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Modeling Wound-Closure Response Over Time in Douglas-Fir Trees

Dryw A. Jones, Constance A. Harrington, and David Marshall

Wound closure is an important component of tree recovery from bole damage. Damage to young Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco) stands in the precommercial and commercial stages is common, yet few studies have looked at how trees at these stages of stand development respond to common forms of damage. Using data from a 10-year study of artificially damaged Douglas-fir trees, we found reduced potential for relative wound closure with increasing initial tree bole diameter, and increasing initial relative bole area damaged. Wound-closure rates increased for longer periods of time in more vigorous trees, trees on better-quality sites, and trees with intact live crowns. Wound-closure rates were reduced for trees with more relative bole damage, smaller live crown cross-sections, slower relative diameter growth, and more crown competition. Trees with low levels of bole damage relative to lower bole surface area produced more callus tissue than was necessary to cover the original wound, suggesting that long-term tree stability should recover for low levels of bole damage.

Keywords: Douglas-fir, wound closure, nonlinear mixed-effects modeling, bole damage

How quickly trees recover from bole damage can significantly impact their survival and their future timber value (Han et al. 2000). Complete enclosure of tree wounds increases mechanical stability when it results in shifting the damaged wood closer to the central axis of the tree stem (Ciftci et al. 2014) and may help prevent infection from decay fungi (Pearce 1996). Wounded trees begin to form callus tissue around the edges of the wound (Oven and Torelli 1999, Stobbe et al. 2002), with most callus formation occurring during the early part of the growing season (Neely 1988b). This callus-formation process typically continues until the entire wound is covered (Stobbe et al. 2002).

How trees respond to wounding depends on damage severity, wounding depth, tree species, growth rate, vigor, and types of tree tissue damaged. When wounding penetrates past the periderm, two primary responses occur: (1) growth of callus tissues over the wound either from the vascular cambium or from re-differentiated xylem parenchyma cells (wound closure); and (2) the compartmentalization of decay in the xylem (Romero et al. 2009). When wound closure is combined with the laying down of clear wood, the process may be referred to as wound occlusion (O'Hara 2007). Much of the research on tree response to pruning wounds has looked into decay response (e.g., Shigo et al. 1977, Armstrong et al. 1981, Vasaitis et al. 2012) and time to occlusion (e.g., Roth 1948, O'Hara and Buckland 1996, Petruncio et al. 1997). Time to occlusion is a critical factor in determining the return on pruning investments (Petruncio et al. 1997). Some of the research on tree response to pruning wounds has found that branch stub length and diameter growth rate at the site of the wound are critical components of the time to occlusion (e.g., Roth 1948, O'Hara and Buckland 1996, Petruncio et al. 1997). In contrast to live crown pruning wounds, bole wounds have no stubs to grow over, and photosynthetic material is not removed concurrent with wounding. Bole wound research that uses external observations of wound response has focused on the process of wound closure (e.g., Neely 1979, 1988a, b, Armstrong et al. 1981, Filip et al. 1992, 1995, Dujesiefken et al. 2001, Huggett et al. 2007, Romero et al. 2009, Delvaux et al. 2010) because these observations do not require the destructive sampling of a tree that is required in order to determine if clear wood is being created (the end-point of the occlusion process).

The timing of bole wounds may also trigger different responses within the tree (Armstrong et al. 1981, Dujesiefken et al. 2005, Copini et al. 2014). The formation of tissue over the wound area and the formation of compartmentalization barriers are important mechanisms for preventing infections from occurring and resisting

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Affiliations: *Dryw A. Jones (drywjones@fs.fed.us) and Constance A. Harrington (charrington@fs.fed.us), USDA Forest Service, Pacific Northwest Research Station, 3625 93rd Ave SW, Olympia, WA 98512. David Marshall (david.marshall2@weyerhaeuser.com), Weyerhaeuser Company Research Center, 505 N Pearl Street, Centralia, WA 98531.*

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the spread of decay when it does occur (Pearce 1996). Wound-closure response varies by tree species, size and type of wound, and tree growth rates (Neely 1970, 1988a). The primary factors that appear to be most strongly correlated to wound-closure rates are tree vigor, season of wounding, and location and size of the tree wound (Neely 1988b). Of these factors, tree vigor as expressed by diameter increment appears to be the most strongly correlated with wound-closure rates (Roth 1948, Neely 1988b).

While some studies on bole wound closure in conifers exist, they have focused primarily on wound-closure rate response (e.g., Filip et al. 1992, 1995, Han et al. 2000, Schneuwly-Bollschweiler and Schneuwly 2012). Wound-closure rates are an important aspect of tree wound response, but the length of time that a wound remains open is related to more than just the rate of wound closure. Using concepts from growth modeling, wound closure can be thought of as having a maximum potential closure (asymptote) related to when the wound is fully closed, a point in time at which annual wound-closure rates may begin to decline (inflection point), and an average wound-closure increment over time (rate). Each of these three components is meaningful in describing tree wound response, yet no study has analyzed all three components. Given that these three aspects of wound response influence time to wound closure, it would be appropriate to attempt to understand how these components of wound closure relate to individual tree, bole damage, and stand metrics.

Young Douglas-fir (*Pseudotsuga menziesii* var. *menziesii*) stands in the Pacific Northwest are commonly damaged by animal activity (Kanaskie et al. 2001), as well as management activity (Tesch et al. 1993). Bear damage is especially prevalent, with individual bears capable of damaging 50–70 trees per day (Schmidt and Gourley 1992). Bears show a preference for Douglas-fir trees (Barnes and Engeman 1995) and a greater preference for trees with higher concentrations of sugars (Kimball et al. 1998). Precommercial size Douglas-fir trees are more likely to be damaged by bears (Schmit and Gourley 1992) and more easily damaged by management activities because of their smaller size and thinner bark. Because some of these young trees will be harvested in the future, understanding how they respond to bole damage and what tree characteristics are related to this process, is important in determining which wounded trees to keep for future crop trees and which trees to thin.

We used data from artificially damaged young Douglas-fir trees to answer the following questions:

1. What tree, damage, and stand metrics significantly impact relative wound-closure potential in young Douglas-fir stands?
2. What tree, damage, and stand metrics significantly impact the time at which relative wound-closure rates begin to decline?
3. What tree, damage, and stand metrics have significant impacts on the rates of relative wound closure?

Materials and Methods

Stand, Plot, and Tree Selection

Stands were established within the Capitol State Forest (Olympia, WA). The selected stands represent young Douglas-fir plantations typical of early commercial thinning structures. The even-aged stands were planted in a grid pattern and established between 1983 and 1986 with either vegetation control or broadcast burns used for site preparation. Stands were selected around a central latitude of 46.8949° and a longitude of –123.125°. All stands had received a precommercial thinning treatment 5–14 years prior to the beginning of the study with spacings between 3.2 and 4.1 m. All stands were on fine, mixed, active, mesic Xeric Palehumults soils. Slopes of the stands ranged from 5 to 40 percent, and elevation ranged from 130 to 340 m. The ranges of initial stand average tree metrics were: diameter at breast height (dbh) at 1.3 m between 14 and 28 cm, total tree height (ht) between 12.4 and 20.0 m, and height to crown base (hcb) between 2.7 and 10.6 m. Reineke's (1933) stand density index (sdi) for the stands ranged from 126 to 300, and the number of trees per hectare ranged from 633 to 995. A summary of tree and stand metrics showing average values and standard deviations is provided in Table 1.

One plot containing at least 240 Douglas-fir trees greater than 10 cm dbh was established within a 24 × 24 row area of each stand in the spring of 2006. Plots were as uniform as possible, dominated by undamaged Douglas-fir, with minimal to no indication of root rot pockets. Plots had stream buffers of at least 64 m, and road buffers of at least 32 m to reduce the potential for vandalism, and an additional 20 m buffer around the plots was established to avoid edge effects. Plots sizes were between 0.58 and 0.85 hectares.

Prior to the growing season of 2006, all trees 4 cm or greater were measured for dbh (±1 mm), and any existing damage noted. Measured trees were tagged and labeled with a unique number for each plot. If a branch whorl existed at 1.3 m along the bole, the measurement was offset vertically up the bole by 10 cm, and the diameter and height of the bole at that location were recorded. A stratified random sampling approach, with stratification performed across dbh measurements, was used to assign trees to treatment groups, thereby ensuring similar mean diameter measurements across treatments. Tree height and hcb were recorded for all treatment trees. Height measurements were to the nearest 0.1 m.

Bole Damage and Wound Area

Ten bole damage treatments were applied to groups of trees in each plot. The damage treatments fell into two categories, 0.9 m bole treatments (called 1 m treatments hereafter) and 1.8 m bole treatments (called 2 m treatments hereafter). In both groups, wound width was determined as a percentage of bole circumference at the midpoint of the wound (lengthwise) with treatment percentages of 20, 40, 60, 80, or 90 percent. Bark was removed

Management and Policy Implications

The time it takes a tree to close over wounds is an important factor in trees regaining bole structural integrity. Our study found that trees with a larger initial bole diameter and larger wounds relative to tree size reached lower relative wound-closure values in a 10-year time frame. Trees with greater vigor maintained positive wound-closure rates for a longer period of time than trees that were less vigorous, and overall wound-closure rates were reduced for trees with higher amounts of relative bole damage, smaller live crown cross-sections, slower relative diameter growth, and higher levels of crown competition. Trees with bole damage less than 20 percent of the lower bole surface area are likely to produce more callus tissue area within a 10-year time frame than is necessary to cover the initial wound. This suggests that low levels of relative bole damage are not likely to reduce the structural stability of trees for the long term.

vertically from the bole at the same width along the entire length of the wound, which was either 0.9 m or 1.8 m, creating a rectangular wound area. After bark was removed, the cambium was scarified using a hand saw to mimic the roughening of cambium typical of bole wounds. The initial wound area was calculated as the width of the wound times the length of the wound. Relative wound closure was calculated by dividing the estimated callus tissue area at a given point in time by the original wound area. The mean width of callus tissue on the sides of the wound, along with the mean callus length from the top and bottom of the original wound, was used to estimate the total callus tissue area. Because of the nature of wound callus growth, the callus area that accumulates at full closure can be greater than the original wound area. The use of relative wound closure accounts for the differences in initial tree sizes within the stand, because larger trees would have had larger wound areas, and that could have skewed the analysis.

Root Damage

Two root-damage treatments were applied to trees with a bole-damage severity of 40 percent. In these treatments, the soil was removed to expose the tree roots. The cross-sectional areas of first lateral roots were measured until the sum of cross-sectional areas equaled 25 percent or 50 percent of the total estimated root area. Small roots (on small trees) were severed with clippers, and roots that were too large to be severed by clippers were girdled with a pocket chainsaw. Damage to the roots was kept close to the stem of the tree. Research into root area relationships in pines (Carlson and Harrington 1987) determined that the root area was directly proportional to the cross-sectional area of the bole at ground level. The target root damage area in this current study was based on those relationships. Analysis of the data from this study published in Gould and Harrington (2008) later determined that the root cross-sectional area was nonlinearly related to stem cross-sectional area. Recalculating the achieved cross-sectional area damaged based on the findings in Gould and Harrington (2008), the 25 percent target root damage group had an estimated damage ranging from 15 percent to 23 percent, whereas the 50 percent target root damage group had an estimated damage ranging from 31 percent to 45 percent.

Each of the damage treatments was replicated 15 times within each plot following the stratified random sampling described earlier. Table 2 contains summary data for the treatments. All treatments were applied in the spring of 2006, with the exception of the fall (B40-1F) treatment in the 0.9 m damage group, which was applied in the fall of 2006. Treatment tree dbh, ht, and hcb were remeasured prior to or at the beginning of the growing season in 2007, 2008, 2010, 2012, 2014, and 2016. Callus thickness measurements (width of visible callus tissue along the edges of the wound) were taken prior to the beginning of the 2012, 2014, and 2016 growing seasons. Wound closure was assumed to be zero immediately after the treatment was applied.

Wound-Closure Modeling

To visualize wound-closure relationships with initial tree size, relative wound closure over time was plotted by initial dbh quartiles, with the smallest quartile representing trees with diameters in the lower 25 percent of the data, then trees between 25 percent and 50 percent of the data for the next quartile, and so on. Initial inspection of the wound data revealed a nonlinear curve in the relative wound-closure response over time. The best baseline model was determined from the following model forms: power, logarithmic, Gompertz (Gompertz 1825), and Weibull (Weibull 1961). The models were fit using nonlinear mixed-effects (NLME) approaches described in Pinheiro and Bates (2000). A nested random effect parameter at the tree within-stand level was added to each rate parameter for all models in order to allow for the models to account for stand level and individual tree-level variation in wound-closure

Table 1. Summary of initial stand metrics for the six studied stands.

Stand #	Dbh (cm)	ht (m)	hcb (m)	ba (m^2)	sdi	tph	Age (years)
1	13.4 (4.1)	11.4 (2.3)	2.6 (0.6)	9.4	1,183	1,001	21
2	15.9 (5.7)	13.1 (2.7)	4.0 (0.7)	12.9	1,076	1,050	22
3	19.7 (5.5)	16.0 (2.3)	7.0 (0.4)	20.5	998	960	24
4	22.7 (9.8)	18.0 (3.8)	10.8 (0.8)	23.2	880	677	24
5	14.0 (5.5)	11.1 (2.3)	2.5 (1.2)	10.8	1,125	757	21
6	27.4 (5.7)	18.6 (1.7)	9.2 (0.5)	26.6	874	638	24

Note: Diameter at 1.3 m (dbh), tree height (ht), and height to crown base (hcb) are summarized for each stand with standard deviations shown in parentheses following the mean value. Stand level basal area (ba), Reineke's stand density index (sdi), trees per hectare (tph), and age are shown for each stand. Metrics are for measurements taken at the beginning of the study.

Table 2. Summary of initial tree metrics for bole circumference damage treatments.

Treatment ID	dbh (cm)	ht (m)	hcb (m)	Percentage circumference removed	Percentage root damage	Treatment group
B20-1S	20.8 (6.8)	15.6 (3.5)	6.5 (3.4)	20	0	1 m
B40-1F	21.0 (6.9)	15.8 (3.6)	6.39 (3.6)	40	0	
B40-1S	20.8 (6.8)	15.8 (3.4)	6.77 (3.5)	40	0	
R25-B40-1S	20.9 (6.9)	15.7 (3.7)	6.27 (3.3)	40	25	
R50-B40-1S	20.9 (6.9)	15.8 (3.3)	6.66 (3.4)	40	50	
B60-1S	20.7 (6.8)	15.8 (3.6)	6.69 (3.5)	60	0	
B80-1S	20.7 (6.7)	15.6 (3.7)	6.61 (3.6)	80	0	
B90-1S	20.7 (6.9)	15.6 (3.6)	6.51 (3.5)	90	0	
B40-2S	20.8 (6.8)	15.9 (3.4)	6.56 (3.5)	40	0	2 m
B80-2S	21.0 (6.9)	15.7 (3.5)	6.55 (3.5)	80	0	

Note: Mean values for bole diameter at 1.3 m from the ground (dbh), tree height (ht), and height to the base of branch node with at least three live branches (hcb) are followed by standard deviations in parentheses. Metrics are for measurements taken at the beginning of the study.

rates. The best-fit model form was determined by lowest AIC value. The Weibull growth curve shown in Equation 1 was determined to be the best-fit model form compared with the other forms tested (Table 3). This model form was then used to test if there were any significant relationships between additional covariates and: the potential relative wound area closed (α), the time point at which wound-closure rates begin to decline (β), and the rate of relative wound area closed (δ). Additional covariates related to tree growth, initial wound and tree size, site quality, competition, and tree vigor were tested for relationships with the three parameters of the wound-closure response function. We used crown cross-sectional area at the base of live crown (ca_{blc}), live crown ratio (lcr), and relative diameter growth (rg_d) as covariates related to tree vigor. Adding m covariates to a model parameter (e.g., α, β, and δ), along with associated parameters for those covariates, creates a $1^{*}m$ parameter-covariate matrix in place of the original model parameter. This can be thought of as a series of parameters multiplied by their associated covariates all added together in place of the original model parameter. The term parameter-covariate matrix will be used to describe these model components. A covariate was left in a given parameter-covariate matrix when adding the covariate and associated parameter estimate met the following two criteria: (1) the covariate significantly improved the model AIC using log-likelihood ratio testing; (2) and the covariate parameter estimate was significantly different from 0. NLME modeling was performed using the NLME package (Pinheiro et al. 2015) in the R-statistical platform (R Development Core Team 2015). Models used during the covariate testing process were fit using maximum likelihood methods to allow for meaningful comparisons between models. The best-fit NLME model was refit using reduced maximum log-likelihood methods because this method results in less biased parameter estimates. The location of the random-effects parameter φ_{ij} was chosen based on AIC comparisons of models with random effects for each parameter, and this parameter location resulted in significantly better model log-likelihoods than all others tested. The best-fit model was used to test whether bole circumference damage categories performed as well as relative bole area damage metrics.

Wound-Closure Model

$$y_{ij} = \alpha(1 - e^{-\beta t^{(\delta+\varphi_{ij})}}) \quad (1)$$

with y_{ij} equal to the relative wound area closed on tree j, in stand i, at t years from wounding, e is Euler's constant, and α, β, and δ are parameter-covariate matrixes. φ_{ij} represents nested random-effects estimates at the stand, and tree within-stand levels used to account for individual tree and stand-level variation in wound-closure rates.

Table 3. Base model testing.

Model #	Model description	AIC	Model test	*P*-value
1	Weibull	–8,611	1 versus 2	<.0001
2	Power	–7,213	2 versus 3	<.0001
3	Logarithmic	–4,926	3 versus 4	<.0001
4	Gompertz	–668		

Note: Model forms tested for base model. Lower AIC values indicate a better model fit given the data. Models were compared using log-likelihood ratio testing with *P*-values of the test shown for the given model comparison.

Model Behavior

Equation 1 is a form of the Weibull growth curve (Weibull 1961). The α parameter controls the maximum estimated relative wound closure. The β model parameter controls the inflection point of the curve with consecutively lower values of β resulting in higher estimates of relative wound closure for a given time period, all else being equal. The δ parameter controls the rate of relative wound closure with higher values related to steeper relative wound-closure curves, all else being equal.

Results

By the end of the study, the relative wound area closed ranged from 0.21 to 1.90, with a mean of 0.77. The relative wound closure from the sides (sum of callus width from the left and right sides of the wound divided by the initial wound width) of the wound ranged from 0.18 to 1.92 with a mean of 0.73. The relative wound closure from the top (width of the callus tissue from the top divided by the initial wound length) ranged from 0 to 0.16, with a mean of 0.07, whereas wound closure from the bottom (the callus tissue from the bottom divided by the initial wound length) ranged from 0 to 0.36, with a mean of 0.08.

The final model using initial relative damage metrics performed significantly better than a similar model that used damage category values (Table 4). This significant improvement in model performance suggests that damage area better explains wound response than percent circumference damage.

Wound-Closure Potential

There were significant differences in relative wound-closure potential (α) between bole circumference damage categories as shown by their nonoverlapping 95 percent confidence intervals in Figure 1. Lower circumference damage categories had higher relative wound-closure potential with the 20 percent category showing average wound-closure values greater than 1 by the end of the 10-year study period (Figure 1). Root damage categories showed no difference from their related bole damage categories indicating minimal to no impact from root damage on relative wound-closure potential. The 2-m bole damage categories demonstrated reduced relative wound-closure values compared with their 1-m damage category counterparts (40-1S versus 40-2S, 80-1S versus 80-2S), with a greater reduction in wound closure shown between the 80 percent damage groups than between the 40 percent damage groups (Figure 1). This suggests that longer wound lengths tend to have lower relative wound-closure potentials than do shorter wounds, likely because of the larger wound area created by longer wounds.

Relative wound closure by initial diameter quartile showed decreasing closure potential with increasing size quartile (Figure 2). This is in line with the wound-closure modeling, which also suggested

Table 4. Model comparisons.

Model #	Model description	AIC	Model test	*P*-value
5	Weibull—continuous	–10,123.3	5 versus 6	<.0001
6	Weibull—categories	–9,804.1	6 versus 1	<.0001

Note: Model comparisons using best-fit base model with additional covariates (Model 5), or treatment as a categorical variable (Model 6). Model 5 uses relative bole area damage metrics, whereas model 6 uses categorical variables related to bole circumference removed during treatment. Model 1 was the base Weibull model shown in Table 3. Lower AIC values indicate a better model fit to the data. Significant differences were determined using log-likelihood ratio tests.

that relative wound-closure potential had negative relationships with initial tree size (dbh_i), and initial relative bole damage severity (d_{ri}) (Table 5). This suggests that larger trees produce less callus tissue relative to their size than do smaller trees, and trees with larger proportions of bole damage are less likely to fully close over the wound within 10 years. This relationship indicates that wound categories alone may not accurately predict tree response to bole damage, because tree size and relative wound area are important factors that are not easily incorporated into a single category. The relationship between potential wound closure and initial relative bole damage severity likely explains the lower wound closure demonstrated by the 2-m groups relative to their corresponding 1-m damage groups (40-1S versus 40-2S, and 80-1S versus 80-2S) shown in Figure 1.

Wound-Closure Inflection Point

Trees with higher initial relative heights (ht_{ri}) and larger live crowns (ca_{blc}*lcr) that were on better-quality sites (si) had later inflection points (β) suggesting that wound-closure rates continue to increase for longer periods of time as those metrics increase. Loss of crown portions (lc_l) resulted in inflection points that were earlier than in trees with crown portions intact indicating that wound-closure rates decline sooner for trees that have damage to their crowns. Taken together, these metrics point to tree vigor being positively correlated with longer periods of increasing wound-closure rates, all else being equal. Root damage and bole damage metrics were not significantly related to β.

Wound-Closure Rates

Relative wound-closure rates (δ) had negative relationships with initial relative damage severity (d_{ri}), and with crown competition (cc_{66}). This indicates that trees with high levels of relative bole damage severity will have reduced wound-closure rates compared with trees with lower levels of relative bole damage severity. Trees that are under high levels of crown competition will also take longer to close wounds. Trees with large live crowns (ca_{blc}) and high relative diameter growth (rg_d) rates showed higher relative wound-closure rates, indicating that vigorous trees will close wounds at a faster rate than less vigorous trees. Root damage and damage to the live crown were not significantly related to δ.

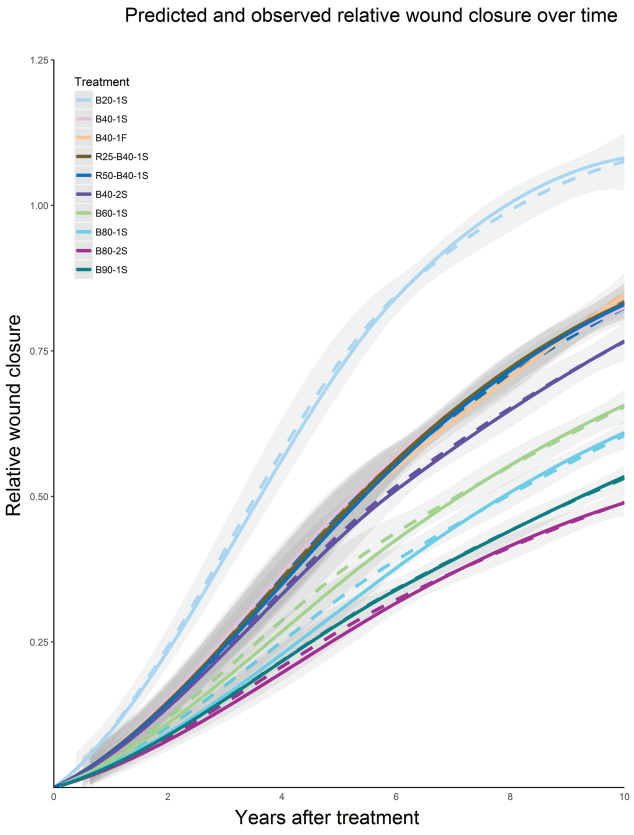

Figure 1. Predicted (dashed lines) and observed (solid lines) relative wound closure over time shown with LOESS regression trend lines by bole circumference damage treatment category. Shaded regions are the 95 percent confidence intervals of the data trend lines. Data do not include measurements of trees on or after mortality was observed, or measurements after wound closure was observed. No measurable wound closure occurred in the B100-1S treatment before all trees died so that treatment was dropped for this figure. The legend shows the color coding for the bole damage treatment categories.

Discussion

Wound-Closure Potential

The negative relationships between potential wound closure and initial tree diameter (Figure 2 and Table 5) found in our study are similar to a finding by Schneuwly-Bollschweiler and Schneuwly (2012) that smaller trees responded better to wounds than did larger trees. It is likely that the larger trees, because of their larger diameters, may have smaller relative diameter growth increments

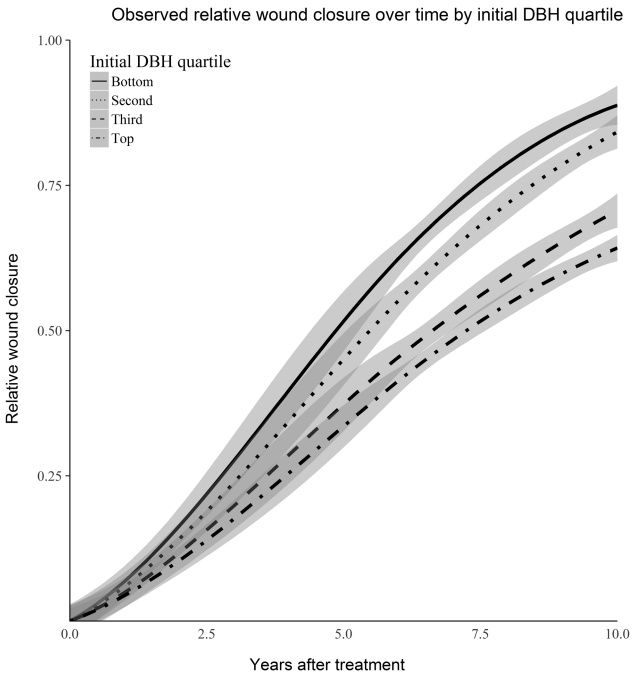

Figure 2. Observed relative wound-closure trend lines over time shown for initial diameter quartiles for all data. Shaded regions are the 95 percent confidence intervals of the data trend lines. Trees in the bottom quartile for initial diameter show the highest relative wound closure followed by the second quartile, then third, and finally the top quartile. Data do not include measurements of trees on or after mortality was observed, or measurements after wound closure was observed.

Table 5. Parameter-covariate matrix results for final wound-closure model.

Covariate parameter matrix	Covariate	Covariate parameter estimate	Covariate parameter SE	*P*-value
α	int	2.6459	0.0413	<.001
α	dbh_i	–0.0244	0.0017	<.001
α	d_{ri}	–1.4248	0.0897	<.001
β	ht_{ri}	6.6981	2.5064	.0076
β	si	0.3473	0.0356	<.001
β	lc_l	-2.0018	0.9240	.0304
β	ca_{blc}*lcr	0.0487	0.0056	<.001
δ	int	1.1901	0.0411	<.001
δ	d_{ri}	–0.2449	0.0583	<.001
δ	ca_{blc}	0.0010	0.0001	<.001
δ	cc_{66}	–0.1225	0.0135	<.001
δ	rg_d	1.1012	0.1254	<.001
ϑ	Stand	0.0000	0.0000	na
ϑ	Tree	0.0000	0.1486	na

Final model parameter estimates and standard errors are shown relative to each parameter-covariate matrix in Equation 1. INT refers to intercept values; dbh_i is the initial tree diameter at 1.3 m from the ground; d_{ri} is the initial bole area damaged divided by bole surface area from the top of the wound to the base of the stem; ht_{ri} is the height of subject tree divided by the mean height of the stand; si is breast height site index at 25 years of age; lc_l is the amount of live crown lost to top damage; ca_{blc} is the cross-sectional crown area at the base of live crown; lcr is the live crown ratio; cc_{66} is a crown competition index; rg_d is the relative diameter growth of the tree; Stand and Tree refer to random effect estimate level with Tree nested within Stand.

leading to smaller relative callus growth around the wound site. This finding may also suggest that the proportion of available photosynthate allocated to wound closure is not constant with tree size. If the proportion of photosynthate allocated to wound closure were constant, we would expect to see relatively equal potential wound closure across tree size. The fact that we see lower relative wound closure in larger trees than in smaller trees suggests that tree bole wounds may trigger response mechanisms that allocate a fixed amount of photosynthate to wound closure. This could explain why increasing relative damage proportions have lower potential wound-closure values, because a fixed amount of growth from the perimeter of the wound would result in larger wounds taking longer to close.

The negative relationship between bole damage severity and potential wound-closure tracks the pattern for wound closure by bole circumference damage category shown in Figure 1. This is likely due to the use of a relative damage metric that somewhat captures the impacts of larger wounds caused by the 2-m treatments, while also accounting for the impacts of wider relative wound widths. The initial relative damage metric (d_{ri} in Table 5) compares the initial wound area with the bole surface area from the top of the wound to the ground line. Because the 2-m treatments extend the damage width to a higher point in the tree, the relative area of these treatments is higher than that of comparable 1-m treatments. The study by Schneuwly-Bollschweiler and Schneuwly (2012), which found that trees responded more slowly to larger wounds than to smaller wounds, is in agreement with our findings, but is in contrast to those of Neely (1988b), because that study found that trees closed larger wounds faster than they did smaller wounds. This discrepancy could be attributed to the greater range in damage inflicted on tree boles in our study and the Schneuwly-Bollschweiler and Schneuwly (2012) study compared with the range in Neely (1988b), or to the difference in tree species between studies. For young Douglas-fir trees of the sizes found in our study, it is clear that increasing relative bole damage severity will decrease the potential for the tree to fully close over the damaged area within a 10-year time frame.

It is possible that, given enough time, surviving trees with high levels of damage would completely close their wounds and that a reanalysis of the data at that time could result in different parameter estimates for potential relative wound closure. The bole damage severity predicted to reduce wound-closure potential below a relative wound-closure value of 1 is relatively high. Using the parameters from the α parameter-covariate matrix (Table 5), a 40-cm tree would have to have a relative bole damage severity of 50 percent in order to decrease the wound-closure potential to below 1. However, as shown in Figure 1, the average wound closure does not reach a value of 1 within a 10-year time frame for any circumference damage category above 20 percent. This failure to close wounds leaves trees more susceptible to stem breakage because of the reduced mechanical stability caused by tree wounds that are not fully enclosed (Ciftci et al. 2014). These findings have important implications for long-term risks of stem breakage in wounded trees.

Wound-Closure Inflection Points

Wound-closure inflection points were positively correlated to tree vigor metrics. We are unaware of any studies on tree wound closure examining the inflection point of wound-closure response, so no comparisons can be made between our study and others. The influence of crown on wound closure is important because it suggests that trees with larger live crowns will maintain wound-closure growth rates at higher levels over time than trees that are less competitive, whereas trees that experience damage to their crowns will experience earlier declines in wound-closure rates. Trees on high-quality sites (as measured by site index) will be less impacted by damage severity than trees on low-quality sites. This suggests that bole damage to understory trees is likely more problematic for wound closure than bole damage to dominant trees, so trees of

different competitive classes should not be expected to respond to wound damage in the same manner.

Wound-Closure Rates

Although relative damage is a different damage metric than that used by Neely (1988a), our findings and the findings from that paper show that wound-closure rates are positively correlated to diameter growth rates. This positive correlation between diameter growth rate and wound occlusion is also common in tree wound response to pruning (e.g., Roth 1948, O'Hara and Buckland 1996, Petruncio et al. 1997, Wang et al. 2016), although the largest portion of the explained variation in those studies appears to be related to the length of branch stub that must be grown over before tissue can close over the wound (O'Hara and Buckland 1996, Petruncio et al. 1997, Wang et al. 2016), and stub length was not a factor in our research. Interestingly, the Schneuwly-Bollschweiler and Schneuwly (2012) study found no relationship between closure rates and diameter growth or tree vigor prior to wounding. There are several possible explanations for this, because our study, the Neely (1988a) study, and the Schneuwly-Bollschweiler and Schneuwly (2012) study all looked at different species. Although the Schneuwly-Bollschweiler and Schneuwly (2012) paper looked at Pearson correlations between wound closure and other covariates across multiple time periods, our analytic approach explicitly accounted for the variation in the data attributable to time, and this could explain the difference in findings because the variation in wound-closure values across time is not insignifcant, as shown in Figure 1.

In contrast to the paper by Neely (1988a), we found that wound-closure rates were negatively related to initial relative wound size. This difference in findings may be related to the much smaller range of relative damage inflicted in the Neely (1988a) study, or to the different species studied. The Schneuwly-Bollschweiler and Schneuwly (2012) study is in agreement with our findings, suggesting that there may be different responses between conifers and broadleaved trees in relation to wound closure and initial wound size. The differences may be species-specific, and both the Schneuwly-Bollschweiler and Schneuwly (2012) and the Neely (1988a) studies found differences in growth rates between species.

In contrast to previous studies, our large dataset included stand-level information, and our approach to modeling wound closure allowed for the inclusion of factors related to competition and tree vigor. The significant impacts of the competition and factors related to vigor (crown cross-sectional area and relative diameter growth rate) in the δ parameter-covariate matrix have important implications for stand dynamics because reduced relative diameter growth would be expected in suppressed trees, which would also be expected to have higher crown competition. Because wounded understory trees experience increasing competition during stand development, their relative growth rates would decrease, and their wound-closure rates would be expected to slow down even more. This could have important implications for closed stands that experience bole damage. In stands that have been thinned, this process is less likely to be an issue because thinning would increase relative growth rates, reduce crown competition, and allow for larger crown cross-sectional areas over time. One important implication of this is that trees under different levels of competition will not respond equally to bole damage, and so broad damage categories may not be useful in determining future crop trees.

Conclusion

Using data from a 10-year study of artificially damaged Douglas-fir trees, we found reduced potential for relative wound closure with increasing initial tree size and increasing relative bole damage. More vigorous trees, trees on better-quality sites, and trees with intact live crowns maintained wound-closure rates for longer periods of time than other trees. Wound-closure rates were reduced for trees with larger relative bole damage, smaller live crown cross-sections, slower relative diameter growth, and more crown competition.

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