Quaternary Science Reviews 29 (2010) 2052–2070

Contents lists available at ScienceDirect

Quaternary Science Reviews

journal homepage: www.elsevier.com/locate/quascirev

Glacial populations and postglacial migration of Douglas-fir based on fossil pollen and macrofossil evidence

Paul F. Gugger [a,*], Shinya Sugita [b]

[a] Department of Ecology, Evolution and Behavior, University of Minnesota, 100 Ecology Building, 1987 Upper Buford Circle, Saint Paul, Minnesota 55108, USA
[b] Institute of Ecology, Tallinn University, Uus-Sadama 5, 10120 Tallinn, Estonia

ARTICLE INFO

Article history:
Received 7 July 2009
Received in revised form
19 March 2010
Accepted 24 April 2010

ABSTRACT

To understand how temperate forests might respond to future episodes of global warming, it is important to study the effects of large-scale climate change brought about by rapid postglacial warming. Compilations of fossil evidence have provided the best evidence of past plant range shifts, especially in eastern North America and Europe, and provide a context for interpreting new molecular datasets from modern forests. In western North America, however, such reviews have lagged even for common, widespread taxa. Here, we synthesize fossil evidence for Douglas-fir (*Pseudotsuga menziesii*) from nearly 550 fossil pollen, sedimentary macrofossil, and packrat midden macrofossil sites to develop hypotheses about the species' late Quaternary history that can be tested with molecular phylogeographic studies. For both the coastal and interior varieties, we identified alternative hypotheses on the number of glacial populations and postglacial migration patterns that can be characterized as single-population versus multiple-population hypotheses. Coastal Douglas-fir may have been subdivided into two populations at the Last Glacial Maximum (LGM) and colonized British Columbia from populations in Washington and Oregon. Interior Douglas-fir could have been subdivided along major topographic barriers into at least three LGM populations and colonized British Columbia and Alberta from populations in northwest Wyoming and/or northeast Utah. For both varieties, we calculated migration rates lower than previous studies, which could have been as high as 100–220 m/yr if Douglas-fir reached its modern distribution 9000 cal yr BP, or as low as 50 m/yr if it reached its modern range at present. The elevational range of populations in California and the southern Rockies shifted upslope by 700–1000 m. If there were multiple LGM populations, these elevational shifts suggest that those populations did not contribute to the colonization of Canada. Our findings emphasize the possibility of low-density northern LGM populations and that populations within species react individualistically in response to large-scale climate change.

1. Introduction

Dated fossil pollen and macrofossil records from late Quaternary lake sediments have been compiled for many European and eastern North American species indicating that species ranges shifted dramatically as they tracked favorable climates. For example, Davis (1981a, 1983) marked the first arrival of tree taxa in deglaciated regions in eastern North America and found that thermophilous trees spread at rates of 100–1000 m/yr into these landscapes from small populations restricted south of the ice sheets at the Last Glacial Maximum [LGM; 21 000–18 000 calendar years before present (cal yr BP)]. Similarly, Huntley and Birks (1983) reviewed the late Quaternary history of European trees, finding that many taxa were restricted to the Iberian, Italian and Balkan peninsulas during the LGM and expanded to their present distributions at rates up to 2000 m/yr. Because these rates are higher than those considered possible based on empirical estimations in modern forests (Clark et al., 2001), rare long-distance seed dispersal by weather or animal vectors has been proposed as a mechanism (Davis, 1987; Johnson and Webb, 1989; Clark et al., 1998).

For many species, this relatively simple scenario in which one or a few restricted populations concurrently and rapidly expanded northward in response to warming has been challenged as fossil data are re-interpreted and other independent types of data become available for comparison (Bennett and Provan, 2008). In particular, molecular genetic data from modern populations have

---

* Corresponding author. Tel.: +1 862 371 2138; fax: +1 612 624 6777.
E-mail addresses: gugg0030@umn.edu (P.F. Gugger), sugita@tlu.ee (S. Sugita).

0277-3791/$ – see front matter © 2010 Elsevier Ltd. All rights reserved.
doi:10.1016/j.quascirev.2010.04.022

been used to infer past changes in distribution because the effects of past isolation and expansion on the distribution of genotypes often endure to the present (Hewitt, 2000; Petit et al., 2003).

One key insight has been the detection of additional source populations farther north than previously thought (Stewart and Lister, 2001). For example, American beech (*Fagus grandifolia*) and red maple (*Acer rubrum*) might have colonized their northern ranges from scattered, low-density populations near the ice margin (McLachlan et al., 2005) and not from a single, small refugium in the South (Davis, 1981a). Low-density populations could have escaped detection in the fossil record altogether or could have been overlooked where pollen percentages were below thresholds used to define presence. Similarly, molecular data suggest low-density populations of white spruce (*Picea glauca*) persisted the LGM in Alaska in addition to the known LGM populations south of the ice (Anderson et al., 2006). In Alaska, *Picea* pollen accounts for less than 2% of pollen assemblages dating to the LGM (Brubaker et al., 2005). If populations were farther north during the LGM than previously thought, postglacial migration rates were likely much lower than previously thought (<100 m/yr), more consistent with empirical observations of seed dispersal (Clark et al., 2001).

Another important insight is that often only a subset of populations expands, while others remain stable or even shrink. For example, the northern latitudes of the range of red maple (McLachlan et al., 2005; Gugger et al., 2008) were only colonized by populations near the ice margin and not by populations to the south. A comparison of fossil and molecular data for European beech (*Fagus sylvatica*; Magri et al., 2006) revealed that populations from Mediterranean countries did not contribute to the colonization of central and northern Europe, as was inferred in early fossil studies in the region (Huntley and Birks, 1983). And in some cases, those populations may have been isolated for more than one glacial cycle. Instead, populations from central Europe expanded to colonize middle and high latitudes.

Fossil surveys and their comparison to molecular datasets in western North America have lagged those in Europe and eastern North America because the climate history and topography are more complex and generally fewer fossil sites have been analyzed. Phylogeographic studies in the region suggest migration into western Canada from multiple northern source populations in Washington and the northern U.S. Rocky Mountains (Richardson et al., 2002; Carstens et al., 2005; Mimura and Aitken, 2007; Godbout et al., 2008; O'Connell et al., 2008), and some fossil studies concur (Tsukada, 1982; Rosenberg et al., 2003). In the Southwest, more complex histories of long-term isolation, elevational shifts, and migration are suggested in fossil (Spaulding et al., 1983) and molecular (Mitton et al., 2000; Galbreath et al., 2009) data. For temperate trees set in a topographically complex region like western North America, LGM populations could have been scattered and discontinuous and only some may have expanded in response to postglacial climate warming, while others retreated to higher elevation or migrated regionally.

Combined fossil and molecular studies have highlighted some limitations of the fossil record, which can include difficulty detecting low-density populations and the inability to resolve the independent histories of different populations within a species. However, fossils still provide the most direct, dated evidence of a species presence or absence through time compared to the imprecise date estimates inferred from molecular data. Without the backdrop of fossil evidence, patterns of molecular variation cannot confidently be attributed to particular geologic or climatic events. Moreover, the fossil record is an important source of hypotheses as phylogeography turns to more sophisticated statistical methods requiring a priori hypotheses (Knowles and Maddison, 2002; Carstens and Richards, 2007).

We synthesize late Quaternary fossil records of Douglas-fir (*Pseudotsuga menziesii*) for the specific purpose of estimating the location of populations during the LGM and patterns of postglacial range shifts that can be tested in future surveys of molecular variation. To do so, we have compiled fossil pollen, sedimentary macrofossil, and packrat (*Neotoma* spp.) midden macrofossil data from hundreds of previously published records spanning almost the entire modern range of Douglas-fir and extending back to just before the LGM. Our approach emphasizes the possibility of low-density glacial populations and the possibility that populations had independent histories. The various interpretations are discussed as alternative hypotheses that can be tested with future molecular phylogeographic studies and additional fossil evidence.

1.1. *Study organism*

Douglas-fir is a wide-ranging economically and ecologically important conifer in western North America. Two varieties are commonly recognized (Hermann and Lavender, 1990): coast Douglas-fir (*P. menziesii* var. *menziesii*) and interior or Rocky Mountain Douglas-fir (*P. menziesii* var. *glauca*). Coast Douglas-fir is found from central California to central and coastal British Columbia at elevations from sea level near the coast to 2300 m in the Sierra Nevada. Interior Douglas-fir ranges from British Columbia and Alberta to central Mexico, though Mexican populations are occasionally regarded as a different variety, or even species (Martínez, 1949). Compared to coast Douglas-fir, interior Douglas-fir inhabits drier, higher elevation sites primarily in the montane zone but can be found from 500 m to 3200 m depending upon latitude and local conditions. The range becomes increasingly fragmented in the Southwest and Mexico. The two varieties meet in a transition zone in southern, central British Columbia (Li and Adams, 1989; Ponoy et al., 1994).

Douglas-fir's late Quaternary history has been partially reviewed in two previous publications (Tsukada, 1982; Hermann, 1985). Tsukada (1982) focused on the Pacific Northwest and using fossil pollen records found that Douglas-fir migrated north from the Willamette Valley of northern Oregon into southern British Columbia at a rate of about 450 m/yr. Subsequent studies cast doubt on the precise location of populations at the LGM (Barnosky, 1985a; Worona and Whitlock, 1995). Hermann's (1985) survey was broader in temporal and spatial scope, encompassing most of the range and extending back to the earliest fossil records in the Miocene and Oligocene. Hermann's (1985) interpretation generally agreed with that of Tsukada (1982) in the Northwest. In the interior, he concluded that Douglas-fir rapidly migrated into southwestern Alberta from populations in the southern Rockies. Since then, a number of new fossil records have been published, which may shed new light on the late Quaternary history of Douglas-fir.

2. Regional Setting

The topography of western North America is characterized by two sets of major north-south mountain chains: the combination of the Rocky Mountains and Sierra Madre and the combination of the Coast Range, Sierra Nevada, and Cascade Mountains (Fig. 1). The arid Great Basin and Columbia Plateau separate these two sets of mountains. Today, the climate varies substantially from cool, moist Pacific coastal habitats to the drier, summer-monsoonal Rocky Mountains to the intervening arid deserts.

Late Quaternary climate change in western North America is as complex as the geography, owing to changes in circulation in a topographically diverse region. Generally, the LGM was attained about 18 000 cal yr BP during the maximum extent of the Fraser (Northwest), Tioga (California), and Pinedale (Rockies) advances of