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ORIGINAL ARTICLE

Variation in phenology and height increment of northern *Ulmus glabra* populations: Implications for conservation

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Abstract
Variation in budburst, height increment and growth cessation within and among five Norwegian *Ulmus glabra* (Huds.) populations was recorded in an experimental trial during the fourth and fifth growing seasons. Budburst occurred first in inland populations and last in coastal populations, and latitude of origin was less important for timing of budburst than distance from the coast. Height increment and date of growth cessation were correlated to latitude, height increment decreased with increasing latitude of origin, whereas growth cessation occurred first in northern populations and later with increasing southern origin. Thus, the phenological traits vary in accordance with the climate from where the populations have been derived. There was a general large within-population variation in phenological traits. The results are discussed in relation to conservation of adaptive trait variation of the species.

Keywords: *Adaptive traits, conservation, Dutch elm disease.*

Introduction

Ulmus glabra is a wind-pollinated tree species, widespread in Europe from the Mediterranean to Scandinavia, and as far as the Ural Mountains in the east (Richens, 1983). In Norway, *U. glabra* has a scattered distribution in most of the lowlands in the south and along the coast to the polar circle, which is the northern fringe of the species (Lid & Lid, 1998). The northernmost populations of several tree species are found in Norway (Hultén, 1971), owing to the Gulf Stream, which skirts the coast.

Tree species with wide ranges typically exhibit clinal variation in timing of onset and cessation of growth along climatic gradients. For example, in northern Europe a shorter critical night length for growth cessation of northern versus southern origins has been convincingly demonstrated (Heide, 1974; Håbjørg, 1978). Similarly, budburst of southern and coastal provenances of broadleaved trees such as *Quercus petraea* (Liebl.) and *Betula* spp. (Ehrh.) occurs later than northern provenances when studied in the same environment (Jensen, 1993; Myking & Heide, 1995; Myking, 2000). This pattern is not always consistent across species and regions. *Alnus glutinosa* (Gartn.) is remarkable for the small differences in timing of budburst among populations from climatically very diverse sites, such as Scotland, Norway and Italy (DeWald & Steiner, 1986; Kohmann & Lexerød, 2004). In *Fagus sylvatica* (L.) and *Quercus petraea* from continental Europe budburst occurs latest in the northern origins (Liepe, 1993; von Wuehlisch et al., 1995), possibly as an adaptation to the milder climate of the North Sea that could otherwise trigger premature budburst (Campbell & Sugano, 1979; Myking, 1997). These adaptation patterns have a genetic basis (Jensen, 1993) and are critical for survival. Large provenance transfers may result in severe frost damage, usually in spring or autumn, because of inadequate synchronization of the growth rhythm with the climate (Skrøppa & Dietrichson, 1986; Liepe, 1993). Thus, the distributions of alleles regulating adaptive traits are influenced by natural selection, which promotes genetic differentiation under diversifying selection. This can lead to contrasting patterns of variation relative to neutral markers (Savolainen & Kuittinen, 2000).

As a scattered noble hardwood species at the northern distribution margin, more than 100 conservation units have been established for *U. glabra* in Norway (Myking & Skrøppa, 2001). The conservation effort has a broad scope and aims to protect forest biodiversity in general; therefore, it far exceeds the requirements purely for conservation of genetic variation in *U. glabra* (Namkoong, 1984; Eriksson et al., 1993). As a result of Dutch elm disease (DED), *U. glabra* has recently been included in the revised Norwegian red list, as "near threatened" (Kålås et al., 2006). DED is caused by certain fungi (*Ophiostoma* spp). It is one of the most serious diseases known to trees and has ravaged elm populations all over Europe. In Norway, DED was identified for the first time in Oslo in 1963 (Gibbs, 1978), but without causing serious harm. From 1981 onwards, however, several devastating attacks on *U. glabra* were recorded at different places around the Oslofjord (Gibbs, 1978; Solheim, 1991), which have subsequently spread in eastern Norway (H. Solheim, personal communication, 2006). This poses a challenge for future conservation of *U. glabra*, which in turn necessitates more knowledge about the distribution of variation in adaptive traits in the species.

Knowledge about variation in phenological traits in elms is scarce. In the recently finalized European Union (EU) project on conservation of European elms (RES-GEN CT 96-78; Collin et al., 2004) the study of adaptive traits was limited to budburst variation in clone collections of *Ulmus minor* (Mill.) from southern and central Europe (Santini et al., 2004; Ghelardini et al., 2006). Phenological traits have also been studied in *Ulmus laevis* (Pallas) populations from central and northern Europe (Whiteley et al., 2003). Thus, the aim of this paper was to study variation in phenological traits and height increment within and among the northern fringe populations of *U. glabra*, to assess conservation strategies for the species. This is the first scientific paper to deal with variation in adaptive traits in *U. glabra*.

Materials and methods

The field trial was established in 2003 in Bergen (60°15′ N, 5°20′ E), Norway, approximately 60 m a.s.l. Five populations, which cover the main geographical gradients in the distribution of *U. glabra* in Norway (Figure 1), were represented by seven to 15 families in each population from seeds collected after open pollination. Collection of more populations, especially more families within populations (≥ 20), was planned, but not achieved owing to a lack of seeds. Availability of seeds was least in the north-ernmost population (Table I, Figure 1), probably because of insufficient flowering and seed maturation associated with low summer temperatures. The trial was established on agricultural soil in a single-tree plot randomized block design with 40 replicates at 1 m spacing, i.e. all families were represented once within each replicate, if present. Results presented here refer to the fourth and fifth (2004 and 2005) growing seasons of the trees, in which budburst, height increment and growth cessation were recorded. For further details on plant cultivation, see Myking and Yakovlev (2006).

Budburst was assessed in classes from 0 to 5 (0: no development; 1: week swelling, the bud light brown at the tip; 2: swelling, the bud green at the tip; 3: budburst, foliage showing; 4: whole leaves visible; 5: leaves fully unfolded with petioles). The assessments were done as an average of the upper third of the plants and were undertaken once in 2004 (22 April) and twice in 2005 (13 and 20 April). Growth cessation was assessed in two classes, as either apical shoot growing or winter bud formed, and assessment was done once in 2004 (23 August) and twice in 2005 (15 and 30 August). Budburst and growth cessation were assessed when there was a satisfactory distribution in the different classes, to cover as much as possible of the variation present. To study properly the progress of these traits over time, however, more than one or two assessments would have been needed. Tree height (cm) was measured each autumn after termination of growth, and height increment was calculated as the difference between the heights measured in 2005 and 2003.

Statistical analyses

Owing to poor soil conditions and high mortality in part of the trial, six replicates were omitted from the statistical analyses, and families with fewer than eight measured trees were also excluded. This meant that two families from each of the Bergen and Alstahaug populations were omitted, leaving 64 families for the analyses. Categorical observations (budburst and growth cessation) were transformed to normal scores based on midpoint values of the cumulative frequency distribution in each block (Danell, 1991) and approximated to a normal distribution with expectation of 0. Overall analyses of variance were performed for these variables and the height increment, including population as a fixed effect and family within populations and blocks as random effects. Appropriate *F* tests were performed, applying the TEST option in the RANDOM statement of PROC GLM in SAS (SAS Institute, 2001). Family variance components for these traits were estimated within each population by PROC VARCOMP and were
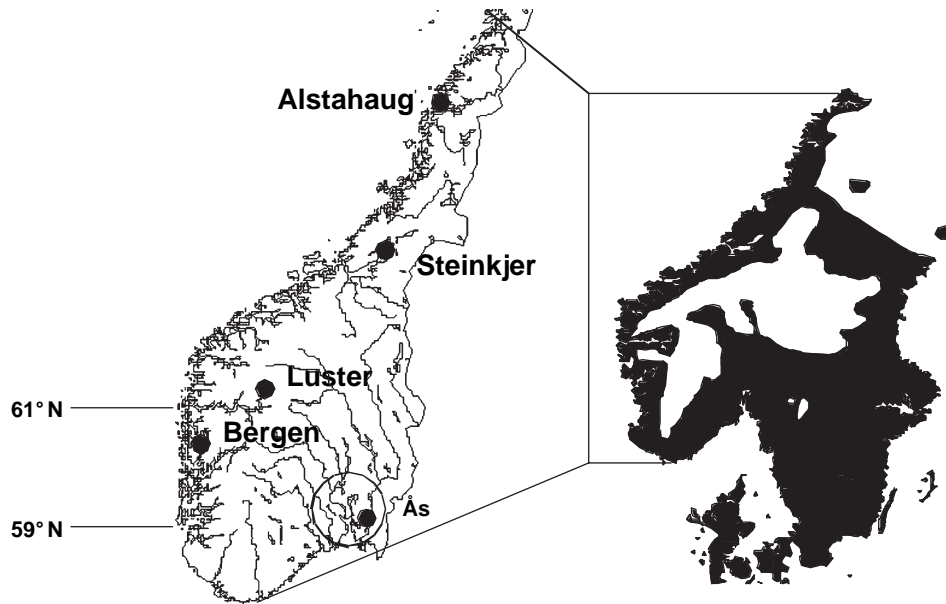
Figure 1. Origins of the five populations included in the experimental field trial established in Bergen, and the distribution of *Ulmus glabra* in Scandinavia (Hultén, 1971). The approximate distribution of Dutch elm disease is encircled (right).

used to estimate heritabilities within each population. Approximate standard deviations (SDs) of the heritability estimates were calculated by the method of Falconer and Mackay (1996).

Results

Variation among populations

There were large and rather consistent differences among populations in terms of increment and timing of budburst and growth cessation (Tables II and III), which were attributable to distance from the coast and latitudinal origin of populations. Budburst occurred first in the northern and slightly continental population from Steinkjer, followed by the more continental, and southern populations from Luster and Ås, respectively. The latest budburst development was recorded in the coastal populations from Bergen and Alstahaug, even though they are separated by about six degrees of latitude. The correlation in budburst between years (2004–2005), as well as between the two assessments within the same year

(2005), was strong and significant at the population level ($r \geq 0.95$). The interval of 7 days between the two assessments in 2005 increased the budburst percentage by 37%, as a grand average of all populations.

Growth cessation was early in the two northernmost populations and progressively later with increasing southern origin. In accordance with this, height increment decreased with increasing latitude (Table II). There was a significant relationship between increment and timing of growth cessation at the population level ($r = -0.94$). In contrast, there was no relationship between height increment and timing of budburst ($r \leq 0.39$). The correlations in growth cessation between years (2004–2005), and between assessments within the same year were strong and significant ($r \geq 0.88$).

Variation within populations

For growth cessation only slight significant differences were present among families in the overall

Table I. Number of families and plants per population, and latitude and longitude of populations.

Population	No. of families	No. of plants	Latitude (N)	Longitude (E)
Alstahaug	7	200	65° 54′	12° 26′
Steinkjer	14	463	64° 00′	11° 30′
Luster	15	527	61° 27′	7° 28′
Bergen	14	471	60° 24′	5° 30′
Ås	14	538	59° 42′	10° 46′

Table II. Population means of height increment (2004 and 2005), budburst (stage 3, 13 April 2005) and growth cessation (15 August 2005) of the five populations.

Population	Increment (cm)	Budburst (%)	Growth cessation (%)
Alstahaug	73	22	51
Steinkjer	70	48	51
Luster	82	42	40
Bergen	86	15	35
Ås	96	28	31

Table III. Results from analyses of variance presented by *F*-ratios and associated *p*-values of increment, budburst (13 April 2005) and growth cessation (15 August 2005).

Trait	Level	*F*	*p*
Increment	Population	9.68	<0.0001
	Family	2.04	<0.0001
	Block	34.34	<0.0001
Budburst	Population	10.53	<0.0001
	Family	2.75	<0.0001
Growth cessation	Population	12.25	<0.0001
	Family	1.35	0.043

Note: no block effects were present in the analyses for the last two traits owing to the normal score transformation.

analyses of variance (Table III). This may partly be due to the fact that this trait was assessed in only two classes, leaving limited resolution for the statistical testing. Only the populations from Bergen and Luster had significant family variation (Table IV) for growth cessation. The three northernmost populations had high and significant variance components for height increment, whereas no significant family variation was found for this trait at Ås and Bergen. For budburst, only the Steinkjer and Ås populations had significant variance components (Table IV). Thus, the patterns of within-population family variation vary among both populations and traits studied. The estimated heritabilities were generally low, and this may be due to large experimental error and inadequate number of families per population. The highest values were obtained for budburst ($h^2 \leq 0.31$, SD $=0.08$), and the lowest for growth cessation ($h^2 \leq 0.08$, SD $=0.04$) and height increment ($h^2 = 0.12$, SD $=0.06$).

Discussion

The interpretation of differences in budburst development among populations is not straightforward since the effect of latitude is confounded by the coast–inland climatic gradient. It is still evident, however, that inland origin contributes to early budburst, whereas coastal populations have late budburst (Table II). Thus, these results corroborate the coast–inland cline previously found for Norwegian birch populations (Myking, 1997) and North American Douglas fir populations (Campbell & Sugano, 1979). Earlier budburst in northern than in southern populations is also commonly observed (Kriebel & Wang, 1962; Worrall & Mergen, 1967; Hänninen, 1990; Whiteley et al., 2003). Although the second northernmost *U. glabra* population (Steinkjer) had the earliest budburst, and the latest budburst occurred among the southern populations (Bergen), the influence of latitude was subordinate to the coast–inland cline in the present study. For instance, in the coastal populations from Bergen and Alstahaug, separated by about six degrees of latitude, budburst occurred about at the same time. Moreover, the Bergen and Luster populations come from about the same latitude, but have different distances from the coast and vary widely in the timing of budburst. Most of the Norwegian coastline experiences forcing temperatures ($>0°C$) throughout the winter (Aune, 1993) owing to the influence of the Gulf Stream. Compared with continental populations, coastal populations have adapted to a milder and more variable climate by developing a more extensive winter dormancy to avoid frost damage associated with premature budburst (Myking, 1997). The sequence of budburst in *U. laevis* on a European level follows a latitudinal pattern, with high-latitude populations flushing first (Whiteley et al., 2003; cf. Myking & Heide, 1995). In *U. minor*, however, southern Italian clones flushed earlier than clones from northern Italy and France, possibly as an adaptation to the drought in spring and summer in the Mediterranean area (Santini et al., 2004; Ghelardini et al., 2006). Such differences within *Ulmus* may be due to the geographical scope of the different studies, but clearly also to the specific climatic gradients to which these species have become adapted.

Growth cessation of populations followed a consistent latitudinal pattern; budset occurred first in the northernmost populations and progressively later with increasing southern origin (Table II). This is in agreement with other Scandinavian trees and shrubs

Table IV. Estimates of variance components within populations and their associated *p*-values for increment, budburst (13 April 2005) and growth cessation (15 August 2005).

Population	Increment		Budburst		Growth cessation	
	Variance	*p*	Variance	*p*	Variance	*p*
Alstahaug	158.21	0.05	0.026	0.07	0.019	0.06
Steinkjer	133.92	0.001	0.076	<0.0001	0.002	0.29
Luster	148.92	<0.0001	0.012	0.11	0.017	0.001
Bergen	21.18	0.14	0.001	0.54	0.015	0.009
Ås	3.37	0.39	0.046	<0.0001	0.003	0.66

and probably due to a shorter critical night length for growth cessation of northern versus southern populations (Håbjørg, 1978; Vihera-Aarnio et al., 2006). The adaptive significance of this is to synchronize growth cessation and winter hardening with the ambient climate experienced by the populations, since delayed growth cessation may cause frost damage in autumn (Skrøppa & Dietrichson, 1986). Height increment decreased with increasing latitude (Table II) and was strongly and negatively correlated with timing of growth cessation rather than budburst. Accordingly, late growth cessation is more important than early budburst for the height increment and duration of the growing season (Chmura, 2006).

In addition to the extensive population variation in adaptive traits across Norway, a general large variation was also present within populations (Tables III and IV). Heritability estimates were low (≤ 0.31), but still within the range (0.0–0.7) found for phenological traits in, for example, *Betula* spp. (Billington & Pelham, 1991) and *U. laevis* (Whiteley et al., 2003). Large differentiation among families in phenological traits has also been demonstrated within Scandinavian *Betula pendula* and *Acer platanoides* (L.) populations (Eriksson et al., 2003). The large variation observed within the *U. glabra* populations, with partly overlapping distributions, makes it unlikely that DED significantly reduces the genetic variation of adaptive traits in elm in Norway within the present range of the epidemic.

In populations severely struck by DED, subsequent coppice regeneration from rootstock sprouts may be substantial and presumably capable of producing seeds before they are reattacked by DED, as shown in the Lower Wye Valley in the UK (Peterken & Mountford, 1998). Even if the elm persists as fast turnover populations that never reach the canopy, the number of elm individuals may increase (Peterken & Mountford, 1998), with possible small consequences for the effective population size and genetic variation. Production of novel genotypes available for natural selection will, however, be reduced if seed production is constrained by the size of the trees. Inventories have recently been initiated in affected areas in Norway to study regeneration and mortality, to evaluate whether *ex situ* conservation is desirable. Preliminary results indicate that natural regeneration balances the mortality due to DED (H. Solheim, personal communication, 2006). If, however, *ex situ* conservation is regarded as necessary, this should be undertaken in areas not affected by DED and in a climate similar to that of eastern Norway, so as not to violate the limits to which the populations are adapted. Regarding latitude and spring temperature regime, the inner

fjord areas of western Norway, between 59 and 61° N, would probably be suitable (Figure 1). The spread of DED would be constrained by the mountain ridge running north–south and, hopefully, by effective disease management along the coast.

In conclusion, the adaptive traits of *U. glabra* display large variation both among populations along climatic gradients and within populations. The large within-population variation may be an important assurance against loss of genetic variation if *U. glabra* populations are increasingly destroyed by DED in the future.

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