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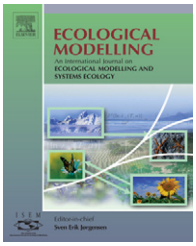

A tree and climate assessment tool for modelling ecosystem response to climate change

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ABSTRACT

Understanding how vulnerable forest ecosystems are to climate change is a key requirement if sustainable forest management is to be achieved. Modelling the response of species in their regeneration niche to phenological and biophysical processes that are directly influenced by climate is one method for achieving this understanding. A model was developed to investigate species resilience and vulnerability to climate change within its fundamental-regeneration niche. The utility of the developed model, tree and climate assessment (TACA), was tested within the interior Douglas-fir ecosystem in south-central British Columbia. TACA modelled the current potential tree species composition of the ecosystem with high accuracy and modelled significant responses amongst tree species to climate change. The response of individual species suggests that the studied ecosystem could transition to a new ecosystem over the next 100 years. TACA showed that it can be an effective tool for identifying species resilience and vulnerability to changes in climate within the most sensitive stage of development, the regeneration phase. The TACA model was able to identify the degree of change in phenological and biophysical variables that control tree establishment, growth and persistence. The response to changes in one or more of these variables resulted in changes in the climatic suitability of the ecosystem for species and enabled a measure of vulnerability to be quantified. TACA could be useful to forest managers as a decision support tool for adaptation actions and by researchers interested in modelling stand dynamics under climate change.

1. Introduction

The distribution of vegetation, in the absence of competitive constraints, is most commonly determined by climate (Woodward, 1987; McKenzie et al., 2003a). Complex interactions between climate, biophysical variables and disturbances create a mosaic of vegetation types and ecosystems across landscapes. However, changes in climate are expected to shift the distribution of species along environmental gradients if their current environmental tolerance is exceeded (Miller and Urban, 1999). This will potentially result in the development of new species assemblages within broader ecosystem groupings. The new ecosystems will reflect the result of complex interactions between biophysical variables such as soil type, climate, disturbances and land-use (Allen and Breshears, 1998; McKenzie et al., 2003b).

Despite the complex interactions that influence the presence or absence of species on a landscape, an understanding of the possible distribution of vegetation types under climate change is still possible if based on predictable environmental controls (Hilbert and Muyzenberg, 1999). To predict shifts in the distribution of vegetation under climatic change,

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modelling can be used to simulate responses of vegetation at a variety of scales, ranging from the individual tree to biomes (Zolbrod and Peterson, 1999). Species-specific responses are masked at broad scales, and species-level modelling is therefore advocated as the most suitable method for predicting the responses of threatened, keystone or target species (Bakkenes et al., 2002). The modelling of individual species responses is primarily done using statistical modelling (Iverson and Prasad, 2001; Schwartz et al., 2001; McKenzie et al., 2003a,b) or mechanistic modelling (Urban et al., 1993; Burton and Cumming, 1995; Sykes and Prentice, 1995; Cumming and Burton, 1996; He et al., 1999; Miller and Urban, 1999; Zolbrod and Peterson, 1999).

Statistical models, also referred to as equilibrium models (Eeley et al., 1999; McKenzie et al., 2003a), attempt to correlate climate to vegetation empirically under the assumption of a static relationship between climate and vegetation (Fischlin and Gyalistras, 1997). These types of models generally provide no explanation of the mechanisms of change and are poor predictors of forest growth and succession under different management and environmental conditions (Kimmins, 2004). Even with robust parameters, the assumption of a static climate–vegetation relationship is still a fundamental part of any statistical model. This limits the inferences that can be derived from statistical models, due to the uncertainty that exists in the assumption that the future relationship between climate and vegetation will be the same as in the past.

The static nature of statistical models can be overcome by using mechanistic models that are driven by empirically derived parameters. Gap replacement models, based on JABOWA (Botkin et al., 1972) and FORET (Shugart and West, 1977), are the most commonly used mechanistic models for predicting species response and forest succession under climatic change (Zolbrod and Peterson, 1999). Kimmins (2004) provides a thorough summary of the evolution of gap models from the original JABOWA model. Gap models simulate the regeneration, growth and mortality of individual trees on an annual time step with growth modelled deterministically and mortality and regeneration modelled stochastically (Burton and Cumming, 1995). Growth responses are based on the sum of growing degree days (GDD), soil moisture levels and light availability (Urban, 1993). Competition between species is based primarily on light with nutrient, moisture and temperature constraints used to modify the growth of different species (Botkin, 1993).

Many modelling studies depend on an understanding of the role of the niche. The fundamental niche (Hutchinson, 1957; Schoener, 1989) of a species is determined by a combination of environmental variables and processes, whereas the realised niche of a species is governed by the competition for the same niche space with other species. Realised niches are not static. They are characterised by dynamic shifts in niche breadth due to changes in resource availability over time and space (Schoener, 1989). To address this, one of two characteristics is usually quantified: species abundance or distribution. Measures of abundance attempt to predict species abundance through the modelling of either the proportion of cover, biomass or basal area a species occupies within a community. The quantification of species distribution investigates whether an individual species will be present or absent on a site due to climate change (McKenzie et al., 2003b). McKenzie et al. (2003b) state that good predictors of species abundance may not be good predictors of species distribution, so different modelling techniques and response variables are needed. Central to these approaches is the theory that species presence/absence and abundance is highest where optimal conditions exist, defined as the centre of each species environmental gradient (Gauch et al., 1974).

Paleoecological studies have identified that species typically increase or decrease in abundance and range in response to climate-driven changes in niche breadth rather than disappear from landscapes (Bradshaw et al., 2000; Davis and Shaw, 2001). Mature individuals have been found to survive well outside of their modern ranges due to favourable microclimatic conditions, reproducing sporadically when climate conditions allow (Bradshaw et al., 2000). Niche breadth is therefore affected by a species' phenology and its regenerative niche (Grubb, 1977). The regeneration niche of trees is narrower than their fundamental niche, typically reflecting the optimal portion of a species' fundamental niche (McKenzie et al., 2003b). However, the dynamic nature of a species' niche usually results in a species dominating the suboptimal portion of its niche over time in the presence of competition (Rehfeldt et al., 1999). The modelling of presence/absence reflects the regeneration niche of a species, because presence is directly related to establishment, providing a modelling approach that is robust to life-history changes in species (McKenzie et al., 2003b). Species are at their most susceptible to climatic variation in their regeneration niche (Grubb, 1977); this sensitivity impacts the distribution of species (Battaglia, 1996). The breadth of a species' regenerative niche impacts overall niche breadth, with species decreasing or increasing over time as changes in the ability of species to regenerate cascade through their fundamental and realised niches. This mechanism will gradually reduce or increase a species abundance and distribution.

In this study, an aspatial model, tree and climate assessment (TACA), was developed to assess the resistance and resilience (Holling, 1996; Gunderson et al., 2002) of tree species and ecosystems to climate change by examining change in the breadth of a species regeneration niche. TACA analyses the influence of predicted changes in climate on the ability of a tree species to regenerate. This approach is used to gain an understanding of the risks associated with the loss of mature ecosystems to both natural and anthropogenic disturbance. TACA is designed to evaluate species response to climate change when they are at their most sensitive stage of their life cycle, regeneration. TACA is based on the patch model ZELIG++ (Burton and Cumming, 1995) which itself is a modified version of the JABOWA-FORET genre patch model ZELIG (Urban, 1993). The two versions of ZELIG differ in their representation of temperature response behaviour. ZELIG++ uses a phenological event-based response versus the standard growing degree day response curves of traditional patch models (Burton and Cumming, 1995). Cumming and Burton (1996) found that ZELIG++ predicted current species composition in British Columbia with greater accuracy then ZELIG. TACA utilises the same phenological event-based response as ZELIG++ but differs from this model and ZELIG by not incorporating growth equations and allometric estimates of biomass or timber volume. A case study is presented that tests the utility of TACA for modelling tree species response to climate change in south-central British Columbia.

2. The TACA model

2.1. *Development and parameters*

TACA is a mechanistic model derived from ZELIG++ and reprogrammed from a C++ programming language into Microsoft Excel (Microsoft, 2002). The model analyses the response of trees in their fundamental-regeneration niche to climate-driven phenological and biophysical variables. TACA is a vulnerability analysis tool that uses the following driving variables to determine the probability of species presence/absence:

- growing degree day thresholds (GDD Min and GDD Max);
- species-specific threshold temperature (T_{base});
- minimum temperature (Min T);
- chilling requirement (CR);
- bud break (BB);
- drought;
- frost.

The model variables are based on Burton and Cumming (1995), and the determination of presence or absence is event-driven, as proposed by Cannell and Smith (1986). As the model is based on presence/absence and does not predict species abundance, the need to model individual tree growth is removed (McKenzie et al., 2003b). The model uses the degree growth stage model developed by Fuchigama et al. (1982) and utilised by Burton and Cumming (1995) to determine if a species is vulnerable to climate-driven phenological events. The determination of presence/absence is described below and illustrated in Fig. 1.

Minimum and maximum GDD thresholds are used to determine the lower and upper relationship limits between temperature and growth (Urban, 1993). If the minimum threshold is not met or the maximum threshold is exceeded, it is assumed that the regeneration niche of a species is exceeded. If the maximum and minimum requirements are not met, minimum growth rates occur that can result in species mortality (He et al., 1999). Increases in temperatures can restrict and prevent species from re-establishing on a site (Franklin et al., 1992). The regeneration niches of species are narrower than mature trees so this assumption may not limit the presence/absence of mature trees (McKenzie et al., 2003b); however, only moderate increases may be required to prevent seedling establishment (Dale et al., 2001). In TACA, if the GDD thresholds are not met, a species is assumed to be absent. GDD are calculated by summing the number of degree days above a species-specific baseline temperature for an entire year.

Species-specific baseline temperatures are used to initiate physiological activity (Fuchigama et al., 1982). The accumulation of degree days above the basal temperature threshold occurs until a species-specific heat sum is reached, which then initiates bud break (Fuchigama et al., 1982). The timing of bud break is expected to occur at earlier dates due to climatic change, which may increase the risk of damage by early spring frosts (Cannell and Smith, 1986; Lavender, 1989).

Species-specific susceptibility to early and growing season frosts is based on Burton and Cumming (1995) and Klinka et al. (2000). Species, whose chilling requirements are satisfied, even under increased temperatures due to climate change, will have the date of mean bud break occurring at a lower mean temperature than is presently the case, increasing the risk of frost damage from late spring cold events (Lavender, 1989; Kimmins and Lavender, 1992). Species are most susceptible to frost damage and mortality during the regeneration phase (Murray et al., 1994). Frost modifiers are used to limit the probability of species presence. In the ZELIG++ model, early and growing season frosts are used to severely limit growth (Cumming and Burton, 1996). As growth is not modified, frost susceptibility affects the probability of successful establishment. Growing season frosts can kill buds and terminal twigs or the entire plant. In addition, plants damaged by frost are more susceptible to damage by disease and insects (Murray et al., 1994; Dale et al., 2001; Kimmins, 2004). For these reasons, species have their probability of presence reduced if subjected to an early growing season frost event. In TACA, the more frost events that a species is subjected to, the more its presence-probability will be modified. Frost events are assumed to occur when temperatures fall below 0 °C. Minimum temperature thresholds are used to determine if winter killing frosts occur. In TACA, if a minimum temperature is reached or exceeded then tree fatality occurs (Burton and Cumming, 1995).

Species-specific chilling requirements are measured to determine if frost hardiness is induced (Cumming and Burton, 1996). Some species are very sensitive to late spring frosts, resulting in very high chilling requirements being required before bud break will occur (Sykes and Prentice, 1995). Climate change may interfere with the ability of trees to meet their chilling requirements for bud break, flowering and germination (Loehle and LeBlanc, 1996). The inability of a species to obtain its chilling requirement can seriously affect the species' ability to re-establish after disturbance, facilitating changes in community composition (Shafer et al., 2001). In TACA, if the chilling requirement is not met then a species is assumed to be absent. Chilling requirements are calculated by summing the number of days that are between −5 and 5 °C from the midpoint of the growing season onwards.

Drought plays a direct role in shaping species distributions (Swetnam and Betancourt, 1998; Aber et al., 2001; Hannah et al., 2002). It is regarded as a major limiting factor for determining the range limits of tree species (Sykes and Prentice, 1995). Drought can cause rapid mortality and increase the susceptibility of species to insect attack (Allen and Breshears, 1998). Hogg and Wein (2005) identified that forests are very sensitive to drought during the regeneration phase and state that drier conditions due to climatic change could exacerbate this vulnerability and restrict or prevent regeneration. Drought conditions have and will prevent establishment of species on a site and cause mortality of established seedlings (Spittlehouse and Childs, 1990; Bawa and Dayanandan, 1998;

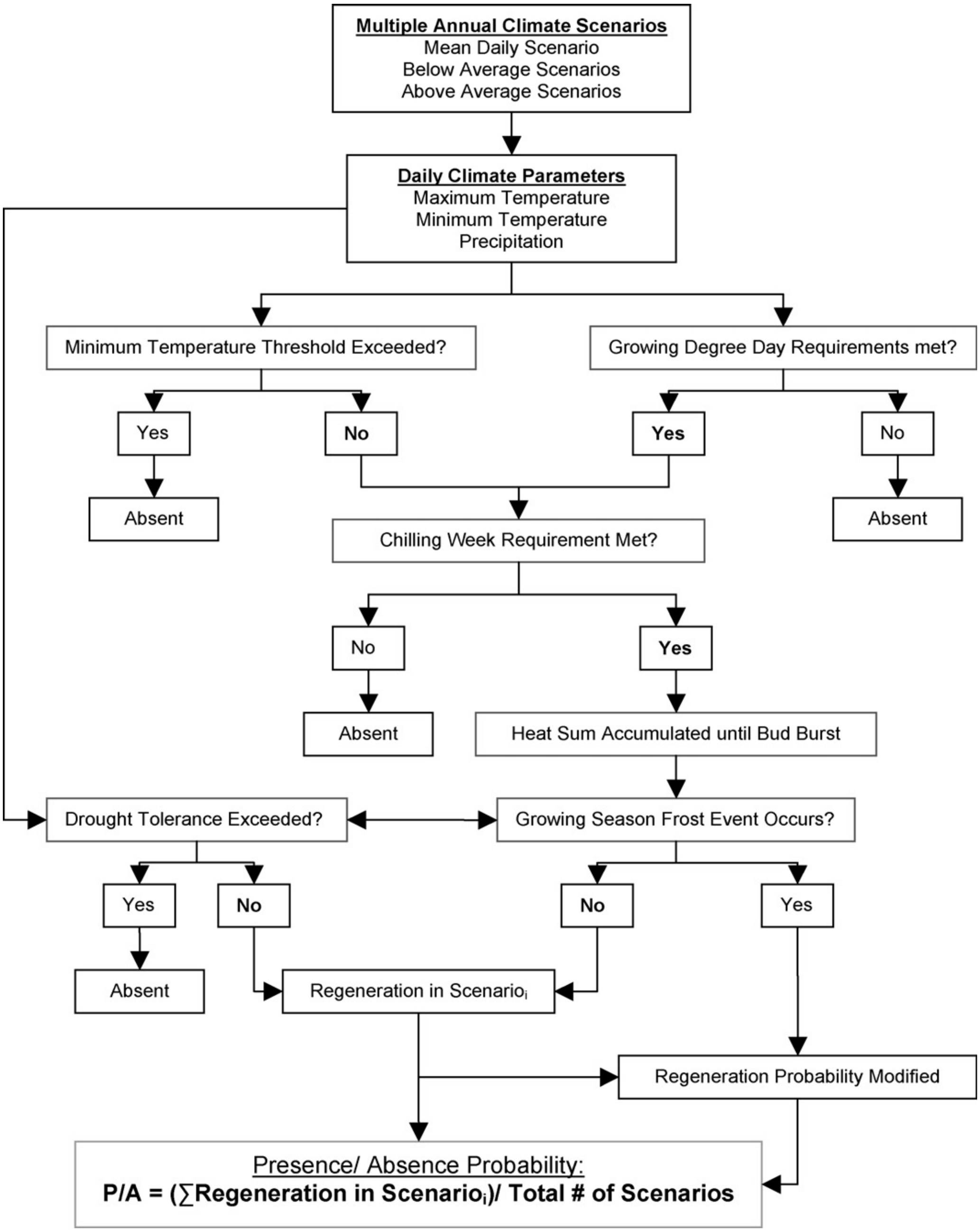

Fig. 1 – Diagram of model components and information flow in TACA.

Fleming and Candau, 1998; Whitmore, 1998; Midgley et al., 2002). Drought in TACA is defined by the number of months where rooting-zone groundwater is absent during the growing season (Klinka et al., 2000). Drought is calculated based on the ratio of actual evapotranspiration (AET) to potential evapotranspiration (PET), which is determined by the annual water balance (Thornwaite and Mather, 1955; Thornwaite et al., 1957; Oke, 1987). Species-specific drought tolerance is based on Burton and Cumming (1995) and Klinka et al. (2000). In TACA, presence/absence under drought is determined by species-specific thresholds related to the proportion of the growing season that can be survived under a water deficit (Burton and Cumming, 1995). If the threshold is exceeded then a species is assumed to be absent from the site.

3. Species parameters

The phenology and biophysical variables of 17 tree species were parameterised for use in TACA. Table 1 summarises the species available for use in TACA.

Species-specific parameters used in TACA (Table 2) follow Bonan (1989), Urban et al. (1993), Burton and Cumming (1995), Cumming and Burton (1996), Zolbrod and Peterson (1999), McKenzie et al. (2003a,b). All parameters, with the exception of two species, are based on empirical relationships between tree species and climate and have been used in modelling the response of tree species to climate change. Observations by Klinka et al. and McKenzie et al. were used to estimate

Table 1 – Tree species parameterised for TACA

Common name	Scientific Name
Black cottonwood	*Populus balsamifera* ssp. Trichocarpa (Torr. & Gray) Brayshaw
Trembling aspen	*Populus tremuloides* Michx.
Pacific silver fir	*Abies amabilis* (Dougl. ex Loud.)
Grand fir	*Abies grandis* (Dougl. ex D. Don)
Subalpine fir	*Abies lasiocarpa* (Hook.) Nutt.
Western redcedar	*Thuja plicata* Donn ex D. Don
Mountain alder	*Alnus incana* ssp. Tenuifolia (Nutt.) Breit.
Paper birch	*Betula papyrifera* Marsh.
Douglas-fir	*Pseudotsuga menziesii* var. *glauca* (Beissn.) Franco
Western larch	*Larix occidentalis* Nutt.
Whitebark pine	*Pinus albicaulis* Engelm.
Lodgepole pine	*Pinus contorta* Dougl. ex Loud. var. *latifolia* Engelm.
Western white pine	*Pinus monticola* Dougl. ex D. Don
Ponderosa pine	*Pinus ponderosa* Dougl. ex P. C. Laws
Black spruce	*Picea mariana* (Mill.) BSP
Engelmann spruce	*Picea engelmannii* Parry ex Engelm.
Hybrid white spruce	*Picea glauca* (Moench) Voss x *engelmannii* Parry ex Engelm.

parameters for whitebark pine (Pa), which had no standard parameter estimates. Mountain alder (Dm) parameters were modified from red alder (*Alnus rubra*) parameters, presented in Zolbrod and Peterson (1999), using the ecological and silvical description provided by Klinka et al. (2000). The parameters are amalgamations based on multiple studies. They were derived to create parameters that are representative of all study areas and were based on the ecological and silvical characteristics described by Klinka et al. (2000).

4. Climate parameters

TACA utilises minimum temperature, maximum temperature, and precipitation on a daily time step for a period of 1 year. Each year represents one climatic scenario. Multiple climate scenarios can be run in TACA and are required to determine a species presence/absence probability under historic, current and/or future climatic scenarios. Future scenarios can be based on predictions from global circulation models or can be user defined to examine the responses of warmer temperatures with or without changes in precipitation and vice versa. The incorporation of multiple scenario analyses is required to address problems of uncertainty, interdependence and complexity (Schoemaker, 1993). A multiple scenario approach, used in conjunction with TACA, provides the boundaries of species vulnerability under current and uncertain future conditions which is a form of sensitivity analysis that can identify the tolerance levels for each parameter for each species.

4.1. *Determining the probability of presence/absence*

Species presence/absence can be determined for both water deficit (WD) and non-water deficit (NWD) sites. For WD sites, the probability of presence/absence was determined based on the average probability of a species meeting all phenological and biophysical criteria. If a species did not meet growing degree day, chilling requirement, minimum temperature and/or drought parameters in any scenario, the species was determined to be absent from the site. If a species met all of these requirements in at least one scenario then the presence probability was modified by the probability of frost damage from early and growing season frosts. Frost damage is a product of the probability of frost events occurring mul-

Table 2 – Selected species parameters used in model (*: estimated species)

Species	T_{base}	BB	CR	Min T	Drought	Frost	GDD Min	GDD Max
Black cottonwood	4.6	175	10	−60	0.2	0.5	280	2491
Trembling aspen	3.5	189	10	−80	0.4	0.1	280	2461
Pacific silver fir	4.3	176	16	−30	0.2	0.5	296	1925
Grand fir	4.3	307	13	−35	0.4	0.5	545	2193
Subalpine fir	2.6	119	10	−67	0.1	0.1	294	2386
Western redcedar	4.1	282	13	−35	0.3	0.5	528	2681
Mountain alder*	5.3	451	18	−46	0.2	0.1	600	3680
Paper birch	3.7	231	11	−80	0.3	0.1	280	2036
Douglas-fir	3.4	255	15	−37	0.5	0.5	340	3761
Western larch	3.4	180	10	−40	0.4	0.5	280	3400
Whitebark pine*	3	120	10	−55	0.5	0.1	200	2200
Lodgepole pine	2.9	116	9	−85	0.3	0.1	276	2600
Western white pine	4.4	468	14	−85	0.3	0.3	297	3165
Ponderosa pine	3.9	250	11	−41	0.5	0.5	600	4000
Black spruce	3	123	8	−69	0.3	0.1	247	1911
Engelmann spruce	3.1	145	7	−45	0.2	0.1	280	1911
Hybrid white spruce	2.9	146	6.5	−58	0.2	0.1	280	1911

T_{base} (°C): species-specific threshold temperature; BB (Heat Sum): heat sum required to initiate bud burst (BB); CR (weeks): number of chilling weeks required for chilling requirements to be achieved; Min T (°C): a temperature below this threshold is considered fatal to a tree; Drought (threshold: % of season which can be survived under a water deficit); Frost (presence probability modifier); GDD Min and GDD Max (degree days): minimum growing degree days required for survival and maximum growing degree days that limits growth through heat stress.

tiplied by the frost modifier for a species. For NWD sites, the drought parameter was excluded and the same procedure followed. A species that met all criteria received a presence score of one and the climate conditions were assumed to be in the optimal range of the species regeneration niche. A score of zero meant that that species never achieved a combination of required parameters, and that climate conditions were outside a species' regeneration niche. Probabilities between one and zero were a result of parameters being met in a proportion of the scenarios and/or the species being subject to frost damage. Presence/absence probability between one and zero reflect the species-specific variation in climatic suitability and suggest that current and future climate conditions can fluctuate between adverse and favourable conditions for regeneration. Species may be able to regenerate successfully in 1 year but not in the next or over a period of years depending on climate conditions.

4.2. *Distinguishing resilience from response*

The resilience measure of a species to climate change is inversely proportional to the modelled probability of presence. A species with a presence probability that increases is very resilient to climatic change and will likely benefit under the new climate regime. Conversely, a decline in a species' presence probability results in a decrease in resilience. The lower the probability the more vulnerable (less resilient) a species is to the current or future climate conditions. A species that has probability decline to zero is categorised as not being resilient to climatic change.

4.3. *Model limitations*

TACA is an aspatial model that assesses the likelihood of the presence or absence of a species. The model assumes that a site is available to all species after disturbance and does not assume reforestation or natural regeneration at any specific density. The model uses the relationship between species and climate to determine the susceptibility of a species to climate-driven changes in important phenological and biophysical requirements for successful establishment and growth. Competition is not included, which limits TACA to being a fundamental-regeneration niche model. The use of the regeneration niche suggests that species that can persist at this phase will remain resistant to climate change once they are established, increasing the robustness of the model (McKenzie et al., 2003b).

TACA was based on established models and simplified to remove the assumptions of succession and tree growth used in these models. It investigates if a species will be present or absent and the vulnerability of that species to climate change. By adding competition for light, moisture and nutrients, the response could be masked by the assumed responses of competing species. The parameters used in TACA are based on published ranges of unknown validity, and the model is therefore dependent on the robustness of those parameters.

The model does not take into account any changes in water-use efficiency that may be induced by increased atmospheric carbon dioxide concentrations. This remains a controversial area (Gifford, 2004), and while there is evidence that under experimental conditions water-use efficiency may be increased, the results of studies undertaken under natural conditions are mixed (Tognetti et al., 2000; Soulé and Knapp, 2006).

The final limitation is the lack of microclimate representation. The influence of topography, edaphic conditions and forest canopy is not included. To reduce the impact of these limitations, TACA assumes that a site is either water-shedding or water-receiving and that at a broad scale the local ecosystems are reflective of the sites occupied by the weather stations used in the analysis. The microclimate on a site is also generalised into two categories: (1) water deficit (WD) sites or (2) non-water deficit (NWD) sites. The influence of topography is based on the assumption that sites positioned on crests and upper slopes are water-shedding sites, lower slope positions and sites in depressions are assumed to be water-receiving sites, while mid-slope positions are assumed to be both water-shedding and receiving sites. Based on these assumptions, the mid-slope positions are the most difficult to predict and based on edaphic conditions could reflect either WD or NWD site. To determine NWD sites, the drought parameter was excluded from the analysis. The influence of forest canopy was assumed to be removed by disturbance, either naturally or by human activities. Despite these limitations, TACA provides a simple method for gaining a broad understanding of which species are vulnerable to climate change in their regeneration niche.

5. An application of TACA

To test TACA, the response of 17 species to current and climate change scenarios was evaluated for an ecosystem located in the North Okanagan region of British Columbia, Canada (50°12′24″North, 119°28′48″West). The ecosystem is classified as the interior Douglas-fir (IDF) zone within British Columbia's biogeoclimatic (BEC) ecosystem classification scheme (Meidinger and Pojar, 1991). The interior Douglas-fir zone is located between 350 and 1450 m in elevation and has a continental climate characterised by warm, dry summers and cool winters (Hope et al., 1991a). The growing season in the IDF is characterised by the common occurrence of substantial moisture deficits and frosts (Hope et al., 1991a). The IDF zone in the selected research area represents the very dry and hot sub-zone of the IDF ecosystem. In general, the IDF zone is characterised by extensive mature stands of Douglas-fir, with mixed stands of lodgepole pine and Douglas-fir occurring where crown fires are common. Hybrid white spruce, western larch, grand fir, western white pine, western red cedar, mountain alder, paper birch, black cottonwood, and trembling aspen can all occur on non-water deficit sites while ponderosa pine can form seral and climax stands throughout the drier portions of the IDF (Hope et al., 1991a; Klinka et al., 2000).

The Fintry fire weather station (50°12′24″, 119°28′48″West), located within the selected ecosystem, was used to test the TACA model. The weather station is located at 670 m in elevation and has been operation since 1989; the data used in this study range from 1989 to 2003.

5.1. *Climate scenarios*

Seventy scenarios, using a daily resolution, were used to represent current climate and climate change scenarios for the IDF ecosystem. The climate change scenarios were produced by the Canadian Global Circulation Model I (CGCM1), Canadian Global Circulation Model II (CGCM2), and the Hadley Centre Global Circulation Model III (HadCM3) global circulation models (GCM). For a description of the Canadian models see Flato et al. (2000) and for the Hadley model see Johns et al. (2003). Climate change outputs were obtained from the Canadian Institute for Climate Studies, Canadian Climate Impacts and Scenarios Project (2005). Three emission scenarios were chosen: CGCM1-gax, CGCM2-A2x and HadCM3-A2x; for a description of the scenarios refer to the Canadian Institute for Climate Studies (2006) and Nakicenovic et al. (2000). A direct adjustment approach was used to integrate climate change scenarios into seven current climate scenarios. One scenario represents the average climate at a weather station and six are randomly generated scenarios based on the variance of climate data around the daily means for temperature and precipitation. The randomly generated scenarios represent a combination of above/below temperature conditions with above/below average precipitation conditions. The generated scenarios were used to represent the year to year variability that exists in the temperature and precipitation regimes for the study area. A scenario was created for each GCM in each time period (2025, 2055 and 2085), equating to 70 scenarios overall. Nitschke (2006) provides a detailed description on weather scenario generation and the integration of climate change scenarios.

5.2. *Test results*

The results of the TACA model test are provided in three steps. The first shows the response of the biophysical components that drive TACA. The second is the response of the 17 tree species to each biophysical component, measured by its presence/absence probability, in each climatic period (current to 2085). The responses from all scenarios were used to calculate the average biophysical and species response in each climatic period. This aggregated the response to all three global circulation models in each predicted climatic period (2025, 2055, and 2085). To support the biophysical component response results, confidence intervals were calculated to provide both an estimate of the effect and a measure of uncertainty. It is the estimates of the magnitudes of effect with associated errors that are important, rather than subjecting the results to statistical significance tests (Johnson, 1999). The third step illustrates the overall species response to current and predicted future climate scenarios. This final step identifies which species could be present under current and future climate conditions. The modelled presence/absence probability illustrates the climatic suitability for each species in its regeneration niche. The closer this probability is to 1.0 the more favourable the climate conditions are for regeneration. The closer this probability is to 0.0 the more adverse the climate conditions are for successful regeneration.

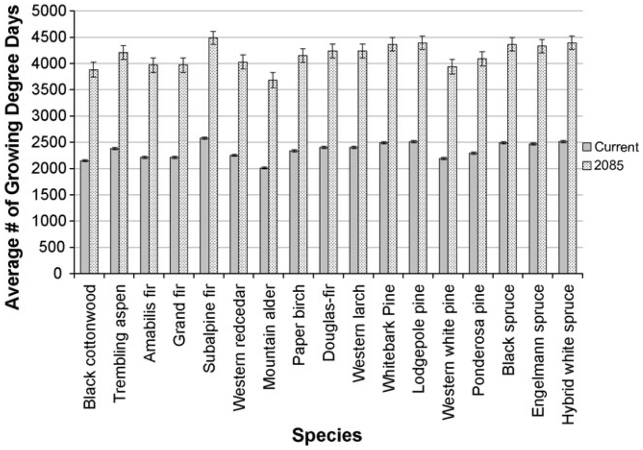

Fig. 2 – Change in the number of growing degree days from the current climatic period to the 2085 predicted climatic period.

5.3. *Growing degree days*

Fig. 2 illustrates the change in the number of growing degree days (GDD) due to climatic change within the test ecosystem. For brevity, the results from only the current and 2085 climatic period are provided. The results suggest that a 1500–2000 increase in the number of growing degree days may occur by the 2085 climatic period. Fig. 3 shows the species response to the number of growing degree days from the current to 2085 climatic period. Seven of the 17 species had their maximum GDD threshold exceeded in all of the current climate scenarios (probability of 1.0). By the 2085 climatic period, 15 species had their maximum GDD threshold exceeded in every scenario. Ponderosa pine and mountain alder were the only two species that did not have their GDD threshold exceeded in every 2085 scenario. However, they had their GDD threshold exceeded one-third of the time due to the predicted climatic change. All species achieved their minimum GDD threshold in each climatic period. Overall, the results from the TACA model suggest that the number of species having their GDD thresh-

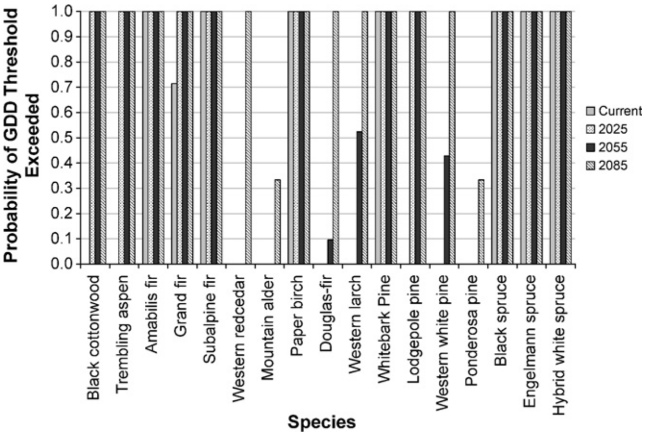

Fig. 3 – Probability of the maximum growing degree day threshold being exceeded from the current to 2085 climatic periods.

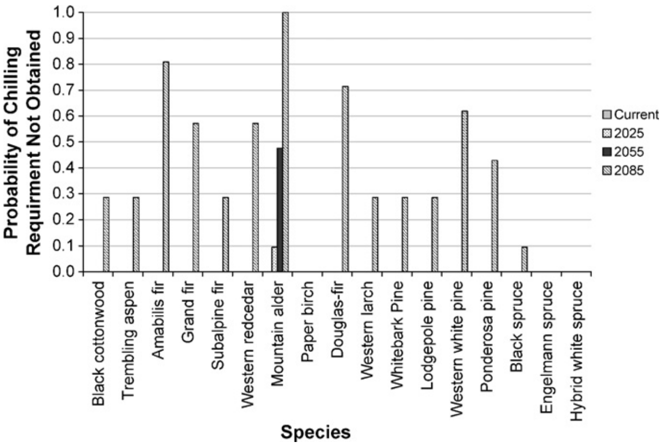

Fig. 4 – Probability of a species not obtaining its chilling requirement between the current to 2085 climatic periods.

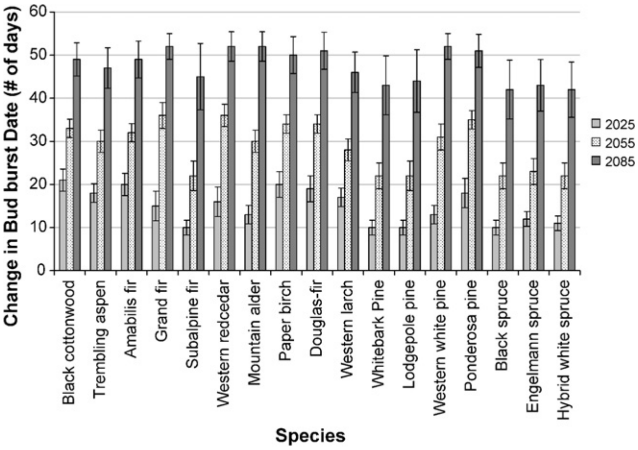

Fig. 5 – Change in the number of chilling weeks between the current climatic period and the 2085 predicted climatic period.

old exceeded will increase from 41% in the current time period to 88% by 2085.

5.4. *Chilling requirements*

The number of chilling weeks changed due to climatic change. The results suggest that there may be 10 fewer weeks for species to achieve their chilling requirements by the 2085 climatic period. In the current climate scenario, 22 chilling weeks (95% confidence interval (CI): 0.74) were modelled which decreased to 20 weeks (95% CI: 0.64) by 2025, 18 weeks (95% CI: 0.60) by 2055, and 12 weeks (95% CI: 1.45) by 2085. The species responses to the number of chilling weeks from the current to 2085 climatic period are shown in Fig. 4. All 17 species achieved their chilling requirements in all of the current climate scenarios (probability of 0.0). By the 2085 climatic period, only three species met their chilling requirements in every scenario, while one species, mountain alder, failed to achieve its chilling requirements in any of the scenarios. By 2085, 13 species failed to achieve their chilling requirements in one or more scenarios due to predicted climatic change. The results from the TACA model suggest that the average probability of chilling requirements not being obtained will increase from 0% in the current to 38% by 2085.

5.5. *Bud burst and frost*

Fig. 5 illustrates the species-specific changes in the bud burst date due to climatic change. The results from all predicted climatic period scenarios are provided, and suggest that bud burst may occur 10–21 days earlier by 2025, 22–36 days by 2055, and 42–52 days earlier by 2085. Fig. 6 shows the species-specific probability of early growing season frost damage occurring from the current to 2085 climatic period. The occurrence of bud burst at earlier times of the year will increase the risk of species being affected by growing season frosts. The vulnerability of species to growing season frosts is at its highest within the first few weeks after bud burst. Six species had a frost damage probability of zero during the current climate scenarios, while two species, mountain alder and western white pine, had a 100% probability of suffering frost damage during this period. The remaining nine species suffered frost damage in some but not all of the current climate scenarios. Of these nine species, grand fir and western redcedar suffered frost damage greater than 70% of the time and ponderosa pine just over 40% of the time. The remaining six species all incurred frost damage in less than 30% of the scenarios. Between the current and 2085 climatic periods the probability of frost damage fluctuated for all species but by 2085 twelve species had higher frost damage probabilities than modelled for the current climate scenarios. Douglas-fir, the most dominant species in the IDF, showed an increase in frost damage potential from 29% in the current to 76% in the 2085 scenarios. The remaining five species all showed a decrease in frost damage potential from the current to 2085. No species suffered frost damage in every scenario from 2055 onwards. Overall the number of species subjected to frost damage will increase, however some species will incur less damage by 2085. The results from the TACA model suggest that the average frost damage probability between species will increase from 32% in the current to 51% by 2055 and 2085.

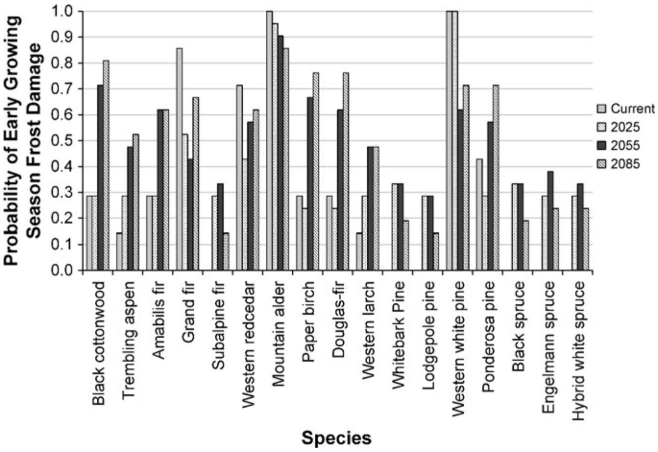

Fig. 6 – Probability of early growing season frost damage between the current and 2085 climatic periods.

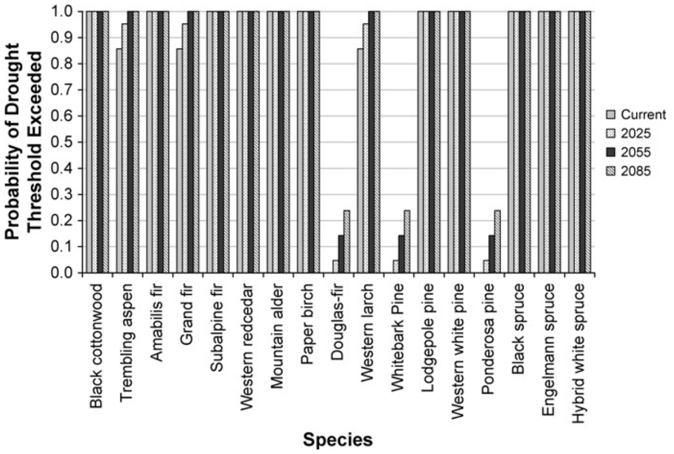

Fig. 7 – Probability of a species drought threshold being exceeded from the current to 2085 climatic periods.

5.6. *Drought*

Climatic change resulted in the change in the actual evapotranspiration/potential evapotranspiration (AET/PET) ratio within the test ecosystem. In the current climate scenario, an AET/PET ratio of 0.53 (95% CI: 0.008) was modelled which decreased to 0.52 (95% CI: 0.005) by 2025, 0.50 (95% CI: 0.004) by 2055, and 0.49 (95% CI: 0.005) by 2085. The results suggest that the AET/PET ratio will decrease by 7.5% by 2085. The decrease in the AET/PET ratio signifies a predicted reduction in the amount of water that can be used by plants and trees for growth due to future climate change. The calculated ratio (>0.30 and ≤0.55) suggests that the driest sites within the study ecosystem, in relation to precipitation inputs, evaporation and run-off outputs, be classified as excessively dry and, as such, are subject to a water deficit for >5 months but ≤7 months of the year (Klinka et al., 2000). This classification remains the same between modelled climate scenarios. Despite the maintenance of the current site classification, species were found to respond to changes in water availability due to climate change. Fig. 7 shows the species-specific probability of their drought threshold being exceeded from the current to 2085 climatic period. Eleven species were modelled to have their drought threshold exceeded during all current climate scenarios. Six species were modelled to have their drought threshold exceeded in some of the current climate scenarios. Trembling aspen, western larch and grand fir exceeded their drought thresholds in 85% of the current scenarios while ponderosa pine, whitebark pine and Douglas-fir exceeded their drought thresholds in only 5% of the current scenarios. In the 2085 scenarios, all species except ponderosa pine, whitebark pine and Douglas-fir had their drought threshold exceeded in every scenario. The probability of drought affecting ponderosa pine, whitebark pine and Douglas-fir did increase however from 5% to 25% of the scenarios by 2085. Overall, the results from the TACA model suggest that the number of species that will always have their drought threshold exceeded will increase from 71% in the current to 94% by 2085. A summary of species response in relation to each driving variable used by TACA is provided in Table 3.

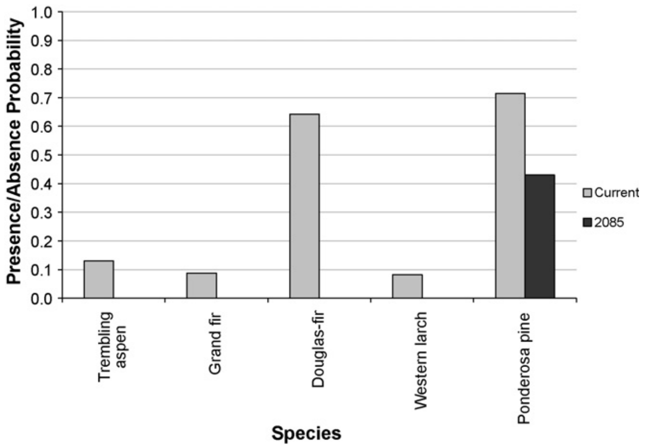

Fig. 8 – Change in species presence/absence probability from the current climate conditions to the 2085 predicted climate conditions on water deficit sites.

5.7. *Species and ecosystem response*

Figs. 7 and 8 present the modelled presence/absence probabilities for species on water-deficit and non-water deficit sites, respectively. The drought threshold function was turned off to represent non-water deficit sites. To simplify the presentation of the models results only species that had a presence probability greater than zero are provided for the current and 2085 climatic periods. The results demonstrate the climatic suitability for each species in its regeneration niche. The closer the probability is to 1.0 the more favourable the climate conditions are for regeneration. The closer this probability is to zero the more adverse the climate conditions are for successful regeneration. On both water deficit and non-water deficit sites the TACA model did reasonably well in modelling the current presence and absence of species. The TACA model was able to model the presence of ten out of twelve potential species and the absence of all five of the expected absent species. Only hybrid white spruce and paper birch were not modelled on non-water deficit sites, likely because the modelled ecosystem is a very dry and hot sub-zone of the IDF zone. Spruce and birch are generally found in the cooler and wetter sub-zones of the IDF (Klinka et al., 2000). Based on these results it seems that the accuracy of TACA for modelling the IDF ecosystem is greater than 90% (presence/absence of 15 of 17 species, plus spruce and birch justification).

We can determine the potential ecosystem response to climate change by using the individual species responses (Figs. 8 and 9). In this study, the IDF, currently dominated by Douglas-fir, may become dominated by ponderosa pine across all sites by 2085 if climate changes within the predicted range covered in this study. The increase in dryness and heat may prevent all species other than ponderosa pine from regenerating on most water and non-water deficit sites. The increase in frost damage and reduction in chilling weeks will further limit the regeneration of all species that do manage to regenerate on sites with favourable edaphic conditions in the future. Edaphic conditions allow species to persist within areas that climatic changes make unsuitable for persistence

Table 3 – Case study summary of species response to climate change for each driving variable used by TACA to determine probability of regeneration

Species	GDD requirements not met (%)		Chilling requirement not met (%)		Frost damage occurs (%)		Drought tolerance exceeded (%)	
	Current	2085	Current	2085	Current	2085	Current	2085
Black cottonwood	0	100	0	29	29	81	100	100
Trembling aspen	0	100	0	29	14	52	86	100
Amabilis fir	100	100	0	81	29	62	100	100
Grand fir	71	100	0	57	86	67	86	100
Subalpine fir	100	100	0	29	0	14	100	100
Western redcedar	0	100	0	57	71	62	100	100
Mountain alder	0	33	0	100	100	86	100	100
Paper birch	100	100	0	0	29	76	100	100
Douglas-fir	0	100	0	71	29	76	0	24
Western larch	0	100	0	29	14	48	86	100
Whitebark pine	100	100	0	29	0	19	0	24
Lodgepole pine	0	100	0	29	0	14	100	100
Western white pine	0	100	0	62	100	71	100	100
Ponderosa pine	0	33	0	43	43	71	0	24
Black spruce	100	100	0	10	0	19	100	100
Engelmann spruce	100	100	0	0	0	24	100	100
Hybrid white spruce	100	100	0	0	0	24	100	100

The table presents the proportion of scenarios that the growing degree day (GDD) or chilling requirement was not met, frost damage occurred due to early bud burst and/or drought tolerance threshold was exceeded under current and 2085 climate conditions.

(Kirkpatrick and Fowler, 1998; Theurillat and Guisan, 2001; Burke, 2002; Rouget et al., 2003). Even the climatic suitability of the ecosystem for ponderosa pine decreased in response to the modelled increases in GDD, drought, frost damage and a reduction in chilling weeks. Despite the decrease in climate suitability for ponderosa pine the results suggest that by 2085 this IDF ecosystem could evolve into a ponderosa pine dominated ecosystem. Currently, a ponderosa pine zone is located at elevations immediately below the IDF zone (Meidinger and Pojar, 1991). In British Columbia, the ponderosa pine zone is currently the hottest and driest forest zone, characterised by large moisture deficits during the summer growing season (Hope et al., 1991b). Climate change within this region will likely increase the moisture deficit and heat stress within the hot and dry IDF ecosystems and facilitate the replacement of this ecosystem by one dominated by ponderosa pine.

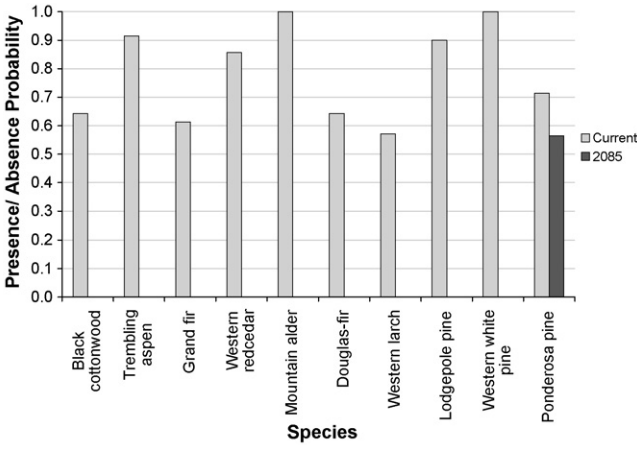

Fig. 9 – Change in species presence/absence probability from the current climate conditions to the 2085 predicted climate conditions on non-water deficit sites.

6. Discussion

Ecosystems are the basic units of nature on earth and are governed by the interaction between the biotic and abiotic components of its environment (Tansley, 1935). Changes in any biotic or abiotic component can threaten the stable dynamic equilibrium that exists between organic and inorganic components leading to creation of new equilibrated systems (Tansley, 1935). The regeneration phase is a critical life stage for species in which changes in climatic controls hinder or enhance a species response to change (Bradshaw et al., 2000). Fagerström and Ågren (1999) found that the changes in phenology and productivity during regeneration can change the competitive interactions between species influencing species distribution. Changes in climate therefore alter the relationship between controlling variables and processes that define an ecosystem. When changes in control variables result in the breadth of a species regeneration niche being exceeded the maintenance of an ecosystem in a resilient state cannot occur (Noss, 2001; McKenzie et al., 2003b). Thus, over time, disturbance and succession will gradually lead to the replacement of species that cannot widely regenerate by ones that can. If the dominant climax species of an ecosystem are not resilient then the integrity and character of the system will be altered, leading to the formation of a new state in the form of a new ecosystem (Holling, 1996). The greatest threat to ecosystems therefore lays in the ability of their species to regenerate under changes in climate which impact the biophysical and phenological mechanisms that limit establishment and subsequent growth. The TACA model can be used to examine these key processes.

6.1. Model comparison: TACA in relation to other modelling approaches

TACA utilises phenological and biophysical constraints to determine the probability of a species regenerating. Rather than focus on modelling germination and seedling growth, TACA focuses on the phenological and biophysical factors that prevent the initiation of growth, or cause mortality, to determine the probability of a species being able to regenerate under a myriad of historic, current or predicted climate conditions. The processes of seedling germination and growth are very complex and would require assumptions that would decrease the precision of the model. The JABOWA genre gap models also ignore the complex processes of germination and seedling growth by establishing trees as saplings (Kimmins, 2004). The presence/absence ratio identifies the sensitivity of a species to changes in climate and the potential change in the breadth of a species regeneration niche not growth which makes it different from the ZELIG models it is derived from.

TACA is fundamentally different from bioclimatic envelope modelling techniques that use statistical relationships between historical climate norms and current species/ecosystem distributions. Hamann and Wang (2006) predicted the potential changes of species and ecosystem in British Columbia using a bioclimatic envelope technique which established a relationship between monthly climatic norms and tree species in their realised niche. Rehfeldt et al. (1999) identified that species tend to dominate the suboptimal portion of its niche over time in the presence of competition (i.e. the realised niche) so this approach may not accurately reflect the fundamental or regeneration niche of a species. Hamann and Wang (2006) also used the observed frequencies of species within a particular ecosystem as a measure of abundance. This is a broad technique that requires an assumption that species are distributed evenly within a zone, ignoring the microclimatic and edaphic conditions that impact local abundance and distribution. This type of modelling provides a coarse representation of potential change that is detached from modelling of processes that impact growth and mortality with the portion of a species niche that is most sensitive to change in climate. TACA focuses on this crucial aspect and thus provides a finer scale representation of species response that could work in accompaniment with this technique and other gap models.

Another important feature of TACA, which is similar to ZELIG++, is the use of a daily time step versus a monthly time step. Both ZELIG and the model developed by Hamann and Wang (2006) use average monthly data. Daily data is used because many ecosystems are driven by the daily variability of local weather (Bürger, 1996). The use of daily time step weather scenarios allows for the inclusion of local variability which is of great importance when if climate change scenarios are to be used at the local-scale for use in ecosystem studies (Bürger, 1996). TACA differs from ZELIG++ in its representation of daily weather by using multiple weather scenarios that incorporate the variability in annual climate conditions versus the mean daily climate approach used by ZELIG++. For a model driven by phenological event-based responses, the use of a higher resolution time step with increased variability will allow for the event–response relationships to be modelled with greater precision and realism than using an average monthly climate approach.

6.2. Ecosystem vulnerability and resilience

The TACA model is a tool for understanding species and ecosystem vulnerability to changes in climate controlled variables and processes. If a species cannot regenerate it cannot compete, and this is the first step to understanding ecosystem resilience (Nitschke, 2006). The resilience of ecosystems is based on the ability to revolve through alternative stable states within a domain. Losing the ability for species to regenerate opens the pathways to a new domain characterised by different stable states. This pathway creates new ecosystems that are adapted and resilient to the new climate conditions and disturbance regime. These adapted species, along with the competitive interactions that follow establishment, will determine which stable state will arise within the new domain (Gunderson et al., 2002). The TACA model provides a tool that can be used to address these issues by providing a means to examine ecological response in terms of vulnerability and ecological resilience within the most sensitive stage of development, establishment/regeneration.

6.3. Modelling species response to climate change

The TACA model provides a method for understanding the resilience of species and ecosystems to potential climate change and enables a measure of vulnerability to be established. It should be used to categorise species vulnerability based on the range of responses to potential future climatic conditions compared to the current status quo. A vulnerability-based approach is recommended as the best method for assessing potential climate change impacts (Intergovernmental Panel on Climate Change, 1998). By using presence/absence probabilities, species resilience can be used to quantify species vulnerability. Species responses do not infer loss but instead illustrate the vulnerability of a species or ecosystem to changes in controlling climatic variables. For example, species modelled as having a presence/absence probability of zero will not necessarily disappear from the landscape but will likely decrease in abundance over time and be restricted to sites where topographic and edaphic conditions mediate the direct effects of climate change. The change in presence/absence probabilities on sites also shows the future resilience of a species to future disturbances in the system. The change in this probability reflects an increase in climatic optimality of a species regeneration niche and vice versa. A decrease in optimality can reduce functionality within the system, which in turn would increase the vulnerability of species to future change (Gunderson et al., 2002).

Key to undertaking management actions is the knowledge of species and ecosystem vulnerability from which informed and planned decisions can be made. A species-level approach that examines the probability of presence or absence of a species in its regeneration-niche will provide a means to measure the resilience of a species to any climatic stressor. The collective response of the species in a community can be used to determine ecosystem vulnerability. As a stressor increases in magnitude, a threshold may be reached. This point will vary between species and may cause the eventual disassociation of the current ecosystem and the creation of a new system. Bartlein et al. (1997) identified that predicted climate change will be comparable to that experienced 14,000–9000 years ago in which variations in the seasonal distribution of temperature and precipitation led to the dismantling of ecosystems and creation of a series of rapidly changing biotic associations. The case study used to test TACA also illustrated this potential system response. Species showed divergent responses which left only one species within the IDF ecosystem. This suggests a potential shift to a new ecosystem within the study area due to climate change.

Zolbrod and Peterson (1999) also found that tree species responded individualistically in abundance and distribution rather than ecosystems moving as intact communities. Hamann and Wang (2006) found that species responded individualistically but predicted that communities would remain intact. This is likely a result of using a static-realised niche approach. Cumming and Burton (1996) predicted that there would be no significant changes in species composition or abundance in the interior Douglas-fir zone which differs from the findings of this study. The difference could be due to the GCM predictions used and the microclimatic differences between the areas modelled but also the result of using a finer resolution time step in this study. Despite these differences in predicted species response there were some similarities. Both studies identified and increase in drought conditions and frost damage. Hamann and Wang (2006) predicted and increase in the ponderosa pine zone and interior Douglas-fir zone in British Columbia although, within the site modelled in this study, they predicted and loss of both these zones with a Bunchgrass ecosystem replacing these ecosystems. This study identified that the interior Douglas-fir ecosystem would be replaced by an ecosystem dominated by ponderosa pine. This study did identify a reduction in the potential regeneration niche of ponderosa pine suggesting that under future climatic conditions it may only be able to regenerate 43% of the time. This would provide an opportunity for an expansion of bunchgrass ecosystem species over time into this ecosystem and lead to creation of a savannah or bunchgrass ecosystem. The results from this study are relatively congruent with other studies of tree and ecosystem response to climate change in British Columbia and the Pacific Northwest of the USA. The degree of change differs but the mechanisms and direction of changes in forest ecosystems support each other. These studies all point to degree of vulnerability of forest ecosystems in British Columbia and the Pacific Northwest USA to climatic change. The predicted changes reflect this vulnerability that will require changes in how we should manage these forests. Management plans and policies that incorporate the response of species and ecosystems are required to assist species to respond to rapid environmental change (del Barrio et al., 2006). This and other studies all provide an understanding of species and ecosystem vulnerability which should be integrated in to management plans to either mediate or exacerbate species response and resilience to the stressor of climatic change. The TACA model is a tool that was designed to provide this level of understanding and capability to forest managers for both stand- and landscape-level forest planning and management.

6.4. Limitations and uses of TACA

The local response of forests and species will be mediated by the fine-scale heterogeneity caused by edaphic and microclimate variation due to topography and soil types (Peters, 1992; Urban et al., 1993; Bush, 2002). The TACA model does not account for the mediating effects of topography or soil types; for this reason, species that are modelled as absent from an ecosystem will likely persist on local-scale sites that mediate the effects of climatic change. However, at the landscape-scale, the species will likely be found at lower abundances as their distribution contracts into these specialised sites. In relation to the TACA model, the predicted absence of a species from a site represents a risk to conserving ecosystem diversity and function, but the reduction in the presence probability does not place an ecosystem at the same risk. A difference in vulnerability exists between the ecosystem- and species-level, so species can be at risk but an ecosystem may not and vice versa. This has direct implications for determining the need for coarse- or fine-scale management of species and ecosystems if managers are going to adapt ecosystems to climatic change. The response of species will also be influenced by genetic variation in growth and adaptation traits that influence how they will respond to climatic change (Rehfeldt et al., 1999; Hamann and Wang, 2005). Broad geographic and climatic patterns that do not account for local climatic and genetic variation can over- or underestimate species responses and ability to persist (Rehfeldt et al., 1999; Epperson, 2003). TACA does not account for the influence genetic variation will have on species response; however, the influence of genetic variation is dampened by focussing on the regeneration phase and excluding growth and competition.

The TACA results can be used to hypothesize how ecosystems could change over time and can also be used to aid in the modelling of stand dynamics. The modelled change in a species' presence/absence probability can be used within the regeneration component of models that predict tree competition and forest succession. TACA is a tool for understanding vulnerability. This understanding is a key requirement for managing ecosystems from a sustainable foundation (Turner et al., 2003). TACA is a simple and effective model for achieving this requirement and building a foundation of understanding that can foster the sustainable management of species and ecosystems under changes in climate.

7. Conclusion

This paper has presented the TACA model as tool that can be used to examine the response of tree species and ecosystems to current and future climate conditions. A fundamental/regeneration niche methodology was used to model species response to phenological and biophysical variables influence by climatic conditions in the absence of competition. TACA measures changes in the breadth of a species regeneration niche. This change can be used to describe the resilience of species and ecosystems to changes in climate through the identification of a species' probability of regenerating under multiple climate scenarios.

Climate change is going to have a major impact on species distribution and abundance which will be most prevalent in the regeneration niche of species. The regeneration niche is the portion of a species niche space that is most sensitive to changes in climate. The breadth of the regeneration niche is a driving factor in the determination of a species distribution and abundance across landscapes. The use of a phenological event-based response model provides a more realistic representation of a species' and ecosystem's response to changes in inter-annual climate by allowing for the investigation of the causal relationships that determine the initiation of growth and mortality. Under climate change an increase in growing degree days can be expected which will allow species to achieve their heat sum and initiate bud burst at much early dates. The early occurrence of bud burst will predispose many species to early spring frost damage. For species that are sensitive to frost damage this will limit their ability to move to more northerly and higher elevation portions of a landscape or region. Increase in temperatures will also lead to the reduction in the number of chilling weeks which in turn will impact the ability of species to achieve their chilling requirements. If species cannot achieve their chilling requirements they will be unable to awake from winter dormancy. An increase in drought risk is also expected in many regions and this will lead to range contractions from southerly and lower elevation areas at broad scale and from dry sites to wet sites at a finer scale. The combination of these factors will have a significant impact on the ability of tree species the regenerate which in turn will impact the integrity of ecosystems. In this study, the TACA model predicted the loss of 90% of the species within the IDF ecosystem including the major climax species, Douglas-fir. The loss of species reflects a loss of ecosystem resilience which could result in this ecosystem evolving to a ponderosa pine dominated system over the next 100 years if climate changes within the range utilised in this study. TACA is an effective tool for understanding of species and ecosystem vulnerability and resilience to changes in climate conditions. The TACA model can be an effective decision support tool for forest managers wanting to develop adaptation plans and for researchers that want to model forest succession under climate change.

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