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The buttercup family through the course of the year – interrelationships between plant phenology and basic questions in evolution

Jürgen Momsen

Abstract

The development of the forms of the leaf, shoot and blossom in the annual sequence of growth and flowering of the common native species of Ranunculaceae is discussed.

The annual sequence of the *leaf and shoot forms* reproduces the essential developmental stages of the ontogeny of the dicotyledonous flowering plants. Furthermore, important progressions in the phylogenetic evolution of the dicotyledonous flowering plants are reflected in the sequence of flower forms. Whereas in the leaf sequence the tendency is to juvenilisation (retention), in the flower sequence it is primarily to specialisation and differentiation (anagenesis).

Plant phenology – the study of seasonal phenomena in the plant kingdom

The annually recurring rhythmical changes in appearance of individual plants and the vegetation as a whole are familiar to people in many climatic and vegetation zones of the earth in a way hardly equalled by any other natural event. Sowing and harvesting, seasonal festivals and many customs are founded in this phenomenon. The appearance of the first flowering snowdrop, the cowslip and cherry blossom touches our feelings, each in its own particular way (see also the descriptions in Kranich 1993).

Consideration of the flowering and growing times of individual medicinal plants during the course of the year also plays a role in the medicine and agriculture inspired by anthroposophy. This is based in particular on remarks by Rudolf Steiner on the 'contra-tendency' in the growth process of mistletoe compared with the 'normal' course of the year (Steiner 1920) and on the varying effectiveness of plants which flower or are harvested early in the year, or in mid-summer or autumn (Steiner 1924).

Systematic investigations into the seasonal development patterns of individual plant species according to their germination and flowering times during the year were carried out in previous decades (between 1969 and 1985) especially by Bockemühl and colleagues using container experiments (see e.g. Bockemühl 1973), later also by Heyden (1987).

Longer-term comparative systematic seasonal observations of flowering plants growing in the wild were initiated in Europe by the brilliant biologist Carl Linnaeus (1707–1778) who, as long ago as the mid 18th century, created the first phenological observer network in Sweden with at least 18 recording stations. This, however, only lasted a few years in the first instance. It was followed in 1780 by the first international observer network, created by the Palatinate Meteorological Society (*Die Pfälzer meteorologische Gesellschaft*) in Mannheim (see also Nietzold 1993, p. 50).

Since then observer services have been established in most European countries and numerous non-European ones as aids for agricultural meteorology. Because of this role, their observation lists comprise predominantly agricultural crop plants.

Following on from plant sociology, the development of botanical symphenology has

occurred particularly since around 1970. This branch of research deals with the seasonal emergence and development pattern of vegetation in different habitats (summary in Dierschke 1994, p. 362–391). Dierschke (1990) also compiled a comprehensive bibliography with around 400 entries, which greatly help the familiarisation process with this new area of research. Many of the works mentioned deal with the yearly development pattern of plants in individual vegetation types. The ground layer vegetation of Central European broadleaved woodland is a particularly important topic for study within this field (see e.g. Dierschke 1989). However, a search of the various publications for studies in which changes in the form development of species are described along with changes in the appearance of the plant community, is usually to no avail.

An important step in this direction was made by Hans Vereijken in his study of the seasonal development of meadows in the grounds of the Goetheanum (Dornach, Switzerland), in which he observed in particular the change of form within the succession of species coming into flower (Vereijken, 1992).

Following on from his work, since 1991 (and more intensively in the course of a research project from 1999 to 2002) we have been involved with form development in flowering plants according to their flowering time in seven different vegetation types in the economically important habitats of forest, grassland and arable in the vicinity of Ludwigsburg, near Stuttgart (A. shaded alluvial woodland, sunny woodland on south-facing slope; B. damp meadowland, dry meadowland; C. arable, vineyard, market garden). This study was designed as basic research towards an understanding of the specific characteristics of individual medicinal plants, in the first instance within an overview of their plant communities. It transpired that a particular characteristic seasonal pattern could be identified not only when comparing the sequence with which plants came into flower in the individual habitats, but likewise within each family and genus. The results of this project will be summarised elsewhere (Momsen 2004). Here – inspired by a medicinal plant project with Jochen Bockemühl on the family Ranunculaceae in March 2002 – we would like to describe the form characteristics in the flowering succession of some common native members of this plant family through the seasons.

Seasonal changes in the leaf and shoot form of native species of buttercups and their relatives during the course of the year

The seasonal changes in plant forms is demonstrated by scarcely any of the native plant families as well as by the buttercup family, in particular by the principal genus *Ranunculus* and its close relatives.

Let us look at the series of plant silhouettes arranged by flowering date in Fig. 1 and the set of phenological data for these species or, where these are unavailable, their nearest relatives in Table 1. In addition to the leaf sequence, the habitat of each species is briefly described:

1. At the beginning of March (3.3.), in dry deciduous woodland, the sky-blue, mostly six-parted radial flowers of hepatica/liverleaf (*Hepatica nobilis*) open singly. Its few leaves are arranged in a basal rosette. They are almost entire but divided by a slight indentation into three lobes.

Future prospects

All arguments are in favour of confirming Stenzel's hypothesis about the leaf character of the seed scale. Conifers are clearly at a developmental level above the ferns, but do not fully reach the level of the flowering plants. As is well known, they are much 'older' than true flowering plants. There is evidence of conifers along with the ferns and mosses as early as the late Carboniferous, while the true flowering plants first emerged in the second half of the Jurassic and have only experienced their true 'flowering' in modern times. Only trees (and shrubs) are known from the conifers. In temperate climates at least, the angiosperm trees show a certain similarity as flowering plants to the primitive types of conifers, primarily in that the flowers are morphologically reduced but nevertheless definitely present. In addition, during the first years of growth many deciduous trees produce a conifer-like cone shape with an erect dominant central trunk. In open-grown specimens this shape is gradually superseded. In the process, the characteristic crown shape is progressively established. As in all trees, the deciduous trees are also dominated by the 'mineral-plant'. This appears in the secondary thickening which leads to wood and bark production and gives rise to a kind of individualised structure by way of compensation for the restrained flowering (Rispen 2006).

Taxonomic botany, to the extent that it exists nowadays as generally accepted knowledge, has taken a progressively abstract route since the end of the 19th century. Due to the dramatic rise in genetics in recent decades, also in relation to matters concerning evolutionary origins, a certain high point has now been reached. Morphology related to direct perception of the world of the senses still has only a very secondary role. It is therefore justifiable to go back to researchers whose aim it was to allow themselves to be instructed directly by nature in the Goethean sense. Stenzel is certainly one of their number.

In this article our main objective was to point out the evolutionary divide between conifers and deciduous trees from the point of view of their reproductive organs. This paper is intended as a supplement to my Goethean survey of the conifers (Rispen 2006) and at the same time is aimed at stimulating a more detailed investigation of deciduous trees.⁴ A rational, phenomena-based, answer to the question about the host trees of mistletoe (*Viscum album*), which would be of great practical and medicinal interest (see for example Sommer & Soldner 2000), is largely dependent on this work which is yet to be accomplished.

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⁴ Preliminary approaches to this appear in *Schad* (1982) and *Göbel* (1994).

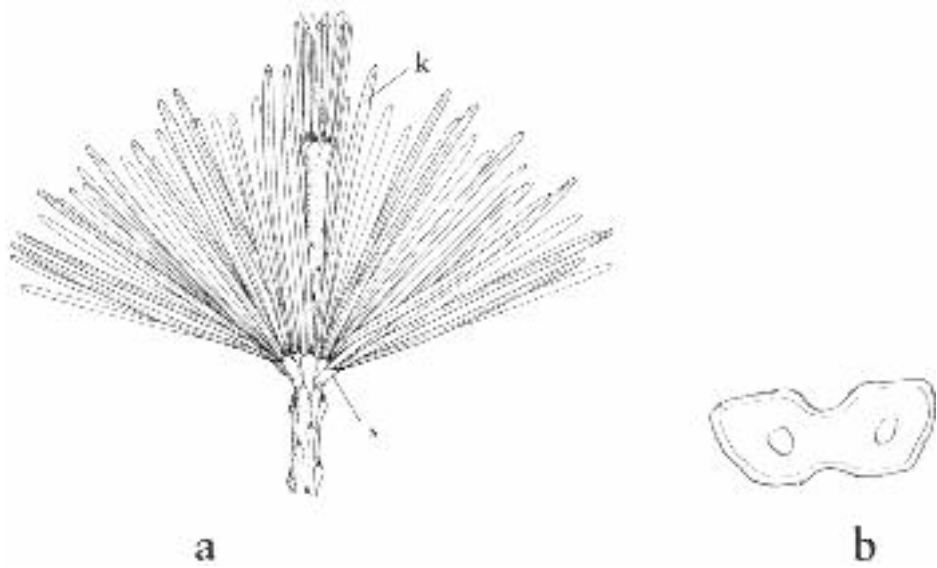


Figure 19. **a:** Umbrella pine (*Sciadopitys verticillata*): twig with one 'umbrella' of needle-shaped short shoots (cladodes) (K) in the axes of scale leaves (S), **b:** cross section through a cladode (phloem above in vascular bundle) (a from Bartels (1993), b after Fukarek *et al.* (1992)).

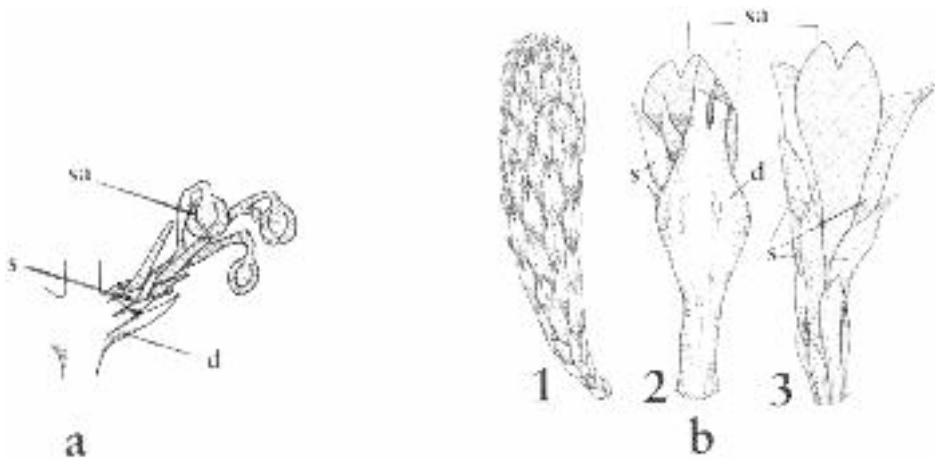


Figure 20. Situation in the oldest Gymnosperms (Cordaitaceae): **a:** 'flower' of *Cordaites pseudofluitens* with bract (d), sterile scales (s) and stalked ovules (sa) (after Florin); **b:** flower of *Lebachia piniformes* (Voltziales); 1: fruiting inflorescence, 2, 3: individual 'fruit shoots' of bract scales (d), sterile scales (s) and flattened atropic ovules (sa) (after Strasburger 1991).

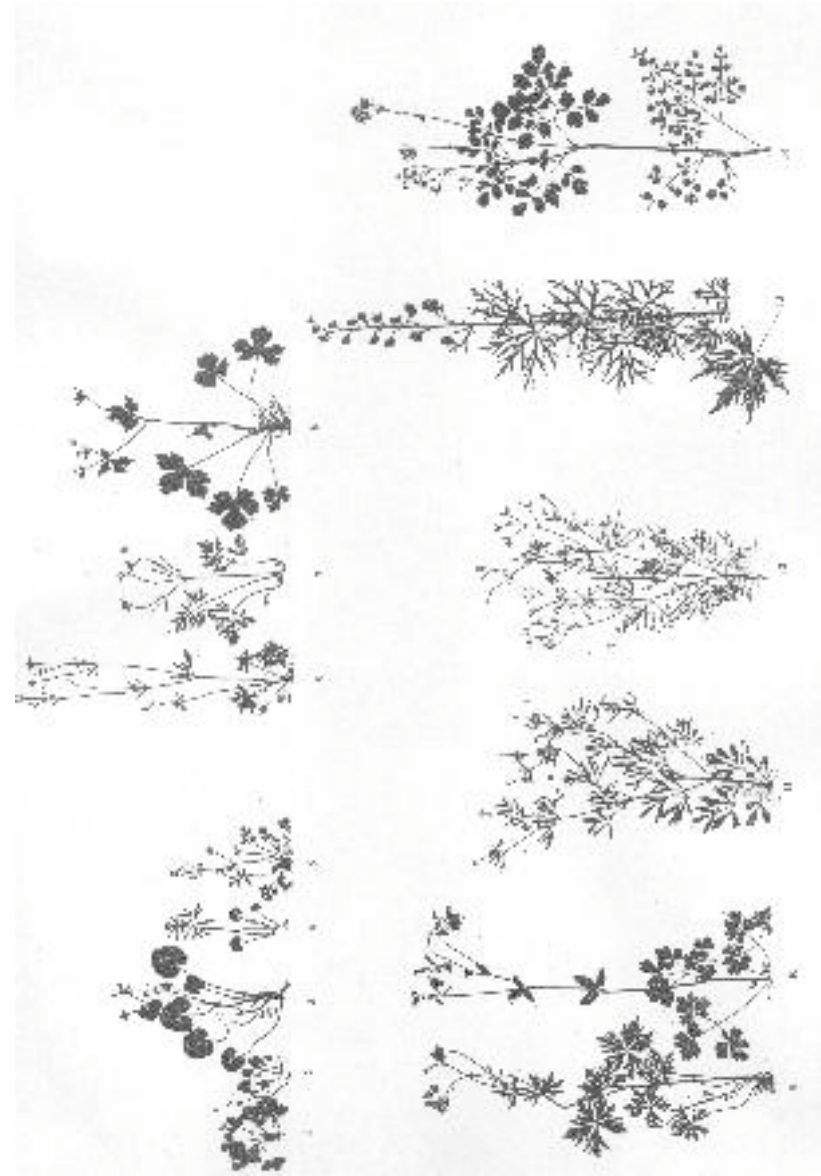


Figure 1. Flowering sequence of native buttercup family species from the genus *Ranunculus* and close relatives. (From the collection of J. Momsen, early 2001 and 2002, primarily from the District of Ludwigsburg, Nos. 13 and 14 from the Botanical Garden, Stuttgart-Hohenheim)

English name	Latin name	Leaf open (ns)	Flower open (ns)	Fruit ripen (ns)	Leaf colour (Julian)	Gen-erance (flure/g)	Vege-ration (days)	Height (m)
Greater celandine	<i>Ranunculus acris</i>	2.1.	2.3.	12.5.	17.10.	71	155	0.87
Lesser celandine	<i>Ranunculus ficaria</i>	22.3.	25.3.	15.5.	15.7.	43	82	0.87
Marsh marigold	<i>Caltha palustris</i>	5.4.	5.4.	16.6.	19.10.	64	221	1.54
Goldilocks	<i>Ranunculus auricomus</i>	25.3.	4.4.	17.6.	27.6.	62	92	1.07
Full-necked buttercup	<i>Ranunculus bulbosus</i>		10.4.					
Black-eyed Susan	<i>R. ranunculus</i>	10.3.	23.4.	12.5.	13.11.	70	212	0.82
Woolly buttercup	<i>R. hederifolius</i>	21.3.	4.5.	25.6.	6.11.	50	272	0.82
Globe Thistle	<i>Thalictrum flavum</i>	24.3.	2.3.	12.6.	25.9.	38	181	0.82
Creeping buttercup	<i>R. repens</i>	12.3.	2.5.	27.6.	7.	36	249	1.2
Chilodactyl	<i>Ranunculus ficaria</i>	15.4.	12.5.	20.6.	15.10.	46	209	0.78
Large-flowered	<i>Ranunculus ficaria</i>	15.3.	1.6.	25.7.	18.10.	57	211	0.77
Black-throated	<i>Ranunculus acris</i>	17.3.	4.5.	7.4.	23.10.	68	61	0.90
Weld	<i>Ranunculus repens</i>	26.3.	4.5.	12.5.	22.10.	73	67	0.83
Common meadow	<i>Thalictrum flavum</i>	2.1.	1.7.	2.5.	6.11.	66	187	0.83

Table 1. Phenological overview of native representatives of the Ranunculaceae arranged according to flowering time.*

- About 3½ weeks later at the end of March (29.3.) the lesser celandine (*Ranunculus ficaria*) begins the series of shiny glossy yellow-flowering native species of the genus *Ranunculus*. It grows in cool damp ground, usually in the half shade of individual trees with patchy vegetation, and has rounded to heart-shaped, slightly indented leaves, which at first appear to form only a rosette. Later in the growing season, however, at first procumbent and later slightly upright elongated flowering shoots develop, which support somewhat smaller more pointed leaves. But the flowers remain mostly procumbent or at least close to the ground surface.
- Soon afterwards i.e. at the beginning of April (5.4.) the first marsh marigolds (*Caltha palustris*) come into flower in wet meadows and bog woodland. To begin with this species also develops undivided rounded leaves in a low basal rosette. As the flowers open, the many-branched flowering stems extend upwards and outwards, so that substantial hemispherical bushes develop, from which the dark yellow terminal flowers shine forth.
- Around ten days later, from mid-April onwards (14.4.) the flowers of goldilocks (*Ranunculus auricomus*) open in the half-shade of woodland and scrub margins on cool damp soils. The first rounded, scarcely-divided basal leaves have already opened about three weeks earlier (from 25.3.). As the flowering stem grows upwards, completely different leaf shapes suddenly appear: the sections of the upper leaves are

* Note 1: the flowering dates in Table 1 and in the text refer to the area around Stuttgart. They are mean values from the observations of J. Nietzold from Stuttgart/Ruit for the years 1960-2000 and from J. Momsen from Vaihingen/Enz (1996-2001). In the first instance we are only considering the sequence of first flowering dates for plants belonging to the buttercup family.

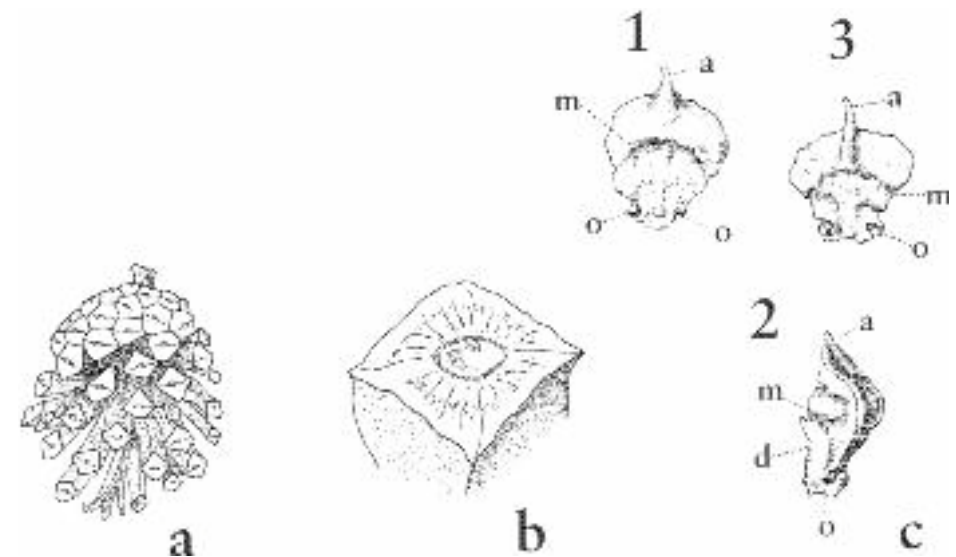


Figure 18. **a**: open cone of *Pinus sylvestris*; **b**: rear (abaxial) side of a seed scale with apophysis and transverse oval centre with a small thorn (*mucro*); **c**: seed scale of *Pinus mugo* (mountain pine) from a recently fertilised fruit-bearing flowering cone; 1) medial seed scale, inner (adaxial) side; 2) seed scale from the side; 3) medial seed scale, outer (abaxial) side; a: apophysis spur, m: transverse swelling, o: ovule, d: bract scale (a and b from Bartels (1993), c from Stenzel (1876)).

cepted to the present day.

Stenzel's fellow campaigners included Alexander Braun (1875) who, like Stenzel, viewed the seed scale as having arisen from two bud scales, a view also held by Caspary (1861). Caspary, however, was of the opinion that the seeds developed on the upper (adaxial) side of the seed scale and not on its lower (abaxial) side.

A phenomenon in the umbrella pine (*Sciadopitys verticillata*) described for the first time by Hugo Mohl (1871) shows similarities in the vegetative realm to the dorsal union of the lateral bud scales to form a seed scale shown by conifer cones (Fig. 19). The needles arranged in an umbrella shape are actually short shoots (so-called cladodes) in the axils of bracts. This is a similar situation to that in *Pinus* (Rispen 2006). Mohl found that 'what has until now been taken to be a simple needle in *Sciadopitys* has arisen from two needles whose posterior edges have united. Its apparent upper (adaxial) surface is therefore in fact the underside, towards which the phloem of the vascular bundle³ lies. Like the seed scales of the Abietineae the two united needles of *Sciadopitys* are ultimately the single developed leaf of an otherwise stunted shoot scale...' (from Stenzel 1876).

³ The vascular bundles in the seed scale also lie with the phloem uppermost, in other words arranged in the opposite direction to the cone axis.

of the scale complex are two-dimensionally arranged, in other words, the five or six sterile scales [belonging to the seed-bearing short shoot, *JAR*] unite to form a five- to seven- pointed “seed scale”. This covers the [stalked, *JAR*] ovules which are also grouped in a plane’. From this we can cautiously conclude – and we are already familiar with this from Stenzel’s intermediate forms – that the (later) seed scales develop from short shoot scales which have grown together, while the seeds arise directly from the short shoot axis. To our knowledge this has not been previously reported. Further development consists of the seed scales and seeds jointly forming a ‘fruiting organ’, in the way we already know from the representatives of present-day conifers. This suggests the hypothesis that the ovules are produced from shoot axis material belonging to the fruiting shoot. The carpel of the gymnosperms, just like that of the angiosperms, clearly possesses a leaf-like character. In the ‘fruit’ (seed scales + seeds) a synthesis of leaf-like and axis-like organs takes place, as is the case for the fruits of angiosperms at a higher level.

The developmental step from the ferns to the gymnosperms is one of moving from a situation where the prothallus is separated from the plant to one where it remains attached to it in a special ‘reproductive’ organ. Microsporophylls still retain a strong resemblance to the fern stage. Pollen is produced by a (scale) bract and released to the environment, which in this situation can be equated with the ovules awaiting pollination. Although the seeds are not enclosed in a carpel, they are, however, borne on a leaf organ (a seed scale), but themselves arise from material belonging to the axis. This development only reaches completion in the angiosperms. In this respect too the microsporangium with its spore-like pollen is reminiscent of the fern stage of development. The fruit, in contrast, being an organ formed by synthesis of a leaf and the axis, creates its own ‘cosmos’ in which the seeds develop. While the fruit of gymnosperms are given up to a hardening process (lignification), it is in the angiosperms that they first achieve the wealth of possible forms which we associate with this organ and often appreciate so much. The angiosperms are the true fruiting and flowering plants. In the case of the gymnosperms it is not really possible to talk about flower and fruit in the true sense of the words. They form a group of their own between the lower plants (ferns) and the flowering plants. Many other phenomenologists agree with this view (cf. Grohmann 1959).

Stenzel found well-known fellow campaigners for the hypothesis that the seed scale is of a purely leaf-like character, but also resolute opponents. Eduard Strasburger (1844-1912), who became known for his botany textbook, was one of the latter group. As a result of studies on pine cones (Strasburger 1872) he developed the view, in contrast to Stenzel, that the seed scale represents a transformed shoot. In the conspicuous apophysis with an oval navel/centre and a small thorn (mucro) which is present in pines, Strasburger thought he saw the stunted meristem of a bud which had been transformed into a seed scale (in the axil of a bract scale) (Fig. 18a, b). Stenzel decisively dismissed this view on the basis of his studies on young mountain pines (*Pinus mugo*; c in Fig. 18). He recognised that the apophysis is a convex outgrowth from the seed scale and the navel/centre with mucro is a fold of the same organ, perhaps even the remains of the posterior bud scale (h; Fig. 14). There can be no question of the axis being involved, because it is the first organ in the stunted bud to be reduced.

As our observations have confirmed, Strasburger’s description has been wrongly ac-

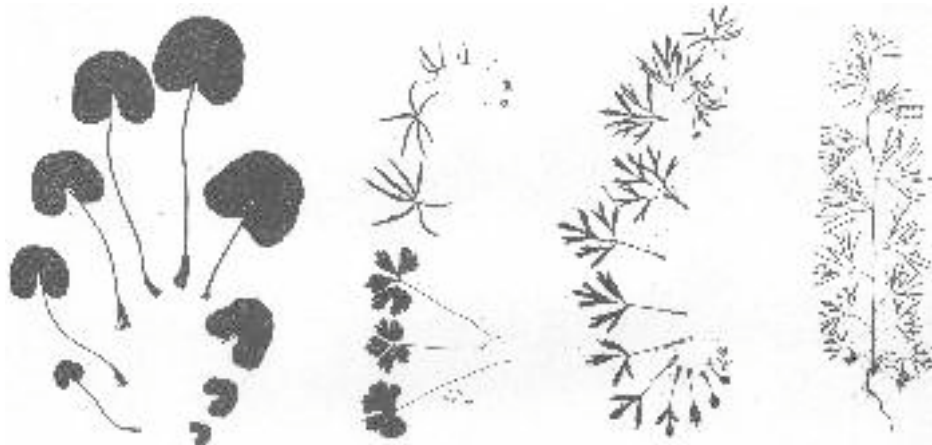
narrow and awl-shaped. A transition from the lower to the upper leaf shapes is not to be found.

- 5 & 6. The flowers of the bulbous buttercup and meadow buttercup (*Ranunculus bulbosus* and *R. acris*) open almost simultaneously, around six and ten days later respectively. The former grows preferentially on dry grassland and meadows, the latter particularly on moist to damp meadows and pastures which are well fertilised. Both species are characterised by the comparatively more strongly divided basal leaves (in *R. bulbosus* mostly with a stalked middle pinna) and the more clearly divided leaves in the upper region of the stem. Nevertheless, in nearly all instances a less pronounced though distinct gap in leaf metamorphosis between the lower and upper leaves is still present.
- 7, 8, 9 & 10. Similar relationships are to be found for the woolly buttercup (*R. lanuginosus*) which comes into flower about two to three weeks later in damp deciduous woodland; the creeping buttercup (*R. repens*) which occurs on damp compacted soils; and the close relatives of the genus *Ranunculus*, the globe flower (*Trollius europaeus*) and aquilegia/columbine (*Aquilegia vulgaris*). In these species the leaf sequences are more complex, the intervals in the leaf metamorphosis smaller, but nevertheless gaps in the metamorphosis persist in either the upper or lower regions of the plant.
11. The corn buttercup (*R. arvensis*) which flowers in mid-May displays a further refinement in leaf-division and the metamorphosis steps.
- 12 & 13. Only the relatively late-flowering (beginning of June) species of the buttercup family – the forking larkspur (*Consolida regalis*) and the monkshood (*Aconitum napellus*) and yellow monkshood – develop flowering stems with a full leaf sequence and subtle intermediate forms in metamorphosis.
14. The much divided delicately-leafed species of meadow-rue (in this instance greater meadow-rue, *Thalictrum aquilegifolium*) also only start to flower from the beginning to middle of June.

Seasonal development in the genus and family in comparison with leaf development in the ontogeny of plants coming into flower and in the flowering sequence of meadow plants

The sequence of buttercup family species ordered according to flowering date displays a progression of leaf metamorphosis from early-flowering predominantly round-leaved rosette species with indistinct metamorphosis, to species with more or less tall, upright flowering stems with deeply divided leaves and distinct subtle metamorphosis steps. The species which flower in the middle period (mid to end of April) in particular, develop both more or less rounded basal leaves and deeply-divided upper stem leaves. Amongst these, the early flowering species most clearly display a gap between the basal leaves and upper stem leaves.

If complete leaf sequences of the species mentioned are used to aid the observation process (see for example Fig. 2a: *Caltha palustris*, Fig. 2b: *Ranunculus auricomus*, Fig. 2c: *Ranunculus arvensis* and Fig. 2d: *Consolida regalis*), then the sequence of rounded leaves of the early-flowering species appears even more clearly. In addition it can be seen



2a: *Caltha palustris* marsh marigold (original J. Bockemühl), mean flowering date 5.4
 2b: *Ranunculus auricomus*, goldilocks, mean flowering date 14.4
 2c: *Ranunculus arvensis*, corn buttercup, mean flowering date 10.5
 2d: *Consolida regalis*, forking larkspur, mean flowering date 20.5

Figure 2. Characteristic leaf series of native members of the buttercup family, arranged according to flowering sequence during the year. From the collection of J. Momsen 2001/02, Ludwigsburg, with the exception of 2a.

that in the species flowering in late spring and early summer the ‘lower’ rounded leaf types are, as it were, missed out in favour of the deeply-divided or pointed forms.

The relationship between individual development and flowering time can be described even more clearly by comparison with a leaf sequence which exhibits the metamorphosis steps in an even more ‘complete’ sequence (see e.g. Fig. 3: *Leonurus sibiricus* = siberian motherwort (*Lamiaceae*)); the early spring flowers (*Hepatica nobilis*, *Caltha palustris* and *Ranunculus ficaria*) form primarily the ‘lower’ leaf shapes of the complete sequence, the late-flowering species produce leaf shapes of the middle and upper regions.

A survey of the flowering plants of a meadow, arranged according to flowering date, shows similar developmental tendencies in the shoot and leaf realms as that described above for the *Ranunculus* genus (see Fig. 4), although in a somewhat more complete sequence and in this case including more than one family: round-leaved rosette plants in the early part of the year, ‘tall herbs’ with divided or narrow leaves in summer and a number of ‘transitional forms’ in between with both rounded and divided leaves as well as pointed ones. Amongst the series of ‘under-canopy’ flowers which grow in the same biotope (Fig. 4b) and open in the partial shade of the tall meadow plants, retarding tendencies in form development become apparent due to the effect of insufficient light. The leaf forms remain rounded even in late spring and the leaf blade scarcely divided. (Further details about the meadow flower sequence such as exact site, species composition and flowering dates are described in Momsen (2000 and 2004)).

This ‘development series’ also shows the influence of forces which operate from the

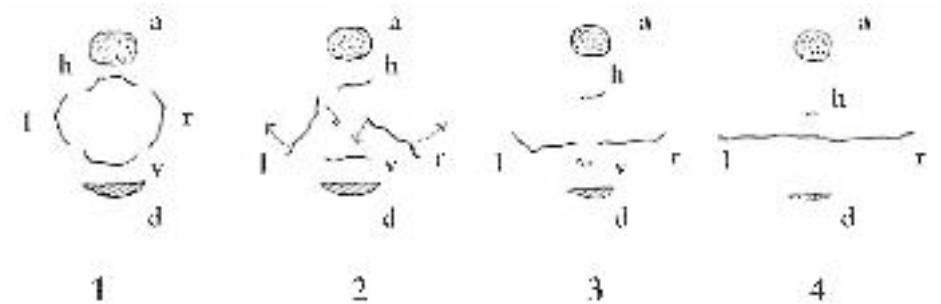


Figure 15. Diagrammatic representation of intermediate forms (seen from above) between a stunted bud (1) with four outer bud scales and a seed scale (4), in which the left (l) and right (r) side scales grow together along the sides facing the cone axis (a) while the front (v) and rear (h) scales are gradually reduced; the broken arrows show the ‘direction of rotation’ of the side scales; d: bract scale.

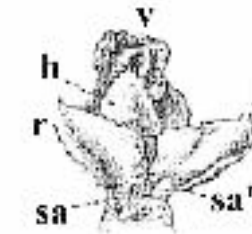


Figure 16. Adaxial side of stunted bud as in Fig. 14; sa / sa’: ovules on the abaxial side (underside) of the two side bud scales (r, l) (from Stenzel 1876).

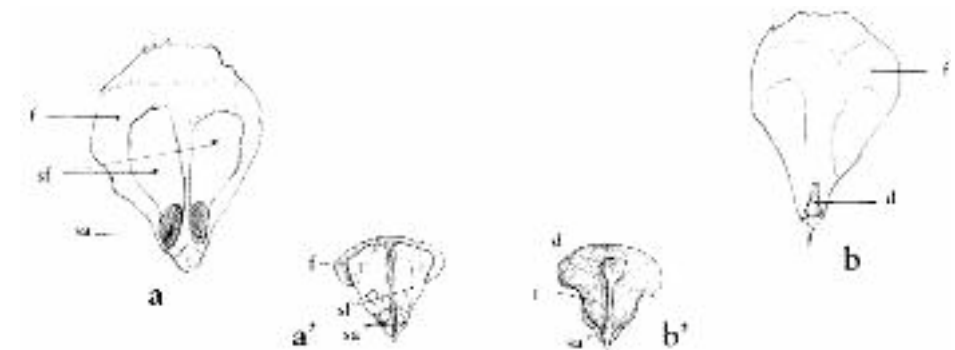


Figure 17. Seed scale of spruce (*Picea abies*); **a**: viewed from the side of the axis (adaxial side) with two winged seeds; **b**: viewed from outside (abaxial side); d: bract scale, visible as a remnant; f: seed scale; sa: seed with seed wing, sf; **a'**, **b'**: the corresponding situation in silver fir (*Abies alba*); the bract scale is well developed in this case.



Figure 14. Various transitional forms between a stunted bud (1 corresponds to Fig. 13b) and an almost completely developed seed scale (7 corresponds to Fig. 13c); stages 2 and 7 are viewed from the cone axis (adaxial side), all other stages from the abaxial side (in most cases the bract scale has been removed); in stage 1 and 2 the bud's outer scales (l, r) have not yet united, but have already clearly turned, in that the edges facing the bract scale (d) are moving away sideways from one another and the edges facing the axis (a in Fig. 15) are coming closer together, before finally growing together to form the seed scale (see also Fig. 15); in some intermediate forms the front (abaxial) bud scale (v) has also united with them; it is, however, completely reduced in the 'pure' seed scale (Stenzel was not entirely certain on this point) and definitely does not produce seeds; l: left outer bud scale, l': left inner bud scale, r: right outer bud scale, r': right inner bud scale, v: front bud scale turned towards the bract scale, h: rear bud scale, turned towards the cone spindle, d: bract scale (from Stenzel 1876).

however, the lower surface of the seed scale becomes the axis and therefore faces upwards. In the angiosperms, both pollen and seeds are enclosed from the upper side by the stamen or carpel respectively. The conifer situation is reminiscent of the ferns, where the reproductive organs (sporangia) are produced on the underside of the leaves and face the ground. This orientation, however, applies only to the pollen sacs of conifers. Although the seeds are carried on the underside of the seed scales, due to twisting of the lateral bud scales they face upwards (towards the cone axis). Conifers are clearly at a higher organisational level than ferns, in that they do not have a separate prothallus, but retain this in the parent plant in a similar way to the angiosperms.

Evolutionary considerations

Fossil remains from ancient conifers (Fukarek et al. 1992, Florin 1938), which textbook botany regards as convincing proof for the shoot character of the seed scale and therefore the shoot character of the cone, throw a new light on our topic. Schultze (in Fukarek et al. 1992; see Fig. 20) describes species from the extinct family of the Voltziaceae: 'This family shows a clear developmental tendency towards the present-day conifers. The parts

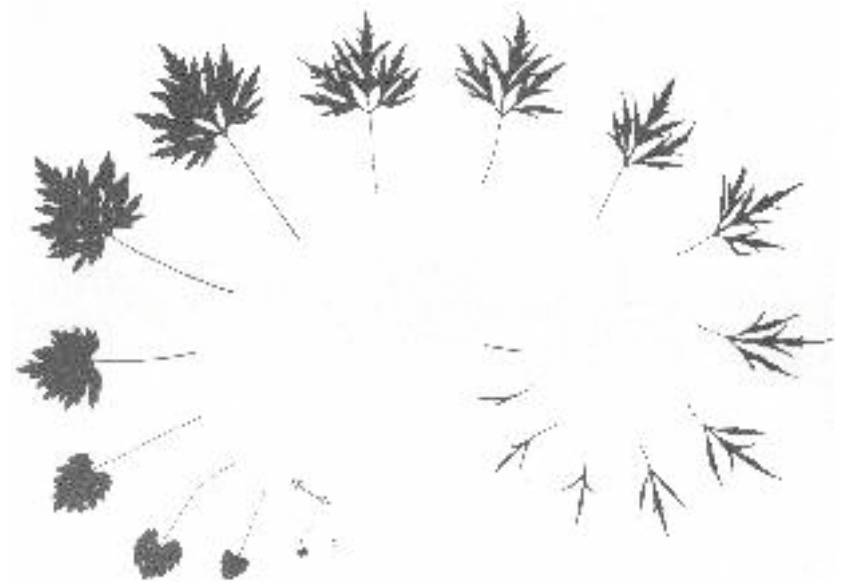


Figure 3. Leaf sequence from *Leonurus sibiricus* – siberian motherwort (*Lamiaceae*), Brazil, as an example of a relatively complete metamorphosis series.

environment during the course of the year and influence form development. These forces take effect principally from above through warmth and light and from below through soil moisture and soil quality. They overwrite and unify the characteristics of family and plant community in the direction of a common symphenological development series.

Suchantke (1983) developed the concept of 'biotope markings' (*Biotoptracht*) based on the example of butterflies' colour harmonisation with their habitat. He confined himself in the first instance to those spatial relationships which could be defined at the time of the study ('*Erscheinungszusammenhang*' after Bockemühl 1977). It is possible – in a descriptive sense and following on from Suchantke – to expand this concept to a temporal aspect of 'seasonal markings' ('*Verwandlungszusammenhang*' after Bockemühl 1977). An even more appropriate concept here would really be 'seasonal biotope markings' because this shows that both aspects – the temporal and the spatial – are closely and almost indissolubly connected in the great majority of cases.

This series of buttercup species and meadow plants coming into flower sequentially through the seasons thus repeat, in their leaf and shoot development, essential features of the development of a single plant (ontogeny, cf. Fig. 3). Echoes of the 'biogenetic law' of Haeckel (1834–1919) thus become apparent – however not in the first instance in the comparison of individual development (ontogeny) with that of the phylum (phylogeny), but in the comparison with the seasonal development of this plant family or the corresponding plant community.

In comparison with other families, the native members of the buttercup family are on the whole characterised by a relatively early average flowering time and consequently by

a predominance of rounded and divided leaf shapes (see also Nietzold 1993, p 158, Momsen 2004).

In comparison to the illustrated flowering sequence of meadow plants (Fig. 4) the buttercups largely lack narrow-pointed leaf shapes. This phenomenon underlines the point that every plant family and every habitat presents a specialisation of the ‘archetype’ of the generalised seasonal development process of herbaceous flowering plants in Central Europe. We can only grasp this through our imagination by comparing different species, families and habitats in order to once again review and enrich the distinctive special phenomena of individual plant species, families or communities.

Up to this point we have focussed on the similarities in developmental characteristics of the seasonal flowering sequence of the native buttercup species and meadow plants, and the metamorphosis of leaf and shoot in the dicotyledonous flowering plants. The sections on ‘flowering plants in relation to seasonal and evolutionary trends...’ and ‘phylogenetic development of the leaf...’ will discuss whether related developmental tendencies exist between the seasonal development and evolutionary tendencies in the phylogeny of flowering plants. First, the relationship of the developmental changes through the seasons (time aspect) to the expression of development changes in different biotopes (spatial aspect) will be investigated.

Are the leaf and shoot forms primarily an expression of habitat conditions or are they an expression of the seasons?

Just as correspondences can be shown between the plant’s form development and the seasons, so relationships are apparent between leaf form and habitat. The early flowering round-leaved species *Caltha palustris*, *Ranunculus ficaria* and in a certain sense also *Ranunculus auricomus* are particularly moisture-loving; the species with finely-divided leaves such as *R. bulbosus* and *R. arvensis* are more usually found in dry habitats. Differentiation according to time of year and habitat are therefore correlated in these examples. For other plants, differentiation of leaf shape according to time of year is really an expression of the fact that in early spring the soil conditions tend to be damp in many habitats, in summer dry soil conditions predominate, and that in the early part of the year plants of damp habitats frequently come into flower more quickly (cf. research report Momsen 2000 and 2001).

However, if we consider the correspondence between habitat and leaf form, aberrant examples are to be found especially in the buttercup family. Thus we find that the predominantly narrow-leaved *Ranunculus* species *R. flammula* (lesser spearwort), *R. lingua* (greater spearwort), *R. sceleratus* (celery-leaved buttercup) do not grow on dry soil – as might have been assumed from the leaf morphology – but preferentially on the wet banks of ditches, ponds and marshes. In contrast they share – in accordance with the leaf form – a late flowering time (end of May/beginning of June until September/November) in comparison with the other species of *Ranunculus*. The relatively narrow-leaved corn buttercup (*R. arvensis*) also only flowers from the end of May.

Conversely, species from the genus *Pulsatilla* which have finely-divided leaves, mostly flower very early in the year, but on dry nutrient-poor grassland.

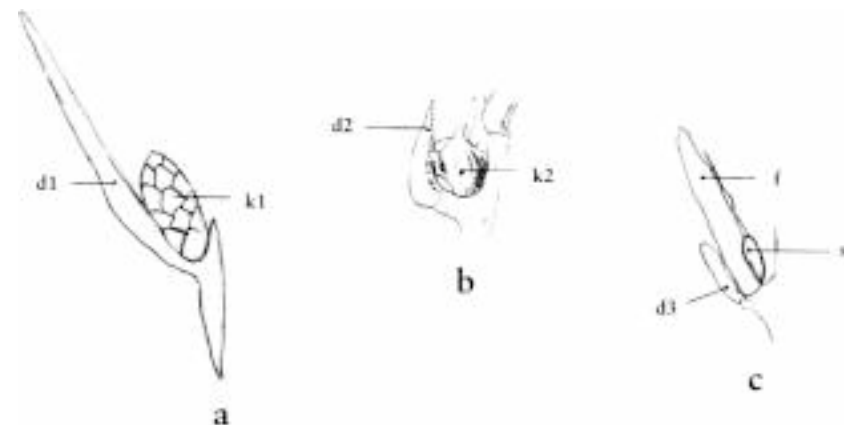


Figure 13. Spruce (*Picea abies*); transformation of **a**: needle with axial bud into **c**: bract scale and seed scale; **b**: intermediate form with stunted bud; d1: needle; d2, d3: bract scale; k1: bud; k2: stunted bud; f: seed scale with seed (sa) (**b** from Stenzel 1876).

tion zone from the cone to the branch (or vice versa), in this case between the bract scales with axillary seed scales and the needles with axillary buds. The seed scale must in fact constitute a transformed shoot bud and not an individual leaf organ as in the case of the pollen scale.

But which part of the bud primordium gives rise to the seed scale? Fig. 14 illustrates a selection from the numerous intermediate forms from a stunted bud and a seed scale which Stenzel discovered and published. This reveals a typical pattern, which we can bring into an inner ‘formative movement’. First the continuation of the axis in the bud is reduced. Soon only the four first outer bud scales are produced. The front (v, abaxial) and back (h, adaxial) ones gradually shrivel (although the front scale can first unite with the side ones in this process), the two side scales (l, r) turn and then unite with the edges facing them across the cone axis, finally giving rise to a unified organ: the seed scale (Fig. 14, right-hand form). Fig. 15 illustrates this process diagrammatically. This makes it clear that the upper (inner, adaxial) side of the seed scale which supports the seeds (Fig. 17) and is turned towards the cone spindle, represents the morphological outer (lower, abaxial) leaf surface, i.e. the outer surface of the axillary bud which gave rise to it. The beginnings of seed development are often to be found on the abaxial side of lateral scales of the stunted side buds where the scales have not yet grown together (Fig. 16). A single ovule per scale is the norm – a further indication that at least two scales are involved in the development of the seed scale in the ‘double seeded’ spruce (and its related conifer species). In species from the families Taxodiaceae and Cupressaceae which in most cases have more than two seeds per seed scale, the question arises as to whether an equal number of bud scales are involved in their development.

Our observations lead to a remarkable conclusion. In conifers, the reproductive material is produced on the morphological underside (abaxial side) of the supporting organs and not, as in the case in the angiosperms, on their upper surface. In conjunction with this,

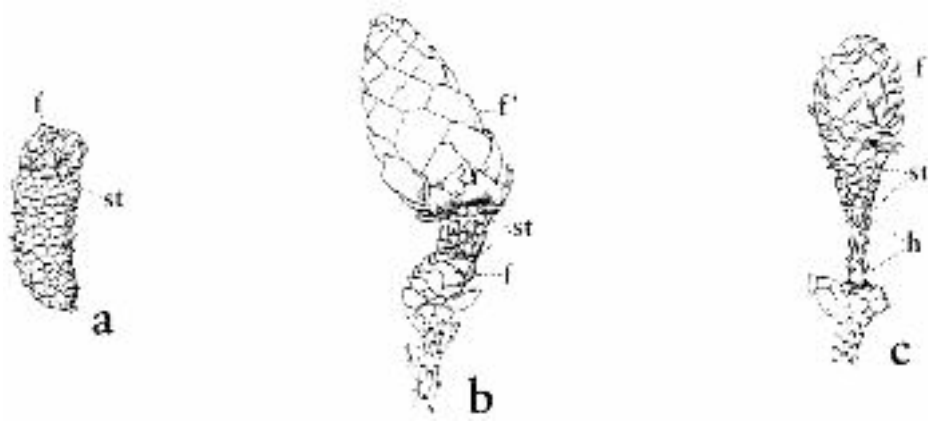


Figure 10. Androgynous cones of *Picea abies*; **a** and **c** are common forms, **b** is rather uncommon; st: microsporophyll, f, f': seed scales, h: membranous scale (from Stenzel 1876).

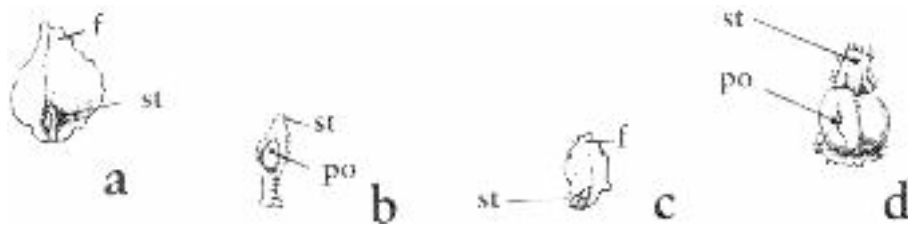


Figure 11. **a, c**: seed scale (f) of *Picea abies* with accompanying microsporangiatic bract scale (microsporophyll); **b, d**: microsporangiatic bract scales (st) enlarged from **a** and **c**; f: seed scale, st: microsporophyll, po: pollen sac, microsporangium; a-c: abaxial side (from Stenzel 1876).

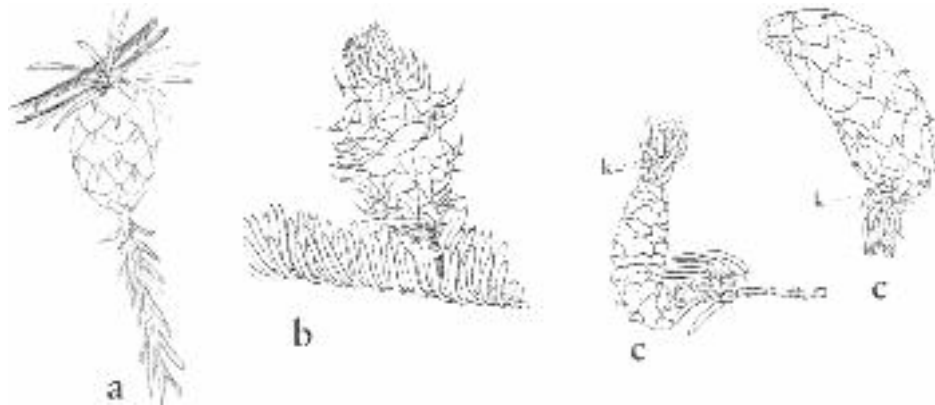


Figure 12. Proliferous cones of: **a**: larch, **b**: fir, **c**: spruce (**b** and **c** from Stenzel 1876).

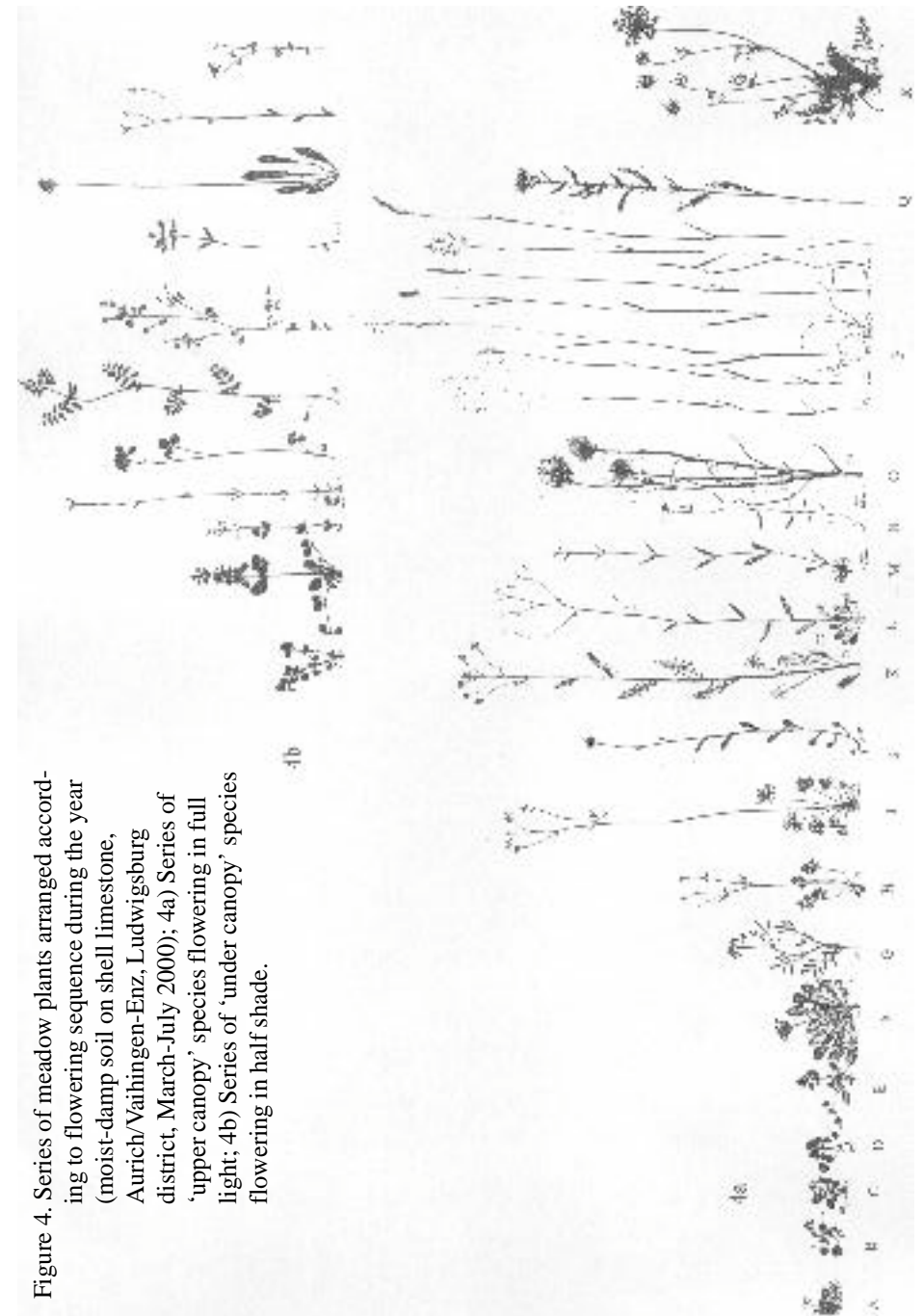


Figure 4. Series of meadow plants arranged according to flowering sequence during the year (moist-damp soil on shell limestone, Aurich/Vaihingen-Enz, Ludwigsburg district, March-July 2000); 4a) Series of 'upper canopy' species flowering in full light; 4b) Series of 'under canopy' species flowering in half shade.

These examples demonstrate that time of year, at least as an additional factor, is just as important as a particular habitat for the understanding of plant form development and that factors of time and space always belong together, even though they have been given little attention until now as regards their relevance for the development of plant form.

Recently, the plant communities of Central Europe have been studied by Vahle (2003) from the viewpoint of biological form. This work is concerned primarily with the form and dynamics of plant communities and therefore complements and extends the particular focus on the seasonal metamorphosis of families and genera presented here.

Seasonal metamorphosis in other genera and families

It is apparently obvious that in addition to ‘time’ and ‘space’ the ‘family relationship’ influences form development, but this has received little detailed investigation in relation to habitat and development season up until now. This aspect is brought out more clearly in a further study by the author where the seasonal development patterns in a number of plant families are compared (Momsen 2004).

Up to this point, this paper has discussed relatively common native species of the genus *Ranunculus* as well as native species of related genera, whose flowering characteristics are easy to understand and order. The wish to study the same criterion (flowering sequence in the course of the year) in other genera of the buttercup family such as species of *Adonis*, *Anemone* and *Pulsatilla* is a justifiable one. However, this does present certain difficulties:

1. It would be necessary to extend the purposely restricted field of observation, because the centres of distribution and abundance of these species and genera occur in many cases in the Alps or in regions of Eastern Europe and Asia Minor and so are largely beyond the study area described here.
2. In species of the *Anemone* group the mostly three-parted whorled upper leaves beneath the flowering head are actually sepals and therefore only partially comparable with the leaves of other genera.

Nevertheless, a comparative study of the seasonal or habitat factors within the respective genera is completely appropriate and – following a survey of the multitude of often non-native species of these genera – still waiting to be made. The species of the genus *Clematis*, whose representatives are the only woody species amongst the Ranunculaceae family, would also benefit from a closer study from this angle.

Flowering time and developmental tendencies in the flowering realm

In the preceding section the *development of the leaf and shoot forms* in relation to their flowering sequence during the year was investigated. We shall now look in a similar way at the sequence of flower form development, considering this from different angles.

Number relationships

The early flowering species discussed, viz. *Caltha palustris*, the *Ranunculus* species and *Trollius europaeus* are characterised by yellow radially symmetrical upturned or helio-

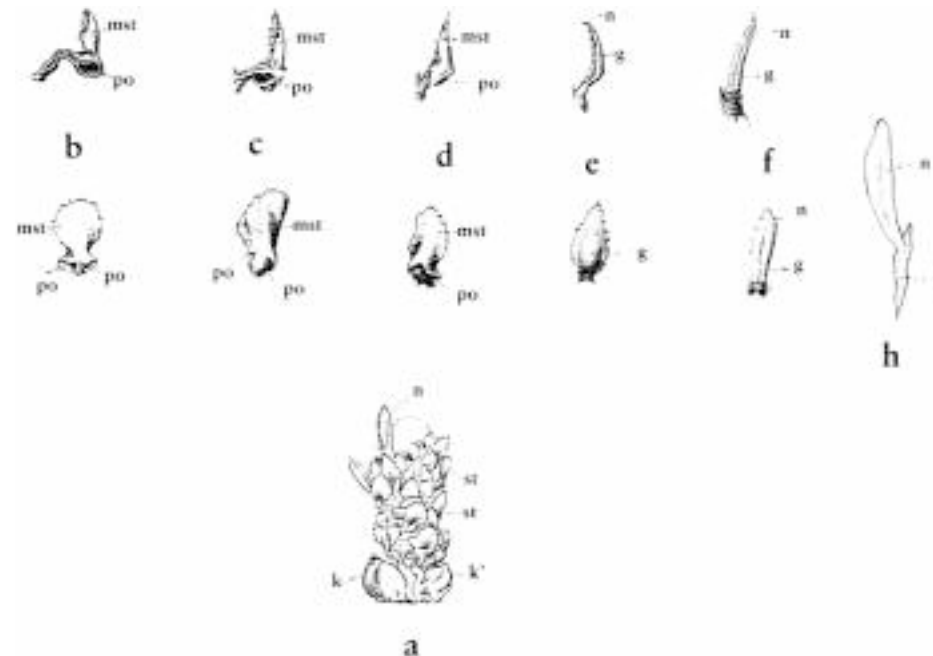


Figure 9. **a**: proliferous pollen-bearing cone of spruce (*Picea abies*) and some intermediate forms between **b**: microsporophyll and **h**: needle; stages **e**, **f** show forms similar to bud scales; the ‘gap’ between stages **f** and **g** is illustrated with additional intermediate forms in Fig. 3; **b-f** top row: side view; **b-f** bottom row abaxial side; **mst**: scale portion; **po**: pollen sac; **g**: needle base; **n**: needle blade; **st**: microsporophyll; **k**, **k'**: vegetative buds (from Stenzel 1876).

found in the transition zone from the pollen part of the flower to the fruit part of the flower. Fig. 11 illustrates two of these extremely rare forms. What is surprising – but following the previous observations this actually makes sense at once – is that the seed scales, which normally develop from the axil of a bract scale, in this case arise directly from the axil of a pollen scale. The latter is always stunted and small in such situations (in a similar way to the spruce, where the bract scale in the fruiting cone is also stunted). This makes it perfectly clear that pollen scales and seed scales have totally different origins and cannot under any circumstances be direct metamorphoses of one another.

Where does the seed scale fit into the picture? Is it a transformed side shoot or even a transformed bud, as its axillary position would suggest? The truth of the latter is evidenced by proliferous fruiting cones, i.e. cones which have produced additional growth. This phenomenon occurs quite often in larches (Fig. 12). There is only one description (Stenzel, Fig. 12 b) of this from a ripe fir cone in the process of shedding its cone scales. Proliferous spruce cones are less frequent than larch, but not uncommon. Stenzel used spruce cones for his observations on proliferous cones (see also Fig. 2).

The most diverse intermediate forms are to be found (Fig. 13) in particular in the transi-

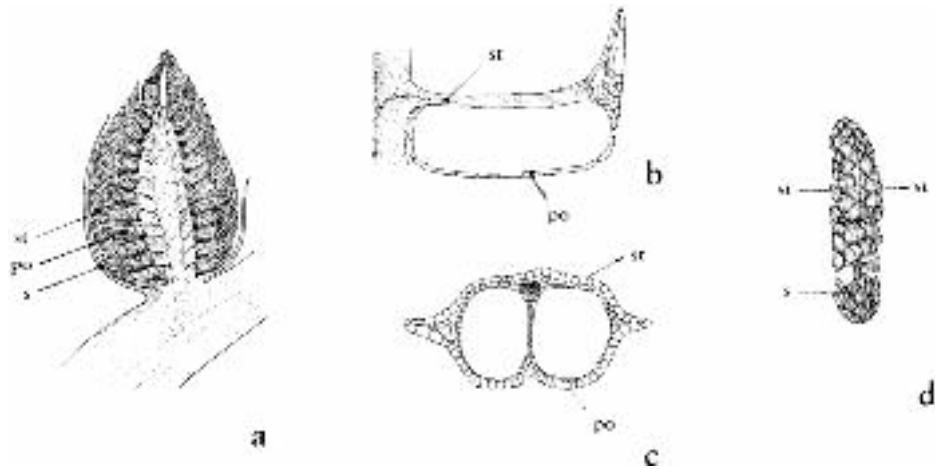


Figure 7. Pollen-bearing cones of **a, b, c:** *Pinus sylvestris* (**b:** longitudinal section through the microsporophyll; **c:** cross section of same) and **d:** *Abies alba* (with burst pollen sacs); the pollen sacs occur on the underside of the microsporophyll (st); the latter represents a transformed bract scale or bud scale; po: pollen sac, s: bud scale (from Strasburger 1991).

scale therefore actually represents a metamorphosis of the needle base and demonstrates its direct relationship with bract and bud scales through this. This is illustrated in the diagram in Fig. 1.

Fruit-bearing flowering cones

Observations on the very rare ‘androgynous’ cones (Fig. 10) lead to even more important insights into the characteristics of cones.

In androgynous flowering cones the pollen-bearing flowers and fruit-bearing flowers occur next to each other but distinctly separate in one and the same inflorescence. In most of these cases the pollen scales occur in the lower part of the cone, the seed scales usually terminally (Fig. 10 a, c). Very rarely, fruit-bearing (flowering) cones are interrupted by a band of pollen scales (Fig. 10 b). Remarkably, a sort of ‘hermaphrodite flower’ can be

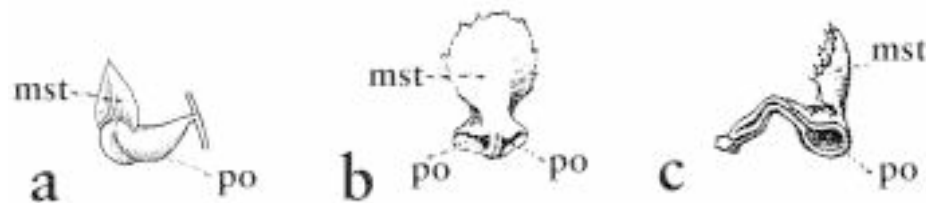


Figure 8. Single microsporophyll of *Picea abies*: **a, c:** side views (**c** with burst pollen sacs); **b:** viewed from behind (abaxial side); mst: scale portion; po: pollen sac (**a** from Strasburger (1991), **b, c** from Stenzel (1876)).

tropic flowers. In the *Ranunculus* species the perianth is divided into calyx and corolla (in which the petals are derived from the nectaries in this instance). It is instructive for our question to consider the number relationships in the flowering series. The earliest flowering species *R. ficaria* frequently has nine, but at times twelve or only eight petals, while the number of sepals fluctuates between three and five.

Goldilocks (*R. auricomus*) which flowers about two weeks later has five petals as a rule, but these are frequently absent, or only two to three or sometimes six to seven are developed. The number of sepals frequently fluctuates in a similar way. (Other early flowering members of the family such as *Hepatica* and *Anemone* also have a large number of petals with a large variation).

It is only later in the series of flowering species when we come to *R. bulbosus*, *R. acris*, *R. lanuginosus*, *R. arvensis* etc., that largely stable number relationships (5 + 5) occur in the flowering realm.

Symmetry, orientation and spatial composition

All native species of the genus *Ranunculus* have free, flat spreading and radially symmetrically ordered sepals. The later flowering species from the genera *Aquilegia*, *Consolida*, *Delphinium* and *Aconitum* (monkshood) exhibit in contrast corollas with markedly incurved petals and, apart from the first-named, also zygomorphic forms with the tendency to form a closed inner space.

In this respect *Trollius europaeus* (globe flower) produces an intermediate form, because the sepals, though choripetalous (free), nevertheless ‘anticipate’ the tendency to create an inner space by retaining a concave form. *Aquilegia* no longer has yellow flowers but pink, blue or chocolate-brown coloured ones, which are adnate (joined) and downward pointing (geotropic instead of heliotropic as in *Ranunculus*). Finally, the flowers of delphinium and monkshood replace the radially symmetrical form with zygomorphic (mirror image) ones. The flower transformation is carried furthest in *Aconitum*, in which the five petals are arranged in such a way as to form their own inner space.

All the late-flowering species from the genus *Thalictrum* (meadow rue cf. Fig. 1, 14) with their largely radially-symmetrical flowers appear to constitute an exception amongst the flowering series of native representatives from the Ranunculaceae family. In this case the seasonal changes in form point in a different direction: the four to five petals are largely reduced, the stamens distinctly elongated, increased in number and mostly brightly coloured. At the same time the flowering shoot is lifted out of the leaf realm and clustered together to a greater or lesser degree. A ‘complex flower’ (synflorescence) appears, which we otherwise know best in the late-flowering species of the *Asteraceae* and *Apiaceae* families.

Flowering plants in relation to seasonal and evolutionary trends (progression)

The developmental tendencies in the flowering realm presented for the seasonal flowering sequence in the buttercup family are tabulated in summary form (see Table 2).

Flowering characteristic symmetry	(Early) spring total = polypometry	Late spring/summer apomorphic = bilateral symmetry
direction of the flowering axis	axial to lateral (axial to lateral)	axial to lateral (axial to lateral)
flowering axis	single flower	flowering axis = complex flower (synflorescence)
number of flowers	single flower	multiple flowers

Table 2. Relationship between flowering parts in native buttercup species and trends in seasonal development and evolution ('progression').

The developmental trends described here also appear to some extent in the flowering sequence of other plant families during the course of the year (*Rosaceae*, *Asteraceae*, *Laminaceae*...), however usually less clearly (see Momsen 2004). In this respect the seasonal developmental trends in the flower realm prove to be identical to the major pathways in the evolution of flowering plants (progression), as comprehensively described by for example Ehrendorfer (1998) in *Strasburger Lehrbuch der Botanik für Hochschulen (Strasburg Textbook of Botany for Universities)* (34th ed., pp. 717–719 and 742) (cf. also Troll 1928).

It has already been pointed out by Nietzold (1993, pp 201-209) in his evaluation of forty years of seasonal observations on more than 700 species of flowering plants that, in the course of evolution in the higher plants, the mean flowering time has become increasingly later and at the same time the fruit-ripening period increasingly reduced. Within the dicotyledons this delay in mean flowering time (B) and reduction in the ripening period (reproduction period = R) is also evident from the apetalous (petals absent), via the polypetalous (free petals) to the gamopetalous (united petals) species. In contrast, the average flowering duration (Bd) and its variation in days (S) increases from the gymnosperms to the monocotyledonous and dicotyledonous angiosperms. Within the last group these values rise consistently from the apetalous via the polypetalous to the gamopetalous species (see also Nietzold 1993, p. 245f and Table 3).

	Mean Flowering time (B) (days from start of year)	Mean Duration of ripening (R) (in days)	Mean flowering duration (Bd) (in days)	Variation in flowering duration (S) (in days)
Gymnosperms		161	127	67
Dicotyledonous		117	39	11
- Monocotyledonous	117	77	27	11.9
- Dicotyledonous	131	38	1.2	26.9
- Apetalous	132	106	337	18.1
- Polypetalous	117	90	37.8	23.1
- Gamopetalous	175	0	17.9	17.9

Table 3. Displacement of the flowering time and the duration of flowering and fruiting during the course of the year from primitive (plesiomorphic) to advanced (apomorphic) systematic plant groups.

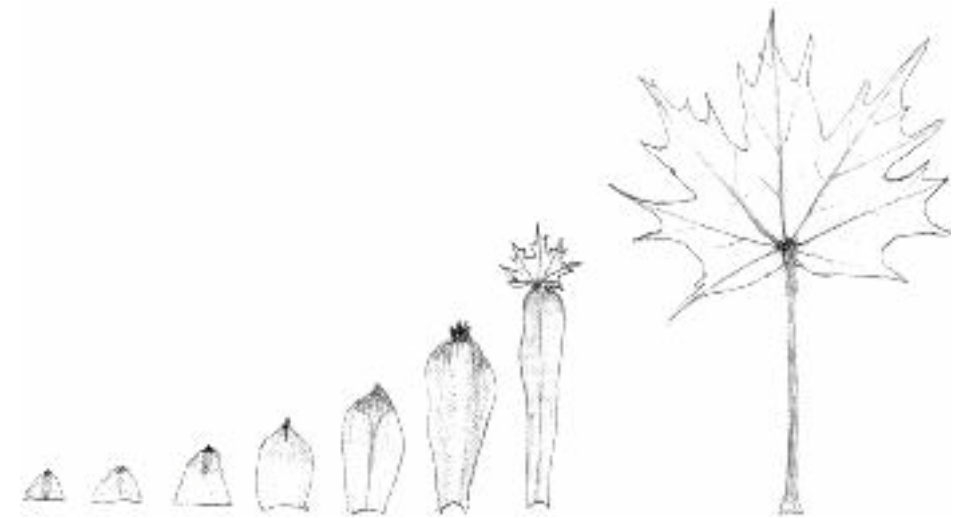


Figure 6. Bud scale sequence in an opening bud of Norway maple (*Acer platanoides*); all scales occur in pairs; abaxial side. Only the first foliage leaf is shown.

example Douglas fir, spruce, larch, Fig. 3), as a rule the needle-like mid portion of the bract scale is conspicuously accentuated. Bract scales are obviously closer to needles than are bud scales, which never possess these kind of points (Fig. 5).

Pollen-bearing flowering cones

Conifers are included in the flowering plants because they possess flowers which produce both pollen and ovules. However, only in rare cases do they manage to produce 'hermaphroditic' (androgynous) sexual organs, in the way that the vast majority of the true flowering plants (the dicotyledons) with their individual hermaphrodite flowers do. We shall now examine the structure of the pollen-bearing and fruit-bearing flowering cones more closely, starting with the pollen-bearing cones.

The pollen-bearing cones are laid down in summer and over-winter, finally coming into flower in spring after a short growth phase in which only the cone axis bearing the pollen scales elongates. The pollen sacs then dry out and release their pollen to the air. Fig. 7 shows pollen-bearing cones of pine (*Pinus*) and fir (*Abies*). The pollen sacs all sit on the underside of the leaf, i.e. the abaxial side considered morphologically, of the individual pollen scales. The pollen scales occur immediately after the bud scales, which suggests that the two organs are homologous.

Stenzel investigated the intermediate forms of pollen scales and needles in proliferous pollen-bearing cones (Fig. 9). The double pollen sacs of the pollen scale develop on the stem-like lower part of the scale, while their upper part remains leaf-like (Fig. 8).

It is obvious from the figures that the two pollen sacs arise from an inrolling of the needle base: they appear on the underside of the leaf in a similar way to ferns. The pollen

of the scale, while the leaf base is transformed into two lateral spreading points (a similarity to the bracts of dicotyledonous leaves is unmistakable).

The scales of vegetative buds also correspond to a transformed needle base (Fig. 5). This leads us to the important realisation that bud and bract scales are homologous. The inner bud scales of Norway maple (*Acer platanoides*, Fig. 6) often develop rudiments of upper leaves and show that the bud scales of deciduous trees are also always derived from the leaf base. Here as well the same form principles exist in the gymnosperms and the angiosperms.

The bud and bract scales separate from the axis to form independent organs, whereas the needle base unites with the axis by forming its bark. This clearly expresses the close relationship between bark and leaf (needle) (Steiner 1923²). The dominance of the axis in conifers is therefore also evident in the leaf realm, in that parts of the needle form a unified organ with the axis. This is a characteristic of fruits.

Intermediate forms between bud scales and bract scales occur by definition where fruit-bearing flowering cones are produced. Fruit-bearing flowering cones are laid down in autumn and overwinter as buds. Their sheath is made of normal bud scales. The entire cone primordium is contained in the bud. When bud break and flowering occur in spring, the bract scales continue to grow – depending on the species of conifer – in contrast to the partially lignified bud scales. The young bract scales are still alive and at the time of flowering have the shape of bud scales. They often wither, however, during the subsequent growth of the fruiting cone. In those species in which they grow vigorously (for

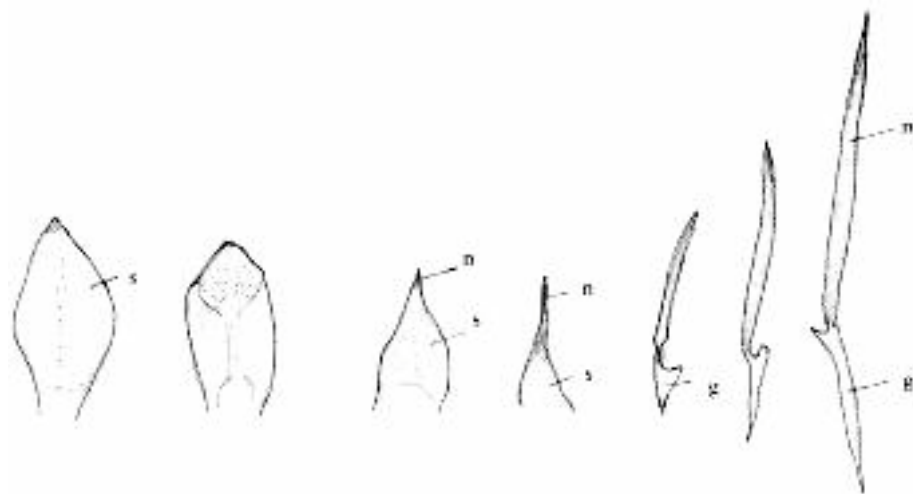


Figure 5. Spruce (*Picea abies*); abaxial side of transitional forms between bud scale (left) and needle (far right), as found in an opening bud (selected stages are illustrated); the needle blade (n) acquires increasing importance; the scale portion (s) is gradually transformed into the needle base (g), which fuses with the shoot axis.

² The 'bark, that still belongs to the leaves'.

Along with the delay in flowering date, the ripening point in dicotyledonous flowering plants is reduced in relation to flowering duration from c. 3:1 in apetalous species to c. 1.5:1 in gamopetalous species. It is thus possible to continue the flowering process increasingly in parallel to the ripening process and to extend it into the light and warmth qualities of late spring and summer. This again reflects the development of flowering plants from the plesiomorphic apetalous groups to the apomorphic gamopetalous groups in respect of their flowering sequence through the year.

This 'echo of the principal evolutionary pathways during the year' is valid for the above survey, but is only this clear-cut with respect to the flowering part of the plant.

Phylogenetic development of the leaf, organogenesis and seasonal development

In contrast, research into the evolution of the leaf realm of the angiosperms shows the rapid appearance of a wide diversity. Ehrendorfer's account of the leaf realm also remains open on this point: 'The leaves of the angiosperms, like those of the cycads were originally based on a pinnate design. However, due to the wealth of forms and their variability, it is not immediately apparent whether the original leaf shape was compound or simple...' (Ehrendorfer 1998, p.717). Nevertheless, in order to investigate this relationship to the course of the year, it is necessary to go somewhat further afield and to add additional observations not only from palaeontology but also from the seasonal development of dicotyledonous flowering plants.

If we follow the accounts in Schweitzer (1990), Thomas and Spicer (1987), Schad (2000), Willis (2002), and especially Suchantke (1998, 2002) of the development over longer periods of time of the leaf realm in the terrestrial plants as a whole then, despite the uncertainty mentioned in relation to the herbaceous flowering plants in a narrower sense, four distinct developmental steps are nevertheless apparent:

1. The earliest, partially amphibious land plants in the Devonian showed by and large no differentiation of the leaf and shoot, they were forked +/- upright shoots (telomes according to Zimmermann).
2. Only towards the end of the Palaeozoic, in the Permian and Carboniferous, did the ferns produce the first systematically divided leaves.
3. Undivided leaf surfaces with anastomosed net venation appeared last and were developed in particular in the dicotyledonous trees.

This phylogenetic sequence of leaf development is not mirrored directly in the ontogeny of herbaceous flowering plants as one might expect, but rather in the organogenesis of the individual leaves, as described originally by Troll (1939) and subsequently by Bockemühl (1977) in the four developmental stages of 'pointing' (*Sprießen*), 'differentiating' (*Gliedern*), 'spreading' (*Spreiten*) and 'stemming' (*Stielen*).

In addition, Suchantke (2002, p. 110-112) points out that this developmental trend which runs parallel to the organogenesis can be demonstrated for narrowly defined groups such as the ginkgo family for example (Fig. in Suchantke 2002, p. 112). In the sequence of bud scales in dicotyledonous woody species a corresponding sequence of forms is also to be found, from awl-shaped, via divided scale tips, to the formation of more or less united leaf blades and lastly more or less elongated leaf stems (Figure in Suchantke 1982, p. 136

and 2002, p. 112 and Göbel 1987, p. 78ff.). In situations where these buds have flower primordia, for example in bush roses, the largely united leaf blade in the leaf sequence is soon reduced again in favour of more strongly divided or contracted forms in the direction of sepals.

4. Only when we reach the youngest stage – from a phylogenetic viewpoint – in the leaf development of the dicotyledonous shrubs and herbs, does the metamorphosis sequence (presented here in relation to the course of the year as ‘regressive’ in terms of organogenesis and phylogenetic development) appear in a more or less complete development of rounded, often basal rosette leaves, via +/- divided leaves on the upright flowering shoot to the +/- contracted upper leaves in transition to the flower (see Fig. 3).

However, if plant communities at different places are examined in a systematic way (Momsen 2004), this ‘familiar metamorphosis sequence’ is only clearly evident in surprisingly few species. Only about ten percent of the dicotyledonous herbs of Central Europe show clear development stages between the leaves. As a rule this applies to annual or perennial herbs with terminal flowering heads and ascending flowering shoot, rather than to those with flowers in the leaf axils or in a rosette. Nevertheless, the metamorphosis trends are present in nearly all angiosperms in a hidden form, they are part of the basic morphodynamics of at least the dicotyledonous herbs, even though this fact has received little attention to date in respect of the ‘hidden’ examples.

Certainly metamorphosis can be suppressed if the plant cannot progress to flowering due to unfavourable natural or artificial conditions (for example shortage of light) (cf. the relevant experiments and descriptions in Bünsow 1982).

Therefore the development of the flower is both ‘cause and aim’ of the reversed metamorphosis direction discussed here. If flowering does not occur or if the flower and leaf realms penetrate each other too deeply, then there is also no distinct transformation of the leaves.

In the course of the year, finely-divided or contracted leaves occur particularly in late spring and summer, preferentially on dry sun-exposed sites. An increased influence of sunlight and warmth are thus requirements for the development of these ‘repressed forms’ in the sense used by Troll (1939). In contrast, the plants with +/- large round entire leaf blades have, from an organogenesis viewpoint, the most highly developed ‘oldest’ leaves. They occur primarily early in the season and in shady moist habitats.

Seasonal development of leaf and flower realms in the light of anagenesis and retention

From the point of view of organogenesis, the progression of leaves during the course of the year is characterised by increasingly juvenile qualities in the leaf form. The Armenian biologist and plant taxonomist Takhtajan (1973) described similar phenomena in the development of monocotyledonous flowering plants using the concepts ‘neotony’, ‘foetalisation’ or ‘retention’, i.e. the retention of juvenile characteristics in the adult stage. This idea was taken up in particular by Schad (2000) and Suchantke (1982, 1998, 2002) for example in order to explain the rapid development of dicotyledonous plants up to the

bract scales in the fruiting cone remain undeveloped in comparison with the seed scales which grow out of their axils, and are not visible on the outside). Fig. 3 illustrates a number of stages of such intermediate forms. Spruce needles have a pronounced leaf base which is united with the shoot axis. The bark of young spruce twigs is made up of the leaf bases of their needles. When the needle blade (the upper leaf) falls off, a ‘bump’ is left behind. In intermediate forms on the way to becoming bract scales, the needle blade portion is reduced while the leaf base, becoming partially independent from the axis, is transformed into a free-standing scale organ. The bract scale therefore develops from the structure and material of the needle base. This is reminiscent of the emergence of the petals of the dicotyledonous flower from the leaf base.

The situation just described can be very clearly seen in the bract scales of Douglas fir, larch and fir cones (Fig. 4). The needle portion is clearly recognisable as the ‘central axis’

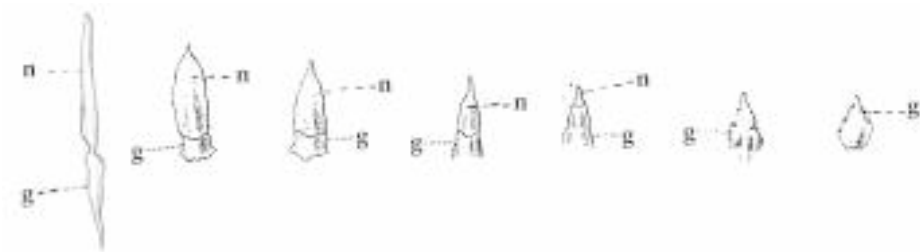


Figure 3. Abaxial side of transitional forms between needle (left) and bract scale (not visible on outside in spruce) in a proliferous fruiting cone: g: needle (leaf) base, still united with the axis in the first three stages, n: needle blade (patent) (from Stenzel (1876), modified and expanded).

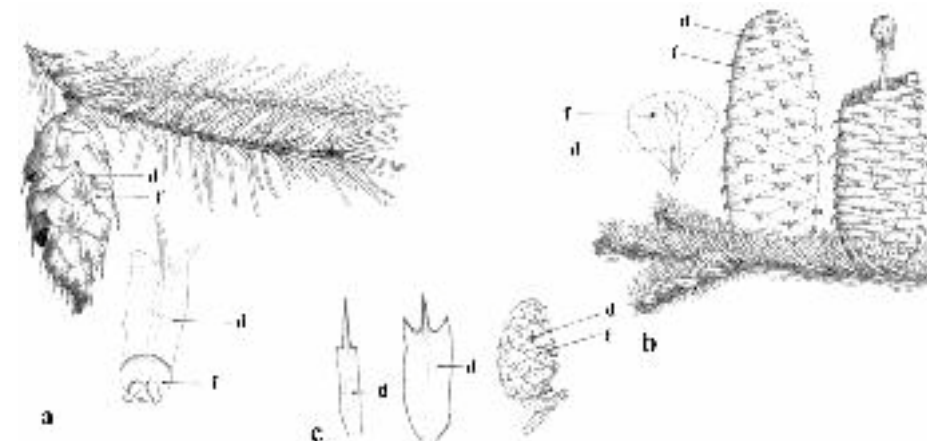


Figure 4. Fruiting cone and cone scales of a: Douglas fir (*Pseudotsuga mensiesii*); below: adaxial side of bract scale and seed scale at flowering time (the seed scale greatly increases in size); b: silver fir (*Abies alba*) and c: larch (*Larix decidua*) (details: abaxial side); d: bract scale; f: seed scale with two seeds (ovules) (from Bartels 1993).

4b). The phenomenon of proliferous cones (Figs. 2 and 12) is certainly not a rare occurrence and also points in the direction referred to, i.e. that cones are transformed shoots. Normal shoots have needles: in what light are the scale organs of the flower and fruiting cones actually to be seen? Stenzel's (1876) material can serve to give us a clear answer to this question.

Proliferous spruce cones

Bract scales and bud scales

Specimens of cones with regrowth from the tip show unmistakably that conifer cones have a shoot-like nature. Fig. 2 illustrates several variations of this in the spruce. The greater the tendency for regrowth, the more the cone portion is reduced at the expense of that of the shoot. The fruiting organ, which in most cases is stunted, is most often situated in the lower part of the axis, but can also develop medially or even terminally.

In the transition from the vegetative axis to the cone portion (or the other way around), intermediate forms¹ between normal needles and bract scales are to be found (in firs the

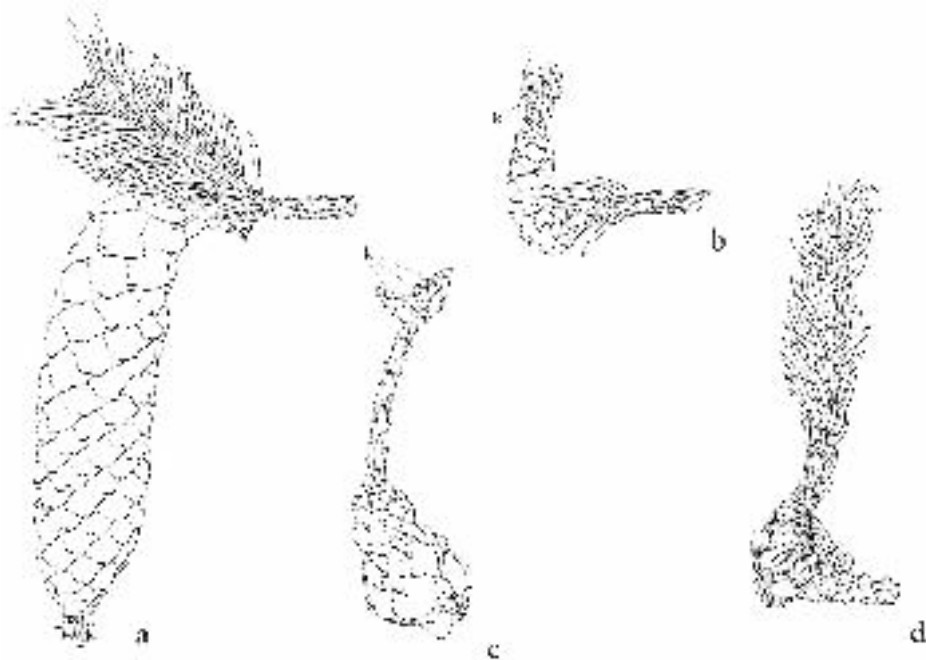


Figure 2. Different types of proliferous spruce cones; **a**: slightly proliferous, normally formed cone; **b**: slightly proliferous, dwarfed cone (k: incompletely developed vegetative bud); **c**: strongly proliferous, stunted cone (with cast needles); **d**: strongly proliferous, largely stunted cone; only the seed scales are visible (from Stenzel 1876).

¹ Stenzel refers to 'intermediate forms'; we shall use this term in what follows.

dominant appearance of the flowers in herbaceous plants.

In this context the parallel development of numerous leaf sequences during the year, from rounded and divided to increasingly simple reduced forms can be understood at least in large part through the concept of neotony. In contrast, the wealth of flowers with their increasingly diverse physical forms appears at first as an example of anagenesis: higher development through differentiation.

However, factors soon become apparent here which show that aspects of neotony are also present in the unfolding of the flower forms.

Thus globe flower (*Trollius europaeus*), at least as far as leaf form and flower colour are concerned, is very similar to the species described for the genus *Ranunculus*, although the late-flowering blossom remains closed like a bud. The tendency to form an 'inner space' discussed in relationship to the late-flowering members of the buttercup family and many additional species of other families can also be described – despite all anagenetic specialisation – as a tendency for retaining the bud form. Likewise, the tendency to form complex flowers (synflorescences) such as heads, umbels and similar, indeed even the flowering tendency itself can be understood as a repression/inhibition phenomenon in relation to the formation of internodes.

Once aware of these questions, the development of the leaf realm of dicotyledonous herbs – although marked by retention in its overall development pathway – can be described as differentiation in the sense of anagenesis because of the numerous specialised forms such as hairs, thickening of the cuticle etc. These often arise as convergent features overlying taxonomic relationships in a particular biotope and are therefore to be regarded as the response of different organisms to the conditions of specific habitats in the sense of the *biotope markings*. These conditions operate on the leaf realm primarily via the specific combination of soil, water, air, warmth and light.

These outer elements, especially the soil and water relationships, are only marginally involved in the anagenetic formation of the specialised flower forms. If we want to expand our understanding of this, we have to look at the relationship to the development of the pollinating agents, particularly those belonging to the animal world: flowers pollinated by wind, bumble bees, hover flies and humming birds – to name but a few – each show manifold convergent differentiation, despite all their differences (cf. Heß 1990, Suchantke 2002, Oltmann 1996), which can only be illuminated by first understanding the relationship with the pollinating agents.

These few examples serve to show how the tendencies for differentiation (anagenesis) on the one hand, and for restriction of development, for the preservation of juvenile forms (retention) on the other, are also connected to the development of the environment and, in numerous cases at least, interact with one another rather than being mutually exclusive. Through the way our thought-processes work we are constrained to focus on first the one and then the other aspect. Only then can the changing relationship of both tendencies be illuminated (see also the contributions to this theme of Schilperoord 2001, Schad 2000 and 2002 and Suchantke 2003 in recent numbers of this journal).

This contribution aims to promote the discussion of questions relating to seasonal development, ontogeny, anagenesis and retention, using the example of the Ranunculaceae.

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The flower cone represents an inflorescence. Its individual 'flowers' are spirally arranged on a central axis. A flowering unit in the fruit-bearing flowering cone consists of a bract scale with a seed scale in its axil (Fig. 1). This latter contains the seeds. It is very inconspicuous at the time of flowering and grows rapidly as the cone develops. In some conifer species, the bract scale is no longer visible in the fully developed cone, or is even shrivelled up, but it is always clearly recognisable at the time of flowering (e.g. Fig. 4a).

No seed scales (or homologous organs) are produced in the pollen-bearing cone; the microsporangia arise directly from the pollen scales (Fig. 7) which, as we shall see later, represent transformed bract scales or bud scales. This fact alone gives an inkling of the fundamental difference between pollen-bearing flowers and fruit-bearing flowers.

Conifers have 'naked seeds' (Gymnosperms). The seeds are not contained in a carpel as in deciduous trees, but lie on top of the seed scale. The seeds in unripe cones are protected from the air due to the cone scales being tightly pressed together and the remaining seams sealed with resin. Only when the cone dries do the scales open and the seeds are exposed 'naked' to the air.

One important characteristic of conifer cones is the progressive lignification of the individual fruits. Lignification is primarily an attribute of the axis: from this point of view, conifer fruits are under its control. The dominance of the axis in the multiple fruit is also underlined by the cone's central spindle. In firs and cedars for example, the spindle remains on the tree like a branch for some time after the cone scales have fallen off (Fig.

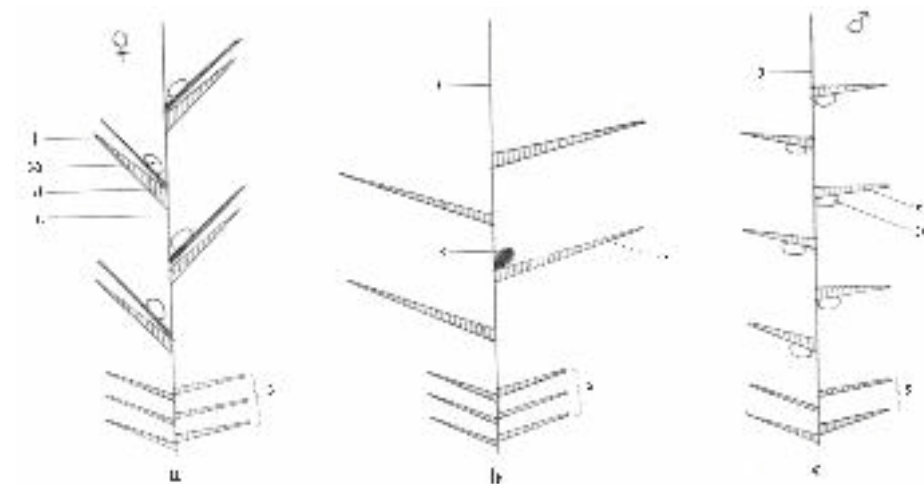


Figure 1. Diagrammatic representation of a long shoot (b) and pair of flowering cones; a: fruit-bearing flowering cone; c: pollen-bearing flowering cone; as shall be shown, the needles, bud scales, bract scales and microsporophylls represent homologous organs; the seed scale lies in the axil of a bract scale, in place of a side shoot (a side-shoot bud); there is nothing of this kind present in the pollen-bearing cone; s: bud scale, d: bract scale, st: microsporophyll, f: seed scale, n: needle, k: bud, sa: seed, po: pollen sac (microsporangium), a: (cone) axis.

The conifer cone

Jan Albert Rispens

Abstract

Conifers get their name from their characteristic cone-shaped flowers and fruit. A flower cone is not a single flower but an inflorescence. When flowering is over, if it is a pollen-bearing cone it dries up and falls off, or, if ovule-bearing, it develops further into a seed cone. The characteristic dominance of the trunk in the overall shape of the conifer tree is also reflected in the shape of the seed cones; these not only develop like little trees but also are strongly subject to lignification processes. Conifers are only classified as 'flowering plants' because, like flowering plants, their flowers produce pollen and fruit. Yet they possess not even the rudiments of a perianth and the seeds lie exposed on the fruit scales, i.e. are not surrounded by a carpel. The question arises as to whether this plant group, one that produces only trees, should be recognised as a completely separate group. Cone samples presented in detail by Stenzel (1876), who has largely been forgotten, can help to develop a new approach to this question.

As is well known, the flowers and fruits of conifers are produced in 'cones'. Is the flowering cone a single flower or is it an inflorescence which appears as a unified flowering organ (pseudanthium)? The answer turns out to lie in favour of the latter possibility (Strasburger 1991), although opinions are still divided regarding the details. This paper aims to draw attention once more to a long-forgotten essay by Karl Gustav Stenzel written in 1876, where the author describes and interprets a series of abnormalities (intermediate forms) in proliferous flower and fruiting cones of spruce, i.e. the shoot has grown through them. These enable deep insights into the inner nature of these organs and lead to far-reaching conclusions for the taxonomic status of the gymnosperms within the plant kingdom.

Conifer flower and fruiting cones

In their flowering behaviour (less so in fruiting) conifers are largely in harmony with the seasons. In Germany, the dawn redwood (*Metasequoia*) flowers as early as the beginning of March, the European conifer species in the first half of May. This flowering is a very inconspicuous event, as is the case for most deciduous trees, apart from the fact that large quantities of pollen are sometimes produced which is released from the trees in clouds and covers our 'civilised' world with a thin layer of yellow dust.

Without exception, conifers produce two different types of flowering cones: pollen-bearing flowering cones that contain the microsporophylls and which wither and fall off after flowering, and fruit-bearing flowering cones which develop into fruiting cones after pollination and fertilisation. While pollen-bearing cones are fully differentiated at the time of flowering, the fruit-bearing flowering cones are somewhat embryonic in form. Their real phase of differentiation only begins after pollination when they continue their development into fruiting cones. This corresponds to a developmental pattern also found in those dicotyledons which have separate flowers for the two sexes (Rispens 1991).

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Thuja orientalis, in contrast, represents the ‘more juvenile’ member within the genus, with its almost succulent fruiting cones and its more shrub-like appearance.

The junipers, which produce almost only shrubs, embody the sulphur aspect of the cypress type. Along with the yews (*Taxaceae*) which produce equally juicy fruits (but no cones), they are the solitary dioecious group amongst the conifers; a juniper bush produces either pollen-bearing cones or flower and fruiting cones. The inner tension of both organs is actually so large, that they are no longer able to grow together on the same bush, which makes a ‘separation of the sexes’ necessary.

The two most important needle-bearing host trees of the mistletoe (*Viscum album*; mistletoe is used in anthroposophical medicine as a remedy for cancer) belong to the Pinaceae. These are the European silver fir (*Abies alba*) and the Scots pine (*Pinus sylvestris*). According to the results of this research – within the pine family, where the conifer archetype is able to develop most fully – these two species constitute the greatest possible contrast and in this respect give rise to polar opposite sites for mistletoe. The differing therapeutic relevance of ‘*Viscum pini*’ and ‘*Viscum abietis*’ arises from the character of these sites (see Steiner 1924b). The tree structure as a ‘mineral plant’ provides the mistletoe with a refuge without which it could not exist on the earth, and at the same time acts formatively as a site with unique characteristics. Our observations on the conifer ‘type’ permits an exact ‘site description’ of these two mistletoe hosts. Our methods began with exact observation. The resulting sequence of pictures should possess ‘mathematical clarity’ (Steiner 1921b) and through living with these pictures, lead to objective imagination. Therapists can use the latter as a basis for expanding their knowledge, to the point of applying host-tree modified mistletoe preparations to individual patients.

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The conifer type – steps in the development of an imaginative understanding of trees

Jan Albert Rispens

Abstract

This article deals with the question of how the being ‘tree’ can be understood in such a way that evidence can emerge which, for instance, makes it possible to recognise the ecological niche of the European mistletoe (*Viscum album*), a plant that could not exist on earth without its particular living host tree. Although trees are plants, they differ from herbaceous plants in many ways. Not only can trees live to great ages compared with other organisms, but also they actively create mountain-like, concrete spaces. From this point of view, the similarity between trees and minerals becomes evident. Therefore, in contrast to herbaceous plants, trees lose their ability to produce impressive flowers. Conifers can be regarded as the most mineral-like group among trees. This article primarily covers the form of the conifer and its variability as well as attempting to achieve a natural systematology of the conifers using a phenomenological approach. Single conifer species, especially the two mistletoe hosts pine (*Pinus sylvestris*) and fir (*Abies alba*), are judged essentially according to their unique expression. This can help towards revealing their curative power.

Introduction

The published literature on Goetheanism has so far only mentioned the topic of coniferous trees in passing (e.g. Grohmann 1989, Pelikan 1997, Julius 1972, Kranich 1983, Leuthold 1998). The aim of this article is to investigate and describe the morphological differences and similarities of the conifers as a group.

The typical conifer form is characterised by a dominant straight central trunk with whorls of relatively weak side branches, without any proper ‘crown’ as we know it in deciduous trees. The evergreen character indicates a durability of the leaves, which compared with deciduous leaves scarcely deserve their name. Indeed, we refer to them as ‘needles’.

But what meaning does ‘tree’ actually have for us? First of all it is the huge, long-lived structure as a whole, which occupies a lot of space and confronts and impresses us. If we compare the tree with the ‘smallest’ amongst the flowering plants, the annual herbs, then we can also discover these on the tree. The leafy shoot put forth by the bud in spring corresponds to the herb, sprouting from the earth and blossoming every year. The herb is rooted in the earth, the new tree shoot in the wood of the tree. The ‘trunk’ or ‘branch’ (twig) has, however, also arisen from the axes of annual tree shoots through ‘secondary thickening’. This secondary thickening does not occur in herbs. It constitutes something basically different from the primary growth of herbs and tree shoots. Secondary thickening takes place from a sheath-like meristem layer (the cambium) of the previously elongated axis, primary growth from a plate-like vegetative point at the end of an axis in the process of elongation. The former results in a relatively uniform physical body (wood, bark), which is largely closed to the senses. The latter produces characteristically shaped leaves, flowers and fruits, which are open to the immediate environment. The herb-like shoots of the tree live on a substrate which itself has arisen from the vegetative world, but

which quickly hardens and which we could describe as ‘mineral-plant in nature’¹. The woody structure of the tree can actually be experienced and recognised as ‘heaped up earth’ (Steiner 1923, 1924a). Numerous herbaceous shoots sprout from this, forming a unity with this ‘earth framework’, a super organism, a kind of ‘elevated meadow’. The heaped up earth is at a more living stage than the purely mineral earth; it is to some extent freed from it as an individual living being in the form of a tree.

Independence from the seasons² is shown more fully by the trunk-dominated conifers. Despite the longevity of its woody structure, the deciduous tree with its herb-like growth by and large follows the changing seasons and in this resembles a meadow. The spring flush and flowering is followed by fruiting in summer, autumn colours and lastly leaf-fall. It is the deciduous trees that enable us to experience the seasons, which they themselves embody in a way.

The predominant impression in the conifers is the monotonous dark green of the needles which remain on the tree for years. Whoever looks for it, of course, notices new shoots and inconspicuous flowering in spring as well as ripening of the fruits in autumn. These living rhythms, initiated directly by the sun’s influence, are, however, largely submerged under the unchanging sclerotised foliage. This is a manifestation of the trunk’s earth activity. The leaf of the conifer becomes a needle and also withdraws physiologically from its environment somewhat, loses vitality and instead becomes tough and durable, timeless as it were. The weaker (Lyr 1992) life processes in the needles, particularly photosynthesis, continue throughout the whole year as long as the outer temperature does not fall too low.

The flowers and fruit, however, also receive a formative influence from the trunk, but in this case not a temporal independence. Conifers do not produce true flowers as we know them from herbaceous plants – our deciduous trees do indeed produce ‘true’ flowers, but mostly very inconspicuous ones. Organs composed of scales, which are designated as ‘flowers’ by taxonomy only because they produce either pollen or ovules, not for their decorative value, are united in trunk-like flowering heads as cones (Rispen 2006). These develop, in the case of the flower and fruiting cones (pollen-bearing cones are shed after flowering), into fruiting cones. Fruiting cones lignify relatively quickly and form small ‘mini trees’ (Grohmann 1989), which often remain on the tree for years and therefore themselves to some extent become part of the woody structure. The seeds lie on the cone scales and are not, as in deciduous trees, enclosed within a carpel. The dominance of the trunk thus acts in a simplifying and hardening way on these organs.

Conversely, conifers show a certain ‘fruit-proximity’ in their vegetative organs: egg deposition by the red and green spruce-gall aphid in the young needle primordia of shoots which have just started growing, transform these for example into structures similar to

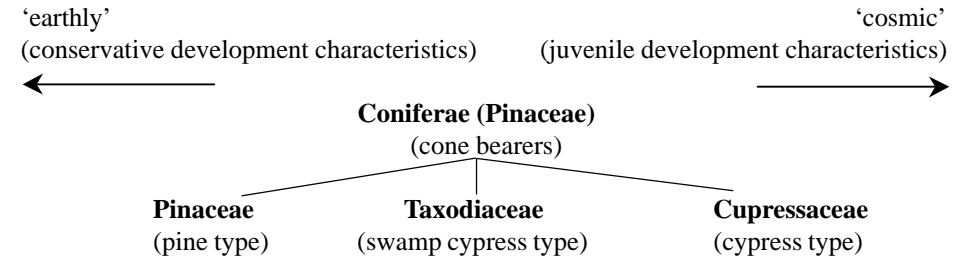
¹ Steiner (1907). In his lecture of, for example, 3rd June he speaks about the mineral-plant nature in the context of the moon incarnation of the earth; a pulpy plant-mass (‘like boiled lettuce’) with certain solid formations like the bark of trees (‘... like a kind of aged plant grown dry’).

² “In the trunk we see springing from the ground the working of the year, made permanent and lasting. This transition of what was first connected with the outer universe into a more inward way of working we see throughout the whole range of nature’s phenomena, in so far as they are cosmic.” (Steiner 1921a)

in a kind of inner competition. This leads to a delay in fruit maturation of one growth period in *Sciadopitys*, as also occurs in the pines.

Future prospects

Our study of the developmental themes of the conifer type leads to a classification which we could show diagrammatically as follows:



In this way each of the three families represents a subordinate type that, of course, is itself in the same ‘tension relationship’. The typical representative of the Pinaceae type is the fir, not the pine. The latter reveals more of a ‘cosmic’ form within the family (naturally attenuated in comparison with the Cupressaceae). It would be better, as was customary in the older literature (cf. Stenzel 1876), to speak of ‘fir family’ (‘Abietaceae’) rather than pine family.

The ‘earthly’ forms within the Cupressaceae are represented by the *Thuja* species. *Thuja plicata* produces a ‘classical’ conical crown and – secondarily – shows to advantage the leaf principle in accordance with the type, in that it forms its two-ranked leaf-shoot sections into distinctive planar organs. In addition, ‘leaf-like’ fruiting cones are produced.

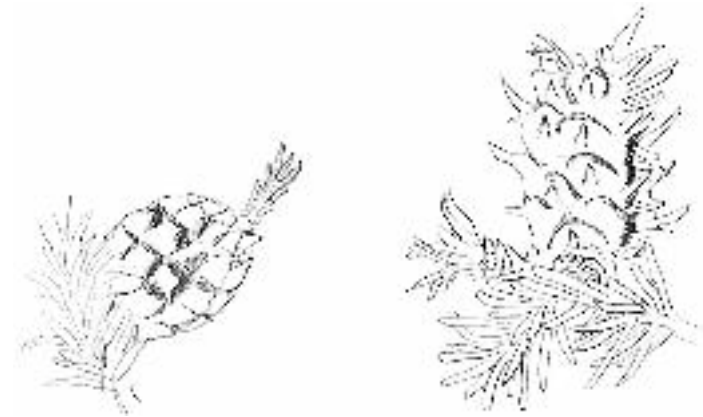


Figure 14. ‘Pineapple gall’ of the spruce gall mite (*Sacchiphantes viridis*) (left) and that of the blade spruce gall adelgid (*Adelges laricis*) (right) on *Picea abies*; in both structures it would appear that cones are involved, although the shoot character is clearly recognisable.

the world, with a trunk diameter of 12.5 metres.

To summarise, we can say that in Taxodiaceae as well the most important thing is the central vegetative shoot axis with its free growth constituting an organ of extreme vitality. Leaves (needles) and shoot can enter into a ‘symbiosis’ in two different ways: either the needle-covered side-shoot sections with restricted growth produce annual ‘leaves’ (*Taxodium*, *Metasequoia*) or the succulent scale-like needles press against the main axis in such a way that a higher-ranking succulent organ is produced (*Sequoiadendron*, also present in *Sequoia*). The more strongly this latter tendency prevails, the smaller are the (terminal) fruiting cones. The genus *Taiwania*, a native of East Asia, produces medium-length needles which are curved towards the axis on the ‘sterile’ long shoots without fruiting cones, whereas on ‘fertile’ long shoots with fruiting cones, the needles merely grow into succulent scales. Characteristically, hardly any difference can then be detected between these and the seed scales of the fruiting cones.

The species-poor genera of the Taxodiaceae form a link between the pine family and the cypress family, without declining into the extreme one-sidedness of these families. The dominance of the trunk in the fir and the one-sided tendency to produce shrubs (crowns) in the juniper exist as though in an inner balance. This can perhaps explain the (often enormous) characteristic forms that distinguish this family and which as a single species often form a genus of their own.

Finally, let us examine a little more closely another ‘exotic’ amongst the swamp cypresses. The Japanese umbrella pine (*Sciadopitys verticillata*) – in a way reminiscent of the true pines – produces long shoots with bracts which wither relatively quickly, from whose axils (only at the shoot tips) grow sylleptical single-needled short shoots that together form the typical umbrella (Fig. 13). On closer inspection it is seen that two needles grow together (so called ‘cladodes’). These short shoots are directly comparable with the two-needle short shoots of the pine. As in the pine, the flowering cones and cladode exist



Figure 13. Umbrella pine (*Sciadopitys verticillata*). Section of long shoot with typical ‘needle umbrella’; the ‘needles’ (K) are actually short shoots with two needles, which have united on their abaxial sides (so called ‘cladodes’); every short shoot grows from the axis of a scale (S); compare with *Pinus sylvestris* (from Bartels 1993).

fruiting cones (Fig. 14). This ‘fruiting organ’, however, exists entirely to serve the insect which is borne (and protected) by the plant and is only able to complete its embryogeny in this way. Naturally, no seeds are produced. This example serves to show – and this can be enlarged upon later by other examples – that the conifer type³ represents a ‘telescoped’ type so to speak. On account of the simplification and ‘generalisation’ of their organs, conifers belong to a simpler level of organisation than the deciduous trees and are defined as gymnosperms as distinct from the angiosperms. Further important differences between the two tree groups can be discussed in more detail when considering the individual conifer genera and species.

An overview of the native conifer species

The best known conifers found in European forests include the pines, firs, spruces and larches, of which only the first two are widely distributed. All belong to the pine family (Pinaceae) which, along with the families Araucariaceae, Taxodiaceae and Cupressaceae (the latter two of which will also be covered in this article), comprise the sub-class of ‘cone-bearers’ (Pinidae or Coniferae).

The Pine family (Pinaceae)

The pine family are usually divided into three sub-families whose most important genera are the following:

Family	Sub-family	Genus
Pinaceae (pine family)	Abietoideae (fir types)	<i>Abies</i> (firs) <i>Picea</i> (spruces) <i>Pseudotsuga</i> (Douglas fir) <i>Tsuga</i> (hemlock)
	Laricoideae (larch types)	<i>Larix</i> (larches) <i>Pseudolarix</i> (golden larch) <i>Cedrus</i> (cedars)
	Piniodeae (pine types)	<i>Pinus</i> (pines)

In order to delve deeper into our topic we shall start with a comparison between *Picea* and *Pinus*, and then incorporate other genera.

The spruce

The Norway spruce (*Picea abies*) is a tree of the cool wet temperate areas of Central Europe. It is basically a mountain species, although it is often planted with success at lower altitudes. The spruce produces the typical conifer form (Fig. 1): a straight central trunk with cone-shaped ‘crown’. It is markedly shallow-rooted and is largely confined to the humus layer of the forest soil. Let us examine its growth more closely.

³ Type (*Typus*) is meant here in the Goethean sense, i.e. it is not an average or generic form but the idea that is active in the particular forms, its entelechy.



Figure 1. Silhouettes of tree shapes: left: conical form of Norway spruce (*Picea abies*); right: beech (*Fagus sylvatica*) in winter and summer (from Edlin 1978).

In May the spruce opens buds with fully preformed shoots and finishes this growth after about six weeks (predetermined growth). The dominance of the terminal bud(s) is therefore established beforehand (this is known as ‘monopodium’). The numerous side-buds on the main shoot in the needle axes directly beneath the terminal bud develop into the characteristic ‘whorls of branches’. This makes it easy to identify the age of the tree from its outer form. Markedly weaker shoots grow from the basal buds on the previous year’s shoot. The spruce only produces long shoots. The needles, which are arranged in tight spirals, have large ‘needle pegs’, which form the bark of the young axis to begin with (Fig. 2 b, c) and after the onset of secondary thickening are gradually replaced by secondary bark in the years following. Steiner (1923) drew attention to the fact that bark constitutes something leaf-like in principle. Here, however, we are dealing with something leaf-like which is dominated by the trunk, which forms a unified organ with it and unmistakably acquires its superimposed imprint. Only the leaf base of the spruce needle is taken over by the axis, its upper leaf can develop freely, but without the ability to become a leaf organ which is genuinely open to the environment, such as we are familiar with in deciduous trees. The very dense arrangement of needles on the brush-like branch, however, means that the spruce nevertheless develops a considerable leaf surface and can enter into an active interaction with the atmosphere. The long life-span of five to ten years, which is extreme for an organ such as the leaf, can also be attributed to the transformation of the ‘tree-herb’ by the mineral-plant.

What kind of flowers does the spruce have? In every species of tree, the woody structure has to reach a certain size before it begins to flower. From then onwards, vegetative growth no longer exclusively serves the vegetative plant and the accumulation of material

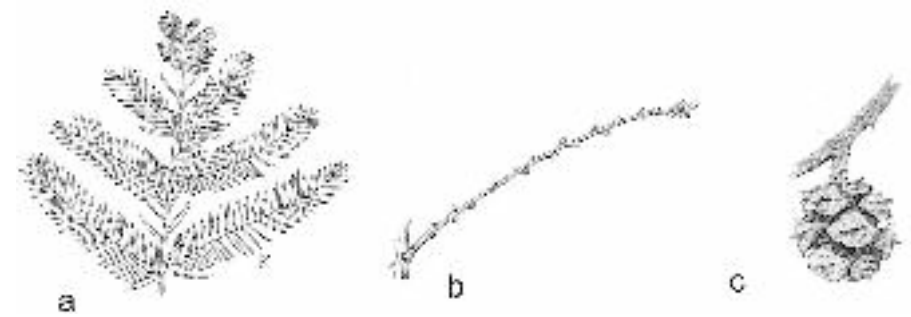


Figure 12. Swamp cypress (*Taxodium distichum*) a: needle-covered long shoot with sylleptically produced parted side shoots (K); b: reproductive side shoot with flower bud in winter dormancy; c: ripe fruiting cone (a from Bartels 1993, b and c from Edlin 1978).

shoot takes on the significance of a single leaf as it were (Fig. 12a), something that we have become familiar with in various ways in the pines and cypresses. In the following year a new shoot develops from a vegetative side bud of this kind of discarded shoot and this shoot is shed in turn in autumn. This can continue in a similar way for a number of years.

The large numbers of pollen-bearing cones are borne laterally, the flower and fruiting cones singly at the end of the side shoots described earlier, which of course are not shed in this case. The same kind of growth mode also occurs in the Asiatic dawn redwood (*Metasequoia*), which likewise has no needles in winter.⁵

The flowering cones of the different species in this family are small in comparison with the cones of spruce, fir and pine, but larger than those of the cypresses. The fruiting cone is a solid structure whose covering scales mostly wither. Characteristically, more than two seeds are produced per seed scale, indicating that several bracts of a seed scale derived from a side bud are involved (see Rispen 2006).

Sequoia, a monotypic genus from North America, also grows in a similar way to the genera already described, with the difference that it only sheds its single needles after two to three years and therefore gives rise to evergreen trees. *Sequoiadendron* (Wellingtonia) displays a phenomenon which forms a link to the cypresses. The needles are shortened in an almost scale-like way and press against the branch, but unlike pines do not dry out but retain their succulence. In this process, secondary shoots are shed in turn complete with scales after a few years, as long as they are not part of the crown structure.

Trees belonging to the swamp cypresses produce the most massive woody structures in the plant kingdom. *Sequoia sempervirens* achieves specimens of 110 metres in height and five metres stem diameter (c. 2000 m³ solid wood). *Sequoiadendrum giganteum* grows to ‘only’ 80 metres in height, but produces a trunk of up to 8 metres diameter (c. 4000 m³ solid wood!). *Taxodium mucronatum* from Mexico is one of the widest trees in

⁵ *Taxodium* and *Metasequoia* turn a brownish-red colour in autumn, quite different from the bright and light yellow of larch needles in late autumn.

demanding species which hardly makes any demands as regards soil conditions. This also makes it unique within its group.

All cypress species typically have scented wood, but no resins can be detected. It is etheric oils which are produced and stored in the wood, without the process of condensation to resins taking place. This is also a consequence of the increased succulence in which shoot, leaf and flower realms are intertwined in the most diverse ways. The wood of the *Cupressaceae* is relatively light and soft, but nevertheless very durable.

Thuja species are popular trees for use as hedges and in cemeteries and gardens. They can be cut back as often as liked and are winter hardy. The varieties 'Aurea' or 'Lutea' are popular and possess a decorative value on account of the permanent yellow colour of their foliage. These specimens with distinctly reduced vigour are obviously more closely associated with desiccating flower-like qualities.

What new aspects does the 'Cupressus type' contribute to the conifer picture which we have acquired? The 'archetype' discovered in the spruce and fir – with predetermined growth of the needle-covered long shoot and, strictly separate from this, the large fruiting cones which occur exclusively on the old wood – is largely 'contracted', and this to an even greater degree than we have seen in the pine. Development in the cypresses is characterised by non-predetermined, sap-producing and fructifying growth and leads to a fruit-like form of all above-ground organs. The progressive simplification of the outer form and the loss of endogenous rhythmicity in comparison to the Pinaceae go hand in hand with this.

The totally juvenilised and yet succulent Cupressus type represents a one-sided fruiting nature: it is the result of permeation by 'water and fire'. One consequence of this is the poisonous, inflammatory foliar sap of many Cupressaceae. The junipers with their shrub form and fleshy berry-like cones take this tendency the furthest. The scale-forming savin juniper (*Juniperus sabina*) is extremely poisonous in all its parts. Only a few drops of its sap will lead to symptoms of acute poisoning and can be fatal. The needle-forming, common juniper, the 'fir amongst the junipers', overcomes this kind of toxicity and manages to produce a tart but exquisite flavour in its fruits.

The swamp cypresses (Taxodiaceae)

This family includes species-poor (even monotypical) genera with representatives which appear primeval, such as *Taxodium* (swamp cypress, Fig. 12), *Metasequoia* (dawn redwood), *Sequoiadendron* (Wellingtonia) and *Sequoia* (coast redwood).

During the growth period, all members of the family display free shoot growth. In so far as winter buds are formed, these remain small; only a small amount of the following year's shoot is preformed, the remainder develops freely. *Taxodium* turns out to be an anomaly. On the long shoots with their spirally arranged needles, shortened side shoots with two-ranked needles are produced sylleptically: these cannot make vegetative buds, but can easily produce reproductive ones. These shoots do not become woody and in autumn, after the needles turn brown, they are shed in their entirety if they do not support any flower buds (while the needles on the main shoot are shed singly). In this situation the

by the trunk, but is also available for the production of flowers and fruit. The latter are 'parasitic' at the expense of the general vitality of the tree, but in a way which, if anything, is 'dissolving' and refining. In this respect, flowering and wood production, by forming opposites, exist in a state of inner competition with one another.⁴

Spruce trees begin flowering at about forty years of age. The spruce is monoecious like the majority of conifers: pollen-bearing flowers and fruit-producing flowers occur within separate cones, but on one and the same tree. Pollen-bearing cones fall off after flowering, the fruit-bearing flowering cones develop further into fruiting cones.

The cone is an inflorescence which emerges as a superordinate organ (*pseudanthium*) which however, unlike for example the composite flower of the Asteraceae, exhibits more of a shoot than a flower character. The lignification of the cone which sets in soon after fertilisation underlines the fact that the flowering and fruiting realms of the conifer are also strongly influenced by the densification and hardening processes of the trunk.

The pollen-bearing cones of the spruce are already laid down as buds in the medial needle axes of short shoots in summer of the previous year. The fruit-bearing flowering cones are initiated as terminal buds on long side shoots in autumn and therefore appear in place of the vegetative terminal buds. The spruce comes into flower in spring shortly before the tree flushes (Fig. 2). The pendulous red-coloured pollen-bearing cones pro-

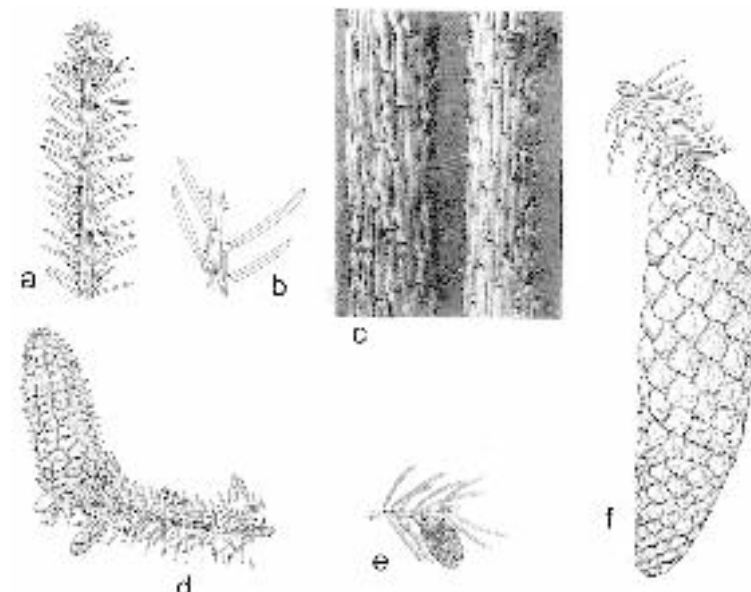


Figure 2. Spruce (*Picea abies*): **a**: long shoot with typical bud arrangement and **b**, **c**: details (left with needles, right without needles; note the 'needle pegs'); **d**: fruit and flowering cone at the end of a long shoot, at flowering time; **e**: pollen-bearing cone; **f**: fruiting cone (a from Bartels 1993; e from Edlin 1978; d and f from Strasburger 1991).

⁴ Modern apple cultivation, e.g. 'spindlebushes' with weak-growing bases, no longer produce trees but only bushes which give a high yield of fruit in only a few years, but are therefore unable to survive to a great age; the plants die off from 'exhaustion' after about ten years.

duce large amounts of pollen. The upright fruit-forming flowering cones are pollinated by the wind. Fertilisation occurs soon after pollination and not, as in pines, months later. The relatively large, now pendulous fruiting cone develops and ripens within the same year.

Each ‘fruitlet’ lies in the axil of a spirally-arranged bract scale and is composed of a seed scale which has two naked winged seeds. In studies of mature spruce cones it has been shown (Stenzel 1876) that the bract scale represents a metamorphosed needle, and therefore a single leaf organ, however the seed scale represents a metamorphosed (side) shoot. More precisely: the seed scale arises from the first two or three scales of a side-shoot bud which grow together (further details of this are in the following article (Rispen 2006) which is devoted entirely to the conifer cone). Stamens, as can be deduced from (rare) ‘abnormalities’ (‘hermaphrodite’ flowering cones), are metamorphosed single bract scales and thus show their relationship to the leaf (needle). What is surprising, is that both pollen sacs and ovules are developed on the morphological underside of their supporting organs. In this way the reproductive organs of the conifers clearly express something of a fern-like nature.

We shall take the spruce as a conifer with an archetypal character which will emerge more clearly in what follows. We shall go into its close relationship to the fir at a later point. First of all, a comparison with the Scots pine as representative of the pine type is in order.

The Scots pine

As with spruce, the seedling of Scots pine (*Pinus sylvestris*) has several (four to seven) cotyledons. Conifers form a plant group which can also be referred to as ‘polycotyledons’.

Figure 3.

Scots pine (*Pinus sylvestris*)
a: shoot section with three years’ growth, the last during shoot extension and flowering; note the three generations of solitary fruiting cones (pollen-bearing cones occur in clusters) (from Strasburger 1991); **b:** seedling with whorl of cotyledons and the first long shoot with primary needles (from Edlin 1978).

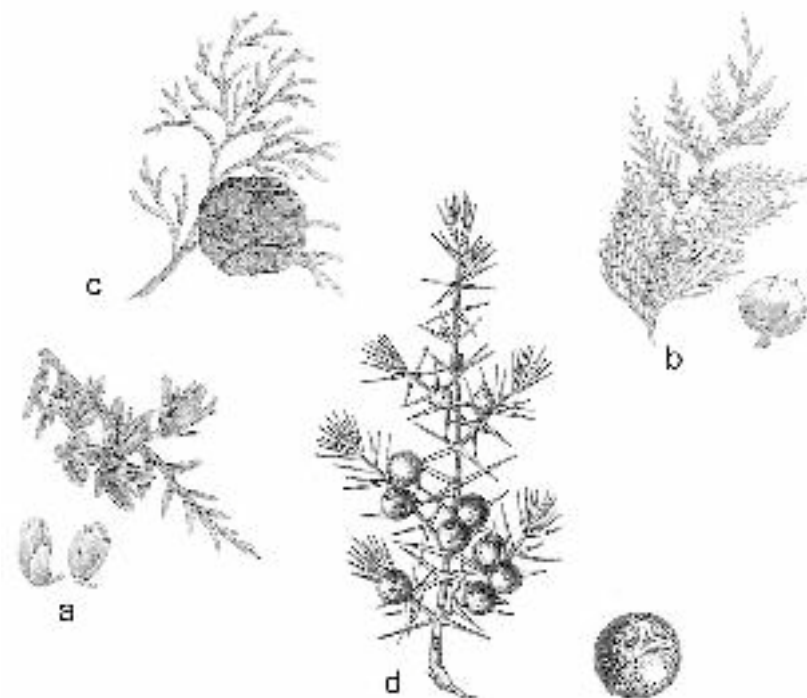
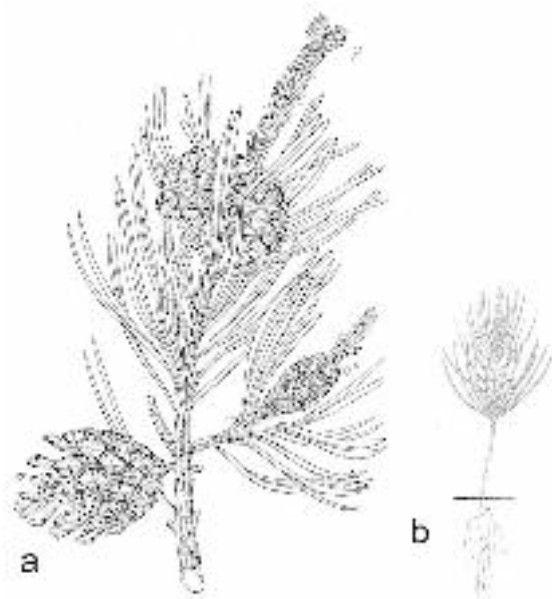


Figure 11. Ripe fruiting cones of **a:** *Thuja*; **b:** *Chamaecyparis*; **c:** *Cupressus* and **d:** *Juniperus*; note the increasing succulence of the fruits in this sequence (a from Hecker 1998, b, c from Hegi 1981, d from Strasburger 1991).

and are thus independent of the shoot. In this species, fertilisation of the flower and fruiting cones is also delayed by a whole year, as in the cypresses and pines. The fruit-bearing cone scales containing seeds are reduced in number to just three, right at the top of the cone. These later grow together and in so doing, increase their succulence to such a point that a kind of berry (false berry) is formed with a sweetish-tart taste and purple colour. Where all other conifer genera become woody, *Juniperus* transfers its succulence to fruit production and thus manages to produce ‘real’ fruit.

A sequence of fruiting cones of increasing succulence arises (Fig. 11). While the individual seed scales of *Thuja* cones are still leaf-like in form, the false cypresses and cypresses produce more solid succulent fruiting cones, which however turn woody in the end. The juniper berries are only to be recognised as conifer cones upon closer inspection; the resinous taste is also a reminder of their status as conifers. The maturation time of the cones increases with increasing succulence of the fruits, as though a prolonged contest was taking place between the hardening and dissolving tendencies.

Although many cypress species can produce large trees (*Chamaecyparis lawsonia* and *Thuja plicata* produce massive structures up to 60 metres in height), the free growth mode often leads to multiple stems. This is so pronounced in *Juniperus* that it only grows as a shrub. Juniper (as one of the few trees which is dioecious) is a true pioneer, a light-

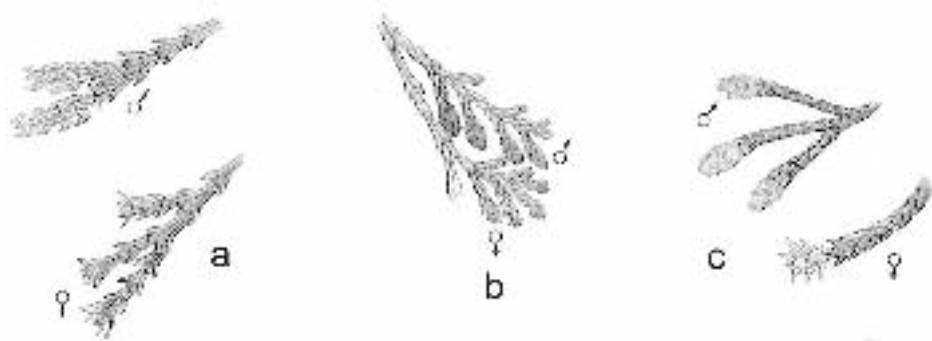


Figure 10. Pollen-bearing cones and fruit-bearing flowering cones of **a**: incense cedar (*Calocedrus decurrens*); **b**: Lawson's cypress (*Chamaecyparis lawsonia*); **c**: Italian cypress (*Cupressus sempervirens*); the fruit-bearing flowering cones in particular can scarcely be distinguished from the shoot in terms of shape as well as colour (from Edlin 1978).

the shoot due to its decussate (rather than spiral) leaf arrangement, but remains very closely associated with the swelling growth. From there it is only a small step to the flowering cone. While vegetative shoot growth and formation of the reproductive organs are strictly separate in the firs, these interpenetrate completely in the cypresses. This leads to the morphological (and also physiological) unification which has been described, in which the shoot and cones can scarcely be distinguished externally from one another. In many cypress species the pollen-bearing cones are much more brightly coloured than the inconspicuous flower and fruiting cones which remain a yellow-green colour. In these latter, no trace of bract scales can be detected. The seed scales almost always have more than two seed primordia, in contrast to the pines. Cypresses are able to produce flowers after only ten years, which is very early for (coniferous) trees. From this point of view these trees resemble the pines.

What comparisons can be made regarding fruit development? Pines are characterised by a notable delay in this particular respect. Fertilisation is delayed and the fruit development remains relatively long in the watery stage, but leads finally however to lignification. This process produces solid bulky fruiting cones. In *Chamaecyparis* and *Thuja*, however, fruit development takes place within one growth cycle. *Thuja* produces open cones with leaf-like seed scales, *Chamaecyparis* has a tendency to form more succulent structures, which harden later (Fig. 11). The true cypresses and junipers, however, actually show similarities to the pines. Pollination and fertilisation are far apart and maturation of the fruiting cones is delayed far into the following growth period. Like the pines, the cypresses produce very solid fruiting cones, which become lignified after a transitional succulent stage. Not so the juniper.

The common juniper (*Juniperus communis*) has needle-like scales arranged in whorls of three. Its succulence is clearly reduced (in contrast to other juniper species which only produce scales), although it exhibits free growth. The flowering cones are not produced terminally – as in the cypresses – but are displaced to a lateral position in the needle axils,

Again like spruce, in the first two to three years, the pine grows long shoots with single primary needles (Fig. 3 b) but unlike the spruce, this 'juvenile stage' is soon left behind. On the long shoots, in place of needles, membranous scales are formed from the axils of which grow sylleptic (in the same growing period) extremely compressed short shoots with two needles. The short shoot is terminated by a more or less developed terminal bud from which, in rare cases, a long shoot can grow (Fig. 4 b). Normally the short shoot does not develop any further. In a way, as a shoot it adopts a leaf (needle) character and, like a needle, is discarded in its entirety after two to three years. The long shoot with scales extends first in spring, the short shoots follow gradually. This produces the characteristic spring image of the pine with its pale green, 'half naked', perfectly straight, long shoots (Fig. 3 a). These shoots resemble spruce twigs in their brush-like appearance. The needle growth on the short shoots only finishes in early autumn and leads to the typical very long, relatively thin needles. A shoot-like transformation of the leaf (the needle) is expressed through this. In conifers and in pines to a very pronounced degree, both organ principles penetrate in multiple ways. The buds on the long shoots are limited to extension to a greater degree than in the spruce, which leads to the young pine exhibiting even more clearly spaced branch whorls.

What gesture is expressed in the growth of the pine? Let us first take a look at the informative flowering process. This differs markedly from that of the spruce. While the

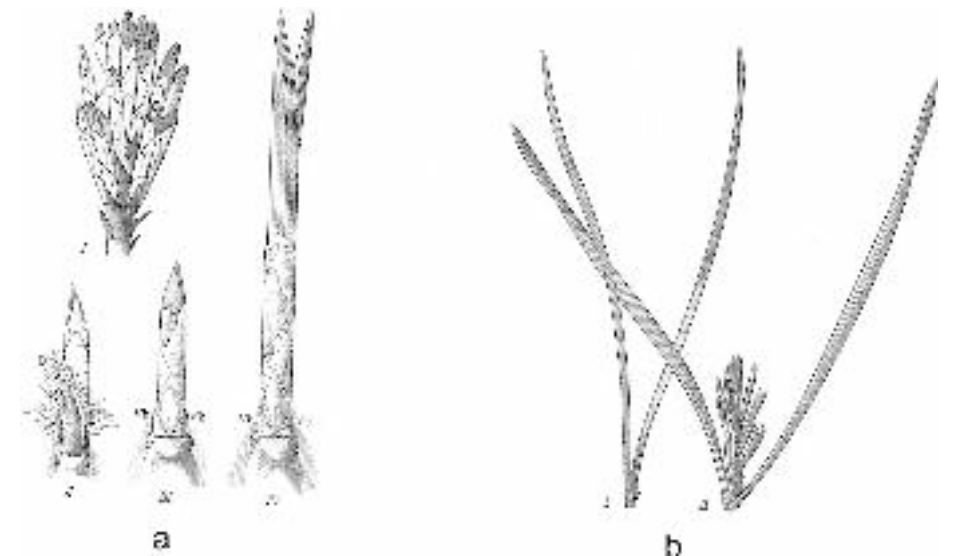


Figure 4. Scots pine (*Pinus sylvestris*) **a**: I: long shoot with young short shoots in the axes of the leaf scales; the scale leaves at the shoot base do not support any short shoots; II-IV: successive developmental stages of the short shoot; D: scale leaf (scale leaves have been cast in stages III and IV); vb: prophyllum (bracteole); the two needles arise from the basal sheath composed of membranous bracteoles; **b**: I: short shoot with stunted terminal bud; II: short shoot with long shoot extension (from Troll 1954).

latter flowers on two-year-old wood, the pine – atypically – flowers on this year’s sprouting shoot, i.e. a year early in a way. But what does ‘flowering’ actually mean for a plant? The organs of a ‘true’ flower arise without exception from the primordia of the leaf node (see for example Suchantke 2002). The informative leaf metamorphoses of *Paeonia officinalis* and *Helleborus foetidus* present classical examples of this (Bockemühl 1985). The sequence of leaves which precede the flower remain at an ontogenetically progressively earlier stage of their development; they become more ‘juvenile’ in form. Only after completion of this juvenilisation – in which not only the leaf organ itself, but also the shoot axis becomes almost totally retracted – can the ‘higher’ level of the flower be reached. This development is typical for the flowering herbs. But the bud organs of trees also exhibit this flower-like juvenilisation. The outer bud scales become cuticular and die off, the inner ones remain living and overwinter. At bud-break in spring these also open, sometimes become red in colour (Norway maple, horse chestnut) and thus remind us strongly of the petals of a flower. The membranous scales on the main shoot of the pine are continuations of such inner bud scales in a certain sense (so-called ‘cataphylls’; Fig. 5), which are laid down early in the overwintering buds instead of needles. At bud-break these grow marginally more, but then immediately wither and fall off.

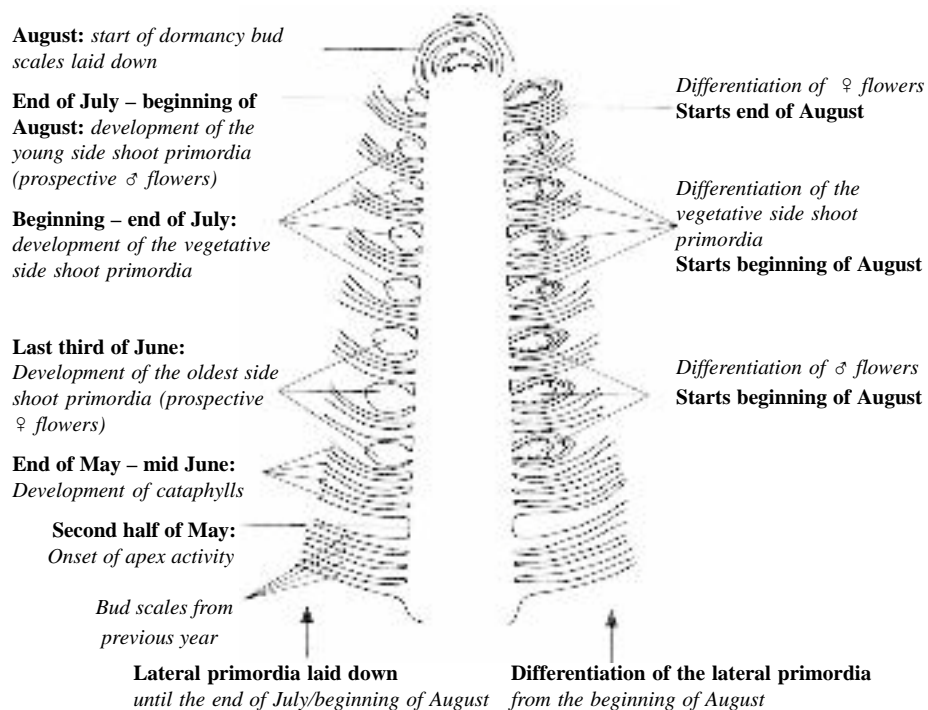


Figure 5. Bud development in *Pinus sylvestris* (diagrammatic longitudinal section through bud). The position on the shoot where the flowering cones are laid down determines their ‘sex’; further details in the text (after Eifler, in Lyr 1992).

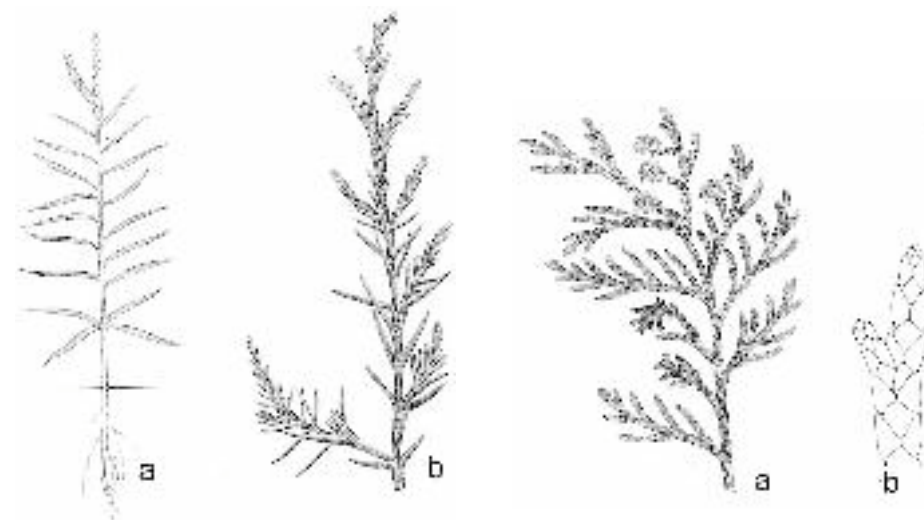


Figure 8. Italian cypress (*Cupressus sempervirens*) **a**: seedling with four cotyledons in a whorl and the first long shoot; the transition from the primary needles to the characteristic succulent scales is clearly visible; **b**: section of shoot with transition points from needle growth to scale growth (a from Edlin 1978, b from Hecker 1998).

Figure 9. Western red cedar (*Thuja plicata*) **a**: shoot section with decussate succulent scales encasing the stem; above: current year’s fruiting cones; below: last year’s open fruiting cones; **b**: detail (a from Edlin 1978, b from Bartels 1993).

in comparison with deciduous trees. The cypress family enhance this gesture. The free growth is also an expression of the general increase in vigour and further phenomena are associated with this.

The needles of *Thuja* species in particular have very mucilaginous sap, a distinctive feature for succulents. The carbohydrates produced are only concentrated into non water-soluble cell and wood substances with difficulty, they remain partly fluid and similar to pectin.

As a result of their two-ranked branching pattern, the false cypresses (*Chamaecyparis*) and *Thuja* species produce planar shoot segments (Fig. 9a and 11b) which are therefore reminiscent of whole leaves and are shed in segments complete with their scales after three to five years.

The flowering cones of members of the cypress family are laid down in autumn and are very small. They occur as ‘male’ or ‘female’ cones at the end of elongating side shoots and cause a temporary halt to shoot growth. The pollen-bearing cones occur on the weaker of the shoots. The flowering cones can only be distinguished with difficulty from the shoot sections (Fig. 10). They do not go through an endogenous resting phase within a bud, but overwinter in a ‘naked’ form. The flower-like quality is basically anticipated in

Additional conifer families

Are the formative themes discovered so far also to be found in the cypresses (Cupressaceae) and swamp cypresses (Taxodiaceae) in a more or less modified form? Do these families show new as yet undiscovered aspects of the conifer type? We shall begin with the cypresses which provide a sharp contrast to the pine family.

The cypresses (Cupressaceae)

The family can be sub-divided as follows:

Family	Sub-family	Genus
Cupressaceae (cypress family)	Cupressoideae (cypress types)	<i>Cupressus</i> (cypresses) <i>Chamaecyparis</i> (false cypresses)
	Thujoideae (white cedar types)	<i>Thuja</i> (white cedar) <i>Thujopsis</i> (hiba) <i>Calocedrus</i> (incense cedar)
	Juniperoideae (juniper types)	<i>Juniperus</i> (juniper) <i>Arceuthos</i>

The first eye-catching and essential feature of the cypresses is the totally free growth of the branching system. (Winter) buds are never produced and length growth continues throughout the whole year, in as far as outer conditions allow. We are familiar with this characteristic, in a limited form, from coppice growth, for example in beech. If the branching system is completely cut back, then what is now an outsized root system has such an enhancing effect on the vigour of the plant, that the normal – predetermined – growth changes to free growth.

A second unusual feature, the strikingly succulent leaves, is directly connected to this. Immediately after germination, cypresses produce a central shoot with spirally arranged needles; this is how every conifer starts its growth, as we know (Fig. 8). This mode of growth is often abandoned in the same year so that, instead of needles, only scale-like leaf organs appressed to the stem are produced. We are already familiar with these kind of juvenile leaves from the pine. In the case of cypresses, however, these organs are fluid-filled and completely enclose the shoot in a decussate leaf arrangement (Fig. 9b). A uniform organ is formed by the leaves and axis, a phenomenon which occurs in succulent plants in all kinds of variations. In the prickly pear cactus (*Opuntia*) for example, the swollen stem spreads and becomes like a leaf, with the real leaves remaining as fine thorns. Some thistles (Asteraceae) also exhibit succulent growth forms in which the axis and leaves are fused. In this case the leaf blade continues partway vertically down the stem, and the ends of the leaf veins emerge from the leaf-blade as pointed ‘thorns’. Succulence is frequently restricted primarily to the leaves, as in stone crops (*Sedum*) or house leeks (*Sempervivum*), where only very simple rounded leaves are formed. Unification and simplification are the basic formative themes in succulents.

Conifers *per se*, with their simple, leathery needles, demonstrate a succulent character

All the vegetative and reproductive organs for the following growth cycle are already laid down in the cataphyll axils of the overwintering buds. Depending on the position of the primordia, short shoots, pollen-bearing cones, flower and fruit-bearing cones or even potential long shoot buds can develop. The time of primordium initiation and the further course of differentiation are also characteristic for specific organs. Pollen-bearing cones develop the most quickly and fully, in the lower region of the axil. Flower and fruit-bearing cones and long shoot buds for the next but one growing period are formed last and go through the winter only partially formed so to speak; they are located at the upper end of the shoot. The short shoots are laid down spatially and temporally between the pollen-bearing and fruit-bearing cones. The further development of the reproductive organs proceeds rapidly when the shoots elongate in spring and leave the short shoots far behind. The pine comes into flower soon afterwards – a year too early compared with spruce (see Fig. 3). The short shoots follow only slowly. Shoot and flowering cones are closely related organs, as regards their location and time of initiation, but differ however in their developmental dynamics. Looked at in this way, the pollen-bearing cones can be understood as propulsive (‘accelerating’) short shoots, the fruit-bearing cones as propulsive long shoots. The latter, as we shall see later, remain at first in embryonic form as organs with ‘flowering potential’ and only become fully differentiated in the fruit formation stage. In contrast, the pollen-bearing cone, being a ‘spent’ organ, is shed after flowering. Short shoots with their two needles are closely related to the (pollen) inflorescence; this is shown by the extreme compression of the axis, correlated with a considerable loss of vitality. They are, however, in comparison with the actual inflorescence, developmentally retarded and remain vegetative. In the end, the dominance of the trunk also exerts its hardening influence on them.

Hence the pine, after leaving the ‘spruce-like juvenile stage’ would be on a level closer to that of a flower than the spruce. A telling point is that flowering begins after only ten to fifteen years in pines. Because the transition to flowering always implies a morphological juvenilisation in the plant kingdom, it is better to denote the ‘spruce state’ as that of maturity (old age). The spruce remains old throughout its lifetime, the pine becomes younger and hence more flower-like (we could also say more ‘sulphur-like’), although the ‘elderly’ dominance of the axis which is so characteristic for conifers in this group naturally remains unmistakable.

An interesting point in connection with this is the crown shape of older pines. In later life they abandon the general pyramidal form with a central trunk and acquire an individualised crown shape similar to deciduous trees, with sweeping irregularly-shaped side branches. The reddish colour of the bark on the upper trunk and branches, contrasting with the silver-green needles gives the crown of the pine the appearance of a warmth and light-filled space: quite different from the cool and damp aura of a spruce or fir.

Despite the pine’s acquired juvenility, its secondary growth leads to lignification. This is also apparent in the production of the extremely hard and compact fruiting cones. Something remarkable is apparent in this context. After pollination, the fruit-bearing flowering cones do not immediately develop into fruiting cones, as is usual in spruces. The female gametophytes need an additional year for differentiation and are only fertilised in

the second spring, a year after pollination. Thus the fruiting cone only develops in the course of the second year after flowering, on two-year wood which has meantime matured. The cone which is upright at flowering time (Fig. 3) turns to the side during the first year, but remains small and green. In the following spring this cone soon develops further (while on the new shoot a new flower and fruiting cone appears), and in the course of the summer finally ripens and lignifies.

Judged against its own flower development, the fruit development in pine is delayed, however, strictly speaking, it takes place at the same time as in the spruce. The pollinated flower and fruiting cone of the pine has the same 'status' as the flower and fruiting cone bud of the spruce in the previous autumn's flowering and closes itself to the environment after flowering (pollination) – like a bud – with a covering of resin. In their reproductive development, the pine and spruce differ fundamentally in the time of flowering, not that of fruiting.

In contrast to the spruce, the pine as a pioneer does not require fertile soil – something which underlines its relationship to the 'flower-like'. It grows well for example on extremely dry soil, a fact often exploited for forestry purposes. In addition the pine is 'light-demanding' which means that it is dependent throughout its development on sun-exposed sites. The whitish green of the needles also expresses this liberation from the earth and the inner movement towards the sun.

Other pine family species

In what ways can the pictures developed so far throw light on the fir, larch and cedar and which new aspects of the conifer type can they show us? Let us begin with the fir.

The silver fir (*Abies alba*) is demanding as far as soil conditions are concerned. It only grows well on damp, mature, forest soils and there it roots considerably deeper than does the pine. Being a pronounced shade-tolerant species, as a young tree it can remain for decades in the under-storey in the half-shade of the wood and then suddenly shoot up when, for example, a neighbouring tree falls over and the light conditions improve. Its ancient cone-shaped monopodial form is typical of the conifers and reminds us strongly of that of the spruce. The whorls of branches are however more noticeable because scarcely any side branches grow between the layers. Like the spruce, its branches bend slightly upwards. The higher order twigs, however, do not hang down, but stretch out horizontally, producing planar branches, as though the fir wanted to compensate for its lack of leaf area in this way. In addition, the arrangement of the needles on either side of the twigs (parting) (Fig. 6a), which is much less pronounced in the spruce, points in this direction. In its vegetative growth the fir emphasises surface area and is more open to the light but also to the air; its sensitivity to air pollution is an indication of this. Its more hidden connection with the warmth element is revealed in the smell of the pressed needles. Although spruce needles smell aromatic, the impression as a whole is dominated by tart constituents. The smell of fir needles is sweet, like the skin of mandarin oranges. The same smell is given off by the crushed seeds, but in an even more pure and intense form. Both organs are pervaded by etheric oils, a flower substance which is however, in the manner of a fruit, withheld and not given off.

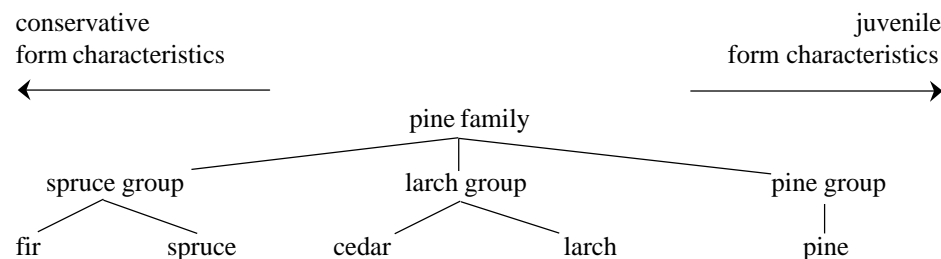
flowering as soon as the short shoots are mature enough for this.

The pines show an even more pronounced flowering tendency. Although predetermined long-shoot growth occurs at the beginning – as in the firs – instead of needles, delicate scales are formed. These leaf organs, just like the homologous bud scales, represent formatively a juvenilisation with an accompanying loss of vigour, as can also be seen in the petals of an angiosperm flower. We might also expect an increased tendency to flowering here, which is in fact the case: the pine flowers with its cones directly on the extending shoots and not with a time delay on the old wood. Thus the stage of the flowering cone buds (as in the spruce group) and that of the vegetative short shoots with reproductive terminal buds (as in the larch group) are missed out to a certain degree.

Pines put out their real vegetative organs, extremely compressed and reduced short shoots, at the same time as their reproductive organs from the axils of the long shoot scales. Flowering cones and side (short) shoots are therefore in inner competition with one another, which also helps to explain the contradictory characteristics of the form of the short shoots. Like a flower, the needle-covered short shoot appears lacking in vitality, as its terminal bud shrivels thus precluding any further elongation of the axis. On the other hand it appears as though the vigour of the axis shifts to the needle growth, exhausts itself in this process and leads to the unusually long, twig-like needles of the pine. These are nevertheless shed complete with the short shoots just like a leaf. The strong influence of the axis again asserts itself only belatedly in the fruiting cone: in its delayed development and ripening processes and in the progressive lignification.

The flower-like pine grows old, but in so doing takes the flowering tendency deep into its development processes. This then becomes visible in the deciduous-tree-like shape of the crown, in the brightly-coloured bark of the trunk, in the resin-filled wood, but also in the dry grey-green of the needles. It is the pine that best manages to recast the dark cool almost mineral-like conifer form, to bring warmth (and dryness) to it in some measure, admittedly without being able to overcome it completely. It would not be a conifer if it could.

The results of our observations can be summarised in the following diagram:



Conservative form characteristics are: long-lasting needle-covered long shoots, large cones, central trunk with conical crown.

Juvenile form characteristics are: frail/delicate leaf organs, formation of short shoots, smaller fruiting cones, crown development.

Preliminary summary

The long shoot with its spirally arranged needles has turned out to be the original form of the conifer type. In the time immediately after germination, all cone-bearing conifers bear only prolific needle-clad long shoots. It is the fir-like group such as spruce, fir, Douglas fir and hemlock which retain this condition throughout life and in this way express a certain conservatism. In the genera of this sub-family, the entire long shoot is laid down in the overwintering bud and opens completely within a few weeks. This is known as pre-formed, predetermined growth. Flower organs are displaced to last year's shoots and laid down as buds on this year's long shoots.

This situation, which also applies to some deciduous trees, indicates an independence of the shoot growth from the immediate influence of the sun and from the seasons. In the case of conifers, this independence from the environment is further increased by the reduction in area of the leaf to a needle. From a phylogenetic viewpoint, the deciduous leaf of the angiosperm trees corresponds, to one of the highest developmental levels in the plant kingdom (Suchantke 1998, 2002), a level which (apart from the bud scales) is retained and, unlike the flowering herbs, is not controlled by a 'juvenilisation' on the way to flowering. In this respect, deciduous trees with their leafy long shoots are also conservative. From a morphological viewpoint, the conifer needle occupies a comparable level to the typical deciduous leaf, but is subject to the greatest suppression in the development of its leaf surface, in which basically only the main vein is developed – a consequence of the typical dominance of the axis in conifers.

The larch group (cedar, larches) begin by extending their preformed short shoots (the supporting long shoots originate from the preceding growth period) which, depending on their status, can change over to free long-shoot growth a few weeks later. We are familiar with this compression of the growing axis into a short shoot, for example from trees of the rose family (Göbel 1988), which enables profuse flowering to take place. Does this permit a similar proliferation in the larch group? Not directly – the flowering buds appear as terminal buds on existing short shoots, not in the needle axils of this year's long shoots, and are thus delayed in a way. But could the larch's short shoots with their soft ephemeral needles not themselves be classified as flower-like? The true flower is primarily a consequence of the direct influence of the sun. The needles of the larch's short shoots undergo their growth cycle of opening, assimilation, change of colour and being shed entirely in accordance with the course of the sun. The flowering cones are perhaps the final crowning of this openness towards the sun shown by the short shoots.

The cedar also demonstrates openness to the environment with its evergreen shoots, but in a different way to the larch. It comes into flower in late summer – too early for a woody plant – at the time when conifers usually lay down their flower buds for the following year and the sun spreads its most intensive warmth. In this respect the cedar resembles a herbaceous perennial (many composite species, for example, only come into flower in late summer).

Both of the phenomena described here can be understood as increased flowering processes, as was already suggested. The larch has a flower-like quality in its foliage, the cedar with its long-lasting vegetative organs is more like the fir, but has an accelerated

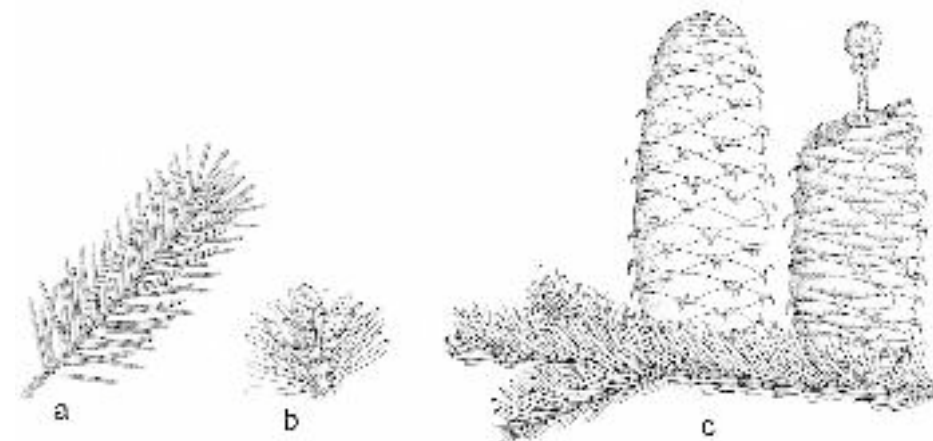


Figure 6. Silver fir (*Abies alba*) **a**: long shoot with 'parted' needles; **b**: terminal bud with side buds which later produce the 'branch whorl'; **c**: ripe (and disintegrating) fruiting cones on last year's long shoot; the needle-like bract scales between the seed scales are clearly visible (from Bartels 1993).

Might we also expect the fir to show an increase in flowering and fruiting in comparison with the spruce? This proves to be true. The flower and fruiting cones are not formed terminally on the branches, but medially like the pollen-bearing cones, as side shoots on last year's long shoots, in positions of reduced vitality. Flower and fruiting cones are confined primarily to the somewhat more vigorous tree-top region, pollen-bearing cones occur preferentially in the lower region of the crown. The flowering process itself is more prominent and colourful in the fir than in the spruce and to a certain extent continues into the process of fruit-formation. The fruiting cone retains its youthful flower-like upright position, reaches a magnificent size and ripens by the autumn. The needle-like cone bracts, as well as the seed scales, are particularly well developed and remain clearly visible, unlike spruce and pine cones (Fig. 6). The cone is not cast in its entirety as happens in the spruces, but disintegrates through the scales flaking off, while the axis remains in place. This indicates that the unifying principle of the trunk acts less powerfully on the fruit formation of the fir, and therefore the bract scales and seed scales are able to express their leaf-character more strongly, just as the fir brings out the surface area motive overall.

The larch (*Larix decidua*) shows us new facets of the conifer type and forms a transition from the fir group to the pines, as we shall discover. In the winter half of the year the larch has no needles. In spring it is one of the first trees to flush. From the preformed buds laid down in autumn in the needle axils or on the shoot tip grow first short shoots with light green soft needles arranged in a compressed crown-shaped spiral. These short shoots possess the potential to change into long shoots. This usually takes place only four to six weeks later and only at the branch tips (Fig. 7b), but can also happen, for example after loss of the terminal bud, on the side shoots which would otherwise only extend a small

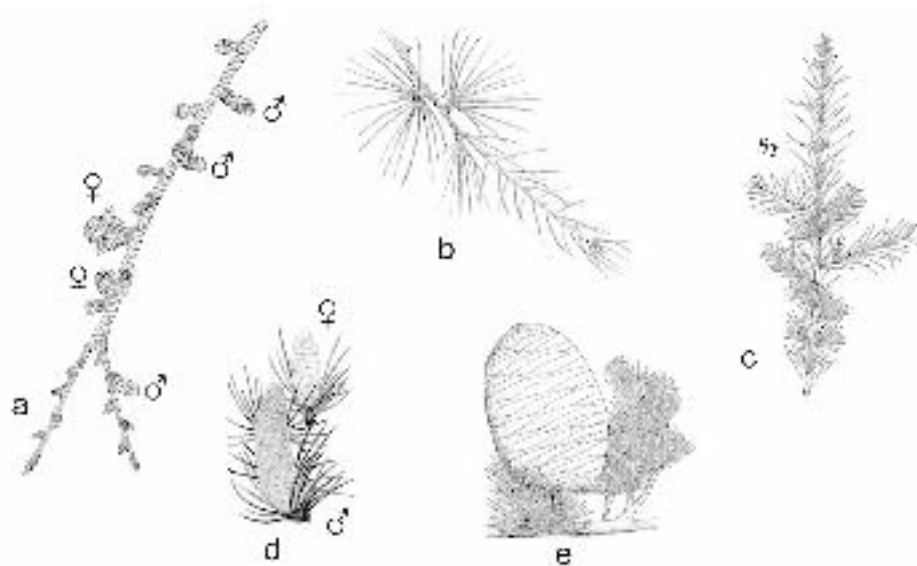


Figure 7 a and b: larch (*Larix decidua*) a: spring flushing of preformed short shoots (unlabelled) and male and female flowering cones (only the fruit-bearing flowering cones have needles round their base); b: twig in late summer; note the short shoots and the neoformed terminal (long) shoot; c-e: Atlas cedar (*Cedrus atlantica*); c: branch with long and short shoots; Sy: sylleptic short shoots on this year's long shoot; d: pollen-bearing cones and fruit-bearing flowering cones on older short shoots; e: ripe fruiting cone on an old short shoot (b, c and d from Edlin 1978, a and e from Bartels 1993).

amount year after year. This free (long shoot) growth continues into the summer. Under favourable conditions, new short shoots can even grow out of needle axils on this year's long shoots (neo-formed, sylleptic growth). However, usually winter buds develop in these places.

The larch displays something pine-like in its growth dynamics, but in a weakened and slowed-down form. A rest period is inserted between the growth of the long shoots and short shoots and this is bridged by bud organs. On the long shoots, instead of scales, leaf organs (this time needles) are formed which although succulent are also 'frail'. Neither do its short shoots become simplified and hardened by any means. Although the individual needles are shed every year, the short shoots can become very old and possibly even develop into long shoots.

The flowering cones of the larch – in a similar way to the closely-related cedar (Fig. 7) – are borne on existing short shoots, i.e. never on last year's long shoots. The pollen-bearing cones, which as usual wither and drop off immediately after flowering, can be produced on the short shoots arising from the long shoots from the year-before-last under favourable circumstances. But very often they also grow from older short shoots, whose

development then comes to an end. Pollen-bearing cones never have needles. It is a different case for the flower and fruiting cones. They support a ring of light green needles around their base, which makes a vibrant contrast to their bright red colour. Flower and fruit-bearing cone buds occur predominantly on short shoots from sections of three-year-old long shoots and come into flower in the following spring. They occur mixed with pollen-bearing cones. In addition to the red colour, the needle-like bract scales are also very eye-catching at flowering time – these are not visible once the cones are ripe. Unlike the pine, the fruiting cones develop in the same year as flowering takes place. The seeds are shed in autumn and winter. The empty dead cone remains on the tree – like a branch – for another five to ten years and is discarded complete with its branch. Until then it forms part of the crown structure. Fruiting cones which have continued to grow are often found on larches, another sign of the close relationship between cone and (long-) shoot.

The cedar is a close relative of the larch. We will take as a representative the Atlas cedar (*Cedrus atlantica*, Fig. 7 c-e), which is grown as an ornamental tree (mostly the blue-needled 'glauca') in parks and gardens. The cedar displays similar growth habits to the larch, with the difference that normally the sylleptic short shoots occur on this year's long shoot. However the needles stay on the tree for three to six years which leads to a dense permanent covering of needles. The cedar's short shoots can live a long time, but always retain the possibility of turning into long shoots without any outer stimulus. These organs thus appear to have more vigour or vitality than those of the larch in some ways, but at the same time are also more self-contained.

Remarkably, the cedar flowers at the beginning of autumn. Both pollen-bearing cones and also flower and fruiting cones occur terminally on existing short shoots: the pollen-bearing cones on last years' short shoots in the middle part of the crown, the flower and fruiting cones on older short shoots in the upper part of the crown. The primordia are laid down in the preceding months and the development is not interrupted by a period of winter dormancy. The flowering likewise shows a premature character, although differently than in pines. In fact, fertilisation only occurs in the summer of the next growth period, as in the pines. Growth and ripening of the cones require at least the remainder of the year. The rule applies here too: premature flowering correlates with delayed fruit development. In contrast to the pine, however, the delay does not lead to extreme lignification of the fruiting cone; the influence of the trunk does not assert itself that strongly. On the contrary: as in the firs, the ripe cedar cone comes apart in flakes and the woody cone axis remains on the tree.

It is not only the cone that is suffused with delicate etheric oil, but aromatic cedar oil can also be distilled from the wood.

Like the larch, the cedar is a light-demanding mountain species.

At this point it is necessary to summarise the main characteristics from the present confusing diversity within the pine family. This shall serve as a guide for understanding the two conifer families which are still to be discussed and for broadening our insight into the conifer type.