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Original article

Latitudinal and altitudinal variation of bud burst in western populations of sessile oak (*Quercus petraea* (Matt) Liebl)

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Summary — Latitudinal and altitudinal variations of bud burst in western populations of sessile oak (*Quercus petraea* (Matt) Liebl) are examined. The phenology of bud burst in 50 populations of sessile oak has been studied in four provenance tests located in France. The authors obtained large variations between populations and these variations are linked to altitude, latitude and spring frost tolerance. The northern populations and those close to the sea level are the latest. These populations are more tolerant to the late spring frost. Due to the geographical structuration, which is linked to adaptative characters, we advise foresters to use sessile oak of local origins.

Quercus petraea **/ phenology / provenance test / frost hardiness / genetic differentiation**

Résumé — Structuration altitudinale et latitudinale du débourrement des bourgeons de populations d'Europe de l'Ouest de chêne sessile (*Quercus petraea* (Matt) Liebl). *Le comportement du débourrement des bourgeons au printemps a été étudié dans un réseau de comparaison de provenances de chêne sessile sur 50 populations. Des variations importantes dans le comportement phénologique entre les populations ont été mises en évidence et elles ont pu être reliées à la latitude et l'altitude ainsi qu'à la tolérance au froid. Les populations tardives sont nordiques ou d'altitude faible. Ces même populations sont plus résistantes aux gelées printanières tardives. Du fait de la structuration géographique observée et de sa liaison avec des caractères adaptatifs, il est conseillé aux forestiers d'utiliser des origines locales pour les reboisements artificiels de chêne sessile.*

Quercus petraea ***/ phénologie / test de provenance / tolérance au froid / différenciation génétique***

INTRODUCTION

Local adaptation results when a population has evolved through natural selection in response to specific ecological conditions. For outcrossing plant species, such as tree species, the efficiency of selection is reduced by a high rate of gene flow (Endler, 1977; Loveless and Hamrick, 1984; Slatkin, 1985). However, forest geneticists have documented genetic differentiation among populations occupying different geographical areas with different markers such as molecular markers (Yeh and O'Malley, 1980; El Kassaby and Sziklai, 1982; Kremer et al, 1991; Kremer and Petit, 1993; Müller-Starck et al, 1993; Petit et al, 1993; Zanetto et al, 1993), physiological characters (Flint, 1972; Liepe, 1993) and quantitative traits (Libby et al, 1969; McGee, 1974; Kriebel et al, 1976; Jensen, 1993; Sork et al, 1993). In this contribution we will report on the geographic variation of bud burst in *Quercus petraea*.

The economic and ecological importance of sessile oak *(Q petraea)* gives the species a high priority for genetic research. The National Forest Service (ONF) and two research institutes (CEMAGREF and INRA) have launched a program to evaluate range-wide genetic diversity to provide a basis for genetic conservation and management. Since 1989, four provenances tests have been established in France along a gradient from west to east and more than 100 provenances will be tested.

The bud phenology has been the subject of numerous studies in forestry and arboriculture. This character is of primary importance since it is linked to frost resistance and avoidance of pests. Furthermore, clinal variation has been reported in various studies (Wright, 1976). The present study gives preliminary results from these provenance tests and tries to determine the origin of bud phenology differentiation between populations of sessile oak.

MATERIALS AND METHODS

Plant material

Sessile oak *(Q petraea)* is widely distributed in Europe from north of Spain to south of Scandinavia and from Ireland to Eastern Europe. It occurs in the plains on most types of soil from sea level to 1 300 m elevation.

Experimental design

The sample of populations covered most of the species range and contained more than 100 populations. However, for this paper only data from western populations were available: from France (42), Ireland (3), Great Britain (2) and Germany (3). Hundred kilograms of seeds were collected from 50 points covering 25 ha per geographic origin.

The populations were collected on 2 successive years (set 1 in 1986 and set 2 in 1987). The seeds were sown in four replicates in the public nursery of Guéméné-Penfao. When seedlings were 3 years old, they were outplanted in field tests (table I) in 1990 (set 1) and 1991 (set 2). Seedlings of the second collection (set 2) were planted in the same field test adjacent to the material of the first collection (set 1) planted during the previous season. A group of six provenances was common to both sets (control provenances).

In each set of field tests, five ecological zones were delineated based on soil description (intensity of the discoloration of the pseudo-gley, depth of the water table and of the bedrock, and texture at different depths) and plant communities prior to plantation of material. These ecological zones were considered as blocks for the experimental design. Two replicates (two plots) were randomly assigned within a block (24 trees per plots). As a result, there were ten replicates per provenances (240 trees). The control provenances were represented by three replicates per block (360 trees/provenance/set). The same procedure was adopted for each set.

Analysis of data

The general model to analyse the data within each set was as follows:

Table I. Location and characteristics of experimental plantations of *Quercus petraea*.

Name of forest	*Department*	*Location*	*Soil*	*Climate*	*Number of populations*	
					Set 1	*Set 2*
Petite Charnie	Sarthe	Western France	Brown soil	Atlantic	19	34
Vierzon	Cher	Central France	Podzol	Dry atlantic	19	34
Vincence	Nièvre	Central France	Brown soil	Dry atlantic	19	37
Sillegny	Meurthe-et-Moselle	Eastern France	Brown soil	Continental	19	37

$$Y_{ijkl} = \mu + P_i + b_j + (Pb)_{ij} + \varepsilon_{ijk}$$

P_i: effect of provenance i (random effect);

b_j: effect of block j (fixed effect);

$(Pb)_{ij}$: interaction between provenances i and block j;

ε_{ijk}: effect of tree k belonging to combination ijk.

From this model provenance means were computed. Linear regression between provenance means of common provenances (six provenances) was used to adjust the data between the two sets.

Characters analysed

Bud burst observations were recorded 3 years after plantation (table II). The procedure was to score the developmental stages of the terminal bud of each tree on a scale from 0 to 5 (0 = dormant bud, 1 = bud swollen, 2 = bud open, 3 = beginning of leaf expansion, 4 = one leaf free, 5 = internodes are elongating). Scoring was done in a single observation.

The field tests suffered from a late spring frost the 21 May 1991. The individuals damaged by this frost have been recorded in the National Forest of Vierzon.

RESULTS

Provenance within and between each set

The provenance mean of bud burst varied between 0.779 to 4.06 according to the testing site and the collection. Provenance variations were highly significant within each collection and site (table III).

Bud burst scores were highly stable between the two collections within a given site, as indicated by the regression between

Table II. Dates of the bud burst observations for the two set in the four sites.

Site	*Set 1 (plantation in 1989)*	*Set 2 (plantation in 1990)*
Petite Charnie	24–25 April 1992	17–19 April 1993
Vierzon	28–29 April 1992	28–29 April 1993
Vincence	1 May 1992	1–2 May 1993
Sillegny	30 April 1992	26 April 1993

Table III. Values of *F* test (ANOVA, provenance effect) for phenological scores.

Set	*Site*			
	Petite Charnie	*Vierzon*	*Vincence*	*Sillegny*
1	67.79 ($P \leq 0.001$)	49.53 ($P \leq 0.001$)	36.97 ($P \leq 0.001$)	67.02 ($P \leq 0.001$)
2	70.72 ($P \leq 0.001$)	34.67 ($P \leq 0.001$)	43.61 ($P \leq 0.001$)	60.83 ($P \leq 0.001$)
1 + 2	121.2 ($P \leq 0.001$)	48.69 ($P \leq 0.001$)	52.01 ($P \leq 0.001$)	69.65 ($P \leq 0.001$)

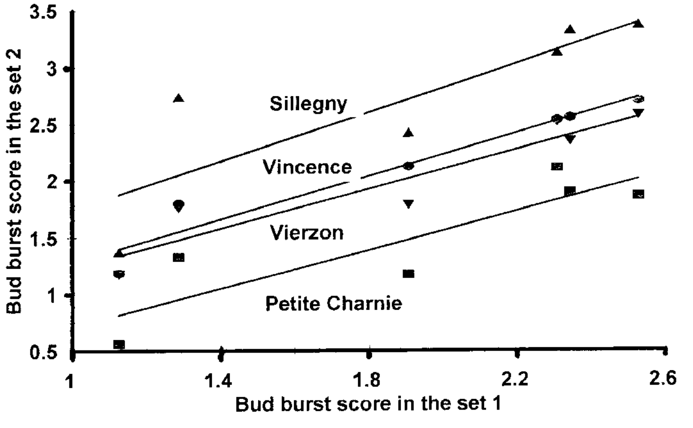

Fig 1. Diagram of the regression between the control provenance mean values of phenological scores in the two different sets. Sillegny (▲): $y = 1.1x + 0.92$, $r = 0.86$, $P = 0.02$; Vincence (▼): $y = 0.81x + 0.4$, $r = 0.88$, $P = 0.02$; Petite Charnie (■): $y = 0.85x - 0.13$, $r = 0.86$, $P = 0.02$; Vierzon (●): $y = 0.65x + 0.65$, $r = 0.89$, $P = 0.02$.

mean values of the control provenance (fig 1). They are independent of the year of plantation, the year of measurement (table II) and the site. As a result this linear model was used to adjust the provenance mean values between the different sets.

Comparison of provenance means

The ranking of the different provenances is remarkably stable, as indicated by the correlation coefficients of provenance means

Table IV. Correlations between population mean values of phenological scores assessed in the different sites.

Experimental plantation	*Petite Charnie*	*Vierzon*	*Vincence*	*Sillegny*
Petite Charnie		0.86	0.89	0.89
Vierzon	1×10^{-15}		0.93	0.91
Vincence	4×10^{-5}	5×10^{-23}		0.95
Sillegny	3×10^{-9}	4×10^{-20}	1×10^{-25}	

Values above the diagonal correspond to the correlation coefficients; values below the diagonal correspond to the probability level.

between the different sites in all pairwise combinations (table IV). Although the correlations are good in general, their values are related to the distance separating the testing sites rather than to the ecological differences between the testing sites. For example, the lowest correlations are observed between sites including the Petite Charnie forest, which is the most western testing site. Although the site of Vierzon is the most differentiated ecologically from the other sites (table I), correlations including the Vierzon plantation are higher than the others.

Two major trends can be observed according to the geographic origin of the provenances:

– Latitudinal trend: correlation between bud burst scores and latitude are significant in all sites (table IV, fig 2). Populations from northern latitudes flush later than populations from southern latitudes.

– Altitudinal trend: significant correlations were observed between altitude and bud burst in all sites (table V, fig 3).

There was a positive correlation between bud burst and frost damage as indicated in

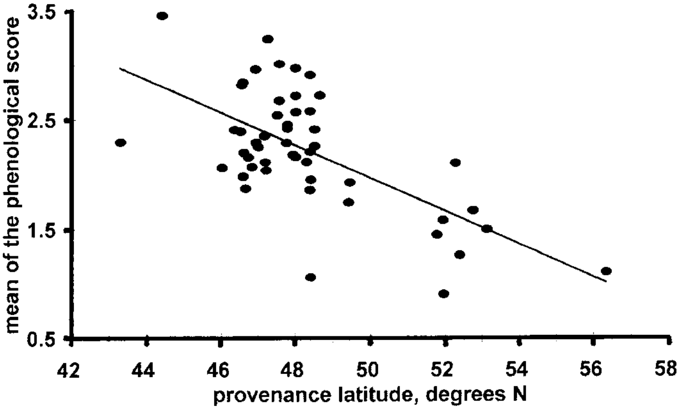

Fig 2. Diagram of the regression between latitude and bud burst. $y = -0.15x + 9.5$, $r = 0.64$, $P = 0.000$. Provenance means values were averaged on the four different plantations.

Table V. Correlation between population mean values of phenological scores and geographical data.

Site	*Latitude*		*Altitude*	
	r	P	r	P
Petite Charnie	0.38	0.0020	0.45	0.0010
Vierzon	0.49	0.0002	0.44	0.0010
Vincence	0.58	< 0.00	0.51	< 0.00
Sillegny	0.67	< 0.00	0.58	< 0.00

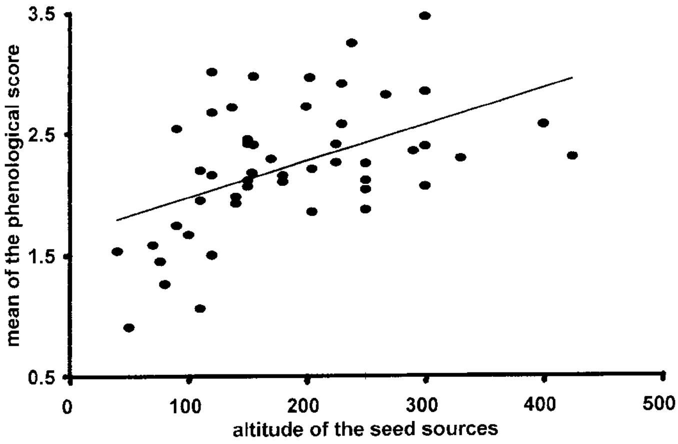

Fig 3. Diagram of the regression between altitude and bud burst scores. $y = 0.003x + 1.7$, $r = 0.48$, $P = 0.0003$.

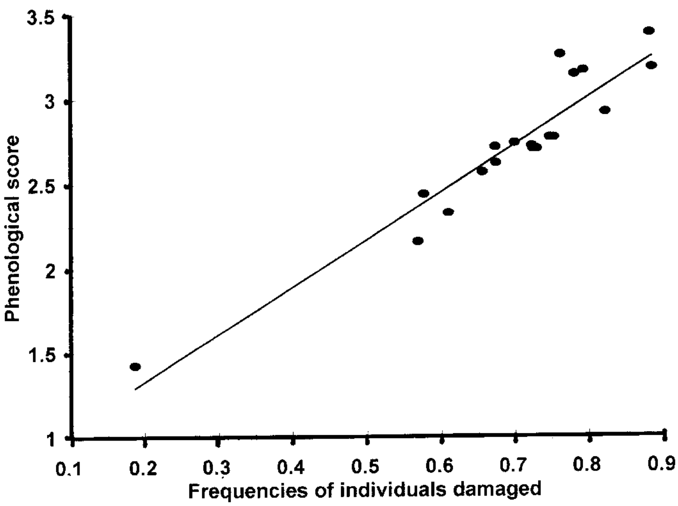

Fig 4. Diagram of the regression between the frequencies of individuals damaged by the spring frost of May 1991 and the phenological score in the forest of Vierzon. $y = 2.79 + 0.77$, $r = 0.94$, $P = 0.000$.

figure 4. There was a large variation of the percentage of damaged trees within provenances (from 18 to 88%). Early flushing trees are likely to suffer more from frost than late flushing trees.

DISCUSSION AND CONCLUSION

In conclusion, considerable geographical variations with respect to spring bud phenology are evident in *Q petraea*. These variations are clinal and related to altitude and latitude. The earliest provenances are those of plateau and the southern origins. This character has an important genetic basis because the phenological rank of the provenances is very stable between the different sets and sites. Jensen (1993) obtained a very high heritability value ($h^2 = 0.87$) for pedunculate oak (*Q robur*).

The latitude trend observed with sessile oak is the opposite to that documented by McGee (1974), Kriebel et al (1976) and Kremer (1994) for northern red oak and for most of the conifers (Wright, 1976) but is the same for the black and Persian walnut (Bey, 1973; Germain, 1992). The altitude gradient has the opposite effect to the previous one, but the range of altitude sampled varies from 35 to 425 m, whereas *Q petraea* is still present at 1 300 m in the southern Alps or Pyrénées. These correlations should therefore be confirmed on a larger sample of populations.

The origin of these trends is not obvious but they probably reflect adaptations to cold and warm conditions and to predators. The sessile oak is sensitive to damage from late spring frost as shown by the results observed in the forest of Vierzon (fig 4). The suceptibility to weather damage is highly correlated with the spring phenology. The earliest provenances were damaged considerably by the spring frost of 21 May 1991. At that time all the individuals had flushed. Therefore the latest origins are more tolerant to frost by avoidance and resistance. These results confirm those obtained by Liepe (1993) in growth chambers. Presumably natural selection should have favored late flushing types, which did not suffer such damage. Selection was counteracted by selection favoring early flushing types which would have a growth advantage in the south or on the plateau. The difference in the date of bud burst is associated with the insect fauna (Crawley and Akhteruzzaman, 1988) and has been considered as a plant defense against leaf herbivores (Tuomi et al, 1989). Moreover, the leaf herbivores have a strong impact on the genetic structural variations between subpopulations of oak (Sork et al, 1993). Therefore variations in insect species and in their abundance across the natural range could also generate phenological gradient.

This geographical structuration demonstrates that natural selection has differentiated populations over the natural range and has counteracted the natural gene flows which are very high in the genus *Quercus* (Ducousso et al, 1993).

The bud phenology has a genetic origin and is strongly correlated with adaptive characters like spring frost tolerance. In arboriculture the introduction of foreign cultivars comes up against difficulties due to differences of phenological behavior, eg, the Californian clone of Persian walnut which is very productive but very sensitive to early spring frost in France (Germain, 1992). Therefore moving acorns from one region to another would increase the exposure of seedlings to the rigors of spring frost and possibly to insect damage since the forest managers do not have a method for preventing frost damage (heating systems or sprinkling). Obviously, the indiscriminate moving of acorns should be avoided.

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