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Genetic variation in seasonal growth patterns in radiata pine in Galicia (northern Spain)

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ABSTRACT

Shoot elongation patterns in 2 and 3-year-old *Pinus radiata* seedlings were monitored twice a month during 2003 and once a month during 2004 in three progeny tests in northern Spain. Fifty-eight half-sib families were studied. Several annual growth parameters were measured in each seedling: initiation, termination and duration of height growth and number of new buds formed each year. Total height, internode length and frost resistance were also measured in each seedling. The variation in these traits among families and sites was studied, as well as the effects of environmental parameters (temperature and rainfall) on growth phenology patterns. The extent to which bud phenology is genetically controlled and related to growth traits was examined. Families differed significantly in total summer shoot growth and number of summer flushes (lammas growth). The number of cycles produced per year ranged from one to four. Monocyclic families grew throughout the year, whereas polycyclic families grew episodically, depending on rainfall.

Heritabilities within sites were moderate and very similar between years and sites for the dates of bud burst and the number of new buds formed. Bud burst was positively genetically correlated with seedling height. Thus, selection for greater growth is expected to delay bud burst. The number of new buds formed each year was negatively correlated with height and internode length, which means that monocyclic families were taller with longer internodes than polycyclic families. Thus, selection for faster stem growth in young progeny tests is expected to increase the length of internodes in the next generation, to reduce the number of flushes per year and to delay the bud burst date, thereby avoiding late spring frost damage.

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1. Introduction

The annual cycle of development plays a crucial role in the adaptation of temperate forest trees to seasonal climate changes in temperate regions (Hanninen, 1995). The timing of spring bud flush in radiata pine is an important adaptive trait (Bollman and Sweet, 1976), because it is a critical factor in initiating the annual growth cycle early in the spring while soil moisture is high, yet late enough to avoid spring frost damage (Kohmann and Johnsen, 1994).

The amounts and types of shoot elongation that occur during the growing season are integral components of the annual sequence of developmental events in seedlings. Two models of shoot growth in conifers are recognised: free growth and predetermined growth. The ability to display free growth is often a juvenile feature that gradually decreases as the plant becomes older (Pollard et al., 1975). Free growth can be regarded as an independent contribution to juvenile height growth, which will be lost with age (Pollard and Logan, 1974), or as a precocious height growth, which will be replaced by predetermined growth of a similar magnitude with age (Ununger and Kang, 1988). Such a growth pattern is called monocyclic because only one cycle of growth (recognised by one cluster of branches marking the end of the cycle) occurs in a year, so that the age of monocyclic growth species can often be determined by counting branch whorls. Somewhere between species with predetermined versus free growth are the recurrently flushing or polycyclic species, which may exhibit free growth during the growing season as long as conditions are favourable (lammas growth). Under unfavourable conditions, recurrent flushing species may produce a temporary or resting bud, and when conditions are once again favourable, the resting bud flushes. Recurrent flushers may flush several times during the growing season, usually with the first flush being the longest, which results in more and thicker branches on the main basal whorl of the spring shoot than on the whorl of summer shoots. The annual shoot consists of one spring shoot arising from

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a winter bud (predetermined growth) and one or more summer shoots (lammas growth) formed by elongation of temporary buds (Yildirim, 1992). These additional cycles may be viewed as supplementary to the strictly seasonal growth. They can, however, represent a large proportion of the annual extension, particularly in 2nd- or 3rd-year seedlings, and they can be highly asynchronous between individuals (Burdon, 1994). Total annual height growth for polycyclic species is a function of both the number of branch clusters and the length of the internodes (Harrington, 1991). The annual height growth pattern of a given genotype will determine the length of internodes, the number of branch clusters and their relative position within the annual cycle (Grace and Carson, 1993). Several authors have stressed the importance of predicting tree internode length because it is an important variable in determining the amounts of clearwood that can be obtained from unpruned logs (Carson and Inglis, 1988; Grace and Carson, 1993). Many current end-uses for radiata pine clearwood require lengths below 2 m (Woollons et al., 2000). At the same time, branch size and number are also well recognized to be vital factors in assessing quality and value of timber (Brazier, 1977; Whiteside, 1982).

Radiata pine produces multiple cycles (Harrington, 1991; Kaya et al., 1994) and the number of internodes in the annual shoot varies between 1 and 6 (Bannister, 1962). Elongation of the first cycle is primarily related to temperature (Boyer, 1970; Bridgwater, 1990; Cremer, 1973). Lanner (1976) indicated that year to year extension can be more effectively influenced by modifying numbers of primordia than by modifying internode elongation between them. The rhythmic pattern of bud formation and elongation occurs until one to several "summer shoots" have become elongated within the same growing season (Lavender, 1985; Birchler et al., 1998). Radiata pine shows an unusual feature in the lack of a defined dormant season in the majority of the trees. The trees that grew episodically do not all become dormant at the same time of year. One main disadvantage of recurrent growth species is that the extension of the shoot growth period and delay in shoot hardening increase the susceptibility of stems to damage from late season drought and early fall frost (Cannell and Johnstone, 1978; Kaya et al., 1989). Moreover, shoots are susceptible to frost damage before hardening in the autumn, when even a slight frost can cause damage. Stem damage often results in the death of the apical buds and needles, but needles proximal to the damaged area remain healthy (Malcolm and Freezaillah, 1975) and may cause future defects such as forks, ramicorns and multiple tops (Adams and Bastien, 1995).

In the first generation, selection in breeding programmes focused on improving volume growth, with some attention to tree form. In many cases, as these programmes enter the second generation of breeding and beyond, there is interest in increasing the size of breeding zones or in moving genetic material among zones (Aitken and Adams, 1997). There is currently interest in increasing the size of the breeding zone for radiata pine in Galicia to include interior zones and eastern Galician mountains, where there is higher risk of early autumn and late spring frosts as well as longer summer drought period. With the prospect of deploying improved materials over greater environmental distances, there is a need to characterize genotypes for traits related to adaptation to environmental stresses (Wheeler et al., 1990). When genotypes, as families, are compared in common environments, the variation in patterns reflects genetic differences in response to the same environmental signals. Cold climates or high elevations will favour genotypes with early development of frost hardiness and early bud set (Johnsen and Skroppa, 2000).

The main aims of the present study were to investigate the yearly cycle of height growth in 58 radiata pine families of 3–4-year-old seedlings in three contrasting sites in northern Spain, in order to evaluate the extent of genetic variation in bud-phenology traits and to determine the course of the annual developmental stages. Further aims were to explain possible changes in the timing of these stages in relation to environmental factors and to use this knowledge in interpreting observed changes in tree performance, such as growth and crown condition, by examining the genetic relationships between growth traits and bud phenology.

2. Materials and methods

2.1. Plant and trial materials

Open-pollinated seed of 50 plus tree progenies, selected in plantations in northern Spain were sown in 2000 with also progenies from six parent clones selected in the Basque Country and two batches of commercial seeds collected from seed stands in Galicia (one batch from the interior and another from a coastal area) as controls. Seedlings were planted as progeny tests at three contrasting sites in northern Spain in May 2001. Details of the site characteristics have been reported elsewhere (Codesido and Fernández-López, 2008; Codesido, 2006). Benade has a continental climate with a mean annual precipitation of 902 mm, mean summer precipitation of 111 mm and 42 annual frost days, whereas Daneiro and Monte Xalo have an oceanic climate with mean annual precipitation of 1776 and 1200 mm, mean summer precipitation of 245 and 136 mm and 27 and 30 annual frost days, respectively. Data (not shown) obtained from meteorological stations near to the three sites tested from 2000 to 2008 (available at www.meteogalicia.es) showed that more than the 50% of the annual frosts were between late February and late March (just during important phenological events like pollen shedding, female strobili receptivity – Codesido et al., 2005 – and bud burst). The sites are within RIUS (Region of Identification and Utilization of forest reproductive material) numbers 1 and 2 (García del Barrio et al., 2000), which a priori constitute the breeding area for the selected material. All sites previously supported radiata pine plantations. Site preparation included clearing, ploughing and ridging before planting. The design was a randomised complete block design with 25 replications of single-tree plots with 3 m $\times$ 3 m spacing.

2.2. Traits measured

Shoot phenology was measured periodically: twice a month between October 2002 and August 2003, and once a month between September 2003 and August 2004. Terminal bud flush was measured at the three sites, with a refined scoring system in which the stage of bud flush was recorded: 0 = dormant bud, not flushed, the entire structured wrapped in, or protected by cataphylls; 1 = bud still closed but swollen (meristematic activity started); 2 = bud burst, the bud opening but no new needles distinguished; 3 = bud open, shoot 0–5 cm long; 4 = shoot 5–10 cm long; 5 = shoot 10–15 cm long; 6 = shoot 15–20 cm long; 7 = shoot 20–25 cm long and 8 = shoot more than 25 cm long. Thereafter, the lengths of all cycles, which comprised the annual leader, were measured on every tree.

The following phenological parameters were derived for each seedling: BB, bud burst or date of height growth initiation, as number of days since January 1st to the day when buds reached phase 2 for the first time in the year; BS, bud set or date of termination of height growth, Dur or duration of shoot growth, calculated as the number of days between bud burst and bud set and NOB or total number of new terminal buds formed every year.

Height, internode length and frost damage resistance were measured at the end of the growing season (Codesido and Fernández-López, 2008; Codesido, 2006).