Soil respiration in a fire scar chronosequence of Canadian boreal jack pine forest

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Abstract

This research investigates soil respiration (R_s) in a boreal jack pine (*Pinus banksiana* Lamb.) fire scar chronosequence at Sharpsand Creek, Ontario, Canada. During two field campaigns in 2006 and 2007, R_s was measured in a chronosequence of fire scars in the range 0 to 59 years since fire. Mean R_s adjusted for soil temperature (T_s) and soil moisture (M_s) ($\overline{R_s}^{T,M}$) ranged from 0.56 µmol $CO_2/m^2/s$ (32 years post fire) to 8.18 µmol $CO_2/m^2/s$ (58 years post fire). Coefficient of variation (*CV*) of R_s adjusted for T_s and M_s ranged from 20% (16 years post fire) to 56% (58 years post fire). Across the field site, there was a significant exponential relationship between R_s adjusted for soil organic carbon (C_s) and T_s ($P = 1.24*10^{-06}$; $Q_{10} = 2.21$) but no effect of M_s on R_s adjusted for C_s and T_s for the range 0.21 to 0.77 volumetric M_s ($P = 0.702$). $\overline{R_s}^{T,M}$ significantly ($P = 0.030$) decreased after burning mature forest, though no significant ($P > 0.1$) difference could be detected between recently burned and unburned young forest. R_s was measured in recently burned boreal jack pine fire scar age categories that differed in their burn history and there was a significant difference in $\overline{R_s}^{T,M}$ between previously 32 v 16 year old ($P = 0.000$) and previously 32 v 59 year old ($P = 0.044$) scars. There was a strong significant exponential increase in $\overline{R_s}^{T,M}$ with time since fire ($r^2 = 0.999$; $P = 0.006$) for the chronosequence 0, 16 and 59 years post fire, and for all these age categories, $\overline{R_s}^{T,M}$ was significantly different from one another ($P < 0.05$). The Joint UK Land Environment Simulator (JULES) was used to model vegetation re-growth over successional time at Sharpsand Creek, though it appeared to perform poorly in simulating leaf area index and canopy height. JULES probably over estimated heterotrophic R_s at Sharpsand Creek when T_s corrected simulated values were compared with measured $\overline{R_s}^{T,M}$. The results of this study contribute to a better quantitative understanding of R_s in boreal jack pine fire scars and will facilitate improvements in C cycle modelling. Further work is needed in quantifying autotrophic and heterotrophic contributions to soil respiration in jack pine systems, monitoring soil respiration for extended time periods after fire and improving the ability of JULES to simulate successional vegetation re-growth.

Acknowledgements

Contents

Keywords

Below ground respiration; boreal forest; Canada; carbon; fire scar chronosequence; forest fire; jack pine; Joint UK Land Environment Simulator (JULES); land surface model; *Pinus banksiana* Lamb.; podzol; soil respiration; soil surface CO_2 efflux; Top-down Representation of Interactive Foliage and Flora Including Dynamics (TRIFFID).

Abbreviations

ADP – adenosine diphosphate; Al – Aluminium; ANOVA – analysis of variance; ATP – adenosine triphosphate; B – burnt in 2007; BFCDM - boreal forest carbon dynamics model; BT – broad leaf trees; C – carbon; C3G – C3 grass; C4G – C4 grass; Can – canopy height; CC – clear cut; CH_4 – methane; CO – carbon monoxide; CO_2 - carbon dioxide; C_s - soil carbon (note C_s values reported for results of *this* research are an estimate of soil organic carbon); *CV* - coefficient of variation; d – deposition; DC – change in carbon; *df* - degrees of freedom; DT – change in time; FC – field campaign; Fe – iron; *FE* – fractional error; e – erosion; E – energy; ETC – electron transport chain; FORTRAN – formula translation; Frac – fractional cover; GPP – gross primary productivity; H_2O – water; IPCC - intergovernmental panel for climate change; *IQR* – inter quartile range; IR – infra red radiation; IRGA – infra-red gas analyser; JULES – joint UK land environment simulator; KC – Kreb's cycle; L – litter fall; LAI – leaf area index; M_d - mass of dry soil; MJP – mature jack pine; MOSES - meteorological office surface exchange scheme; M_s – soil moisture (note M_s values reported for results of *this* research are an estimate of volumetric pore moisture (fraction of pore space)); $M_{s(v)}$ - soil moisture voltage; M_w - mass of wet soil; N – nitrogen; *N* – sample size; NADH - nicotinamide adenine dinucleotide; NB – not burnt in 2007; NCEP - national centers for environmental prediction; NEE – net ecosystem exchange; NEP – net ecosystem productivity; NO_x – oxides of nitrogen; NPFT – non plant functional type; NPP – net primary productivity; NS – not (statistically) significant; NT – needle leaf trees; O_2 – oxygen; OJP – old jack pine; P – phosphorus; *P* - statistical significance; PB – pine barrens; PFT – plant functional type; PP – primary producers;

P_s - soil porosity; PVC - polyvinyl chloride; Q_{10} – rate of (soil) respiration increase for every 10°C rise in (soil) temperature; R – respiration; R_0 – base (soil) respiration rate at reference (soil) temperature; R_a – autotrophic respiration; RC – recent cut; RCF – run control file; R_e – ecosystem respiration; R_h – heterotrophic respiration; R_s - soil respiration; $R_{s(a)}$ – soil autotrophic respiration; R_s^C – soil respiration adjusted for soil organic carbon; $R_s^{C,T}$ – soil respiration adjusted for soil organic carbon and soil temperature; $R_{s(h)}$ – soil heterotrophic respiration; R_s^T – soil respiration adjusted for soil temperature; $R_s^{T,M}$ – soil respiration adjusted for soil temperature and soil moisture; *sf* - significant figure(s); Sh – shrubs; SRC - soil respiration chamber; SRS – soil respiration system; T_0 – reference (soil) temperature at base (soil) respiration rate; TRIFFID – top-down representation of interactive foliage and flora including dynamics; T_s - soil temperature; v – versus; V_s – volume of soil; $\bar{x}$ - mean; σ - standard deviation; $\bar{\sigma}$ - standard error; θ - laboratory derived volumetric soil moisture; θ_p – laboratory derived volumetric soil pore moisture; μmol – micromoles; < - less than; > - greater than; † - 2006 field campaign; + - 2007 field campaign.

Chapter 1: Introduction

1.1 Introduction

This chapter begins by introducing the research, outlining its importance and placing it within the wider context of the relevant literature. Thereafter, the two main research questions are stated. The final section details how the thesis is structured.

1.2 Research context

Over the latter half of the 20th Century, measurements have demonstrated a consistent rise in the atmospheric carbon dioxide (CO_2) concentration (Keeling et al. 1976; Thoning et al. 1989; Conway et al. 1994; Keeling 1997; Tans 2009) and anthropogenic influence from fossil fuel combustion and deforestation has been implicated in an enhanced 'greenhouse effect'. During the last 20 years, climate change has become a serious global concern in both the scientific community and international politics (Plantico et al. 1990; Allen et al. 2000; Florides and Christodoulides 2009). In 1988, the United Nations established the Intergovernmental Panel for Climate Change (IPCC), a collaboration of 2500 scientists, which aimed to provide advice to governments and policy makers (Grace 2004; IPCC 2007). At the Rio Earth Summit (1992), a number of countries agreed to reduce emissions of greenhouse gases (e.g. CO_2) and binding targets were set at the Kyoto Protocol (1997) (Grace 2004).

Soil respiration (R_s) refers to CO_2 efflux at the soil surface. R_s influences nutrient cycling (Zak et al. 1993), carbon (C) balance at ecosystem (Curtis et al. 2005) through global (Raich and Potter 1995) scales, and climate change (Cox et al. 2000) since it represents a direct input of CO_2 to the atmosphere. Indeed, globally R_s produces 75 to

120 Pg CO_2–C yr^{-1}, 11 to 20 times that produced by the combustion of fossil fuels (Hibbard et al. 2005). There has been a substantial amount of R_s research over the last decade, though it remains one of the least understood processes in ecosystem ecology (Martin and Bolstad 2005; Luo and Zhou 2006). Current research campaigns seek to improve our understanding of R_s in a range of different environments e.g. arable (Akbolat et al. 2009), grassland (Zhang et al. 2009) and forest (Campbell et al. 2009) ecosystems.

Forest ecosystems sequester, store and liberate C and have an integral role in the global C balance (Bonan 2008). It has been estimated that boreal forests account for approximately a tenth of Earth's land area (Bonan and Shugart 1989) and a third of Earth's total forested area (Zhang et al. 2003). Boreal forests contain almost half of the C stored in forest ecosystems (Preston et al. 2006) and between one quarter and one third of global soil C (Dixon et al. 1994). Of the 3150 Pg C believed to be contained in the Earth's soils (Sabine et al. 2003), several hundred Pg are thought to reside in boreal systems (Goulden et al. 1998; Hobbie et al. 2000). Climate predictions suggest that anthropogenic induced warming will be most pronounced at high latitudes (Kattenberg et al. 1996) and this has recently been demonstrated for Siberia (Balzter et al. 2007). The boreal forest biome is likely to be especially affected by climate change and average atmospheric temperatures are predicted to increase by 4 to 6ºC in the next 50 to 100 years (IPCC 2001, 2007). This has led to the suggestion that changes in boreal forest soil C storage could significantly alter the global soil C balance (Ohashi et al. 2005).

Fire is an important natural process in many ecosystems, e.g. tropical peat lands and forests (Page et al. 2002), tropical savannahs (Cardoso et al. 2008) and temperate rainforests (Abarzua and Moreno 2008). Fire is widely regarded as the most significant

natural factor controlling succession in the boreal forest biome (Zackrisson 1977). Boreal forest structure and large fuel loads (Stocks 1991) commonly result in large and high intensity wildfires (Bond-Lamberty et al. 2004), which can be responsible for releasing millions of tonnes of CO_2 to the atmosphere (Amiro et al. 2001; Wang et al. 2001). Forest fires are said to drive much of the C flux dynamics in Siberian and North American boreal forests (Kasischke and Stocks 2000) and it is reported that between 1959 and 1999 an average of two million ha of Canadian forest had burnt annually (Stocks et al. 2002). Furthermore, there has been a general increase in the amount of Canadian boreal forest burnt throughout the 1980s and 1990s (Amiro et al. 2001). It is possible that climate change will alter the boreal forest fire regime (e.g. an increase in size, frequency or intensity; Kasischke et al. 1995) and there are a number of ways in which this could modify the global C balance. First, it could lead to greater CO_2 emissions directly from forest fires, a positive feedback mechanism. Second, it would most likely have a profound effect on the C flux dynamics of boreal forest ecosystems. It is possible that a greater frequency of fires will result in a higher proportion of young, relative to intermediate, mature and older forest and the consequences of this are largely unknown. There is also concern that any change in boreal forest age structure may alter albedo and hence climate (Bonan et al. 1992; Foley et al. 1994). However, potential scenarios remain uncertain; for instance Flannigan et al. (1998) actually suggest a future reduction in boreal forest fire frequency.

Boreal forests have been extensively studied in the context of C cycling and climate change (Bond-Lamberty et al. 2004), particularly in Canada (Kasischke and Stocks 2000). C flux research may involve field, laboratory, modelling or remote sensing approaches and are often a combination thereof (Steele et al. 1997; Sullivan et al. 1997; Lo et al. 2001). For

example, eddy covariance measurements from CO_2 flux towers may be used to measure total ecosystem respiration (R_e) (Nakai et al. 2008), though often separation of above- and below- ground processes (Bond-Lamberty et al. 2004) provides more detailed insight into C flux dynamics. This is particularly important for improving the accuracy of C cycle models (Kaduk and Heimann 1996; Crucifix et al. 2005; Huntingford et al. 2008; Sitch et al. 2008). The possibility of changing boreal forest fire regime has led to R_s research being conducted in boreal fire scar chronosequences (Zhuang et al. 2002; Wang et al. 2003; Bond–Lamberty et al. 2004; Czimczik et al. 2006; O'Neil et al. 2006; Singh et al. 2008). Studies of R_s in boreal fire scar chronosequences particularly relevant to this research are reviewed in Chapter 4.

This study investigates R_s in a boreal jack pine (*Pinus banksiana* Lamb.) fire scar chronosequence, of which there has been relatively little research to date. Jack pine is an important component of the North American boreal forest and may become more widespread in the future (Chapter 4; Sect. 4.2). In addition, it is the first study to test the ability of a current land surface model to simulate heterotrophic R_s ($R_{s(h)}$) in a boreal jack pine system. It is intended that the results of the research will lead to a better quantitative understanding of R_s in boreal jack pine systems, facilitate model parameterization and lead to improvements in C cycle models.

1.3 Main research questions

There are two main research questions:

1.   How does measured R_s change over successional time since fire for a boreal jack pine ecosystem?

2.   How well can a current land surface model capture the behaviour of R_s over successional time since fire for a boreal jack pine ecosystem?

After a thorough analysis of the relevant literature, more specific research questions are provided (Chapter 4).

1.4 Thesis structure

This thesis is divided into seven chapters. Following on from this Introduction, **Chapters 2 and 3** provide background information to the research. **Chapter 2** gives a general overview of the boreal forest biome. **Chapter 3** begins with an overview of C cycling in the terrestrial biosphere and moves on to concentrate on R_s, since this is the focus of the research. The studies most relevant to the research are considered in **Chapter 4.** First, a review of key knowledge is provided, allowing comparisons with the results of this research in Chapter 7 (see below). This is followed by an overview of significant gaps in the literature and specific research questions, which this study aims to address. **Chapter 5** describes the materials and methods used in the fieldwork and modelling analyses of the research respectively. In **Chapter 6,** combinations of inferential and descriptive statistics are employed to display the key results of the research. In **Chapter 7**, the results are discussed in the context of relevant literature, the main limitations and suggestions for future research.

1.5 Summary

R_s has an integral role in C cycling, though it is one of the least understood processes in ecosystem ecology. Boreal forests contain almost half of the C stored in forest ecosystems and up to a third of global soil C. Average atmospheric temperatures in the boreal forest

could increase by up to 6ºC in the next 50 to 100 years and changes in boreal forest soil C storage may alter the global soil C balance. Fire is a significant natural factor controlling succession in the boreal forest biome and there has been a general increase in the amount of Canadian boreal forest burnt throughout the 1980s and 1990s. This research, concerned with R_s in a boreal jack pine fire scar chronosequence, is centred around two main research questions and comprised of seven chapters. A review of the boreal forest biome is now provided in Chapter 2.

Chapter 2: The boreal forest biome

2.1 Introduction

This chapter provides a general overview of the boreal forest biome. After introducing the location and climate, it moves on to consider the main soil and vegetation types and the effects of fire in boreal forest ecosystems. Where the emphasis of this chapter is on background information, a review of the studies more specific to this research is provided in Chapter 4.

2.2 Location and coverage

The boreal forest, or taiga, is a large terrestrial biome, occupying 45ºN to 70ºN (Zhang et al. 2003) and is the second largest forest biome on Earth (Martin et al. 2005). The biome encompasses a broad circum-polar band that extends over sub-arctic Russia, North America and parts of northern Europe (Brown and Lomolino 1998; Woodward 2003; see also Fig. 2.1). Some 1.2 billion ha of Earth's surface is covered by boreal forest (a third of Earth's total forested area (Zhang et al. 2003)), the majority of which (900 million ha) is closed or stocked (Conard and Ivanova 1997). Two thirds of Earth's boreal forest is located in Russia (Conard and Ivanova 1997).

Genetically similar species occur in North American and Eurasian boreal forest and this can be explained by the connection of the two land masses during the last ice age (Botkin and Keller 2005). Within the boreal forest biome, increasing latitude results in a progressively shorter growing season and trees become smaller and sparser. Eventually, trees are unable to establish, as the boreal forest merges into the treeless tundra biome. On
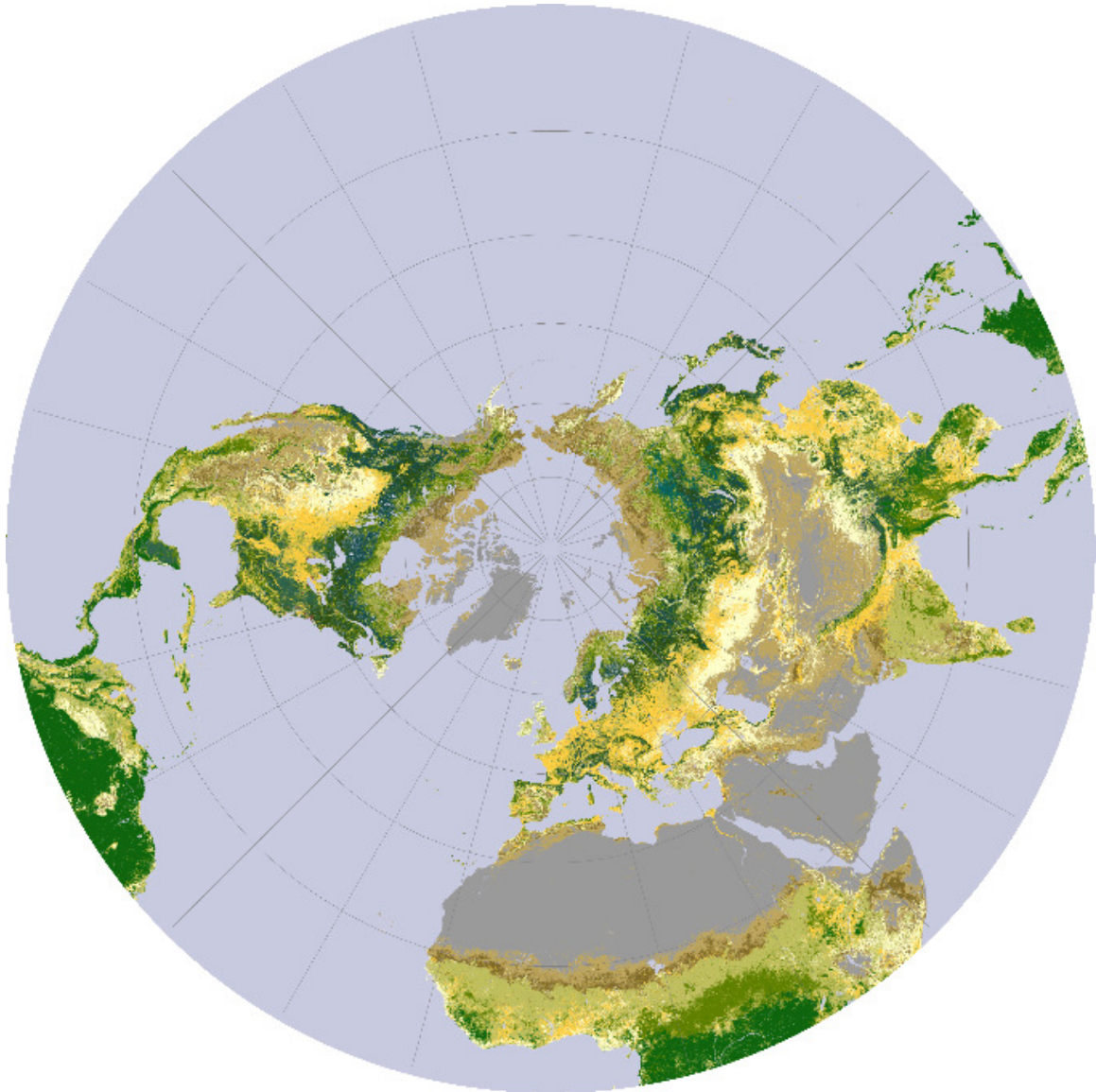
Figure 2.1 The boreal forest biome across the continents, covering parts of Europe, Asia and North America. Dark green = boreal forest; tan = tundra and barren land; yellow = crops and grasslands. Source: Riebeek (2006). Permission granted from Robert Simmon (NASA).

a global scale, the northern-most limit of tree growth closely coincides with the 10°C isotherm, which separates the boreal and tundra biomes (Bailey 1998). In fact, the boreal-tundra boundary is angled across North America from 68°N in Alaska to 58°N in eastern Canada, whilst in Eurasia it predominantly parallels the coastline of the artic ocean a few

hundred km inland (Woodward 2003). At the ecosystem scale, the boundary of the boreal and tundra biomes is determined by the thermal limits for plant growth (Bailey 1998) and post-glacial recovery, which results in a slow pole-ward migration of the biomes (Holden 2005). On its southern latitudinal limits, the boreal forest merges into deciduous forest (coastal regions) or temperate grassland (continental interiors). Holden (2005) discusses how the effects of commercial forestry also influence the natural boundaries of the boreal forest biome.

This chapter is concerned with the boreal forest *biome*, though it should be noted that '*boreal type*' vegetation occurs in temperate latitudes at high elevations, e.g. the cordilleras of western North America all the way to southern Mexico, and large areas of highland Mexico (Brown and Lomolino 1998).

2.3 Climate

The boreal forest experiences a sub-arctic, cold continental climate with one to five months attaining a mean atmospheric temperature >10°C (Brown and Lomolino 1998; Botkin and Keller 2005; Holden 2005). Mean *annual* atmospheric temperature, however, is between 5°C and -5°C (Macdonald 2003). Temperatures vary substantially throughout the year (with the exception of more coastal regions), the record currently held in Verkhoyansk, Russia (daily low of -68°C; daily high of 32°C) (Woodward 2003). Winters are typically long and severe (average January atmospheric temperatures as low as -50°C in central Siberia (McDonald 2003)), with sub-zero mean temperatures for up to six months and just 50 to 100 frost free days in summer (Woodward 2003). Indeed, summers are short and cool to warm (Woodward 2003), with average atmospheric temperatures in July 10 to 20°C (MacDonald 2003).

Since the boreal forest is largely situated in continental interiors, it receives relatively little precipitation, averaging 381 to 508 mm annually (Holden 2005). This is sufficient to support forests, however, due to generally low temperatures and thus low evaporation rates (Woodard 2003). A summer maximum of precipitation is often a result of convection (Holden 2005). Indeed, more than half the annual precipitation falls in summer, with winters often dry (Woodward 2003). Although much of the boreal forest is covered in snow over the long winter period, the potentially high albedos (snow = 0.7 to 0.9: Greuell and Oerlemans 2005; Stroeve et al. 2005) may be 'masked' by the forest canopy (Betts and Ball 1997; Ni and Woodcock 2000).

2.4 Soils

Boreal forest soils are generally young (Woodward 2003), a reflection of the last glaciations affecting large regions of the biome. The common soil type formed is an acidic, nutrient-poor podzol (Fig. 2.2). These soils form where precipitation > evapo-transpiration (Holden 2005). The forming of a podzol, termed podzolization, is a result of extreme leaching.

The litter layer is very resistant to decomposition and may contain three to five times the annual accumulation of acidic coniferous needles (Holden 2005). The slowly decomposing needles produce a shallow acidic mor humus (Richards 1987). This provides chelating agents and fulvic acid, which renders iron (Fe) and aluminium (Al) minerals more soluble. Infiltrating water, e.g. following snowmelt, leaches bases and translocates organic matter and sesquioxides of Fe and Al. Intense leaching is capable of dissolving these less soluble elements and results in loss of an already finite supply of nutrients. The

Figure 2.2 Humo-ferric podzol profile. Note the marked contrast in colour between the different soil horizons. Source: Canadian Soil Information System (2008); reproduced with the permission of the Minister of Public Works and Government Services Canada, 2009.

consequence is an ash-grey bleached A horizon (eluvial layer), composed of mostly silica or quartz (SiO_2). Fe and Al leached from this horizon are deposited lower down in horizon B (illuvial layer), which sits above the parent material (horizon C) (Richards 1987). It is not uncommon for an 'iron pan' to form in horizon B, which can restrict root penetration and may cause water-logging. Indeed, boreal forest soils are often waterlogged (Brown and Lomolino 1998).

Cold, acidic soils are not favourable to microorganisms resulting in relatively low nutrient turnover, compared with that of temperate and tropical biomes (Waring and Schlesinger 1985). There is also a relative lack of soil fauna (Holden 2005), which further slows down decomposition. The low rates of decomposition and lack of mixing agents produce well-defined horizons. An accumulation of peat and humic acids results in many soil nutrients being unavailable for plant growth (Brown and Lomolino 1998). Flora of the

boreal forest must therefore have a relatively low nutrient requirement and be able to tolerate the acidic soils (Brown and Lomolino 1998).

Permafrost (permanently frozen soil) is widespread in boreal soils, as is snow cover for much of the year (Chapman and Reiss 1992). Indeed, pole-ward of the boreal tree-line, it is a continuous layer of permafrost close to the soil surface that prevents tree establishment, rather than climatic conditions (Woodward 2003). As evergreen cover increases with boreal forest succession, the level of permafrost rises and this may inhibit root penetration and availability of plant nutrients, e.g. nitrogen (N) and phosphorus (P) (Waring and Schlesinger 1985). Indeed, soil nutrient availability and pH usually decrease over successional time following fire and with increasing conifer abundance (Hart and Chen 2006). High C:N ratios and acidity of coniferous litter decrease available soil nutrients and pH, as base cations are immobilized in the lignicolous litter, reducing pH, which is further lowered by the acidity of the litter (Van Cleve et al. 1983; Pare et al. 1993; Brais et al. 1995; Pare and Bergeron 1995; Driscoll et al.1999; Wardle et al. 2003; Hart and Chen 2006).

2.5 Vegetation

The boreal forest plant community has been described as having floristic homogeneity (Mcknight and Mess 2008). Indeed, boreal forests are typically dominated by only a few conifer species (Brown and Lomolino 1998) and it is not uncommon for large areas to be occupied by just one or two tree species (Begon et al. 1996). Diversity and productivity are low as a result of cold climates and acidic soils (Brown and Lomolino 1998). In fact, the boreal forest of North America contains only around 20 major species, though some of

these have high commercial value, e.g. white pine (*Pinus strobus*) (Botkin and Keller 2005). Boreal conifers are softwoods and a valuable resource for timber, pulp and paper.

Usually boreal forest trees are relatively small, <30 m in height (Botkin and Keller 2005). Coniferous (needle leaf (NT)) genera dominate, namely spruces (*Picea* spp.), firs (*Abies* spp.), pines (*Pinus* spp.) and larches (*Larix* spp.) (Woodward 2003; see also Fig. 2.3). Evergreen conifers (note larch is a *deciduous* conifer, see below) retain their leaves over winter, usually for several years, shedding only a portion at a time (Chapman and Reiss 1992). The xeromorphic needle leaves of conifers are more resistant to cold and drought than broad leaved trees (BT) and begin photosynthesising as soon as environmental conditions allow (Hora 1981), maximising the growing season (Holden 2005). It is biochemical differences at the cellular level between coniferous and deciduous trees that permit the former to photosynthesise at lower temperatures (Oquist and Huner 2003). The adaptations that make conifers well suited to the boreal climate are summarised in Table 2.1.

There are some deciduous angiosperms in the boreal forest, e.g. poplar (*Populus* spp.), and birch (*Betula* spp.), and these are particularly common in areas of recent or frequent disturbance, such as fire (Woodward 2003; McKnight and Mess 2008). The deciduous conifer larch or tamarack (*Larix* spp.) sheds its needle leaves in winter, adopting the deciduous habit (Chapman and Reiss 1992; Botkin and Keller 2005; McKnight and Mess 2008). Where winters are extremely cold and dry, only the deciduous habit can prevent damage to foliage. In this instance, larches and broad leaved deciduous birches and aspens (*Populus* genus) dominate, as seen in the interior regions of eastern Siberia (Woodward 2003).

Figure 2.3 Stand of mature jack pine (*Pinus banksiana* Lamb.) at Sharpsand Creek experimental burn site, Ontario, Canada. Source: author's collection, June 2006.

Table 2.1 Adaptations of conifers to the boreal forest climate.

Structure / Adaptation	Function / Explanation
Needle- instead of broad- leaves.	Reduction of leaf surface area, decreasing moisture loss.
Retain needle leaves year round (evergreen).	Able to photosynthesise whenever conditions allow.
Tough needles.	Allows survival for many years - important as their manufacture is biologically 'expensive' (antifreeze properties). Needles must also withstand adverse weather e.g. wind, snow and attack by insects and fungi.
Very dark green needles.	Maximises absorption of solar radiation - increases leaf temperatures and promotes photosynthesis earlier in spring than air temperatures alone might allow.
Thick waxy cuticle on needles.	Cuticle waterproof reducing moisture loss.
Hardening of foliage in late autumn.	Increases frost resistance.
Increased concentration of sugar in sap during winter.	Increases moisture uptake by osmosis. Protection against cold and lack of water (plant root absorption of water less efficient in colder conditions).
Sunken stomata.	Stomata shielded from drying winds, reducing moisture loss.
Stomatal closure.	Reduces transpiration rates.
Thickened resinous bark.	Reduces transpiration rates; protects against cold winds in winter and forest fires in summer.
Compact, conical shape with downward sloping, springy branches.	Provides stability against strong winds; allows snow to glide off without breaking branches; lower branches longer minimising snow accumulation.
Layering form of asexual reproduction at northern limits of boreal biome.	Branches touching ground sprout roots which send up leader branch to become new tree. Layering form of reproduction where environmental conditions prevent seed germination.
Fan shaped root system.	Adaptation to shallow soils – fan shape maximises lateral nutrient 'mining'.

Information compiled from: Hora (1981); Chapman and Reiss (1992); Waugh (2000); Woodward (2003); Holden (2005).

The boreal forest undergrowth is not usually dense (McKnight and Mess 2008), though it may be well developed in some mesic sites, comprising acid-tolerant shrubs, mosses, and lichens (Brown and Lomolino 1998). Hart and Chen (2006) discuss how boreal under-storey vegetation is the least understood, yet most diverse component of boreal plant communities (Roberts 2004). Under-storey vascular vegetation development is usually limited by light, though it is often reduced through-fall due to a dense canopy that limits non-vascular plants (Busby et al. 1978; Chen et al. 1996; Chen 1997; Strengbom et al. 2004; Hart and Chen 2006). Common dwarf shrubs include bilberries and cranberries (*Vaccinium* spp.), Labrador Tea (*Ledum palustre*) and Leatherleaf (*Chamaedaphne calyculata*) (Hora 1981). Flowering plants of the forest floor include creeping lady's tresses (*Goodyera repens*), twin flower (*Linnaea borealis*) and one flowered wintergreen (*Moneses uniflora*). Wood sorrel (*Oxalis acetosella*) and grasses (Gramineae) occur in the southern part of the boreal forest biome (McKnight and Mess 2008).

As in all natural ecosystems, ecological succession occurs in the boreal forest resulting in temporal modifications to the plant community and its associated abiotic environment. Lyons et al. (2008) describe how boreal forest post-fire succession is controlled by numerous interactive factors such as fire severity and return interval, site drainage characteristics and seed source availability (Lutz 1955; Viereck 1973; Foote 1983; Viereck et al. 1983; Harper et al. 2002; Johnstone and Kasischke 2005; Johnstone and Chapin 2006). Dense, single storied canopies form by establishment of fast growing shade-intolerant species which colonise after stand-replacing fires, e.g. in North American boreal mixed-woods: jack pine (*Pinus banksiana* Lamb.), trembling aspen (*Populus tremuloides* Michx.) and paper birch (*Betula papyrifera* Marsh.) (Lavoie and Sirois 1998; De Grandpre

et al. 2000; Gauthier et al. 2000; Hart and Chen 2006). Shade-tolerant species may establish in the under-storey, such as balsam fir (*Abies balsamea*), white and black spruce (*Picea glauca* and *Picea mariana* respectively) and eastern white cedar (*Thuja occidentalis*), often within a few years of fire (Carleton and Maycock 1978; Bergeron 2000; Hart and Chen 2006). As the stand develops after fire, under-storey light availability decreases (Hart and Chen 2006). This is most severe after closure of the initial shade-intolerant cohort, but continues as the over-storey becomes increasingly more abundant with shade-tolerant conifers (Hart and Chen 2006). After some time, the shade-intolerant canopy begins to break down and stands become unevenly aged and structurally heterogeneous (Hart and Chen 2006). In the absence of further fire, the shade-tolerant species replace the shade-intolerant ones (Smirnova et al. 2008). For instance, jack pine is commonly replaced by black spruce around 150 years after stand initiating fire (Bergeron and Brisson 1990; Gauthier et al. 1993; Lesieur et al. 2002; Bergeron et al. 2004; Smirnova et al. 2008).

Post-fire succession influences surface energy exchange by numerous processes (Lyons et al. 2008). Consumption of coniferous foliage by fire greatly increases surface broadband albedo when snow is present on the forest floor, as can occur over winter (Liu et al. 2005; Amiro et al. 2006). Furthermore, summer albedo may be greater in early successional communities where deciduous species have leaves and branches with higher albedo than those of coniferous evergreens (Betts and Ball 1997; Amiro et al. 2006; Mcmillan and Goulden 2008). The transition to conifer dominance later in boreal forest succession commonly results in reduced leaf area index (LAI), as coniferous and deciduous species increase and decrease in abundance respectively (Waring and Schlesinger 1985).

However, Waring and Schlesinger (1985) describe how in the absence of fire or some other disturbance (e.g. logging), succession may continue to a climax community termed *muskeg*, where canopy cover is sparse (Reiners et al. 1971; Van Cleve and Viereck 1981; Van Cleve et al. 1983). Muskegs are low laying bogs or water filled depressions and are not uncommon in the boreal forest, often occurring in poorly drained or post-glacial sites (Woodward 2003; Holden 2005).

The boreal-tundra and boreal-deciduous forest / temperate grassland transitions are gradual and marked by zones containing species characteristic of both biomes, the *ecotone*. For instance, the boreal-deciduous forest ecotone is usually represented by mosaics, as opposed to mixed deciduous and coniferous stands (Holden 2005).

2.6 Forest fires

Fire, insect outbreaks and storms are all natural forms of disturbance in the boreal forest (Botkin and Keller 2005) though the former is widely regarded as the most significant factor controlling ecological succession (Zackrisson 1977; see also Fig. 2.4). Although most regions of the boreal forest in North America have fire return intervals of 50 to 200 years, this may increase to 500 years in more mesic sites (Bonan and Shugart 1989). Boreal forest fires may start naturally (lightning strikes) or anthropogenically. The latter may be intentional e.g. to clear land for development, or accidental, e.g. mistakenly dropping a lit cigarette. Eastwood et al. (1998) discuss how statistics from the Canadian Forest Service suggest that approximately 60% of boreal forest fires are anthropogenic in North America and Russia. However, natural fires are usually the largest in the boreal forest since they normally occur in remote areas and are therefore left uncontrolled (Eastwood et al. 1998).

During a forest fire, C is released mainly as CO_2, though methane (CH_4) and carbon monoxide (CO) are also released, along with various nitrous oxides (NO_x), particulate matter and trace gases (Cofer et al. 1998). Forest fires are self-sustaining if conditions allow; that is, sufficient fuel (biomass), oxygen (O_2) and transfer of heat. Michaletz and Johnson (2007) distinguish between *heat*, defined as 'the energy associated with random molecular motion'; and *temperature*, defined as 'the average kinetic energy of the molecules'. Heat can be transferred causing fire to spread, while temperature remains constant (Michaletz and Johnson 2007). Heat transfer occurs through convection, radiation and conduction and may cause damage to the crown, bole and roots of vegetation (Michaletz and Johnson 2007; see also Fig. 2.5). Environmental factors such as strong winds or moist conditions may accelerate or attenuate rate of fire spread respectively.

Figure 2.4 High intensity forest fire (prescribed burn) in a stand of boreal mature jack pine at Sharpsand Creek experimental field site, Ontario, Canada. Source: author's collection, May 2007.
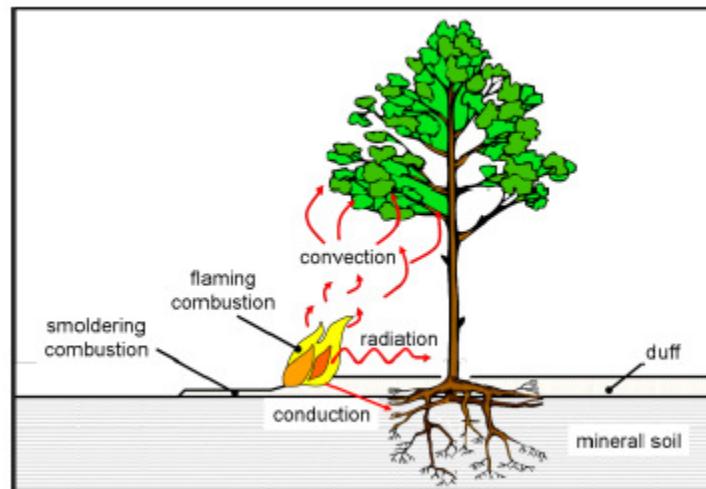
Figure 2.5 Heat transfer processes that cause damage to vegetation during forest fires. Source: Michaletz and Johnson (2007). Permission obtained from *Scandinavian Journal of Forest Research* (Taylor & Francis Group).

Fire intensity is defined as the energy produced by a fire event over an area during a period of time (Smirnova et al. 2008). Fire intensity can be inferred from residual structures (Schimel and Granstrom 1996; Turner et al. 1998; Smirnova et al. 2008) and a number of recent experiments have demonstrated a simple linear relationship between fire radiative energy and biomass consumption (Wooster 2002; Wooster et al. 2005). This relationship has been used to estimate biomass consumption from remotely sensed satellite measurements of fire radiative power (Roberts et al. 2005).

The abundance of soil animals is significantly reduced by forest fires, both those occupying niches above and below the char layer (Malmstrom 2008). Soil microbial biomass is concentrated in the surface layers (decreases rapidly with depth) and as such, the region of greatest biological activity is subjected to the highest temperatures during fire (Knicker 2007). Fire generally reduces microbial biomass, though bacteria may be less affected than fungi (Pietikainen and Fritze 1995; Dumontet et al. 1996; Knicker 2007).

Where fires burn the upper soil layers, release of nutrient cations previously immobilized in organic matter (Brais et al. 2000; Simard et al. 2001; Hart and Chen 2006) causes soil pH to temporarily increase (Certini 2005; Hart and Chen 2006). The partially burnt vegetation and organic soil layer may fertilise soil (Pyne 2001; Knicker 2007) and rising pH levels can initiate biological recovery (Baath and Arnebrant 1994; Chambers and Attiwill 1994; Knicker 2007). The darker charred plant and soil surface results in a low albedo, e.g. 0.06 (Chambers and Chapin 2002; Chambers et al. 2005), which may increase soil temperature (T_s). In addition, a more open canopy may also act to increase T_s, enhancing microbial decomposition (Binkley 1984; Hart and Chen 2006).

The dead soil and plant organic matter (necromass) burnt in forest fires, (also referred to as *char* or black C (Masiello 2004; Knicker 2007)), becomes incorporated into the soil and it has been suggested that previous models may over-simplify its structure and function in the soil system (Knicker 2007). Furthermore, Knicker (2007) describes how microbial attack and dissolution is facilitated by char chemistry, allowing rapid oxidation. Although char decomposition is generally thought to occur more slowly than that of litter, over long periods of aerobic conditions, char degradation may be so great that it cannot be distinguished from naturally formed soil organic matter (Knicker 2007). Pyrogenic soil organic matter is chemically different and less soluble than that formed from biodegradation and humification (Almendros et al. 1990, 1992) and subsequent hydrophobicity can perturb water flow and cause a patchy distribution of nutrients (Knicker 2007).

Lyons et al. (2008) discuss how the frequency of boreal forest fires will probably increase (Flannigan et al. 2005) as a consequence of rising northern surface temperatures

anticipated over the coming centuries (Christensen et al. 2007), assuming no change in management regime. Lyons et al. (2008) attribute this to increasing summer drought stress in coniferous forests (Monson et al. 2005) and prolonged fire seasons (Westerling et al. 2006).

2.7 Summary

The boreal forest is a large terrestrial biome that experiences a sub-arctic, cold continental climate. Soils are generally acidic nutrient-poor podzols with low nutrient turnover. Dominant trees are of the coniferous genera and fire is the most significant natural factor controlling ecological succession. Boreal forest fires impact the physical, chemical and biological properties of soils and this has relevance to C cycling. A review of the terrestrial biospheric C cycle and R_s is now provided in Chapter 3.

Chapter 3: The carbon cycle and soil respiration

3.1 Introduction

Multiple elements e.g. C and N flow in biogeochemical cycles between the atmosphere, geosphere, hydrosphere and biosphere. Importantly, the '*bio*' in biogeochemical cycles indicates that some transfers are biologically mediated, or wholly depend on living organisms. Indeed, the focus of the first section is a general overview of biospheric C cycle dynamics, with particular emphasis on the soil system. Thereafter, a review of ecosystem productivity concepts relevant to this research is provided. Finally, the process of R_s is introduced where its biochemistry, component sources, soil CO_2 transport, influencing factors and field measurements are discussed.

3.2 Carbon cycling in the terrestrial biosphere

In the global C cycle, inorganic C, as CO_2, is extracted from the atmosphere by primary producers (PP) (plants and some microorganisms) by photo- or chemo- synthesis (Fig. 3.1). These organisms are autotrophic, that is, capable of synthesising their own energy (E) and biomass (for maintenance, growth and propagation) from inorganic sources. Those organisms that use sunlight as an E source are termed photo-autotrophs (plants, algae and some bacteria) and those that use inorganic molecules are termed chemo-autotrophs (some bacteria). However, photosynthesis is the process by which the majority of C enters biological systems (Allen et al. 1995; Norris 1995). Photosynthesis occurs in the chloroplasts (cell organelles) of plant leaves, where CO_2 (obtained from the atmosphere via stomata) is combined with water (H_2O) (obtained from soil via plant roots)
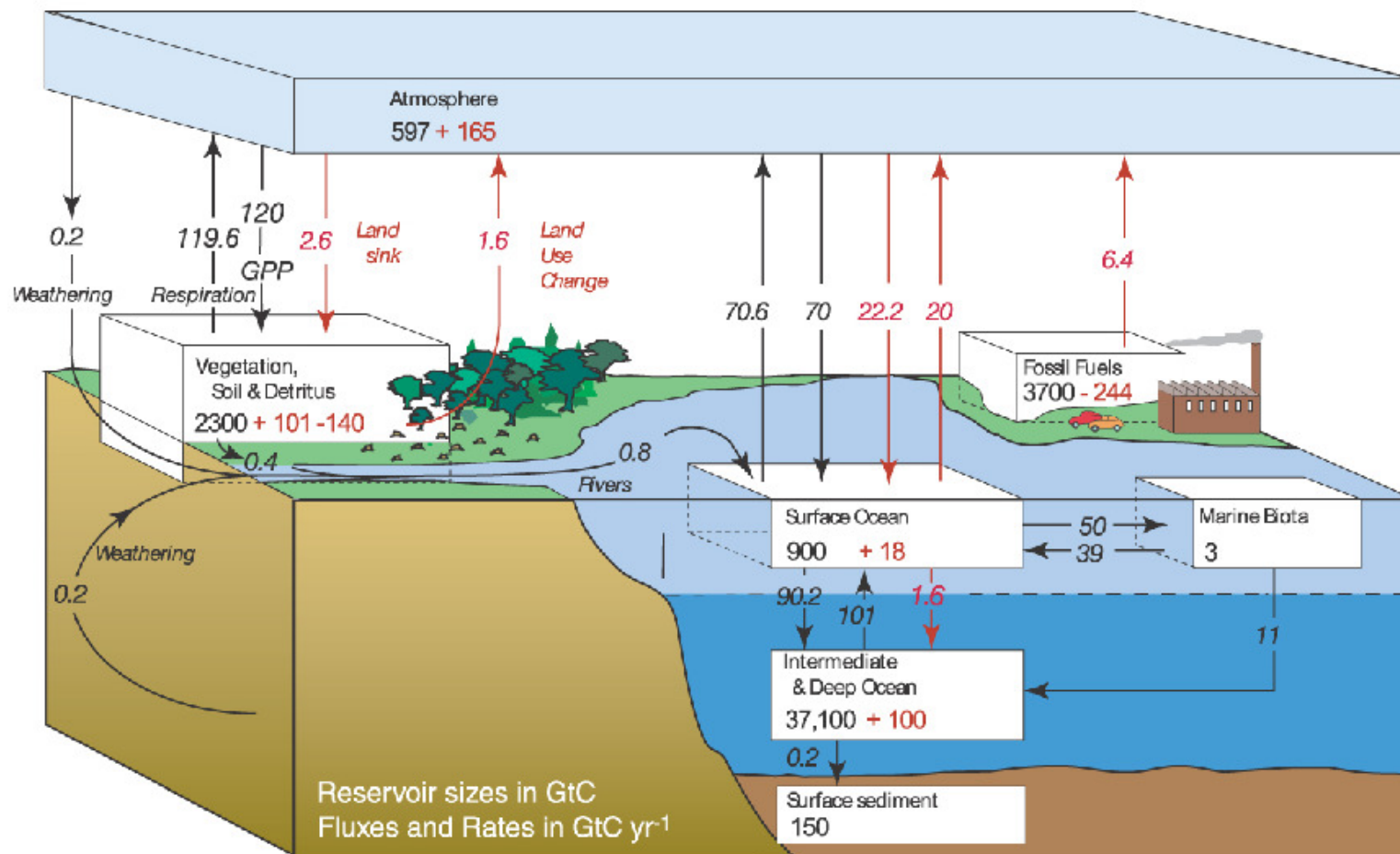
Figure 3.1 Global carbon (C) cycle for the 1990s. Black: pre-industrial natural fluxes; red: anthropogenic fluxes; GPP = gross primary productivity; 1 GtC = 1 PgC. Source: Denman et al. (2007) (modified from Sarmiento and Gruber 2006, with changes in pool sizes from Sabine et al. 2004). Reprinted by permission of Princeton University Press.

in the presence of sunlight and chlorophyll to produce sugars (e.g. glucose ($C_6H_{12}O_6$)), H_2O and oxygen (O_2):

$$6CO_2 \ + \ 12H_2O \ + \ Light \quad \rightarrow \quad C_6H_{12}O_6 \ + \ 6H_2O \ + \ 6O_2 \qquad \text{(Eq. 3.1)}$$
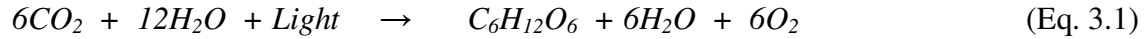
Glucose is a single (monosaccharide) sugar, a simple organic compound from which more complex multi- (polysaccharide) sugars, proteins and lipids are synthesised. Photosynthesis by terrestrial vegetation is responsible for the uptake of around

120 Pg C yr^{-1} from the atmosphere (Luo and Zhou 2006; see also Fig. 3.1). Heterotrophic organisms, e.g. all animals, fungi and many bacteria are unable to synthesise their own organic C from inorganic sources. However, organic C 'fixed' by PP is transferred through trophic (feeding) levels of food chains to herbivorous and carnivorous animals, and microorganisms. Since these consumer organisms obtain their E from organic compounds, they are more properly termed chemo-heterotrophs.

Respiration (R) is the process by which all organisms release E from organic molecules. By far the most dominant form, in the context of global C flux dynamics, is aerobic R (Dilling and Cypionka 1990; Towe 1990; Sone et al. 2004; Spees et al. 2006; Boutin and Johnson 2007; Ma et al. 2007), which involves the oxidation of organic compounds to produce E rich molecules along with the by–products, H_2O and CO_2. Thus, R by auto- and hetero- trophic organisms releases CO_2 back to the atmosphere. The amount of CO_2 released through terrestrial R_e is similar to that of photosynthetic uptake by terrestrial vegetation (Luo and Zhou 2006; see also Fig. 3.1). A more detailed review of cellular R is provided in due course (Sect. 3.4.2).

The quantity of C stored in terrestrial ecosystems is far greater than that of the atmosphere with over two thirds of terrestrial C stored belowground (Hibbard et al. 2005). Changes in soil C content may have a substantial effect on the global C budget (Bellamy et al. 2005). C enters the soil system through plant, animal and microbial dead organic matter from the above ground biosphere. It is estimated that almost 76 Pg C enters global soils via vegetative inputs every year (Jenksinson et al. 1991; Martin and Bolstad 2005). Dead organic matter is broken down by decomposer organisms in the process of decomposition, whereby organic molecules are sequentially degraded into inorganic ones. The decomposition of organic matter involves both physical fragmentation and chemical reactions and an eventual release of mineral nutrients that can be utilised by plants (Luo and Zhou 2006). Decomposers include soil fauna (e.g. earthworms, beetles, ants, micro-arthropods) and microorganisms (Luo and Zhou 2006). Bacteria (e.g. many Bacilli) and fungi (e.g. many Ascomycetes) (Richards 1987) are the primary consumers of the decomposer food web responsible for most mineralization of nutrients in the soil (Wardle 2002). However, the fraction of soil C (C_s) contained within microorganisms at any given time is small, typically 2 to 5% (Ashman and Puri 2002).

Bacteria and fungi both use exo-enzymes in order to hydrolyse complex organic compounds (Richards 1987). Bacteria colonise the surface of dead organic matter, though fungi are also capable of penetrating cell structures (Waring and Schlesinger 1985). Soil microbial species produce enzymes specific to the decomposition of particular litter components (e.g. hemi-cellulose, cellulose or lignin) so that collectively, a community can decompose the different constituents of dead organic

matter (Luo and Zhou 2006). For instance, Richards (1987) describes how different Clostridia ferment cellulose, starch and pectin, amino acids and proteins, or sugars respectively. Fungal biomass is usually three times that of bacterial biomass in the majority of soils, though bacterial populations have higher turnover and E flow rates, and may contribute more to R_s in some ecosystems (Waring and Schlesinger 1985).

Although the soil is widely regarded as part of an ecosystem, it may be considered a sub-system in its own right (Richards 1987). The aforementioned decomposers are not the only types of organisms that inhabit the soil; as in the above ground biosphere, complex food webs support a variety of herbivorous, predatory, parasitic and mutualistic organisms occupying various trophic niches. However, where plants contribute substantially to primary production above ground, primary productivity is relatively insignificant in the soil system, algae being the only organisms capable of photosynthesis (Richards 1987). The soil system thus depends on the importation of allochthonous dead organic matter, since it does not have the capacity to access large amounts of solar energy (Richards 1987).

3.3 Ecosystem productivity concepts

Gross primary productivity (GPP) can be defined as the total rate of photosynthesis and chemosynthesis, including that portion of the organic material produced which is used in R during the measurement period (Allaby 1998). R has autotrophic (R_a) and heterotrophic (R_h) components, the sum of which constitutes R_e:

$$R_e = R_a + R_h \hspace{4cm} \text{(Eq. 3.2)}$$

However, R losses of C will not contribute to an increase in ecosystem biomass. Therefore net primary productivity (NPP) is defined as the rate of biomass production

after some C has been lost to plant R during the measurement period (Allaby 1998). Thus:

$$NPP = GPP - R_a \qquad \text{(Eq. 3.3)}$$

In order to quantify net ecosystem productivity (NEP), R_h must also be deducted, thus:

$$NEP = GPP - (R_a + R_h) \qquad \text{(Eq. 3.4)}$$

hence,

$$NEP = NPP - R_h \qquad \text{(Eq. 3.5)}$$

Deposition (d) and erosion (e) can input and output ecosystem C respectively and this is considered in net ecosystem exchange (NEE):

$$NEE = (GPP - R_e) + d - e \qquad \text{(Eq. 3.6)}$$

3.4 Soil respiration

3.4.1 Introduction

R_s research has increased substantially over the last ten years (Chapter 1), though Luo and Zhou (2006) discuss how studies involving R_s have a notably long history, the earliest dating back to the 19th Century (Wollny 1831; Boussingault and Levy 1853; Moller 1879). Soil CO_2 production occurs via R of animals, plants and microorganisms inhabiting the soil system. The majority of soil CO_2 efflux is a consequence of aerobic R, though CO_2 is also produced by anaerobic R and consumed in chemical reactions (Luo and Zhou 2006). Both these processes are, however, relatively trivial in comparison to aerobic R and indeed most R_s studies do not consider anaerobic

metabolism or weathering (Luo and Zhou 2006). For this reason, the focus of this section will be on aerobic R_s.

3.4.2 Respiration at the cellular scale

R is the biochemical process by which organic molecules are degraded to CO_2, H_2O and Adensosine triphosphate (ATP). In the case of aerobic oxidation of glucose:

$C_6H_{12}O_6 + 6O_2 \rightarrow 6CO_2 + 6H_2O + energy\ (heat\ or\ ATP)$ (Eq. 3.7)
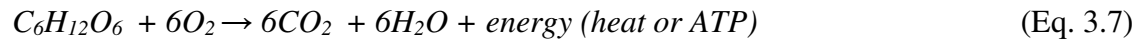
ATP contains an energy rich bond that is spent by the enzyme ATPase to release Adenosine diphosphate (ADP), phosphate (P) and E:

$$ATP \xrightarrow{ATPase} ADP + P + E$$ (Eq. 3.8)

E is required for *all life processes* e.g. cell division, synthesis and maintenance of living tissue and indeed the processes of R and photosynthesis themselves. R takes place in *all living cells* and is hence more properly termed *cellular R*. R is a catabolic process, that is, the breakdown of larger and more complex molecules to smaller, simpler ones, with the release of E (Prescott et al. 1999). It is essentially the reverse of photosynthesis.

The preliminary stage of releasing E involves the catabolism of organic molecules to produce their individual constituents: polysaccharides are broken down to monosaccharides; lipids to glycerol and fatty acids; and proteins to amino acids (Prescott et al. 1999). These simpler organic molecules then undergo a series of reactions to create ATP. The various stages of E release from glucose are now reviewed (see also Fig. 3.2).

Stage one, anaerobic glycolysis, occurs in the cytoplasm of all living cells, where glucose (six C molecule) is broken down to pyruvic acid (or pyruvate)

(CH$_3$COCOOH) (three C molecule) (Prescott et al. 1999). Two net ATP molecules are produced for each molecule of glucose (Raven and Johnson 1999). Electrons are released and removed by Nicotinamide Adenine Dinucleotide (NADH) (C$_{21}$H$_{27}$N$_7$O$_{14}$P$_2$). In *stage two*, pyruvate is
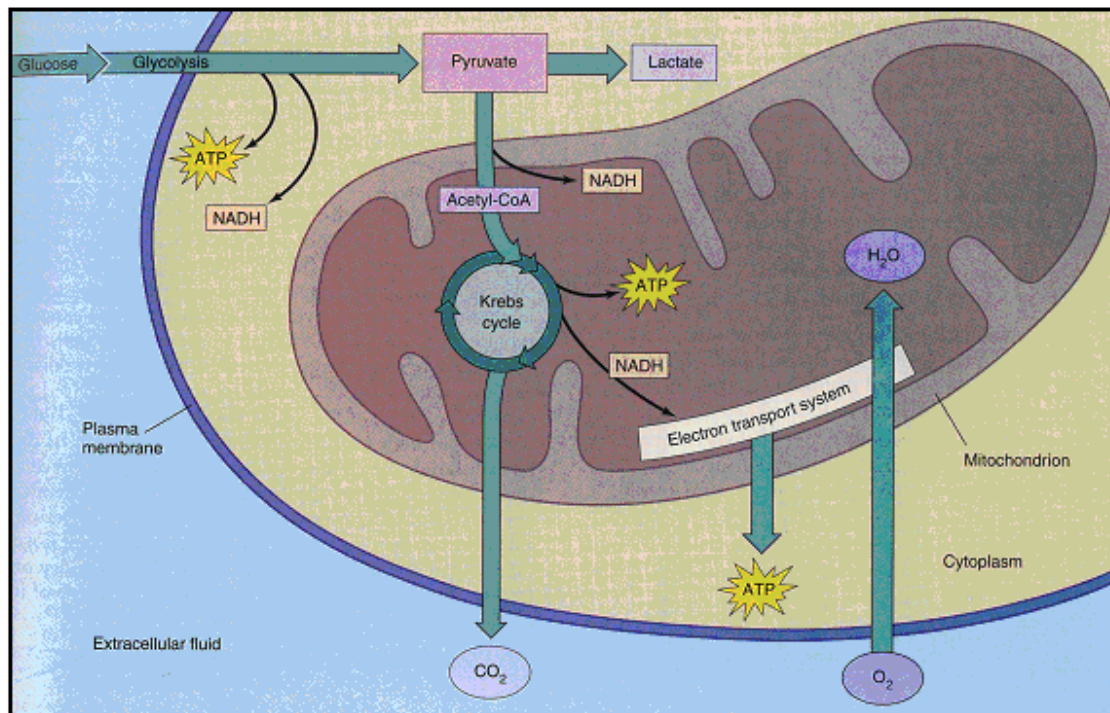
Figure 3.2 Diagrammatic representation of cellular respiration. Source: Raven and Johnson (1999); permission granted by McGraw-Hill.

oxidised to CO$_2$ and acetyl-CoA (C$_{23}$H$_{38}$N$_7$O$_{17}$P$_3$S) producing one molecule of NADH (used to produce ATP via aerobic R) for each pyruvate molecule (Raven and Johnson 1999). NADH accepts electrons released in this process. *Stage three* involves the cycling of acetyl-CoA through nine reactions of the Kreb's Cycle (KC) yielding two molecules of ATP and removing a large amount of electrons by NADH; CO$_2$ and H$_2$O are produced as by-products (Raven and Johnson 1999). In *stage 4*, the electrons

removed by NADH in glycolysis, pyruvate oxidation and the KC pass along carriers of the electron transport chain (ETC), in doing so harvesting large amounts of ATP (Raven and Johnson 1999). A single oxygen (O) atom is the final electron acceptor for two hydrogen (H) atoms, which combine to form H_2O (Raven and Johnson 1999). In *eukaryotes* (higher organisms, with nuclear material enveloped in a nuclear membrane, e.g. animals and plants), carriers of the ETC are proteins located in the cristae (inner membrane) of mitochondria (cell organelles), though in *prokaryotes* (simple organisms, whose nuclear material is *not* enclosed in a nuclear membrane, e.g. bacteria) they are located in the plasma membrane (Prescott et al. 1999; see also Fig. 3.2). The ETC can be similar in prokaryotes and eukaryotes, though it may be shorter in the former and often differs in the electron carriers (Prescott et al. 1999).

Anaerobic R may occur in the absence of O_2, relying solely on ATP produced in glycolysis (Raven and Johnson 1999). In this instance, H atoms are donated to organic molecules (fermentation), often an organic acid, e.g. acetic acid (CH_3COOH) (Raven and Johnson 1999). Aerobic organisms carry out anaerobic R when aerobic R is insufficient to supply a short-term rapid energy release. An 'O_2 debt' is accrued but 're-paid' when O_2 is available to oxidise the accumulated organic acids. Some organisms, however, are solely dependant on fermentation, the so-called obligate anaerobes. Furthermore, some bacteria may carry out anaerobic R by donating electrons to *inorganic* compounds other than O_2, such as sulphur (S) or nitrate (NO_3^-) (Raven and Johnson 1999). Anaerobic R by bacteria that use inorganic molecules as electron acceptors, may produce other waste gases, such as CH_4 and hydrogen sulphide (H_2S) (Raven and Johnson 1999).

CO_2 is a poisonous by-product of aerobic and many forms of anaerobic R and released from organisms in various ways. In mammals, CO_2 is dissolved in blood, exchanged for O_2 in the lungs and exhaled from the body through the mouth. In insects, CO_2 diffuses through a tracheal system and released to the atmosphere through spiracles. Plants release CO_2 through stomata on the leaves, or lenticels on stems and roots. In bacteria, CO_2 diffuses directly out of their plasma membranes.

3.4.3 Soil respiration at the ecosystem scale

R_s is second to photosynthesis in atmosphere-biosphere C flux exchanges from the majority of ecosystems (Davidson et al. 2002; Yim et al. 2002). Moreover, R_s is the largest component of R_e (Ryan and Law 2005) and directly affects NEP. It has been estimated that R_s from forests contributes 60 to 80% of R_e (Law et al. 1997, Janssens et al. 2001, Milyukova et al. 2002; Hubbard et al. 2005). Annual R_s from boreal forests ranges from 150 to 600 g C m^{-2} yr^{-1} (Luo and Zhou 2006).

R_s is comprised of both autotrophic ($R_{s(a)}$) and heterotrophic ($R_{s(h)}$) components (Fig. 3.3), thus:

$$R_s = R_{s(a)} + R_{s(h)} \qquad\qquad\qquad (Eq. 3.9)$$

$R_{s(a)}$ is from plant roots and associated mycorrhizal fungi (Langley et al. 2005; Hughes et al. 2008; Johnson 2008; Bomberg and Timonen 2009). Although some microorganisms are autotrophic, this pool is relatively small and not usually considered part of $R_{s(a)}$. Plant roots commonly form mutualistic, symbiotic associations with mycorrhizal fungi and indeed the majority of vascular plants are believed to have root-mycorrhizal associations (estimates range from 75 to 95% (Prescott et al. 1999)). The

mycorrhizal fungi are filamentous in form with a hyphal (branching, filamentous cells) network that permeates the soil system. Both the plant and fungus benefit from the relationship; the plant obtains an enhanced supply of nutrients in return for supplying the fungus with organic material produced in photosynthesis (photosynthate). Although there is an energy cost to the plant, mycorrhizal fungi increase plant competitiveness (compared to non-mycorrhizal plants) for instance, increasing uptake of nutrients and H_2O, particularly important in nutrient – poor and dry
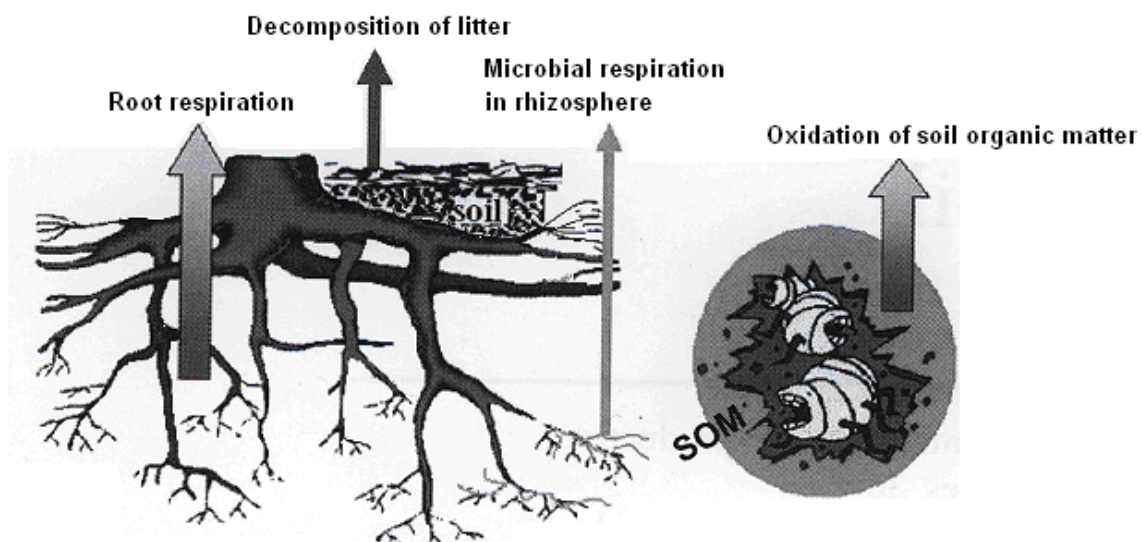
Figure 3.3 The principle component sources of soil respiration. Source: Lou and Zhou (2006); permission granted from Elsevier Academic Press.

soils (Prescott et al. 1999). Although all fungi are heterotrophic, when they obtain carbohydrate from plants in this way they may be considered an autotrophic component of R_s (Ryan and Law 2005). However, whilst fungi commonly play an important role in decomposition, mycorrhizae are generally incapable of decomposing organic matter (Richards 1987). $R_{s(h)}$ refers to the collective soil CO_2 efflux from microorganisms and soil fauna that occupy the different trophic niches of the soil system. Luo and Zhou

(2006) discuss how soil fauna may contribute a non-trivial proportion of R_s, though there is lack of research in this field.

Utilisation and generation of O_2 and CO_2 by R processes yield pressure gradients, usually resulting in net O_2 influx and net CO_2 efflux to and from the soil respectively. CO_2 concentrations in dry soils and litter rarely exceed 0.5%, though in wet soils this value may periodically rise to 10% due to hindered diffusion and enhanced microbial activity (Richards 1987). Soil CO_2 may reside within soil pore spaces, dissolve in soil H_2O or be transported upwards and out into the above-ground atmosphere. There are a number of factors important in the transport of CO_2 in soil including soil texture, soil moisture (M_s), soil porosity and soil tortuosity (Simunek and Suarez 1993; Jensen et al. 1996). Luo and Zhou (2006) discuss how movement of gases is governed by the physics of diffusion (partial pressure gradients: Moldrup et al. 2000a and b) and mass flow (gradient of total gas pressure between two zones: Rolston 1986; Payne and Greggory 1988). Furthermore, soil CO_2 efflux is strongly influenced by gusts and turbulence (Luo and Zhou 2006) and it has been shown that barometric pressure changes can alter deep soil gas diffusion rates by 60% (Kimball 1983).

The principal factors controlling R_s are substrate supply (organic matter), density of fine plant roots, T_s and M_s, though soil texture (Bouma and Bryla 2000; McInerney and Bolger 2000), soil N (Bouma et al. 1996; Magill and Aber 1998; Amthor 2000; Saiya-Cork et al. 2002), soil O_2 (Stolzy 1974; Gambrel and Patrick 1978; Crawford 1992) and soil pH (Kowalenko et al.1978; Situala et al. 1995; Rao and Pathak 1996; Xu and Qi 2001) can also be important. Substrate supply may be linearly related to R_s, e.g. soil organic matter content (Franzluebbers et al. 2001) or litter supply (Maier

and Kress 2000). R_s may also be linearly related to fine root density (Shibistova et al. 2002), though specific root R rates are also important (Holthasen and Caldwell 1980). Both substrate supply and root density are indirectly related to ecosystem productivity, which has been shown to correlate positively with R_s (Janssens et al. 2001; Reichstein et al. 2003).

R_s is generally accepted to respond exponentially to T_s (root R: Berry 1949; Atkin et al. 2000); (microbial R: Flanagan and Veum 1974; Mikan et al. 2002); (total R_s: Lloyd and Taylor 1994). R_s response to T_s is usually modelled using a dimensionless Q_{10} function. A Q_{10} value models the expected factorial increase in R_s for every 10°C rise in T_s, though Q_{10} may not always be constant over a range of T_s (Flemming et al. 2006). Lou and Zhou (2006) state how Q_{10} values generally range from 2.0 to 6.3 for European and North American forest ecosystems (Davidson et al. 1998; Janssens and Pilegaard 2003).

Climate change may be reinforced by increasing R_s as a result of rising T_s, though this is a topic of continuing debate (Bellamy et al. 2005). Short-term rates of $R_{s(h)}$ are strongly and positively dependant on T_s (Kirschbaum 2006), though long-term response to T_s is uncertain (Bradford et al. 2008). A number of field experiments have shown increased R_s in response to higher T_s, but R_s has returned to pre-warming rates within a few years (Jarvis and Linder 2000; Oechel et al. 2000; Luo et al. 2001; Rustad et al. 2001; Melillo et al. 2002; Eliasson et al. 2005). It has been suggested that the temperature sensitivity of decomposition is greater in litter than old soil C in forest systems (Liski et al. 1999) though this is debatable (Giardina and Ryan 2000; Kirschbaum 2004; Eliasson et al. 2005; Fang et al. 2005; Knorr et al. 2005; Hartley et

al. 2007). In addition, thermal adaptation of microbial R to increasing T_s may occur (Oechel et al. 2000; Luo et al. 2001; Reichstein et al. 2005; Davidson and Janssens 2006). The acclimation of R_s to T_s is currently a topic of debate in *Ecology Letters*. Hartley et al. (2008) showed how warming induced changes in the microbial community of arctic soils may amplify R_s and that soil microbial R_s does *not* acclimate to temperature. However, Bradford et al. (2008) showed how acclimation of R_s to T_s in a mid-latitude forest resulted from the combined effects of decreased soil C pools and microbial biomass, and thermal adaptation of microbial R_s (changes in the microbial community).

Fleming et al. (2006) discuss that while most studies of R_s in temperate and boreal forest systems report strong R_s versus (v) T_s relationships, M_s responses of R_s have been detected less frequently (Schlentner and Van Cleve 1985; Law et al. 1999a; Lavigne et al. 2004). This may reflect limited variation in M_s (Drewitt et al. 2002) and / or analytical difficulties in determining R_s v M_s responses (Davidson et al. 1998). Luo and Zhou (2006) discuss how understanding of the R_s v M_s relationship is limited and has been modelled using linear, quadratic, parabolic, hyperbolic and exponential functions. Soil microbial R is often expected to increase with M_s (water limiting) up to some optimal level, thereafter declining (aeration limiting) with further increases in M_s. Foster et al. (1980) describe that as soils approach saturation, O_2 becomes limiting to aerobic metabolism and R_s is suppressed (Bernier 1960; Roberge 1976). The optimal M_s may be well-defined (Papendick and Campbell 1981) or plateau over a range of values (Liu et al. 2002; Xu et al. 2004). Fleming et al. (2006) discuss how most field studies of R_s reveal little response to M_s over broad ranges of intermediate M_s values

(Law et al. 1999b; Fang and Moncrieff 2001; Drewitt et al. 2002). Details of R_s responses to T_s and M_s more relevant to this research are provided in Chapter 4.

R_s may be highly spatially variable along gradients of latitude (Santruckova et al. 2003), altitude (Kane et al. 2003) and topography (Kang et al. 2003). R_s rates are known to vary at biome (Raich and Schlesinger 1992) and ecosystem (Janssens and Ceulemans 1998) scales. Luo and Zhou (2006) describe how R_s can exhibit high spatial variability at the stand level, even in relatively homogeneous soils, such as arable systems. Temporal variability can occur at diurnal (Xu and Qi 2001), seasonal (Borken et al. 2002), inter-annual (Irvine and Law 2002) and decadal (Singh et al. 2008) scales.

In Chapter 1, it was discussed how the possibility of changing boreal forest fire regime has led to C flux research being carried out in fire scar chronosequences. The majority of studies have demonstrated a reduction or no change in R_s following fire and a greater difference is seen the more severe the fire (Reinke et al. 1981; Weber 1985; Weber 1990; Fritze et al. 1993; Fritze et al. 1994; Burke et al. 1997; Sawamoto et al. 2000; O'Neil et al. 2002; Amiro et al. 2003; Singh et al. 2008). Decreased rates of $R_{s(a)}$ could occur if roots are directly affected by fire or plant R is suppressed as a result of damage to above ground soil organs. Post fire succession may result in a gradual increase in $R_{s(a)}$ as the vegetation recovers from disturbance. $R_{s(h)}$ however, may increase soon after fire in forest ecosystems, due to increased T_s (more open canopy, lower albedo of charred soil surface, and heat from fire itself) and / or accumulation of dead organic matter (Pregitzer and Euskirchen 2004; Yermakov and Rothstein 2006). N mineralization rates may increase immediately after fire but subsequently decrease, paradoxically as organic matter accumulates (Yermakov and Rothstein 2006). It is

believed that the combination of decreased organic matter quality and altered soil microclimate can reduce microbial activity (Van Cleve and Noonan 1975; Van Cleve and Viereck 1981; Zackrisson et al. 1997; DeLuca et al 2002; Wardle et al. 2003). The consensus is that organic matter mineralization decreases with successional time in northern forest systems, with consequently low nutrient availability in mature seres (Van Cleve and Viereck 1981; Van Cleve et al 1983; Paster et al 1987; Bormann and Sidle 1990; DeLuca et al. 2002; Yermakov and Rothstein 2006). $R_{s(h)}$ may therefore be lower in later seral stages (Yermakov and Rothstein 2006).

In reality, multiple factors interact to determine R_s rates and it may be difficult to separate individual responses (Luo and Zhou 2006). Like other eco-physiological processes, R_s usually responds to the most limiting factor (Luo and Zhou 2006). Carlyle and Bathan (1988) showed that R_s is responsive to T_s at high M_s (<0.75 volumetric M_s) but insensitive to T_s at low M_s (0.1 to 0.25 volumetric M_s). Vanhala (2002) showed that when T_s is constant at 14°C, R_s is controlled by M_s and pH, but when M_s is constant at 60% water holding capacity (WHC), it is pH and the quantity of organic matter that predominantly constrains R_s.

3.4.4 Field measurements of soil respiration

There are numerous methods that have been employed to measure R_s e.g. open dynamic chamber method (Pumpanen et al. 2001), closed static chamber method (Grogen 1998), alkali trapping (Kabwe et al. 2002), soda lime trapping (Yim et al. 2002) and gas chromatography (Abnee et al. 2004). Furthermore, various techniques have been used to separate component sources of R_s e.g. trenching (Edwards and Norby 1998), tree girdling (Hogberg et al. 2001) and use of stable or radioactive isotopes (Pendall et al.

2004). However, this section will focus on field measurements of total R_s, using the closed dynamic chamber approach since this is the method used in the research.

R_s can be measured in the field using a Soil Respiration System (SRS) (Fig. 3.4). SRS's consist of a R_s chamber (SRC) connected to an Infra-Red Gas Analyser (IRGA). In order to measure R_s, the SRC may be placed over a soil collar (often made of Polyvinylchloride (PVC)) (Fig. 3.5), providing an air-tight seal between it and the soil surface. CO_2 diffuses upward from the soil into the SRC causing its CO_2 concentration to increase over time. This is monitored by the IRGA (Fig. 3.6). Soil collars are normally inserted prior to measurement (at least 12hrs before; Wang et al. 2005) in order to minimise disturbance and subsequent over-estimation of CO_2 efflux (CO_2 spring-out effect (Licor 1997)). Furthermore, they can be used to take repeated measurements of R_s at the same location. Wang et al. (2005) showed how R_s was directly affected by soil collar insertion depth. Insertion at shallow depths may lead to over-estimation of R_s caused by unstable collars and CO_2 spring–out, though deeply inserted collars can sever plant roots and lead to an under-estimate of R_s (Wang et al. 2005). Mosses and grasses growing on the soil surface may be clipped prior to measurement to eliminate above ground R_a.

IRGA's e.g. CIRAS-1 (PP Systems), utilise the Infra-Red (IR) absorption characteristics of certain molecules (Fig. 3.7). CO_2 is a diatomic molecule that strongly absorbs photons of IR radiation (PP Systems 2003). Indeed, CO_2 molecules absorb photons particularly strongly at a wavelength of 4.3 µm (PP Systems 2003). At one end of a tube, photons of IR radiation are emitted from a light source and at the other end, a sensor detects these photons. The addition of CO_2 to the tube results in absorption of

some of the photons, thereby decreasing the reading on the sensor. CO_2 continuously circulates to the IRGA (via an internal pump) through connecting tubes where it is analysed. In CIRAS-1, the measured change in CO_2 concentration (DC; units ppm) and elapsed time (DT; units s) are used in the calculation of R_s (units: g CO_2 m^{-2} hr^{-1}).

Figure 3.4 The PP Systems Soil Respiration System consisting of an infra-red gas analyser (CIRAS-1) (background) connected to a soil respiration chamber (SRC-1) (foreground). Source: author's collection.

Figure 3.5 Soil collar inserted prior to measurement of soil respiration. A soil respiration chamber (connected to an infra red gas analyser) can be placed over the collar when taking measurements of soil respiration. Source: author's collection.
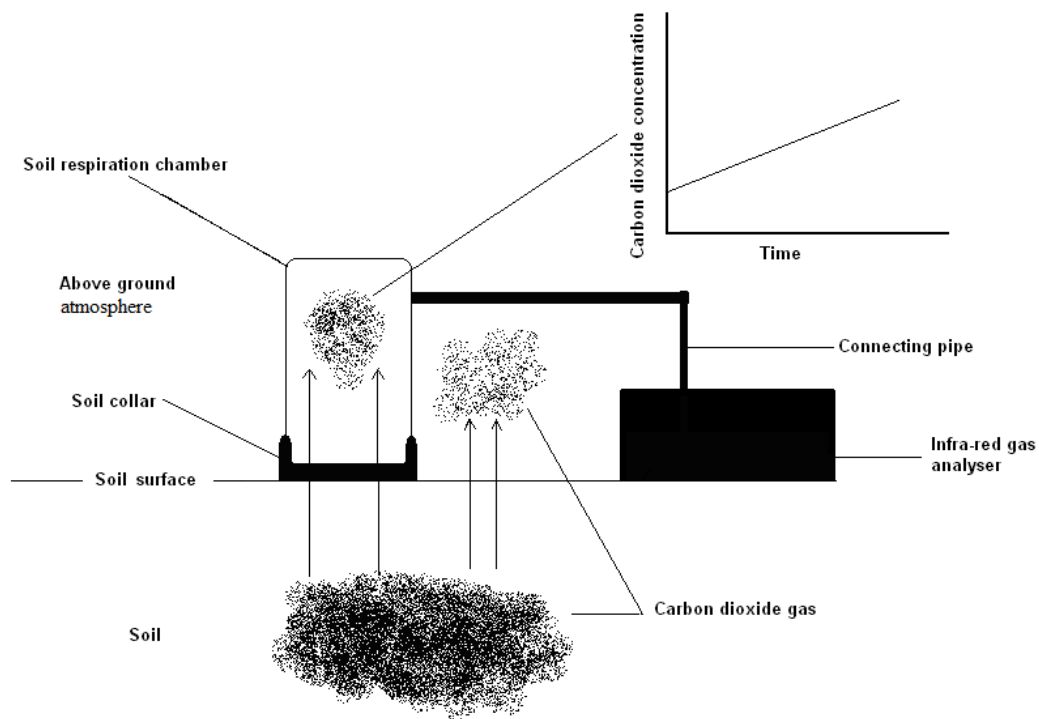
Figure 3.6 Principle of soil respiration (R_s) measurement. Soil carbon dioxide (CO_2) moves upward into the R_s chamber causing its CO_2 concentration to increase over time in an approximately linear relationship. This increase is monitored by the infra-red gas analyser attached to the R_s chamber. Not to scale.
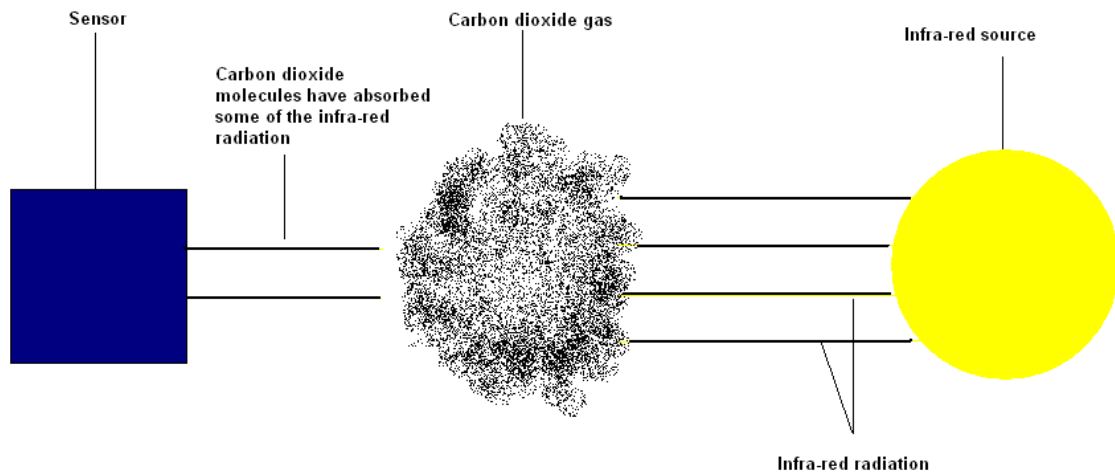
Figure 3.7 Principles of an infra red gas analyser. A light source emits infra red (IR) radiation strongly at 4.3 μm, which is detected by a sensor. The addition of carbon dioxide (CO_2) to the system absorbs some of the IR radiation, thereby reducing the amount of IR radiation reaching the sensor. The sensor reading is subsequently lowered by the addition of CO_2. Not to scale.

3.5 Summary

The C cycle describes the way C flows between the atmosphere, geosphere, hydrosphere and biosphere. C enters the biosphere through photosynthesis and exits via R. C enters the soil system via plant, animal and microbial remains from the above ground biosphere and organic matter is broken down in the process of decomposition. R_s is comprised of $R_{s(a)}$ (roots and associated mycorrhizal fungi) and $R_{s(h)}$ (microorganisms and soil animals) and is controlled primarily by T_s, M_s, C_s and soil fine root content. R_s can be measured in the field using a SRS comprised of an IRGA connected to a SRC. The next chapter reviews the literature most relevant to the research, that is, R_s in jack pine dominated ecosystems.

Chapter 4: Soil respiration in jack pine ecosystems

4.1 Introduction

This chapter reviews the literature most relevant to the research, specifically R_s in jack pine dominated ecosystems. The focus of the next section is an overview of jack pine systems. This is followed by a review of those studies that have considered the spatial variability of R_s in jack pine forests. Thereafter, the T_s and M_s responses of R_s in jack pine systems are considered respectively, followed by an overview of R_s in jack pine fire scar chronosequences. The literature where a modelling approach has been used to simulate R_s in jack pine systems is then reviewed. Subsequently, the main gaps in the literature are considered and this is followed by specific research questions.

4.2 Jack pine ecosystems

Jack pine (*Pinus banksiana* Lamb.) is a short-lived, early successional species (Yermakov and Rothstein 2006) and one of nine tree species dominant and widespread in boreal regions of North America (Payette 1992; Euskirchen et al. 2006; see also Chapter 2, Fig. 2.3). Jack pine covers in excess of $2*10^{12}$ m^2 of predominantly well drained uplands in northern North America (Law and Valade 1994; Lowe et al 1994; Striegl and Wickland 2001; Howard et al. 2004), though the species can also be found in northern temperate regions (Barnes and Wagner 1996).

Jack pine commonly grows on dry areas in sandy, gravel or thin soils (Little and Garrett 1990; Rudolph and Laidly 1990; Day et al. 2005), though the species may also grow on clay soils (Beland et al. 2003). Jack pine is able to grow on soils low in nutrients and M_s (Cayford and McRae 1983), where other species cannot establish

themselves (Yermakov and Rothstein 2006). Beland et al. (2003) describe how jack pine requires a seedbed of usually mineral soil (Chrosciewicz 1990) and is shade intolerant, requiring full sunlight for growth (though some shade may benefit germination) (Burns and Honkala 1990; Chrosciewicz 1990). Although jack pine may be replaced in succession e.g. by black spruce (Bergeron and Brisson 1990; Gauthier et al. 1993; Lesieur et al. 2002; Bergeron et al. 2004; Smirnova et al. 2008), long term maintenance may occur through disturbances such as harvest, insect outbreaks and fire (Striegl and Wickland 2001).

Natural regeneration of jack pine is poor after harvesting and Beland et al. (2003) discuss how jack pine is dependant on fire for its maintenance (Cayford and McRae 1983). Heat from forest fires opens the serotinous cones, releasing seeds and initiating a new generation of trees within the immediate vicinity. High population densities and combustible foliage render jack pine systems prone to fire (Rowe and Scotter 1973; Yermakov and Rothstein 2006). In fact, boreal jack pine forests have fire return intervals of 40 to 80 years and are one of the most fire prone ecosystems in North America (Carroll and Bliss 1982; Cogbill 1985; Desponts and Payette 1992; Larsen 1997; Yermakov and Rothstein 2006). North American jack pine stands are generally even aged as a result of stand replacing, high intensity fires (Smirnova et al. 2008). However, moderate intensity fires may be tolerated by jack pine and situations can occur whereby mature trees survive amongst a new cohort. Here, the post-fire stand retains legacies from the pre-fire community (Desponts and Payette 1992; Gauthier et al. 1993; Smirnova et al. 2008).

It is possible that with future warming of the boreal forest, jack pine could become more abundant due to increasing fire regimes (size, frequency, intensity) and drier soils. Since jack pine systems are particularly prone to fire, this may further increase fire regimes, a positive feedback mechanism.

4.3 Spatial variability of soil respiration in jack pine ecosystems

The spatial variability of R_s in jack pine systems has been rarely addressed. The first quantitative assessment of R_s spatial variability in jack pine systems reported a coefficient of variation (CV) for mean monthly R_s of 9 to 28% (Weber 1985). Although Burke et al. (1997) observed considerable variability in daily R_s they provided no CV or estimate of sample size (N). On average, CV of R_s (CV_{R_s}) was 31.3% at old jack pine (OJP) and 30.1% at clear-cut (CC) sites in a study by Striegl and Wickland (1998). Striegl and Wickland (2001) added to this by reporting average CV_{R_s} of 22.8% at young jack pine (YJP) and 30.4% at recent cut (RC) sites.

In a recent study of a jack pine chronosequence, Singh et al. (2008) showed within site CV_{R_s} to range from 26 to 61%, with a mean of 35%. Generally R_s at the 1998 fire scar (youngest) was most spatially variable. R_s in the older site had significantly lower variability than the younger sites, which did not significantly differ in variance themselves ($P > 0.05$). Furthermore, for any given site, the greatest within site CV_{R_s} occurred at different months, the 1998 fire scar in July, 1989 scar in June and the 1977 scar in August. They report necessary N of 25, 10 and 12 for estimating mean

R$_s$ ($\bar{R}_s$) within a fractional error (*FE*) acceptance of 20% (of the true mean) for the 1998, 1989 and 1977 fire scars respectively.

4.4 Soil temperature response of soil respiration in jack pine ecosystems

Research into the T$_s$ response of R$_s$ in jack pine systems has a very short history. Brooks et al. (1997) were among the first to study the R$_s$ v T$_s$ relationship in 40 to 60 year old jack pine forest, though no empirical functions or Q_{10} values were reported (Fig. 4.1). Subsequently, a number of studies of the R$_s$ v T$_s$ response have been carried out in jack pine forests of a specific age. Euskirchen et al. (2006) investigated the T$_s$ response of R$_s$ in a young naturally regenerating (CC in 1988) jack pine ecosystem, near the town of Alberta, Michigan, USA (46°N, 88°W). Over three years of study, they report Q_{10} values of 1.1 (2001), 2.3 (2002) and 1.9 (2003), and 2.2 over all years of data combined. Fleming et al. (2006) also investigated the R$_s$ v T$_s$ response in a post-harvest (CC in 1993) jack pine forest in Wells Township, Ontario, Canada (46°21'N, 83°23'W). This site, at the southern boundary of boreal forest biome, yielded Q_{10} values in the range 1.8 to 2.8 (Fig. 4.2). Other studies have investigated the R$_s$ v T$_s$ relationship in two ages of jack pine forest. Striegl and Wickland (1998) found T$_s$ to explain at least 50% of the variability in R$_s$ for two ages of jack pine forest, with Q_{10} values ranging from 2.02 to 2.68 (Fig. 4.3).
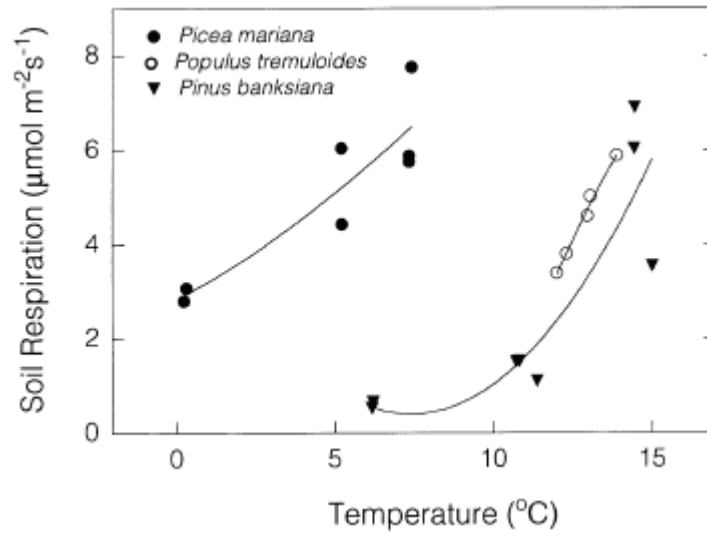
Figure 4.1 Soil respiration versus soil temperature for three forest stands in the BOREAS (Boreal Ecosystem-Atmosphere Study) northern study area (northern limits of the boreal forest in central Canada; 55.928°N, 98.622°W), 1994. ▼ Jack pine (*Pinus banksiana*) stand 40 to 60 years old. Source: Brooks et al. (1997); permission granted from Oxford University Press.
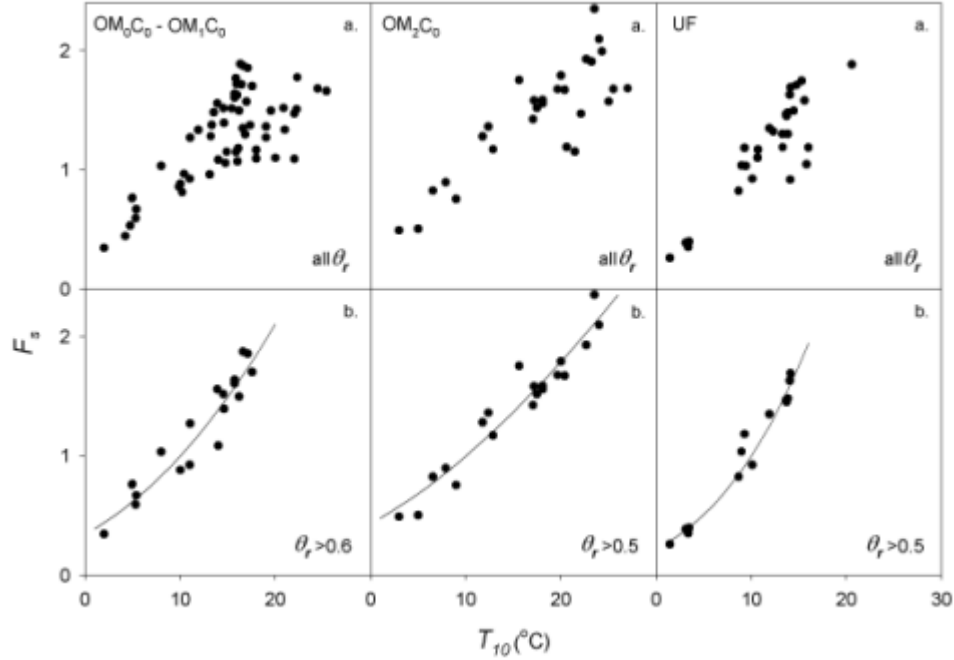
Figure 4.2 Scaled soil respiration (F_s) versus soil temperature (T_{10}) in jack pine systems. T_{10} = soil temperature 10 cm below surface. F_s = measured soil respiration / baseline soil respiration at 10°C under non-limiting volumetric soil water content (θ). Relative soil water content ($θ_r$) = θ at 0 to 10 cm depth / maximum θ at 0 to 10 cm depth. OM_0C_0 = stem only harvest; OM_1C_0 = full tree harvest (stems plus crowns removed); OM_2C_0 = full tree harvest with surface soil removal; UF = uncut forest. Soil respiration measured during 1996 to 1998 snow free seasons. F_s versus T_{10} produced r^2 of 0.92 to 0.98 when θ large. Source: Fleming et al. (2006); permission granted from *Canadian Journal of Forest Research***; The Canada Institute for Scientific and Technical Information (CISTI).**
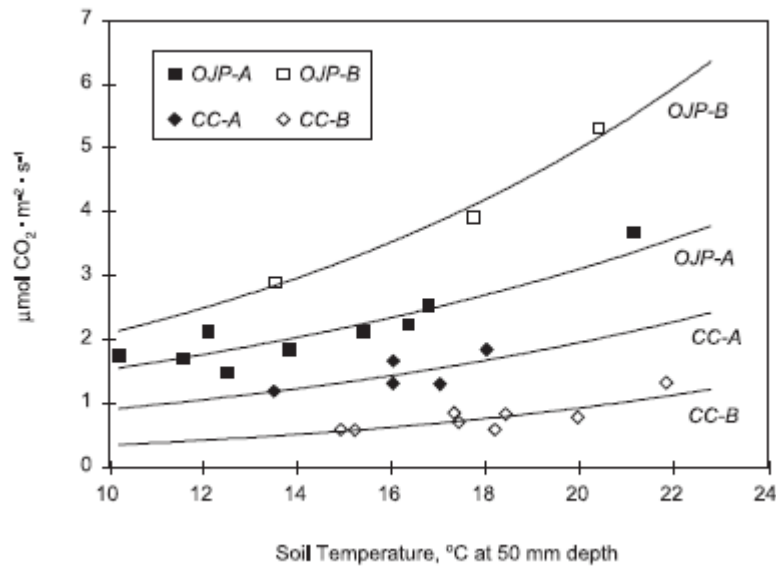
Figure 4.3 Soil respiration† (R_s) versus soil temperature at old (OJP) and clear-cut* (CC) jack pine sites located in the BOREAS (Boreal Ecosystem-Atmosphere Study) southern study area (SSA), approximately 100 km north east of Prince Albert, Saskatchewan, Canada (53.916°N, 104.691°W). †Each R_s value is the mean of six chamber measurements taken May through September 1994. *Jack pine trees harvested from the CC site during the winter of 1993 to 1994. For the four exponential curves: (OJP-A; r^2=0.8; Q_{10} = 2.02); (OJP-B: r^2= 0.98; Q_{10}= 2.38); (CC-A: r^2=0.5; Q_{10}=2.16); (CC-B: r^2=0.68; Q_{10}=2.68). Source: Striegl and Wickland (1998); permission granted from *Canadian Journal of Forest Research*; The Canada Institute for Scientific and Technical Information (CISTI).

Euskirchen et al. (2003) studied R_s and T_s interactions in mature jack pine (MJP) and open canopy jack pine barrens (PB) burned <7 years previously. Here they report significant exponential relationships ($P < 0.0001$) of R_s versus T_s, though T_s explained more of the variation in R_s at the younger site (MJP: $Q_{10} = 1.67$; $r^2 = 0.45$); (PB: $Q_{10} = 1.92$; $r^2 = 0.66$) (Fig 4.4).

Finally, research has investigated the R_s versus T_s response in jack pine dominated chronosequences. In one such study, R_s was plotted against T_s for a jack
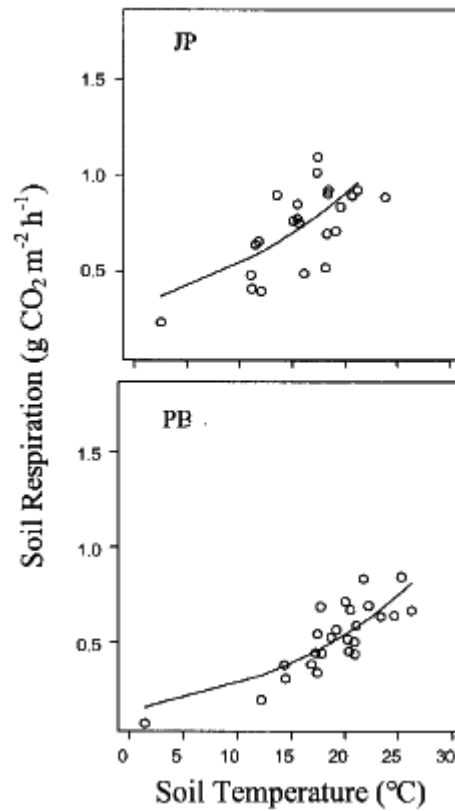
Figure 4.4 Soil respiration (R_s) versus soil temperature (T_s) for jack pine (JP) and open canopy jack pine barrens (PB) in the Washburn Ranger District of the Chequamegon National Forest, Wisconsin, USA (46º30 to 46º45'N, 91º02 to 91°22'W). Data points represents means among three replicates of each patch type for each sampling session, or 30 individual measurements. R_s versus T_s revealed significant exponential relationships ($P < 0.0001$): (JP: $R_s = 0.3235*e^{(0.0514*T_s)}$; standard error = 0.0798; $Q_{10} = 1.67$; $r^2 = 0.45$); (PB: $R_s = 0.1466*e^{(0.0653*T_s)}$; standard error = 0.0365; $Q_{10} = 1.92$; $r^2 = 0.66$). Standard errors are of the intercept term. Source: Euskirchen et al. (2003); permission granted from Springer-Verlag.

pine chronosequence, though exponential functions which represented $Q_{10} = 2$ were fitted to the data, as opposed to calculation of more precise Q_{10} values (Striegl and Wickland 2001; personal communication; see also Fig. 4.5 to 4.7). Howard et al. (2004) found R_s to be significantly affected by T_s ($P < 0.0001$) and T_s explained a large

50

Figure 4.5 Soil respiration (R_s) versus soil temperature (T_s) at the BOREAS site in central Saskatchewan, Canada. Old jack pine (OJP): established after fire in early 1900s, over-storey composed entirely of mature jack pine 60 to 75 years in 1994. Empirical functions:
OJP early/late (5/26 to 6/29 and 7/30 to 9/14): $R_s = 0.7595e^{(0.07030*T_s)}$; $r^2 = 0.8$; $Q_{10} = 2.0$;
OJP mid (6/30 to 7/29): $R_s = 0.8807e^{(0.0867*T_s)}$; $r^2 = 0.98$; $Q_{10} = 2.0$
Source: Striegl and Wickland (2001); permission granted from *Canadian Journal of Forest Research*; The Canada Institute for Scientific and Technical Information (CISTI).

amount of observed variation in R_s (adjusted r^2 range: 0.73 to 0.88). Q_{10} values were high and ranged from 3.77 in a five year old stand to 7.12 in a 29 year old stand, though there was no clear pattern of Q_{10} change over time (Table 4.1). Yermakov and Rothstein (2006) found R_s to be significantly affected by T_s (linear regression: ln R_s = 0.034*T_s+3.366; $P < 0.001$; $Q_{10} = 1.40$), though the strength of the relationship was limited ($r^2 = 0.302$). Monthly measurements of R_s positively correlated with average T_s
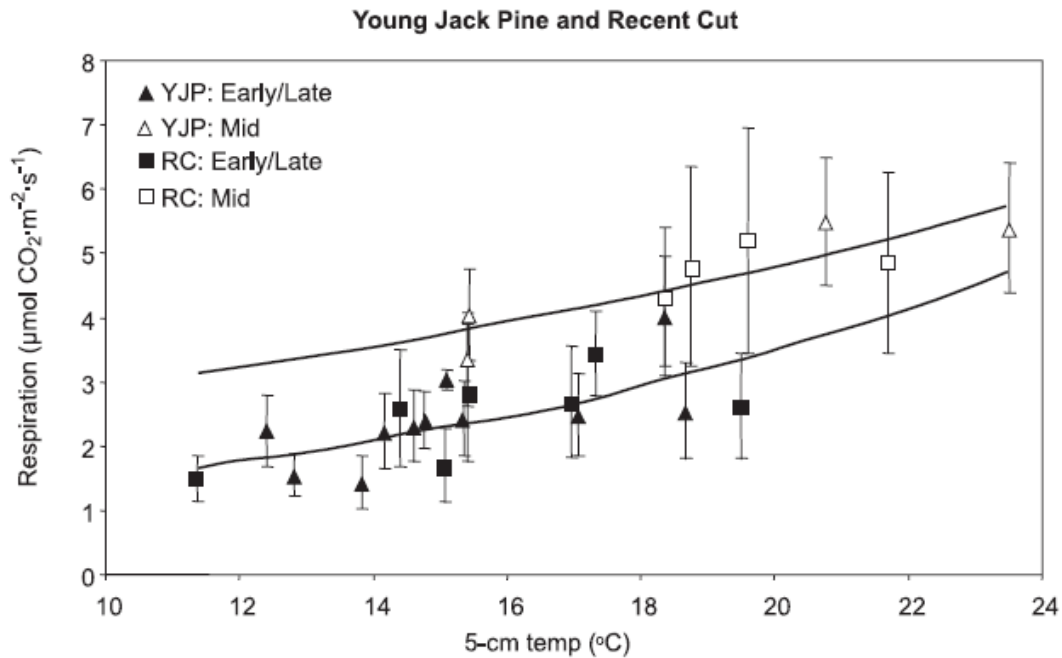
Figure 4.6 Soil respiration (R$_s$) versus soil temperature (T$_s$) at the BOREAS site in central Saskatchewan, Canada. Young jack pine (YJP) - clear cut in late 1970's, 16 to 20 year old jack pine in 1994; Recent cut (RC) – formally mature jack pine. Empirical functions:

YJP and RC early/late (5/26 to 6/24 and 8/3 to 9/15) = 0.63e^(0.0858*T$_s$); r^2=0.47; Q_{10} =2.0;

YJP and RC mid (6/25 to 8/2): R$_s$ =1.7558 e^(0.0505*T$_s$); r^2 = 0.73; Q_{10} = 2.0;

Source: Striegl and Wickland (2001); permission granted from *Canadian Journal of Forest Research*; The Canada Institute for Scientific and Technical Information (CISTI).

(r = 0.591) though the strength of the relationship declined with stand age from correlation values of 0.978 in the youngest stand (age 1 year) to 0.511 in the oldest stand (age 72 years).
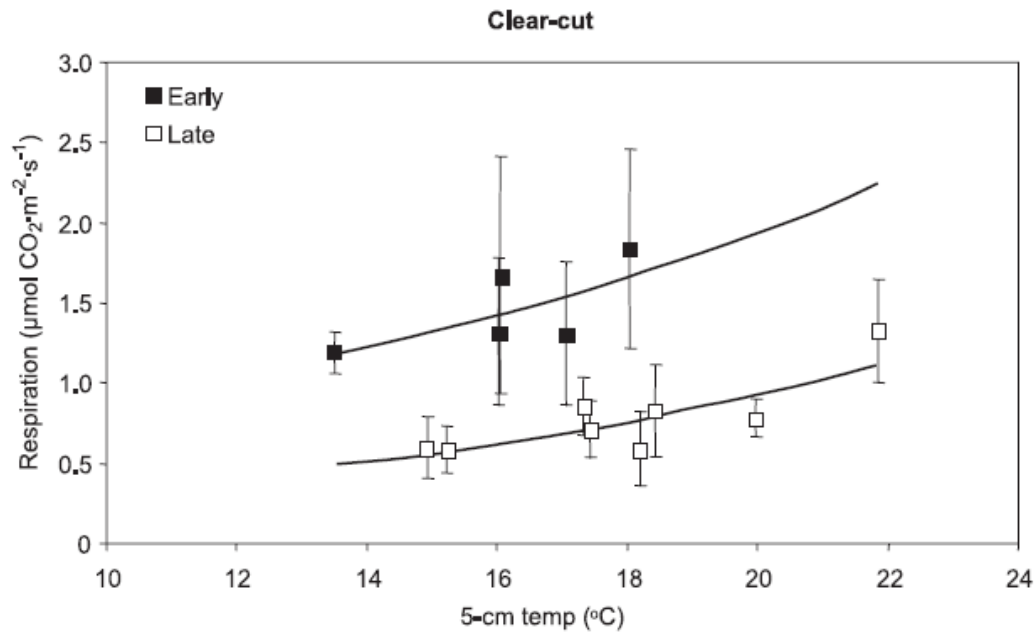
Figure 4.7 Soil respiration (R_s) versus soil temperature (T_s) at the BOREAS site in central Saskatchewan, Canada. Clear cut (CC): performed in mid- 1980's - formally mature jack pine stand; jack pine trees 8 years old in 1994; CC during autumn and winter of 1993 to 1994; summer of 1994 most of soil surface bare or covered with dead / dying vegetation or slash. Empirical functions:

CC early (5/26 to 7/24) = 0.4185e^(0.0769*T$_s$); r^2 = 0.50; Q_{10} = 2.0;

CC late (7/25 to 9/14) = 0.1298e^(0.984*T$_s$); r^2=0.67; Q_{10} = 2.0

Source: Striegl and Wickland (2001); permission granted from *Canadian Journal of Forest Research*; The Canada Institute for Scientific and Technical Information (CISTI).
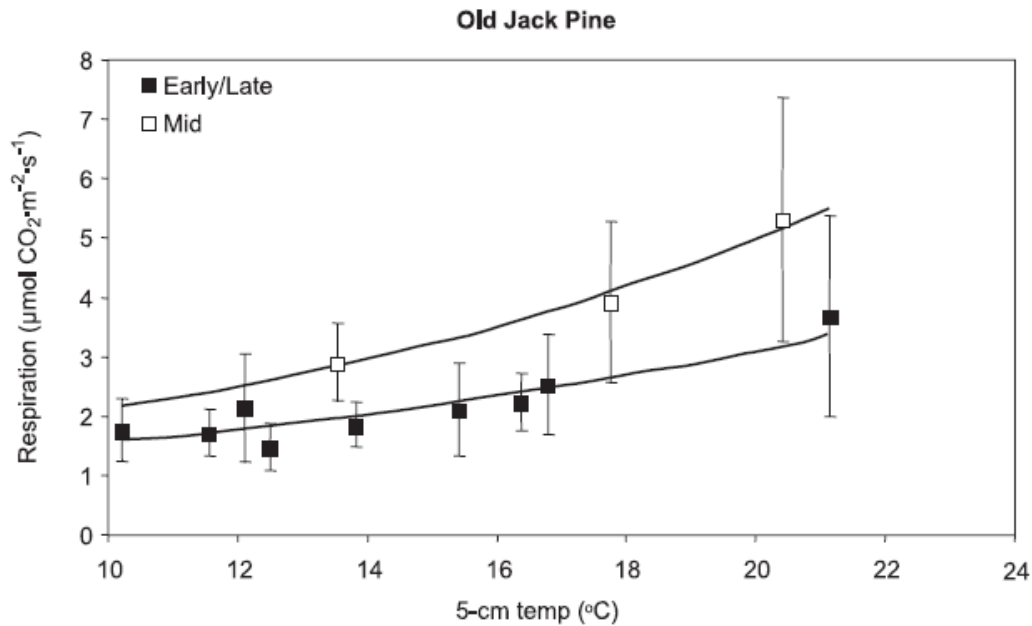
Table 4.1 Soil respiration (R_s) versus soil temperature (T_s) regressions in a chronosequence of harvested† jack pine

Stand age	Regression equation	n	r^2	F	P	Q_{10}
0	$\log_e R_s = -1.20005 + 0.1635 * T_s$	143	0.78	507	< 0.0001	5.13
5	$\log_e R_s = -1.65280 + 0.1328 * T_s$	145	0.73	377	< 0.0001	3.77
10	$\log_e R_s = -1.33644 + 0.1509 * T_s$	151	0.78	514	< 0.0001	4.51
29	$\log_e R_s = -1.23751 + 0.1963 * T_s$	136	0.88	967	< 0.0001	7.12
79	$\log_e R_s = -1.44210 + 0.1670 * T_s$	194	0.73	531	< 0.0001	5.31

†Except 79 year old fire scar. Study area near the southern limit of the boreal forest in Saskatchewan, Canada. R_s was significantly affected by T_s ($P < 0.0001$ in all cases) and T_s explained a large amount of observed variation (adjusted r^2 range: 0.73 to 0.88; $P < 0.0001$ for all coefficients) in R_s. Soil moisture did not improve the regression models. Q_{10} values calculated by Daniel Smith. Modified from Table 4 in Howard et al. (2004). Permission granted from Wiley-Blackwell.

4.5 Soil moisture response of soil respiration in jack pine ecosystems

The relationship between R_s and M_s has received relatively little attention in jack pine systems compared with that of the R_s v T_s response. However, the first research to investigate the M_s dependence of R_s in jack pine forests (Foster et al. 1980) was published 17 years prior to that of the first study of the R_s v T_s relation (Brooks et al. 1997). Foster et al. (1980) performed an incubation study to investigate the M_s response of microbial R_s in humus from a 45 year old jack pine stand in the Missinaibi-Cabonga section of the boreal forest near Chapleau, Ontario, Canada. Over the M_s range 40 to 100% (6 to 15% WHC),

initial R_s was directly related to initial M_s. However, total R_s summed over 13 days was similar at constant M_s levels of 60 to 300% (9 to 45% WHC). Indeed, only <60% M_s content did significant reductions in R_s occur, until R_s ceased at 20% M_s. Foster et al. (1980) suggest that since the maximum M_s tested was < saturation, O_2 diffusion in the soil was unlikely to have limited R_s. However, no direct R_s v M_s relationship was quantified.

A considerable amount of time elapsed between the work of Foster et al. (1980) and the second investigation into the M_s response of R_s in jack pine systems. In a study by Euskirchen et al. (2003), prediction of R_s from T_s and M_s in open canopy jack pine barrens (burned <7 years previously) was substantially improved (greater r^2) when an M_s, and T_s * M_s interaction term was incorporated into their T_s model. Indeed, models that used both T_s and M_s explained between 46 and 74% of the variability in R_s. Only very recently has the R_s v M_s relationship been displayed graphically by polynomial type curves (Fleming et al. 2006; see also Fig. 4.8).
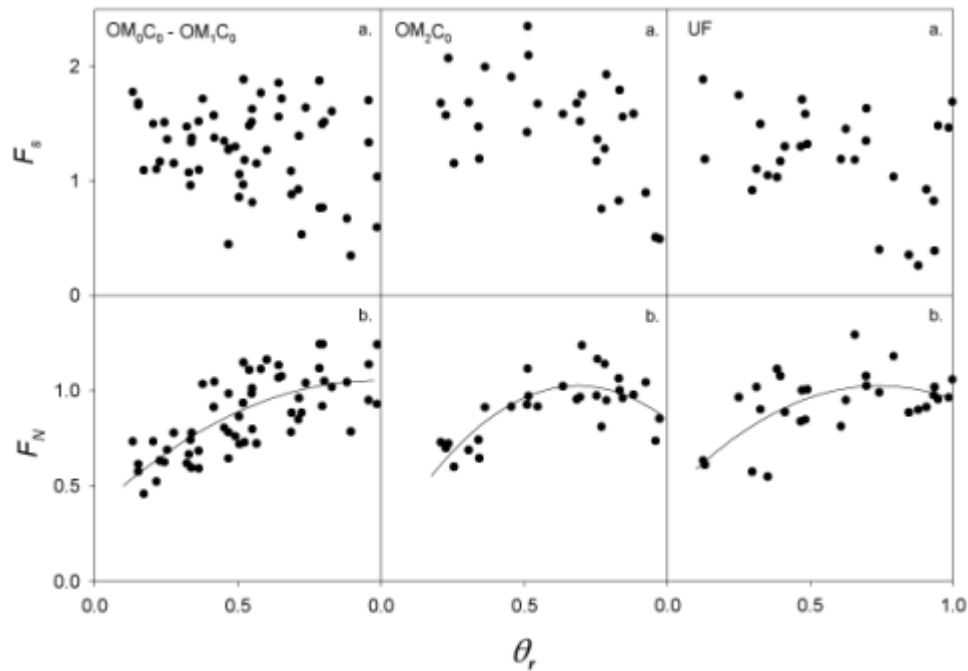
Figure 4.8 Scaled soil respiration (R_s) versus relative soil water content (θ_r). Scaled R_s = measured R_s / baseline R_s at 10°C under non-limiting volumetric M_s. (a) – scaled R_s (shown here as F_s) not temperature normalised; (b) – temperature normalised scaled R_s (shown here as F_N). θ_r = volumetric soil moisture at 0 to 10 cm depth / maximum volumetric soil moisture 0 to 10 cm depth. OM_0C_0 = stem only harvest; OM_1C_0 = full tree harvest (stems plus crowns removed); OM_2C_0 full tree harvest with surface soil removal; UF = uncut forest. Source: Fleming et al. (2006); permission granted from *Canadian Journal of Forest Research*; The Canada Institute for Scientific and Technical Information (CISTI).

4.6 Soil respiration in jack pine dominated fire scar chronosequences

R_s research has been conducted in boreal jack pine dominated post-harvest chronosequences (Striegl and Wickland 2001; Howard et al. 2004), boreal fire scar chronosequences dominated by species other than jack pine (Zhuang et al. 2002; Wang et al. 2003; Bond–Lamberty et al. 2004; Czimczik et al. 2006; O'Neil et al. 2006) and a boreal jack pine fire scar of a single age category (Striegel and Wickland 2001). However,

the focus of this section will be R_s in *jack pine dominated fire scar chronosequences* since this is most directly relevant to the research.

Weber (1985) was the first to investigate R_s in a jack pine fire scar chronosequence, detecting significant differences between fire scars that differed in their burn history (Table 4.2). Burke et al. (1997) investigated R_s in unburned and burned (~ five years old) jack pine forest. R_s measurements were made in spring and summer from the BOREAS northern study area (NSA) near Thompson, Manitoba, Canada (55.91°N, 98.42°W). R_s ranged from 0.36 to 7.46 g C/m^2/d (transformed units: 0.35 μmol CO_2/m^2/s to 7.20 μmol CO_2/m^2/s). Unburned had significantly greater median R_s than burned forest: unburned = 1.34 g C/m^2/d (transformed units:

1.29 μmol CO_2/m^2/s); burned = 1.01 g C/m^2/d (transformed units: 0.97 μmol CO_2/m^2/s).

Savage et al. (1997) measured R_s in old (OJP) and young (YJP) jack pine forest of the BOREAS NSA from May through September 1994 at weekly intervals. Average R_s ± standard deviation (σ) values were: OJP-lichen, R_s = 4.8 ± 2.9 g CO_2/m^2/d (transformed units: 1.26 μmol CO_2/m^2/s); OJP-aspen, R_s = 8.0 ± 2.9 g CO_2/m^2/d (transformed units: 2.10 μmol CO_2/m^2/s); OJP-moss, R_s = 4.8 ± 2.2 g CO_2/m^2/d (transformed units: 1.26 μmol CO_2/m^2/s); YJP, R_s = 6.3 ± 3.2 g CO_2/m^2/d (transformed units: 1.66 μmol CO_2/m^2/s). Euskirchen et al. (2003) studied R_s in jack pine forests within the Washburn Ranger District of the Chequamegon National Forest, Wisconsin, USA (46°30 to 46°45'N, 91°02 to 91°22'W). R_s measurements were taken from three replicates of (1) mature jack pine forest (MJP) and (2) open canopy jack pine barrens (PB) (burned <7 years previously) during June through September 1999 and April through October 2000. No significant differences (Bonferroni corrected t tests;

$P < 0.05$) in $\overline{R}_s$ between MJP and PB were detected in either 1999 or 2000

Table 4.2 Multiple comparison matrix of means (± standard errors) from overall seasonal forest soil respiration (R_s) (mg CO_2/m^2/day) on five burning treatments.

Treatment	Comparison			
1920(4504±140)	1963			
1962(4244±114)	1964	1920*	1963**	
1963(4571±123)				
1964(4315±134)	1920	1963*		
1977 (4219±94)	1962	1964	1920*	1963**

Five jack pine fire scar sites located in the middle Ottawa forest section within the great lakes – St. Lawrence, eastern Ontario, Canada. Chronosequence: wildfire (1920); under-storey experimental burn (1962); under-storey experimental burn (1963); wildfire (1964); experimental burn of 1964 age class (1977). Two replicate stands for each of the five burning treatments. R_s measurements taken May through November 1983. Transformed units for means: (1920: 1.18 μmol CO_2/m^2/s); (1962: 1.12 μmol CO_2/m^2/s); (1963: 1.20 μmol CO_2/m^2/s); (1964: 1.14 μmol CO_2/m^2/s); (1977: 1.11 μmol CO_2/m^2/s). *Significant difference in mean R_s at $P < 0.05$; **Significant difference in mean R_s at $P < 0.01$. Re-drawn from Weber (1985). Permission granted from *Canadian Journal of Forest Research*; The Canada Institute for Scientific and Technical Information (CISTI).

(MJP 1999 = 0.8 g CO_2/m^2/hr (transformed units: 5.05 μmol/CO_2/m^2/s); PB 1999 = 0.6 g CO_2/m^2/hr (transformed units: 3.79 μmol/CO_2/m^2/s); MJP 2000 = 0.7 g CO_2/m^2/hr (transformed units: 4.42 μmol CO_2/m^2/s); PB 2000 = 0.5 g CO_2/m^2/hr (transformed units: 3.16 μmol CO_2/m^2/s)).

In a recent study of a 72 year old jack pine wildfire chronosequence, growing season R_s showed no clear pattern with stand age, ranging from 156 g C/m^2 to 254 g C/m^2 in 7 and 22 year old stands respectively (Yermakov and Rothstein 2006; see also Fig. 4.9) Yermakov and Rothsetin (2006) suggest that fire related changes in T_s, M_s and soil chemistry increase R_s in early seral stages. A subsequent rapid decrease
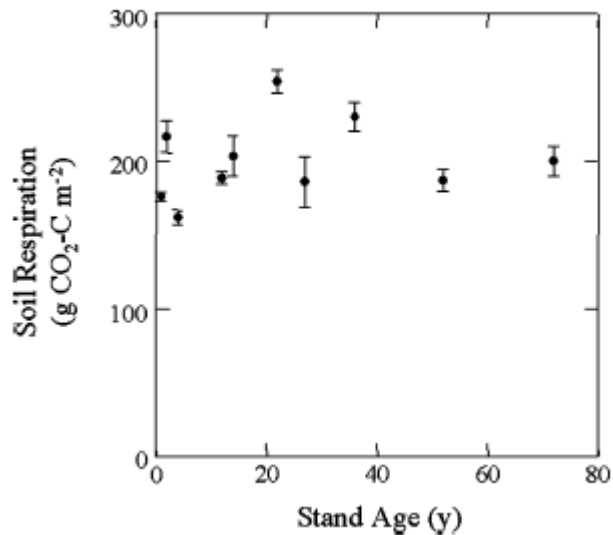
Figure 4.9 Soil respiration (R_s) over the growing season for a jack pine wildfire chronosequence. All study sites were located in northern Michigan, USA (44°30'N, 84°30'W). Though there were obvious significant differences in R_s between certain age categories, there was no general temporal trend. Source: Yermakov and Rothstein (2006); permission granted from *Oecologia*, Springer.

would occur as organic matter is depleted, followed by a slower increase as organic matter accumulates over time. Furthermore, Yermakov and Rothstein (2006) hypothesised that tree mortality results in low $R_{s(a)}$ after fire (Wang et al. 2002) but increases with successional time. Thus, differential $R_{s(a)}$ versus $R_{s(h)}$ may account for the absence of a clear R_s relationship over time.

Singh et al. (2008) investigated R_s in a boreal forest fire scar chronosequence (1977, 1989, 1998) in Saskatchewan, Canada (Fig. 4.10). There were significant differences in $\overline{R}_s$ among sites in both years of study. The 1989 site had significantly greater $\overline{R}_s$ than other sites in 2005, though in 2004, $\overline{R}_s$ was significantly greater than other sites in July only.
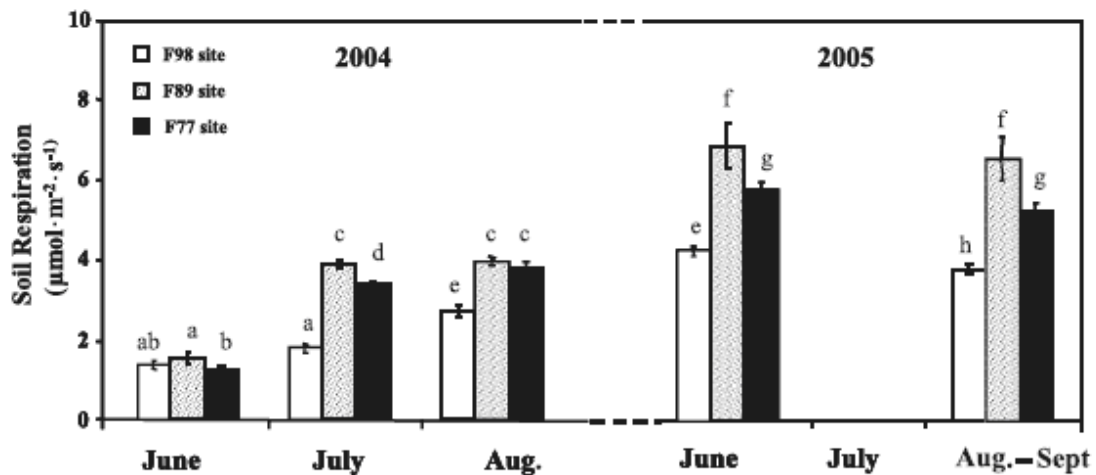
Figure 4.10 Mean soil respiration (R_s) during the growing season of 2004 and 2005 at three fire scars. Error bars indicate standard errors. Different letters indicate a significant difference ($P < 0.05$) among sites and sampling periods within a given year. All fire scars contained jack pine though other species such as black spruce, trembling aspen, balsam poplar, white birch and green alder were sometimes present. Source: Singh et al. (2008); permission granted from *Canadian Journal of Forest Research*; The Canada Institute for Scientific and Technical Information (CISTI).

The youngest site generally had lowest R_s in the chronosequence and it was suggested that the likely cause was lower root biomass at the site. However, Singh et al. (2008) show that the 1989 site had less root biomass compared with the 1977 site, but generally had greater R_s. It was suggested that species differences could account for this since the 1989 site had a greater broad leaved species component than the 1977 site. It was concluded that in early successional post-fire boreal forest systems, R_s is constrained more by root biomass than forest floor organic layer thickness.

4.7 Models of soil respiration in jack pine ecosystems

Striegl and Wickland (1998) were the first to model R_s in jack pine ecosystems. Here R_s v T_s response curves were applied to continuously measured T_s in order to model R_s for Old Jack Pine (OJP) and Clear Cut (CC) sites (Fig. 4.11). Modelled R_s was within one
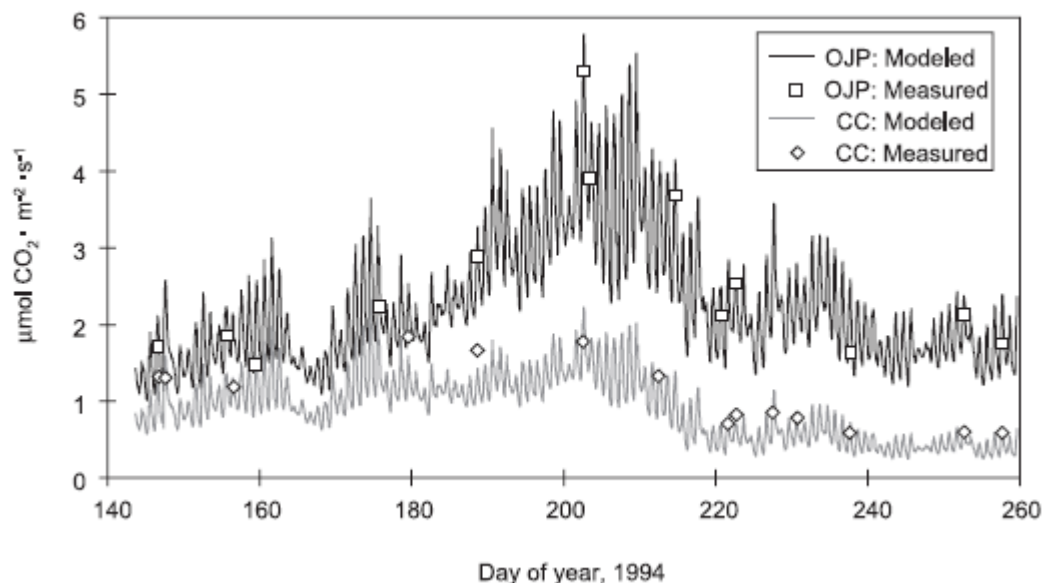
Figure 4.11 Measured and modelled soil respiration (R_s) at old jack pine (OJP) and clear cut (CC) sites. R_s modelled on the basis of soil temperature (T_s). Measured points are the mean of chamber measurements along a transect. Source: Striegl and Wickland (1998); permission granted from *Canadian Journal of Forest Research*; The Canada Institute for Scientific and Technical Information (CISTI).

standard deviation of mean measured R_s for 12 of 13 and 14 of 14 measurement periods at OJP and CC respectively. Striegl and Wickland (2001) used T_s to simulate R_s and found that for 48 of 52 measurement periods, modelled R_s fell within one standard deviation of measured R_s (Fig. 4.12). However, total modelled R_s for the season was 10 to 30% lower than the total R_s estimated from interpolation of the mean measured values.

Howard et al. (2004) used site-specific regression models for predicting R_s from T_s to estimate annual R_s in jack pine sites from May 1999 through April 2000.
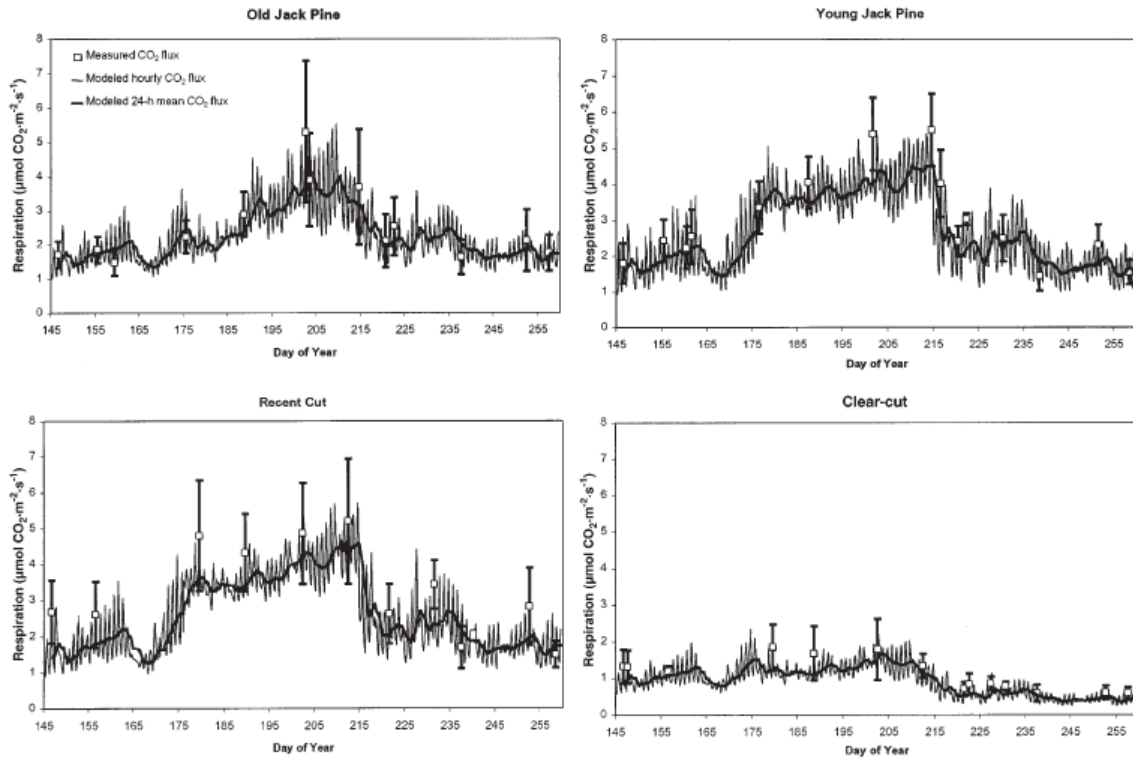
Figure 4.12 Measured and modelled soil respiration for the 1994 growing season for old jack pine, young jack pine, recent cut and clear cut sites. Source: Striegl and Wickland (2001). Permission granted from *Canadian Journal of Forest Research*; The Canada Institute for Scientific and Technical Information (CISTI).

Modelled estimates were 4.4 ± 0.1, 2.4 ± 0.0, 3.3 ± 0.1, 5.7 ± 0.3 and 3.2 ± 0.2 (Mg C/ha/yr $\pm$ 1 standard deviation) for 0, 5, 10 and 29 year old harvested stands, and a 79 year old stand that originated after wildfire.

Euskirchen et al. (2003) modelled R_s on the basis of T_s (Fig. 4.13), T_s and M_s (Figs. 4.14 to 4.15) and compared modelled and measured R_s in both 1999 and 2000 (Fig. 4.16). Although average simulated R_s was similar to field measured values in 2000, in 1999 the simulated values tended to under-predict R_s in the pine barrens.
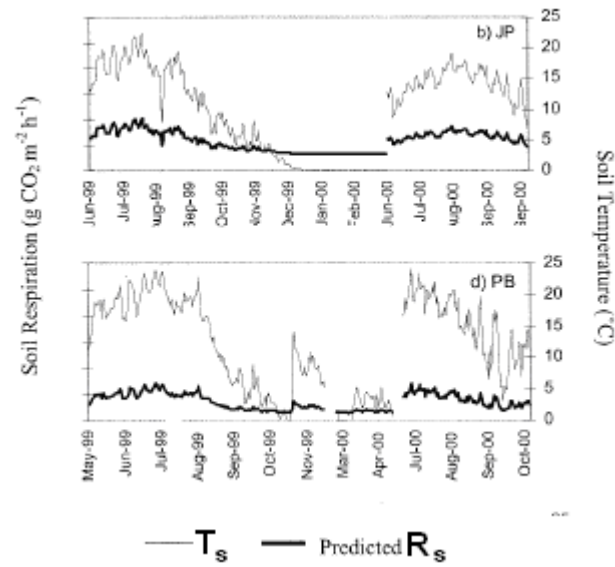
Figure 4.13 Soil respiration (R_s) modelled on the basis of soil temperature (T_s) for jack pine (JP) and pine barrens (PB). Source: Euskirchen et al. (2003); permission granted from Springer.
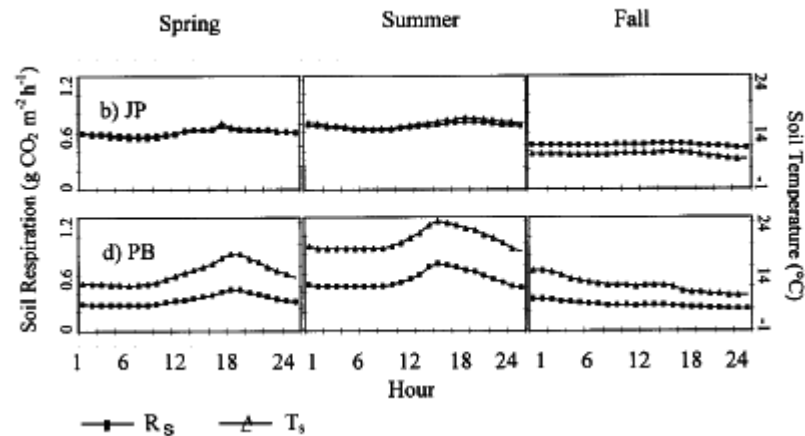
Figure 4.14 Modelled and measured soil respiration (R_s) and soil temperature (T_s) respectively over three seasons for JP (jack pine) and PB (pine barrens) systems. R_s modelled on basis of T_s and soil moisture (M_s). Source: Euskirchen et al. (2003); permission granted from Springer.
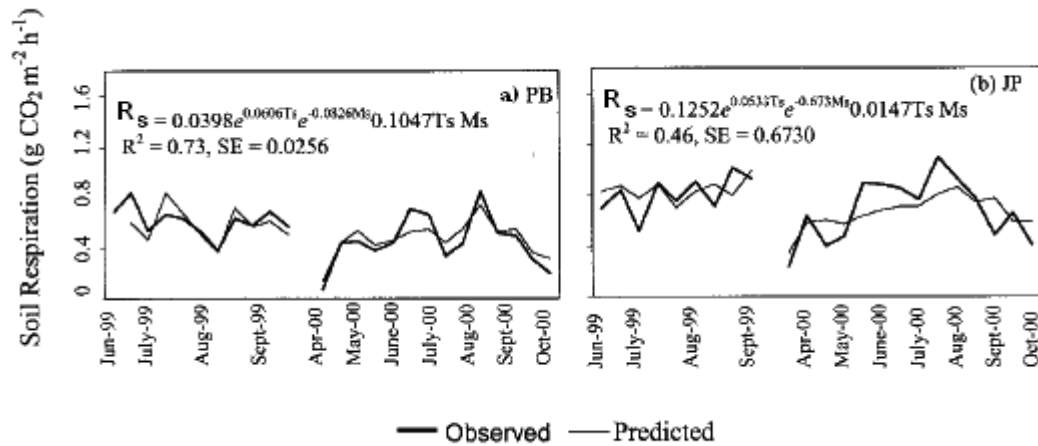
Figure 4.15 Modelled versus measured soil respiration (R_s) for pine barrens (PB) and jack pine (JP) systems. R_s modelled on the basis of soil temperature (T_s) and soil moisture (M_s). Empirical functions:
a) PB: $R_s = 0.0398e^{\wedge}(0.0606*T_s)\ e^{\wedge}(-0.0826M_s)*0.1047T_s*M_s$; $r^2 = 0.73$; *SE= 0.0256*
b) JP: $R_s = 0.1252e^{\wedge}(0.0533*T_s)\ e^{\wedge}(-0.673M_s)*0.0147T_s*M_s$; $r^2 = 0.46$; *SE= 0.6730*
For all models $P > F$ is < 0.0001 and *SE* = standard error of intercept term. Source: Euskirchen et al. (2003); permission granted from Springer.

Nalder and Wein (2006) used the Boreal Forest Carbon Dynamics Model (BFCDM) to simulate R_s and compare the results to those reported in the literature for jack pine fire chronosequences. The BFCDM model was designed to be capable of incorporating the effects of fire and was able to simulate $R_{s(h)}$ but not $R_{s(a)}$. Consequently, simulated R_s for BOREAS sites were lower than that of other studies where total R_s was measured, though results were consistent in magnitude with the literature when considering absence of $R_{s(a)}$.

Euskirchen et al. (2006) modelled R_s for a jack pine ecosystem using two exponential models (Figure 4.17). The first model incorporated only T_s and was statistically significant ($P < 0.0001$) with T_s explaining between 68 and 77% of the
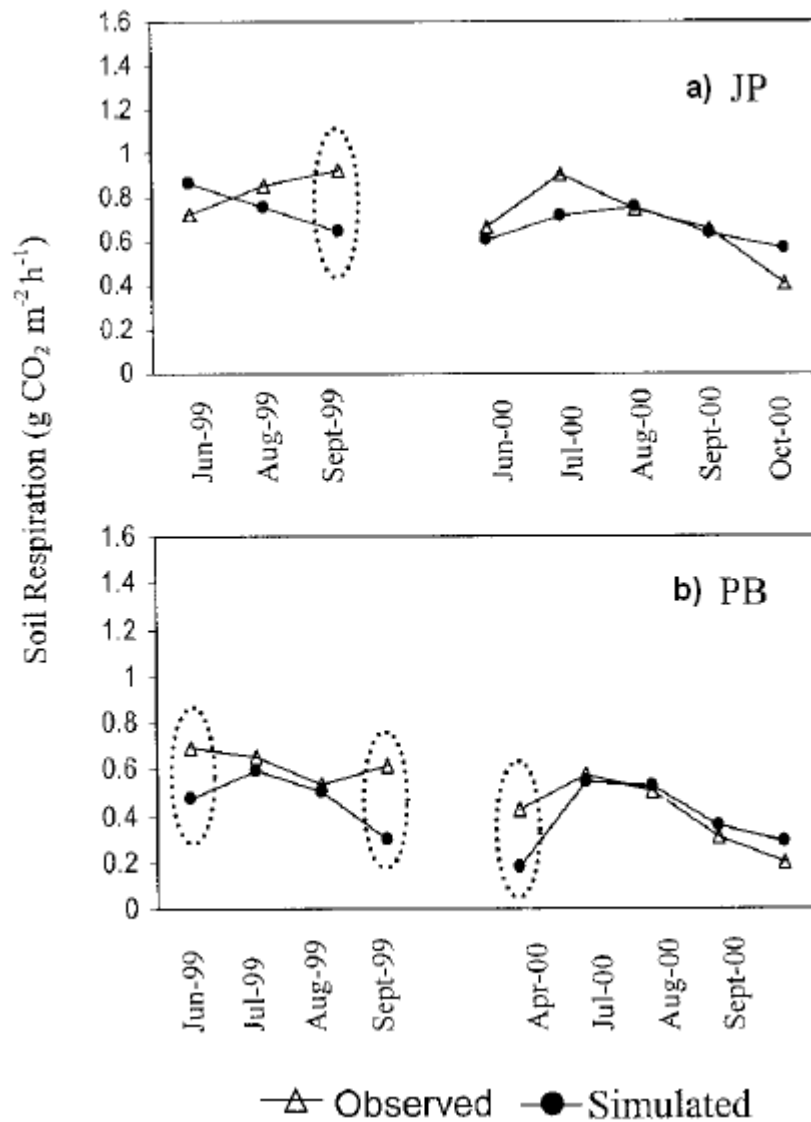
Figure 4.16 Measured versus modelled average monthly soil respiration (R_s) for jack pine (JP) and pine barren (PB) systems. R_s modelled on the basis of soil temperature. Significant differences between data point pairs (t test; $\alpha = 0.05$) are shown by circles. Source: Euskirchen et al. (2003); permission granted from Springer.

variability in R_s. The second model, which included both T_s and M_s, was also statistically significant ($P < 0.0001$) and explained more of the variability in R_s (75 to 88%).
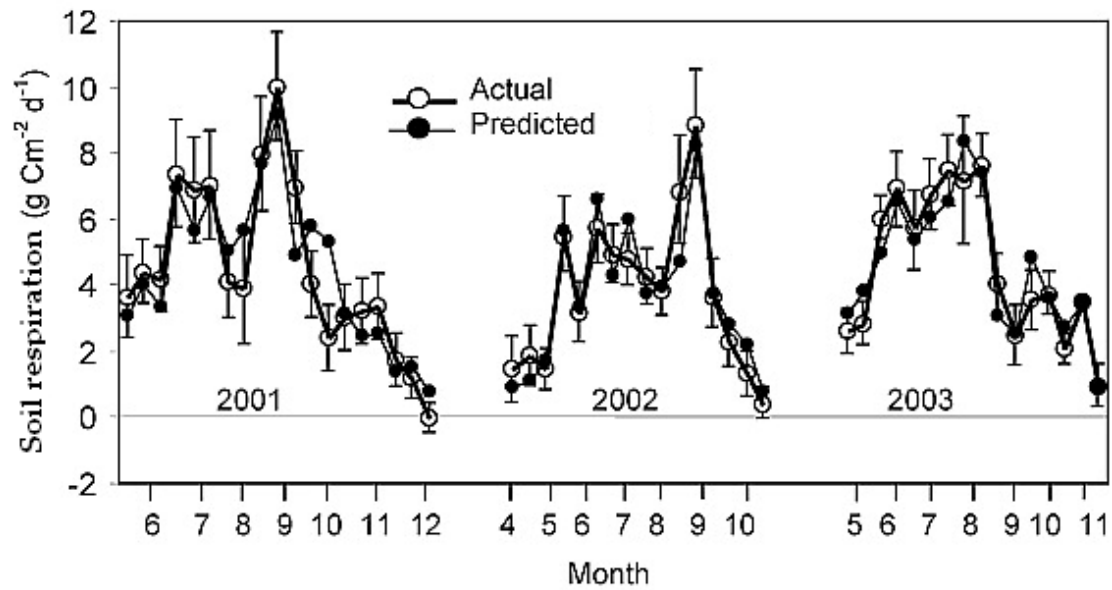
Figure 4.17 Comparison of actual (± 1 standard deviation) and modelled soil respiration for a jack pine ecosystem over three study years. Modelled estimates based on soil temperature. Source: Euskirchen et al. (2006); permission granted from *Journal of Geophysical Research*; American Geophysical Union.

4.8 Main gaps in the literature

Though there has been some documentation of the spatial variability of R_s in jack pine systems, the information is somewhat limited and the effects of T_s and M_s have not been accounted for. Moreover, only in one paper has necessary N been suggested. The R_s v T_s relation has received some attention in jack pine systems, though rarely have the effects of M_s been accounted for and never has C_s been accounted for. The R_s v M_s relation has received very little attention in jack pine systems and again the effects of C_s have not been accounted for. There have been some studies of R_s in jack pine fire scar chronosequences, though to date, research has rarely involved use of replicate fire scars. In addition, there has yet to be any comparison of R_s in un-burnt v burnt scars immediately after fire. Furthermore, there has yet to be any comparison of R_s in recently burnt fire scars that differ

in their burn history and previous studies have not adjusted for T_s and M_s when comparing different fire scar age categories. There has been some modelling work of R_s in jack pine systems based on T_s and M_s, but to date, R_s has only been simulated over short time periods e.g. days to one or two years. Moreover, R_s has not been simulated over longer time scales that would imply jack pine development over successional time. Furthermore, R_s has yet to be simulated for a jack pine system using a fully-fledged land surface model where R_s is constrained by C_s, T_s and M_s, which are themselves controlled by additional modelled processes.

4.9 Specific research questions

There are six *specific* research questions that aim to address the two *main* research questions stated in Chapter 1 (Sect. 1.3) and the present gaps in the literature.

1. What is the spatial variability of measured R_s for a boreal jack pine ecosystem after accounting for the effects of T_s and M_s?

2. What is the general T_s dependence of measured R_s for a boreal jack pine ecosystem after accounting for the effects of C_s?

3. What is the general M_s dependence of measured R_s for a boreal jack pine ecosystem after accounting for the effects of C_s and T_s?

4. What is the immediate effect of burning on measured R_s in young and mature boreal jack pine ecosystems after accounting for the effects of T_s and M_s?

5. Are there any significant differences in measured R_s from recently burnt boreal jack pine fire scars that differ in their burn history, after accounting for the effects of T_s and M_s?

6. How well can a current land surface model simulate vegetation re-growth over successional time for a boreal jack pine ecosystem?

Specific research questions 1 through 5 relate to *main* research question 1, but are also required for *main* research question 2, since model results will be compared with field observations. *Specific* research question 6 relates largely to *main* research question 2, with the notion that an understanding of modelled vegetation re-growth is required to explain modelled R_s.

4.10 Summary

Previous studies in jack pine ecosystems report CV_{R_s} in the range 9 to 61% and necessary sample size of up to 25 R_s measurements for estimating $\overline{R}_s$ within a *FE* acceptance of 20% (of the true mean). Research into the T_s response of R_s in jack pine systems has documented Q_{10} values in the range 1.1 to 7.12. A recent study showed M_s dependence of R_s by polynomial functions in jack pine forest. There have been some studies comparing R_s in different aged jack pine fire scars and reported R_s values range from 0.35 to 7.2 µmol $CO_2/m^2/s$. Some simulations of R_s have been within one standard deviation of measured values, though other models have under-predicted R_s. There are six *specific* research questions that aim to address the current gaps in the literature and relate to the *main* research questions stated in Chapter 1. The next chapter describes the materials and methods used in the research.

Chapter 5: Materials and methods

5.1 Introduction

This chapter describes the materials and methods used in the research and is comprised of two main sections. The first is concerned with the fieldwork component of the study, where information on the field site, instruments used, experimental designs and data analyses is provided. The second section introduces the land surface model used in the research and describes how it was used to simulate R_s at the field site.

5.2 Fieldwork

5.2.1 Field site

Sharpsand Creek is a boreal forest experimental burn site of the Canadian Forest Service located approximately 60 km North of Thessalon, Ontario, Canada (latitude 46°47' N, longitude 83°20' W). Since the mid- 1970's, numerous prescribed burns have been carried out on forest plots (0.4 to >3 ha) (Table 5.1; Figs. 5.1 to 5.4). Further data from prescribed burns, e.g. fire weather index system components and fuel consumption are provided in Stocks (1987). Sharpsand Creek is an excellent site for addressing the specific research questions (Chapter 4; Sect. 4.7); the site is dominated by jack pine, and the availability of replicate, different aged fire scars at similar geographic location minimizes the effect of confounding variables that may influence R_s measurements (Chapter 3).

The Sharpsand Creek area experiences short, warm summers and long, cold winters, with mean daily atmospheric temperatures of 16°C and -17°C in July and January respectively (Stocks 1987). Mean annual precipitation is 760 mm, of which

Table 5.1 Fire scars at Sharpsand Creek used in the pilot study and field campaigns 1 and 2 of this research.

Field campaign	Fire scar	Age category †	Burnt in 2007 wildfire?	Time since fire (years)
1	A	1948	no	58
1	B	1948	no	58
1	C	1948	no	58
1	2	1991	no	15
1 + P	7	1991	no	15
2	A	1948	yes	0
2	B	1948	yes	0
2	C	1948	yes	0
2	5	1975	yes	0
2	6	1975	yes	0
2	Ac	1975	yes	0
2	2	1991	yes	0
2	7	1991	yes	0
2	8	1991	yes	0
2	1A	1948	no	59
2	2 *	1991	no	16

† - excluding fire on 13 May 2007; P - pilot study; 2* - part of scar 2 not burnt in 2007 wildfire. Replicates for 1948 and 1991 age categories not burnt in 2007 unavailable due to the extent of the 2007 wildfire.

approximately one third falls as snow (Stocks 1987). The growing season has a mean annual length of 162 days, beginning early May and ending mid– October (Stocks 1987). The site is located on level ground (Stocks 1987) above a granite substratum. Soils in the area are nutrient-poor petawawa outwash sands (humo-ferric podzols) that have high water-washed boulder contents due to their glacio-fluvial origin (Timothy Lynham – personal communication).

The field site is dominated by jack pine (*Pinus banksiana* Lamb.), which grows quickly after fire and out-competes any established sedges or grasses. Fire has the effect
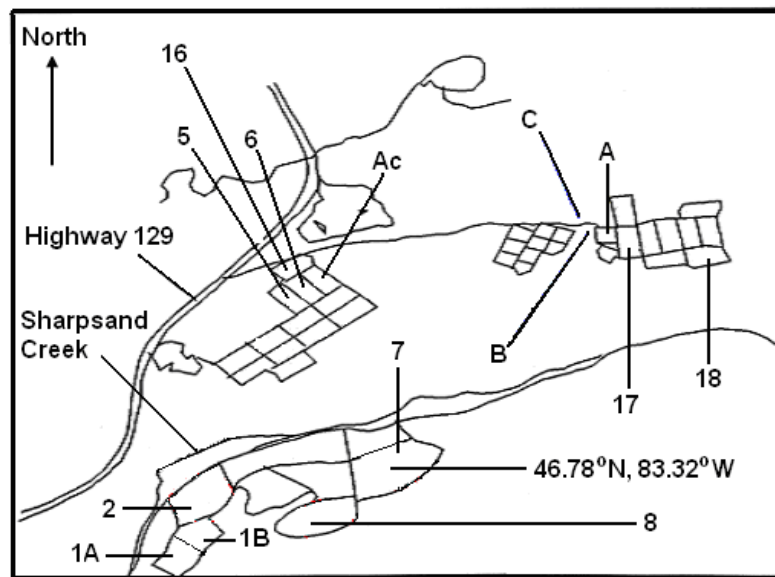
Figure 5.1 Organisation of fire scars at Sharpsand Creek last burnt* in: 1948 wildfire (1A, 1B, A, B, C); 1975 prescribed burns (5, 6, Ac); 1981 prescribed burns (16, 17, 18); 1991 prescribed burns (2, 7, 8). *Excluding 13 May 2007 prescribed burn at 1B and subsequent wildfire across large areas of whole field site. Modified with permission of Timothy J. Lynham (personal communication).
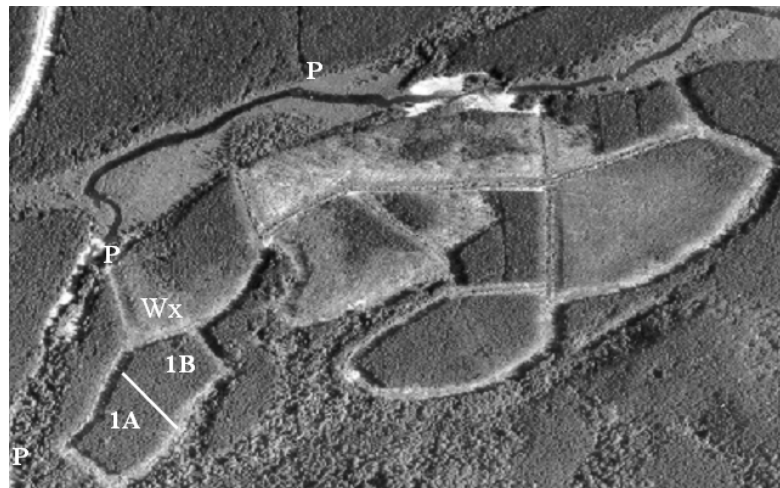
Figure 5.2 Aerial photograph (1992) of part of Sharpsand Creek field site. The fire scars and fire breaks around their perimeter are clearly visible. Scar 1A was last burnt in a 1948 wildfire. On 13 May 2007, a prescribed burn was carried out on scar 1B (previously burnt in 1948 wildfire). 'Wx' represents the location of a Canadian Forest Service weather station. 'P' represents the location of water pumps used in fire suppression. Photograph included with permission of Timothy J. Lynham (personal communication); Ontario Ministry of Natural Resources.

Figure 5.3 Photograph taken inside scar A at Sharpsand Creek, last burnt in a 1948 wildfire. Source: Daniel Smith (June 2006).

Figure 5.4 Photograph taken inside scar 7 at Sharpsand Creek, last burnt experimentally in 1991. Source: Daniel Smith (June 2006).

of releasing seeds from jack pine cones and this happens immediately after passage of the fire front. Seeds may germinate within days and population densities after fire can reach thousands of jack pine seedlings per ha (Brian Stocks – personal communication). Post-fire recovery is dependant on fire intensity. Surface fires of low intensity and flame height may not kill the jack pine trees, though small shrubs and herbs in the under-storey will usually not survive. More intense fires may kill the jack pine trees, but like other boreal species, they remain standing for five to six years in the absence of strong winds. After the trees have fallen to the forest floor, it can take several decades for them to decompose completely by a succession of fungi and bacteria. Small shrubs such as blueberry (*Vaccinium* spp.) and sweet fern (*Comptonia peregrina*) appear around 12 months after fire and are able to thrive in the shady under-storey of the new jack pine stand. In this research, age categories for jack pine at Sharpsand Creek are defined as: young (0 to 20 years, as in Euskirchen et al. 2006); intermediate (20 to 50 years); mature (50 to 90 years) and over-mature (>90 years). At Sharpsand Creek trees are normally harvested after 70 to 80 years.

On 13 May 2007, a prescribed burn was carried out on plot 1B (size = 0.9 ha; Figs. 5.1 and 5.2) last burnt in a 1948 wildfire. An unprecedented number of spot fires and fire whirl behaviour caused the fire to escape from the plot and burn through large areas of the whole field site. The total area burned from the ensuing wildfire was estimated at 1557ha (Timothy Lynham – personal communication). Before 2007, Sharpsand Creek was also subject to the Chapleau-Mississagi wildfire (6 to 8 June 1948) that burnt in excess of 260,000 ha between Thessalon and Chapleau, Ontario (Stocks and Walker 1973). It is believed that previous wildfires occurred in the Sharpsand Creek area in 1850, 1880, 1901 and 1919 (Stocks 1987).

5.2.2 Instruments

R_s point measurements were made at Sharpsand Creek with the PP Systems (Hitchin, Hertfordshire, UK) SRS, which consists of a cylindrical R_s chamber (SRC-1: height = 15 cm; diameter = 10 cm; ground surface area = 78 cm^2) connected to an IRGA (CIRAS-1) (PP Systems 2003; see also Chapter 3, Fig. 3.4). CIRAS-1 has an absolute precision for CO_2 measurements of 0.2 μmol/mol at 0 ppm and 0.7 μmol/mol at 2000 ppm (PP Systems 2003). Furthermore, CIRAS-1 has a linearity >1% throughout the measurement range 0 to 9999 μmol/mol (PP Systems 2003). Two SRS's were serviced approximately two months prior to use in the pilot study (Sect. 5.2.3.1) and field campaign (FC) 1 (Sect. 5.2.3.2). A preliminary test (10/06/06) showed no significant difference in median R_s measured between the two CIRAS-1 IRGA's (Mann Whitney U test: $N = 10$ (5+5); $U = 6$; $P = >0.1$). Where required, chemical reagents were replaced in the SRS's prior to use in FC 2 (Sect. 5.2.3.2).

T_s was measured with the Cole Parmer pH/mV/°C Meter and soil moisture voltage ($M_{s(v)}$) with the Delta T ML2 Theta probe connected to a voltmeter (Maplin Electronics Digital Multi Media Sinometer MS8230B). $M_{s(v)}$ values were calibrated to volumetric pore moisture (fraction of pore space) (θ_p) obtained from soil cores collected in FC 2 (Sect. 5.2.3.2) to give an M_s value for each location ($M_s = 1.0252 * M_{s(v)}$). M_s values reported for the field component of this research are thus an estimate of volumetric pore moisture (fraction of pore space).

5.2.3 Experimental design

5.2.3.1 Sampling regime

Over the pilot study and both FC's at Sharpsand Creek, sampling points for measurements of R_s, T_s, $M_{s(v)}$ and C_s were arranged as regularly as possible, but some irregularities may have resulted e.g. due to the position of jack pine trees and dead woody debris. Where necessary, soil surface vegetation was removed prior to taking R_s measurements (e.g. litter removed; moss layer peeled back; grasses clipped) in order to minimise autotrophic respiration from the soil surface. Measurements were taken from areas considered representative of the fire scars (in terms of dominant vegetation cover).

5.2.3.2 Pilot study

The pilot study was conducted on 24 June 2006 in order to estimate the spatial variability of R_s at Sharpsand Creek. The experiment was carried out on fire scar 7 (Table 5.1; Figs. 5.1 and 5.4), burnt experimentally in 1991 and one of the youngest fire scars available at the time. This scar was selected with the assumption that spatial variability of R_s would be greatest in the younger fire scars (Singh et al. 2008). The aim was to collect a large number of R_s measurements in order to obtain a CV_{R_s} value for the scar.

Thirty sampling points were marked out randomly within an area 30 m * 30 m considered to be representative of the fire scar. Concurrent R_s (two independent SRS's) and T_s (at 11.7 cm depth) measurements were taken from each sampling point. CV_{R_s} adjusted for T_s ($CV_{R_s^T}$) was calculated using:

$$CV_{R_s^T} = \frac{\sigma_{R_s^T}}{\overline{R}_s^T} \qquad \text{(Eq. 5.1)}$$

where: $\sigma_{R_s^T}$ is standard deviation of R_s adjusted for T_s; and $\overline{R_s}^T$ is mean R_s adjusted for T_s.

Minimum estimated sample size (N) of R_s measurements required to be 95% confident the sample $\overline{R_s}^T$ lies within specified fractional errors (FE) of the true $\overline{R_s}^T$ was calculated using Eq. 5.2 (Steele and Torrie 1960):

$$N \geq \left(\frac{2 * CV_{R_s^T}}{FE} \right)^2 \qquad\qquad \text{(Eq. 5.2)}$$

5.2.3.3 Field campaign 1

On 3 July 2006, concurrent R_s, T_s (at 11.7 cm depth) and $M_{s(v)}$ (to 6 cm depth) measurements were taken from five fire scars at Sharpsand Creek (Table 5.1). Two independent CIRAS-1 IRGA's were used, though the same SRC was used for all measurements. Point measurements were carried out on two parallel 10 m line transects (spaced 5m apart) at 0, 5 and 10 m.

5.2.3.4 Field campaign 2

The burning of large areas of Sharpsand Creek from the escaped prescribed burn on 13 May 2007, provided an opportunity to take R_s measurements from recently burned fire scars as well as from those areas the fire did not affect. Between 17 and 21 May 2007, measurements of R_s, T_s (at 2 cm depth) and $M_{s(v)}$ (to 6 cm depth) were taken from 11 fire scars (Table 5.1). At each fire scar, PVC collars (diameter = 10.1 cm; height = 5 cm) were inserted into the soil (2 to 3 cm depth) at least 12 hours prior to measuring R_s (Wang et al. 2005) in order to minimize soil disturbance at the time of measurement (Luo and Zhou

2006). Three parallel 10 m line transects were set up (spaced 5 m apart) and soil collars placed at 0, 5 and 10 m along each of the transects. An additional soil collar was placed randomly within the 10 m * 10 m area, making a total of ten soil collars per fire scar. R_s was measured over the soil collar using a single PP systems SRS. After R_s, T_s and $M_{s(v)}$ measurements were taken, soil cores (depth = 5 cm; volume = 132.10 cm^3) were delicately extracted from three random collars in each scar and put into labelled, air tight soil tins. Each of the soil samples were weighed before, and after oven drying at 105°C. Laboratory derived volumetric moisture (θ) of each of the samples was derived by:

$$\theta = \frac{M_d}{M_w} * V_s$$

<div align="right">Eq. 5.3</div>

Where M_d is the mass of dry soil;

M_w is the mass of wet soil;

V_s is the volume of each soil core = 132.10 cm^3.

Laboratory derived volumetric pore moisture (fraction of pore space) (θ_p) was calculated by:

$$\theta_p = \frac{\theta}{P_s}$$

<div align="right">Eq. 5.4</div>

Where P_s is the porosity of soil = 0.38 (McWhorter and Sunada 1977; value for sand).

Dry soil samples of known weight were placed in a Sybron/Thermdyne muffle oven for 16 hours at 375°C in order to oxidise organic matter. Soils were then re-weighed to estimate organic C content (Page et al. 1982; Kalra and Maynard 1991) expressed as bulk density. During this process, some mass loss may occur through combustion of inorganic C. However, soil inorganic C content e.g. carbonates was assumed to be negligible due to the high level of leaching that occurs in podzolic soils (Chapter 2).

5.2.4 Data analyses

5.2.4.1 Soil respiration adjustments for soil temperature

R_s is dependant on some function of T_s, M_s and C_s and usually modelled as:

$$R_s = R_0 * f(T_s, M_s) * C_s \qquad \text{(Eq. 5.5)}$$

where R_0 is base R_s rate at reference T_s (T_0).

  To estimate the general T_s and M_s dependence of R_s at Sharpsand Creek, the R_s measurements from FC 2 were used, for which T_s, M_s and C_s were known. In order to account for the effect of C_s (Eq. 5.3), R_s measurements were first adjusted using:

$$R_s{}^C = \frac{R_s}{C_s} \qquad \text{(Eq. 5.6)}$$

where $R_s{}^C$ is R_s adjusted for C_s.

  R_s is commonly assumed to be exponentially dependant on T_s (Davidson and Janssens 2006), modelled using a Q_{10} value:

$$R_s = R_0 * Q_{10} \wedge \left(\frac{T_s - T_0}{10} \right) \qquad \text{(Eq. 5.7)}$$

  $R_s{}^C$ was plotted against T_s and an exponential function fitted to derive Q_{10}. This indicated a general T_s response of R_s across the field site. R_s adjusted for C_s and T_s ($R_s{}^{C,T}$) (using $Q_{10} = 2.21$ and $T_0 = 10°C$) versus M_s revealed no effect of M_s on $R_s{}^{C,T}$ over the range 0.21 to 0.77 M_s (Chapter 6). Since very few R_s measurements had associated M_s values outside the range 0.21 to 0.77 M_s (Chapter 6) these R_s values were excluded from the analysis. All remaining R_s data from FC's 1 and 2 had associated M_s values in the range 0.21 to 0.77 M_s. Therefore R_s measurements used in FC 1 and 2 were adjusted for T_s using:

$$R_0 = \frac{R_s}{Q_{10} \wedge \left(\dfrac{T_s - T_0}{10}\right)}$$ (Eq. 5.8)

where $Q_{10} = 2.21$ and $T_0 = 10°C$.

Note that Eq. 5.6 accounts for the effects of T_s and M_s but not C_s (C_s was only taken in three locations per fire scar FC 2 (Sect. 5.2.3.4)). Each R_s measurement yielded an R_0 that varied due to differences in C_s between locations. R_0 is hereafter referred to as $R_s^{T,M}$, implying R_s has been 'adjusted' for the effects of T_s and M_s.

5.2.4.2 Statistical procedures

Statistical analyses were performed in Microsoft Office Excel 2003 and SPSS version 15. All R_s measurements (y axis) were plotted against DC/DT (x axis) to visually identify outliers, which were subsequently removed. For R_s and C_s data obtained in FC 1 and 2, after removing additional outliers (>1.5 * *Inter Quartile Range* (*IQR*)), data were analysed for normality and homogeneity of variances by Kolmogorov-Smirnov and Levene's tests respectively. Since Levene's test indicated significant differences in the variances of both R_s and C_s between fire scar age categories ($F = 25.75$; $df = 6, 104$; $P = 0.000$ to 3 *sf*), the non-parametric Kruskal-Wallis test was used instead of Analysis of Variance (ANOVA) to test for any significant differences in median $R_s^{T,M}$ and C_s between fire scar age categories. Independent samples t tests (Students t test where Levene's $P > 0.05$; unequal variance t test (Ruxton 2006) where Levene's $P < 0.05$) were subsequently used to test for significant differences in $\overline{R_s}^{T,M}$ and $\overline{C_s}$ between specific fire scar age categories. *P* values were corrected for multiple hypotheses testing using the Ryan-Holm step-down Bonferroni procedure (Holm 1979; Aickin and Gensler 1996; Ludbrook 2000) to minimise the occurrence of Type 1 errors. Due to large spatial variability of R_s and C_s measured in the

field, and small sample sizes, it was decided to set α = 0.1; i.e. $P < 0.1$ to be statistically significant when comparing $\overline{R_s}^{\,T,M}$ and $\overline{C_s}$ between fire scar age categories (NS $P > 0.1$; *$P < 0.1$; **$P < 0.05$; ***$P < 0.01$). Setting a high α value (compared with e.g. 0.05 used in similar studies of jack pine systems (Weber 1985; Euskirchen et al. 2003; Singh et al 2008)) increases statistical power, reducing the chance of committing a Type 2 error. Correlations of $R_s^{\,C}$ v T_s, $R_s^{\,C,T}$ v M_s and $\overline{R_s}^{\,T,M}$ v time since fire were performed using regression analyses. The fire scars 1975B, 1991NB and 1948NB were chosen to represent the chronosequence 0, 16 and 59 years since fire respectively. 1975B was chosen to represent 0 years, since the burn history more closely matched those of the other scar age categories (1975B, 0 years since most recent fire, *burnt 32 years previously*; 1991NB, 16 years since fire, *burnt 43 years previously*; 1948NB, 59 years since fire, *burnt 29 years previously*). P values are reported as output by the application used.

5.3 Modelling

5.3.1 Overview of JULES

The Joint UK Land Environment Simulator (JULES) is a land surface model developed from the Meteorological Office Surface Exchange Scheme (MOSES), the land surface model used in the unified model of the UK Meteorological Office (Cox et al. 2000). JULES comprises two coupled models: (1) MOSES; and (2) TRIFFID (Top-down Representation of Interactive Foliage and Flora Including Dynamics). MOSES is concerned with simulating surface energy flux and hydrological processes whereas TRIFFID is designed to simulate vegetation and soil dynamics. JULES was released to serve two purposes: (1) to

make the model freely available to the scientific community; and (2) to enable model development (JULES 2009).

JULES is written in the high level programming language FORmula TRANslation (FORTRAN). JULES adopts a modular structure comprised of routines and sub-routines and divides the land surface into grid boxes, which may be occupied by a number of Plant Functional Types (PFT's) and Non Plant Functional Types (NPFT's). Up to five PFT's can occupy a grid box, namely: broad leaf trees (BT); needle leaf trees (NT); C3 grasses (C3G); C4 grasses (C4G); and shrubs (Sh). In addition, up to four NPFT's may occupy a grid box, namely: urban, inland water, soil and ice. JULES adopts a tiled structure in that surface processes are calculated separately for each surface type, or tile. JULES can be run on point (single grid box) or global scales.

The specifications of a JULES model run are controlled in the run control file (RCF). Here, the user specifies the details of the simulation, such as time, location, PFT and NPFT fractional coverage (Frac), various parameters, initial conditions and desired output (Table 5.2). JULES requires a number of climate forcing data, specifically: air temperature, precipitation, wind-speed, humidity, air pressure, downward short-wave radiation, and downward long-wave radiation (Best 2005). Although there have been some papers published concerning JULES (diffuse sunlight effects: Alton et al. 2007a; sensitivity analysis: Alton et al. 2007b; global vegetation modelling: Hughes et al. 2006; radiation interception and photosynthesis: Mercado et al. 2007), there has yet to be any published studies on using JULES to simulate R_s for a boreal jack pine ecosystem.

5.3.2 Soil respiration modelling in JULES

Change in C_s storage is modelled using a differential equation where litter fall (L) and microbial R_s ($R_{s(h)}$) increase and decrease C_s respectively:

$$\frac{dC_s}{dt} = L - R_{S(h)}$$

(Eq. 5.9)

$R_{s(h)}$ is assumed to be a function of C_s, T_s and M_s, modelled as:

$$R_{s(h)} = k * C_s * f(T_s) * g(M_s)$$

(Eq. 5.10)

Where k is the specific $R_{s(h)}$ rate at 25°C and f and g are T_s and M_s dependant functions respectively.

T_s dependence is modelled as:

$$f(T_s) = Q_{10}^{0.1(T_s - 25)}$$

(Eq. 5.11)

The M_s dependence of $R_{s(h)}$ is modelled using a piece-wise approach based on McGuire et al. (1992):

$$g(M_s) = \begin{cases} 1 - 0.8\{S - S_o\} & for\ S > S_o \\ 0.2 + 0.8\left\{\dfrac{S - S_W}{S_o - S_W}\right\} & for\ S_W < S \leq S_o \\ 0.2 & for\ S \leq S_W \end{cases}$$

(Eq. 5.12)

Where S is the unfrozen M_s

S_w is the wilting M_s

S_o is optimum M_s

5.3.3 JULES simulations at Sharpsand Creek

It was first attempted to run JULES from initial conditions set to represent a post-fire environment, assuming total vegetation mortality to occur as a result of the 1948 wildfire at Sharpsand Creek. Although jack pine trees remain standing for some time after fire (Sect. 5.2.1), JULES version 2.0 is unable to distinguish between live and dead PFT's. Therefore initial conditions of leaf area index (LAI), canopy height (Can) and Frac were set to ~ zero across the PFT's. However, the display of 'not a number' (NaN) values in spun-up dump files implied that JULES was unable to calculate necessary output and calculations in the main run would be incomplete.

Model runs were set to commence on 07/06/1963 (day/month/year) (15 years after the 1948 wildfire at Sharpsand Creek) due to the availability of C_s, Can, and LAI data from 15 and 16 year old fire scar age categories at Sharpsand Creek. Initial conditions of C_s and NT Can were obtained from FC 2 (1991 scar age category; data collection 2007; 16 years post fire; Table 5.2). Initial conditions for LAI were obtained from a recent study of above ground biomass at Sharpsand Creek (1991 scar age category; data collection 2006; 15 years post fire) (Mottram 2009; see also Table 5.2). National Centers for Environmental Prediction (NCEP) reanalysis data were used for model forcing (temporal resolution = three hourly): NOAA (2008). Since JULES is able to interpolate to higher temporal resolutions, the model time-step was set to 300 s, increasing the frequency of calculations, optimizing model performance. JULES was coded to spin-up repeatedly over ten year cycles in order to produce physically stable soil conditions (T_s and M_s) prior to commencement of the main model runs. The number of PFT's and NPFT's were set to 5 and 4 respectively. A radiative canopy with heat capacity and representation of snow

beneath the canopy was selected from the JULES options. JULES was programmed to use the phenology, TRIFFID and van Genuchten models (Best 2005). JULES was set to use a canopy radiation model with a multilayer approach for both radiation interception and canopy photosynthesis, the latter calculated separately for sunlit and shaded leaves (Sellers et al. 1992, Best 2005). JULES was coded to calculate solar zenith angle and use spectral albedo, which included a prognostic snow albedo (Best 2005). A summary of the RCF set up for simulations at Sharpsand Creek is shown in Table 5.2 (see also Appendix 1 for JULES RCF replicate 1).

Three model replicate runs (RR 1, 2 and 3) were performed that had various parameters modified to 'match' the Sharpsand Creek field site (Table 5.2), though all other parameters were the JULES standard (Best 2005). The three model RCF's differed only in the initial C_s values that corresponded to three values measured in the field for a 16 year old fire scar (scar 2; FC 2) (Table 5.2). Field measured C_s replicate 1 was used for initial C_s in RR 1, field measured C_s replicate 2 was used for initial C_s in RR 2 and field measured C_s replicate 3 was used for initial C_s in RR 3 (Table 5.2). Output variables on a mean annual basis included $R_{s(h)}$, C_s, T_s, M_s, NT LAI and NT Frac. Output variables for specific time periods since fire (month and year) included $R_{s(h)}$, C_s, NT LAI and NT Can (means calculated from the three RR) allowing comparisons with field data (Table 5.3). Model output was analysed with the Grid Analysis and Display System (GrADS) (GrADS 2009).

Table 5.2 Set up of the JULES run control file for model runs at Sharpsand Creek

Model scale / component	Variable / Parameter	Value	Units	Reference
Temporal scale	Time-step	300	s	This study
	Dates main run	19630607 - 20071201	Year/month/day	This study
	Dates spin up	19630607 - 19730607	Year/month/day	This study
Spatial scale	Number grid points	1	-	This study
	Latitude	46.7833	Decimal degrees	This study
	Longitude	-83.3333	Decimal degrees	This study
Atmosphere component	Atmospheric CO_2 concentration	5.25e-04	mmr	Tans (2009)
Soil component	Depth soil layer 1	0.05	m	This study
	Depth soil layer 2	0.15	m	This study
	Depth soil layer 3	0.8	m	This study
	Depth soil layer 4	2.0	m	This study
	b	3.39	Dimensionless	Bonan (1996)
	Saturated hydraulic conductivity	1.79	kg/ m^2/s or mm/s	* Schaap and Leij (1998)
	Soil moisture content at saturation	0.373	m^3/m^3	*Bonan (1996)
	Permanent wilting point	0.09325	m^3/m^3	+ Campbell and Norman (1998)
	Dry heat capacity	2140000	J / m^3 / K	* Bonan (1996)
	Dry thermal conductivity	8.61	W / m / K	* Bonan (1996)
	Soil albedo	0.10	Proportion	† Campbell and Norman (1998)
	Q_{10} for soil respiration	2.21	Dimensionless	This study
	Minimum C_s	1.0e-6	kg / m^2	This study
	Initial C_s replicate 1	68.33	kg / m^2	This study and ▼ Jobbagy and Jackson (2000)
	Initial C_s replicate 2	33.36	kg / m^2	This study and ▼Jobbagy and Jackson (2000)
	Initial C_s replicate 3	21.83	kg / m^2	This study and ▼ Jobbagy and Jackson (2000)
Vegetation component	Temperature below which leaves dropped for NT	230	K	This study
	Minimum LAI NT, Sh	1.63	Dimensionless	Mottram (2009)
	Minimum LAI C3G, C4G	0.1	Dimensionless	This study
	Initial canopy height NT	2.54	m	‡ This study
	Initial canopy height Sh	1	m	This study
	Initial canopy height BT, C3G, C4G	0.001	m	This study
	Initial fractional cover NT	0.995	Proportion	This study
	Initial fractional cover BT, C3G, C4G, Sh, S	0.001	Proportion	This study
	Initial LAI NT, Sh	1.63	Dimensionless	▲Mottram (2009)
	Initial LAI BT, C3G, C4G	0.1	Dimensionless	This study

NT = needle leaf tress; BT = broad leaf trees; C3G = C3 grass; C4G = C4 grass; Sh = shrub; S = soil; C_s = soil carbon; b = exponent in soil hydraulic characteristics; Q_{10} = rate of soil respiration increase for 10°C rise in soil temperature; LAI = leaf area index; mmr = mass mixing ratio, mean annual for 1985 at Mona Loa; *value for sand; †mean value for coniferous forest and within range for dark soil; + approximately 1/4 of volumetric soil moisture at saturation; ▼ 50% carbon in top 20cm soil and remainder in 20 to 100cm soil depth; total soil depth = 1m; ‡ mean from field campaign 2 (2007) field data N = 5 from fire scars 2,7 and 8 (total N=15); ▲mean LAI measured in 2006 for fire scars 2 and 7 last burnt experimentally in 1991.

Table 5.3 Comparison of measured and modelled variables by month and year at Sharpsand Creek

	Time since fire (years)															
	15		**16**		**25**		**26**		**31**		**32**		**58**		**59**	
Variable	**Meas**	**Mod**	**Meas**	**Mod**	**Meas**	**Mod**	**Meas**	**Mod**	**Meas**	**Mod**	**Meas**	**Mod**	**Meas**	**Mod**	**Meas**	**Mod**
R_s	July 2006	May 1963	May 2007	May 1964	-	-			-	-	-	-	July 2006	July 2006	May 2007	May 2007
C_s	-	-	May 2007	May 1964	-	-	-	-	-	-	-	-	-	-	May 2007	May 2007
Can	June 2006	-	May 2007	May 1964	June 2006	June 1973	May 2007	May 1974	June 2006	June 1979	May 2007	May 1980	June 2006	June 2006	May 2007	May 2007
LAI	June 2006	-	-	June 1964	June 2006	June 1973	-	-	June 2006	June 1979	-	-	June 2006	June 2006	-	-

Meas = measured; Mod = modelled; R_s = soil respiration; C_s = soil carbon; Can = canopy height; LAI = leaf area index; field data obtained in 2006 and 2007 from fire scars last burnt in 1991 (15 to 16 years since fire), 1981 (25 to 26 years since fire), 1975 (31 to 32 years since fire) and 1948 (58 to 59 years since fire). May = 31 days; June = 30 days; July = 31 days; – variable not measured or modelled; note comparisons could only be made where Meas and Mod data available at various years since fire.

5.4 Summary

Fieldwork was carried out in 2006 and 2007, which involved taking measurements of R_s, T_s, $M_{s(v)}$ and C_s (2007 only) from various fire scar age categories at Sharpsand Creek. The pilot study was used to estimate spatial variability of R_s^T. The effects of T_s on R_s^C and M_s on $R_s^{T,C}$ were analysed using regression analysis. Significance testing for statistical differences in $\overline{R}_s^{T,M}$ and $\overline{C}_s$ between fire scar age categories was performed using Holm-Bonferroni corrected t tests. JULES was used to model $R_{s(h)}$, C_s, T_s, M_s, NT LAI, NT Can and NT Frac over successional time at Sharpsand Creek. The next chapter presents the results of the research.

Chapter 6: Results

6.1 Introduction

This chapter presents the results of the research and is comprised of three main sections. The first section details the results of fieldwork at Sharpsand Creek, specifically the pilot study of R_s spatial variability, differences in $\overline{C_s}$ between fire scar age categories, T_s and M_s responses of R_s and differences in $\overline{R_s}^{T,M}$ between fire scar age categories. The second section presents the results of the modelling analyses for Sharpsand Creek, specifically simulations of $R_{s(h)}$, C_s, T_s, M_s, NT LAI and NT Frac for the chronosequence. In the third section, field results of R_s, C_s, NT Can (this study) and NT LAI (concurrent study: Mottram 2009) are compared to those obtained from the modelling analyses at specific times since fire.

6.2 Fieldwork

6.2.1 Pilot study

Analysis of R_s data from the pilot study suggested high spatial variability in R_s^T ($\overline{R_s}^T$ = 3.20 µmol CO_2/m^2/s; σ = 1.41 µmol CO_2/m^2/s; CV = 44%) (two R_s outliers removed due to dubious R_s readings). Table 6.1 shows estimated sample size (N) requirements to be 95% confident that the sample $\overline{R_s}^T$ lies within various FE of the true $\overline{R_s}^T$. For instance, it is estimated that to be 95% confident the sample $\overline{R_s}^T$ lies within 20% of the true $\overline{R_s}^T$, N = 20 is required.

Table 6.1 Estimated minimum sample size (*N*) requirements of soil temperature (T$_s$) normalised soil respiration (R$_s$^{T}) to be 95% confident sample mean R$_s$^{T} ($\overline{R_s}$ ^{T}) lies within various fractional errors of the true $\overline{R_s}$ ^{T}.

Fractional error acceptance	Estimated minimum *N*
0.10	78
0.15	35
0.20	20
0.25	13
0.30	9

R$_s$^{T} adjusted to base soil respiration rate at T$_s$ = 10°C using Q_{10} = 2.0; based on 28 measurements taken from an area 30 m * 30 m from scar 7 (scar age category 1991; 15 years since fire) at Sharpsand Creek, June 2006. *N* rounded up to nearest integer.

6.2.2 Soil organic carbon analyses

C$_s$ contents of samples collected during FC 2 are shown in Table 6.2 and Fig. 6.1. Mean C$_s$ ($\overline{C_s}$) ranged from 0.060 g C/cm^3 (1975B, fire scar age = 0 years) to 0.103 g C/cm^3 (1991NB, fire scar age = 16 years). After removing 1 outlier (Chapter 5, Sect. 5.2.4.2), it was checked that the C$_s$ data for the five scar age categories were normally distributed (Kolmogorov-Smirnov test: $P > 0.1$ for all scar age categories). To test for differences between scars, ANOVA was inappropriate due to evidence of a statistically significant difference in variances between fire scar age categories (Levene's test: $W = 8.833$; $df = 4$, 27; $P = 0.000$ to 3 *sf*). Therefore a non-parametric test was performed, which indicated significant differences in median C$_s$ between one or more scar age categories (Kruskal-Wallis test: $\chi^2 = 11.031$; $N = 32$; $df = 4$; $P = 0.026$). Subsequent t tests (Students t test where Levene's $P > 0.05$; Unequal variances t test where Levene's $P < 0.05$) revealed a

Table 6.2 Descriptive statistics of soil samples analysed for organic carbon (C$_s$) collected from various fire scar age categories at Sharpsand Creek.

†Scar age category	Time since fire (years)	N replicate scars	N soil samples	$\overline{C}_s$ (g / cm^3)	σ_{C_s} (g / cm^3)	$\overline{\sigma}_{C_s}$ (g / cm^3)	CV_{C_s} (%)
1948 B	0	3	9	0.088	0.012	0.004	13.6
1948 NB	59	1	3	0.088	0.028	0.016	31.8
1975 B	0	3	8	0.060	0.014	0.005	23.3
1991 B	0	3	9	0.074	0.016	0.005	21.6
1991 NB	16	1	3	0.103	0.061	0.035	59.2

Soil samples collected during field campaign 2 (May 2007). †Scar age category corresponds to year of last burn (excluding 2007 burn). B = burnt in 2007; NB = not burnt in 2007. N = sample size; $\overline{C}_s$ = mean soil organic carbon; σ = standard deviation; $\overline{\sigma}$ = standard error; CV = coefficient of variation. 1 outlier removed (>1.5*inter quartile range).

statistically significant difference in $\overline{C}_s$ between 1948B and 1975B ($P = 0.000$ to 3 *sf*), though other comparisons were not statistically significant ($P > 0.1$) (Fig. 6.2; Table 6.3).
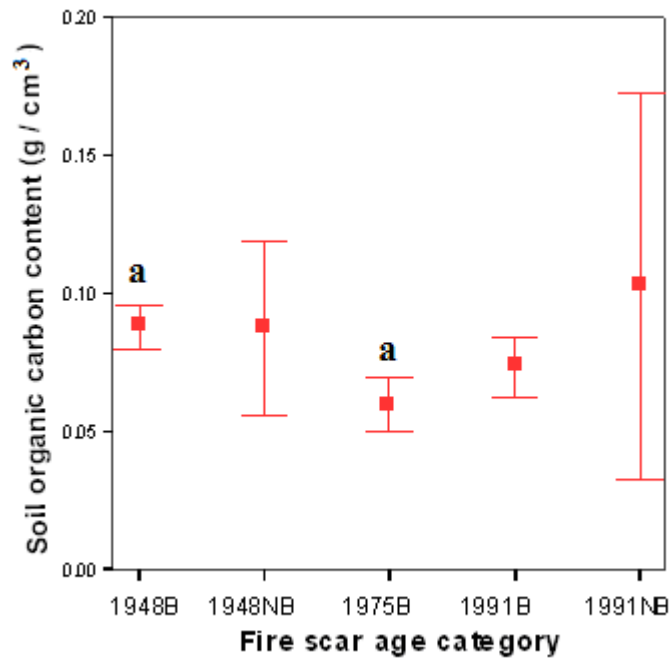
Figure 6.1 Mean soil organic carbon ($\overline{C_s}$) for five scar age categories at Sharpsand Creek. Soil samples collected during field campaign 2 (May 2007). Scar age category corresponds to year of last burn (excluding 2007 burn). B = burnt in 2007; NB = not burnt in 2007. Error bars represent mean ± 2 standard errors. Same letters are significantly different from one another (α = 0.1).

Table 6.3 Statistical tests for significant differences in mean soil organic C ($\overline{C_s}$) between various fire scar age categories at Sharpsand Creek.

Fire scar age category comparison	Levene's test		t test				
	F	*P*	Type	t	*df*	*P* raw	*P* Holmed
1948NB v 1948B	6.432	0.030	UV	0.041	2.242	0.971	1.0 NS
1948B v 1975B	0.112	0.742	S	4.602	15	0.000	0.000 ***
1991B v 1948B	2.166	0.160	UV	2.155	14.427	0.048	0.329 NS
1948NB v 1975B	3.832	0.082	S	2.294	9	0.047	0.329 NS
1991NB v 1948 NB	2.565	0.184	S	-0.401	4	0.709	1.0 NS
1975B v 1991B	0.960	0.343	S	-1.857	15	0.083	0.415 NS
1975B v 1991NB	14.748	0.004	UV	-1.213	2.076	0.345	1.0 NS
1991B v 1991NB	13.818	0.004	UV	-0.824	2.098	0.493	1.0 NS

Scar age category corresponds to year of last burn (excluding 2007 burn); B = burnt in 2007; NB = not burnt in 2007; v = versus; *F* = Levene's test statistic; *P* = statistical significance; NS = not statistically significant; t tests: S = students t test (where Levene's *P* > 0.05); UV = unequal variance t test (where Levene's *P* < 0.05); *df* = degrees of freedom; *P* values for t tests are 2 tailed; Values to 3 significant figures; *P* Holmed = Holm-Bonferroni correction for multiple hypothesis testing; NS *P* > 0.1; *P<0.1; **P<0.05; ***P<0.01.
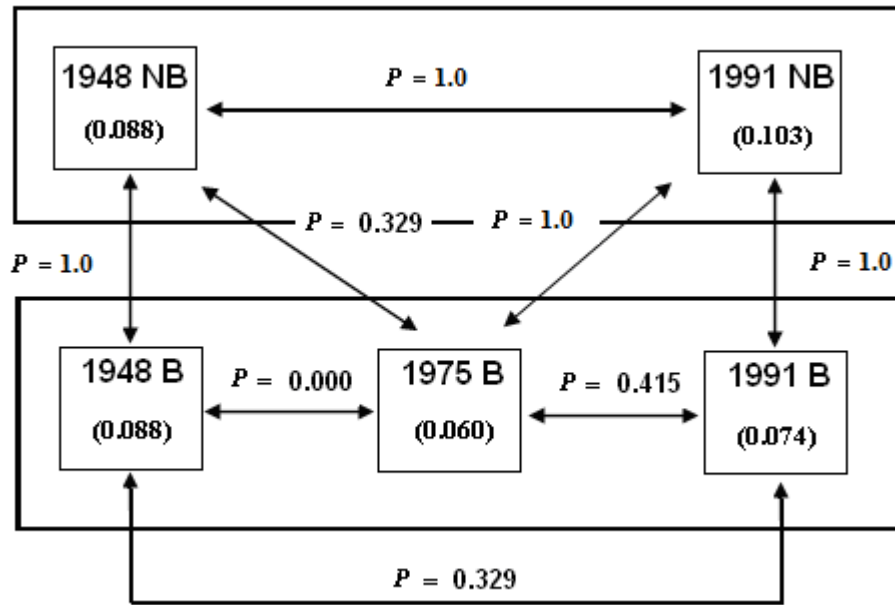
Figure 6.2 *P* **values from t tests for significant differences in mean soil organic carbon** $\overline{C}_s$ **(Parenthesis; units g/cm³) between various fire scar age categories at Sharpsand Creek. Arrows indicate t tests between two scar age categories; scar age category corresponds to year of last burn (excluding 2007 burn); B = burnt in 2007; NB = not burnt in 2007; for details of statistical tests see Table 6.3.**

6.2.3 Soil temperature response of soil respiration

R_s data for which C_s were known were adjusted for C_s (R_s^C) and plotted against T_s at 2 cm depth (Fig. 6.3; see also Chapter 5, Sect 5.2.4.1). There was a significant exponential relationship between R_s^C and T_s (logarithmic transformed linear regression: $N = 28$; $df = 27$; $r^2 = 0.60$; $P = 1.24 \ast 10^{-6}$); $Q_{10} = 2.21$ (five outliers visually identified prior to analysis and discarded).
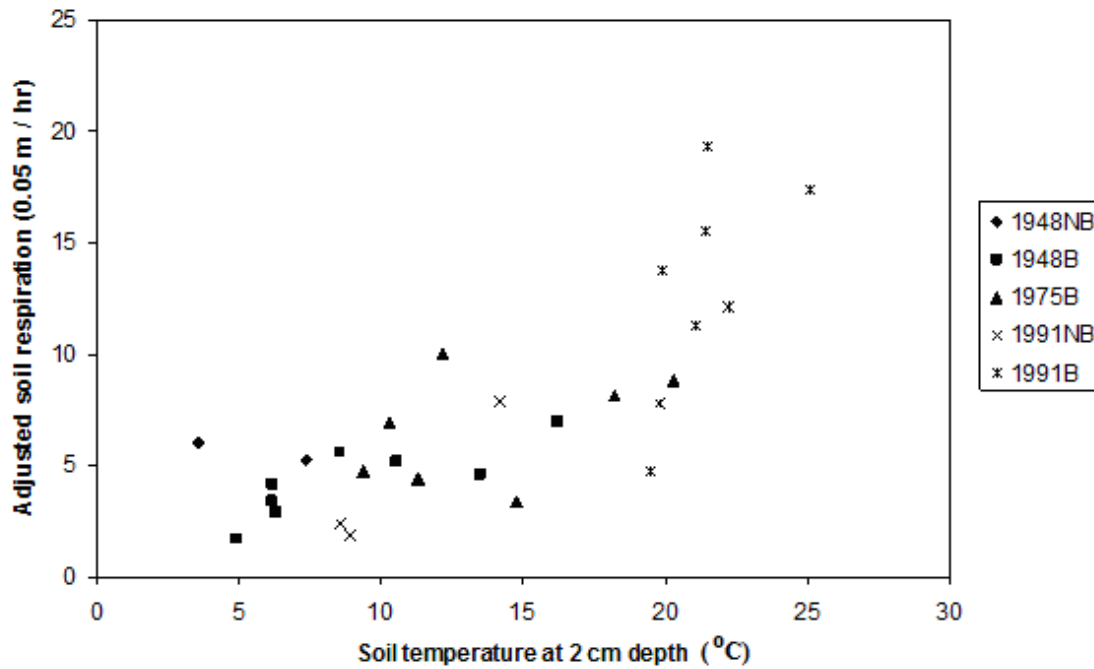
Figure 6.3 Soil respiration (R_s) adjusted for soil organic carbon (C_s) (R_s^C) versus soil temperature (T_s) at 2cm depth. $R_s^C = R_s/C_s$. Exponential function: $R_s^C = 2.0542exp(0.0794*T_s)$; $Q_{10} = 2.21$. Ln R_s^C versus T_s linear regression: $N = 28$; $df = 1, 26$; $r^2 = 0.60$; $P = 1.24*10^{-6}$. Based on measurements taken across Sharpsand Creek field site in May 2007.

6.2.4 Soil moisture response of soil respiration

R_s^C adjusted for T_s ($R_s^{C,T}$) (using $T_0 = 10°C$ and $Q_{10} = 2.21$) v M_s revealed no effect of M_s on $R_s^{C,T}$ over the range 0.21 to 0.77 M_s (linear regression: $N = 27$; $df = 26$; $r^2 = 0.006$; $P = 0.702$) (Fig 6.4; see also Chapter 5, Sect. 5.2.4.1) (one outlier visually identified prior to analysis and discarded).
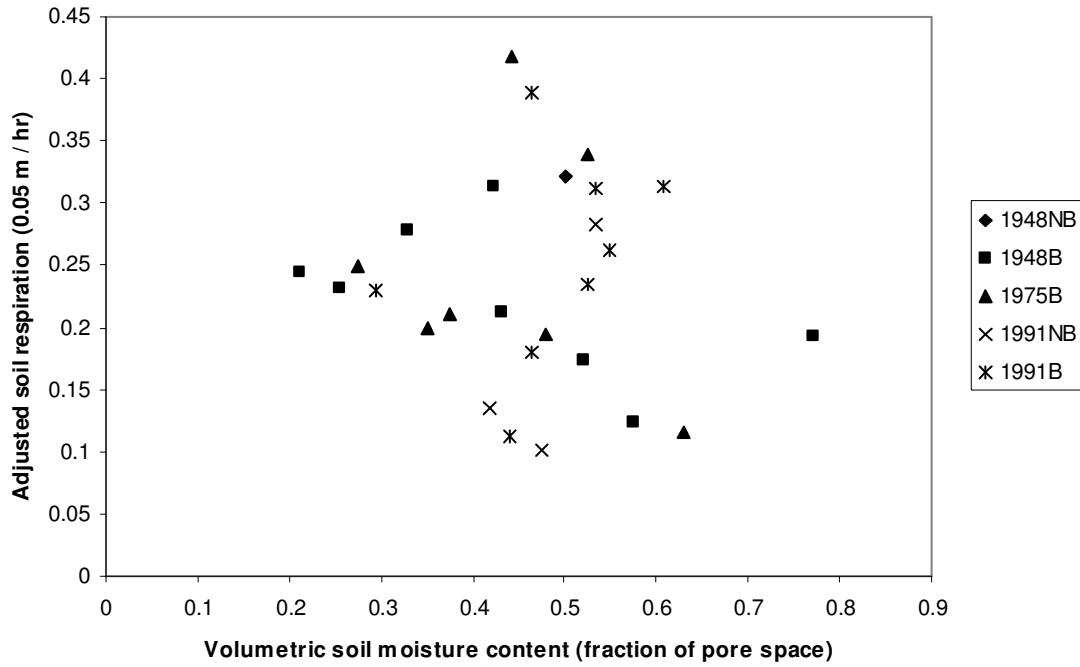
Figure 6.4 Adjusted soil respiration (R_s) versus volumetric soil moisture (M_s). R_s adjusted for soil organic carbon (C_s) (R_s/C_s), then adjusted for T_s (base $T_s = 10°C$; $Q_{10} = 2.21$). Linear regression: $N = 27$; $df = 26$; $r^2 = 0.006$; $P = 0.702$.

6.2.5 Differences in soil respiration between fire scar age categories

$\overline{R_s}^{T,M}$ along with N and variability coefficients for the fire scar age categories at Sharpsand

Creek are shown in Table 6.4 (see also Chapter 5, Sect. 5.2.4.1 (for T_s and M_s adjustments

of R_s) and Sect. 5.2.4.2 (for outlier identification). In FC 1 $CV_{R_s^{T,M}}$ was higher (56%) in

older fire scars (1948†; 58 years since fire) than younger ones (1991†; 15 years since fire)

(22%). When comparing the same scar age categories from FC 2, $CV_{R_s^{T,M}}$ was somewhat

lower in 1948NB (41%) and slightly lower in 1991NB (20%) compared with FC1, though,

$CV_{R_s^{T,M}}$ was still higher in the older scar age category.

For the different fire scar age categories that were all subject to burning in 2007 (1948B; 1975B; 1991B), it appeared that the previously younger fire scar age category (1991B) had lowest $CV_{R_s^{T,M}}$ (26%) followed by 1948B (49%) and 1975B (55%). Although it appeared that burning increases $CV_{R_s^{T,M}}$ immediately after fire (1948NB < 1948B; 1991NB < 1991B), $CV_{R_s^{T,M}}$ for 1991B was still lower than that obtained for 1948B.

N for 1948† was 12 and this is < minimum $N = 32$ to be 95% confident the sample $\overline{R_s}^{T,M}$ lies within 20% of true $\overline{R_s}^{T,M}$ for this scar age category (Sect. 7.2.1). N for 1948NB was 8 and this is < minimum $N = 17$ to be 95% confident the sample $\overline{R_s}^{T,M}$ lies within 20% of the true $\overline{R_s}^{T,M}$ for this scar age category. N for 1948B was 24 and this is < minimum $N = 25$ to be 95% confident the sample $\overline{R_s}^{T,M}$ lies within 20% of the true $\overline{R_s}^{T,M}$ for this scar age category. N for 1975B was 27 and this is < minimum $N = 31$ to be 95% confident the sample $\overline{R_s}^{T,M}$ lies within 20% of the true $\overline{R_s}^{T,M}$ for this scar age category. N for 1991† was 7 and this is < minimum $N = 20$ to be 95% confident the sample $\overline{R_s}^{T,M}$ lies within 20% of the true $\overline{R_s}^{T,M}$ for this scar age category (calculations based on the pilot study). However, N for 1991† was 7 and this is > minimum $N = 5$ to be 95% confident the sample $\overline{R_s}^{T,M}$ lies within 20% of true $\overline{R_s}^{T,M}$ for this scar age category (calculations based on FC 1 as opposed to pilot study). N for 1991NB was 8 and this is > minimum $N = 4$ to be 95% confident the sample $\overline{R_s}^{T,M}$ lies within 20% of the true $\overline{R_s}^{T,M}$ for this scar age category. N for 1991B was 25 and this is > minimum $N = 7$ to be 95% confident the sample $\overline{R_s}^{T,M}$ lies within 20% of the true $\overline{R_s}^{T,M}$ for this scar age category.

Table 6.4 Mean soil respiration (R_s) adjusted for soil temperature (T_s) and soil moisture (M_s)
($\overline{R_s}^{T,M}$) along with sample sizes (N) and variability coefficients from various fire scar age categories in
field campaigns 1 (2006) and 2 (2007) at Sharpsand Creek.

Scar age category	N_1	N_2	$\overline{R_s}^{T,M}$ (μmol CO_2/m^2/s)	$\sigma_{\overline{R_s}^{T,M}}$ (μmol CO_2/m^2/s)	$\overline{\sigma}_{\overline{R_s}^{T,M}}$ (μmol CO_2/m^2/s)	$CV_{\overline{R_s}^{T,M}}$
1948†	3	12	8.18	4.60	1.33	0.56
1991†	2	7	2.61	0.58	0.22	0.22
1948NB+	1	8	1.91	0.79	0.28	0.41
1948B+	3	24	0.83	0.41	0.08	0.49
1975B+	3	27	0.56	0.31	0.06	0.55
1991NB+	1	8	0.79	0.16	0.06	0.20
1991B+	3	25	0.91	0.24	0.05	0.26

T_s adjustment: Q_{10} = 2.21; reference T_s = 10°C; M_s adjustment: exclusion of R_s values with associated M_s outside the range 0.21 to 0.77 volumetric M_s; scar age category = year of last burn (not including 2007 wildfire); † Field campaign 1 (2006); + field campaign 2 (2007); NB = not burnt in 2007; B = burnt in 2007; N_1 = number of replicate scars; N_2 = number of R_s measurements; σ – standard deviation; $\overline{\sigma}$ - standard error of mean; CV – coefficient of variation.

There was evidence of one or more statistically significant differences in median $R_s^{T,M}$ between fire scar age categories (Kruskal-Wallis test: N = 111; χ^2 = 67.176; df = 6; P = 0.000 to 3 sf), see also Fig. 6.5). Holm-Bonferroni corrected independent samples t tests revealed significant differences (α = 0.1) in $\overline{R_s}^{T,M}$ (Table 6.5; Fig 6.6). $\overline{R_s}^{T,M}$ was significantly greater in 1948 than 1991 age categories in both FC 1 (15 v 58 years since

Table 6.5 t tests comparing mean soil respiration (R_s) adjusted for soil temperature (T_s) and soil moisture (M_s) ($\overline{R}_S{}^{T,M}$) between various scar age categories at Sharpsand Creek.

Fire scar age category Comparison	Levene's test			t test			
	F	*P*	**Type**	*t*	*df*	*P* raw	*P* Holmed
1948† v 1991†	9.793	0.006	UV	4.130	11.598	0.001	0.009 ***
1948NB+ v 1948B+	10.332	0.003	UV	3.713	8.289	0.006	0.030**
1948NB+ v 1975B+	24.943	0.000	UV	4.719	7.632	0.002	0.014**
1948B+ v 1975B+	1.547	0.219	S	2.632	49.0	0.011	0.044**
1948NB+ v 1991NB+	20.228	0.001	UV	3.943	7.599	0.005	0.030**
1948B+ v 1991B+	6.297	0.016	UV	-0.849	36.571	0.402	0.402 NS
1975B+ v 1991NB+	6.325	0.017	UV	2.693	22.530	0.013	0.044**
1975B+ v 1991B+	2.917	0.094	S	4.533	50.0	0.000	0.000***
1991NB+ v 1991B+	2.269	0.142	S	-1.370	31.0	0.181	0.362 NS
1948† v 1948NB+	9.643	0.006	UV	-4.615	11.958	0.001	0.009***
1991† v 1991NB+	6.255	0.027	UV	8.020	6.826	0.000	0.000***

T_s adjustment: Q_{10} = 2.21; reference T_s = 10°C; M_s adjustment: exclusion of R_s values with associated M_s outside the range 0.21 to 0.77 volumetric M_s; scar age category = year of last burn (not including 2007 wildfire); † field campaign 1 (2006); + field campaign 2 (2007); NB = not burnt in 2007; B = burnt in 2007; 'Type': S = students t test (where Levene's P > 0.05); UV = unequal variance t test (where Levene's *P* < 0.05). *P* Holmed = Holm-Boferroni adjustment for multiple hypothesis testing; *P* values 2 tailed; NS *P* > 0.1; *P < 0.1; **P < 0.05; ***P < 0.01.
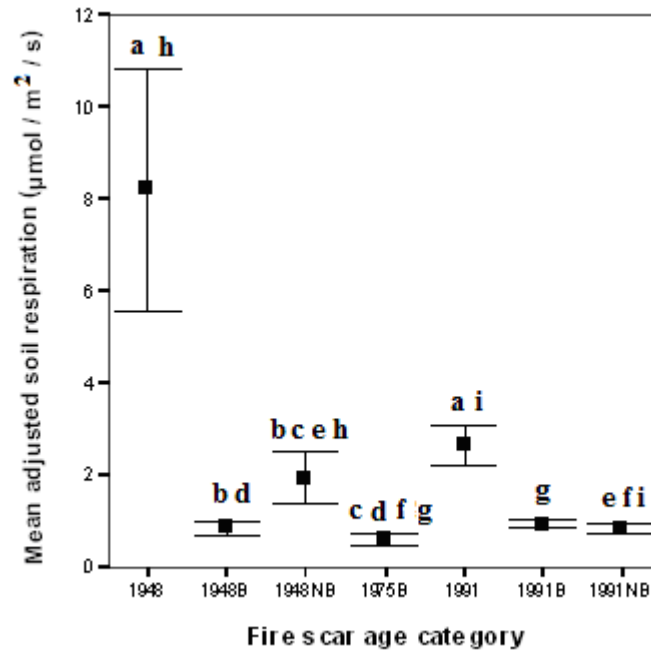
Figure 6.5 Mean soil respiration (soil surface CO_2 efflux) adjusted for soil temperature (T_s) and soil moisture (M_s) ($\overline{R_s}^{T,M}$) for various fire scar age categories at Sharpsand Creek. T_s adjustment: Q_{10} = 2.21; reference T_s = 10°C; M_s adjustment: exclusion of R_s values with associated M_s outside the range 0.21 to 0.77 volumetric M_s; data collected over field campaign 2 (2007) except 1948 and 1991 categories – data collected during field campaign 1 (2006). Scar age category corresponds to year of last burn (excluding 2007 burn). NB = not burnt in 2007; B = burnt in 2007. Error bars represent mean ±2 standard errors.

fire) and FC 2 (16 v 59 years since fire) (FC 1: 1948† $\overline{R_s}^{T,M}$ = 8.18 µmol CO_2/m^2/s; 1991†

$\overline{R_s}^{T,M}$ = 2.61 µmol CO_2/m^2/s; FC 2: 1948NB+ $\overline{R_s}^{T,M}$ = 1.91 µmol CO_2/m^2/s; 1991NB+

$\overline{R_s}^{T,M}$ = 0.79 µmol CO_2/m^2/s. However, $\overline{R_s}^{T,M}$ was significantly greater in FC 1 than FC 2

when comparing the same scar age category (1948NB+ v 1948†; 1991NB+ v 1991†).
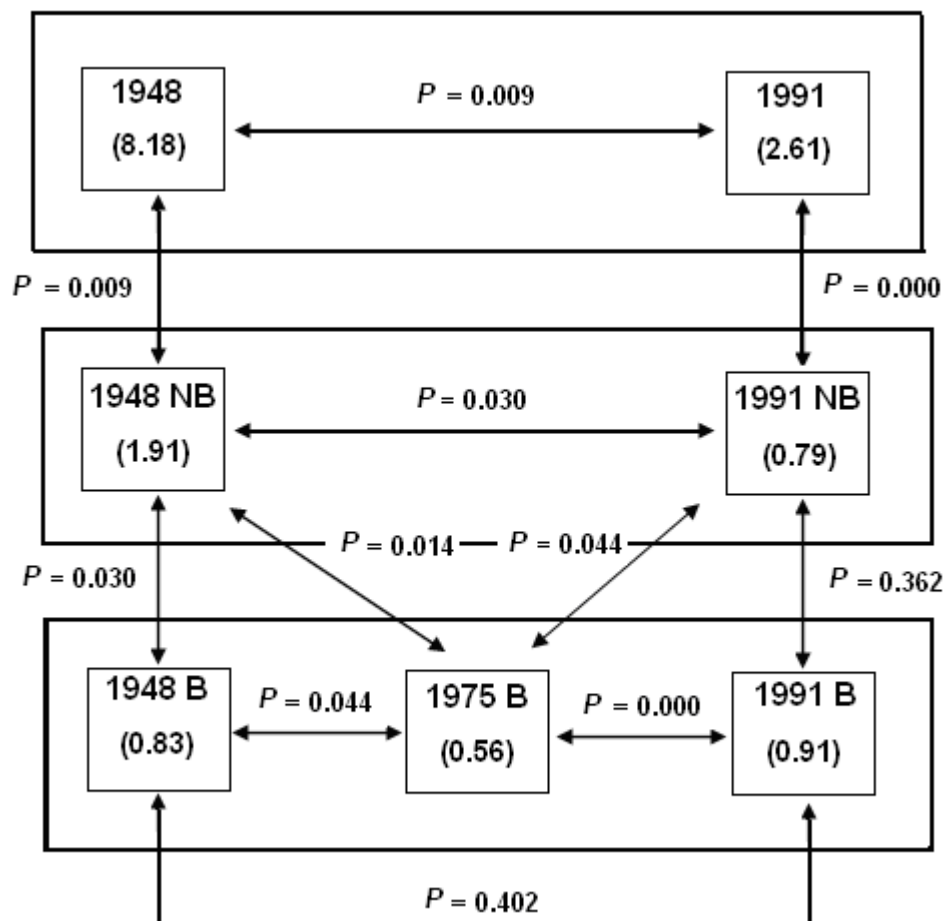
Figure 6.6 Diagrammatic representation of t tests for significant differences in mean soil respiration adjusted for soil temperature (T_s) and soil moisture (M_s) ($\overline{R}_s^{\,T,M}$) (values in parenthesis; units: μmol $CO_2/m^2/s$) between various fire scar age categories at Sharpsand Creek. Arrows indicate t tests between two scar age categories; T_s adjustment: Q_{10} = 2.21; reference T_s = 10°C; M_s adjustment: exclusion of R_s values with associated M_s outside the range 0.21 to 0.77 volumetric M_s; scar age category corresponds to year of last burn (not including 2007 wildfire); NB = not burnt in 2007 wildfire; B = burnt in 2007 wildfire; data collected in field campaign 2 (2007) except scar age category '1948' and '1991' collected in field campaign 1 (2006); for details of statistical tests see Table 6.4.

There was a strong significant exponential increase in $\overline{R_s}^{T,M}$ with time since fire (logarithmic transformed linear regression (Ln R_s v time since burn): $N = 3$; $df = 2$; $r^2 = 0.999$; $P = 0.006$); see also Fig. 6.7.
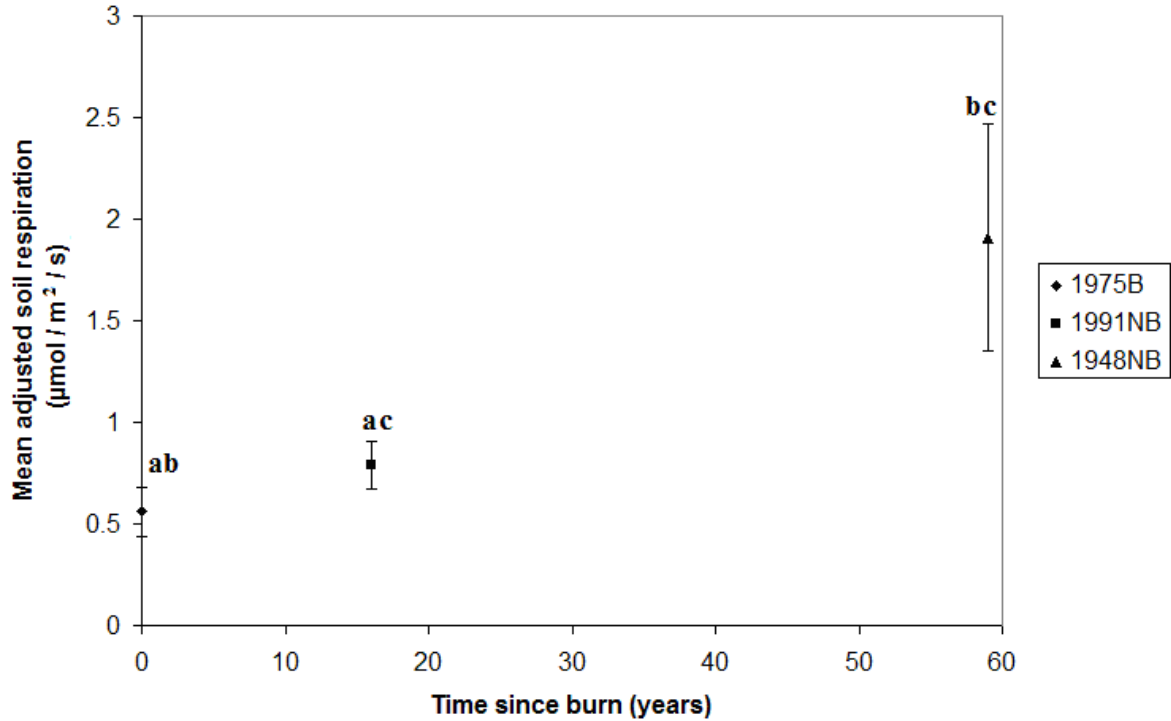
Figure 6.7 Mean soil respiration (soil surface CO_2 efflux) adjusted for soil temperature (T_s) and soil moisture (M_s) ($\overline{R_s}^{T,M}$) versus time (t) since last fire at Sharpsand Creek. Based on three scar age categories: 1975B (0 years since fire), 1991NB (16 years since fire), 1948NB (59 years since fire). T_s adjustment: $Q_{10} = 2.21$; reference $T_s = 10°C$; M_s adjustment: exclusion of R_s values with associated M_s outside the range 0.21 to 0.77 volumetric M_s; measurements made during field campaign 2 (May 2007). Empirical function: $\overline{R_s}^{T,M} = 0.5629exp(0.0207*t)$; transformed linear regression (Ln R_s v time since burn): $N = 3$; $df = 2$; $r^2 = 0.999$; $P = 0.006$. Error bars represent mean ± 2 standard errors.

6.3 JULES simulations at Sharpsand Creek

Annual, mean $R_{s(h)}$ ($\overline{R}_{s(h)}$) for the three simulations showed no overlap across the chronosequence with RR 1 > RR 2 > RR 3 (Fig. 6.8). Furthermore, $\overline{R}_{s(h)}$ showed high inter-annual fluctuation (RR 1 > RR 2 > RR 3). In RR 1, $\overline{R}_{s(h)}$ generally decreased between 1965 and 1995 though in RR 2 and RR 3, $\overline{R}_{s(h)}$ showed no obvious overall change over this period. There was a general increase in $\overline{R}_{s(h)}$ for all three simulations between 1995 and 2007.
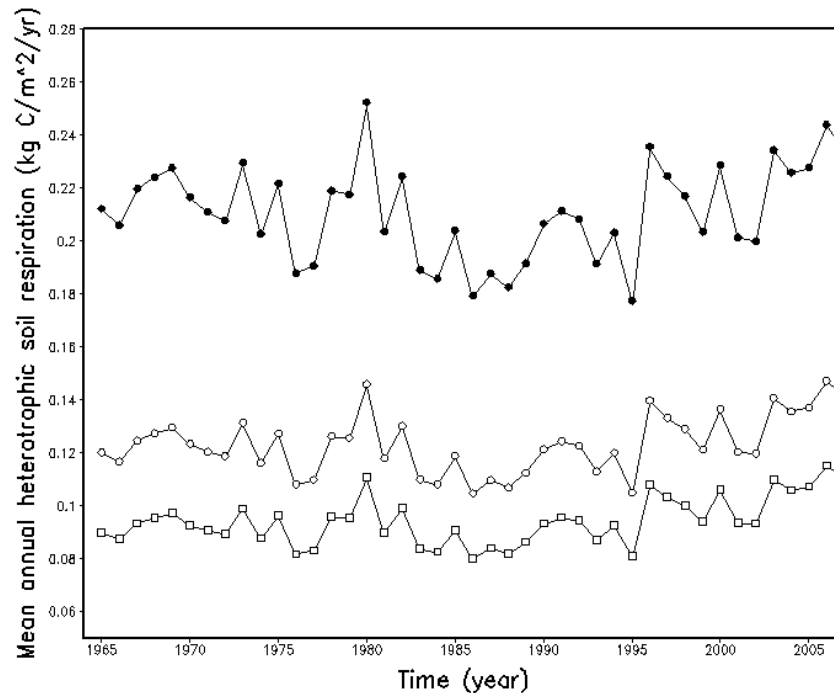
Figure 6.8 Mean annual heterotrophic soil respiration for the three simulations at Sharpsand Creek for the period 1965 through 2007. Filled circles = replicate run 1; open circles = replicate run 2; squares = replicate run 3.

Instantaneous C_s for the three simulations showed no overlap across the chronosequence with RR 1 > RR 2 > RR 3 (Fig. 6.9). RR 1 showed an approximately linear decrease in C_s over the chronosequence and this was also true for RR 2, though the rate of decline was less. However, C_s did not appear to change over the chronosequence for RR 3.
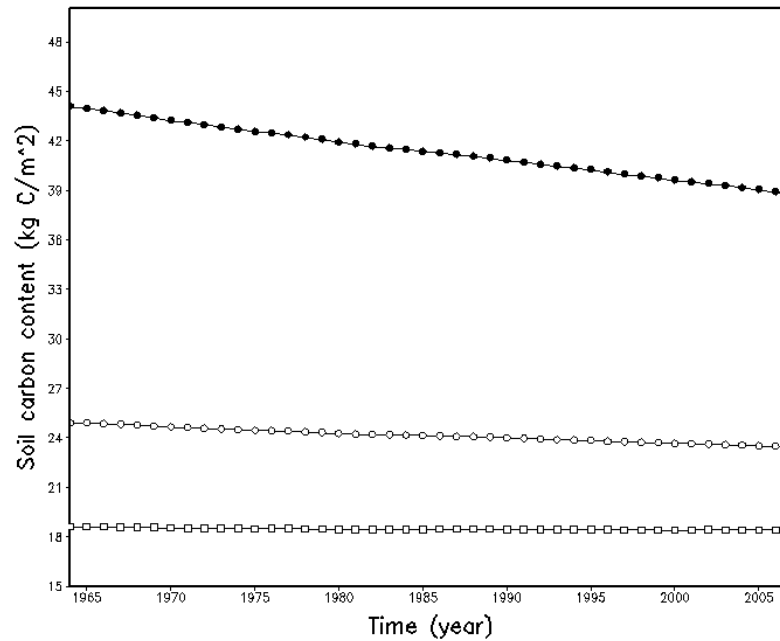
Figure 6.9 Instantaneous soil carbon for the three simulations at Sharpsand creek for the period 1964 through 2007. Soil depth assumed to = 1m. Filled circles = replicate run 1; open circles = replicate run 2; squares = replicate run 3.

As expected, there were no differences in instantaneous NT LAI between simulations across the chronosequence (Fig. 6.10). With the exception of four sharp declines, NT LAI did not appear to change significantly between 1964 and 1996, though did show a slight increase from 1996 to 2007.
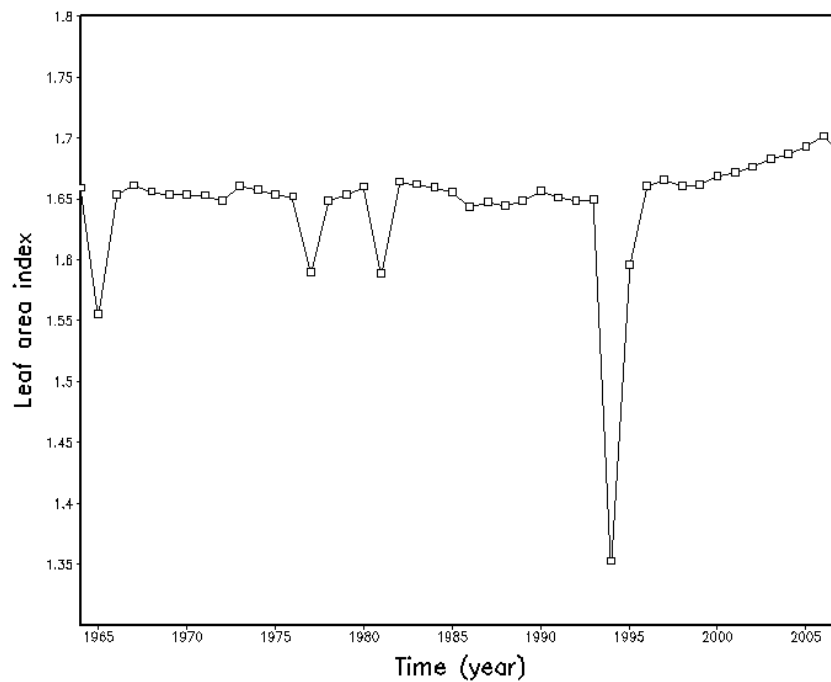
Figure 6.10 Instantaneous leaf area index of needle leaf trees for the three simulations at Sharpsand Creek for the period 1964 through 2007.

As expected, there were no differences in annual $\overline{T}_s$ between the three simulations, which fluctuated between 1965 and 1995, though showed a significant increase between 1995 and 2007 (Fig. 6.11).
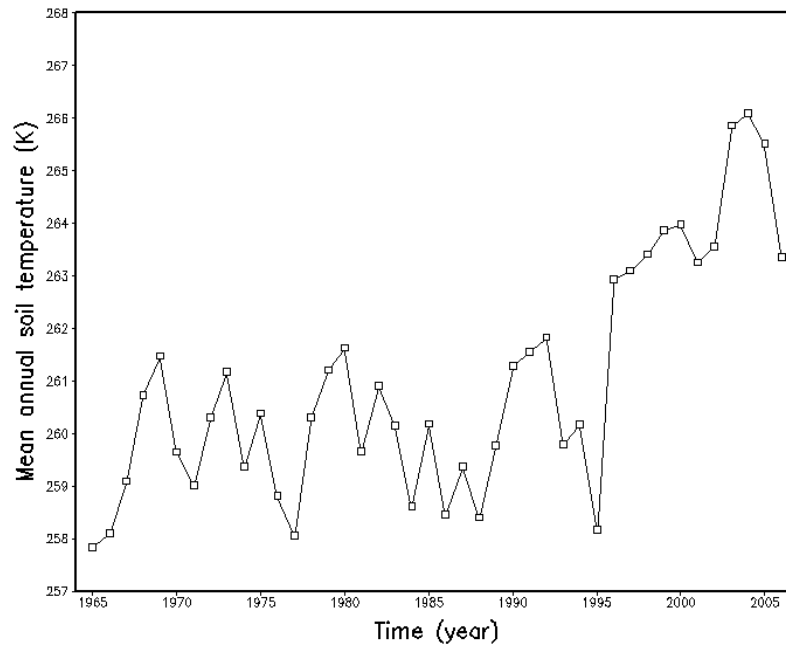
Figure 6.11 Mean annual soil temperature for the three simulations at Sharpsand Creek for the period 1965 through 2007. Simulations for soil layer 1 (surface to 0.05m depth).

As expected, there were no differences in annual $\overline{M}_s$ between the three simulations, which showed high inter-annual fluctuation, though there was a general decline from 1965 through 1990, thereafter increasing more noticeably to 2007 (Fig. 6.12).
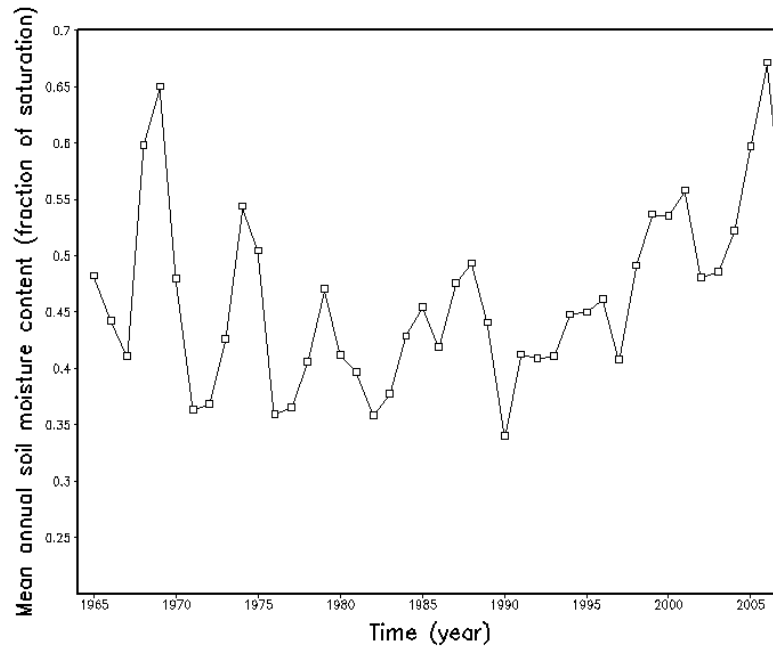
Figure 6.12 Mean annual soil moisture content for the three simulations at Sharpsand Creek for the period 1965 through 2007. Simulations for soil layer 1 (surface to = 0.05 m depth).

As expected, there were no differences in annual NT Frac between the three simulations, which showed an approximately linear decline over the chronosequence (Fig. 6.13).
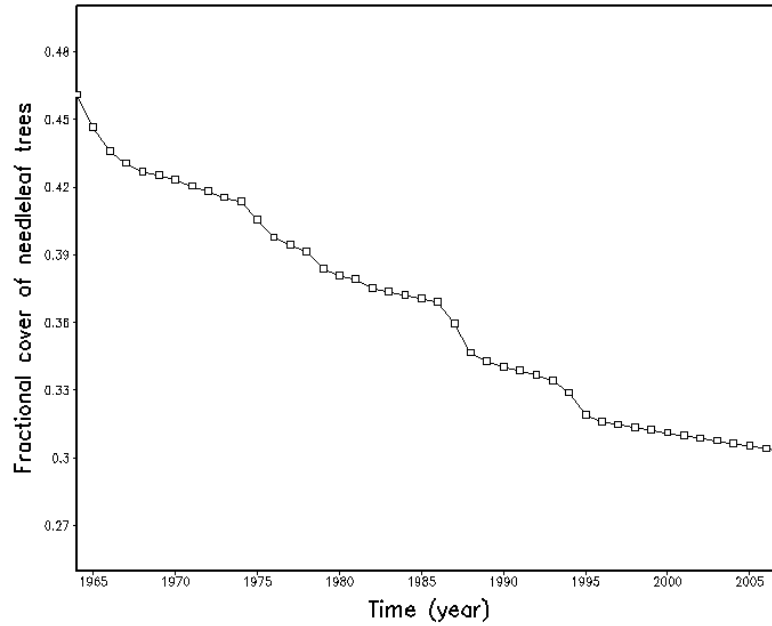
Figure 6.13 Instantaneous fractional cover of needle leaf trees for the three simulations at Sharpsand Creek for the period 1964 through 2007.

6.4 Field versus modelled observations

Measured $\overline{R_s}^{T,M}$ (2.61 μmol CO_2/m^2/s) was > modelled $\overline{R_{s(h)}}^{T}$ (1.72 μmol CO_2/m^2/s; T_s adjustment using $Q_{10} = 2.21$; $T_0 = 10°C$) at 15 years since fire, though σ overlapped (Table 6.6). Measured $\overline{R_s}^{T,M}$ fell within 2σ of modelled $\overline{R_{s(h)}}^{T}$ and modelled $\overline{R_{s(h)}}^{T}$ fell within 2σ of measured $\overline{R_s}^{T,M}$ at 15 years since fire.

Table 6.6 Comparison of measured and modelled variables at specific times since fire at Sharpsand Creek.

Var	Units	Scar age category	Month/year measured	Month/year modelled	Time since fire for measured and modelled (years)	Measured Mean	Measured σ	Measured CV	Modelled Mean	Modelled σ	Modelled CV
R_s	μmol CO_2/m^2/s	1991	July 2006	May 1963	15	2.61	0.58	0.22	1.72	0.77	0.45
		1991	May 2007	May 1964	16	0.79	0.16	0.20	1.17	0.51	0.44
		1948	July 2006	July 2006	58	8.18	4.60	0.56	1.54	0.62	0.40
		1948	May 2007	May 2007	59	1.91	0.79	0.41	1.58	0.62	0.40
C_s	kg C / m^2	1991	May 2007	May 1964	16	25.73	15.13	0.59	29.25	13.27	0.45
		1948	May 2007	May 2007	59	21.88	6.89	0.31	26.92	10.62	0.39
LAI	dimensionless	1981	June 2006	June 1973	25	1.02	0.75	0.74	1.64	0	0
		1975	June 2006	June 1979	31	2.28	1.42	0.62	1.63	0	0
		1948	June 2006	June 2006	58	2.28	0.82	0.36	1.66	0	0
Can	m	1991	May 2007	May 1964	16	2.54	0.60	0.24	9.00	0	0
		1981	May 2007	May 1974	26	6.93	0.81	0.12	9.00	0	0
		1975	May 2007	May 1980	32	9.02	0.81	0.09	9.04	0	0
		1948	May 2007	May 2007	59	15.68	1.32	0.08	9.13	0	0

Var = variable; R_s = soil respiration; C_s = soil carbon; LAI = leaf area index; Can = canopy height; 2006 = field campaign 1; 2007 = field campaign 2; σ = standard deviation; CV = coefficient of variation; R_s measured adjusted for soil temperature (T_s) (adjustment: Q_{10} = 2.21; reference T_s = 10°C) and soil moisture (M_s) (adjustment: exclusion of R_s values with associated M_s outside the range 0.21 to 0.77 volumetric M_s). R_s modelled (heterotrophic) adjusted for T_s Q_{10} = 2.21; reference T_s = 10°C. LAI measured during June 2006, Can measured in May 2007.

Measured $\overline{R_s}^{T,M}$ (0.79 μmol CO_2/m^2/s) was < modelled $\overline{R_{s(h)}}^{T}$ (1.17 μmol CO_2/m^2/s) at 16 years since fire, with overlap of σ. Measured $\overline{R_s}^{T,M}$ fell within 1σ of modelled $\overline{R_{s(h)}}^{T}$ and modelled $\overline{R_{s(h)}}^{T}$ fell within 3σ of measured $\overline{R_s}^{T,M}$ at 16 years since fire.

Measured $\overline{R_s}^{T,M}$ (8.18 μmol CO_2/m^2/s) was > modelled $\overline{R_{s(h)}}^{T}$ (1.54 μmol CO_2/m^2/s) at 58 years since fire with no overlap of σ. Modelled $\overline{R_{s(h)}}^{T}$ fell within 2σ of measured $\overline{R_s}^{T,M}$ and measured $\overline{R_s}^{T,M}$ fell within 11σ of modelled $\overline{R_{s(h)}}^{T}$ at 58 years since fire.

Measured $\overline{R_s}^{T,M}$ (1.91 μmol CO_2/m^2/s) was > modelled $\overline{R_{s(h)}}^{T}$ (1.58 μmol CO_2/m^2/s) at 59 years since fire with overlaps in σ. Modelled $\overline{R_{s(h)}}^{T}$ fell within 1σ of measured $\overline{R_s}^{T,M}$ and measured $\overline{R_s}^{T,M}$ fell within 1σ of modelled $\overline{R_{s(h)}}^{T}$ at 59 years since fire.

Where measured $\overline{R_s}^{T,M}$ increased from 2.61±0.58σ μmol CO_2/m^2/s at 15 years since fire to 8.18±4.60σ μmol CO_2/m^2/s at 58 years since fire and was significantly different (P = 0.009) (FC1), modelled $\overline{R_{s(h)}}^{T}$ decreased from 1.72±0.77σ μmol CO_2/m^2/s to 1.54±0.62σ μmol CO_2/m^2/s during same period, but the difference was considered NS due to overlap of σ.

Where measured $\overline{R_s}^{T,M}$ increased from 0.79±0.16σ μmol CO_2/m^2/s at 16 years since fire to 1.91±0.79σ μmol CO_2/m^2/s at 59 years since fire and was significantly different (P = 0.030) (FC 2), modelled $\overline{R_{s(h)}}^{T}$ also increased from 1.17±0.51σ μmol

$CO_2/m^2/s$ at 16 years since fire to 1.58±0.62σ μmol $CO_2/m^2/s$ at 59 years since fire, but differences were considered NS due to overlap of σ.

Measured $\overline{C_s}$ (25.73 kg C/m^2) was < modelled $\overline{C_s}$ (29.25 kg C/m^2) at 16 years since fire (Table 6.6). Measured $\overline{C_s}$ fell within 1σ of modelled $\overline{C_s}$ and modelled $\overline{C_s}$ fell within 1σ of measured $\overline{C_s}$ at 16 years since fire.

Measured $\overline{C_s}$ (21.88 kg C/m^2) was < modelled $\overline{C_s}$ (26.92 kg C/m^2) at 59 years since fire and σ overlapped. Measured $\overline{C_s}$ fell within 1σ of modelled $\overline{C_s}$ and modelled $\overline{C_s}$ fell within 1σ of measured $\overline{C_s}$.

Where measured $\overline{C_s}$ decreased from 25.73±15.13 σ kg C/m^2 at 16 years since fire to 21.88±6.89σ kg C/m^2 at 59 years since fire though was NS (P = 1.0), modelled $\overline{C_s}$ also decreased from 29.25±13.27σ kg C/m^2 to 26.92±10.62σ kg C/m^2 from 16 to 59 years since fire and this was also NS due to overlap of σ.

Modelled NT $\overline{LAI}$ changed very little over the chronosequence: 1.64±σ, 1.63±σ, 1.66 ±0σ at 25, 31 and 58 years since fire respectively (Table 6.6). This is in contrast to measured NT $\overline{LAI}$ which increased from 1.02±0.75σ at 25 years since fire to 2.28±1.42σ at 31 years since fire and 2.28 ±0.82σ at 58 years since fire.

Modelled NT $\overline{Can}$ also remained similar across the chronosequence: 9.00±0σ m, 9.00±0σ m, 9.04±0σ m, 9.13±0σ m for 16, 26, 32 and 59 years since fire respectively

(Table 6.6). This is in contrast to measured NT $\overline{Can}$ which increased from 2.54±0.60 σ m to 6.93±0.81 σ m to 9.02±0.81 σ m to 15.68±1.32 σ m at the same years since fire.

6.5 Summary

Two field campaigns were carried out at Sharpsand Creek in 2006 and 2007. $\overline{R_s}^{T,M}$ ranged from 0.56 μmol $CO_2/m^2/s$ (32 years post fire) to 8.18 μmol $CO_2/m^2/s$ (58 years post fire). $CV_{R_s^{T,M}}$ ranged from 20% (16 years post fire) to 56% (58 years post fire). Across the field site, there was a significant exponential relationship between R_s^C and T_s ($P = 1.24*10^{-06}$; $Q_{10} = 2.21$) but no effect of M_s on $R_s^{C,T}$ for the range 0.21 to 0.77 M_s ($P = 0.702$). $\overline{R_s}^{T,M}$ significantly ($P = 0.030$) decreased after burning mature forest, though no significant ($P > 0.1$) difference could be detected between recently burned and unburned young forest. R_s was measured in recently burned boreal jack pine fire scar age categories that differed in their burn history and there was a significant difference in $\overline{R_s}^{T,M}$ between previously 32 v 16 year old ($P = 0.000$) and previously 32 v 59 year old ($P = 0.044$) scars. There was a strong significant exponential increase in $\overline{R_s}^{T,M}$ with time since fire ($r^2 = 0.999$; $P = 0.006$) for the chronosequence 0, 16 and 59 years post fire, and for all these age categories, $\overline{R_s}^{T,M}$ was significantly different from one another ($P < 0.05$). JULES was used to model $R_{s(h)}$, C_s, T_s, M_s, NT LAI, NT Can and NT Frac over successive time at Sharpsand Creek. JULES appeared to perform poorly in simulating vegetation re-growth and seemed to over estimate $R_{s(h)}$ when T_s corrected simulated values were compared with measured $\overline{R_s}^{T,M}$. The next, and final chapter discusses the results of the fieldwork and modelling analyses in the context of relevant literature, the main limitations and suggestions for future research.

Chapter 7: Discussion

7.1 Introduction

This chapter is comprised of five main sections. The first section discusses the results of fieldwork at Sharpsand Creek, specifically spatial variability of R_s, T_s and M_s responses of R_s, and differences in $\overline{R_s}^{\text{T,M}}$ between fire scar age categories. Thereafter, the results of JULES simulations over the chronosequence are considered, followed by a discussion of field observed versus modelled variables at specific times since fire. The study is then concluded and this is followed by directions for future research.

7.2 Fieldwork at Sharpsand Creek

7.2.1 Spatial variability of soil respiration

7.2.1.1 Interpretation of results

The pilot study indicated high spatial variability in R_s^T ($CV_{R_s^T} = 44\%$) in a 15 year old fire scar. Moreover, it was estimated that to be 95% confident sample $\overline{R_s}^{\text{T}}$ lies within 20% of the true $\overline{R_s}^{\text{T}}$, $N = 20$ is required in 15 year old fire scars. Over FC 1 and 2, $CV_{R_s^{T,M}}$ for the different fire scar age categories ranged from 20% (FC 2; 1991NB; 16 year old scar) to 56% (FC 1; 1948†; 58 year old scar). In FC 1, where soil collars were *not* used for R_s measurements, $CV_{R_s^{T,M}}$ was higher in older fire scars (1948†; 58 years since fire; $CV_{R_s^{T,M}} = 56\%$; minimum $N = 32$ to be 95% confident sample $\overline{R_s}^{\text{T,M}}$ lies within 20% of true $\overline{R_s}^{\text{T,M}}$) than younger ones (1991†; 15 years since fire; $CV_{R_s^{T,M}} = 22\%$; minimum $N = 5$ to be 95% confident sample $\overline{R_s}^{\text{T,M}}$ lies within 20% of true $\overline{R_s}^{\text{T,M}}$). When comparing the same scar

age categories from FC 2, $CV_{R_s^{T,M}}$ was somewhat lower in 1948NB ($CV_{R_s^{T,M}}$ = 41%;

minimum N = 17 to be 95% confident sample $\overline{R_s}^{T,M}$ lies within 20% of the true $\overline{R_s}^{T,M}$)

and slightly lower in 1991NB ($CV_{R_s^{T,M}}$ = 20%; minimum N = 4 to be 95% confident sample

$\overline{R_s}^{T,M}$ lies within 20% of the true $\overline{R_s}^{T,M}$) compared with FC 1, though, $CV_{R_s^{T,M}}$ was still

higher in the older scar age category. The absence of soil collars may have resulted in

greater spatial variability, accounting for higher $CV_{R_s^{T,M}}$ measured in FC 1, though

measurements were also taken approximately a year apart.

For the different fire scar age categories that were all subject to burning in 2007, it

appeared that the previously younger fire scar age category (1991B) had lowest $CV_{R_s^{T,M}}$

($CV_{R_s^{T,M}}$ = 26%; minimum N = 7 to be 95% confident sample $\overline{R_s}^{T,M}$ lies within 20% of the

true $\overline{R_s}^{T,M}$) followed by 1948B ($CV_{R_s^{T,M}}$ = 49%; minimum N = 25 to be 95% confident

sample $\overline{R_s}^{T,M}$ lies within 20% of the true $\overline{R_s}^{T,M}$) and 1975B ($CV_{R_s^{T,M}}$ = 55%; minimum N =

31 to be 95% confident sample $\overline{R_s}^{T,M}$ lies within 20% of the true $\overline{R_s}^{T,M}$). Although it

appeared that burning increases $CV_{R_s^{T,M}}$ immediately after fire (1948NB < 1948B; 1991NB

< 1991B), $CV_{R_s^{T,M}}$ for 1991B was still lower than that for 1948B, perhaps retaining legacies

from pre-fire conditions. The fact that $CV_{R_s^{T,M}}$ for 1975B was higher than that obtained for

1948B and 1991B could imply a high $CV_{R_s^{T,M}}$ in 1975NB (32 years since fire, or an

intermediate aged jack pine ecosystem), though this scar age category was unavailable at

Sharpsand Creek.

$CV_{R_s^{T,M}}$ may increase immediately after fire due to the patchy effect of burning on the soil (Michaletz and Johnson 2007). For instance, some areas may be more severely burnt than others and subsequent changes to the physical, chemical and biological properties of soils may have differential consequences on $R_{s(a)}$ and $R_{s(h)}$ (Pregitzer and Euskirchen 2004; Yermakov and Rothstein 2006). As the stand recovers from disturbance, $CV_{R_s^{T,M}}$ may decrease for some time (lower $CV_{R_s^{T,M}}$ in 15 and 16 year old scars) due to a new cohort of jack pine trees established at approximately the same time and hence all having similar root development (Smirnova et al. 2008). However, with increasing time since fire, differential development of root and / or microbial communities could account for higher $CV_{R_s^{T,M}}$ in mature systems (58 and 59 years since fire). For instance, decreased organic matter quality and altered soil microclimate are believed to suppress organic matter mineralization over successional time in northern forest systems (Van Cleve and Viereck 1981; Van Cleve et al 1983; Bormann and Sidle 1990; DeLuca et al. 2002; Yermakov and Rothstein 2006), though this may not occur in complete spatial uniformity.

7.2.1.2 Comparisons with other studies

Minimum N estimated in the pilot study is somewhat larger than that of Singh et al. (2008) who found in their study that $N = 10$ is required for estimating $\overline{R}_s$ within a *FE* of 20% of the true $\overline{R}_s$ for a 15 year old jack pine fire scar. However, results from FC 1 suggest smaller minimum N may be required (1991†; 15 years since fire; $CV_{R_s^{T,M}} = 22\%$; minimum $N = 5$ to be 95% confident sample $\overline{R}_s^{T,M}$ lies within 20% of the true $\overline{R}_s^{T,M}$). Furthermore, results from FC 2 suggest even less measurements may be required in jack pine systems 16

years post fire (1991NB; $CV_{R_s^{T,M}}$ = 20%; minimum N = 4 to be 95% confident sample

$\overline{R_s}^{T,M}$ lies within 20% of true $\overline{R_s}^{T,M}$). However, estimates from Singh et al. (2008) were

based on a different sampling area (18 m * 18 m) and larger R_s sample sizes (N = 100).

The $CV_{R_s^{T,M}}$ from FC 1 and 2 are consistent with previous studies in jack pine

systems that report CV_{R_s} in the range 9 to 61% (Weber 1985; Striegl and Wickland 1998;

Striegl and Wickland 2001; Singh et al. 2008). However, except recently burned scars, both

FC's suggest higher $CV_{R_s^{T,M}}$ in mature as opposed to young jack pine systems. This was

also the case in a study by Striegl and Wickland (1998) who found on average CV_{R_s} was

31.3% at old jack pine (age not given) and 30.1% at clear-cut (approximately 6 months to a

year after clear-cutting) sites. However, Singh et al. (2008) found that generally R_s at their

youngest site (three post fire scar age categories: 6 to 7 years since fire; 15 to 16 years

since fire and 27 to 28 years since fire) was most spatially variable, though R_s was not

measured in a mature or old jack pine system.

7.2.1.3 Limitations

The absence of soil collars in the pilot study and FC 1 may have resulted in an over-

estimate of $CV_{R_s^{T}}$ and $CV_{R_s^{T,M}}$ respectively and hence minimum N. Furthermore, the

estimate of $CV_{R_s^{T}}$ for the pilot study is based on adjusting for T_s assuming a Q_{10} of 2, since a

generalised R_s v T_s relationship had yet to be obtained for the site (obtained during FC 2).

Accounting for M_s in addition to T_s may further reduce spatial variability and in this

instance, R_s is likely to be controlled primarily by C_s and fine root content. The number of

fire scars tested and sampling points within fire scars was not always consistent for FC 1

and 2 and sample sizes and sample area may have been too low to accurately quantify $CV_{R_s^{T,M}}$.

7.2.2 Soil temperature response of soil respiration

7.2.2.1 Interpretation of results

There was a significant exponential relationship between R_s^C and T_s (r^2 = 0.60; *P* = 1.24*10^{-6}; Q_{10} = 2.21) derived from the set of measurements that comprised T_s as well as C_s. This implies a more than doubling of R_s^C for every 10°C rise in T_s. This Q_{10} is based on a *general* relationship between *total* R_s ($R_{s(a)} + R_{s(h)}$) v T_s, incorporating measurements from *different* aged fire scars.

7.2.2.2 Comparisons with other studies

Comparing the T_s response of R_s with other studies of jack pine ecosystems, the Q_{10} was remarkably similar to that found by Euskirchen et al. (2006): Q_{10} of 2.2 over three study years; range 1.1 to 2.3. The Q_{10} reported herein is also within the range documented by Striegl and Wickland (1998) (2.02 to 2.68) and Fleming et al. (2006) (1.8 to 2.8). However, two studies report lower Q_{10} values (Euskirchen et al. 2003: 1.67 to 1.92); (Yermakov and Rothstein 2006: 1.40) and one study reports much higher Q_{10} values (Howard et al. 2004: 3.77 to 7.12), perhaps a result of not effectively accounting for the effects of C_s, M_s or fine root content.

Since a general R_s^C v T_s exponential relationship fit the Sharpsand Creek field site, implying a constant Q_{10}, it may be that R_s does not acclimate to T_s. It could be argued that this finding supports the work of Hartley et al. (2008), but disagrees with Bradford et al. (2008), though both these studies were concerned with microbial R_s, in contrast to this research which measured total R_s.

7.2.2.3 Limitations

There are three main limitations. First, there was no attempt to derive separate T_s responses of $R_{s(a)}$ and $R_{s(h)}$ respectively, since only total R_s was measured. Second, the R_s v T_s relationship was not derived separately for individual fire scar age categories, which may have differential $R_{s(a)}$:$R_{s(h)}$ ratios (Wang et al. 2002; Yermakov and Rothstein 2006). Third, the effects of fine root content were not accounted for, which has been shown to influence R_s (Shibistova et al. 2002).

7.2.3 Soil moisture response of soil respiration

7.2.3.1 Interpretation of results

$R_s^{C,T}$ v M_s revealed no significant effect of M_s on $R_s^{C,T}$ over the range 0.21 to 0.77 M_s ($r^2 = 0.006$; $P = 0.702$) to which this study is limited after removal of outliers (Chapter 6). This is based on a *general* relationship between *total* $R_s^{C,T}$ ($R_{s(a)}$ + $R_{s(h)}$) v M_s, incorporating measurements from *different* aged fire scars.

7.2.3.2 Comparisons with other studies

Although most field studies of R_s reveal little response to M_s over broad ranges of intermediate M_s values (Law et al. 1999b; Fang and Moncrieff 2001; Drewitt et al. 2002), this research is the first to demonstrate this in post-fire jack pine systems. The results are in agreement with Howard et al. (2004) who found that M_s did not improve regression models of R_s v T_s in a chronosequence of harvested jack pine. The results are, however, in contrast to a recent study of a jack pine system, which showed M_s dependence of R_s by polynomial functions (Fleming et al. 2006), perhaps a result of not effectively accounting for the effects of T_s, C_s or fine root content.

7.2.3.3 Limitations

In addition to the limitations outlined in 7.2.2.3, there are the following limitations. Firstly, the M_s dependence of R_s was derived after accounting for T_s and is therefore dependant on the validity of the R_s^C v T_s relation. Although this research indicated no M_s response of R_s over the range 0.21 to 0.77 M_s, the response at low (<0.21) and high (>0.77) M_s was not investigated. For instance, it is likely that as soils approach saturation, O_2 becomes limiting to aerobic metabolism and R_s is suppressed (Bernier 1960; Roberge 1976; Foster et al. 1980).

7.2.4 Differences in soil respiration between fire scar age categories

7.2.4.1 Interpretation of results

$\overline{R_s}^{T,M}$ was significantly greater in 1948 than 1991 age categories in both FC 1 (15 v 58 years since fire; $P = 0.009$) and FC 2 (16 v 59 years since fire; $P = 0.030$) (FC 1: 1948† $\overline{R_s}^{T,M} = 8.18$ µmol $CO_2/m^2/s$; 1991† $\overline{R_s}^{T,M} = 2.61$ µmol $CO_2/m^2/s$; FC 2: 1948NB $\overline{R_s}^{T,M} = 1.91$ µmol $CO_2/m^2/s$; 1991NB $\overline{R_s}^{T,M} = 0.79$ µmol $CO_2/m^2/s$). However, $\overline{R_s}^{T,M}$ was significantly greater in FC 1 than FC 2 when comparing the same scar age category (1948NB v 1948†, $P = 0.009$; 1991NB v 1991†, $P = 0.000$). The differences could be a result of measurements being taken a year apart and particularly the absence of soil collars in FC 1, which may have led to an over estimate of soil surface CO_2 efflux (Licor 1997).

There was a strong significant exponential increase in $\overline{R_s}^{T,M}$ with time since fire ($r^2 = 0.999$; $P = 0.006$) for the chronosequence 1975B ($\overline{R_s}^{T,M} = 0.56$ µmol $CO_2/m^2/s$), 1991NB ($\overline{R_s}^{T,M} = 0.79$ µmol $CO_2/m^2/s$) and 1948NB ($\overline{R_s}^{T,M} = 1.91$ µmol $CO_2/m^2/s$) and for all these age categories $\overline{R_s}^{T,M}$ was significantly different from one another ($P < 0.05$).

An overall increase in $\overline{R_s}^{T,M}$ over successive time could be a result of increased contribution of $R_{s(a)}$ as the vegetation component recovers from disturbance (Wang et al. 2002; Yermakov and Rothstein 2006).

$\overline{R_s}^{T,M}$ in 1948NB was significantly ($P = 0.030$) greater than that obtained for 1948B implying that burning has an immediate affect of decreasing $\overline{R_s}^{T,M}$ in mature jack pine stands, probably as a result of decreased $R_{s(a)}$ (Wang et al. 2002; Yermakov and Rothstein 2006). However, there was no significant ($P > 0.1$) difference when comparing $\overline{R_s}^{T,M}$ for 1991NB v 1991B. Though fire may suppress $R_{s(a)}$ in these younger scars, an increase in $R_{s(h)}$ as a result of fire (Pregitzer and Euskirchen 2004; Yermakov and Rothstein 2006) could mask this effect and account for no *overall* change in *total* R_s. This may be a result of higher $R_{s(h)} : R_{s(a)}$ ratios in younger jack pine systems. Although $R_{s(h)}$ may increase as a result of fire in mature jack pine systems, lower $R_{s(h)} : R_{s(a)}$ ratios may imply the increase in $R_{s(h)}$ is insufficient to mask the reduction in $R_{s(a)}$ in response to burning. Indeed, absence of a significant ($P > 0.1$) difference in $\overline{R_s}^{T,M}$ between 1948B and 1991B (where before burning there *was* a significant difference, see above) is further evidence that fire suppresses R_s in older, but not younger jack pine systems. Where before fire, $\overline{R_s}^{T,M}$ was significantly greater in 58 versus 15 and 59 versus 16 year old scars, fire induced reduction in $\overline{R_s}^{T,M}$ in the older scars could explain the absence of significant differences after fire.

The absence of a 1975NB category prevents any firm conclusions into the effect of fire on $\overline{R_s}^{T,M}$ in 32 year old jack pine systems (intermediate age category), though there was a significant difference between 1975B v 1991B ($P = 0.000$) and 1975B v 1948B

(P = 0.044). This does provide evidence that significant differences in $\overline{R}_s^{\,T,M}$ *can* occur

between previously different aged fire scars that have all been subjected to the same fire. In

essence, jack pine stands can retain legacies of pre-fire conditions. The fact that 1975B had

significantly lower $\overline{R}_s^{\,T,M}$ than 1991B or 1948B was possibly due to higher $R_{s(a)}$: $R_{s(h)}$

ratios in 32 year old (or intermediate aged) jack pine systems.

The t tests for significant differences in $\overline{C}_s$ between fire scar age categories

revealed a significant difference only between 1948B and 1975B (P = 0.000) with all other

comparisons P > 0.1). The likely cause is sample sizes being too small resulting in

insufficient statistical power to detect significant differences. Therefore it was not

appropriate to relate $\overline{C}_s$ to changing $\overline{R}_s^{\,T,M}$ over successional time.

7.2.4.2 Comparisons with other studies

$\overline{R}_s^{\,T,M}$ values reported herein are within the range 0.35 to 7.20 μmol $CO_2/m^2/s$ reported in

the literature for jack pine systems (Burke et al. 1997; Savage et al. 1997; Euskirchen et al.

2003). The results of this study also agree with the literature in that the majority of studies

have demonstrated a reduction or no change in R_s following fire (Reinke et al. 1981; Weber

1985; Weber 1990; Fritze et al. 1993; Burke et al. 1997; Sawamoto et al. 2000; Amiro et al.

2003; Singh et al. 2008).

The significantly greater $\overline{R}_s^{\,T,M}$ in mature (58 to 59 years since fire) compared to

young (15 to 16 years since fire) scars (except recently burnt scars) is in agreement with

another study of jack pine ecosystems: (63 years since fire > 21 years since fire; 63 years

since fire > 6 years since fire; 20 years sine fire > 6 years since fire (Weber 1985; note α =

0.05 in this study)). Singh et al. (2008) also found that their youngest site generally had

significantly lower R_s in a jack pine fire scar chronosequence (6 to 7 years since fire; 15 to 16 years since fire; 27 to 28 years since fire), but although $\overline{R_s}$ was significantly greater in 16 year old v 7 year old scars, $\overline{R_s}$ in 16 year old scars was significantly greater than that in 28 year old scars (Singh et al. 2008; note $\alpha = 0.05$ in this study).

This research is the first to report a significant exponential increase in $\overline{R_s}^{T,M}$ over successional time in post-fire jack pine systems. In a recent study of a 72 year old jack pine wildfire chronosequence, growing season R_s showed no clear pattern with stand age (Yermakov and Rothstein 2006).

7.2.4.3 Limitations

There are a number of limitations. Firstly, soil collars were absent in FC 1 which may have led to over-estimated CO_2 efflux. There were no replicate scars available for 1948NB and 1991NB in FC 2, and there were no 1975NB scars available, or intermediate aged jack pine systems.

R_s was adjusted for the generalised T_s and M_s responses and not responses specific to scar age categories, which may have differential $R_{s(a)}$: $R_{s(h)}$ ratios (Wang et al. 2002; Yermakov and Rothstein 2006). Moreover, there was no attempt to separate $R_{s(a)}$ and $R_{s(h)}$. R_s measurements were made at different times of the day and over a number of days. Although it was attempted to account for T_s and M_s, other factors could have influenced R_s; for example, R_s can vary temporally at diurnal scales (Xu and Qi 2001) due to barometric pressure changes (Kimball 1983).

R_s sample sizes were small and statistical power may not have been high enough to always detect significant differences (Type 2 error) in $\overline{R_s}^{T,M}$ between fire scar age

categories. In addition, sample sizes may not have been large enough to capture spatial variability of R_s. However, small sample sizes were in part due to exclusion of outliers necessary for statistical analyses (Chapter 5).

Finally, the FC's were short and do not replicate measurements temporally e.g. months of the growing season, or over individual years. Temporal variability of R_s can occur at seasonal (Borken et al. 2002) and inter-annual (Irvine and Law 2002) scales.

7.3 JULES simulations at Sharpsand Creek

7.3.1 Interpretation of results

Annual $\overline{R}_{s(h)}$ for the three simulations showed no overlap across the chronosequence with RR 1 > RR 2 > RR 3. In RR 1, $\overline{R}_{s(h)}$ generally decreased between 1965 and 1995, which could be the result of decreasing C_s and / or $\overline{M}_s$. In RR 2 $\overline{R}_{s(h)}$ showed no obvious overall change between 1965 and 1995 even though C_s and $\overline{M}_s$ generally decreased, possibly due to increased $\overline{T}_s$ (though this is not clearly visible at the displayed temporal resolution). In RR 3 $\overline{R}_{s(h)}$ showed no overall change between 1965 and 1995 and since C_s was relatively constant over this period, this is further evidence for a possible increase in $\overline{T}_s$ which would have countered the effects of decreasing $\overline{M}_s$. The general increase in $\overline{T}_s$ between 1995 and 2007 and $\overline{M}_s$ between 1990 and 2007 explains the increase in $\overline{R}_{s(h)}$ for all simulations between 1995 and 2007, even though C_s decreased in RR 1 and RR 2. The general increase in $\overline{T}_s$ between 1995 and 2007 could be a result of higher air temperatures. Indeed, the global land and marine surface temperature record from 1850 to 2008 show the ten

warmest years on record as 1997, 1998, 2001, 2002, 2003, 2004, 2005 2006, 2007 and 2008 (Brohan et al. 2006; Jones 2009).

NT LAI stayed relatively constant over the chronosequence with the exception of a slight increase between 1996 and 2007 (possibly due to increased air temperatures, see above) and four abrupt declines (which may be the result of large volcanic eruptions e.g. Mt. St. Helens, 1980). The relatively constant NT LAI and decline in NT Frac implied JULES was unable to accurately simulate successional vegetation re-growth from the prescribed initial conditions and in turn, unable to reliably quantify L input to the C_s pool. The small increase in NT LAI between 1996 and 2007 was insufficient to prevent C_s declining in RR 1 and RR 2. Since C_s declined in RR 1 and RR 2, $\overline{R}_{s(h)}$ was $>$ L, though in RR 3 $\overline{R}_{s(h)}$ was $\approx$ L therefore C_s remained relatively constant.

The results of this study show how JULES, in its current state (version 2.0), is unable to reliably simulate vegetation re-growth (LAI, Can and Frac) for a NT ecosystem. The lack of increase in NT Can may be a result of inter-specific competition with other PFT's. The tree (NT and BT) and grass (C3G and C4G) PFT's co-compete with competition coefficients depending on their relative heights (Best 2005). Changes in vegetation C density (leaf, root and stem C) are allometrically related to changes in balanced LAI, and Can is calculated from total stem C (Best 2005). If LAI does not change, this implies Can cannot change. The sole dependence of LAI on Can is probably unwise as this study has shown that NT Can may continue to increase over successional time, when NT LAI remains constant.

7.3.2 Comparisons with other studies

The general decrease in $\overline{R}_{s(h)}$ in RR 1 between 1965 and 1995 is in agreement with the majority of studies, which report that organic matter mineralization decreases with successional time in northern forest systems (Van Cleve and Viereck 1981; Van Cleve et al 1983; Bormann and Sidle 1990; DeLuca et al. 2002; O'Neill et al 2006; Yermakov and Rothstein 2006) and that $R_{s(h)}$ may therefore be lower in later seral stages (Yermakov and Rothstein 2006). However, the simulated decrease in $\overline{R}_{s(h)}$ was probably caused by declining C_s content in contrast to the majority of forest systems where organic matter accumulates (Yermakov and Rothstein 2006). In reality, it is believed that the combination of decreased organic matter *quality* and altered soil microclimate suppresses microbial activity over successional time (Van Cleve and Viereck 1981; Zackrisson et al. 1997; DeLuca et al 2002; Wardle et al. 2003). Pregitzer and Euskirchen (2004) suggest $R_{s(h)}$ increases slightly over successional time in boreal systems and although this is not apparent in simulations between 1965 and 1995, it *is* seen between 1995 and 2007. This was likely caused by elevated $\overline{T}_s$ and $\overline{M}_s$ and not by changes to C_s quality and the soil microclimate, which are thought to occur in real forest systems (Van Cleve and Viereck 1981; Zackrisson et al. 1997; DeLuca et al 2002; Wardle et al. 2003).

7.3.3 Limitations

There are three main limitations. First, only three RR were performed, limited by the three C_s values obtained for an appropriate initial condition. Second, JULES does not consider the change in soil C quality that is thought to occur over successional time and

its impact on $R_{s(h)}$. Third, JULES was unable to accurately simulate vegetation re-growth and this in turn impacts on L input to the soil and $R_{s(h)}$.

7.4 Field v modelled observations

7.4.1 Interpretation of results

Measured $\overline{R_s}^{T,M}$ (0.79 μmol $CO_2/m^2/s$) was < modelled $\overline{R_{s(h)}}^{T}$ (1.17 μmol $CO_2/m^2/s$) at 16 years since fire, with overlap of σ. Measured $\overline{R_s}^{T,M}$ fell with 1σ of modelled $\overline{R_{s(h)}}^{T}$ and modelled $\overline{R_{s(h)}}^{T}$ fell within 3σ of measured $\overline{R_s}^{T,M}$ at 16 years since fire. Even if no difference is assumed (overlap of σ) between measured $\overline{R_s}^{T,M}$ and modelled $\overline{R_{s(h)}}^{T}$, JULES probably over estimated $R_{s(h)}$ since it does not consider $R_{s(a)}$, which would contribute to *total* R_s

Measured $\overline{R_s}^{T,M}$ (1.91 μmol $CO_2/m^2/s$) was > modelled $\overline{R_{s(h)}}^{T}$ (1.58 μmol $CO_2/m^2/s$) at 59 years since fire with overlaps in σ. Modelled $\overline{R_{s(h)}}^{T}$ fell within 1σ of measured $\overline{R_s}^{T,M}$ and measured $\overline{R_s}^{T,M}$ fell within 1σ of modelled $\overline{R_{s(h)}}^{T}$ at 59 years since fire. Even though measured $\overline{R_s}^{T,M}$ was > modelled $\overline{R_{s(h)}}^{T}$, overlaps of σ suggest no significant differences between them. Considering the absence of simulated $R_{s(a)}$, JULES again probably over estimates $R_{s(h)}$ here.

Where measured $\overline{R_s}^{T,M}$ increased from $0.79\pm0.16\sigma$ μmol $CO_2/m^2/s$ at 16 years since fire to $1.91\pm0.79\sigma$ μmol $CO_2/m^2/s$ at 59 years since fire and was significantly different ($P = 0.030$) (FC 2), modelled $\overline{R_{s(h)}}^{T}$ also increased from $1.17\pm0.51\sigma$ μmol $CO_2/m^2/s$ at 16 years since fire to $1.58\pm0.62\sigma$ μmol $CO_2/m^2/s$ at 59 years since fire, but

differences were considered NS due to overlap of σ. Modelled $R_{s(h)}$ probably did not increase due to C_s decreasing, in turn caused by JULES' inability to accurately simulate vegetation re-growth from the initial conditions.

Measured $\overline{C_s}$ (25.73 kg C/m^2) was < modelled $\overline{C_s}$ (29.25 kg C/m^2) at 16 years since fire. Measured $\overline{C_s}$ fell within 1σ of modelled $\overline{C_s}$ and modelled $\overline{C_s}$ fell within 1σ of measured $\overline{C_s}$ at 16 years since fire. Measured $\overline{C_s}$ (21.88 kg C/m^2) was < modelled $\overline{C_s}$ (26.92 kg C/m^2) at 59 years since fire and σ overlapped. Measured $\overline{C_s}$ fell within 1σ of modelled $\overline{C_s}$ and modelled $\overline{C_s}$ fell within 1σ of measured $\overline{C_s}$. Where measured $\overline{C_s}$ decreased from 25.73±15.13σ kg C/m^2 at 16 years since fire to 21.88±6.89σ kg C/m^2 at 59 years since fire, though was NS (P = 1.479), modelled $\overline{C_s}$ also decreased from 29.25±13.27σ kg C/m^2 to 26.92 ±10.62σ kg C/m^2 from 16 to 59 years since fire and this was also considered NS due to overlap of σ. Though JULES appears to accurately simulate C_s, N of field measured C_s was probably too low to be a reliable representation of C_s at Sharpsand Creek (N = 3 for 1948NB and 1991NB. In addition, JULES' inability to reliably simulate vegetation re-growth and hence L input to the soil casts doubt over simulated C_s values.

Modelled NT $\overline{LAI}$ changed very little over the chronosequence: 1.64±σ ,1.63 ±σ , 1.66 ±0σ at 25, 31 and 58 years since fire respectively. This is in contrast to measured NT $\overline{LAI}$, which increased from 1.02±0.75σ at 25 years since fire to 2.28±1.42σ at 31 years since fire and 2.28±0.82σ at 58 years since fire (Mottram 2009). Modelled NT $\overline{Can}$ also remained similar: 9.00±0σ m, 9.00±0σ m, 9.04±0σ m, 9.13±0σ m for 16, 26, 32 and 59

years after fire respectively. This is in contrast to measured NT $\overline{Can}$, which increased from 2.54±0.60σ m to 6.93±0.81σ m to 9.02±0.81σ m to 15.68±1.32σ m over the same time period. NT LAI and NT Can data provide further evidence that JULES was unable to accurately simulate vegetation re-growth from the prescribed initial conditions. Indeed, it is possible that initial NT Can and / or NT LAI were too low to stimulate vegetation re-growth.

7.4.2 Comparisons with other studies

Other modelling studies in jack pine systems have also found modelled R_s to be within 1σ of measured R_s. For example, modelled R_s (on the basis of T_s) was within 1σ of measured $\overline{R_s}$ for 12 of 13 and 14 of 14 measurement periods at OJP and CC respectively (Striegl and Wickland 1998). Striegl and Wickland (2001) used T_s to simulate R_s and found that for 48 of 52 measurement periods, modelled R_s fell within 1σ of measured R_s, though total modelled R_s for the season was 10 to 30% lower than the total R_s estimated from interpolation of the mean measured values. However, the apparently over - simulated $R_{s(h)}$ obtained in the present study was in contrast to other studies. Although Euskirchen et al. (2003) found average simulated R_s was similar to field measured values in 2000, in 1999 the simulated values tended to under-predict R_s in pine barrens. Nalder and Wein (2006) used the BFCDM to simulate R_s, which was designed to be capable of incorporating the effects of fire (unlike JULES) and was able to simulate $R_{s(h)}$ but not $R_{s(a)}$ (like JULES). Simulated R_s for BOREAS sites was lower than that of other studies where total R_s was measured, though results were consistent in magnitude with the literature when considering absence of $R_{s(a)}$ (Nalder and Wein 2006).

7.4.3 Limitations

In addition to the limitations outlined in 7.2 and 7.3 there are two main limitations. First, JULES is only capable of simulating $R_{s(h)}$ and therefore direct comparisons with measured R_s, which includes $R_{s(a)}$ and $R_{s(h)}$, is compromised. Second, modelled $R_{s(h)}$ was only adjusted for T_s as opposed to measured R_s which was adjusted for T_s and M_s.

7.5 Conclusions

Referring back to the *specific* research questions (Chapter 4; Sect. 4.9), the following conclusions may be drawn:

1. The spatial variability of measured R_s was investigated at Sharpsand Creek and $CV_{R_s^{T,M}}$ was estimated to be in the range 20% (FC 2; 1991NB; 16 year old fire scar) to 56% (FC 1; 1948†; 58 year old fire scar).

2. The relationship between measured R_s^C and T_s was investigated at Sharpsand Creek and found to be significantly exponential in form ($r^2 = 0.60$; $P = 1.24*10^{-6}$; $Q_{10} = 2.21$).

3. The relationship between measured $R_s^{C,T}$ and M_s was investigated at Sharpsand Creek and there was no significant effect of M_s on $R_s^{C,T}$ over the range 0.21 to 0.77 M_s ($r^2 = 0.006$; $P = 0.702$).

4. The immediate effect of burning was investigated at Sharpsand Creek and it appeared that measured $\overline{R_s}^{T,M}$ is significantly ($P = 0.030$) decreased after burning mature jack pine forest, though no significant ($P > 0.1$) difference could be detected between recently burned and unburned young jack pine forest.

5. R_s was measured in recently burned boreal jack pine fire scar age categories that differed in their burn history and there was a significant difference in $\overline{R_s}^{T,M}$ for 1975B v 1991B (P = 0.000) and 1975B v 1948B (P = 0.044) at Sharpsand Creek.

6. JULES was used to model vegetation re-growth over successional time at Sharpsand Creek, though it appeared to perform poorly in simulating NT LAI and NT Can.

Referring back to the two *main* research questions (Chapter 1; Sect 1.3), the following conclusions may be drawn:

1. There is evidence to suggest that the null hypothesis, of no change in measured $\overline{R_s}^{T,M}$ over successional time at Sharpsand Creek, should be rejected. Measured $\overline{R_s}^{T,M}$ increased exponentially over successional time at Sharpsand Creek.

2. There is no evidence against the null hypothesis, that JULES is unable to accurately simulate R_s at Sharpsand Creek. JULES probably over-estimated $R_{s(h)}$ at Sharpsand Creek when simulated $\overline{R_{s(h)}}^{T}$ was compared with measured $\overline{R_s}^{T,M}$.

The results of this study contribute to a better quantitative understanding of R_s in boreal jack pine fire scars and will facilitate improvements in C cycle modelling.

7.6 Future research

There are numerous areas for future research. Firstly, measurements of *both* $R_{s(h)}$ and $R_{s(a)}$ in jack pine chronosequences will allow more detailed insight into changes over successional time. The T_s and M_s responses of R_s in jack pine systems needs to be quantified for $R_{s(h)}$ and $R_{s(a)}$ and in different aged jack pine systems. Also the M_s

dependence of R_s at low (<0.21) and high (>0.77) M_s needs investigating in jack pine systems. This research has shown that R_s may decrease after burning mature jack pine but not young jack pine, though further work with replicate scars is needed to confirm this. This is particularly important since the proportion of young jack pine ecosystems may increase with future increases in boreal forest fire size, frequency, or intensity. In addition, comparisons of recently burned and unburned intermediate and old jack pine systems should be investigated. This research has suggested that R_s increases exponentially with successional time since fire in jack pine systems, though further work with replicate fire scars is needed. In addition, monitoring R_s for an extended time period after fire is a fertile avenue for future research.

Further work is needed in improving the ability of JULES to simulate vegetation re-growth over successional time and this will also likely improve modeling of $R_{s(h)}$. JULES version 2.0 was clearly unable to simulate NT LAI and NT Can at Sharpsand Creek. Since Can is dependant on LAI, it would be intuitive to begin by focusing on how JULES simulates LAI. In TRIFFID, LAI is a function of balanced LAI and phenological status e.g. litter fall rate and budburst (Best 2005) and it is possible that these may be inaccurately simulated. Further work could be to repeat the simulations in this research with a range of litter fall and budburst rates and investigate the impact on LAI. Since this study has shown that Can may continue to increase when LAI remains constant, it could be argued that Can should be controlled not only by LAI, but other processes, such as nutrient uptake. It is also possible that competition coefficients for NT are too low, compared with C3G and / or C4G, restricting an increase in NT vegetation C density and Frac. Further work could repeat the simulations using a range of competition coefficients to see if this allows more

NT C accumulation and prevents decline in NT Frac over successional time reported in this research.

The further work suggested herein will aid the incorporation of two coupled models into JULES (Ecosystem Demography (ED) and SPITFIRE), with the overarching aim of improving simulation of post-fire ecosystem succession.

Appendices

Appendix 1 JULES run control file

```
# File used to control a run of the JULES code at Sharpsand Creek...
##########################################################################
#######

## Model options.
>INIT_OPTS

5,4        !   npft,nnvg
9          !   ntiles

'BT', 'NT', 'C3G', 'C4G','shrub'   !  pftName
'urban', 'lake', 'soil', 'ice'     !  nvgName

1,1        !   nxIn,nyIn
4          !   sm_levels
4          !   can_model
3,10       !   can_rad_mod,ilayers
T,T        !   l_cosz
T,T,F      !   l_phenol,l_triffid,l_trif_eq

F          !   yrevIn
T          !   echo
48         !   print_step

##########################################################################
#######
## Date and time information
>INIT_TIME

300                                       !  timestep:
19630607,'12:00:00', 20071201,'12:00:00' !  dateMainRun,timeRun
(start and end)
19630607,19730607,50                      !  dateSpin,nspin:
T                                         !  terminate run if spin-up
fails (T,F)
T, F, 1.0                                 !  soil moisture:
spinVar,spinTolPercent,spinTol
T, F, 0.1                                 !  Tsoil
1,1                                       !
phenol_period,triffid_period
F                                         !  l_360

##########################################################################
#######
## Model grid and points to use.
```

```
>INIT_GRID

T,F                     !  pointsList,landOnly
F,F                     !  subArea,subAreaLatLon
2,5,1,4                 !  xcoord(1:2),ycoord(1:2)
1                       !  npoints

F                       !  readFilePoints
'input/mask.dat'        !  fileNamePoints

##############################################################################
#######
# Land fraction.
>INIT_LAND
F                       !  readFileLand )
'asc'                   !  fileFormatLand
'input/mask.dat'        !  fileNameLand

>ASCBIN
0,0                     !  nheaderFileLand,nheaderFieldLand
1                       !  fieldLand

>NC
1                       !  nlandDim
'Land'                  !  landDim
'lfrac'                 !  varNameLand

##############################################################################
#######
# Latitude and longitude of points.
>INIT_LATLON
F                       !  regLatLon:
52.168, 5.744           !  regLat1,regLon1
1.0,1.0                 !  regDlat

F                       !  readFile
'asc'                   !  fileFormat
'input/latlon.dat'  !  fileName

>ASCBIN
0,0                     !  nheaderFile,nheaderField
1,2                     !  fieldLat,fieldLon

>NC
1                       !  nLatLonDim
'Land'                  !  latLonDim
'lat','lon'             !  varNameLat,varNameLon

##############################################################################
#######
# Data for points, land fraction and lat/lon.

>DATA_POINTS
1                       !  mapIn (DA 1-d integer array of points)
```

```
>DATA_LAND
1.0                      !  flandg



>DATA_LATLON
46.7833                  !
-83.3333                 !

###########################################################################
######
## Fractional cover.
>INIT_FRAC
T     !  readFracIC
F                            !  readFile:
'asc'                        !  fileFormat
'input/frac.dat'             !  fileName

>ASCBIN
0,0                      !  nheaderFile,nheaderField
1                        !  fieldNum

>NC
1                        !  nfracDim
'Land','Psuedo'          !  fracDim
'frac'                   !  varName

# Data fields to be read from this file should appear below here.
>DATA
0.355, 0.355, 0.208, 0.0, 0.0, 0.0, 0.0, 0.082, 0.0   ! frac(:,:)

###########################################################################
#######
## Soil layer details.
>INIT_DZSOIL

>DATA
0.05, 0.15, 0.8, 2.0    !  dzsoil(1:sm_levels)

###########################################################################
#######
## Soil hydraulic and thermal characteristics, and soil albedo.
>INIT_SOIL

T                        !  l_vg_soil
F,F                      !  constZ,
F                        !  readFile
'nc'                     !  fileFormat (quoted)
'/home/JULES/data/gswp/baseline/PARAM/qrparm_islscp_newk_vector.nc'
!  fileName (quoted)

>ASCBIN
0,0                      !  nheaderFile,nheaderField
```

```
>VARS
b          1                ! name,field number
sathh      2
satcon     3
sm_sat     4
sm_crit    5
sm_wilt    6
hcap       7
hcon       8
albsoil    9
>ENDVARS


>NC
1                          ! nSoilDim
'Land'                     ! soilDim
>VARS
b          field1381       ! name,name of SDF variable
sathh      field342
satcon     field333
sm_sat     field332
sm_crit    field330
sm_wilt    field329
hcap       field335
hcon       field336
albsoil    field1395
>ENDVARS


>INIT_SOIL2
1.0,1.0    !  multi for satcon

# Data fields to be read from this file should appear below here.
>DATA
3.39, 3.39, 3.39, 3.39       ! b or 1/(n-1)
0.049460, 0.049460, 0.049460, 0.049460 !  sathh
1.79, 1.79, 1.79, 1.79 !  satcon
0.373, 0.373, 0.373, 0.373      !  smvcst
0.1865, 0.1865, 0.1865, 0.1865 !  smvccl
0.09325,   0.09325 , 0.09325, 0.09325   !  smvcwt
2140000, 2140000, 2140000, 2140000     !  hcap
8.61, 8.61, 8.61, 8.61           !  hcon
0.10   !  albsoil

################################################################################
#######
# PFT parameters
>INIT_VEG_PFT

F                                        ! readFile:
'/home/JULES/data/gswp/baseline/PARAM/standard_pft_param.dat'       !
fileName (quoted)
5                                        ! npftInFile

# Data fields to be read from this file should appear below here.
```

```
>DATA
    'BT',   'NT','C3G',  'C4G','shrub'      !  pftName
    1,       1,      1,       0,      1     !  c3
  19.01, 16.38,   0.79,   1.26,   1.00      !  canht_ft
    5.0,    4.0,    2.0,    4.0,    1.0     !  lai
   0.50,   0.50,   0.50,   0.50,   0.50     !  catch0
   0.05,   0.05,   0.05,   0.05,   0.05     !  dcatch_dlai
   0.05,   0.05,   0.10,   0.10,   0.10     !  dz0v_dh
    0.1,    0.1,    0.1,    0.1,    0.1     !  z0h_z0m
   4.00,   4.00,   2.00,   2.00,   2.00     !  infil_f
   3.00,   1.00,   0.50,   0.50,   0.50     !  rootd_ft
      0,      1,      0,      0,      0     !  snowCanPFT
   0.15,   0.15,   0.60,   0.60,   0.40     !  albsnc_max
   0.30,   0.30,   0.80,   0.80,   0.80     !  albsnc_min
   0.10,   0.10,   0.20,   0.20,   0.20     !  albsnf_max
   0.50,   0.50,   0.50,   0.50,   0.50     !  kext
   0.50,   0.50,   0.50,   0.50,   0.50     !  kpar
      0,      0,      0,      0,      0     !  orient
   0.08,   0.08,   0.08,  0.040,   0.08     !  alpha
   0.45,   0.35,   0.58,   0.58,   0.58     !  alnir
   0.10,   0.07,   0.10,   0.10,   0.10     !  alpar
   0.15,   0.15,   0.15,   0.17,   0.15     !  omega
   0.70,   0.45,   0.83,   0.83,   0.83     !  omnir
   0.65,   0.65,  0.005,  0.005,   0.10     !  a_wl
  10.00,  10.00,   1.00,   1.00,  10.00     !  a_ws
  1.667,  1.667,  1.667,  1.667,  1.667     !  b_wl
   0.01,   0.01,   0.01,   0.01,   0.01     !  eta_sl
   0.25,   0.25,   0.25,   0.25,   0.25     !  g_leaf_0
    0.0,    0.0,    0.0,    0.0,    0.0     !  dgl_dm
    9.0,    9.0,    0.0,    0.0,    9.0     !  dgl_dt
 1.0E-6,1.0E-6,1.0E-6,1.0E-6,1.0E-6         !  glmin
  0.090,  0.060,  0.100,  0.075,  0.100     !  dqcrit
  0.015,  0.015,  0.015,  0.025,  0.015     !  fd
  0.875,  0.875,  0.900,  0.800,  0.900     !  f0
   0.00,   0.00,   0.00,   0.00,   0.00     !  fsmc_of
 0.8e-3,0.8e-3,0.8e-3,0.4e-3,0.8e-3         !  neff
  0.040,  0.030,  0.060,  0.030,  0.030     !  nl0
   1.00,   1.00,   1.00,   1.00,   1.00     !  nr_nl
   0.10,   0.10,   1.00,   1.00,   0.10     !  ns_nl
   0.25,   0.25,   0.25,   0.25,   0.25     !  r_grow
 0.0375,0.1000,0.0250,0.0500,0.0500         !  sigl
 273.15,230.0,258.15,258.15,243.15          !  tleaf_of
    0.0,   -5.0,    0.0,   13.0,    0.0     !  tlow
   36.0,   31.0,   36.0,   45.0,   36.0     !  tupp

#######################################################################
######
# Vegetation (PFT) parameters that vary with time and/or location.
```

```
>INIT_VEG_VARY

0            !  nvegVar
21600 ,0        !   vegDataPer;VegUpdatePer
60,-2        !  nvegFileTime
F            !  vegClim
F        !  readList
'/home/JULES/data/gswp/baseline/PARAM/qrparm_lai_vector_fracked.nc'    !
file name (quoted)
1480101,'00:00:00'                ! vegFileDate(1); vegFileTime(1)
(quoted)
F                                 ! vegEndTime
'nc'                              ! fileFormat


>ASCBIN
18                                ! nfieldVegFile
1,2,0                             !
nvegHeaderFile,nvegHeaderTime,nvegHeaderField
T                                 ! noNewLineVeg
'lai',   't', 6, 'nf', 'laifile'  !  name,flag,field
number,interpolation type, name  used in file name

>NC
3                                 ! nvegDim
'Land','Psuedo','Time'            ! vegDim
'lai', 'tx', 'i', 'lai', 'laifile' !  name varable,flag,interpolation
type,name netCDF variable, name used in file name


###########################################################################
#######
# Non-veg parameters
>INIT_NONVEG

F                                      !   readFile
'/home/JULES/data/gswp/baseline/PARAM/standard_nonveg_param.dat'       !
fileName (quoted)
4                                      !   nnvgInFile

# Data fields to be read from this file should appear below here.
>DATA
'urban',  'lake', 'soil', 'ice' !  nvgName
 0.40,    0.80,   0.80, 0.80     ! albsnc_nvg
   0.18,    0.06,  -1.00,  0.75  ! albsnf_nvg
   0.50,    0.00,   0.00,  0.00  ! catch_nvg
   0.00,    0.00,   1E-2,   1E6  ! gs_nvg
   0.10,    0.00,   0.50,  0.00  ! infil_nvg
   1.00,    3E-4,   3E-4,  1E-4  ! z0_nvg
    0.1,     0.1,    0.1,   0.1  ! z0h_z0m
  0.28E6,   0.00,   0.0,  0.00   ! ch_nvg
    1.0,    0.00,   0.0,  0.00   ! vf_nvg

###########################################################################
#######
## Snow parameters
```

```
>INIT_SNOW
 250.0,                  !  rho_snow
 0.63e6,  0.265          !  snow_hcap,snow_hcon
 50.0, 2000.0            !  r0,rmax
 0.6, 0.06, 0.23e6       !  snow_ggr(1:3)
 0.98, 0.7               !  amax(1:2)
 2.0,  0.3               !  dtland,kland (incl. dtland in denominator)
 0.2                     !  maskd
 4.4, 0.7, 0.4           !  snowLoadLAI,snowInterceptFact,snowUnloadFact

#########################################################################
#######
## TRIFFID parameters.
>INIT_TRIF
F                                      !    readFile
'PARAM/standard_trif_param.dat'        !    fileName (quoted)
5                                      !    npftInFile




# Data fields to be read from this file should appear below here.
>DATA
    'BT',  'NT','C3G', 'C4G','shrub'    ! trifName
     0,      0,     0,     0,     0     ! crop
  0.005, 0.004,  0.25,  0.25,  0.05     ! g_area
  20.00, 20.00, 20.00, 20.00, 20.00     ! g_grow
   0.25,  0.25,  0.25,  0.25,  0.25     ! g_root
   0.01,  0.01,  0.20,  0.20,  0.05     ! g_wood
   9.00,  9.00,  4.00,  4.00,  4.00     ! lai_max
   0.1, 1.63, 0.1, 0.1, 1.63            ! lai_min

#########################################################################
#######
## Agricultural fraction.
>INIT_AGRIC

F                        !  readFile
'asc'                    !  fileFormat
'input/agr.dat'          !  fileName

>ASCBIN
0,0                      !  nheaderFile,nheaderField
1                        !  fieldNum

>NC
1                        !  nagrDim
'Land'                   !  agrDim
'frac_agr'               !  varName

# Data fields to be read from this file should appear below here.
>DATA
10000*0.0                !  frac_agr

#########################################################################
#######
## Miscellaneous surface and carbon/veg parameters.
```

```
>INIT_MISC

 5.7E4, 1.1E4                    !  hleaf,hwood
 0.83, 0.93                      !  beta1,beta2
 0.5, 2.0e4                      !  fwe_c3, fwe_c4
 2.0                             !  q10_leaf
 0.5e-8, 2.21                    !  kaps, q10_soilk
 1.0e-6                          !  cs_min
 5.25e-04                        !  co2_mmr
 1.0e-6, 0.01                    !  frac_min, frac_seed
 20.0                            !  pow (for SIGM)

###########################################################################
#######
>INIT_DRIVE

21600                   !  driveDataPer)
60,-2                   !  ndriveFileTime ; driveFilePer
T                       !  readList
'drivefile_ncep_reanalysis_surface_gauss_gswp_grid' !  file name (quoted)
19820701,'03:00:00'     !  driveFileDate(1),driveFileTime(1)
F                       !  driveEndTime
'nc'                    !  driveFormat

1,F                     !  ioPrecipType; 1_point_data
274.0                   !  tForSnow
373.15,0.3              !  tForCRain ; conFrac
1,F                     !  io_rad_type, ioWindSpeed
10.0, 2.0               !  z1_uv; z1_tq=height


>ASCBIN
8                       !  nfieldDriveFile
5,0,0                   !
ndriveHeaderFile,ndriveHeaderTime,ndriveHeaderField
T                       !  noNewLineDrive
>VARS
pstar      7  nf  psfc ! name,field number, interpolation type, name as
in file name
t          5  nf  t
q          8  nf  q
wind       6  nf  wind
lw_down    2  nf  lw
sw_down    1  nf  sw
precipTR   3  nf  liqp
precipTS   4  nf  solp
>ENDVARS

>NC
2                       !  nDriveDim
'XAX1_15238' 'TIME'     !  driveDim
>VARS
pstar      GPRES     pres.sfc.gauss.gswp.      i ! name,name of SDF
variable, name as in file name, interpolation type


t          GAIR      air.2m.gauss.gswp.        i
```

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```
q               GSHUM       shum.2m.gauss.gswp.        i
u               GUWND       uwnd.10m.gauss.gswp.       i
v               GVWND       vwnd.10m.gauss.gswp.       i
lw_down         GDLWRF      dlwrf.sfc.gauss.gswp.      nb
sw_down         GDSWRF      dswrf.sfc.gauss.gswp.      nb
precip          GPRATE      prate.sfc.gauss.gswp.      nb  !
>ENDVARS


###########################################################################
#######
# initial state.
>INIT_IC

F                                   !    readFile
'asc'                               !    fileFormat (quoted)
'/home/drs20/SHARPSAND_CREEK/ncep1_vgT_final_dump.19850201_SC.extr'    !
fileName (quoted)
F     !  zrev
>ASCBIN
0,0                         !  nheaderFile,nheaderField
>VARS
sthuf       1     0.9    !  varName,varFlag, constVal
canopy      2     0.0
snow_tile   3     0.0
tstar_tile  4   275.0
t_soil      5   278.0
cs          6     0.0
gs          7     0.0
rgrain      8     0.0
canht_ft    9     0.0
frac        10    0.0
lai         11    0.0
snow_grnd   12    0.0
>ENDVARS


>NC
2               !  nDim
'Land','Soil'   !   dim
>VARS
sthuf       1     0.9     sthuf   !  varName,varFlag, constVal,SDF varname
canopy      1     0.0     canopy
snow_tile   1     0.0     snow_t
rgrain      1     0.0     rgrain
tstar_tile  1   275.0     tstar_t
t_soil      1   278.0     t_soil
cs          1     0.0     cs
gs          1     0.0     gs
snow_grnd   1     0.0     snow_grnd
>ENDVARS



# Data fields to be read from this file should appear below here.



>DATA
```

```
0.749, 0.743, 0.754, 0.759   !  sthu+sthf(1:sm_levels)(top to bottom)
9*0.0                         !  canopy(1:ntiles)
9*0.0                         !  snow_tile(1:ntiles)
9*276.78                      !  tstar_tile(1:ntiles)
276.78, 277.46, 278.99, 282.48  !  t_soil(1:sm_levels)(top to bottom)
68.33                         !  cs
0.0                           !  gs

9*50.0                        !  rgrain(1:ntiles)

0.001, 2.54, 0.001, 0.001, 1.0            !  canht_ft(1:npft)
0.001, 0.995, 0.001, 0.001, 0.001, 0.0, 0.0, 0.001, 0.0  !  frac(1:ntype)
0.1, 1.63, 0.1, 0.1, 1.63        !  lai(1:npft)
9*0.0               !  snow_grnd(1:npft)
########################################################################
#######
########################################################################
#######
########################################################################
#######
########################################################################
#######
## Output selection.
>INIT_OUT

'drs20'    !  run_id (QUOTED)
'bin'                       !  outFormat )
'/home/drs20/PhD_THESIS/final_clean_folder_for_all_in_one_dir_analysis_19
63'   ! directory
'replace'   !  outStatus (QUOTED)
F,F     !  yrevOut ; zrevOut
T               !  numMonth
T               !  useTemplate
20  !  number of output profiles
-1.0e20      !  missing/undefined data value for output (undefOut)
0.06, 0.06    !  zsmc, zst
'little_endian'  !  outEndian
4,'replace'       !  dumpFreq; dumpStatus
##
########################################################################
###
#Each output 'profile' should appear below here.
# A profile starts with >NEWPROF.
# Within each profile, the list of variables appears between >VARS and
>ENDVARS.
########################################################################
########################################################################
###############################
>NEWPROF
'p21b'                  !  outName
-2,-8                 !  outPer, outfileper
0                     !  outSamPer
19630607,'12:00:00'        !  outDate(start); outTimestart
20070607,'12:00:00'   !  outDate(end); outTime(end) (hh:mm:ss)

0,0                  !  pointsFlag(1:2)
```

```
T                      !  outAreaLL
10,20,10,50            !  outRangeX(1:2) ,outRangeY(1:2)
F,T                    !  outCompress ; outLLorder

F                      !  readFile
'input/outgrid1.dat' !  fileName

1                      !  pointsOut
1                      !  mapOut(1:pointsOut,1)
1                      !  mapOut(1:pointsOut,2)

>GRID
1,1                    !  outNx,outNy


>VARS
S respSDrOut
>ENDVARS

###########
```

Appendix 2 Field data

See compact disc of field data

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