Chapter 3
The Onset, Course and Intensity of the Pollen Season

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Abstract The onset, duration and intensity of the period when pollen is present in the air varies from year to year. Amongst other things, there is an effect upon the quality of life of allergy sufferers. The production and emission of pollens are governed by interacting environmental factors. Any change in these factors may affect the phenology and intensity of the season. Readiness to flower in a plant, and the amount of pollen produced, is the result of conditions during an often long period foregoing flowering. When a plant is ready to flower, temporary ambient circumstances e.g., irradiation and humidity, determine the timing of the actual

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pollen release. In order to understand variation between years and to be able to safely predict future situations, not least due to the ongoing climate change, it is necessary to know the determinants of all related processes and differences between and within species, here reviewed.

Keywords Anemophily • Allergenic plants • Phenology • Readiness to flower • Vernalization • Onset of anthesis • Chilling • Dormancy • Forcing • Pollen release • Pollen emission • Circadian rhythms • Pollen season duration • Pollen index • Flowering intensity • Masting • Pollen season severity • Pollen production • Climate change

3.1 Introduction

Aerobiology studies the behaviour of biological particles in the atmospheric medium. Due to their abundance and allergenic properties, fungal spores and pollen grains, primarily from wind-pollinated (anemophilous plants), are the most important of these particles. Pollen grains from this group of plants are small, very light in mass, aerodynamic, with a relatively thin wall, low sculpturing and a powdery, non-sticky surface.

As "pollen season", we define the period during which pollen is present in the air. The term is used either collectively, referring to pollen from any plant taxon or from each taxon separately. Evidently, the pollen season in a certain area is related to the local flowering season, as for pollen to be present in the air, it has to be previously produced and emitted by mature flowers. However, pollen seasons and flowering seasons usually do not fully coincide; this is the result of intervening winds that allow for mid- and/or long-range transport. The abundance of pollen grains in the air is described by the term pollen season intensity: the more there are, the more intense the season is.

Pollen in the air, which is the result of pollen production and the different aerobiological processes, emission, dispersion and/or transport and deposition, is controlled by factors associated with climate. Any change in these factors may affect the phenological and quantitative features of the season. Monitoring airborne pollen provides substantial information on plants' performance under different environmental conditions and could allow predictions of their response under the ongoing climate change.

The onset, duration and intensity of the pollen season varies from year to year. In order to understand this variation and be able to safely predict future situations, it is necessary to know the determinants of all related processes. At an applied level, this is particularly important because the pollen season and its intensity affects the quality of life of allergic persons, who constitute a considerable part of the human population, particularly in the industrialized countries.

In this chapter, we will attempt to identify the strength and weaknesses in our knowledge and, hence, the requirements for future activity. To this end, we will deal with the factors known to affect pollen-related processes in anemophilous plants giving emphasis to taxa of allergenic importance in both the north and south of Europe.

3.2 Readiness to Flower

The major environmental factors that determine the readiness to flower are photoperiod, temperature and water stress. Water stress can also be important through its effect on growth rate. In some plants, e.g. in many temperate grass species, floral buds are produced only after a sequence of environmental cues that may occur several months apart. The term “readiness” denotes a state of maturity. When a plant is ready to flower, it is temporary ambient circumstances e.g., irradiation and humidity that determine the timing of the actual pollen release (Fig. 3.1). The latter circumstances are described in Sect. 3.3 of this chapter.

3.2.1 The Influence of Light as Day Length and Light Intensity

A photoperiod response is a biological response to changes in day length at latitudes where this cue is associated with seasonal progression. Plants discriminate day from night by means of photoreceptors, i.e., pigments that capture different wavelengths that may promote or inhibit flowering. These pigments synchronize biological activities with the day/night cycle, the so-called circadian clock. Plants that are governed by photoperiod may respond to day lengths surpassing a critical threshold in late spring or early summer, securing time for seed maturation, or in contrast, when nights become long so that as much of spring and summer as possible can be used for vegetative growth. For instance, in *Ambrosia artemisiifolia*, floral initiation is not possible before summer (Lewis et al. in Rogers et al. 2006).

Recent studies indicate that plants perceive day length through the degree of coincidence of light with the expression of the gene CONSTANS (CO). This gene encodes a clock-regulated protein that controls the expression of the floral integrator FT, which is ubiquitous in plants, in a light-dependent manner. Although long- and short-day plants contrast in their reactions to light, the differences are due to modifications of the same common basic pathway. Other floral integrator genes react to temperature and/or developmental cues such as hormone levels (Kim et al. 2009). Whereas a response to photoperiod is often overriding in short-lived plants, an interaction between photoperiod and temperature is common in perennials (King and Heide 2009).

Additionally, increasing light intensity during springtime and early summer is likely to influence flowering in summer-flowering plants. This increase can modify the effect of the photoperiod, but also act independently upon the FT-gene in long-day plants (King and Heide 2009).

3.2.2 Temperature

Each vital process in living organisms is adjusted to a certain temperature range. The optimal amplitude of this fluctuation range varies between plants adapted to

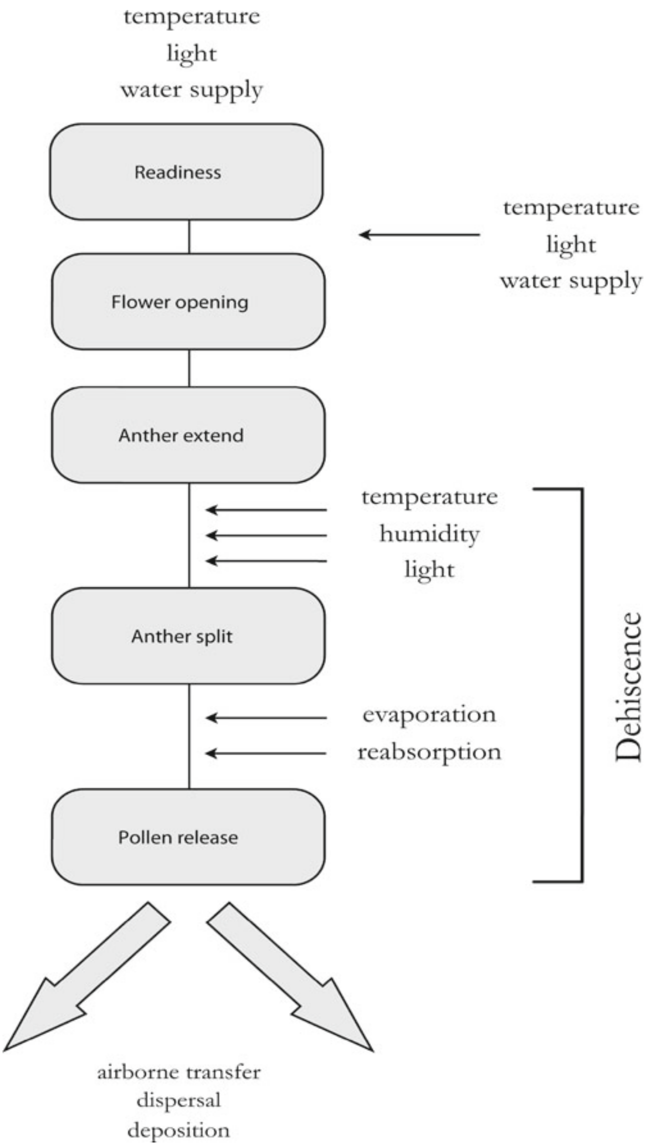

Fig. 3.1 Scheme of the processes involved in the readiness of flowering and anther dehiscence of anemophilous plant species. Modified after Linskens and Cresti (2000)

different climate regimes. For each species/ecotype and process, and for the development of different structures, there is a specific response curve. Below the base temperature, development is zero. Above this threshold, development rate increases linearly up to an optimum temperature at which the rate of development is at a maximum. Above this point, development rate decreases linearly until an upper limit, above which development is again zero. In most temperate woody species and some perennial herbs (Rathcke and Lacey 1985), flowering time is mainly controlled by temperature which usually acts through accumulation of heat above a threshold level.

In temperate regions, many species need a period of exposure to low, but non-freezing temperatures to acquire reproductive competence, as an adaptation to fit flowering and fruiting to periods when the risks for frost and/or detrimental drought are low. This process is called vernalization (from Latin word *vernus*, meaning “of the spring”) and confers the ability of the plant to respond to the correct day length and to initiate flowers. Thus, it is not equal to floral initiation, but must forego this. Many vernalization-requiring species have a winter-annual or biennial habit and many are long-day plants (Kim et al. 2009).

Unlike cold acclimation, which is a relatively rapid process and which follows a separate physiological pathway, the vernalization process must go on for a prolonged period. Otherwise, the plants could be “tricked” into flowering by transient warm conditions before winter is really over. The low temperatures are perceived by the apical meristem, which later will develop into a flower or an inflorescence. Once it has been exposed, the meristem “remembers” that it is vernalized. This memory is stable throughout mitosis, and all daughter cells – also after grafting on a different plant – will retain the reproductive competence as a “memory of winter”. In contrast, the effect is not transmissible to tissues that do not originate in the exposed meristem. Although vernalization may have evolved multiple times and thus not necessarily involve identical pathways, it generally appears to be a slow epigenetic process that triggers a series of chromatin modifications, ultimately resulting in silencing of genes that would repress flowering in an active state (King and Heide 2009; Kim et al. 2009).

3.2.3 Resource Accumulation

In plants, there is often a plastic response in flowering time to the availability of water, nutrients and carbon dioxide. Plants of some species are said to reach a level of reproductive maturity only after they have accumulated a threshold level of resources, often measured by plant size. In annuals, large individuals that are large since they have accumulated resources quickly, often flower earlier in the growing season to that of smaller individuals of the same species. The latter are assumed to be slower in resource acquisition (Rathcke and Lacey 1985). In perennial or woody plants, where time between bud formation and flowering is generally longer, one could predict that seasonal resource accumulation determines when floral buds are formed, but that flowering itself is triggered by a more predictable environmental cue. This situation has been documented in three shrubs belonging to the family Ericaceae (Reader in Rathcke and Lacey 1985).

The atmospheric carbon dioxide concentration stimulates leaf-level photosynthesis, which may or may not stimulate growth and, in this way, indirectly influence flowering time, which may be accelerated, delayed or unchanged with increasing CO_2 concentration. The response to elevated concentrations appears to be highly variable both among and within species, and even within populations (Nord and Lynch 2009).

3.2.4 Readiness to Flower in Grasses and Other Herbaceous Plants

In Europe, most indigenous grasses, and with a few exceptions (e.g., the cosmopolitan weed *Cynodon dactylon*), most of those that are important for allergies, belong to the sub-family Pooideae. They are herbaceous plants that may be annual, or more commonly, perennial. A grass plant generally consists of a parent shoot, which has developed from the epicotyl, and a number of lateral shoots or tillers that originate from axillary buds. Each leaf at the base of the parent shoot can subtend such a tiller. Each shoot or tiller is monocarpic, i.e. flowers only once and then dies away after fruiting.

The origin of the subfamily Pooideae is connected with a shift from tropic to temperate regions, and it is postulated that a vernalization requirement originated early within the group, after this shift (Colasanti and Coneva 2009). Many perennial grasses, however, need a dual induction of flowering (King and Heide 2009). In the late autumn, a tiller that is exposed to short day conditions and/or a vernalization period will be able to initiate inflorescence primordia, either directly or after transition to long-day conditions. But these primordia will not develop further, until a secondary induction caused by exposure to long day conditions takes place: hence, the latter is necessary for culm elongation, inflorescence development and anthesis. Each tiller of a perennial species then has a biennial life cycle.

Critical temperatures and day lengths, as well as the critical duration of exposure for primary induction vary greatly among the grass species and may also vary much among ecotypes of different geographic origin within the same species. For a number of temperate grasses of Scandinavian origin, 9°C appears to the most effective temperature to promote flowering during short-days conditions (King and Heide 2009). Generally, ecotypes from high latitudes and especially arctic and alpine ecotypes, have wider ranges of inducing temperatures and photoperiods, and they require fewer cycles of efficient day lengths than their low-latitude and maritime counterparts; for these ecotypes or species, 3–6 weeks can be sufficient, whereas for those at mid-latitudes 16–18 weeks of vernalization could be necessary. The latter is the case for species belonging to the genera *Deschampsia* and *Festuca*. In the Mediterranean grass *Phalaris tuberosa* L., plants from Morocco and Israel have little or no vernalization requirement, but flowering in these ecotypes is accelerated by low temperatures. Populations of the same species from more northern latitudes in Turkey and Greece require up to 8 weeks vernalization to induce complete flowering. Their respective requirements are related to the severity of winters at the collection sites (McWilliam 1968).

Significant variation in vernalization requirements in accordance with different selection regimes is also found in annual grasses like *Bromus tectorum* and *Aegilops tauschii,* which can be found in a variety of habitats that differ in altitude and/or aridity (Meyer et al. 2004; Colasanti and Coneva 2009).

After induction, the morphological changes of the apex by which the various parts of the inflorescence and flower primordia are laid down take place. This occurs during short-day conditions in the autumn in a number of arctic alpine ecotypes and in early-flowering low-latitude species like *Alopecurus pratensis* and *Anthoxanthum odoratum.* In many dual induction grasses, however, morphological changes at the apex take place only after a shift from short to long days. In *Phalaris arundinacea*, *Agrostis alba*, *Lolium perenne*, *Dactylis glomerata* and *Festuca* species, which all have large vernalization requirements, initiation takes place in the spring (King and Heide 2009).

Floral initiation in the non-grass weeds *Ambrosia artemisiifolia* and *Artemisia vulgaris,* belonging to the family Asteraceae, depends on different day-light regimes. In *Ambrosia,* initiation takes place in short-day conditions (Rogers et al. 2006). In *Artemisia vulgaris*, the required photoperiod for flower induction is 4–16 h for 4 weeks (Barney and DiTommaso 2002); hence, it is not a pronounced short-day plant.

After induction and the earliest morphological changes, further development of inflorescences and flowers is a growth process that is much influenced by temperature and day length. In grasses, this development is associated with rapid stem elongation (heading or bolting). Grasses begin growth in spring, when soil and daytime temperatures reach more or less species-specific thresholds that trigger initiation of growth, if soil moisture is available. At this stage, the time to heading decreases with increasing temperature, at least up to about +25°C (King and Heide 2009).

Many different species, with different responses to environmental conditions, contribute to the grass pollen content in the air. Since allergy sufferers react to most grass pollen, and the different taxa are not distinguished in the traditional pollen analysis, it is necessary to find generalized parameters for pollen, if prediction models are to be developed. In spite of the apparent importance of long-day conditions for inflorescence development even to begin, a number of authors have successfully used temperatures even from the pre-equinox part of late winter and early spring (Frenguelli et al. 1989; Spieksma and Nikkels 1998; Emberlin et al. 1993; Smith and Emberlin 2005, Table 3.1). In addition, a correlation between the amount of precipitation and onset of anthesis is found in a number of studies, alone or interacting with temperature; i.e., the more rain, the earlier is the start of flowering (Jones 1995; Ong et al. 1997; Stach et al. 2008).

The December–January–February averages of The North Atlantic Oscillation (NAO) index (i.e. the difference in pressure between Iceland and the Central North Atlantic, see Sect. 3.6.1) was found to be one of the most important predictors of the start of the grass pollen season in Poznan, Poland, as in several other locations in Europe; the strongest associations generally near the Atlantic Coast. A high value of the NAO index is associated with over-average temperatures and precipitation in North Europe. Also, the relationship between the NAO index and terrestrial ecosystems is well-documented (Stach et al. 2008; Smith et al. 2009).

Table 3.1 Environmental variables that have been successfully used to predict the onset of the grass pollen season

Study	Temperature	Precipitation	Other factor	Country
Frenguelli et al. (1989)	Mean and maximum; heat units minus base temperature (5°C)			C. Italy
	March–April			
Spieksma and Nikkels (1998)	Mean temperature			The Netherlands
	April–May			
Emberlin et al. (1993)	Cumulative temperature (>5.5°C)			UK
	March–April + forecast May forecast			
Jones (1995)	10-day aggregated data	10-day aggregated data		UK
	End of winter, spring	Spring		
Stach et al. (2008)	Mean temperature	Mean daily rainfall	North Atlantic Oscillation Index	Poland
		Days 61–70 from January 1st		
	May	March	December–February	
Ong et al. (1997)		Total rainfall		Australia
		July (a winter month)		
Smith and Emberlin (2005)	Minimum temp			UK
	Days 81–90, from January 1st			
	Maximum temperature			
	Days 101–110, from January 1st			

Cleland et al. (2006) investigated responses of phenology to four experimentally simulated changes in warming, elevated CO_2, nitrogen deposition, and increased precipitation in grassland species. Elevated CO_2 delayed flowering in grasses and greening of the canopy at an ecosystem level, whereas N addition dampened the acceleration of greening caused by warming. In this study, increased precipitation had no consistent impacts on phenology.

In the weed *Ambrosia artemisiifolia*, temperatures during early spring seem to have an indirect effect on flowering date through their effect on germination. A difference in the date on which first pollen release was recorded was found among cohorts of transferred-from-cold conditions to climate-controlled green-houses, at 15-day intervals. There was a consistent trend towards a later first date of anthesis in later cohorts. Therefore, in contrast to floral initiation, the onset of anthesis is apparently not controlled by photoperiod (Rogers et al. 2006).

3.2.5 Readiness to Flower in Woody Plants

3.2.5.1 Chilling and Forcing

Many woody plants in temperate areas alternate between a period of active growth in spring and summer, with a period of dormancy in autumn and winter, during which growth and development is temporarily suspended. The ability to survive unfavourable periods and to evade risk for freezing damage of new shoots is essential not only to the plant's fitness, but also for the competence to maximize the duration of the growing season (Repo et al. 1990).

When the environment imposes dormancy, e.g., by low temperatures, the dormant bud is said to be quiescent or ecodormant. When, in contrast, innate agents maintain dormancy, the bud is said to be in rest, or endodormant. Arora et al. (2003) recommend the use of the terms eco- and endodormant (following the Lang et al. 1987 proposal), since they are more physiologically descriptive than the older terms quiescence and rest. During endodormancy, many metabolic and developmental processes go on in the buds and twigs. These processes include respiration, photosynthesis, cell division, enzyme synthesis, production of growth stimulators, and dissipation of growth inhibitors. But growth is arrested: an endodormant bud cannot elongate even under very favourable circumstances. In poplars, the cells in the growing points within buds are cytoplasmically isolated from one another within 5 days after endodormancy induction. In *Betula*, the cell-to-cell communication in the growing points diminishes in association with the start of endodormancy, since the plasmodesmata, the intercellular "communication channels", decrease in number and diameter. They appear to be blocked by 1-3-beta-D-glucan and thus the possibility for the apical meristem to act as an integrated whole is shut down. Endodormant buds have had less free water than ecodormant buds. Bound water status appears to be associated with low temperature stress tolerance rather than directly to dormancy itself. It has been suggested that dormancy induction may be, in part, regulated through dehydration stress via alterations in the quantity or activity of aquaporins, membrane-bound water-channel proteins that are able to increase water transport across membranes 20-fold over diffusion alone. Another class of ubiquitous proteins, the dehydrins, are suggested to be responsible for the binding of free water. Dehydrins appear to be activated by low temperatures and the plant hormone abscisic acid. They also add to cold acclimation (Arora et al. 2003).

The development of endodormancy and cold hardiness, though which a plant can sustain freezing temperatures without being damaged, are from a physiological point of view two separate processes, although they usually occur simultaneously. Both states are usually triggered by decreasing day length and low temperature (Arora et al. 2003). According to prevailing theories and experimental evidence (e.g., Myking 1999), growth-arresting conditions are eliminated when buds are exposed to chilling temperatures for a certain period. For many temperate plants, the optimal temperature for chilling appears to be within the interval 5–7°C (Richardson et al. 1974; Myking 1999).

Winter chilling is associated with a change in the ratio between endogenous gibberellins and some growth inhibitors, such as abscisic acid. When, how and to what degree hormones are involved in dormancy release is still uncertain and evidence both supporting and refuting various growth regulators can be found in the recent literature (Arora et al. 2003). It was suggested that chilling-requirement satisfaction is associated with the gradual release of water into the cytoplasm by the action of gibberellins, and the removal of a permeability barrier that prevents nutrients from entering the bud. Chilling may also lead to restoration of cell-to-cell signalling networks among individual cells of the apical meristem, allowing for symplastic movement of small signalling molecules, hormones, or proteins responsible for dormancy release (Rohde et al. 2000; Arora et al. 2003).

In the northern hemisphere, chilling requirements are generally met in December-February, depending on species and region (Myking 1999). The actual chilling requirement has been related to the risk of freezing damage in different environments (e.g. Chuine and Cour 1999). Plants growing in cold areas could be expected to need a longer chilling period (and a shorter forcing period) than those in a comparatively warmer region (e.g., Jato et al. 2000; Rodriguez-Rajo et al. 2003). However, the important factor for selection of a long period of dormancy may not be the low temperatures *per se.* During endodormancy, growth is prevented during transitory periods of warm temperatures (Arora et al. 2003). Thus, chilling requirements are expected to be inversely related to the length and stability of the winter, rather than to its severity (Table 3.2). Ecotypes of *Betula* from Northern Norway have earlier bud burst than ecotypes from Mid-Norway and Denmark, when they all were kept at the same equal temperature and light regime (Myking 1999). During winter in south Scandinavia, conditions often fluctuate between temperatures above and below the limit for frost damage (−5°C), whereas in the very north, warm temperatures are rare in wintertime. A similar variation in chilling requirements is found between *Betula* ecotypes from areas differing in their degree of continentality. In a transfer experiment, ecotypes native to mild oceanic winters were later released from dormancy than those of lowland continental origin. In contrast, a

Table 3.2 Chilling and forcing base temperatures, and chilling requirements for different tree species, as recorded in literature

Species and area	Chilling base temp	Chilling upper limit	Chill units	Forcing base temp	Source
Alnus glutinosa, Scandinavia	>−9.7°C			−3°C	Myking (1998)
Alnus glutinosa, Denmark, Copenhagen			1,550	+2°C	Andersen (1991)
Alnus glutinosa, Spain, Galicia			800	+5.5°C	Rodriguez-Rajo et al. (2004)
Alnus glutinosa, Spain, Léon			848	+6.5°C	Gonzalez-Parrado et al. (2006)
Alnus glutinosa, Italy, Perugia			950		Jato et al. (2000)
Betula pendula, Italy, Perugia (Perugia, Italy)	+7°C				Rodriguez-Rajo et al. (2003)
Betula pendula, Norway	<−9.7°C			0–+1°C	Myking (1998)
Betula pendula, Spain, Vigo, Spain	+5.75°C				Rodriguez-Rajo et al. (2003)
Betula spp., Scandinavia		+12°C			Myking & Heide (1995)
Betula, Pinus, Finland	−3.4	+10.4°C			Sarvas (1974)
Buxus sempervirens, Platanus acerifolia, Southern and Central Europe	(−5°C)–3.4°C	+10.4°C (+15°C)			Chuine et al. (1999)
Californian plants	0	+7.2°C			Aron (1983)
Cupressaceae, Mediterranean area	+7.1°C				Fuertes-Rodriguez et al. (2007)
Fruit trees		+14°C			Richardson and Anderson (1986)
Northern deciduous trees				0°C	Heide (1993), Myking (1997b)
Olea europaea, Córdoba				12.5°C	Galán et al. (2005)
Olea europaea, Priego				5°C	Galán et al. (2005)
Olea europaea, Granada				6°C	Galán et al. (2005)
Olea europaea, Jaen				7°C	Galán et al. (2005)
Olea europaea, Málaga				10°C	Galán et al. (2005)
Olea, Spain, Mesomediterranean area				5–5.5°C	Alcalá and Barranco (1992)
Olea, cultivar “Picudo”, from Southern Spain			997		Orlandi et al. (2004)
Olea, cultivar “Ascolana”, from Central Italy			1,848		Orlandi et al. (2002)
Olea, Portuguese cultivars				9–9.7°C	Ribeiro et al. (2006)
Olea, Southern Spain				10–13°C	García-Mozo et al. (2002)
Prunus padus	>−9.7°C				Myking (1998)
Quercus, Southern Spain				8–11°C	García-Mozo et al. (2002)
Tree species, spp., Southern of S. Spain				5–5.5°C	García-Mozo et al. (2002)

continental Mediterranean climate provides a larger freezing damage risk to new *Olea* tissues than a maritime one from an area where frost seldom occurs (Orlandi et al. 2004), thus creating a larger demand for chilling. Myking (1999) suggested a second explanation to the observed differences: that in a region where the growing season is short, early alleviation of dormancy (i.e. a low chilling requirement) secures rapid growth as soon as temperatures are favourable.

Since chilling requirements are usually low in Mediterranean species, thermal time models with temperature accumulation starting around 1 January are often considered to be sufficient for the prediction of flowering start. Any difference in chilling from 1 year to another is considered to be unimportant. However, the importance of chilling is not zero in Mediterranean species, as illustrated in *Olea europea*. Every olive cultivar appears to require its own amount of chilling in order to flower (Table 3.2).

When endodormancy is released, the buds are fully growth competent. But they still need stimulation from the environment before they can burst or flowering can begin. This stimulation has generally been presumed to be the occurrence of forcing temperatures i.e. temperatures above a certain base or threshold temperature. In many studies, 5°C has been considered as the standard threshold (basic) temperature for growth in boreal and temperate species (refs. in Myking 1999; Rodriguez-Rajo et al. 2004), irrespective of origin. However, in several studies, a clinal within-species variation, related to latitude, altitude, and different degrees of continentality, has been demonstrated (Table 3.2). The threshold may also vary with the age and developmental stage of the individual plant, as well as with environmental factors (Wielgolaski 1999).

Although it is possible to experimentally identify the date for the breaking of dormancy, and to approximate it in a model based on phenological and meteorological records, the temporal limitation between endo- and ecodormancy is not necessarily clear-cut. Forcing temperatures may be effective even if chilling requirements have not been fulfilled. In several studies, a dynamic relationship has been observed, i.e. the longer the chilling period, the fewer days of heat accumulation are needed to start the flowering (e.g. Rodriguez-Rajo et al. 2004; Emberlin et al. 2007). However, the range of chilling and forcing intervals is not satisfactorily known (Chuine and Cour 1999), nor is it clarified when and how chilling and forcing temperatures act on bud growth when they alternate. Warm temperatures have been suggested to be able to reverse the effects of previous chilling (e.g. Fuertes-Rodriguez et al. 2007), when they occur before endodormancy release; moreover, temperatures below a certain threshold during the forcing period have been suggested to nullify the effect of heating (Linkosalo et al. 2006). There appears to be a considerable overlap between the intervals when chilling and forcing temperatures are efficient, and their effects are easily confounded. It has been stated (references in Myking 1999) that the most efficient temperature for resumption of growth in dormant buds was the temperature that is both low enough to break endodormancy (through chilling), and high enough to stimulate growth when dormancy diminishes (through forcing). Outdoor fluctuating temperatures have been claimed to be more effective for budburst than artificial constant temperatures in many woody plants. This would imply that the thermal time requirement for budburst is less when the temperature fluctuates than when it is constant. However, in an experiment with *Betula pendula* and *B. pubescens*, no such difference could be detected (Myking 1999).

Results from experiments with tree seedlings of boreal and temperate species (Linkosalo et al. 2006) indicate that there is a gap between dormancy and bud growth. Several analyses of phenological tree series suggest that the starting date of ontogenetic development of buds, usually initiated in previous seasons, falls somewhere in late winter or early spring. The fulfilment of chilling requirements appears usually to be 3–4 months earlier, in late autumn or early winter. The delay is generally explained with prevailing low temperatures, which do not allow growth. However, a number of authors, e.g. Linkosalo et al. (2006), have claimed that something more may be missing from the traditional models. For the ontogenetic development to start, a cue from the diurnal light regime might be necessary. A light dependency would guarantee that development does not take place when temperatures giving frost injury still are likely to occur. While the climate is varying between years, the cyclic changes in light conditions remain stable at certain latitude. Photoperiod has been claimed to be the most important factor to promote flowering in late-successional species like *Fagus sylvatica* and *Quercus robur* (Körner and Basler 2010), but Chuine et al. (2010) argued that no study has shown that it was dominant over temperature even in these genera. Linkosalo et al. (2000) suggested that for *Betula pendula*, the cue could be a combination of day length or night length and twilight conditions. For that species, the initiation of bud development is suggested to occur around spring equinox. After this date, the temperature seldom falls below −5°C, which is the upper limit for freezing damage to occur in *Betula*. Chilling requirement is then a necessary, but not sufficient control mechanism for flowering to take place. In *B. pendula* and *B. pubescens*, short-day conditions stabilize dormancy, whereas long days promote dormancy release (Myking 1999).

3.2.5.2 Similarities and Differences Within and Between Species

The local and regional adaptation of the reproductive phenology of wind-pollinated trees may be surprising, since there generally is a large gene flow, as well as an overlap between generations, that would be expected to counteract selection. Moreover, in north Europe, trees arrived at their present locations fairly recently in the perspective of generation length. A number of quantitative trait loci, and in a few cases single loci that affect induction of endodormancy, chilling requirement and date of bud burst have been identified in *Malus*, *Populus* and *Vaccinium.* In these studies, some of the traits appear to have a large heritability, which would make natural selection possible. On the other hand, heritability of bud burst is very variable in *B. pendula* populations in north Scotland (Arora et al. 2003).

Whereas members of the same genus and species from different climatic regions often differ with regard to reproductive phenology, species of the same genus that grow in the same region often respond in the same way to temperature. There can also be differences within genera, e.g., between *Betula pendula* and

B. pubescens, where the former usually has a lower chilling demand than the latter (Myking 1999).

The similarity is also valid for species from different families, when selection pressures are strong and the successful responses limited. *Salix pulchra* and *Betula nana* from the Arctic had similar mean dates of bud break and could be predicted with the same model parameters (Pop et al. 2000). But there are several other examples where chilling requirements and threshold temperature vary with environmental conditions, ecology, and presumably, with phylogeny. The chilling requirements of *Betula pendula* and *B. pubescens* are in northern Europe often met with already in December, in *Populus tremula* in January, and in *Alnus glutinosa*, in February. *Alnus* has a larger chilling requirement than *Betula*, but flowers much earlier and quite soon after endodormancy alleviation. The low basic temperature may explain its quick growth resumption (Myking 1999).

Although they may have different demands, temperate tree species in the same region come into leafing and flowering in the same sequence from 1 year to another and their flowering dates are highly correlated. The heat accumulation of *Ulmus glabra*, counted from the beginning of flowering of *Alnus glutinosa*, varies little (Frenguelli and Bricchi 1998). The date of alder flowering could thus be used to predict elm flowering.

3.3 Pollen Release and Pollen Traits

3.3.1 Anther Morphology and Pollen Maturation

In terrestrial plants, the life cycle is an alternation between a diploid, spore-producing multicellular generation (the sporophyte) and a haploid, also multicellular generation (the gametophyte), producing sperm and/or egg cells. A pollen grain contains the male gametophyte of the seed plant, i.e., the sperm-producing generation. In seedless plants, gametophytes are generally independent from the sporophyte, and consist of hundreds of cells; evolution of the seed-bearing habit involved dependence of the gametophytes upon sporophytes and reduction of their size. Thus, in gymnosperms, the male gametophyte has up to ten cells, whereas in angiosperms, there is only one vegetative cell apart from the two sperm cells (Fig 3.2). The male gametophyte originates from a spore, generally called a microspore, and is still surrounded by this spore's sporopollenin outer wall, the exine (Fig. 3.3c), at maturity. The gametophyte's own wall is called the intine (Fig. 3.3c). Since a microspore is a single cell, it is not correct to use microspore and pollen as synonyms.

In angiosperms, the pollen grains develop within the anthers. An anther generally consists of two "halves" or theca, connected to a filament. Each theca contains two locules, i.e. microsporangia, separated by a septum. There are several deviations from this pattern, and there may be one or more locules in one theca (Endress 1996 in Pacini 2000). The inside of a locule is covered with the tapetum layer

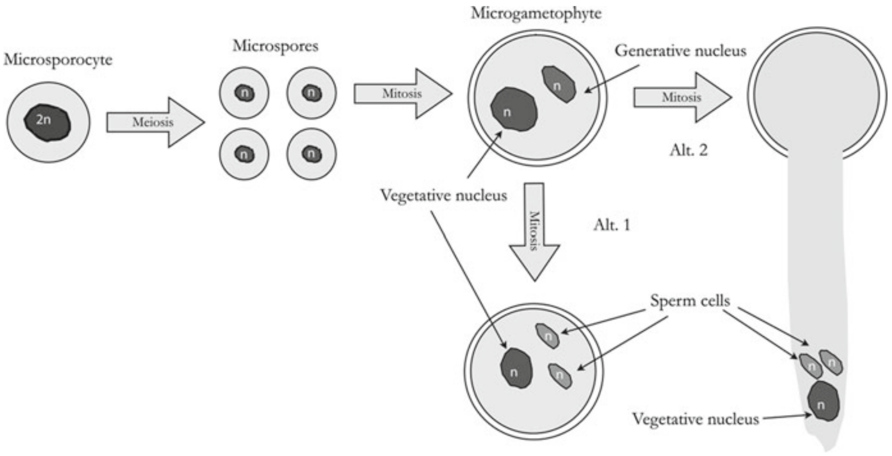

Fig. 3.2 The development of a pollen grain, i. e. a microgametophyte with a resistant outer wall. A gametophyte is the haploid, sexual generation of terrestial plants; a microgametophyte produces sperm cells. A diploid microsporocyte in one of the microsporangia of the anther (see Fig. 3.3a) divides by meiosis into four haploid microspores. Each microspore develops further by mitosis, into a binucleate microgametophyte with a vegetative and a generative cell. During this process, sporopollenin synthesised by the tapetum of the microsporangium is deposited on the microspore to form the exine, the outer pollen wall (see Fig. 3.3c). The generative cell divides to produce two sperm cells, either within the pollen grain before dispersal (Alt. 1) or after germination, within the pollen tube (Alt.2). The alternative locations differ between plant families. (2n = a diploid nucleus, n = a haploid nucleus)

(Fig. 3.3a), which provides the developing spores with nutrients, enzymes and sporopollenin, conveyed through a liquid, the locular fluid. The tapetum disintegrates shortly before anther opening (Fig. 3.3b).

There is also a mechanical layer, which may consist of one or more layers of cells situated in different parts of the anther. They are often dead at the time of pollen maturity, and may have lignified thickenings of different functional types within the same anther. As a result of the drying of all, or part of the anther, and in relation to the disposition of the thickened areas, the cells of the mechanical layer change their shape, causing stretching and folding. This action leads to opening of the anther and pollen presentation or expulsion (Manning 1996; Bianchini and Pacini 1996 in Pacini 2000). In the epidermis of the part of the anther wall that faces the septum, there are one or two thin-walled zones or apertures called stomia (sing, stomium).

At the time of maturation and degeneration, the tapetum also secretes viscous substances, e.g. tryphine (Brassicaceae) or pollenkitt. They cause the pollen to clump together mostly in entomophilous species but have also other functions, e.g. to keep the pollen to remain in the anther until dispersal. In anemophilous species, pollenkitt is usually lacking; this is not the case for *Parietaria judaica* (Fotiou et al. 2010) or *Olea europea* that has relatively "recent" entomophilous ancestors (Pacini 2000). The remaining structures of the disintegrating tapetum are called orbicules (or Ubisch bodies) and consist of sporopollenin, just as the

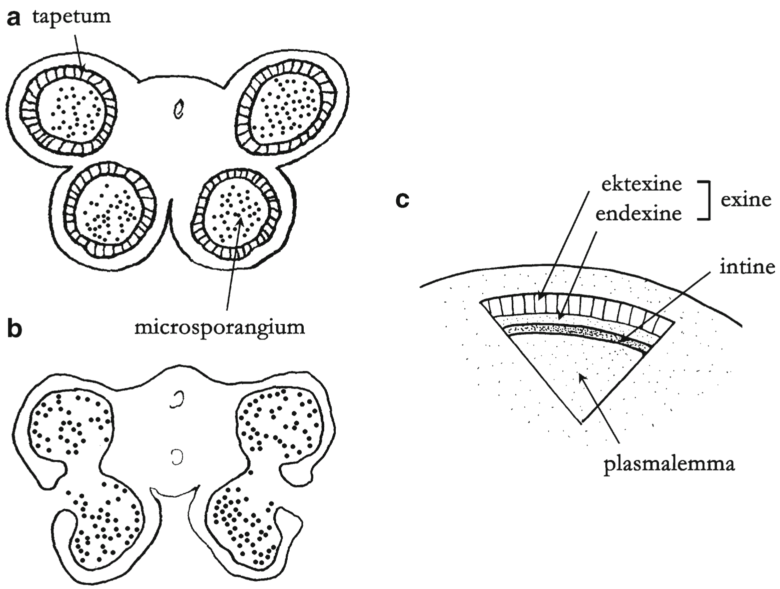

Fig. 3.3 (**a**) A cross section of an immature anther with two microsporangia, each containing numerous microspores and a tapetum layer that provides the microspores with various nutrients and sporopollenin. (**b**) A mature, dehisced anther with pollen grains. The tapetum is now consumed. (**c**) A part of a pollen grain with a cross section of the pollen wall, showing the two layers of the exine (endexine and ectexine) and the largely pectocellulosic intine, which in contrast to the exine is derived from the microgametophyte

pollen exine. Orbicules can be seen on the surface of pollen from some gymnosperms, e.g. *Taxus baccata* and *Juniperus communis*. They may or may not co-occur with pollenkitt, but appear to be absent from the anthers of many predominantly entomophilous angiosperm families, such as Asteraceae. In Fagales, and Poaceae, orbicules are present without pollenkitt. Since they have the same physical properties and electrostatic charge as the pollen grain surface, they have been suggested to facilitate pollen detachment from the anther, which is advantageous in a wind-pollinated species (Pacini and Hesse 2004). They have also been suggested to be allergen carriers (El-Ghazaly et al. 1995).

3.3.2 Anther Dehiscence

Pollen release could be considered to occur in two simple steps: first, the locular fluid disappears and second, the anther wall bursts (Pacini and Hesse 2004; Laursen et al. 2007). The first of these steps may be due to evaporation through the anther wall, or to reabsorbtion through the anther vascular bundles, or to both. The rate of evaporation depends on the ambient relative humidity, although it can be limited by

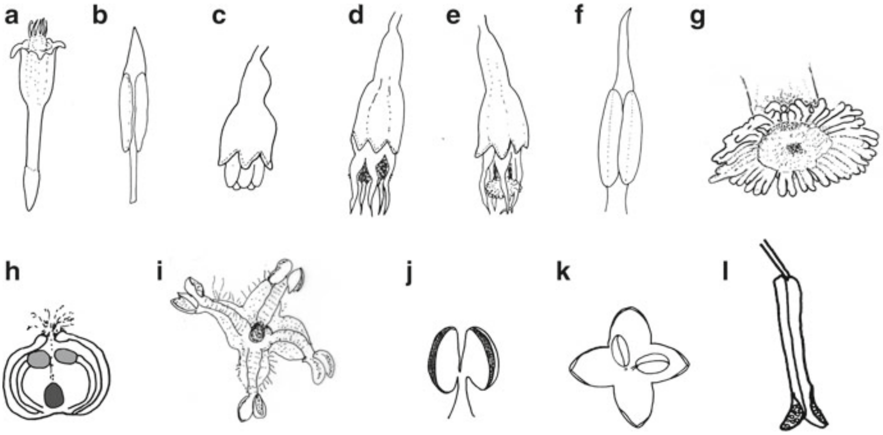

Fig. 3.4 (**a**–**b**) *Artemisia vulgaris*. (**a**) Male flower in the pollen-presenting stage. (**b**) Stamen. (**c**–**g**) *Ambrosia artemisiifolia* (**c**–**e** redrawn after Bianchi et al. (1959); **b** and **g** redrawn after Curtis and Lersten (1995); see also illustrations in Martin et al. (2009, 2010). (**c**) Male flower of with extending anthers. (**d**) Male flower in the pollen-presenting stage. (**e**) Male flower after pollen dispersal. The pistillodium is visible. (**f**) Stamen. (**g**) Pistillodium. (**h**–**i**) *Parietaria judaica*. (**h**) Bisexual flower in the female stage. The anthers are under tension and pressed towards each other. (**i**) Open flower with straight filaments and released pollen. (**j**) *Betula pendula.* Stamen with cleft anther and open thecas. (**k**) *Olea europaea*, male flower. (**l**) Grass stamen with two apical stomia

specific mechanisms. But reabsorbtion is a programmed process that is regulated by the plant. It enables anther opening at any time of day, whereas evaporation may occur only in the driest hours of the day. The relative importance of the two processes differs among species. The minimum temperature during the 24 h-cycle is also important as it determines whether anthers will dehisce or not. This is corroborated in studies from different taxa, such as Poaceae (Galán et al. 1995), Cupressaceae and *Olea europea* (Cariñanos et al. 2010), Urticaceae (Galán et al. 2000), and *Ambrosia artemisiifolia* (Bianchi et al. 1959).

In anemophilous trees, which flower in early spring, high temperature, low humidity, and moderate wind speed favour a passive dehydration, which then leads to a bursting of the anthers (Pacini and Hesse 2004). There are, however, considerable differences among these species as to whether all pollen will be released simultaneously or if the anther will open and close again according to variations in humidity, e.g. during a rainy day.[1] Apart from generalizing statements, very little is found in the literature on this matter.

In grasses, the anther opens either along a longitudinal slit, or the opening is limited to the apex or both to the apex and the base of this slit (Fig. 3.41). In *Oryza*, *Hordeum* and probably also in other grass species, dehiscence occurs when the pollen grains swell due to a potassium movement from locular fluid to the grain (Matsui et al. 2000). This is a moisture-requiring process, whereas the widening of

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[1] Dahl, personal observation.

the splits in both the upper and lower part of the anther wall is caused by desiccation (Matsui et al. 1999). This has been proposed to be the result of evaporation as well as of active retraction (van Hout et al. 2008).

In *Parietaria* and other Urticaceae, pollen is released explosively. All anthers in the flowers are juxtaposed and under tension. The filaments are incurved and form an arch inside the perianth, which compresses the anthers against one another (Fig. 3.4h). Their walls have transverse thickenings (ribs) in their upper two-thirds, whereas there is no mechanical layer in the anther (Franchi et al. 2007). When the anthers dehydrate, they shrink and lose contact with one another. This triggers all the stamen filaments to straighten violently (Fig 3.4i), and the pollen is released as a small cloud through the single stomium (Pacini and Hesse 2004).

3.3.3 Pollen Hydration and Vitality

The pollen wall is perforated by numerous micropores that allow for the transport of water, and it is to a certain degree elastic. At the time of exposure, pollen may contain from 1 to 70% water in its cytoplasm. As a rule, the higher the water content, the more active the metabolism of the pollen. In most species, the pollen grain is partially dehydrated just before or at the time of anther opening, a process that contributes to its longevity. These pollen grains often become ovoid at dispersal due to folding along their colpi (furrow-shaped apertures). Their carbohydrate content contributes to their water capacity and to their ability to stay vital and intact during humidity changes. In general, their longevity is increased at low relative humidities and low temperatures until germination, which generally requires high relative humidity (Gomez-Casero et al. 2004). In contrast, in a number of species that remain partly hydrated at dispersal, e.g. of Urticaceae and Poaceae, there are no adaptations to prevent water loss. Their pollen grains are usually spherical in shape and devoid of colpi, and they do not change in shape when water is lost; instead, they may eventually collapse due to a thin pollen wall, as is usually the case in grass pollen (Pacini 2000). Pollen that is partly hydrated at the time of dispersal is usually short-lived and cannot stand dehydration (Pacini and Hesse 2004). In the context of pollen allergies, it is important to distinguish pollen viability and allergenicity. The pollen allergens, which are glycoproteins produced by the pollen, may retain their impact on the human immune system for a long time, after the pollen grain is essentially dead (e.g. Yli-Panula and Rantio-Lehtimäki 1995).

3.3.4 Diurnal Patterns of Pollen Release

Pollen release may be synchronous or staggered within flowers, inflorescences and entire plants, depending on life form, adaptations or ambient meteorological factors. High temperatures usually speed up maturation and shorten the duration of anthesis.

In many anemophilous trees high temperature, low humidity and moderate wind speed favour a passive dehydration which then leads to bursting of the anthers (Helbig et al. 2004). In grasses, it is well known that each species sheds its pollen at its own time of day, and often with "clock-like regularity". Anthesis starts when filaments elongate and push the anthers outside the florets. In a study of several Indian grass species, Subba Reddi et al. (1988) concluded that each grass species follows the same course of pollen release on successive days with normal weather, but that variation occurs in the initiation, progress and termination of the daily course, when weather changes. They claimed that each course appears to be adapted to a certain "evaporating power", presumably degree of relative humidity and the related vapour pressure deficit. In a study of the circadian rhythm of *Zea mays*, the actual time of pollen release differed from day to day and depended on the time required for the anther tips to dry and open (van Hout et al. 2008), which in turn was affected by the presence or absence of morning dew. In this study, the first pollen concentration peak, detected in Rotorod samplers situated at canopy height, happened shortly before the direct irradiance peak on the anthers suggesting that direct solar irradiation might be important for the desiccation process. The temperature range that prevailed during the study period, 20–30°C, did not seem to have noticeable effects. Jarosz et al. (2003) related the initial morning emission of *Zea* to a decrease in relative humidity below 100 %, corresponding to vapour pressure deficit values of 0.2–0.5 kPa around the anthers.

In a study undertaken in India, 50 of the 52 investigated species shed pollen during only one diurnal period, which lasted for 2–16 h (Subba Reddi et al. 1988). The main period, when more than 50 % of the pollen was shed, could occur at any time, night or day, but always at the same time for the same species and always at the same time from one date to another. Some grass species are reported to exhibit a bimodal diurnal pollen release pattern (Subba Reddi et al. 1988), e.g., *Holcus lanatus*, *Festuca rubra*, and *Lolium perenne*. In all these species as well as in *Cynodon dactylon*, most pollen was released during the second period. In another investigation of *Festuca rubra* and *Lolium perenne* (Liem and Groot 1973 in Subba Reddi et al. 1988), a clear diurnal periodicity with regard to anther emergence was found: most of it took place from noon to midnight, and much less during the reverse period, from midnight to noon. Anthers must protrude from the flowers for pollen to be released, but anther emergence and pollen release are not synchronous. In this investigation, pollen release was not correlated to temperature or light either, but it was to low relative humidity. More pollen was released if the relative humidity fell below 50 %. There was no clear periodicity, and pollen could be released just at any time, depending on when the sufficient minimum humidity was reached. All emerged anthers in a plant were closed or opened simultaneously, which was inferred as a dependence on the same environmental factors. In *Zea mays* (van Hout et al. 2008) the observed bimodal pattern of pollen emission was compared to meteorological factors. The cause of the bimodality was reduced mean wind velocity during mid-day and could not be related to any other meteorological factor. *Imperata cylindrica* and *Pennisetum americanum* studied by Subba Reddi et al. (1988), released pollen during all 24 h, irrespective of weather.

Divergence in daily flowering among grass species has been suggested to act as a regulating mechanism to avoid waste of pollen, stigma sites, and ovules through unwanted "nonsense" pollination (cf. van der Pijl 1978), and also to promote reproductive isolation between closely related species, which otherwise might produce hybrids with low fitness (Grant 1983).

In *Artemisia* and *Ambrosia*, which both belong to Asteraceae, several flowers ("florets") are closely packed together in an inflorescence, a capitulum. The Asteraceae are characterized by secondary pollen presentation, i.e., after anther opening, the pollen is deposited and presented to dispersing agents in other parts of the flower. In *Ambrosia* and some species of *Artemisia* the flowers are unisexual and positioned in likewise unisexual capitulae, whereas in *Artemisia vulgaris*, pollen-producing flowers are hermaphrodite and situated in the centre of the capitulum, surrounded by flowers containing only pistils. In both species, the pollen-producing flower is tube-like and narrow, with five stamens arranged vertically on the inside. In the centre of the flower there is a pistil, which in *Ambrosia* is modified into a columnar structure with a cap of clavate hairs, a pistillodium (Fig. 3.4g). As described above, the anthers open inwardly (Fig. 3.4f). In *Artemisia*, the pollen adheres to the style by means of pollenkitt. When the style subsequently lengthens, it carries the pollen out of the flower (Fig. 3.4a, b). The tips of the stigma lobes are modified into brush-like structures that help in this process (Garnock-Jones 1986; Pacini 2000). In *Ambrosia*, the elongation of the filaments appears to be the main force to cause the complete emergence of the pollen from the mouth of the corolla (Fig. 3.4c, d). But the pistillodium plays a role in the "sweeping out" of the pollen mass also in this species (Fig. 3.4e), at least of the pollen grains that still remain in the anthers after dehiscence, or in the open space between them. The result is a bimodal pollen release (Bianchi et al. 1959; Martin et al. 2010).

In studies of *Artemisia vulgaris* pollen is released during 4.00–8.00 (Finland, Käpylä 1981) and during 6.00–11.00 o'clock (Germany and Poland, von Wahl and Puls 1989; Kazlauskas et al. 2006). However, it is retained by the apical appendages of the anthers. Pollen detachment from the capitulum is therefore likely to be temporarily separate from the actual anther opening within the flower, and thus could take place any time during the day when there is enough wind. Kazlauskas et al. (2006) found a negative correlation between pollen concentration in the air and rain during the morning and forenoon hours, but point out that there is no study on the possibility that anther dehiscence is postponed to the afternoon, if the weather dries up. There is also no study as to the relationship between the role of active reabsorbment and of evaporation for anther opening. In an investigation of *A. tridentata* from sagebrush steppe in Wyoming, USA (Laursen et al. 2007), a baseline diurnal pattern of increasing presentation, release, and transport from late morning to mid- to late afternoon was found. The data suggested that the actual degree and timing of anther development and dehiscence are modified by diurnal variations in temperature and humidity. Evening hours of high humidity were suggested to promote anther development, while early morning hours of decreasing humidity most likely drive anther dehiscence, a process also driven by temperature which in this arid environment generally is inverse to humidity. Wind was responsible for actual pollen detachment.

There was not a linear relationship between wind speed and detachment, but there may be a lower critical limit, which in the Wyoming study was estimated to 2.67 m/s. This fairly mild breeze apparently was strong enough to remove pollen from the capitulae and keep them suspended for subsequent transport as winds continued to increase into the morning. Also Kazlauskas et al. (2006) found a relationship with wind speed and pollen concentration in the air. Finally, Munuera Giner et al. (1999) did not discern any diurnal pattern that could be related to meteorology in the results from their *Artemisia* pollen concentration measurements in Murcia, Spain. Intradiurnal patterns of pollen concentrations were similar for late summer and winter species (*A. campestris* and *A. barrelieri*). During autumn-blooming, the intradiurnal pattern of *A. herba-alba* was particularly erratic. As pointed out by Laursen et al. (2007), will temporal patterns of release from individual plants be obscured when their pollen merge into the well-mixed air streams of the general atmosphere? Moreover, when data are interpreted from pollen traps situated at different elevations, diurnal patterns will appear to differ according to when vertically transported aerosols emitted at ground level reach the trap, as shown by von Wahl and Puls (1989) and others.

In *Ambrosia*, the pollen grains are released from the anthers about or shortly after sunrise, and the pistillodium has swept out the remaining ones about 5 h later (Martin et al. 2010). Pollen grains tend to stick together in clumps, which stay on the capitulae or fall on adjacent vegetation prior to reflotation by wind (Bianchi et al. 1959; Ogden et al. 1969; Martin et al. 2009). Their detachment from the deposition surface is likely to be impeded by the occurrence of morning dew, and the highest concentrations of airborne *Ambrosia* pollen grains are then generally found during midday (Bianchi et al. 1959; Ogden et al. 1969; Solomon and Mathews 1990). Like in *Artemisia*, actual pollen dispersal is also related to wind speed and relative turbulence. Peak releases have been reported to occur in connection with unstable weather with increasing wind forces and shifting wind directions (Barnes et al. 2001).

If populations are gregarious, turbulence will facilitate effective dispersal. But when conspecific plants are separated, turbulence may cause much pollen go to waste (Subba Reddi et al. 1988). Species that tend to appear in low density would be selected to shed pollen when conditions are stable, and pollen concentration at the source can be maintained at high level. Subba Reddi and Reddi (1986) identified 30 such grass species.

3.4 Duration of the Pollen Season and the Shape of the Pollen Curve

The duration of the period, when pollen from a certain taxon is found in the air, and the shape of the curve that describes the change in pollen concentration over time, depend on a number of factors. First, a pollen taxon may comprise one species or an entire family, depending on the taxonomic level where morphological identification is possible. The taxon Poaceae is an amalgam of different species with varying ecology, mating systems and heating requirements, and thus, the curve can have several peaks (e.g. Gonzalez Minero et al. 1998).

The second important factor is the specific schedule for pollen emission, as a result of the proportion of flowers open per day (flowering rate) and of floral or inflorescence longevity (Kudo and Hirao 2006). Flowering may be synchronous or staggered, at the population and/or at individual levels (Rathcke and Lacey 1985; Primack 1985). In wind-pollinated plants, which are the main contributors to the atmospheric pollen load, synchrony among conspecific plants promotes outcrossing and pollen tube competition among a maximum number of potential mates. A high concentration of pollen in the air surrounding a maternal plant is beneficial to the fitness of its progeny. Furthermore, the period for efficient pollination can be limited by predictable environmental changes, selecting for a synchronous behaviour. In temperate regions, many deciduous trees flower before leafing, in the springtime. In the Mediterranean, summer drought is ubiquitous, and at a certain point in time during spring, many annual species allocate their resources away from vegetative growth, into an intense and final period of reproduction. Plants that flower in late summer and autumn, such as *Ambrosia artemisiifolia*, can be limited by the risk for early frost. When flowering is synchronous in a population or even in a region, the pollen curve is often positively skewed (Primack 1985) and the peak of pollen concentration will follow in a fairly short time after flowering onset.

Staggered or asynchronous flowering, on the other hand, can be the case when the outcome of flowering, fruit set or seed germination is uncertain due to the risk of adverse conditions (Rathcke and Lacey 1985; Kudo and Hirao 2006). The result is a platykurtic pollen curve. In contrast to the annuals mentioned above, other annual herbs and grasses, and a number of perennials such as *Parietaria judaica,* are opportunists with indeterminate growth. Their flowers are produced from lateral meristems, i.e., on side shoots, whereas the top of the plant continues to grow vegetatively. This growth pattern permits simultaneous vegetative and reproductive growth and allows for risk-spreading, as well as for the possibility to exploit favourable conditions. This growth pattern allows for pollen dispersal all the year around if there is no frost, although there may be a maximum, e.g., in late spring (Guardia and Belmonte 2004). In winter-flowering trees, such as *Corylus* and *Alnus* (Rodriguez-Rajo et al. 2004), pollen-producing catkins are not injured by frost. In Northwest-Europe, winter temperatures often fluctuate between mild and sub-zero centigrades. In low but frost-free temperatures, only a few anthers open at one time. Moreover, a platykurtic pollen curve can be due to the existence of environmental and genetic variation for flowering time within populations and species, as has been documented for numerous species (Primack 1985; Wielgolaski 1999; Chuine and Belmonte 2004).

Thirdly, apart from the inherent flowering behaviour, flowering rate and therefore also the duration and the timing for the peak of the pollen season, are affected by weather conditions. Temperature affects the rate of growth and development, depending on the species. The main pollination period of *Betula* (mainly *B. pendula*, and in the north, also *B. pubescens*) varies considerably with temperature, as recorded in several studies from different parts of Europe (Mendez et al. 2005). The length and timing of the peak of the grass pollen season in Bilbao (Spain) differ between years, according to temperature (Antepara et al. 1995). When nights are not hot enough as to favour anther dehiscence (i.e. >10–15°C) in mid-autumn, the pollen curve tails off in *Ambrosia artemisiifolia* (Bianchi 1959; Stark et al. 1997), although there may not have been any night frost. The effect of heating and of related meteorological variables can alter as the season progresses, especially as a result of changes in the amounts of remaining pollen to be dispersed or of pollen production (Smith and Emberlin 2005; Vázquez et al. 2003). Heat favours anther dehiscence in *Olea europaea* during the pre-peak period but makes flowering decrease during the post-peak period (reference in Galán et al. 2001).

Rainfall before anthesis can have an effect on the grass pollen season: in southern Spain, an abundant rainfall during development leads to a short and intense peak, whereas drier conditions will cause the season to be long and without a pronounced maximum (Gonzalez Minero et al. 1998). In contrast, rainfall and a high relative humidity during anthesis will prolong the season in Poaceae (Antepara et al. 1995), in *Olea* (Gonzalez Minero and Fernandez-Mensaque 1996) and probably also in other species since they hamper anther dehiscence.

García-Mozo et al. (1999) investigated variations in the *Quercus* sp. pollen season at selected sites in Spain and detected that no relationship was observed between the amount of pollen produced (the pollen index, see subchapter 3.5.1) and season duration: years with higher pollen counts did not have a longer pollen season and vice-versa. However, there was a connection between the number of days on which more than 50 grains/m^3 were recorded and the pollen index, in years with lower pollen production, fewer days were registered despite the season maintaining its normal duration.

3.5 Factors That Influence the Magnitude of the Pollen Index/Pollen Sum

3.5.1 The Pollen Index Parameter

Ever since Blackley constructed the first pollen trap in the late 1860s, the amount of registered airborne pollen during defined period of time has become a basic aerobiological parameter. The amount of pollen registered during a year is described as the "annual pollen sum" or the "pollen index". This has become the standard parameter both for quantitative descriptions of the registered airborne pollen within the same monitoring site.

The magnitude of the pollen sum/index reflects the flowering intensity of the pollen-producing plants. The availability of pollen can be important for successful pollination and fertilization, and is of interest in studies of plant reproduction behaviour (McClanahan 1986) or of the production of agricultural anemophilous crops, such as *Olea* (Galán et al. 2001) and *Vitis* (Cristofolini and Gottardini 2000). The annual variations in the amount of registered pollen indicate variations in abundance of the source. Thus, changes in the amount of registered pollen have been used in studying changes in vegetation (Pidek 2007; Kobzar 1999) and in environmental conditions (e.g. Damialis et al. 2007), which could be of particular interest for forecasts. However, the pollen index can be a biased measure of the reproductive output of the plants, as it is influenced by factors such as the atmospheric transport and deposition of pollen, and weather factors affecting the emission process (Ranta et al. 2008). Episodes of long distance transport from remote sources occur at a regular basis, and can contribute significantly to the counts registered at a certain site (Mahura et al. 2007). Although the reproductive output of tree species could be synchronized at a large geographical scale (Ranta et al. 2008), the local pollen index may be influenced by factors acting far away from the immediate environment.

3.5.2 Flowering Intensity in Grasses and Other Herbaceous Species

Pollen concentrations experienced by allergy sufferers depends on the weather during anthesis. Nevertheless, in temperate areas, the potential severity of the pollen season of grasses and other herbaceous species is mainly determined earlier, by the accumulated temperature and precipitation from the beginning of the growth period and onwards during the spring, when the culms elongate and pollen is formed in the anthers. Thus, the important factors are about the same that influence the start date. They are difficult to foresee far in advance, but forecast is possible when some time into the development period has passed. As emphasized in Emberlin et al. (1999), specific forecast models must be developed for different sites, since the absolute time periods that are important differ. Emberlin et al. (1993) found that for London, they could predict the likely severity of the season at the end of May or alternatively when 75 pollen grains were recorded, by using cumulative temperatures for March and April, combined with forecasts of temperature and precipitation in June in multiple regression analyses based on pollen data over a 20-year period. Predictions could be made even earlier, at the end of April, replacing the latter variables with long-term weather forecasts for May. The severity of the Poaceae pollen seasons was also modelled at a network of sites in the UK (Jones 1995). Total monthly rainfall, daily average temperatures compiled to monthly mean and cumulated temperatures as day degrees above 5.5°C were used as variables in a multiple regression analysis. It was, however, found that 10-day aggregated variables often gave the best results. Three models were developed, enabling the prediction of the grass pollen season within 4 days of the actual start dates, but with varying success at London, Cardiff and Derby, respectively. Emberlin et al. (1999), employed 10-day aggregates of cumulative daily temperatures above 5.5°C and precipitation at the same locations, and achieved a high level of explanation for them all.

In the Mediterranean parts of South Europe, precipitation is an especially strong limiting factor to determine flowering intensity, not least because of the fact that it is irregular. In Sevilla, Southern Spain, the annual pollen index of grass pollen appeared to decrease over a period with recurring drought (Gonzalez Minero et al. 1998). A lack of water will have a general negative effect on vigour and growth potential in all grasses since they have shallow roots, and especially in annual species, which constitute a relatively large proportion of the Mediterranean flora. Galán et al. (1995) observed that the number of rainy days was even more important than the amount of precipitation collected in these areas, since rain tends to be torrential and almost all is lost as run-off. In the Mediterranean area, the grass pollen season may continue throughout the year, but is most intense in late spring and early summer. In contrast to the results from Sevilla, Recio et al. (2010) found increasing grass pollen counts and more days with numbers over 100 grains/m^3 in Malaga during the springs 1992–2007, which they related to increased temperature and minimum temperatures during early spring, i.e., at seed germination and vegetative growth. Also the study from Sevilla, Spain (Gonzalez Minero et al. 1998), the total pollen index increased with increasing rainfall between 1 January and 2 months onward. However, neither temperature prior to anthesis nor autumn precipitation was found to be important. In Melbourne, Australia, with a semiarid climate, the seasonal total of grass pollen was significantly correlated to the rainfall sum of the preceding year (Schappi et al. 1998). Craine et al. (2010) found an interspecific difference in the response to precipitation during the growing season at different times in three American tallgrass prairie grass species, which they related to differences in their phenology of resource uptake.

In a study of *Artemisia vulgaris*, the highest annual pollen indexes were recorded during years when the maximum temperature was moderately high (between 22 and 25°C) and there also was a high amount of precipitation during the 4 months preceding flowering. Higher maximum temperatures combined with lower precipitation, i.e., a tendency to drought, were correlated to a lower annual total. Especially, rainfall recorded in the first fortnight of July had a positive effect on pollen season intensity (Stach et al. 2007b).

Studies on yield in grass species used for forage indicate that in northern temperate areas, growth conditions in the year previous to flowering could affect the annual pollen index. Thus, the carbohydrate status at the time of floral induction can influence the magnitude of reproductive output during the next summer. In several cool-season perennial grasses, as much as 92 % of the seed yield is said to be set before the onset of conditions favouring vernalization, i.e. during the growth season previous to flowering. But there is a variation among species. In *Poa pratensis* and *Festuca rubra*, the tiller height at the end of post-harvest regrowth period was consistently related to flowering and seed yield. A connection between the basal diameter of vegetative tillers in autumn and flowering and seed yield was found in young stands of the same species, but not in older ones. Also, in *Dactylis glomerata* and *Festuca arundinacea*, there was an age-related correlation between the number and size of vegetative tillers before induction with flowering and seed yield in young stands. Vegetative characteristics were not related to flowering and seed production in *Lolium perenne* and

Agrostis castellana (Chastain and Young 1998). Nitrogenous fertilizers applied before the onset of primary induction increase the number of inflorescences in several dual induction grasses (Heide 1994); again, the effect is mainly indirect through an increase in the number and vigour of inducible tillers in autumn.

Grass pollen counts derive from many different species, which may result in multiple peaks. The long-term (26 year) dataset of daily airborne grass pollen concentrations in Leiden was analysed (Spieksma and Nikkels 1998) in order to identify trends and variations. Analysis showed that individual years had their own characteristic periods of high and low grass pollen concentrations, very often with multiple peaks. Average daily grass pollen concentrations over the 26-year period showed that the data had a tendency towards a bimodal distribution, as observed by Norris-Hill (1995), with a main peak in mid-June followed by a secondary peak in the first week of July.

In the Mediterranean, Poaceae anthesis may continue throughout the year. It is generally most intense in late spring and early summer, but peaks may appear also in early spring and later, during summer, the latter depending on rainfall during May (Gonzalez Minero et al. 1998). In North Europe, the grass pollen period continues from late spring until early autumn. Models of the course of grass pollen anthesis can be strengthened when the grass pollen season is divided into three periods (Smith and Emberlin 2006). Pollen counts during the earliest period (end of May) can be used to predict the counts in July and August.

The intensity of the grass pollen season has a positive correlation with duration, because both rely on common variables. Davies and Smith (1973) used cumulated temperature divided with the number of days during two months prior to anthesis to predict the peak date. In a study from Bilbao, both season length, as well as the time to the peak date, was related to cumulated temperatures (800–900°C). The results of Emberlin and her colleagues (Emberlin et al. 1993, 1999) show that an early start date for the pollen season will lead to a higher total pollen catch. A similar relationship to phenology was confirmed by a model based on the dates when the cumulated pollen counts reach a particular value (Davies and Smith 1973). The earlier these cumulated counts are obtained, the greater is the likelihood of a high pollen index.

3.5.3 Flowering Intensity in Trees

In trees and other perennial plants, it is common that reproductive effort varies among years, e.g. in *Betula* (Emberlin et al. 1993; Dahl and Strandhede 1996; Mahura et al. 2007; Ranta et al. 2008), *Olea* (Galán et al. 2001), *Alnus* (Rodriguez-Rajo et al. 2006) and *Quercus* (Jato et al. 2007). During one year, many flowers and fruits are produced in a population and in an entire region, whereas in other years, reproduction is moderate or sparse. The phenomenon is called masting, and a year of high abundance is called a mast year.

A number of non-mutually exclusive hypotheses as to the evolutionary advantages of masting have been proposed. The result would be efficient pollination, especially in wind-pollinated trees, abundant fruit set, satiating seed predators (Janzen 1971), and vigorous progeny (Ranta et al. 2008). In contrast, the resource matching hypothesis states that reproductive output will vary in response to environmental variation in the absence of selection for (or against) masting (Kelly 1994).

Many species are claimed to have an innate flowering rhythm, where mast years recur every second or third year, depending on specific characteristics and processes within the tree. A biannual cycle has been described for *Betula* (Jäger et al. 1991; Jato et al. 2002; Latałowa et al. 2002), *Olea europaea* (Lavee 2007), *Alnus glutinosa* (Rodriguez-Rajo et al. 2006) and *Quercus ilex* (Latorre 1999 in Weryszko-Chmielewska et al. 2006). In *Fraxinus*, there is a tendency to a 3-year cycle, corresponding to the number of seasons between floral initiation and pollen emission (Dahl and Wallander, personal data).

The specific cycle length appears to be affected by the shoot architecture, the schedule of development of different organs and their relative demands, and possible competition for energy (Dahl and Strandhede 1996). These properties could actually be interpreted as evolutionary constraints for a constant reproductive output. For various fruit species, the developing fruit has been suggested to act as a sink competing for metabolites (Monselise and Goldschmidt 1982), but the negative effect upon future reproduction is not universal (Dahl and Strandhede 1996; Lavee 2007). In contrast, Dahl and Strandhede (1996) found evidence for competition for resources between elongating inflorescences and expanding leaves in the same shoot in *Betula pendula*, resulting in a diminished assimilation capacity and a negative effect on the development of new inflorescence initials and the following pollen-production. In a study of *Styrax obassia*, Miyazaki et al. (2002) found a lower amount of starch in reproductive than in non-reproductive shoots during the growing season of a mast year. Leaves of reproductive shoots had a significantly smaller area, a lower mass per area and lower concentrations of nitrogen than leaves of non-reproductive shoots, indicating a similar competition between reproductive and assimilating organs.

In *Olea*, differences in growth regulators in leaves and buds between the so-called "on" (heavy flowering) and "off" (lean flowering) years have been reported (Lavee 2007). They indicate that masting indeed appears to be the result of selection in this species, and not just the result of morphological and physiological constraints. The growth regulators are supposed to balance the development of vegetative and reproductive shoots and, at the same time, act as vectors to initiate the specific metabolic activity controlling the flowering and fruit potential for the next year. According to resource-budget hypotheses (Isagi et al. 1997), a tree will reproduce when accumulated resources exceed a certain threshold, which can be determined by the cost of reproduction in the species in question, e.g. according to fruit size, but not necessarily by environmental factors.

As a support for the resource-matching hypothesis, several studies show the effects of varying environmental conditions, causing a high degree of synchronization between conspecific trees in the same region, and even, as found by Ranta et al. (2008) for *Betula pendula* and *B. pubescens,* over wide geographical areas.

Such a pattern may be more evident in areas where environmental conditions are limiting factors to reproduction. In *Olea europaea*, winter chilling (below 9°C) was suggested to cause such synchronization in for flowering bud differentiation in areas where relatively warm winters are common (Hartmann and Prolingis 1957 in Lavee 2007) A correlation between the amount of chilling and the pollen index has been reported; rainfall during the vegetative period exerted the greatest influence on olive flowering intensity in Spain (Galán et al. 2001). In oak, rainfall and temperature prior to the pollen season are the most important independent variables for predicting the pollen season intensity for *Quercus* in the Iberian peninsula (Garcia-Mozo et al. 2006). Similarly, the amount of rainfall during the rainy season of the year previous to flowering is positively correlated to the annual pollen sum for oak in northern California (reference in Antepara et al. 1995). In North Europe, a number of studies show the importance of the weather conditions during the previous growing season for the intensity of birch flowering (Emberlin et al. 1993; Dahl and Strandhede 1996; Rasmussen 2002; Ranta et al. 2005; Ranta and Satri 2007). Emberlin et al. (1993) used pre-seasonal meteorological parameters as independent variables in a multiple regression model. Among the tested parameters, precipitation and temperature values until the end of April, performed best.

A number of authors emphasize the importance of combining biological and meteorological factors when predicting pollen intensity in anemophilous trees. Lavee (2007) described the intricate interaction between endogenous processes and the environment in *Olea*. Dahl and Strandhede (1996) found that favourable conditions could compensate for the innate competition between leaf expansion and flowering in *Betula*. If late spring and early summer are warm enough, assimilation will be promoted and hence the trade-off effects caused by competition between the catkins from the previous year and those from the current year decreased. If a number of favourable years follow one another, the endogenous flowering rhythm, in the case of *Betula* a biannual cycle, will not be apparent. Ranta et al. (2008) tested a combined resource-budget and environmental effect model developed in Japan by Masaka and Maguchi (2001) for birch. This model is based on the assumption that abundant flowering and seeding in a mast year depend on resource accumulation over several years, affecting the amount of catkin initiation in springtime, as well as weather factors stimulating catkin growth and development during late spring and early summer during the year prior to flowering. They suggested that the model is not suitable for data sets longer than 10 years, if there is some long-term trend in environmental conditions affecting the amount of flowering such as increase in mean annual temperatures induced by climate change. However, for shorter time-spans, the annual fluctuations are well explained.

3.5.4 The Effects of Atmospheric Carbon Dioxide

Besides temperature and water, atmospheric CO_2 could be considered as an important environmental factor influencing plant physiology, principally through its direct effects on photosynthesis, photorespiration, dark respiration and stomatal physiology.

Due to projected rates of future atmospheric CO_2 increase given by current climate change scenarios, scientists became interested in the impacts of CO_2 on growth and pollen production, especially in plants with C3-type photosynthesis that are currently carbon-limited. The increase of CO_2 is suspected to stimulate photosynthesis, resulting in increased vegetative growth and pollen production (Skjoth et al. 2007). For ragweed, it was shown that large plants produce more pollen grains and seeds than small ones (Fumanal et al. 2007). As is experimentally confirmed any ecological factor resulting into biomass increase inevitably leads to increased pollen production per plant (references in Rogers et al. 2006).

Ziska and Caulfield (2000, in Rogers et al. 2006) performed a highly controlled experiment involving ragweed reared in growth chambers. Pollen production per plant increased significantly with increasing CO_2 concentration: 132 % more pollen was produced by plants living in the current CO_2-concentration as compared to plants that were exposed to pre-industrial CO_2-levels. Another study (Rogers et al. 2006) confirmed these results. It also showed that earlier germination induces higher pollen production. Similar responses of ragweed plants to increased CO_2 concentrations were also found in field studies. This has implications (increasing biomass and pollen production) for plants that live in areas enriched with greenhouse gases. In places like roadsides, it was experimentally proved that an enriched CO_2 environment induces increased levels of *Amb a* 1 allergen in the pollen grains, although their total protein content remained unchanged (references in Rogers et al. 2006)

Elevated CO_2 concentrations resulted in greater biomass and/or seasonal pollen production in loblolly pine (*Pinus taeda*) at the Duke University forest Free-Air CO_2 Enrichment (FACE) site (reference in Rogers et al. 2006) and in field studies of soybean (*Glycine max*), velvetleaf (*Abutilon theophrasti*) and tomato (*Lycopersicon esculentum*) (Ziska et al. 2001).

3.6 Impacts of Climate Change on Plants

During the twentieth century, the average annual surface temperature has increased by 0.8°C in most of Europe. Results of the Intergovernmental Panel on Climate Change (IPCC), Working Group II on Impact, Adaptation and Vulnerability (Alcamo et al. 2007) showed that from 1901 to 2005, average temperature in Europe increased by 0.9°C, with a larger increase in winter than in summer. During the most recent period (1979–2005), the trend is considerably higher (+0.4°C/decade). Precipitation trends in the twentieth century showed an increase (10–40 %) in northern Europe and a decrease in southern Europe (up to 20 % in some parts).

3.6.1 Impact of Climate on Phenological Events

Climate change affects the physiology, phenology and distribution of European plant and animal species. Phenological data are simple to record, and the scientific community has pointed out the value of historical phenological databases for the climate change research. A meta-analysis, comprising different species in European countries, has shown that the response of spring phenology to temperature is unquestionable (Menzel et al. 2006). Changes in phenology depend on the season when they take place, and also on climatic trends (Gordo and Sanz 2005). In general it has been demonstrated that greater phenological changes are recorded in those events that occur earlier in the year, from early spring to summer. This emphasizes the fact that changes in temperature are more pronounced in winter and early spring (Scheifinger et al. 2002; Peñuelas et al. 2002; Menzel et al. 2006). However, for phenological events that occur in autumn, it is more difficult to define a pattern since greater interannual oscillations occur (Menzel et al. 2006; Gordo and Sanz 2005).

In Europe, an increase of annual mean temperature in the last 30 years has been associated with an advance of the growing season start and increase of its duration; the end of the growing season showed a lower variability in all regions of Europe (Chmielewski and Rötzer 2001). Studies at regional scale have shown that the rate of change is higher in Western Europe and Scandinavia, and that different phenological rhythm and trends occur in the Eastern part of Europe (Ahas et al. 2002; Chmielewski and Rötzer 2001). Most long-term phenological studies to date have been focused on Northern Europe, while comparatively few have addressed the Mediterranean region (Peñuelas et al. 2002; Gordo and Sanz 2005). For instance, it is important to consider that in the Mediterranean region other variables related with changes in rainfall and water availability are also important (Peñuelas et al. 2004). However, Gordo and Sanz (2005) suggested that the relationship between water availability and different phenological phases is difficult to quantify.

Furthermore, at regional level in Europe, it is important to consider the role of North Atlantic Oscillation (NAO) in governing the temporal variability of the lower atmosphere, and thus phenological dates in Europe (Scheifinger et al. 2002; Chmielewski and Rötzer 2001). The NAO is the dominant mode controlling (above all winter and spring) climate over Europe. It is characterised by the longitudinal oscillation of atmospheric mass between the two dominant pressure systems over the North Atlantic sector, namely the Azores high and the Icelandic low. Its positive state (high pressure difference between the Azores high and the Icelandic low) is connected with increased zonal flow and causes northern Europe to experience wet and mild winters while over southwestern Europe, winters are anomalously dry (Xoplaki et al. 2004). During its negative state, northern Europe experiences dry and cold winters while the winters in the western Mediterranean are wetter than normal (e.g. Wanner et al. 2001). For central Europe, however, the NAO is of minor importance as this region is located at a transition zone of the main centers of action (Azores high, Icelandic low and Russian high). For a detailed discussion of this phenomenon see Wanner et al. (2001). The NAO accounts for a significant amount of the interannual variation in temperatures in the North Atlantic (Menzel et al. 2006; Post and Stenseth 1999). Plant phenology in this region is therefore influenced by year-to-year variations in the NAO (D'Odorico et al. 2002; Stenseth et al. 2002). The maximum influence of the NAO on phenological dates is found on early phases and decreases with an increasing number of days after January 1st (Scheifinger et al. 2002). The influence of the NAO is also reduced with increasing distance from the Atlantic coast (Scheifinger et al. 2002; Ahas et al. 2002; Menzel et al. 2006).

Climate change may also influence the behaviour of the NAO. This may enhance or mask climate change on a regional level, which may lead to regionally very different implications of climate change on plant phenology. In this context the influence of the NAO on phenological trends should be mentioned. A recent example is the change of the NAO from predominantly negative to positive states around 1990. This change advanced many phenological dates leading to pronounced trends. Hence recent trends in phenological time series should be interpreted along with changes in the NAO.

3.6.1.1 Impact of Climate on Pollen Content in the Air (Floral Phenology)

Many studies point out the role of phenology as one of the most important bio-indicators to study the direct impact of global warming on different species, both at temporal and spatial level. Climate-related morphological changes in many plants are also good bio-indicators of different conditions that characterize the climes. The pollen content in the air offers a quantitative variable to describe the floral phenology of anemophilous plants. For this reason, pollen season and pollen intensity historical databases have a relevant importance on global warming adaptation studies. For example, a report published by the Minister of Environment in Spain recommends the support of phenological networks, including aerobiology among others, to monitor impacts on plant biodiversity (Fernández-González et al. 2005). In a report produced on an assignment from the Swedish Environmental Agency, it is stated that monitoring of airborne pollen and allergens could be necessary to follow the possible health effects of global warming, and the same agency supports the development of a national phenological network. It should be noted, however, that certain characteristics of the pollen season (such as start or intensity) can be affected by long-distance transport, Therefore, it is necessary to make allowances for this when interpreting the data.

3.6.1.2 Climate Impacts on the Timing of Pollen Seasons

As the World Health Organization (WHO) has concluded in the document on Phenology and human health, allergic disorders, an earlier start and peak of the pollen season is currently more pronounced in species that start flowering earlier in the year, whereas the duration of the season becomes extended in summer flowering species (Huynen et al. 2003).

Different aerobiological studies, based on long historical databases, have shown earlier pollen seasons during recent years as a result of temperature increase, most of them related to spring flowering trees (Garcia-Mozo et al. 2006; Galán et al. 2005; Emberlin et al. 2007; Damialis et al. 2007; Frei and Gassner 2008; Bonofiglio et al. 2009; Orlandi et al. 2009). The greater advances observed in earlier rather than later spring pollen seasons are probably due to the higher dependency on temperature of early spring tree species, such as hazel, alder and birch. This fact could also be explained by the influence of the NAO on pollen season start (D'Odorico et al. 2002; Smith and Emberlin 2006; Smith et al. 2009). The seasonality of the NAO suggests that the phenomenon is more likely to affect ecological mechanisms in winter (Hurrell 1995; Ottersen et al. 2001). Indeed, some relationship was found between grasses and the NAO (Smith et al. 2009), but it should be remembered that several factors other than temperature affect the flowering date, like photoperiod and water availability.

However, it is important to take into consideration that the pollen season advance or delay depends on the period of time selected for the study and the temperature trends during these years, i.e. a moderate increase of temperature resulted in a delay in winter/early spring tree pollen season start (Emberlin et al. 2007; Tedeschini et al. 2006). It also depends on regional characteristics (Orlandi et al. 2009; Recio et al. 2009), what may confound patterns. This is possibly the reason why there are no clear systematic patterns on pollen season dates in South-Eastern Europe, i.e. Greece (Damialis et al. 2007).

An advance in reproductive phenology could give rise to a greater risk of exposure to late frosts, with plants being more exposed to cold stress episodes that can provoke damage on the reproductive structures (Linkosalo et al. 2000; Scheifinger et al. 2002; Garcia-Mozo et al. 2001). In addition, increases on climatic variability and incidences of extreme events are aspects of climate change that can affect less drought-tolerant species (Huynen et al. 2003).

There are also differences in response to climate change depending on the species. Although earlier and longer pollen seasons also occur in some spring flowering herbaceous plants, such as *Artemisia* in Eastern Europe (Stach et al. 2007b), the long-term trends seem to be less remarkable for grass and weeds than for trees (D'Amato and Cecchi 2008). Stable trends, with a slight tendency to delayed weed pollen season start, have been observed in southern Europe (Alcázar et al. 2009; Recio et al. 2009).

3.6.2 Climate Impacts to Pollen Season Severity and Projections

As previously mentioned (Sect. 3.5.2), different researchers have observed an increase in annual pollen index in some winter-spring flowering trees (Garcia-Mozo et al. 2006; Damialis et al. 2007; Frei and Gassner 2008; Bonofiglio et al. 2009), being regulated by weather factors together with the system of resource allocation among years (Dahl and Strandhede 1996; Ranta et al. 2005). It should also be noted that there are possible interactions with other components of global change. For instance, it is important to consider that atmospheric increases of CO_2 and the deposition of nitrogenous compounds favour plant activity and photosynthesis, which favours an increase in floral intensity (Garcia-Mozo et al. 2006; Rogers et al. 2006; Ziska et al. 2001, 2008). In general, long-term trends are more evident in the amount of pollen produced by trees and shrubs than by herbs (Damialis et al. 2007). Precipitation trends in Europe may also affect floral intensity. This is because of the generally low water availability in the Mediterranean region; especially for herbs and grasses, declining precipitation can provoke declining annual pollen counts (Recio et al. 2010). However, relating changes of pollen season intensity to climate change cannot be straightforward. Relationships between climate change and pollen production increase are not always evident and depend on the site and the period of time studied (Clot 2003). Among the factors that may influence pollen counts are changes to land use and urban green space designs (like the planting of ornamental plants in urban areas).

The NAO may have an influence on the intensity of the pollen season. There is a significant positive relationship between total pollen count and averages of the NAO the previous year in Poznan (Poland). The city has a continental climate, but it is located in an area where winds arrive predominantly from the west and southwest (Woś 1994; Stach et al. 2008; Corden et al. 2000). In the likewise Polish city Krakow, the intensity of *Betula* pollen seasons do not appear to be influenced by the NAO, which is probably the result of a more continental climate. Also, in contrast to the situation in Poznan, in Worcester and London, the temperatures and averages of the NAO during the year previous to pollen dispersal were negatively related to the pollen counts. Instead, the intensity of the birch pollen season at these locations was positively correlated to temperatures and averages of the NAO during winter and spring in the current year (Stach et al. 2008).

Predictive modelling based on climate projections is an important tool to allow the adoption of mitigation measures for the anticipated impacts. However, only few studies in aerobiology have focused on this topic. Future meteorological data modelled by the Hadley Meteorological Centre, included in the Intergovernmental Panel on Climate Change (IPCC), have been used for estimating future projections on pollen season start dates and intensity for different trees in the Iberian Peninsula (Garcia-Mozo et al. 2006; Galán et al. 2005) and the UK (Emberlin et al. 2007). Studies on some spring flowering trees in southern Europe indicated that, under a double CO_2 scenario, at the end of the twenty-first century pollen seasons for these species will start from 1 week to 1 month earlier, depending on the plant and the study area, with stronger effects in inland areas.

3.6.3 Climate Impacts on Plant Migration

With climate change, non-native species from adjacent areas may cross over frontiers and become new elements of the biota. When such movements cover long distances, they can usually be attributed to human activity (Walther et al. 2002). Either plant invasion or long-range transport of foreign allergenic pollen exposes citizens to new allergenic pollen grains.

Ragweed (*Ambrosia*) is an important cause of pollen allergy in Eastern and Central Europe and can be presented as a recent example of biological invasion.

It has been introduced in Europe with cereal grain from North America (Smith et al. 2008; Stach et al. 2007a). Ragweed populations do not tend to thrive under a maritime climate and in northern Europe the growing season is often too short for seed maturation (Comtois 1998; Dahl et al. 1999; Saar et al. 2000). *Ambrosia* has been recorded as far north as Poland, the Baltic States and even Sweden, but populations are often ephemeral and scattered and reliant on the regular introduction of seeds from outside sources (Dahl et al. 1999; Saar et al. 2000; Stepalska et al. 2002). Often, ragweed does not reach maturity in northern latitudes and so the occurrence of *Ambrosia* pollen may be reliant on conditions being appropriate for both germination and flowering or long-range transport (Stach et al. 2007a). However, when seed set does occur, it may contribute to a persistent seed bank. Climate change may therefore allow ragweed to spread to areas where populations have not previously been able to establish.

3.6.4 Climate Impacts on Public Health

Climate change can prolong or shorten pollen seasons, increase or decrease pollen season intensity and aid the spread of species with allergenic interest. In addition, the higher occurrence of heavy precipitation events and an increase of episodes of urban pollution can provoke or aggravate health problems (Ziska et al. 2008; D'Amato and Cecchi 2008) including negative effects on respiratory allergic diseases. However, the data and tools currently available make predictions quite uncertain. To face this limitation, a number of activities should be undertaken. As also recommended by Cecchi et al. (2010), (a) aerobiological data should be collected in a structured way at the European level, (b) multidisciplinary research teams should be created, promoted and supported, (c) there should be more attention to and emphasis on the pollen/spore exposure in the guidelines for the diagnosis and treatment of respiratory and allergic diseases, and (d) communicating the importance of aerobiological research and lobbying the European Union and other funders to finance this research should become priority activities.

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