

Geographic variation and bud dormancy in beech seedlings (*Fagus sylvatica* L)

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Summary – Italian populations of beech, originating from zones of similar altitudes but different latitudes (38°16'–43°49'N), were studied. The seedlings, 1 and 2 years old, were grown in Florence (43°45') under natural conditions or in climate-controlled chambers with short (SD) or long day (LD) after having been exposed, or not, to winter chilling (CH and NCH, respectively). Differences observed in precociousness of sprouting, thermal time, growth in length and duration of growing season all indicate a variation among the populations tied to the latitude of their zones of origin. Winter chilling was demonstrated to be the principal factor in the removal of dormancy in all the populations studied. In the northernmost populations a significant effect on sprouting was attributable also to photoperiodic regime. The interaction chilling x long day indicates that LD is able to partially substitute winter chilling and that once the need for removal of dormancy has been satisfied, temperature is presumably the principal environmental factor that controls sprouting.

bud dormancy / chilling / *Fagus sylvatica* / growing season / photoperiod

Résumé – **Variation géographique et dormance des bourgeons chez de jeunes plants de hêtre (*Fagus sylvatica* L).** Sur de jeunes plantules de hêtre, on a étudié la variation géographique du débourrement printanier et l'influence qu'ont le froid pendant l'hiver et le régime photopériodique sur la sortie de dormance. Les altitudes des lieux de provenance du matériel sont identiques, mais les latitudes sont différentes. Dans la première expérience on a cultivé les plantules des trois populations (Bagno di Romagna, latitude 43° 49' N ; Pacentro, latitude 42° 03' N ; Aspromonte, latitude 39° 09' N) à Florence (latitude 43° 45' N) aux conditions climatiques naturelles. Avec l'augmentation de la latitude des stations de provenance le débourrement printanier devient plus précoce (fig 1) et la croissance en longueur, le « thermal time » et le temps entre le débournement du bourgeon apical et celui des bourgeons latéraux raccourcissent (tableau I). D'après la deuxième expérience effectuée sur les plantules de deux provenances (Casentino, latitude 43° 48' N, et Aspromonte, latitude 38° 16' N) exposées ou non au froid hivernal puis cultivées en conditions naturelles à Florence, les résultats de la première expérience ont été confirmés en ce qui concerne le débournement et la croissance (tableau II, figs 2 et 3). En outre un polycyclisme très net chez la population méridionale et une forte dépendance du débournement vis-à-vis de la période de froid préalable ont été démontrés (tableau II, figs 2 et 3). Chez les deux provenances les plantules exposées au froid en hiver présentent un débournement plus précoce et plus rapide par comparaison avec celles qui n'ont pas été exposées. Cet effet est particulièrement évident dans le cas des bourgeons latéraux (figs 2 et 3). Lorsqu'on élève en chambre climatisée, à jours longs ou courts, les plantules des populations de la deuxième expérience en les

ayant exposées ou non au froid hivernal, les différences entre populations sont confirmées en ce qui concerne la précocité du débourrement, la croissance en longueur et la durée de la période de végétation (tableau III et fig 4). L'effet très net du froid hivernal sur la sortie de dormance (tableau III) et sur le débourrement qui s'ensuit des bourgeons apicaux et axillaires (tableau V) est aussi confirmé. En effet la période nécessaire pour obtenir la totalité du débourrement est plus longue de 100–150 jours (fig 4) chez les plantules non exposées au froid. On a aussi observé un effet du photopériodisme, qui semble être une caractéristique de la population la plus septentrionale (tableaux V, VI et VII). Les effets des jours longs sont nets sur les temps moyens et sur le pourcentage de débourrement et sur la somme des degrés-jours. L'interaction entre jour long et froid en hiver laisse penser que le jour long est très impliqué dans la sortie de dormance et peut se substituer partiellement aux besoins en froid. Une fois satisfaites les exigences pour la sortie de dormance, c'est la température qui intervient comme principal facteur du milieu contrôlant le débourrement. Les différences observées au cours de toutes les expériences en ce qui concerne la précocité de débourrement, la croissance en longueur et la durée de la saison de végétation indiquent toutes l'existence parmi les populations de variations liées à la latitude des lieux d'origine.

dormance des bourgeons / exposition au froid / *Fagus sylvatica* / saison de végétation / photopériode

INTRODUCTION

The seedlings of many tree species follow a rhythmic alternation of growth and nongrowth when they are maintained under constant conditions in long days or a 24 h day (Lavarenne et al, 1971; Barnola et al, 1986). The nature of the nongrowth phase is not the same in all species, however (Barnola et al, 1977, 1986).

Wareing (1953) reported that for *Fagus sylvatica* L seedlings the nongrowth phase was a state of dormancy, and that it was induced by short days (SD), and broken by long days (LD). The photoperiodic nature of stimulus perceived by the bud was shown by Wareing (1953, 1954). More recently, however, Bagni et al (1980) reported that under natural conditions sprouting in *F. sylvatica* seedlings in spring also depended upon prior chilling received. Falusi and Calamassi (1990), also working with seedlings, found that chilling was in fact the predominant factor determining rapid release from bud dormancy and bringing about the internal changes in the seedlings that lead to an acrotal vegetative habit. Heide (1993) reported that in beech provenances from northern and central Europe, both chilling and sub-

sequent long days were required for normal bud sprouting, but he found no variation in critical photoperiod among the ecotypes he studied.

The diversity of these findings suggests that differences in the qualitative and quantitative requirement for dormancy release may be due to geographical differences. Wareing (1953) suggested that the controlling factor for budding in beech was the photoperiod for southern populations and thermic conditions for the northernmost populations. Later studies (Galoux, 1966; Teissier-du-Cros et al, 1988) on beech have shown that spring budding, which is characterized by strong genetic control and genotype x environment interaction, is different under natural conditions in populations at low and high elevation.

Geographical variation in the factors that bring about release from dormancy is found in many other tree species (Heide, 1974; Campbell and Sugano, 1975; Downs and Bevington, 1981; Worrall, 1983; Oleksyn et al, 1992).

In a previous study on beech (Falusi and Calamassi, 1990), a weak interaction was observed between chilling and daylength to achieve dormancy release. The present study was undertaken to investigate

whether the role of daylength varied with latitudinal origin of the provenances.

MATERIALS AND METHODS

Plant material

Seeds were collected from 20 trees growing at least 50 m apart in each of five areas (located at similar altitudes): i) Appennino Tosco-Emiliano (Bagno di Romagna, latitude 43°49'N, altitude 1 300 m), ii) Abruzzo (Pacentro, latitude 42°03' N, altitude 1 070 m), iii) Aspromonte (Monte Basilicò, latitude 39°09'N, altitude 1 400 m), iv) Casentino (Pratovecchio, latitude 43°48'N, altitude 1 170 m), v) Aspromonte (Oppido Mamertino, latitude 38°16'N, altitude 1 050 m).

The seeds were stratified for 6 weeks at 3 ± 0.5 °C and germinated during spring in darkness at 20 ± 0.5 ° in transparent polystyrene germinators (diameter 12 cm) on filter paper saturated with deionized water. The resulting seedlings were transferred to pots containing beech-wood loam and were grown under natural conditions in Florence (43°45'N), and used as needed for the experiments. The seedlings, which spent a year in the nursery before being used (experiment 3) were watered and fertilized regularly (as indicated later) and protected during summer by a Umbratex netting which reduces light intensity by 40–50%.

Methods

Experiment 1

This experiment comprised 50 1-year-old seedlings per provenance from provenances 1, 2 and 3. The seedlings had been transplanted at the beginning of autumn in the year of germination (1987) to pots (diameter 18 cm, depth 30 cm) containing 50% fir and chestnut loam and turf and 50% sand; they were then maintained in the nursery, with a plant density of 30 plants/m², in Florence, during the winter and the following growing season. Plants were watered and fertilized when it was needed alternately with 150 cm³ of deionized water or an equal amount of half strength Knop's nutrient solution amended with microelements.

Sprouting and shoot development, the selected measures of dormancy release, were examined on all the buds of all the seedlings, initially every 3 days and then once a week until

the end of September. Sprouting was scored on the scale of Malaisse (1964). Only the first three stages were utilized in this study (stage 1: fusiform elongated buds, 2: buds are swollen and somewhat lengthened, 3: bud scales have separated and the green tips of the first leaves are emerging) while the other four stages were not used because they were not pertinent to this work. Shoot development was defined by the two parameters of length of the new shoot from the bud and the number of leaves produced.

For the statistical analysis, percentages were transformed to square root of arcsin percent (shown as actual percentage in text and tables). The data were analysed by one-way analysis of variance and comparisons were made with the LSD test.

Experiment 2

One hundred 1-year-old seedlings from provenance 4 (Casentino) and an equal number from the southern provenance 5 (Aspromonte - Oppido Mamertino) were used in this experiment. The seedlings were repotted at the beginning of autumn in the year of germination (1989) in cylindrical plastic pots (diameter 12 cm, depth 50 cm) filled with a 1:1:2 (v/v) mixture of coarse vermiculite, fine vermiculite and perlite. In October, before the onset of the cold season, 50 seedlings of each provenance were moved to a heated greenhouse (minimum temperature 16 °C) where they remained until the end of the experiment 11 months later (unchilled NCH group). Every other day the pots were given alternately 150 cm³ of deionized water or an equal amount of half strength Knop's nutrient solution amended with microelements. The remaining 50 seedlings per provenance were overwintered outside to experience winter chilling under fully natural conditions (chilled CH group). Starting from March 1990 these seedlings were watered and fertilized as those in the greenhouse. Sprouting and bud growth parameters were measured as in experiment 1. The plant density was approximately 69 plants/m². The data were analysed by two-way analysis of variance, and comparisons were made with the LSD test.

Experiment 3

Thirty-two seedlings per provenance from provenances 4 and 5 (Casentino and Aspromonte - Oppido Mamertino), as in experiment 2, were used for this experiment. When the

seedlings were in their second growing season (1990) from germination, they were repotted in cylindrical plastic pots (diameter 16 cm, depth 60 cm) filled with a 1:1:2 (v/v) mixture of coarse vermiculite, fine vermiculite and perlite. As in experiment 2, half the seedlings from each provenance were maintained in a greenhouse with a minimum temperature of 16 °C (unchilled NCH group), and half were overwintered outside to experience winter chilling under fully natural conditions (chilled CH group).

In the first week of the following March 1991, both chilled and unchilled seedlings were transferred to controlled environment chambers where half the seedlings from each category (CH and NCH) were maintained at a 9 h day (SD), the remainder at a 13 h day (LD). In both chambers, lighting was provided by fluorescent tubes producing 32 W m⁻² at crown level, day/night temperature was 24/13 ± 0.5° and relative humidity 70–75/80–85%. There were therefore four treatments: NCH-LD, CH-LD, NCH-SD, and CH-SD, each comprising eight seedlings per provenance. The plant density was approximately 35 plants/m². Plants were watered and fertilized as

in experiment 1. The trial in the controlled environment chambers lasted 235 days.

Sprouting and bud growth parameters were measured as in experiment 1. For the statistical analysis, percentages were transformed to the square root of arcsin percent. The data were analysed by two- and three-way analysis of variance, and comparisons were made with the LSD test.

RESULTS

Experiment 1

Apical buds sprouted earlier with higher latitudinal origin of the provenance (fig 1). The differences in sprouting times were caused by different requirements for resuming growth in the buds because the rate and the pattern of the successive development of the bud were much the same in all provenances; therefore, for example, there were no statistical differences in the transition times from stage 2 to stage 3 among

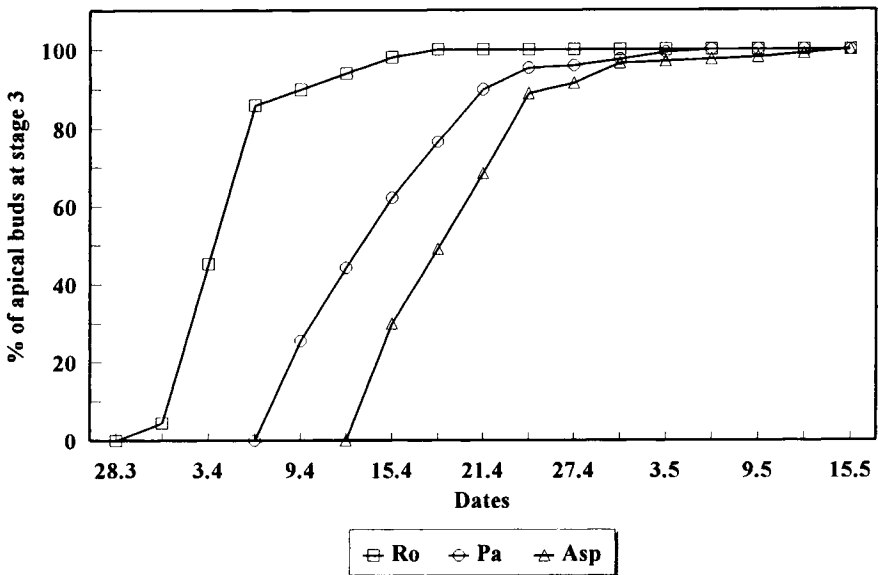


Fig 1. Sprouting pattern of apical buds of the Bagno di Romagna (Ro), Pacentro (Pa) and Monte Basilicò (Asp) provenances (experiment 1).

Table I. A. Relations among buds during sprouting and **B.** mean growth values in length of the Bagno di Romagna (Ro), Pacentro (Pa) and Monte Basilicò (Asp) provenances (experiment 1).

	I	II	III	IV	V
A	19.32 ^{ab}	43.90 ^a	39.02 ^b	17.08 ^c	2.73 ^a
Ro	14.59 ^a	43.75 ^a	45.83 ^b	10.42 ^b	4.41 ^{ab}
Pa	23.55 ^b	76.00 ^b	24.00 ^a	0.00 ^a	5.56 ^b
Asp					
B					
Ro	90.68	2.10 ^a	26.98	56.66 ^a	147.34 ^a
Pa	90.18	5.12 ^b	25.87	132.46 ^b	222.64 ^b
Asp	83.02	13.34 ^c	24.39	325.40 ^c	408.42 ^c

A: I: percentage of lateral buds sprouted before the apical buds; II: percentage of seedlings with lateral buds sprouted before their apical bud; III: percentage of seedlings in which the lateral buds sprout at the same time as their apical bud; IV: percentage of seedlings in which the lateral buds sprout later than their apical bud; V: advance (in days) between sprouting date of the lateral buds and that of the apical buds. **B:** I: apical shoot growth (mm); II: number of lateral shoots; III: mean growth of one lateral shoot (mm); IV: total growth of lateral shoots (mm); V: total growth (apical + lateral) (mm). Means followed by different letters are significantly different at 1% in LSD test.

the provenances (Bagno di Romagna [Ro] = 10.7 ± 0.72 , Pacentro [Pa] = 9.2 ± 0.88 , and Monte Basilicò [Asp] = 9.5 ± 0.58 days).

The sprouting time lags between apical and lateral buds for each provenance are shown in table I.A. In Aspromonte, the southernmost provenance (where sprouting, in any case, occurs later in the year), this time lag was longer, and involved a greater number of seedlings than in the other provenances (table I.A).

The required thermal time (accumulated day/degrees > 5 °C, from 1 February until 50% sprouting of apical buds) also decreased with higher latitude (Asp = 396, Pa = 340, Ro = 292 day/degrees).

Total growth decreased with higher latitude (ie, with earlier sprouting [table I.B]). The greater growth in the more southernly provenance was not caused by longer individual shoots so much as by more shoots being produced (table I.B). It should be noted that the growth recorded for the southernmost provenance, Aspromonte, would have been greater still if the precocious sprouting of new buds on the current-year shoots (lammas shoots) had been

added to the sum. This type of sprouting was investigated only on the apical shoots and it was found to be most pronounced in the Aspromonte seedlings (46.49% of lammas shoots vs 25.74 and 29.95 for the other two provenances, $P = 0.01$).

Experiment 2

In both provenances, chilled seedlings sprouted sooner and faster than unchilled seedlings (table II). This difference between chilled and unchilled seedlings was substantial in the apical buds, but was still greater for the lateral buds (figs 2 and 3).

When seedlings had been chilled, the apical and lateral buds sprouted more or less simultaneously in each provenance; however, in the unchilled seedlings the apical buds sprouted earlier than the lateral buds in the Casentino provenance and later in the Aspromonte provenance (table II). The thermal time for the chilled seedlings was 247 and 257 day/degrees for Casentino and Aspromonte, respectively. These values indicate that the chilling requirements of the species had not been met because of the particular mild winter for the test year (Murray et al, 1989). The seedlings

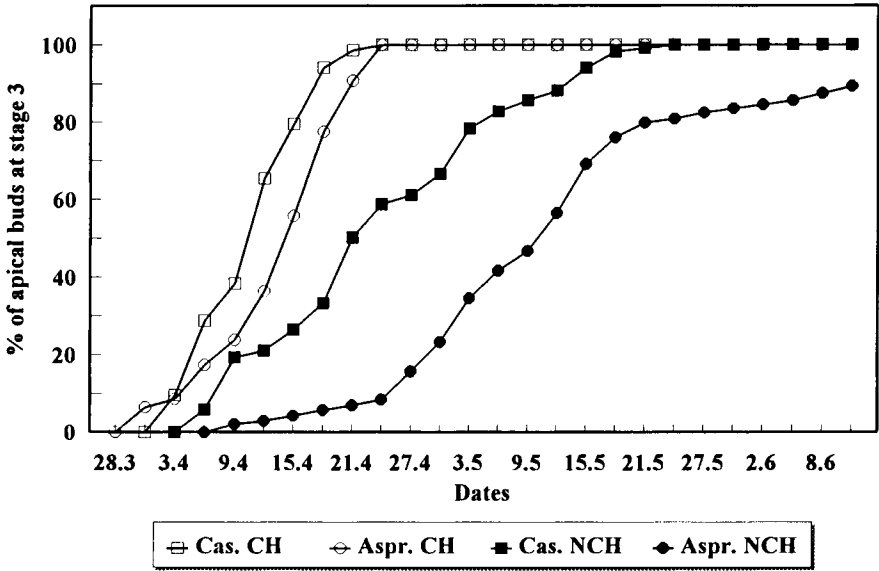


Fig 2. Sprouting pattern of apical buds of Aspromonte (Asp) and Casentino (Cas) seedlings (experiment 2). CH: chilled seedlings; NCH: unchilled seedlings.

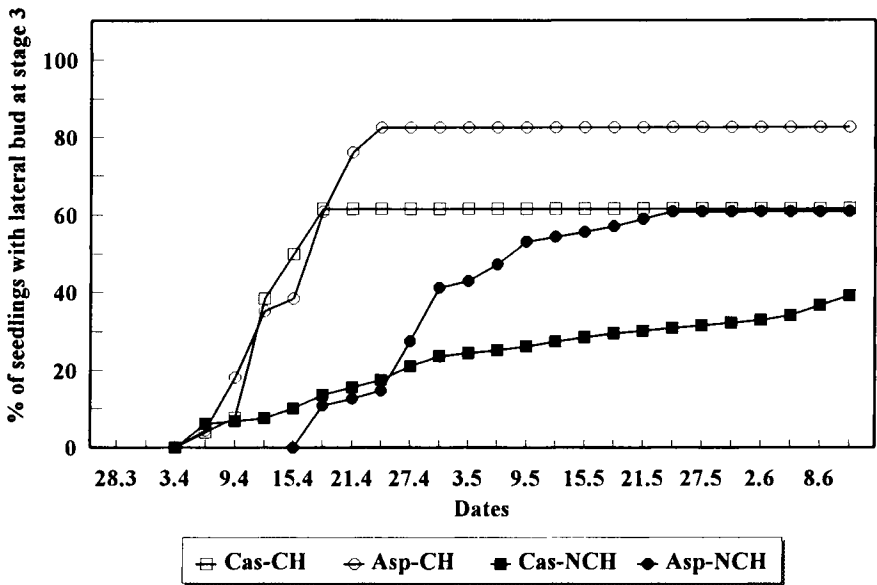


Fig 3. Percentage of Aspromonte (Asp) and Casentino (Cas) seedlings with at least one sprouted lateral bud (experiment 2). CH: chilled seedlings; NCH: unchilled seedlings.

Table II. Mean number of days (from 1 February) required for apical buds and earliest lateral bud to reach phenological stage 3 (experiment 2).

	<i>Apical bud</i>			<i>Lateral bud</i>		
	<i>Unchilled</i>	<i>Chilled</i>	<i>Mean</i>	<i>Unchilled</i>	<i>Chilled</i>	<i>Mean</i>
Casentino	83.18 ^b	70.37 ^a	77.77 ^a	112.04 ^c	72.50 ^a	92.27 ^b
Aspromonte	104.79 ^c	73.63 ^a	89.21 ^b	94.37 ^b	75.53 ^a	84.96 ^a
Mean	94.98 ^b	72.00 ^a		103.21 ^b	74.02 ^a	

Means followed by different letters are significantly different at 1% in LSD test.

of the more northerly Casentino provenance exhibited earlier sprouting of the apical buds than the seedlings from the southerly Aspromonte provenance (table II).

Height growth in beech follows a fully pre-determined pattern, with one or more growth flushes, which always end with the formation of a new apical bud (Gellini, 1975). In the Casentino seedlings the apical bud produced a single flush during the test season; however, in about 40% of the Aspromonte seedlings the apical bud produced more than one flush (average 1.51). The growing season for the Aspromonte seedlings was much longer, continuing until the end of August, while the Casentino seedlings stopped growing in the beginning of May. The apical shoot growth reflected this difference: by the end of the growing season, apical shoots were significantly longer in the Aspromonte seedlings (82.0 ± 10.6 vs 51.2 ± 2.1 mm). In Aspromonte seedlings, the greater growth in length had two causes. Winter apical buds had a number of preformed internodes not statistically different between the two

provenances (6.7 ± 0.19 and 7.2 ± 0.73). However, the average length reached by these internodes was greater in the Aspromonte population (9.0 ± 0.53 vs 7.0 ± 1.32). In addition, as previously mentioned, approximately 40% of these seedlings produced more than one flush, characterized by 5.4 ± 1.1 internodes of average length of 10.2 ± 1.5 mm.

Experiment 3

In this experiment chilling greatly hastened subsequent sprouting. When data for apical and lateral buds were combined, sprouting was rapid after chilling, being virtually complete in 40–50 days for Casentino and in 50–90 days for Aspromonte. Sprouting was very slow without chilling: 140–150 days for Casentino, 230 days for Aspromonte (fig 4). The mean time to budburst (stage 3, counting from the day in which the seedlings had been transferred to the controlled environment chambers) was significantly faster in the Casentino

Table III. After transfer in climate-controlled chambers, mean number of days required for apical buds to reach phenological stage 3 (experiment 3).

	<i>Short day</i>	<i>Long day</i>	<i>Mean</i>	<i>Unchilled</i>	<i>Chilled</i>	<i>Mean</i>
	Casentino	70.19	46.75	58.47 ^a	83.50	33.44
Aspromonte	79.94	64.06	72.01 ^b	99.94	44.06	72.01 ^b
Mean	75.06 ^b	55.41 ^a		91.72 ^b	38.75 ^a	

Means followed by different letters are significantly different at 1% in LSD test.

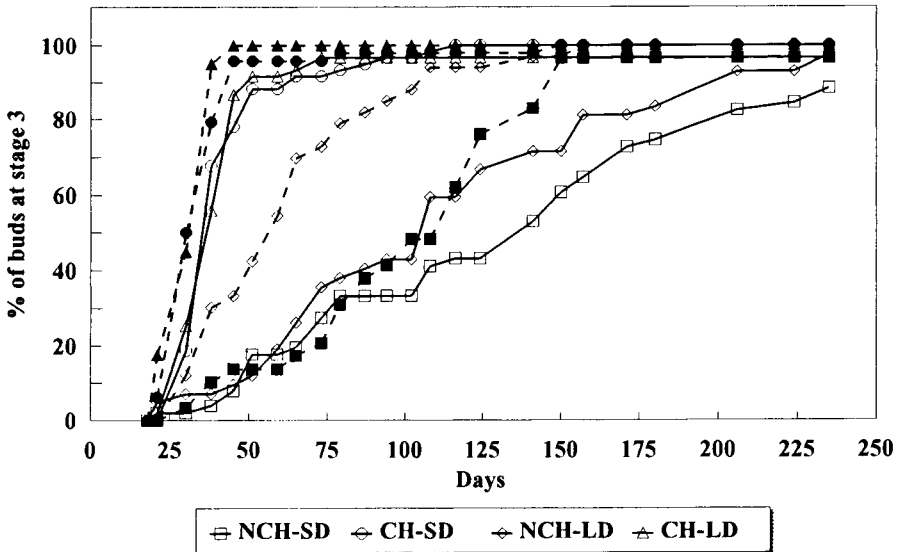


Fig 4. Sprouting pattern of total buds (apical + lateral) in Aspromonte (open symbols) and Casentino (closed symbols) seedlings (experiment 3). CH: chilled; NCH: unchilled; SD: short day; LD: long day.

seedlings than in the Aspromonte seedlings (table III).

Bud sprouting was significantly earlier with the chilled plants compared with the unchilled plants between days 30 (32.89 vs 6.47%, $P = 0.01$) and 180 (99.27 vs 89.32%, $P = 0.01$). The effect of the long day treatment on bud sprouting was only significant between days 65 (75.90 vs 57.03%, $P = 0.01$) and 102 (85.61 vs 69.65%, $P = 0.05$). During the latter period, there was a significant interaction between chilling and the photoperiod.

A difference in the percentage of sprouted buds between the two provenances was evident only between day 141 (95.60 vs 82.47%, $P = 0.01$) and 180 (99.22 vs 89.87%, $P = 0.01$). This difference was, however, preceded and accompanied by significant interactions between the provenance and either chilling or daylength, suggesting that differences in sprouting behaviour between the proven-

ances were due primarily to differences in their response to daylength.

To test this hypothesis, the effects of chilling and daylength on some sprouting parameters (mean time to budburst, percent of sprouted buds, transition time between stage 2 and stage 3 and time lag between lateral and apical budburst) were analysed statistically for each provenance separately. The effect of LD noted earlier turned out to be exclusive to the Casentino seedlings; thus, in this population a LD was partly able to replace chilling (table IV). The different behaviour of the two provenances is evident from the graphs (fig 4).

The percentage of buds that had sprouted by some key dates was also analysed statistically (table V). This confirmed that sprouting in the Aspromonte seedlings depended entirely on chilling (table V). In the Casentino seedlings, a clear daylength effect and a significant interaction between chilling and LD appeared with evidence (table V).

Table IV. Mean number of days required for apical and lateral buds to reach phenological stage 3 (experiment 3).

	<i>Apical bud</i>			<i>Lateral bud</i>		
	<i>Unchilled</i>	<i>Chilled</i>	<i>Mean</i>	<i>Unchilled</i>	<i>Chilled</i>	<i>Mean</i>
<i>Aspromonte</i>						
Short day	109.25	50.63	79.94	139.26	44.11	91.69
Long day	90.63	37.51	64.06	112.84	45.96	79.40
Mean	99.94 ^b	44.06 ^a		126.05 ^b	45.03 ^a	
<i>Casentino</i>						
Short day	104.88 ^c	35.51 ^a	70.19 ^b	100.61 ^c	38.43 ^a	69.52 ^b
Long day	62.13 ^b	31.38 ^a	46.75 ^a	62.08 ^b	33.81 ^a	47.94 ^a
Mean	83.51 ^b	33.44 ^a		81.34 ^b	36.12 ^a	

Means followed by different letters are significantly different at 1% in LSD test.

Table V. Percentage of sprouted buds at selected dates during experiment 3.

	<i>Aspromonte</i>			<i>Casentino</i>		
	<i>Unchilled</i>	<i>Chilled</i>	<i>Mean</i>	<i>Unchilled</i>	<i>Chilled</i>	<i>Mean</i>
<i>38 days</i>						
Short day	7.15	71.21	39.18	7.29	73.95	40.62
Long day	8.75	55.01	31.88	29.16	95.00	62.08
Mean	7.95 ^a	63.11 ^b		18.23 ^a	88.12 ^b	
<i>51 days</i>						
Short day	16.83	88.38	52.61	14.59	96.91	55.75
Long day	17.51	92.48	54.99	40.64	100.00	70.32
Mean	17.17 ^a	90.43 ^b		27.62 ^a	98.45 ^b	
<i>65 days</i>						
Short day	19.33	91.08	55.21	20.84 ^a	96.91 ^c	58.87 ^a
Long day	33.89	96.65	65.27	64.58 ^b	100.00 ^c	82.29 ^b
Mean	26.61 ^a	93.87 ^b		42.71 ^a	98.45 ^b	
<i>102 days</i>						
Short day	38.40	96.43	67.42	48.96 ^a	97.91 ^c	73.44 ^a
Long day	54.74	98.21	76.48	90.64 ^b	100.00 ^c	95.32 ^b
Mean	46.57 ^a	97.32 ^b		69.81 ^a	98.96 ^b	
<i>171 days</i>						
Short day	76.11	100.00	88.06	96.88	100.00	98.44
Long day	77.10	98.21	87.66	100.00	100.00	100.00
Mean	76.61 ^a	99.11 ^b		98.44	100.00	
<i>205 days</i>						
Short day	88.30	100.00	94.15	96.88	100.00	98.44
Long day	92.81	98.21	95.51	100.00	100.00	100.00
Mean	90.56 ^a	99.11 ^b		98.44	100.00	

Means followed by different letters are significantly different at 1% in LSD test.

Table VI. Mean number of days required for bud development to proceed from stage 2 to 3 (experiment 3).

<i>Aspromonte</i>	<i>Apical bud</i>			<i>Lateral bud</i>		
	<i>Unchilled</i>	<i>Chilled</i>	<i>Mean</i>	<i>Unchilled</i>	<i>Chilled</i>	<i>Mean</i>
Short day	27.0	9.6	18.3	9.1	7.6	8.4
Long day	17.7	6.5	12.1	9.6	7.4	8.5
Mean	22.3 ^b	8.1 ^a		9.4	7.5	
<i>Casentino</i>						
Short day	22.2	6.6	14.4	20.1	7.0	13.5 ^b
Long day	14.7	5.0	9.9	9.6	4.8	7.2 ^a
Mean	18.5 ^b	5.8 ^a		14.9 ^b	5.9 ^a	

Means followed by different letters are significantly different at 1% in LSD test.

The sprouting patterns were defined by the transition times from stage 2 to stage 3. Chilling hastened this transition in the apical buds of *Aspromonte* seedlings, and in both the apical and lateral buds of *Casentino* seedlings; in this latter provenance, the lateral buds also exhibited a marked LD effect (table VI).

The importance of the LD effect in the *Casentino* provenance is confirmed by the thermal time data in the absence of chilling: unchilled *Casentino* seedlings required 41% less thermal time to reach 50% sprouting of apical buds under a LD than under a SD, whereas with unchilled *Aspromonte* seedlings the reduction in thermal time when going from a SD to a

LD was only 13%. Seedling habit (bud growth distribution along the seedling) was examined for variations due to chilling, day-length or both. In the *Aspromonte* seedlings, chilling reduced the advance in the sprouting of the lateral buds over the apical buds to about 11 days. In the *Casentino* seedlings, chilling all but eliminated this advance, although LD also played a role here (table VII).

Both the bud sprouting sequence and the distribution of total shoot growth in the seedling differed sufficiently between the provenances to differentiate the seedling habits. By the end of the experiment, the average *Aspromonte* seedling had about 50% of its sprouted buds located in the

Table VII. Mean number of days which the first lateral bud to reach stage 3 was in advance of the first apical bud (experiment 3).

<i>Aspromonte</i>	<i>Unchilled</i>	<i>Chilled</i>	<i>Mean</i>
Short day	77.5	18.0	47.7
Long day	57.1	4.2	30.6
Mean	67.3 ^b	11.1 ^a	
<i>Casentino</i>			
Short day	56.2	5.0	30.6 ^b
Long day	26.4	0.6	13.5 ^a
Mean	41.3 ^b	2.8 ^a	

Means followed by different letters are significantly different at 1% in LSD test.

lower portion of the crown, compared with only 24% in the average Casentino seedling. The total shoot growth distribution also reflected these proportions (35 vs 18%).

In this, as in the previous experiment, the Casentino seedlings exhibited a shorter vegetative season (46.1 vs 87.3 days, $P = 0.01$) and achieved less height growth than the Aspromonte seedlings (66.5 vs 107.8 mm, $P = 0.01$).

DISCUSSION AND CONCLUSION

It seems significant that although the test populations examined in this study differed but little in their latitude of origin, in all the experiments, especially experiment 1, a more northerly origin was linked to earlier sprouting, as well as to lower total growth, because of a shorter vegetative period, a lower sprouting percentage or both. Such variations between provenances from different geographical origins, but growing experimentally at the same site, have also been found in other species (Farmer, 1983). Concerning some of these aspects (eg, vigour and time of budding), studies on genetic and ecological variability in European beech (Galoux, 1966; Dupré et al, 1986; Teissier-du-Cros et al, 1988) have come to similar conclusions. In a recent study conducted on Italian beech populations (Borghetti et al, 1993), spring sprouting was observed to be later in southernmost populations.

In our study another behaviour (incidence of polycyclism) seems to differentiate the studied provenances. For Galoux (1966), beech polycyclism seemed to be genetically controlled at family and population levels. Later studies on the architecture and form of the tree (Dupré et al, 1986; Teissier-du-Cros et al, 1988) indicated the existence of a strong genotype x environment interaction, due to polycyclism sensibility to fertility and competition. Therefore, Dupré et al (1986) concluded that under ordinary conditions provenance effect played an import-

ant role in the apparition of polycyclism but when conditions (climatic, edafic, etc) improved, polycyclism became more frequent and the provenance effect diminished.

The present study provides evidence for the view of Falusi and Calamassi (1990) that chilling in *F. sylvatica* seedlings is important to remove bud dormancy. It is significant that natural chilling achieved such an effect in our study; the winters during the years of the experiments were milder than the mean of the century. From December to February, the average monthly temperatures were, in fact, approximately 2–3 °C above the 100-year average, so that chilling levels were relatively low, and in fact the thermal time for the outdoor seedlings in experiment 1 showed that the chilling requirements of the species had not been completely met (Murray et al, 1989). Even so, these poorly chilled seedlings, particularly those from the Aspromonte provenance, sprouted much earlier than the wholly unchilled seedlings in the greenhouse. Since in the Aspromonte seedlings the dependency on chilling to break dormancy was almost total, insufficient chilling led necessarily to incomplete release from dormancy. This was indicated not only by the long thermal time, but also by temporal relationships of sprouting of apical and lateral buds, and by growth distribution along the seedling axis.

The fact that in the Aspromonte seedlings the apical buds sprouted later than the lateral buds is interesting. It can be related to the finding of Worral (1983) that a greater total chilling requirement for the apical bud in a tree was a defence mechanism evolved in areas (as in Aspromonte; Walter and Lieth, 1967) where temperature fluctuations around the time of budburst could otherwise harm these buds. Under these conditions of 'spring uncertainty', the time of budburst is determined by the chilling requirement, as indicated by Farmer and Reinholdt (1986), with true postdormancy being absent or short.

In the unchilled Casentino seedlings the apical buds began to sprout vigorously in the first half of April (experiment 2), much earlier than in the unchilled Aspromonte seedlings (it was of course later than in the chilled Casentino seedlings). This suggests that in the Casentino seedlings LD also played a role in removing dormancy and/or initiating growth.

The findings of experiment 3 supported this hypothesis. In the Casentino seedlings a LD reduced the thermal time, accelerated sprouting and enhanced the sprouting percentage.

In contrast, the exclusive dependency on chilling in the Aspromonte provenance was evident in all parameters examined. The fact that at the end of the experiment the chilled Aspromonte seedlings had in the lower part of the crown a high percentage of sprouted buds which experienced vigorous growth can be considered as a consequence of the low amount of chilling experienced during the very mild cold season of the experiment. Similar behaviour was observed in *Castanea sativa* Miller (Pezet-Si-Mohamed, 1988) and beech (Falusi and Calamassi, 1990) and it was attributed to an incomplete removal of dormancy.

A chilling x daylength interaction was already reported by Falusi and Calamassi (1990) for a more northerly Italian beech provenance than Casentino, and by Heide (1993) for provenances from northern and central Europe. This interaction has been interpreted by Heide (1993) as a dual dormancy control mechanism of considerable adaptive significance, in which, once fully satisfying the chilling requirement, the daylength is the main controlling factor for budburst in beech. The present series of experiments provides evidence for the view that the photoperiodic response is a factor which some, but not all, provenances can call upon to break dormancy when levels of chilling have been insufficient to do this alone.

The interaction between chilling and the photoperiod found in this study and in a previous one (Falusi and Calamassi, 1990) is reminiscent of the partial substitution of chilling by long photoperiods observed in *Cornus florida* L (Downs and Borthwick, 1955) and in *Pinus taeda* (Garber, 1983). In this latter work, a 14 h photoperiod appeared to strongly stimulate sprouting in unchilled plants, but this effect decreased rapidly with the increase of chilling levels. It became negligible when the plants had completely filled their chilling requirements: in this case no sprouting difference appeared between the plant exposed to 10 or 14 h of the photoperiod.

In our study, chilled seedlings of beech showed the same behaviour when they were grown with a 13 or 9 h photoperiod (the shortest daylength accounted in Florence). The results suggest that, as in *P. taeda*, when the chilling requirement for budbreak has been satisfied, the temperature is presumably the main environmental factor which controls the budbreak.

REFERENCES

- Bagni N, Falusi M, Gellini R, Torrigiani P (1980) La dormienza delle gemme di alcune provenienze di Faggio. Aspetti metodologici e funzionali. *Giorn Bot It* 114, 122-123
- Barnola P, Champagnat P, Lavarenne S (1977) Mise en évidence d'une dormance rythmique chez le noisetier *Corylus avellana* L. cultivé en conditions contrôlées. *CR Acad Sci Paris* 284, 745-748
- Barnola P, Lavarenne S, Gendraud M, Jallut N (1986) Étude biochimique d'une dormance rythmique chez le frêne (*Fraxinus excelsior* L.) cultivé en conditions contrôlées (12EC jours longs). *CR Acad Sci Paris* 303, 239-244
- Borghetti M, Leonardi S, Raschi A, Snyderman D, Tognetti R (1993) Ecotypic variation of xylem embolism, phenological traits, growth parameters and allozyme characteristics in *Fagus sylvatica*. *Funct Ecol* 7, 713-720
- Campbell RK, Sugano AI (1975) Phenology of bud burst in Douglas-Fir related to provenance, photoperiod, chilling and flushing temperature. *Bot Gaz* 136, 290-298
- Downs RJ, Borthwick HA (1955) Effect of photoperiod on growth of trees. *Bot Gaz* 117, 310-326

- Downs RJ, Bevington JM (1981) Effect of temperature and photoperiod on growth and dormancy of *Betula papyrifera*. *Am J Bot* 68, 795-800
- Dupré S, Thiébaud B, Teissier-du-Cros E (1986) Morphologie et architecture des jeunes hêtre (*Fagus sylvatica* L). Influence du milieu, variabilité génétique. *Ann Sci For* 43, 85-102
- Falusi M, Calamassi R (1990) Bud dormancy in beech (*Fagus sylvatica* L). Effect of chilling and photoperiod on dormancy release of beech seedlings. *Tree Physiol* 6, 429-38
- Farmer RE Jr (1983) Latitudinal variation on height and phenology of balsam fir. *Silvae Genet* 32, 148-153
- Farmer RE Jr, Reinholdt RW (1986) Genetic variation in dormancy relations of balsam poplar along a latitudinal transect in northwestern Ontario. *Silvae Genet* 35, 38-42
- Galoux A (1966) La variabilité génécologique du hêtre commun (*Fagus sylvatica* L) en Belgique. *Min de Agric Stat de Rech des Eaux et Forêts*, Belgium, 11
- Garber MP (1983) Effects of chilling and photoperiod on dormancy release of container-grown loblolly pine seedlings. *Can J For Res* 13, 1265-1270
- Gellini R (1975) *Botanica forestale*. Clusf, Florence, Italy
- Heide OM (1974) Growth and dormancy in Norway spruce (*Picea abies*). I. Interaction of photoperiod and temperature. *Physiol Plant* 30, 1-12
- Heide OM (1993) Dormancy release in beech buds (*Fagus sylvatica* L) requires both chilling and long days. *Physiol Plant* 89, 187-191
- Lavarenne S, Champagnat P, Barnola P (1971) Croissance rythmique de quelques végétaux ligneux des régions tempérées cultivés en chambre climatisée à température élevée et constante et sous diverses photopériodes. *Bull Soc Bot France* 118, 131-162
- Malaisse, F. (1964) Contribution à l'étude des hêtraies d'Europe occidentale, note 4. Quelques observations phénologiques des hêtraies en 1963. *Bull Soc R Bot Belgique* 97, 85-97
- Murray MB, Cannell MGR, Smith RI (1989). Date of budburst of fifteen tree species in Britain following climatic warming. *J Appl Ecol* 26, 693-700
- Pezet-Si-Mohamed Y (1988) Approche biochimique du déterminisme de l'acrotonie et de la basitonie chez le châtaignier (*Castanea sativa* Miller). *Bull Soc Bot France* 135, 71-79
- Oleksyn J, Tjoelker MG, Reich PB (1992) Growth and biomass partitioning of populations of European *Pinus sylvestris* L under simulated 50° and 60° N daylengths: evidence for photoperiodic ecotypes. *New Phytol* 102, 561-574
- Teissier-du-Cros E, Thiébaud B, Duval H (1988) Variability in beech: budding, height growth and tree form. *Ann Sci For* 45, 383-398
- Walter H, Lieth H (1967) *Kimadiagramm-weltatlas*. G Fischer, Jena, Germany
- Wareing PF (1953) Growth studies in woody species. V. Photoperiodism in dormant buds of *Fagus sylvatica* L. *Physiol Plant* 6, 35-40
- Wareing PF (1954) Growth studies in woody species. VI. The locus of photoperiodic perception in relation to dormancy. *Physiol Plant* 7, 261-277
- Worrall J (1983) Temperature-bud burst relationships in amabilis and subalpine fir provenance test replicated at different elevations. *Silvae Genet* 32, 203-209