Forest Ecology and Management 325 (2014) 18–25

Contents lists available at ScienceDirect

Forest Ecology and Management

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

Pinus sylvestris sapling growth and recovery from mammalian browsing

Julianne M. O'Reilly-Wapstra [a,*], Ben D. Moore [c], Mark Brewer [d], Joan Beaton [e], David Sim [e], Natasha L. Wiggins [b], Glenn R. Iason [e]

[a] School of Plant Science and National Centre for Future Forest Industries, University of Tasmania, Private Bag 55, Hobart, Tasmania 7001, Australia
[b] University of Utah, Department of Biology, 257 South 1400 East, Salt Lake City, UT 84112, United States
[c] Hawkesbury Institute for the Environment, University of Western Sydney, Locked Bag 1797, Penrith, NSW 2751, Australia
[d] Biomathematics and Statistics Scotland, Craigiebuckler, Aberdeen, Scotland AB15 8QH, UK
[e] James Hutton Institute, Craigiebuckler, Aberdeen, Scotland AB158QH, UK

ARTICLE INFO

Article history:
Received 24 September 2013
Received in revised form 22 March 2014
Accepted 24 March 2014
Available online 22 April 2014

Keywords:
Genetic variation
Plant secondary metabolites
Red deer
Re-growth
Scots pine
Tolerance

ABSTRACT

Plants employ a range of resistance and tolerance mechanisms to counteract the effects of herbivory and research is still unravelling which strategies are most effective against which herbivores. In commercial forestry, research has focused on understanding the genetic basis of resistance traits and using resistance as a management strategy. However, there has been less focus on addressing the basis and utility of tolerance traits. Scots pine (*Pinus sylvestris*) is a well-studied forest tree due to its wide distribution, commercial importance and use in forest restoration of degraded lands as an important foundation tree species. Several herbivore species browse Scots pine and, here, we examine the genetic basis of recovery of Scots pine saplings following browsing by red deer (*Cervus elaphus*) and attempt to describe which plant traits are associated with sapling tolerance. Three hundred saplings from five different open pollinated mothers (five families) were offered to deer in a feeding trial and saplings were left to recover from browsing for one and a half years (two annual growth seasons) in a randomised, replicated common garden. Seven sapling traits were assessed at this time: survival, stem diameter below the leading bud, stem diameter at the base of the sapling, total sapling height, length of the leading bud, average length of three lateral buds, and the total number of lateral buds. Results indicate that browsing of Scots pine by deer influences sapling survival and recovery ability. There were significant family differences in morphological growth traits and these differences were maintained in the presence and absence of browsing. For one recovery trait, length of the leading bud, overcompensation in response to browsing was evident in all families. These data, matched with our finding of no negative relationships between any recovery traits, indicate that Scots pine is quite robust to once-off browsing events by deer. We suggest that at the sapling stage, Scots pine do not employ resistance as a strategy against deer, but tolerate deer browsing to counteract the negative impacts of herbivory. Hence, the use of recovery traits as a management tool to mitigate the negative impacts of browsing is an option worthy of further investigation.

1. Introduction

Plants are eaten and infested by multiple herbivores and pathogens throughout all life stages, causing potential fitness costs to the plant (Strauss and Irwin, 2004). To counter-act these pressures plants employ two main strategies; *resistance* is the ability of plants to prevent browsing from occurring in the first place and *tolerance* incorporates a suite of strategies to reduce fitness impacts once browsing has occurred. In many cases, these strategies have evolved due to the selective pressures imposed by the offending organisms. Earlier theory proposed a trade-off between these two strategies, assuming they should be mutually redundant if there are costs associated with producing resistance and tolerance traits (Vandermeijden et al., 1988; Fineblum and Rausher, 1995). However, trade-offs are often not evident and plants can employ a range of both resistance and tolerance mechanisms (Mauricio et al., 1997; Leimu and Koricheva, 2006; Nunez-Farfan et al., 2007; Carmona and Fornoni, 2013). Mixed strategies appear necessary as no single strategy would be effective against all herbivores and pathogens consuming the plant (Carmona and Fornoni, 2013). Despite over 50 years of research in plant/herbivore interactions, understanding which strategies have evolved to be effective against which enemies remains an important and exciting research

* Corresponding author. Tel.: +61 3 62262482.
E-mail address: joreilly@utas.edu.au (J.M. O'Reilly-Wapstra).

http://dx.doi.org/10.1016/j.foreco.2014.03.038
0378-1127/

question (Gershenzon and Dudareva, 2007; Gomez, 2008; Iason et al., 2011; Utsumi, 2013; Moore et al., 2014).

Determining which strategies plants employ against particular herbivores is also important for mitigating the negative impacts of herbivores in managed plant systems (Miller et al., 2009; Russel and Kimball, 2010). Browsing of saplings and trees in commercial plantations and semi-natural forests is a world-wide problem (Bulinski and McArthur, 2003; Gomez-Aparicio et al., 2005; Oswalt et al., 2006; Mann et al., 2012; Bergqvist et al., 2013). It can result in large economic losses for companies, not only through decreased growth rates and reduced productivity, but through costs in re-planting due to plant losses. Additionally, severe browsing can reduce biodiversity values and carbon gains in re-forestation efforts, where these benefits are prioritised (Ayres and Lombardero, 2000; Persson et al., 2005).

Recent research on natural plant resistance has shown considerable genetic based variation in resistance traits (e.g. plant secondary metabolites; PSMs) that leads to decreased mammalian browsing in the field (Miller et al., 2009). For example, in *Eucalyptus globulus* (a globally-planted temperate hardwood species) large-scale commercial field trials showed plants with increased levels of PSMs (e.g. sideroxylonal and 1,8-cineole) received less browsing than seedlings containing lower concentrations of these compounds (Miller et al., 2009, 2011). This defensive effect also lasted longer in the field than more traditional methods such as tree guards and use of repellents (Miller et al., 2009). Such genetic variation (including relatively high coefficients of genetic variance and high narrow-sense heritabilities of these traits; O'Reilly-Wapstra et al., 2013) offers the opportunity to select for more resistant genotypes in breeding programs. Since resistance is rarely absolute and there may be limitations in this approach (Henery, 2011), the ability of a plant to recover could also prove to be a useful strategy to mitigate damage. Some plants recover fully from browsing while others even over-compensate for browsing by achieving greater net biomass gains and improved fitness than un-browsed plants (Hjalten et al., 1993; Haukioja and Koricheva, 2000; Gard et al., 2013). While research in managed systems has focused on understanding the genetic basis of resistance traits and using resistance as a management strategy, there has been less focus on understanding the genetic basis of recovery traits and investigating tolerance mechanisms as a management tool.

Scots pine (*Pinus sylvestris*) is a well-studied forest tree due to its wide distribution, commercial importance and use in forest restoration of degraded lands as an important foundation tree species and Caledonian pine forests in the UK are a conservation issue (Mason and Alia, 2000; Mason et al., 2004). Scots pine seedlings and saplings are browsed by a range of herbivores including red deer (*Cervus elaphus*) (Gill, 1992). It is rich in monoterpenes – a hugely diverse class of PSMs, many of which have anti-herbivore properties (Gershenzon and Dudareva, 2007). Some of the dominant terpenes in young Scots pine act as defences against molluscs, capercaillie (*Tetrao urogallus*) and moose (*Alces alces*) (Sunnerheimsjoberg, 1992; O'Reilly-Wapstra et al., 2007; Iason et al., 2011), providing some evidence of the need for a diversity of compounds (Iason et al., 2011). However, these defences in saplings do not appear to have the same effect on red deer, with only a weak relationship detected between increased δ^3-carene levels and decreased browsing of needles in one of two different feeding trials (Iason et al., 2011). One possibility is that Scots pine may have a propensity to recover from deer browsing.

Responses of Scots pine to simulated and deer browsing damage appears varied with some studies reporting poor recovery (Miller et al., 1982; Hester et al., 2004; Herrero et al., 2012) and others reporting some recovery (Palmer and Truscott, 2003; Hodar et al., 2008). Variability seems to relate to timing and type of damage (Honkanen et al., 1994). Despite several studies examining recovery of this ecologically and commercially important species from browsing and investigation of some of the factors that may lead to variation in recovery, little research has examined the genetic basis of Scots pine recovery (Honkanen et al., 1994). Large genetic variation exists in many traits such as photosynthetic activity, spring phenology and monoterpenes within the species, including among and within populations (O'Reilly-Wapstra et al., 2007; Salmela et al., 2011, 2013) and variability in recovery may be due to genetic differences which could be used advantageously in managed forest stands, or in conservation and restoration.

In this paper we examine the genetic basis of recovery of Scots pine saplings following browsing by red deer and attempt to describe which plant traits are associated with sapling recovery. We specifically ask: (1) Can saplings recover from browsing? (2) Is there genetic variation in sapling recovery traits? (3) Is there evidence of any negative correlations (indication of possible trade-offs) between sapling morphological traits in recovery? (4) Does the amount of damage by deer influence the likelihood of recovery? (5) Do sapling morphological and chemical traits prior to browsing correlate with recovery?

2. Materials and methods

2.1. Plant genetic stock and experimental design

Three hundred seedlings of the same age were grown in a randomised design from seed sourced from five open-pollinated maternal trees (60 seedlings were randomly selected from each mother and these offspring from each mother will be referred to as a family) from Ballochbuie Wood, Balmoral, Aberdeenshire, UK (latitude: 57°3′N, longitude: 3°16′E). These families from one population were selected for the deer feeding trial (Iason et al., 2011) as they represented three distinct chemotypes – high, medium and low δ^3-carene. To distinguish these families we arbitrarily assigned them the numbers 1–5. Seedlings were maintained in a glasshouse and then moved to an outside enclosure at Craigiebuckler, Aberdeen, Aberdeenshire, UK. Seedlings were potted in 2 L pots and grown in Scotts M2a compost (Scotts, Ipswich, Suffolk, UK). At age three, these saplings were offered to six female red deer (*C. elaphus*) in a one week feeding trial in summer 2006, with three of the deer run in one week (week 1) and three in the following week (week 2) due to logistical constraints. The trial was run indoors and deer were individually housed in pens. Deer were fed a maintenance diet of hay, supplemented by Scots pine branches for five days before the start of the trial. The trail was run in an arena (18×10 m) with a concrete floor and 25 saplings were offered in pots in five heterogeneous patches (one sapling of each of the five families was allocated randomly in each patch) spread evenly around the arena. Deer entered the arena individually and were allowed to move freely between and around the patches. At the time of the feeding trial, saplings had elongated new buds, but had not yet burst new seasons needles (that is, prior to budburst). Immediately, prior to being offered to the deer, five morphological traits were measured on each sapling; stem diameter below the leading bud (mm), stem diameter at the base of the sapling (mm), length of the leading bud (mm), total sapling height (mm) and number of lateral spring buds. Monoterpene concentration of the new spring buds and needles from the previous year was also assessed from each sapling at this time (see below). In the feeding trial, the height of the sapling eaten by deer (% height lost) was measured as a percentage of the starting height. There was variation in the degree to which individual saplings were eaten by deer where deer ate a greater proportion of plants that had longer buds. The full design and results of this trial can be found in Iason et al. (2011).