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Downed woody debris in Tasmanian eucalypt forest: modelling the effects of stand-replacing disturbance dynamics

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Summary

Australian cool-temperate wet eucalypt forests are fire-driven ecosystems that can accumulate massive volumes of living wood and downed woody debris (DWD) between disturbance events. Because of their productivity and forestry potential, they are the subject of major concerns over the impacts of harvesting on biodiversity and on carbon. Downed woody debris is a major resource for biodiversity, as well as being a major carbon pool. To explore the relative effects of harvesting and wildfire disturbances on DWD, we developed DELTA (‘Dynamics of Eucalypt Logs in Temperate Australia’). This aspatial, process-based, deterministic model explores temporal changes in DWD volume and mass in highly productive stands of lowland wet eucalypt *Eucalyptus obliqua* forest of Tasmania, Australia. We used DELTA to explore six disturbance scenarios, based on repeat cycles simulated over 1200 years, differing only in return interval. All scenarios predicted large changes in total DWD over the course of a cycle. Four wildfire (WF) scenarios (WF100 – i.e. a 100-year return interval, WF200, WF300 and WF400) predicted initial increases in total DWD volume, followed by a decrease only under WF300 and WF400. Wildfire scenarios also predicted much higher quantities of DWD than the two clearfell, burn and sow (CBS) scenarios (CBS100 and CBS200), with mean volumes peaking, under WF200, at over 900 m^3 ha^{-1}. Even the troughs in the wildfire cycles represented higher levels of DWD than were reached at any stage of the CBS cycles (other than the initial spike). CBS scenarios predicted gradual decreases in DWD quantity over the course of a cycle, with cycle means ranging from 132 m^3 ha^{-1} for the first cycle (which benefited from large quantities of legacy DWD) to as low as 43 m^3 ha^{-1} (for CBS100) in later cycles (lacking much legacy DWD). The distribution of DWD by decay-class and diameter-class over the course of a cycle varied by scenario. Decay-classes remained relatively constant under wildfire scenarios, and hence the ratio of volume to mass also did; but showed a general progression towards later decay-classes with time under CBS scenarios, with a concomitant dramatic change in the ratio of volume to mass. Larger-diameter DWD was more prevalent in scenarios with longer return intervals. Our findings add weight to the idea that CBS has a limited ability to emulate wildfire disturbance dynamics, even under longer-than-usual rotations. In this context, aggregated retention is one promising alternative; long-term retention of mature forest in the vicinity of CBS coupes is another.

Introduction

Downed woody debris (DWD) is increasingly recognised as a key component of forest ecosystems, with major roles as habitat for biodiversity (Grove, 2002; Lassauce *et al.*, 2011) and as a reservoir of carbon (Harmon and Marks, 2002). Yet while DWD can be inventoried using a range of well-tested standard techniques (e.g. Van Wagner, 1968), it is not an attribute that remains static over time. This makes its management problematic unless its dynamics are sufficiently understood. This understanding is increasingly apparent in some parts of the world (Hagemann *et al.*; Fraver *et al.*, 2002; Groot *et al.*, 2004; Gibb *et al.*, 2005; Gough *et al.*, 2007), but scarcely so in cool-temperate Australia, despite the high ecological, commercial and social importance of the forests in this region (Lindenmayer and Franklin, 2002).

Downed woody debris may be generated through self-thinning and senescence, or through major disturbance events such as wildfires or clearfell harvesting. Forest management and frequent wildfires often increase the proportion of younger forests in the landscape. Neither short silvicultural rotations, nor short wildfire return intervals, allow for the development of large, old trees in many forest systems that are ostensibly capable of supporting them (Fall *et al.*, 2004; Siipilehto and Siitonen, 2004; Moroni *et al.*, 2011), neither do they allow the generation of the larger-diameter DWD that such trees produce. Logs of different initial diameters may support different suites of species as they decompose (Siitonen and Saaristo, 2000; Jonsson and Kruys, 2001; Yee *et al.*, 2001; Grove, 2002); they may also decompose along different trajectories (Grove *et al.*, 2011) and at different rates. In order to ensure that the ecological and other values associated with DWD in all its diversity are given due consideration in management, it is important to understand DWD dynamics. Empirical data on changes in DWD quantities over wide temporal scales and over a wide range of management or disturbance scenarios is often limited; hence this is one area where modelling can assist in objective decision-making (Porte and Bartelink, 2002; Turner *et al.*, 2002). There have been many recent attempts at modelling DWD dynamics in different parts of the world (e.g. Tinker, 2001; Ranius *et al.*, 2004), but to date none has done so for cool-temperate Australian lowland eucalypt forests, despite some recent attempts to explore carbon dynamics in these forests (Dean *et al.*, 2003; Dean and Wardell-Johnson, 2010; Moroni *et al.*, 2011).

The cool-temperate lowland eucalypt forests of Tasmania are dominated by a single tree species, *Eucalyptus obliqua* L'Hér. They are naturally fire-prone, with a return wildfire interval of 100-400 years (Gilbert, 1959; Jackson, 1968), or occasionally longer (Wood *et al.*, 2010). Typical wildfires in this forest type have often been assumed to be stand-replacing events (Jackson, 1968), although in reality many are only partially stand-replacing (Hickey *et al.*, 1999; Turner *et al.*, 2009). In either case, wildfires may generate large amounts of DWD through killing trees, although they will also consume some of those same trees and some of the existing DWD.

The concept of stand-replacing wildfires inspired ‘clearfell, burn and sow’ (CBS) silviculture and helped provide some ecological justification for it (Gilbert and Cunningham, 1972). This form of harvesting and regeneration has been the standard in the commercial production forests of this region for the past half-century, and has now been applied to tens of thousands of hectares of previously unharvested (but fire-derived) lowland wet eucalypt forest in Tasmania. When first introduced, the lack of a pulpwood market (Elliott *et al.*, 2008) meant that much less wood was considered merchantable than is the case today, and post-harvest DWD loads were consequently higher. Nevertheless, even today, high post-harvest fuel-loads (i.e. harvest residue and legacy DWD from the previous stand) are generally considered a fire-risk and an impediment to regeneration. They are effectively reduced through the application of a post-harvest regeneration burn (Slijepcevic, 2001). While stands regenerating after CBS support large amounts of DWD, ecological concerns have been expressed about the future fate of DWD under repeat cycles of CBS (Grove and Meggs, 2003). Longer rotations have been suggested as one improvement on CBS (e.g. (World Heritage Committee, 2007), while aggregated retention is one alternative that has been increasingly operationalised (Forestry Tasmania, 2009). However, to date, the dynamics of DWD have not been characterised in either wildfire-derived or CBS-derived forests sufficient to allow a clear assessment of the management issues associated with CBS or its alternatives.

This paper describes our development and use of a model to explore a range of wildfire and harvesting scenarios, as a means of better understanding key patterns and processes in DWD dynamics in these forests and their management implications, and of identifying knowledge gaps for future research.

Methods

We developed DELTA (‘Dynamics of Eucalypt Logs in Temperate Australia’) using the visual modelling environment of *Simile*, version 4.4 (Muetzelfeldt and Massheder, 2003). We considered that our basic requirements were for a model able to predict total volume and mass of DWD by decay-class, by diameter-class distributions, and by a combination of these. We had previously determined the relationship between DWD volume and mass, and how this varies as wood decomposes (Grove *et al.*, 2009). Because the proportional contribution of carbon to DWD mass is relatively fixed (at about 50%), we were also able convert the output to carbon.

DELTA is an aspatial, process-based, deterministic model. Figure 1 describes its main elements. Conceptually, simulations in DELTA involved five stages: (1) growing the stand of living trees; (2) converting living trees into standing dead trees following self-thinning or a stand-replacing disturbance event; (3) allowing standing dead trees to fall over and enter the DWD pool; (4) decomposing DWD in the DWD pool, factoring-in losses due to wildfire or harvesting activities; and (5) aggregating and outputting data on DWD in the DWD pool. Each of these stages is considered in further detail in Appendix 1. To separately model wildfire and harvesting scenarios, we developed two versions of DELTA. DELTA-WF was developed to model the dynamics of DWD under recurrent wildfires, while DELTA-CBS was developed to model DWD under recurrent CBS cycles.

We ran six scenarios, for 1200 years each. Each scenario started with a 150-year-old living even-aged stand of *E. obliqua* with a site-index indicative of a highly productive stand, ‘seeded’ with 340 m^3 ha^{-1} of DWD (see Appendix 1). Each scenario was subjected to its first disturbance event in Year 0 of the simulation.

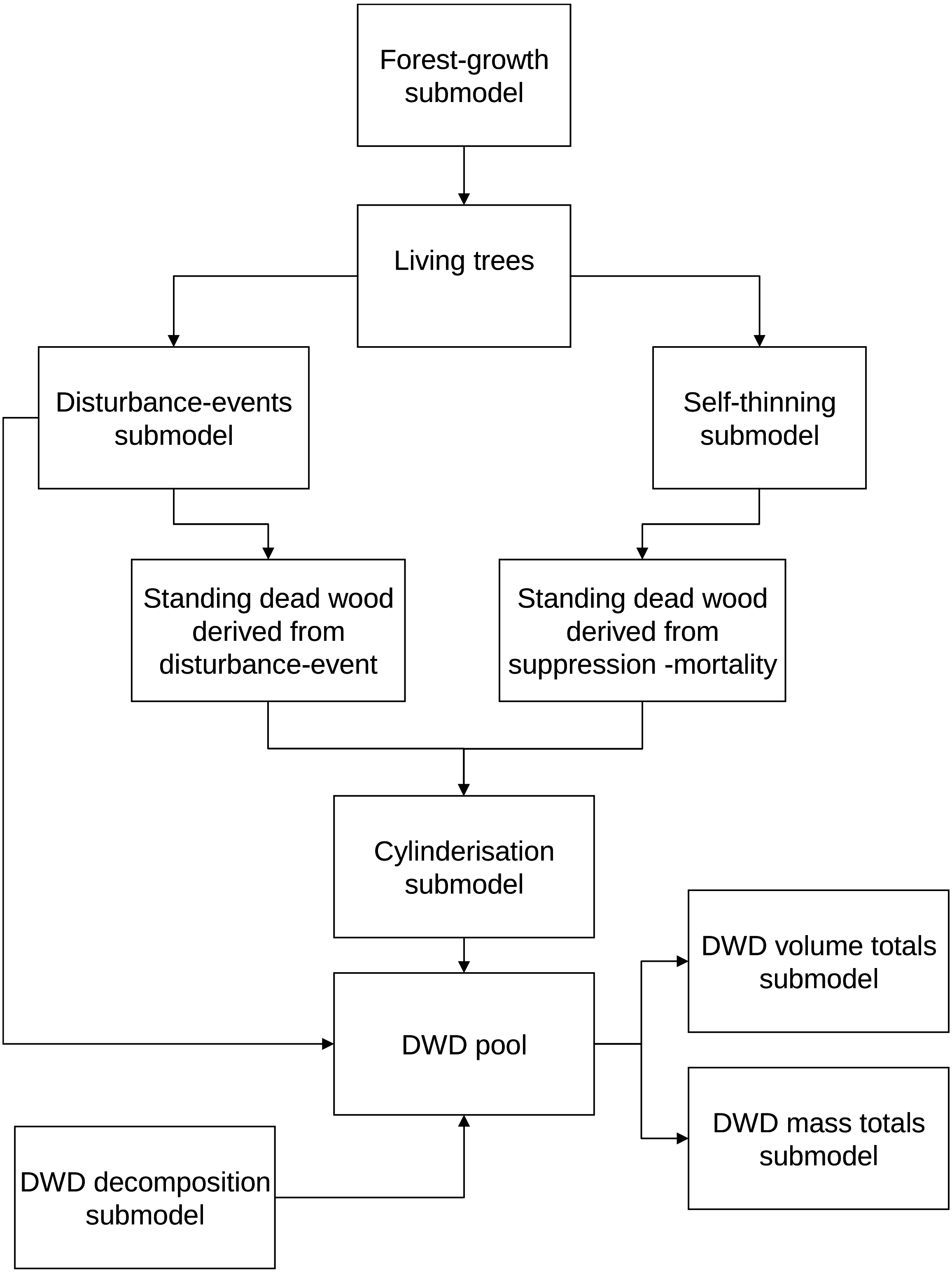

Figure 1. The main elements of DELTA and their relationships.

The four DELTA-WF scenarios (WF100, WF200, WF300 and WF400) employed wildfire return intervals of 100, 200, 300 and 400 years respectively as these all lie within the feasible range of intervals experienced by forests in the study-region

(Gilbert, 1959; Jackson, 1968; Bowman, 2000; Wood *et al.*, 2010). The two DELTA-CBS scenarios (CBS100 and CBS200) employed harvesting cycles of 100 and 200 years respectively. The former is close to the notional 90-year rotation on which harvesting schedules are based in Forestry Tasmania's planning purposes; while the latter may correspond to the 'longer-rotation' forestry that is sometimes suggested as a more suitable silviculture in environmentally sensitive areas (e.g. World Heritage Committee, 2007).

Results

Sensitivity analysis

For DELTA-WF, we tested the individual effects on output DWD volumes of a 10% increase and decrease in the values of eight key model parameters. We ran the model through two cycles of WF300 and considered model sensitivity in relation to the output maximum and minimum DWD volumes in the second of these. Sensitivity was assessed on the basis of comparing relative change in output to change in input (Ranius *et al.*, 2004; Tinker and Knight, 2000).

Under these conditions, percentage changes in outputs varied from 0 to 17.9 (Table 1). The model proved relatively sensitive to four of the parameters. It was most sensitive to a change in the modelled relationship between tree age and diameter for suppressed trees; it was also quite sensitive to a change in the modelled relationship between a log's decay-progression and its diameter-loss. It was partially sensitive (i.e. in relation to maximum volume only) to changes in the site-index employed in the growth submodel; and marginally sensitive (in relation to minimum volume only) to changes in the residence times employed for logs in different decay-classes. It proved insensitive to changes in the modelled relationships between tree age and the volume of suppressed trees; between forest age and the number of suppressed trees; between DWD decay-class and the proportion lost to combustion; and between the diameter of a fire-killed tree and the time taken for it to fall over and enter the DWD pool.

Table 1. Sensitivity of DELTA-WF model (second cycle of WF300) to a 10% increase (decrease) in selected parameter values, as gauged by proportional change in minimum and maximum values for total volume of DWD during the cycle.

Parameter	% change in min vol DWD	% change in max vol DWD
Diameter of suppressed trees of a given age	16.6 (-14.8)	17.9 (-15.6)
% volume reduction from one decay-class to the next	12.1 (-11.0)	15.3 (-13.4)
Site-index	7.9 (-9.2)	15.6 (-15.1)
Residence times	10.4 (-10.6)	8.6 (-8.8)
Volume of suppressed trees dying per year	6.8 (-6.8)	7.0 (-7.0)
Number of suppressed trees per hectare at a given time	6.8 (-6.8)	7.0 (-7.0)
% lost to combustion in wildfire	-0.6 (0.1)	0 (0)
Average fall-time (dead trees post-wildfire)	0.2 (-0.5)	0.1 (-0.1)

Comparisons among scenarios

Figure 2 shows total volumes and masses of DWD predicted for each scenario over the entire period of simulation. A trend common to all wildfire scenarios is the immediate massive decline in DWD following the wildfire (as a proportion of legacy DWD is combusted), followed by gradual recovery (as fire-killed trees gradually fall over and enter the DWD pool). Under WF100, WF200 and WF300 the recovery begins immediately, while under WF400 the decline in DWD continues for a few years before recovery begins (because old-aged, fire-killed trees take longer to fall over than younger trees). The rate of recovery in DWD then slows with time under all wildfire scenarios (because the rate of input of fire-killed trees declines, while decomposition of DWD continues apace). Under WF300 and WF400, recovery is eventually superseded by increasingly rapid decline (because decomposition continues apace in the absence of any further substantial inputs). Under WF100 and WF200, the next wildfire interrupts recovery before a decline can set in.

The WF300 model equilibrates after just one cycle, while WF100 equilibrates after seven cycles. Neither WF200 nor WF400 fully equilibrate during the period of simulation, but approach equilibrium after five and two cycles respectively. The model's 'seed' conditions are best matched with the WF300 scenario, in that its equilibrium cycles span a range of quantities of DWD similar to that of the initial cycle, whereas the equilibrium cycles for WF400 seem set to span significantly lower quantities, and those of WF100 and WF200 significantly higher quantities. However, all scenarios, including WF300, return significantly higher volumes of DWD at all stages of every cycle than the initial volume with which each scenario was seeded.

For CBS scenarios, there is an initial massive 'spike' of DWD, representing felled trees (i.e. a mixture of merchantable wood and harvest residue). Immediately after harvest, there is a rapid decrease in DWD as harvesting is followed by the regeneration burn (which combusts a proportion of both the harvest residue and the legacy DWD). For the initial cycle, the height of the post-harvest spike is the same in each scenario (because the stand-age at time of harvest is the same), but subsequent cycles of CBS200 produce higher spikes than those of CBS100 (because the stand has grown older and larger prior to harvest). Beyond this early spike, DWD quantities gradually and continually decrease, at a rate that itself declines over time (because there is little further input of DWD other than some early self-thinning, and because decomposition continues apace). Both scenarios approach equilibrium in their second cycle, with WF200 doing so at a higher level than WF100 (because at harvest the larger stand generates higher volumes of DWD, and because the rate of decay is slow enough for a legacy effect on successive cycles for both scenarios). Other than immediately after initiation, the quantities of DWD at all stages of all cycles in the CBS scenarios are considerably lower than quantities in the wildfire scenarios (because much of the wood otherwise destined to become DWD is harvested, and because inputs of DWD more or less cease immediately after the harvest rather than continuing for many years as fire-killed trees fall over).

Considering only the final cycle (i.e. the cycle closest to equilibration) for the four wildfire scenarios (Figure 3), the proportional representation by volume of the different decay-classes changes relatively little over the course of the cycle, and varies little among scenarios. Decay-class 1 is scarcely represented in any cycle except in the first few years (because its main period of input is immediately after tree death).

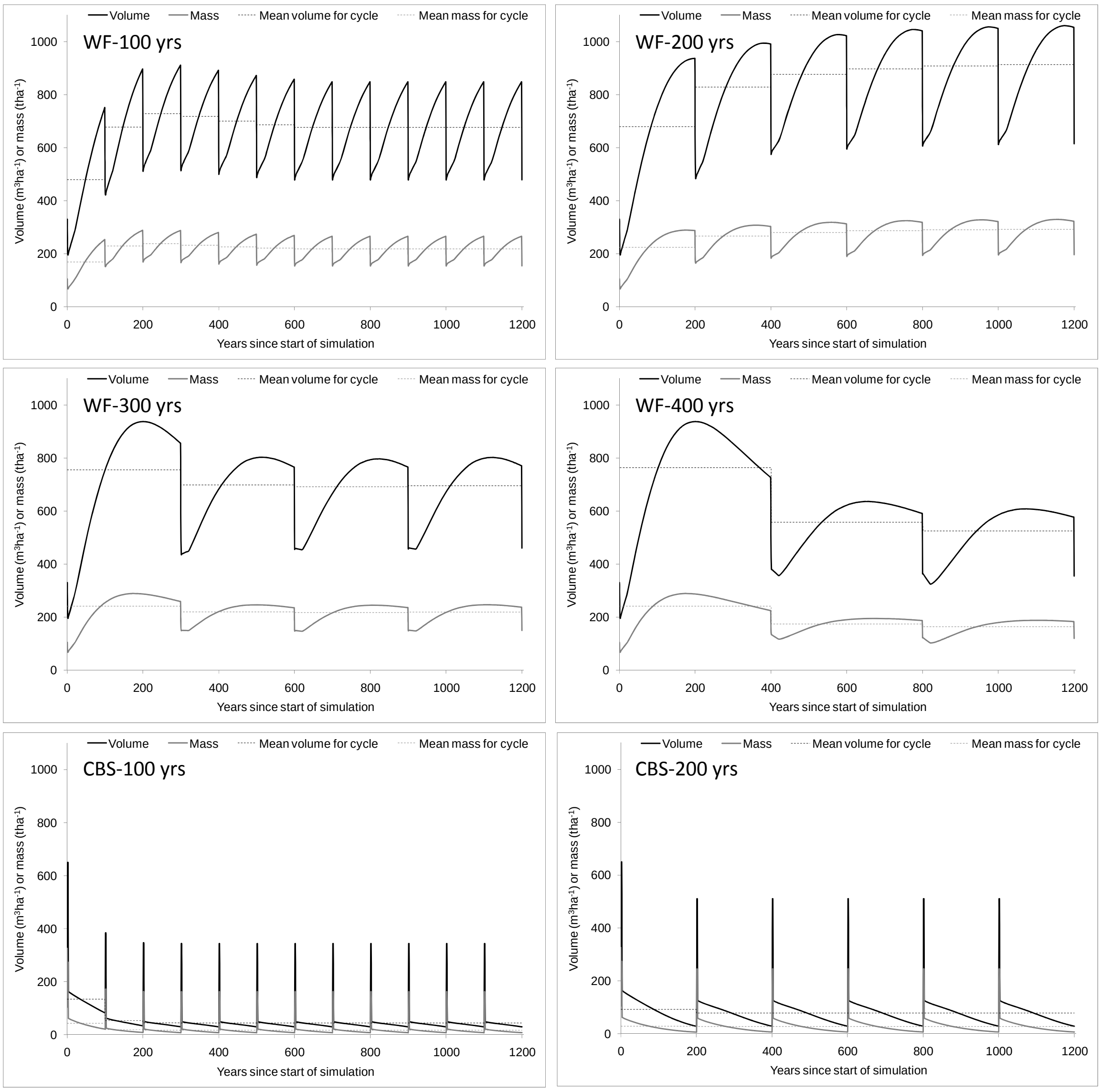

Figure 2. Output of 1200-year simulations of various scenarios of DELTA-WF and DELTA-CBS, expressed as total DWD volume and mass and as means of these per cycle. Note that the initial component of the ‘spike’, comprising felled but as-yet unharvested DWD, has been removed from these figures, to allow greater spread of underlying DWD quantities on the y-axis.

The other four decay-classes are more or less equally represented throughout the cycle (because decomposition of DWD leads to its passing along successive decay-classes). Differences are more apparent in the proportional representation of the different diameter-classes, both over the course of the cycle and among scenarios (because the diameter-class distribution of stands of different ages varies, as does the rate at which trees of different diameters fall over; and because larger-diameter DWD passes down through successively smaller diameter-classes as it decomposes). With increasing time-since-wildfire, there is a progressive shift towards larger-diameter DWD, though this shift doesn’t commence until about 20 years into the cycle (because large-diameter fire-killed trees take many years to start falling over and entering the DWD pool). In WF400, this trend is dampened by a trend for the proportion of largest-diameter DWD to decline over the first 200 years (because this period is dominated by decomposition of legacy DWD, since the fire-killed stand was sparse and supplies little new DWD for many decades).

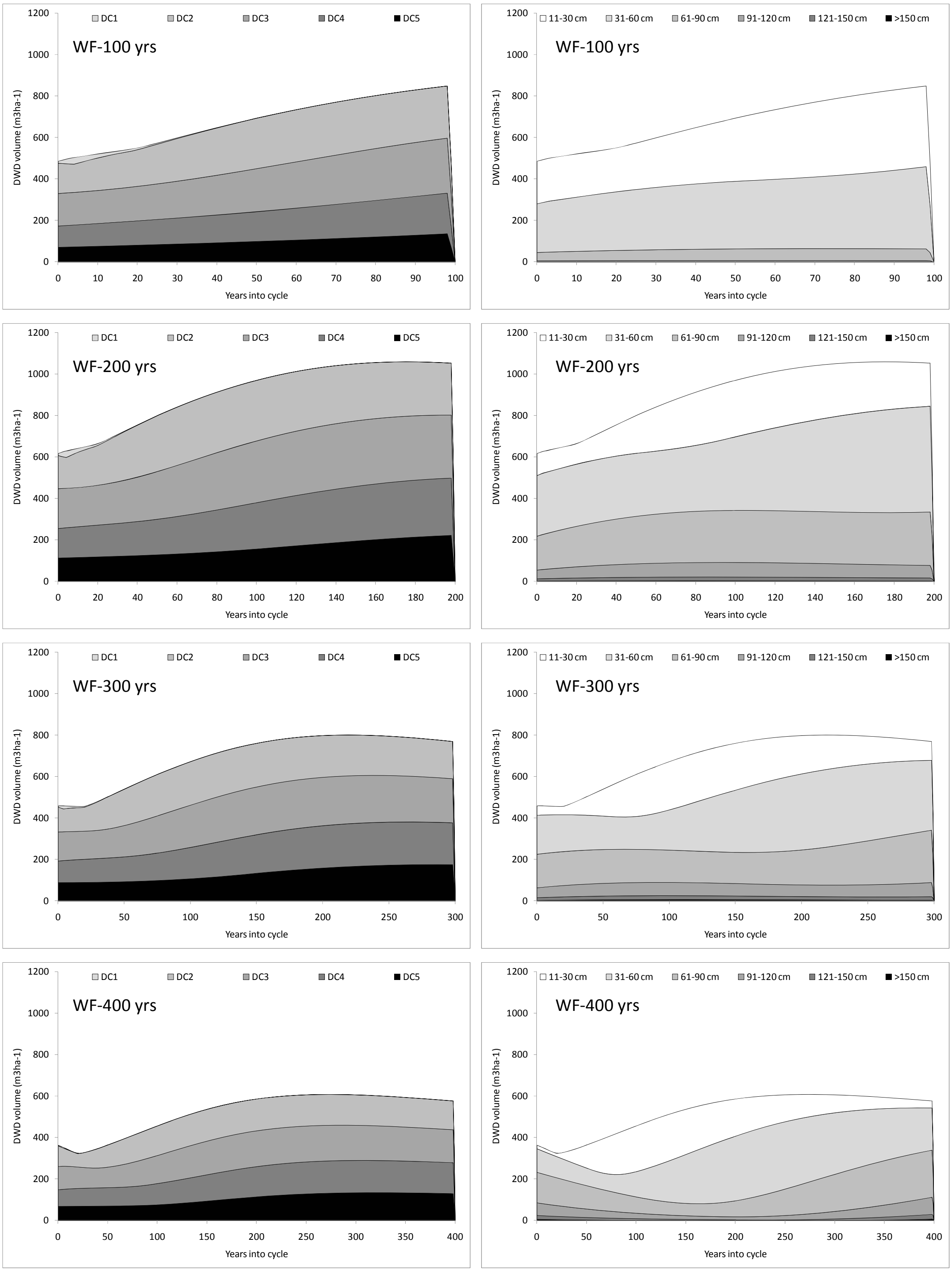

Figure 3. Output of the final cycles of 1200-year simulations of various scenarios of DELTA-WF, expressed as volume of DWD over time by decay-class (left) and by diameter-class (right).

WF100 generates very little DWD over 60 cm diameter at any stage in the cycle (because the stand wasn't that large when burnt), but the three other scenarios do so. In these three scenarios, most DWD over 60 cm diameter is in the 61-90 cm range, with DWD in diameter-classes larger than this contributing relatively little to total volumes (because they comprised a diminishing proportion of total stand volume).

For CBS scenarios, we compare the first and final cycles in Figure 4.

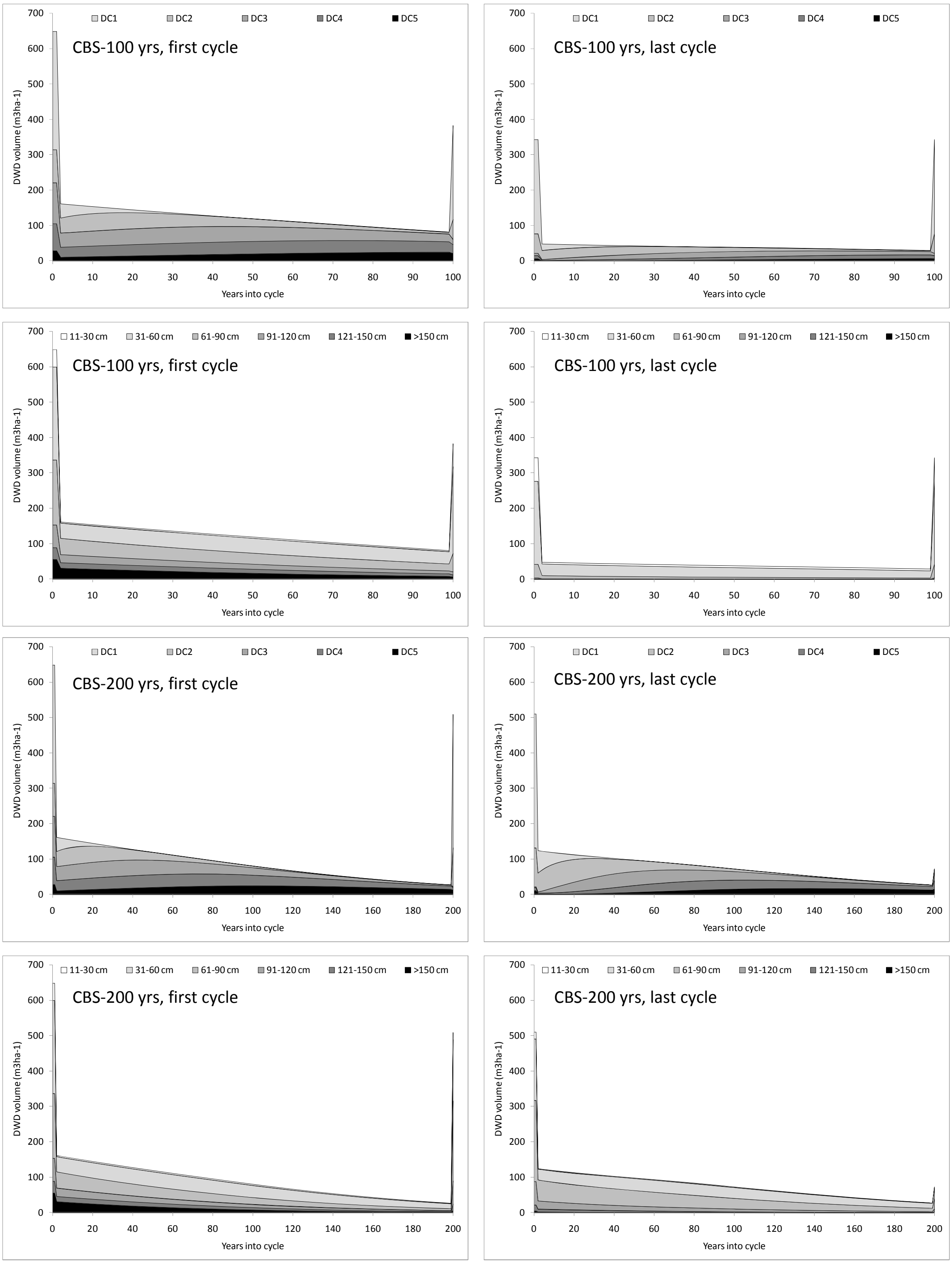

Figure 4. Output of the first (left) and final (right) cycles of 1200-year simulations of the two scenarios of DELTA-CBS, expressed as volume of DWD over time by decay-class (upper) and by diameter-class (lower). Note that the initial component of the ‘spike’, comprising felled but as-yet unharvested DWD, has been removed from these figures, to allow greater spread of underlying DWD quantities on the y-axis.

The first cycle is the model's simulation of silvicultural regeneration under current practices, since CBS is still generally in its first cycle in the study-region and is therefore seeded with legacy DWD from previously-unharvested forest. The final cycle is the model's simulation of tomorrow's silvicultural regeneration that will lack this legacy. Considering the final cycles first, the CBS scenarios stand in contrast to the equivalent wildfire scenarios, predicting a gradual succession towards later decay-classes over the course of the cycle (reflecting the near-complete lack of input of 'fresh' DWD after the harvest). This succession is most pronounced under CBS200 (because under CBS100 it is curtailed by the next disturbance event). Also in contrast to the wildfire scenarios, these CBS scenarios show a progressive decline in the prevalence of larger-diameter DWD (because in the absence of significant inputs after the harvest, extant DWD gradually reduces in diameter as it decomposes). This decline is most pronounced under CBS200 (because under CBS100, the stand scarcely reaches a size large enough to generate significant quantities of DWD over 60 cm diameter). In comparison to the final cycles, the first cycle features, under each scenario, more DWD, more later-decay-class DWD, and more larger-diameter DWD, than the final cycle (reflecting the legacy DWD and the larger-diameter harvest residue inherited by the first cycle). The differences between the first and final cycles are much more apparent for CBS100 than for CBS200 (because CBS100 represents a starker difference between the implied cycle-length of the pre-harvest stand - and the consequent size of trees in the stand - and that of the successive CBS cycles).

Wildfire and CBS scenarios also differ greatly in how the relationship between DWD volume and mass varies over the course of the cycle (Figure 5).

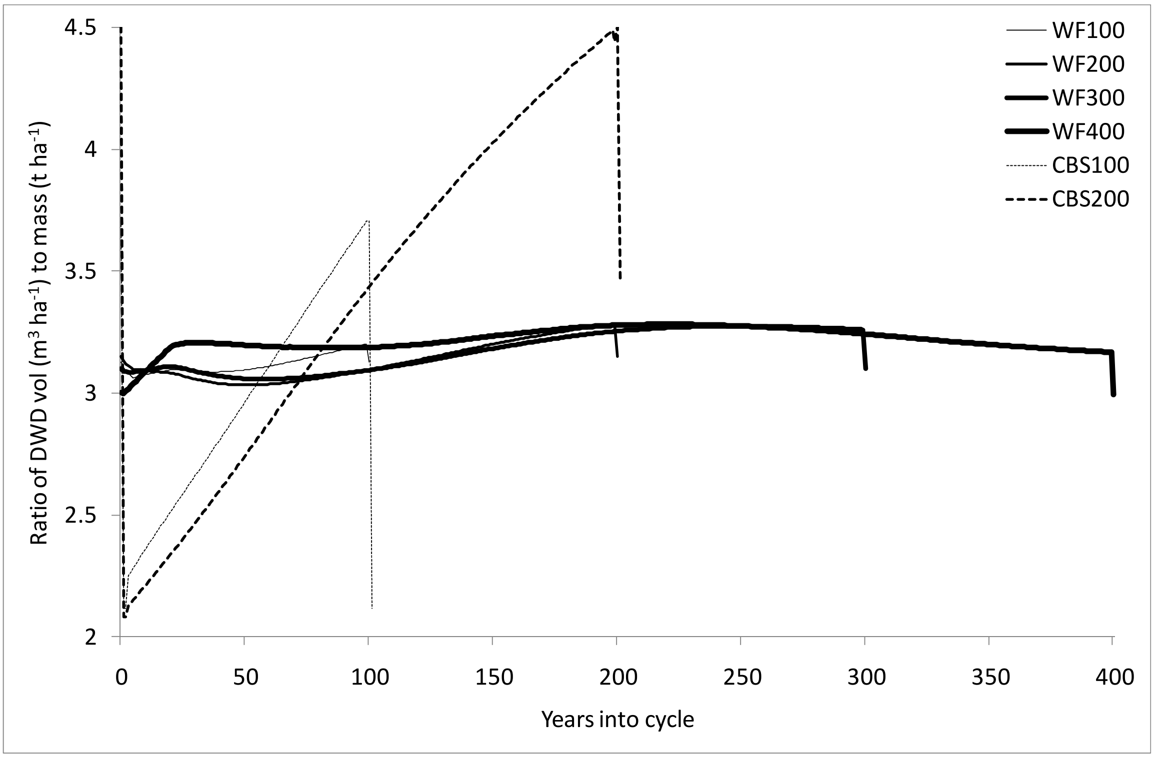

Figure 5. Output of the final cycles of 1200-year simulations of the various scenarios of DELTA-WF and DELTA-CBS, expressed as the ratio of DWD volume to mass over time.

Under wildfire scenarios, the ratio of DWD volume to mass changes little over the course of the cycle, ranging from about 3 to 3.5, regardless of scenario (because the underlying proportional representation of the different decay-classes varies little). Under CBS scenarios, the range is much broader. After the regeneration burn, it sits at a little over 2, but increases more or less linearly over the cycle to a peak of 4.5 just before the next regeneration burn (because of the volume- and density-reduction associated with the increasing proportional representation of later decay-classes).

Model validation

We attempted to validate the output of DELTA-WF through comparing model outputs with empirical data on DWD volumes recorded from a series of eight 50 x 50 m plots chosen for their successional positions along a wildfire chronosequence in the Southern Forests (Sohn *et al.*, in review). Near-stand-replacing wildfires in 1898, 1934 and 1967 were thought to have been individually responsible for the even-aged regrowth in six (three pairs) of these plots, although it is possible that the two plots characterised as arising from the 1898 wildfire may also have been subjected to the 1934 wildfire. The time-since-wildfire for the pair of old-growth plots in this chronosequence was unknown, but for the purpose of this validation exercise was characterised as 250 years.

The validation was in two parts. The first was aimed at validating overall volumes of DWD predicted by each scenario of the final cycle of DELTA-WF at various stages post-wildfire (Figure 6).

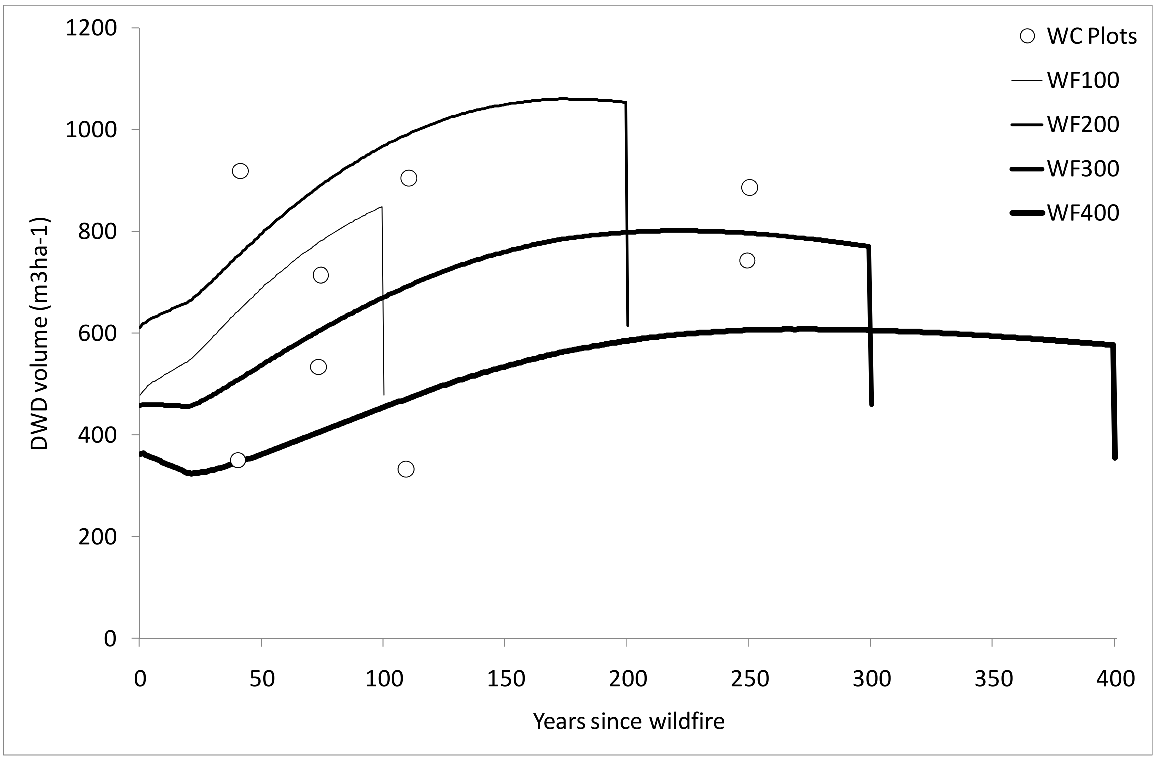

Figure 6. Output of the final cycles of 1200-year simulations of the various scenarios of DELTA-WF, expressed as total DWD volume over time, and overlaid with empirical data recorded from wildfire chronosequence (WC) plots of known or estimated time-since-wildfire (from (Sohn *et al.*, in review).

For data from Sohn *et al.* (in review), we applied a conversion factor of 1.163, derived from their data, to factor-in the contribution of DWD below their generalised measurement threshold of 40 cm diameter but above our modelling threshold of 10 cm diameter. The plot-level data showed great variation in DWD volumes for a given time-since-wildfire, and did not convincingly demonstrate the generally upward trajectory predicted by any of the modelled scenarios. The most closely 'matched' scenario was WF300, in the sense that the recorded DWD volume of one member of each time-since-wildfire pair of plots sat above the line of prediction while that of the other member of the pair sat below it; had the volumes for pair-members been averaged, the 'fit' would have appeared closer still.

The second part of the validation of DELTA-WF aimed to validate the decay-class composition of the DWD pool at various stages post-wildfire. For this purpose, we again made use of the empirical data from the wildfire chronosequence data of Sohn *et al.* (in review), by comparing the proportions of DWD in different decay-classes from these plots with those from the equivalent time-since-wildfire points in the final cycle of the wildfire scenario simulations (Figure 7). For the 40-year-old and 70-year-old chronosequence plots, all four scenarios could be compared; for the 109-year-old plots we had to exclude WF100; while for the notional 250-year-old 'old-growth' plots we also had to exclude WF200. There was little match between the simulations and the plots. At all times-since-wildfire, the simulations predicted higher proportions of DWD in decay-classes 2 and 5 than were present in the plots, while the corresponding proportions in decay-classes 3 and/or 4 were lower.

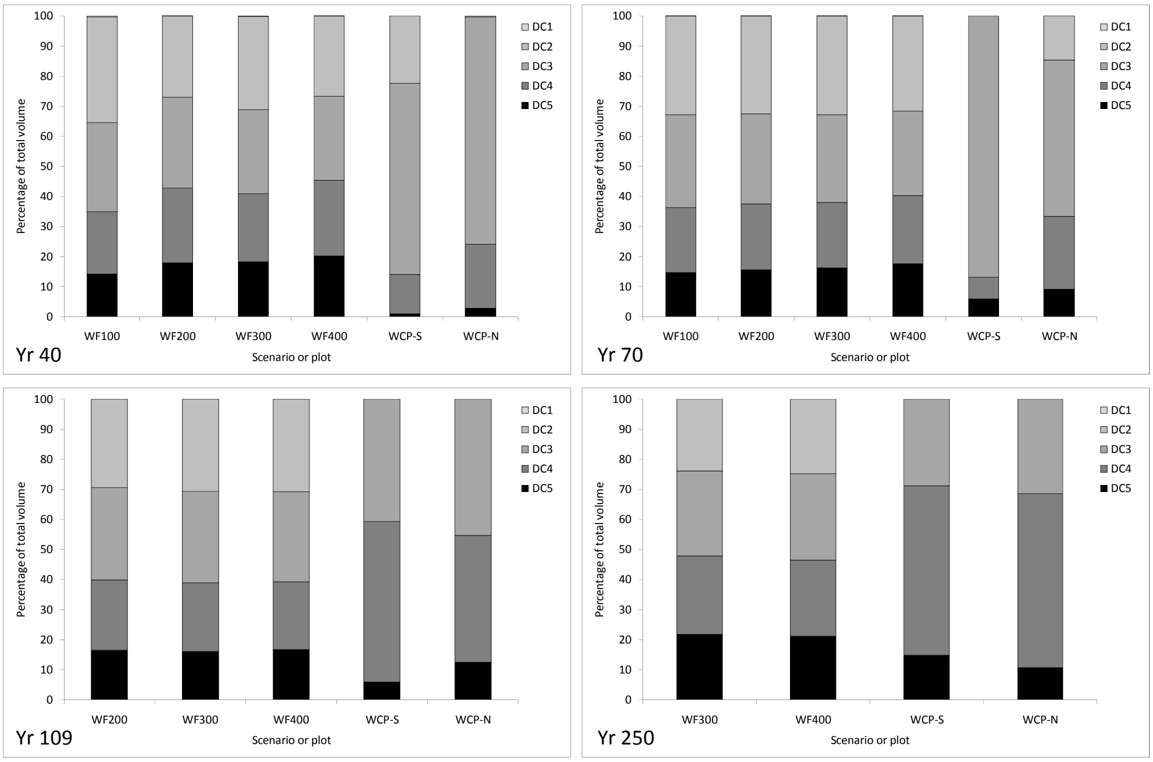

Figure 7. Output of the final cycles of 1200-year simulations of the various scenarios of DELTA-WF, expressed as proportion of total DWD volume in different decay-classes at specified times-since-wildfire, and presented alongside empirical data recorded from wildfire chronosequence (WC) plots known or estimated to be from the same specified time-since-wildfire (from (Sohn *et al.*, in review).

The four scenarios predicted little change in the relative contributions of different decay-classes to total DWD volume, whereas the plots showed greater variation, with a more prominent succession towards later decay-classes with time-since-wildfire.

Validating the output of DELTA-CBS proved difficult because of changing forestry practices over the past half-century, and because all CBS to date has taken place in previously-unharvested forest (i.e. it represents the first silvicultural cycle and therefore inherits variable quantities of ‘legacy’ DWD, depending in part on the age and fire-history of the stand at time of harvest). When CBS was first widely applied in Tasmania, there was no market for pulpwood (Elliott *et al.*, 2008), which meant that post-harvest DWD volumes (comprising legacy DWD and harvesting residue) were often much higher than they have been since the establishment of a pulpwood market in the 1970s. For instance, Woldendorp and Keenan (2005) recorded 1615 m^3ha^{-1} of DWD (>15 cm diameter) in a Southern Forests plot of 35-year-old silvicultural regeneration arising following CBS in 1966; corresponding figures for Southern Forests plots in 40-year-old silvicultural regeneration, recorded by Sohn *et al.* (in review), are approximately 1084 and 830 m^3ha^{-1}. DELTA-CBS instead predicted DWD volumes of around 128 m^3ha^{-1} at this stage in the forest’s post-harvest regeneration – which equates to only 12-15% of those recorded volumes. In comparison, Mannes (2002) recorded mean volumes of DWD in Southern Forests coupes immediately post-clearfelling (and before the regeneration burn) of 621 m^3ha^{-1} for mature forest (based on 3 coupes, range: 528-716 m^3ha^{-1}), 522 m^3ha^{-1} for mixed-aged forest (based on 7 coupes, range: 223-711 m^3ha^{-1}) and 344 m^3ha^{-1} for regrowth (i.e. <110 year-old) forest (based on 6 coupes, range: 202-536 m^3ha^{-1}). These would have been a little higher had they not excluded wood in decay-stages 4 and 5, and pieces shorter than about 100 cm. The volume predicted by DELTA-CBS for this stage in the first cycle is 650 m^3ha^{-1}, which is very close to the mature-forest mean and within the range of values recorded for both mature and mixed-age forest.

Discussion

Modelling framework and parameterisation

Parameterising DELTA for Tasmanian lowland wet eucalypt forest allowed us to identify many local data-gaps in relation to DWD, wildfire dynamics and harvesting. While we were generally able to implement mathematical ‘fixes’ for these gaps (see Appendix 1), their existence suggests the need to (a) find ways of filling them with empirical data and (b) interpret the model’s output with caution in the mean time. In particular, the model should not be used as a means of demonstrating *absolute* quantities of DWD at different times-since-disturbance under different scenarios. However, given the findings of the sensitivity analysis, we feel that it should prove up to the task of comparing trends in *relative* quantities among the different scenarios, and in providing ecological and management insights accordingly.

Insights arising from attempting to validate the model

Validating the output of DELTA proved difficult, yet insightful. The challenge in validating DELTA-WF was in finding suitable areas of forest of known time-since-wildfire and in compiling data on DWD from such areas. The difficulty in finding suitable areas is itself a reflection of recent research that is increasingly concluding that stands that have regenerated following stand-replacing wildfires represent a very small part of the landscape and tend to occur in patches of only a few hectares each, whereas over far larger and more contiguous areas those same wildfires have been only partially stand-replacing (Hickey *et al.*, 1999; Turner *et al.*, 2009). Thus the reality is that DELTA-WF is only capable of simulating DWD dynamics for a small part of our study-region. Furthermore, modelling the stand-level growth of a multi-aged wet eucalypt forest, let alone its DWD dynamics, is currently beyond our capabilities. A further challenge is in obtaining reliable data on DWD from those suitable parts of the landscape. DWD is such a heterogeneous and 'hit-and-miss' resource that data from small-scale plots are prone to enormous variability (Woldendorp *et al.*, 2004). While in 'seeding' our model we controlled for this somewhat by using mean volumes from multiple line-intersect samples from mature forest, for validation purposes the only data-set available was from a small number of small plots in notionally even-aged stands that sat at known points in time along a wildfire chronosequence (Sohn *et al.*, in review). Given that some of the largest-diameter logs in these plots were longer than the longest dimension of the plot, it is not surprising that the plots showed such great variation in total volumes and no clear trend with time-since-wildfire. This is a difficulty that others attempting to validate their DWD models in more homogeneous and lower-stature forests, such as Sturtevant *et al.* (1997) in Newfoundland, did not have to face. In this context, it is interesting that DELTA-WF predicted volumes of DWD at different times-since-wildfire that were at least within the range of values recorded in these plots of similar ages.

The lack of correlation between the decay-class distributions at different times-since-wildfire predicted by DELTA-WF and those recorded in the few wildfire chronosequence plots may also have arisen through a mismatch between how DELTA categorises DWD by decay-class and how human observers do so. While DELTA was of course parameterised by human observers, deriving the exponential decomposition curve was a multi-stage process (Grove et al., 2009) that involved first assigning logs of known age to decay-classes, then applying to these a set of density values that had been derived from other logs (of unknown age) that had also been assigned to decay-classes. It is possible that only those logs that could be assigned to a particular decay-class with a high degree of confidence were selected for these stages, excluding more ambiguous cases. Yet when it comes to recording DWD in plots and in line-intersect samples, all DWD has to be allocated to one class or another, and any ambiguity is masked. Under such circumstances, logs in an intermediate stage of decomposition may tend to get lumped into decay-class 3 or sometimes 4, perhaps to the extent of artificially inflating the proportion of DWD in these categories at the expense of earlier or later decay-classes. Certainly it is difficult to see how the model could have been parameterised to produce a different balance of decay-classes in the output, while still keeping true to the principle that DWD decomposition follows a negative exponential curve with an empirically-derived decomposition constant.

The main challenge in validating DELTA-CBS lies in the fact that forestry practices have changed since CBS was first introduce in the 1950's (Elliott *et al.*, 2008), to the extent that the quantity of legacy DWD left today is probably typically an order of magnitude lower than what was left before the 1970s. This means that it is not valid to compare outputs of DELTA-CBS (as currently parameterised) against DWD quantities in, say, 30- or 40-year-old regeneration arising following CBS, because the model was parameterised assuming today's more-intensive harvesting practices. When such comparisons are made, it is instructive to note that the model predicts

DWD levels that are less than a fifth those derived from CBS as practised a few decades ago. Validation of DELTA-CBS requires examining the output from the first few years of the first simulated cycle only, and comparing this with current practice. Forests currently being subjected to CBS are very varied, ranging from even-aged regrowth to mixed-age stands and occasionally to even-aged oldgrowth; and their wildfire history is seldom known in detail. Furthermore, there are few comprehensive assessments of DWD post-harvest. Despite this, it is heartening that DELTA-CBS predicts volumes of DWD immediately post-harvest that are very close to those that have actually been recorded, suggesting that the model is 'seeded' with suitable volumes of DWD for the age and structure of at least some of the stands that are currently the target of CBS operations.

Comparisons among scenarios and with other systems

Overall, the degree of fit of the WF300 scenario to the empirical chronosequence data, coupled with its relatively consistent performance over successive cycles, may suggest that it is the most realistic scenario for emulating 'real' stand-replacing wet eucalypt forest dynamics in Tasmania's Southern Forests. However, it must be recognised that wildfire events in these forests are probably stochastic, and so the concept of a 'mean' return interval may have no more relevance over most readily observable timescales here than it does in the better-studied forest landscapes of the Pacific Northwest, which share somewhat similar disturbance dynamics and where the natural proportion of old-growth in the landscape is considered to vary greatly over timescales of hundreds or thousands of years (Spies, 2009).

The 'humped' shape of the DWD accumulation and decline curves under DELTA-WF appears to be attributable to two interacting processes. One is the slow rate at which large-diameter fire-killed trees fall over and become DWD; the other is the slow rate of decomposition of DWD. Together, they keep DWD levels relatively high compared to most studied ecosystems, even at the point in the cycle when the amount of DWD reaches a minimum. Empirical data, such as from our wildfire chronosequence plots, offer some validation of this aspect of the model's output. This trajectory stands in stark contrast to the u-shaped curves more typically determined in fire-disturbance-driven forests elsewhere. For instance, Spies *et al.* (1988) determined a u-shaped trajectory for DWD in Douglas-fir forests in the U.S. Pacific Northwest. The shape was explained by assuming that the input of DWD after wildfire was insufficient to counteract decomposition for many decades, before sufficient larger-diameter (suppressed or fire-killed) trees fell over to replenish the DWD pool. A different situation again was described for post-harvest ('second-growth') boreal forest in Newfoundland (Sturtevant *et al.,* 1997). In that case, the initial u-shaped curve was eventually followed by an asymptote as the forest entered more steady-state, pre-disturbance conditions.

Under CBS, DWD dynamics are relatively simple, because nearly all the input happens at the start of the cycle, after which the dominant process is decomposition. While decomposition is always slow enough to ensure the presence of some DWD at every stage in the cycle, the amount of DWD that CBS can maintain is far lower than that possible under any feasible wildfire scenario. Especially in second-rotation cycles onwards, particular combinations of (larger) diameter-class and decay-class are likely to be virtually absent. Many DWD-dependent species are thus likely to be progressively excluded from stands managed by CBS (Grove and Meggs, 2003), particularly those with an association with larger-dimension DWD (Jonsell *et al.*, 1998; Yee *et al.*, 2001; Grove and Forster, in review).

Management implications

In Tasmanian lowland wet eucalypt forests, foresters have long claimed that CBS silviculture is guided by the natural wildfire dynamics (Gilbert and Cunningham, 1972). However, it is clear from this study that the resultant DWD dynamics bear little resemblance to those of a wildfire-driven system, and many commentators have questioned the relevance of clearfelling in the 'new' forestry (Swanson and Franklin, 1992; Franklin *et al.*, 2002; Lindenmayer *et al.*, 2006). In particular, CBS lacks the standing dead and dying trees that are a fundamental part of the wildfire system and which provide habitat for a significant proportion of forest-dependent species even before they fall over to become DWD (Hunter, 1990; Koch *et al.*, 2008; Wardlaw *et al.*, 2009); and which provide for a more extended period of input of DWD than does clearfelling (Grove *et al.*, 2002). Silvicultural rotations are also probably much shorter than the 'usual' wildfire return interval in these forests, resulting in a relative lack of continued input of the larger-diameter DWD which provides the habitat for a specialised saproxylic biota. Our study demonstrates that the current availability of larger-diameter DWD in stands regenerating after clearfelling is atypical, and is a function of both the inheritance of legacy DWD from the previously-unharvested stand, and the former lack of a market for lower-grade logs at the time when many of these stands were regenerated (Elliott *et al.*, 2008).

Developing alternatives to clearfelling in Tasmania's lowland wet eucalypt forests, conceived in part to address these ecological concerns, has proven technically challenging (Hickey *et al.*, 2006). However, Forestry Tasmania's recent progressive adoption of one such alternative, aggregated retention (Forestry Tasmania, 2009), holds out the promise of better emulation of wildfire dynamics, particularly the retention of old-growth attributes in the regenerating stand (Bauhus *et al.*, 2009) and their associated biodiversity (Baker *et al.*, 2009; Lefort and Grove, 2009). It is also important to note that many parts of the Tasmanian production forest matrix are excluded from harvesting for environmental reasons (Forest Practices Board, 2000), while as a result of a series of science-based assessments the state also has very high levels of forest reservation (e.g. Commonwealth of Australia, 1997). In some parts of the forest estate, these excluded or reserved areas may occur at a sufficiently fine spatial scale (the 'coupe-context scale') as to mitigate some of the ecological shortcomings of clearfelling.

Carbon

DELTA was not built specifically to simulate carbon dynamics. However, because the proportional contribution of carbon to DWD mass is relatively fixed (at about 50%), the carbon signature of different scenarios is evident in some of DELTA's outputs. For wildfire scenarios, a fire return interval of some 200 years returned higher mean DWD mass, and hence carbon, than either longer or shorter intervals. For CBS scenarios, a 200-year harvesting interval returned higher mean DWD mass than a 100-year interval. Notably, the ratio of volume to mass varied greatly through a CBS cycle. In some instance, ignoring this change in ratio and basing an understanding of DWD mass or carbon on a single conversion factor from DWD volume could lead to some serious miscalculations. Regarding forest harvesting scenarios, Harmon (2009) determined a similar model outcome to ours in the

Douglas-fir – western hemlock forests of the Pacific Northwest. Managers of forests subject to stand-replacing disturbance dynamics will have to be cognisant of DWD as a major carbon pool whose size fluctuates with time-since-disturbance, as demonstrated by our study, and which undergoes long-term variation due to the stochasticity inherent in fire regimes. It would, for instance, be simplistic to advocate longer rotations solely on the basis of our model, since it captures only one aspect of the ability of wood to store or sequester carbon, whereas over time, other aspects such as the living trees or storage in wood products may prove more significant (Waterworth and Richards, 2008).

Conclusion

Building a model of DWD dynamics such as DELTA requires careful consideration of many ecological and anthropogenic processes, from the growth and death or harvesting of the trees to the decomposition and combustion of the resultant DWD. Despite many uncertainties, we have demonstrated the utility of DELTA in simulating a range of scenarios for comparison of their relative, rather than absolute, effects on DWD dynamics (volume, mass and, by extension, carbon). The model provides a window into the relationship between the frequency of disturbance events (driving DWD input) and the decomposition of DWD (driving its output). It demonstrates that the amount of DWD present at any point in time is a product of the interplay between these two processes, with the added complexity that the total amount and dimensions of DWD in a regenerating stand is also strongly dependent on how old the previous stand was prior to that last disturbance. The model has also demonstrated some of the fundamental differences in DWD dynamics between wildfire and CBS regimes. It adds weight to the idea that CBS has a limited ability to emulate wildfire disturbance dynamics, even under longer-than-usual rotations. In this context, aggregated retention is one promising alternative; long-term retention of mature forest in the vicinity of CBS coupes is another.

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Appendix 1. Details of the submodels in DELTA

(1) Growing the stand of living trees. DELTA's *'forest-growth'* submodel employs a stand-level growth-and-yield model, and predicts living-tree volumes per hectare by 1-cm-bandwidth diameter-classes (diameter at breast height over bark, DBHob) at every time-step (year). This submodel was developed within Forestry Tasmania (Goodwin, 1992; Grove *et al.,* 2002), based on empirical data from hundreds of permanent and temporary inventory plots (Whiteley, 1999). The equations rely on a 'site-index' function (defined as the dominant height in metres of the stand at age 50 years). We ran all simulations using a site index of 27, which corresponds to a highly productive stand; all simulations assumed an initial stand-age of 150 years, which corresponds to forest towards the lower end of what could be called 'mature' in the study-region (Stone, 1998; Forestry Tasmania, 2010).

(2) Converting living trees into standing dead trees. In DELTA, trees can die as a result of either self-thinning or a stand-replacing disturbance event. The *'self-thinning'* submodel describes the volume per hectare by diameter class (DBHob) of suppressed trees dying due to competition in a given year, transferring this volume to a 'standing dead wood derived from self-thinning' compartment in the time-step (year) immediately following the mortality. This model was developed within Forestry Tasmania, based on empirical data from hundreds of permanent inventory plots (Whiteley, 1999).

The *'disturbance-events'* submodel is a schedule of disturbance-events by year, for the duration of the model (e.g. wildfires every 100 years for 1200 years). When a disturbance-event occurs, the age of the growing stand in the *'forest-growth'* submodel is reset to zero, while the extant volumes of living trees are transferred to a 'standing dead wood derived from disturbance-event' compartment in the time-step (year) immediately following the disturbance event. We parameterised this submodel with different values for the disturbance return interval depending on the scenario modelled.

(3) Allowing standing dead trees to fall over and enter the DWD pool
Implementation of this stage in DELTA involves simulating treefalls, and 'cylinderising' the standing dead trees as they fall (see below). In DELTA-CBS, all trees fall over in the year of harvest, while in both DELTA-CBS and DELTA-WF, standing dead wood arising from self-thinning falls over in the year of death. In DELTA-WF, we modelled the relationship between a wildfire-killed tree's mean residence-time as a standing dead tree prior to falling over, and its diameter-class, with a simple linear equation (Mean residence time = -5.9 + 2.05*DBHob) that aimed to capture the likelihood of smaller-diameter standing dead trees having shorter residence-times than larger-diameter trees At each time-step, standing dead trees then 'fall over' at a rate proportional to their mean residence time. This equation was derived from a study that compared the density of standing dead trees visible in aerial photographs of parts of the Southern Forests taken at multiple time-intervals after wildfire (FT unpublished data).

As long as dead wood resides in the 'standing dead wood' compartments, it is characterised by its diameter (DBHob) only. However, on leaving these compartments and before entering the DWD pool, DELTA employs a ‘*cylinderisation’* submodel that applies matrix multiplication to FT’s taper equations (Goodwin, 1992) to allocate each short section of trunk to its respective cylinder-diameter-class, in 1 cm increments (Figure 8). The volumes are then summed by cylinder-diameter-class, and passed to the DWD pool. Cylinderisation ensures that the diameter-distribution of DWD is accounted for in subsequent parts of the model, and ensures that outputs are more directly comparable with empirical data on diameter-distributions derived from probability-based sampling approaches such as line intersect sampling (Van Wagner and Wilson, 1976).

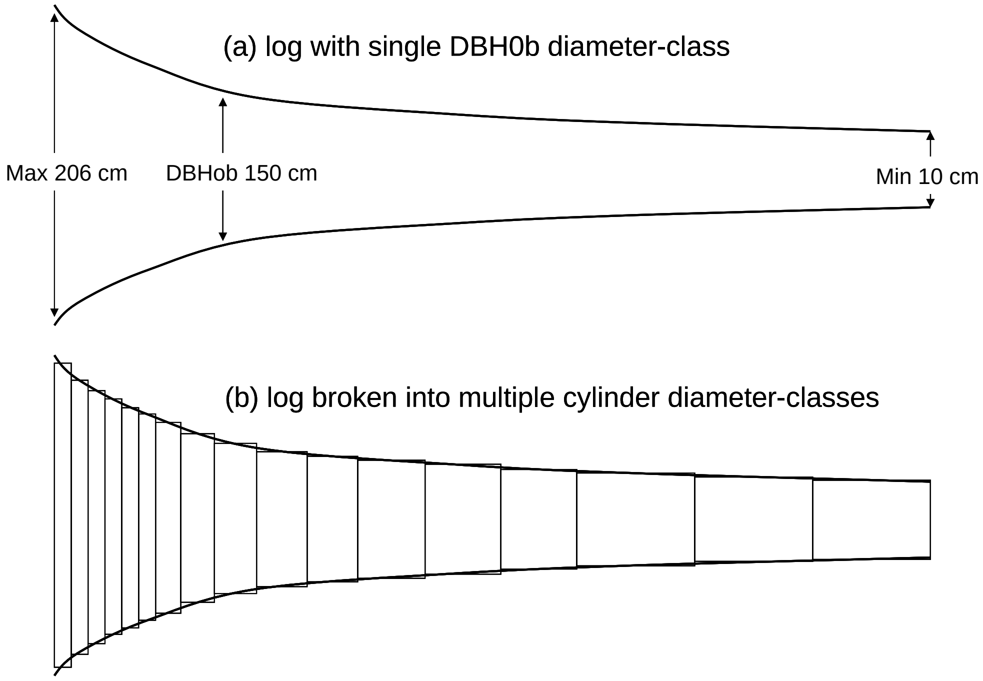

Figure 8. Representation of the process of ‘cylinderisation’ of logs in DELTA.

(4) Decomposing DWD in the DWD pool

DELTA’s *‘DWD decomposition’* submodel passes the volume of DWD in each cylinder-diameter-class through successive decay-class pools and factors-in decomposition-related loss in volume (due to fragmentation, shrinkage or compression) for each of the individual cylinder-diameter-classes with each progression to the next decay-class. We followed (Kruys *et al.*, 2002) and (Vanderwel *et al.*, 2006) in modelling these transitions using a Markov-chain approach (Markov, 1971). We specified a mean residence-time for each decay-class. At each time-step, DWD leaves a particular decay-class pool at a rate inversely proportional to its mean residence time. As it does so, the submodel adopts a further Markov-chain approach that ensures that DWD is passed into a lower cylinder-diameter-class if sufficient volume (and hence diameter, assuming the piece is cylindrical) has been lost. We also specified that DWD would only enter the decay-class 1 pool if it had been standing for five years or fewer, but would enter the decay-class 2 pool if it had been standing for longer than this. The DWD pool was initially ‘seeded’ with volume data by decay-class and diameter-class combinations so as to reflect the DWD compliment typical for the modelled age of the forest at the start of the simulation.

DELTA also removes a proportion of the volume of DWD in the DWD pool at the time of each disturbance event to simulate losses from combustion due to wildfire (DELTA-WF) or to harvest and the subsequent post-harvest regeneration burning (DELTA-CBS). These losses are modelled as varying by decay-class and by diameter-class. In DELTA-CBS, harvest-losses are modelled as occurring in the year of disturbance, while losses to the post-harvest regeneration burn are modelled as occurring in the subsequent year.

We parameterised the residence-time parts of this submodel with data derived from (Grove *et al.*, 2009), in which a set of empirical observations enabled DWD of *E. obliqua* to be characterised as comprising 5 decay-classes, and its decomposition to be represented as a negative exponential decay-curve, with a decay-class constant *k* of -0.011. We determined that mean residence-times for our five successive decay-classes of 12, 34, 44, 46 and 50 years respectively resulted in near-perfect correlation of the submodel's output (r^2=0.99) with this exponential model. We parameterised volume-losses by diameter-class from one decay-class to the next as equations that were based on unpublished data on fragmentation, shrinkage and compression reported in (Stamm, 2006), and which were collected in association with the wood-density findings reported in (Grove *et al.*, 2009). We 'seeded' the submodel with 340 m^3ha^{-1} of DWD, which represents the mean volume of DWD in mature lowland wet eucalypt forest, determined from line-intersect samples across hundreds of temporary inventory plots (FT unpublished data); we divided this volume up into the mean decay-class and diameter-class combinations that had been determined through a smaller-scale but more detailed line-intersect sampling program conducted in the Southern Forests only (FT unpublished data) (Figure 9).

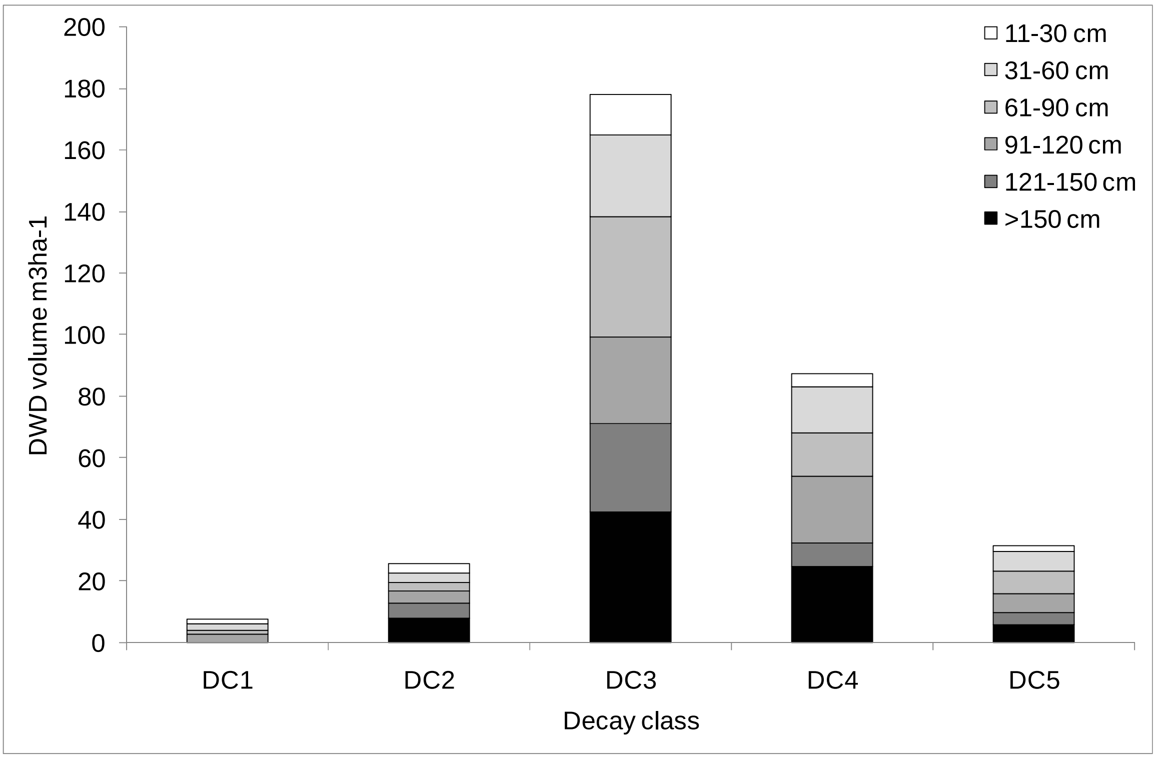

Figure 9. 'Seed' volumes of DWD in different diameter-classes and decay-classes in DELTA at the start of a simulation.

In DELTA-CBS, we used third-order polynomial functions to represent the relationship between DWD diameter and the proportion harvested following clearfelling (and prior to the regeneration burn), and applied different functions for different decay-classes, such that rates of harvest of earlier decay-stage and larger-diameter DWD were highest while rates of harvest of later decay-stage and smaller-diameter DWD were lowest (Figure 10). The main target of harvest (for sawlogs or veneer) is the larger-diameter 'fresh' wood, which DELTA characterises as decay-class 1; hence the function ensures that nearly all such wood is harvested. For the pulpwood market, decay-class 2 and some decay-class 3 DWD is targeted for harvest, but rates of recovery are lower than for sawlogs (e.g. because of fragmentation of the log into pieces too small to be merchantable, or because of the avoidance of log-sections containing commercially undesirable heart-rot). DWD in decay-classes 4 and 5 is not targeted for harvest, but some is nonetheless crushed or damaged by machinery to an extent whereby a proportion was considered to no longer function as DWD for the purposes of this model.

In both DELTA-CBS and DELTA-WF, we used negative exponential functions to represent the relationship between DWD diameter and the proportion lost to combustion or regeneration burning, and applied different combustion constants for different decay-classes and disturbance-types (Figure 11). The higher rate of combustion implicit in the constant for all decay-classes under the CBS scenarios reflects the high intensity of regeneration burning, whose aim is to ensure that the eucalypt seed sown in the days after the fire lands on a receptive (mineral-earth plus wood-ash) seed-bed (Neyland *et al.*, 2009). The lower rate implicit in the constant for decay-classes 4 and 5 under wildfire scenarios reflects the relatively high moisture content of DWD in later stages of decomposition and the likelihood of such material lying in more fire-protected settings (such as partly submerged in the soil and litter layer, or under logs in earlier decay-classes)(Mount, 1979).

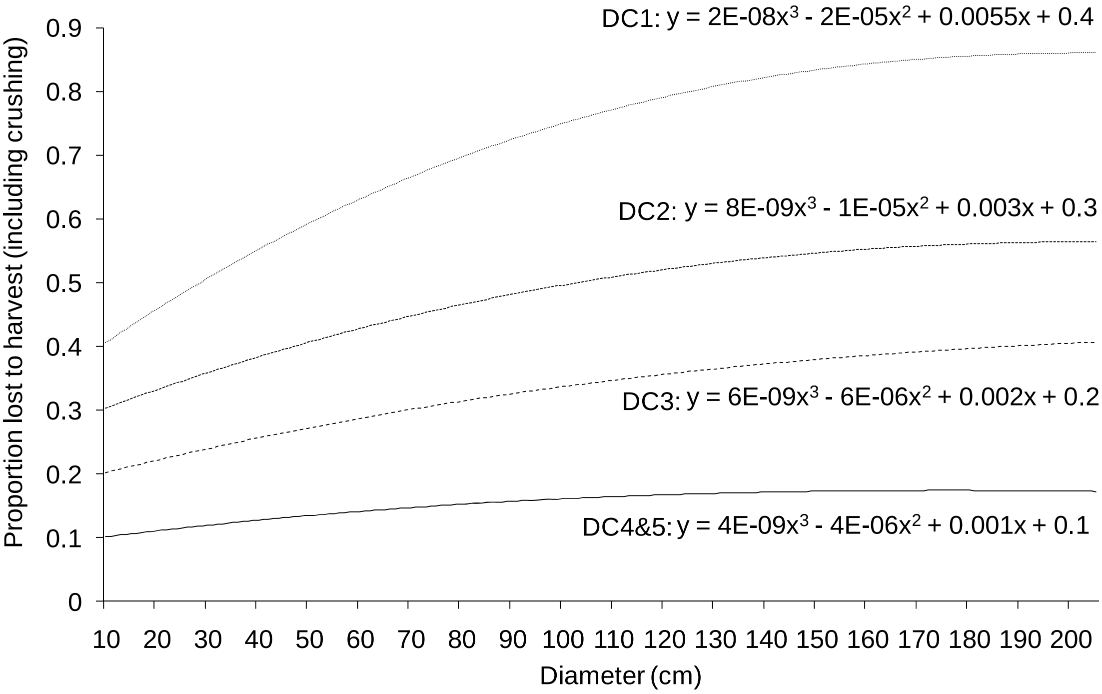

Figure 10. Modelled relationships in DELTA-CBS between the diameter of DWD and the proportion lost to harvest (including by crushing), contingent on its decay-class.

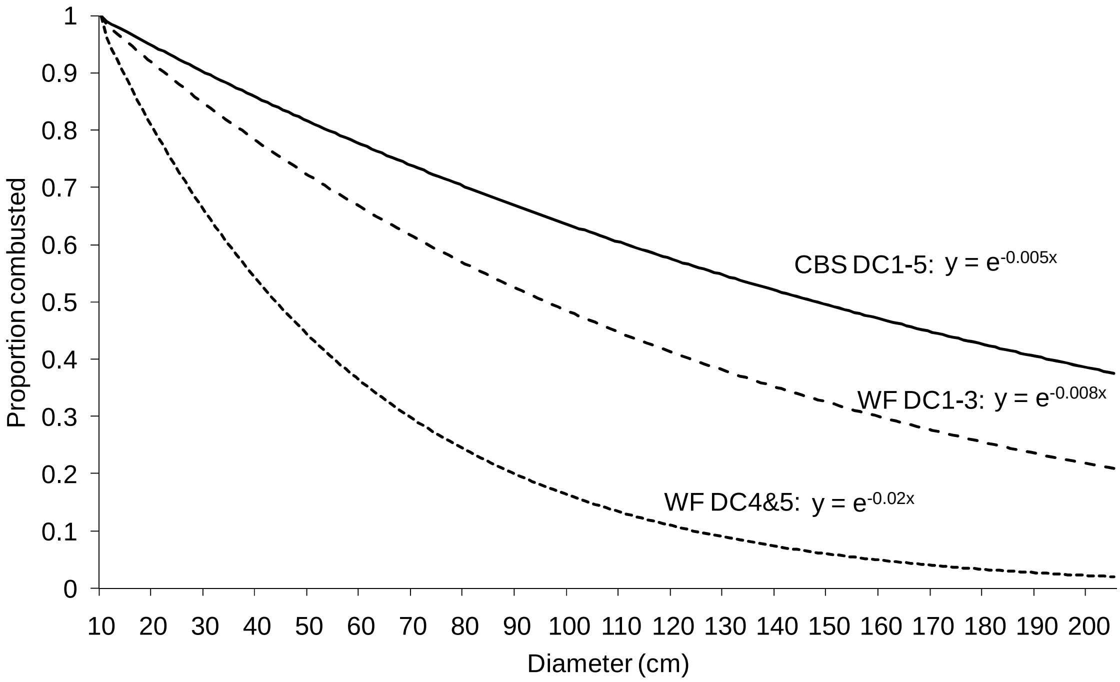

Figure 11. Modelled relationships in DELTA between the diameter of DWD and the proportion combusted in a disturbance event, contingent on the nature of that event (CBS or WF) and on decay-class.

(5) Aggregating and outputting data on DWD

DELTA is able to output quantities of DWD in terms of both volume (m^3 ha^{-1}) and mass (t ha^{-1}) for each year of simulation. In each case, the 1 cm cylinder-diameter-classes of DWD are grouped into 30-cm diameter-classes. We chose these because they make the data more amenable to comparison with standard Forestry Tasmania inventory data, which is also often collected in this format. Since volume is the basic unit modelled in DELTA, the *'DWD volume totals'* submodel simply aggregates modelled DWD quantities for every time-step. However, the *'DWD mass totals'* submodel converts volume data to mass, by each decay-class volume by a corresponding density as described above. We parameterised this part of the model using the wood-densities reported in Grove *et al.* (2009).