Trees (2014) 28:1197–1207
DOI 10.1007/s00468-014-1030-1

ORIGINAL PAPER

The influence of stem guying on radial growth, stem form and internal resin features in radiata pine

John R. Moore · David J. Cown · John R. Lee · Russell B. McKinley · Rod K. Brownlie · Trevor G. Jones · Geoffrey M. Downes

Received: 27 January 2014 / Revised: 22 February 2014 / Accepted: 2 May 2014 / Published online: 23 May 2014

Abstract

Key message **Stem guying to prevent wind-induced swaying of radiata pine trees resulted in significant changes in radial growth, but did not affect the frequency of compression wood or resin features.**

Abstract Mechanical stress resulting from wind forces acting on trees can cause a number of direct and indirect effects ranging from microscopic changes in cambial activity through to stem breakage and uprooting. To better understand these effects on radial stem growth and wood properties, an experiment was established in a 13-year-old radiata pine (*Pinus radiata* D Don) stand in which 20 trees were guyed to prevent them from swaying. Radial growth was monitored in these trees and 20 matched controls at monthly intervals for 5 years. The trees were then felled and radial growth, resin features and compression wood were assessed on cross-sectional discs taken at fixed locations up the stem. There was a significant reduction in radial growth at breast height (1.4 m above the ground) in the guyed trees, but an increase in growth immediately above the guying point. A total of 277 resin features were observed in the growth rings formed following guying. The overall frequency of such features was related to height within the stem and annual ring number. No effect of stem guying was found on the incidence of compression wood. Interestingly, the distribution of resin features also did not differ between guyed and un-guyed trees. There was no evidence of a link between stem restraint as a result of guying and the incidence of resin features, suggesting that other factors, such as soil moisture may be more influential.

Keywords Biomechanics · Wind sway · Wood properties · Stem form · Resin

Introduction

Tree stems are dynamic organisms, reacting to both general site conditions and to their local environment (Larson 1965; Telewski 1995). Apart from edaphic factors, rainfall and temperature, the direction, frequency and intensity of wind can be some of the most influential factors affecting tree survival, growth and morphology (Zhu et al. 2004). The damaging effects of wind range from large-scale catastrophic damage in which whole trees are uprooted or broken, through to malformation of stems resulting from branch or leader breakage (Telewski 1995). Operationally, wind exposure can be a constraint on silvicultural options, particularly thinning and also affects the choice of rotation length (Savill 1983; Quine et al. 1995).

Wind exposure can also have a strong influence on stem and crown shape, and wood properties. A number of studies have shown that trees subjected to mechanical stimulus such as wind loading typically have reduced height growth and increased radial growth, leading to a more tapered form (Burton and Smith 1972; Rees and

---

Communicated by T. Fourcaud.

J. R. Moore (✉) · D. J. Cown · J. R. Lee ·
R. B. McKinley · R. K. Brownlie · T. G. Jones
Scion, Private Bag 3020, Rotorua 3046, New Zealand
e-mail: John.Moore@scionresearch.com

Present Address:
T. G. Jones
The New Zealand Institute for Plant and Food Research Limited,
Private Bag 11600, Palmerston North 4442, New Zealand

G. M. Downes
Forest Quality Pty. Ltd., P.O. Box 293, Huonville, TAS 7109,
Australia

Grace 1980; Telewski and Jaffe 1986; Holbrook and Putz 1989; Telewski 1995; Meng et al. 2006). There has also been much debate in the literature about the influence of wind on stem shape, with a number of authors arguing that the shape of tree stems results in uniform stress in the outer fibres when a tree is subjected to wind loading (the so-called "uniform stress hypothesis"). This in turn helps to prevent weak points being created at localised regions of high stress (Metzger 1893; Larson 1963; Mattheck 1991; Dean and Long 1986; Morgan and Cannell 1994). Trees can also respond by adopting a more streamlined crown shape, which results in less wind drag and is assumed to reduce the risk of wind-induced failure (Telewski 1995, 2012). Sellier and Fourcaud (2009) demonstrated that tree sway and response to high winds is more sensitive to changes in the geometry of tree axes, including length, diameter and branch insertion angles, than to alterations of material properties. However, thigmomorphogenetic responses have been observed in a number of wood properties. These include: altered cell dimensions (Bannan and Bindra 1970), compression wood formation (Cown 1973a, 1974; Nicholls 1982; Timell 1986), resin pockets (Frey-Wyssling 1938; Cown 1973b; Temnerud 1997; Watt et al. 2009), spiral grain (Kubler 1991; Eklund and Sall 2000; Skatter and Kucera 1997), increased organic extractives content (Telewski and Jaffe 1986) and a reduction in stiffness (Telewski 1989; Pruyn et al. 2000; Bascuñán et al. 2006; Bruchert and Gardiner 2006).

In order to better understand the effects of wind-induced swaying on tree morphology and wood properties, several studies have compared different traits on guyed and un-guyed trees (Jacobs 1939, 1954; Burton and Smith 1972; Holbrook and Putz 1989; Meng et al. 2006; Valinger 1992). Arguably, the most notable of these studies was carried out by Jacobs (1954) who compared the growth and stem form of guyed and un-guyed radiata pine (*Pinus radiata* D. Don) trees for 19 years. He observed that guying decreased radial growth in the lower bole, but increased it higher up above the guy point, a result confirmed in loblolly pine by Burton and Smith (1972). These authors also observed a reduced incidence of compression wood in the lower stems of guyed trees, but a progressive increase above the guying points.

Wind-induced stem bending resulting in damage to the cambium has been suggested as one possible mechanism responsible for the rupture of resin canals and formation of resin features in wood (Frey-Wyssling 1938; Temnerud et al. 1999). In radiata pine, along with other softwoods, resin features (hereafter taken to include resin pockets and other resinous defects) have been observed to be universally present at a low level (Park 2004) and can occasionally be a serious defect in clear lumber and veneer (Cown et al. 2011; Temnerud 1996; Watt et al. 2011). Resin features have been observed to be random with respect to directional orientation within stems, but tend to increase outwards from the pith and vertically from the base (Gjerdrum and Bernabei 2007; Wernsdorfer et al. 2002). In addition to wind-induced damage to the cambium, drought and pathogens have been suggested as potential causal mechanisms (Cown 1973b; Temnerud 1997; Seifert et al. 2010; Tsoumis 1991; Larson 1994). In some radiata pine forests, notably those on the Canterbury Plains of New Zealand where high winds and drought are common, the incidence of resin features can reach "epidemic" proportions (Clifton 1969; Cown 1973b; Watt et al. 2009). A recent analysis of resin feature data from 281 radiata pine stands sampled in four regions of New Zealand (Woollons et al. 2008) found that their frequency was positively associated with vapour pressure deficit, solar radiation, wind and negatively associated with available water. This analysis used the frequency of broken tree tops as a surrogate for wind exposure; therefore, the direct influence of wind-induced swaying on the formation of resin features in radiata pine was not examined.

In order to better understand and quantify the effects of wind-induced sway on resin features in radiata pine, guying trials were established at three sites in 2006. Two of these trials were installed at locations on the Canterbury Plains (McLeans Island and Balmoral Forest), while the third was installed at a more productive site in the North Island. Results from the guying study at McLeans Island (Lat. 43.47° S, Long. 172.39° E; Elev. 90 m a.s.l.), which was the site with the highest incidence of resin features, have already been presented by Watt et al. (2009). They found that there was a significant reduction in stem growth after guying, accompanied with a decrease in incidence of resin features, particularly in the lower stem. In this paper, we present the results from the guying study at Ohurakura Forest, which had the highest productivity and the lowest incidence of resin features in the lower stem of the three sites (Watt et al. 2011).

Materials and methods

Site description and treatments

This guying trial was established in an existing radiata pine "female tester trial" located at Ohurakura Forest, Hawke's Bay, New Zealand (Lat. 39° 15′ S; Long. 176° 42′ E, Elev. 425 m a.s.l.). The trial was planted in 1993 at an initial density of 625 trees/ha and was pruned to 2.0 m. It was designed to test the general combining ability of progeny of five female clones with candidate pollen parents and has not been thinned. The trial is a first rotation stand growing on an ex-pasture site of high fertility, which is a mixture of flat and sloping terrain with a southeast aspect. The site is exposed to strong northwest winds, has an average annual rainfall of 1,675 mm and contains some swampy patches. The average annual temperature at the site is 11.8 °C, average relative humidity 81 %, and average wind speed of 4.1 m $s^{-1.}$ (National Institute of Water and Atmospheric Research Ltd). The soil type is Puketitiri sandy silt, which is classified as an Orthic Pumice Soil under the NZ Soil Classification (Hewitt 1998).

In 2006, at age of 13, 40 trees consisting of 20 pairs of guyed and un-guyed trees of similar height and diameter at breast height, located in close proximity, were selected for the study. Trees were selected on the flatter areas of the stand order to facilitate guying. All trees were also selected on the basis that they exhibited some signs of external resin bleeding, which is often an indicator of internal resin features (Kumar 2004; Cown et al. 2011). Trees were not selected on the basis of their genetic origin, but the genetic origin of each tree was noted. Tree heights ranged from 17.5 to 23.0 m at the time of selection, and average breast height diameter (DBH) of selected stems was 395 mm with a range of 303–469 mm. Each tree was guyed using three wire ropes attached to metal stakes driven into the ground to a depth of 1,200 mm at 120° intervals around the stem base. A collar was placed on the stem directly above the branch whorl located closest to one-third of total tree height, corresponding to a position up the stem of ~10–12 m. Collars comprised an 8-mm braided wire rope contained inside a 15-mm plastic tube and were only placed on the guyed stems. The guy ropes were attached to this collar and moderately tensioned to reduce tree sway. A comparison of DBH measurements at the time of trial initiation indicated that the guyed trees and their un-guyed controls were not significantly different. Manual band dendrometers (Agricultural Electronics Corporation, Tucson, Arizona, USA) were installed at breast height (1.4 m above the ground) on each of the 40 sample trees, and growth data were collected at monthly intervals for 59 months (i.e. ~5 years).

Disc collection and assessment

Two guyed trees were removed in 2010, because the collars to which the guy ropes were attached had partially girdled the stems and caused the tree tops to break off. The remaining 38 trees were felled in May 2012 and wood samples collected. At the time of felling, all guyed stems showed some signs of trauma such as greatly increased radial growth immediately above the guy point and reduced crown health; two trees were dead at the time of final sampling and had to be harvested earlier. A 1-m section centred about the point of guy-rope attachment was cut from each stem. These sections were then divided longitudinally along the pith and surfaced using the disc skimming tool (Lee 2009). The annual rings were identified to better understand the pattern of growth allocation immediately above and below the point of guying.

In contrast to the previous study (Watt et al. 2009, 2011), cross-sectional discs (50-mm thickness) were removed from all the sample trees at consistent intervals up the stem (i.e. 0, 1.4, 3, 5, 7, 9, 11, 13, 15 and 20 m). The 11-m discs were taken from below the point of guy wire attachment, while the 13-m discs were taken from above this point. Bar code labels were attached to each disc so that they could be tracked. All discs were surfaced in the fresh green condition using a specifically constructed disc skimming tool (Lee 2009), to yield a smooth and clean surface on which to measure growth rings and the number, type and location of resin features. While previous studies in radiata pine have classified resin pockets into three types (Type 1, Type 2 and Type 3) based on size, shape and occlusion characteristics (Somerville 1980; Donaldson 1983), no distinction is generally made between Type 2 and Type 3 resin pockets (Watt et al. 2009). Therefore, in this study resin features were grouped into two classes: Type 1 resin pockets and "other". Type 1 resin pockets are radially narrow discontinuities in the wood that are oval in the tangential–radial plane and filled with oleoresin and callus tissue (Frey-Wyssling 1938). There is a continuum of expressions of "other" resin features arising from obvious physical cambial damage to unspecified causes—epicormic shoots, galls, needle traces, insect damage (Cown et al. 2011).

Each disc was placed in a purpose-built photo booth and photographed using a high-resolution camera at a fixed distance to create a permanent record of visible features. For each disc sampled from 9 m and above, the location of annual growth rings was identified from these images using digitizing software (Engauge Digitizer V4.1). The basal area of each growth ring was calculated along with diameter under bark. In some cases, it was difficult to identify the outermost growth rings in the discs from the guyed trees. In these cases, the best estimate of the annual ring corresponding to the year of guying was made, so that the basal area following guying could be calculated. For discs sampled from below 9 m, the diameter at 2006 and the diameter under bark were determined from the images. The amount of compression wood in each disc (on a percentage area basis) was assessed visually on all discs, without regard to severity. For those discs taken from 9, 11, 13, 15 and 20 m from the base of the stem, compression wood content was assessed separately for the periods before and after the guying treatment was applied as this part of the stem was assumed to be most affected by guying. The distance between the pith and the geometric centre of the disc was determined for each disc as this provides an indirect measure of the effects of wind-induced sway on the formation of compression wood and eccentric growth.

Data analysis

The cumulative diameter increment at breast height was determined from the dendrometer data for the 59-month period following the application of the guying treatment. The main and interactive effect of treatment and time since guying on cumulative diameter increment was examined using a mixed effects model that accounted for the repeated nature of measurements. The study was considered to be a randomised complete block experiment with repeated measurements on the experimental units in a block/cluster of two trees. There were missing data points due to missed measurements or death of trees in some of the blocks. The data were analysed using the SAS MIXED procedure, which adjusts the hypotheses tests accordingly to account for the missing data points. The following linear model was fitted to the data:

$$dbhrel_{ijk} = \mu + \alpha_i + b_j + \tau_k + (\alpha\tau)_{ik} + \gamma dbh0_{ij} + \varepsilon_{ijk} \quad (1)$$

where $dbhrel_{ijk}$ is the diameter increment in the jth cluster ($j = 1, 2, \ldots 20$) of the ith treatment ($I = 1,2$) at the kth time ($k = 1,2,.. 59$); α_i is the effect of the ith treatment; b_j is the random effect of the jth cluster; $(\alpha\tau)_{ik}$ is the ith treatment by kth time interaction effect; γ is the effect of the initial dbh of the treatment i tree in cluster j ($dbh0_{ij}$); and ε_{ijk} is the random error due to the kth time measurement on the treatment i tree in the jth cluster. The Kenward–Roger denominator degrees of freedom adjustment method was used to correct for possible across treatments' constant variance issues and the spatial power correlation model [a generalisation of the autoregressive first-order (AR (1)) model when measurement time intervals are not equal] used to model the correlations among residuals from the same tree. The treatment by time least square means predicted by model 1 and their 95 % confidence intervals were recovered from the SAS MIXED procedure and used to determine when the guying treatment started to have a significant effect on diameter increment.

The effect of guying on stem form was examined by normalising the under-bark diameter of each disc by the breast height diameter of the corresponding tree. The vertical profile of normalised diameter was determined for guyed and un-guyed trees and the effect of the guying treatment was examined using two-way ANOVA. The basal area increment between 2006 and 2012 was determined for each disc, while the basal area of each annual ring was also determined on discs sampled from 9 m and above.

Data on the number of resin features were summarised by type, year of formation and height up the stem for guyed and un-guyed trees. The frequency of resin pockets was expressed on a unit area basis using the basal area of each ring and disc. Mixed effects models with a nested structure were used to test the main and interactive effects of guying treatment, year, and height on incidence of resin features. Separate models were developed for Type 1 resin pockets and other resin defects. In these models, the effect of guying on resin feature incidence was examined for the 59-month period following the application of guying treatments in 2006. A generalised linear mixed effects model was used in which the frequency of resin features was assumed to follow a Poisson distribution. These data were analysed using the R open source statistical software (R Development Core Team 2013). The temporal trend in resin feature occurrence was compared with annual trends in rainfall and wind speed to look for any obvious patterns. Meteorological data for these comparisons were obtained from the National Climate Database (National Institute of Water and Atmospheric Research Ltd) for the nearest meteorological station to the experimental site.

Results

Growth and stem form

Data from the breast height dendrometer bands showed that for some pairs of guyed and un-guyed trees there was little or no difference in diameter increment following guying, while for other pairs of trees differences of 30–50 mm were observed 5 years after the application of the guying treatment (Fig. 1). Overall, there was a significant treatment by time interaction ($p < 0.001$). Thus, the effect of the guying treatment depended on the time interval since the guying treatment was applied. Diameter increment did not show a relationship with initial DBH at the time of guying ($p = 0.13$). The effect of guying treatment on diameter increment became significant after 26 months (Fig. 2). After 59 months since the treatments were applied, the guyed trees had on average 17.7-mm less diameter growth at breast height compared with the un-guyed controls. No obvious genetic differences in the response to guying were observed.

On average, the guyed trees at the time of sampling had lower relative diameter just below the guying point compared with the un-guyed trees, but had increased relative diameter immediately above the guying point (Fig. 3). Radial–longitudinal sections through the point of guy wire attachment to the stem showed the substantially greater radial growth immediately above the point of attachment (Fig. 4). These sections also showed that in some trees, the outermost annual rings appeared to stop at the point of attachment where the collar had girdled the stem and interrupted the phloem flow in particular.

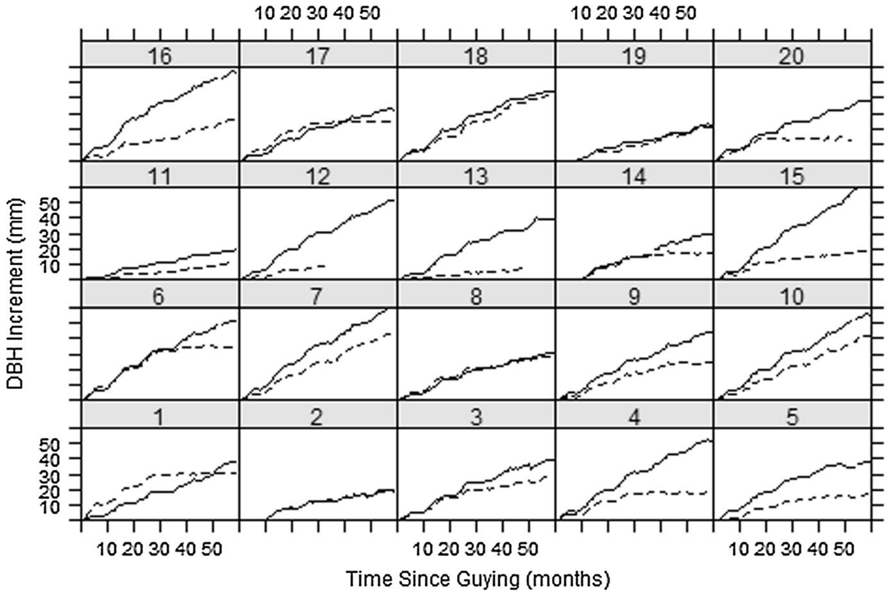


Fig. 1 Comparative diameter increment at breast height for the 59-month period following the application of the guying treatments. Data are shown for the 20 pairs of guyed (*dashed line*) and un-guyed (*solid line*) trees

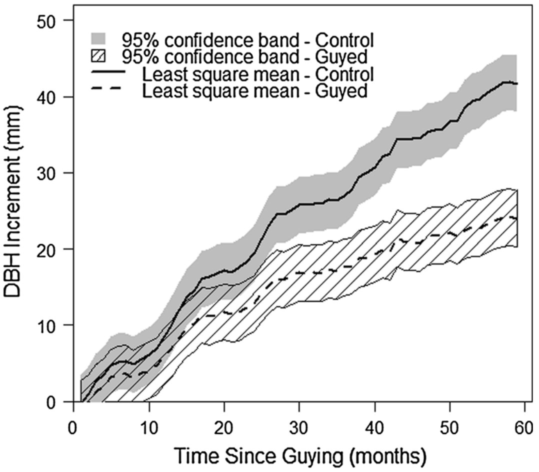


Fig. 2 Average diameter increment at breast height for the 59-month period following the application of the guying treatments. Values are based on the model given by Eq. 1 in the text

Comparison of the basal area increment between 2006 and 2012 for the discs sampled between 0 and 20 m up the stem shows that immediately above the guying point (i.e. at 13 m), the guyed trees had on average 10 cm^2 more basal area growth per year than the un-guyed controls (Fig. 5). The increase in basal area increment became apparent ~2 years after the application of the guying treatment and is responsible for the change in shape that was observed in the guyed trees. On some of the surfaced discs from the guyed trees, there appeared to be a significant reduction in or even cessation of growth. In the most extreme cases, annual rings were absent from part of the circumference of the disc. This was assumed to be due to the girdling effect of the collar that the guy ropes were attached to, which likely limited the cambial activity of the tree.

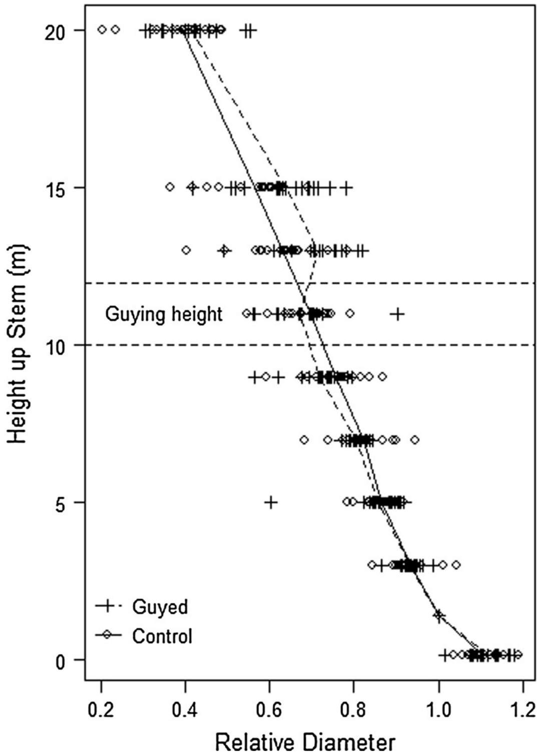


Fig. 3 Vertical profiles of normalised stem diameter for guyed and un-guyed trees. Stem diameter for each tree was normalised by the diameter at breast height. Lines pass through the mean value for guyed and un-guyed trees at each sampling height

Resin features

A total of 728 resin features were observed on the disc surfaces, which corresponded to a frequency of 24.3 features m^{-2}. There were 28 Type 1 resin pockets and 700

Fig. 4 Longitudinal-radial section through the region of the stem centred about the guying point. The growth rings have been highlighted to show the increased radial growth in the region immediately above the guying point

other resin defects (Table 1). The overall Type 1 resin pocket frequency was 0.94 m^{-2}. The mean frequency of resin features increased with height up the stem, reaching a peak of 65.7 m^{-2} in the discs taken from 15 m. However, the variability in resin feature frequency also increased with height up the stem (Fig. 6). The maximum number of resin pockets in the breast height discs was observed in the annual ring formed in 2005 (Fig. 7). Because the area of the innermost rings was lower, the frequency of resin pockets per m^2 was highest in the rings formed in 2001 and 2002 (data not shown). There was no obvious effect of climate on the incidence of resin features as both rainfall and wind speed in the 2004 years were close to the long-term means for the site.

In the period following the application of the guying treatment a total of 277 resin features were observed, which consisted of 18 Type 1 resin pockets and 259 other resin defects. Four of the Type 1 resin pockets were in the un-guyed control trees and the remaining 14 were in the guyed trees (Table 1). Seven of these were observed in the discs taken from 13 and 15 m in the guyed trees, i.e. immediately above the guying point where there is the highest bending stress. In the region below the guying point, four Type 1 resin pockets were observed in control trees and six were observed in the guyed trees. However, the small number of observations of type resin pockets meant that meaningful comparisons between guyed and un-guyed trees could not be made. Of the 259 other resin defects that were observed, 140 were found in the control trees and 119 in the guyed trees. The generalised linear mixed model fitted to these data showed that there were significant positive effects of ring number and disc height, but no significant effect of guying treatment (Table 2).

Compression wood

The proportion of total cross-sectional area of the sampled discs containing visible compression wood ranged from 0 % up to 50 %. Approximately one-third (36 %) of discs contained no more than 5 % visible compression wood, and the overall mean proportion of compression wood was 14 %. There was no trend in the occurrence of compression wood in wood formed after 2006 with height up the stem

Fig. 5 Comparison of the total basal area increment from 2006 to 2012 at different heights up the stem for the guyed and un-guyed trees (*top graph*). The basal area of each annual ring in the guyed and un-guyed trees for the disc sampled at 13 m is shown in the *lower graph*

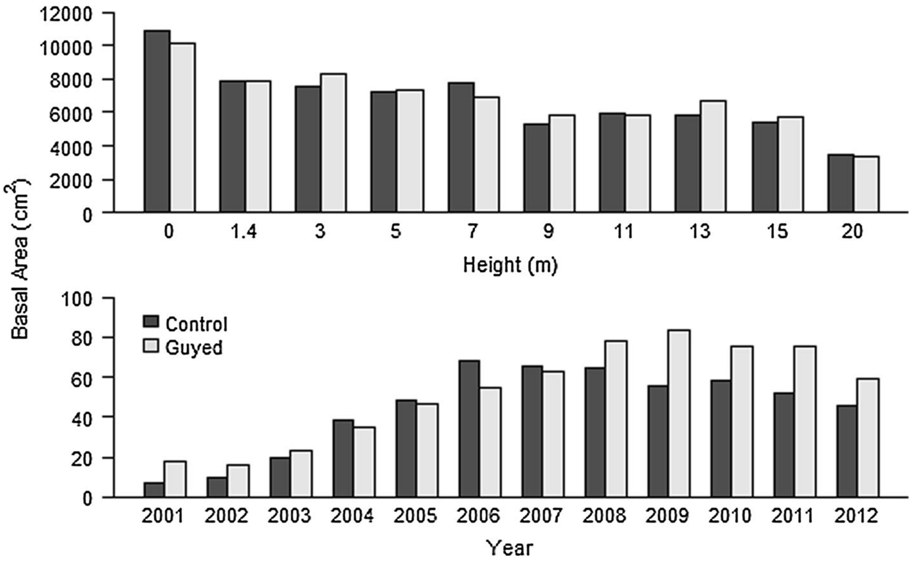


Table 1 Occurrence of Type 1 resin pockets and other resin features in guyed trees and un-guyed controls

Disc height (m)	Control				Guyed			
	Post-2006		Total		Post-2006		Total	
	Other	Type 1	Other	Type 1	Other	Type 1	Other	Type 1
0.15	6 (5.5)	1 (0.9)	25 (7.6)	2 (0.7)	0 (0.0)	0 (0.0)	23 (8.6)	1 (0.4)
1.4	2 (2.5)	2 (2.5)	53 (21.9)	2 (0.8)	3 (3.8)	0 (0.0)	34 (16.0)	1 (0.4)
3	3 (4.0)	0 (0.0)	46 (21.6)	0 (0.0)	3 (3.6)	1 (1.2)	38 (20.6)	2 (1.2)
5	10 (13.7)	1 (1.4)	56 (30.2)	2 (0.9)	22 (29.9)	3 (4.1)	44 (28.8)	5 (2.9)
7	15 (19.3)	0 (0.0)	51 (34.1)	0 (0.0)	11 (15.8)	1 (1.4)	23 (19.4)	1 (0.8)
9	9 (14.3)	0 (0.0)	33 (25.1)	0 (0.0)	6 (9.78)	1 (1.6)	12 (10.0)	1 (0.6)
11	24 (35.9)	0 (0.0)	45 (42.1)	0 (0.0)	14 (23.1)	0 (0.0)	19 (23.1)	0 (0.0)
13	21 (32.7)	0 (0.0)	43 (41.7)	0 (0.0)	28 (40.4)	4 (5.8)	38 (37.9)	5 (4.3)
15	33 (55.0)	0 (0.0)	51 (80.7)	0 (0.0)	26 (44.0)	3 (5.1)	35 (43.1)	4 (6.0)
20	17 (44.1)	0 (0.0)	23 (51.2)	0 (0.0)	6 (18.2)	1 (3.0)	8 (26.5)	2 (5.5)
Total	140 (19.8)	4 (0.6)	426 (35.7)	6 (0.2)	119 (17.3)	14 (2.0)	274 (23.3)	22 (2.1)

Values are given for both the entire tree and for the wood formed after 2006. The frequencies of resin features per m^2 of transverse section are given in parentheses

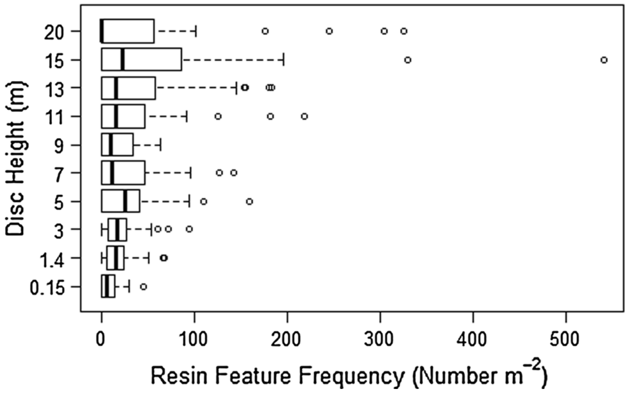


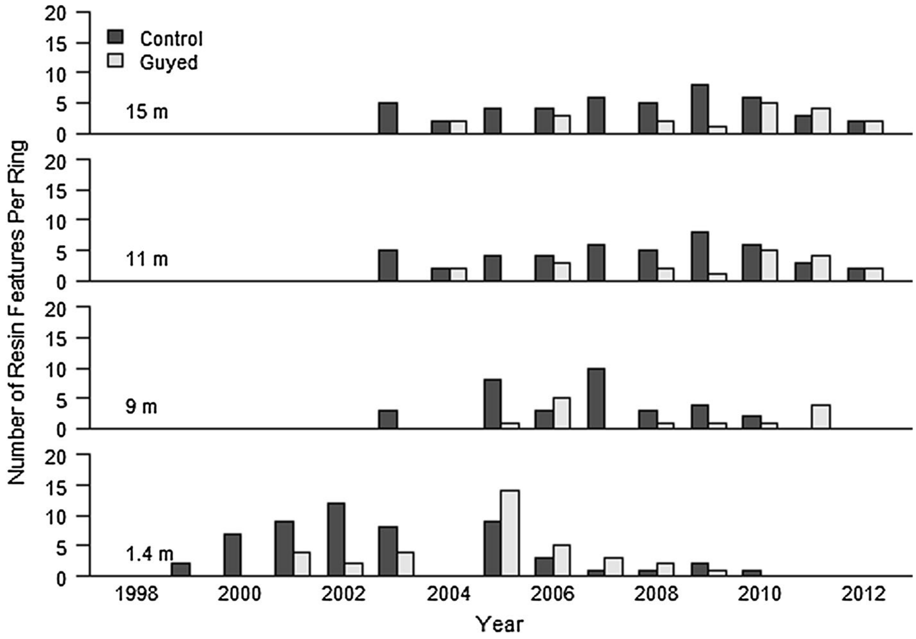
Fig. 6 *Box* and *whisker diagram* showing the overall frequency of resin features at different heights in the stem. The edges of the *boxes* correspond to the upper and lower quartiles of the distribution of resin features, while the median is shown by a thicker *black line*. The *whiskers* correspond to ±1.96 standard deviations from the mean and values outside this are shown as *open circles*

($p = 0.60$) and no effect of treatment ($p = 0.55$). The distance between the pith and the geometric centre of the disc decreased with height up the stem (Table 3). There was a significant effect of the interaction between guying treatment and disc height on the pith offset distance ($p = 0.02$). Those discs taken from the bottom 3 m of the guyed stems had an offset distance that was 4–7 mm less than in discs taken from the same heights in the un-guyed controls.

Discussion and conclusions

The main emphasis of the study was to document aspects of wood formation, particularly radial growth and resin features as they are affected by the elimination of stem movement. This study confirmed the results from a number of earlier studies (Jacobs 1939, 1954; Burton and Smith 1972; Holbrook and Putz 1989; Watt et al. 2009; Valinger 1992), which showed that tree sway can influence the diameter growth at different points along the stem. Compared with the control trees, radial growth was reduced in the lower part of the guyed stems, but was greater for the region of the stem extending for several metres above the point of guy-rope attachment. In the earlier guying study on radiata pine, Jacobs (1954) observed similar enhanced radial growth, or swelling, immediately above the point at which the trees were guyed. A similar result was also observed in Scots pine (*Pinus sylvestris* L.) by Valinger (1992). This is assumed to be a physiological response to the increased bending stress that occurs in the outermost part of the stem at this point. A number of studies have suggested that new wood is accumulated more rapidly in regions subject to higher mechanical stress to keep the stress more or less uniform along the length of the stem (Riech and Ching 1970; Metzger 1893; McMahon 1975; Dean et al. 2002). While the uniform stress hypothesis is a matter of some debate in the literature (Niklas and Spatz 2000a, b; Mattheck 2000), the results from the study reported here indicate that radial growth is lower in regions of lower stress (i.e. the lower part of the stem of guyed trees) and higher in regions of high stress (immediately above the point of guy rope attachment). However, it is not possible to conclude that the differences in radial growth that were observed are solely a response to altered patterns of mechanical stress along the stem. The collar to which the guy ropes were attached eventually acted to girdle the stem, which would have interrupted the phloem transport to the lower stem and roots. This could have elicited a response similar to that resulting from stem girdling in which carbohydrate produced by the crown is retained in the region of

Fig. 7 Number of resin features per annual ring at selected heights up the stem



the stem above the girdle and is used for growth (Wilson 1968; Wilson and Gartner 2002; Daudet et al. 2005; de Shepper et al. 2010). After several years following the application of the guying treatment, many of the guyed trees began to show some signs of distress such as a loss of vigour and missing growth rings. In the most extreme cases two of the guyed trees died, while the stems of another two broke immediately above the point of guy-rope attachment. For future studies, it is recommended that either an expanding collar or eye-bolts are used to avoid the problems that were encountered here. In addition, the collar or bolts should be applied to the control as well as the guyed trees.

Table 2 Results from significance tests on the parameters included in the generalised linear mixed effects model examining the effects of guying treatment, disc height, ring number and their interactions on the incidence of other resin features

Source of variation	*p* value
Treatment	0.846
Disc height	<0.001
Ring number	<0.001
Treatment × disc height	0.304
Treatment × ring number	0.830

The analysis was not run for Type 1 resin pockets due to the low number of these features observed in the study

Table 3 Occurrence of visible compression wood and the distance between the pith and the geometric centre of sampled discs from guyed trees and un-guyed controls

Disc height (m)	Control				Guyed			
	Visible compression wood (%)			Off-centre pith (mm)	Visible compression wood (%)			Off-centre pith (mm)
	Pre-2006	Post-2006	Whole disc		Pre-2006	Post-2006	Whole disc	
0.15	–	–	16	30	–	–	11	26
1.4	–	–	15	31	–	–	12	23
3	–	–	15	31	–	–	10	24
5	–	–	10	25	–	–	9	25
7	–	–	13	24	–	–	11	18
9	23	19	10	20	19	15	11	19
11	16	23	16	21	13	21	18	20
13	14	21	16	19	14	24	18	18
15	15	29	21	15	9	17	15	16
20	2	18	15	6	10	18	13	7

Values are given for both the entire tree and for the wood formed before and after 2006

While guying affected both radial growth and stem form, it did not significantly affect the incidence of resin features or compression wood. There were few resin features close to the pith in the lower stem, which is in agreement with the results of the study by Watt et al. (2011), but an increasing frequency with height up the stem, as was noted previously by Clifton (1969). Only a small number of Type 1 resin pockets were observed in this study and "other" resin features, which are sometimes classified as Type 2 and Type 3 resin pockets (Somerville 1980; Donaldson 1983; Cown et al. 2011) outnumbered Type 1 resin pockets by a factor of ten in the guyed trees and 70 in the un-guyed controls. This is similar to some past studies which have differentiated between different types of resin features (Watt et al. 2011). The incidence of resin features was related to both year of annual ring formation and height up the stem. Across all trees, the incidence of resin features was greatest in the 2004–2005 annual ring, which was the same year that the peak was observed in trees sampled in a related study at McLeans Island in Canterbury (Watt et al. 2009). Both stands of trees were planted at a similar time, i.e. 1992 and 1993, but there was no obvious climatic signal that appeared to be associated with the high incidence of resin features in the 2004–2005 annual ring. In contrast to recent studies (Watt et al. 2009, 2011) which only sampled the lower 5 m of trees, we collected information on resin feature frequency up to a height of 20 m in the stem. The observation that the frequency of resin features increased with height up the stem was in broad agreement with Clifton (1969) who found higher concentrations of Type 1 pockets in the second log (i.e. ~6–12 m up the stem) in radiata pine trees.

In contrast to other studies (Frey-Wyssling 1938; Temnerud 1997; Watt et al. 2009; Jones et al. 2013) that have found a positive relationship between stem bending and the incidence of resin pockets, we found no effect of stem guying on the incidence of resin features. A similar result was found by Seifert et al. (2010) who could not establish a connection between resin pocket incidence and wind direction or speed. While the Ohurakura site had a higher mean wind speed than the other sites sampled in the study by Watt et al. (2011), it also had the highest rainfall—more than double the average annual rainfall of the McLeans Island site, where a significant effect of guying was observed on the frequency of Type 1 resin pockets (Watt et al. 2009). In comparison to the study at McLeans Island in which the trees were guyed for 2 years before being destructively sampled, the trees in this study were guyed for 5 years. Therefore, it was assumed that any response to guying would have been more pronounced. However, earlier results presented by Watt et al. (2011) showed that the trees growing at the McLeans Island site had almost ten times the resin feature frequency as those at the Ohurakura site. The low incidence of Type 1 resin pockets observed in this study meant that any effect of guying was not able to be detected, but could also mean that moisture deficit is a key factor affecting the occurrence of resin features (Cown 1973b; Woollons et al. 2008; Seifert et al. 2010). By comparing the results of this study with those from the McLeans Island study (Watt et al. 2009), a tentative conclusion could be drawn that prevention of wind-induced stem sway only affects the occurrence of resin features on those sites where trees are subjected to prolonged moisture stress due to low rainfall. While guying, the trees had a clear influence on stem growth and form in this trial, there is no evidence to suggest the reduction in tree sway influenced the formation of resin features or compression wood. Sampling of the trees in the guying experiment at Balmoral Forest on the Canterbury Plains, which has the lowest mean annual rainfall and mean wind speed of the three sites that guying experiments were established at, would provide more evidence to support or refute this conclusion.

Author contribution statement JRM was the primary author and analysed most of the data. DJC and RBMcK collected data on resin features and contributed to the interpretation of results. JRL arranged the collection of discs, undertook preliminary analysis of the data and assisted with an early draft of the manuscript. RKB assisted with monitoring of the trial, collection and photographing of the discs. TGJ helped with developing the initial trial design and collected data on tree growth during the guying period. GMD and JRM conceived the initial concept of the trial, developed the work plan and obtained funding.

Acknowledgments Funding for the initial establishment of this experiment was provided by the Wood Quality Initiative Ltd. Future Forests Research Ltd. provided funding for the ongoing data collection, felling of the trial and analysis of the data. Rayonier | Matariki Forests provided the site for this experiment. Scion colleagues Mark Miller and Kane Fleet installed the guying cables and with Jason Bennett assisted in the felling of the trial. Dr Charles Sabatia provides assistance with the analysis of the growth response data. Dr Damien Sellier, Dr Jonathan Harrington and two anonymous reviewers provided helpful comments on earlier versions of the manuscript.

Conflict of interest The authors declare that they have no conflict of interest.

References

Bannan MW, Bindra M (1970) The influence of wind on ring width and cell length in conifer stems. Can J Bot 48:255–259

Bascuñán A, Moore JR, Walker JCF (2006) Variations in the dynamic modulus of elasticity with proximity to the stand edge in radiata pine stands on the Canterbury Plains, New Zealand. NZ J For 53(1):4–8

Bruchert F, Gardiner B (2006) The effect of wind exposure on the tree aerial architecture and biomechanics of sitka spruce (*Picea sitchensis*, Pinaceae). Am J Bot 93(10):1512–1521

Burton JD, Smith DM (1972) Guying to prevent wind sway influences loblolly pine growth and wood properties. US Department of Agriculture, Forest Service, Southern Forest Experiment Station Research Paper SO-80, New Orleans, p 8

Clifton NC (1969) Resin pockets in Canterbury radiata pine. NZ J For 14(1):38–49

Cown DJ (1973a) Effects of severe thinning and pruning treatments on the intrinsic wood properties of young radiata pine. NZ J For Sci 3:379–389

Cown DJ (1973b) Resin pockets: their occurrence and formation in New Zealand forests. NZ J For 18(2):233–251

Cown DJ (1974) Comparison of the effects of two thinning regimes on some wood properties of radiata pine. NZ J For Sci 4:540–551

Cown DJ, Donaldson LA, Downes GM (2011) A review of resin features in radiata pine. NZ J For Sci 41:41–60

Daudet F-A, Ameglio T, Cochard H, Archilla O, Lacointe A (2005) Experimental analysis of the role of water and carbon in tree stem diameter variations. J Exp Bot 46(409):135–144

de Shepper V, Steppe K, van Labeke M-C, Lemeur R (2010) Detailed analysis of double girdling effects on stem diameter variations and sap flow in young oak trees. Environ Exp Bot 68:149–156

Dean TJ, Long JN (1986) Validity of constant-stress and elastic-instability principles of stem formation in *Pinus contorta* and *Trifolium pratense*. Ann Bot 58:833–840

Dean TJ, Roberts SD, Gilmore DW, Maguire DA, Long JN, O'Hara KL, Seymour RS (2002) An evaluation of the uniform stress hypothesis based on stem geometry in selected North American conifers. Trees 16:559–568

Donaldson LA (1983) Longitudinal splitting of bark: a likely cause of "type 3" resin pockets in *Pinus radiata*. NZ J For Sci 13:125–129

Eklund L, Sall H (2000) The influence of wind on spiral grain formation in conifer trees. Trees 14:324–328

Frey-Wyssling A (1938) The formation of resin pockets. Holz Roh und Werkstoff 9:329–332

Gjerdrum P, Bernabei M (2007) Three-dimensional model for size and location of resin pockets in stems of Norway spruce. Holz als Roh und Werkstoff 65(3):201–208

Hewitt AE (1998) New Zealand soil classification, 2nd edn. Landcare Research Science Series, Lincoln

Holbrook NM, Putz FE (1989) Influence of neighbors on tree form: effects of lateral shade and prevention of sway on the allometry of *Liquidamber styrafaciflua* (Sweet gum). Am J Bot 76(12):1740–1749

Jacobs MR (1939) A study of the effects of sway on trees. Commonwealth Forestry Bureau, Canberra

Jacobs MR (1954) The effect of wind sway on the form and development of *Pinus Radiata* D. Don. Aust J Bot 2:35–51

Jones TG, Downes GM, Watt MS, Kimberley MO, Culvenor DS, Ottenschlaeger M, Estcourt G, Xue J (2013) Effect of stem bending and soil moisture on the incidence of resin pockets in radiata pine. NZ J For Sci 43:10

Kubler H (1991) Function of spiral grain in trees. Trees 5:125–135

Kumar S (2004) Genetic parameter estimates for wood stiffness, strength, internal checking, and resin bleeding for radiata pine. Can J For Res 34(12):2601–2610

Larson PR (1963) Stem form development of forest trees. For Sci Monogr 5:1–42

Larson PR (1965) Stem form of young Larix as influenced by wind and pruning. For Sci 11:412–421

Larson PR (1994) The vascular cambium: development and structure. Springer, Berlin

Lee J (2009) Assessment of the end grain of log ends and discs. Scion Wood Process Newslett 43:5–6

Mattheck C (1991) Trees: the mechanical design. Springer, Berlin

Mattheck C (2000) Comments on "Wind-induced stresses in cherry trees: evidence against the hypothesis of constant stress levels" by K. J. Niklas, H.-C. Spatz, Trees, (2000) 14:230–237. Trees 15:63

McMahon TA (1975) The mechanical design of trees. Sci Am 233:93–102

Meng SX, Lieffers VJ, Reid DEB, Rudnicki M, Silins U, Jin M (2006) Reducing stem bending increases the height growth of tall pines. J Exp Bot 57(12):3175–3182

Metzger C (1893) Der Wind als massgebender Faktor fur das Wachstum der Baume. Mundener forstl Hefte 3:35–86

Morgan J, Cannell MGR (1994) Shape of tree stems—a re-examination of the uniform stress hypothesis. Tree Physiol 14:49–62

Nicholls JWP (1982) Wind action, leaning trees and compression wood in *Pinus radiata* D.Don. Aust For Res 12:75–91

Niklas KJ, Spatz H-C (2000a) Response to Klaus Mattheck's letter. Trees 15:64–65

Niklas KJ, Spatz H-C (2000b) Wind-induced stresses in cherry trees: evidence against the hypothesis of constant stress levels. Trees 14:230–237

Park J (2004) The incidence of resin pockets. NZ J For 49(3):32

Pruyn ML, Ewers BJ III, Telewski FW (2000) Thigmomorphogenesis: changes in the morphology and mechanical properties of two Populus hybrids in response to mechanical perturbation. Tree Physiol 20:535–540

Quine CP, Gardiner BA, Coutts MP, Pyatt DG (1995) Forests and wind: management to minimise damage. Forestry Commission Bulletin 114, HMSO, London

R Development Core Team (2013) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna

Rees DJ, Grace J (1980) The effects of wind on the extension growth of *Pinus contorta* Douglas. Forestry 53:145–153

Riech FP, Ching KK (1970) Infuence of bending stress on wood formation of young Douglas-fir. Holzforschung 24:68–70

Savill PS (1983) Silviculture in windy climates. For Abstr 44(8):473–488

Seifert T, Breibeck J, Seifert S, Biber P (2010) Resin pocket occurrence in Norway spruce depending on tree and climate variables. For Ecol Manage 260(3):302–312

Sellier D, Fourcaud T (2009) Crown structure and wood properties: influence on tree sway and response to high winds. Am J Bot 96(5):885–896

Skatter S, Kucera B (1997) Spiral grain—an adaptation of trees to withstand stem breakage caused by wind-induced torsion. Holz Als Roh-Und Werkstoff 55(4):207–213

Somerville A (1980) Resin pockets and related defects of *Pinus radiata* grown in New Zealand. NZ J For Sci 10:439–444

Telewski FW (1989) Structure and function of flexure wood in *Abies fraseri*. Tree Physiol 5:113–121

Telewski FW (1995) Wind-induced physiological and developmental responses in trees. In: Coutts MP, Grace J (eds) Wind and trees. Cambridge University Press, UK, pp 237–263

Telewski FW (2012) Is windswept tree growth negative thigmotropism? Plant Sci 184:20–28

Telewski FW, Jaffe MJ (1986) Thigmomorphogenesis: anatomical, morphological and mechanical analysis of genetically different sibs of *Pinus taeda* in response to mechanical perturbation. Physiol Plant 66:219–226

Temnerud E (1996) Pitch pockets in *Picea abies:* variation in amount, number and size within trees and within a stand. Scand J For Res 11:164–173

Temnerud E (1997) Formation and prediction of resin pockets in *Picea abies* (L.) Karst. Doctoral thesis Acta Universitatis Agriculturae Sueciae Silvestria 26:56

Temnerud E, Valinger E, Sundberg B (1999) Induction of resin pockets in seedlings of *Pinus sylvestris* L. by mechanical bending stress during growth. Holzforschung 53:386–390

Timell TE (1986) Compression wood in gymnosperms, vol 1–3. Springer-Verlag, Berlin

Tsoumis G (1991) Wood science and technology of wood—structure, properties, utilisation. Chapman & Hall, New York

Valinger E (1992) Effects of wind sway on stem form and crown development of Scots pine (*Pinus sylvestris* L.). Aust For 55:15–21

Watt MS, Downes GM, Jones T, Ottenschlaeger M, Leckie AC, Smaill SJ, Kimberley MO, Brownlie R (2009) Effect of stem guying on the incidence of resin pockets. For Ecol Manage 258(9):1913–1917

Watt MS, Kimberley MO, Downes GM, Bruce J, Ottenschlaeger ML, Jones TG, Brownlie RK, Leckie AC, Smaill SJ, Xue J (2011) Characterisation of within-tree and within-ring resin-pocket density in *Pinus radiata* across an environmental range in New Zealand. NZ J For Sci 41:141–150

Wernsdorfer H, Reck P, Seeling U (2002) Mapping and predicting resin pockets in stems of Norway spruce (*Picea abies* (L.) Karst.). In: Proceedings of the Fourth Workshop IUFRO 50104, Harrison Hot Springs, British Columbia, Canada, September 8–15:68–77

Wilson BF (1968) Effect of girdling on cambial activity in white pine. Can J Bot 46:141–146

Wilson BF, Gartner BL (2002) Effects of phloem girdling in conifers on apical control of branches, growth allocation and air in wood. Tree Physiol 22:347–353

Woollons R, Manley B, Park J (2008) Factors influencing the formation of resin pockets in Pruned radiata pine butt logs from New Zealand. NZ J For Sci 38(2–3):323–334

Zhu J, Liu Z, Li X, Matsuzaki T, Gonda Y (2004) Review: effects of wind on trees. J For Res 15:153–160