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Estimation of compensatory growth of coastal Douglas-fir following pre-commercial thinning across a site quality gradient

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ABSTRACT

This study is aimed to address the issue of whether the volume loss in stands with partial cutting such as pre-commercial thinning (*PCT*) treatments could catch-up with the ones of unthinned stands, employing the lens of compensatory growth (CG) in plant ecology to ask the question of how long one could expect to see the complete CG to happen, if any. CG is the ability of plants or vegetation to vary their growth to offset damage caused by disturbances. Though it has been demonstrated in annual plants such as crops and grasslands, it has not been well studied in trees except Douglas-fir under different *PCT* regimes in the Swiss Central Plateau, trembling aspen seedlings under different fertilization regimes, and fast-growth willow coppice with clipping, etc. Our data from a long-term silvicultural trial (combined *PCT* and fertilization) near Shawnigan Lake, Vancouver Island, British Columbia, Canada, demonstrate complete CG in coastal Douglas-fir 40 years after treatments at both the tree and stand levels. We present a method of estimating the length of time required to achieve complete CG in stand volume. Our results also show that different patterns of complete CG could be expected under different site conditions differentiated by levels of fertilization. Without fertilization a long length of time would be required to reach complete CG, and the length of time could be reduced by increased fertilization application. Potential forest management implications are discussed including possible alternative shapes of yield curves for managed stands and hence the forecast of future wood supply, positive economic evaluation of *PCT* and fertilization, and contribution to regional carbon budget.

1. Introduction

Compensatory growth (CG), or “catch-up” growth, often refers to the process of accelerated growth of an organism following a disturbance or a period of slowed development due to nutrient deprivation. The majority of CG research is conducted at the level of individual plants; however, it has also been studied in agroecosystems at the level of population as crop compensation when damage is not uniform (Sadras and Henggeler, 1994). In rangeland ecosystems, CG as a special case of growth response (GR), has also been studied at the level of population (or community) focusing on measurements of standing crop, net above-ground primary production (NAPP) and forage quality (leaf nitrogen content) (Zellmer et al., 1993). In forestry, this has often be referred to as GR after disturbances expressed as faster growth rate of residual plants due to the redistribution of space and nutrients (Smith, 1986). Furthermore, the terminology of compensative effect was used to describe stand productivity after different thinning regimes to Douglas-fir plantations in the Swiss Central Pleteau (Schütz et al., 2015).

Although the exact biological mechanisms for CG are poorly understood, the phenomenon has been observed in a wide variety of animals and plants. In animals, homeostatic and homeorhetic processes are involved in abnormally high growth rates. Homeostatic processes usually affect CG in the short term (Gerrard and Grant, 2006), whereas homeorhetic processes usually have a long-term effect (Lawrence and Fowler, 2002). In plants, complete CG (referred to as the state of no difference in biomass between disturbed and undisturbed sites) and over CG (referred to as the state of biomass in the disturbed sites exceeded that from the sites without disturbances) have been observed in grasslands, agroecosystems, trembling aspen (*Populus tremuloides*) seedlings, and fast-growing willow (*Salix*) coppice. On the basis of the observational data and the statistical relationships between plant productivity and grazing, McNaughton (1985) tested a hypothesis that

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grazing can increase grassland productivity and showed that aboveground productivity due to grazing was maximal at intermediate grazing intensities for mid-slope and flatland grasslands. The results suggested that CG mechanisms might be the driving forces determining plant productivity (McNaughton, 1985). In agroecosystems, the mechanism of CG has been employed to increase cotton yield through early removal of the reproductive organs of flower buds and squares, which was evaluated at the level of crop or population (Eaton, 1931). In trembling aspen, seedlings in a resource-rich environment showed compensation (or complete CG; in contrast responses ranged from undercompensation (or under CG) to compensation (or complete CG) in a resource-limited environment (Erbilgin et al., 2014). In fast-growing willow coppice, Guillet and Bergström (2006) found that in both the new plantation and in the older coppice, the willows fully compensated (complete CG) for biomass losses after winter clipping, irrespective of clipping intensity. On the other hand, total biomass production usually decreased after high-intensity summer clipping.

Many studies conducted in agricultural ecosystems have found CG after disturbances such as herbivory (Crawley, 1983; McNaughton, 1985) and insect pest infestation (Eaton, 1931). These results suggest that it is possible for a plant to experience CG or even over CG compared with its normal growth without disturbances. Research has even gone further, investigating whether the quality of crop products would be influenced by artificial disturbances that mimic the damage caused by insect infestation (Eaton, 1931). Research on the economic threshold in pest management has suggested that at the population (crop) level, CG could be used to increase crop yield with lower costs for pesticide applications (Sheng, 1988). All these results have supported decisions to achieve management objectives.

The phenomenon of CG has not been well explored in perennial plants, especially trees, which have a much longer life-span than grass and agricultural crops. Over the course of a tree's long life-span, its growth can be influenced by not only physical site conditions but also natural and anthropogenic disturbances. Trees subjected to frequent natural disturbances such as fire, insect outbreaks, animal browsing, droughts, and ice storm have developed protective mechanisms such as thickened bark (Pausas, 2015; Schafer et al., 2015), increased sprouting (Masaka et al., 2000), and bigger leaves (Rea and Massicotte, 2010). Under anthropogenic disturbances such as harvest, without changing land use, forestland can be renewed by either natural regeneration or plantation to initiate a new cycle of succession. When partial cutting is involved, growth of released crop trees, as a kind of CG at the level of population, has been observed and used as a management option to increase the sizes of residual trees (e.g., Lindgren et al., 2007).

Pre-commercial thinning (*PCT*) is a thinning method performed prior to trees reaching merchantable size for reducing stand density and increasing the growth of the remaining trees (Weetman and Mitchell, 2013). *PCT* can serve as an example of anthropogenic disturbances to forest ecosystems, and such partial cutting can display diverse consequences of CG. Many *PCT* studies have shown that at the individual tree level, tree sizes in terms of diameter at breast height (*DBH*) and total height (*TH*) increase much faster in thinned plots than in unthinned plots in a relatively short period (e.g., Aussenac and Granier, 1988; Brix, 1993; Morris et al., 1994). At the stand level, however, the total volumes in thinned plots are not always able to catch up with those in unthinned plots (e.g., Rice et al., 2001). However, exceptions were also reported such as different thinning regimes do not have much impact on stand productivity 41 years after treatments in Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco) in a plantation in Swiss Central Plateau (Schütz et al., 2015). Similar observations were from Douglas-fir forests in the Malcolm Knapp Research Forest of UBC in Maple Ridge, British Columbia, where more or less the same forest productivity was observed about 50 years after different thinning regimes (Cheryl Power, Pers. Comm., Dec. 2017). More or less similar forest conditions can also be observed for aspen mixedwood forests near Calling Lake, Alberta 40–50 years after various silvicultural treatments (Derek Sidders, Canadian Wood Fibre Centre, Pers. Comm., Nov. 2017). Also, Pitt and Lanteigne (2008) reported that thinned stand volumes exceeded volumes in unthinned stands in the balsam fir (*Abies balsamea*) dominated stands in northwestern New Brunswick, Canada, 42 years after *PCT*, in which thinned plots contained 15% more total gross volume than unthinned plots.

Because of the slow growth of trees and the relatively short career lengths of researchers, most observations have been made in a relatively short period after thinning treatments. For example, it was suggested that a l0-year period of growth was generally sufficient to show potential growth rate, stem and branching characteristics, and susceptibility to various types of damage (Reukema, 1975). This has limited researchers' ability to study the CG of trees at the forest level. While relative differences do tend to decline over time, if one has data to produce growth curves then the trajectories of these curves can be examined to predict longer term trends. Consequently, volume (i.e., cumulative growth) assessment has become essential in studying CG and its impact on sustainable forest management planning and evaluation of silviculture.

Whether the volume loss in stands with *PCT* treatments could catch-up with the ones of unthinned stands remains one of the major issues for decisions of forest management and forestry. This is not only an issue of evaluating silvicultural operations, but also important in forecasting regional wood supply, which appears critical in sustainability of forest resources, and practical forest management planning of forest industries and the forest sector as a whole. Despite the examples mentioned above, which could lead to positive implications to forestry such as shortening the number of years to reach harvest operability and hence enhanced forecast of regional wood supply, considerable literature has shown that the answer to this issue is probably nonpositive. This may lead to nonpositive implications for the forecast of regional wood supply (Curtis et al., 1982; Smith, 1986); assumptions of yield curves of managed stands (Nigh, 2013); contribution to regional carbon budget (Bradford and D'Amato, 2012; Schaedel et al., 2017); and economic evaluation of forestry under silvicultral treatments (Duke et al., 1989), etc.

The lens of CG has been successfully adopted to explain the plant morphological observations that fall outside of the normal ranges characterized in the dichotomous identification keys (Rea and Massicotte, 2010). This inter-disciplinary approach has also been adopted in plant science in terms of using ideas from behavioural ecology to understand plants (e.g., Cahill, 2015). In current study, the lens of CG is employed to explore the forest GR under different silvicultural treatments. Despite of similar biological meanings, CG and GR are continuums developed independently from different fields. We used CG for putting more weight on identifying conditions for over CG towards positive management applications and possible mechanisms.

The objectives of this study are two-fold. The first objective is to test a hypothesis that CG after *PCT* and fertilization will allow the volume in thinned plots to catch up with the volume in unthinned plots. This test will be conducted through applying the concept of CG in plant ecology to address the question of how long one could expect the complete CG to take place, and by analyzing data from the latest remeasurement in 2012, 40 years after the initial treatments from the Shawnigan Lake Project (Crown and Brett, 1975), a long-term Douglas-fir *PCT* and fertilization trial near the Shawnigan Lake, British Columbia, Canada. If this hypothesis is true, the volume in thinned plots will catch up with or even exceed the volume in unthinned plots, provided that the time horizon is long enough to allow realization of CG in full. This investigation also uses some existing results published in previous Shawnigan Lake Project studies. The second objective is to explore how this new information could be used in forestry practice such as how the carbon storage in biomass pool would be influenced by different treatments of *PCT* and fertilization. If the null hypothesis is true, there should eventually be no significant difference in biomass carbon pool under different treatments.