possibly less useful in high resource environments
Effective nutrient storage	Of most advantage in short growing seasons	Of advantage where conditions reduce length of growing season	Soil poverty may increase advantage	Possibly less useful in high resource environments
Effective root competition	Possibly effective in all climates		Soil poverty likely to reduce advantage	Likely to reduce effectiveness as a competing mechanism
Ruderality	Possibly of most advantage in short growing seasons	Of advantage where conditions reduce length of growing season	Soil poverty likely to increase advantage	Competition likely to reduce likelihood of recruitment
Low mollusc palatability	Possibly of greatest advantage in short growing season climates			May be important factor in survival or elimination of species in dense planting

(1) *Short growing season* is understood to refer to situations where either the length of time with suitable temperatures for growth or of moisture availability is short.

(2) *Soil poverty* is understood to refer to low availability of nutrients, or other factors that limit access to available nutrients such as low moisture, water logging, soil chemistry, low light etc.

Table 9.1

The likely impact of increasingly localised environmental factors (from right to left) on bundles of plant characteristics.

9.1.4 Implications for practitioners

To summarise, the implications for practitioners seeking to select species with good competitive ability or ability to persist long-term:

9.1.4.1 Macro factors and micro-climatic factors

Practitioners working in climates with a short growing season can be expected to find factors which involve high biomass production such as ramet production or large lower leaf canopy production to be of less value in selecting plants for competitive effect – as the short growing season will limit the growth of all plant species.

Practitioners working in climates with short but intense growing seasons where competition for high levels of resources are extreme, such as continental North America can expect that high biomass and extensive ramet production are the most useful. Early growth or phenological plasticity might be less useful. The upright nature of most prairie species suggests that competition for light is of supreme importance – more so than the ability to shade out competition early in the year (Givnish 1982 & 1987). It might also be supposed, from the evidence in 6. *Evaluating the competitiveness of herbaceous perennials using a phytometer in open ground conditions* and *5.Assessing competition with two grasses of contrasting productivity in standardised container culture* that root competition is also extremely important. However given the presence of species such as *Baptisia australis* which appear to have a conservative resource recycling and storage strategy, and geophytes such as *Camassia* species, in the prairie, other strategies than those discussed by Grime (2001) as purely competitive may have a place. Practitioners should be able to make use of these in designing plantings.

Practitioners working in climates with some maritime character can be expected to find that early growth, effective basal cover and phenological plasticity make a contribution in addition to high biomass and extensive ramet distribution to competitive ability, and are consequently important characteristics to look for in seeking taxa for EBPS.

Microclimatic variations may be expected to enhance or reduce the importance of phenological plasticity depending on the impact of moisture availability or temperature.

9.1.4.2 Soil conditions

Reduced access to nutrients or to opportunities to sustain their absorption and use can be expected to, as discussed by Grime (2001), reduce biomass, and so reduce competition. Strategies involving resource conservation and recycling are commonly observed amongst species of less productive soils. Practitioners in areas of low soil productivity may find that higher levels of diversity in plantings are easier to sustain, as high biomass production is limited. Very low soil productivity will require focusing on species which exhibit the characteristic morphological features of effective nutrient recycling.

9.1.4.3 Competition

Evidence gathered here does support the conclusions of Grime (2001) regarding high biomass, morphological plasticity, etc. and the ability to compete effectively. Practitioners need to understand that competition exists on a gradient, and that perennial-based planting schemes can be placed on a gradient (see table 9.2).

minimal competition	**moderate competition**	**high competition**	**intense competition**
traditional border planting	High density, low maintenance. e.g. 'mixed planting'	EBPS with low maintenance.	Hay meadow management. High resource environments e.g. bog gardens.

Table 9.2

The gradient of competition and various management systems.

The characteristics 1-11 listed above in 9.1.1 *Traits and Characteristics* generally favour competitive ability, and those which do not, such as nutrient recycling and geophytic tendency may favour exploitation of particular niches, or long-term survival in competitive environments. Disturbance favours ruderal character and species with extensive ramet production (Grime 2001).

Clearly, the more competitive the environment, the more practitioners need to use species with clear competitive character, but at the same time they must expect these competitive characteristics to be less effective the more competitive an environment becomes.

As resources levels increase, the greater the likelihood of a virtual monoculture developing (Grime 2001) – analogous to areas in some wild tall herb floras (Ellenberg 1988) (see table 9.3). It is well established that plant biomass or height varies predictably along natural gradients of stress and disturbance, the less of either factor being linked to greater biomass (Gaudet & Keddy 1988, Menges & Waller 1983). It has also been noted that clonal species, i.e. those most likely to establish a monoculture are more common on wetter soils (Klimes, Klimesova, Hendriks, van Groenendael 1997). Competition involving a multiplicity of species and interactive effects is noted as being strongest in situations where high nutrient levels and reduced disturbance result in the highest level of biomass (Wilson & Keddy 1986). The Wilson and Keddy study noted that mutualism could result in higher biomass for interacting species, but that this only occurred in exposed sites.

a.	**Decreasing level of management>>>>>>>>>>>>>>>>>>>>>> Increasing level of plant community density>>>>>>>>>>>>>>>**		
Increasing soil nutrient		steppe type open border (1)	hay meadow type community
v			
v v v v v			high-biomass, low diversity, tall-herb type flora (3)
v			
v v	conventionally managed border	open border (2) ·	monocultural blocks (3)

b.	**Decreasing level of management>>>>>>>>>>>>>>>>>>>>>> Increasing level of plant community density>>>>>>>>>>>>>>>**		
Increasing disturbance	conventional perennial border	steppe type open border	hay meadow type community
v			
v v		*increasing ruderal component*	
v			
v v	conventional annual plantings		annual meadows (4)

Table 9.3

Perennial planting styles for a gradient of decreasing levels of management (and a concomitant level of increasing plant density, i.e. numbers of individuals per unit area) and a. a gradient of increasing levels of nutrient and b. of increasing disturbance. Species which express morphological and phenological characteristics that enhance competitive abilities will be indicated as increasingly relevant towards the bottom-right of a., with the trade-off of probable loss of diversity. Such plants will not necessarily have much advantage in ruderal situations as in b.

(1) E.g. Munich Westpark steppe area (Kingsbury & von Schoenaich 1995).

(2) E.g. areas at Cowley Manor discussed in *3.The use of transects to investigate established ecologically-based plantings*

(3) E.g. areas of tall-herb flora in semi-shade at Hermannshof discussed in *3.The use of transects to investigate established ecologically based plantings.*

(4) E.g. as developed at Sheffield University

The most competitive situation for ornamental forbs can be assumed to be grass managed as hay, i.e. cut once or twice a year (as on the right-hand side of table 9.3). Evidence presented here suggests that the ability to shade out competition, root competition, early growth and ramet production are all of particular importance in such situations. Work reported by Hitchmough (2007), indicates that relatively few species are able to survive and increase long-term in rough grass managed as hay meadow, at least in the strongly maritime British climate. The same author emphasises the role of slugs in eliminating or reducing species in this habitat, and in the creation of prairies in the UK (Hitchmough & de Fleur 2006). Regeneration may also be limited in grass with high sward height (Hitchmough 2003).

A particular aesthetic implication of the use of species with extensive ramet production in densely species-packed plantings is that instead of becoming monocultures they may be forced to develop a more scattered distribution, with a high level of inter-species spatial integration – this situation is may often be particularly visually pleasing, but also place limitations on the spread of very invasive species. As an example *Euphorbia cyparissias,* noted for its extensive ramet formation, is readily observed in the wild on the European mainland to be scattered in open grass-dominated habitats and in hay-meadow managed grass (see *Investigating the growth of ornamental herbaceous perennials in grass swards)*; in the conventional border it is noted as being 'invasive' and forming large mats (Jelitto & Schacht 1990) (see illustrations A4-A5 and fig.9.2).

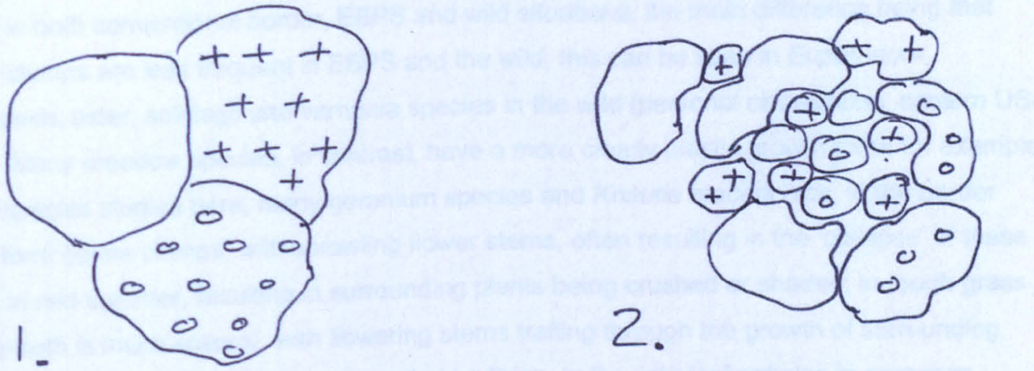


Fig. 9.2

Phalanx and guerrilla spread and long-term development of EBPS

Vigorously competitive species which phalanx spread can be expected to form monocultural blocks in high productivity situations (1), with the expectation that eventually one will overwhelm the others. In theory species which spread by guerrilla extensions would form more complex patterns of interpenetrated ramets and clumps as in (2) in a similar situation. In practice, one species probably would overwhelm the others eventually, but occasional maintenance in either limiting the more aggressive species, or simple random disturbance might enable a complex pattern to survive for longer. Random disturbance, in the form of mowing is, arguably an additional reason (to intense competition) why *Euphorbia cyparissias* develops a sparse distribution pattern in hay meadow situations.

Given what has been noted regarding competitive species forming monocultures (see 3. *The use of transects to investigate established ecologically based plantings*) it is important to ask the question – when does a species form a monocultural block and when does it form a scattered distribution? Grime (2001)notes the tendency of a limited number of species in high resource environments to form monocultures, but these are exceptional species, noted for rapid expansion of foliage and very persistent litter. It is unlikely that species as aggressive as *Pteridium aquilinum* would be seen as desirable in any kind of landscape horticulture. The monocultural blocks observed at Hermannshof are in semi-shade – the habitat in which much similar tall-herb flora is observed (Ellenberg 1988); in full sun, grass is far more likely to dominate, resulting in the scattering of species such as *Euphorbia cyparissias*. It is suggested, that light-shade with high level of resources (i.e. analogous to many tall-herb flora situations) is most favourable to the development of monocultures by species with the ability to spread vegetatively and mechanisms for effective shading of neighbours.

9.1.4.4 Morphological plasticity

There does appear to be a difference in morphological plasticity between species occurring in different habitats. Erect growers, generally late-flowering, tend to form a similar shape in both conventional border, EBPS and wild situations, the main difference being that dense clumps are less frequent in EBPS and the wild; this can be seen in *Eupatorium maculatum*, aster, solidago and vernonia species in the wild (personal observation, eastern USA, 1994). Many meadow species, in contrast, have a more clearly plastic growth form; for example, of the species studied here, many geranium species and *Knautia macedonica*; in the border these form dense clumps, with sprawling flower stems, often resulting in the 'collapse' of these stems in mid-summer, resulting in surrounding plants being crushed or shaded; in rough grass their growth is much sparser, with flowering stems trailing through the growth of surrounding plants (mostly grasses) and being supported by them, in the wild leaf petioles in geranium species are likewise able to penetrate/be supported by surrounding vegetation, enabling laminae to be positioned in the sun with great flexibility (*Knautia macedonica* – personal observation, Cowley Manor, 1998) (*Geranium pratense* – personal observation, Gloucestershire, 1998), (*Geranium phaeum* – personal observation, Austria, 2002). *Astrantia major* can be seen similarly, particularly with regard to leaf petiole penetration of surrounding vegetation in a slightly different habitat, woodland edge, with generally non-graminoid neighbours (personal observation – Austria, 1995). Hitchmough 2000 suggests that the long petiole length itself, of e.g. *geranium* promotes survival in dense swards. The outcomes of the two extreme situations, in borders and meadows is illustrated in fig.9.3

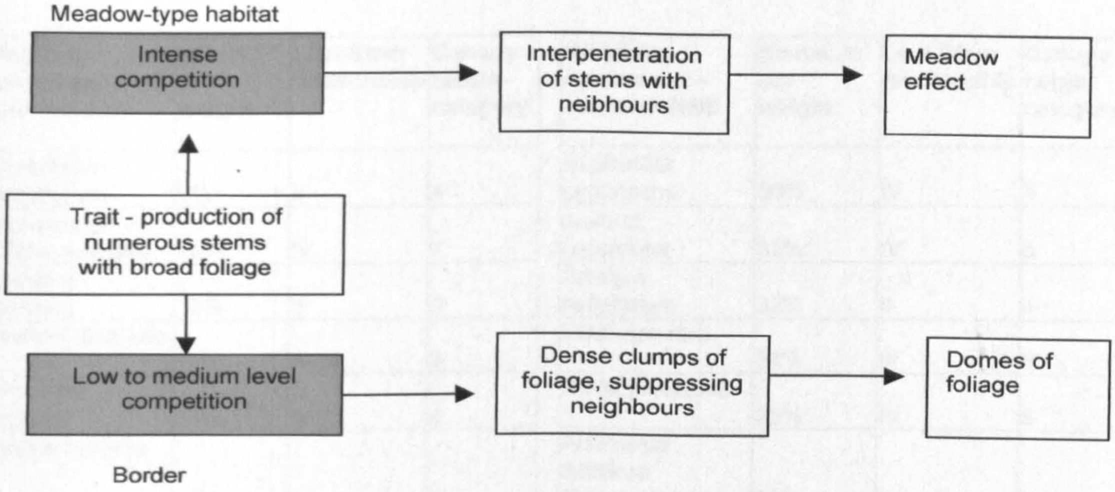


Fig. 9.3

The effect of different environments: meadow-type and conventional border, on the expression of traits in *Geranium endressii*. Competition effects expression of traits governing stems and foliage, and thus overall plant shape, with consequences for visual effects.

A similar effect may be the case with those species which produce stems which branch, where branching ability which may be reduced in the wild for the same reason as rapid multiple ramet production is reduced – notably neighbour competition, but are able to produce branching stems in less-competitive cultivation conditions – the resulting branching may well enable the plant to then became an enhanced ability to suppress neighbouring vegetation. This can be clearly appreciated in the case of *Nepeta x faassenii*, which forms a dense mat of prostrate branching stems, and was observed to have a particularly effective shading ability.

The morphological plasticity which is so useful to the horticultural practitioner is dependent on the basic architecture of the plant allowing for sufficient flexibility to allow for plasticity – essentially this means the existence of stem tissue, in the form of petioles and supporting stems which potentially offer flexibility in that they can extend but without compromising photosynthetic efficiency. Additionally, it can be supposed that the size of photosynthetic surfaces (i.e. leaf laminae) have to be large enough to justify expenditure on potentially long supporting structures. A key issue is also the physical capacity to bend, as opposed to remain rigid. It is supposed that a lower dry matter content might make this more likely.

Table 9.4 shows the % dry weight of mature flowering stems of 43 species:

Weighing carried out – summer 2005	**Stems, % dry weight**	**Leaf-Stem relationship**	**Canopy height category**
Symphytum caucasicum	9%	II	4
Aconogonon 'Johanneswolke'	10%	IV	7
Acanthus spinosus	12%	II	4
Papaver orientale	12%	II	3
Geranium phaeum	13%	II	4
Lunaria rediviva	15%	IV	4
Cephalaria gigantea	17%	II	7
Campanula latifolia	18%	IV	4
Macleaya cordata	18%	IV	7
Nepeta x faassenii	18%	IV	3
Alchemilla mollis	19%	II	3
Salvia nemorosa	19%	IV	3
Astrantia major	20%	*III*	4
Knautia macedonica	21%	IV	3
Thermopsis Carolina	21%	IV	5
Lysimachia punctata	22%	IV	5
Dianthus carthusianorum	23%	IV	2
Anemone x hybrida	24%	II	6
Anaphalis triplinervis	25%	IV	3
Aquilegia vulgaris	25%	II	3
Aruncus dioicus	25%	IV	5
Bergenia 'Abendglut'	25%	II	2
Phlomis russelliana	26%	II	3
Amsonia orientalis	27%	IV	3
Baptisia australis	28%	IV	5
Euphorbia cyparissus	30%	IV	3
Inula cf. racemosa	31%	IV	6
Achillea millefolium	32%	II	4
Echinops ritro	34%	III	6
Phlox paniculata	35%	IV	5
Artemesia lactiflora 'Rosenschleier'	36%	IV	6
Stipa arundinacea	36%	IV	3
Aconitum arctuatum	38%	IV	6
Calamagrostis x acutiflora 'Karl Foerster'	38%	IV	4
Eupatorium maculatum ssp.purpureum	38%	IV	8
Miscanthus sinensis	43%	IV	7
Solidago rugosa	53%	IV	4

Table 9.4

Dry matter content of a selection of the ornamental herbaceous species studied. Arranged in order of dry matter content, with leaf-stem relationship category and height category.

It can be appreciated from table 9.1 that there appears to be a tendency for meadow species to have less dry matter invested in strong stems than other species. In terms of the evolution of hay meadow as an anthropogenic habitat, this is to be expected, since mid-summer cutting might be expected to minimise the advantage of investment in upright stems.

Grasses and prairie species are noted as being particularly high, along with a number of species from tall-herb or woodland edge habitats. Shorter species with less dry matter invested in stems are more likely to have a leaf-stem relationship weighted towards larger lower stem leaves (i.e. Leaf-Stem categories I-III see 7.5.3.5 An analysis of plant traits and characteristics) the latter to more evenly distributed foliage (i.e., Leaf-Stem category IV). It is indeed to be expected that tall species might have particularly high dry-matter in stems. The low dry matter content of the *Aconogonon* 'Johanniswolke' is noted – its stems are very clearly hollow, yet show considerable strength. It is suggested that perhaps one reason for the ability of this and the related *Fallopia* species to achieve dominance is the ability to use minimum resources rapidly to build stems of sufficient strength to support foliage that can overtop and shade out neighbours. However it is noted that this, and macleaya, also a notably tall species with hollow stems, are plants of tall-herb habitats, where wind damage is likely to be less than in open habitats, such as grassland.

The high dry matter content of *Aconitum arctuatum* is also noted. This woodland edge species is noted by Wynne-Jones (2008), as being a semi-climber. In cultivation it is noted as having a climbing mechanism radically different to any other species observed, in that a rigid upright stem encountering an obstacle such as a shrub branch suddenly bends, so projecting the foliage and flowers in the direction of light, but remaining rigid (personal observation, Montpelier Cottage 2997).

Pons and Jordi (1998) discuss how erect-growing herbaceous plants have leaves which rapidly replace each other as the lower ones become shaded, so are able to have resources re-allocated to new, higher ones – by extension it can be assumed that species which are not erect growers, are also able to re-allocate resources. Whilst many species in cultivation typical of prairie and tall-herb floras have sturdy upright stems which last an entire growing season (leaf/stem relationship III and IV), meadow species are more likely to have leaf/stem relationship III, with stems, as in the knautia and geranium species studied here, which do not last an entire growing season, and it is noted, may be replaced during the course of the growing season. There is a trade-off here: high investment in strong stems with high dry matter content which last a whole season, as opposed to less investment in shorter-lived, less structurally strong, more plastic stems; the latter trait however lead to species with it to be selected for in the dynamics of the development of hay meadow communities.

It is suggested that morphological plasticity is a trait of considerable value in both conventional horticulture and EBPS. In conventional horticulture, many species of *geranium* are used, with a clump-forming habit seen as visually pleasing and with a dense network of ramets and large leaves combining to ensure complete coverage of the surface of the clump and a high level of shading effectiveness, resulting in the noted usefulness of the plant for weed suppression and amenity ground cover (Thomas 1970). Thomas's praise of them as first-rate ground covers is based on their ability to maintain a monoculture. However, after flowering the frequent collapse of flowered stems is seen as undesirable. In EBPS, the growth of the plants may be closer to that seen in the wild, where stems are closely integrated with, and partly supported by neighbouring vegetation. The tendency of the stems to collapse after flowering can also be appreciated as potentially reducing the growth of neighbouring plants through smothering, which when combined with the relatively high level of persistent litter makes them effective competitors. It is noted how well some geranium taxa thrive in rough grass (see 4.*Investigating the growth of ornamental herbaceous perennials in grass swards*). Some, notably those with long flowering stems such as *G. x oxonianum* and *G. procurrens* can also scramble into the lower branches of shrubs. Their flexibility also makes them more useful in lightly shaded situations where their foliage can grow to face into the light whereas species with strongly upright stems tend to lean over unattractively.

In the conventionally-managed garden *Geranium endressii* types and *G.phaeum* appear to illustrate a strong competitive *effect*, i.e. dense weed-suppressing clumps; in a semi-natural plant community (i.e. in the wild, or when naturalised (author observation, Bath and Brilley, England) this is much less apparent, but instead they clearly show a strong competitive *response* - the ability to survive amongst grasses. In EBPS their appearance may be anything between the two extremes, as is shown by their performance in the transects at Cowley and Hermannshof, where a strong tendency to suppress growth of neighbours was noted but where integration was also observed (see Illustrations A8, A9). It is suggested that the position on a monoculture-integration gradient is dependent upon i) growth traits of neighbouring species and ii) density of planting.

Similar habits can be observed in several other species observed. The *Perennial Data Table* (7.Appendix 1) in *7. An analysis of plant traits and characteristics* lists 'Angle of flower-bearing stems' amongst the characteristics observed. Species stems well away from the upright are classed as category 3. - *Initially erect, frequently falling to the horizontal, or initially horizontal, arching upright.*

	Leaf-stem relationship category
Alchemilla mollis	II
Geranium asphodeloides *	II
Geranium sanguineum	II
Geranium x oxonianum *	II
Knautia macedonica *	IV
Lysimachia ciliata *	IV
Origanum laevigatum	IV
Salvia nemorosa *	IV

* = indicates tendency to produce substantial new growth after spring.

Table 9.5

Species with flowering stems which are frequently observed to tend towards the horizontal in specimens studied.

Table 9.5 illustrates that where flowering stems tend towards the horizontal the leaf-stem relationship may either be weighted towards a preponderance of lower stem leaves or be more evenly distributed.

	Leaf-stem relationship category
Calamintha grandiflora	IV
Euphorbia polychroma *	IV
Geranium 'Rozanne' *	III
Nepeta x faassenii *	IV
Persicaria affinis	IV
Vinca minor	IV

* = indicates tendency to produce substantial new growth after spring.

Table 9.6

Species with foliage which is observed to be largely procumbent in specimens studied.

Table 9.6 lists species studied where stems are normally procumbent, of them, *Persicaria affinis* is grown as a rockery plant and the vinca as ground cover in shade; thus the level to which they may be combined with other species in this study may be limited. The other taxa here are all species which are commonly used in conventional herbaceous planting. It is suggested that the ability of these species to form either tight clumps (in conventional borders, or ground cover plantings) or to send out stems which are able to integrate themselves spatially with those of neighbouring plants, in some cases relying on them for support, makes them particularly suitable for EBPS, especially denser and more competitive plantings.

9.1.4.5 Phenological plasticity

An additional factor should be noted, that of phenological plasticity. It was noted in the *Perennial Data Table* that some species produced greater or less amounts of new growth from either the base or from shoot tips after the main spring production of new growth. These are marked above with * in table 9.6 above. *Geranium* 'Roxanne' is also included, as its spring production of new growth never really stops until September, producing long trailing stems.

The combination of morphological and phenological plasticity suggests that species which combine these two characteristics are in a position to exploit advantages presented to them in both space and time, in a way in which species which are genetically pre-determined to grow straight up, spreading sideways only through the longer-term process of ramet production are at a competitive advantage in EBPS, especially in maritime climates. Additionally, the tendency shown by *Geranium x oxonianum* and *G. asphodeloides* to produce very early season growth is a further competitive advantage in climates with a long growing season. It is suggested that the combination of morphological and phenological plasticity combined with early-season growth are amongst the strongest reasons why geranium species have become so commercially successful in Britain since the 1980s. The introduction and evaluation of further taxa and of other genera with a similar combination of traits is therefore strongly suggested.

Schmidt recognises the value of strongly competitive species for fertile soils, where their weed suppressing character can be invaluable; he makes a distinction between early summer and late summer/autumn (overwhelmingly North American) flowering species in terms of management, as the earlier flowering group are effectively remontant, so can be cut back after flowering to produce fresh new foliage, and sometimes re-flower (Schmidt 2006b). Some geranium species are good examples of this – a useful characteristic in terms of aesthetic interest, particularly for hay-meadow type management.

In the long growing-season of a maritime-influenced climate, the opportunities for herbaceous plants to grow are arguably more varied than that offered by other climates. A particularly important aspect of a maritime climate is the level of wintergreen foliage present; species which in their native region may not have foliage which overwinters, or is normally buried in snow, may be able to effectively photosynthesise through the winter, either because their old foliage has not died, or because relatively high winter temperatures encourage the production of new shoots, which may be able to undertake useful photosynthesis. The different performance of species from the same geographical origin in a different climate zone is something that may make a considerable difference to competitiveness, and therefore value for low maintenance situations or EBPS. In other words, species from the same geographic origin may show considerable variation in phenological plasticity – but this can only be discovered through evaluation in climates where the opportunities for growth outside that which is customarily experienced in their region of origin.

9.1.4.6 Nutrient recycling and mobilisation in species which show high resilience to competition but slow spreading ability

It has been noted (7.5.5.2 *An analysis of plant traits and characteristics*, and 6.*Evaluating the competitiveness of herbaceous perennials using a phytometer in open ground conditions*) that some ornamental herbaceous species show characteristics which reflect traits towards nutrient storage or recycling and persistence in one location, and others exhibit related traits towards nutrient storage and rapid mobilization in spring. The extremes of these tendencies are cesspits grasses and geophytes, respectively. It is suggested that these tendencies give an advantage to plant species in competitive environments, even though they are not strategies of competition, but of resilience, or of competition avoidance. As such they may play an important part in EBPS, although there is an important proviso, that by being spatially limited and relatively immobile, their ability to recover from disturbance is likely to be limited.

An awareness of the potential importance of these strategies is highly pertinent to the performance of some widely used monocots in horticulture. Caespitose graminoids, chiefly *Carex* species, are particularly popular in contemporary garden design. It is to be expected that their capacity to compete with weeds and neighbouring plants is reduced by their small size, low rate of vegetative spread and moderate shading ability (see 7. *An analysis of plant traits and characteristics*), however the results of the open ground trial (see *6. Evaluating the competitiveness of herbaceous perennials using a phytometer in open ground conditions*) indicates that when grown in groups their foliage meshes to form a highly effective blanket shading the ground.

Caespitose grasses and other species which do not strongly spread vegetatively, and which may start growth late (as in C4 grasses) may perform well in less productive soils where neighbour competition is reduced, but they may be readily out-competed in more productive environments by more competitive neighbours, or by weeds if maintenance is reduced. However species which have a broadly similar habit, but possibly exert effective root competition or shading competition, such as *Baptisia australis*, may fare better – at least if they survive mollusc predation when young – a problem noted by Hitchmough and de Fleur (2006) and potentially an important limiting factor on this type of slow-growing plant. Other slow-growing species however e.g. *Veronicastrum virginicum*, they suggest, may benefit from their unpalatability to molluscs, giving them a breathing space within which to establish.

Species which store enough nutrient in their roots, as is possibly the case with *Iris sibirica*, and certainly with *Crocosmia* 'Lucifer' (see.8.2.4.6 *An analysis of plant traits and characteristics)* to make rapid growth in spring and replenish nutrient reserves before being overshadowed by neighbours, can be likened to those geophytes which also flourish in dense communities on productive soils, such as camassia species in prairie habitats (Ladd 1995). In the case of the iris highly persistent and wide-spreading leaf litter may be expected to contribute. A similar strategy, but with later-season growth appears to be exhibited by crocosmia taxa.

9.1.5 Exploring possible relationships between annual growth cycle, region of origin, climate, habitat and competitiveness.

Here an attempt is made to explore possible connections between a variety of plant traits and characteristics to wild habitat and climate zone, in order to see if there are any broad indications as to which plant traits might be expected from species from particular geographic regions and habitat types. Only a broad indication can be expected, for two reasons: one is that the selection of plants under study might be regarded as limited, and secondly and more seriously, the severe lack of information regarding the description of the habitat details of most of the species under study. Whilst Ellenberg's numbers (Ellenberg 1988) could be of great use in the study of central European species, there is nothing like this level of accuracy or schematic organisation of information is available for other floras. Habitat descriptions are often vague in the extreme in published floras.

Having established broad relationships between habitat and climate zone and phenology and morphology, consideration is then given to the usefulness of these relationships to plant usage in EBPS.

9.1.5.1 Region and habitat of origin

Information given about the natural environment of the species studied are in Appendix 1. *Region and habitat of origin.*

Making comparisons between plants growing in the wild and in cultivation is of only limited value because:

- The difference often observed between fundamental and realised niches (Burrows 1990) indicates that a knowledge of conditions in the wild can only be of limited value to the horticulturalist.
- That the composition of wild plant communities is the result of contingency and to a large extent the outcome of chance. Contemporary thinking is summarised by Budiansky 1995.

Individuals in the wild are generally considerably smaller (Hitchmough 1994), the outcome of more intense competition. EBPS practitioners are working with plants in competitive combination, unlike conventional horticulture and landscape professionals, and so might be expected to be able to make more useful comparisons of plants in the wild and in cultivation.

Comparison of plant form, growth rate and competitive ability between individuals in the wild and in garden conditions does not appear to have been systematically undertaken.

The usefulness of the chart '*Region and habitat of origin*' is indicated by the fact that the knowledge that a particular species originates in a particular climate zone or habitat is useful because it points to the fact that in this realised niche, in conditions of competition, it can survive. Such information is more useful in determining conditions of sufficiency for growth than the knowledge that it can survive in garden conditions with a particular set of climate conditions.

Notes: For citations for plant species habitat information here, see appendix: habitats. *Habitat etc. information for taxa of hybrid origin are given for parents where known.*

9.1.5.2 Growth cycle groups and environment of origin

For Growth cycle of plant species in the study see 4.2 of 7.*An analysis of plant traits and characteristics.*

Growth cycle groups as defined here, are a characteristic, the result of a bundle of traits that would require a major research project to unravel. Amongst these might be expected the following:

- Growth rate as a response to temperature
- Growth rate as a response to light levels
- Traits involved in governing foliage longevity, e.g. resource allocation to foliage vis a vis other parts of the plant, leaf survival during cold or dry weather.

GROUP 1. Wintergreens/Evergreens, i.e. foliage surviving for at least one year

Group 1	Region of origin	Climate	Habitat	ECA	CSR
Bergenia 'Abendglut'	Himalayas	continental/montane	slopes	3	C
Carex dipsacea	New Zealand	Maritime	swamps, woods	2	SC
Epimedium perraldianum	N Africa	montane/Mediterranean	woodland	3	C/SC
Helleborus x hybridus	Balkans	Mediterranean/continental	woodlands, thickets	3	C
Liriope muscari	E Asia	Continental	woods	3	CR
Ophiopogon bodinieri	S.China	Continental	forest, scrub, slopes	3	C/SC
Phlomis russelliana	Turkey	Continental	woodland clearings	4	C
Stipa gigantea	Iberian peninsula	continental/ Mediterranean	rocky slopes, usually at altitude	3	S/SC
Vinca minor	Balkans	Mediterranean/continental	woods, hedges, rocks	3	SC

Climate, region of origin and wild habitat

Woodland habitats, where it is well established that having wintergreen foliage is an advantage, and Mediterranean climates, where cool moist winter conditions favour species with wintergreen foliage, predominate (Aerts 1995).

What is immediately noticed is that all, apart from the *Carex dipsacea*, are of old world origin. However, it is suggested that there are historical reasons for this: plant introductions to north European horticulture were in no way systematic, and the many evergreen perennials and sub-shrubs of North America were poorly represented in the range of species introduced (Stuart 2004).

However it is noted that species with persistent winter foliage are to be overwhelmingly found in particular habitats, notably woodland and exposed environments, and are almost entirely absent from temperate zone productive grass-dominated habitats, such as meadow and prairie. None of the species are from areas that regularly experience prolonged very cold winters, e.g. northern China or American mid-west.

Most of the species have some stress-tolerant character, this being expected from CSR theory (Grime 2001).

Morphology

Canopy height is relatively low, mostly under 600mm, methods and rate of vegetative spread vary; what is distinctive is that the leaf-stem relationship is dominated by leaves, indeed most of these species have no, or minimal, leaf-bearing stems. It would appear that evergreen foliage and development of upright foliage-bearing herbaceous stems is mutually exclusive. There would appear to be a trade-off between canopy height and having a long season of photosynthetic activity.

Competitiveness

ECA is generally medium, the only exception being *Phlomis russeliana* at 4; this species has particularly large leaves creating a very dense shade zone around the clump; it also shows a strong ability to spread laterally through ramet growth; it should however be noted that this species is only wintergreen in maritime climates. Some species do have a long inter-ramet distance, notably the ophiopogon (through rhizomes) and the vinca (stems which root at the nodes). *Vinca minor* has also been observed to effectively grow over and eventually suppress other strong-growing species in shade below trees, notably *Alchemilla mollis, Geranium macrorrhizum* and *Luzula sylvatica* (author observation, Cowley Manor). Being evergreen clearly is not involved in a trade-off in competitiveness, in certain environments – shade; it is suggested that being evergreen and an ability to spread laterally rapidly are part of an effective competitive strategy for the domination of forest floor environments.

Habitat information suggests that all these species apart from *Bergenia 'Abendglut'*, *Stipa gigantea* and *Carex dipsacea* are woodland species. The latter two are typical in many ways of caespitose grasses/sedges, a clearly defined group, both morphologically and taxonomically, with a particular and important role in habitats where water loss is liable to be high (Briske & Derner 1998).

It is suggested that the distinctive character of evergreen growth, the close link with (shaded) habitat and with a particular morphological features (minimal leaf-bearing stems), makes this a very clear and obvious character.

Usage

The value of evergreen, or at least wintergreen, species for landscape ground cover is well established (Thomas 1970, MacKenzie 1999). Species selection is heavily dependent upon climate zone, e.g. the usage of *Liriope* and *ophiopogon* species for example seems largely restricted to regions which offer a long enough season of warmth to maintain substantial foliage growth, e.g. south-east USA, Mediterranean.

Evergreens are an attractive proposition for monocultural ground cover plantings, particularly if they have a spreading habit; bergenia, epimedium and vinca species are frequently used in northwest Europe for this purpose. It is noted from the trial described in 6. *Evaluating the competitiveness of herbaceous perennials using a phytometer in open ground conditions* that bergenia is slow to establish and vulnerable to competition in the first year; given that it, epimedium and all other species with thick wintergreen foliage can be expected to grow slowly, given the need to grow fleshy foliage, it might be expected that this result would be expected from all wintergreen species with this type of foliage. However all are plants of shaded habitats where the growth of resource-hungry competitors would be reduced – and indeed this is where standard horticultural practice suggests these plants are used (Thomas 1970, MacKenzie 1999). A more visually exciting appearance would result from an intermingled style of planting, as in EBPS. There is every reason to expect that such plantings should be successful, so long as the rate of spread through ramet production and extension from the parent plant occurs at a similar rate. This would rule out the inclusion of species with a caespitose habit or slow ramet production, such as *Carex dipsacea*.

Phlomis russelliana is an anomaly here – it is not noted as a plant for shade, and its combination of a clump-forming habit and widely spreading wintergreen foliage makes it apparently ideal for monocultural weeds-suppressing plantings.

GROUP 2. Very strong tendency to substantial later season basal growth, replacing spring growth

Group 2	Region of origin	Climate	Habitat	ECA	CSR
Centaurea montana	Europe	Continental	tall herb flora, open places	5	
Cirsium rivulare	C Europe	continental/ montane	wet meadows, moorland	3	
Geranium asphodeloides	Balkans	continental/ Mediterranean	woodlands, thickets	3	C/CR
Geranium x oxonianum	S.Europe	maritime and montane	moist, woodland edge	4	CR
Nepeta x faassenii	SW Europe/W Asia	continental/ Mediterranean	dry places	3	C/SC
Persicaria bistorta	Eurasia	continental/ montane + maritime	damp woods, meadows	5	C/CR
Salvia nemorosa	C& E Europe	Continental	dry meadows, arid places	2	CR
Symphytum caucasicum	Caucasus	Continental	meadows, roadsides, streamsides	5	C/CR

This group is not clearly defined (see 7. *An analysis of plant traits and characteristics*) is one end of a spectrum, the nature of which is the ability to produce new foliage at low temperatures/light levels, which is also linked to a fast turnover of foliage (although this is not necessarily the case with *Nepeta x faassenii*). *Achillea millefolium* could for example arguably be included here – its reduced ability to produce winter growth compared to the species included is simply one of degree.

Climate and habitat

Given that the length of growing season is such a key defining characteristic of a maritime climate, the ability of these species to respond to it, suggests that this category has considerable usefulness for practitioners in these climate zones; conversely it could be seen as possibly much less relevant for those in strongly continental climates.

Some species here are from regions where mild winters might be expected to confer an advantage on species which can produce photosynthetic tissue and new ramets, e.g. *Geranium x oxonianum* parents are from the Mediterranean region. Others are not – there is no obvious reason why continental climate species such as the cirsium and the centaurea should be so adapted. However it is noted that species from continental climates which exhibit leaves as early as February when grown in Britain will also do so at a similar time of year in their home region: *Aster divaricatus* and solidago sp. (author observation, New York State). The ability to produce foliage during the winter, or in the case of North American species which do this, during the autumn, for overwintering (this is also observed in UK gardens for *Rudbeckia fulgida*), is a trait who value may be marginal in most circumstances, but which confers advantage in certain exceptional ones, i.e. unusually mild American winters or early springs (see Illustration A10). What may be only of occasional or latent advantage in the home region may turn out to confer a more definite competitive advantage in EBPS in milder winter climate zones. In addition the ability to produce a second set of foliage during the summer is an obvious advantage in hay meadows, although most other herbaceous species are capable of doing this if the first set of growth is removed. In a natural environment, this trait may confer an advantage, or in regions with a short continental growing season, it may not, but rather, as with the winter growth issue discussed above may be an occasional and latent advantage. It is worth noted that with *Cirsium rivulare,* the form in cultivation in Britain, 'Atrosanguineum' is largely senescent in August, the second set of growth not starting until September; the wild species can be seen in full growth in Slovakia in August (author observation, Nizhky Tatry, SK) – whether this difference is due to genetic difference or climate is impossible to say.

Salvia nemorosa is an anomaly in terms of habitat, however an ability to produce new foliage in favourable conditions is an obvious advantage in habitats where moisture availability in unpredictable.

Morphology

With such a small group it is difficult to gain any clear idea of possible links between phenology and morphology. The four genera here have three very different morphologies: the geranium and the centaurea offer two clear cut examples of the main range of leaf-stem relationships amongst the dicot species being studied: that dominated by pseudobasal and lower stem leaves in the former and upright stem with small more evenly scattered leaves in the latter. The *Cirsium rivulare* is somewhere in the middle. The phenology of both the geranium species and the centaurea involves a mid-season collapse of old foliage, whilst the nepeta's more or less prostrate stems and continuous production of new foliage provides a similar effect – physical suppression of neighbours, through a different mechanism.

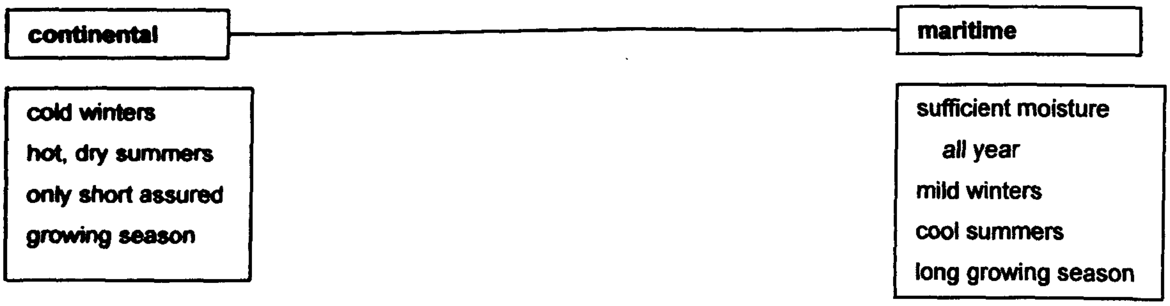
Mechanism and extent of vegetative spread varies – the fact that all these species (with the exception of the *Salvia nemorosa*) are able to grow vigorously over a long growing season and to put on strong new growth twice a year is not extended to making unduly extensive vegetative spread.

Competitiveness

The ECA records the persistence or competitive aspect of these species in EBPS and horticultural situations. The introduction of further species with this trait or hybridisation involving them, could lead to valuable new additions to the range of taxa that can be used in maritime climates. The *Centaurea montana* and *Geranium x oxonianum* are renowned as amongst the most robust garden perennials (Rice 2006). *G. asphodeloides* is persistent rather than aggressive, but in fact can self-sow very effectively.

Usage

It is suggested that the usefulness of these species is highly related to a continentality-maritime gradient:



With the exception of *Salvia nemorosa*, all these are species which are frequently used in a range of lower-maintenance herbaceous planting schemes including EBPS, in both maritime (British) and continental (southern German) schemes, testifying to their vigour and resilience. Their ability to produce growth in suitable conditions throughout the summer and part of the cooler seasons would appear to make them potentially very useful for meadow-grass type and low maintenance management in maritime climates. However their use in maritime climates would appear to involve a trade-off: useful for their ability to compete with weeds and rough grass is countered by a tendency towards suppression of less vigorous species included in planting schemes, notably those where canopy height is similar or less and where new growth is produced only in spring.

GROUP 3. Early dormancy

Species	Region of origin	Climate	habitat	ECA	CSR
Acanthus spinosus	S Europe	Continental	woodlands, meadows	5	
Aconitum napellus	C Europe	continental/ montane	tall herb flora, moist woodland	3	
Papaver orientale	W Asia	Continental	rocky slopes, dry meadows	3	C/CR

These species have a tendency so summer dormancy, inevitable in the case of *Papaver orientale*, from dry meadow habitats in a region with very hot summers, less likely in the case of *Acanthus spinosus* in the British Isles (though common in Mediterranean climates). The performance of *Aconitum napellus* in this respect is something of an anomaly, as early dormancy is uncommon amongst tall-herb flora species.

Usage

Hitchmough and Woudstra 1999 suggest that the good performance of *Papaver orientale* in ornamental meadow-grass management schemes is linked to its early growth, and opting out of competition later in the year. It would be interesting to trial the other two species here in a meadow grass regime. The performance of the *acanthus* makes it useful where unpredictable moisture may be a problem – its early production of dramatic foliage makes it a valuable design element too. It is suggested that it is a particularly good plant (Chatto 1993) for less maritime zones of north-west Europe, such as eastern England where a combination of mild winters and dry summers require the use of species which are able to initiate growth at low light and temperature levels but are able to survive drought by dying back if necessary. For a continuity of visual appearance in dry summers it would be sensible to combine such species with evergreen sub-shrubs. Climate change and associated dry summers would suggest that the sourcing of more herbaceous plants with this growth cycle would be sensible.

GROUP 4. Maximum height achieved by June

Group 4a. Flowering no later than May

Group 4a	Region of origin	Climate	Habitat	ECA	CSR
Aquilegia vulgaris	Eurasia	Continental	light woods, meadows, mountains	3	C/CR
Brunnera macrophylla	Caucasus	Continental	grassy slopes, woodland	3	
Euphorbia polychroma	C Europe	Continental	dry woodland, infertile meadows	3	
Geranium phaeum H	Europe	Continental	meadows, woodland edge	4	C/CR
Geranium sylvaticum H	Europe	continental/ montane	meadows	3	
Lunaria rediviva	C Europe	Continental	tall herb flora, moist woodland	3	C/CR
Pulmonaria officianalis	C Europe	Continental	woodland	3	C/CR
Thermopsis caroliniana	SE N.America	humid continental	woodland edge	5	C/SC

Climate, region of origin and wild habitat

All are of old world origin, except *Thermopsis caroliniana s.* It is interesting to speculate whether this is due to historic factors, as argued above with evergreens or whether it reflects a difference in morphology between the taxonomic groups represented on either side of the Atlantic – which is marked. There is a strong tendency for these species to be from productive environments: tall-herb, wet meadow, riverside etc. Of the European species several can be found in hay meadows (H), and indeed some are very typical of this anthropogenic habitat – their phenology fits into the cutting regime – growth complete by late June, and with the ability to strongly regrow after cutting (Ellenberg 1974). *Thermopsis caroliniana* is unusual amongst taller North American forbs in cultivation in that it is earlier-flowering than most, which may be a function of its woodland edge rather than prairie habitat.

Morphology

There is a variety of leaf-stem relationships, but the majority emphasise the relationship already noted whereby woodland edge or woodland species tend to have leaf distribution lower down the stem than species of higher resource environments (Givnish 1987).

It is suggested that this group is dominated by species which are adapted to the broad regional climate zone in which the British Isles is situated, where a slow start to the growing season and unpredictable temperature conditions mean that an adaptation to complete the bulk of vegetative growth by mid-summer's day, when solar radiation will be at its strongest, confers advantages.

Competitiveness

Where CSR was assessed, all species had C character and the majority R. ECA assessments were 3 or above, except for the majority of those from dry habitats which were generally 2. The number with '4' or '5' ratings was notably high, which could be due to the fact that many are from a climate zone not too dissimilar to that of the British Isles, so these species would be growing near to their optimum conditions.

Usage

The tendency of earlier-flowering species to be most useful in cultivation as conventional border or woodland edge habitats is noted. Of these, only the two *Geranium* speciesand *Thermopsis caroliniana* are grown in hay meadow schemes in full sun, the *Geranium* species being common meadow species throughout montane central Europe; *Aquilegia vulgaris* is frequently encountered naturalised in light grass in partial shade. The reaction of *Thermopsis* species to a hay-meadow cutting regime is not known. It can be supposed that species such as the two *Boraginaceae* here would be uncompetitive in denser plantings owing to the bulk of their foliage being near ground level; unlike geranium and astrantia species, their short petioles and lack of morphological plasticity would be expected to render them relatively uncompetitive.

GROUP 4b. Mid-summer flowering, where flowering either begins no later than July, soon after the time of maximum solar radiation intensity

Group 4b	Region of origin	Climate	Habitat	ECA	CSR
Achillea millefolium	Eurasia	Maritime + continental	meadows, open places	4	C-S-R/C-R
Aconogonon 'Johanneswolke'	Sakhalin, Japan	continental/high summer rainfall	coastal	3	
Alchemilla mollis	Europe	Continental	open places, roadsides, meadows	4	
Anaphalis triplinervis	Himalayas	Montane	clearings, pasture	2	CR
Artemesia lactiflora 'Rosenschleier'	S China	Montane	streamside, woodland edge	2	C/CR
Aruncus dioicus	Eurasia	continental/ montane	woodland, tall-herb flora	3	
Calamagrostis x acutiflora 'Karl Foerster'	Eurasia	Continental	woodland edge, river banks, roadside	3	CR
Calamintha grandiflora	S and SE Europe, W Asia	continental/ Mediterranean/montane	woods in mountains	3	CR
Campanula latifolia	Europe	continental/ montane + maritime	tall herb flora	3	
Cephalaria gigantea	Caucasus	Continental	wet meadows	3	
Cirsium canum	C Europe	Continental	wet meadows, moorland	3	CR
Clematis heracleifolia				3	
Dianthus carthusianorum	Europe	Continental	calcareous, dry meadows	1	CR
Eryngium bourgatii	Mediterranean	Mediterranean	dry rocky places	2	CR
Euphorbia schillingii	Himalayas	continental/ montane	rocky slopes	3	
Filipendula rubra 'Venusta'	N America, IO southwards	Continental	wet prairie, marshes	4	C
Filipendula ulmaria	Eurasia	continental + maritime	wet meadows, marshes	4	C/S-C
Geranium 'Johnsons Blue'	Eurasia/Himalaya	continental + maritime	scrub and open country	4	
Geranium pratense	Eurasia	primarily continental	scrub, meadows	3	
Geranium 'Rozanne'	Himalayas	continental/ montane	forests, scrub, open slopes	3	
Geranium sanguineum	Europe, Turkey	continental + maritime	dry scrub and open situations	3	
Hemerocallis 'Golden Chimes'	Eurasia	Continental	wet meadows	3	

Heuchera micrantha	NW N America	Maritime	rocky places, stream banks	2	
Hosta fortunei	E Asia	continental	moist	3	
Group 4b *Continued*	**Region of origin**	**Climate**	**Habitat**	**ECA**	**CSR**
Inula cf. racemosa	Himalayas	continental/ montane	waste ground near habitation	3	
Iris sibirica	Eurasia	continental	marshlands, wet meadows	4	C
Lysimachia punctatum	C & SE Europe	continental	tall herb flora, damp places	5	
Lythrum salicaria	Eurasia	continental	marshes, lake sides	3	C-S-R/C-R
Macleaya cordata	E Asia	continental	grassy places, open woodland	3	C
Persicaria amplexicaule	Himalayas	continental/montane	meadows, streamsides	4	C/CR
Stipa calamagrostis	C & S.Europe	continental/ montane	pioneer, dry slopes	2	
Tanacetum macrophyllum	Balkans	continental/Mediterranean	moist woods	5	
Tanacetum parthenium	SE Europe	continental	scrub, rocky placdes	3	
Thalictrum aquilegifolium	Eurasia	continental/ montane	woods, tall herb flora	3	

Geranium 'Rozanne' may achieve maximum height by March, but this is in fact a procumbent plant, with flowering stems carrying foliage continuing to lengthen until September.

Climate, region of origin and wild habitat

Notably few are of North American origin, only *Filipendula rubra* being a prairie species. There is no particular habitat noted as predominant. It is suggested that these are species which respond to a relatively continental climate but with a less extreme continentality than is normal in much of Midwestern and east coast North America.

Morphology

Is noted as varied, with no obvious pattern.

Competitiveness

Several notably competitive species of grassland: e.g. *Achillea millefolium, Alchemilla mollis* are noted, The presence of several tall-herb flora species is noted – their flowering and completion of maximum canopy height by mid-summer's day is possibly linked to the shaded nature of much tall-herb flora habitat.

Usage

The competitive species here are amongst those which show considerable potential for EBPS. This group includes a range of species which combine maximum visual impact in early to mid summer with a robust character.

GROUP 4c. Late summer flowering

Group 4c	Region of origin	Climate	Habitat	ECA	CSR
Aconitum arctuatum	E Asia	continental	woodland edge	4	
Aster cordifolius 'Little Carlow'	NE N.America	continental	woodland edge	4	CR
Aster puniceus	NE N.America	continental	moist/wet	3	C/CR
Chelone obliqua	E N America	continental	wet woods, swamps	3	
Rudbeckia fulgida var. deamii	Mid West USA	continental	moist open, woodland edge	4	C
Sanguisorba tenuifolia	Japan	continental	moist places	3	

The existence of this group would appear to be a construct of the research question, that of separating out time of flowering and that of achieving maximum canopy height; that the latter was observed in the year of measurement could well have been an anomaly, or the pattern may be general at the location, but untypical of the species. It is suggested that it be most usefully amalgamated with Group 5.

GROUP 5. Maximum height achieved later than July

Group 5	Region of origin	Climate	Habitat	ECA	CSR
Amsonia orientalis	Greece, Turkey	continental/ Mediterranean	wet places near sea	3	C/CR
Anemone x hybrida	China	continental	rocky places, woods	4	
Aster novi-belgii	coastal E N America	continental but maritime influenced?	swamps near coast	5	
Aster umbellatus	E N.America	continental	moist meadows	4	C
Astrantia major	Europe	continental	moist, fertile woodland, tall-herb	3	CR
Baptisia australis	E N America, IO, PA south	continental	dry mesic	3	
Echinaea purpurea	mid-west N America	continental	moist prairie, open woodland	3	
Echinops ritro	S Europe	continental/ Mediterranean	rocky places, steppe	4	
Eupatorium maculatum ssp.purpureum	E N.America	continental	Moist	3	C/CR
Euphorbia cyparissus	Europe	continental	dry limestone meadows	5	
Euphorbia palustris	Europe	continental	wet meadows	3	C/CR
***Group 5** Continued*	**Region of origin**	**Climate**	**Habitat**	**ECA**	**CSR**
Helianthus 'Lemon Queen'	E N.America	continental	moist open places	4	C/CR
Knautia macedonica	SE Europe	continental/Mediterranean	scrub, meadows	3	CR
Leucanthemella serotina	SE Europe	continental	wet meadows	4	

Lysimachia ciliata	E N America	continental	damp woods, wetlands	4	CR
Lysimachia clethroides	E Asia	continental	open grassy places	3	
Miscanthus sinensis	E Asia	continental	open places, moist	4	CR
Molinia caerulea subsp. arundinacea	C and S Europe	continental/ montane	dry woods, slopes, moorland	3	
Monarda hybs.	E N America	continental	variety of open and lightly shaded habitats	1	
Origanum laevigatum	Turkey	continental/ Mediterranean	meadows, dry open woodland	2	
Phlox paniculata	E Coast N America	continental	meadows, roadsides, fertile soils	4	
Rudbeckia 'Juligold'	E N.America	continental	moist thickets	4	
Sedum spectabile	S China	continental	woodland edge, dry rocksy slopes	3	
Solidago rugosa	E N.America	continental	moist places	3	C/CR
Stipa arundinacea	New Zealand	maritime	woodland, woodland edge	2	S/SC

Climate, region of origin and wild habitat

Taking group 4c and 5 together, it is noted that they are overwhelmingly species of productive, and generally moist habitats, including both open and woodland edge. Prairie species are noticeable, as are species from what could be assumed to be broadly similar habitats in Eurasia (*Leucanthemella serotina, Lysimachia clethroides, Miscanthus sinensis*).

The presence of woodland edge species can be explained as a tendency towards plasticity in cessation of growth in species which tend to be found in habitats where moisture availability may be expected to vary greatly owing to competition for this key resource by trees and shrubs. When moisture is plentiful they can be expected to continue to grow later than in seasons when moisture is less available.

Morphology

Leaf-stem relationship is all IV or occasionally III, bearing out Givnish's (1987) findings regarding small, rapidly-replaced foliage on tall stems being typical of productive environments, and the findings regarding dry-stem weight noted earlier.

Several anomalies stand out, generally smaller species of notably drier habitats, the argument concerning moisture availability in woodland edge habitats could apply here too. *Euphorbia cyparissias* is noted as producing considerable quantities of tip growth long after its flowering season, thus improving its competitiveness when moisture is available.

Competitiveness

Competition is generally estimated as high, as might be expected from species of productive habitats.

Usage

Many of the species here play or can be expected to play major roles in EBPS in situations where soil productivity is high. Other species, more typical of more stressed habitats, e.g., *Euphorbia cyparissias, Knautia macedonica, Astrantia maxima* are noted for their ability to continue to make growth and therefore to compete when conditions allow. This is in contrast to species which have a strong tendency to become dormant such as *Papaver orientale* or which do not produce extra growth later in the year such as *Brunnera macrophylla*. It is also in contrast to species that produce new basal growth in flushes, i.e., those in Group 2. The fact that new growth is produced continuously largely from shoots which originated in spring rather than the base suggests that many of these species would be unsuitable for hay-meadow management schemes, unless it can be shown that they are also capable of regeneration from the base.

9.2 ISSUES IN PLANTING DESIGN AND EBPS

Making use of the body of research here involves attempting to relate findings to practice, or possibilities for the further development of practice. In Kingsbury (2003a), an attempt is made to classify planting design using a grid; of particular relevance here is the axis 'static < - > dynamic', where conventional practice is described by the 'static' end of this gradient and minimal maintenance EBPS practice (e.g. hay meadow management) at the 'dynamic' end. For the purposes of this research this axis will be used as a basis from which to discuss the relevance of the findings.

Proceeding from the most 'static' to the most dynamic, the following planting styles are considered:

- Block planting – e.g. 'classic' Oehme van Sweden, typical of 1980s 1990s, Petra Pelz
- Small block planting – e.g. Oudolf, 1980s to early 2000s.
- Limited combination – e.g. much recent Oudolf, some recent Oehme van Sweden.
- Plant community creation – e.g. much current German *Lebensbereich* work (e.g. Hermannshof), author's work, Mixed Planting (*Perennemix*) and Integrated Planting System.
- Minimal management – e.g. Hay meadow type management.

The following issues need to be considered:

- Ability of a planting to resist weed infiltration
- Degree of species spatial integration - Functional monocultures as opposed to diversity
- Durability of planting: longevity and/or replacement through recruitment?
- Implications for management
- Implications for aesthetic interest

9.2.1 Monocultural block planting

This is the simplest and most cost-effective method (Kircher 2004). The more architectural use of large monocultural blocks for plantings in large public spaces is associated with the work of Oehme van Sweden in the US (Oehme & van Sweden 2002). A similar approach has been used by Pelz in Germany. Pelz recognised and articulates the case for reduced levels of diversity, arguing that visual effect at a variety of distances and the need for simplified maintenance in public spaces are best met by very simple bold schemes (Kuhn 2001, Pelz 2001, 2002).

Species which readily form monocultural blocks through relatively extensive ramet formation are clearly very suitable, and have the advantage that the clumps which result will be relatively immune to weed infiltration owing to root and foliage competition. Species which do not form extensive clumps, but which are included for aesthetic reasons present the possibility that the spaces between them may be colonised by weeds, although this likelihood is likely to be reduced if the species used are wintergreen. Herbaceous species which spread vegetatively by ramets should not present any longevity problems – on the contrary they generally could be expected to survive almost indefinitely. The *Perennial Category Grid* (see 7.5.5). *An analysis of plant traits and characteristics*) should assist the task of plant selection though its use of Pattern of Spread as one axis. The selection of species on the Leaf-stem relationship axis is then largely a decision to be made on the basis of suitability for the site and aesthetic criteria.

9.2.2 Small monocultural block planting

In many ways the issues are the same as above, except that practitioners tend to use, and are often strongly committed, to using many more plant taxa. It could be said that this approach is the dominant one for larger public gardens, public herbaceous planting and larger gardens (Robinson 1992). More sophisticated examples are the smaller-scale (often domestic) work undertaken by Oehme van Sweden and most of the Oudolf work to date (Oehme & van Sweden 1997, Kingsbury & Oudolf 1999). Ease of maintenance is often put forward as the main justification for this planting style (Kircher 2004, Kingsbury & Oudolf 2005), as well as that it provides an effective visual contrast and is easy to draw and lay out (Robinson 1992).

Extensive ramet formation leading to highly competitive behaviour would be regarded as undesirable. Some practitioners, most notably Oudolf, have developed a style based on 'structural planting' which emphasises plant form as a primary aesthetic quality; most of the plants he classes as 'structural' have a leaf-stem relationship III or IV; in contrast to the amorphous 'filler plants' included for flower or seasonal interest - these are generally leaf-stem relationship I or II. He claims to use a ratio of 3:1 to achieve the visual appearance he seeks (Kingsbury & Oudolf 1998).

9.2.3 Limited combination

The combination of small numbers of taxa in blocks is a recent refinement of the above, allowing for more sophisticated visual textures, colour combinations and seasonally interesting effects. Oudolf has begun to use it (Kingsbury & Oudolf 2005). Kloerters (2006) uses a variation of it, using only two taxa per block, in order to minimise maintenance but to provide more interest than monocultural blocks. Oehme van Sweden have also begun to use it (Brady 2006).

Selection of species for this planting style would need to be very precise, as the likelihood of one species out-competing the other is high, and the result would be seen over the entire area of the planting. Practitioners of this planting style would benefit from the analysis of plant morphology and phenology here, in particular: time of emergence, pattern of spread and shading effectiveness.

9.2.4 Plant community creation

In many ways this is the heart of EBPS, where intermingled plant combinations are created which are intended to function at least partly ecologically. Whether maintenance is more difficult than with block planting is debatable – it may be in the early years, but with time dense assemblages of plants can be built up which require little maintenance input, as at Cowley Manor.

A number of approaches to this planting style are discussed in Kingsbury (2003a). More recently other planting systems have begun to become commercialised in Germany and Switzerland that emphasise a random rather than aesthetically structured planting – they could be described as 'modular planting'. Some go so far as to start the entire plant community as seedlings on mats of coconut fibre (Rücker 2002). Better established are the 'Mixed Planting' system developed by a number of workers including Kircher and Schönfeld, and the 'Integrated Planting System' by Föhn and colleagues; all share the same basic idea – that a combination of compatible plant taxa are chosen, for aesthetics, for their known ability to thrive in a given environment and for their approximately similar competitive ability. Suitable proportions are worked out and the resulting list of plants can then be planted at random (Bachtiger et al. 2001, Föhn 2002, 2005, Schmidt nd, Kircher 2000, 2004, Messer 2002, Schönfeld 2000, 2001).

All planting systems which intermingle taxa face similar management problems:

- Identification of weeds or appropriate desirable level of recruitment of component species by maintenance personnel
- Eventual domination by the most effectively competitive taxa in the mix
- Change in composition over time may reduce visual interest

9.2.4.1 Number of species used

Reducing the number of species used can make for greater coherence and 'readability' and make it easier for maintenance personnel to learn to distinguish between desirable and undesirable spontaneous plants.

Given that a very low number of intermingled taxa (two or three) is particularly liable to be eventually dominated by one, it is suggested that increasing the number of taxa is likely reduce this effect. The Mixed Planting system can be assumed to offer the minimum number of taxa in an EBPS, as it is a deliberately simple modular system; mixtures developed by Kircher, Messer and colleagues each include around 12 herbaceous perennials (geophytes and other *Streupflanzen* are additional) (Kircher et al. nd.). Schmidt is of the opinion that higher numbers confer a greater chance of success and long-term ecological stability, but that this can be commercially difficult (Schmidt 2008).

9.2.4.2 Plant selection issues

Plant selection issues are inevitably dominated by issues of aesthetics. Selection for different environmental conditions plays a role, but given that most herbaceous ornamentals are generalists, which is almost certainly a reflection of the fact that plant selection has over the years favoured species which establish quickly; it is noted that in general, species with broad ecological amplitude establish more successful than those with narrow (Cottam & Wilson, 1966).

Borchardt has devised a system of categories for the planning of herbaceous plantings (see fig.9.3):

Solitärstauden – solitary plants
Gerüststauden – framework plants
Gruppenstauden –grouped plants, i.e. species best used in aggregate
Streupflanzen – strewing/scatter plants (generally geophytes)
Bodendecker – ground cover [1]

This system is very largely aesthetic – and in design terms a very useful one. However regarding long-term management and development issues, the category system proposed here may be more informative. This illustrates that design imperatives and management ones may find

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[1] See Borchardt 1997, and Hansen & Stahl 1993. The terminology used here is not fully developed in either of these works, although the concept clearly is. Schmidt 2008 is the source for the information concerning the origin of this concept and terminology with Borchardt.

useful quite different systems of categorisation – it follows that both have validity, but serve different purposes.

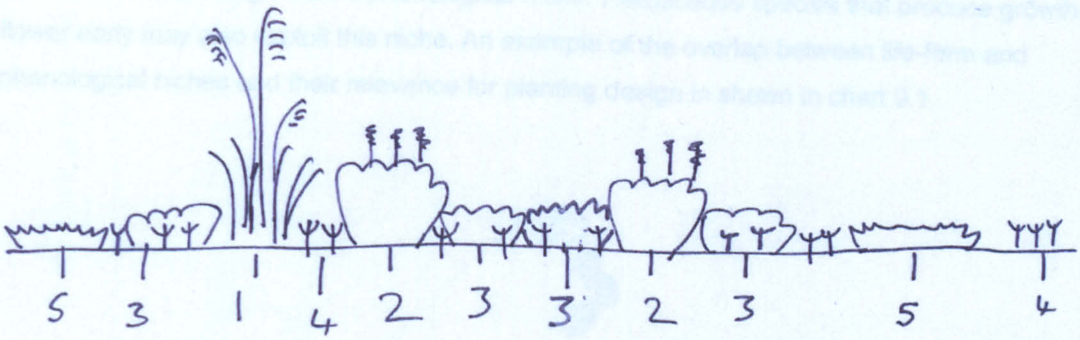

Fig.9.4

The Borchardt system of categorising herbaceous plants according to design functionality.

1. Solitary plants
2. Framework plants
3. Grouped plants
4. Scatter plants
5. Ground-cover

Grubb's identification of four morphological and phenological niches (Grubb 1986) (see Introduction*1.2.5*) may serve to inform issues of plant selection:

- Habitat niche.
- Life Form Niche.
- Phenological niche.
- Regeneration niche.

It is suggested that the Perennial Category Grid has a role to play in guiding practitioners to the necessity of selecting species with a level of vegetative spread appropriate to the size and management requirements of the planting (e.g. greater spreading capacity is more appropriate for large sites with reduced management), i.e. *Regeneration niche* whilst at the same time guiding them towards an awareness of plant architecture as manifested by the Leaf-stem Relationship categories, i.e. *Life form niche*. The recognition that plants in any kind of herbaceous planting need to vary in shape (i.e. *Life form niche*) is one learned, albeit intuitively, very early on; Borchardt's classification elaborates this, as does Oudolf's stress on structure (Kingsbury & Oudolf 1999).

The Growth Cycle Groups also have a role to play: in situations where recurrent growth or wintergreen foliage would be an advantage both functionally or visually, such as maritime climates, practitioners can be guided towards appropriate species, i.e. *Phenological niche.* In any case, the use of bulbs (or *scatter plants* in the Borchardt system) is a commonly used example of practitioners exploiting Grubb's *phenological niche*. Herbaceous species that produce growth and flower early may also exploit this niche. An example of the overlap between life-form and phenological niches and their relevance for planting design in shown in chart 9.1.

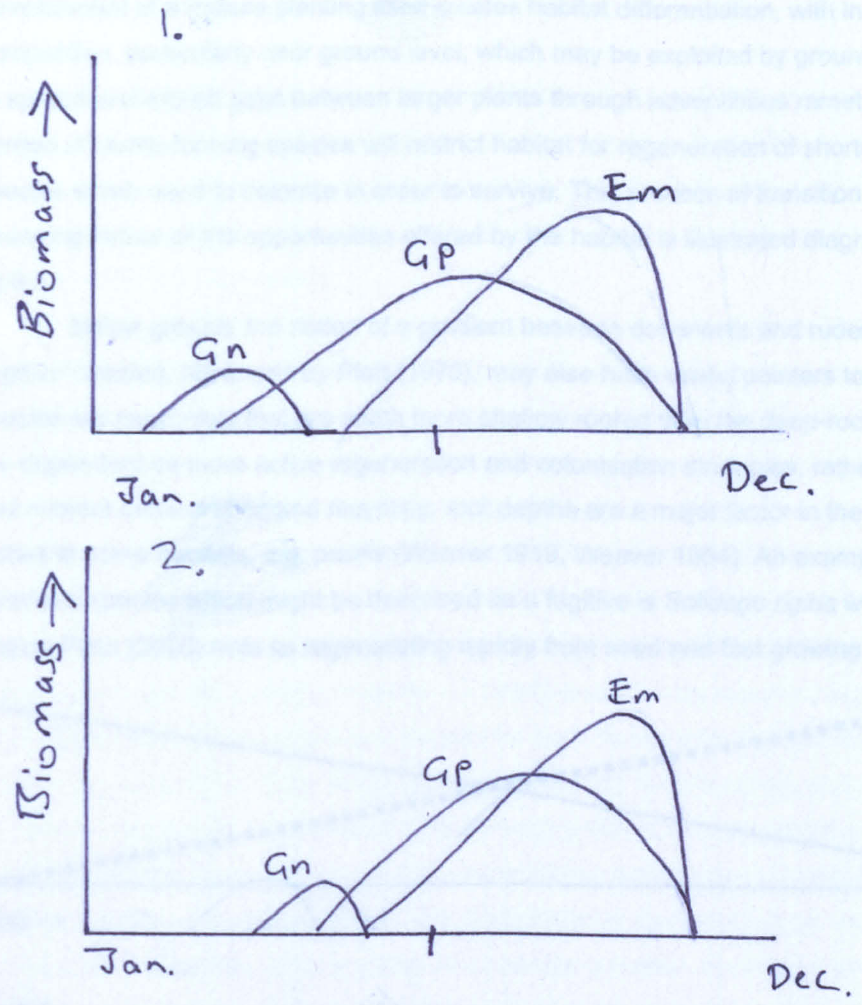

Fig.9.1
Overlap of phenological and life-form niches

The growth in aboveground biomass in three species over the year in two climate zones: (1) maritime and (2) continental.

Gn = *Galanthus nivalis*, Gp = *Geranium phaeum,* Em = *Eupatorium maculatum.*

The three species (a bulb, a distinctly spreading clump-forming perennial, and a slowly-spreading very upright perennial respectively) succeed each other in the time at which they initiate growth, flower and achieve maximum biomass. However the succession is concertinaed in the short intense summer of continental climate. This could possibly exacerbate a problem sometimes observed in British gardens, that the vigorous growth of early-growing geranium species can suppress that of species which initiate growth later.

Habitats within most sites for EBPS are often uniform, but a gradient of conditions (most likely to be shade or moisture availability) present options for different *Habitat niches*. The development of a mature planting itself creates habitat differentiation, with increasing shade and competition, particularly near ground level, which may be exploited by ground cover species able to spread and exploit gaps between larger plants through adventitious ramets. However the spread of clump-forming species will restrict habitat for regeneration of shorter-lived species and species which need to colonise in order to survive. This process of transition and the constantly changing nature of the opportunities offered by the habitat is illustrated diagrammatically in fig.9.5.

Below ground, the notion of a gradient between dominants and ruderals, to include 'fugitive' species, advanced by Platt (1975), may also have useful pointers to EBPS. Fugitive species are perennials that are much more shallow rooted than the deep-rooted dominants, and are dependent on more active regeneration and colonisation strategies, rather than persistence and nutrient conservation and recycling; root depths are a major factor in the defining of habitat niches in some habitats, e.g. prairie (Weaver 1919, Weaver 1954). An example of a soundly perennial species which might be described as a fugitive is *Solidago rigida* which Hitchmough and de Fleur (2006) note as regenerating rapidly from seed and fast growing.

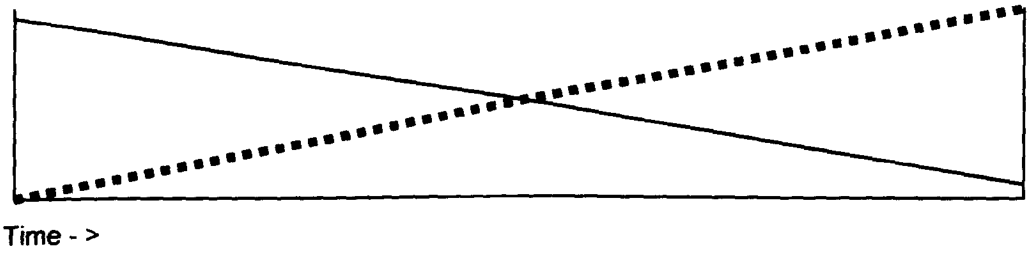

Fig.9.5

Changing opportunities for diversification of habitat niche and therefore floristic diversity in a planting on a productive site over time, with no active intervention to promote diversity.

As species in a planting mature (left to right), they create more diverse habitat by creating microhabitats around them – allowing more species to find niches (dotted line) - theoretically. No research has been seen on this topic for horticulturally managed plantings. Author observation (Elmtree Cottage, 1997-2006) suggests that this is in fact limited, and only very low-growing species with effective vegetative colonising mechanisms are able to exploit emerging habitat niches – mostly spontaneous species such as *Veronica persica* and *Ranunculus repens*.

As a planting matures, it would be expected that diversity of species in the original planting will decline (Grime 2001) (unbroken line).

It is suggested that future research needs to focus on the long-term dynamics of created plantings in order to resolve the questions raised here.

Another way of looking at this chart is to see the dotted line as representing the rising biomass of long-lived dominant species over time and the solid line as representing fugitive or ruderal species dependent upon colonising opportunities declining over time.

The 'Caespitose-type' strategy identified in 7.5.5.2 *Analysis of plant traits and characteristics* would potentially highlight such dominants. Species with more active foraging and spreading capacities may possibly be described as fugitives, the ability of some to dominate ground in monocultures possibly the result of absence of potential dominants than their ability to establish long-term dominance.

With regard to the exploitation of niches in planting design, Grubb points out that niche differentiation can be expected to be important between species of high abundance within a community, but not necessarily between species of low abundance (Grubb 1986). Rabinovitz et al. (1984) introduce the paradoxical notion that rare species are most abundant when surrounded by common ones. Translating this into planting design terms suggests that it is possible to regard the concept of 'facilitator species' as valid (see 3.11 in *Introduction*). However it would not be possible to draw any conclusions from the research carried out here, as only long-term combination trials could be used to reach any sort of conclusion. However, the noted tendency of species with vigorous patterns of spread to create exclusionary monocultures suggests that low rates of ramet production might be indicated for such 'facilitators', for they might allow other species to exploit other niches between them – primarily habitat niches, but also potentially life-form and phenological. It is noted that Hitchmough (1994a) has suggested planting schemes based on interplanting amongst a matrix of caespitose grasses (and Oudolf has used such a planting scheme (Bury Court, Hants. UK). Caespitose or caespitose-type species with a strategy of resource conservation and recycling may indicate potential 'dominants' for EBPS; conversely, foraging and colonising 'fugitives' indicate another niche. Indeed it might be possible that this identification of dominant and other niches in EBPS planting schemes may be more useful for the development of low-maintenance planting designs than the current mode of design.

It is therefore suggested that design strategies for minimising maintenance in EBPS should perhaps be based on one of two basic approaches:

1. Coloniser-based.

Large blocks of monocultural mats of strongly spreading colonising species. Variety linked to exploitation of phenological niche only (i.e. geophytes).

2. Dominant-based.

Caespitose-type species with strong persistence, nutrient recycling and effective root competition, with a variety of other species in the interstices. Possibility of exploiting phenological, habitat, life form and regeneration niches.

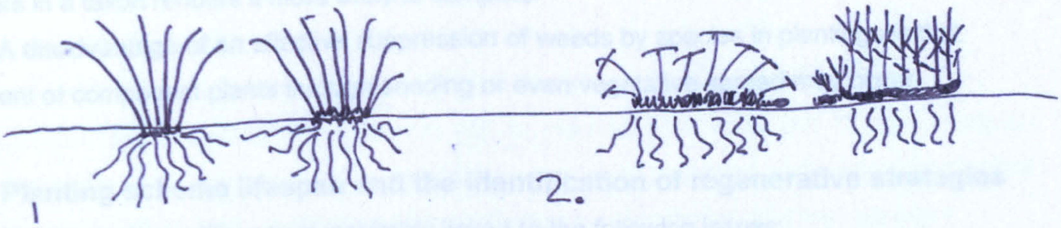

Fig. 9.6

Plantings dominated by coloniser and dominant species.

In (1) dominants, with dense and only very slowly expanding clumps, leave (in theory) gaps between both their above and below growth for other species to grow. However their foraging ability might be so effective as to limit resources for neighbouring plants; some potential species, e.g. *Stipa arundinacea* and *Sporobolus heterolepis*, also produce so much foliage which flops over laterally, that this might serve to limit the spatial possibilities for other species to exploit. In (2) the lateral vegetative spread of colonising species can be expected to eventually cover all the available ground surface, so greatly reducing habitat for neighbours.

9.2.4.3 Weed suppression

Ornamental perennials with a strongly competitive character can be expected to compete well with weeds, through the various mechanisms explored in this study.

Early growth is potentially important in maritime climates where the both established plants, fragments and seedlings of many weedy species are able to germinate and grow at low temperature and light levels.

Ground shading capacity, particularly early in the season, to suppress weed seedlings and fragments.

Large biomass, and *root competition*, both through denial of space and resources to unwanted species.

Extensive vegetative spread - this *ipse facto* denies space to weeds, but also it should be stressed that the physical extension of new growth into new territory puts the desired plant in a position to compete effectively in the season to come. This can be appreciated by the performance of *Lysimachia punctata*, (see *4.3.2* in 7. *Evaluating the competitiveness of herbaceous perennials using a phytometer in open ground conditions.)* where poor growth in competition with achillea was observed, but knowledge of the long-term performance of the plant and the wide spread of ramets in this trial suggests that it will eventually out-compete the competition.

It should be noted that none of the evidence suggests that any one of these on its own enables a plant species to out-compete weeds, indeed it is suggested that a combination of characters in a taxon renders it more likely to compete.

A disadvantage of an effective suppression of weeds by species in plantings is that recruitment of component plants through seeding or even vegetative spread may occur.

9.2.4 4 Planting scheme lifespan and the identification of regenerative strategies

Planting scheme lifespan is inevitably linked to the following issues:

1. Genetically determined lifespan of component taxa – do shorter-lived components have the opportunity to regenerate from seed?
2. Reduction in taxa diversity and therefore visual and bio-diversity interest through competition – is there opportunity to regenerate vegetatively?
3. Loss of diversity through weed competition – how effectively do component species suppress weeds?

Where species with a ruderal component to their survival strategy (as defined by Grime 2001) are used, some loss of diversity is probably inevitable – as regeneration depends on there being enough gaps for seedlings to grow. Vegetative regeneration is particularly important and successful in the later stages of succession where there is little scope for regeneration from seed owing to a lack of suitable sites for successful seedling growth (Luken 1990). Schmidt notes that horticultural experience spells out what is known from ecological studies, that competitive species reduce species diversity in plantings over time (Schmidt 2006b, Lessen et al. 2004). Such species are therefore suitable for block or monocultural plantings (see 3. *The use of transects to investigate established ecologically based plantings*) – unless disturbance is introduced as an occasional maintenance tool. Such competitive species will be the most effective at competing with weeds but will inevitably be the most likely to eliminate others from the planting and reduce diversity. It is to be expected that species able to achieve dominance will vary between climate zones and resources levels; in short and intense growing seasons, competition for light would suggest that tall species (e.g. typical prairie species) would be the most competitive, in long growing seasons: ability to grow early, ability to shade competition with lower foliage and phenological plasticity would be more competitive.

The Integrated Planting System (IPS) recognises that constituent species have different strategies of reproduction so the ongoing development of the planting will be dictated by these strategies. The ability of the species included to cover ground rapidly is fundamental to the success and value of this system (Föhn 2005). The combination of species with different vegetative regeneration strategies may well result in maintaining diversity for longer, primarily this means a range of spreading strategies on the guerrilla/phalanx gradient. Clearly this could be re-addressed as a dominant - fugitive gradient.

9.2.4.5 Management strategies in EBPS

Interest in EBPS is likely to be increased if it can be shown that visual interest (and concomitant low levels of seasonal untidiness) can be maintained at lower and cheaper levels of maintenance than is required for more conventionally managed plantings. It therefore follows that consideration should be given to the interaction between plant selection and management strategies and programmes which can simultaneously maximise both usage of resources and visual impact. An example is the work on summer (June) mowing of perennial plantings, in addition to winter mowing, by Kietsch and Kircher 2005, which appeared to show that some species performed better, and that the visual appearance of plantings was improved, due to increased flowering and a tidier impact. Reduction to ground level, analogous to a summer hay cut, affects plant phenologies and changes the nature of habitat niches in a number of ways, for example by limiting the upward growth of taller perennial species and enabling lower-growing species to have more access to light. It is suggested that the growth of very vigorous species, a and thus by extension their tendency towards forming monocultural blocks, might be limited by this technique, thus enhancing the ability of managers to maintain floristic diversity. It is suggested that the categorisation of growth cycle groups and morphological categories developed in this study may be a useful guide to a further development of this and similar techniques. The work of DiSabato Aust 2006, based on a systematic survey of the response of ornamental perennials to mid-summer pruning is also seen as relevant here.

9.2.4 The genetics of competitive species

A major difference between horticultural planting systems and natural or semi-natural habitats is, with the exception of seed-derived hay-meadow managed grassland or seed-derived prairie plantings (both essentially habitat restoration, as defined in Kingsbury 2003a) is the nature of the genepool. Horticultural plantings, including most EBPS, have a very narrow genepool compared to wild populations. This is because many plants in cultivation are propagated clonally, or even if grown from seed, the seed has been 'improved' through a process of mass or pedigree selection for the purposes of predictable horticultural quality. A reduced genepool may arguably reduce the ability of a planting to reproduce itself effectively through seeding because of insufficient clonal diversity to allow fertilisation, or with enough genetic variation to cope with changes in abiotic conditions.

There is another dimension to the narrow genepool problem. Aarssen 1989 suggests that one reason why plant communities continue to maintain high levels of species diversity is that levels of competitive ability vary within species populations – a reflection of the varied levels of genetic input and its expression. The implication for EBPS is that the widening of genetic variation might allow for greater levels of what Aarssen calls 'interaction avoidance', which would allow for a denser packing of species and individuals.

9.3 METHODOLOGIES

It was noted earlier (see section 4 in 1. *Introduction)* that the nature of research into plant ecology by most of those working in the field was only of limited value to practitioners. A fundamental problem in research is the trade-off between depth and width, i.e. whether a few examples are studied in great depth or many more very widely. The real world of practitioners presents situations where knowledge and theory has to be applied to highly complex situations. An intuitive, and therefore unarticulated application of knowledge and theory is generally the result.

The approach taken here to methodology has tried to explore a practitioner friendly approach to research. A container-based trial, based on a methodology typical of academic research, was found to be unsuitable for busy practitioners. An open-ground trial was suggested as an alternative, and found to be very much easier to manage and far more productive of meaningful results per unit of time and money expended. Observational work, in the form of transects of existing plantings was tried, and found to be very useful in measuring plant performance and spatial integration. In addition a programme of data collection was carried out, which aimed at addressing unresolved issues in the lack of very basic data concerning plant development and performance. The collection of data in this way requires very little specialist knowledge or training.

Inadequacies in the methodologies used are noted as follows:

- Sample sizes of trials may often be too small, or in trials there may be insufficient replicates
- Sample sizes, i.e. of taxa studied, may be too skewed towards particular genera (e.g. geranium)
- Sample sizes are arguably not representative of the full range of species used in EBPS
- Sampling or observational procedures may need further work in order to produce data which can be readily quantified – in particular techniques for measuring vegetative spread and foliage shading.

The possibilities for ongoing development and integration of the methodologies used here are discussed below in *Future research.*

9.4 CONCLUSIONS - SPECIES, PLANT COMMUNITY AND HABITAT RELATIONSHIPS

There has long been debate about the nature of plant communities; the modern view is not too dissimilar to Gleason's view of the community as 'not an organism, but merely a co-incidence' (quoted in Crawley 1997b, p.477); plant communities are the result of an immensely complex series of interactions over time, and cannot be compared to an 'organism' in a holistic sense, in the way in which Clements tended to propose (Budiansky 1995).

The assemblages of plants which are the result of EBPS can be seen as artificial plant communities, allowed to pursue and develop their own dynamic within certain, human imposed, limits. This is most clearly seen in situations where these associations have been allowed to develop with little outside input over time, e.g. at Cowley and some Hermannshof plantings.

The view is taken here, that linkages between the wide range of morphological and phenological traits of forbs used in ornamental horticulture are not sufficiently strong to form obvious and clear-cut categories; each plant species has a unique combination of intensities of expression of these traits. The performance of a particular plant species in a given situation is the outcome of the operation of a range of environmental operators and of competition from neighbours on the range of traits possessed by the plant species. Taking the Gleasonian view of 'co-incidence', the existence together of a given range of plant species within a particular habitat, does not therefore imply that these plant species will always be found together in similar habitats, or that these species can simply be transplanted *en masse* to a recreated habitat elsewhere and be expected to perform just as they do 'back home' or that they can be expected to perform in a similar habitat (Gleason 1964).

Much horticultural literature takes such a simplistic view of relating plant species to environment that many practitioners tend to see an all-too rigid link between plant and habitat. The view that practitioners can learn useful information about where plants grow in the wild is all too easily made into a simple equation: species – environment. In fact this is a relationship mediated by plant traits; a species grows in a particular environment in its region of origin because of the outcome of the trait-environment relationship and the operation of that species' traits in the context of the operation of the traits of neighbouring species. A natural plant community is composed of species which may display a wide range of trait combinations, enabling them to flourish in a range of different niches. The knowledge gained about the habitat origin of a species needs to be appreciated not as a simplistic link between plant and habitat but plant and the environmental factors operating in that environment. In many cases this will mean that a species will thrive in similar conditions in cultivation as in the wild, but this can never be assumed. The actual performance of a species in the wild will also be the result of the outcome of its ability to compete with neighbours, or responses to predation; this further complicates the translation of knowledge of habitat of origin to usage in cultivation. As has been discussed above a species may perform differently in the wild and in cultivation, or indeed in the wild in its region of origin and when naturalised elsewhere – hence the problem with invasive alien species. Indeed the behaviour of invasive aliens, and the immensely more common fact of species in cultivation not surviving without constant human management input – despite apparent similarities in basic environmental conditions between region of origin and place of cultivation/naturalisation, points to the need to make clear that no simple equations can be made between region of origin and place of cultivation.

The performance of plant species can only be understood in terms of the expression of traits which enable them to (or disable them from) surviving and competing in specific locations, which themselves can only be understood in terms of their offering particular sets of conditions of moisture and nutrient availability etc. and in terms of the other species with which they will have to compete for moisture and nutrients.

It is argued here then that more useful than knowledge of habitat of origin is a knowledge of plant traits, and indeed perhaps the most useful aspect of knowledge concerning knowledge of origin is that particular plant traits are more likely to be found amongst species from particular climatic regions or habitats, e.g. North American prairie species with traits for rapid production of tall stems and small, rapidly-disposed of leaves. The practitioner's role is to apply their knowledge of these plant traits in order to control gene x environment interaction to reach the outcomes they desire through management processes e.g. mowing. Further management input may be required in order to control various biotic impacts on plant growth and the expression of traits such as the negative impact of weed competition. The outcome is the result of a complex series of interactions, the basics of which are illustrated in fig.9.7.

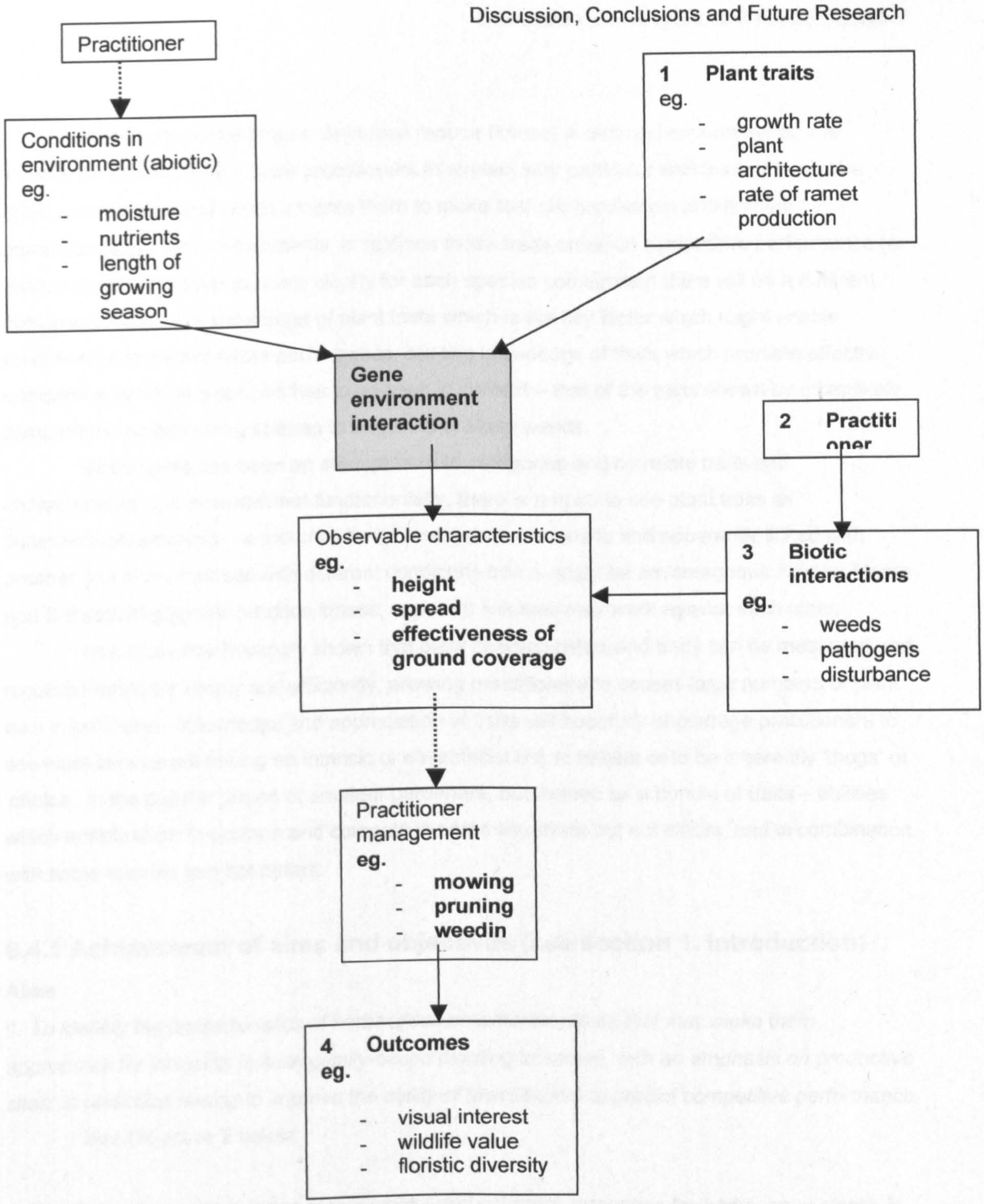

Fig.9.7
A flow-chart illustrating the relationships between biotic and abiotic environmental conditions, plant traits, characteristics, and outcomes. The role of the practitioner is to amend the conditions presented by the environment in order to influence gene x environment interaction and the impact of further biotic influences in order to meet desired outcomes.

Plant traits confer fitness (or indeed reduce fitness) in different environments; it is knowledge of these which allow practitioners to explain why particular species will thrive in a given environment and which enables them to make realistic predictions about future performance in other environments. In addition these traits enhance competitive performance (or reduce it) vis a vis other species; clearly for each species combination there will be a different outcomes. Again, it is knowledge of plant traits which is the key factor which might enable practitioners to predict future performance; but this knowledge of traits which promote effective competitive ability in a species has to be seen in context – that of the traits shown by other likely competitors: neighbouring species in an EBPS or likely weeds.

Whilst there has been an attempt here to categorise and correlate traits and characteristics, it is stressed that fundamentally, there is a need to see plant traits as 'independent operators' - a trait may be advantageous in one site and apparently linked with another, but in another site with different conditions trait A might be advantageous / confer fitness and B disadvantageous / reduce fitness; apparent linkages may work against each other.

This study has hopefully shown that plant characteristics and traits can be measured and recorded relatively simply and efficiently, allowing practitioners to assess large numbers of plant taxa in cultivation. Knowledge and appreciation of traits will hopefully encourage practitioners to see plant taxa as not having an intrinsic or essentialist link to habitat or to be inherently 'thugs' or 'choice', in the popular jargon of amateur gardeners, but instead as a bundle of traits – abilities which enable them to perform and compete in some situations but not others, and in combination with some species and not others.

9.4.1 Achievement of aims and objectives (see section 1. Introduction)

Aims

1. To identify the characteristics of herbaceous ornamental plants that may make them appropriate for inclusion in ecologically-based planting schemes, with an emphasis on productive sites; in particular aiming to improve the ability of practitioners to predict competitive performance.

See Objective 2 below.

2. To attempt to create a series of meaningful and coherent categories for herbaceous plants, in order to improve the ability of practitioners to specify taxa, plan for visual quality and plan management strategies.

Herbaceous perennials are not amenable to placing in general categories, as morphological and phenological traits do not frequently co-incide, and yet the value of categories for design and management purposes is recognised. It is proposed in section 7 (An analysis of plant traits and characteristics.....) that the most useful system of categorisation involves separate morphological phenological indices.

- A system of groups of species based on time of initiation of growth and dormancy is proposed – this reflects underlying traits of physiological response to temperature and light.
- A grid to summarise morphological character is proposed, described by two axes: *Leaf-stem relationship* and *Pattern of Spread.* Pattern of spread is also indicated as being correlated with a gradient described as caespitose – rapidly-colonising/fugitive.

3.To evaluate the suitability of methodologies for testing competitiveness for practitioners outside academia.

A variety of research methodologies have been suggested as being easy to use, time-efficient and inexpensive, in particular the use of transects (see section 3. (Use of transects to investigate established ecologically-based plantings) and the use of trials in open-ground conditions (see section 6 (Evaluating the competitiveness of herbaceous perennials using a phytometer in open ground conditions).

Objectives

1. Can CSR theory and description of the CSR character of ornamental herbaceous plant taxa contribute to an understanding of plant selection for EBPS?

CSR theory is useful as a general guide to the development and management of particular planting schemes but ordination of individual species is of little use to horticultural practitioners, at least outside region of origin.

2. What are the morphological and phenological characteristics of ornamental herbaceous taxa that might make them potentially valuable for EBPS?

This study has focussed on the selection of species for productive habitats where competitive ability is regarded as important. Sections 3 (Use of transects to investigate established ecologically-based plantings), 4 (Investigating the growth of herbaceous perennials in grass swards), 6 (Evaluating the competitiveness of herbaceous perennials using a phytometer in open ground conditions) and 8 (An investigation into the relationship between herbaceous plant traits and characteristics and competitiveness) indicated, and to a large extent agreed a range of characters which appear to enhance competitive ability.

Competitive ability is indicated by the following factors:

- High biomass, particularly as represented by maximum canopy height x distance between ramets.
- Effective shading of the ground by expansive lower foliage. Less expansive foliage may enhance competitive ability if combined in monocultural blocks to form a multiplier effect.

- Early start to growth.
- Phenological plasticity, i.e. the ability to produce substantial new basal growth after main period of growth in spring.
- Extensive ramet production.
- Effective root competition.

It is indicated that combination of the above factors is important for effective competition, especially as plantings move along a gradient of increasing plant density and reduced management, i.e. become more like natural or semi-natural vegetation. It is also indicated that combination of factors may be more important for competitive ability in regions with a long growing season, i.e. maritime climates.

4. What are the major factors that result in plant taxa having a low maintenance requirement in EBPS?

5. What are the plant characteristics that might help facilitate long-term community stability in species-diverse EBPS?

Selection of species with competitive ability will ensure that weed infiltration (a major element of maintenance) will be reduced in productive sites. Persistence is indicated as potentially as important to practitioners as competitive ability. In some cases persistence may be a sign of dominance, or potential dominance. Two strategies for minimising maintenance in EBPS are indicated. One is the use of colonisers with extensive ramets for the formation of monocultural blocks, the other the use of dominants with diverse subsidiary species exploiting a range of niches.

However it is noted (see Section 3 (Use of transects to investigate established ecologically-based plantings) that some species which form stable monocultures which may effectively reduce maintenance but also reduce visual interest and bio-diversity. Research into plant characters which facilitate long-term stability is recognised as being beyond the scope of this study, but the ability to persist in diverse EBPS situations through the potential to avoid competition through occupation of niches and the exploitation of a gradient of dominant-fugitive behaviour is also recognised (see 9. Discussion).

6. To produce outline indications for horticultural professionals which would enable them to identify taxa that are potentially valuable for EBPS.

It is suggested that the traits and characteristics outlined in section 7 (An analysis of plant traits and characteristics.....) and 8 (An investigation into the relationship between herbaceous plant traits and characteristics and competitiveness) could be used to develop such a list of indicators for particular horticultural purposes.

9.5 FUTURE RESEARCH

9.5.1 Introduction

The research in this study is very much introductory. The relevance and importance of the application of plant ecology science to the development of long-term and sustainable plantings, in particular to EBPS, cannot be underestimated. What plant ecology science can offer in terms of definite answers however is very limited. It was noted in the introduction (see *4.1*) that there is very little middle-ground between the observational, almost anecdotal, level of much horticultural discourse about plant performance, and the systematic, highly focused, inevitably reductionist nature of much work in plant ecology science. The latter is dealing with issues of great complexity, which once more than a few species are involved, produces interactions which rapidly becomes mathematically indescribable (Budiansky 1995); inevitably horticulture and landscape practice is going to have to continue to be based on an unsystematic, observationally-based and often intuitive knowledge base. However, it is hoped that this study has shown how plant ecology science linked with more detailed and systematic observational work than is currently found in horticulture (but less rigorous than is currently acceptable in plant ecology science) can produce a knowledge base which goes some way to improving our ability to understand and predict herbaceous plant performance, and which is accessible to practitioners.

Here a number of directions for future research are indicated, based on the continuation of work carried out here, or which address identified lacunae, or which aim to further investigate phenomena observed in the research.

9.5.2 Long-term pair wise competition plots

Traits identified in this research as being linked to competitive character in EBPS need to be tested vis a vis each other. A number of pairs of species with particular character could be planted in plots as in 7. *An analysis of plant traits and characteristics*, on a long-term basis and their performance measured.

The following grid, based on the expression of traits which this research suggests are most important in conferring competitive ability in EBPS in north-west Europe, would show how 36 combinations of plant species could be tested pair wise against each other. In practice however, possession of characteristics may not be so distributed amongst species which it is either desirable or practicable to test, that allow a neat separation into clear categories.

	Extensive ramet production	**Effective basal cover**	**High biomass**	**Early growth**	**Phenological plasticity**	**Morphological plasticity**
Extensive ramet production						
Effective basal cover						
High biomass						
Early growth						
Phenological plasticity						
Morphological plasticity						

The evaluation of these characteristics is important not just for understanding competition in EBPS, but because they are often themselves of importance in the aesthetic value of the plant and its role in the design of plantings, e.g. early growth is a valuable quality visually; 'effective basal cover' is clearly linked to the possession of large, visually-striking, basal leaves.

The following expressions of traits are indicated as playing a role in either competition or ability to persist (or the taxon to persist) in EBPS. They too could be investigated in relation to the above characteristics:

Root competition
Nutrient recycling
Nutrient storage
Ruderality
Low mollusc palatability

9.5.3 Facilitator species

In the *Introduction* it was suggested that certain species could in effect stabilise a plant community. In the *Discussion* it was proposed that such a role might be assigned to dominants in certain semi-natural plant communities, such as certain grasses in prairie or meadow habitats. In order to further investigate this the following research could be undertaken:

- The 'dominance' of possible dominant species vis a vis strongly competitive colonising and ruderal components of ornamental floras in regions outside the region of origin, and weedy species e.g. can North American prairie dominants remain dominant in EBPS in north-west Europe. It is quite possible that these species would not survive long-term when faced with the competition of species that are very fit in ecological terms, circumstantial evidence from *4.Investigating the growth of ornamental herbaceous perennials in grass swards* suggests that caespitose grasses may be readily out-competed by tillering species in north-west Europe. However it may be possible for meta-stable communities based on caespitose grasses can be maintained by low levels of maintenance.

- An exploration of competition between possible dominant species and other visually or functionally important components, focusing on the possible co-existence within reasonable time frames for cost-effective maintenance regimes. A concrete proposal would be:

1. The selection of a sample of herbaceous species which gave a long season of visual interest and exhibited a range of morphological and reproductive strategies.
2. Its repetition a number of times in identical environmental conditions alongside a number of potential dominant or facilitator species, plus a control.
3. Annual measurement of dry matter production over a number of years, plus visual evaluations.

9.5.4 Speed of establishment from seed, ramet trials

It was apparent from 6.*Evaluating the competitiveness of herbaceous perennials using a phytometer in open ground conditions* that the performance of the species trialled was affected by age, in particular that of the *Baptisia australis* which showed reduced competitive performance and yet is known to be slow-developing and persistent over time. The majority of herbaceous perennials used in ornamental horticulture do however develop very quickly from both seed and vegetative propagation. The fact that some, such as the baptisia do not, and the fact that this species and quite possibly others with a caespitose-type habit, possibly including some grasses, develop slowly but show great persistence over time, strong visual character, and may play an important role as dominants in a meta-stable community, suggests that further research into the speed of development is perhaps more important than at first sight this relatively small group of species may warrant. It should be noted that when attention is turned from open productive habitats for EBPS, to shaded, less productive ones, that the importance of slowly developing species becomes much greater, as species with these characteristics play a proportionately larger role in woodland habitats. In this study *Helleborus x hybridus* could be described as being one of this group of plants.

Speed of establishment is an important issue for the development of EBPS. There is a clear impact on competition between species within the planting; the impact of faster-establishing species on slower establishing could well be deleterious, as with the baptisia example just discussed, which could impact on the development of long-term stability. High rates of growth may be desirable if low-maintenance and weed competition are expected to be problems.

Speed of establishment would be relatively simple to measure, as 'established size' could be defined as the achievement maximum canopy height and flowering.

9.5.5 Development and exploration of a dominant-fugitive gradient

The concept of dominant plants and fugitives may be a more useful gradient to work with than CSR for practitioners in this field, or at least the use of this gradient within a particular environment, i.e. different dominant-fugitive gradients could be recognised for different levels of environmental stress, as suggested in fig 9.8. As discussed above, re. *Helleborus x hybridus* in woodland habitat, the relative importance of slower-growing long-lived dominants versus fast-spreading but ultimately shorter-lived fugitives varies between habitats.

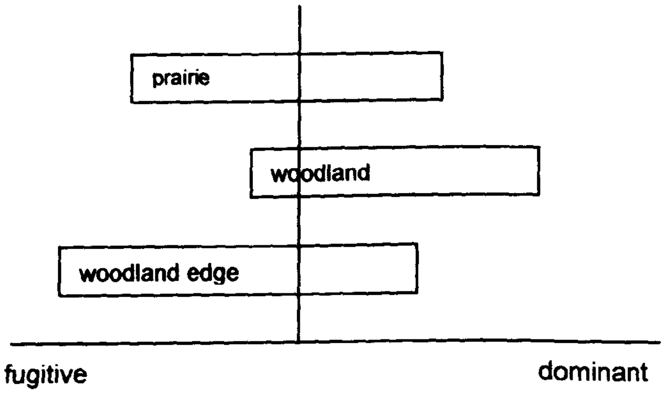

Fig.9.8

A hypothetical illustration of the weighting of the proportion of dominant and fugitive species amongst those which could be potential components in three EBPS habitats

Fugitives are clearly related to Grime's definition of ruderals in CSR theory, yet may not cover exactly the same set of traits; in particular some longer-lived ones may register as having strong C character. Likewise some dominants may show some S character. A comparison of the concept with the CSR model would be valuable.

The possibly greater value of a concept of a dominant-fugitive gradient for practitioners of EBPS is that it may relate more clearly and meaningfully to issues of plant selection, establishment and longer-term management than a classic CSR model. However given the coherence and explanatory power of Schmidt's practitioner-orientated version of the CSR model (Schmidt 2006, Schmidt & Hoffman 2003) (see 2. *The CSR model of plant functional types – an evaluation of its value in ecologically based ornamental horticulture*), it would be important to integrate the two.

9.5.6 Ramets

Given that a great many of the species used in both conventional horticultural practice and EBPS are clonal, the importance of a greater understanding of clonal plants over time is considerable. Several issues which have a major impact on any herbaceous planting have been highlighted in this study which could be investigated further (see *An analysis of plant traits and characteristics*):

- Patterns of ramet spread,
- Persistence of previous years' ramets,
- Rate of ramet production
- Distance of ramet spread.

In addition, further aspects were not investigated but could form a part of future study, notably: the balance of dormant and active buds on basal/root growth,

- The role of dormant ramets as an insurance against damage
- Levels of integration/disintegration.

The rate and pattern of clump formation could readily be measured in a trial plot, with the very considerable proviso that rate at least would be highly conditional on soil productivity and length and temperature range of the growing season. However an extensive enough trial conducted at the same place over the same period of time would produce results where rate etc. was measured *relative* to each other, and therefore have some validity.

9.5.7 Roots and Below-ground competition

It is quite clear, from 5. *Assessing competition with two grasses of contrasting productivity in standardised container culture* and 6.*Evaluating the competitiveness of herbaceous perennials using a phytometer in open ground conditions*, that root competition is a major component of overall competition.

Methods of separating out above and below ground competition do exist (Grime 2001) but are technically complex. More useful might be less rigorous, observationally based methods of comparing the root systems of different species. Characteristics could be identified which could be tentatively related to underlying traits related to competition. These could include:

- Root depth – it is noted how different suites of prairie species have roots at different soil levels (Weaver 1919, Platt 1975), serving to differentiate zones of foraging and therefore niches.
- Foraging ability – is related to how fine-textured root systems are, and how far they extend laterally (Grime 2001).

9.5.8 Nutrient storage and mobilisation of nutrients in spring

It has been suggested (see *4.5.2.* in *7. An analysis of plant traits and characteristics*) that species which store nutrients over winter in root tissues can be seen as being on a gradient which puts them closer to true geophytes than it does with species which store little over winter (or a drought-induced dormant season). This allows them to put on a spurt of growth in spring that puts their foliage above that of competitors for a crucial period of good moisture availability.

Further investigating this tendency would require analysing the dry matter content of roots, and relating this to the dry matter content (and thus assumed nutrient content) available to each ramet likely to make growth in the spring.

9.5.9 Response to temperature and light in growth initiation

In 7. *An analysis of plant traits and characteristics* it was suggested that there is a considerable difference in the genetically determined predisposition to start growth at particular temperatures and light intensities; although temperature is suggested as the key variable (Grace 1987).

Whilst it is observed that several species studied here which make a notably late start to growth are from strongly continental climates, e.g. *Eupatorium maculatum* and *Desmodium canadense* from the North American Midwest, it must not be assumed that there is a necessary link between climate of region of origin and the ability to start growth, as is shown by the behaviour of aster, rudbeckia, and solidago species (see *Discussion* 2.2). Species which start growth late may be expected to be at a competitive disadvantage in a climate with an early start to the growing season, but those which are able to respond to exceptional early warmth might be expected to be at advantage in short continental growing seasons in that their greater phenological plasticity enables them to take advantages over those species which are obligate late emergers.

Therefore, rather than assume that species from particular regions will respond to particular temperature and light conditions, it is suggested that instead species will have to be tested for their responses. Whilst only the expense of controlled-environment greenhouses will give an accurate measure of response, observation, ideally made over several growing seasons will give good enough results for most practitioner purposes.

9.5.10 Response to moisture availability, temperature of established plants

In the characterisation of Growth Cycle Groups 2 and 3, and in section 4.5.6 of 7. *An analysis of plant traits and characteristics*) it is suggested that the sensitivity of the degree to which some ornamental forbs respond to changing conditions makes them particularly suitable for use in climates where growing conditions are unpredictable, as in much of north-west Europe, conversely, an understanding of these issues would help practitioners in plant selection in more severe but predictable climates. It is suggested that a better and more systematic understanding of the response to these environmental variables could potentially be very valuable in plant specifying.

9.5.11 Refinement of measure of Estimated Competitive Ability (ECA)

The measure of ECA proposed in 7. *An analysis of plant traits and characteristics* should be regarded only as a crude starting point for further research. The expression of plant performance through a quantitative measure based on essentially subjective judgements is potentially a valuable way of gathering data from practitioners, but with the strong proviso that judgements need to be made through the grading of performance by definite and varied criteria. The concept of ECA needs to be broken down into components which more accurately reflect defined behaviours, e.g. ability to spread extensively, to persist in occupied space, to suppress neighbours – each of which can be graded, so that ECA then becomes a measure based on a more finely-textured range of judgements.

It is noted that there is little systematic collection of data about plant performance or characteristics in the horticultural literature. One way to do this, and which has the virtue of gathering data from potentially a wide range of different situations, is the survey. Participants could be asked to fill in gradings for a range of performance criteria for taxa of which they have experience. This would be a way to record, and potentially be able to make accessible information that is otherwise only passed on anecdotally.

9.5.12 Perennials in grass

The potential for naturalising perennials in hay-meadow managed grass in climates like those of northwest Europe does appear to be limited, as indicated by work discussed in 4. *Investigating the growth of ornamental herbaceous perennials in grass swards* and Hitchmough 2007. Nevertheless the ability to use even a small number of taxa in such situations could make a considerable difference to the floristic and visual diversity of areas of rough grass in amenity situations. The technique is also potentially valuable as a research too because it presents multiple and demanding challenges to plant survival and spread – what survives will clearly be a strong competitor and/or show strong persistence.

Trialling in a variety of situations over periods of five or more years is necessary in order to achieve meaningful results. Once set up, such trial plots require little maintenance and are therefore, if enough participants can be found, easy to run. The maintenance of control plots for each location, which would need to be kept competitor free, in fact presents a higher maintenance demand.

9.5.13 Future plant trialling and selection work

The future of EBPS as a dynamic and visually exciting technique depends on the ability to be able to choose from as wide a range of taxa as possible. Active searching for new species, or for varieties or hybrids derived from taxa already in cultivation and their trialling is thus important. Searching for and trialling needs to reflect on the one hand the likely sources of potentially valuable species and the other on the needs of EBPS.

The following are the expressions of traits which have been identified in this study as conducive to competitive ability:

Extensive ramet production

This can be perceived as either potentially useful or problematic, depending on usage. Considerations of invasive potential also need to be considered. Colonising species of high resource environments are the most likely sources of new material.

Effective basal cover

This has value for visual quality as well as for competitive ability, and can be regarded as particularly important in conventional horticulture as well. Woodland edge and meadow habitats seem to be the most important potential sources.

Morphological plasticity

So distinctive of geranium species, this characteristic is an expression of a trait that has been noted as very useful for competition in crowded EBPS but also for the development of a tighter, weed-suppressing and visually attractive habit in less densely packed plantings. Woodland edge and meadow habitats seem to be the most important potential sources.

High biomass

High biomass is not always a desirable characteristic, as large herbaceous plants have limited use in most EBPS and landscape plantings. They can however create considerable visual drama. Tall herb habitats are a pre-eminent source of such species.

Early growth and Phenological plasticity

These are important for maritime climate regions. However given what has been said above, potential species need not be sought only in regions with such climates. It is possible that the traits underlying these characteristics may vary considerably within species, necessitating attention to provenance and genetic variation.

The following have also been noted as possibly important, either for competitive ability or persistence:

Nutrient recycling

Given the possible role such characteristics might have in ensuring the long-term persistence or dominance in some communities, the identification of species with a relatively closed nutrient cycle and associated caespitose-type habit may have considerable value, especially for species which might have value for a visually important or matrix role. Such species may be expected to be found in habitats where disturbance is low, and also where soil productivity is low.

Nutrient storage

A geophytic tendency has been indicated as a strategy whereby some species seem to be able to compete or at least persist. Attention to the ability to make rapid spring growth and possession of swollen root tissues is indicated.

Some ruderal character, and resistance to mollusc predation are also characteristics that will have value in EBPS.

9.5.14 Trends in floristic diversity in designed plantings over time

Long-term mapping, measurement and evaluation of ornamental herbaceous plantings have never been consistently carried out. Such a project would be relatively easy to integrate into an existing feature, and could reveal much valuable material on plant spread (rates and mechanisms), long term survival, recruitment, the growth of spontaneous species, change in ornamental character etc.

9.5.15 Genetic Variation

Many species in cultivation have a low level of genetic variation. One aspect of this is that taxa in cultivation may reflect a very narrow range of provenance, which potentially can seriously limit the range of conditions in which a species may be used (Dosmann 1999). Limited genetic variation can also limit the ability of a species to reproduce or to maintain a sufficiently wide genepool in a dynamic plant community where replacement through seedling recruitment is essential for long-term persistence. Genetic variation as expressed through on-going recruitment to a designed plant community may also be expected to play a role in the adaptation of that community to changing conditions. Conventionally, genetic variation has not been regarded as important when species are introduced into cultivation (although provenance has been); the demands of EBPS suggest that more attention be paid to this in future. The idea that a genetic variation plays a role in diversity is another reason (Aarssen 1989).

One implication of this is that cultivar selection may have only limited value for dynamic planting schemes, as cultivars are by definition genetically uniform or almost so. Combinations of cultivars though may allow sufficient genetic variation for a healthy genepool to be maintained.

Given the enormous difference between species in how much genetic variation there is within a species (Diboll 1993), this would seem to be a fruitful and important area for future research.

Appendix 1.

Region and habitat of origin

Making comparisons between plants growing in the wild and in cultivation is of only limited value (see *3.10 Natural habitats and horticultural habitats*), because:

- The difference often observed between fundamental and realised niches (Burrows 1990) indicates that a knowledge of conditions in the wild can only be of limited value to the horticulturalist.
- That the composition of wild plant communities is the result of contingency and to a large extent the outcome of chance. Contemporary thinking is summarised by Budiansky 1995.

Individuals in the wild are generally considerably smaller (1994 Hitchmough), the outcome of more intense competition. EBPS practitioners are working with plants in competitive combination, unlike conventional horticulture and landscape professionals, and so might be expected to be able to make more useful comparisons of plants in the wild and in cultivation.

Comparison of plant form, growth rate and competitive ability between individuals in the wild and in garden conditions does not appear to have been systematically undertaken.

The usefulness of the table *Region and habitat of origin* is indicated by the fact that the knowledge that a particular species originates in a particular climate zone or habitat is useful because it points to the fact that in this realised niche, in conditions of competition, it can survive. Such information is more useful in determining conditions of suffficiency for growth than the knowledge that it can survive in garden conditions with a particular set of climate conditions.

	Region	Climate	habitat	Source of inf	parent species of hybrid taxa
					Habitat information is given for parents of hybrids
Acanthus spinosus	S Europe	continental	woodlands, meadows	Polunin 1980	
Achillea millefolium	Eurasia	Maritime + continental	meadows, open places	Polunin 1969, Fitter 1978	
Aconitum arctuatum	E Asia	continental	woodland edge	Wynne-Jones 2007	
Aconitum napellus	C Europe	continental/ montane	tall herb flora, moist woodland	Adler et al. 1944,	
Aconitum carmicha	C and S China	continental	woodland edge, grassy slopes	Flora of China	
Aconogonon 'Johanneswolke'	Sakhalin, Japan	continental/high summer rainfall	coastal	Ohwi 1965	hybrid of A. *weyrichii and ?*
Alchemilla mollis	Europe	continental	open places, roadsides, meadows	Adler et al. 1944,	
Amsonia orientalis	Greece, Turkey	continental/ Mediterranean	wet places near sea	Tutin et al. 1968	
Anaphalis triplinervis	Himalayas	Montane	clearings, pasture	Polunin & Stainton 1984	
Anemone x hybrida	China	continental	rocky places, woods	Phillips and Rix 1991	descended from A.hupehensis and others
Aquilegia vulgaris	Eurasia	continental	light woods, meadows, mountains	Adler et al. 1944, Polunin 1969	
Artemesia cf.cana	N.America, Plains	Dry continental	steppe type habitat	Britton & Brown 1898, Barr 1983	
Artemisia lactiflora	S China	Montane	streamside, woodland edge	Flora of China	
Aruncus dioicus	Eurasia	continental/ montane	woodland, tall-herb flora	Adler et al. 1944,	
Aster cordifolius	NE N America	continental	woodland edge	Britton & Brown 1898	
Aster novi-belgii	coastal E N America	continental but maritime influenced?	swamps near coast	Britton & Brown 1898	
Aster puniceus	NE N.America	continental	moist/wet	Britton & Brown 1898	
Aster umbellatus	E N.America	continental	moist meadows	Britton & Brown 1898, Cullina 2000	
Astrantia major	Europe	continental	moist, fertile woodland, tall-herb	Adler et al. 1944, Polunin 1969	
Astrantia maxima	Caucasus	continental/montane	woods, damp meadows	Phillips and Rix 1991	
Baptisia australis	E N America, IO, PA south	continental	dry mesic	Britton & Brown 1898, Jones and Foote 1990	

	Region	**Climate**	**habitat**	**Source of inf**	**parent species of hybrid taxa**
Bergenia 'Abendglut'	E Asia	continental/momontane	rocks, slopes, grassy places, *mountain meadows*	Polunin & Stainton 1984, Phillips and Rix 1991	parents from similar habitat, assumed to be largely B.stracheyi (Phillips and Rix 1991)
Brunnera macrophy	Caucasus	continental	grassy slopes, woodland	Phillips and Rix 1991	
Calamagrostis x acutiflora 'Karl Foerster'	Eurasia	continental	woodland edge, river banks, roadside	Adler et al. 1944,	Parents are C.arundinacea and C.epigeios
Calamintha grandiflora	S and SE Europe, W Asia	continental/ Mediterranean/montane	woods in mountains	Polunin 1980, Polunin 1969	
Campanula latifolia	Europe	continental/ montane + maritime	tall herb flora	Adler et al. 1944,	
Carex dipsacacea	New Zealand	maritime	swamps, woods	Moore & Edgar 2004	
Carex pendula	W.C. & S.Europe	Maritime + continental	moist woods	personal observation	
Centaurea montana	Europe	continental	tall herb flora, open places	Adler et al. 1944,	
Cephalaria gigantea	Caucasus	continental	wet meadows	Phillips and Rix 1991	
Chelone obliqua	E N America	continental	wet woods, swamps	Gleason and Cronquist 1963, Cullina 2000	
Cirsium canum	C Europe	continental	wet meadows, moorland	Adler et al. 1944,	
Cirsium rivulare	C Europe	continental/ montane	wet meadows, moorland	Adler et al. 1944,	
Clematis heracleifolia	N & C China	continental	woodland edge	Flora of China	
Crocosmia 'Lucifer'	E.South Africa	montane	wet meadows	Plantzafrica 2005	C.masonorum x C.paniculata
Desmodium canadense	E N America	continental	moist places	Gleason and Cronquist 1963	
Dianthus carthusianorum	Europe	continental	calcareous, dry meadows	Adler et al. 1944, Polunin 1969	
Dictamnus albus	C & S.Europe	continental/ Mediterranean	warm, dry, light woodland	Adler et al. 1944, Polunin 1969	
Dryopteris felix-mas	Temperate N. Hemisphere	Maritime + continental	light shade	personal observation	
Echinacea purpurea	mid-west N America	continental	moist prairie, open woodland	Ladd 1995	
Echinops ritro	S Europe	continental/ Mediterranean	rocky places, steppe	Polunin 1969, Adler et al. 1994	
Epimedium perraldianum	N Africa	montane/Mediterranean	woodland	Phillips and Rix 1991	
Eryngium bourgatii	Mediterranean	Mediterranean	dry rocky places	Phillips and Rix 1991	
Eupatorium maculatum	E N.America	continental	moist	Britton & Brown 1898	
Euphorbia cyparissus	Europe	continental	dry limestone meadows	Adler et al. 1944, Polunin 1969	
Euphorbia myrsinites	Balkans	continental/ Mediterranean	rocks, grassy places	Polunin 1980	
Euphorbia palustris	Europe	continental	wet meadows	Adler et al. 1944, Polunin 1969	

	Region	**Climate**	**habitat**	**Source of inf**	**parent species of hybrid taxa**
Euphorbia polychroma	C Europe	continental	dry woodland, infertile meadows	Adler et al. 1944,	
Euphorbia schillingii	Himalayas	continental/ montane	rocky slopes	Phillips and Rix 1991	
Filipendula rubra 'Venusta'	N America, IO southwards	continental	wet prairie, marshes	Jones and Foote 1990	
Filipendula ulmaria	Eurasia	continental + maritime	wet meadows, marshes	Polunin 1969, Fitter 1978	
Geranium asphodeloides	Balkans	continental/ Mediterranean	woodlands, thickets	Polunin 1980	
Geranium 'Johnsons Blue'	Eurasia/Himalaya	continental + maritime	scrub and open country	Yeo 1985	G.himalayense x G. pratense
Geranium phaeum	Europe	continental	meadows, woodland edge	Adler et al. 1944, Polunin 1969	
Geranium pratense	Eurasia	primarily continental	scrub, meadows	Fitter 1978, Polunin 1969	
Geranium renardii	Caucasus	continental/ montane	cliffs, rocky meadows	Phillips and Rix 1991	
Geranium 'Rozanne'	Himalayas	continental/ montane	forests, scrub, open slopes	Bath and Jones 1994, Polunin & Stainton 1984	G.wallichianum x G.himalayense
Geranium sanguineum	Europe, Turkey	continental + maritime	dry scrub and open situations	Polunin 1969,Adler et al. 1994	
Geranium sylvaticum	Europe	continental/ montane	meadows	Yeo 1985	
Geranium x oxonianum	S.Europe	maritime and montane	moist, woodland edge	Tutin et al. 1968	hybrid of G.endressi (Pyrenees) and G.versicolor (Balkans)
Helianthus 'Lemon Queen'	E N.America	continental	moist open places	Cullina 2000	H. pauciflorus var. subrhomboideus x Helianthus tuberosus
Helleborus x hybridus	Balkans	Mediterranean/continental	woodlands, thickets	Polunin 1980	parentage assumed to largely H.orientalis
Hemerocallis 'Golden Chimes'	Eurasia	continental	wet meadows	Phillips and Rix 1991	parents assumed to be various, similar habitats
Heuchera micrantha	NW N America	maritime	rocky places, stream banks	Phillips and Rix 1991, Hitchcock and Cronquist 1973	
Hosta fortunei	E Asia	continental	moist	Phillips and Rix 1991	assumed to be a hybrid
Inula cf. racemosa	Himalayas	continental/ montane	waste ground near habitation	Phillips and Rix 1991	reference is to I.racemosa
Iris sibirica	Eurasia	continental	marshlands, wet meadows	Adler et al. 1944,	
Knautia macedonica	SE Europe	continental/Mediterranean	scrub, meadows	Phillips and Rix 1991	
Kniphofia cvs.	S Africa	warm temperate/ montane	wet grasslands	Plantzafrica 2005	hybrids of various origins.
Lamium orvala	N.Balkans	continental	woodland	Polunin 1980, personal observation	

	Region	**Climate**	**habitat**	**Source of inf**	**parent species of hybrid taxa**
Leucanthemella serotina	SE Europe	continental	wet meadows	Phillips and Rix 1991, Polunin 1980	
Ligularia 'Zepter'	China	continental	wet places	Phillips and Rix 1991	assumed to be a hybrid of L.veitchiana and L.przewalskii
Liriope muscari	E Asia	continental	woods	Phillips and Rix 1991	
Lunaria rediviva	C Europe	continental	tall herb flora, moist woodland	Adler et al. 1944,	
Lysimachia ciliata	E N America	continental	damp woods, wetlands	Phillips and Rix 1991	
Lysimachia clethroides	E Asia	continental	open grassy places	Phillips and Rix 1991	
Lysimachia punctatum	C & SE Europe	continental	tall herb flora, damp places	Adler et al. 1944,	
Lythrum salicaria	Eurasia	continental	marshes, lake sides	Polunin 1980	
Macleaya cordata	E Asia	continental	grassy places, open woodland	Phillips and Rix 1991	
Miscanthus sinensis	E Asia	continental	open places, moist	Phillips and Rix 1991, Ohwi 1965	
Molinia caerulea subsp. 'arundinacea'	C and S Europe	continental/ montane	dry woods, slopes, moorland	Adler et al. 1944,	
Monarda hybs.	E N America	continental	variety of open and lightly shaded habitats	Jones and Foote 1990, Philips and Rix 1991	assumed to descended from M.didyma and M.fistulosa
Nepeta x faassenii	SW Europe/W Asia	continental/ Mediterranean	dry places	Phillips and Rix 1991	N. racemosa x N.nepetella
Ophiopogon bodinieri	S.Cbina	continental	forest, scrub, slopes	Flora of China	
Origanium laevigatu	Turkey	continental/ Mediterranean	meadows, dry open woodland	Phillips and Rix 1991	
Papaver orientale	W Asia	continental	rocky slopes, dry meadows	Phillips and Rix 1991	
Persicaria amplexicaule	Himalayas	continental/montane	meadows, streamsides	Phillips and Rix 1991	
Persicaria bistorta	Eurasia	continental/ montane + maritime	damp woods, meadows	Fitter 1978, Polunin 1969	
Persicaria affinis	Himalayas	continental/ montane	rocky places	Flora of Pakistan	
Phlomis russelliana	Turkey	continental	woodland clearings	Phillips and Rix 1991	
Phlox paniculata	E Coast N America	continental	meadows, roadsides, fertile soils	Jones and Foote 1990, Cullina 2000	
Pulmonaria officianalis	C Europe	continental	woodland	Adler et al. 1944,	
Rudbeckia fulgida var. deamii	Mid West USA	continental	moist open, woodland edge	Hilty 2006	

	Region	**Climate**	**habitat**	**Source of inf**	**parent species of hybrid taxa**
Rudbeckia 'Juligold'	E N.America	continental	moist thickets	Britton & Brown 1898, Jones and Foote 1990	assumed to be derived from R.laciniata
Salvia nemorosa	C& E Europe	continental	dry meadows, arid places	Polunin 1980	
Salvia verticillata	E Europe	continental	dry meadow	Adler et al. 1944,	
Sanguisorba tenuifolia	Japan	continental	moist places	Phillips and Rix 1991	
Sedum spectabile	S China	continental	woodland edge, dry rocksy slopes	Flora of China	
Senecio tanguticus	China	continental	moist meadows	Phillips and Rix 1991	
Solidago rugosa	E N.America	continental	moist places	Cullina 2000	
Stipa arundinacea	New Zealand	maritime	woodland, woodland edge	Manaaka 2004	
Stipa calamagrostis	C & S.Europe	continental/ montane	pioneer, dry slopes	Adler et al. 1944,	
Stipa gigantea	Iberian peninsula	continental/ Mediterranean	rocky slopes, usually at altitude	Phillips and Rix 1991	
Symphytum caucasicum	Caucasus	continental	meadows, roadsides, streamsides	Phillips and Rix 1991	
Tanacetum macrophyllum	Balkans	continental/Mediterranean	moist woods	Polunin 1980	
Tanacetum parthenium	SE Europe	continental	scrub, rocky placdes	Polunin 1980	
Thalictrum aquilegifolium	Eurasia	continental/ montane	woods, tall herb flora	Adler et al. 1944,	
Thermopsis caroliniana	SE N.America	humid continental	woodland edge	Radford et al. 1964	
Trachystemon orientalis	Caucasus	continental	woodland, riverbanks	Phillips and Rix 1991	
Vernonia crinita	N America, MS to TX	continental	prairie, streamsides	Britton & Brown 1898	
Veronica spicata subsp. incana	E Europe	continental	Dry slopes	Tutin et al. 1968	
Veronicastrum virginicum	E N.America	continental	moist, open & woodland edge	Britton & Brown 1898	
Vinca minor	Balkans	Mediterranean/continental	woods, hedges, rocks	Polunin 1980	

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Appendix 2.

RESEARCH LOCATIONS

1. Data collected for 7.*An analysis of plant traits and characteristics* was from plants growing at:

Cowley Manor, Gloucestershire, UK
51:49:58N
2:03:27W
250m
medium loam over oolitic limestone

Tinpenny Cottage, Gloucestershire, UK
51:58:40N
2:06:58W
15m
heavy clay loam

Elmtree Cottage, Gloucestershire, UK
51:55:32N
2:29:56W
140m
sandy clay loam

2. Data collected for 3. *The use of transects to investigate established ecologically-based plantings*:

Cowley Manor

Hermannshof, Weinheim, Germany
49:33:08N
8:39:57E
135m
loamy sand

3. Research plots for 6. *Evaluating the competitiveness of herbaceous perennials using a phytometer in open ground conditions:*

Pershore College, Worcestershire, UK
52:06:51N
2:04:50W
40m
alluvial silty clay loam

Montpelier Cottage, Brilley, Herefordshire, UK
52:07:44N
3:04:59W
110m
sandy clay loam

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A1.

Anaphalis triplinervis. The very dense production of shoots from a small base is reminiscent of the growth habit of cespitose grasses. It is not sufficient to deter competition from species growing very near to the clump however.
April, Elmtree.

A2.

***Calamagrostis x acutiflora* 'Karl Foerster'** A dense clump is resistant to penetration by other species.

A3.

***Centaurea montana*, naturalised in hedge bottom, Brilley, Herefordshire.**
Established here for at least 15 years.
Early June.

A4.

***Euphorbia cyparissias* in the wild, Luxembourg.** The plant is intermingled with other vegetation on a sunny bank. July, presumably after a hay cut.

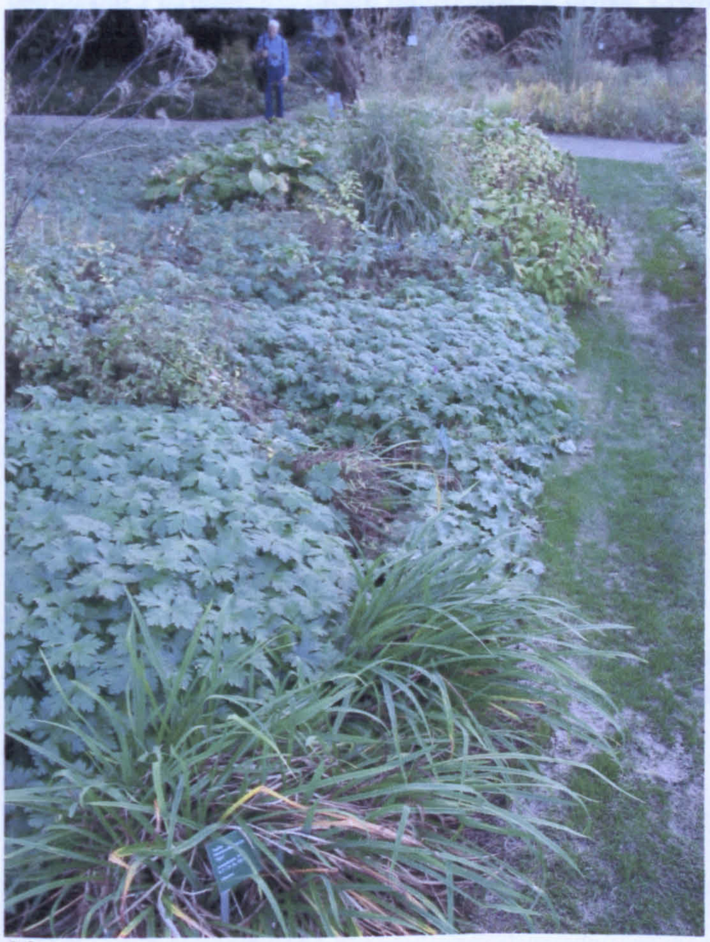
A5.

***Euphorbia cyparissias* in cultivation.** The plant has occupied all available space producing much more dense ramet production than it does in the wild. Note how it appears to be unable to penetrate a neighbouring clump of *Geranium sanguineum*.
July

A6.

***Euphorbia palustris* in the wild, vanishing lake of Cerknica, Slovenia.** Fewer stems are produced from the base compared to cultivated situations. Stems are also more upright.
June.

A7.
***Euphorbia palustris*, in cultivation,** illustrating the very small area of the base of the plant. April, Elmtree.



A8.
***Geranium endressii* var. in border at Hermannshof.**

The dense clumps formed by these plants are typical of how the species performs in standard border cultivation.
Early June.

A.9.

***Geranium x oxonianum* group naturalised in grass, Cowley manor**. Stems tending to interpenetrate grass stems. June.
June

A10.

***Geranium x oxonianum* group**. Production and maintenance of foliage at lower temperatures than other species arguably gives this taxon a great competitive advantage.
January.

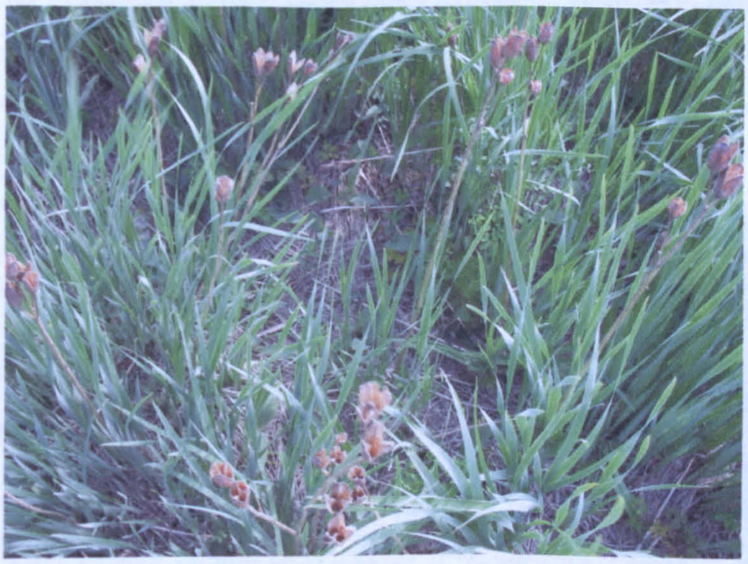
A11.

Geranium **'Johnson's Blue'** is typical of most herbaceous ornamentals in that its foliage does not overwinter. However it leaves a dense thatch of dead growth which may inhibit late winter germination of potentially competitive seedlings. In this example, the foliage has nearly all fallen one way, down a steep slope, illustrating great vulnerability to competition on the upward side. January, Elmtree.

A12

Geranium phaeum **naturalised in lightly-shaded roadside verge, Brilley, Herefordshire.** A meadow species not native to Britain which can clearlycompete with native vegetation. June.

A 13.
***Geranium phaeum* naturalised, detail.** Showing weak grass growth beneath leaves.
June.



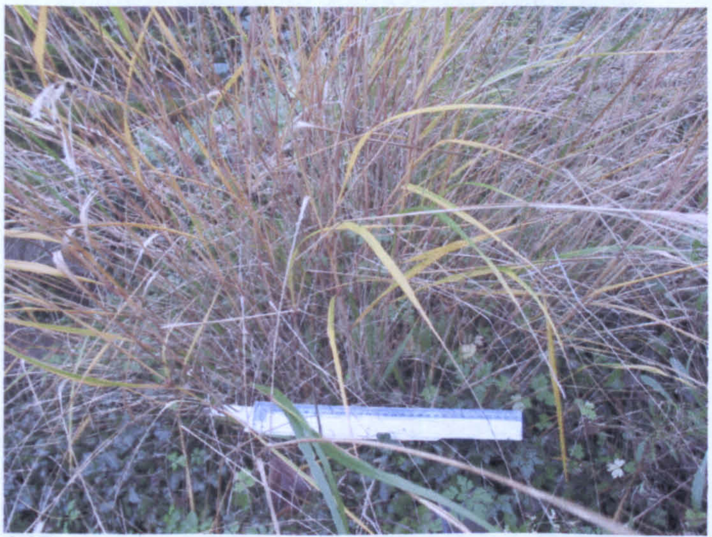
A14.
***Iris sibirica*, in the wild, Nanos, Slovenia.** Note dense thatch of previous year's deal foliage.
June.

A15.

Phlomis russeliana. Leaves living for a year resulting in effective year round shading of the ground in and around the clump.
April, Cowley.

A16.

Phlox paniculata. Illustrating a phalanx habit, followed by death of older ramets and increasing tendency of resulting ring to break into separate independent clumps.
April, Cowley.



A17.

Stipa calamagrostis**.** Note the open character of the clump and penetration by *Ranunculus repens.*
January, Elmtree.

A18.

Stipa gigantea**.** A Mediterranean species with foliage which lives for more than one year, ensuring shading around the base – this shading is however reduced in effectivenes by its linear nature which gradually reduces the shading effect nearer the tips; it is also very light and easily blown by the wind, so further reducing shading.
September, Elmtree.

A 19

Young growth of Eupatorium fistulosum.

The presence of residual leaf laminae at widely-spaced nodes is noted. Rapid growth is made during May, with expansion of appreciable foliage canopy only beginning at around 600mm above ground. First week June. Montpelier Cottage.