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Evidence for the widespread occurrence of ancient forests on cliffs

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Abstract

Aim The objective of this work was to determine if the existence of ancient forests on cliffs was specific to the Niagara Escarpment, Canada, or part of a globally widespread pattern.

Location Sixty-five cliff sites were visited in five countries in the temperate climatic zone, and trees were sampled for age and growth rate on forty-six of these.

Methods Two hundred and twenty-four core samples or cross-sections were taken from trees on cliffs that varied in height, aspect, rock-type, and exposure. General observations were also made of regeneration of the tree species forming the mature canopy, and other habitat conditions.

Results The evidence shows that ancient slow-growing forest occurs on most cliffs. Age and growth rate distributions were similar at all treed sites. Small-statured *Thuja, Juniperus*, or *Taxus* stems with age estimates in excess of 1000 years were found in the United States, the United Kingdom and France, and small *Pinus and Quercus* stems nearly 400 years in Germany. There was a high rate of recurrence of plants in the genera *Polypodium*, *Asplenium*, *Cystopteris*, *Campanula*, *Rosa*, *Prunus*, *Hedera*, and *Sorbus*. Most of the sites appear to be habitats of completely natural origin.

Conclusions We conclude that ancient natural forest is a normal feature of cliffs, at least in the temperate zone.

Keywords
Cliffs, undisturbed habitat, escarpment, ancient forest, tree age, growth rates.

INTRODUCTION

The conversion of natural self-regenerating forest into sites that provide goods and services for people (Vitousek, 1994) has been relentless over the past century. A high priority for ecologists and conservationists has been to find and protect sites that represent the best examples of ancient refuge ecological systems under natural controls (Whitney, 1987; Hunter, 1989). In North America work has been done to locate and protect the remaining stands of old-growth forest (Findley, 1990; Davis, 1996), especially ones with a very wide spectrum of age classes, and a consistent assemblage of associated understorey species. Similar projects have been carried out in Europe (Spencer & Kirby, 1992; Peterken, 1996; Wulf, 1997) and recent work using radiocarbon-dating methods have identified the location of ancient woodland in Amazonia (Chambers *et al.*, 1998). One of the problems in the identification and protection of such forest is that the current search image for old-growth (or virgin) forest is dominated by visions of large diameter tall trees with a complex multilayered understorey (Stahle, 1996a, 1996b). Such forests exist in large tracts in the western parts of temperate North America (Findley, 1990), in many parts of tropical Central and South America (Villalba, 1990; Stahle & Cleaveland, 1993), and elsewhere as a small number of isolated stands (Peterken, 1996), but there is no ecological

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reason why ancient woodland or forest should necessarily have this form. For example, it is well known from the work of Edmund Schulman (Schulman, 1954) that stunted and widely space bristlecone pine (*Pinus longaeva* Bailey) occurs as a forest type at high altitudes in California & Nevada, U.S.A. and Stahle & Chaney (1994) have shown that ancient stunted oak woodland in Arkansas (U.S.A.) only occurs in remote or rocky areas that deterred commercial exploitation of trees by people.

Recently it has been shown that some of the least disturbed and most temporally stable refuge woodlands in all of North America occur as stunted forests on vertical limestone cliffs of the Niagara Escarpment, southern Ontario, Canada (Larson & Kelly, 1991; Kelly *et al.,* 1994; Larson & Melville, 1996; Kelly & Larson, 1997). As with other remnant stands of ancient forest, these areas were not exploited commercially by people. The cliff forests are dominated by *Thuja occidentalis* L. (eastern white cedar) that can reach 1890 years of age. The coarse woody debris in these cliff forests can persist for 4000 years or more (Larson & Melville, 1996). When trees are randomly sampled over large geographical scales smooth negative exponential age distributions typical of undisturbed old-growth forests have been found (Larson & Kelly, 1991; Kelly & Larson, 1997). Disturbance from humans is absent or very site specific despite the proximity of a densely populated industrial/agricultural landscape. Sporadic rockfall is the main natural disturbance but much of the rock is Silurian-aged dolomitic limestone and very stable. The understorey of such cliff forests has a disturbance-intolerant vegetation and faunal community that displays a large number of species that are either highly restricted to the cliffs, or completely endemic to them (Larson *et al.*, 1989; Nuzzo, 1995; Matthes-Sears *et al.*, 1997; Nekola, 1999). While these results confirm the prediction by Stahle & Chaney (1994) and Therrell & Stahle (1998) that unproductive rocky landscapes will support the best local examples of ancient forest, there have been few larger-scale tests of the hypothesis as it applies to cliffs. Larson *et al.* (1999) have recently presented evidence that age and growth rate frequency distributions were the same for trees on North American to European cliffs, but few additional details were provided in that work.

Here we present the results of an investigation that addresses the question 'To what degree do partly wooded cliffs in the temperate zone support ancient forest, and what habitat variables such as cliff height, rock type, aspect, and exposure influence the age and growth rate structures?'. To answer these questions, cliffs were visited and trees sampled in five countries. A cursory examination was also made of the local flora, the presence of seedling recruitment, coarse woody debris, and disturbance from human and livestock activities. The results were then compared with those already obtained for the cliffs of the Niagara Escarpment. We predicted that if cliffs generally support ancient woodland, then such sampling would reveal the same right-hand side of the negative exponential age distribution previously described for cliff forests of the Niagara Escarpment. We also predicted that such cliffs would support seedlings, saplings, and coarse woody debris of the same trees forming the forest.

METHODS

Cliffs were sought only in climatic zones roughly similar to southern Ontario: temperate latitudes with rainfall between 500 and 1500 mm per year and average annual temperatures between 0 and 20 °C. These conditions bracket those of southern Ontario (950 mm annual precipitation and average annual temperature of nearly 10 °C). We think that temperature and precipitation are important considerations because rates of mass wasting are tightly controlled by these variables (Ritter, 1978). We also think that cliff faces that weather very rapidly (because of excessive precipitation or extreme cold) would be very unlikely candidates to support an ancient biota, and at the other end of the spectrum, cliffs that weather very slowly (because of hot/dry conditions) would be unlikely to support woody species (Larson *et al.*, 2000). The assumption of an association between rock stability in different climatic zones and the development of an ancient biota will be tested in the future.

We do not claim that our selection of regions, sites, or cliffs was random. We argue that if the ecological characteristics of the Niagara Escarpment are in any way duplicated on cliffs generally in the north or south temperate zones with the above conditions of temperature and precipitation, then trees on cliffs however sampled ought to have similar age and growth rate characteristics. With this thinking in mind, we sampled trees on cliffs in the United States from Iowa to Massachusetts, and as far south as Tennessee (Table 1). Also we sampled in central, eastern and southern Germany, southern France, and north-western England and north Wales. A small amount of sampling was also carried out in New Zealand. The total number of sites visited was sixty-five. Rock-climbing equipment was used to gain access to cliff faces. At each site genera of vascular plants that were common on the cliffs were noted but we do not claim to have conducted a proper systematized vegetation survey. In cases where the cliffs were sampled outside of the growing season, lists of the names of common taxa were obtained from local sources (Lindsey *et al.*, 1969; Clapham *et al.*, 1987; Ellenberg, 1988; Rodwell, 1991; Wardle, 1991; Fleckenstein, 1992). Cliffs were considered suitable for sampling when the outcrop was a large and significant landscape feature generally > 0.5 km in length and sufficiently stable to ensure the safety of field workers. Topographic maps were examined for each site. Latitude and longitude were recorded as well as the rock type for the formation as a whole. Also listed for each site was the aspect of the cliff face, the presence or absence of overlying tree canopy shading, the average height of the cliff face (m) above the talus slope at its base, the stability of the rock (+ indicating very stable and minimally fractured, – indicating very loose and highly fractured), the presence of disturbance from people or livestock (indicated by signs of cutting, livestock browsing, or livestock dung), and the presence of *in situ* coarse woody debris. When mature woody plants were found on cliff edges, cliff faces, or talus slopes (close to the base of the cliff), increment cores were taken from a small number of mature trees at each site, or cross sections were taken from parts of stems that had died recently. The number of samples from each site varied because

Table 1 Sites visited including information on place name; nearest town or village plus state, Province or Department; latitude and longitude (degrees and minutes); rock type (conglom. = conglomerate; dev. = devonian; ordov. = ordovician; carbonif. = carboniferous); aspect (N,E,S,W) of the main part of the face that was examined; exposure in terms of an overlying deciduous or coniferous canopy (+ = sheltered, – = exposed); approximate cliff height in the areas sampled (m), stability of rock on cliff (+ = solid, – = weak); the presence of disturbance in the form of hiking (hike), climbing (climb), sheep, sea spray, industry, or roads; the presence or absence (+ or –) of seedling recruitment and the presence or absence (+ or –) of coarse woody debris.

Place name	Town/State	Lat/Long	Rock	Asp.	Expos.	Ht.	Stab.	Dist.	Seed.	Wood.
United States										
Mt. Tom	Holyoke, Massachusetts	42°12′N; 72°37′W	basalt	W	+	25	–	none	+	+
Shawangunks	New Paltz, New York	41°45′N; 74°05′W	conglom.	W,E	+	30	+	climb	+	+
Cohoes Falls	Cohoes, New York	42°45′N; 73°43′W	Dev. shale	W,N,E	+	10	–	industry	–	–
Letchworth St.Pk.	Castile, New York	42°38′N; 78°04′W	Dev. shale	NE	+	200	–	none	+	+
Pennsylvania Grand Canyon	Wellsboro, Pennsylvania	41°45′N; 77°18′W	Dev. shale	S	+	200	–	none	+	+
Middle Bluff	Fayette State Park Michigan.	45°43′N; 86°37′W	Silurian dolomite	W	+	30	+	none	+	+
Ellison Bay State Park	Ellison Bay, Wisconsin	45°04′N; 87°17′W	Silurian dolomite	W	+	30	+	none	+	+
Greenleaf	Green Bay, Wisconsin	44°25′N; 88°02′W	Silurian dolomite	W	–	20	+	none	+	+
Ship Rock	Baraboo, Wisconsin	44°05′N; 88°02′W	Cambrian sandstone	N,S	–	15	+	hike/climb	–	–
Mississippi River Bluffs	Dakota, Minnesota	43°55′N; 91°24′W	Ordov. dolomite	E	+	30	+	none	+	+
Turkey River Mounds	Guttenberg, Iowa	42°48′N; 91°06′W	Ordov. dolomite	W,S	+	30	+	hike	+	+
Backbone St.Pk.	Dundee, Iowa	42°41′N; 91°32′W	Silurian dolomite	W,E	+	20	+	hike	+	+
Palisades-Kepler St.Pk.	Mount Vernon, Iowa	41°25′N; 91°03′W	Silurian dolomite	W	–	15	+	hike	+	+
Palisades-Dows St.Pr.	Mount Vernon, Iowa	41°56′N; 91°26′W	Silurian dolomite	E	–	15	+	none	+	+
Farm Creek	Andrew, Iowa	42°11′N; 90°37′W	Silurian dolomite	W	+	25	+	none	+	+
Ice-Cave City Park	Decorah, Iowa	43°18′N; 91°49′W	Ordovician dolomite	S	+	20	+	none	+	+
Bluffton Hemlock St.Pr	Bluffton Iowa	43°28′N; 91°51′W	Silurian limestone	N	+	35	+	none	+	+
Devil's Lake St.Pk.	Ontario, Wisconsin	43°43′N; 90°36′W	Precambrian quartzite	W	+	30	+	hike	+	+
Picture Rock	Harper's Ferry, Iowa	43°29′N; 91°20′W	Ordovician dolomite	E	+	70	+	none	+	+
Mississippi Palisades St.Pk.	Savanna, Illinois	42°06′N; 90°07′W	Silurian dolomite	W	–	30	+	climb	+	+
Apple River Canyon	Apple River, Illinois	42°25′N; 90°26′W	Silurian dolomite	N	+	20	+	none	?	+
Cedar Bluffs	Bloomington, Indiana	39°10′N; 86°31′W	Silurian limestone	N	+	20	+	hike	+	+
Natural Tunnel St.Pk.	Duffield, Virginia	36°52′N; 82°07′W	Silurian dolomite	N,W	+	100	+	hike	+	+
Potomac River	Sharpsburg, Maryland	39°27′N; 77°46′W	Silurian limestone	N	–	10	–	road	+	+
Watauga River	Watauga River Tennessee	36°17′N; 81°55′W	quartzite	NE	+	25	+	industry	+	+
New River	Pembroke, Virginia	37°19′N; 80°39′W	limestone	E	+	60	+	none	+	+
Germany										
Sächsische-Schweiz	Bad Schandau, Sachsen	50°58′N; 13°58′E	Cretaceous sandstone	W	+	200	+	climb	+	+
Höllental	Blankenstein, Bayern	50°23′N; 11°41′E	granite	S	+	50	+	hike	–	–
Ahrtal	Altenahr, Nordrhein-Westfalen	50°31′N; 7°00′E	greywacke quartz	S,W	–	10	+	hike	+	+

Table 1 *continued*

Place name	Town/State	Lat/Long	Rock	Asp.	Expos.	Ht.	Stab.	Dist.	Seed.	Wood.
Dahner Felsenland	Hinter Weidenthal, Rheinland-Pfalz	49°12′N; 7°46′E	red sandstone	E	+	30	+	hike	+	+
Maintal	Miltenberg, Bayern	49°42′N; 9°16′E	red sandstone	N	–	30	+	industry	+	–
Nahetal	Kirn, Rheinland-Pfalz	49°47′N; 7°28′E	volcanic schist	SE	+	100	+	none	–	–
Battert	Baden-Baden, Baden-Württemberg	45°47′N; 8°15′E	conglom	W	+	30	+	climb	+	–
Fränkische—Schweiz	Pottenstein, Bayern	49°46′N; 11°20′E	limestone	W	–	10	+	none	+	+
Oberes Donautal	Beuron, Baden-Württemberg	48°5′N; 8°58′E	limestone	N	+	100	+	hike/cimb	+	+
France										
Rivière Doubs	Baumes Les Dames	47°24′N; 6°28′E	limestone	S	+	30	+	road	+	+
Haute Jura	Ponts des Pierres, Ain	46°21′N; 5°43′E	Jurassic limestone	S	+	100	+	none	+	+
Chabestan	Chabestan, Haute Alpès	44°28′N; 5°48′E	Jurassic limestone	S	+	200	+	none	+	+
Digne	Digne, Alpes-des Haute Province	43°53′N; 6°26′E	Jurassic limestone	E	+	100	+	none	+	+
Gorges du Verdon	Moustier-Ste-Marie Var	43°45′N; 6°22′E	Jurassic various limestone		+	500	+	climb	+	+
Les Gaudes	Grenoble, Isère	45°14′N; 5°45′E	Jurassic limestone	E	+	50	+	none	+	–
Belevedere de Bénedegand	Champagnole, Doubs	46°44′N; 5°55′E	limestone various		–	30	+	none	+	+
Les Mées	Les Mées, Alpes-des-Haute Province	44°03′N; 6°00′E	conglom.	N	+	50	+	road	–	–
United Kingdom										
Whitbarrow	Newby Bridge, Cumbria	54°15′N; 2°49′W	Carbonif. limestone	W	–	25	+	none	+	+
Scout Scar	Witherslack, Cumbria	54°18′N; 2°46′W	Carbonif. limestone	W	+	25	+	none	+	+
Askam in Furness	Askam in Furness, Cumbria	54°12′N; 3°13′W	Carbonif. limestone	SW	+	10	+	sea-spray	–	–
Dovedale	Thorpe, Derbyshire	53°05′N; 1°47′W	Carbonif. limestone	W	+	30	+	hike	+	+
High Tor	Matlock Bath Derbyshire	53°07′N; 1°47′W	Carbonif. limestone	W	–	100	+	climb	+	+
Froggatt Edge	Froggatt, Derbyshire gritstone	53°17′N; 1°37′W	Carbonif.	W	+	10	+	climb	–	–
Lake District	Grasmere, Cumbria	54°31′N; 3°3′W	stockdale various shales		+	10	+	sheep	+	+
Helm Crag	Grasmere, Cumbria	54°30′N; 3°1′W	stockdale shales	W	+	25	+	hike	+	+
Miller's Dale	Bakewell, Derbyshire	53°15′N; 1°45′W	Carbonif. limestone	SW	+	20	+	none	+	+
Malham Cove	Malham, Yorkshire	53°5′N; 2°5′W	Carbonif. limestone	SW	+	100	+	none	+	+
Gordale Scar	Malham, Yorkshire	53°5′N; 2°4′W	Carbonif. limestone	W	+	70	+	none	+	+
Arncliffe	Arncliffe, Yorkshire	53°9′N; 2°3′W	Carbonif. limestone	SW	+	30	+	none	?	?
Eglwyseg	Llangollen, Denbighs	52°59′N; 3°10′W	Carbonif. limestone	SW	+	40	+	climb	+	+
Tremadog	Tremadog, Gwynedd	52°57′N/4°8′W	Cambrian slate	SW	+	40	+	climb	–	–
Great Orme	Llandudno, Gwynedd	53°20′N; 3°45′W	Carbonif. limestone	N	+	100	+	sea-spray	?	+
Markland Grips	Clowne, Derbyshire	53°16′N; 1°14′W	Permian magnesian limestone	SE	–	10	+	none	+	+
Mam Tor	Castleton, Derbyshire	53°21′N; 1°47′W	Carbonif. sandstone	E	+	70	–	none	–	–
Peak Cavern	Castleton, Derbyshire	53°21′N; °45′W	Carbonif. limestone	W	–	40	+	none	?	+

Table 1 *continued*

Place name	Town/State	Lat/Long	Rock	Asp.	Expos.	Ht.	Stab.	Dist.	Seed.	Wood.
New Zealand										
Kaikoura	Kaikoura, South Island	42°27′S; 173°35′E	Tertiary limestone	E	+	50	+	none	+	+
Waima Gorge	Mirza, South Island	41°40′S; 173°50′E	Tertiary limestone	NE	+	25	+	none	+	+
Bullock Creek	Punakaiki, South Island	42°07′S; 171°19′E	Tertiary limestone	N	+	100	+	none	+	+
Paparoa Nat.Pk.	Punakaiki, South Island	42°08′S; 171°20′E	Tertiary limestone	N,S	+	100	+	none	+	+
Tiropahi Track	Charleston, South Island	41°52′S; 171°22′E	Tertiary limestone	W	+	60	+	none	+	+
Broken River Karst	Broken River South Island	43°20′S; 171°51′E	Tertiary limestone	S	+	30	+	none	+	+
Lake Maraetai	Mangakino, North Island	37°48′S; 175°22′E	Whakamaru ignimbrite	W	+	50	+	none	+	+
Waitomo River	Waitomo, North Island	38°10′S; 174°55′E	Oligocene limestone	E	–	15	+	none	+	+
Miriwai Beach	Auckland, North Island	36°30′S; 174°31′E	volcanic sandstone	W	+	50	+	sea-spray	?	?

of site-specific variability in the number of trees present, or the ease of access to the cliff faces. Most cliffs had four or five trees sampled. The diameter of the bole (cm) at the core height (cm) was recorded for each sample. Ring counts were made on each of the 224 specimens so collected. An age estimate was then made by assuming that visible rings were annual but no attempt was made to crossdate the material. While false rings are a normal problem in some species of *Juniperus* (Schweingruber, 1993) their frequency was exceptionally low in these slow-growing cliff-face trees. A similar phenomenon has been observed by Guyette *et al.* (1989) for *Juniperus virginiana* L. growing on cliffs in the Ozark Mountains, U.S.A. When core samples or cross sections did not include the pith, an estimate was applied using methods described elsewhere (Kelly & Larson, 1997). The radial growth rate of wood of each tree was calculated by dividing the distance between the innermost ring closest to the pith and the outermost ring closest to the cambium (mm), by the ring count (yr).

The results were plotted as frequency distributions for age estimate and growth rate, and comparisons were made among countries (France, Germany, U.S., and U.K.), habitat types (edge vs. face), aspect (E,S,W,N), cliff height (small (< 10 m), medium (11–30 m), and large (> 31 m), rock-type (calcareous *v.* noncalcareous), and shading (+ or –). Each of these categories was coarse because we felt that the size of the complete data set would not permit finer divisions of each variable. Equivalence of frequency distributions was assessed using two nonparametric tests: the Watson U^2 test (Zar, 1974) that is particularly sensitive to differences in distributions based on the pattern of the variance, and the Cramér-von Mises W^2 test (Conover, 1971; Zar, 1974) that is more sensitive to differences in the mean. All P-values were adjusted for multiple comparisons. When both of these tests showed statistically different frequency distributions, we took this as an indication of a very strong trend. When only one of the two tests showed differences, we were more cautious in our interpretation.

RESULTS

General trends in vegetation

While we do not claim that the cliffs examined were randomly sampled, all were vegetated to some degree and most of them supported woody taxa. A few sites in the northern hemisphere, and most of the sites in New Zealand supported only herbaceous vegetation. For example the extremely unstable rock of Mam Tor, U.K., supported a largely graminoid vegetation between the loose rocks, while the extremely stable concrete-like conglomerate rock of Les Mées, France, supported plants only at the summits of the cliffs. Exposed sea-cliffs at Askam in Furness, U.K., mainly supported populations of *Plantago maritima* L. In New Zealand cliffs in areas exposed to abundant precipitation on the west coast of the South Island, supported herbaceous plants such as *Phormium cookianum* (Le Jolis), but such plants could not be dated. With these exceptions, cliffs supporting a woody vegetation were selected in all countries, and on virtually all of them there was seedling recruitment of the canopy trees, and abundant standing and fallen coarse woody debris.

There was a high rate of recurrence of certain genera of canopy and understorey plants. *Betula papyrifera* Marsh. was common in northern and central North America, while *B. alleghaniensis* Britt. was common on cliffs in the eastern and southern United States. In Europe *B. pendula* Roth. occurred in exactly the same cliff-face microsites as did the other birches in North America. Similarly, *Thuja occidentalis* L. was common on alkaline rocks in the eastern and northern portions of North America and was replaced by *Juniperus virginiana* L. in the central, southern and eastern states visited. *Taxus*

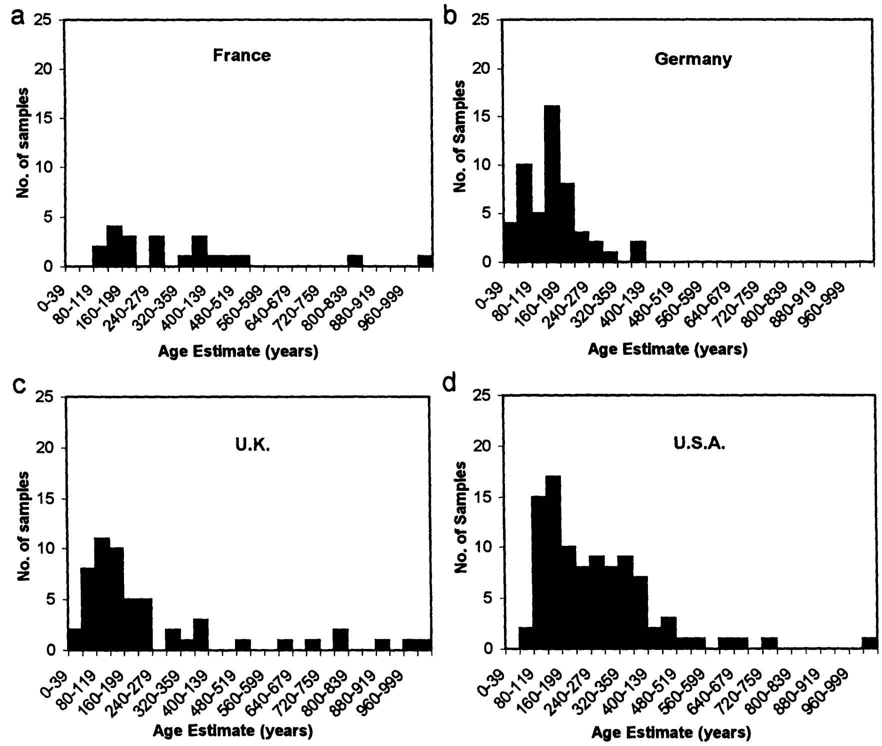

Figure 1 Frequency distribution of the estimated age of trees sampled on cliffs in different regions: (a) France, $n = 21$ (b) Germany, $n = 51$ (c) United Kingdom, $n = 55$ (d) United States of America, $n = 97$.

canadensis Marsh. was also frequently encountered on limestone outcrops. On acid rocks, the main tree species encountered was *Pinus rigida Mill.* In Europe, *Taxus baccata* L., *Juniperus communis* L., *J. oxycedrus* L., and *J. phoenicea* L. were present on limestone outcrops while *Pinus sylvestris* L. and *Quercus petraea* Liebl. were found in areas of more acidic rock. Smaller woody plants and shrubs in the genera *Sorbus*, *Buxus*, *Hedera*, *Prunus*, *Fraxinus*, and *Crataegus* were commonly found on the cliffs that were sampled. Likewise, climbing plants such as *Rosa*, *Hedera*, *Vitis* or *Rhododendron* were found on cliff faces or rooted at the bottom of many cliffs. Plants in *Campanula* (*usually C. rotundifolia L.*) were also very frequently observed, and ferns including species in *Polypodium* (*P. virginianum* L. & *P. vulgare* L.), *Cystopteris* (*C. fragilis* L., *C. bulbifera L.*), *Asplenium* (*A. ruta-muraria* L., *A. trichomanes L.*, *A.* viride Huds.), and *Phyllitis* (*P. scolopendrium* L.) recurred commonly among the sample sites.

Quantitative analysis of age in woody cliff vegetation

Only samples from adult trees growing on cliffs in Europe and North America were included in this analysis. Thus tree age and growth rate data were only obtained from forty-six sites. The samples from New Zealand were excluded because of the small sample size, but the few *Pachystegia insignis* (Hook.) plants that were sampled were old (~200 years) and slow growing (< 0.25 mm/year). The 224 samples that were included in the analysis and they were mainly *Thuja occidentalis*, *Juniperus communis*, *J. virginiana*, *J. oxycedrus*, *J. phoenicea*, *Taxus baccata*, *Taxus canadensis*, *Pinus sylvestris*, and *Quercus petraea.* Most cliffs had four or five mature trees sampled.

The results for age estimate show similar trends among sites: extremely uneven age distributions with shapes consistent with the negative exponential age distribution were found in all countries (Fig. 1). Despite these general similarities, there were some differences when countries were compared. Trees on cliffs in Germany were younger and less variable in age than those on cliffs in the U.S. ($P < 0.001$). When the radial growth rates of these trees were compared (Fig. 2) the only statistically significant difference was between trees with very low growth rates in France and those sampled in the U.K. ($P < 0.001$). Trees with age estimates near or over 1000 years were found in Wisconsin, Michigan, and Tennessee. Trees over the millennium age estimate were also found in France and the U.K. Radial growth rates of all trees found on cliffs were exceptionally small: the median radial growth rate for the entire population of trees sampled was less than 1.00 mm/year. All of the trees sampled exhibited extensive cambial mortality as well as stunting: for example, *Juniperus phoenicea* (Verdon Gorge, France) had a radius (also its diameter) of 8 cm, and an annual radial growth rate of 0.06 mm over a 1025-year period. This tree was typical of most cliff trees in that it had suffered partial cambial mortality apparently caused by mass wasting of rock that undercut the base of the trees and killed sectors of the root system.

The influence of habitat characteristics

When frequency distributions for age estimate were

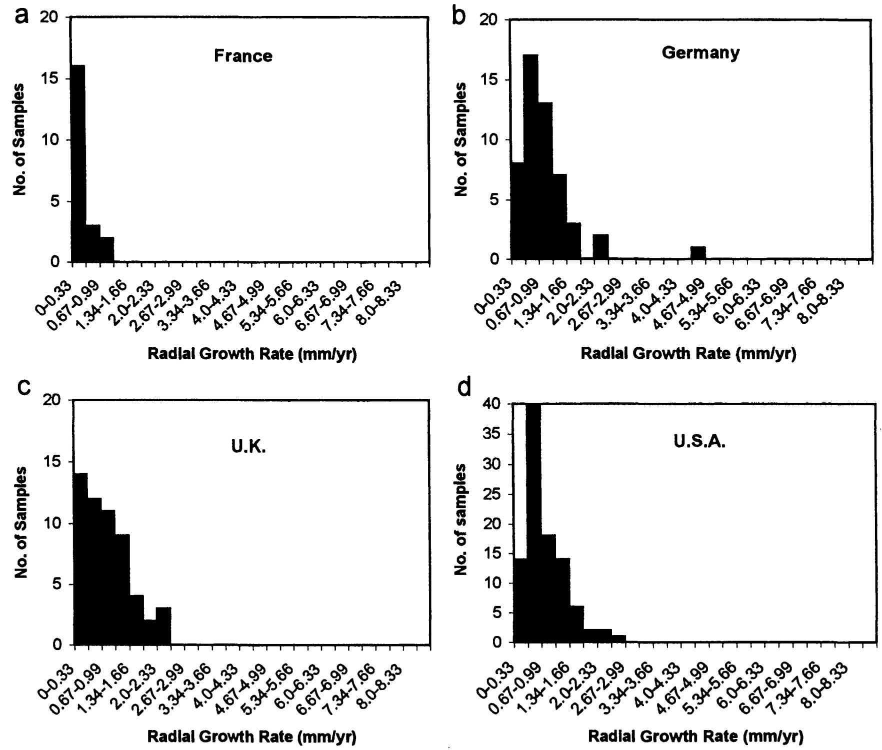

Figure 2 Frequency distribution of the radial growth rate of trees sampled on cliffs in different regions: (a) France, $n = 21$ (b) Germany, $n = 51$ (c) United Kingdom, $n = 55$(d) United States of America, $n = 97$.

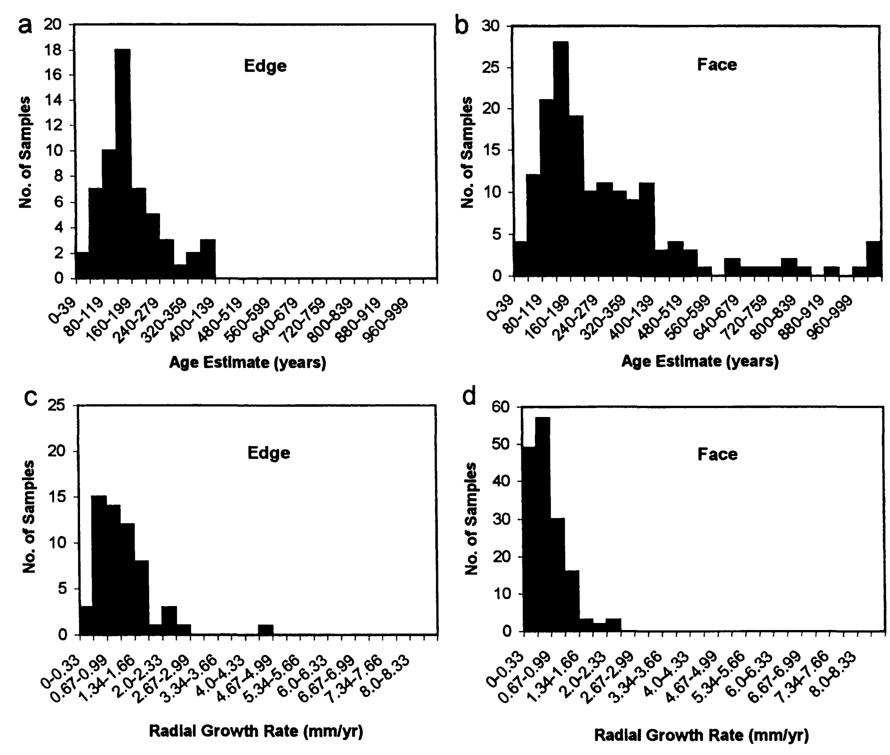

Figure 3 Frequency distribution of the estimated age (a,b) and radial growth rate (c,d) of trees sampled on cliffs as a function of habitat of origin: (a,c) cliff edges, $n = 58$ (b,d) cliff faces, $n = 160$.

compared among different habitat types, cliff-face trees were shown to be slightly older than cliff-edge trees ($P < 0.05$). None of the trees cored in level ground and talus habitats adjacent to the cliffs were over 200 years of age. Level-ground trees and those growing on talus slopes had growth rates up to 10 mm/year while trees on cliff edges grew much more slowly, and cliff-face trees the slowest of all ($P < 0.001$) (Fig. 3c,d). Trees on cliffs of all heights (short, medium and

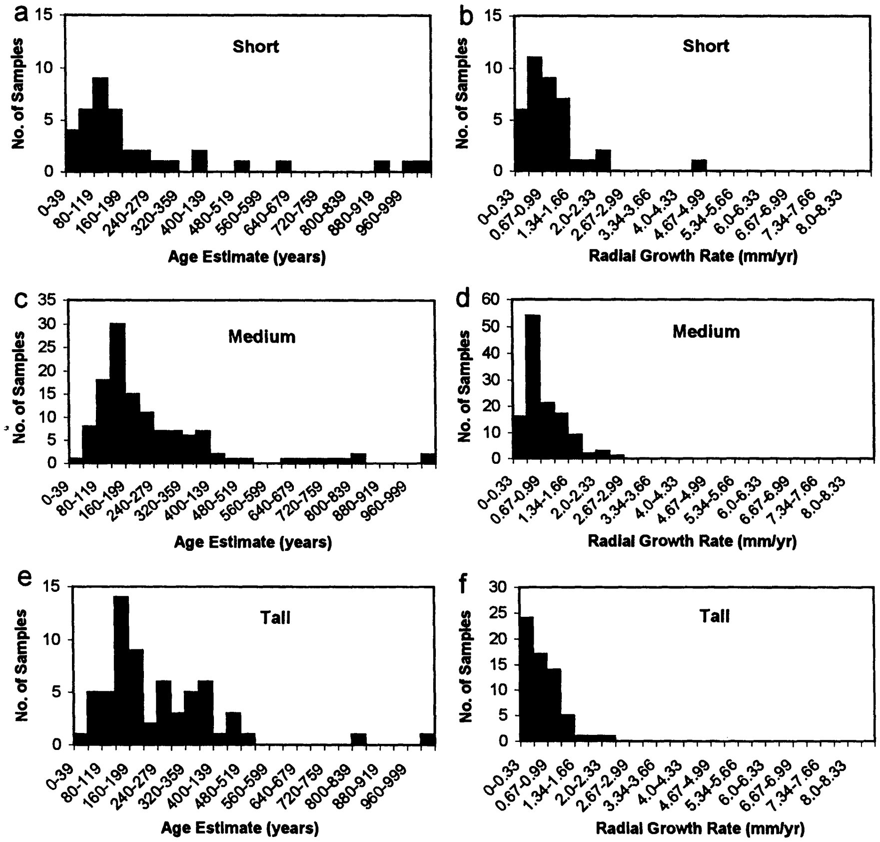

Figure 4 Frequency distribution of the estimated age (a,b,c) and radial growth rate (d,e,f) of trees sampled on cliffs as a function of the height (size) of the cliffs: (a,d) small cliffs < 10 m, n = 38(b,e) cliffs > 10 < 30 m, n = 123 (c,f) trees from cliffs > 30 m tall, n = 63.

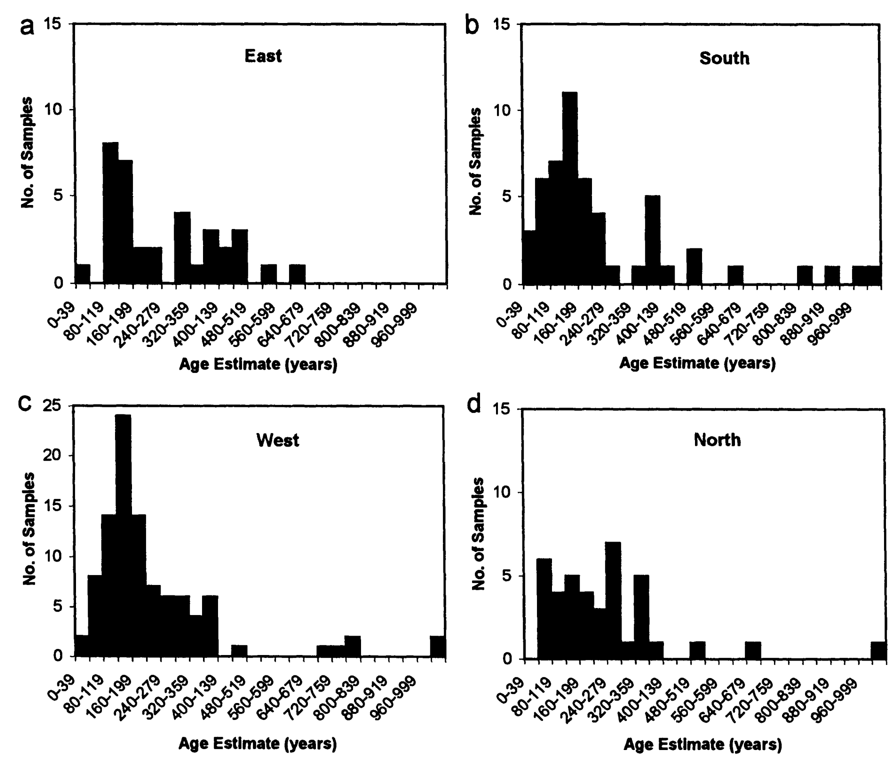

Figure 5 Frequency distribution of the estimated age of trees sampled on cliffs as a function of the aspect of the cliff face: (a) cliffs facing east, n = 35 (b) cliffs facing south, n = 52 (c) trees facing west, n = 98 (d) trees facing north, n = 39.

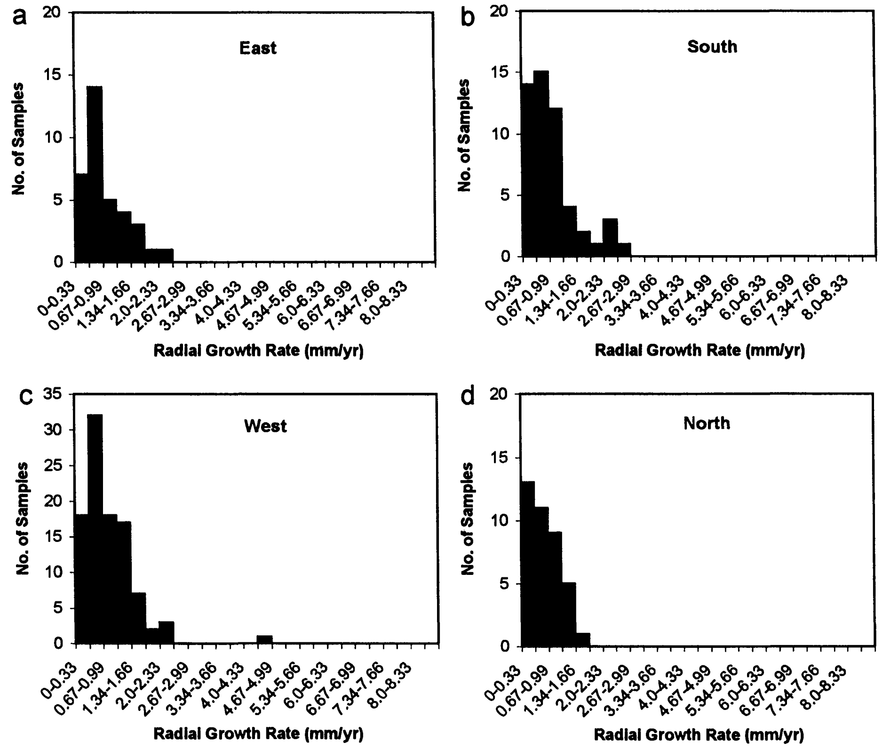

Figure 6 Frequency distribution of the radial growth rate of trees sampled on cliffs as a function of the aspect of the cliff face: (e) cliffs facing east, n = 35(f) cliffs facing south, n = 52 (g) trees facing west, n = 98 (h) trees facing west, n = 98.

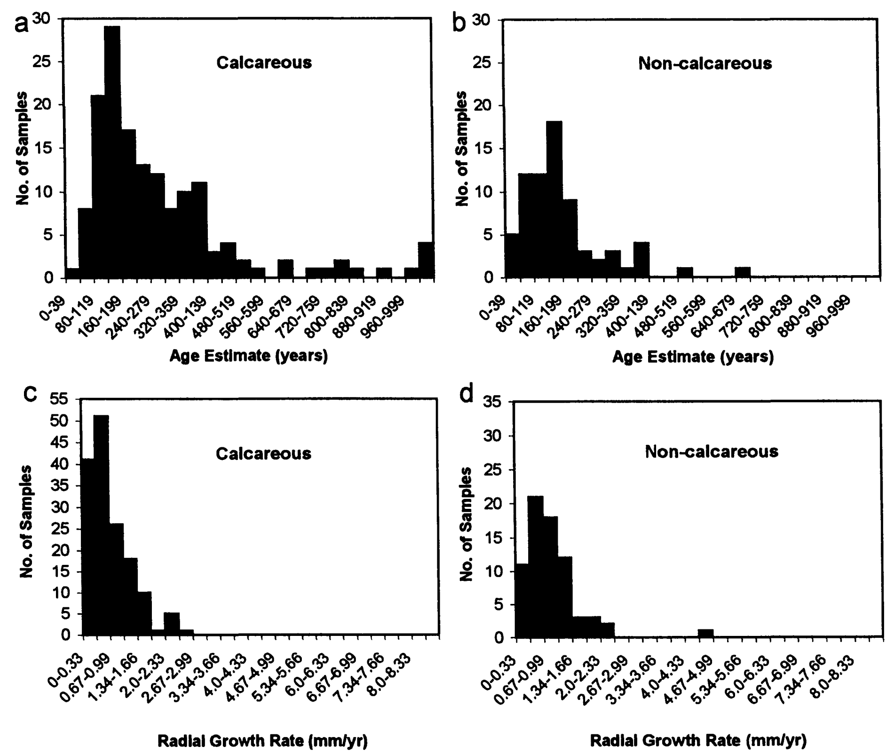

Figure 7 Frequency distribution of the estimated age (a,b) and radial growth rate (c,d) of trees sampled on cliffs as a function of rock type: (a,c) calcareous rock, n = 153 (b,d) noncalcareous rock, n = 71.

tall) had the same frequency distribution of age estimate and growth rate (Fig. 4a-f, $P > 0.05$). For the variables 'aspect' (Figs 5a-d, 6a-d), 'rock-type' (Fig. 7a-d), and 'shading' (Fig. 8a-d) all distributions were similar ($P > 0.05$), indicating that the existence of ancient woodland on cliffs is independent of particular orientations of the vertical surfaces, the underlying chemistry of the rocks, or the extent to which the sites have dense overlying canopies that shade the cliff-face.

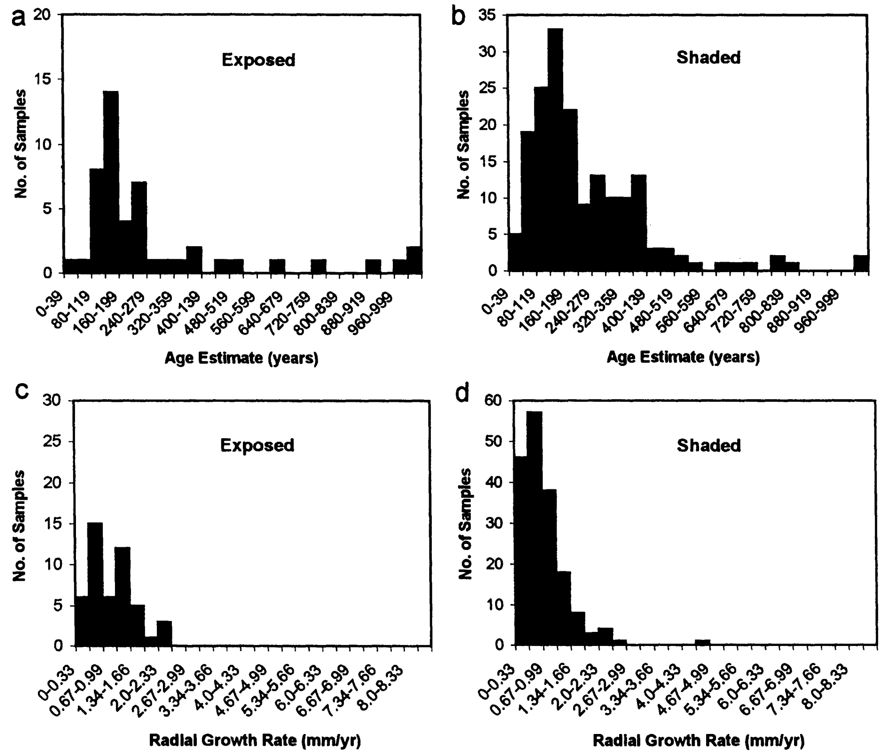

Figure 8 Frequency distribution of the estimated age (a,b) and radial growth rate (c,d) of trees sampled on cliffs as a function of exposure of the cliffs exposed to open sky (a,c), n = 48, or shaded (b,d), n = 176.

DISCUSSION

The conversion of land from natural structures and processes to ones dominated by people has accelerated over the past 200 years in North America and the southern hemisphere, and over the past 2000 years in Europe (Clark *et al.*, 1989). Vitousek (1994) presents evidence that between 40 and 50% of the terrestrial surface of the earth has been transformed or otherwise significantly influenced by people. Some have argued that this conversion of land from natural to commercial functions has reduced the area of old-growth forest in North America from over 50% to much less than 1% in the period from 1850 to the present (Paullin, 1932; Findley, 1990). In Europe, the reductions have been reported to be as significant, but have occurred over a much longer period of time, leading to the curious situation in which the term 'ancient woodland' can sometimes refer to 'continuous woodland, not to the age of the trees or to the naturalness of the stands' (Peterken, 1981; Peterken, 1996; Wulf, 1997). One suspects that the reason such a relaxed definition of 'ancient woodland' is used is because most spontaneous self-regenerating woodland in Europe is strongly influenced by people, and not populated by particularly old trees. In other words, a more strict definition of ancient or virgin woodland would lead some to the conclusion that such woodland is extinct. Peterken (1996) presents a map (Fig. 3.4) suggesting that truly virgin forests are absent from the United Kingdom, from most of Germany, and from almost all of France. Our results, however, agree with those of Stahle (1996a,b) who points out that these estimates of the amount of remaining old-growth forest ignore the large contributions that may be made by rocky low-productivity lands such as the ones studied here.

The extent of ancient forests on cliffs

The results of the present research show that conventional ideas about the magnitude of remaining old-growth forest need to be modified. Despite the limited, nonrandom, and broad-scale sampling involved here when compared with the intensive sampling that we have done on the cliffs of the Niagara Escarpment (Larson & Kelly, 1991; Kelly *et al.*, 1992, 1994; Kelly & Larson, 1997), the present results show features that are similar to what we have described before and very different from the surrounding level-ground forests that are commonly plantations in western Europe and second growth conifer or deciduous forest in North America. Old, exceptionally slow-growing, deformed, and widely spaced trees are found growing from cracks, crevices and solution pockets on most of the cliffs sampled. There is a common perception that aspect and shading have a large impact on the ecology of organisms that live on rock, but from these results we must conclude that cliff height, aspect, rock-type, and shading may have little influence on the age and growth-rate structure of these ancient woodlands. We must conclude that the ecologically important factor that governs the appearance of such forests is simply the presence of vertical rock that restricts fire and limits access by humans and their livestock. In the landscapes surrounding all of the cliffs sampled, intense human use, livestock grazing, and fire were evident and coarse woody debris was largely absent. In contrast, the cliffs showed no signs of human or animal use other than recreational rock climbing, no sign of fire, and an abundance of *in situ* coarse woody debris. In addition the vegetation community on the cliffs in different regions contains plants in many of the same genera, and even some individual species consistently recurred at many sites. We conclude that cliffs are refuge sites that support ancient forests in many temperate locations on the earth and this conclusion is consistent with the ideas of Davis (1951). Wardle (1991) and Ellenberg (1988) have observed that between 40 and 60% of the remaining endemic taxa in New Zealand and central Europe, respectively, are restricted to refuge sites on steep slopes or cliffs, and our results add significantly to these conclusions by showing precisely how old and undisturbed some of these sites can be.

Explaining the lack of previous recognition

It is not surprising that such sparsely vegetated ancient cliff forests would have escaped previous detection or have only been acknowledged by dendrochronologists (Stahle, 1997). The conventional model of 'old-growth forest' (Hunter, 1989; Kirby *et al.*, 1991; Spencer & Kirby, 1992; Peterken, 1996) places emphasis on the height, girth, age and density of trees, a large areal extent of the forest when mapped, and a low ratio of edge to interior space. Mature trees in these 'traditional' old-growth forests are massive and not necessarily slow growing but almost always in high demand in commercial forestry. In fact, the major pressure that still exists on 'conventional' old-growth forests, comes from those who wish to harvest them. Hence, it makes sense that many of those who seek to identify and protect the remaining stands of old-growth forest do so by adopting the same large erect-tree search image held by commercial loggers.

In contrast, the forests described here are composed of small, slow-growing, and widely spaced trees on a substrate that has zero area when mapped using aerial photographs. The commercial value of the trees in these forests is nearly zero. Cliff forests also have linear shapes with an exceptionally high edge to interior ratio—leading to a low assessed conservation value when viewed from the perspective of 'traditional' old-growth forest. Some workers have tried to point out that truly ancient woodland in central and eastern North America can take on very unusual forms when it occurs on rocky sites (Stahle & Chaney, 1994), but this alternate view of what ancient forests can look like has not been embraced by the mainstream community of forest ecologists. The literature generally regards the trees in such settings as mere 'bushes' (Ward, 1982; Peterken, 1996) making it extremely difficult to have these sites recognized as any kind of 'forest'.

For example in the United Kingdom, Rodwell (1991) interprets areas of cliff and rock outcrop dominated by *Taxus* to be components of mixed deciduous vegetation, or an unusual northern outlier of *Taxus* woodland found throughout south-east England, but the possibility is never acknowledged that such rocky sites themselves represent a type of free-standing ancient woodland or forest. Most of the literature argues that *Taxus* regeneration requires shading, a nurse cover of Juniper, and steady supplies of precipitation for seedlings (Watt, 1926; Williamson, 1978; Hulme, 1996). In our experience young *Taxus* plants rooted directly in rock and fully exposed to direct radiation and wind were found on most of the cliffs where mature *Taxus* was present. This kind of observation leads us to believe that cliffs dominated by stunted slow-growing *Taxus* or *Juniperus* in Europe, or *Juniperus* or *Thuja* in North America may represent a primary forest type from which these species expanded following the appearance of habitat openings caused by people. The presence of fruit on all of the trees sampled suggests that all of taxa studied could migrate to adjacent habitats from refuges on cliffs. Several authors have suggested that this may be true (Godwin, 1956; Marks, 1983; Ficht *et al.*, 1995).

CONCLUSIONS

We conclude that temperate-zone cliffs in general have ecological properties in common with the Niagara Escarpment in southern Ontario, Canada, including the property of supporting ancient, primary or virgin woodland. We also believe that these cliffs have been overlooked as sites that support such ancient woodland for many of the same reasons that applied in southern Ontario, namely the small size and unusual appearance of the forest. When one considers the high rate of encounter with ancient trees that we experienced while sampling these cliffs and the relatively modest sampling effort that was executed by us at any one site, it would appear that future intensive studies of the structure and function of cliff forests around the world will be extremely productive within the context of the identification and preservation of primary natural and ancient forest.

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BIOSKETCH

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