Estimating forest net primary production under changing climate: adding pests into the equation

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Received September 15, 2010; accepted May 11, 2011; published online July 11, 2011; handling Editor Annikki Makela

The current approach to modelling pest impacts on forest net primary production (NPP) is to apply a constant modifier. This does not capture the large spatial and temporal variability in pest abundance and activity that can occur, meaning that overestimates or underestimates of pest impacts on forest NPP are likely. Taking a more mechanistic approach that incorporates an understanding of how physiology is influenced by pest attack, enables us to better capture system feedbacks and dynamics, thereby improving the capacity to predict into novel situations such as changing climate, and to account for both changes in pest activity and host responses to the growing environment now and into the future. We reviewed the effects of pests on forest NPP and found a range of responses and physiological mechanisms underlying those responses. Pest outbreaks can clearly be a major perturbation to forest NPP, and it seems likely that the frequency and intensity of pest outbreaks, and the ways in which host species respond to pest damage, will change in the future. We summarized these impacts in the form of a conceptual model at leaf, tree and stand scales, and compared the physiological processes embedded within that framework with the capacity of a representative range of NPP models to capture those processes. We found that some models can encapsulate some of the processes, but no model can comprehensively account for the range of physiological responses to pest attack experienced by trees. This is not surprising, given the paucity of empirical data for most of the world’s forests, and that the models were developed primarily for other purposes. We conclude with a list of the key physiological processes and pathways that need to be included in forest growth models in order to adequately capture pest impacts on forest NPP under current and future climate scenarios, the equations that might enable this and the empirical data required to support them.

Keywords: climate change, models, pests, photosynthesis, respiration.

Introduction

Net primary production (NPP) is the net production of carbon (C) by plants in an ecosystem, and is defined as photosynthesis less autotrophic respiration (Binkley et al. 1997). It is an indication of the capacity of ecosystems to sequester C (Chertov et al. 2009) and represents one of the major components of total ecosystem C flux (Li et al. 2003). When losses associated with heterotrophic respiration are accounted for, NPP becomes net ecosystem exchange (NEE), and when mortality associated with disturbance or changed climatic conditions is considered, NEE becomes net biome productivity (NBP) (Kirschbaum et al. 2001). Net primary productivity is difficult to estimate empirically (Roxburgh et al. 2004), with methods revolving around either monitoring changes in above- and belowground biomass, or measuring CO₂ fluxes in chambers or the atmosphere (Clark et al. 2001). Both methods provide considerable challenges (Roxburgh et al. 2004), and hence empirical estimates of NPP are sparse in both time and space. Consequently, there is a strong reliance on mathematical models for estimating NPP.

Forest NPP is strongly influenced by site and climatic conditions, plant attributes and disturbance events (Binkley et al. 1997). Pest activity has the potential to substantially affect NPP. Pests (defined as insects and fungi damaging to trees) are an
We reviewed the effects of pests on NPP and identified a range of responses and physiological mechanisms underlying those responses. From this we developed a conceptual model for processes at leaf, tree and stand scales, and compared the physiological processes embedded within that framework with the capacity of a representative range of forest NPP models to capture these processes. Finally, we summarized the key physiological processes and pathways that need to be included in forest growth models in order to adequately capture pest impacts on forest NPP, and the ways that these processes might be incorporated into models.

How might pests affect forest NPP?

The bulk of our understanding of tree physiological responses to pest attack comes from observation and experimentation with defoliating pests, and of necessity the following discussion focuses largely on the potential impacts of defoliating pests on NPP. Root and stem pests have the potential to have a much more dramatic effect on forest NPP than defoliating pests because they are more likely to kill trees, but our understanding of host physiological responses to such pests is limited.

Pest impacts on photosynthesis

Reductions in leaf area associated with pest activity have the potential to substantially affect whole-tree photosynthesis, with resultant reductions in NPP. However, a common response of host species to defoliating insects is to increase the photosynthetic rates of the remaining foliage (Ayres 1992, Prins and Verkaar 1992, Reich et al. 1993, Pinkard et al. 2007), at least until the foliage removed by defoliation has been replaced (Pinkard and Beadle 2000). This response has been attributed to a reduction in the source:sink ratio that occurs with defoliation. Thus, increased demand for carbohydrates to rebuild defoliated crowns results in an increase in the rates of the photosynthetic C reduction cycle (Geiger 1987, Wareing and Patrick 1975, Stitt et al. 1990). Photosynthetic upregulation in response to defoliation is associated with increased carboxylation efficiency and ribulose-1,5-bisphosphate (RuBP) regeneration capacity (Hodgkinson 1974, von Caemmerer and Farquhar 1984, Layne and Flore 1995). Photosynthetic upregulation has been attributed to changes in hydraulic conductance of the soil to leaf pathway resulting in increased stomatal conductance (Pataki et al. 1998, Oren et al. 1999, Quentin et al. 2011). However, the increase in the ratio of photosynthesis:leaf conductance observed in a number of studies (Ovaska et al. 1993a, Reich et al. 1993, Pinkard et al. 1998) suggests that this is not the whole story. Likewise, there is inconsistency in the literature about the role of leaf nitrogen (N) in facilitating photosynthetic upregulation, with some studies observing increases in foliar N (Prins and Verkaar 1992, Suzuki and Takano 2004) and others demonstrating
an increase in N use efficiency (Ovaska et al. 1993a, Pinkard et al. 1998).

Photosynthetic upregulation, combined with changes in patterns of biomass allocation to favour leaf development, can result in complete compensation for defoliation, and thus little if any impact on NPP (Eyles et al. 2009). However, there will always be a maximum photosynthetic rate above which no further increase will be observed despite greater source limitation, related to limitations in the rates of biochemical reactions of photosynthesis (von Caemmerer and Farquhar 1981, Sharkey 1985). This means that, although photosynthetic rate may increase in response to defoliation, when defoliation is severe and/or chronic the increase is commonly insufficient to allow complete compensation, with resultant reductions in NPP. It also suggests that we can expect a non-linear response to defoliation. It can be anticipated therefore that it is pest outbreaks, rather than chronic low or background levels of defoliation, that are likely to have a major influence on NPP.

The level of defoliation above which compensation is incomplete varies widely between species (Pinkard and Beadle 2000). In fast-growing 1- to year-old eucalypts, for example, trees can rapidly recover biomass following 50% defoliation by increasing photosynthetic rates and leaf production (Pinkard and Beadle 1998), but above this level they can only partially compensate. In other species, this level is much lower (Hoogesteger and Karlsson 1992, Reich et al. 1993, Layne and Flore 1995, Lavigne et al. 2001), suggesting that the threshold may be related to relative growth rate.

Environmental constraints on production can influence photosynthetic responses to defoliation (Prins and Verkaar 1992). High N and water availability have been shown to increase the rates of recovery from defoliation by increasing photosynthetic rates (Prins and Verkaar 1992, Otronen and Rosenlund 2001, Suzuki and Takano 2004), although these conditions may in some instances increase the severity of future pest damage through changes in secondary defence chemistry (e.g., decreased concentrations of tannins, phenolics, essential oils) that favour pests (Forkner and Hunter 2000, Lower and Orians 2003, Rekhi et al. 2004, O’Reilly-Wapstra et al. 2005, Prudic et al. 2005).

Unlike defoliating insects, many foliar pathogens do not induce an increase in photosynthetic rates following tissue damage (Ayres 1992), and a decrease may in fact be observed associated with reduced ribulose-1,5-bisphosphate carboxylase oxygenase activity and changes in the capacity for RuBP regeneration (Scholes 1992, Bassanezi et al. 2002, Pinkard and Mohammed 2006). This is particularly the case with biotrophic and hemi-biotrophic pathogens. Following attack by necrotrophs, an increase in photosynthesis may be observed in the unaffected tissue (Scholes 1992). Pathogenic fungi may influence photosynthesis of asymptomatic as well as symptomatic tissue, related to hyphal invasion (Scholes 1992). For example, reductions in photosynthetic rate were proportionally greater in Eucalyptus globulus infected by Teratosphaeria (=Mycosphaerella) spp. than might be expected from the reduction in green leaf area as a result of the disease (Pinkard and Mohammed 2006).

Host responses to insect defoliation are influenced by severity, frequency, timing and pattern of pest attack (Collett and Neumann 2002, Pinkard et al. 2007). Rates of photosynthesis have been shown to increase with greater severity/frequency of defoliation (Pinkard et al. 2006) and the seasonality of pest attack can also be important. For example, late-season defoliation resulted in larger reductions in the growth of E. globulus than early-season defoliation, which was associated with a delay in photosynthetic upregulation until the following growing season (Pinkard et al. 2007). Patterns of defoliation can have a large influence on the physiological responses of the host plant. For example, although both upper- and lower-crown defoliation resulted in similar levels of photosynthetic upregulation, upper-crown defoliation had a larger impact on growth than lower-crown defoliation, highlighting the importance of changes in patterns of biomass allocation as well as photosynthesis (Pinkard et al. 2006).

Attack by a range of insect and fungal defoliating pests has been shown in many studies to increase the longevity of the remaining foliage within the crown (Prins and Verkaar 1992). This response occurs irrespective of the pattern of defoliation, meaning it is not necessarily a direct response to altered crown light conditions. This sort of response may influence whole-tree NPP following a defoliation event.

A general observation is that trees experiencing defoliation alter patterns of biomass allocation to favour leaf development (Prins and Verkaar 1992). Hence the above:belowground biomass ratio decreases in the short term (Cannell 1985). In addition, the specific leaf area (SLA) of new foliage often increases compared with that of undefoliated trees (Prins and Verkaar 1992). Both these responses can enhance C uptake under source-limited conditions (Valentine 1985, Cannell and Dewar 1994).

Understanding the effects of root and stem pests on photosynthetic processes is much less well developed than for foliar pests. Root pests, by reducing root biomass and growth, affect the capacity of the host for water and nutrient uptake, which may indirectly affect photosynthetic processes. Phytophthora cinnamomi, for instance, causes necrosis of roots and stem tissue in eucalypts (Podger et al. 1980, Podger and Brown 1989), resulting in foliage discoloration, premature leaf senescence, and potentially, mortality. In infected Castanea sativa, P. cinnamomii resulted in a 19% reduction in photosynthetic rate (Dinis et al. 2008). Other species of root-infecting Phytophthora, for example Phytophthora alni on Alnus glutinosus (Clemenz et al. 2008), and Phytophthora citriodora on Fagus spp. (Fleischmann et al. 2005), caused rapid reductions in pho-
tosynthetic capacity and transpiration rates, but if the host survived the initial infection, these physiological responses were only transient (Clemenz et al. 2008). The rapid nature of the response to *P. citriodora* infection in *Fagus* spp. suggested the involvement of a mobile signal triggering early changes in leaf physiological processes by root infection (Fleischmann et al. 2005).

Pests that target stems may affect the transport system for water and nutrients. Bark beetles such as *Phorocantha* spp. and *Ips* spp., for example, damage cambial tissue, with resultant leaf mortality and crown dieback (Pook and Forrester 1984). Relatively little is known about the effects of stem pests on host physiology.

**Pest impacts on autotrophic respiration**

Leaves infected with biotrophic fungi, such as rust or powdery mildew, commonly have increased rates of dark respiration (Farrar 1992). This is most likely related to an increase in respiration rates of the healthy tissue associated with defence responses, as well as respiration associated with the growth and development of the pathogen. The impacts of insect defoliation on respiration are less clear, and both increases and decreases have been reported (Ovaska et al. 1993a, Reich et al. 1993, Layne and Flore 1995, Pinkard et al. 2007).

**Climate change: another level of complexity**

The physiological processes associated with defoliation and refoliation, and the relationships with allocation, photosynthesis and ultimately growth, are very complex. Changing climate and particularly elevated atmospheric CO$_2$ (eCO$_2$) also influence these processes, and not necessarily in the same direction as pest attack (Table 1). There are likely to be instances where changing climate will increase the effects of pests on NPP (Chiang et al. 2008, Chertov et al. 2009, Pinkard et al. 2010), and others where host responses to climate change may reduce the impacts of pests on NPP (Ayres and Lombardero 2000). There have been numerous reviews of the likely impacts of climate change on forests (e.g., Long et al. 2004, Ainsworth and Long 2005, Hyvonen et al. 2007); in the following we focus on changes that may influence pest damage and ultimately NPP.

**Pest abundance and levels of damage**

Temperature plays a major role in determining the abundance and distribution of insects and fungi (Ayres 1992). Increasing winter temperatures are likely to increase the abundance of many insects and pathogens (Ayres and Lombardero 2000, Margarey et al. 2005). Increasing summer temperatures may accelerate development and reproductive potential (Ayres and Lombardero 2000, Whittaker 2001) and increase the number of generations per year (Tobin et al. 2008). These kinds of change can result in rapid population build-up during periods of active growth (Whittaker 2001), and increased damage during the host growing season. Of particular concern is increased damage late in the growing season, which has been shown to have a larger impact on the productivity of eucalypts (Pinkard et al. 2006) and pines (Ericsson et al. 1980), than early-season damage.

Little is known about the direct effects of eCO$_2$ on pest abundance and activity. Phloem feeders are the main guild of insects showing increased development and reproduction

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**Table 1.** A comparison of the impacts of defoliation, leaf tissue damage and elevated CO$_2$ on tree physiological processes that are likely to influence NPP. ↑ = an increase in the variable; – = no change in the variable; ↓ = a decrease in the variable. An empty cell indicates insufficient information to draw a conclusion. Where more than one response is indicated, it implies a lack of consensus in the literature.

<table>
<thead>
<tr>
<th>Plant attribute</th>
<th>Defoliation</th>
<th>Leaf tissue damage</th>
<th>Elevated CO$_2$ + climate change</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td>C:N ratio</td>
<td>↓</td>
<td>↓</td>
<td>↑</td>
<td>Hyvonen et al. (2007)</td>
</tr>
<tr>
<td>Photosynthesis</td>
<td>↑</td>
<td>– or ↓</td>
<td>↑</td>
<td>Ainsworth and Long (2005); Ayres and Lombardero (2000); Ayres (1992) and Prins and Verkaar (1992)</td>
</tr>
<tr>
<td>Dark respiration</td>
<td>↓ or ↑</td>
<td>↑</td>
<td>↓</td>
<td>Drake et al. (1997); Farrar (1992); Pinkard et al. (2007)</td>
</tr>
<tr>
<td>Stomatal conductance</td>
<td>↑</td>
<td>– or ↑</td>
<td>↓</td>
<td>Ainsworth and Long (2005); Ayres and Lombardero (2000); Ayres (1992); Prins and Verkaar (1992)</td>
</tr>
<tr>
<td>Above:below biomass allocation</td>
<td>↑</td>
<td>↑</td>
<td>↑</td>
<td>Long et al. (2004); Prins and Verkaar (1992)</td>
</tr>
<tr>
<td>Leaf longevity</td>
<td>↑</td>
<td>↑</td>
<td></td>
<td>Prins and Verkaar (1992)</td>
</tr>
<tr>
<td>Specific leaf area</td>
<td>↑</td>
<td>↑</td>
<td>↓</td>
<td>Ainsworth and Long (2005); Prins and Verkaar (1992)</td>
</tr>
<tr>
<td>Water use efficiency</td>
<td>↑</td>
<td>↑</td>
<td></td>
<td>Ayres (1981); Hyvonen et al. (2007)</td>
</tr>
<tr>
<td>Foliar N</td>
<td>↓ or ↑</td>
<td>↓ or ↑</td>
<td>↓</td>
<td>Long et al. (2004); Ovaska et al. (1993b); Reich et al. (1993)</td>
</tr>
<tr>
<td>Standing biomass</td>
<td>↑, – or ↓</td>
<td>– or ↓</td>
<td>↑</td>
<td>Ayres and Lombardero (2000); Hyvonen et al. (2007); Prins and Verkaar (1992)</td>
</tr>
</tbody>
</table>
Pathogens may show more rapid growth following invasion of host tissue (Chakraborty 2005, Chakraborty et al. 2008), and pathogen fecundity and aggressiveness have been shown to increase under eCO$_2$ (Burdon et al. 2006, Kobayashi et al. 2006, Jeger and Pautasso 2008). These responses suggest that, for at least some host–pest interactions, the impact on NPP may be larger at higher atmospheric concentrations of CO$_2$.

Drought increases the susceptibility of many tree species to stem borers and stem and root pathogens (Old and Stone 2005, Haavik et al. 2008). This has been related to factors such as decreased concentrations of secondary defence compounds in the stem (Kainulainen et al. 1998), increased concentrations of compounds favouring pathogen development, such as glucose (Desprez-Loustau et al. 2006), changes in host tissue water content that favour pathogens (Desprez-Loustau et al. 2006), and increased entry points to the stem via bark and cambial cracks (Pook and Forrester 1984). Increases in water use efficiency of host trees associated with eCO$_2$ (Ainsworth and Long 2005) may improve plant water status and hence reduce susceptibility to borers and root/stem pathogens. However, the expected increase in the frequency of severe drought may offset increases in water use efficiency and increase damage from these organisms.

**Foliage properties and levels of damage**

Reductions in foliage N content, and an increase in the C:N ratio, associated with eCO$_2$ (Long et al. 2004, Hyvonen et al. 2007) are likely to affect the palatability of foliage to pests (Harrington et al. 2001, Coll and Hughes 2008). Herbivores with chewing feeding habits that are reared on foliage growing under eCO$_2$ typically have longer development times, lower survivorship, reduced adult weight and lower fecundity than those reared under ambient CO$_2$, as was observed for *Chrysophtharta flaveola* feeding on *Eucalyptus tereticornis* growing under eCO$_2$ (Lawler et al. 1997, Coll and Hughes 2008). This has been associated with an increase in C-based metabolites in leaves growing under eCO$_2$ (Hyvonen et al. 2007). A 9-year experiment examining plant–herbivore interactions under eCO$_2$ found reduced abundance of leaf miners, which was attributed to increased death rates from natural enemies and greater ingestion of tannins (Stiling and Connelissen 2007). A meta-analysis supported the experimental results for a broader range of leaf chewers.

Compensatory feeding by the pest may occur when foliage has an increased C:N ratio (Ayres and Lombardero 2000). However, this may not necessarily translate into greater overall damage levels if population levels are reduced, as suggested above (Stiling and Connelissen 2007).

Decreased SLA is often observed in response to eCO$_2$ (Curtis 1996, Roden and Ball 1996). Decreased SLA deters some defoliating insects in eucalypts (Steinbauer 2001). Decreased SLA can also restrict the development of foliar pathogens. Smith et al. (2006) determined that reduced SLA was an indicator of increased cell density in *E. globulus* and *Eucalyptus nitens*, and enhanced the capacity of the host species to fight infection from foliar pathogens by firstly restricting the intercellular pathways available for mycelial development and hence increasing pathogen development times, and secondly by enhancing the capacity of the host to rapidly develop effective barrier zones between healthy and infected tissue. Hence foliar pathogens may be disadvantaged by reduced SLA in the host.

How well do existing models represent pest damage?

Most NPP models do not explicitly represent the effects of pests, but instead apply a uniform discount rate (Roxburgh et al. 2004). We have illustrated that this may not be appropriate because the key dynamics between host and pest are likely to be missed, with resultant over- or under-prediction of NPP. Taking a more mechanistic approach that incorporates an understanding of how physiology is influenced by pest attack enables us to better capture system feedbacks and dynamics, thereby improving our capacity to predict into novel situations and to account for both changes in pest activity and host responses to growing environment.

We summarized the impacts of defoliating pests into a conceptual model (Figure 1), and used this framework to examine the capacity of existing NPP models to capture the processes associated with host–pest interactions. Seven commonly used and well-cited forest NPP models were selected:

- **CenW** (Kirschbaum 1999) is a generic forest growth model that simulates the fluxes of C and water, light interception and the dynamics of nutrient cycling through plant and soil organic matter pools. It runs on a daily timestep, and C gain is calculated based on light absorption, temperature, soil water status, foliar N and any foliage damage due to extreme temperatures during the preceding days. Daily respiration rate is calculated as a constant fraction of gross primary productivity (GPP), or as a function of temperature and nutritional status. A single-layer canopy is assumed. Allocation of C is determined by plant nutrient status, tree height and species-specific allocation factors. Water use is calculated using the Penman–Monteith equation.
- **G’Day** (Commins and McMurtrie 1993) also simulates the cycling of C, N and water in plant and soil. Processes represented include CO$_2$ uptake and respiration, plant water and N uptake, tissue growth and senescence, litter and soil decomposition, and soil N availability. Photosynthesis depends on CO$_2$ concentration and temperature, and respiration depends on temperature. The model has a daily timestep, where C gain is a function of absorbed light, leaf
N, temperature, soil moisture and autotrophic respiration. Respiration is usually represented as a constant fraction of GPP but can also be represented as proportional to N content. The canopy is considered as a single layer. Allocation is based on fixed proportions. Water balance is calculated using either the Penman–Monteith equation or the RESCAP model of Dewar (1996).

- **PnET** (Aber and Federer 1992) is a lumped-parameter model of C and water balances of forests, applicable to stand and small catchment scales. It predicts leaf area, and water and C balances on a monthly timestep. Radiation, temperature, water stress during the previous month and foliage N content are used to calculate GPP and respiration for leaves at the top of the canopy. A light attenuation coefficient, a photosynthetic light response curve and foliar longevity are used on a daily timestep to calculate monthly canopy photosynthesis. Carbon allocation is determined by allometric equations.

- **3-PG** (Landsberg and Waring 1997) is a generalized stand model applicable to plantations or even-aged homogeneous

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**Figure 1.** Conceptual model of the ways that defoliation by insect and fungal pests can affect physiological processes at the leaf, tree and stand scales, and issues for modelling that arise from responses to defoliation at each of these scales. Solid lines indicate material flows; hatched lines indicate signalling or influences.
forests. GPP is the product of absorbed radiation and canopy quantum efficiency, which is modified for soil water availability, vapour pressure deficit and temperature. The canopy is assumed to be a single layer. Respiration is assumed to be a constant fraction of GPP, and biomass allocation patterns are based on allometric relationships. 3-PG has a monthly timestep.

- **CABLE** (Kowalczyk et al. 2006) is a model of biosphere atmosphere exchange allowing for interactions between microclimate, plant physiology and hydrology (Kowalczyk et al. 2006). Light interception is calculated using Goudriaan’s model. Photosynthesis differentiates between sunlit and shaded leaves, with the photosynthetic reactions limited by rates of biochemical reactions or sink demand. Respiration is calculated as a constant proportion of GPP.

- **CABALA** (Battaglia et al. 2011), modified from Battaglia et al. (2004), is a linked C–N–water model, where the simultaneous effects of leaf loss on C uptake, biomass allocation, transpiration and water use, and N reallocation can be assessed. It was developed for even-aged homogeneous forests. It uses a combination of ray-tracing and big-leaf light interception models, and assumes a multi-layer canopy. Foliar respiration is considered to be proportional to photosynthesis. Photosynthetic upregulation is linked to altered source:sink balance, and a combination of goal seeking and allometrics is used to allocate biomass. The model operates on a daily timestep.

- **Forest-BGC** (Running and Coughlan 1988) is a stand level model that calculates hydrologic balance, plant water availability and canopy gas exchange on a daily timestep, but allocates C on a yearly timestep. The forest canopy is treated as a homogeneous 3D leaf with depth proportional to leaf area index. Carbon and N budgets are dynamic and interacting (Running and Gower 1991). Allocation of C is determined using predefined parameters. Growth respiration is calculated as a proportion of photosynthate, and subtracted after C has been allocated to biomass pools.

While some models encapsulated some of the processes identified in our conceptual framework, no model could comprehensively account for the range of responses to defoliation experienced by trees (Table 2). This is understandable, given the paucity of empirical data on the impacts of pest outbreaks on NPP for most of the world’s forests, and that the models were not developed specifically to examine pest effects. The two models that best represented pest effects were CABALA, as modified by Battaglia et al. (2011), and CenW, as modified by Kirschbaum et al. (2007).

In CenW insect damage is accounted for through modifications to respiration, carbohydrate loss and photosynthesis to account for the effects of leaf necrosis and loss of photosynthetic

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**Table 2.** The degree to which existing NPP models capture the impacts of defoliating pests on NPP. D = daily timestep; M = monthly timestep; A = annual timestep.  

<table>
<thead>
<tr>
<th>Model</th>
<th>Photosynthesis linked to changing source: sink balance</th>
<th>Spatial heterogeneity in leaf properties mimic observed responses to leaf pest attack</th>
<th>Spatial heterogeneity in leaf properties mimic observed responses to pest attack</th>
<th>CO₂ effects captured</th>
<th>Leaf longevity variable as per responses to pest attack</th>
<th>Respiration varies with pest type</th>
<th>Spatial heterogeneity in leaf properties mimic observed responses to carbohydrate and nutrient stores</th>
<th>Spatial heterogeneity in leaf properties mimic observed responses to carbohydrate and nutrient stores</th>
<th>Plant water availability treated dynamically for recovery from pests</th>
<th>Biomass allocation</th>
</tr>
</thead>
<tbody>
<tr>
<td>CenW</td>
<td>Y</td>
<td>Y</td>
<td>N</td>
<td>N</td>
<td>N</td>
<td>Y</td>
<td>N</td>
<td>N</td>
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<td>N</td>
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<tr>
<td>G'Day</td>
<td>N</td>
<td>N</td>
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<td>N</td>
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<td>Y</td>
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<td>PnET</td>
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<td>3-PG</td>
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<tr>
<td>CABLE</td>
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<tr>
<td>CABALA</td>
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<td>Forest-BGC</td>
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</table>

First letter denotes the timestep for photosynthetic calculations; second letter denotes the timestep for biomass allocation.
area on productivity. Changes in biomass allocation associated with insect damage are not explicitly addressed in the model and are dealt with through transient reparameterization of allocation parameters. Kirschbaum et al. (2007) used the modified model to examine the effects of a sapsucking insect on native E. delegatensis NPP, and demonstrated the value of being able to separate out the effects of pest damage and drought on NPP.

By comparison with CenW, CABALA allows for more detailed analysis of the effects of severity, frequency, pattern and timing of defoliation events on crown light conditions, photosynthetic processes, and patterns of biomass and resource allocation. However, it does this for the simpler plantation system rather than the more complex native forest system tackled by CenW. It does not capture the ways in which autotrophic respiration, carbohydrate stores and within-stand heterogeneity are affected by defoliation. The modifications in CABALA were possible because of recent intensive studies of physiological processes associated with defoliation in the main plantation species in Australia (E. globulus, E. nitens, Pinus radiata) (Pinkard et al. 2007, Pinkard et al. 2008, Eyles et al. 2009, Quentin et al. 2010). It also reflects simplifying assumptions about canopy structure applicable to plantations and not native forests which allow greater process representation (a case in point of the trade-off between generality and complexity referred to in the early review of process-based models by Battaglia and Sands (1996)).

One of the reasons that most NPP models do not deal effectively with pest damage is because there is limited empirical understanding of levels of pest damage and impacts in forest systems. Most information comes from forests managed for timber production (Candy et al. 1992) rather than for conservation. CABALA, for example, was modified to incorporate defoliation effects to meet a specific need within the plantation industry, for species with well-documented tree physiology and where a history of forest health surveillance has resulted in a well-developed understanding of pest issues and potential impact, and there is an economic imperative to estimate impacts of damage on forest productivity. Plantations comprise a relatively small proportion of Australia’s forests (National Forest Inventory 2010) and detailed information of pest effects required for this level of modelling is rare.

Improving our capacity to model pest impacts on NPP

Many tree species have great capacity to withstand pest attack, and it is possible that in many situations forest NPP will not be unduly affected by defoliation. Nevertheless, it is important to understand the conditions under which defoliation may reduce NPP. Future studies will add to this knowledge, but in order to understand the enormous range of pest by site by host condition interactions, modelling will be a necessary tool for assessing pest impacts. Without capturing within models the dynamics and feedbacks that are inevitable in pest–host systems, predictive ability will be low.

The impacts of defoliation by pests at the leaf level have consequences that scale to the tree and then to the stand level. Modelling at any one of these levels must consider how impacts at lower levels scale up and lead to change at the scale of interest. We have attempted to capture this in a conceptual framework (Figure 1). What is evident from Figure 1 is that, as we move from leaf to stand scale, there is increasing complexity in responses in terms of the interactions between plant and biogeochemical processes, and more broadly on ecological processes such as forest structure and demography. Figure 1 raises some issues for modelling at each of these scales, and below we address these and provide suggestions of how they might be addressed in models. Clearly not all these influences and effects need to be considered in every modelling exercise, and the application of sensitivity analysis can indicate which are important in particular situations.

There is an additional scale that we do not consider in our assessment: the landscape scale. At this scale it is generally net ecosystem exchange or net biome productivity that is of interest, and issues for modelling revolve around questions such as the impacts of pests on host species composition, and the stochastic nature of pest distribution and movement in the landscape.

Issues for modelling at the leaf scale

Leaf respiration rates may change

Assumptions about constant respiration ratios, either through the 3-PG type stand level ratio (e.g., Landsberg and Waring 1997) or through the ratio of photosynthetic activity to canopy respiration rate (e.g., Battaglia et al. 2004), may be invalidated by changes in respiration as a direct response to pests. Kirschbaum et al. (2007) accounted for loss of photosynthate due to sapsucking insects through a user-defined loss rate, and a similar approach could be used to model changes in leaf respiration following pest damage. The difficulty in this approach is determining the size and duration of changes in respiration. An alternative is to use the approach that Battaglia et al. (2011) use to regulate photosynthesis following defoliation, with a predetermined change in respiration that is scaled to a canopy effect using the proportion of leaves damaged. Control of the duration of changes in respiration could be linked to either the duration of pest attack, or the time taken for lost foliage to be replaced.
Photosynthesis up- or downregulates in response to pest damage

While in most NPP models photosynthetic rate is determined by some combination of light, N and water availability, the changes in photosynthetic rate following pest damage are not necessarily linked to these variables (Ovaska et al. 1993a, Reich et al. 1993, Pinkard et al. 2007). This has been accounted for in some models by applying a predetermined change in photosynthesis that is scaled to the canopy. Kirschbaum et al. (2007) accounted for reductions in photosynthetic rate following pest damage are not necessarily linked to these variables (Ovaska et al. 1993a, Reich et al. 1993, Pinkard et al. 2007). This has been accounted for in some models by applying a predetermined change in photosynthesis that is scaled to the canopy. Kirschbaum et al. (2007) accounted for reductions in photosynthetic capacity associated with leaf necrosis using a discount factor on the N, temperature, CO₂ and water-limited maximum assimilation rate. Battaglia et al. (2011) applied a similar approach to account for photosynthetic upregulation in response to insect defoliation, but allowed this to be varied for each of nine predefined canopy zones. The duration of response was linked to rates of refoliation.

An alternative approach is to link photosynthetic rate to the source:sink balance. Battaglia et al. (2011) conceptualized this as:

\[ P_{U} = U P_{f} \text{ if } B < B^* \]

where \( U \) is the upregulation factor for photosynthesis (defined empirically); \( B \) is the ratio of photosynthetic tissue to sapwood in the tree at the current time; \( B^* \) is that ratio at the time of defoliation; and \( W_f, W_{bsw}, W_{ssw}, W_{fr} \) and \( W_{crsw} \) are masses of foliage, branch sapwood, stem sapwood, fine roots and coarse root sapwood. This is clearly an approximation, with the mass of growing tissue a surrogate for meristematic potential. It is underlain by a presumption that the sources and sinks are in balance at the time of defoliation. A more plausible framework for a stand level model might be to include a storage pool in the model and link photosynthetic upregulation to the depletion of this pool. Conceptually, the most rigorous approach may be to invoke the transport-resistance model (Thornley 1998) and make photosynthetic regulation a function of photosynthate accumulation in leaves, notwithstanding the parameterization difficulties this invokes.

Leaf retention rates may change

In most NPP models leaf longevity is a function of a user-defined maximum leaf lifespan, which in some cases may be moderated by water and nutrient limitation. This is not consistent with experimental observations of responses to pest damage, where both increases and decreases in leaf lifespan have been observed.

Kirschbaum et al. (2007) defined decreased leaf retention rates associated with psyllid damage as

\[ S_p = k_p \]

where \( k_p \) is a user-defined constant that gives the additional foliage senescence per day resulting from insect damage. Increased leaf retention after defoliation is not simulated by any of the models reviewed. Progress in this area probably requires an understanding of determinants of leaf senescence. The common use of age as a surrogate for the many contributing factors (e.g., self-shading, nutrient withdrawal, phenology, hydraulics) to leaf fall may need revision if altered leaf retention is a significant tree adaptation to defoliation.

Specific leaf area may vary spatially in the crown

Specific leaf area in many models is calculated as a function of either N concentration or stand age (e.g., CABALA, 3-PG, CenW), and hence the capacity to model variable SLA within the crown is limited. Foliage formed following a defoliation event may have a very different SLA to that formed prior to defoliation, irrespective of where in the crown leaf area has been lost. In general one would expect changes in SLA to have a minor effect on NPP; however, if it was felt necessary to model this response the most appropriate approach might be a transport-resistance model with SLA made a function of leaf level carbohydrate and N stores.

Issues for modelling at the tree scale

Interactive effects of C:N; water supply on net assimilation and growth

Models need to be able to capture the interactive effects of pests on the C, N and water economy of the tree to simulate the effect of site and ontogenetic controls of response to damage. Many of the models reviewed here couple these cycles (e.g., Forest-BCG, G’Day, CenW, CABALA) but they vary to the extent to which the limitations to growth of one or more of these resources are used to regulate physiological processes. All these models co-limit assimilation rate with (at least some of) nutrients, water and light. However, the interaction of these factors on C allocation is only captured in a few. Given the highly lumped representation of the process of allocation and coordination in tree level models, and the poor understanding of the mechanisms involved, it is difficult to recommend modelling approaches to improve on this other than to suggest that NPP and pest models should be able to simulate site, silvicultural and ontogenetic effects on tree recovery.

Role of C stores

Our conceptualization shows C stores to be an important intermediary between pest impacts and tree response, and clearly C storage is important to stimulate tree refoliation following complete defoliation. None of the models reviewed here has C storage terms in the biomass. Creation of a C storage pool, perhaps proportional to sapwood mass, is a relatively straightforward addition to these models. Requiring more consideration is the
Changes in light distribution and production

The pattern of defoliation affects subsequent NPP and GPP (see modelled example in Figure 2; see also Pinkard et al. 2006). A portion of this difference is due to changes in crown level light use efficiency and light interception. Big-leaf models that only simulate defoliation as the loss of uniformly distributed leaf area with no consideration of the subsequent spatial distribution of leaf area will not capture the effects of patterns of defoliation on NPP. The application of light interception models that allow for spatially variable leaf density and photosynthetic properties in crowns will be required in order to capture the effects of pattern of defoliation on NPP. If all trees are uniformly affected in a stand and canopy closure is maintained then this can be easily dealt with through a multi-layer approach to big-leaf modelling, with each layer having different leaf area density and photosynthetic properties (see also Shi et al. (2010) for importance of assumptions about foliar properties in a layered model on the predicted radiation adsorption and CO₂ and H₂O fluxes). To allow dynamic prediction of effects of defoliation on NPP and patterns of recovery, consideration of where new leaf area grows within canopies and from where leaf loss occurs will be required. Simulating pre-canopy closure effects will be more difficult and some form of three-dimensional canopy modelling will be required (e.g., Wang and Jarvis 1990, Battaglia et al., 2011). Medlyn et al. (2007) showed an example of this scaling from leaf properties to crown with MAESTRA that has applicability to pest damage simulations.

Issues for modelling at the stand scale

Changes in energy partitioning in a stand

Defoliation changes the radiation reaching the understorey and potentially the forest floor, with consequences for growth and transpiration of the understorey and soil evaporation. There may be consequences for soil temperature with flow-on effects to soil respiration and mineralization processes. Many of the models we review deal with the decrease in light interception and the consequent increase in forest floor radiation. The models as originally developed do not allow for understorey effects but subsequent development of CenW (Kirschbaum et al. 2007) and 3-PG (Almeida et al. 2007) does allow for this.

Nutrient and C cycling

If trees respond to defoliation by changing leaf chemistry and retaining leaves longer, there will be flow-on effects to litter quality and quantity. On nutrient-limited sites this could have short- to medium-term effects on leaf area and NPP. Models that do not include the bio-geo-mechanical cycle and instead rely on a fertility index or measure of site quality may not be able to simulate this effect of defoliation.

Increased within-stand heterogeneity

Pest attack rarely affects all trees within a stand uniformly, resulting in a spatially more heterogeneous stand. This will affect intra-specific competition, flowing through to size class distribution of trees and patterns of mortality, and may affect resource use efficiency (Binkley et al. 2002). The models reviewed here generally assume a uniform canopy, although CenW (Kirschbaum et al. 2007) and 3-PG (e.g., Nightingale et al. 2008) have both been applied to more heterogeneous forest structures. However, in those cases they were parameterized for specific situations and it is less clear whether they would deal with the situation when imposed dynamically. Another approach is to partition stand level estimates of NPP to trees within the stand based on a matrix of tree attributes and use this to drive stand level properties such as mortality (e.g., Korol et al. 1995 with Forest-BCG; Grote et al. 2011 with MoBILE-PSM).

Future research

In order to use models to explicitly address issues of pest impact, it will be necessary to fill a number of research gaps. Firstly, very few forest host–pest systems have been studied in detail and hence empirical data sets for model validation are rare. Of particular importance for validating pest effects in NPP models is better understanding of photosynthesis, respiration, nutrient and carbohydrate responses to defoliation in a broad range of species; and changes in patterns of biomass allocation in response to varying patterns and severities of defoliation. Secondly, there is little understanding of background levels of pest damage, patterns of pest outbreaks (frequency, severity, seasonality) and threshold levels of damage above which NPP is affected, and how these might change under future climates. This limits our capacity to define appropriate
levels of damage to use in models. The conceptual framework presented in Figure 1 provides a guide to the sorts of empirical data required to support model development. Sensitivity analysis can be used to identify the physiological processes most important to capture in models in order to improve predictions of pest damage.

Conclusions

In circumstances where the past is a good indicator of the future, it may be appropriate to assume that disturbances such as pest attack are ‘taxing’ a fixed proportion of NPP. There is clear evidence of discontinuity in at least the climate drivers on NPP making such assumptions contestable. In this work we have explored how pests might be affected by climate change and the sort of effects this might have on NPP. Our desiderata for the processes to be included into models may guide future NPP modelling, or at least provide a checklist that can be used to evaluate the robustness of predictions.

Acknowledgments

We acknowledge the financial contribution of the Australian Department of Climate Change (Project no. 715).

Funding

We thank the Australian Department of Agriculture, Fisheries and Forestry for funding contributed to this project via AGO Project No. 0715.

References


Pest effects on net primary production under changing climate


