

Podocarps in Africa: Temperate Zone Relicts or Rainforest Survivors?

Hylton Adie and Michael J. Lawes

ABSTRACT. Podocarp distribution in Africa follows a discontinuous mountainous belt from Cameroon to Angola in the west and from Ethiopia in the northeast to the southern Cape in South Africa. Besides a relict population of *Afrocarpus falcatus* in coastal lowland forest in northeastern South Africa and southern Mozambique, African podocarps are generally limited to highland (Afrotemperate) regions. All podocarps are restricted to montane regions in Madagascar. Afrotemperate landscapes are characterized by a patchy mosaic of forest and grassland. Processes in the matrix, such as fire, are important drivers of forest distribution in the highland regions. Here we examine the relative performance of podocarps and angiosperms along an altitudinal gradient from temperate highlands to subtropical coastal regions in eastern South Africa. *Podocarpus latifolius* is a successful component of temperate highland forest, where it dominates old-growth stages. The success of podocarps is attributed to their greater longevity and ability to regenerate in shade, whereas many potential competing angiosperms are less capable of doing so. Regeneration by *P. latifolius* and associated angiosperms is less successful in high-light gap environments, where ferns and grasses suppress establishment. Podocarps are rare in coastal scarp forest, where the population is dominated by adult individuals. They are unable to regenerate in very deep shade (<3% daylight), which may account for the lack of *P. latifolius* regeneration beneath the dense canopy of coastal scarp forest. Low-nutrient soils did not favor podocarps over angiosperms, although the fact that soil nutrients do not appear to be limiting and the scarcity of shade-tolerant angiosperms in forests may influence this outcome. The relative role of light and soils on angiosperm-conifer competition is unknown for lowland forest, although current evidence from montane forests suggests that under prevailing soil conditions, light is the more important axis of niche differentiation.

Hylton Adie, School of Biological and Conservation Sciences, Forest Biodiversity Research Unit, University of KwaZulu-Natal, Private Bag X01, Scottsville 3209, South Africa. *Michael J. Lawes*, Research Institute for the Environment and Livelihoods, Charles Darwin University, Darwin, Northern Territory 0909, Australia. **Correspondence:** Michael.Lawes@cdu.edu.au.

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INTRODUCTION

The subtropical forests of southern Africa are characterized by a mixed angiosperm-*Podocarpus* composition that ranges along a productivity gradient from angiosperm dominance in coastal and mid-altitude (1,100–1,500 m above

sea level) forests to podocarp dominance in high-altitude montane forests. The dynamics of these main components are poorly understood, and mechanisms explaining their dominance have not been examined in detail (Adie and Lawes, 2009a). In temperate forests, the mechanisms conferring component dominance are proposed variously as climatic and soil nutrient constraints on angiosperm seedling growth rates in favor of slow-growing conifers at high altitudes (Bond, 1989), conifer shade tolerance (Midgley et al., 1990), a less-competitive reproductive system in terms of the ability of conifers to colonize or capture space relative to most angiosperms (Bond, 1989), competitive exclusion of podocarps by the understory vegetation, especially herbs and grasses in more productive environments (Midgley and Bond, 1989; Midgley et al., 1995a), prevention of shade-tolerant conifers from escaping angiosperm competition in deep shade (Coomes et al., 2005), and the intensity and frequency of large-scale disturbances (Ogden and Stewart, 1995; Ogden et al., 2005). In the Southern Hemisphere podocarps appear to have the competitive edge relative to associated angiosperms in seasonally colder temperate sites that experience periodic intense disturbance, and they are a successful component of montane forests in tropical latitudes but are rare in lowland tropical forests (Enright, 1995; Enright and Jaffré, this volume).

We examined the dynamics of high-altitude podocarps in the subtropics and focused on regeneration patterns of the two principal forest canopy components: conifers, represented by *Podocarpus latifolius*, and angiosperms (all other species). Angiosperms are reported to have poor regeneration in many inland forests (Moll, 1972; Everard et al., 1995; West et al., 2000; Lawes et al., 2007b), possibly due to shade intolerance (Midgley et al., 1995b). In a landmark paper, Bond (1989) explored factors limiting the distribution of conifers. He argued that faster-growing and competitively superior angiosperms outperform conifers in the early regeneration phase, restricting conifers to edaphically or climatically suboptimal sites. Bond's proposal continues to stimulate interest (Becker, 2000; Coomes et al., 2005). In this chapter we examine the question: What enables podocarps to persist in angiosperm-dominated environments? As an introduction to the African Podocarpaceae we briefly discuss the taxonomic status of African and Madagascan species. Next, we examine the historical biogeography of African Podocarpaceae and propose an explanation for distribution anomalies consistent with differences in dispersal and reproductive biology between podocarp taxa. Finally, we explore a case study that investigates the regeneration

ecology in eastern South African montane forests to understand the angiosperm–conifer contest.

TAXONOMY

Compared with the rest of the Southern Hemisphere, Africa and Madagascar are relatively depauperate in species belonging to the Podocarpaceae (Farjon, 2001; Mill, 2003). In this review we refer collectively to members of African Podocarpaceae as podocarps. Two genera (*Afrocarpus*, *Podocarpus*) and 13 to 17 species are recognized from the continent and associated islands (Table 5.1). All taxa were previously placed in the genus *Podocarpus* (for a recent review see Barker et al., 2004), but recent morphological (Kelch, 1997) and molecular (Kelch, 1998; Conran et al., 2000; Sinclair et al., 2002; Barker et al., 2004) data support the decision to raise the section *Afrocarpus* to generic level as proposed by Page (1989). *Afrocarpus* is more closely related to the podocarp genera *Nageia* (Southeast Asia, India, Japan, Philippines, Indonesia) and *Retrophyllum* (South America, Indonesia, New Caledonia) than to the rest of the African species incorporated into *Podocarpus* (Conran et al., 2000; Sinclair et al., 2002). The genus-level identity of podocarp pollen is confounded by the failure to separate *Podocarpus* from *Afrocarpus* in the pollen record. Where podocarps appear in West African pollen cores they are assumed to be *Podocarpus* because of the present West African distribution of the genus.

The present status of several podocarp taxa in Africa and Madagascar is uncertain. Dowsett-Lemaire and White (1990) adopt the view that the four podocarp species from South Africa (*A. falcatus*, *P. henkelii*, *P. latifolius*, *P. elongatus*) are the only true species on mainland Africa. In support of this notion, de Laubenfels (1985) considered *P. ensiculus* collected from the western Usambaras of Tanzania (Melville, 1954) to be a synonym of *P. henkelii*, endemic to the midlands of southeastern South Africa. More recently, the *henkelii-ensiculus* group has been recorded from the highlands of Malawi (Dowsett-Lemaire and White, 1990). Farjon (2001) recognizes differences between temperate southern Africa and tropical Africa by assigning the formerly pan-African species *A. falcatus* and *P. latifolius* to southern Africa and acknowledging *A. gracilior* from east Africa and the central African *P. milanjanus*, respectively. Using DNA sequence data, Barker et al. (2004) were unable to separate *P. milanjanus* from *P. latifolius*. These authors concede, however, that failure to detect sequence differences does not negate

TABLE 5.1. Podocarpaceae species from Africa and Madagascar (after Farjon, 2001).

Species	Broad distribution
<i>Afrocarpus dawei</i>	East African highlands (Kenya, Tanzania, Uganda, Democratic Republic of the Congo)
<i>Afrocarpus falcatus</i>	Southern South Africa (Swellendam) eastwards through highlands of Eastern Cape, KwaZulu-Natal, north into Mpumalanga and Northern Province, and into southern Mozambique (coastal)
<i>Afrocarpus gausсенii</i>	Eastern plateau of Madagascar
<i>Afrocarpus gracilior</i>	Highland regions of Ethiopia, Kenya, Tanzania, Uganda
<i>Afrocarpus mannii</i>	São Tomé Island in the Gulf of Guinea
<i>Afrocarpus usambarensis</i>	Burundi, Rwanda, Congo, Tanzania
<i>Podocarpus</i> (section <i>Podocarpus</i>)	
<i>Podocarpus elongatus</i>	Winter rainfall region of Western Cape, South Africa
<i>Podocarpus latifolius</i>	Southern South Africa (Swellendam) eastwards through highlands of Eastern Cape, KwaZulu-Natal, Mpumalanga, and Northern Province
<i>Podocarpus</i> (section <i>Scytododium</i>)	
<i>Podocarpus capuronii</i>	Endemic to Madagascar, mountainous regions
<i>Podocarpus henkelii</i>	Highland regions of Eastern Cape and KwaZulu-Natal provinces of South Africa
<i>Podocarpus humbertii</i>	Endemic to Madagascar, mountainous regions in north
<i>Podocarpus madagascariensis</i>	Endemic to Madagascar
<i>Podocarpus rostratus</i>	Endemic to Madagascar, mountainous regions

species distinctness, given that morphologically distinct *A. falcatus* and *A. gracilior* have identical markers for the same region tested. In this review we consider *P. milanjinus* to be a synonym of *P. latifolius* (Drummond, 1975; Barker et al., 2004). In Madagascar, de Laubenfels (1985) proposed that *P. woltzii* and *P. perrieri* be synonymized within *P. capuronii* and *P. rostratus*, respectively. Stockey et al. (1998), however, comment that the rarity of some Madagascan podocarp species may have resulted in their incorporation into a single taxon. Using cuticle micromorphology, these authors found some evidence to split the *P. capuronii*–*P. woltzii* and *P. rostratus*–*P. perrieri* pairs into distinct species.

In Africa, all podocarp species occur in highland regions or, if coastal, then mostly at temperate latitudes (e.g., *A. falcatus* and *P. latifolius* in the southern Cape). The distribution of *A. falcatus* in coastal lowland forest at subtropical latitudes of northeastern South Africa and southern Mozambique is unusual and probably relictual, a legacy of former cooler periods during the late Pleistocene and Holocene (Mazus, 2000; Finch and Hill, 2008; Neumann et al., 2008). Confined to the winter rainfall region of the southwestern Cape, *P. elongatus* is unique among African members of the Podocarpaceae in its ability to regenerate from roots (Midgley et al., 1995a).

BIOGEOGRAPHY

The earliest records of African taxa possibly belonging to the Podocarpaceae arise in the Jurassic in Morocco, followed by Egypt in the Eocene and Ethiopia in the Miocene (Dupéron-Laudoueneix and Dupéron, 1995). Miocene pollen records of Podocarpaceae associated with now extinct taxa in the southwestern Cape support the hypothesis of a common Gondwanan flora (Coetzee and Muller, 1984). Consistent with this proposal are the vicariant distributions of *A. mannii* on São Tomé Island (Maley, 1996b) in the Gulf of Guinea and podocarp genera on Madagascar (Schatz, 1996). With five to seven podocarp taxa, Madagascar has been a center of radiation and, given its Gondwanan distribution adjacent to East Africa, also a site of *Afrocarpus* radiation, suggesting podocarps have expanded their distribution from East Africa. Podocarp fossils first appear in East Africa 14 MYA (Bonnefille, 1994) and in West Africa 2.7 MYA (Morley, 2000, 2003, this volume).

The distribution of podocarps on mainland Africa is reasonably well known, and the family has featured prominently in reconstructing paleoenvironments for the last 150,000 years. In general, African podocarps are restricted to highland archipelagos (sensu White, 1981) that

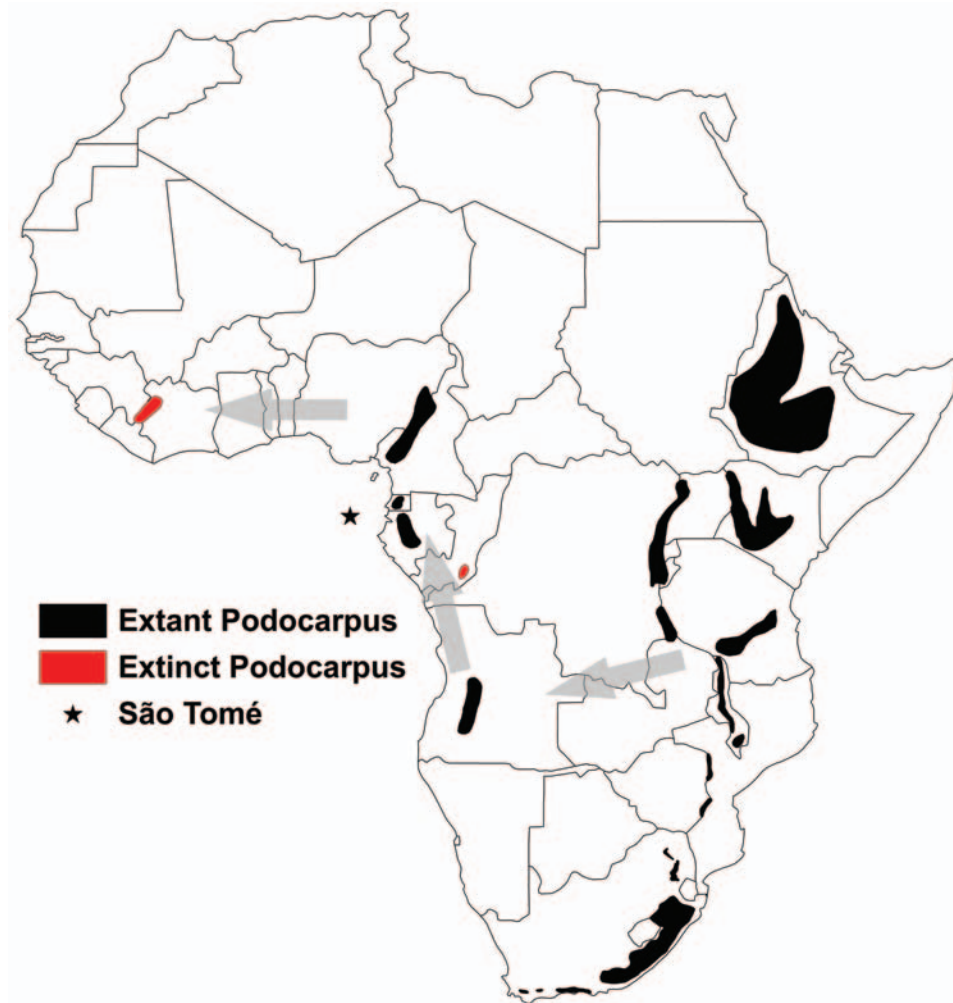


FIGURE 5.1. Highland regions in Africa where Afromontane forest is distributed (adapted from White, 1981). Areas in red indicate now extinct distributions of what is assumed to be *Podocarpus latifolius*. Arrows indicate proposed migration route of Afromontane elements from the East African highland region into West Africa via the Zambezi-Congo watershed (adapted from Maley, 1989). The West African distribution of *P. latifolius* was compiled from multiple sources: western Cameroon highlands (Maley and Brenac, 1998), Equatorial Guinea (Parmentier et al., 2001), the Chaillu massif in Gabon (Maley et al., 1990), west central highlands (Huambe) of Angola (Huntley and Matos, 1994), southeastern Congo highlands (Malaisse, 1967). Pollen cores from multiple marine and terrestrial sites in West Africa attest to a former distribution in the Guinean highlands (Maley, 1993; Dupont et al., 2000) and the Batéké Plateau of Congo (Elena et al., 1991).

correspond with regions of high species richness and endemism that are considered refuges during extreme paleoclimatic conditions (White, 1981; Maley, 1989; Linder, 2001; Figure 5.1). The principal Afromontane forest belt extends intermittently from Ethiopia southward to the southern Cape. *Afrocarpus* is distributed throughout this region but is absent from West Africa. *Podocarpus* has an isolated distribution in West Africa, extending from the

Cameroon highlands as far south as central Angola, and occurs throughout the East African mountain chain but is absent from Ethiopia. At the landscape scale, Afromontane forests persist as relatively small patches within a grassland or fynbos/heathland matrix (Figure 5.2).

Sharing of Afromontane faunal and floral elements between the Cameroon highlands and East Africa has long been recognized (Moreau, 1966; Kingdon, 1971;

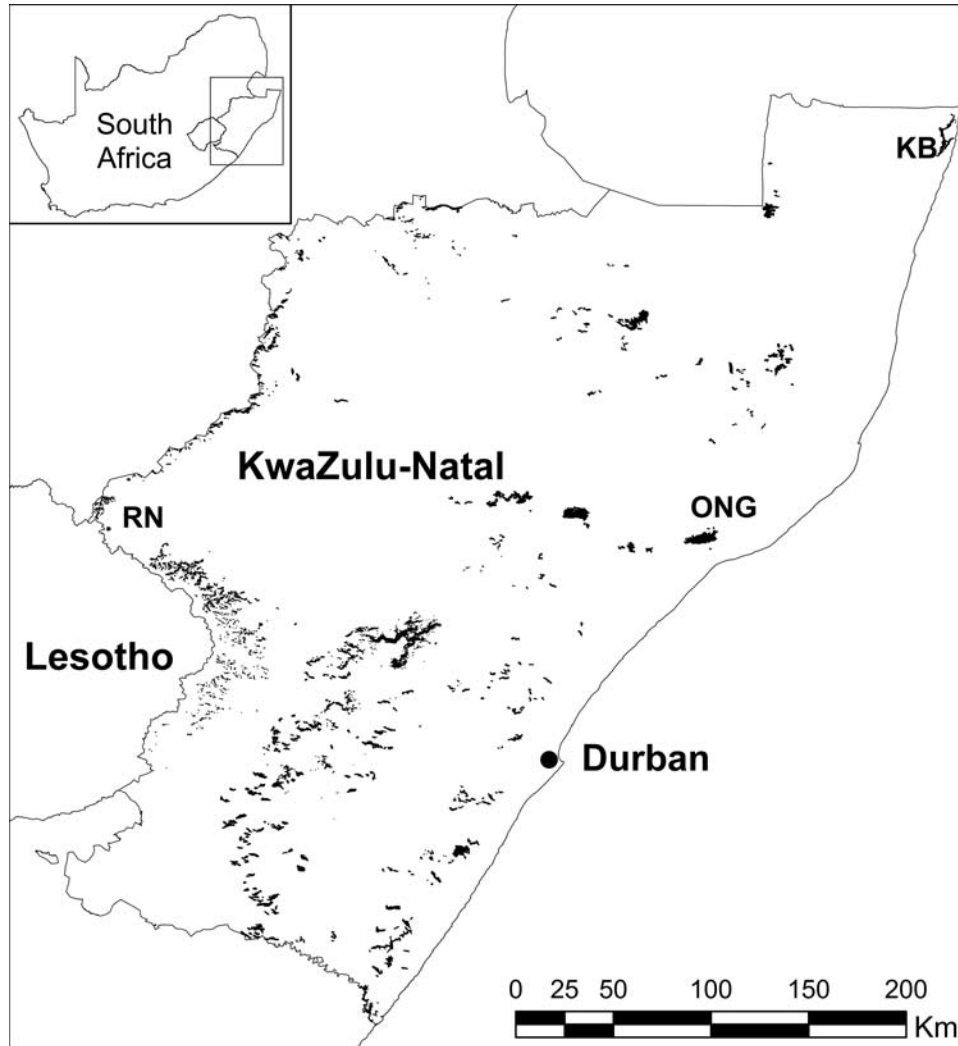


FIGURE 5.2. Indigenous forest in KwaZulu-Natal, South Africa, showing the patchy distribution at the landscape scale. Sites referred to in the text are Royal Natal (RN), Ongoye (ONG), and Kosi Bay (KB).

White, 1978, 1981; Hamilton, 1989; Dawson and Powell, 1999). An explanation for this disjunct distribution is that a direct dispersal corridor opened during drier climatic periods (Moreau, 1966; Van Zinderen Bakker, 1967; Coetzee and Van Zinderen Bakker, 1970; Kingdon, 1971). On the basis of montane floral elements, however, White (1981), and later Maley (1989, 1996a), proposed a more southern migration route that avoided the central Congo basin (Figure 5.1). In support of this pathway, Linder (2001) recently identified the Zambezi–Congo watershed, extending from northern Zambia to central Angola, as an important center of plant species diversity and endemism.

Determining the timing of migration between East and West Africa is difficult given the long history of podocarps in West Africa (2.7 MYA; Morley, 2000, 2003, this volume). Repeated climatic oscillations in the last 800,000 years, and in particular the last 150,000 years, for which the pollen record is well known (Maley, 1993; Dupont et al., 2000), provide adequate opportunity for biotic movement via the proposed Zambezi–Congo watershed corridor to West Africa. The significant increase in montane elements (particularly podocarps) in East Africa from 115,000 to 95,000 years ago reflects the expansion of montane forest taxa to lowland areas associated with cooler and dryer conditions (Cohen et al., 2007). At

much the same time, two phases of cool and dry conditions (115,000–105,000 and 95,000–85,000 years ago) resulted in maximum expansion of montane elements in West Africa (Fredoux, 1994; Maley, 1996a; Dupont et al., 2000). At no stage, even during the Last Glacial Maximum (18,000 years ago), does podocarp pollen dominate the record as much as in that earlier time period.

Even though the taxonomy and systematics of African Podocarpaceae require further refinement, the intriguing differences in distribution between *Podocarpus* and *Afrocarpus* invite speculation. In West Africa, podocarp pollen assumed to be *P. latifolius* was last recorded from the Guinean highlands approximately 74,000 years ago (Fredoux, 1994; Jahns et al., 1998; Dupont et al., 2000) and from the Batéké Plateau in the Congo Republic just prior to the Holocene (Elanga et al., 1991). Apart from the isolated distribution of *A. mannii* on São Tomé Island in the Gulf of Guinea, *Afrocarpus* has not been recorded from West Africa. *Afrocarpus* is the only podocarp in Ethiopia but coexists with *Podocarpus* throughout East and southern Africa. The absence of *Podocarpus* from Ethiopia is unusual since many common Afromontane tree species occur in the region (White, 1978; Dawson and Powell, 1999). Regional extinction is plausible given the history of local extinction of *Podocarpus* (assumed) in West Africa (Elanga et al., 1991; Dupont et al., 2000). The relatively impoverished bird and butterfly faunas of Ethiopia and the high endemism of the latter (Carcasson, 1964; Moreau, 1966) suggest the region has long been isolated, adding support to the extinction hypothesis. However, shared bird subspecies between Ethiopia and Kenya imply a recent biotic exchange (Moreau, 1966), at least for vagile animal species, but does not explain the absence of *P. latifolius*, an otherwise widely distributed podocarp, from Ethiopia.

A consistent pattern from soil cores in Africa is the concomitant increase in podocarp and grass pollen, associated with the regression of rainforest elements (Meadows, 1984; Fredoux, 1994; Dupont et al., 2000; Neumann et al., 2008). Even when an increase in podocarp pollen is associated with a simultaneous decline in grass (e.g., DeBusk, 1998; Cohen et al., 2007), the proportion of grass in the pollen record is still high (20% or more). An abundance of grass in pollen cores is always characteristic of open habitats (Vincens et al., 2006) and is frequently associated with cooler conditions. In East and West Africa, temperature declines of 4°C or more were associated with the expansion of Afromontane elements to lower elevations and the contraction of tropical (lowland) rainforest (Van Zinderen Bakker, 1982; Bonnefille et al., 1990; Maley, 1996a). Given the

abundance of grass during these cooler periods, Afromontane forest is unlikely to have extended its distribution as a continuous belt. Indeed, contemporary Afromontane landscapes are a patchy mosaic of forest and grassland, with forest patches usually situated on south-facing slopes or in valley heads (Everard, 1986; Meadows and Linder, 1993; Adie and Lawes, 2009b; Figure 5.2). Fire in the grassland matrix is the dominant process responsible for this patchy and isolated distribution of forest (Geldenhuys, 1994). The migration of Afrotropical elements during late Pleistocene climatic fluctuations is therefore most likely to have followed the “stepping-stone” process (DeBusk, 1998), which requires dispersal across an inhospitable grassland matrix. This proposal is consistent with the forest-grassland mosaic typical of the Drakensberg Mountains of eastern South Africa, where all forest tree species, and especially *P. latifolius*, persist in fire refugia situated in the grassland matrix (Adie and Lawes, 2009b; Figure 5.3). Being bird dispersed and capable of rapid germination (4–6 weeks, H. Adie and M. J. Lawes, unpublished data; Geldenhuys, 1993) in a variety of habitats, *P. latifolius* displays traits typical of a highly vagile species. *Podocarpus latifolius*, therefore, fits the model of a good disperser with a high probability of establishment within a grass-dominated environment, provided it can escape fire. However, the species appears to be a weak competitor at the regeneration phase when faced with lowland angiosperm species (Adie and Lawes, unpublished), which may account for its failure to persist in isolated refuges once warmer conditions return that favor lowland forest species.

In contrast to *Podocarpus*, the absence of *Afrocarpus* west of the Eastern Afromontane chain suggests this taxon never extended farther westward. We propose that the westward expansion of *Afrocarpus* has been constrained by its reproductive biology. Dispersed by birds, bats, monkeys, and baboons (Geldenhuys, 1993; Teketay and Granstrom, 1997; Negash, 2003; Hitimana et al., 2004), the *falcatus-gracilior* group is unlikely to be dispersal limited, even across the open grass-dominated landscapes that characterize the Afrotropical region. However, the hard sclerotesta of *A. falcatus* cones delays germination for a year or more and leads to high postdispersal damage by mammals, resulting in low recruitment rates (Geldenhuys, 1993). In addition, seed viability declines by more than 50% within 12 months of harvesting (Negash, 2003). Loss of viability and postdispersal mortality combined with infrequent seed production (mast fruiter) all reduce the probability of colonizing new habitat. At the landscape scale, *Afrocarpus* appears to be a poor colonist but persists well once established. The minor radiation



FIGURE 5.3. Mature *Podocarpus latifolius* persisting in a fire-safe topographic refuge situated in a regularly burnt grassland matrix at Royal Natal.

of *Afrocarpus* in East Africa and the discovery of distinct *A. falcatus* provenances in South Africa (Geldenhuis and Von dem Bussche, 1997) are consistent with the hypothesis that the genus is restricted by stepping-stone dispersal and imply that the distribution of *Afrocarpus* in Africa is an ancient one.

PODOCARP ECOPHYSIOLOGY

The ecophysiology of African podocarps is largely unknown. Nevertheless, explanations for conifer distribution in Africa have been based in large part on physiological differences between conifers and competing angiosperms

(Bond, 1989). Bond argued that functional constraints such as tracheids and nonvascularized leaves place conifers at a competitive disadvantage at the regeneration phase, restricting them to edaphically or climatically sub-optimal sites where they perform better than angiosperms.

The dual role of mechanical support and hydraulic function performed by wood leads to trade-offs in performance with important ecological implications (Chave et al., 2009). Angiosperms solved this problem by separating mechanical support from hydraulic function with the evolution of xylem vessels, multicellular conduits for water transport, and a matrix of fibers for support (Sperry et al., 2006). Released from their structural function, angiosperm vessels achieve greater conducting efficiency by increasing

their diameter (Tyree and Ewers, 1991; Sperry et al., 2005). In contrast, conifer tracheids are limited by their unicellularity and the need to provide both mechanical support and hydraulic function to the plant (Sperry et al., 2006; Lusk, this volume; Brodribb, this volume). The dual role of tracheids leads to a trade-off between their two primary functions, a constraint that conifers have overcome to some extent with the evolution of the torus-margo pit, a membrane that joins conduit end-walls, allowing significantly higher conductivity compared with the longer vessels of angiosperms (Hacke et al., 2004; Pittermann et al., 2005). Nevertheless, conifers grow more slowly than angiosperms (Coomes and Bellingham, this volume).

Compared to angiosperms, conifer leaves are poorly vascularized and have low stomatal conductance and low specific leaf area, resulting in lower photosynthetic capacity (Lusk et al., 2003; Brodribb et al., 2005a, 2005b). Photosynthetic capacity increases with xylem vessel conductance (Brodribb and Feild, 2000; Hubbard et al., 2001), but large vessels are at risk of embolism in cold environments (Sperry et al., 1994). Photosynthetic yield (measured by the leaf area to stem area ratio) has been shown to be much greater in angiosperms measured in high light, but this advantage over conifers tends to be neutralized in low light (Brodribb et al., 2005a). A pervasive pattern among African podocarps is superior shade tolerance compared with associated angiosperms, which demand more light (Midgley et al., 1995b; Adie and Lawes, 2009a). However, Coomes and Bellingham (this volume) point out that many shade-tolerant podocarps are capable of regenerating in shaded environments yet fail in deep shade, where light levels are ~2% of daylight. This is consistent with the finding that plants, in general, are substantially more responsive to nutrient supply at light levels of >5% of daylight compared with deep understory shade, where light levels are often <2% of daylight (Coomes and Grubb, 2000). Thus, it is not surprising that relative shade tolerance of podocarps is strongly implicated in the coexistence of African podocarps and angiosperms and is likely the dominant determinant of mixed angiosperm–conifer tree community structure in African forests (Adie and Lawes, 2009a).

ECOLOGY

MIXED ANGIOSPERM–CONIFER FORESTS

Here we examine podocarp regeneration along an altitudinal gradient extending from the Drakensberg,

a mountainous region situated in the northwest of KwaZulu-Natal province, to lowland forest on the east coast of South Africa (Figure 5.2). Mixed angiosperm–conifer forests in the montane region are characteristically small, usually less than 5 ha and rarely exceeding 30 ha (Lawes et al., 2007a), and exist as an archipelago within a grassland matrix between 1,400 and 1,830 m above sea level. Forest distribution is limited by fire and is therefore generally restricted to moist south-facing slopes and steep-sided ravines (Everard, 1986; Geldenhuys, 1994) situated beneath tall sandstone cliffs. Lowland forest lies on the plains inland of the coastal dune cordon (Mucina and Rutherford, 2006) and is well represented just south of Kosi Bay in northern Maputaland (Figure 5.2). The forests have a well-developed canopy and subcanopy, and the semiwoody herb *Isoglossa woodii* (Acanthaceae) frequently dominates the shrub layer. Intermediate between the inland mountains and coastal lowlands is coastal scarp forest, a species-rich subtropical forest type that is derived from, and hence owes its diversity to, tropical coastal forests and inland Afromontane elements (Lawes, 1990; Griffiths and Lawes, 2006). Situated in a mosaic of grasslands and rocky granitic outcrops, Ongoye Forest Reserve lies between 300 and 500 m elevation and is 2,600 ha in extent (Boudreau et al., 2005).

Three species of Podocarpaceae are distributed along the described altitudinal gradient. *Podocarpus latifolius* is an abundant and widespread species throughout the Drakensberg and KwaZulu-Natal midlands and extends toward the coast, where it is an uncommon component of scarp forest. Known from only one forest in the Drakensberg, *P. henkelii* is rare in the montane region but common in mist belt forests of the midlands (H. Adie, personal observation). *Afrocarpus falcatus* has a patchy but locally common distribution in the Drakensberg, is widespread and relatively common in the midlands, is present but uncommon in scarp forest, and is the only podocarp found in the subtropical lowland forests of the coastal plains, where it is scarce.

BIOPHYSICAL FACTORS

Light is a critical factor determining plant growth and survival in forest ecosystems (Denslow, 1987), in which the differential response to light during the regeneration phase drives plant community composition and dynamics (Kobe et al., 1995; Bloor and Grubb, 2003). In mixed angiosperm–conifer forests of the Southern Hemisphere, regeneration following both autogenic and allogenic disturbance is driven by differences in plant shade tolerance

(Lusk and Ogden, 1992; Ogden and Stewart, 1995; Lusk and Smith, 1998). Deep shade (~2% daylight) in southern forests tends to favor angiosperms at the expense of podocarps (Lusk, 1996; Coomes et al., 2005).

To understand regeneration patterns in Afromontane forest, two forest types that differed substantially in structure and, therefore, in light environment were compared. Angiosperm forest, as the name implies, is dominated by angiosperm canopy species. Tree density in this forest type is relatively high, and the forest canopy is moderate in stature (<20 m). *Podocarpus latifolius* is usually present in the angiosperm forest canopy, but at low density. Forests dominated by the conifer (>60% of canopy trees) differ structurally from those dominated by angiosperms by having a higher canopy (20–25 m) and larger trees with greater nearest neighbor distances, resulting in an open mid-story and “cathedral-like” structure. The two forest types differ in terms of the quality and quantity of light

reaching the forest floor beneath the intact canopy and in canopy gaps (Adie and Lawes, 2009a; Figure 5.4). Photosynthetically active radiation was high (~17% irradiance) in canopy gaps in both forest types, but light quality (measured as the ratio of red to far red light; Capers and Chazdon, 2004) in angiosperm canopy gaps, which were small ($84.6 \pm 13.7 \text{ m}^2$, $n = 10$), showed far less variation and was lower compared with the much larger gaps ($183 \text{ m}^2 \pm 36.6$, $n = 10$) in *Podocarpus* forest (Adie and Lawes, 2009a). We also sampled forest tree regeneration outside true forest, in a thicket environment dominated by *Rhus tomentosa*. The thicket habitat, which had a low canopy of 4–6 m, was less shaded than the two forest habitats, but light quality was substantially lower, probably because of the high stem density of the habitat (Lee, 1989; Smith and Whitelam, 1997).

The structural conditions described above cause important differences in the light reaching the forest

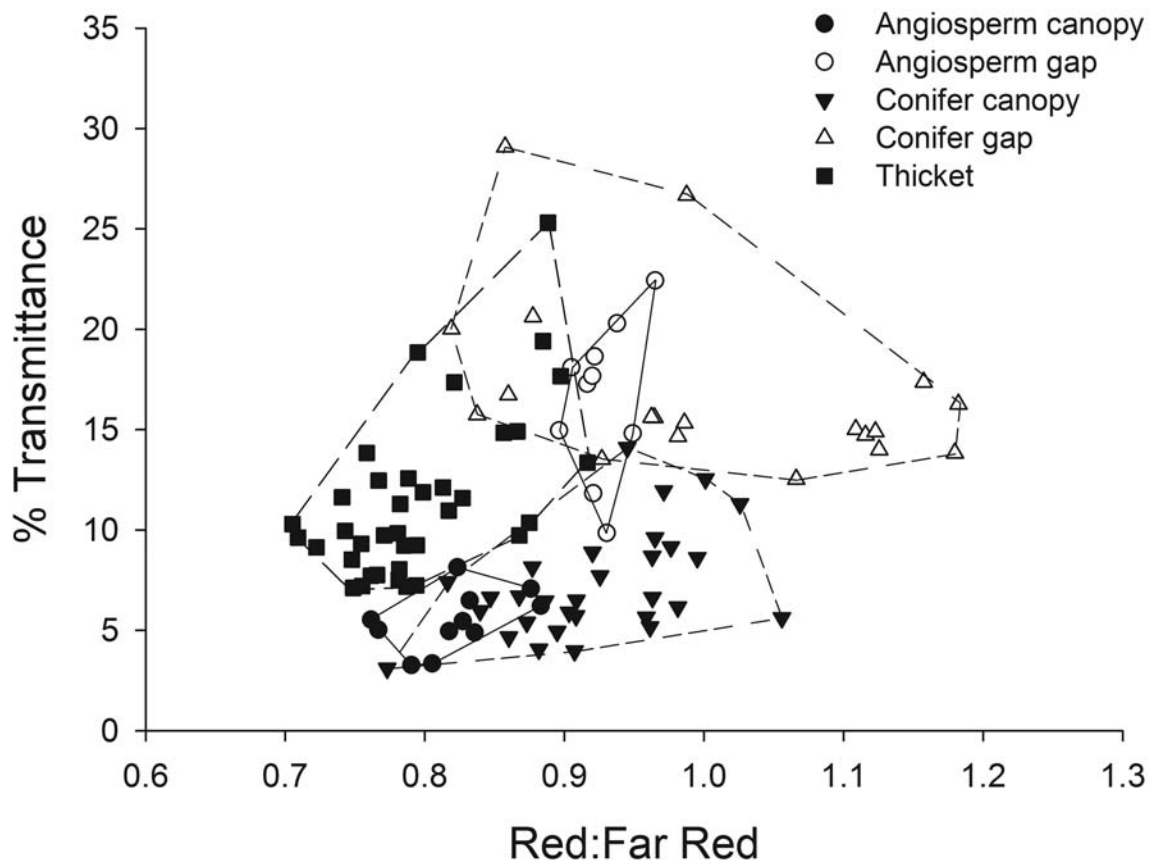


FIGURE 5.4. Light characteristics (percent light transmittance, red:far red) at ground level in *Rhus tomentosa* thicket and two habitats (canopy, gap) in forest dominated by angiosperms and conifers.

understory environment, and both light and the understory vegetation act in combination to restrict regeneration by forest canopy species (Adie and Lawes, 2009a). Grass was the principal ground cover beneath the intact *Podocarpus* forest canopy, but was absent from both angiosperm forest and thicket. Bare ground or a sparse covering of litter dominated the thicket habitat and angiosperm forest. Gaps in both forest types were frequently choked by a combination of grasses, vines, ferns, and understory shrubs. With this background to the physical environment, we discuss the relative success of angiosperm and conifer regeneration in Afrotropical forest.

THE ROLE OF DISTURBANCE IN MIXED ANGIOSPERM-CONIFER FORESTS IN SOUTH AFRICA

GAP-PHASE DYNAMICS

Gap-phase dynamics is an important driver of forest structure and dynamics in New Zealand and South America (Lusk and Ogden, 1992; Ogden and Stewart, 1995). In these temperate forests, the differential response to gaps at the juvenile stage leads to canopy species coexistence (Lusk and Smith, 1998; Gutierrez et al., 2004; Gutierrez et al., 2008). In contrast, canopy gaps have a limited role in the regeneration dynamics of Afrotropical forests (Adie and Lawes, 2009b), where poor regeneration by angiosperm canopy species results from their shade intolerance (Midgley et al., 1995b; Adie and Lawes, 2009a).

Gaps in angiosperm forest are created by lateral branch breakage and stem snapping, resulting in relatively small gaps. Young gaps tend to be larger than old gaps, suggestive of progressive canopy closure with age due to lateral ingrowth of adjacent canopies. Interestingly, seedling and sapling densities do not differ among gap sizes or from densities recorded beneath the closed canopy (Adie and Lawes, 2009a). Thus, in spite of elevated light levels, the gap environment offers no new regeneration opportunities for angiosperms or *P. latifolius*. Even though angiosperm seedlings were abundant, very few saplings or poles were recorded in gaps or beneath the canopy (Figure 5.5), suggesting that light conditions were inadequate for growth into larger size categories. Young conifer trees were abundant in these regeneration environments, but less so in older gaps, implying self-thinning or suppression by ground cover (Beckage et al., 2000; Coomes et al., 2005). In addition, *P. latifolius* saplings (1–5 cm diameter at breast height [dbh]) and poles (5 cm < dbh ≤ 10 cm)

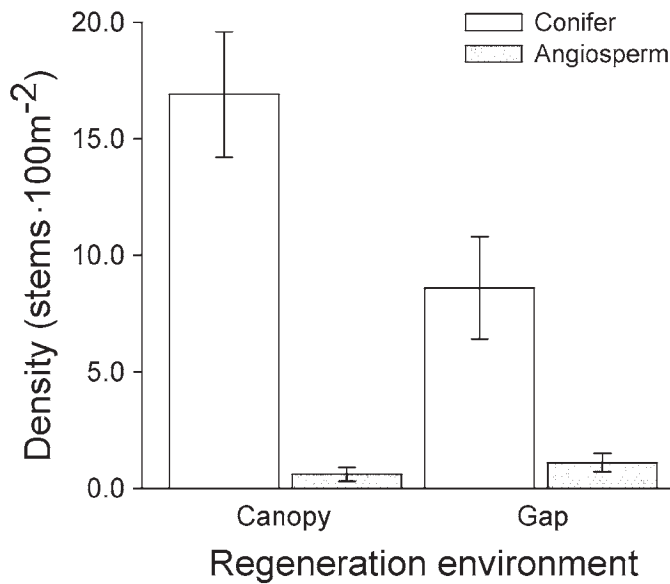


FIGURE 5.5. Mean density (\pm standard error, $n = 10$) of young conifer and angiosperm trees in two regeneration environments in Afrotropical forest.

were common in young tree fall gaps (<24 months old), demonstrating that successful gap fillers were drawn from individuals in the advanced regeneration phase that established prior to gap creation (Adie and Lawes, 2009b). Being shade tolerant, or more shade tolerant than associated angiosperm species, the conifer outperformed angiosperms at gap formation because it was able to establish profusely beneath the angiosperm canopy.

In contrast to the high rate of establishment by *P. latifolius* in angiosperm forest, regeneration by the conifer in *Podocarpus*-dominated forest was substantially less than that recorded for angiosperms (Adie and Lawes, 2009a). Canopy gaps in *Podocarpus* forest were generally created by uprooting of large-canopy individuals (Adie and Lawes, 2009b). Consequently, canopy gaps in *Podocarpus* forest were relatively large compared with angiosperm forest, yet they offered no new regeneration opportunities to angiosperms or *P. latifolius*. Curiously, unlike angiosperm forest, there were almost no *P. latifolius* seedlings beneath the intact canopy of *Podocarpus* forest. Grass, the dominant ground cover in *Podocarpus* forest, suppressed *P. latifolius* seedlings, causing high mortality (Adie and Lawes, 2009b). Even in gaps, the abundant grass cover resulted in relatively low densities of *P. latifolius* (0.9 ± 0.3 per 0.01 ha) and angiosperm canopy species (1.2 ± 0.3 per 0.01 ha).

Besides grass, dense understory vegetation and vines may also dominate gaps. An inverse J-shaped distribution of angiosperm stem sizes in *Podocarpus* forest suggests that grass does not suppress angiosperm seedlings in the same way it does *P. latifolius*. Seedlings were common, but the scarcity of saplings implies growth suppression, with possibly light limitation restricting the growth of seedlings into larger size categories. Notwithstanding the low density of both angiosperms and *P. latifolius* in gaps, the contest between these two plant groups in *Podocarpus* forest is equivocal, with both apparently having an equal opportunity to occupy gaps. Tree fall gaps therefore offer one mechanism to maintain angiosperm diversity in Afrotropical forest, but in old-growth forest only (Adie and Lawes, 2009a).

CATASTROPHIC DISTURBANCE

Large-scale natural disturbances (earthquakes, cyclones, landslides, volcanic eruptions) have had a pervasive influence on the structure and dynamics of mixed angiosperm–conifer forests in New Zealand (Stewart and Rose, 1989; Ogden and Stewart, 1995; Wells et al., 2001) and South America (Veblen and Ashton, 1978; Veblen et al., 1995). The Afrotropical landscape in the subtropics is relatively benign in that it lacks the climatic, topographic, or geological extremes that cause stand-destroying disturbance in many southern temperate forest environments. Fire has also been reported as an important process controlling stand structure in mixed forests in South America (Burns, 1993), and extensive precolonization fires in New Zealand probably caused a mosaic of seral and mature forest communities (Ogden et al., 1998). Natural fire is also implicated in the total destruction of podocarp forests following drought on New Zealand's South Island (Kershaw and McGlone, 1995) and in New Guinea *Araucaria* forest (Enright, 1995). In tropical environments, fires are more likely during drought years, when fragmented forests are particularly vulnerable (Cochrane and Laurance, 2002). South American gallery forest, a naturally fragmented form of tropical moist forest that exists within a savanna matrix (Kellman and Meave, 1997), is more prone to fire in the late dry season, when plant material is more ignitable (Biddulph and Kellman, 1998). Drakensberg montane forest is not unlike gallery forest in that it exists as small patches within a fire-prone grassland matrix (Everard, 1986), yet fire has largely been de-emphasized as a process driving forest change in South Africa (Mucina and Rutherford, 2006), a viewpoint that is not unexpected since fire is unusual in South African forests (Midgley et al., 1997).

Forests with a canopy dominated by angiosperms do not burn (Bond, 1997) because of low fuel loads and high leaf moisture levels (van Wilgen et al., 1990) or high fuel moisture content (Eriksson et al., 2003). Nevertheless, it is notable that most Afrotropical forests establish and persist in fire refugia, where they escape the prevailing grassland fire direction (Geldenhuys, 1994).

Although rare under the present grassland management system in the subtropics of southern Africa, fire may have been a critical historical driver of inland forest structure and dynamics by destroying old-growth *Podocarpus* forest. Catastrophic disturbance provides relatively rare regeneration opportunities for angiosperm trees in the Afrotropical landscape. Historical records report catastrophic fires devastating indigenous forest, particularly in the temperate *Podocarpus* forests of the southern Cape (Geldenhuys, 1994). In most cases fires were preceded by several days of hot berg wind conditions (van Wilgen, 1984; Geldenhuys, 1994; Bond, 1997). The open physiognomy of *Podocarpus*-dominated forests is highly susceptible to the desiccating effect of berg winds and, coupled with high levels of volatile compounds in long-lived sclerophyllous leaves (Kershaw and McGlone, 1995) and the well-developed grass cover in old-growth forests, predisposes *Podocarpus* forest to fire.

DOES PATTERN AND PROCESS IN AFROMONTANE FORESTS CONFORM TO OTHER SOUTHERN HEMISPHERE PODOCARP FORESTS?

Regeneration patterns of canopy trees in montane forests are consistent with the temporal stand replacement model (TSRM; Ogden, 1985; Enright et al., 1999; Ogden et al., 2005), with important exceptions. The TSRM was proposed to explain the dominance of long-lived pioneer conifer cohorts and the widespread regeneration failure reported from temperate forests in New Zealand (Veblen and Stewart, 1982; Stewart and Rose, 1989) and South America (Veblen et al., 1980, 1995). Under the TSRM, sites are colonized by a pioneer cohort, usually a long-lived conifer, following stand-destroying disturbance. In the absence of further disturbance, synchronous senescence by the colonizing cohort causes overstory mortality, creating gaps that offer diminishing regeneration opportunities for the first-generation conifer in favor of more shade-tolerant species, usually an angiosperm (Enright et al., 1999; Ogden et al., 2005).

Regeneration failure by the angiosperm canopy component is a recurrent pattern in South African inland forests

(Moll, 1972; Everard et al., 1995; West et al., 2000; Lawes et al., 2007b). Drakensberg montane forests, with a near absence of advanced angiosperm regeneration beneath the intact canopy, are no exception (Adie and Lawes, 2009b). However, angiosperm regeneration was recorded from scrub thicket sites and a grassland fire-exclusion site, leading us to propose that many angiosperm species assume a colonizing role and establish as a pioneer cohort following disturbance (Adie and Lawes, 2009b). Unlike temperate forests elsewhere, *P. latifolius* was slow to regenerate in these scrub environments, possibly because of slow seedling growth rates relative to angiosperms (Bond, 1989). The prevalence of angiosperm-dominated canopies among forests that were logged extensively (i.e., catastrophic disturbance) during the colonial era from the early to mid-1800s to the early twentieth century (Fourcade, 1889; Hutchins, 1905; McCracken, 1986) is consistent with the proposal that angiosperms assume the colonizing role following major disturbance. Therefore, in South Africa a suite of angiosperm species take on the pioneer role that is usually filled by a long-lived gymnosperm species in New Zealand. The slow colonization of fire-protected grassland sites by angiosperm tree species demonstrates that catastrophic disturbance, another key feature of the TSRM, is not a necessary requirement for forest development in the Afrotropical landscape.

Podocarpus latifolius regenerated continuously beneath the intact angiosperm-dominated canopy in the Drakensberg, confirming shade tolerance in this species. Age data for *P. latifolius*, which shows that *Podocarpus*-dominated forest is considerably older than angiosperm forest, confirms the replacement of angiosperms by the conifer and is consistent with the TSRM as a two-phase system with phases separated in time (Adie and Lawes, 2009b). Continuous regeneration by the shade-tolerant conifer eliminates the need for the synchronous canopy senescence that is a key feature of the TSRM in other southern temperate forests. Conifer persistence, the central feature of conifer–angiosperm competition, appears to be curtailed by more shade-tolerant angiosperms elsewhere. Superior angiosperm shade tolerance in Chilean temperate forest prevents conifer regeneration in deep shade (Lusk, 1996), and productive alluvial forest habitats in New Zealand appear too dark for even the most shade-tolerant conifers (Coomes et al., 2005). Indeed, the progressive replacement of the colonizing cohort by more shade-tolerant angiosperm species in southern temperate forest is a key feature of the TSRM (Enright and Ogden, 1995; Ogden et al., 2005). In these temperate forests, canopy gaps favor recruitment by conifers, leading to their coexistence with

angiosperms (Lusk and Smith, 1998). The differential response by tree species to varying light conditions is a critical driver of forest structure and dynamics in New Zealand (Ogden and Stewart, 1995). More recently, soil nutrient availability has been shown to have an important role in plant community development, with conifers performing better than angiosperms on nutrient-poor sites (Richardson et al., 2004; Coomes et al., 2005; Carswell et al., 2007).

SOIL NUTRIENTS

Superior shade tolerance of *P. latifolius* in the Afrotropical environment relative to angiosperms weakens the proposition that conifers are restricted to suboptimal environments (climate, nutrients) by competitively superior angiosperms at the regeneration phase (Bond, 1989). Angiosperm shade intolerance removes competition at the conifer seedling phase and ultimately results in the replacement of angiosperms by the podocarp. Do depleted soil nutrient levels affect the tortoise–hare contest in favor of the conifer as Bond (1989) predicted? In New Zealand, soil nutrient status alters regeneration success among podocarps (Carswell et al., 2007), and podocarps perform better on infertile (phosphorus-limited) and poorly drained soils relative to co-occurring angiosperms (Richardson et al., 2004; Coomes et al., 2005). The role of soil fertility in altering the outcome of the angiosperm–podocarp contest has not been examined directly in African forests. At fynbos sites, known to be very infertile, shaded microhabitats were more important than soil organic matter content for germination of forest species (Cowling et al., 1997), and in the southern Cape, topography and aspect, rather than soil type, determined forest distribution (Geldenhuys, 1994). In these regions fire was the overriding process determining forest distribution (van Wilgen et al., 1990; Geldenhuys, 1994; Cowling et al., 1997).

Compared with *P. latifolius*, which showed no nutrient effect, seedling growth of angiosperm canopy species was consistently higher at high nitrogen (half-strength Hoagland's solution containing 10% of the recommended nitrogen concentration; Hewitt, 1966) compared with low nitrogen (1% nitrogen) levels, but there was a steady decline in performance with diminishing light (Figure 5.6). In Chilean temperate rainforest, shade-tolerant conifers were associated with nutrient-poor and climatically stressed sites, but these species were also associated with high-disturbance gap sites (Lusk, 1996), suggesting response to light is equally, if not more, important to regeneration success. Coomes et al. (2005) showed variable performance by conifers along a productivity gradient,

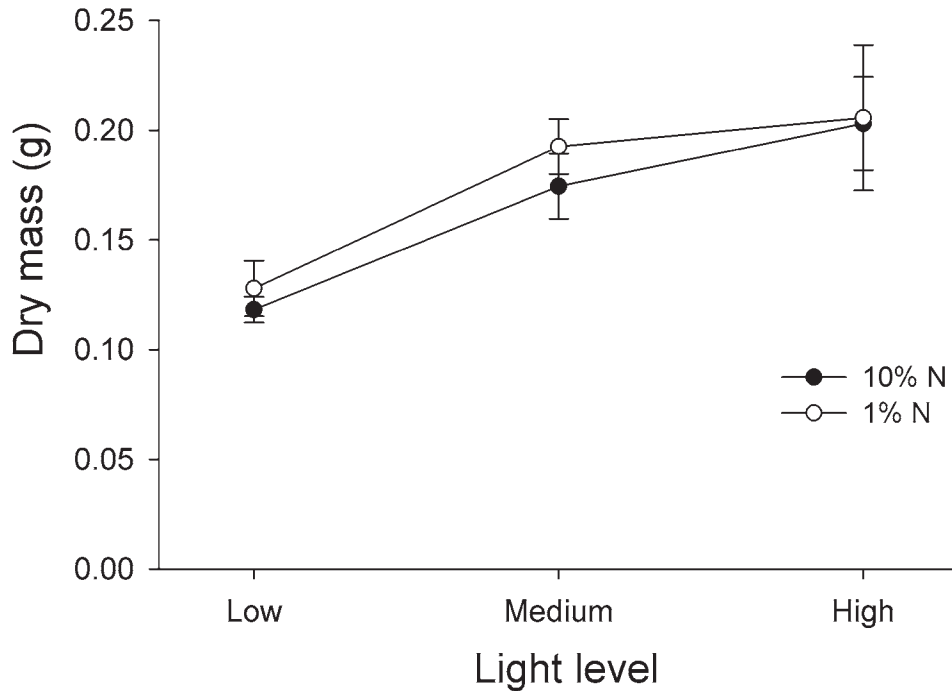


FIGURE 5.6. Seedling mass (mean \pm standard error, $n = 6$) of *P. latifolius* after three months growth under three light treatments (low = 2.4% photosynthetically active radiation (PAR), medium = 8.0% PAR, and high = 13.5% PAR) and two nutrient levels (10% nitrogen and 1% nitrogen).

the conifers performing better in lower-nutrient (yet more open) terrace forest, where they established in gaps. In contrast, shadier habitats and ferns limited regeneration opportunities for conifers at the upper end of the productivity gradient. In Afromontane forests of the South African Drakensberg Mountains we found no association between conifer or angiosperm community dominance and soil chemical composition (M. J. Lawes, unpublished data). Nitrogen does not appear to be a limiting soil nutrient in African forest sites. In the Munesa region of the Ethiopian southeastern highlands, where *A. falcatus* is an important canopy species, the soil carbon to nitrogen ratio was 12.6 (Solomon et al., 2002). This value is no different from values for Drakensberg and subtropical forest sites in KwaZulu-Natal (Table 5.2) but is substantially lower than nutrient-poor sites in New Zealand (Richardson et al., 2004; Coomes et al., 2005). We have no comparable values for total phosphorus, which has been shown to be a strong driver of plant community structure in New Zealand forests (Richardson et al., 2004; Coomes et al., 2005; Carswell et al., 2007). However, available phosphorus, the quantity of phosphorus that is easily extracted and directly available to the plant (Holford, 1997), does not seem to

be limiting in the Drakensberg or subtropical scarp forest sites (Table 5.2). Concentrations of available phosphorus $>10 \text{ mg kg}^{-1}$ (Ambic-2 method; Thibaud et al., 1994) in similar soils are not considered severely limiting for annual agricultural crops in KwaZulu-Natal; it is therefore unlikely that concentrations $>5 \text{ mg kg}^{-1}$ would be limiting for slow-growing forest trees (A. Manson, Soil Fertility Analytical Services, KZN Department of Agriculture and Environmental Affairs, personal communication). Available phosphorus recorded in forests in the central Ethiopian highlands (31.7 mg kg^{-1} ; Bray II method; Michelsen et al., 1996) was similar to Ongoye forest. These data indicate that soils in southeastern Africa are neither nitrogen nor phosphorus limited, and it is possible that soil moisture may have an importance not recognized in other Southern Hemisphere locations where podocarps are present.

Arbuscular mycorrhizal fungi provide an important mechanism to overcome growth constraints imposed by nutrient-poor soils (Brundrett, 2002). Such fungi have a significant effect on seedling growth (Janos, 1980), particularly in soils where available phosphorus concentrations are low (Chen et al., 2005; Lambers et al., 2008), and have the potential of causing differential regeneration success

TABLE 5.2. Soil chemical characteristics (mean \pm standard error, $n = 6$) from forest sites in the Drakensberg (Monk's Cowl, Royal Natal) and a subtropical site (Ongoye Forest Reserve) in KwaZulu-Natal. Available phosphorus was analyzed using the Ambic-2 method (Thibaud et al., 1994).

Site	C:N	Total N (%)	Available P (mg P kg ⁻¹)
Royal Natal	12.06 \pm 0.81	0.91 \pm 0.045	12.89 \pm 0.876
Monk's Cowl	12.55 \pm 0.62	1.21 \pm 0.171	9.88 \pm 1.04
Ongoye	11.77 \pm 0.60	0.71 \pm 0.215	27.68 \pm 1.42

and therefore affecting species diversity in forests (Kiers et al., 2000; Chen et al., 2005). Phosphorus uptake by conifer roots is stimulated by the presence of arbuscular mycorrhizal fungi (Morrison and English, 1967; Baylis, 1969), and Dickie and Holdaway (this volume) propose that root nodules serve to increase the volume of the root cortex volume, resulting in greater fungal infection. Arbuscular mycorrhizas have been identified in *A. falcatus* (Allsopp and Stock, 1993; Wubet et al., 2003) and *P. latifolius* (Hawley and Dames, 2004) and are also present in many associated angiosperm species in Afrotemperate forest (Hawley and Dames, 2004). The importance of arbuscular mycorrhizal fungi at the regeneration phase, and whether it affects the conifer–angiosperm contest, is unknown for Afrotemperate forests but is unlikely if phosphorus is not limiting.

PODOCARPS IN COASTAL FOREST

The presence of podocarps in coastal forest is probably a legacy of climatic extremes during the Last Glacial Maximum, when inland forests are thought to have retreated toward the coast (Eeley et al., 1999). *Podocarpus latifolius* persists as large-canopy individuals in scarp forest, but the continuous regeneration so prevalent in montane forest is absent. Seedlings and saplings beneath the canopy are rare and tend to be spindly in appearance (Adie and Lawes, unpublished data). However, angiosperm species are similarly absent from the understory at Ongoye, which contradicts the view that direct competitive interactions limit the conifer beneath the forest canopy in subtropical environments (Midgley et al., 1995a). Either (1) shade tolerance of *P. latifolius* in scarp forest differs from that in montane forest populations, which is not an unreasonable hypothesis since there is evidence for distinct *A. falcatus*

provenances in southern Africa (Geldenhuys and Von dem Bussche, 1997), or (2) the response to light by *P. latifolius* does not differ between the two forest habitats, but there is a lower limit below which the conifer is unable to perform. Incoming photosynthetically active radiation beneath the intact canopy at Ongoye was substantially lower than that recorded in Afrotemperate forests (Figure 5.7) because of a more-productive angiosperm canopy and many shade-tolerant mid-canopy species in scarp forest. Deep shade (<2% photosynthetically active radiation) and not direct competition from understory angiosperms, which were absent beneath the canopy, seems to be a more likely mechanism suppressing *P. latifolius* regeneration in scarp forest. Many podocarp species persist in deep shade but do not regenerate continuously in these habitats (Coomes and Bellingham, this volume).

Conifer regeneration opportunities were similarly restricted in productive alluvial forest habitats in New Zealand (Coomes et al., 2005). Saplings of *P. latifolius* growing adjacent to forest roads and on the forest edge at Ongoye were robust (Adie and Lawes, unpublished data), reflecting successful growth and supporting our contention that light, rather than direct angiosperm competition at the regeneration phase, ultimately suppresses growth of this species in scarp forest. Enhanced productivity in scarp forest, which may result from a combination of soil fertility and climate, is a proximate factor that operates indirectly by altering light levels that suppress *P. latifolius* performance.

The differential response to light between angiosperms and conifers appears to be the critical factor driving lowland forest dynamics. An isolated population of *A. falcatus* exists in tropical coastal lowland forest at Kosi Bay in northern Maputland (Figure 5.2). *Afrocarpus falcatus* is a shade-tolerant tree (Fetene and Feleke, 2001; Tesfaye et al., 2002) that regenerates continuously in forest but has higher seedling growth rates in gaps compared with more shaded sites (Teketay, 1997). The latter point concurs with the observation of Laughton (1938), who considered *A. falcatus* more light demanding than *P. latifolius* in southern Cape forests.

At Kosi Bay the structure of the *A. falcatus* population is consistent with regeneration failure. Very large canopy individuals (>60 cm diameter at breast height) form an integral part of the angiosperm-dominated canopy, with a preponderance of young plants (including seedlings but few saplings) beneath the canopy (R. Kyle, personal communication). Intermediate-sized trees are rare or absent. Saplings and poles are a valuable resource to local communities because the wood is hard and the poles are

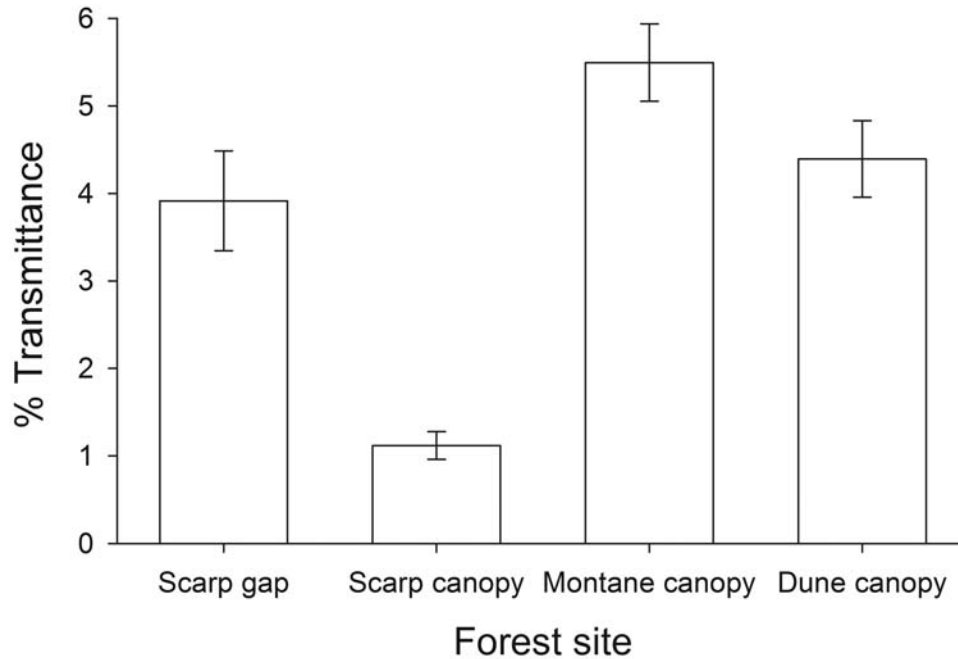


FIGURE 5.7. Mean light transmittance (\pm standard error, $n = 12$) in a scarp forest understory gap and beneath the canopy of scarp forest and angiosperm-dominated Afromontane forest. The gap in scarp forest was created artificially by felling eight mid-canopy tree species.

straight. Consequently, there is heavy harvesting pressure on juvenile plants, which presumably accounts for the paucity of medium-sized trees. Kyle (personal communication) reports that fruiting trees produce abundant fruit and that the high number of seedlings noted in the forest reflects good germination.

Were it not for the intense harvesting pressure on juvenile stages, we suggest that *A. falcatus* would show continuous regeneration in coastal forests. Their establishment beneath the canopy and the straight nature of poles is consistent with shade tolerance for this conifer. It is not clear whether the persistence of *A. falcatus* in subtropical lowland forest is directly associated with its ability to establish in shade or whether there is an interactive effect with soil nutrient status. Coastal forests are dominated by light-demanding angiosperms, with few species showing successful establishment beneath the shaded closed canopy and pervasive shrub layer (Griffiths et al., 2007). The understory herbaceous shrub *Isoglossa woodii* influences forest dynamics by suppressing tree recruitment in dune forest (Griffiths et al., 2007; Tsvuura et al., 2007). The proposition that *A. falcatus* persists in subtropical lowland forest through shade tolerance mirrors our finding for *P. latifolius* in Afromontane forest. However, some

podocarp species are able to persist in lowland tropical forest where soil conditions are poor (Coomes and Bellingham, this volume). Soils in the Kosi Bay system are sandy and infertile (Maud, 1980) and may favor *A. falcatus* over competing angiosperms given the superior ability of conifers to acquire and retain nutrients (Coomes and Bellingham, this volume).

The persistence of *A. falcatus* in coastal lowland habitats is an enigma. Several aspects of the biology of this species would seem to conspire against long-term success. First, regeneration failure is not uncommon among mast-fruited species (Blundell and Peart, 2004), and logging has been shown to reduce the extent and intensity of mast-fruited events, resulting in regeneration failure (Curran et al., 1999). Second, the threat of extinction among dioecious plants, particularly woody species, is high (Vamosi and Vamosi, 2005). Reduced mate assurance leads to pollination failure (Pannell and Barrett, 1998), or reduced seed production limits the effective size of the breeding population (Heilbut et al., 2001). Third, recruitment rates are generally low because of delayed germination and high postdispersal damage by mammals (Geldenhuys, 1993) and loss of seed viability (Negash, 2003). Finally, sustained harvesting of *A. falcatus* poles has a significant

impact on regeneration success (Tesfaye et al., 2002; Lawes et al., 2007b). The ability to regenerate in shaded environments, compared with an angiosperm component dominated almost entirely by light-demanding species, explains this species' persistence in lowland coastal forest.

CYCLICAL REGENERATION AND PODOCARP PERSISTENCE

The TSRM promotes a deterministic successional process that relies on catastrophic disturbance to initiate the sequence (Ogden, 1985; Ogden and Stewart, 1995). However, catastrophic disturbance is not always necessary to explain forest structure and the persistence of podocarps (Six Dijkstra et al., 1985; Lusk and Ogden, 1992). Podocarps are able to maintain their dominance, or coexistence with angiosperms, through cyclical regeneration driven principally by endogenous disturbance and the differential response of trees at the juvenile stage to canopy opening (Lusk and Smith, 1998). At the landscape scale, tree species coexistence is mediated through temporal (progressive overstory collapse) and spatial (microsite, degree of canopy closure) segregation (Ogden and Stewart, 1995). The duration of the proposed regeneration cycle may last 650–700 years (Beveridge, 1973; Six Dijkstra et al., 1985). In South African Afromontane forests, it is not clear what follows the old-growth *Podocarpus*-dominated phase since not only is this type of forest rare, but these old-growth forests appear to be relatively young. Trees exceeding 600 years in age are routinely recorded from southern temperate forests in New Zealand and Chile (e.g., Lusk and Ogden, 1992; Lusk, 1996; Smale et al., 1997), yet we dated the largest *P. latifolius* to a little over half that age (Adie and Lawes, 2009b).

Several lines of evidence lead to a model that proposes the persistence of old-growth *Podocarpus* forest in the absence of stand-destroying disturbance in South Africa. First, grass suppresses the establishment of *P. latifolius*, restricting regeneration to occasional episodes that may be associated with higher than usual rainfall (Adie and Lawes, 2009a). This finding, combined with the continuous regeneration of *P. latifolius* during the angiosperm phase, results in a multi-aged *P. latifolius* canopy at the old-growth phase, which eliminates synchronous canopy senescence and the associated progressive overstory collapse (Adie and Lawes, 2009b). Second, angiosperm canopy trees in Afromontane forests are relatively shade intolerant, resulting in very limited angiosperm regeneration in

old-growth forest. Finally, gap creation, frequently caused by multiple tree falls, provides angiosperms with a limited opportunity of reaching the canopy in old-growth forest.

SUMMARY

Members of the Podocarpaceae, especially *P. latifolius*, are exceptionally successful in South African inland forests. The genus was decimated by colonial logging, and its present abundance in forest throughout its range is largely a consequence of that disturbance. Given adequate time, and in the absence of further catastrophic disturbance, *Podocarpus* will dominate the angiosperm flora. *Podocarpus* dominance is attributed to its longevity (Lawes et al., 2006) and ability to regenerate in shade, where all potential competing angiosperms are less capable of doing so (Adie and Lawes, 2009b).

To explain the geographical distribution of podocarps in South Africa, Midgley et al. (1995a) proposed that competitively superior angiosperms limit conifers in the more productive tropical environments. Indirectly, this claim holds in that deeply shaded habitat, resulting from higher angiosperm productivity, suppresses growth of *P. latifolius* seedlings. However, we found no evidence for direct competitive interaction between angiosperms and podocarps at the regeneration phase, with angiosperms appearing to be equally suppressed by the shaded conditions. We contend that the response by *P. latifolius* to light is the dominant and ultimate factor explaining the relatively poor performance of the conifer in scarp forest. Thus, the persistence of *P. latifolius* in this productive subtropical forest type is driven by disturbance that creates elevated light levels. Canopy gaps, however, do not facilitate *P. latifolius* regeneration in coastal scarp forests (e.g., Ongoye) because gaps are rapidly colonized by fast-growing vines (e.g., *Flagellaria guineensis*) that suppress canopy tree regeneration. Catastrophic disturbance, linked with the general longevity of podocarps, may offer one mechanism driving persistence.

We have no reason to suggest that African podocarps behave differently from other members of the Podocarpaceae. Rather, the prevalence of a generalist life history among competing angiosperms is important, and it is within this context that African podocarp ecology needs to be evaluated. African podocarps and their associated angiosperm flora have been shaped by Pleistocene climatic fluctuations. During the relatively benign interglacials that favored angiosperms, podocarps persisted by retreating to

their ancestral temperate zone refuges in montane regions. The intervening cold glacial periods drove podocarp expansion into lowland habitats, where they were able to compete successfully with angiosperms. African podocarps are thus temperate forest relicts and are not lowland rainforest survivors. The regression of Afrotemperate forest is likely to have placed floras under increasing risk of extinction by processes associated with fragmentation and those operating in the grassland matrix causing widespread species filtering that left a temperate angiosperm flora bereft of shade-tolerant species (Adie and Lawes, 2009b). *Podocarpus latifolius* is capable of establishing in relatively high light conditions and does not suffer the same constraints that place shade-tolerant species at risk of extinction in a fragmented landscape. The resulting relative difference in shade tolerance between conifers and angiosperms is an important determinant of forest structure and dynamics in Africa.

FUTURE RESEARCH DIRECTIONS

1. Palynological studies are needed to differentiate between *Afrocarpus* and *Podocarpus* to test the hypothesis that the present distribution of *Afrocarpus* is old (pre-Pliocene) whereas the more vagile *Podocarpus* is more recent (Pleistocene), reflecting rapid colonization followed by local extinction. *Podocarpus*, the older lineage compared with *Afrocarpus* (Biffin et al., this volume), is widespread in Africa, perhaps because of life history traits that promote dispersal, but local extinctions suggest the taxon is susceptible to climatic upheavals. It is tempting to suggest that the variable climate associated with volcanism and rifting in East Africa (Pik et al., 2008) and cooling (Kender et al., 2009) in the early to mid-Miocene led to the selection of traits that reinforced persistence but compromised dispersal ability in *Afrocarpus*. Recent research on the Maputaland coastal plain (northeastern South Africa) documents expansion and regression of podocarp forest (Mazus, 2000; Finch and Hill, 2008; Neumann et al., 2008). It is not clear whether the species represented in the pollen record is *A. falcatus*, present in lowland forest on the coastal plain, or *P. latifolius*, found in scarp forest just inland of the coast.

2. *Podocarpus latifolius* is the dominant species at altitude (inland mountains), where it dominates canopies. The mechanisms suppressing their performance in coastal scarp sites require examination, which will provide insight into why this species was unable to persist once lowland

forest extended its distribution following relaxation of glacial maxima (West Africa).

3. In spite of intensive colonial logging, *A. falcatus* has persisted and continues to be successful in forest habitats from the coastal lowlands to temperate highlands. Understanding the persistence of this species is particularly relevant in the face of severe logging pressure elsewhere in Africa (Wubet et al., 2003, 2006) and also as a window to the potential response of podocarps to climate change. Superior drought resistance (cf. Brodribb and Hill, 1998) may explain the persistence of *A. falcatus* on the coast in place of *P. latifolius*. The performance of *A. falcatus* under varying light and soil moisture and nutrient conditions requires testing, as we have done for *P. latifolius*.

4. The proposed long-term persistence of *A. falcatus* relative to *P. latifolius* may result from their contrasting reproductive biology and seed physiology. *Afrocarpus falcatus* is a dioecious masting species with a periodicity of six to seven years between reproductive events (Geldenhuys, 1993). *Podocarpus latifolius*, on the other hand, is an annual seeder, resulting in less episodic recruitment and lower vulnerability to climatic instability compared with *A. falcatus*, which may partly explain the wider and more continuous distribution of *P. latifolius*. In addition, shade-tolerant species rely on seed reserves for energy and nitrogen (Kitajima, 2002), and large energy reserves enhance establishment (Kitajima and Fenner, 2000). The high lipid content of *A. falcatus* seed (20%; Wirminghaus et al., 2002) may contribute to the success of this species in shaded environments and in competition with grasses in old-growth podocarp-dominated forests. Trials testing relative germination and establishment success with competing C₃ grasses are required to test the persistence hypothesis.

5. The recovery by *A. falcatus* and *P. latifolius* after colonial logging activities differ markedly, and understanding this relationship may offer insight into differences in their ecology and distribution. In the Drakensberg Mountains the response by *A. falcatus* was slow, resulting in a relatively low abundance and restricted distribution compared with the dominance of *P. latifolius*.

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