# The growth and phenology patterns of herb Paris (*Paris quadrifolia* L., *Trilliaceae*): relation to soil and air temperatures

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The phenology and development of *Paris quadrifolia* L. has been related to variations in soil and air temperatures during four seasons (1997–2000). Its emergence appeared to be strongly dependent on soil temperature. Plants became visible as soon as the daily mean maximum soil temperature reached *ca*. 7 °C. Variations in soil temperatures could delay Paris emergence by almost one month during the study period. The plants needed on average 18 days to develop from 10% to 95% of maximum height, and flowers were developed after *ca*. 30 days. The growth and phenology pattern of Paris is therefore not typical of a light-demanding early spring plant. Its need for a relatively long developmental period is compensated for by its ability to survive by vegetative growth during low light periods. The investigation showed that the temperature sum is not a useful tool for predicting phenological events in areas where frozen soil occurs. Two populations separated by *ca*. 6 m had a two-week difference in emergence due to differences in soil temperature. Sterile plants were generally lower than 14 cm and fertile plants were mostly taller than 20 cm. This pattern appeared to be the same in different geographical areas.

**Key words:** *Paris quadrifolia,* phenology, temperature, soil, air

## INTRODUCTION

Paris is a clonal rhizomatous species which is common on fertile and moist soils over most of Northern Europe. In parts of Southern Europe it is rare and considered endangered, and according to Kranczoch (1997) it can be used as an indicator species for historically old forests. However, it has been shown recently that *Paris quadrifolia* L. is more common in young than in old stands (Elofsson et al., 2000). Paris is mostly primarily adapted to shadow and is frequently found in edaphically rich and dense vegetation (Čiuplys, 2001; Diekmann, 1996; Odland, 1992).

Paris starts to develop relatively early in spring (April) and usually flowers in May (Falinska, 1972). The growth of the underground rhizome starts later in the season, after the above-ground shoots start to decay. (The growth of the aerial shoots and the rhizome does not take place at the same time (Schroeder, 1921)). When the aerial shoot has died off, the rhizome increment is completed. Its annual length increment ranges mostly from 2 to 8 cm (Kranczoch, 1997).

There is generally a major difference in final height between fertile and sterile Paris plants (Kranczoch, 1997), but they seem to emerge at the same time in spring. It is, however, not known if these patterns are the same in different geographic areas.

Diekmann (1996) showed that its timing of flowering could be predicted by the cumulative sum of daily temperatures higher than 5 °C after January 1. The date at which the plants appear in spring and when they flower is determined by an interaction of both genetic and environmental factors. Though flowering may be controlled by photoperiod (*e. g*., (Vince-Prue, 1975)), most investigations have shown temperature to be the prime controlling factor (Chapin, 1974; Diekmann, 1996; Fitter et al., 1995). In most cases, the phenology of plants has been related or modelled in relation to air temperatures. This may, however, not always give a highly predictive estimate of phenological events. Soil temperature has long been recognised as an important factor affecting plant growth (Anderson et al., 1972; Nielsen et al., 1966) and thereby influencing species distribution (Kramer, 1942). Most plants have a soil temperature threshold, and they will not start to emerge before that is reached, despite favourable air temperatures (Holway et al., 1975; Odland, 1995). Karlsson and Nordell (1996) showed that variation in growth could be more affected by soil temperature than by nutrient level.

The main aim of the current work was to study important phenological events and patterns of development of Paris in relation to air and soil temperature.

## MATERIALS AND METHODS

Data on plant development and measurements of soil and air temperature were collected in Norway during the summers of 1997–2000 within homogeneous Paris populations. Five different populations were studied, population A was studied both in 1997 and 1999 (Table 1). The populations lied within an ecotone between meadows and *Alnus incana* forests. The study site was located at Hørte in SE Norway (59° 20‘ N, 9° 2‘ E) *ca*. 70 m a.s.l. Mean July and January temperatures for the closest meteorological station (Gvarv, 26 m a.s.l.) were 16.0 and –6.6 °C, respectively (Aune, 1993). Average annual precipitation was 780 mm (Førland, 1993).

Soil temperatures were recorded every hour with a data-logger, with the sensor placed 5 cm below the soil surface. The daily maximum and minimum values at a given depth are assumed to influence plant growth most (Richards, 1952).

Mean daily air temperature data were provided by the Norwegian Meteorological Institute (data from 1997 were not available). In the spring of 1999 and 2000, 5 and 10 plants respectively within different Paris populations were selected at random and labelled as they appeared above soil. Their heights were measured until they were fully grown. “Date of emergence” is here defined as the day when more than five Paris plants within the population have become more than 5 cm high. The number of days the plants needed to develop from 10 to 95% of maximum height was counted (Odland, 1995). All phenological events were given as days since April 20 (day 1). Maximum relative growth rate (RGR) was calculated and given as the percentage of height growth per day in relation to the final height.

The height (from the soil surface and up to the leaf bases) was measured on plants within populations from different parts of Norway and Lithuania. (The following numbers of plants and populations were studied: Western Norway – 142 plants from 11 populations; South East Norway – 223 plants from 18 populations; Troms County, North Norway – 227 plants from 12 populations; Finnmark County, North Norway – 65 plants from 3 populations.) The populations in Western and North Norway were mostly situated in *Alnus incana* forests and in South Eastern Norway in *Alnus incana – Picea abies* forests.

The height of fully grown sterile and fertile plants of *Paris quadrifolia* was measured in six Lithuanian populations in July 11–24, 2001. Six natural populations of herb Paris were chosen: three populations in Varėna district, two populations in Labanoras forest (Molėtai district) and one population in Grigiškės (Trakai district). All the populations grew in moist *Alnus glutinosa* forests.

## RESULTS AND DISCUSSION

The relationship between the day of emergence of Paris and soil temperature is shown in Table 1. During the study period, emergence varied from April 24 (2000) to May 19 (1999), *i. e*. within almost a month. Figure 1 shows the variation in soil temperatures during 1997 and in soil and air temperatures during the spring of 1998–2000. There was a gradual increase in soil temperatures, but the pat-

Table 1. **Dates of emergence and flowering of *Paris quadrifolia* L. and soil temperatures in 1997–2000**

| Year | Population | Day of emergence | Day number | Maximum daily soil temperature, °C | Minimum daily soil temperature, °C | Date of flowering | nD[a] | Tsum[b] |
|---|---|---|---|---|---|---|---|---|
| 1997 | A | May 1 | 12 | 6.0 | 4.1 | May 30 | 29 | |
| 1997 | B | April 30 | 11 | 6.0 | 2.0 | May 30 | 30 | |
| 1998 | C | April 27 | 8 | 6.0 | 3.9 | | | 98.0 |
| 1999 | A | May 5 | 16 | 8.3 | 3.4 | May 31 | 26 | 200.3 |
| 1999 | D | May 19 | 30 | 8.2 | 4.8 | | | 331.5 |
| 2000 | E | April 24 | 5 | 5.5 | 4.1 | May 25 | 31 | 124.3 |
| Mean ± SD | | | | 6.7 ± 1.2 | 3.7 ± 1.0 | | 29.0 ± 2.1 | 188.5 ± 104.7 |

[a] Number of days from emergence until the flowers were developed.
[b] Cumulative air temperature (sum of mean daily temperatures above 5 °C) until plant emergence.

tern was highly variable and obviously influenced by frozen ground, air temperatures and snow. During a day, there was mostly a 2–4 °C difference between the maximum and minimum soil temperatures, but in periods with low air temperatures the difference was smaller. Table 1 shows that two populations (A and D, Fig. 1 d and 1 e) separated by only 6 m showed a two-week difference in emergence in 1999. Population D (Fig. 1e) was obviously influenced by frozen ground as there was a slow increase in soil temperature. Days of emergence are shown in Table 1 and Fig. 1. On average, Paris started to emerge when the maximum soil temperature exceeded 6.7 °C and the minimum exceeded 3.7 °C. The flowers were fully developed one month after emergence (Table 1).

The cumulative air temperature until Paris emergence is given in Table 1, and the values varied greatly, so air temperature sum appeared to be a poor predictor of Paris emergence in this area. The

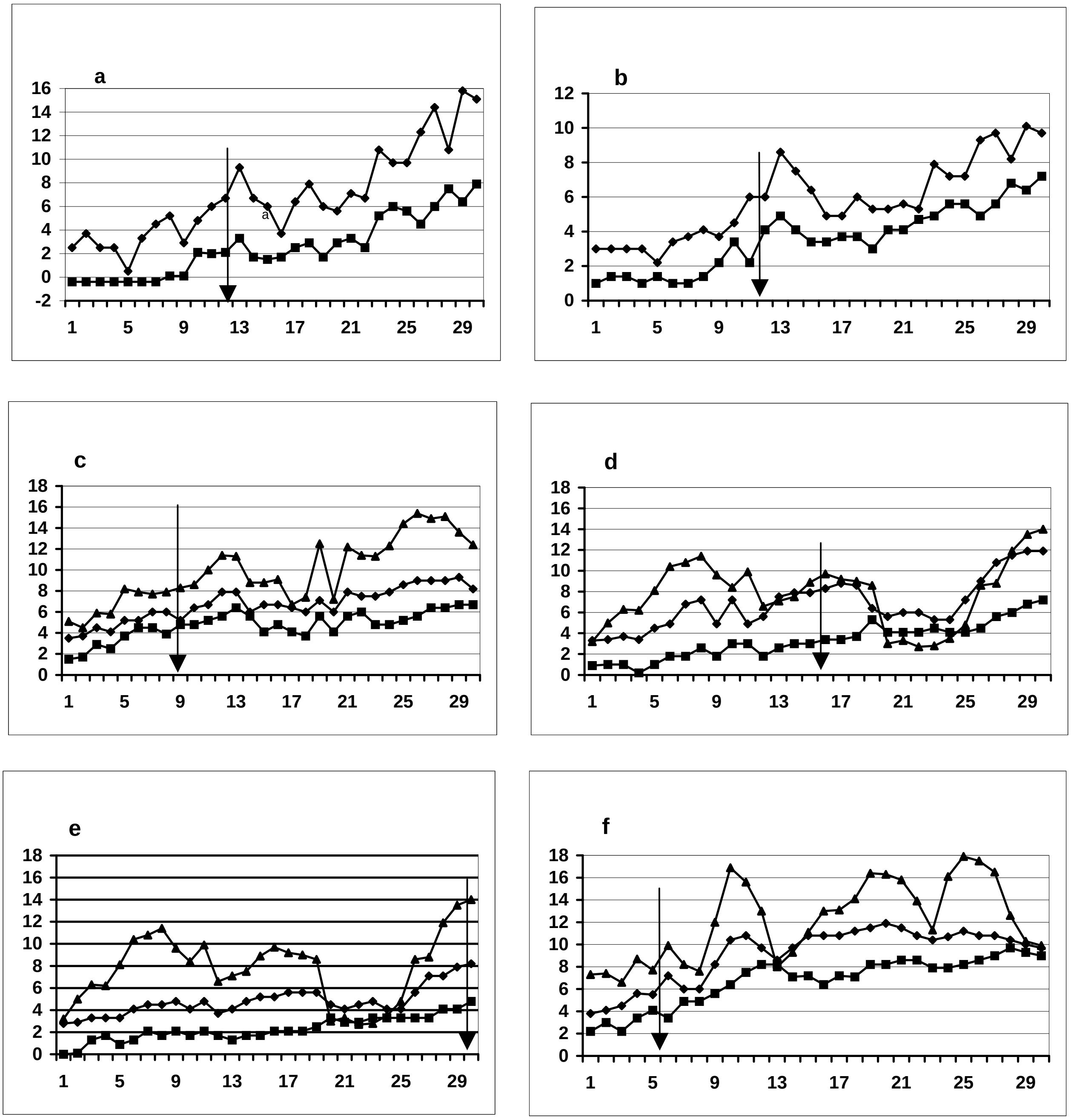


Fig. 1. Variation in maximum (♦) and minimum (■) soil temperature and air temperature (▲) (vertical scale) during the period from April 20 (day 1) until May 19 (day 30) (horizontal scale): *a* – population A in 1997, *b* – population B in 1997, *c* – population C in 1998, *d* – population A in 1999, *e* – population D in 1999, and *f* – population E in 2000. Day of Paris emergence is indicated with a vertical arrow (see also data in Table 1)

cumulative temperature sum associated with the development of flowers during the summer of 2000 was 425.5 degree-days.

Data on Paris plant development in 1999 and 2000 are given in Table 2. There was a difference between fertile and sterile plants both with regard to final plant height and maximum growth rate. Variations in mean plant height of fertile and sterile shoots of Paris from different populations of Norway and Lithuania are shown in Fig. 2. In general, sterile plants were lower than 14 cm and fertile ones taller than 20 cm. Norwegian plants were generally taller than Lithuanian, except for population 6. Maximum Relative Growth Rate (RGR) was reached after about 8 days, and it varied between 10 and 15% day$^{-1}$ (Table 2). Despite that the date of emergence was highly different between these years, there was only a small variation in the number of days the plants needed to develop from 10% to 95% of maximum plant height. The cumulative sum of daily temperatures needed until the final plant height was highly different in 1999 and 2000, as was the sum for the developmental period from 10% to 95% of maximum plant height.

The study shows that a certain soil temperature threshold has to be reached before *Paris* plants start to emerge. At the maximum daily soil temperatures below 7 °C the growth was poor. Similar values have also been recorded for several other plants (Hagan, 1952; Odland, 1995). According to Diekmann (1996), Paris may be classified as an early-flowering species: he found the average full flowering date to be May 28. Compared to, *e.g*., *Hepatica nobilis* (April 21), *Carex digitata* (April 29), *Ranunculus ficaria* (May 3) and *Anemone nemorosa* (May 3), this was, however, not particularly early.

The Paris plants studied needed on average 18 days to develop from 10% to 95% of full size, and flowers developed *ca*. 30 days after emergence. This is not a particularly rapid developmental rate. One of its frequent competitors, *M. struthiopteris,* can produce all its vegetative fronds over a period of 14–31 days, depending on air temperatures (Odland, 1995), and also initiated its growth at the same soil temperature threshold.

Table 2. **Development of randomly selected Paris *quadrifolia* plants in 1999 and 2000**

| Year | Number of plants | Day of emergence | Reproductive phase[a] | RGR[b] | Mean maximum plant height, mm | nD[c] | Tsum1[d] | Tsum2[e] |
|---|---|---|---|---|---|---|---|---|
| 1999 | 9 | May 19 | F | 10.0 | 262 | 18 | 506.1 | 207.3 |
| 1999 | 1 | May 19 | S | 9.6 | 180 | 18 | 506.1 | 207.3 |
| 2000 | 2 | April 24 | F | 15.5 | 230 | 17 | 373.9 | 249.6 |
| 2000 | 3 | April 24 | S | 13.4 | 145 | 19 | 407.9 | 283.6 |

[a] F – fertile, S – sterile plants.
[b] Mean maximum relative growth rate (%) of maximum plant height day$^{-1}$.
[c] Mean number of days needed for the plants to develop from 10% to 95% of maximum plant height.
[d] Temperature sum (cumulative sum of mean daily temperatures above 5 °C) since January 1 to 95% of final plant height was reached.
[e] Temperature sum needed for the plants to develop from 10% to 95% of final plant height was reached.

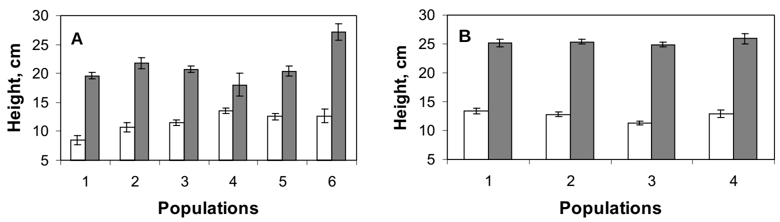


Fig. 2. Average height of sterile and fertile plants in different populations from Lithuania and Norway. 2A – populations from Lithuania: *1* – Varėna, population A; *2* – Varėna, population B; *3* – Varėna, population C; *4* – Labanoras, population A; *5* – Labanoras, population B; *6* – Grigiškės. Sterile plants – open columns, fertile plants – filled columns. 2B – data from four regional districts in Norway: *1* – Western Norway (11 populations); *2* – Southeastern Norway (18 populations); *3* – Troms County, North Norway (12 populations); *4* – Finnmark County, North Norway (3 populations). Vertical bars indicate standard error of the mean

Sterile and fertile shoots needed the same period of time to reach final plant height, and hence fertile shoots had a higher RGR.

Paris plants in different parts of Norway had almost exactly the same average height of both sterile and fertile plants. The variation in Lithuanian plants was somewhat greater. Similar studies of Paris from Oldenburg, Germany showed the same difference between sterile and fertile shoots, with 25 cm as a minimum size for fertile plants (Kranczoch, 1997). In that study, however, shoot height was measured from the rhizome, and it is generally situated about 5 cm below soil surface. These data indicate that the size of *Paris* shoots is fairly equal from north to south in Europe, but locally smaller shoots can be found.

The relationship between important phenological timing of a plant in relation to competitors and its photosynthetic response to light is highly important. It was studied by Sparling (1967), and he found a strong relationship between the phenology of Ontario woodland herbs and their photosynthetic responses. Species whose leaf development preceded canopy expansion had higher light requirements than those whose leaf development occurred later.

Paris is generally categorised as a shade-adapted plant, because it is mainly found in forest understories, and according to Ellenberg et al. (1997) its light indicator number is 3 on a 1–9 scale. According to Ögren and Sundin (1996), the photosynthetic response of Paris was also typical of a shade plant. It is capable of an effective use of lightflecks relative to continuously high light. Shade plants are generally characterised by an efficient use of varying light conditions.

This investigation shows that the cumulative air temperature sum may be a poor predictor for the phenology of plants emerging in spring. In Boreal and Alpine areas emergence may be strongly delayed due to frozen ground. A temperature threshold of 5 °C in the calculation of the temperature sum may also be questioned, since plants certainly will grow also at lower temperatures when the soil temperatures have exceeded a certain threshold.

## ACKNOWLEDGEMENT

This work was funded by the Research Council of Norway.

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**ŽOLINIO AUGALO (*Paris quadrifolia* L., *Trilliaceae*) AUGIMAS IR FENOLOGIJA: PRIKLAUSOMYBĖ NUO DIRVOS BEI ORO TEMPERATŪRŲ**

S a n t r a u k a

Keturlapė vilkauogė (*Paris quadrifolia* L.) yra daugiametis vasaržalis klonus sudarantis šakniastiebinis žolinis augalas. Šiaurės Europos plačialapiuose bei mišriuose miškuose derlingų ir pakankamai drėgnų dirvų sąlygomis *P. quadrifolia* yra ganėtinai dažnas augalas, tuo tarpu Pietų Europoje rūšis yra reta, kartais netgi priskiriama nykstantiems miškų komponentams.

Pagrindiniai *P. quadrifolia* fenologijos bei antžeminių dalių augimo tyrimai atlikti Norvegijoje per keturis vegetacijos sezonus nuo 1997 iki 2000 metų. Tirtos penkios homogeniškos, miško su *Alnus incana* prieigose lokalizuotos *P. quadrifolia* populiacijos, Lietuvoje *P. quadrifolia* šešių populiacijų tyrimai atlikti 2001 metais. Visos tirtos populiacijos tarpo vidutinio drėgnumo *Alnus glutinosa* miškuose.

Tyrimų metu nustatyta, kad *P. quadrifolia* vegetacijos laikas ir tempas tiesiogiai priklauso nuo dirvos temperatūros, *P. quadrifolia* antžeminės dalys pavasarį pradeda augti, kai dirvos temperatūra 5 cm gylyje per parą įšyla vidutiniškai iki 7 °C. Dėl žemesnių dirvos temperatūrų *P. quadrifolia* vegetacijos pradžia atskirose populiacijose tyrimų metu vėlavo beveik mėnesį. *P. quadrifolia* vegetatyviniai organai 95% išsivystymo lygį pasiekia vidutiniškai per aštuoniolika plėtros dienų, o generatyvinės struktūros susidaro maždaug per 30 dienų. Tokiu būdu, *P. quadrifolia* augimo ir fenologijos ypatumai nėra tipiški ankstyva pavasarine vegetacija pasižymintiems šviesiniams augalams, nes šios rūšies vegetatyvinės plėtros periodas yra santykinai ilgas. Kita vertus, *P. quadrifolia* gali sėkmingai augti ir esant mažam apšvietimui miškuose po medžių sulapojimo. Tyrimai parodė, kad temperatūrų suma nėra patikimas rodiklis fenologiniams reiškiniams prognozuoti tose vietose, kuriose dirvos įšąla. Dviejų *P. quadrifolia* populiacijų, tarp kurių atstumas buvo vos apie 6 m, plėtros laikas dėl nevienodų dirvų temperatūrų skyrėsi net dviem savaitėmis. Sterilūs *P. quadrifolia* individai paprastai yra trumpesni nei 14 cm, tuo tarpu fertilūs augalai – dažniausiai aukštesni nei 20 cm. *P. quadrifolia* augimo bei fenologijos ypatumai yra analogiški skirtingose geografinio arealo vietose.

**Raktažodžiai**: *Paris quardrifolia*, fenologija, temperatūra, dirvožemis, oras