The ecology of the climbing fern *Dicranopteris linearis* on windward Mauna Loa, Hawaii

ANN E. RUSSELL, JAMES W. RAICH and PETER M. VITOUSEK*

Department of Botany, 353 Bessey Hall, Iowa State University, Ames, IA 50011–1020, USA; and *Department of Biological Sciences, Stanford University, Stanford, CA 94305–5020, USA

**Summary**

1 *Dicranopteris linearis* (Gleicheniaceae), a native fern common throughout the Old World tropics and Polynesia, forms dense thickets > 3 m deep over large areas of open-canopy, oligotrophic, wet Hawaiian rainforests. Our objectives were to identify leaf- and whole plant-level traits that are key to its success and to determine its community- and ecosystem-level consequences in primary successional sites.

2 Along an elevational gradient from 90 to 1660 m, mean maximum net assimilation rates of *Dicranopteris* ranged from 2.9 to 5.0 μmol m⁻² s⁻¹, compared with 3.6–9.5 μmol m⁻² s⁻¹ in the codominant tree *Metrosideros polymorpha*. Gas-exchange characteristics did not explain *Dicranopteris'* success, nor its trends in production.

3 However, indeterminate, clonal growth form, shallow rhizomes, marcescent leaves with low decomposability, and a mat-forming capacity enabled *Dicranopteris* to colonize sites and to maintain dominance via high effective leaf area, despite its low biomass. Phosphorus use efficiency, which reached 24 kg g⁻¹, was exceptionally high, allowing colonization of phosphorus-poor sites.

4 *Dicranopteris* contributed up to 74% of above-ground net primary productivity in a site where it contained only 14% of live biomass. It accounted for up to 57% and 47% of total nitrogen and phosphorus uptake by plants, respectively, where it contained only 24% and 30% of plant nitrogen and phosphorus. *Dicranopteris* leaves are short-lived and slow to decompose; thus, fixed carbon is transferred quickly to soil detrital pools where it contributes to aggrading soil organic matter pools and may exacerbate oligotrophic conditions, thereby strongly influencing soil genesis and ecosystem development.

5 The fern therefore influences forest-floor light regimes and directs later community development. An exclusion experiment demonstrated that *Dicranopteris* competed with *Metrosideros*, but lack of revegetation in 40% of the exclusion area after 39 months showed that *Dicranopteris* also colonized microenvironments unavailable to its endemic codominants. *Dicranopteris* may play an important role in resisting invasions of exotic species into Hawaiian rainforests.

**Keywords:** clonal plant, *Dicranopteris linearis*, ecosystem development, fern ecology, growth form, Hawaiian rainforests, Mauna Loa, Hawaii, nutrient use, primary succession


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**Introduction**

On windward Mauna Loa, Hawaii, ecosystem processes such as biomass accumulation, net primary productivity and nutrient cycling correlate closely with climate and substrate age (Aplet & Vitousek 1994; Raich *et al.* 1997). In other locations such processes are also controlled by the characteristics of the specific organisms present (e.g. Chapin *et al.* 1996). The floristically depauperate ecosystem of Mauna Loa offers an opportunity to evaluate the effects of individual species. *Dicranopteris linearis* (N. L. Burm.) Underw. (Gleicheniaceae), a climbing, thicket-forming fern, is especially appropriate for examining species–ecosystems relationships because it varies widely in abun-
dance along well-defined environmental gradients and contributes substantially to production and nutrient cycling (Raich et al. 1997).

_Dicranopteris linearis_ is one of the most widely distributed ferns throughout wetter parts of the Old World tropics and subtropics (Holtum 1959; Page 1979), including all of Polynesia, and is intolerant of shade, drought and frost but tolerant of poorly drained and oligotrophic soils (Holtum 1938; Page 1979; Russell 1996). As a result, the fern’s most common habitat is wet, open-canopy sites on low-fertility soil (Holtum 1959), and in the Hawaiian Islands it is especially prolific at middle elevations of windward slopes, where rainfall is maximum (Jacobi 1989). Throughout its range, this sun-demanding fern can be a pioneer species on primary successional sites such as lava flows, mountain ridges, precipices and taluses (Atkinson 1970, Holtum 1959; Scott 1969). It colonizes secondary successional sites such as landslides, road-cuts, abandoned logging decks and roads, post-agricultural sites, plantation understoreys and degraded forest lands in India, Sri Lanka, Malaysia and China (Maheswaran & Gunatilleke 1988; Brown et al. 1995; Cohen et al. 1995; A.E.R., J.W.R., personal observation). Its congenor, _D. pectinatus_, colonizes landslides in wet forests of the New World tropics (Wardlaw 1931; Guariguata 1990; Walker 1994; Walker et al. 1996).

Once established, this native fern may persist for a long time but is eventually shaded out by overtopping trees, except where fronds climb into the canopy (Holtum 1959; Kochummen 1977). In Hawaii, _Dicranopteris_ may become dominant late in primary succession if the forest canopy opens as a result of natural dieback of the entire overstorey of _Metrosideros polymorpha_ (Mueller-Dombois 1985). This species is believed to play an important role in community dynamics by suppressing tree regeneration (Gerrish & Mueller-Dombois 1980; Cohen et al. 1995), and it is credited with preventing erosion on steep slopes where few other native species can become established (Kepler 1983). This fern accumulated organic matter and conserved nutrients in deforested areas of Sri Lanka (Maheswaran & Gunatilleke 1988, 1990).

_Dicranopteris_ can form dense, extensive thickets > 3 m deep, dominating large areas of wet and mesic Hawaiian rainforests. However, relatively little is known about the mechanisms that contribute to its ability to dominate a site, or its influence on ecosystem processes such as organic matter dynamics and nutrient cycling. Our objectives were to identify those leaf- and whole plant-level traits that control this species’ success, and to determine the community- and ecosystem-level consequences of these traits.

**Materials and methods**

To assess which traits of _Dicranopteris_ were likely to contribute to its success, we evaluated traits with the potential to regulate carbon and nutrient acquisition, focusing on physiological and morphological attributes and comparing _Dicranopteris_ with its codominants. To characterize the functional importance of _Dicranopteris_, we evaluated its dominance in terms of leaf area index, biomass and net primary production, and nutrient pools and cycling, relative to its codominants in a range of Hawaiian rainforests. To examine the effect of _Dicranopteris_ on community-level processes such as regeneration and competition, we conducted a manipulative experiment in which we excluded _Dicranopteris_ from experimental plots for 3.25 years.

_Dicranopteris_ is clonal; individuals expand horizontally by means of shallowly rooted, dichotomously branching, indeterminate rhizomes (Fig. 1a). The fronds, technically all leaf tissue, are also indeterminate in growth. The basic morphological unit of growth and our level of accounting for growth studies is the leaf segment, defined as all products of determinate growth of a single fiddlehead (Fig. 1b). The rachis grows by expansion of the tip (fiddlehead) to form a new leaf segment. Under favourable environmental conditions, the main rachis branches dichotomously and the lateral fiddleheads thus formed continue to branch dichotomously while the fiddlehead atop the main rachis rests. If this dormant fiddlehead becomes active, it produces the next leaf segment of the main rachis together with its lateral branches. This sequence of growth is repeated, enabling _Dicranopteris_ to propagate above-ground both horizontally and vertically. The over-ground portion can attain a height of > 10 m if supported by a tree, but otherwise develops into self-supported thickets that may attain heights of > 3 m. The leaf rachis functions as, and in this study is referred to as, a ‘stem’, while the blade portion is referred to as the ‘leaf’ (Fig. 1). _Dicranopteris_ leaves are marescent, i.e. no abscission occurs as they senesce (Fig. 1a).

**STUDY SITES**

In 1990 we established permanent 50 m × 100 m plots in six sites (described by Raich et al. 1997) at four elevations on the island of Hawaii centred at 19°20’N, 155°40’W, along windward (east) flanks of Mauna Loa Volcano. One site at each of four elevations, 290, 700, 1130 and 1660 m, was situated on a young (110- or 136-year-old) lava flow. At 700 and 1660 m, a second site was established on an adjacent 3400-year-old lava flow. Two additional young sites at 90 m (110-year-old lava flow) and 1500 m (136-year-old lava flow) were used to measure gas-exchange characteristics across a broader elevational range. The old site at 700 m had undergone overstorey dieback at least once, as evidenced by the open canopy, standing dead trees and fallen logs. On all sites, primary succession has proceeded without major disruption due
to landslides, fire, or human or feral pig (Sus scrofa) activities.

Lava chemistry differs little within and among flows on these sites (Wright 1971; Wright & Helz 1987). The basaltic pahoehoe substrate is characterized by a ropy-textured morphology. Soils are lithic tropofolists (Sato et al. 1973), mucky, peaty soils that have gravimetric water contents often exceeding 500%. Soil pH ranges from 4.7 to 5.1. Mean soil depths range from <1 to 8 cm on young flows and from 15 to 22 cm on the old flow (Raich et al. 1997). During periods of high rainfall, standing water can exist at these sites. Mean rainfall ranges from 2500 to 6000 mm year\(^{-1}\) along the elevational gradient, with a maximum at 700 m that corresponds with maximum attenuation of solar radiation. Mean annual temperature ranges from 23.6 to 13.1°C along the elevational gradient from 10 m to 1640 m on Mauna Loa (Juvin & Nullet 1994).

Each of our 0.5-ha sites contained only 20–35 vascular plant species. Angiosperm nomenclature follows Wagner et al. (1990). All overstoreys were dominated by a single tree species, M. polymorpha (Myrtaceae), but on old sites Acacia koa (Fabaceae), a nitrogen-fixing tree, was also present. Dicranopteris was a dominant understory plant at all sites except on the young flow at 1660 m.

LEAF-LEVEL MEASUREMENTS

We measured maximum net assimilation rates (\(P_{\text{max}}\)), stomatal conductance to water vapour, transpiration and water-use efficiency of photosynthesis (WUE) using an LI-6200 Portable Photosynthesis System (LI-COR 1987). Dicranopteris was sampled most intensively at 290, 700, 1130 and 1500 m on young flows where, at each site, a total of 49–56 leaves was sampled between 09:30 and 13:00 each day over 3 days in summer (July 1994) and 6 days in winter (December and January 1994–95). Measurements over the remaining sites were taken in winter 1994–95 when a
minimum of 10 leaves was sampled per species and site. At that time we also measured gas exchange of
*M. polymorpha* and the tree ferns *Cibotium glaucum* (Sm.) Hook. & Arnott and *Sadleria cyathoides* Kaulf. All leaves were newly fully expanded.

Each measured leaf was harvested, its area measured using a ΔT Area Meter (Delta Devices, Ltd, Cambridge, UK), and leaf mass per area (LMA) measured after drying at 70°C. Foliar N concentrations were determined from biomass harvests (described below) in the six main sites and from foliar sampling in two additional sites. We determined stomatal density on five leaves per site, with 10 randomly located observations per leaf, using the method described by Hilt & Randall (1984). All counts were made on newly fully expanded leaves, in an intravelen, mid-leaf location. We determined leaf area index (LAI) for both live and dead (but still attached) leaves of *Dicranopteris* by measuring the leaf area of leaves harvested from a known area of land. LAI was calculated as the product of specific leaf area (m² leaves g⁻¹) and leaf mass (g m⁻² ground).

All other dry weights of plant tissues were based on drying at 105°C, but nutrient analyses were conducted on separate subsamples oven-dried at 70°C and finely ground. For all studies except the exclusion experiment, total N and P concentrations were measured as described by Vitousek et al. (1988), with a mercuric oxide catalyst on a block digestor (Technicon Instrument Systems 1976). For the exclusion experiment, samples were analysed for N using an NA 1500 N/C/S Elemental Analyser (Carlo Erba Strumatazione, Milano, Italy). For P, samples were ashed at 500°C and digested in aqua regia; extracts were then analysed colorimetrically using an automated ion analyser (QuickChem 4100, Lachat Instruments Division, Zellweger Analytics, Inc., Milwaukee, Wisconsin).

Nutrient resorption after senescing leaves reduces dependence of the plant on soil nutrient supplies by recycling nutrients internally (Clark 1977; Turner 1977; Jonasson & Chapin 1985). We sampled mature (green) and newly senesced leaves in all six sites and calculated resorption as the difference between concentrations in mature and newly senesced leaves, divided by the concentration in mature leaves. We assumed that leaching losses were minimal and could be ignored because these leaf tissues were extremely low in N and P concentrations (cf. Tukey 1970; Chapin & Kedrowski 1983).

We monitored births and deaths of all *Dicranopteris* leaf segments for 13 months in the six main study sites. We randomly selected and framed with PVC pipes 10 1 m x 1 m quadrats per plot, as described by Raich et al. (1997). At the young site at 1660 m, clones were so small that the entire population was monitored. Each month, each new cohort of leaf segments was tallied and tagged at the fiddlehead stage with wires colour-coded for the cohort’s birth month.

We used cohort life-table analysis (Keyfitz 1968; Seber 1982) to determine leaf-segment life expectancy, limiting analyses to the three oldest cohorts. Three developmental stages were identified: (i) initial leaf expansion, 0–100 days; (ii) leaf maturation, 101–300 days; and (iii) leaf senescence, 301–400 days. A separate mean mortality rate, qₙₒₒₒ (Seber 1982), was calculated for each stage at each site. Mean mortality rates over the youngest age interval were based on eight cohorts per site, for the intermediate interval on three cohorts and on the two oldest cohorts for the final interval.

**NUTRIENT POOLS, NET PRIMARY PRODUCTIVITY AND NUTRIENT UPTAKE**

Biomass and nutrient pools were measured in three to four randomly selected locations per site. All above-ground vegetation was removed from a 1 m x 3 m quadrat and sorted by species and plant part (leaves, stems and large branch), by status as live or dead, and weighed and subsampled as described by Raich et al. (1997). For *Dicranopteris*, total (live and dead) rhizome mass was measured. We assumed that the ratio of live:dead rhizomes within a site equalled that in stems. Fine roots were not measured.

We measured all above-ground tissue produced by *Dicranopteris* over a 13-month period. Herbivory losses were minimal in this species. Above-ground net primary productivity (ANPP) of *Dicranopteris* was measured in the same 1-m³ quadrats using the same plants and set-up as described above for the leaf demography study. Tagged leaf segments that died over the study period were harvested and weighed. At the end of 13 months, all tagged leaf segments were harvested, separated by status (live or dead), birth date and plant part, and subsampled for dry weight and nutrients. *Dicranopteris* leaf segments continue to increase in mass for several months after birth. This biomass increment could not be measured directly, but was estimated under the assumption that the number of unexpanded leaves present at the initiation of measurements equaled the number present at the end of the study (Russell 1996).

Nutrient uptake was defined in this study as the pool of nutrients taken up in new growth, minus nutrients resorbed from senescing leaves. Nutrient losses due to leaching were not measured, but probably did not exceed 5–10% of annual N and P flux as reported elsewhere (Cole & Rapp 1981; Van Cleve & Alexander 1981). Nutrient uptake was calculated as the product of tissue nutrient concentrations (at the end of resorption) and organic matter production (ANPP). Nutrient concentrations for live stems from the biomass study were used to calculate uptake by that plant component. Nutrient use efficiency was defined as the amount of biomass produced per unit nutrient taken up from the environment.
EFFECTS OF EXCLUDING DICRANOPTERIS

To investigate *Dicranopteris*’ effects on other plant species, we excluded the fern from plots within the 50 m x 100 m permanent plot on the young site at 290 m. We used a stratified design in which we categorized six plots, 10 m x 10 m in size, according to three levels of overstorey tree density: low, medium and high. We randomly assigned which plots received the fern exclusion treatment. In June–July 1992, the fern was cut and left to decompose in three exclusion plots that were surrounded by undisturbed vegetation. In three control plots, the fern was left undisturbed. We created little disturbance to the remaining understorey and soil during cutting. *Dicranopteris* contained only 1.9 g N m−2 and 0.12 g P m−2 so nutrient inputs to the soil from cut fronds were minimal. We cut through the shallow (generally < 5 cm) soil to bedrock around the perimeters of the plots, severing only fern rhizomes, as *Metrosideros* was deeply rooted in cracks. Only minimal weeding was required once a year thereafter to prevent *Dicranopteris* cover from exceeding 2%.

We measured *Metrosideros* growth directly in the exclusion and control plots, measuring height and circumference of each tree at intervals of 12–15 month for 39 months. Circumferences were measured to the nearest 1.0 mm with a metal tape at exact locations marked by paint on the bole. We estimated total tree, leaf, branch and bole biomass using site-specific regression equations of Raich et al. (1997). Relative growth rate (RGR) was calculated as net growth per year divided by total mass, on a plot basis. In all plots > 20 leaves were sampled annually for *Metrosideros, Palhinhaea cernua* (L.) Franco & Carv. Vasc., *Machaerina angustifolia*, *Arundina graminifolia* and *Melastrum candidum*. We established a single 10 m x 1 m subplot centred and orientated diagonally (with randomly selected direction) within each plot in June 1994 to monitor seedling demographics. All seedlings > 0.5 cm tall were mapped, identified and tagged with wires; heights were measured in July 1994 and September 1995.

We measured soil temperature at 2 cm depth in all plots on two sunny days, one each in June and July 1994, at 0.5-m intervals along a single 10-m long, randomly selected transect per plot. In September 1995, we collected all soil to bedrock in five randomly selected 10 cm x 10 cm squares in each plot. Samples were dried at 70°C, sieved through a 2.00-mm mesh and hand-sorted to remove plant litter, roots and lava rocks. Remaining soil was ground with mortar and pestle to pass through a 0.25-mm mesh and then analysed for C and N using the Carlo-Erba Analyser. We estimated percentage plant cover once at the end of the experiment (after 39 months) at 20 cm intervals along three randomly selected 10 m long transects per plot, by suspending a pole vertically and recording all species that touched the pole at heights from 0 to 2 m above-ground at each sample point (total n = 150 plot−1). Total cover per plot could exceed 100%.

Results

LEAF PHYSIOLOGY AND MORPHOLOGY

Rates of maximum net assimilation ($P_{\text{max}}$) and transpiration in *Dicranopteris* decreased with increasing elevation in winter ($r^2 = 0.84$ and 0.71, $P = 0.01$ and 0.04, respectively) but not in summer (Table 1). In general, however, summertime $P_{\text{max}}$ was higher at elevations < 1130 m. Neither $P_{\text{max}}$ nor transpiration were significantly different in young compared to old sites. Transpiration, $P_{\text{max}}$ and stomatal conductance on young sites were all higher in summer than in winter (Mann–Whitney, $P \leq 0.05$ in all tests) (Table 1).

Mean (± SE) wintertime $P_{\text{max}}$ in *Dicranopteris* ranged from 1.8 ± 0.2 to 5.0 ± 1.2 μmol m$^{-2}$ s$^{-1}$ along the young-flow elevational gradient (Table 1), whereas rates of codominants were 3.6 ± 0.6–9.5 ± 0.4 μmol m$^{-2}$ s$^{-1}$ for *Metrosideros*, 2.2 ± 0.7–5.6 ± 0.6 μmol m$^{-2}$ s$^{-1}$ in *Cibotium glaucum* and 6.6 ± 0.6–7.5 ± 0.7 in μmol m$^{-2}$ s$^{-1}$ in *Saideria cya-ntheoides*. Mean (± SE) WUE (in units of mmol CO$_2$ mol$^{-1}$ H$_2$O) in *Dicranopteris* was 1.5 ± 0.1–2.4 ± 0.1, while WUE was 1.5 ± 0.1–2.7 ± 0.3 in *Metrosideros*, 1.6 ± 0.7–2.8 ± 0.4 in *Cibotium* and 1.7 ± 0.2–2.2 ± 0.2 in *Saideria*. Additional comparisons with other species at individual sites yielded similar results (Russell 1996). Thus, $P_{\text{max}}$ and WUE in *Dicranopteris* were similar to those of the remaining species sampled on Mauna Loa, and to scioiphytes in general (Larcher 1995). In general, the amplitude of physiological responses by *Dicranopteris* over environmental gradients was low compared to other species on Mauna Loa.

LMA increased with elevation on young sites ($r^2 = 0.90$, $P = 0.004$ for summer leaves) (Table 1), as in the codominant species *M. polymorpha* (Vitousek et al. 1992; Joel et al. 1994). In *Dicranopteris*, foliar concentrations of N decreased with elevation ($r^2 = 0.72$, $P = 0.02$) and thus LMA and foliar N concentrations were negatively correlated ($r^2 = 0.75$, $P = 0.02$). As a result, on young flows, N mass on an areal basis did not vary significantly with elevation, a condition that is typical of montane plants in general (Körner 1989) and of *Metrosideros* as well (Vitousek et al. 1992). The relative similarity in N mass per leaf area in *Dicranopteris* may contribute to the lack of difference in $P_{\text{max}}$ along the elevational gradient (Mooney et al. 1978; Medina 1984; Field & Mooney 1986). Stomatal density in *Dicranopteris* was consistently high (286–386 per mm$^2$) among all sites (Table 1). *Dicranopteris* adjusted its leaf morphology and rate of carbon gain in a standard fashion.
Table 1. Leaf and gas exchange characteristics in *Didranopteris linearis* on Mauna Loa, Hawaii. Air temperature measurements were taken with daytime gas exchange measurements. Methods and sites are described in the text. Winter (December-January) and summer (July) measurements are denoted by W and S, respectively.

<table>
<thead>
<tr>
<th>Site (flow age/elevation (m))</th>
<th>Season</th>
<th>Air temperature (°C)</th>
<th>LMA (g m⁻²)</th>
<th>Foliar N (g m⁻³ of leaf)</th>
<th>Stomatal density (n m⁻²)</th>
<th>Transpiration (mmol H₂O m⁻² s⁻¹)</th>
<th>Stomatal conductance for H₂O (cm s⁻¹)</th>
<th>Maximum net assimilation rate (Pₙₐ₅, μmol m⁻² s⁻¹)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Young/90</td>
<td>W</td>
<td>30.1 ± 0.2</td>
<td>87 ± 3</td>
<td>0.84</td>
<td>323 ± 20</td>
<td>3.4 ± 0.3</td>
<td>0.331 ± 0.028</td>
<td>4.66 ± 0.24</td>
</tr>
<tr>
<td>Young/270</td>
<td>W</td>
<td>27.5 ± 0.3</td>
<td>99 ± 4</td>
<td>0.84</td>
<td>332 ± 14</td>
<td>2.2 ± 0.1</td>
<td>0.313 ± 0.017</td>
<td>4.97 ± 0.19</td>
</tr>
<tr>
<td>S</td>
<td></td>
<td>32.0 ± 0.3</td>
<td>95 ± 2</td>
<td>0.76</td>
<td>47 ± 0.2</td>
<td>4.7 ± 0.2</td>
<td>0.637 ± 0.046</td>
<td>7.30 ± 0.40</td>
</tr>
<tr>
<td>Young/700</td>
<td>W</td>
<td>25.6 ± 0.2</td>
<td>128 ± 4</td>
<td>0.86</td>
<td>386 ± 11</td>
<td>2.2 ± 0.1</td>
<td>0.270 ± 0.014</td>
<td>4.58 ± 0.25</td>
</tr>
<tr>
<td>S</td>
<td></td>
<td>27.6 ± 0.3</td>
<td>122 ± 4</td>
<td>0.86</td>
<td>3.0 ± 0.1</td>
<td>0.790 ± 0.068</td>
<td>9.70 ± 0.25</td>
<td></td>
</tr>
<tr>
<td>Young/1130</td>
<td>W</td>
<td>25.3 ± 0.2</td>
<td>162 ± 3</td>
<td>0.86</td>
<td>382 ± 5</td>
<td>1.8 ± 0.1</td>
<td>0.219 ± 0.016</td>
<td>2.90 ± 0.19</td>
</tr>
<tr>
<td>S</td>
<td></td>
<td>29.9 ± 0.6</td>
<td>131 ± 4</td>
<td>0.79</td>
<td>3.4 ± 0.2</td>
<td>0.458 ± 0.041</td>
<td>6.00 ± 0.40</td>
<td></td>
</tr>
<tr>
<td>Young/1500</td>
<td>W</td>
<td>24.6 ± 0.2</td>
<td>143 ± 3</td>
<td>0.90</td>
<td>351 ± 10</td>
<td>1.7 ± 0.1</td>
<td>0.289 ± 0.019</td>
<td>3.23 ± 0.24</td>
</tr>
<tr>
<td>S</td>
<td></td>
<td>29.8 ± 0.7</td>
<td>139 ± 4</td>
<td>0.90</td>
<td>4.8 ± 0.3</td>
<td>0.563 ± 0.049</td>
<td>6.10 ± 0.30</td>
<td></td>
</tr>
<tr>
<td>Young/1660</td>
<td>W</td>
<td>25.7 ± 0.1</td>
<td>171 ± 5</td>
<td>0.96</td>
<td>345 ± 23</td>
<td>1.8 ± 0.2</td>
<td>0.141 ± 0.017</td>
<td>1.84 ± 0.22</td>
</tr>
<tr>
<td>Old/700</td>
<td>W</td>
<td>26.3 ± 0.1</td>
<td>109 ± 6</td>
<td>1.03</td>
<td>268 ± 6</td>
<td>2.1 ± 0.1</td>
<td>0.271 ± 0.023</td>
<td>3.65 ± 0.26</td>
</tr>
<tr>
<td>Old/1660</td>
<td>W</td>
<td>25.0 ± 0.2</td>
<td>123 ± 2</td>
<td>0.71</td>
<td>320 ± 10</td>
<td>1.4 ± 0.1</td>
<td>0.141 ± 0.015</td>
<td>2.32 ± 1.00</td>
</tr>
</tbody>
</table>

**NUTRIENT RESORPTION, LEAF PHENOLOGY AND DEMOGRAPHY**

Nitrogen resorption varied relatively little among sites, ranging from 43% at the young site at 1660 m to 59% on the old site at 700 m. However, P resorption varied widely, ranging from 49% at the old site at 1660 m to 82% at the young site at 1130 m. Nitrogen resorption values were similar to other species on Mauna Loa (Russell 1996) and elsewhere (Chapin & Kedrowski 1983). However, the higher P resorption observed was among the highest reported values (Chapin & Kedrowski 1983; Killingbeck 1996).

Birth rate of fiddleheads varied considerably among sites; the maximum number of fiddleheads produced on the young sites ranged from < 0.001 to 45 m⁻² month⁻¹ at 1660 m and 290 m, respectively. On old sites, maximum rates were 86 and 36 m⁻² month⁻¹ at 700 and 1660 m, respectively. Within a site, *Didranopteris* maintained a relatively constant production of leaf segments year-round. Leaf-blade phenology was remarkably variable across the range of sites. Three months after blade expansion, sorus development began. Sori matured by 4 months and released spores for the next 3–4 months, after which sori became deciduous. Spore production occurred year-round. All leaf blades died within 11 months at all sites. The survivorship curves of leaf segments were similar among sites, with mortality rates increasing with leaf-segment age (Fig. 2 and Table 2). Leaf-segment life expectancy ranged from 299 to 328 days among young sites and, in general, did not differ significantly among sites nor among cohorts (Table 2).

Leaf-segment mortality rates were higher on the old site at 700 m during the maturation stage (Kruskal-Wallis, *P* = 0.05) (Fig. 2), with a mean life expectancy of 248 days at the 700-m old flow compared with 327 days at the adjacent young site (Friedman’s and multiple comparison tests, *P* = 0.05). Segments comprising the indeterminate, bladeless main rachis were the oldest surviving leaf segments, whereas lateral branches were relatively short lived (Fig. 1). Thus higher mortality rates on the old flow were the result of a greater proportional allocation to lateral branches, which were leafy. Mortality rates were also high at the young site at 1660 m, where plants were severely stressed by drought and cold.

**LEAF AREA, BIOMASS AND NUTRIENT POOLS**

LAI of live *Didranopteris* leaves was roughly similar to that of *Metrosideros* on the three lowermost young
Table 2 Mean (+ SE) mortality rates (fractions of survivors dying per month) over three life stages and life expectancies (days) of Dicranopteris linearis on windward Mauna Loa, Hawaii. Life stages are defined in the text.

<table>
<thead>
<tr>
<th>Site (age/elevation (m))</th>
<th>Mortality rates (by life stage)</th>
<th>Life expectancy</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Expansion</td>
<td>Maturation</td>
</tr>
<tr>
<td>Young/290</td>
<td>0.012 ± 0.003</td>
<td>0.066 ± 0.011</td>
</tr>
<tr>
<td>Young/700</td>
<td>0.012 ± 0.002</td>
<td>0.050 ± 0.014</td>
</tr>
<tr>
<td>Young/1130</td>
<td>0.015 ± 0.004</td>
<td>0.032 ± 0.004</td>
</tr>
<tr>
<td>Young/1660</td>
<td>0.014 ± 0.005</td>
<td>0.021 ± 0.033</td>
</tr>
<tr>
<td>Old/700</td>
<td>0.033 ± 0.005</td>
<td>0.114 ± 0.006</td>
</tr>
<tr>
<td>Old/1660</td>
<td>0.033 ± 0.006</td>
<td>0.063 ± 0.025</td>
</tr>
</tbody>
</table>

Dicranopteris LAI greatly exceeded that of Metrodora on the old site at 700 m. Maximum combined live and dead (marcescent) LAI of Dicranopteris exceeded 16 in one study quadrat on the old site at 700 m.

Total above-ground biomass of Dicranopteris on the young sites varied with elevation (Table 3). Live leaf mass was lower at the 1660-m site than at the three lower elevation sites (Kruskal–Wallis, $P = 0.05$). Biomass of all plants parts increased from young to old sites (Mann–Whitney, $P < 0.05$ in all tests). At 700 m, live above-ground mass increased 11-fold over 3400 years of succession, reaching 1022 g m$^{-2}$; at 1660 m, it increased from < 0.001 to 441 g m$^{-2}$.

The proportion of biomass in leaf blades, stems and rhizomes varied as a function of biomass (Fig. 4). A greater proportion of biomass was contained in leaves at intermediate-biomass sites (the young sites at 700 and 1130 m), whereas more mass was represented in stems, i.e. structure, at the lowest and highest biomass sites (Kruskal–Wallis, $P = 0.05$). Rhizomes contained 15–25% of the biomass in all sites. Proportional biomass distribution in Dicranopteris is consistent with Tilman’s (1988) pattern for a competitively superior morph, in that maximum proportion of biomass in leaves occurred at sites intermediate in biomass.

On the old flow, foliar N concentrations were lower at 1660 m than at 700 m (Mann–Whitney, $P = 0.02$) (Table 3). Foliar P concentrations were higher on the old compared to the young site at 700 m (Mann–Whitney, $P = 0.05$), but not at 1660 m; there was no discernible elevational trend in foliar P concentrations on the young flows. Above-ground masses of N and P contained in Dicranopteris were very low in these ecosystems, but varied with elevation and increased with substrate age (Table 3).


ANPP of Dicranopteris decreased from 291 to 0.032 g m$^{-2}$ year$^{-1}$ with increasing elevation along the young-flow elevation gradient ($r^2 = 0.89$, $P = 0.06$). Similarly, ANPP decreased from 658 to 263 g m$^{-2}$ year$^{-1}$ as elevation increased from 700 to 1660 m on the old flow (Table 4). At both elevations, ANPP was greater on old than on young sites (Mann–Whitney, $P < 0.0001$). As ANPP increased, above-ground production was increasingly allocated to stems and especially to side branches. Presumably this increasing allocation to structure facilitated carbon gain by reducing the self-shading that inevitably occurs with increasing plant size.

Nitrogen uptake by Dicranopteris was very low, ranging from 0.0001 to 0.826 g m$^{-2}$ year$^{-1}$ on young sites and from 1.173 to 2.353 g m$^{-2}$ year$^{-1}$ on old sites (Table 4). Phosphorus uptake was 0–0.040 g m$^{-2}$ year$^{-1}$ on young sites and 0.064–0.116 g m$^{-2}$ year$^{-1}$ on old sites. Uptake of N and P declined with increasing elevation on young sites, as did ANPP. Uptake of both N and P was greater on old compared to young sites. Uptake decreased with increasing leaf-segment life span ($r^2 = 0.77$ and 0.81, $P = 0.02$ and 0.01 for N


![Fig. 3 Leaf area index for live and dead Dicranopteris linearis and live Metrodora polymorpha leaves on the six main study sites on Mauna Loa, Hawaii.](image)
Table 3 Organic matter and nutrient pools of *Dicranopteris linearis* from six study sites on Mauna Loa, Hawaii. Nutrient concentrations of live leaves were representative composites of all stages of maturation and senescence. Values are means ± 1 SE of two to four samples. ND, no data

<table>
<thead>
<tr>
<th></th>
<th>Site 1</th>
<th>Site 2</th>
<th>Site 3</th>
<th>Site 4</th>
<th>Site 5</th>
<th>Site 6</th>
</tr>
</thead>
<tbody>
<tr>
<td>Site age (year)</td>
<td>110</td>
<td>136</td>
<td>136</td>
<td>136</td>
<td>3400</td>
<td>3400</td>
</tr>
<tr>
<td>Elevation (m)</td>
<td>290</td>
<td>700</td>
<td>1130</td>
<td>1660</td>
<td>700</td>
<td>1660</td>
</tr>
</tbody>
</table>

**Live leaves**

<p>| | | | | | | |</p>
<table>
<thead>
<tr>
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</tr>
</thead>
<tbody>
<tr>
<td>Biomass (g m⁻²)</td>
<td>208 ± 47</td>
<td>63 ± 13</td>
<td>106 ± 30</td>
<td>0.014</td>
<td>361 ± 80</td>
<td>206 ± 32</td>
</tr>
<tr>
<td>N concentration (%)</td>
<td>0.765 ± 0.064</td>
<td>0.703 ± 0.041</td>
<td>0.601 ± 0.006</td>
<td>0.561 ± 0.076</td>
<td>0.941 ± 0.068</td>
<td>0.578 ± 0.048</td>
</tr>
<tr>
<td>P concentration (%)</td>
<td>0.047 ± 0.002</td>
<td>0.028 ± 0.003</td>
<td>0.027 ± 0.001</td>
<td>0.041 ± 0.003</td>
<td>0.046 ± 0.003</td>
<td>0.037 ± 0.004</td>
</tr>
</tbody>
</table>

**Live stems**

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<thead>
<tr>
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</tr>
</thead>
<tbody>
<tr>
<td>Biomass (g m⁻²)</td>
<td>222 ± 20</td>
<td>26 ± 4</td>
<td>58 ± 23</td>
<td>0.029</td>
<td>661 ± 99</td>
<td>235 ± 58</td>
</tr>
<tr>
<td>N concentration (%)</td>
<td>0.168 ± 0.009</td>
<td>0.158 ± 0.013</td>
<td>0.157 ± 0.006</td>
<td>ND</td>
<td>0.191 ± 0.005</td>
<td>0.198 ± 0.053</td>
</tr>
<tr>
<td>P concentration (%)</td>
<td>0.013 ± 0.004</td>
<td>0.010 ± 0.003</td>
<td>0.006 ± 0.002</td>
<td>ND</td>
<td>0.014 ± 0.002</td>
<td>0.017 ± 0.003</td>
</tr>
</tbody>
</table>

**Dead leaves**

<p>| | | | | | | |</p>
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<thead>
<tr>
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</tr>
</thead>
<tbody>
<tr>
<td>Biomass (g m⁻²)</td>
<td>220 ± 43</td>
<td>56 ± 15</td>
<td>209 ± 72</td>
<td>0.068</td>
<td>441 ± 168</td>
<td>246 ± 49</td>
</tr>
<tr>
<td>N concentration (%)</td>
<td>0.504 ± 0.045</td>
<td>0.391 ± 0.049</td>
<td>0.398 ± 0.038</td>
<td>ND</td>
<td>0.675 ± 0.057</td>
<td>0.339 ± 0.036</td>
</tr>
<tr>
<td>P concentration (%)</td>
<td>0.020 ± 0.007</td>
<td>0.013 ± 0.002</td>
<td>0.015 ± 0.004</td>
<td>ND</td>
<td>0.027 ± 0.001</td>
<td>0.022 ± 0.002</td>
</tr>
</tbody>
</table>

**Dead stems**

<p>| | | | | | | |</p>
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<tr>
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</tr>
</thead>
<tbody>
<tr>
<td>Biomass (g m⁻²)</td>
<td>273 ± 20</td>
<td>25 ± 10</td>
<td>279 ± 168</td>
<td>0.039</td>
<td>1441 ± 201</td>
<td>541 ± 188</td>
</tr>
<tr>
<td>N concentration (%)</td>
<td>0.153 ± 0.010</td>
<td>0.145 ± 0.023</td>
<td>0.139 ± 0.037</td>
<td>ND</td>
<td>0.132 ± 0.036</td>
<td>0.188 ± 0.015</td>
</tr>
<tr>
<td>P concentration (%)</td>
<td>0.003 ± 0.001</td>
<td>0.009 ± 0.003</td>
<td>0.007 ± 0.005</td>
<td>ND</td>
<td>0.010 ± 0.003</td>
<td>0.015 ± 0.002</td>
</tr>
</tbody>
</table>

**Rhizomes (live and dead)**

<p>| | | | | | | |</p>
<table>
<thead>
<tr>
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</tr>
</thead>
<tbody>
<tr>
<td>Biomass (g m⁻²)</td>
<td>192 ± 65</td>
<td>61 ± 16</td>
<td>208 ± 99</td>
<td>0.029</td>
<td>1286 ± 234</td>
<td>165 ± 69</td>
</tr>
<tr>
<td>N concentration (%)</td>
<td>0.228 ± 0.021</td>
<td>0.278 ± 0.041</td>
<td>0.234 ± 0.033</td>
<td>ND</td>
<td>0.361 ± 0.078</td>
<td>0.285 ± 0.015</td>
</tr>
<tr>
<td>P concentration (%)</td>
<td>0.014 ± 0.005</td>
<td>0.013 ± 0.002</td>
<td>0.013 ± 0.005</td>
<td>ND</td>
<td>0.019 ± 0.004</td>
<td>0.018 ± 0.004</td>
</tr>
</tbody>
</table>

**Live above-ground mass (g m⁻²)**

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<table>
<thead>
<tr>
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<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Total biomass</td>
<td>430</td>
<td>89</td>
<td>164</td>
<td>0.043</td>
<td>1022</td>
<td>441</td>
</tr>
<tr>
<td>Total N</td>
<td>1.91</td>
<td>0.48</td>
<td>0.73</td>
<td>trace</td>
<td>4.55</td>
<td>1.72</td>
</tr>
<tr>
<td>Total P</td>
<td>0.12</td>
<td>0.02</td>
<td>0.03</td>
<td>trace</td>
<td>0.26</td>
<td>0.12</td>
</tr>
</tbody>
</table>

Fig. 4 Proportional biomass allocation patterns as a function of biomass in *Dicranopteris linearis* on the six main study sites on Mauna Loa, Hawaii. Biomass was the sum of live leaves, stems and rhizomes. Live rhizome biomass was estimated by multiplying total (live and dead) mass by the proportion of live : dead stems as determined from the biomass harvests.

and P, respectively) (Fig. 5). This result related directly to the growth form of *Dicranopteris*; in general, where nutrient uptake was higher, investment in relatively short-lived lateral branches was greater.

**EFFECTS OF DICRANOPTERIS EXCLUSION**

Exclusion of *Dicranopteris* from 100-m² subplots on the young site at 290 m, where its percentage cover is 81%, resulted in increased growth of *Metrosideros*, with greater diameter increments in the second year of the study and greater relative net growth in the second and third years after removal (Mann–Whitney, $P = 0.04$ in all 1-sided tests) (Fig. 6). In general, exclusion of *Dicranopteris* also led to higher foliar nutrient concentrations and lower LMA in remaining species, but few differences were significant (Table 5). The 110 woody seedlings found in subplots represented
Table 4 ANPP and nutrient uptake of *Dicranopteris linearis* in six study sites on Mauna Loa, Hawaii. Values of ANPP are means of ± 1 SE of 11 measurements taken at intervals of 4–6 weeks. Nutrient uptake values are the products of mean ANPP and mean nutrient concentrations of newly senesced tissues.

<table>
<thead>
<tr>
<th>Site</th>
<th>Site 2</th>
<th>Site 3</th>
<th>Site 4</th>
<th>Site 5</th>
<th>Site 6</th>
</tr>
</thead>
<tbody>
<tr>
<td>Site age (year)</td>
<td>110</td>
<td>136</td>
<td>136</td>
<td>136</td>
<td>3400</td>
</tr>
<tr>
<td>Elevation (m)</td>
<td>290</td>
<td>700</td>
<td>1130</td>
<td>1660</td>
<td>700</td>
</tr>
<tr>
<td>Leaves (g m⁻² year⁻¹)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Biomass</td>
<td>189 ± 22</td>
<td>92 ± 12</td>
<td>52 ± 9</td>
<td>0.026 ± 0.005</td>
<td>332 ± 40</td>
</tr>
<tr>
<td>N uptake</td>
<td>0.641</td>
<td>0.297</td>
<td>0.138</td>
<td>&lt; 0.001</td>
<td>1.436</td>
</tr>
<tr>
<td>P uptake</td>
<td>0.245</td>
<td>0.006</td>
<td>0.002</td>
<td>&lt; 0.001</td>
<td>0.052</td>
</tr>
<tr>
<td>Stems (g m⁻² year⁻¹)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Biomass</td>
<td>64 ± 7</td>
<td>14 ± 2</td>
<td>4 ± 1</td>
<td>0.002 ± 0.000</td>
<td>271 ± 37</td>
</tr>
<tr>
<td>N uptake</td>
<td>0.166</td>
<td>0.023</td>
<td>0.007</td>
<td>&lt; 0.001</td>
<td>0.764</td>
</tr>
<tr>
<td>P uptake</td>
<td>0.010</td>
<td>0.002</td>
<td>&lt; 0.001</td>
<td>&lt; 0.001</td>
<td>0.056</td>
</tr>
<tr>
<td>Primary segments (g m⁻² year⁻¹)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Biomass</td>
<td>39 ± 8</td>
<td>10 ± 3</td>
<td>6 ± 1</td>
<td>0.004 ± 0.001</td>
<td>54 ± 14</td>
</tr>
<tr>
<td>N uptake</td>
<td>0.069</td>
<td>0.018</td>
<td>0.010</td>
<td>&lt; 0.001</td>
<td>0.153</td>
</tr>
<tr>
<td>P uptake</td>
<td>0.006</td>
<td>0.001</td>
<td>&lt; 0.001</td>
<td>&lt; 0.001</td>
<td>0.009</td>
</tr>
<tr>
<td>Total above-ground (g m⁻² year⁻¹)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Biomass</td>
<td>291 ± 29</td>
<td>116 ± 16</td>
<td>62 ± 11</td>
<td>0.032 ± 0.006</td>
<td>658 ± 69</td>
</tr>
<tr>
<td>N uptake</td>
<td>0.826</td>
<td>0.338</td>
<td>0.155</td>
<td>&lt; 0.001</td>
<td>2.353</td>
</tr>
<tr>
<td>P uptake</td>
<td>0.040</td>
<td>0.008</td>
<td>0.003</td>
<td>&lt; 0.001</td>
<td>0.116</td>
</tr>
</tbody>
</table>

Fig. 5 N (solid circles) and P (clear triangles) uptake as a function of leaf life span in *D. linearis* at the six main study sites on Mauna Loa, Hawaii.

Fig. 6 Mean (± SE) diameter increment and relative growth in *Metrosideros polymorpha* in plots where *D. linearis* was excluded from 1992 to 1995. Significant differences between control and exclusion plots are indicated by *. The experiment was conducted on the young site at 290 m elevation on Mauna Loa, Hawaii.

Only four species: the endemics *Metrosideros polymorpha* and *Myrsine* sp. and the exotics *Melastoma candidum* and *Psidium cattleianum*. *Dicranopteris* exclusion had no significant effect on woody seedling densities (1.5–1.9 seedlings m⁻²), recruitment rates (0.02–0.03 seedlings m⁻² year⁻¹), mortality rates (0.01–0.02 seedlings m⁻² year⁻¹) or seedling growth rates.

Percentage cover of all vascular species in the understory (excluding *D. linearis*) increased from 34% in the control to 57% in the exclusion plots after 39 months (Figs 7 and 8), mostly via expansion of pre-existing individuals. Total understory cover by all vascular species including *D. linearis* was lower in exclusion than in control plots (Mann–Whitney, *P* = 0.04), with 39.6% of the exclusion-plot area hav-
Table 5  Foliar characteristics of four dominant species in control and exclusion experimental plots on the young flow at 290 m, Mauna Loa, Hawaii. LMA is in g m⁻²; foliar nutrient concentrations are in percentage. Values are means (± SE) of three plots per treatment where 30–50 leaves were bulked in each plot. Significant differences between control and exclusion means (Mann-Whitney tests, z = 0.05) are denoted by *; LMA could not be determined (ND) for microphylls.

<table>
<thead>
<tr>
<th>Plant Species</th>
<th>LMA (Control)</th>
<th>LMA (Exclusion)</th>
<th>Foliar N (Control)</th>
<th>Foliar N (Exclusion)</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Machaerina angustifolia</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Year 1</td>
<td>228 ± 7*</td>
<td>213 ± 1</td>
<td>1.53 ± 0.09*</td>
<td>1.64 ± 0.10</td>
</tr>
<tr>
<td>Year 2</td>
<td>233 ± 20</td>
<td>220 ± 17</td>
<td>1.51 ± 0.08</td>
<td>1.51 ± 0.08</td>
</tr>
<tr>
<td>Year 3</td>
<td>232 ± 30</td>
<td>241 ± 13</td>
<td>1.65 ± 0.01*</td>
<td>1.58 ± 0.05</td>
</tr>
<tr>
<td><em>Melastoma candidum</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Year 1</td>
<td>78 ± 5</td>
<td>84 ± 7</td>
<td>1.12 ± 0.15</td>
<td>1.68 ± 0.53</td>
</tr>
<tr>
<td>Year 2</td>
<td>83 ± 1</td>
<td>89 ± 11</td>
<td>0.92 ± 0.14</td>
<td>1.07 ± 0.01</td>
</tr>
<tr>
<td>Year 3</td>
<td>90 ± 5</td>
<td>88 ± 2</td>
<td>0.91 ± 0.03*</td>
<td>1.08 ± 0.03</td>
</tr>
<tr>
<td><em>Metrosideros polymorpha</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Year 1</td>
<td>172 ± 7</td>
<td>155 ± 3</td>
<td>0.63 ± 0.02*</td>
<td>0.74 ± 0.04</td>
</tr>
<tr>
<td>Year 2</td>
<td>160 ± 8*</td>
<td>140 ± 1</td>
<td>0.65 ± 0.04</td>
<td>0.71 ± 0.04</td>
</tr>
<tr>
<td>Year 3</td>
<td>153 ± 5</td>
<td>158 ± 6</td>
<td>0.70 ± 0.04</td>
<td>0.65 ± 0.05</td>
</tr>
<tr>
<td><em>Paspalium cernuum</em></td>
<td>ND</td>
<td>ND</td>
<td>0.70 ± 0.07</td>
<td>0.83 ± 0.05</td>
</tr>
<tr>
<td>Year 2</td>
<td>ND</td>
<td>ND</td>
<td>0.84 ± 0.01</td>
<td>0.89 ± 0.12</td>
</tr>
<tr>
<td>Year 3</td>
<td>ND</td>
<td>ND</td>
<td>0.85 ± 0.01</td>
<td>0.91 ± 0.10</td>
</tr>
</tbody>
</table>


Discussion

Regarding no plant cover (litter or bare soil) compared with 2.5% in the control plots (Fig. 7). Mean (± SE) soil temperature at 2 cm depth was higher in exclusion plots, 23.7 (± 0.6) °C, than in the control, 21.6 (± 0.4) °C (Mann-Whitney, P = 0.04). Mean (± SE) soil N concentrations were higher in exclusion plots, 1.44 ± 0.05%, than in the control, 1.29 ± 0.05% (Mann-Whitney, P = 0.01).

Specific traits may represent keys to competitive success if they enable a species to capture or regulate resources in a unique manner, or if plasticity of the trait provides competitive advantages in specific sites. Many traits of *Dierocopteris* vary along the elevational gradient on Mauna Loa in a fashion similar to its codominants. For example, trends in biomass, height, ANPP and foliar N concentrations for *Dierocopteris* closely mirror those of *M. polymorpha*, a completely unrelated species (Fig. 9). Physiological attributes of *Dierocopteris* are neither unique nor highly plastic in response to environmental gradients when compared to other species on Mauna Loa, and hence cannot explain its success. *Dierocopteris* does, however, possess a suite of traits that result in unique
Fig. 8 Landscape view of the exclusion experiment at the young site at 290 m, Mauna Loa, Hawaii. (a) *Dicranopteris linearis* was excluded from the plot for 39 months. (b) *Dicranopteris* was left undisturbed in control plots.

Fig. 9 Means per site of biomass, height, above-ground net primary productivity (ANPP) and foliar N concentrations in two contrasting taxa, *Dicranopteris linearis* (black, right y-axis in top graphs) and *Metrosideros polymorpha* (white, left y-axis in top graphs) on four young sites on Mauna Loa, Hawaii.

or competitive solutions for colonizing, persisting and utilizing nutrients in these particular environments and these attributes have important consequences for community and ecosystem dynamics.

**Colonization and Persistence**

On young successional sites on pahoehoe lava, very little mineral soil has formed over 134 years of primary succession. The most favourable microsites for initial colonization by all plant species are cracks in lava slabs where moisture and detritus accumulate. Once established in these microsites, a clonal habit of indeterminate, branching, rhizomatous growth enables *Dicranopteris* to creep beyond cracks and onto more severe microenvironments, planar slabs of lava. Three years following removal of *Dicranopteris* from our young site, 40% of the area was still bare soil. We do not believe that allelopathy (e.g. Aragon 1975) or toxic effects due to aluminium accumulation
(Moomaw et al. 1959) cause lack of revegetation, primarily because other species quickly colonize our older, more fertile sites following removal of Dicranopteris (see also Cohen et al. 1995). We speculate that at this site, excessive soil temperatures and regular desiccation of shallow organic soils create harsh conditions for other species. Dicranopteris competes with these species in hospitable microsites, but it also colonizes microenvironments unavailable to its competitors.

Dicranopteris is also abundant on old pahoehe sites, where we suggest that anaerobic soil conditions create the major impediments to plant growth. The pseudodichotomous, indeterminate, clonal growth form of Dicranopteris endows it with a capacity to cover an area with one to several layers of live leaves, and thereby exploit resources over large areas. The combination of short-lived, marcescent leaves with low decomposability (Russell & Vitousek 1997) results in formation of a canopy of live and dead leaves that can be >3 m thick with an effective (live plus dead) LAI of >16. Such high site coverages reduce light transmission to the soil surface, inhibiting growth of other species and preventing tree regeneration. Accumulations of slow-to-decompose Dicranopteris stems (Russell & Vitousek 1997) form a durable meshwork that traps litter, forming a litter layer 0.5–1 m thick. This layer, perched approximately 1 m above the boggy forest floor and suffused with Dicranopteris rhizomes and fine roots, can support a person’s weight – most of the time – and enables the fern to bypass waterlogged soils. Finally, the highly recalcitrant litter produced by Dicranopteris may act as a nutrient sink, exacerbating nutrient limitations to plant growth and promoting persistence of oligotrophic conditions while offering Dicranopteris a competitive advantage over more nutrient-demanding species.

NUTRIENT USE

The relatively short, invariable blade life span of Dicranopteris differs distinctly from that of Metrodiosorus, in which life span ranges from 1 to >5 year (A.E. Russell, unpublished data). In oligotrophic sites, increased leaf longevity is considered to be a key trait for success (Chapin et al. 1980; Berendse & Aerts 1987). Dicranopteris may lack the capacity to alter its blade life span because its blades bear the reproductive organs. Thus, in exchange for sexual reproduction, Dicranopteris loses an important adaptation for nutrient conservation. Although leaves are short-lived, they are positioned for efficient carbon gain because new leaves are produced above older leaves, thereby avoiding self-shading. (Fig. 1).

Nitrogen-use efficiency (NUE), amount of organic matter produced per N taken up, in Dicranopteris is quite high at 224–400 g g⁻¹ compared with NUE values of 140–170 g g⁻¹ in fine litter and 250 g g⁻¹ in above-ground biomass in other low-nutrient ecosystems (Medina & Cuevas 1989). However, at our Mauna Loa sites, above-ground NUE values are equally high in other species, 135–391 g g⁻¹ (Raich et al. 1997) (Fig. 10). Apparently, high NUE is a common plant attribute in our N-poor sites. What sets Dicranopteris apart from other species is its extremely high P-use efficiency (PUE) (Fig. 10). High PUE may be an extremely valuable trait in our early successional sites where P is limiting (Raich et al. 1996). High PUE would also enable Dicranopteris to colonize the myriad of P-poor sites in which it is found throughout the humid tropics, e.g. highly degraded sites such as mined soils, logging decks, abandoned plantations and fields; very old soils such as laterites, oxisols and ultisols; and sites virtually devoid of surface-soil such as landslides, road cuts, precipices and taluses. We conclude that growth form and, in some sites, high PUE resulting from unusually efficient P resorption, rather than increased photosynthetic capacity or water-use efficiency, are the main characteristics that enable this fern to be highly successful over a broad range of high-light, high-rainfall, oligotrophic sites.

SPECIES IMPACTS AND ECOSYSTEM CONSEQUENCES

It might be argued that Dicranopteris arrests succession in post-dieback forests in Hawaii as a consequence of its impact on regeneration (e.g. Cohen et al. 1995). Nevertheless, Dicranopteris has coexisted with

\[ \text{NUE (g OM g}^{-1} \text{N)} } 
\[ \begin{align*} 
\text{DICRANOPTERIS} & \quad \text{OTHER SPECIES} \\
290 & \quad 290 \\
700 & \quad 700 \\
1130 & \quad 1130 \\
1660 & \quad 1660 \\
700 & \quad 700 \\
1660 & \quad 1660 \\
\end{align*} 
\]

\[ \text{PUE (g OM g}^{-1} \text{P)} } 
\[ \begin{align*} 
\text{DICRANOPTERIS} & \quad \text{OTHER SPECIES} \\
290 & \quad 290 \\
700 & \quad 700 \\
1130 & \quad 1130 \\
1660 & \quad 1660 \\
700 & \quad 700 \\
1660 & \quad 1660 \\
\end{align*} 
\]

\[ \begin{align*} 
\text{Elevation (m) / substrate age} \\
\text{Young} & \quad \text{Old} \\
290 & \quad 290 \\
700 & \quad 700 \\
1130 & \quad 1130 \\
1660 & \quad 1660 \\
\end{align*} 
\]
endemic species in the Hawaiian Islands for millennia (S.C. Hotchkiss & J.O. Juvik, unpublished data). Invasive species can threaten the function and development of native Hawaiian ecosystems by significantly altering ecosystem processes (e.g. Vitousek et al. 1987). Invasion by exotic species is perhaps the most serious threat facing otherwise protected Hawaiian ecosystems today. Exotic species such as Tibetania herbacea, Psidium cattleianum, Setaria palmitifolia and Crocosephalum crepidoidea, rather than endemics, rapidly colonized our most fertile site where Dicranopteris was cut for trails. We suggest that an important function of Dicranopteris is to resist the invasion of exotic species into these unique Hawaiian rainforests.

Live Dicranopteris constitutes a very small storage pool of organic matter and nutrients in our primary successional sites on Mauna Loa. However, Dicranopteris plays a disproportionate role in carbon and nutrient cycling, with its activity very high relative to its mass. Over all sites, Dicranopteris accounts for at most 14% of the biomass, but contributes up to 51% of ANPP on our young sites (Fig. 11). The importance of Dicranopteris increases over succession: it accounts for 74% of ANPP, 57% of the N uptake and 47% of the P uptake on the old site at 700 m, despite its small mass (Fig. 11). Although Dicranopteris comprises at most 24% and 13% of standing stocks of N and P on young flows, it accounts for up to 52% of N and 31% of P uptake (Fig. 11). Moreover, of nutrients stored in the fern, 81–83% of N and 76–78% of P are contained in live leaf blades with short life spans. As a result, nutrients taken up by Dicranopteris are relatively quickly transferred to the detrital pool, which is the sole source of soil organic matter, and soil, in these sites.

High rates of nutrient resorption in Dicranopteris result in C-rich, nutrient-poor litter that decomposes very slowly (Russell & Vitousek 1997). Consequently, Dicranopteris contributes substantially to soil accretion that occurs over successional time (Raich et al. 1997). During early succession on bare rock, soil formation facilitates plant growth by increasing water- and nutrient-storage capacities of the ecosystem. However, inputs of low-quality litter may decrease nutrient uptake by plants. On Mauna Loa, nutrient fluxes in litterfall are approximately twice as high in forests with understoreys dominated by tree ferns (Cibotium spp.) compared to those with Dicranopteris understoreys (Vitousek et al. 1995; Raich et al. 1997; Raich, in press). In late succession, soil organic matter accumulation impedes soil drainage and contributes to waterlogged conditions, further promoting oligotrophic conditions. Dicranopteris may dominate such sites for centuries and the result is an ecosystem with few trees.

Fig. 11 Pools of organic matter, nitrogen and phosphorus in live mass and rates of above-ground net primary productivity (ANPP), and nitrogen and phosphorus uptake of Dicranopteris linearis (shaded) compared with all other species combined (clear) in the six main study sites on Mauna Loa, Hawaii. For pools, values are means per site based on three to four quadrats per site with organic matter in units of kg m⁻² and N and P pools in g m⁻². Process means are based on 10 quadrats per site and are in units of g m⁻² year⁻¹. Young and old substrates are 110–134 and 3400 years old, respectively.
Dicranopteris could be viewed as a specialist in colonizing open-canopy, wet, oligotrophic – especially low-P – sites. That Dicranopteris is a specialist is suggested by the fact that in > 3 years no other species filled the vacuum created by removal of the fern on the early successional site. Growth form and nutrient use in Dicranopteris render this species unrivalled in terms of its ability to vegetate harsh landscapes and maintain dominance by blanketing a site with leaves. Carbon gain in Dicranopteris under nutrient-poor conditions can be substantial, resulting in important impacts on regeneration, ecosystem-level productivity, nutrient uptake, soil genesis and, consequently, ecosystem development. These community- to ecosystem-level consequences can all be viewed as resulting directly from traits that enhance the competitive success of Dicranopteris in rainforests on windward Mauna Loa.

Acknowledgements

We are very grateful to the many people who assisted in this research. We thank D. Turner who oversaw most of the nutrient analyses. We thank T. Bellfield, H. Farrington, D. Fernandez, F. Hughes, D. Paul and T. Schuur for assistance in the field. D. Friedrich provided the drawing of Dicranopteris. S. Cordell, G. Goldstein, T. Jurik, N. Lersten, P. Matson, M. Ryan, R. Shirables and D. Sundberg provided advice and/or equipment for the gas exchange and stomatal density work. We thank all of the research staff at Hawaii Volcanoes National Park in the National Biological Service, the US Fish and Wildlife, and the US Geological Survey who provided logistical support, advice, information and insights, especially D. Foote, J. Jacobi, J. Lockwood, L. Pratt and C. Stone. We thank A. Blackmer, W. Clark, D. Farrar, G. Gerrish, T. Jurik, M. Kaiser, P. Marks, D. Muller-Dombois, L. Walker and two anonymous referees for their useful and insightful comments and suggestions. This work was funded by National Science Foundation grant BSR 8918003 to Stanford University, by National Science Foundation grant DEB 9311526 to Iowa State University, and by two Sigma Xi Grants-In-Aid-of Research.

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Received 21 August 1997
revision accepted 16 February 1998