Title Early successional processes of basaltic lava ecosystems on Mt.Etna (Sicily) with additional comparative studies of Mauna Loa (Hawaii)

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2004

University of Luton

Early Successional Processes of Basaltic Lava Ecosystems on Mt.Etna (Sicily) with additional comparative studies of Mauna Loa (Hawaii)

by

M. P. Carpenter M.Sc.

A thesis submitted to the University of Luton in partial fulfilment of the requirements for the degree of Doctor of Philosophy.

January 2004

Early Successional Processes of Basaltic Lava Ecosystems on Mt.Etna (Sicily) with additional comparative studies of Mauna Loa (Hawaii).

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Abstract

Primary succession on the basaltic lava flows of Mt.Etna was studied using chronosequence theory to investigate the first 500 years of ecosystem development. Separate experiments were conducted to look at how plant species, nutrient availability and lichen activity on the lava changed over time under different conditions based on the site location (age, aspect and altitude on the volcano). By comparing the results of these different areas of study, close links were observed between soil development and nutrient availability. Lichens were found to be an important stage in primary succession introducing biomass to form a developing soil as well as weathering the lava surface. The plant species present on the lava were found to change as plants first colonised the lava and were then replaced as further species appeared over time. Nutrient availability was investigated in living plant material by measurement of the enzyme nitrate reductase and also in the developing soil. Two large inputs of nitrogen were observed in the chronosequences. An early input believed to be lichen derived and another steadily increasing input associated with the soil. The biomass of the nitrogen fixing lichen *Stereocaulon vesuvianum* on the lava flows was found to change over time with a rapid increase over the first 100 years of the chronosequence followed by a slower decline as competition and shading from vascular plants covered available habitat. *S.vesuvianum* was also found to be an efficient weathering agent on the lava altering the surface morphology. This weathering was observed qualitatively by detailed visual examination of the lava surface by scanning electron microscopy. Weathering was also measured quantitatively using an intelligent machine vision computer system, to collate the surface changes of many images simultaneously and compare surface change to a baseline chronosequence, allowing discrimination of fine differences in the extent of weathering. Two of the experiments conducted on Mt.Etna (nitrate reductase activity and lichen weathering) were repeated on a second volcano, Mauna Loa (Hawaii). This tested if the trends observed on Etna were typical of primary succession on lava and the impact of a different climate regime (tropical) compared to Etna (temperate). Nitrate reductase activity was found to be very

low in the primary colonising species studied on Hawaii indicating that nitrogen is limited on the early lava flows. Lichen weathering by *Stereocaulon vulcani* on Hawaii was found to occur in a comparable manner to *S.vesuvianum* on Etna, and was similarly controlled by the lichen biomass and associated climatic conditions.

Quotations

"From such a mountain mouth as breathes fire and smoke over Sicily came forth the stern king of Hades, to drive in his iron chariot across that fair isle, where the ground heaves beneath fruitful crops, and ruin is strangely mingled with the richest green."

From the story of Persephone and Hades, Classical mythology.

"Nature is a process, not a state – a continuous process. A striving to keep alive. No species has the *right* to exist; it simply has the ability or the inability. It survives by matching its fecundity against the forces that threaten it with destruction. It may appear for a time to have struck a balance, a fluctuating balance, but it has not. All the time there is change - change of competitors, change of environment, change of evolution – and sooner or later any species will prove inadequate and be superseded."

Taken from John Wyndham's "Web."

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Declaration

I declare that this thesis is my own unaided work. It is being submitted for the degree of Doctor of Philosophy at the University of Luton. It has not been submitted before for any degree or examination in any other University

Michael Carpenter 9 / 1 / 2004

Acknowledgements

Thanks to all…

To my parents for their continuing support for my need to further my education – and for continually asking "haven't you finished it yet?" which was an unending source of irritation and encouragement to finish.

To my colleagues in Luton:

David Orwin for his unfailing support, encouragement and assistance during the field work and subsequent write up. Angus Duncan for his huge help during course of this project and having to read all these chapters about green things! Peter James, for his invaluable insights into soil development and letting me use the Liverpool University soil laboratories. Pauline Oliver, for help in the field work on Etna. Roy Wood for his great assistance in using the SEM. And finally the graduate school, whose faces may have changed over the years – but there's usually been someone up for a beer at the end of the day.

To my colleagues in Italy:

Professor Emelia Poli and Virginia Puzzulo from the Ecology department of Catania University. Dr.Annamaria Panico of the Biochemistry and Pharmacology department, for the loan of equipment and chemicals for the NR work on Etna.

To my colleagues in Hawaii:

To Professor Peter Vitousek of Stanford University for allowing me to join his group in Hawaii for the summer field season and his invaluable knowledge of the Hawaiian ecosystems. Dave Penn and the Stanford PhD students lucky enough to be working on Hawaii full time for their help and company during the Field trip. And finally Heraldo Farringdon for his huge assistance in getting me to my sites and willingness to use his shotgun to get me leaf samples from the tops of the trees.

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Chapter 1: Introduction

1.1. Succession

Succession is often referred to as the first major ecological theory and was first proposed by Clements (1916). A loose definition would describe succession as 'a directional change in species composition, whether in terms of species present or of their relative abundances' (Grubb 1986). However a complete definition of the process must include the three main trends: **1)** It is a time dependent process with changing vegetation characteristics such as density, cover and species richness, diversity and composition, **2)** it results from a modification of stress and disturbance regimes, **3)** it changes ecosystems which are unstable to stable, concerning cover, biomass and/or diversity information content (Glen-Lewin *et al* 1992; Tsuyuzaki 1995). This change can often be seen as a clear progression in vegetation change as propounded by Clements (1916) but is more often a more random occurrence of chance events or discontinuities (Gleason and Cronquist 1964). For example the migrations of some plants at different times of the year may lead to a different species colonising an area first.

This replacement of species over time can usually be divided into two distinct types: primary and secondary. Primary succession is the establishment and subsequent development of the first assemblage of species on a previously unvegetated surface (Miles and Walton 1993). It only occurs following the destruction of biosystems where the ground surface is covered by rocks and/or inorganic soil substrates (Vitousek and Walker 1987; del Moral and Bliss 1993; Bradshaw 1983). In essence, this is where nature is starting from scratch on a completely raw substrate where plants and animals have not existed before. These conditions are rare in nature and occur only in areas such as sand dunes, mountain scree, lava flows, tephra cover and freshly exposed moraines due to glacial retreat (Miles and Walton 1993).

Secondary succession, is distinct from primary succession and can be defined as 'the changing pattern of dominance by species present through most or all of the succession period'. This process is usually initiated by a sudden catastrophic event which strips away the dominant vegetation, whilst leaving the soil structure, nutrients and seed bank intact. This can occur in two particular forms. 'Internal successions' that are part of the natural regeneration process in many types of vegetation (Grubb 1986) and 'Man-induced succession' on sites such as old-fields and forest clearcuts. For example, if a forest is felled, the initial regrowth will incorporate elements of the old vegetation (from the seed bank and root stock) as well as new species which move in to exploit the new conditions (e.g. increased light availability). These species are commonly recruited from a wide range of habitats and have not evolved together to the same degree as species involved in 'internal succession.' Normally, gaps caused by natural events such as fire, flood or animal activity are re-colonised by species that are an integral part of the community. Examples of this vary, from the fires that frequently decimate the eucalyptus forests of Australia, (and hence cause the seeds from many species to germinate), to wind felled trees in the rainforest, which open gaps in the canopy, allowing other species present in the seed bank to exploit the light.

In order to study primary succession there are several key processes that need to be considered:

1) Colonisation:

   This is the obvious first stage. The plants must first arrive and colonise the new substrate. In order to do this these species must *be available in the vicinity* and able to *disperse* effectively. This can lead to a stochastic effect on the succession as some areas closer to the edge are more readily colonised. The different dispersal mechanisms employed by the plants may also influence this. For example a wind-borne coloniser like a lichen which produces huge amounts of spores and fragments capable of colonising a bare surface will arrive on the whole of a new surface practically simultaneously. In contrast seed plants may require alternative methods of dispersal (e.g.

animals) which produce a time factor of colonisation as they move in from the edge and this adds to the heterogeneity of the system.

2) Establishment:

   This is closely related to the colonisation of the substrate – after all it is no use if what arrives cannot become established and this is controlled by the ability of the species to survive in the new harsh environment. This is controlled by seed *germination,* as the plants will not be able to germinate until the conditions are favourable. So here is a process of *selection* in which only those species adapted to the conditions can survive (Bradshaw 1993). As the conditions change over time (sometimes brought about by the plants on the surface at the start – e.g. producing a precursor soil) new species colonise the surface and a true succession occurs as new species replace the old. This is further controlled by *species interaction* and may lead to the formation of *facilitation* effects (symbiosis) which cause beneficial interactions or *inhibition* effects (competition) which cause negative interactions leading to species exclusion.

3) Growth:

   Nothing will happen on a substrate if the plants cannot grow. This can only be achieved by the *acquisition of nutrients* by the plants. This leads to a consideration of the sources of nutrients and their subsequent build up and recycling through the ecosystem. For example nitrogen is very important for plant growth and is usually extremely limited on early ecosystems as it must first be fixed and then cycled through the system. Many influences can affect the *nutrient accumulation* during succession as the sources of nutrients may be allogenic (weathering and inputs of nutrients from the air) or autogenic as the actions of living organisms (nitrogen fixation, organic matter accumulation and cycling processes).

The purpose of this project is to investigate each of these processes in turn occurring on the newly formed substrate of lava. This study investigates changes over primary successional period from the initial bare substrate, to the development of complex communities, as the lava flows are initially colonised by cryptograms (lichens and mosses), then by seed plants (annuals and shrubs) and tree seedlings leading to a forest ecosystem. In order to follow this succession a methodology has been employed utilising the relatively new idea of chronosequence theory.

1.2. Chronosequence Theory

One of the many problems faced with studying successional processes is the time that must elapse before an appreciable change can be measured. In the short term, permanent plots or quadrats can be set up which allow continuous monitoring of the vegetation change. This direct observation of vegetation change with the associated factors of soil development, nutrient accumulation and climatic variation, produce incontrovertible evidence of successional development over time. In other words, it is possible to document change that has actually happened. Studies of primary succession on tephra deposits on Krakatau (Whittaker *et al* 1989; Thornton 1997) fresh lava on Hawaii, (Smathers and Mueller Dombois 1974; Kitayama *et al* 1995) and the recently de-glaciated terrain of Glacier Bay (Crocker and Major 1955) are all of this type. This is clearly the best form of study for looking at succession, if it could only be done over a long enough period. However, given that the development of the more complex ecosystems (e.g. forests) can take from hundreds to thousands of years, this is clearly impossible. Therefore, when looking at successional development over long periods other methods must be employed.

For long term studies a chronosequence or 'substitution of space for time', can be employed (Aplet and Vitousek 1994). In this case a series of sites of different ages are selected, where the successional processes can be studied in terms of vegetation change and concurrent changes in soil nutrient content. At each site measurements of plant species presence, abundance, percentage cover can be taken simultaneously with nutrient availability in the soil and plants. Each of these sites is then assumed to represent the dominant vegetation / nutrient status of the succession at a particular time, giving a series of 'snapshot' pictures of ecosystem change and development over time. Inherent in this method, is the assumption that each site in the study will develop over time to produce the same ecosystem represented by the next 'snapshot,' and is subject to the same environmental conditions. When using this theory consideration must be given to minor topographical and environmental differences in the sites as these could cause variation in the outcome of the successional processes.

As such, in a chronosequence, great care must be taken to ensure that the only important variable affecting plant succession is the time elapsed since the deposition of the substrate. Other factors capable of influencing vegetation development include: climate, organisms (e.g. grazing), relief and parent material. It is often difficult to locate sites where these factors can be controlled. However, where these factors can be controlled (e.g. by selecting sites at the same altitude) the chronosequence approach can be very useful in predicting ecosystem change and development. This was proved by Foster and Tilman (2000), who tested the validity of the chronosequence by monitoring permanent plots over a 14-year period on a chronosequence of 19 old-field sites. They concluded that the initial static chronosequence survey (essentially the year 1 data) accurately predicted many of the observed changes in species abundance and confirmed the validity of the method in its approach to infer basic patterns of successional change.

1.3. Volcanic ecosystems

1.3.1. Volcanic activity

Volcanoes are a common feature around the globe, and reflect internal processes in our dynamic planet. There are some 600 active and several thousand extinct volcanoes on the continents or exposed above the sea as islands. 40 % of all the rock in the Earth's crust is basaltic (much of it intrusive) which is the major rock produced by volcanism (Press and Siever 1986). Many volcanoes erupt harmlessly and may be regarded as beneficial, as most materials erupted by volcanoes are rich in valuable nutrients. A layer of volcanic ash scattered in the fields stimulates yields almost as much as artificial fertiliser. For example, excellent crops were produced after the eruption of Mount St.Helens in 1980 (Dale 1988; 1991; Scarth 1994; del Moral *et al* 1995). Weathered volcanic soils like those on the lower slopes of Etna are amongst the richest in the world. This topic will be discussed further in the soils chapter (4) of this thesis.

Volcanoes can also cause massive changes in local and global climatic conditions simply by injecting huge volumes of gas and dust into the atmosphere. For example the huge eruption of Tambora on 10-11 April 1815 produced about 150km^3 of ash, more than any other known eruption in the last 10,000 years. The ash cloud rose about 43km into the stratosphere and spread around the world. Within three months the eruption was causing optical effects in the atmosphere of Europe. During the next year, 1816, the summer was cool wet and gloomy and resulted in crop failure and famine – almost certainly precipitated by the Tambora aerosol cloud (Huggett 1995).

Continuing work on colonisation patterns of flora and fauna on islands over time such as Krakatoa (Thornton 1997) and Surtsey (Fridrickson 1975; 1989) are increasing our knowledge of biogeography and evolutionary pressures and processes.

1.3.2. Volcanic substrate types

Volcanic substrates vary greatly and strongly affect the rate of succession depending on its topographical, morphological and elemental composition. Blong (1984) and del Moral (1993) described six major substrate types: Lava, Pumice, Scoria, Pyroclastic flow deposits, Lahars and Tephra. Each is the result of, or a consequence of different eruption events. However, this is a bit of a misnomer as Pumice, Tephra, Scoria and Pyroclastic flow deposits can all be defined as 'Pyroclasts'. These variations in substrate greatly affect both the speed and the subsequent outcome of the succession.

1. Lava

Lava is molten rock or magma extruded from craters or vents which solidifies on cooling. It can vary in composition from the rhyolitic forms, which are high in silica to the basaltic forms, which are low in silica. Lava is a difficult surface for plants to colonise due to its thickness, hard surface and typically large extent. This substrate undergoes succession very slowly as most plants cannot grow on the surface until a soil structure has formed (even if this is just a scrape or hollow in a rock filled with wind blown debris). As a result mosses and lichens dominate early succession on exposed lava surfaces (Eggler 1963; Kurina and Vitousek 1999). A great many factors can alter the rate of colonisation of this material, resulting in a lava field often having concurrent successions developing at different rates on separate sections of the flow (e.g. distance from edge, altitude, climate and amount of wind blown debris or pyroclasts). This substrate comes in many different morphological forms and which are covered in greater depth later in this chapter. Few authors have looked at primary succession on lava.

2. Pyroclastics - Tephra

Tephra includes all airborne materials ejected form a volcano. But divided into three principal forms:- **ash** (size <2mm), **lapilli** (between 2 and 64mm) and **blocks / bombs** (size >64mm). Tephra can cause a great deal of damage by clogging plant pores and even snapping off the leaves of plants (Kent *et al* 2001). Whittaker *et al* (1989) studied the effects of ash on islands neighbouring Krakatoa. However, usually only thick deposits kill vegetation as many species simply re-grow up through the deposit (Kent *et al* 2001). Eruptions on Mt.Katmai (Griggs 1932) and Paricutin (Eggler 1963; Rejmanek *et al* 1982) provided early opportunities for studying the effects of deep tephra deposits. However, the impact of tephra may be more important in the development of soil on open lava, as it provides a base of fine material for roots; aids in water retention and a provides a ready supply of nutrients as it weathers.

2.1. Fall deposits – Pumice and Scoria

Pumice consists of pale volcanic fragments riddled with gas holes, formed by the expansion of contained gases as the magma reaches the surface, and exploded violently over vast areas during an eruption (Scarth 1994). It is difficult for plants to invade due to low nutrient status and surface instability (del Moral 1993). Plant colonisation requires stable substrates followed by amelioration.

Scoria is basaltic vesicular ejecta. It is denser than pumice and weathers readily. It occurs on volcanoes such as Mt.Etna and Mauna Kea. This substrate has a tendency to be local to particular volcanoes. All the cinder cones of Etna are composed of scoria as are large areas of Surtsey (Fridrickson 1975).

2.2. Pyroclastic flow deposits

Pyroclastic flows (also known as nuée ardente) describes an incandescent cloud or glowing avalanche of hot gas and fragments of all sizes, including ash, cinders, pumice and rock debris in an aerosol-like emulsion expelled by explosive eruptions, which travels across the ground at very high speeds and gives off billowing clouds (Scarth 1994). Plant colonisation of the flow deposits is usually slow (Beard 1976) although after a few years dispersal barriers may inhibit colonisation more than substrate conditions. Mount St.Helens located in south-western Washington state, which erupted on 18th May 1980 generated extensive pyroclastic flow deposits. Many studies have been conducted into successional processes on this substrate, (del Moral 1981; 1993; del Moral and Wood 1993a; 1993b; Titus and del Moral 1998).

3. Lahars

Lahar is an Indonesian word used to describe a volcanic mudflow commonly formed when an eruption melts part of an ice-cap; disturbs a crater lake; or even the mobilisation of tephra by heavy rainfall (Mt.Pinatubo is an example of this). These mudflows travel down-slope at high speed destroying everything in their path (Scarth 1994) producing a stripped surface ready for primary colonisation. However, the water saturated debris often picks up seeds, rhizomes and other organic material that can rapidly initiate succession once deposited. The 1980 eruption of Mount St.Helens (del Moral 1998) generated several lahars caused by the rapid glacier melt during the early stages of the eruption.

1.3.3. Primary succession on volcanoes

Primary succession following volcanic eruptions is perhaps the least well documented form of succession. The continuing study by Fridrickson (1987) on Surtsey is a good example of volcanic succession but the isolation of the island is a factor in the slow rate of colonisation of the lava. A great many studies of island biogeography and invasion of colonising species are a direct result of volcanic activity producing 'new' volcanic islands such as Surtsey (Fridrickson 1975; 1987) and Krakatoa (Whittaker *et al* 1989; Thornton 1997; Whittaker *et al* 1999).

Lava substrates produce an excellent opportunity for research on successional processes. Often the age of a lava flow may be known to a high degree of accuracy (especially in historically long inhabited areas) since volcanic eruptions can be important events to chronicle. In addition, it is relatively easy to select sites in order to control for the factors affecting succession outlined above (e.g. select all sites at the same altitude). Since lava flows often occur at the same climate, altitude, aspect and can be separated by relatively short distances, these factors can be isolated - provided that an allowance is made for minor variations in the substrate. This last problem can often be compensated for by careful selection of sites whilst accepting the fact that over time weathering processes will have changed the initial morphology.

1.3.4. Lava Morphology

Basaltic lava shows great variation in morphology between two extremes (Peterson and Tilling 1980; Pinkerton and Sigurdson 1987; Kilburn 2000). Relatively fluid lava erupted with low rates of shear, forms '*Pahoehoe*' lava, which is generally smooth or ropy (Fig 1.1). 'A*a*' lava is created by relatively viscous magma emplaced with high rates of shear, forms rough rubbly lava made up of many separate blocks, which are irregular and spinose (Fig 1.2). These differences in morphology can have a profound effect on plant colonisation. The smooth pahoehoe substrate produces a surface far more resistant to colonisation by plants, with the exception of cracks in the lava sheet, where plants can gain a purchase (Eggler 1971; Smathers and Mueller Dombois 1974; Drake 1992). These cracks provide a 'safe site' for colonisation by concentrating water and nutrients from 'micro-watersheds' on the surface of the flow (Aplet *et al* 1998). This produces a disjointed colonisation process, where the cracks support a high diversity of plants while the bulk of the surface is too smooth to allow colonisation of anything other than crustose lichens and mosses. Eventually, the areas of high diversity spread out over the surface of the lava by depositing organic material over the ropy surface and by weathering action breaking up the lava sheets.

In contrast, the aa form is colonised by lichens almost immediately and the greater surface area affords a growth advantage due to higher availability of nutrients or to the provision of an aerated root system (Aplet *et al* 1998). This lava initially has a relatively low vascular plant diversity, until a sufficient soil structure has formed in the large interstitial spaces between the lava blocks. Once a sufficient soil structure has formed the whole aa lava surface is colonised, producing a high biomass. These attributes are illustrated in Fig 1.3.

Figure 1.1. Pahoehoe lava form on Hawaii, note the relatively smooth and ropy structure. (Picture by M.Carpenter).

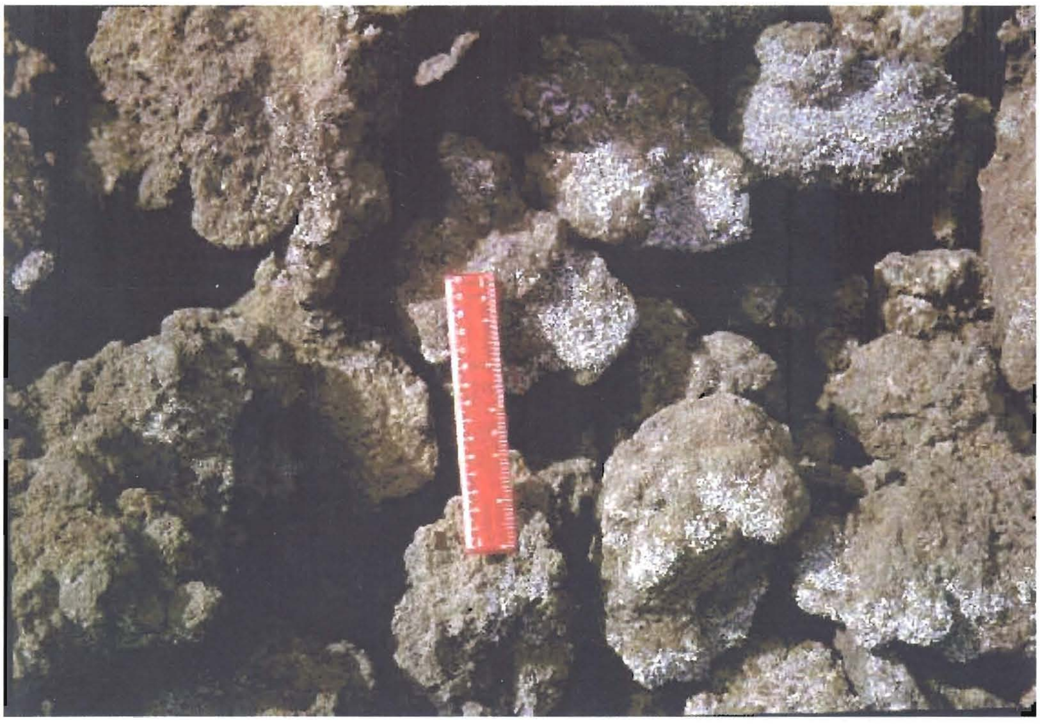


Figure 1.2. aa lava form on the 1981 lava flow of Mt.Etna. The surface of the lava is separated into many irregularly shaped blocks. The white areas are the lichen *Stereocaulon vesuvianum* (Picture by M.Carpenter).

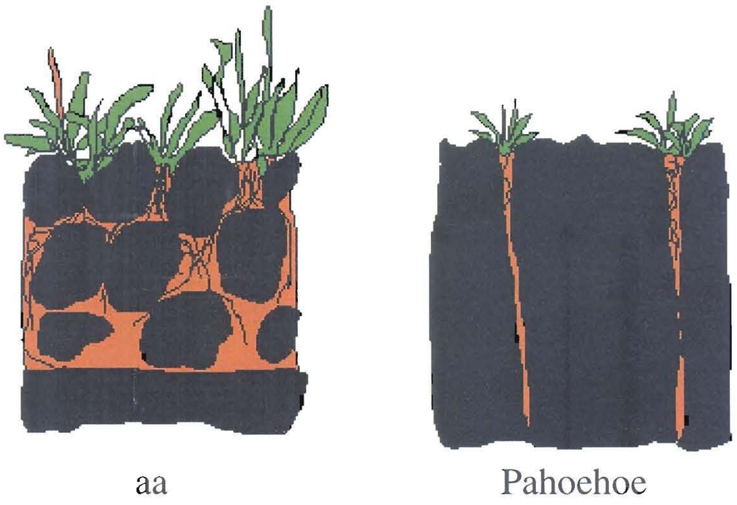


Figure 1.3. Colonisation of the different morphological types of lava with the greater plant biomass found on the aa type, where black denotes rock and brown is soil. Initially the pahoehoe form produces a higher species diversity as nutrients become concentrated in the cracks.

Between these two extremes of lava there are many intermediate types (sheet pahoehoe - slabby pahoehoe, large boulder aa – clinker type) and many lava flows incorporate many of the different types as different areas of the flow, reflecting the complexity of flow field formation. This results in surface heterogeneity, which is subject to differences in colonisation and succession (Chapin and Bliss 1988; Bjarnason 1991; Pinder *et al* 1997). However, as mentioned previously, this can be controlled by careful site selection.

1.4. Volcanoes studied for the project

This project is primarily based on chronosequences of lava flows on Mt.Etna (Sicily), which has a wide spread of available lava flows covering many different aspects and altitudes - and hence climatic conditions. However the second part of the project compares Mt.Etna with several lava flow fields on Mauna Loa on the Big Island of Hawaii . Both of these volcanoes were chosen as they each have a large spread of accurately dated lava flows, of similar chemical composition yet both have variable climatic conditions.

1.5. Mt. Etna

Mount Etna (Fig 1.4), situated on the east coast of Sicily (Fig 1.5), is one of the most active volcanoes in the world (Chester *et al* 1985). Periodic eruptions have produced a large number of dated historic lava flows, of basaltic composition with remarkably consistent chemistry, extending back over several thousand years. These flows range in altitude from over 3000m at the summit to sea level on the eastern flank (Chester *et al* 1985). In addition, lava flows of both aa and pahoehoe morphology occur on Mt. Etna. Accordingly it is possible to put together well-defined chronosequences that vary strongly and largely independently of aspect, precipitation and parent material, but are very similar in other respects.

Figure 1.4. Mt.Etna (Picture by M.Carpenter).

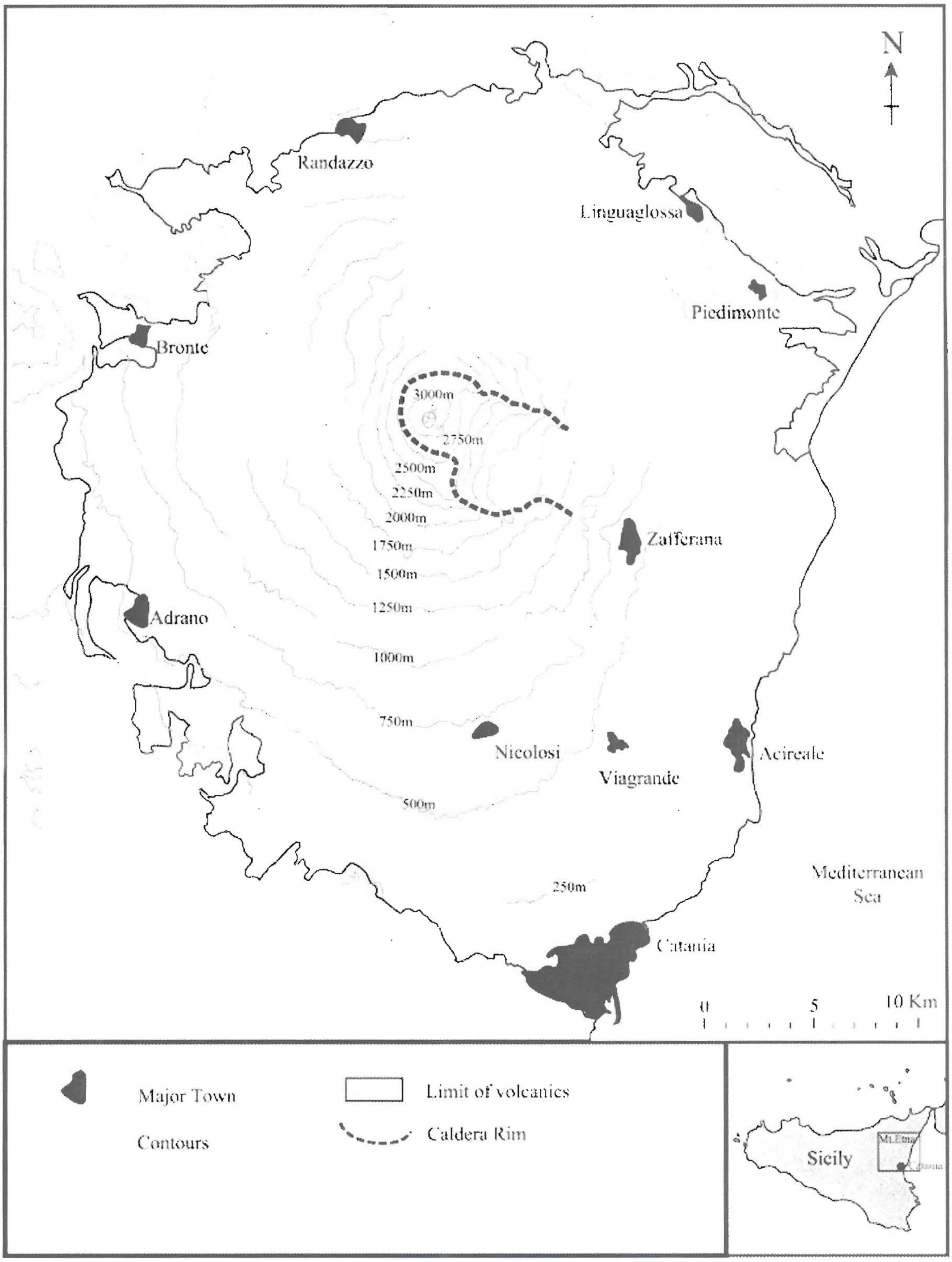


Figure 1.5. Topographical map of Mt.Etna showing the principal towns and its relative position in Sicily.

1.5.1. The Climate around Mt.Etna

The climate of Mt.Etna varies quite substantially around the volcano with both aspect and altitude (the orographic effect) which combine to produce a series of sectorially and altitudinally defined zones. There is detailed climatological data from weather stations in most of the principal towns and villages located around the volcano. However the spatial coverage of the stations decreases with altitude and near the summit area observations have only been made at the observatory of Serra la Nave. The east facing aspects (north-east, east and south-east) show markedly higher annual rainfall than the west. (Fig 1.6). However, this increased rainfall is seasonally orientated, with the higher rainfall occurring during the winter/spring period (Fig 1.7).

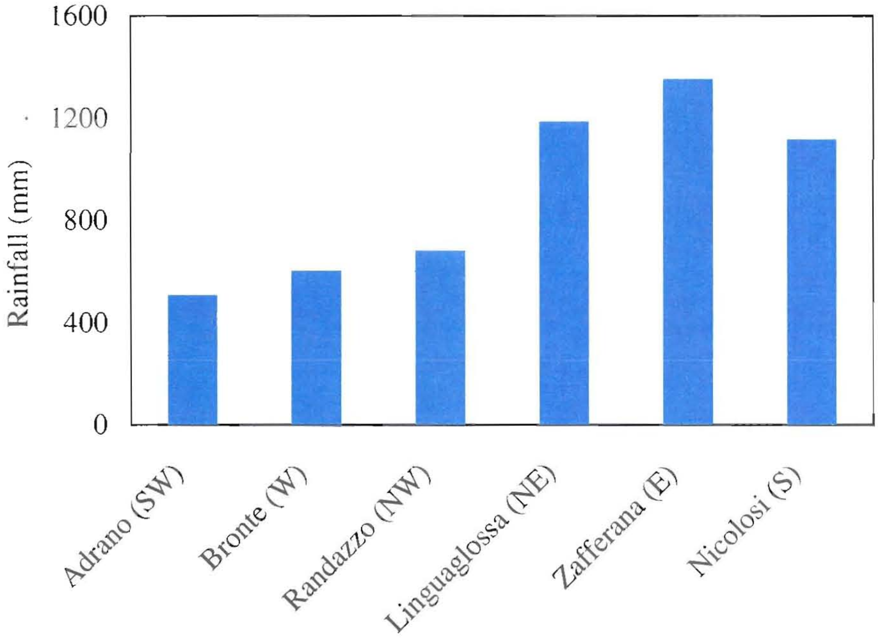


Figure 1.6. Average annual precipitation from meteorological stations in the principal towns from the different aspects of the Mt.Etna. (Raw data compiled and presented via personal communication from V.Puzzulo)

Figure 1.7 shows the standard climate diagrams used in biogeography (an example can be seen in Mueller-Dombois 2000). Each graph is divided into months (x-axis) and temperature (10°C intervals) on the left y-axis and precipitation (20mm intervals) on the right y-axis. Within the body of the graph is the curve for mean monthly temperatures (lower line) and the curve for mean monthly precipitation (higher line). The different shading where these lines overlap indicates seasonal changes in climate. The relative period of drought (dotted), relative humid season (vertical hatching), and the period when mean monthly precipitation exceeds 100mm (black). For example a large dotted area shows a very hot and dry season, whereas a large area of black shading would indicate a very wet season (rainforests typically show this as occurring all year).

The greatest difference in climate on Etna can be seen by comparing the weather data for the towns on the west and east aspects of the volcano. Adrano in the west shows a very low average rainfall pattern all year round with a dry season extending for five months from the end of April to the beginning of October (Fig 1.7). This compares to Zafferana in the east, which has a smaller dry season (four months), and a wet season which commonly exceeds over 100mm of rain. Durbin and Henderson-Sellars (1981) used older precipitation data to form a contoured precipitation map for Mt.Etna. This also shows the same rainfall change with altitude and aspect, this has been adapted for Fig 1.8.

In addition to the variation caused by aspect, there is a marked change in precipitation due to altitude. This is demonstrated in Fig 1.9 (data from Poli *et al* 1981) where annual rainfall measured at three sites of increasing altitude on the south aspect of the volcano clearly increases.

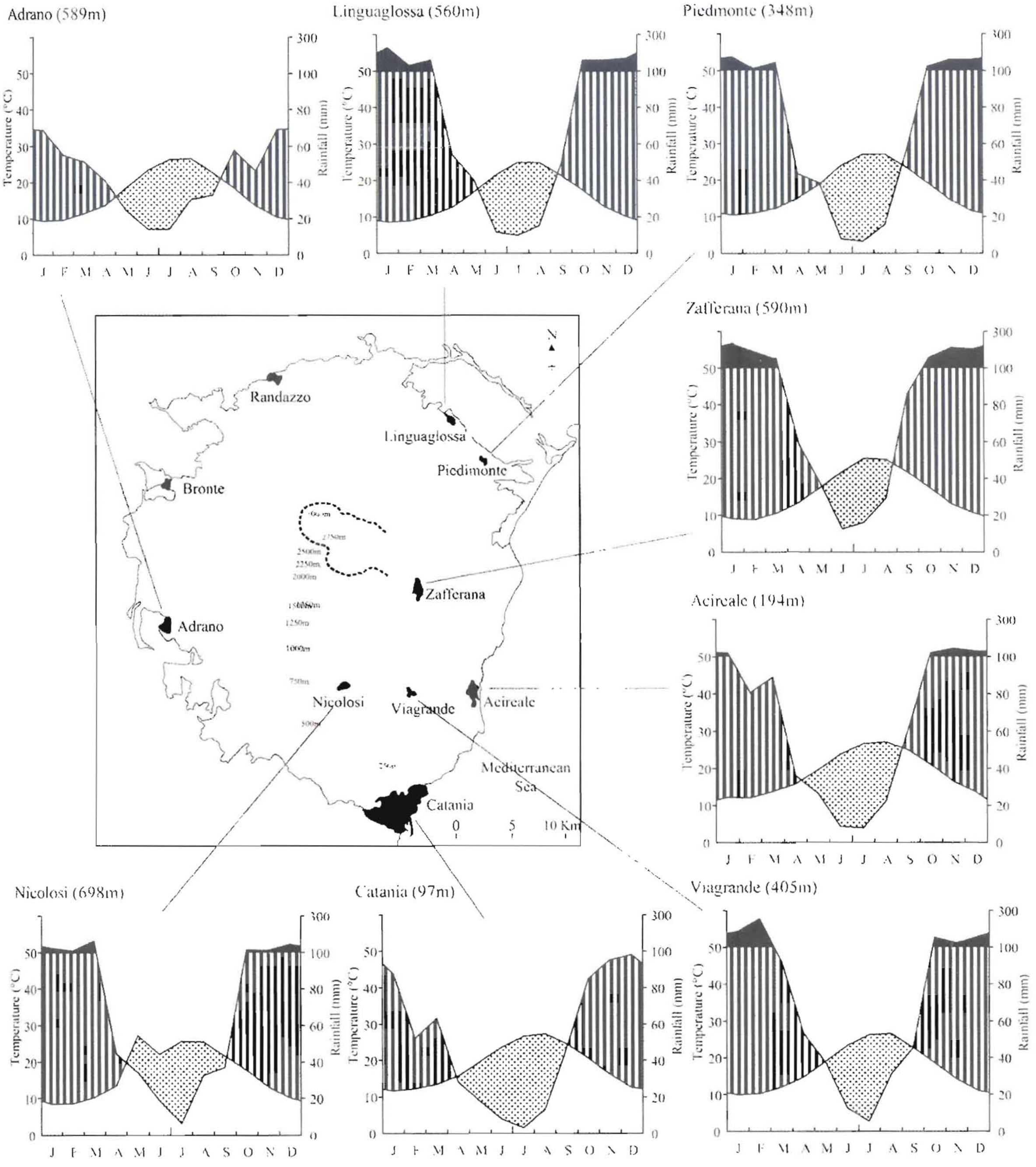


Figure 1.7. Standard graphs of climate from meteorological stations in the local towns around Mt.Etna. (Raw data compiled and presented as personal communication from V.Puzzulo)

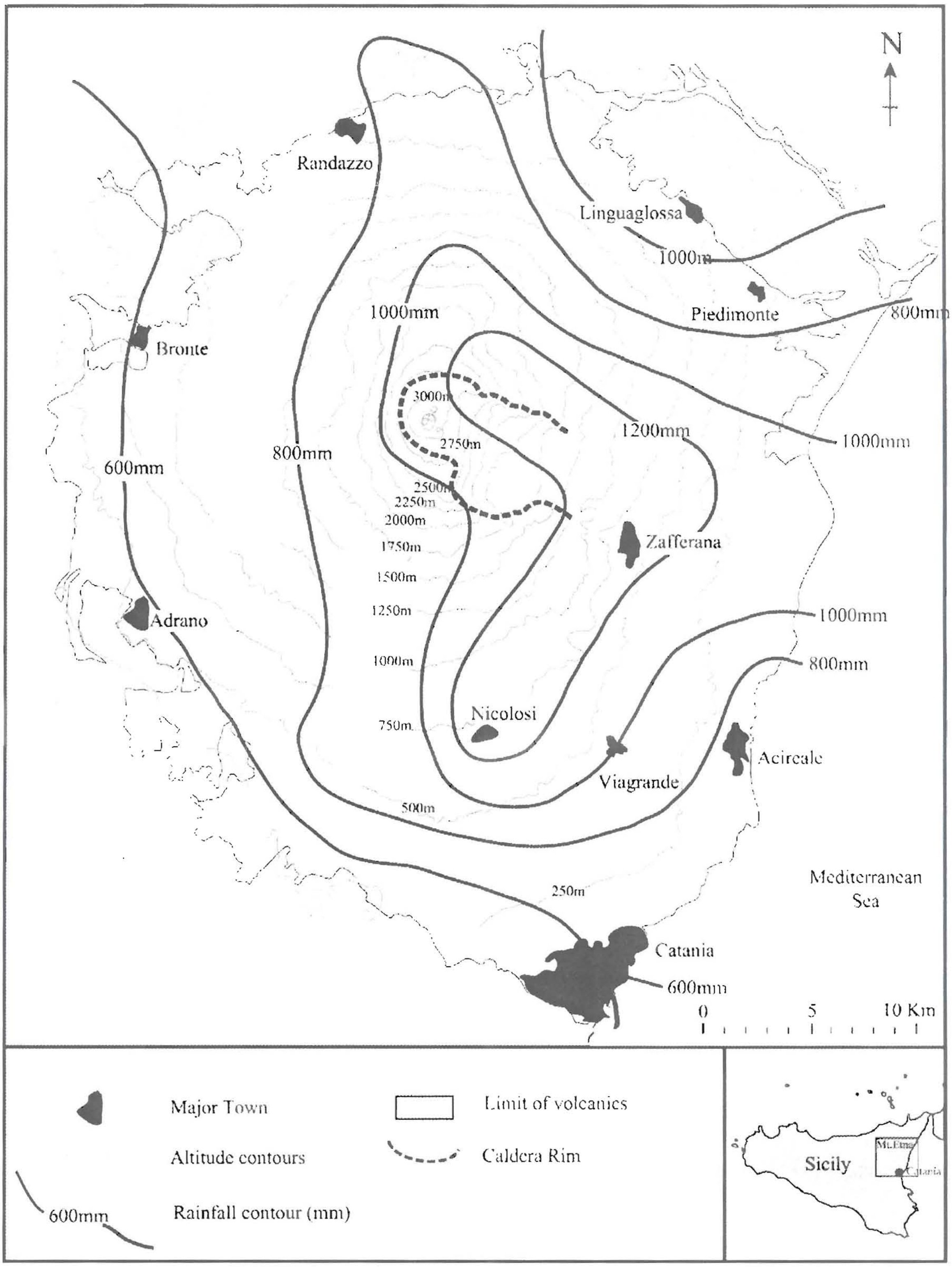


Figure 1.8. Mean annual rainfall on the slopes of Mt.Etna. Adapted from Durbin and Henderson-Sellers (1981).

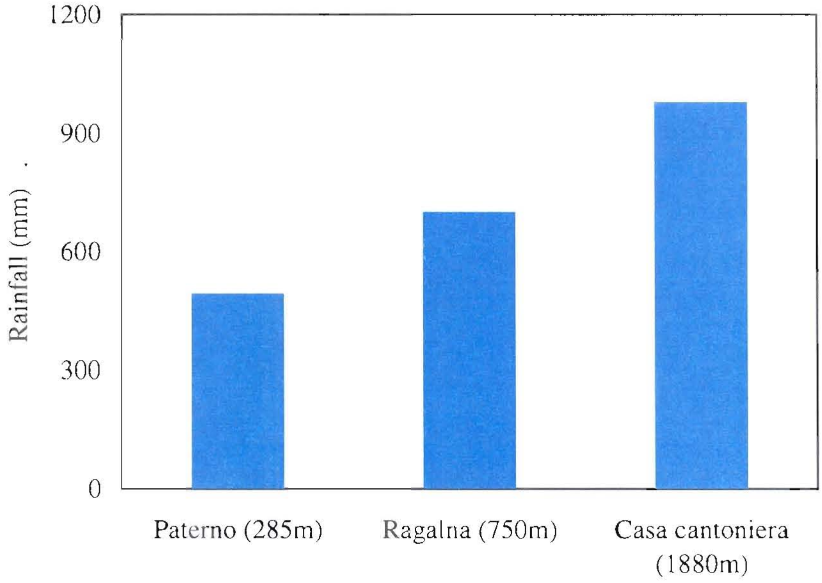


Figure 1.9. Increasing annual rainfall with altitude on the south aspect of Mt.Etna (data from Poli *et al* 1981).

This trend for increasing rainfall with altitude is also seasonally orientated as can be seen in Fig 1.10. The temperature drops substantially as altitude increases, such that Serra la Nave at 1725m does not exceed 20° even during the summer months (Fig 1.10). The extent of the dry season is also clearly decreasing with altitude (as the dotted area shrinks) such that it lasts for only three months at 1725m, but extends for a full six months in Catania (97m).

Although there is seasonal change in the climate of the Etna region, as well as variation from year to year, there has been no significant long-term climate change over the last 2000 years. This has been shown by the research of Sadori and Narcisi (2001) who discovered that there has been no perceptible climate change in Sicily for the last 2000 years by researching lake sediments. Although there have undoubtedly been short periods of climate change (e.g. the 'little ice-age' in the sixteenth century) these have not caused significant vegetational changes and therefore do not affect the chronosequence methodology. This is an important factor in this project as one of the primary tenets of using chronosequence theory is that environmental factors should remain as constant as possible.

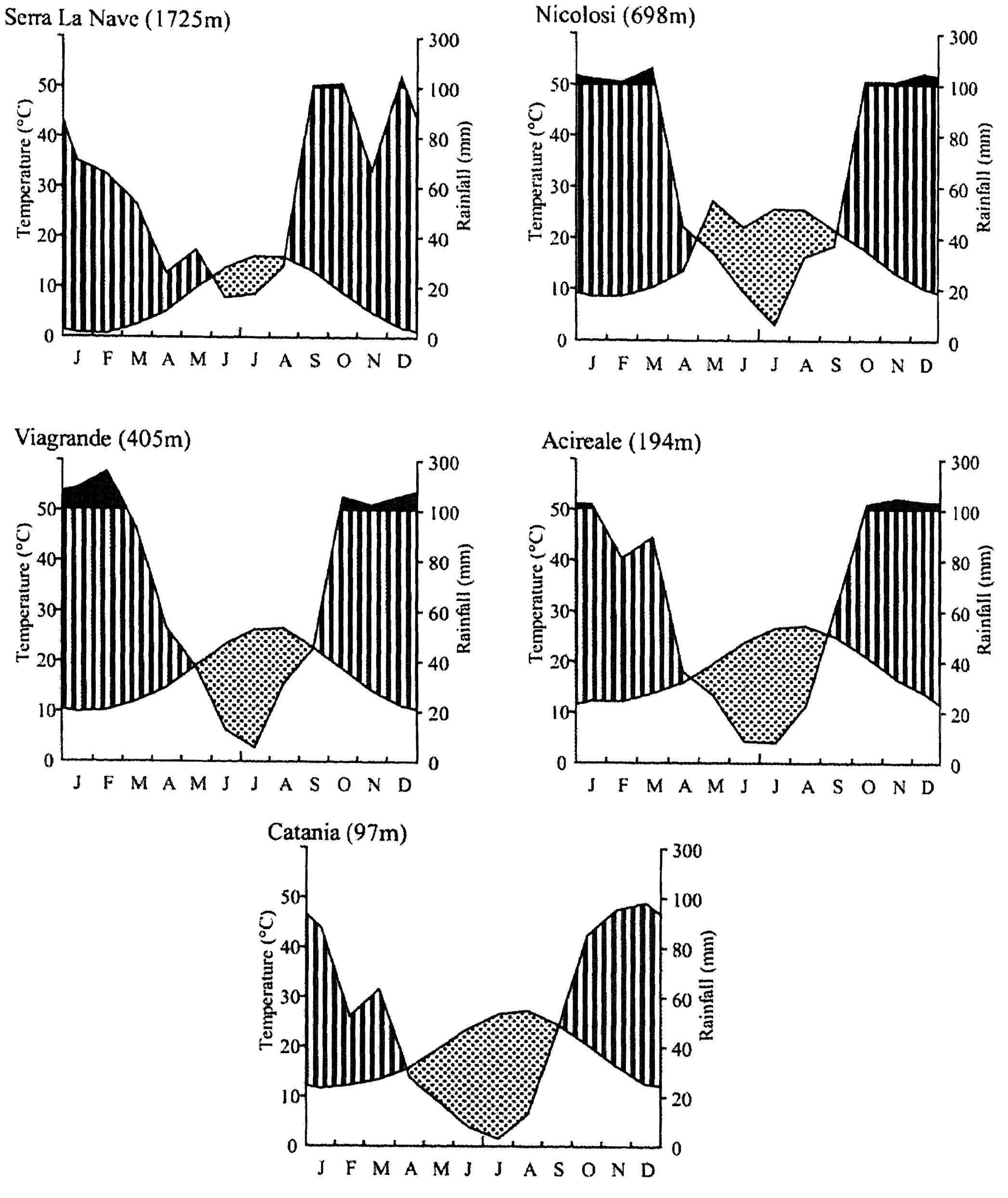


Figure 1.10. Standard graphs of climate from the south aspect of Mt.Etna over increasing altitudes. Raw data compiled and presented via personal communication from V.Puzzulo. Serra la Nave data from Poli *et al* 1981.

1.6. Mauna Loa - Hawaii

The second volcano studied as part of this investigation was Mauna Loa on the Big Island of Hawaii. This volcano was chosen as many of the environmental variables of age, aspect and lava morphology can all be selected for by careful site selection in the same way as Mt.Etna. In addition, the lava of Mauna Loa has a very similar chemistry to that found on Etna (see appendix p270), which excludes substrate variation as a factor. However, the climatic conditions on Hawaii are very different to Etna, with many areas on the east aspect of the island dominated by dense tropical rainforest with an annual precipitation of over 6m (Giambelluca *et al* 1986; Austin and Vitousek 1998). This allows expansion of the project in terms of the climatic conditions and vegetation type (tropical systems). Many authors have studied the succession (Smathers and Mueller–Dombois 1974; Kitayama *et al* 1995) and nutrient cycling on Hawaii (Vitousek *et al* 1995; Raich *et al* 1996; Kitayama *et al* 1997), and it has been used as the base model of chronosequence theory (Vitousek *et al* 1992; Chadwick *et al* 1999).

In order to avoid confusion with Etna, the information regarding the lava flows and climatology of Mauna Loa is presented later in thesis in the sections relating to the comparison of the volcanoes.

1.7. The Project

Over time there is change in the flora, fauna, available nutrients and even in the structure of the lava itself as it is compacted, weathered and finally covered by developing soil and plants. This creates a very wide-ranging number of topics for observing primary succession on volcanic ecosystems. This succession can continue for many hundreds to thousands of years, as seen on Hawaii where Vitousek *et al* (1983; 1988; 1995) have looked at chronosequences of several million years. However, many of the most obvious changes are occurring in the very early stages (0-500 years) of colonisation and very few authors have looked at this early stage in the ecosystem development. As will be seen, this period on Mt.Etna can cover the change from a completely bare new lava flow, through initial colonisation by cryptogams to the development of a young oak woodland. After this period, although succession continues, it is slower and mainly concerns changes in the species composition, species interaction and concurrent changes in soil biogeochemistry. Therefore this project only looks at the earliest primary succession and has been limited to a time frame of the initial 500 years. Additionally this project has concentrated on only one form of lava morphology (aa).

Earlier on in the chapter the key processes identified, which must be considered in primary succession are *colonisation*, *establishment* and *growth*. In order to study these processes the project will look at three distinct topics for study over the 500 year time period of the succession of the project

1) Plant community change:- An initial colonisation by vascular plants and subsequent species change and replacement over the course of succession.
2) Nutrient cycling:- over time there is a significant change in nutrient availability as the nutrients which are initially in very short supply are both cycled and added to as the system accumulates more biomass and aeolian material.

3) Lichen activity:- In the very early stages of colonisation the primary colonisers of Etna are the lichens and they dominate the landscape of the lavas for approx. 150 years in many areas. These lichens have a considerable impact on the accumulation of biomass (organic material), nutrient accumulation and weathering of the underlying rock material (releases many elements which are limited on the lava flows and which when leached become available to other parts of the ecosystem). Lichens also contribute to the precursor soil and the formation of microsites for subsequent plant colonisation.

Though these three main sections of the project at first appear to be discrete and separate entities, they are in fact closely linked together. For example, the factors affecting early nutrient cycling can be linked to early weathering and biomass accumulation of lichens. In addition, plant succession may be related to nutrient availability and also the formation of suitable germination sites (even if this is just a tiny accumulation of matter in a rock crevice) which may not occur or until the rock has been weathered enough to produce a crevice in which the roots can take hold. As a result further nutrient cycling processes later in the succession will be dependent on the increasing biomass and species composition of the preceding successional stages.

Although several authors have studied different facets of primary colonisation on volcanoes before, for example Smathers and Mueller-Dombois (1974) on vegetation change and Kurina (1998) on lichen biomass, this comprehensive examination of the different elements of primary succession on volcanic ecosystems is unique. This integration also allows direct observation of links between different facets of primary succession which have not been previously investigated (e.g. lichens and nutrient cycling).

1.8. Aims an objectives

The main areas of interest in this study can be summed up by the following key aims and objectives:

I. To assess the vegetation change over a range of chronosequences on the lava flows of Etna, to assess the impact of aspect and altitude on plant diversity. Further, to study several key primary colonising species and look at the changes occuring in the frequency and percentage cover. To observe interactions between species and the climate in order to measure the impact of different environmental conditions.

II. To test if the method of nitrate reductase measurement within plant tissue can be used as an indicator of change in key plant species over the chronosequences. To test this method on a range of chronosequences which can then be compared and the impact of different climatic conditions assessed.

III. To study soil development and nutrient availability by measuring changes in soil and foliar nutrients on a range of chronosequences evaluate changes in available nutrients in the soil and in the leaves of plants over the chronosequences.

IV. To determine the impact of lichens on the lava flows in both their contribution to soil biomass and as a weathering agent of the lava surface which introduces valuable trace elements into the soil.

V. To compare the results found on Etna of the nitrate reductase and Lichen weathering patterns with those found on another volcano (Hawaii) in order to look observe the impact of different climatic conditions.

VI. To link up all of the information gathered on succession and ecosystem change on both volcanic systems and produce a model of ecosystem development on basaltic lava systems.

1.9. Organisation of the thesis

In order to observe the three main areas of interest outlined a number of discrete and separate experiments were conducted on many areas of succession utilising many different methods (from observational to completely analytical). These experiments also looked into many of the factors affecting this succession other than age (e.g. climate, aspect, and altitude) over the 500-year period. As a result of the variety of interrelated topics studied these data are presented in chapters dealing with each topic in turn.

The thesis is broken down into seven experimental chapters, each dealing with a different set of experiments looking at a particular facet of primary colonisation. Each of these chapters has been further broken down into its own introduction, methods, results and discussion. The final integration of many of the different areas of study occurs in the final discussion chapter.

The first of the experimental chapters (2) studies the vegetation changes during the chronosequence. Plant succession is one of the most important factors in the volcanic ecosystem. Species colonisation and replacement are continuous and dynamic processes producing a complex interrelationship between species as factors of competition and symbiosis alter the vegetation structure.

Nutrient change and the associated soil development is the subject of chapters 3 & 4. Chapter 3 is a focused look at the availability of nitrogen as measured by the enzyme nitrate reductase in the leaves and roots of several key primary colonising species. In contrast, chapter 4 is a broader study of nutrient change as seen in the soil and leaves

Lichens dominate much of the early stages of primary succession on many volcanoes including Mt.Etna and Mauna Loa. As a result, they have a substantial impact on both early nutrient cycling and the succeeding successional stages. Chapters 5 and 6 demonstrate many of these impacts. These shall be covered in terms of the very visible contributions made by the physical structures of the lichens (biomass, contribution of organic matter to soil development and species change, chapter 5); before focusing on the less visible effects of lichen weathering of the lava surface (chapter 6). Although mosses are also an early lava coloniser they have not been studied in this project, as they are a smaller component in the cryptogamic stage of development (in terms of biomass and diversity). This project has concentrated on the dominant lichen impacts.

The two Hawaiian chapters (7 & 8) repeat two of the experiments conducted on Etna on this different volcano in order to test whether several of the processes observed on Etna hold true for other volcanic systems. These last two experimental chapters will demonstrate a comparison of nitrate reductase activity on Hawaii (chapter 7) and lichen weathering patterns (chapter 8).

The final discussion (chapter 9) draws together many of the threads of these individual experiments and point out many of the links which have become apparent over the course of the project – and which would not have been obvious without this broad and integrated approach to primary succession.

1.10.Notes on the ages of the lava flows

On many of the subsequent chapters many lava flows were examined and the year when the lava flow was erupted is noted in the text (e.g. 1981 or 1809). In other areas this date has been translated into the actual age of the site when the sample or study was conducted. In the case of most of the Etna samples these were taken during the year 2000 sampling period (except where referred to otherwise in the text). For example, a 1981 flow was 19 years old in 2000.

All Hawaiian samples were taken in 2001 and the age of the lava flows is calculated from this date (e.g. 1984 flow has an age of 17 years).

Chapter 2: Plant community change on the lava flows of Mt.Etna

2.1. Introduction

One of the most obvious and fundamental changes that will occur over any successional sequence is the alteration in plant species composition. As a site ages the plant available nutrients increase and a significant soil structure forms, thereby altering the prevalent conditions and allowing the colonisation of further species. Over time, the initial conditions of a nutrient poor and harsh environment (e.g. extremes of temperature and water availability) are gradually ameliorated as organic matter and nutrients accumulate (Chapin *et al* 1994). In addition, the colonising plants create shade increasing water retention, which in turn allows other plants to enter the developing habitat. As the conditions change and become suitable to other species, inter-species competition occurs, producing succession as one species is superseded by another. However, as time passes this process becomes increasingly complex as the plant species diversity increases. The individual needs of the plants become harder to distinguish and other factors such as symbiosis and the appearance of soil mycorrhizae allow the appearance of species that would otherwise be excluded. In addition, the heterogeneous nature of the habitat allows many taxonomic plant groups to become established more or less concurrently within a relatively small area (Clarkson 1990; Titus and Del Moral 1998).

Consequently, the first assessment of the primary succession is the study of vegetation change that occurs over time and an investigation of the dominant plant species present at specific time periods. Since vegetation is linked to nutrient availability and climate, patterns emerge which show the importance of the dominant species at each particular stage of the succession. Although the ultimate ecosystem formed may be a forest, a study of the intermediate ecosystems involved (and their dominant species) will lead to an understanding of the contribution played by these species over time.

This process is perfectly illustrated on volcanic substrates where these intermediate stages are clearly visible on a chronosequence formed by regular eruptions. In addition, the underlying substrate and mineralogy of the lava substrate tends to be uniform throughout the chronosequence. Hence, the processes of weathering which occur over time will introduce nutrients into the ecosystem in a relatively predictable manner (providing that the environmental conditions have not varied much over the length of the chronosequence). However, this may be complicated by depositions of tephra.

2.1.1. Properties of vegetation

When looking at the plant species of a particular area there are five main properties of vegetation to take into account:

1) **Species composition:** composition ranges from simple to very complex, depending on the habitat conditions and the relative richness of the local flora.
2) **Structure:** some vegetation is structurally very simple, but often a degree of structural complexity and organisation is evident. The structural patterns arise from the different stature and growth forms of the constituent plant species and their spatial disposition relative to each other.
3) **Physiognomy:** the general appearance of vegetation results from the relative abundance of species possessing distinctive stature, form, colour and texture of shoot systems and foliage.
4) **Spatial pattern:** the species composition of vegetation varies in space because the component species respond differently to sets of habitat conditions, which are themselves spatially variable.
5) **Temporal patterns:** the species composition of vegetation varies with time – this point is the main crux of this chapter.

Two terms must be clarified at this point. The term 'Vegetation' is the plant cover of an area in which species play different roles in terms of their abundance or rarity and in terms of their life forms, life histories, and physiology. When plants interact together they form communities. 'Plant communities' can be distinguished by differences in life-form structure – such as forests versus shrub or grassland - or by differences in species assemblages (Mueller-Dombois and Fosberg 1998).

There are two principal factors used when assessing a species within these communities – these are the **density** or number of plants per unit area and **cover** or percentage of the total area covered by the aerial parts of plants of a species. These variables can cause problems in the interpretation of the importance of a species on a site due to the different growth forms between species and the different patterns of distribution of individuals of different species on the ground (Tsuyuzaki 1996). For example, a weedy lawn may include at one extreme a grass such as *Poa annua*, which has a high density of shoots but relatively low cover value per shoot, whereas, a rossette weed like *Plantago major*, has few shoots which cover a relatively large amount of ground (Greig-Smith 1983).

One further minor problem with observing vegetation patterns over time is the time-scales involved in measuring plant occurrence. Plants gradually moving in and out of an ecosystem over the course of many years are measured on a macro scale (primary or secondary succession over long periods). However, on a much smaller time scale is the time taken for a seed to arrive on the site. Minor differences in environmental conditions, landscape morphology as well as the factor of blind chance (whether a seed is deposited in the right place at the right time) may cause variation in a species distribution over a relatively small area. As a result, any study on plant communities must always recognise the dynamic and heterogeneous nature of the ecosystem.

The smallest time-scale level is the factor of the time of year of the study, as the biota of any region will vary with the seasons (Phenology). Although the more obvious perennial species of trees and shrubs will be distinguishable all year round, many annuals may be in flower for only a short period of the spring or summer and hence not recognisable during the other periods. This problem can be solved by only comparing sites at the same time of year – in the case of this project the vegetation study was conducted in the late spring (May / early June).

2.1.2 Analysis of specific plant species over time

The species that colonise a volcanic ecosystem soon after the eruption will be dependent biologically on the locally abundant species and their seed/spore dispersal mechanisms (Van der Maarel 1988). Once the seed/spore of a species has arrived on the lava, the abiotic factors of local climatic conditions prevalent in the area as well as nutrient availability and substrate morphology will influence its germination and hence its survival to be a primary coloniser. Micro-organisms (including bacteria, fungi and some algae) are very abundant in nature. They or their spores are dispersed into the air and carried by the wind to settle on suitable substrate. The same process holds true for the mosses, lichens and some ferns allowing these groups to gain a foothold on the new lava substrate almost as soon as the lava has cooled. In addition, the considerable fecundity of these groups allows a simultaneous colonisation of almost the entire lava surface. The later vascular plant species have a slower and haphazard method of seed dispersal which leads to a mosaic structure to the vegetation with small patches or populations of plants which gradually increase in size. In addition this will be controlled by the ability of these seeds to germinate on the substrate. The species with the slowest seed dispersal systems (e.g. trees) have greatest difficulty colonising a flow. These species will gradually encroach from the edge by seed dropping, wind dispersal mechanisms or they may be reliant on the activities of animals to carry their seeds any distance onto a flow. As such, at any particular time on a lava flow there will be a range of successional communities occurring. Species diversity in these communities will be dependent on which species have managed to encroach furthest onto the flow and the biogeophysical conditions that occur there (once a seed arrives on a site the climatic or nutrient status may prevent germination).

In dealing with an area with a potential botanical content of 9,000 species (Poli 1991; DiBenedetto 1983), it quickly becomes apparent that to be manageable botanical survey needs to concentrate on specific species, given the time scale of the project. This is made evident by the fact that many of the plant and lichen species are completely indistinguishable except for minor morphological differences in flowers or seeds, which might not be available at the time of the study. Consequently, this project identifies the general trends in botanical change over the chronosequence as the plant community evolves.

2.1.3. Aspect

The location of the chronosequence on the slopes of Mt.Etna has a profound effect on the vegetation found on each site, as observed by Poli *et al* (1989 and 1995). Variations in climate on the different aspects as outlined in Chapter 1, will encourage the growth of some species whilst impeding others. This could lead to different rates of succession and change the ultimate outcome and biota of each chronosequence.

2.1.4 Altitude

There is a distinct change in vegetation with altitude on the slopes of Mt.Etna, which has been observed by various authors (Poli 1970a; 1970b; 1971; King 1973; Poli 1991). However, in many places the impacts of agriculture and other forms of human activity have completely altered the types of vegetation present. King (1973) noted that the forest belt of Etna (1,500 – 2,000m) has been much depleted over time due to timber cutters and charcoal production with only the higher altitude stands of oak, beech and larch surviving. This is notable on the north aspect where a tourist village has been constructed among the trees.

However, since the establishment of Mt.Etna as a national park, human impact has been much reduced. In addition, there are many pockets or areas of lava, which are still in the natural state either because they are in remote locations or because it has been protected by the landowner.

Poli *et al* (1981) identified and mapped many of the forested areas of Mt.Etna. This allowed the differentiation of dominant species at different altitude zones as illustrated in Fig 2.1.

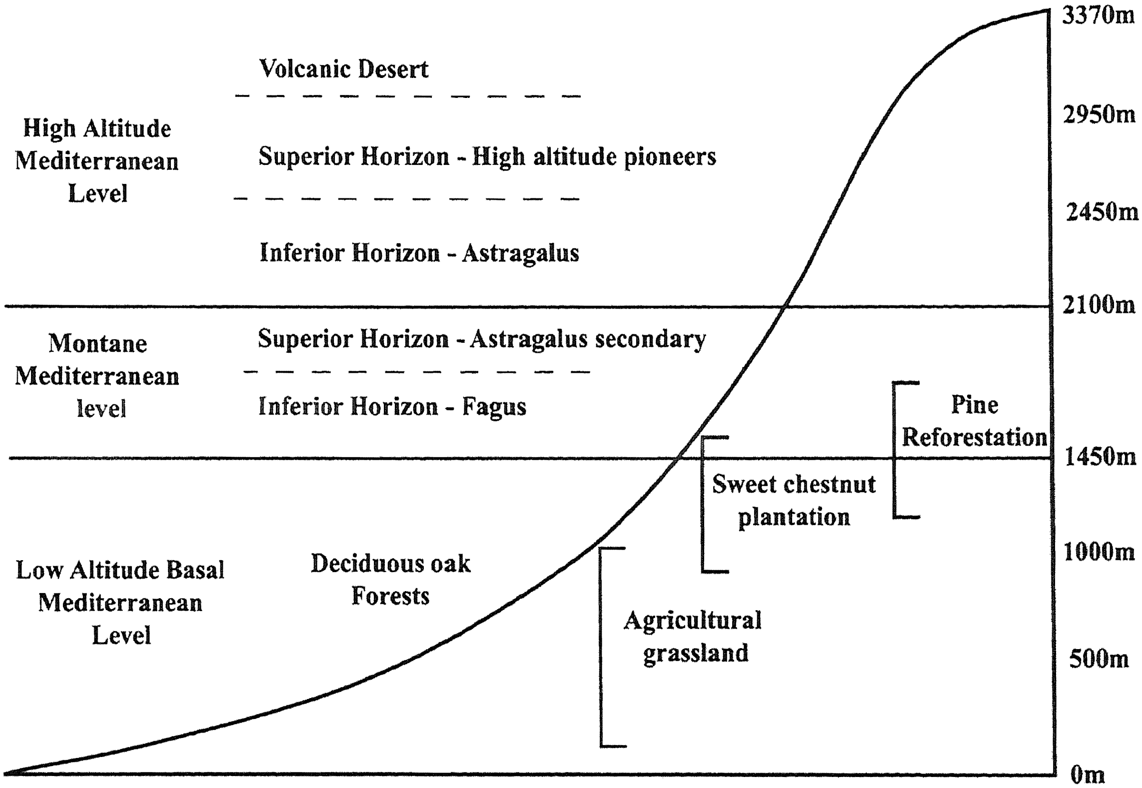


Figure 2.1. Vegetation change with altitude on Etna. Translated and adjusted from Poli (1991).

2.1.5. Seed dispersal – Dagalas and the edge effect

The colonisation process can only occur if there is a source of propagules from which the plants can spread and is also dependent on the species seed dispersal mechanisms (Tsuyuzaki 1987 & 1989; Tsuyuzaki 1991; Chapin 1993).

Those species, which are wind dispersed, are quickly spread over the new substrate (depending on the efficiency of their mechanism). Other species are slower to colonise the lava, as they must encroach gradually from the edge of the flow by seed dropping, being carried by animals or vegetative spreading by stolons or rhizomes. In these cases the distance from the edge can become a factor in the time taken for a species to appear on the lava flow. In the case of lava flows, however, the edge of the flow might not be the only source of propagules. Occasionally when a lava flow is moving down the slope of the volcano a minor topographical feature (small rise or hill) may cause the lava to split around it and then rejoin on the other side. This leads to the isolation of a small pocket or island of older substrate located within the new lava field. This phenomenon is known locally as a Dagala (or Kipuka in Hawaii) and can provide a source of propagules and organic material for the new lava flow acting as a spreading centre of colonisation within the new lava field.

2.1.6. Notes on the experiments

In order to control for human impact (agriculture and areas of habitation) as a factor during this project, sites were chosen away from the villages and towns around Mt.Etna and in the more remote areas where activity was limited. In addition, careful selection often identified those sites, which have been disturbed recently, and these could then be removed from study.

This chapter is restricted to the successional change of the vascular plants on the volcano. Cryptogamic species also show succession on the lava flows and their interactions are an important step in the colonisation process (in most cases they are the first step). However, the succession of lichens on the rock surface and the subsequent changes in biomass are sufficiently different from vascular plants to merit separation into another chapter (Chapter 5).

2.2. Methods

2.2.1. Site selection

The methods used were very similar to those described by Clarkson (1997). A total of 35 sites were visited on the lava flows of Mt. Etna on each of the four cardinal aspects and at different altitudes (between 750 and 1500m). These sites were separated into three chronosequences, on the north (nine lava flow fields), south (ten lava flow fields) and east (six lava flow fields) aspects. A western chronosequence was not possible as there is no sequence of lava flows on this aspect, however two lava flows (1843 and 1646) were selected and compared to similar aged lava flows on each of the three other aspects for a direct comparison of the four aspects of Etna. Similarly, other lava flows in a sequence of increasing altitude from 750m – 1500m on two lava flows (one nineteenth and one seventeenth century flows) on the south aspect, were selected to investigate the impact of altitude and aspect. All the chronosequence sites were pre-selected using the geological maps of Mt.Etna lava flows (Romano *et al* 1979 (accurate up to 1974), Abrams *et al* (1996) and the more recent tourist maps to 2001. Sites were selected to give a good range of ages in the 0-500 year period of interest (see Fig 2.2).

All sites were selected using stringent controls over topographical, landscape and environmental parameters in order to equalise these factors as much as possible. Each site was located on a level area to eliminate the effects of slope such as rainwater run-off and shading which could cause variation between sites. All sites were located on aa lava. In addition, all sites were located a minimum of 50m from the roadside to limit human impact and the damage caused during the cutting of the road. Similarly, all sites were located a minimum of 50m from the adjacent lava flows to minimise the edge effect on colonisation and measure *in-situ* colonisation rather than the pattern of spread (with the exception of the experiment to study this phenomenon).

Figure 2.2. Map of the most recent lava flows of Mt.Etna. Different shadings indicate different lava flows (0-600 years). Revised and adjusted from the original Romano *et al* (1979) lava flow map.

2.2.2. Sampling methods

During the start of this project a number of vegetation sampling methods were initially employed on the Etna lava flows, each of which was standard for the different ecosystems that had developed on the sites. For example, small quadrats on the younger habitats dominated by cryptogams ($400cm^2$) and a far larger quadrat for the forested areas ($400m^2$). This became a problem when comparing each site directly. Consequently a standard format for comparing each site using the same criteria was developed. On each site five quadrats of 20m x 20m ($400m^2$) were laid out. This size was chosen as it encompasses all the larger vascular plant species such as trees and yet was not impractical for the younger flows since species diversity was relatively low (the cryptogamic species are covered later). The site of the first quadrat was chosen non-randomly (due to the stringent controls on surface morphology). Each subsequent quadrat was set at least 10m apart except in those areas where this was prohibited by the size of the lava flow. For example, the 1809 flow on the north aspect is represented by only a relatively small pocket of vegetation, due to inundation by more recent lava flows (1911 & 1923). On this site the five quadrats were grouped together but still at the prescribed 50m distance from the road and edge of the flow.

Within each quadrat the abundance of nine species was determined – by a direct measurement of the number of individuals of each species present per $400m^2$. These nine species were chosen as they were all common on Etna and present over a long period of successional time. Of these species: *Centranthus ruber, Rumex scutatus, Genista aetnensis, Helichrysum italicum, Isatis tinctoria, Spartium junceum* and *Senecio bicolor* were the commonest primary colonisers and the oak species of *Quercus ilex* and *Quercus pubescens* were typical of a later stage. In the case of *R.scutatus* and *S.bicolor* which are colonial species, where it was impossible to ascertain the exact number of individuals present within a clump, the clump was taken as an individual. These species were documented to observe how species change over time. In addition, estimates were taken of the percentage cover of the commonest species found on Etna by subjective observation by the author. In one quadrat from each site all vascular plant species present were recorded, and measurements taken of their abundance (P=present 1-5 individuals present, O=occasional 6-15 or C=common 16+). Plants were identified using reference guides (Polunin 1969; Blamey and Grey-Wilson 1993; Press and Gibbons 1993; Davies and Gibbons 1993; Poli 1991).

2.2.3. Plant community change on the northern chronosequence

A chronosequence of sites was selected on the northern aspect of the volcano, ranging from 19 to 464 years old. These consisted of lava flows erupted in: 1981, 1947, 1923, 1879, 1809, 1646, 1614-24, 1566 and 1536 (Fig 2.3). Map grid references for all the sites can be seen in the appendix (p272). Each site was located at an altitude of approximately 1000m, using the parameters of topography, distance from the edge and lava morphology as outlined in 2.2.1.

2.2.4. Plant community change on the southern chronosequence

A chronosequence of sites was selected on the southern aspect of the volcano, ranging from 17 to 566 years old. These consisted of lava flows erupted in: 1983, 1910, 1886 (also marked as 1892), 1780, 1766, 1634, 1537, 1536 and 1444 (Fig 2.4). An older 812-1169 lava flow was included in the vegetation survey only. Each site was located at an altitude of approximately 1000m, using the same parameters of topography, distance from the edge and lava morphology as 2.2.1.

2.2.5. Plant community change on the eastern chronosequence

A chronosequence of sites was selected on the eastern aspect of the volcano, ranging from 8 to ~311 years old. These consisted of lava flows erupted in: 1992, 1971, 1928, 1865, 1792 and 1689. (Fig 2.5). Each site was located at an altitude of approximately 1000m, using the same parameters of topography, distance from the edge of flow and lava morphology as outlined in 2.2.1.

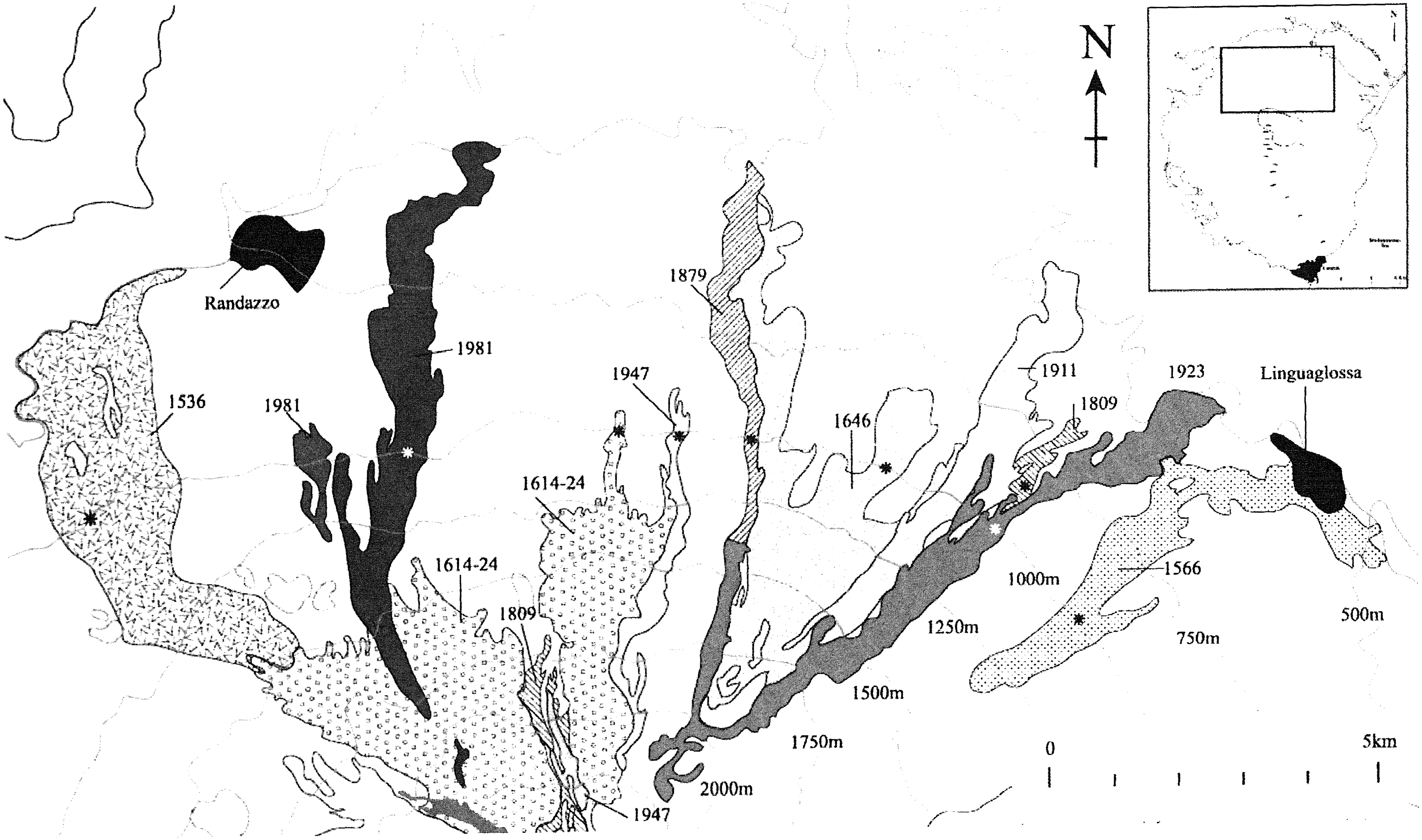


Figure 2.3. Sites on the northern chronosequence. * (black or white colouration) marks the position of the sites.

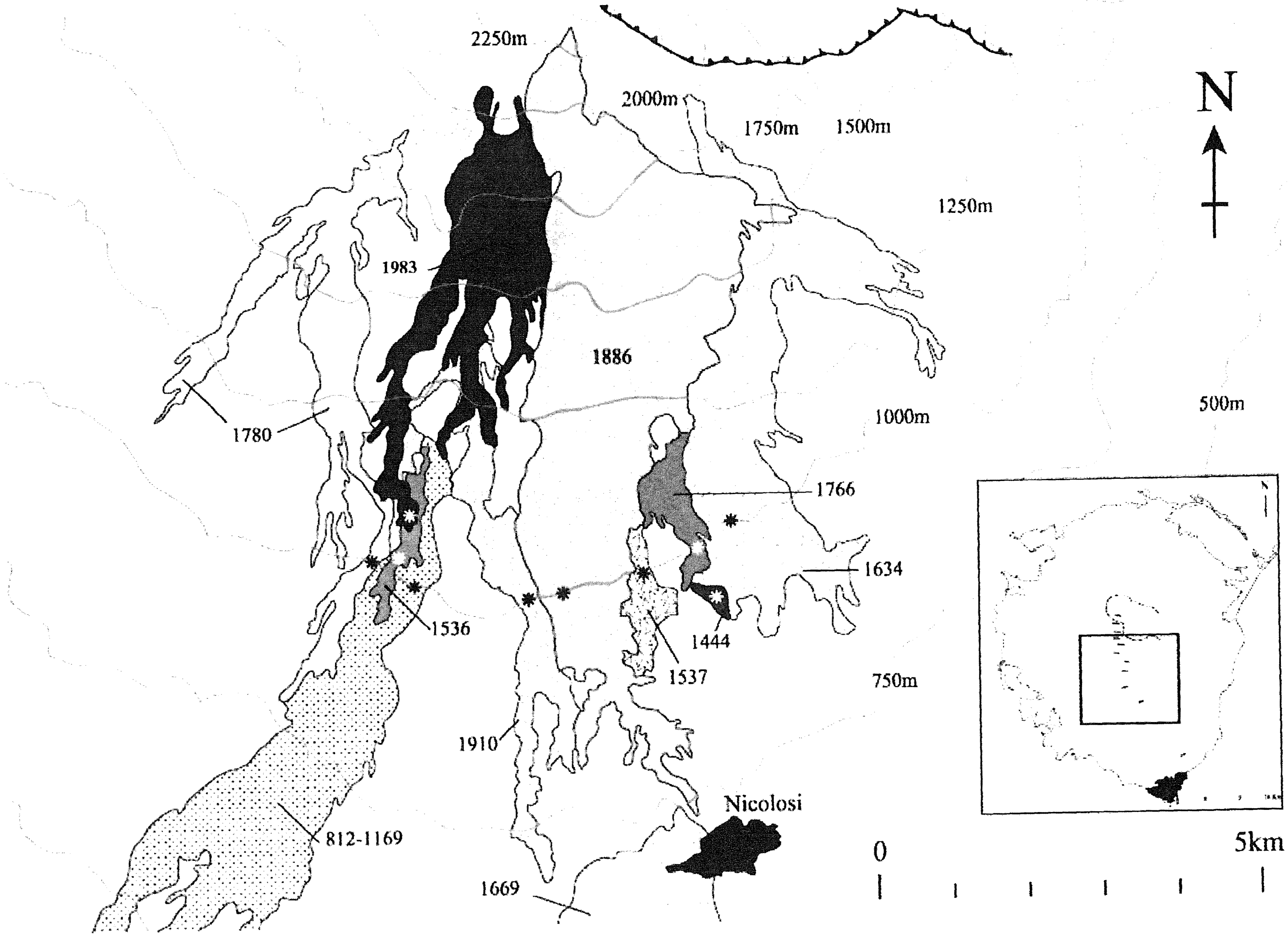


Figure 2.4. Sites on the southern chronosequence. * (black or white colouration) marks the position of the sites.

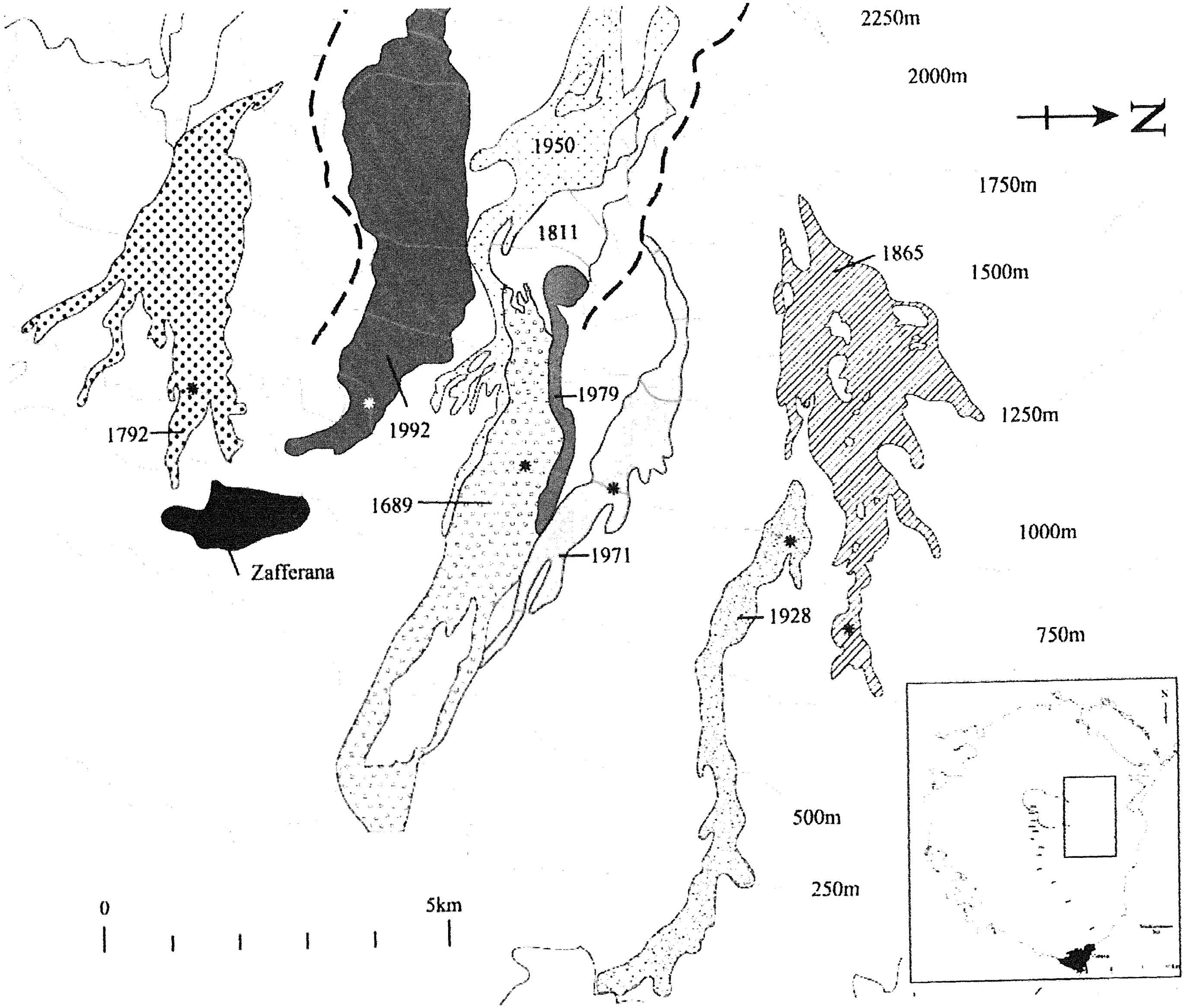


Figure 2.5. Sites on the eastern chronosequence * (black or white colouration) marks the position of the sites.

2.2.6. Plant community change on the four aspects of the volcano from two different aged lava flows

Two lava flows were selected on each of the four aspects of the volcano. These lavas were selected for comparable age – one nineteenth century and one seventeenth century lava flow, to test variation caused by aspect and age. The lavas selected were: 1879 and 1646 on the north aspect; 1865 and 1689 on the east aspect; 1892 and 1634 on the south aspect; and 1843 and 1651 on the west aspect of Etna (Fig 2.6). Each site was located at an altitude of approximately 1000m. Each site was selected using the same parameters of altitude, topography, distance from the edge of flow and lava morphology as outlined in 2.2.1.

2.2.7. Plant community change on a range of altitudes

A further seven sites were selected on the south aspect of the volcano in order to assess the impact of altitude on plant diversity and percentage cover. These sites were located at 1500 m and 1250 m for the 1886 and 1634 lava flow fields. Other sites in the altitude sequence were the 1892 flow (800 m), 1634 flow (780 m) and 1910 flow (750m) (Fig 2.7). The results from these sites were combined with those taken at 1000 m in the southern chronosequence to give a near continuous altitude transect from 750 m to 1500 m on two different aged lava flows. Each site was selected using the same parameters of topography, distance from the edge of flow and lava morphology as outlined in 2.2.1.

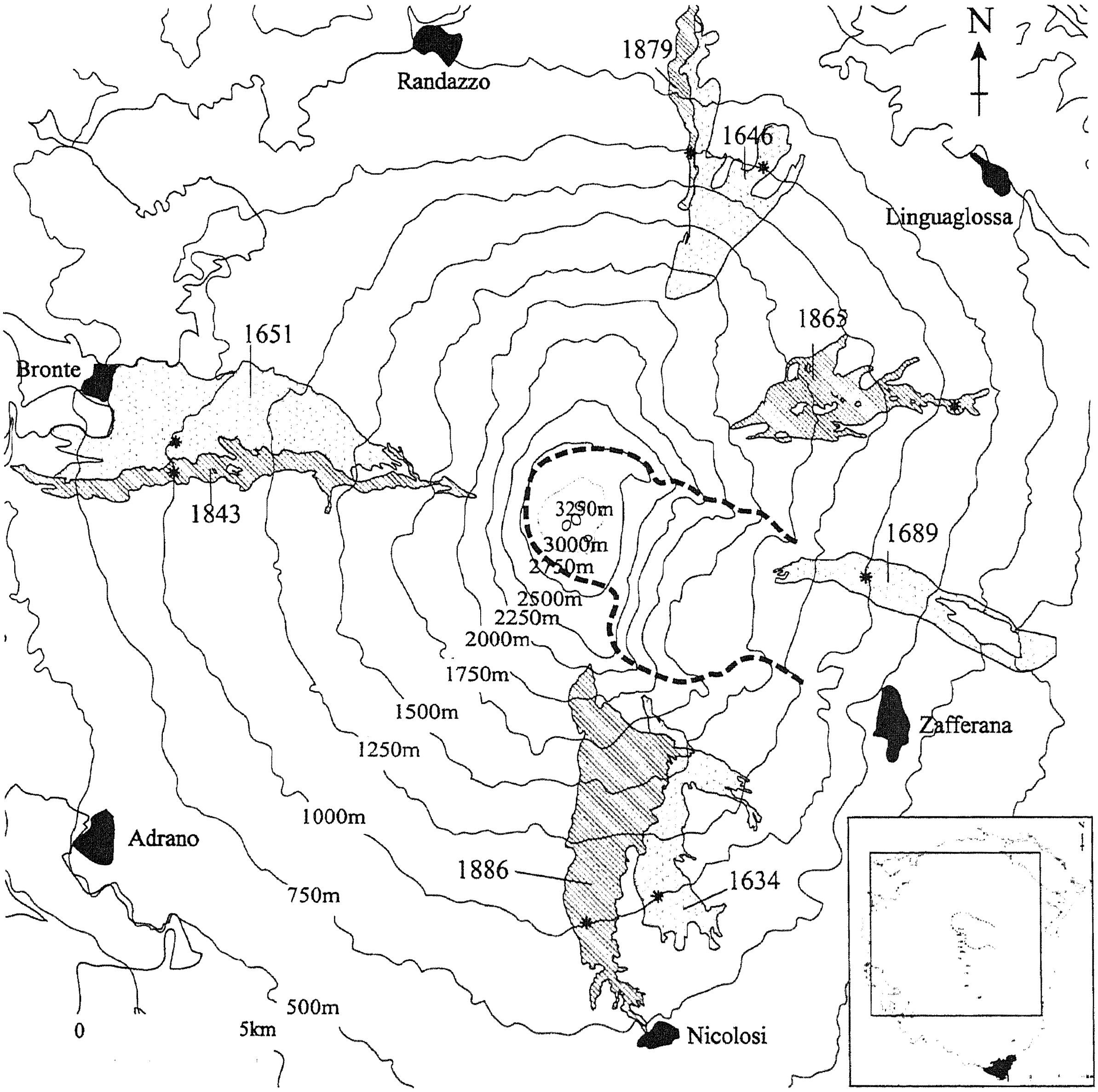


Figure 2.6. Comparison of two similarly aged lava flows (one from the nineteenth and one seventeenth century) located on the 4 aspects of Etna. * marks the position of the sites.

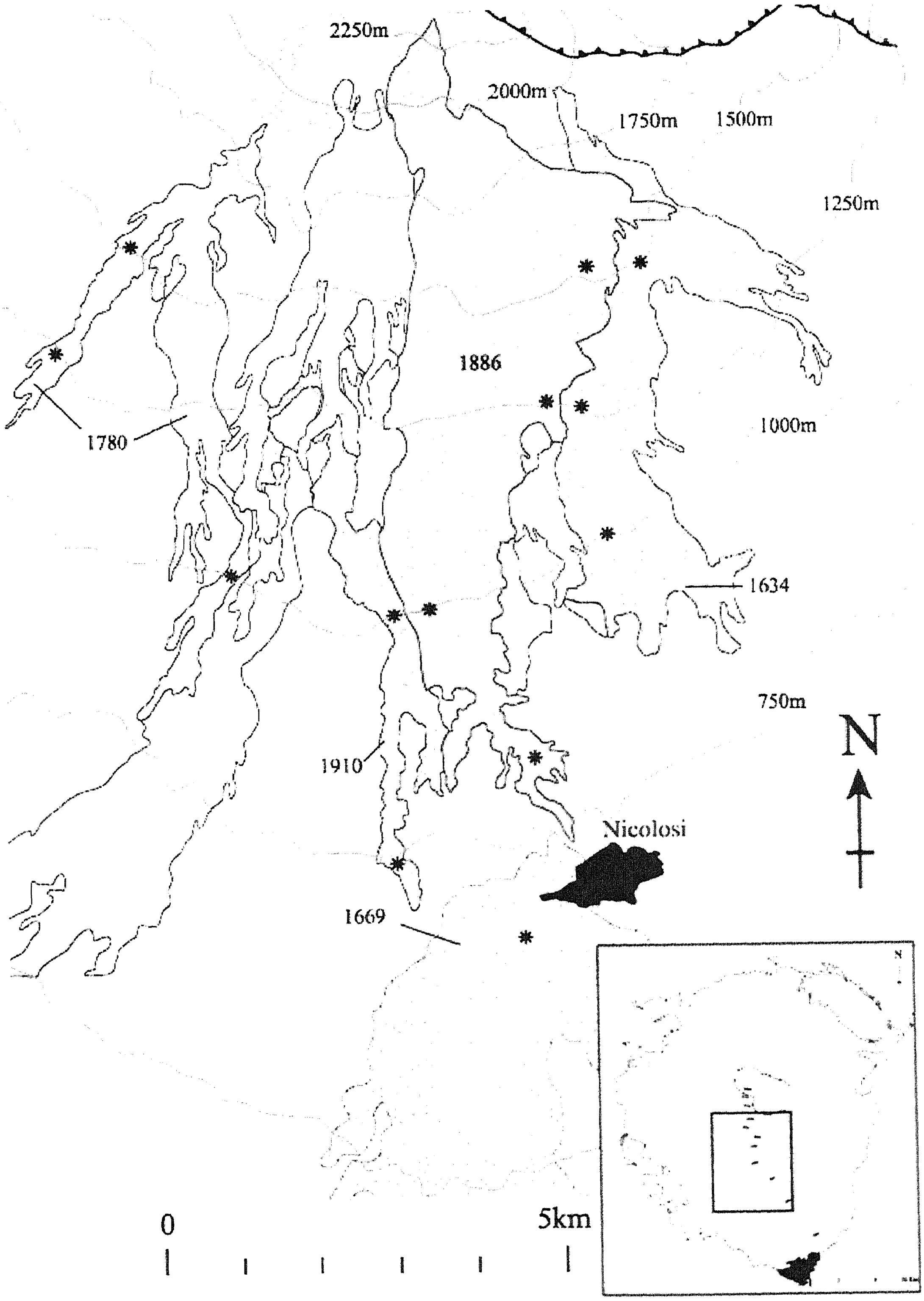


Figure 2.7. Map of the sites sampled for altitude Etna where * marks the position of the site

2.2.8. The Edge effect: Change in species abundance on the 1928 lava flow (72 years old) as a factor of distance from the edge of the flow.

Plant species abundance and diversity are linked to the source of the seeds and these are dependent on the individual species seed dispersal mechanisms. The dispersal of three primary colonising vascular plants was measured on a recent lava flow to see how some species colonise from the edge of a lava flow. The lava flow which erupted in 1928 on the east aspect of Etna (Fig. 2.5), inundated an ancient lava flow (>8,000 years old). There is a very clear differentiation of the two lava flows with the ancient flow acting as a source for colonisation of the new flow.

To measure the frequency and distance that these species have moved onto the younger flow four transects were placed on the 1928 flow running from the edge to 50m into the flow. Along these transects the position of vascular plant species from the edge was noted. The data from the four transects was then combined and sorted into 5m sections. These data were then plotted as a bar graph of increasing distance from the edge of the flow.

2.3. Results

2.3.1. Changing species diversity on Mt.Etna

Each of the three chronosequences on the south, north and east aspects of Mt.Etna show a rapid increase in species diversity with time. In the south and north chronosequences this is a steady increase over the 500 years. However the east chronosequence shows a much faster rate of increase and has attained the same diversity (42) in only 300 years (Fig 2.8).

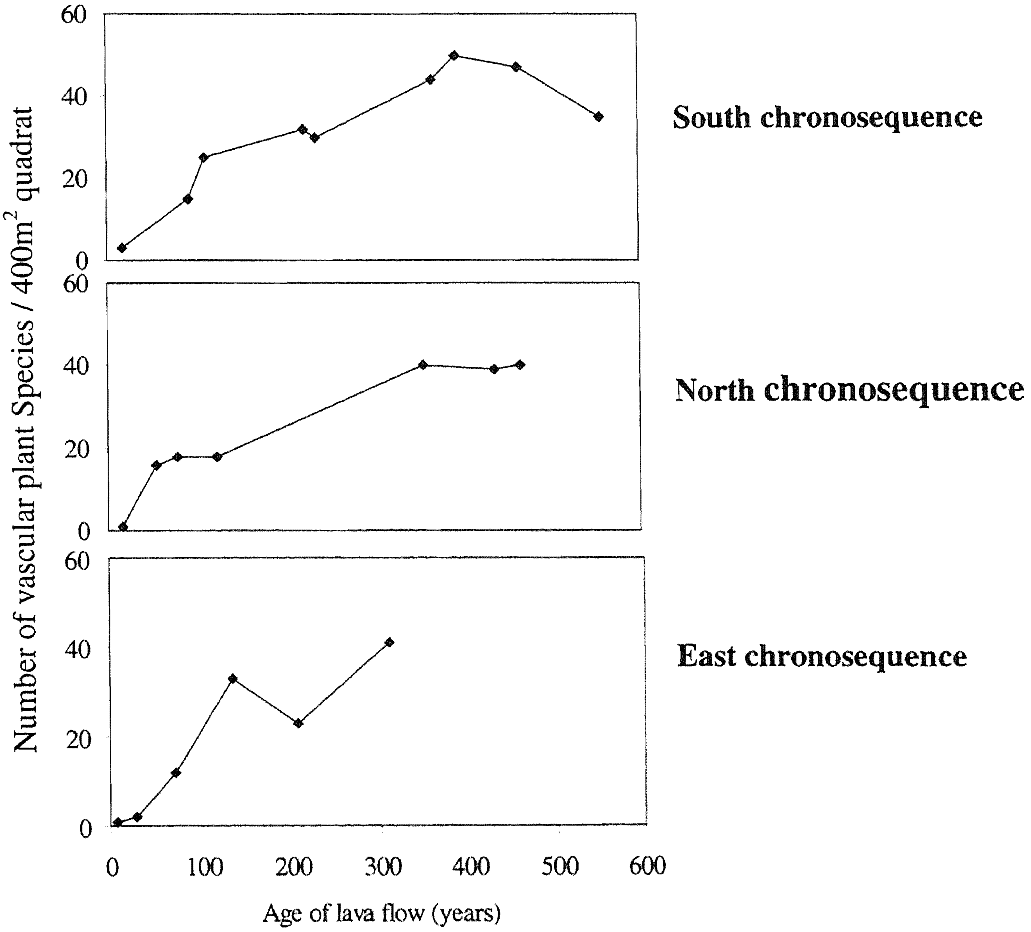


Figure 2.8. Species diversity on three chronosequences on Mt.Etna.

On the three lava flows studied there is a clear decline in species diversity as altitude increases (Fig 2.9). On the 1634 flow it declines from 50 at 800m down to 35 at 1500m; the 1780 lava flow declines from 34 (1000m) to 26 (1500m) and the 1892 from 24 (1000m) to 18 (1500m)

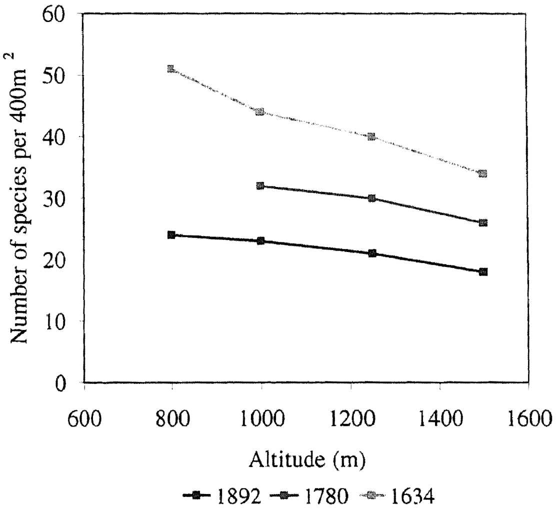


Figure 2.9. Species diversity on a range of altitudes on Mt.Etna.

A full list of the species found on the southern and northern lava flows and a measurement of their abundance and percentage cover can be seen in the appendix.

2.3.2 Species change over time on Mt.Etna. Examples of nine species abundance and percentage cover

All of the nine species studied on the lava flows of Etna show changes in their mean abundance and percentage cover over the chronosequences. Some species quickly colonise the flows and achieve a high abundance on the younger flows (*C.ruber*, *R.scutatus*, *H.italicum*, *I.tinctoria* and *S.bicolor*) before declining slowly (Figs 2.10 – 19). Whereas, other species become dominant later in the chronosequence (*G.aetnensis*, and *S.junceum* (Figs 2.20-23)). The final stage species appear in low numbers but quickly attain dominance through a high percentage and these are characterised by the two oak species; *Q.ilex* and *Q.pubescens*. Each of these nine species varies on the different chronosequences as shall be shown on an individual basis.

Centranthus ruber:

This species is an early coloniser of the lava flows achieving its highest abundance (17 per 400m^2) on the southern aspect of Etna after only 90 years (1910 flow) (Fig 2.10a). After this period it gradually declines in abundance. After an initial fast colonisation on the northern aspect (reaching an average of 5 after 50 years), the abundance very gradually declines through the rest of the chronosequence (50-500 years) (Fig 2.10b). In the east it reaches its highest abundance (13) on the 1865 lava flow (135 year old) after which it gradually declines. The mean abundance of this species on all four aspects of Etna (Fig 2.10d) is always higher on the younger nineteenth century lava flows than on the seventeenth century flows. In addition, there is a clear drop in abundance on the northern aspect compared to the other three aspects (Fig 2.10d). These trends in the abundance of *C.ruber* are repeated on the graphs of percentage cover (Fig 2.11). However the percentage cover of this species is low and reaches its highest on the southern aspect (5.8) at the 90 year mark (Fig 2.11 a).

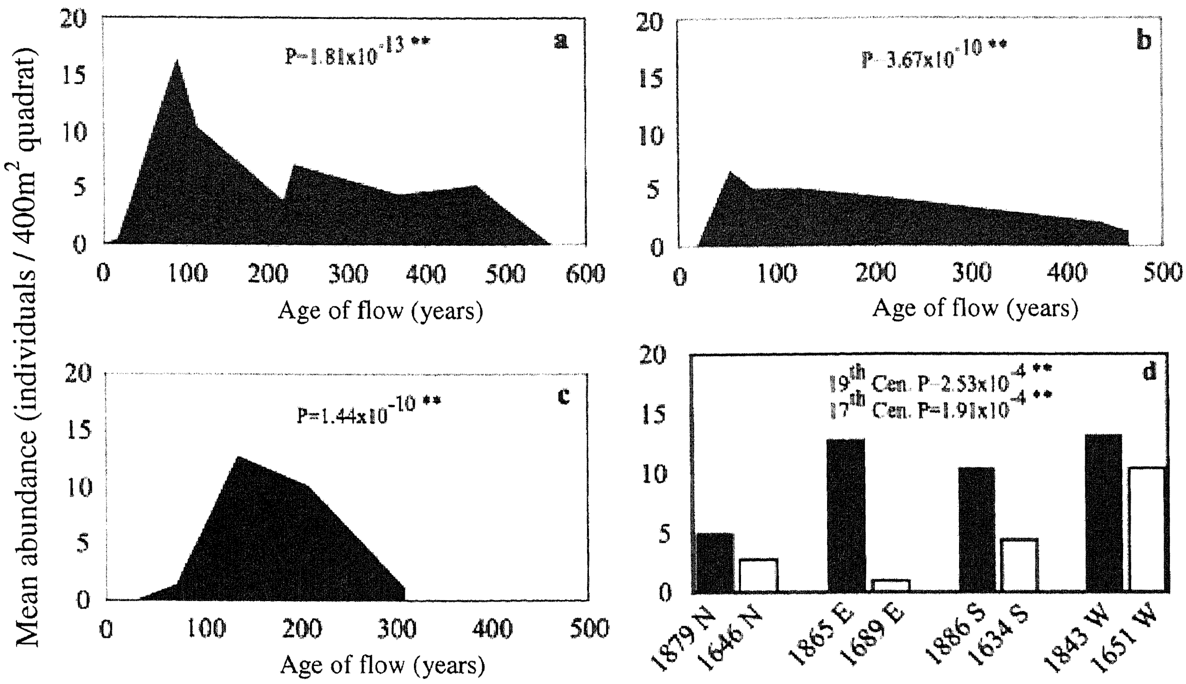


Figure 2.10. Mean abundance of *Centranthus ruber* on the three chronosequences where **a** is the south, **b** north and **c** the east chronosequences. **d** compares two similar age groups on all four aspects.

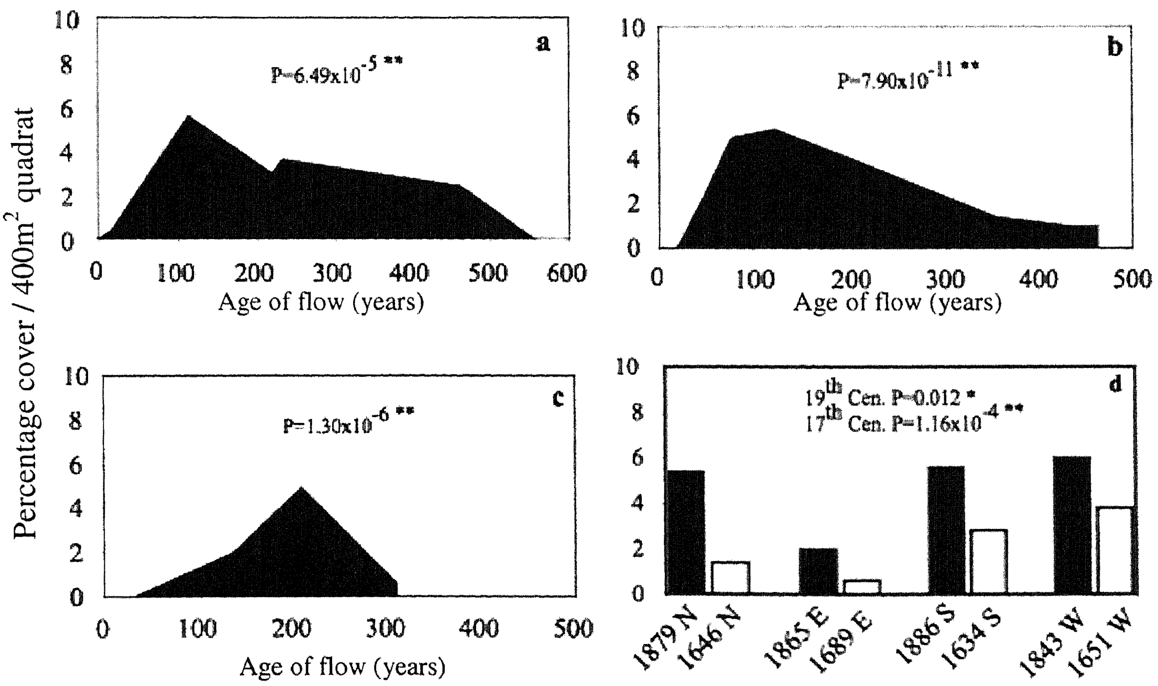


Figure 2.11. Percentage cover of *Centranthus ruber* on the three chronosequences where **a** is the south, **b** north and **c** the east chronosequences. **d** compares two similar age groups on all four aspects.

Rumex scutatus

This species is the most abundant of all the nine vascular plant species studied in this project. It is present on all the sites (although rare on the oldest sites) and favours the young open lava fields before declining in both abundance (Fig 2.12) and percentage cover (Fig 2.13). On the south aspect of Etna it demonstrates a fast colonisation of the flows becoming very abundant by the 90 year old flow (density of over 20 per 400m^2 (Fig 2.12a)). After this the abundance appears to drops down to 10 per 400m^2 before increasing again to a second peak at the 220year old flow. However, this drop does not occur in the percentage cover graph of the same period (Fig 2.13a), and this is the better indicator of the true state of this species over time. The trend for high abundance on the younger flows is repeated on the north chronosequence (Fig 2.12b) where it reaches a density of 12 per 400m^2 after only 52 years, before declining slowly. On the east aspect *R.scutatus* reaches its maximum abundance on the 208 year old lava flow (Fig 2.12c) with 20 per 400m^2. These trends of early dominance on the younger lava flows are clearly visible on the graphs of the species percentage cover (Fig 2.13). On the four aspects together (Fig 2.12d), the lowest abundance and cover (Fig 2.13d) occurred on the eastern lava flows with a level of 1 per 400m^2 and less than 1% cover on the 1689 lava flow. This compares to the similarly aged 1651 west lava flow, which has a density of 10 per 400m^2 and cover of 4%.

Helichrysum italicum

This species has low abundance on each of the three chronosequences examined on Etna (Fig 2.14). On the south chronosequence (Fig 2.14a) it colonises the younger lava flows and remains present for approximately 350 years. This trend is repeated on the north chronosequence, which peaks at 6 per 400m^2 quadrat before declining gradually throughout the rest of the sequence. In contrast, *H.italicum* is rare on the eastern chronosequence and only appears briefly at the 200 year mark, where it averages 1 per 400m^2 quadrat (Fig 2.14c) and less than 1% cover of the flow (Fig 1.15c). This is confirmed by the results of the comparison of all four aspects of the volcano where the highest abundance and percentage cover is seen on the west aspect (Fig 2.14d & Fig 2.15d respectively).

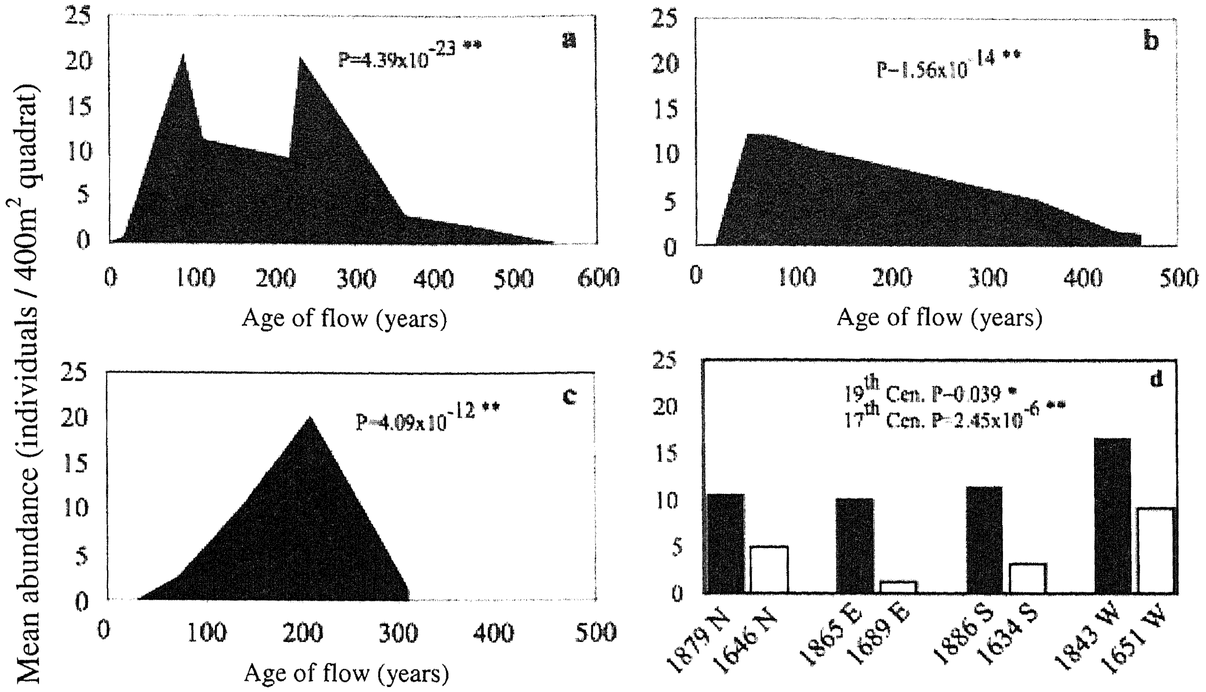


Figure 2.12. Mean abundance of *Rumex scutatus* on the three chronosequences where **a** is the south, **b** north and **c** the east chronosequences. **d** compares two similar age groups on all four aspects.

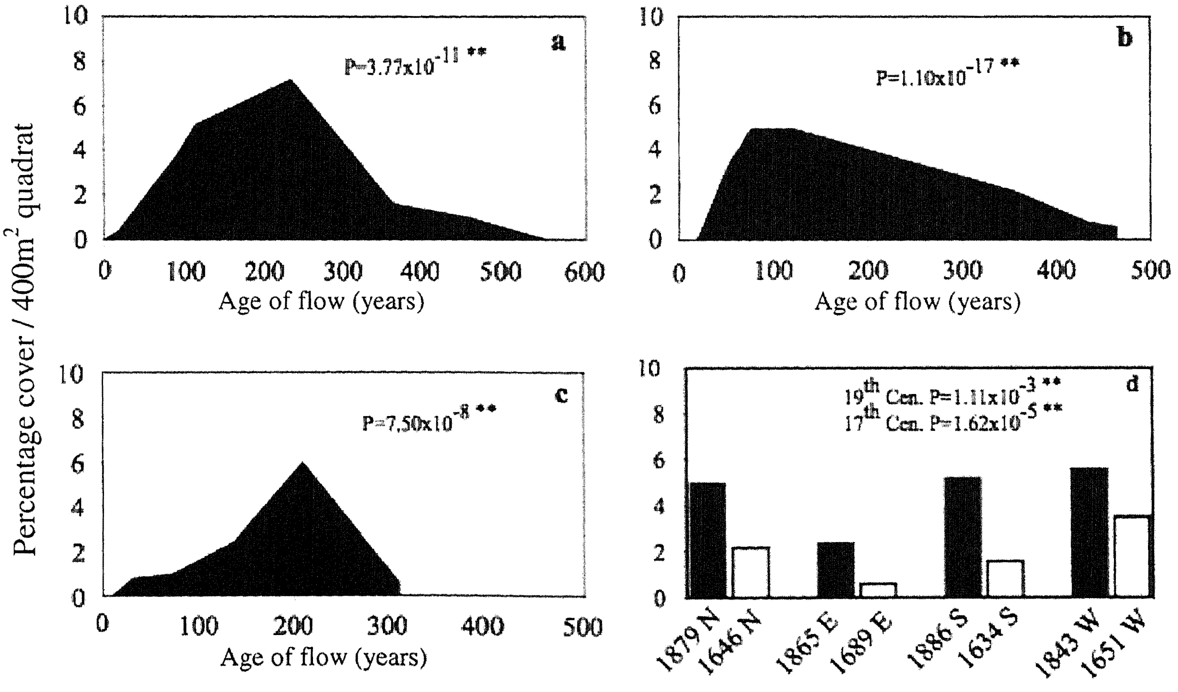


Figure 2.13. Percentage cover of *Rumex scutatus* on the three chronosequences where **a** is the south, **b** north and **c** the east chronosequences. **d** compares two similar age groups on all four aspects.

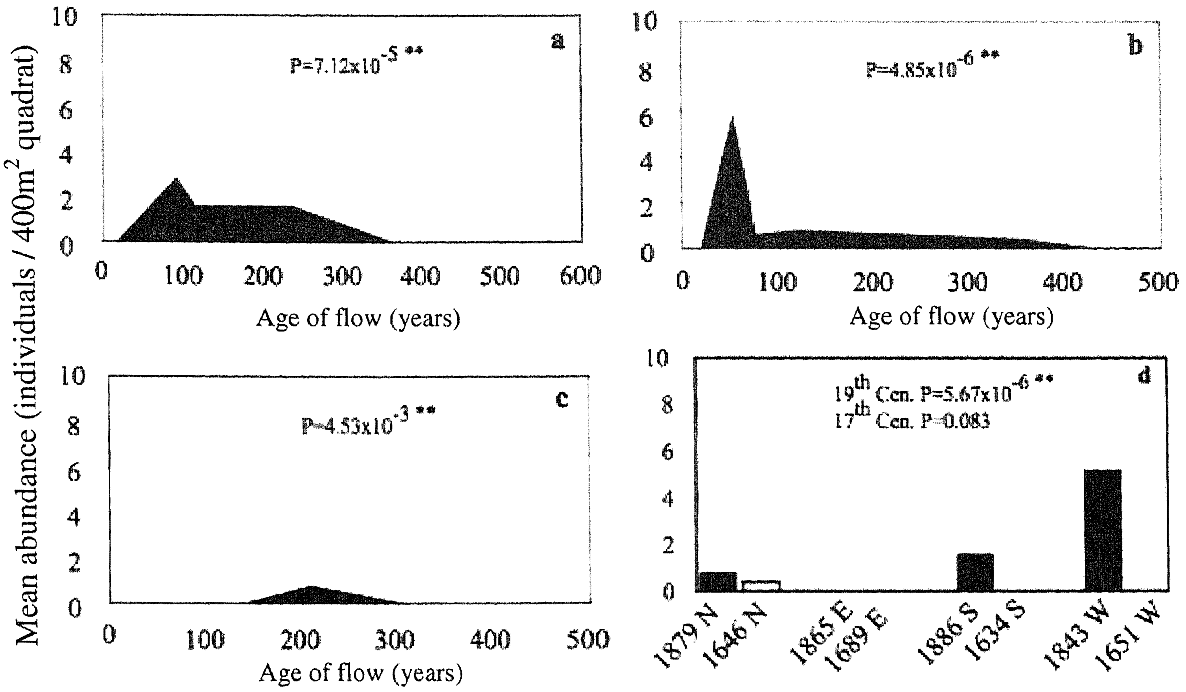


Figure 2.14. Mean abundance of *Helichrysum italicum* on the three chronosequences where **a** is the south, **b** north and **c** the east chronosequences. **d** compares two similar age groups on all four aspects.

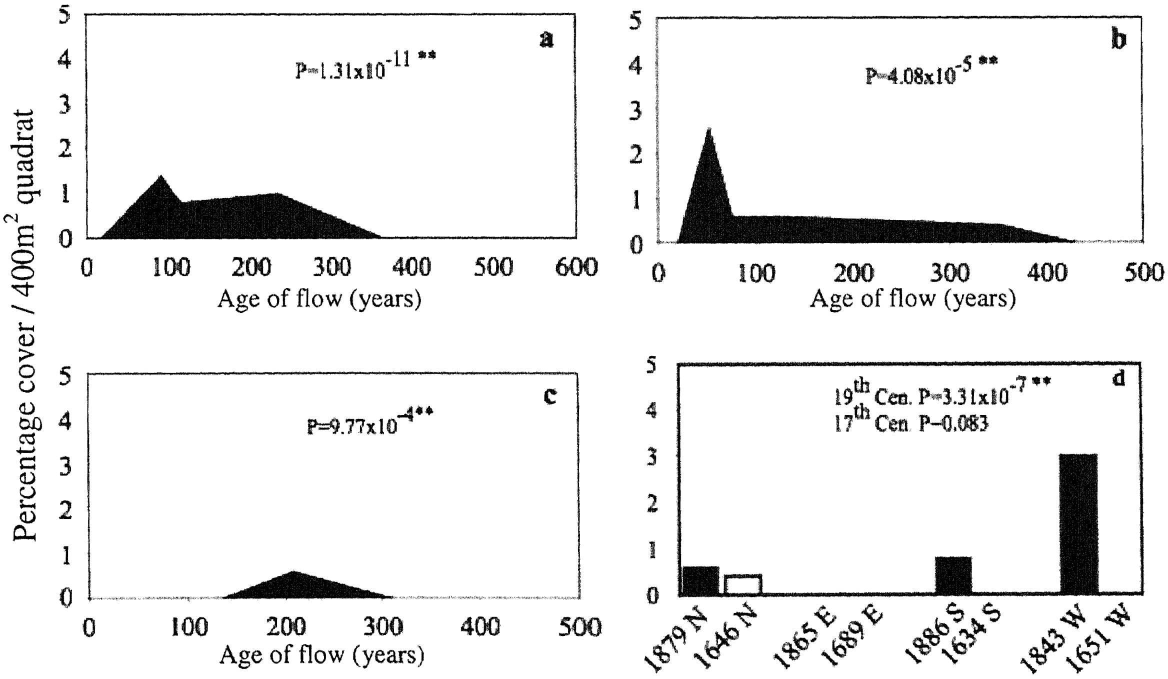


Figure 2.15. Percentage cover of *Helichrysum italicum* on the three chronosequences where **a** is the south, **b** north and **c** the east chronosequences. **d** compares two similar age groups on all four aspects.

Isatis tinctoria

This is a common species throughout the chronosequences of Etna colonising the very young lava flows and then maintaining a presence throughout the chronosequences. It is most common on the southern chronosequence where it reaches a peak density of 12 per 400m^2 on the 220 year old lava flow (1780) after which it declines steadily (Fig 2.16a). In the north its density remains fairly constant between 2 - 6 per 400m^2 throughout the chronosequence (Fig 2.16b). On the east chronosequence the abundance peaks on the 135 year old lava flow (Fig 2.16c) again with a density of 12 per 400m^2. The average percentage cover of *I.tinctoria* remains fairly constant on all three of the chronosequences (Fig 2.17a,b,c) as well as on the comparison of all four aspects (Fig 2.17d) varying between 1 and 2%.

Senecio bicolor

This species is abundant on the southern aspect of Etna. However, it is very rare on both the northern and eastern aspects (Fig 2.18a,b,c). On the southern aspect it reaches its highest abundance on the 90 year old flow, reaching an average of 17 per 400m^2 quadrat (Fig 2.18a). As the age increases the abundance drops sharply (<2 per 400m^2) from 200 years onward, and though present on the flows is very rare. In a comparison of all four aspects (Fig.1.18d) the species is absent on the two age groups of lava flows on the north and east but is common on both the western sites (10 per 400m^2 on the 1651 flow). This trend is repeated in the species percentage cover (Fig 2.19) where it achieves highest cover (3%) on the 1910 (90 year old flow) on the southern aspect after which it declines.

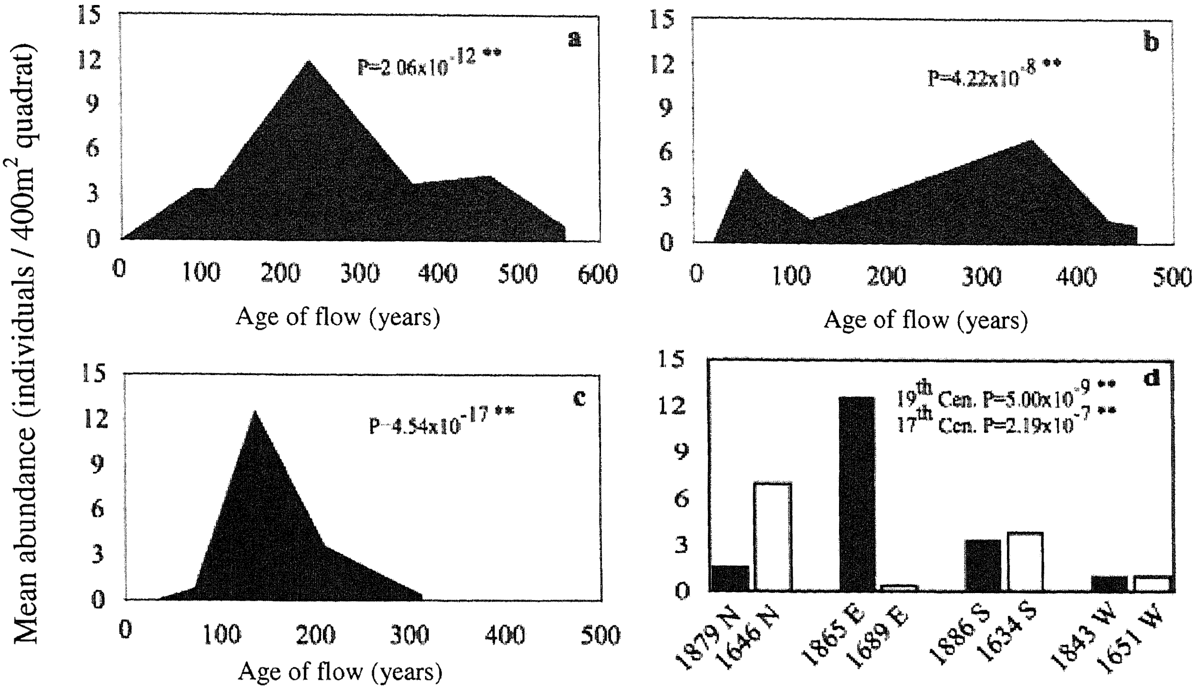


Figure 2.16. Mean abundance of *Isatis tinctoria* on the three chronosequences where **a** is the south, **b** north and **c** the east chronosequences. **d** compares two similar age groups on all four aspects.

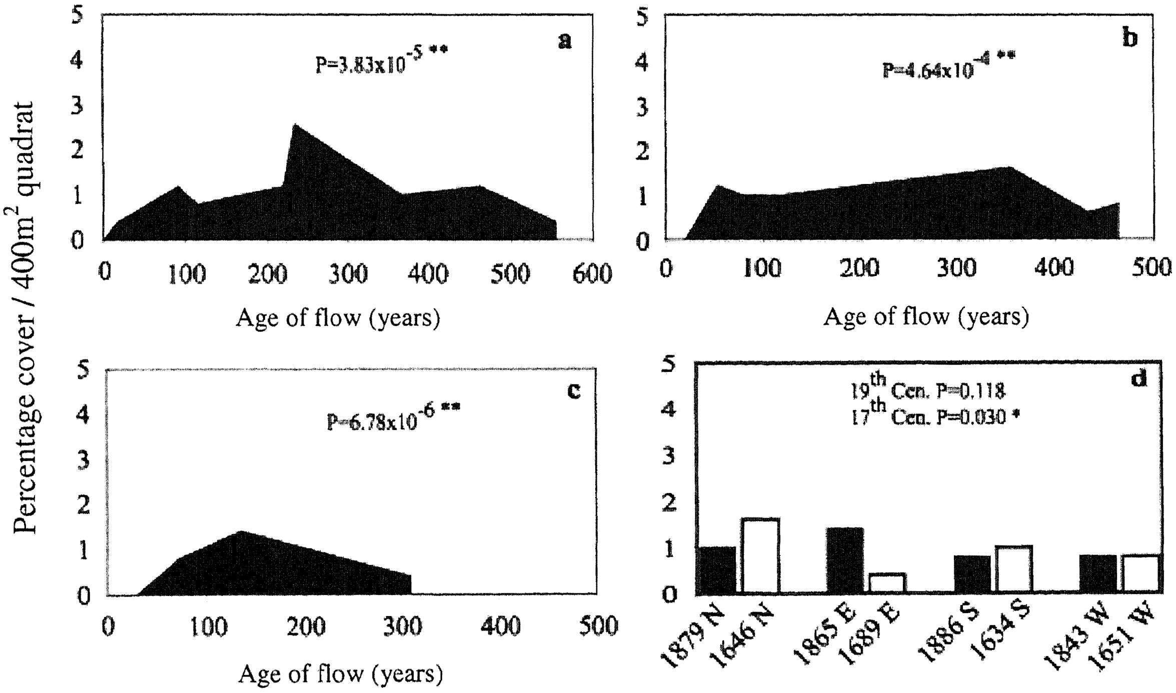


Figure 2.17. Percentage cover of *Isatis tinctoria* on the three chronosequences where **a** is the south, **b** north and **c** the east chronosequences. **d** compares two similar age groups on all four aspects.

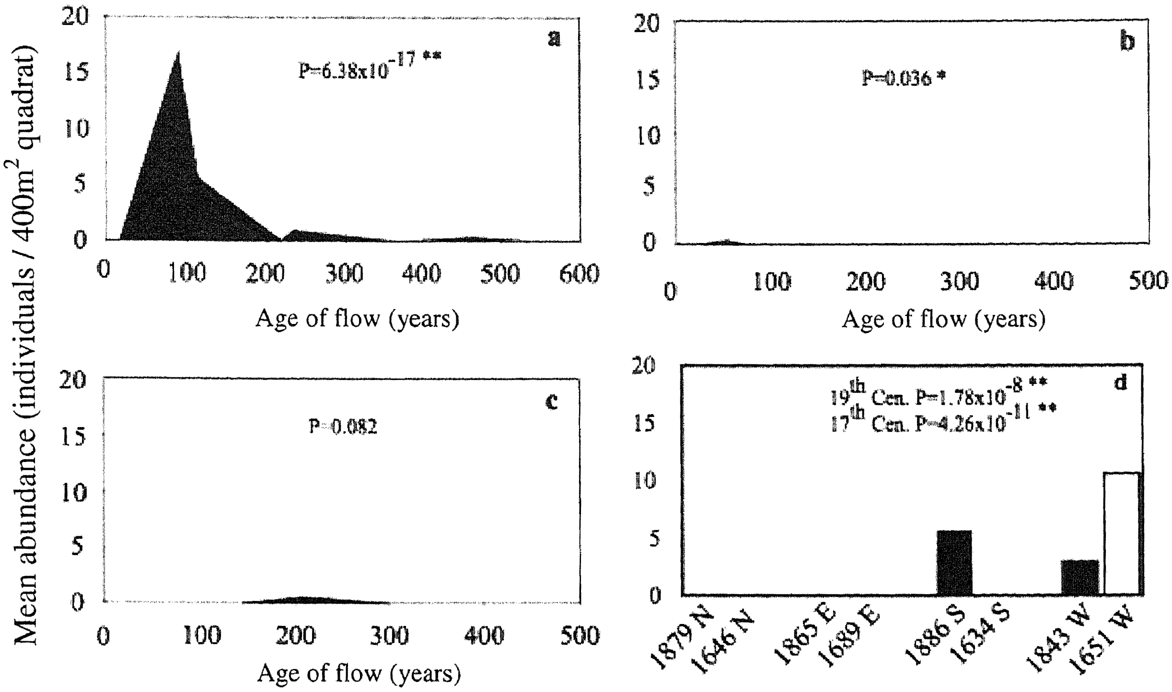


Figure 2.18. Mean abundance of *Senecio bicolor* on the three chronosequences where **a** is the south, **b** north and **c** the east chronosequences. **d** compares two similar age groups on all four aspects.

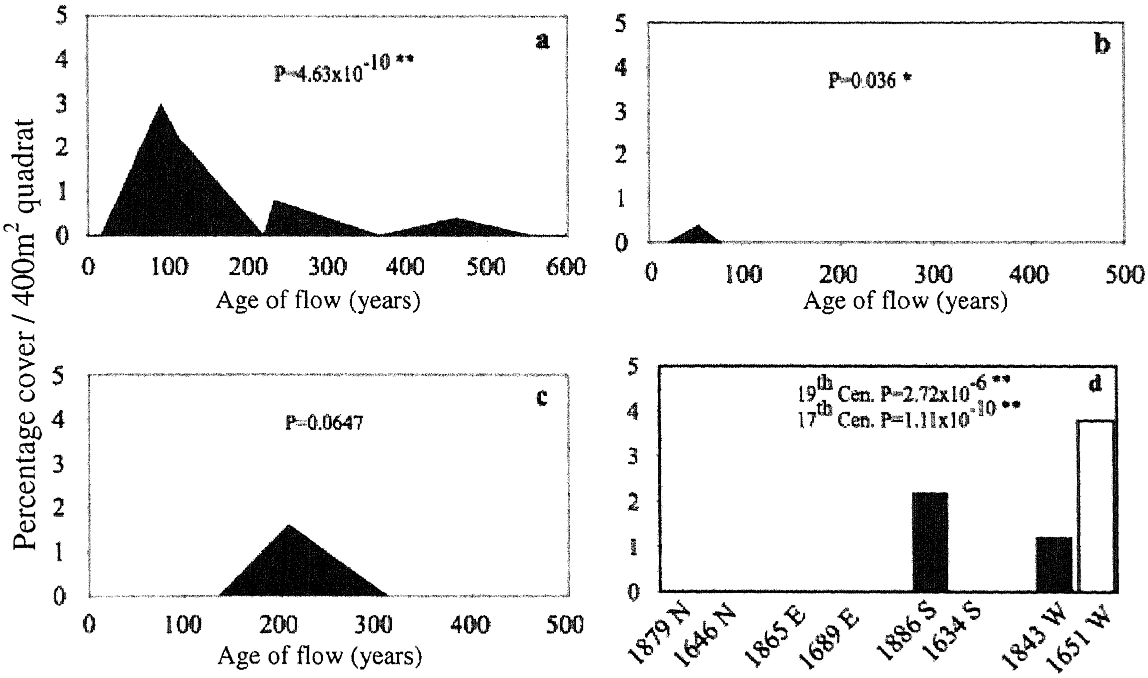


Figure 2.19. Percentage cover of *Senecio bicolor* on the three chronosequences where **a** is the south, **b** north and **c** the east chronosequences. **d** compares two similar age groups on all four aspects.

Genista aetnensis

This species is common on all aspects of the volcano except the west (Fig 2.20d). On the south chronosequence abundance gradually increases over time until the 464 year old flow where it has a density of 4 per $400m^2$ (Fig 2.20a) and a percentage cover of 21% (Fig 2.21a). On the northern chronosequence it peaks at a density of 3.7 per $400m^2$ after 121 years and the size of the *G.aetnensis* is obviously bigger as the percentage cover is up to 37% (Fig 2.21b). However the plants are smallest in the east where the percentage cover remains at about 10% from 100-300 years of age (Fig 2.21c).

Spartium junceum

This species appears early on in all three of the chronosequences. However there is a marked difference on the three aspects. On the south it has a low abundance until 366 years when it increases until 465 years when it averages over 7 per $400m^2$. After this it declines. In contrast the northern chronosequence shows a much steadier increase in abundance (Fig 2.22b) before peaking at 354 years and then declining. The biggest difference is on the eastern aspect where the species reaches its maximum abundance after only 135 years (averaging 6.6 per $400m^2$) and then declining quickly and becomes rare on lava flows older than 200 years (Fig 2.22c). This species was absent from the western lava flows studied on Etna (Fig 2.22d). These three trends for *S.junceum* abundance are paralleled in the average percentage cover (Fig 2.23). Clearly on the eastern aspect of the volcano it has become a dominant species after only 135 years (Fig 2.23c) attaining 30% cover. On the south and north chronosequences it is much slower to appear only achieving 25% cover after 464 years in the south (Fig 2.23a) and 20% on the north after 356 years at their respective peaks (Fig 2.23b).

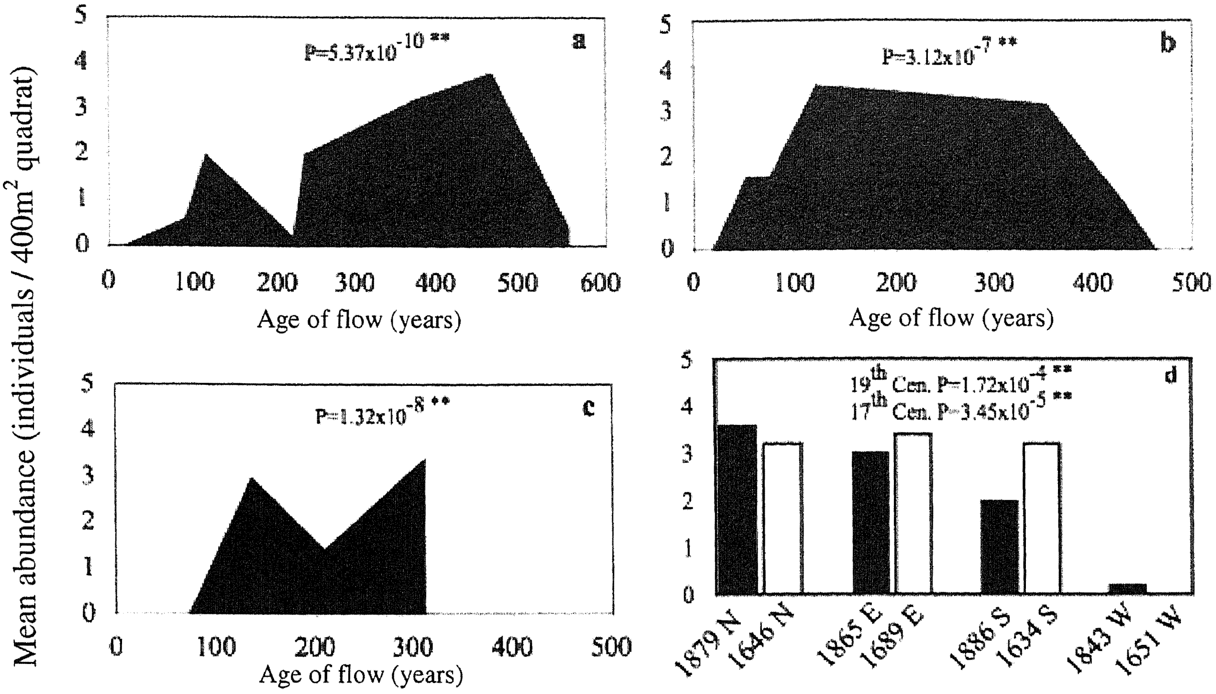


Figure 2.20. Mean abundance of *Genista aetnensis* on the three chronosequences where **a** is the south, **b** north and **c** the east chronosequences. **d** compares two similar age groups on all four aspects.

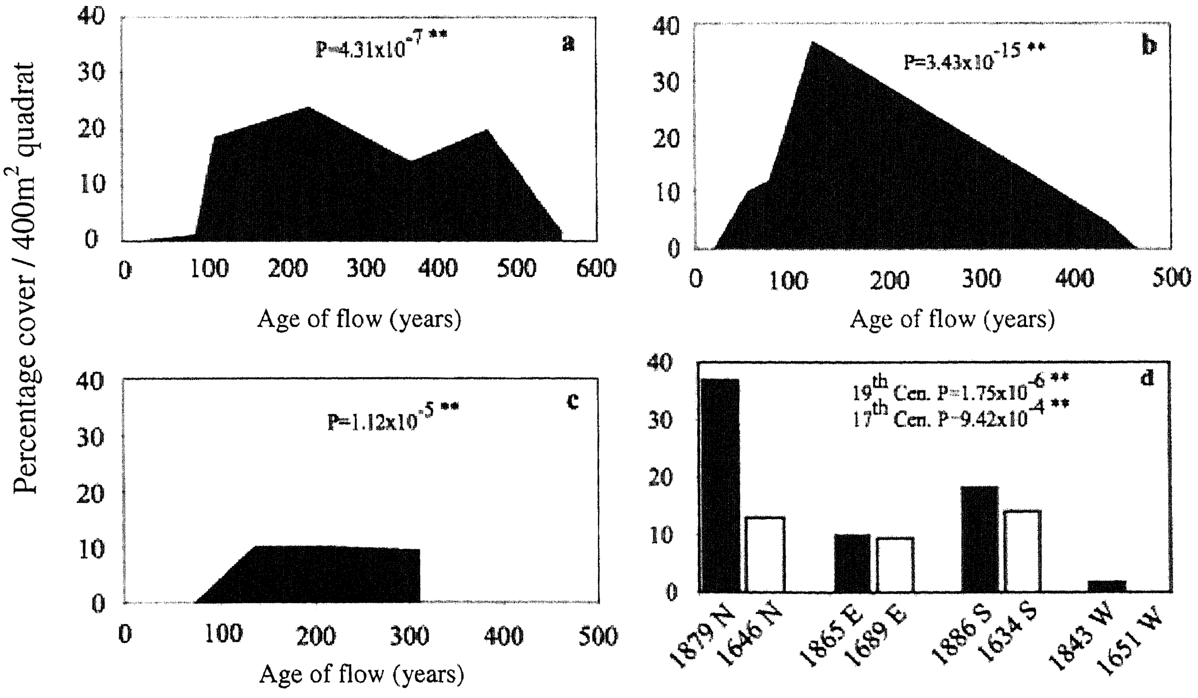


Figure 2.21. Percentage cover of *Genista aetnensis* on the three chronosequences where **a** is the south, **b** north and **c** the east chronosequences. **d** compares two similar age groups on all four aspects.

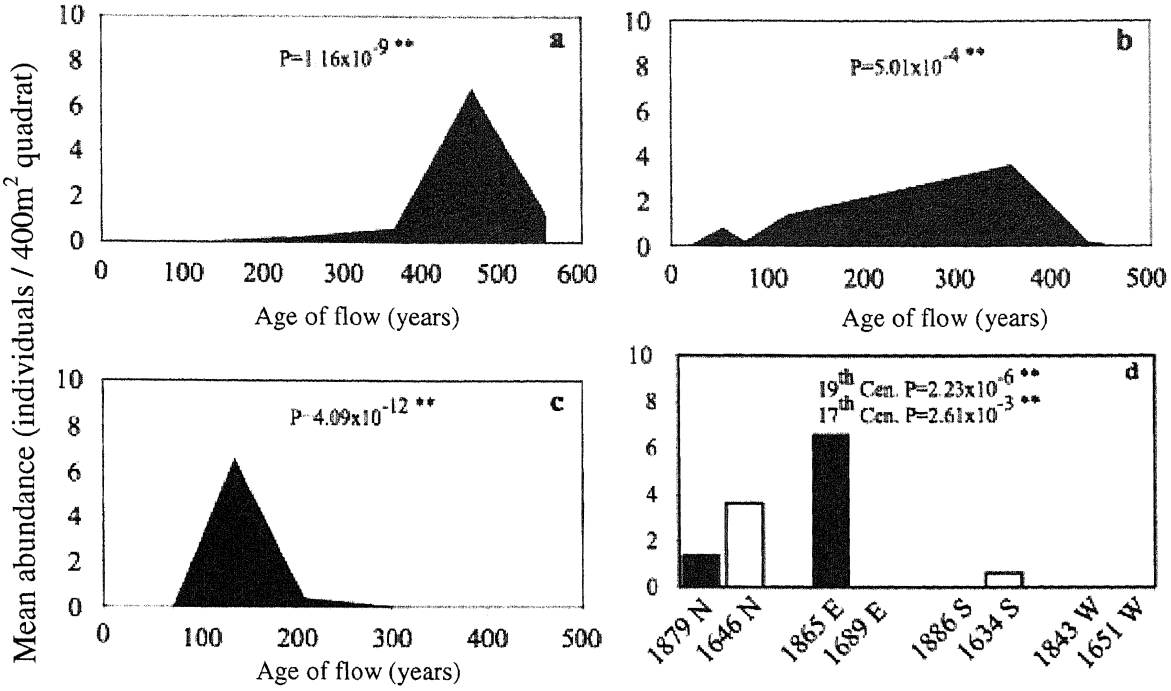


Figure 2.22. Mean abundance of *Spartium junceum* on the three chronosequences where **a** is the south, **b** north and **c** the east chronosequences. **d** compares two similar age groups on all four aspects.

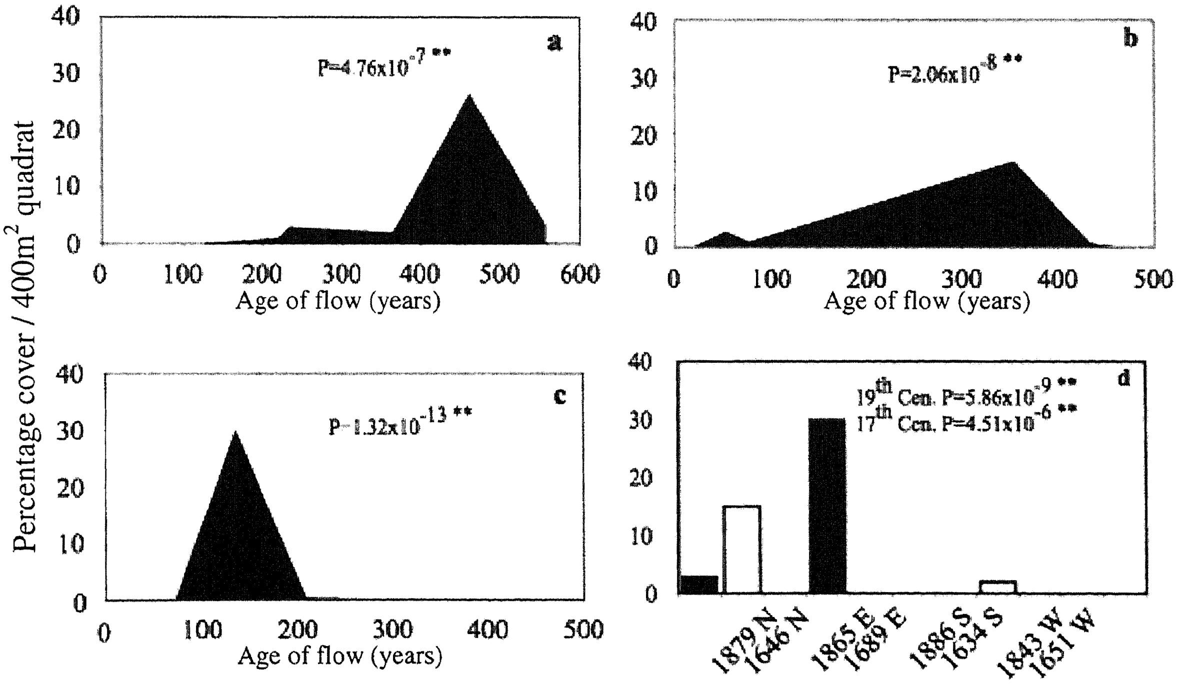


Figure 2.23. Percentage cover of *Spartium junceum* on the three chronosequences where **a** is the south, **b** north and **c** the east chronosequences. **d** compares two similar age groups on all four aspects.

Quercus ilex

This species favours the southern aspect of the volcano where it appears after about 100 years and gradually increases in abundance (Fig 2.24a) to an average level of 14 per 400m^{2}quadrat in the oldest site investigated (1444, 556 years old). It is rare in the north and east chronosequences (Fig 2.24 b and c) and absent from the western sites examined. (Fig 2.24d). As shown on Fig 2.25a the percentage cover of this species has reached nearly 100% by the end of the southern chronosequence and the area is a dominant *Q.ilex* woodland.

Quercus pubescens

In contrast to *Q.ilex* (the other oak species found on Etna) *Q.pubescens* clearly favours the east aspect of the volcano where it has achieved almost total dominance after only 311 years (1689 lava flow) averaging 13 per 400m^2 (Fig 2.26c) and nearly 100% cover (Fig 2.27c). Although present on the north and south chronosequences its abundance is low (<3 per 400m^2) and it is totally absent from the two western sites (Fig 2.26d). It does reach a percentage cover of 20% on the southern chronosequence after 364 years (Fig 2.27a) and at this time is co-dominant with *Q.ilex* which has 40% cover during the same period (Fig 2.25a). However, after this point it declines in abundance and *Q.ilex* becomes totally dominant.

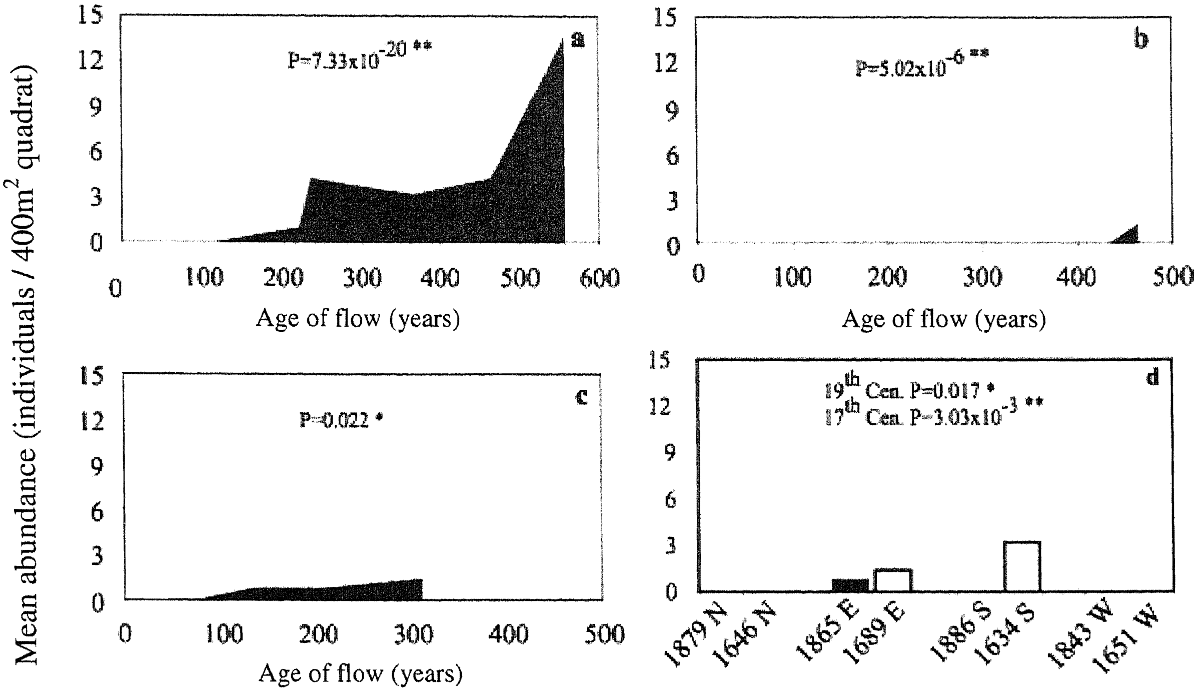


Figure 2.24. Mean abundance of *Quercus ilex* on the three chronosequences where **a** is the south, **b** north and **c** the east chronosequences. **d** compares two similar age groups on all four aspects.

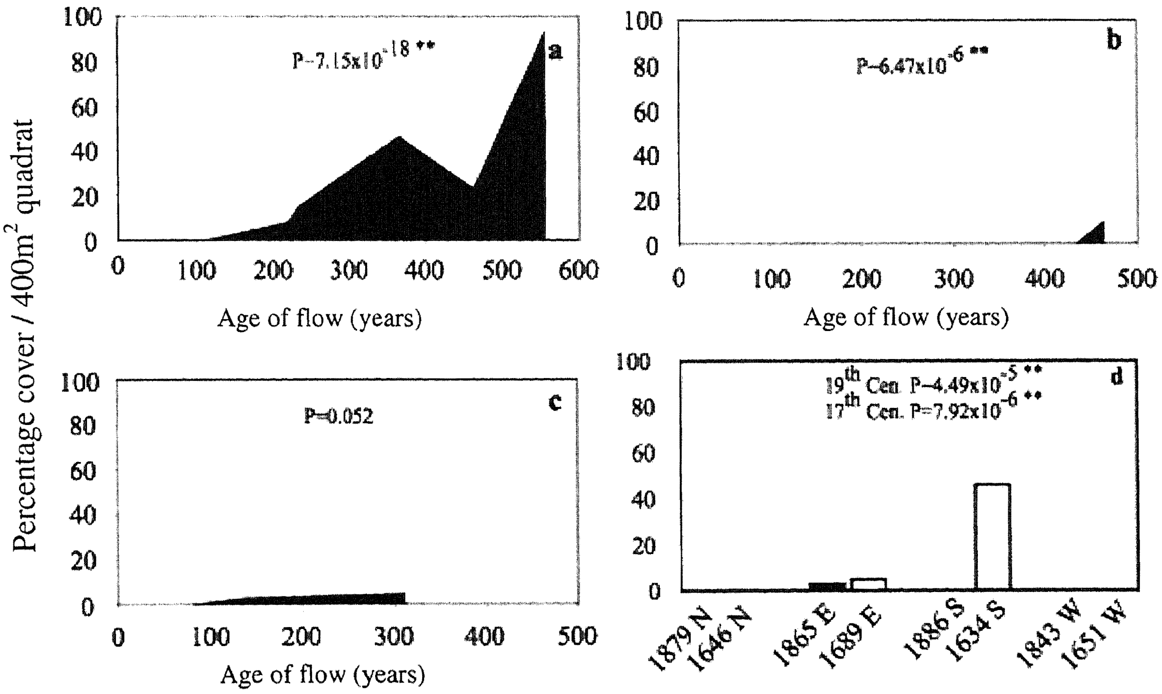


Figure 2.25. Percentage cover of *Quercus ilex* on the three chronosequences where **a** is the south, **b** north and **c** the east chronosequences. **d** compares two similar age groups on all four aspects.

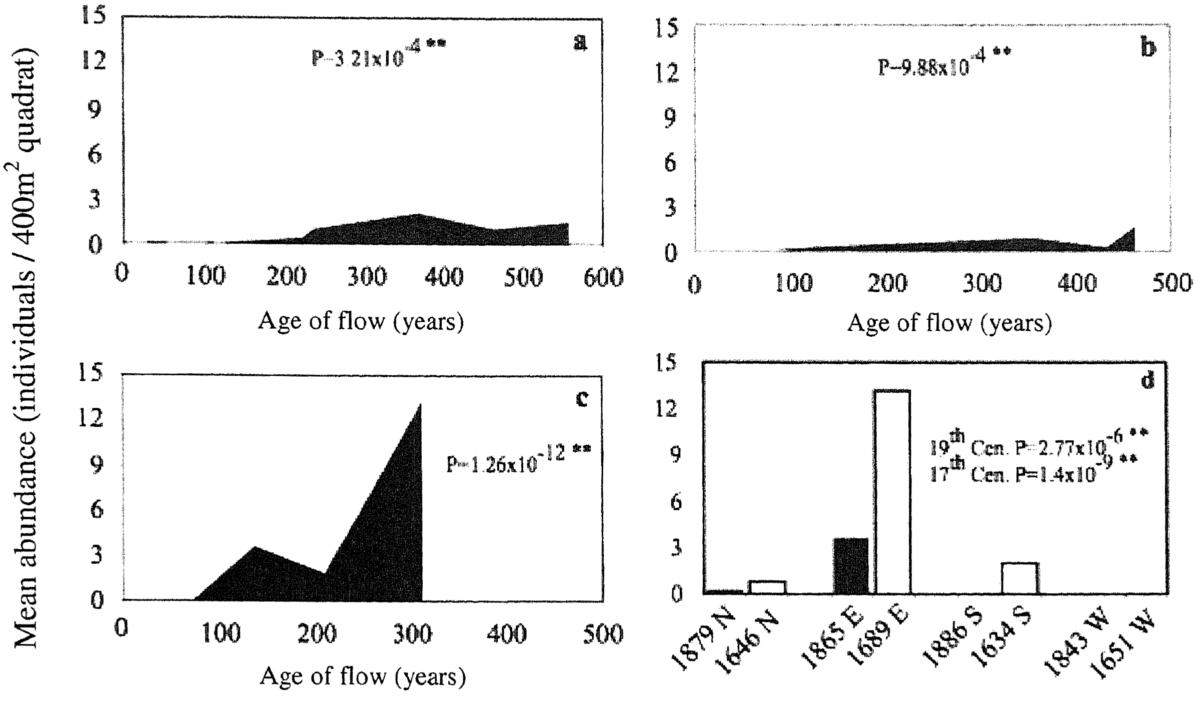


Figure 2.26. Mean abundance of *Quercus pubescens* on the three chronosequences where **a** is the south, **b** north and **c** the east chronosequences. **d** compares two similar age groups on all four aspects.

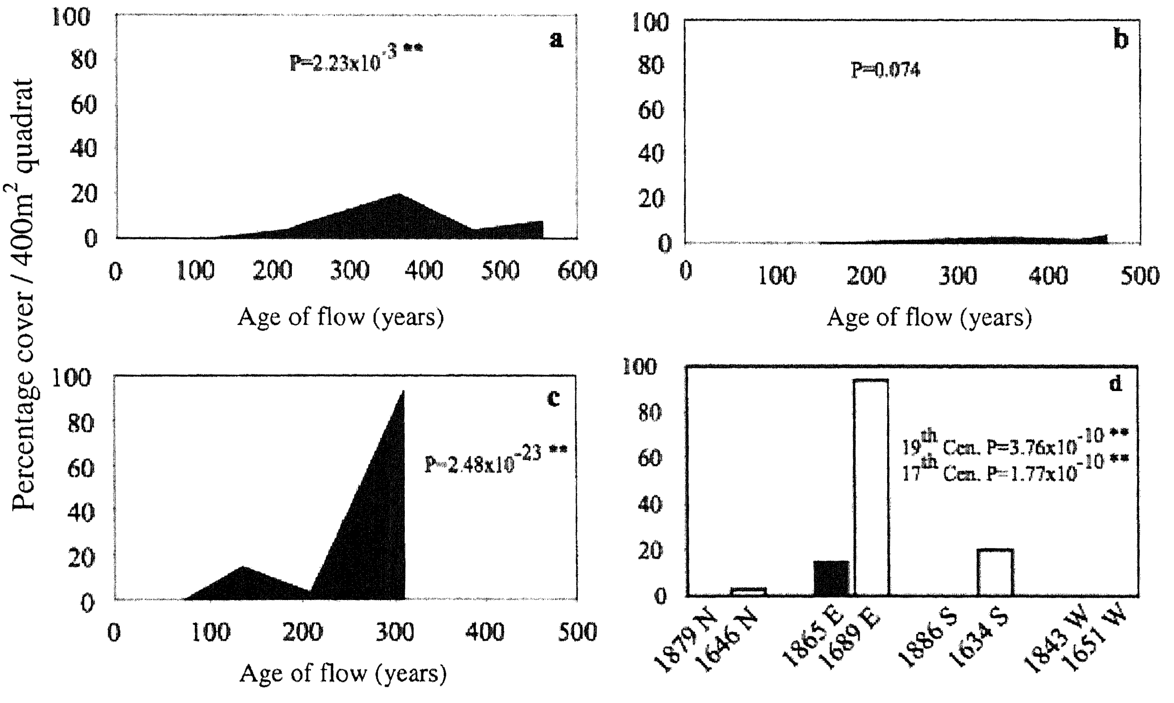


Figure 2.27. Percentage cover of *Quercus pubescens* on the three chronosequences where **a** is the south, **b** north and **c** the east chronosequences. **d** compares two similar age groups on all four aspects.

2.3.3 The abundance and percentage cover of nine primary colonising species over a range of altitudes on the south aspect of Etna

Centranthus ruber

C.ruber is abundant on the lower altitudes of the nineteenth century lava flow (1886) attaining 10 per 400m^2 at 1000m (Fig 2.28a blue line). As altitude increases this abundance declines to a level of 2 per 400m^2 by 1500m. In contrast, on the seventeenth century lava flow (1634) it has highest abundance 15 per 400m^2 at an altitude of 1250m (Fig 2.28a green line). This trend is repeated in the graph of percentage cover (Fig 2.28b).

Rumex scutatus

Clearly from the data (Fig 2.29) *R.scutatus* favours the younger lava flow – as it has a higher abundance at all altitudes on the 1886 flow than on the 1634. Species abundance and percentage cover remain constant with altitude on the seventeenth century lava flow (1634 flow - green line – Fig 2.29a and 2.29b). However, there is a drop in the percentage cover of *R.scutatus* from its peak value of 5% at 1000m to 2% on the higher 1500m site on the younger flows (Fig 2.29b)

Helichrysum italicum

This species clearly favours the higher altitudes of the south aspect of Etna. Both lava flows show an increase in abundance and percentage cover (Fig 2.30a and b) with increasing altitude. On the seventeenth century flow this rises from 0 on the 1000m site to 12 per 400m^2 quadrat at 1500m. During the same period the nineteenth century flow rises from 1.5 per 400m^2 at 1000m to 7 at 1500m. This trend is repeated in the species percentage cover (Fig 2.30b).

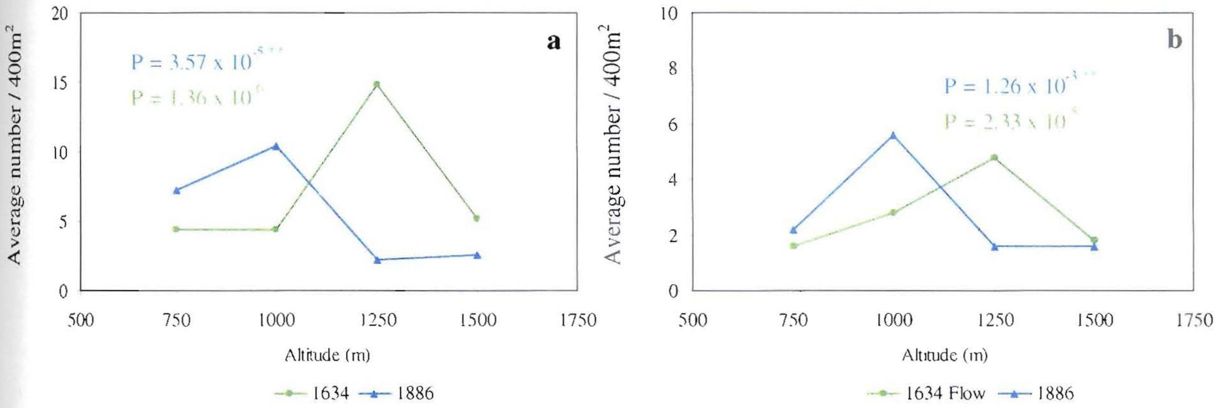


Figure 2.28. *Centranthus ruber* (**a**) abundance and (**b**) percentage cover over a range of altitudes on two lava flows on the south aspect of Mt.Etna.

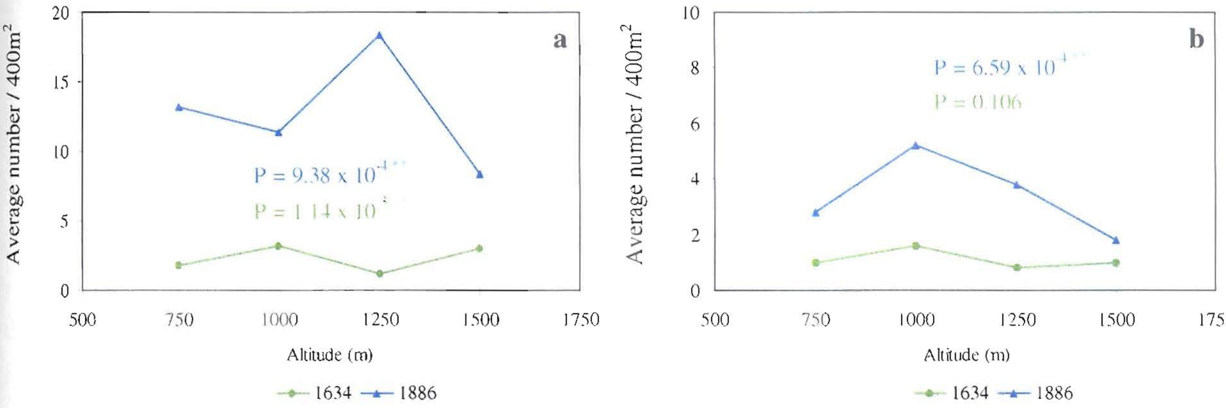


Figure 2.29. *Rumex scutatus* (**a**) abundance and (**b**) percentage cover over a range of altitudes on two lava flows on the south aspect of Mt.Etna.

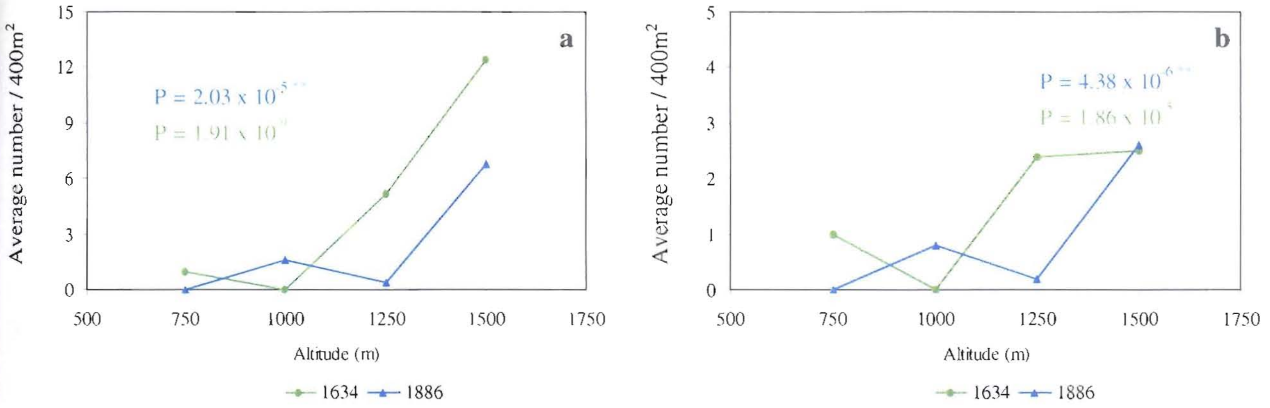


Figure 2.30. *Helichrysum italicum* (**a**) abundance and (**b**) percentage cover over a range of altitudes on two lava flows on the south aspect of Mt.Etna.

Isatis tinctoria

This species abundance and percentage cover remains constant on the 1886 flow with changing altitude (Fig 2.31a and 2.31b). In contrast, the seventeenth century flow (1634 green line) shows a large increase in abundance and percentage cover with altitude. *I.tinctoria,* rises from a low density of 1 per $400m^2$ at 750m to more than 20 at 1500m altitude (Fig 2.31a) and a rise from less than 1% to 3% cover (Fig 2.31b) over the same altitude change. This is a small plant so a change of cover of this size is quite significant.

Senecio bicolor

This species' abundance and cover changes with altitude and clearly favours the mid range altitude sites on the nineteenth century lava flow. Here, it shows peak abundance at 1000m (Fig 2.32a) with just under 6 per $400m^2$ before declining gradually on the higher altitudes. On the seventeenth century flow (green line – Fig 2.32a) it shows low abundance on the lowest altitude sites and peaks at 1250m. (4 per $400m^2$) this trend is repeated in the species percentage cover (Fig 2.33b)

Genista aetnensis

This species abundance remains constant on the 1886 flow with changing altitude (Fig 2.33a) however its percentage cover drops over the same range – from 23% at 750m to less than 10 on the 1250 and 1500m sites (Fig 2.33b). This clearly shows that the species has grown well on the lower sites and is growing more slowly on the upper slopes. In contrast, the seventeenth century flow (1634 green line) shows a large increase in abundance and percentage cover with altitude. Rising from a low density of 2.5 per $400m^2$ at 750m to more than 15 at 1500m altitude (Fig 2.33a) and a rise from 10% to 55% cover over the same altitude range (Fig 2.33b). Clearly the species takes a while to colonise the younger flows on which it grows well at the lower altitudes.

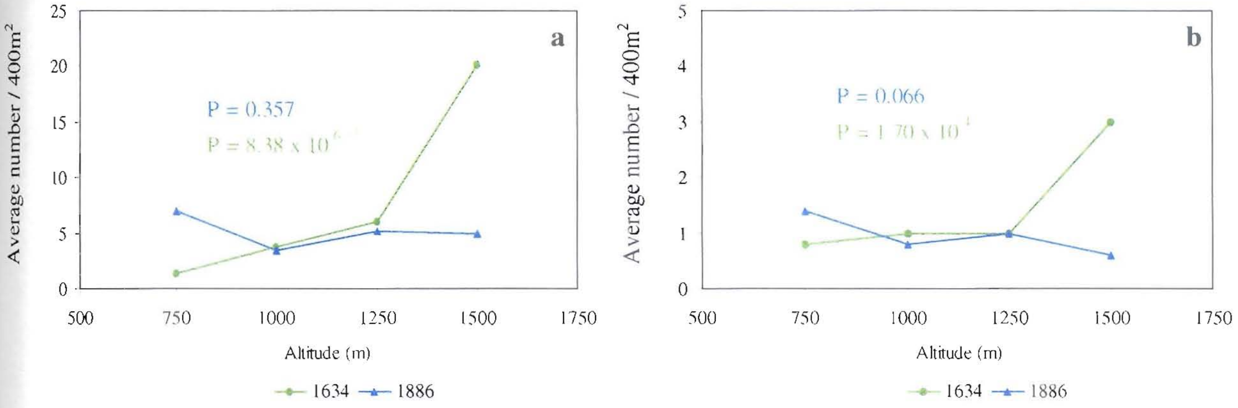


Figure 2.31. *Isatis tinctoria* (**a**) abundance and (**b**) percentage cover over a range of altitudes on two lava flows on the south aspect of Mt.Etna.

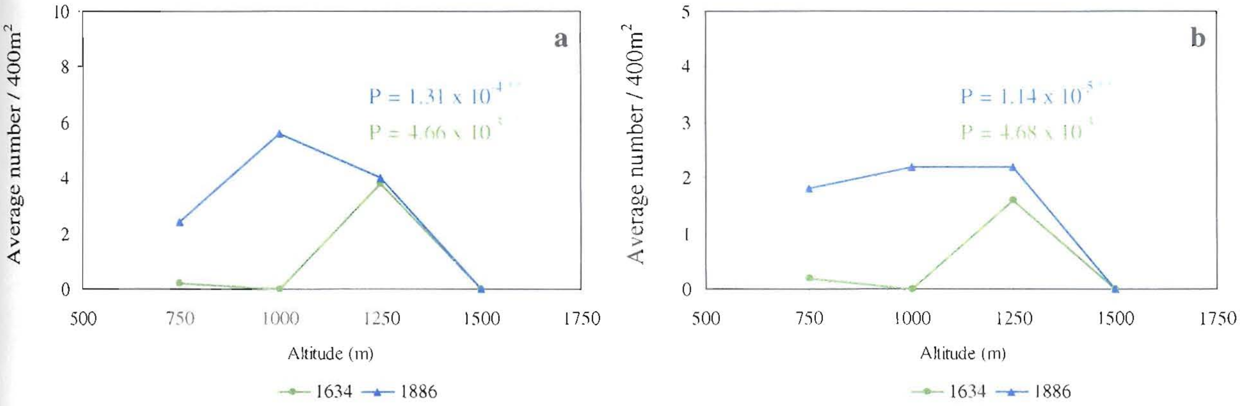


Figure 2.32. *Senecio bicolor* (**a**) abundance and (**b**) percentage cover over a range of altitudes on two lava flows on the south aspect of Mt.Etna.

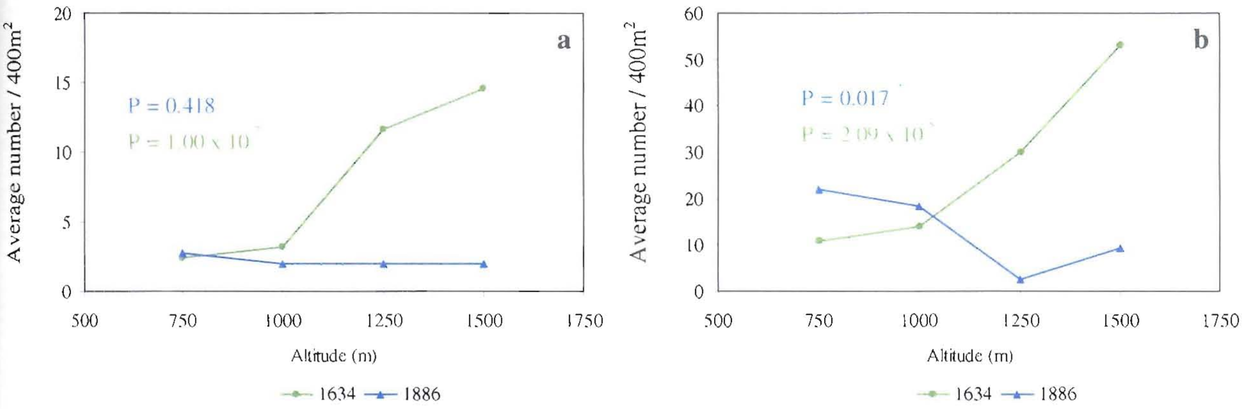


Figure 2.33. *Genista aetnensis* (**a**) abundance and (**b**) percentage cover over a range of altitudes on two lava flows on the south aspect of Mt.Etna.

Spartium junceum

This species is absent on the younger nineteenth century flow (Fig 2.34a). On the seventeenth century flow (1634) *S.junceum* shows a sharp drop in abundance with altitude. It is very common on the lowest altitude (750m, density of 11 per 400m^2 quadrat and 30% cover). After which it declines to a low level on the 1000m flow (density of 1 per 400m^2 quadrat and 2% cover Fig 2.34a and b). It is absent from the higher altitudes.

Quercus ilex

This species is present on the lowest altitude measured (750m) on the nineteenth century flow (1886) after which it declines and is absent from the higher altitude sites (Fig 2.35a). In contrast, on the seventeenth century flow 1634 it is absent on the lowest site (750m) but is common on the 1000m and 1250m. This species clearly favours the 1000m altitude on this age lava flow as it reaches a level of 47% cover (Fig 2.35b) before declining with higher altitude.

Quercus pubescens

This species is absent on the younger nineteenth century flow (Fig 2.36a). On the seventeenth century flow (1634) *Q.pubescens* shows a sharp drop in abundance with altitude after 1000m. This is reflected in the percentage cover where it has achieved 20% on the 1000m flow but is virtually undetectable on the higher altitudes (Fig 2.36b)

These data for each species over the different altitudes and aspects of Etna correlated with environmental data and the numerous links between species abundance/percentage cover and the environmental conditions can be seen in the correlation tables in the appendix.

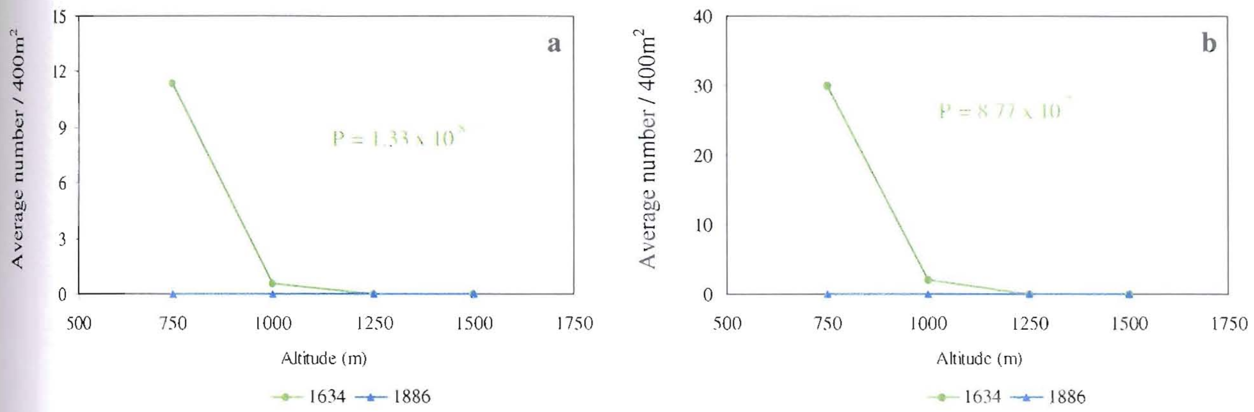


Figure 2.34. *Spartium junceum* (**a**) abundance and (**b**) percentage cover over a range of altitudes on two lava flows on the south aspect of Mt.Etna.

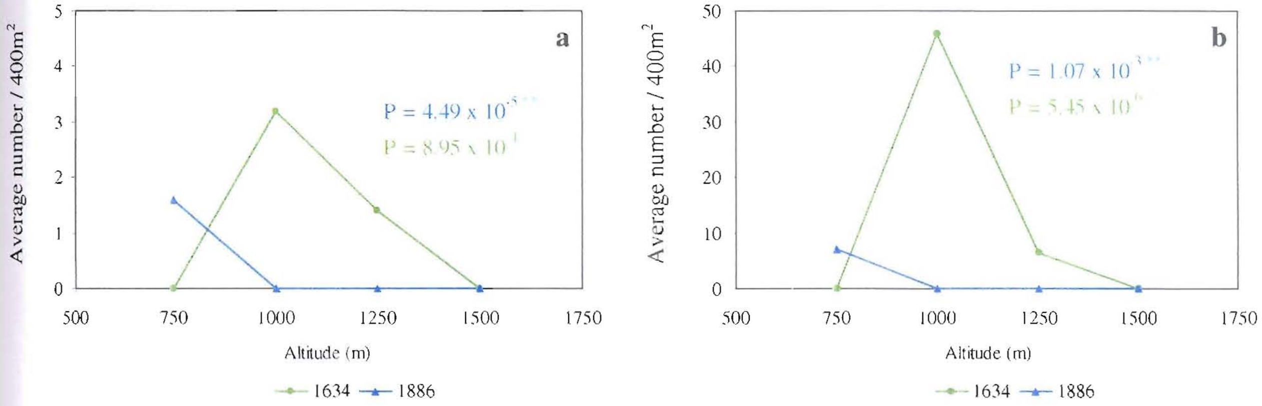


Figure 2.35. *Quercus ilex* (**a**) abundance and (**b**) percentage cover over a range of altitudes on two lava flows on the south aspect of Mt.Etna.

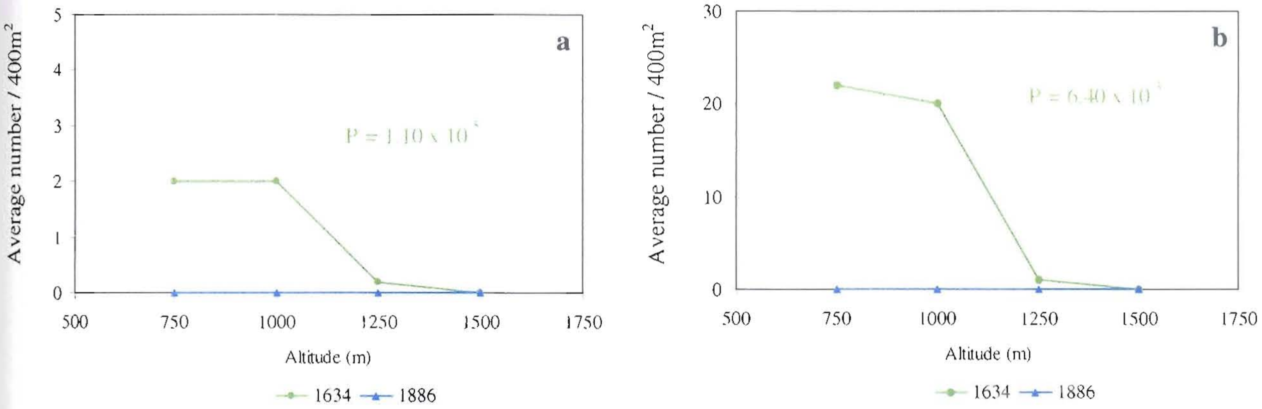


Figure 2.36. *Quercus pubescens* (**a**) abundance and (**b**) percentage cover over a range of altitude s on two lava flows on the south aspect of Mt.Etna.

2.3.4. Impact of the edge effect

On the 1928 east lava flow there is a link between the distance from the edge of the flow and the abundance of the species growing on the lava. The data from the four 50m transects were combined and a sum of each species per 5m length was gained. These data were then plotted on a bar graph. Each species showed a similar trend in the shape of the graphs with an initially high abundance, which declined with distance from the edge (Fig 2.36)

R.scutatus extended furthest onto the lava flow and was found in each of the 5m sections. However, after 15m its density had dropped to a consistent level of approximately three individuals per 5m segment (Fig 2.36.b). *C.ruber* (Fig 2.36a) and *Umbilicus rupestris* (Fig 2.36c) also show a sharp decline in frequency with distance from the edge, after which they become occasional on the lava flow.

The initial lower amount found in the first 0-5m segment from the edge of the flow for *R.scutatus* and *C.ruber* is probably a factor of slope at the edge of the flow. Where the two flows adjoin the younger flow has covered the older – and consequently the levee is steep.

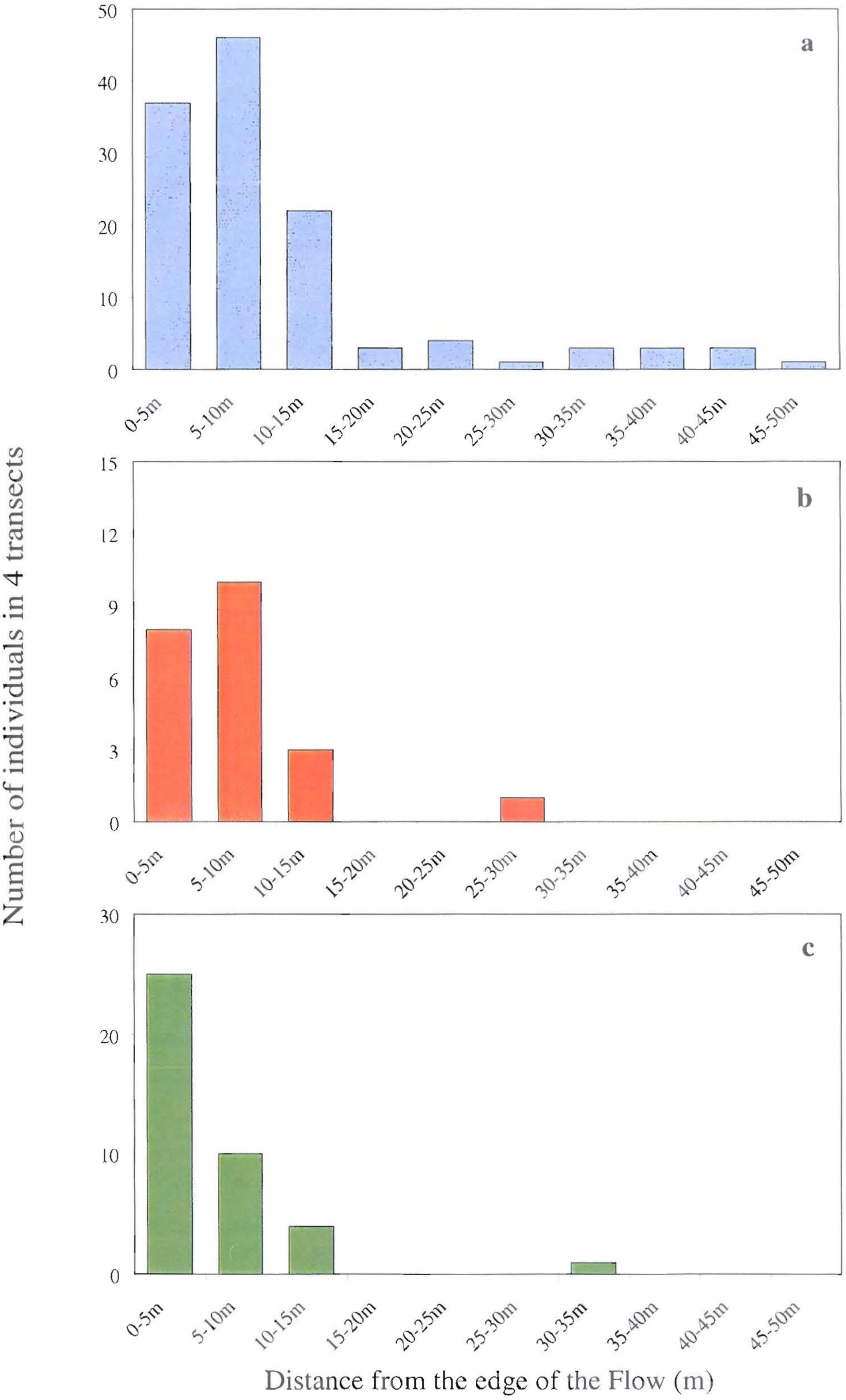


Figure 2.37. Examples of the edge effect on the 1928 lava flow (72 year old) on the east aspect of Etna. Where **a** is *Centranthus ruber*, **b** *Rumex scutatus* and **c** *Umbilicus rupestris*.

2.4. Discussion

These results show that on the chronosequences on three aspects of the volcano the species diversity present on the lava flows is characterised by two phases. During the first phase (0-150 years) there is a rapid colonisation of the lava flows with a high rate of increase in the species diversity over time. Once this initial period of colonisation has ended, a slower period of succession occurs whereby species are replaced as the changing conditions allow new species to enter the area which then competitively exclude other species. Despite the loss of some species, this second phase also shows a steady rise in species diversity over time, which probably continues long past the length of the chronosequences studied in this experiment. Given the nature of this study only the commonest species in an area would be observed and only at specific times of the year, so undoubtedly the true diversity of each site is much higher than shown here. In addition, as the ecosystem becomes richer in nutrients it will support more species, given that symbiotic relationships will form (Hobbie *et al* 2000) allowing more species to interact.

This rate of increase in diversity varies significantly between the three aspects. This can be illustrated on the east aspect of Etna. Here, the number of species increases so rapidly in the early stages that by 150 years it has double the number of vascular plant species present (35) that occur on similarly aged lava flows on the north and south aspects of Etna. There are several factors, which may account for this:

1) Climate:- The higher precipitation and more favourable temperatures in the east (Fig 1.7) will aid plant growth. Cloud formation in the afternoon produces a much cooler environment in the summer than that found on the other three aspects of Etna. This can be seen especially in comparison with the dry west.
2) Tephra:- Deposits of tephra can be found all around the volcano but are mainly found in the east aspect, as the prevailing wind blows most of the fine ash and lapilli from the summit in an easterly direction. This tephra

contributes nutrients and a fine particulate structure to the precursor soil increasing water retention and providing a matrix for the roots to grow in (Kent *et al* 2001).

From the species data there are three distinct groups of plants occupying the recent (0-500 year old) lava flows of Mt.Etna. These groups appear to occupy different time periods of the chronosequence (although there is a great deal of overlap where these species meet). The first group are the earliest **pioneers / colonisers** characterised by *C.ruber, I.tinctoria, R.scutatus, S.bicolor* and *H.italicum*. These five species are the earliest vascular colonisers on the lava and quickly achieve high abundance and percentage cover before gradually declining due to competition with other plant species. Of this group the three species; *R.scutatus*, *C.ruber* and *I.tinctoria* survive over a wide range of ages of lava (50-450 years on the south). However, they are reduced in abundance and superseded by the second group of **mid-range species** that appear to be slower colonisers (partly due to slower seed dispersal and partly the longer generation time as these take longer to produce seeds). These species are characterised by *G.aetnensis* and *S.junceum* (which appear early in the colonisation but with a low abundance). However, as age increases the size of these early colonising woody plant species, can have a significant impact on the overall diversity of flora on the lava flows. For instance a *G.aetnensis* shrub growing on a young (1910) lava flow may act as a diversity hotspot by creating shade and producing leaf litter as nutrient source. This increases the overall diversity and speeds further plant colonisation as these shrubs act as a spreading centre of diversity and colonisation (Certini *et al* 2001). These two species dominate the lava flows with their high percentage cover. In the case of *S.junceum* by up to 20% cover after 300-400 years on the north and south chronosequences and 30% cover on the east at 100 years. *G.aetnensis* has an even greater effect by averaging 20% of the cover on the south chronosequence from 100-450 years. However, both of these species decline after the 450 year old mark, as a result of competition with the third group of colonisers – the deciduous trees. These trees are characterised by the two oak trees, *Q.ilex* and *Q.pubescens*. By the end of the age range of the chronosequences covered by this study the oak species have risen to dominant status. However, *Q.ilex* dominates the south aspect and *Q.pubescens* the east, which by 300 years has produced a large oak forest with a high abundance (averaging 14 in a $400m^2$ quadrat) and percentage cover (90%).

2.4.1. Change of species with aspect

Each of the nine commonest species observed on Etna has specific requirements / preferences in order to survive in an area. For example, the early pioneer species *S.bicolor* clearly shows a preference for the early (50-150 year old) lava flows of the south aspect of the volcano (Figs 2.18 and 2.19) where it achieves an abundance of $17m^{-2}$. In contrast, it is rare on the north and east chronosequences. This could be caused by the different climates zones located around the volcano or specific nutrient requirements of each species. Seedling survivorship will be specific to each species nutrient needs and the sites ability to supply those needs (Del Moral 1993; Tsuyuzaki *et al* 1997)

S.junceum clearly shows the increased rate of colonisation on the east aspect of the volcano. On the north chronosequence it increases gradually from 0 – 360 years before declining. However on the east aspect it reaches its maximum abundance (6 per $400m^2$) after just 135 years and then declines and is superseded by the oak species *Q.pubescens* (as confirmed by Poli *et al* 1981). The diversity and cover of the plant species present on Etna is very complex as the changing conditions of the succession create a zonation of species into specific regions of the volcano (Eggler 1959; Poli *et al* 1981). For example *H.italicum* grows well on the north and south chronosequence but not on the east (Fig 2.14 and 2.15).

2.4.2. The change of species with altitude

There is clearly species change occurring with altitude, but this is also being affected by the age of the flow. In most of the nine species shown here there is a distinct pattern of spread, as species colonise the lower altitudes first before spreading over time further up the lava flow. This difference in species abundance at different altitudes may be due to changes in nutrient availability caused by the different climatic conditions (Austin and Vitousek 1998). This causes an effect similar to the chronosequence itself as colder conditions at higher altitudes slow the succession (Aplet and Vitousek 1994). As new species enter the system they too colonise the lava flow from the bottom - out-competing and replacing the other species, before spreading up the slope. This leads to heterogeneity on the lava flows with altitude.

This is demonstrated when comparing *G.aetnensis* (Fig 2.33) and the two oak species *Q.ilex* and *Q.pubescens*. On the younger lava flow (1886) *Genista* has quickly grown on the lower altitude of 750m (over 20% cover) but declines steadily with altitude – during the same period *Q.ilex* has only appeared on the lowest altitude site (750m Fig 2.35a) and *Q.pubescens* has yet to appear on the flow. In contrast on the older lava flow (1634) *G.aetnensis* has declined in its cover of the lower altitudes (less than 10%) but its peak abundance and cover has now moved up the lava such that it covers over 50% at 1500m. However, *Q.ilex* and *Q.pubescens* have now become common on the lower slopes and covers over 47% and 20% respectively at an altitude of 1000m (Fig 2.35 and 2.36). In effect, *G.aetnensis* has been replaced by the oaks at this stage in the succession.

2.4.3. The edge effect

The experiments on the edge effect undertaken on Mt.Etna demonstrate the need for selecting sites far from the edge of the flow in order to obtain information on a typical site on a particular lava flow. This was one of the reasons why a standard distance of 50m was always chosen in site selection. The gradual encroachment of some species from the edge (e.g. *R.scutatus* Fig 2.36) and the sudden appearance of others simultaneously all over the lava (e.g. the lichen *Stereocaulon vesuvianum*) causes heterogeneity in the vegetation of any particular area of a flow depending on the distance from the edge. As distance increases diversity declines and eventually becomes relatively stable (given that minor topographical features may cause fluctuations in species diversity) as demonstrated by *R.scutatus* (Fig 2.37). In addition, the same can be said of the presence of dagalas on the lava flows. The presence of a small patch of an old, diversity rich area in the middle of a barren young lava will have a significant impact as a 'spreading centre' of colonisation both as a source of nutrients (biomass) and a seed pool. Both the edges of a flow and dagalas aid colonisation in several ways:

1) By producing biomass (e.g. leaf litter) to form a precursor soil.
2) By producing vegetative colonists (runners and stolons) which can encroach from the edges whereby the plant can deposit a new plant in a specific area and continue to support it from a nutrient rich area until it is big enough to support itself.
3) Production of seeds which will colonise the new lava.
4) By supporting an animal population which will cross between edges / dagalas and in so doing spread seeds across the intervening distance and also (by defecation), deposit biomass of a relatively high nutritional content onto the lava flow.

Chapter 3: Nitrate Reductase as an indicator of plant succession

3.1. Introduction

Nitrogen is a vital element for life. As the soil nutrient required in the largest quantities, it contributes between 1 and 3% of the total dry mass of higher plants (Lee and Stewart 1978) compared to carbon which is sourced from the atmosphere and which contributes 40% (Beevers and Hageman 1969). It has been estimated that on a world-wide scale, 200 billion tonnes of carbon are fixed annually by photosynthetic processes. On the basis of approximate analysis, this would require the assimilation of 10 billion tonnes of nitrogen (Beevers and Hageman 1969). Comprising nearly 80% of the atmosphere, nitrogen is fixed by prokaryotic organisms existing either symbiotically within plants (nitrogen fixing plants or lichen) or free-living within the soil matrix. These organisms reduce atmospheric nitrogen (N_2), to form ammonia (NH_3) by adding electrons and hydrogen ions (Campbell 1993). They catalyse the reaction using an enzyme complex called nitrogenase. In soil solution, the ammonia picks up another hydrogen ion to form ammonium (NH_4^+), which some plants can absorb. However, plants usually acquire nitrogen in the form of nitrate (NO_3^-). This nitrate is produced in the soil by nitrifying bacteria that oxidise ammonium (Campbell 1993). Apart from those species that utilise symbiotic nitrogen fixing bacteria, the bulk of plant nitrogen arises from the reduction of nitrate from the soil. Under natural conditions, this inorganic form of nitrogen, occurs at concentrations of 1 mol m^{-3} or less in the interstitial water of soils, although in arid areas greater levels may build up (Andrews 1986). In agricultural soils, nitrate concentration can be as high as 20 mol m^{-3} because of the addition of N fertiliser.

As a result of its importance for plant growth, changes in available nitrogen over successional time can have implications for ecosystem development over a chronosequence. So methods of detecting nitrogen change over time are of inestimable value in this project to study ecosystem change. Therefore this chapter is entirely devoted to the use of nitrate reductase to detect these changes at an ecosystem level which will then be compared with more traditional methods of soil and foliar nutrient analysis outlined in the next chapter.

3.1.1. Nitrate reductase as a successional indicator

A characteristic feature of nitrate metabolism in higher plants is its susceptibility to a range of environmental conditions. It has been established that light, drought, mineral nutrition, and plant age all influence the capacity of nitrate reduction (as shall be demonstrated in the following sections). In most of these cases it appears that the control of nitrate reduction is mediated by the regulation of nitrate reductase. This is a logical conclusion since it is a) the first enzyme in the pathway; b) the rate limiting step; c) substrate dependent; d) relatively unstable (high turnover rate). In addition, the toxic effects of excess levels of nitrite and ammonium ions also indicate the desirability of regulating their production. As a result, nitrate reductase should make an excellent indicator of available nitrate at a set time – as well as how that system may vary under slightly different environmental conditions (e.g. brought about by changes in altitude). Hence, this should make it an extremely useful tool in determining changes in nitrogen availability over successional time over a range of conditions as are found on the lava fields of Mt.Etna.

3.1.2. Function of Nitrate reductase

Within the plant, nitrate must first be reduced to ammonium before being assimilated into amino acids (Beevers and Hageman 1969). This reaction takes place in several stages. Firstly the nitrate is actively transported into root cells (Lee and Stewart 1978) and is then either reduced in the root or transported to the shoot where it is reduced in the leaves (Andrews 1986). The reduction of nitrate to ammonia within the cell occurs in two steps, catalysed by the enzymes nitrate reductase (NR) and nitrite reductase (NiR) (Crawford *et al* 1992) as shown below :

$$NO_3^- \xrightarrow{NR} NO_2^- \xrightarrow{NiR} NH_4^+$$

The process converts nitrate into nitrite as a stable free intermediate and ammonium as a stable end-product and involves the utilisation of NADH and reduced ferredoxin in the donation of eight electrons per molecule of ammonium formed (Hewitt *et al* 1979). Incorporation of the ammonium into amino acids is carried out by the glutamine synthetase-glutamate synthase pathway (Pelsey and Caboche 1992). Nitrate reduction takes place in the cytosol, whereas nitrite reduction and ammonia fixation occur in the chloroplast. This entire set of enzymes and reactions is referred to as the nitrate assimilation pathway (Crawford *et al* 1992).

The first step in the conversion of nitrate to ammonia is thought to play a key role in nitrate assimilation by controlling the flux of nitrate through the pathway. In other words, nitrate reduction is the rate determining step in the nitrate assimilation pathway within the cell. The main evidence for this claim is that nitrate fed plants seldom accumulate an excess of either nitrite or ammonia (Lee and Stewart 1978).

3.1.3. Structure and enzymology of Nitrate reductase

Due to intensive biochemical and molecular studies of nitrate reductase, much has been learned about its structure and enzymatic properties (Crawford and Glass 1998; Campbell 1996; Pelsy and Caboche 1992; Campbell and Remmler 1986). The enzyme shows considerable variation between species in its size and genetic structure but all show the same basic features. A standard model as constructed by Notton and Hewitt (1979), and Crawford *et al* (1992) shows that the enzyme consists of three distinct structures. To quote Crawford *et al* (1992 p378): "The enzyme is a homodimer of 100-110 kDa subunits. Each subunit is thought to be further divided into three distinct domains, which serve as redox centres. A subunit of NR contains Flavin Adenine Dinucleotide (FAD), a heme-Fe and a molybdenum pterin cofactor (MoCo)." These groups are the redox centres that catalyse the transfer of electrons from NADH or NADPH to nitrate, in order to form ammonium.

In addition, one of the features of this enzyme is that it can exist in two stable forms, one active and one inactive and that their mutual interconversion is governed by an oxidation-reduction mechanism. Under reducing conditions the active form is converted into the inactive one. The inactive form recovers its original activity when incubated with ferricyanide (Aparicio and Maldonado 1979).

3.1.4. Location of nitrate assimilation

Almost all tissues of higher plants have or are capable of synthesising the complement of enzymes necessary to assimilate nitrate (Andrews 1986; Smirnoff *et al* 1984; Lee and Stewart 1978; Beevers and Hageman 1969) although there are a few notable exceptions like the *Erica* spp which do not possess nitrate reductase. Evidence regarding the sites of nitrate assimilation can be found by two approaches : analyses of the enzymatic composition of root and shoot tissues and analyses of the nitrogenous compounds exported by the root. Species exhibit marked differences as regards the sites of nitrate assimilation and two groups can be recognised. There are those in which assimilation is restricted to the shoot, particularly the leaves. Plants such as *Borago* spp. and *Xanthium pensylvanicum* (Lee and Stewart 1978) are characteristic of this group. In these species the xylem sap contains 95-99% of its nitrogen in the form of nitrate ions (indicating that it is being transported from the roots and has not been converted to ammonium or amino acids), and no NR is measurable in the roots (Lee and Stewart 1978). The other group consists of plants where assimilation is carried out in the roots. For example *Lupinus* and *Vicia*, (Andrews 1986) and *Picea rubens* (Yandow and Klein 1986). The majority of plants studied show a pattern intermediate between these two extremes. In these, both root and shoot tissues have appreciable levels of NR and the xylem sap contains free nitrate and organic nitrogen (Lee and Stewart 1978).

On the basis of such studies it has been proposed that plants relying on shoot nitrate assimilation have a low capacity for root nitrate reduction. There has been no widespread correlation between the predominance of one particular form and the environment in which it is situated, but it has been proposed that in many species - especially the *Leguminosae* and other species, temperate species carry out most of their nitrate assimilation in the root while tropical species use their leaves (Andrews 1986). From an energetic viewpoint, it is thought that photon and water economy benefits can be gained in light photon flux density (PFD) environments by carrying out photoreduction of nitrate in the leaves or stems as opposed to respiratory driven reduction in the roots. This would explain the predominance of shoot NR activity in tropical species - but causes confusion concerning the temperate species. Andrews (1986) proposed the explanation that although shoot assimilation is an advantage in high PFD environments, it is a disadvantage in low temperatures. He supports this with evidence of work on a cold-sensitive normally spring-sown cultivar of *Vicia faba* L. and an overwintering cold-tolerant variety. When the two cultivars are grown together both the distribution of NRA between root and shoot and xylem sap : reduced N indicate that the proportion of nitrate assimilation is greater in the cold sensitive cultivar than in the cold tolerant. However, when the cold tolerant cultivar is given nitrate and 'forced' to transport nitrate to the shoot, it too shows low temperature stress effects – indicating that decreased shoot assimilation may be a factor in low temperature tolerance (Andrews 1986).

3.1.5. Diurnal variation in activity

The level of NR in leaf tissue varies diurnally and is influenced by the intensity of the illumination (Wyn-Jones and Sheard 1979; Canvin and Atkins 1974; Beevers and Hageman 1969). Extracts from plants exposed to increasing periods of darkness show a progressive decrease in nitrate reducing ability (even when adequate electron donors are present in the medium) which is restored on subsequent illumination (Beevers and Hageman 1969). However, there is no variation in the rate of nitrate uptake from the soil over the diurnal/nocturnal cycle as was proved by Rufty *et al* (1984). The nitrate then accumulates in the root. A large portion of the nitrate, retained in the root in darkness, is translocated and incorporated, into insoluble reduced-N in the shoot, in the following light period. The amount of nitrate assimilated during the light period exceeds the amount of exogenous nitrate acquired from the soil (Rufty *et al* 1984). In this way the maximum amount of nitrate is assimilated in the stem during the light period, utilising nitrate taken up the night before.

Although the mechanisms involved in the link between nitrate assimilation and the diurnal cycle remain unclear, several hypotheses have been proposed. As nitrate assimilation correlates to CO_2 assimilation (Geiger *et al* 1998; Steer 1973) an indirect control by photosynthesis has been suggested. The flow of carbon compounds from the shoots might regulate nitrate uptake, an ATP-dependent process, through root respiration. Diurnal root respiration seems closely related to nitrate uptake rate (Cardenas-Navarro *et al* 1998). As nitrate reduction in woody plants is mostly a photosynthetic process, other hypotheses are based on a control of nitrate uptake either by some assimilation products, or by plant nitrate content itself. Exogenous supply of amino acids or malate, a nitrate assimilation by-product, depress and stimulate nitrate uptake, respectively (Cardenas-Navarro *et al* 1998). However, during the diurnal cycle or following nutritional treatments, reports of correlation between root amino acid content and nitrate uptake are conflicting, and malate production is not specific to nitrogen metabolism.

However, at present these are still only hypotheses, (if backed by circumstantial evidence). It is probably not justified to see any single kind of plant-light interaction as defining the total relationship between white light and nitrate assimilation (Wyn-Jones and Sheard 1979). Only the barest outline of this relationship is currently available.

3.1.6. The effect of drought

Studies on the effects of drought on NR activity have clearly shown, that enzyme activity decreases under rapidly applied water deficits, (Foyer *et al* 1998; Smirnoff *et al* 1985; Rajagopal *et al* 1977). This decrease can be extremely significant to the activity of NR in the plant. For example, Smirnoff *et al* (1985) observed a 30 - 85% loss of NR over 6 days of water stress in barley (*Hordenum vulgare*) and duram wheat (*Triticum durum*). This can also be demonstrated in maize (Shaner and Boyer 1976). Foyer *et al* (1998) noted that foliar NR activity in maize leaves decreased to less than 10% of the original maximal after 7 days of water deprivation. The decrease has also been demonstrated in field grown plants, since Rajagopal *et al* (1977) found crops of wheat grown under drought conditions had lower activities than those grown with irrigation. This is significant since in laboratory experiments small soil volumes can lead to rapid development of stress over a period of days, whereas field grown plants have a much larger volume of soil with a greater capacity for water retention and hence stress develops slowly over the growing season (Smirnoff *et al* 1985).

Nitrate reductase activity recovers quickly once water is restored – which can be important in mediterranean climates where periods of drought are common. Maximal extractable NR activity recovered in Maize (Foyer *et al* 1998) when water was restored three days into the experiment. Similar results were found by Shaner and Boyer (1976), who showed an 80% recovery subsequent to water restoration. Drought induces complex changes in C and N metabolism from water deficits and from modifications in the availability of nutrients. This has the knock on effect of reducing protein synthesis and hence NR production. In consequence, while the rate of enzyme degradation remains constant, the rate of production falls, causing an overall decrease (Shaner and Boyer 1976). This reduced rate of protein synthesis may be the result of a direct effect of the water potential within the plant, or indirectly from an alteration in the signals that in turn control synthesis. The first alternative has been proved in maize (Shaner and Boyer 1976).

It is worth noting at this point that NR activity in young leaves varies little under stress conditions, and it is the older leaves that show a marked decrease. This suggests a link between NR activity and increased senescence caused by the water deficit (Smirnoff *et al* 1985).

3.1.7. Substrate induction

Evidence that nitrate reductase is inducible, (i.e. production is stimulated by addition of nitrate) has been produced by many workers (Min *et al* 1998; Imsande and Touraine 1994; Hofstra *et al* 1985; Shaner and Boyer 1976). One thing that quickly becomes clear, is that different levels of nitrate are required for optimum induction in different species and in some cases high concentrations are needed (Beevers and Hageman 1969). These differences almost certainly relate to differences in rate of uptake. For example in the trembling aspen, (*Populus tremuloides* Michx.) optimum NR activity is achieved 12h after exposure to nitrate around the roots. Whereas in the lodgepole pine (*Pinus contorta* Dougl.) optimum activity does not occur until 4 days later (Min *et al* 1998). Shaner and Boyer (1976) took this one step further when they first lowered, then restored, nitrate to maize plants (*Zea mays* L.) kept under controlled conditions. These plants showed a marked decline in NR activity, but quickly recovered once the nitrate was restored. This rapid recovery allows plants to quickly assimilate nitrate when it becomes available, since this element is usually limiting to plant growth (Imsande and Touraine 1994).

3.2. Methods

During the course of this investigation various methods have been used to determine nitrate reductase activity change over successional time - in order to:- 1) test the sensitivity of the enzyme to changes in the ecosystem properties (environment and nutrient availability). 2) refine the experimental procedure for field work. 3) to compare the field results with those taken from simulated environmental conditions in the laboratory, in order to show that NR activity is a good determination of successional change and not merely random or due to other factors. In addition, to find out which particular factor of ecosystem change has the greatest effect on NR activity.

3.2.1. Species selection

In order to trace variation in NR activity over time on Mt.Etna, it was necessary to select species that are represented over a long period of successional time, starting at the earliest possible phase of colonisation. In addition, these plants would have to produce an easily measurable amount of nitrate reductase. The first factor limited the plant selection to seven species: *Centranthus ruber, Rumex scutatus, Helichrysum italicum, Genista aetnensis, Senecio bicolor, Linaria purpurea* and *Echium vulgare*. Of these species, both *E.vulgare* and *L.purpurea* are small plants of low abundance and biomass. *G.aetnensis* is a leguminous tree with tiny leaves utilising photosynthetic stems – and hence was unlikely to contain nitrate reductase. This was inferred by preliminary testing of a similar *Genista* species prior to the field trip to Sicily. This testing also confirmed the presence of easily measurable amounts of NR within *C.ruber,* which is commonly found in Britain. Time constraints and preliminary testing of some of the species for nitrate reductase activity once in Sicily, indicated that two of the species - *C.ruber*, and *R.scutatus,* were both abundant enough and produced enough leaves, to enable harvesting of some leaves without causing damage to the plants in an area. Both species are primary colonisers of the lava and continue to thrive for many hundreds of years until shading by *Genista* and competition with other species reduces the population. In addition, both species produce large quantities of nitrate reductase in their leaves.

Both *R.scutatus* and *C.ruber* are the first colonisers of aa lava in any great abundance. These species commonly co-occur in clumps on the lava – although it is unknown if this is due to a scarcity of sites for colonisation or due to a symbiotic relationship. It may well be a combination of both, since there does not appear to be any competition between the species with both members in a clump growing extremely vigorously.

3.2.2. Nitrate reductase activity in plant leaves of pre-watered and nitrate treated plants on the northern chronosequence

A chronosequence of sites was selected on the northern aspect of the volcano, ranging from 52 to 463 years old. These consisted of flows erupted in: 1947, 1923, 1879, 1809, 1646, 1614-24, 1566 and 1536 (Fig 2.3 for site locations). Map grid references for all the sites studied can be seen in the appendix. Each site was located at an altitude of 1000m, using the same parameters of topography, distance from the edge of flow and lava morphology as outlined in 2.2.1. On each site, a number of clumps of *C.ruber* and *R.scutatus* were selected (each clump roughly 0.5m x 0.5m). One group of clumps was then watered with 1L of 5mol Nitrate and another with 1L of water. Both induce nitrate reductase activity in the plants, but the addition of nitrate induces higher levels. After two days samples consisting of the top two leaves (the youngest) were taken from each species and amalgamated to form an average representation of each site. These leaves were then taken and analysed using a variation of the method described in Stewart and Orebamjo (1979).

Leaf tissue was cut into 1-2mm strips, 400mg was then taken and incubated at 25°C in the dark, under a vacuum, in 10ml of the following assay medium: 100 mol potassium phosphate buffer, pH 7.5 containing 75 mol m^{-3} potassium nitrate and 1% propanol. Incubation lasted 45 minutes after which 4ml of the assay mix was taken and mixed with 4 ml of Sulphanilic acid (1% Sulphanilic acid in 3 M HCl) and 4 ml of 0.02% Napthyl ethylene diamine hydrochloride (NED) (Stewart and Orebamjo 1979). The subsequent colour change after 20 minutes was measured at 540nm, using a Hatch DR/2000 spectrophotometer. Four replicates were taken of each species from which an average and standard error was determined.

The results were compared to a standard of sodium nitrite in the 1-100 nmol range, to determine the amount of nitrite formed as a result of enzyme activity. This value was then converted into the amount of nitrite in nmol formed per gram of fresh weight of leaves per hour (nmol GFW^{-1} h^{-1}) to give a standard format of readings for comparison between sites.

A second experiment compared samples taken from plant clumps of both species on the 1879 flow. These plants, taken from both treatment types (nitrate and water), were compared to leaves of untreated 'natural condition' plants to determine the effect of the treatments on the plants to determine how necessary it is to treat the plants before sampling.

3.2.3. Nitrate reductase activity in plants on the two chronosequences

A series of sites were selected on the southern aspect of the volcano, ranging from 89 to -566 years old. These consisted of flows deposited in: 1910, 1886, 1766, 1634, 1537, and 1444 (Fig 2.4). Map grid references for all the sites studied can be seen in the appendix. Each site was located at an altitude of 1000m, using the same parameters of topography, distance from the edge of flow and lava morphology as outlined in 2.2.1. At each site, leaf samples of *C.ruber* and *R.scutatus* were taken from plants using the same method outlined in 3.2.2. with the exception that none of the plants was pre-watered or given additional nitrate - from this, measurements of NR activity of plants in their natural state were taken. These samples were amalgamated and analysed using the same method in 3.2.2. This experiment was repeated on two separate occasions at two different times of the year; once in the autumn (29th October – 2nd November 1999) and once in the spring (May 2000). In addition, the northern chronosequence was sampled again using this method at the same time of the year (May 2000) in order to directly compare the two chronosequences.

3.2.4. Nitrate reductase activity in plants from the four aspects of the volcano from two different aged lava flows

Two lava flows were selected on each of the four aspects of the volcano. These lavas were selected for comparable age – one nineteenth century (approx. 1850) and one seventeenth century lava flow (approx. 1650) to test variation caused by aspect and age. The lavas selected were : 1879 and 1646 on the north aspect, 1865 and 1689 on the east aspect, 1886 and 1634 on the south aspect, and 1843 and 1651 on the west side of Etna. Each site was selected using the same parameters of altitude, topography, distance from the edge of flow and lava morphology as outlined in 2.2.1. NR activity was measured using a variation of the method described in Stewart and Orebamjo (1979) as outlined in the field experiment 3.2.2.

3.2.5. Nitrate reductase activity in the leaves of plants taken from a range of altitudes

Two lava flows on the southern aspect of Mt.Etna were selected - one from the 17th Century (1634) and one from the 19th Century (1882). At 250m intervals from 1500m down to 400m, leaves of the two target species were gathered and analysed for NR activity using the method outlined in 3.2. The sites were located at 1500m, 1250m, 1000m, 750m and 400m (1634 lava flow) and 1500m, 1250m, 1000m, 800m (1892 lava flow). Each site was selected using the same parameters of topography, distance from the edge of flow and lava morphology as outlined in 2.2.1. NR activity was measured using a variation of the method described in Stewart and Orebamjo (1979) as outlined in the field experiment 3.2.2.

3.2.6. Laboratory nitrate reductase activity experiments – The effects of drought

Twelve pots of *R.scutatus* were grown under artificial light under controlled conditions of 20°C day length 16 hours. These plants were well watered for three weeks and saturated with water at the start of the experiment, to the carrying capacity of the soil. At this point leaves were harvested from each pot and measured for NR activity and percentage water content. From this point on the plants were not watered and the pots allowed to dry out. Every seven days after this, leaves were harvested and analysed for NR activity, up until the plants died of water stress. Concurrently, measurements of soil water content were made by wet/dry weight samples (drying the soil at 70°C for three days and re-weighing) and by direct measurement using a moisture probe (theta meter) on the pots and a control pot. NR activity was measured using a variation of the method described in Stewart and Orebamjo (1979) as outlined in the field experiment 3.2.2.

3.2.7. Laboratory nitrate reductase activity – plants under different Nitrogen treatments

Twelve pots of *R.scutatus* were grown under artificial light under controlled conditions of 20°C day length 16 hours. These twelve pots were separated out into three experimental treatments. Four pots were used as a control and were watered once a week for a two month period with 1L of distilled water only. Four pots were watered once a week with for a two month period with 1 L of a 2.5 mol nitrate solution. Four pots were watered once a week with 1L of a 5.0 mol nitrate solution over a two month period. After the two months leaves of each treatment were harvested from each pot and measured for NR activity. NR activity was measured using a variation of the method described in Stewart and Orebamjo (1979) as outlined in the field experiment 3.2.2.

3.3. Results

3.3.1. Nitrate reductase activity in plant leaves of pre-watered and nitrate treated plants on the northern chronosequence (May 1999)

The activity of nitrate reductase in the leaves of *R.scutatus* (Fig 3.1) and *C.ruber* (Fig 3.2) varied considerably over the chronosequence, both between species and treatments. Increased activity was induced in both species as a result of adding nitrate to the plants (hence activity is consistently higher in nitrate fed plants as evidenced by the red line always being above the blue), but the extent of inductance varied depending on site. Both species showed maximum rates of inductance on the oldest sites (1535 and 1624 lava flows).

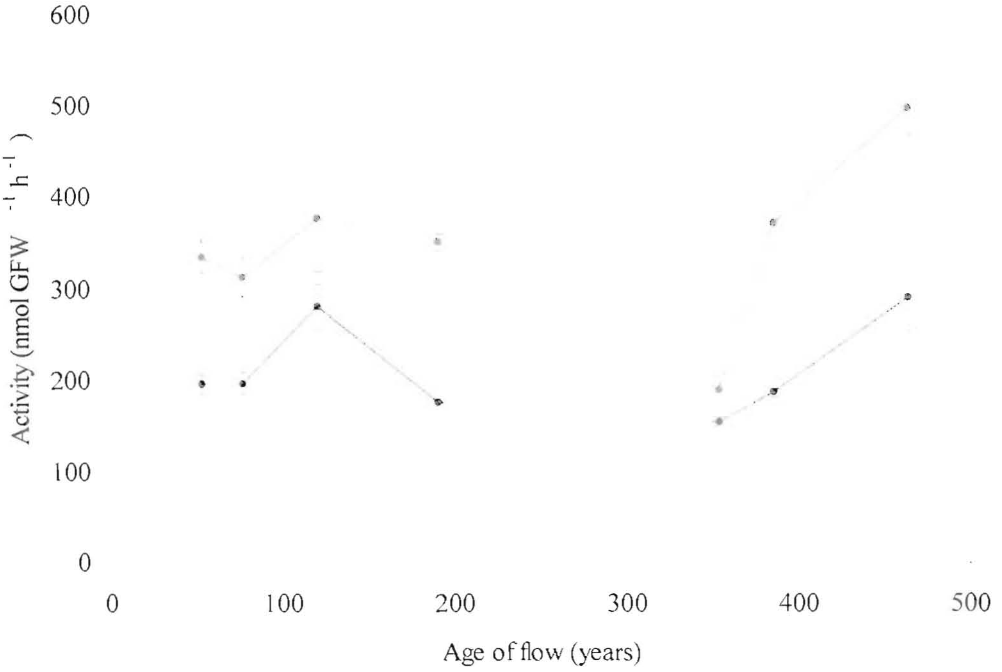


Figure 3.1. Nitrate reductase activity in *R.scutatus* leaves from plants on the northern chronosequence, in both nitrate treated plants (red line) and water treated plants (blue line) (n=4,+/- S.E.).

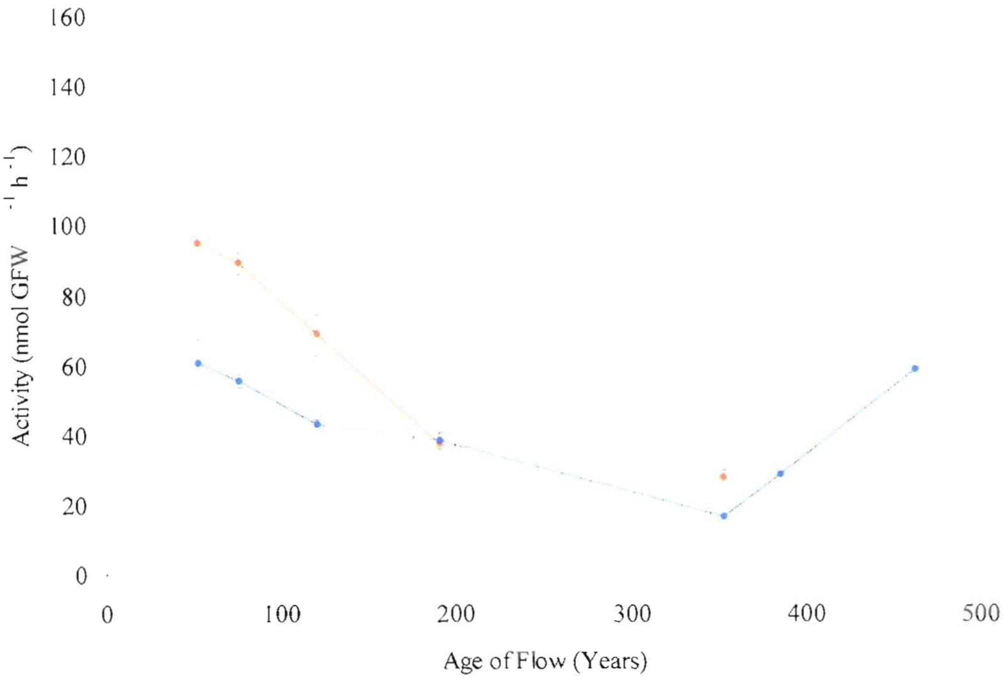


Figure 3.2. Nitrate reductase activity in the leaves of *C.ruber* on the northern chronosequence, in both nitrate treated plants (red line) and water treated plants (blue line)(n=4,+/- S.E.).

In addition, both species displayed a trend for high enzyme activity in the younger flows (attaining 280 GFW^{-1} h^{-1} in watered *R.scutatus* on the 1879 flow and 60 GFW^{-1}h^{-1} in watered *C.ruber* on the 1947 flow). This activity then declined with age between 200 and 300 years reaching a low point of 189 GFW^{-1} h^{-1} in *R.scutatus* and 16.5 GFW^{-1} h^{-1} in *C.ruber* on the 1646 flow. After this point the enzyme activity rapidly increased again on the oldest sites attaining levels of 290 GFW^{-1} h^{-1} in *R.scutatus* and 59 GFW^{-1} h^{-1} in *C.ruber* respectively. During the course of this experiment, it was decided to drop the results of the 1566 site as this lava flow was later reclassified as slabby pahoehoe morphological type. This occurred, as it is often difficult to discern the underlying lava morphology of the older flows and a definitive conclusion is only reached after more observation.

The second experiment to determine the effect of watering and nitrate treatment as compared to plants in their natural state showed that nitrate treatments induced a considerable increase in the NR activity of both plant species. *R.scutatus* gave an average of 377 GFW^{-1} h^{-1} in the nitrate treated plots against 280 GFW^{-1} h^{-1} in the water treated plants on the 1879 lava flow. However there was only a slight inducement of NR activity on the water treated plants as compared to the untreated 'natural' plants, which averaged 258 GFW^{-1} h^{-1} (Fig. 3.3).

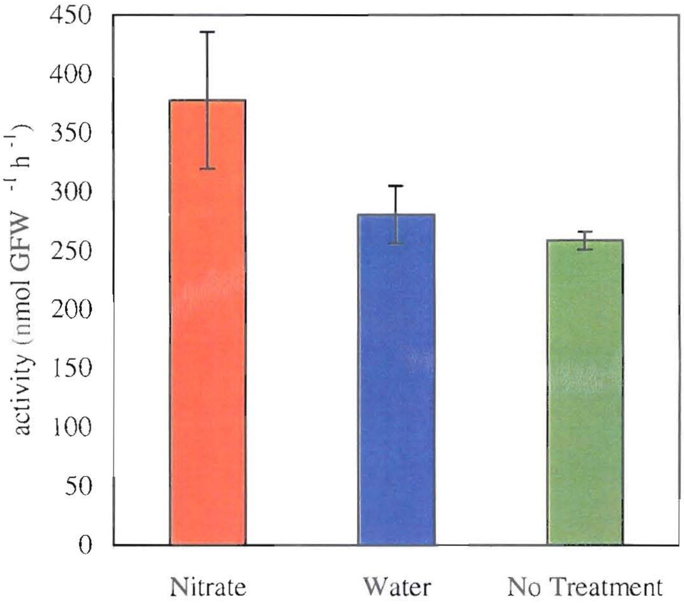


Figure 3.3. Average nitrate reductase activity in the leaves of *R.scutatus* plants on the 1879 lava flow under three treatments : nitrate addition (red), water addition (blue) and no treatment control (green), (n=3 +/- S.E.).

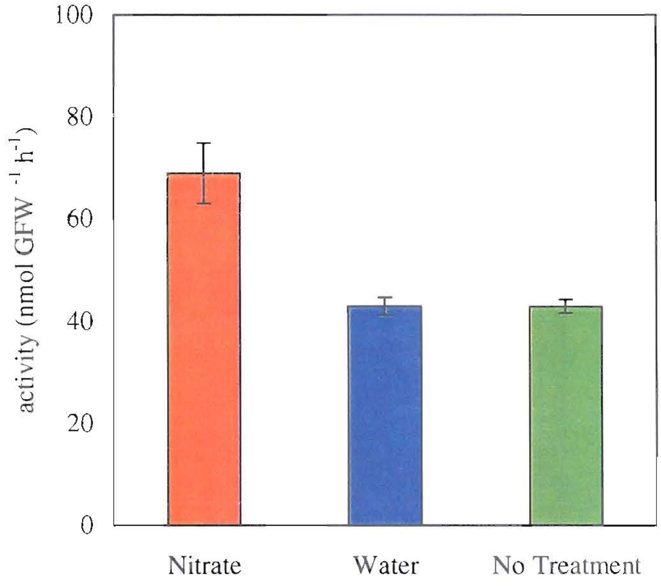


Figure 3.4. Average nitrate reductase activity in the leaves of *C.ruber* plants on the 1879 lava flow under three treatments – nitrate addition (red), water addition (blue) and No treatment (green) (n=3 +/- S.E.).

Similarly, *C.ruber* was induced to produce more NR activity in the nitrate treated plots with an average of 69 GFW^{-1} h^{-1} against 43 GFW^{-1} h^{-1} in the water treated plants on the 1879 lava flow. However there was no inducement of NR activity on the water treated plants as compared to the untreated 'natural' plants, which averaged 258 GFW^{-1} h^{-1} (Fig. 3.4).

As a result of these findings, that there was little effect of giving water to the plants in the field, it was decided to change the methodology for further field experiments to exclude treatments as this was logistically difficult. By discontinuing this method the number of sites was increased in the available time.

3.3.2. Nitrate reductase activity in plants on the two chronosequences

There is considerable variation in the activity of nitrate reductase on the lava flows of Mt.Etna. This can be seen clearly in the activity in the leaves of *R.scutatus* on the southern chronosequence in November 1999 (Fig 3.5). There is an initially low level of NR activity (230 GFW^{-1} h^{-1}) which then drops still further until it rapidly increases to reach a peak on the 1634 lava flow (366 y.o) of more than 450 GFW^{-1} h^{-1}.

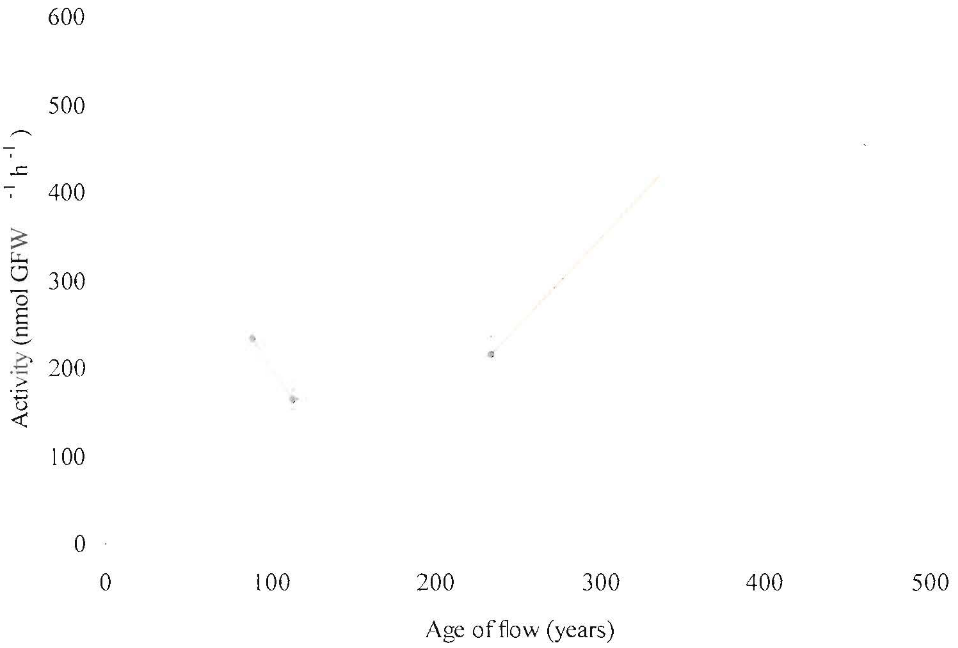


Figure 3.5. NR activity in the leaves of *R.scutatus* on the southern chronosequence of Mt.Etna, November 1999. (n=3, +/-SE).

This pattern was repeated in the leaves of *C.ruber* which initially dropped in activity from 86 GFW^{-1} h^{-1} on the 1910 flow (89 y.o) to a low point of 35 GFW^{-1} h^{-1} before steadily increasing to reach a level of 130 GFW^{-1} h^{-1} on the 1537 lava flow (Fig 3.6).

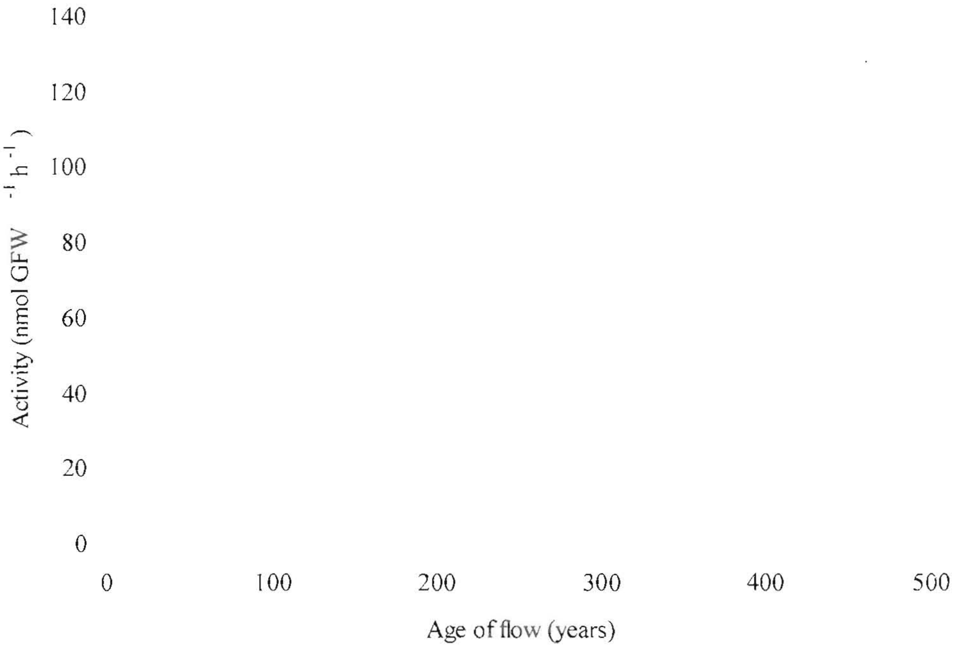


Figure 3.6. NR activity in the leaves of *C.ruber* on the southern chronosequence of Mt.Etna, November 1999. (n=3, +/-SE).

However, the enzyme activity varied considerably when the experiment was repeated on the same sites in the following springtime (May 2000). On this occasion the enzyme activity on the 1892 lava flow for both plant species was very high (341 GFW^{-1} h^{-1} and 103 GFW^{-1} h^{-1} for *R.scutatus* and *C.ruber* respectively) followed by a decline in enzyme activity and then a rise again (this is very clear on Fig. 3.8 and less so on Fig. 3.7)

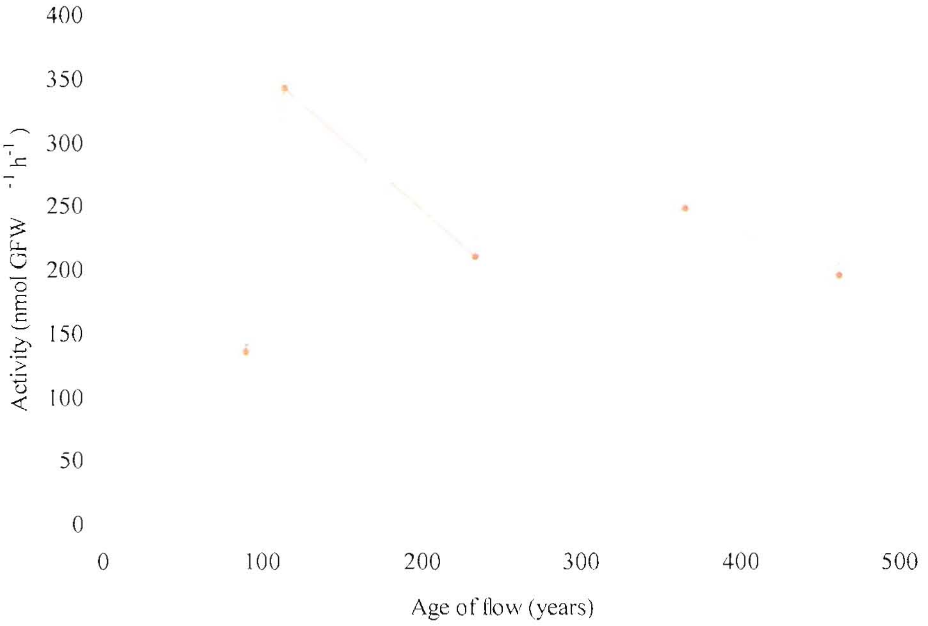


Figure 3.7. NR activity in the leaves of *R.scutatus* on the southern chronosequence of Mt.Etna, May 2000. (n=3, +/-SE).

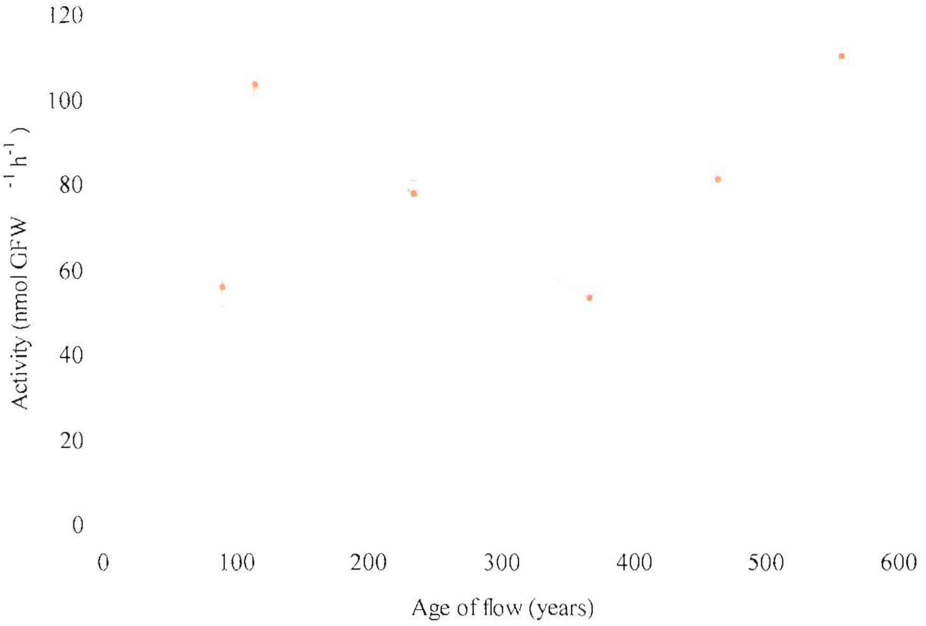


Figure 3.8. NR activity in the leaves of *C.ruber* on the southern chronosequence of Mt.Etna, May 2000. (n=3, +/-SE).

In contrast, the north chronosequence shows much higher levels of NR activity throughout the age range of sites (most of the *R.scutatus* sites averaging more than 300 GFW^{-1} h^{-1}, Fig 3.9). The activity in *R.scutatus* also shows a much more distinctive change over time with the early peak in activity around 100 year old flows and the second rise occurring after 400 years.

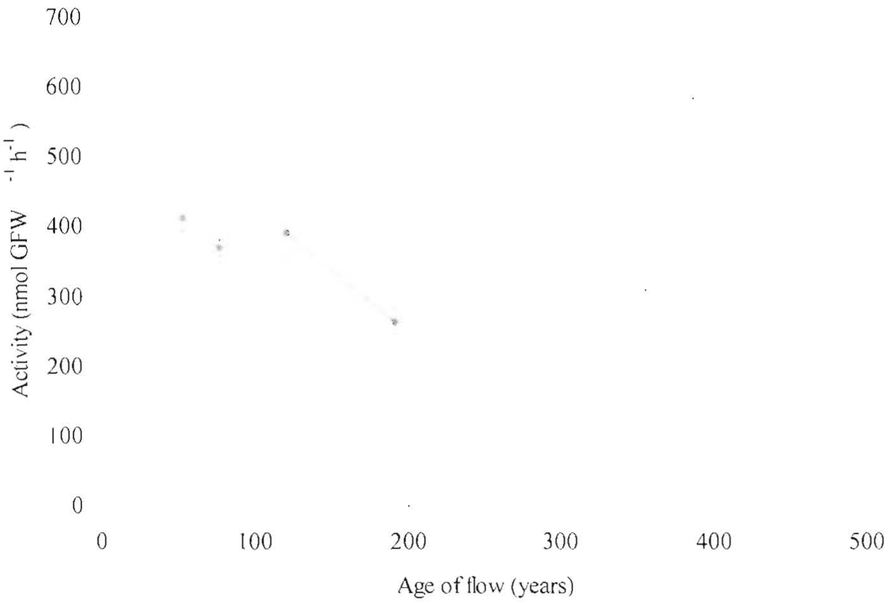


Figure 3.9. NR activity in *R.scutatus* on the northern chronosequence of Mt.Etna, May 2000. (n=3, +/-SE).

The activity in *C.ruber* on the northern chronosequence is also consistently higher than that found on the southern chronosequence. Here, most sites averaged over 140GFW^{-1} h^{-1} (Fig 3.10) compared to less than 120 GFW^{-1} h^{-1} on the southern chronosequence taken at the same time (Fig 3.8).

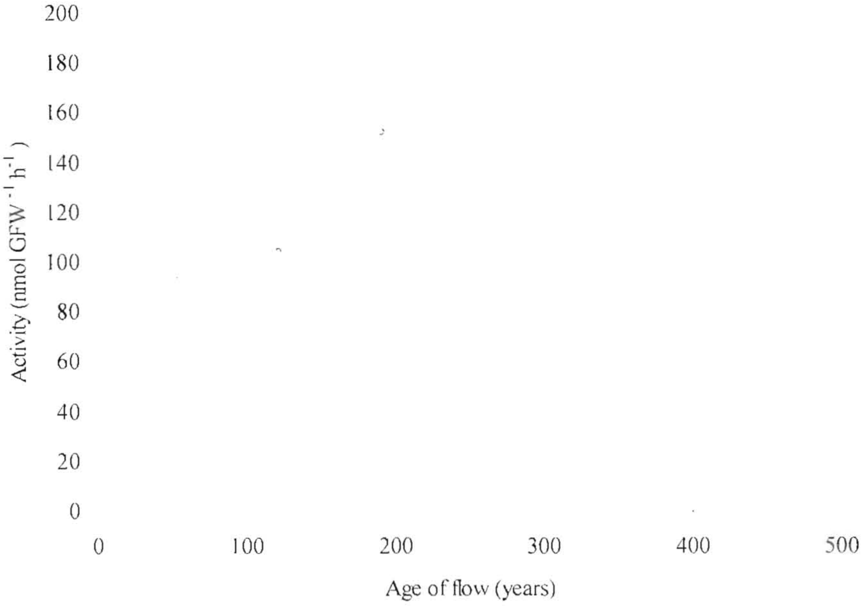


Figure 3.10. NR activity in *C.ruber* on the northern chronosequence of Mt.Etna, May 2000. (n=3, +/-SE).

3.3.3 Nitrate reductase activity in plants from the four aspects of the volcano

There is a marked difference in enzyme activity in the leaves of the two target species on the different aspects of the Mt.Etna on lava flows of similar age and morphology. As Fig 3.11 shows, *R.scutatus* varies widely, with a peak in activity observed on the 1879 North flow (390 GFW^{-1} h^{-1}) a decrease in activity on the south and west aspects (325 GFW^{-1} h^{-1}) and a low point on the east aspect of 250 GFW^{-1} h^{-1}. This trend is almost exactly matched on the 17th Century lava flows (red bars) but at a consistently lower level (e.g. the peak value in the north is 290 GFW^{-1} h^{-1}).

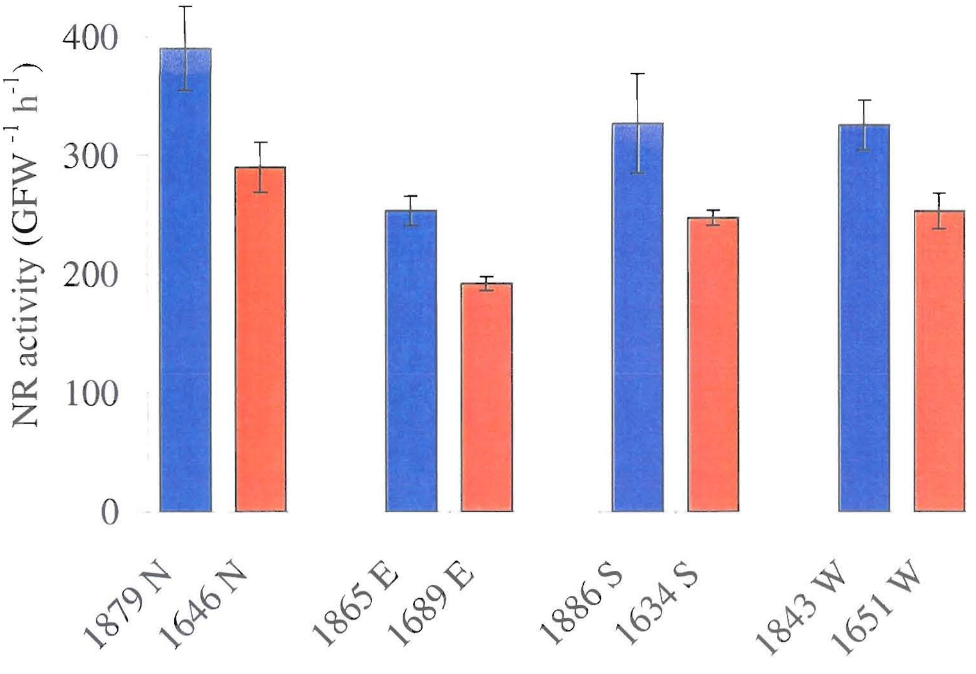


Figure 3.11. Nitrate reductase activity in the leaves of *R.scutatus* on the four aspects of the volcano, Mt.Etna.

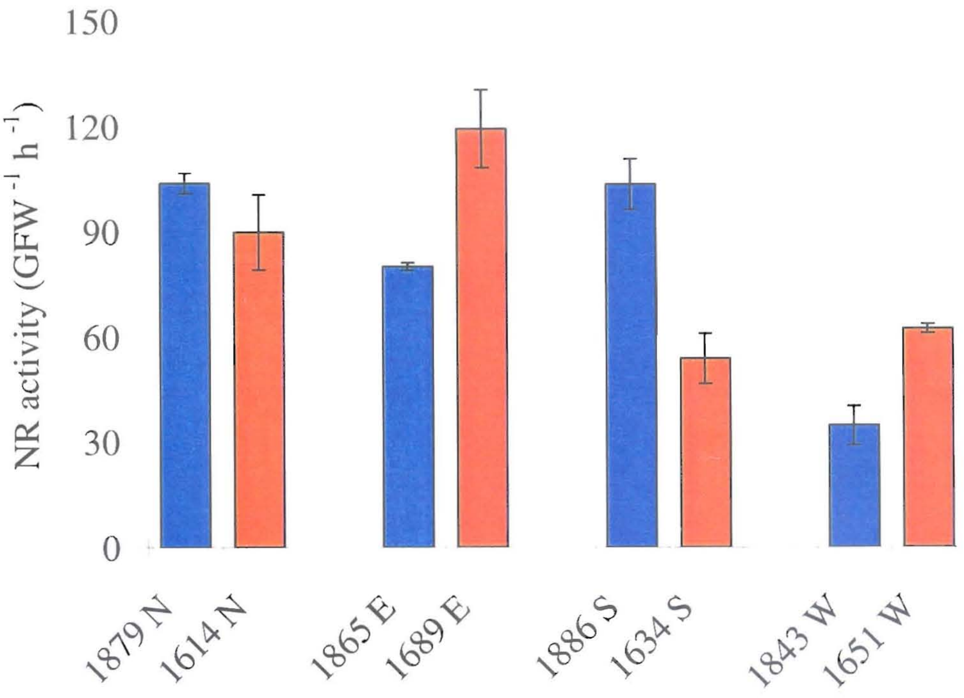


Figure 3.12. Nitrate reductase activity in the leaves of *C.ruber* on the four aspects of the volcano, Mt.Etna.

Activity in *C.ruber* is slightly different, with both the eastern and western aspects producing higher readings on the older lava flows than in their northern and southern counterparts (Fig 3.12).

3.3.4 Nitrate reductase activity in the leaves of plants taken from a range of altitudes

The average nitrate reductase activity in the leaves of the two target species varied with altitude and with age. As altitude increases the enzyme activity in *R.scutatus* also increases. This can be clearly seen in Fig 3.13 where the activity on the 1634 lava flow gradually climbs from 190 to 300 GFW^{-1} h^{-1} (r^2 value = 0.932). The 1892 lava flow shows a similar trend but drops substantially between the altitudes of 1250m and 1500m. In addition, there is a consistent trend of higher activity on the younger lava flow.

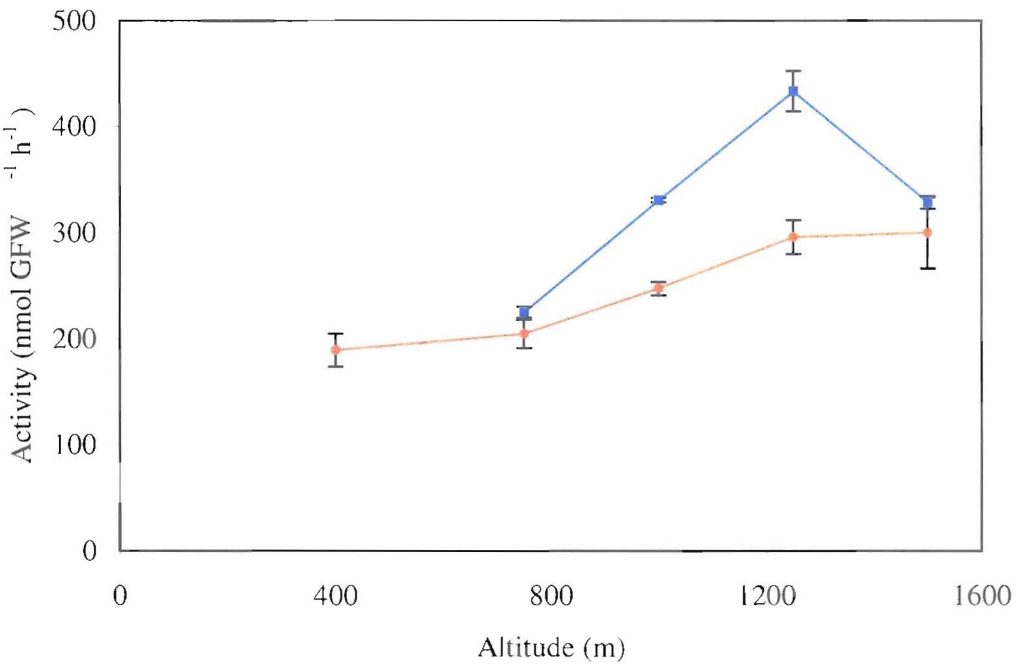


Figure 3.13. Nitrate reductase activity in the leaves of *R.scutatus* over increasing altitude on two lava flows (1634 red line, 1892 blue line).

However, this trend is only partially seen in *C.ruber* where there is a very minor increase in NR activity with altitude ($r^2 = 0.2344$) on the 1634 lava flow (fig 3.14). But the trend for higher activity on the younger (1892) lava flow is clearly visible (hence the blue 1892 line is consistently above the 1634 red).

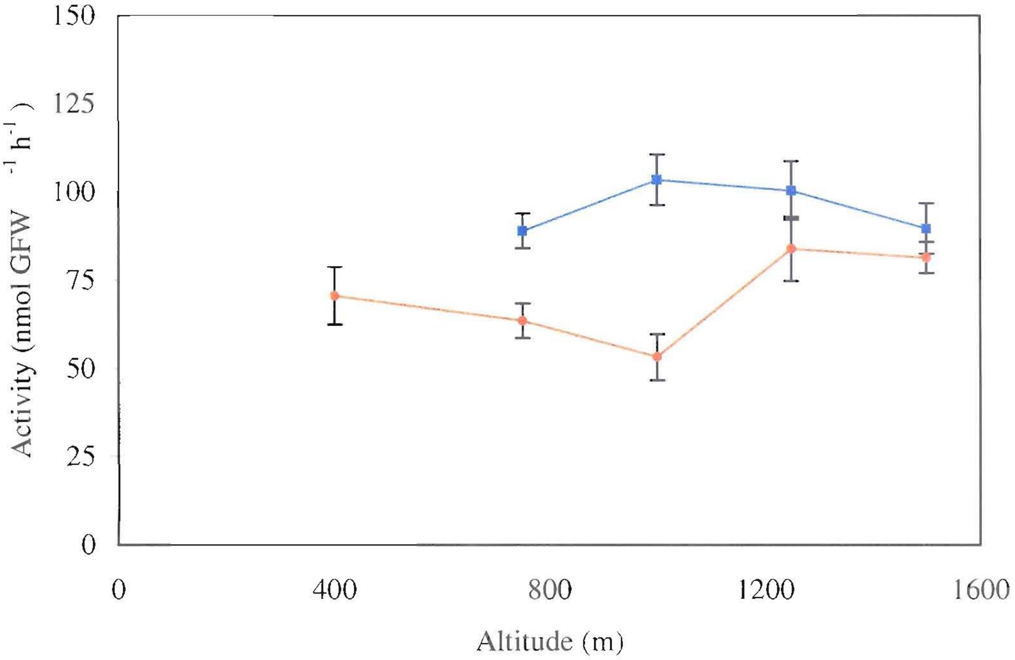


Figure 3.14. Nitrate reductase activity in the leaves of *C.ruber* over increasing altitude on two lava flows (1634 red line, 1892 blue line).

3.3.5. Laboratory nitrate reductase activity experiment – The effects of drought

During the course of this experiment a range of readings were taken to show the effect of drought on Nitrate reductase activity on the species *R.scutatus* in order to compare with the field responses and show the importance of this factor between the sites on Etna. To observe the effects of drought many measurements of the physical changes in the plants and the growth medium (soil) were taken to establish the exact changes that occurred. The change in soil water content (taken as a percentage of mass lost after drying for 3 days at 70°C) over time can be seen in Fig 3.15.

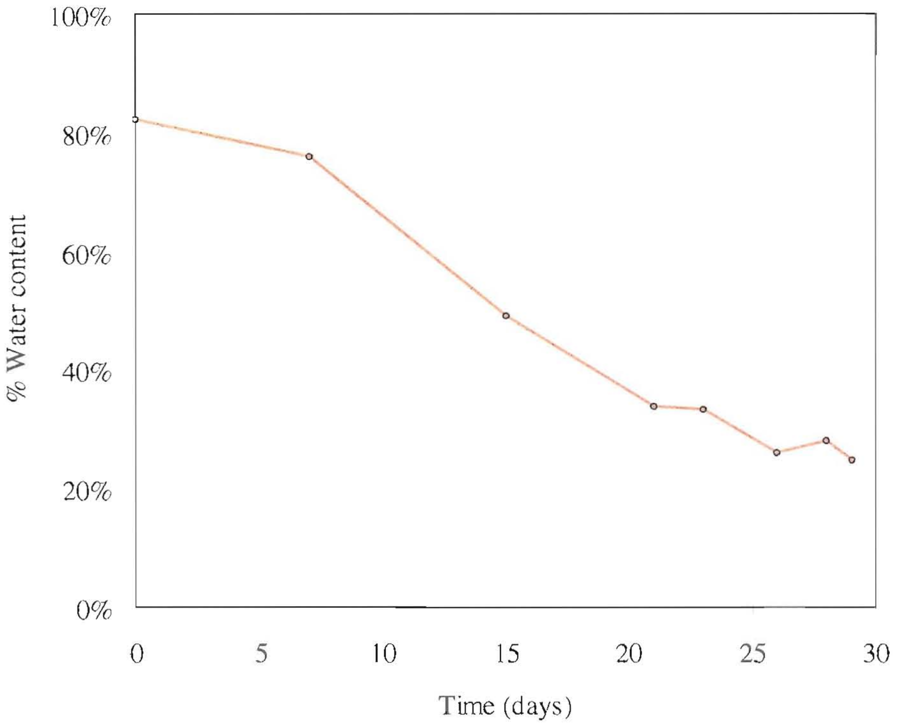


Figure 3.15. Change in the percentage water content of the soil around *R.scutatus* plants calculated using loss of water after three days drying at 70°C.

This clearly shows a linear drop in soil water content with time. This is confirmed with the results from the theta moisture probe which show a similar drop in the amount of soil organic water content (Fig 3.16) and in the mineral water content of the soil (Fig. 3.17).

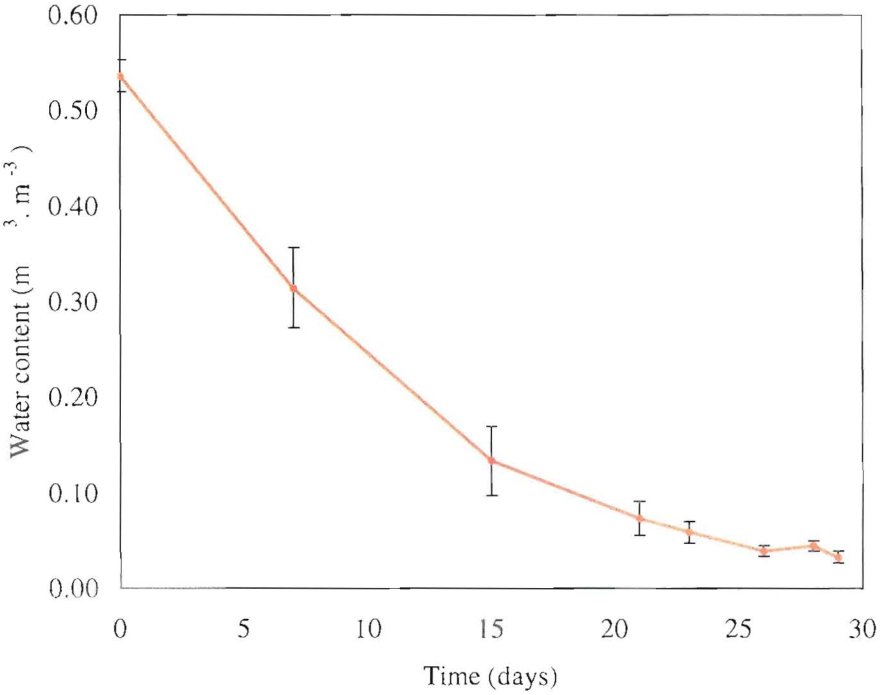


Figure 3.16. Organic water content of the soil around Rumex plants taken using a theta meter (n=4 +/-S.E.).

However, during the course of the experiment, the nitrate reductase activity initially remains constant at a level of about 100 nmol GFW $^{-1}$ h $^{-1}$ for the first week of the experiment, before slowly declining over the remaining time period of the experiment (Fig 3.18).

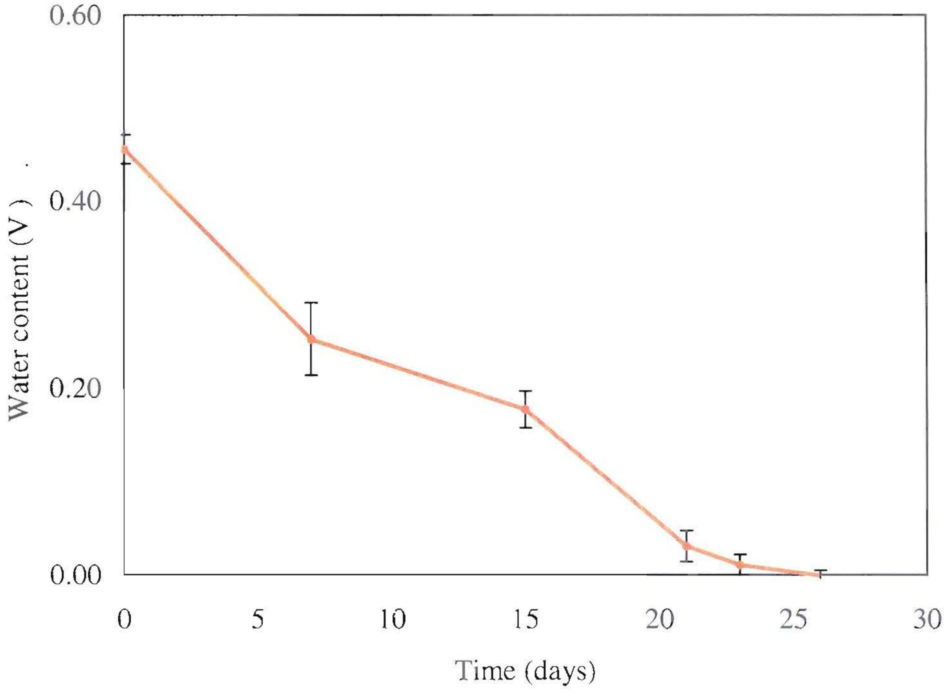


Figure 3.17. Mineral water content of the soil around *R.scutatus* over time of the drought experiment. (n=4 +/-S.E.).

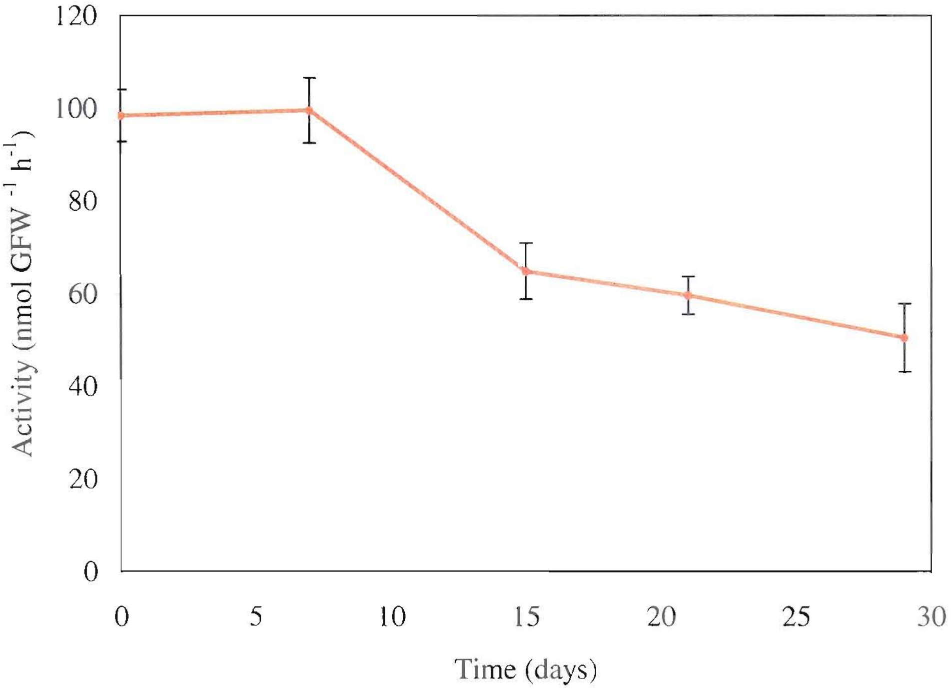


Figure 3.18. Nitrate reductase activity in the leaves of *R.scutatus* over the time frame of the experiment. (n=4 +/-S.E.).

This drop in NR activity after an initial 'plateaux' around 100 nmol GFW^{-1} h^{-1} can be seen more readily when the NR activity and organic soil water content are plotted together (Fig 3.19). From this, it is clear that Nitrate reductase activity remains constant in the leaves until the soil water content drops below 0.3 m^3.m^{-3}.

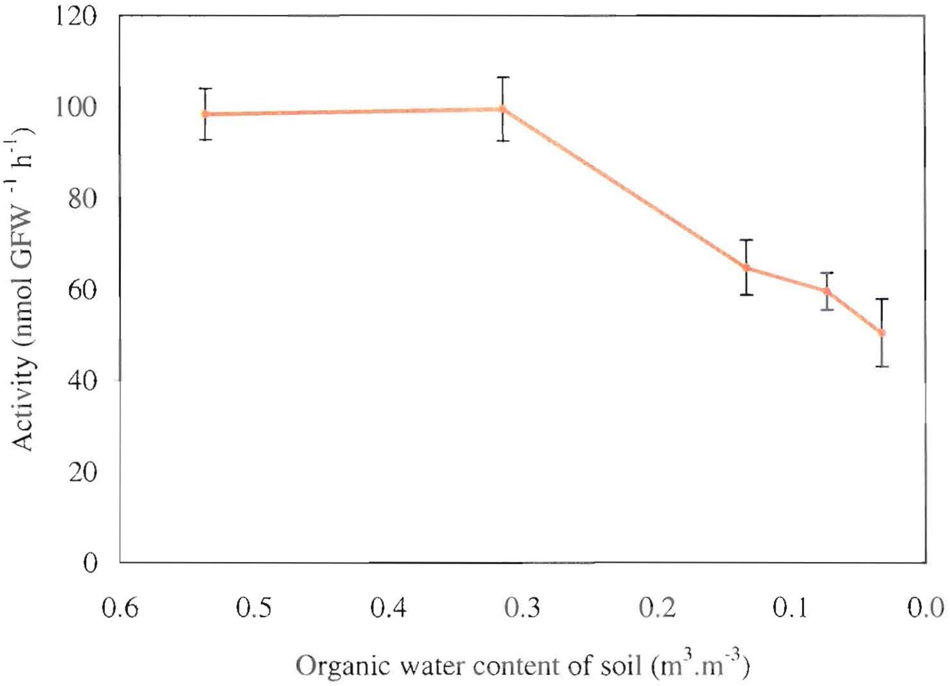


Figure 3.19. Change in nitrate reductase activity in the leaves *of R.scutatus* under increasing drought conditions. (n=4 +/-S.E.).

In addition, the plant does its best to maintain the water content of the leaves for as long as possible, despite the drop in soil moisture. This can be seen in Fig 3.20. which clearly shows the plant maintaining leaf water content at more than 95% until more than 20 days into the experiment. From observation of the plant leaves, it does this by concentrating the water in the youngest / smallest leaves at the growth tips and allows the older leaves to droop and totally desiccate so that they fall off the plant. As a result the NR activity was measured only using these young leaves.

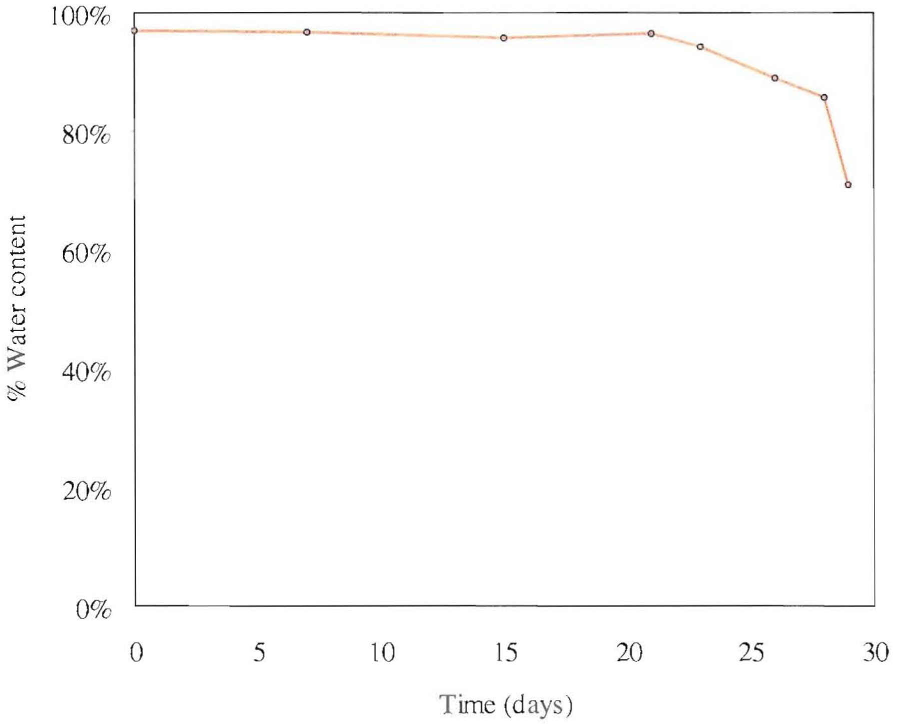


Figure 3.20. Percentage water content of the leaves of *R.scutatus* over time, under simulated drought conditions.

3.3.6. Laboratory nitrate reductase activity – plants under different nitrogen treatments

Plants grown in the laboratory under the three different treatments of nitrate showed a clear difference in their nitrate reductase activity after a two month period. While the control plants showed a reading of about 100 nmol / GFW / hr both the nitrogen treated samples showed an increase in activity with the 2.5 mol treatment giving a reading of 235nmol / GFW / hr and the 5.0 mol treatment giving a 294nmol / GFW / hr respectively (Fig 3.21)

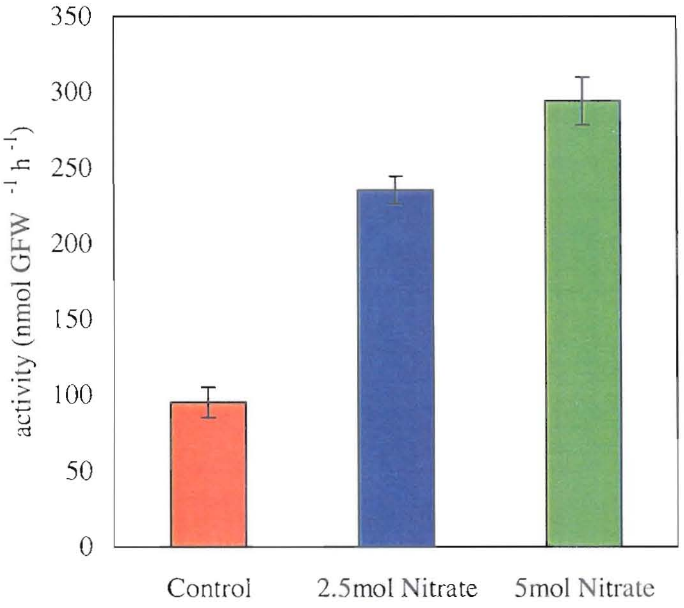


Figure 3.21. Nitrate reductase activity in leaves of *R.scutatus* grown under three treatments of nitrate.

3.4. Discussion

3.4.1. Nitrate reductase activity in plant leaves of pre-watered and nitrate treated plants on the northern chronosequence.

The high rates of inductance found on almost all the sites, indicates that nitrogen is limiting on all the lava flows of the chronosequence. In the younger sites this is due to the lack of soil structure whereas in the later stages it is a result of the increased inter-species competition. However, this experiment has shown that the plants are capable of responding quickly once nitrogen becomes available. The higher rates of inductance in the youngest and oldest sites (as evidenced by the greater gap between the two experimental plots on Figs 3.1 and 3.2) are almost certainly due to higher background levels of nitrogen. This seems to be present at these two stages of development (as indicated by the higher levels of NR when the plants are only water treated). That is that these plants already have a ready source of nitrate reductase present in the leaves with which to utilise the additional nitrogen.

As a result this experiment indicates that there is a two phase system of nitrogen inputs occurring over the succession – an early input occurring at around one hundred years which then declines, and a second gradual rise occurring after 300 years. The second phase can be easily explained if the source of the nitrogen is coming from the soil development increasing the microbial and organic biomass (which is further studied in the next chapter). The first phase however is less easily explained and shall be covered using the other experiments in the proceeding chapters to pinpoint the source of this nitrogen.

3.4.2. Nitrate reductase activity in plants on the two chronosequences

Although the graphs of data (Figs 3.6 - 3.11) show considerable variation between chronosequences and sites over time, there is a distinct trend which is appearing repeatedly within the data – an early peak of nitrogen followed by a decline and then a second rise in activity over the time span of the chronosequence. This confirms the results of 3.4.1 and supports the proposition that there are two large inputs of nitrogen occurring during the chronosequence. The huge variation seen within and between sites is possibly due to the high site heterogeneity and the considerable variation in environmental conditions from day to day – or seasonally. This is one of the major problems of dealing with ecological data. This problem has been addressed here in the only method possible – repeating the experiment several times. The consistency of the trend here confirms the value of repeating the experiment.

The much larger early peak in activity observed in the springtime is partly due to the increased rainfall at this time of year as opposed to the extreme drought conditions of the summer from which the plants are barely recovering in the Oct/Nov sampling.

3.4.3. Nitrate reductase activity in plants from the four aspects of the volcano

On each of the four aspects of Etna there is more nitrate reductase activity in *R.scutatus* on the younger nineteenth century flows than on the older seventeenth century sites (Fig 3.11). However, this trend is only repeated on the north and south aspects in the case of *C.ruber* (Fig 3.12). In addition, there is a high peak of nitrate reductase activity in the east 1651 sample (120nmol). However this is still lower than that seen in *R.scutatus* on the same site (200nmol). Variations between species and sites in this way reflect the stochastic nature of the data, whereby minor changes can reflect in the results. Since this experiment was only done once (whereas most of the others were repeated), these data could be due to minor variations within sites or a major difference in the nitrate reductase activity between the two species. As such this is worthy of further study.

3.4.4. Nitrate reductase activity in the leaves of plants taken from a range of altitudes

There is a clear link between NR activity and altitude in *R.scutatus*, with activity increasing with altitude up the volcano – with the exception of the 1500m point on the 1892 flow which shows a rapid decline. The increase in activity is probably correlated to the increased rainfall and generally cooler, more favourable conditions found higher up the volcano. This will allow more water to remain within the soil profile without evaporating as happens in the harsher conditions lower down the volcano (e.g. 400m). In addition, the higher temperatures lower down the slopes may impede the enzyme activity. However, above 1250m on the 19th century flow there is little vegetation cover and the temperature variation is more extreme with high temperature during the day and low at night - which may partly explain the drop in enzyme activity above 1250m.

3.4.5. Laboratory nitrate reductase activity experiment

The results of this experiment show that nitrate reductase activity in the leaves of *R.scutatus* plants under increasing water stress remains constant at a level of 99 nmol GFW^{-1} h^{-1}, until the organic soil water content drops below 0.3 $m^3.m^{-3}$ (Fig 3.19). After this point the activity gradually declines until the plants die (when the organic water content is less than 0.03 $m^3.m^{-3}$). Other experiments into drought effects on plants by Foyer *et al* (1998); Smirnoff *et al*, (1985) and Rajagopal *et al* (1977), also found decreased nitrate reductase activity.

From observation of physical changes in the plants, the leaves started to wilt at the $0.3m^3.m^{-3}$ point. By $0.13\ m^3.m^{-3}$, there were few healthy leaves left unaffected and many had died completely. There is therefore a strong link between the NR activity and the water content of the leaves. However, as the plant maintains the level of NR activity in light drought conditions – and further that when the NR activity is dropping it is clearly visible in the plants physical appearance (desiccated / wilting leaves). It is therefore possible to extrapolate this to what occurs in plants growing in the field. Hence, by careful selection of plants which are in healthy condition (or using pre-watered plants where this is logistically possible given time / travel constraints) the effects of drought can be removed as a factor influencing the NR activity in *R.scutatus*. Factors that affect nitrate reductase activity in plants include drought, light and available nutrients (Beevers and Hageman 1969). Light can be controlled by locating plants in open areas with little shade. Therefore by selecting plants which show no signs of wilting we can be certain that the major factor causing variation in nitrate reductase activity in the field is the availability of nutrients on lava of different ages.

3.4.6. Laboratory Nitrate reductase activity – plants under different Nitrogen treatments

The results from the plants grown under laboratory conditions show that nitrate reductase is a very good indicator of nitrate availability as nitrate reductase activity clearly increases with available nitrate. The treated plants both showed increased nitrate reductase activity (240nmol / GFW / hr and 294nmol / GFW / hr) over the control (100nmol / GFW / hr mol).

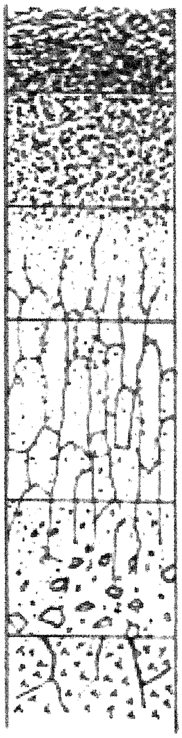
Chapter 4: Soil and Foliar nutrient change

4.1. Introduction

4.1.1. Soil formation and development over time

Once the initial colonisation by lichens, mosses and first stage vascular plant colonisation has occurred soil begins to develop. From that point on plant succession and soil development occur concomitantly. Increases in plant species and in the biomass produced are reflected in the developing soil. In addition, the presence of the lichens and plants serve to trap and bind wind borne particles and tephra. Deposition of organic material following plant growth in and on this initial parent material initiates depth-gradients in the soil profile of many soil characteristics such as pH, bulk density and contents of organic carbon, nitrogen, phosphorous and many trace metals. Over time, the further processes of weathering and leaching cause large gains, losses, transformations and redistributions of many organic and inorganic constituents (Stevens and Walker 1970). By studying a chronosequence of soils, these losses and gains can be observed and the relative importance of the various factors acting on the lava flows can be assessed for their contribution to soil development.

Soil can be defined as a natural body composed of solids (minerals made up of sand, silt and clay size particles and organic material), liquids and gases that form on the rock surface, occupy space and are characterised by horizons or layers (Fig. 4.1). These layers are classified according to their order and mineral content as follows in a temperate soil profile



O Horizons Organic horizons in which the main feature is the accumulation of plant residue with various degree of decomposition

A Horizons Mineral horizons that form at the surface or below an O horizon and are characterized by an accumulation of humified organic matter intimately mixed with the mineral fraction

E Horizons Mineral horizons in which the main feature is loss of silicate clay, Al, Fe, or combination of these, leaving a concentration of sand and silt particles of resistant minerals

B Horizons Horizons that formed below an O, A, or E horizon and are dominated by obliteration of all or much of the original rock structure and by illuvial concentration of silicate clay, Al, Fe, humus, carbonates, gypsum or silica, alone or in combination

C Horizons Horizons or layers, excluding hard rock, that are little affected by soil forming processes and lack properties of the above horizons

R layers Hard rock or bedrock

Figure 4.1. Standard profile of the major horizons present on a well drained and developed soil in temperate humid system (Ping 2000).

O - Organic horizon.

At the top of the soil profile is the organic horizon. Derived from animal and plant remains it consists of humus. Full of microorganisms it is usually dark in colour with 20-30% or more organic matter. It is very important in water retention in the soil profile. Where conditions favour rapid decomposition of organic matter and its mixing with mineral material by organisms, there may be no separate organic horizon. Where a deep organic layer does not accumulate, however, a humus horizon (H) may occur on the soil surface. This is thinner than an O horizon.

R - Rock horizon.

At the bottom of the soil profile consisting of unconsolidated material or bedrock

A, E, B, and C.

These horizons are found between the two extremes of O and R. They are composed of sand, silt and clay and other weathered by-products. These four horizons are collectively known as the solum. The major constituents of the horizons are :

A : Humus and clay, also rich in organic material and hence dark. Bioturbation, the mixing of organic and mineral material within the soil (Singer and Munns1991) is important where organisms such as earthworms, ants and gastropods are favoured.

E : Lighter coloured due to silicate clays and oxides of aluminium and iron which have leached out and descended to lower horizons (caused by eluviation - the removal of fine particles and minerals by water).

B Accumulated clays, aluminium and iron. Dominated by illuviation (depositional process, as opposed to eluviation which is a process of removal). May have red or yellow hues because of mineral content. Where effects of illuviation are minimal a *cambic* B horizon develops as a result of in situ weathering and other changes (Ashman and Puri 2002). On young soils (like those found on Etna chronosequences), a more fully developed B horizon is unlikely. Even a cambic B horizon may not have developed, in which case the soil has an A-C profile.

C Weathered Bedrock - also known as the Regolith. Plant roots and microorganisms are fewer than in the upper horizons although in shallow soils, roots may in fact be concentrated at the rock interface. It lacks clay concentrations and is made up of carbonates, gypsum, or soluble salts or iron and silica, which form cemented soil structures. This system holds true in many mature soils although in very dry systems the net salt movement will be up the soil profile as evaporation draws water up the profile.

The relative age or maturity of a soil is reflected in the degree of differentiation of the horizons. In many instances, the greater the distinction between horizons, the greater the age of the soil and the greater the thickness and intensity the more mature the soil (Stevens and Walker, 1974). Erosion by water or wind is important in removing soil and limiting profile depth where vegetation is disturbed by natural or anthropogenic means.

Soil texture refers to the mixture of sizes of its particles and the proportion of different sizes. All particles smaller than 2mm are considered part of the soil and these particles can be further subdivided by size into three types: Sand (< 2 - 0.05mm), Silt (0.05 - 0.002mm) and Clay (< 0.002mm).

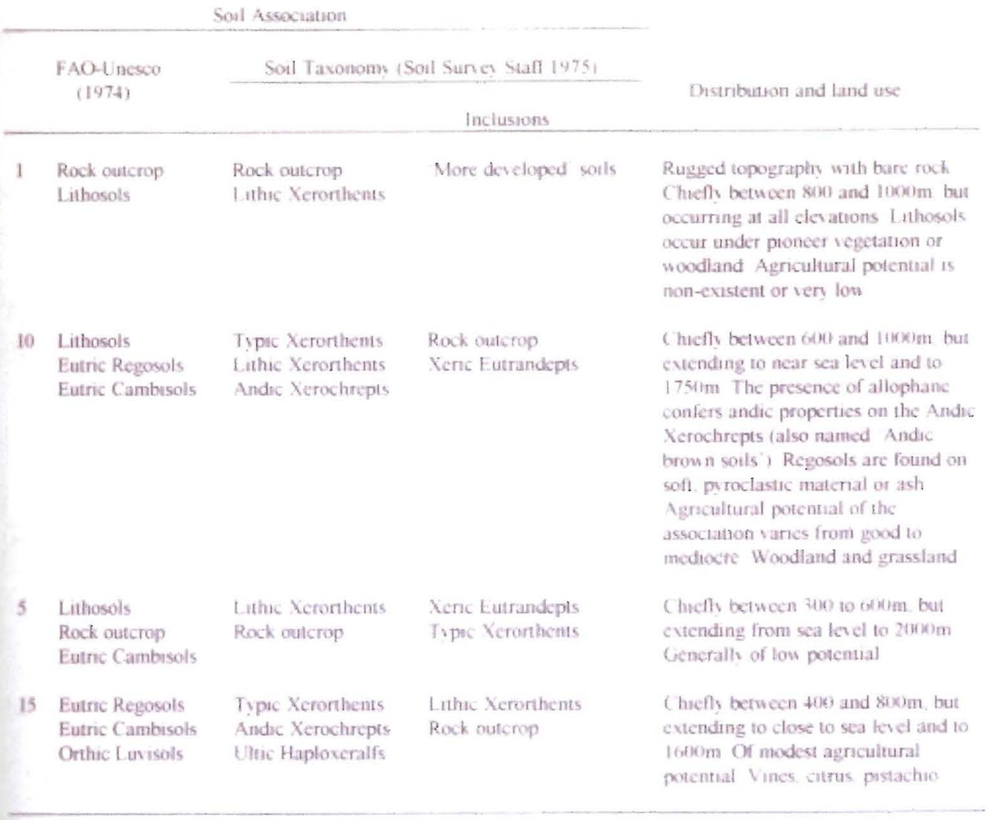
The production of clay minerals is also important in volcanic soils as this influences nutrient holding capacity (particularly exchangeable cations like (Calcium (Ca^{2+}) and Potassium (K^+) and water holding capacity. The clay minerals of tephra soils are very distinctive (less so on lava). Nevertheless clay formation is a major aspect of soil development throughout the early lava flows of this chronosequence.

4.1.2. Volcanic soils

Volcanic ecosystems provide a perfect field for studies of primary succession and the corresponding soil development during a chronosequence. This has been studied by many authors including Dickson and Crocker (1953a), (1953b), (1953c) working on Mt.Shasta; Tezuka (1961) on Oshima; Fridrikson (1975) on Surtsey; Kitayama and Mueller-Dombois (1995) and Vitousek *et al* (1995) working on Hawaii. They have all observed the changing organic and other properties of the soil and the nutrient content at particular points in time.

4.1.3. Etna soils

Four soil associations are classified and mapped for Mt.Etna by Fioretti (1988) the soil taxonomy classes being those of the Soil Survey Staff, 1975 (Table 4.1). Rock outcrops occur frequently on all the lava flows – both as small protrusions on the surface which are hardly visible and as larger sheets or tumuli. The smaller outcrops reflect the initial uneven nature of lava and differences in weathering rates as soil and debris develops in hollows on the surface gradually rising up to cover all but the highest protrusions. This will aid weathering of the surface bringing the underlying rock into contact with roots and organic acids.



	Soil Association			
	FAO-Unesco (1974)	Soil Taxonomy (Soil Survey Staff 1975)		Distribution and land use
			Inclusions	
1	Rock outcrop Lithosols	Rock outcrop Lithic Xerorthents	'More developed' soils	Rugged topography with bare rock Chiefly between 800 and 1000m but occurring at all elevations Lithosols occur under pioneer vegetation or woodland Agricultural potential is non-existent or very low
10	Lithosols Eutric Regosols Eutric Cambisols	Typic Xerorthents Lithic Xerorthents Andic Xerochrepts	Rock outcrop Xeric Eutrandepts	Chiefly between 600 and 1000m but extending to near sea level and to 1750m The presence of allophane confers andic properties on the Andic Xerochrepts (also named 'Andic brown soils') Regosols are found on soft, pyroclastic material or ash Agricultural potential of the association varies from good to mediocre Woodland and grassland
5	Lithosols Rock outcrop Eutric Cambisols	Lithic Xerorthents Rock outcrop	Xeric Eutrandepts Typic Xerorthents	Chiefly between 300 to 600m, but extending from sea level to 2000m Generally of low potential
15	Eutric Regosols Eutric Cambisols Orthic Luvisols	Typic Xerorthents Andic Xerochrepts Ultic Haploxeralfs	Lithic Xerorthents Rock outcrop	Chiefly between 400 and 800m, but extending to close to sea level and to 1600m Of modest agricultural potential Vines, citrus, pistachio

Table 4.1 The four Etna soil associations mapped by Fioretti (1988).

4.1.4. Foliar nutrients

Often when studying changing nutrient status in the soil there is a corresponding change in the amount of elements within the leaf structures of the plants that grow on these surfaces. Clearly if a plant lives on a nutrient rich soil it will have large quantities of essential elements present in the leaves, whereas those living in nutrient poor sites will be nutrient deficient (although there will probably be more obvious differences like number of leaves and size of the plant). By studying the relative amounts of these nutrients in the leaves it is possible to gain more information about the available nutrient status of an ecosystem than a soil analysis on its own. This gives a comparison between the amount of nutrients available to the plants and what the plant is actually utilising. Factors such as competition can affect the amount of nutrients in the plant leaves regardless of the soil nutrient status as some species are better at taking in nutrients than others. In addition, there is the possibility that soil data may be affected on a temporal scale by sudden surges of nutrients (e.g. caused by a rain depositing and redistributing nutrients) whereas the foliar nutrient status will be laid down over the growth of the plant and can give a more accurate reading of a site's true nutrient status.

4.1.5. Soils project

The changing soil properties over the period of the 500 year chronosequence has important implications on the changing ecosystem. Individual plant species have specific nutrient requirements – however these vary between species. Therefore, as nutrient status in the soil changes, species will move in and out of the ecosystem. The purpose of this part of the project is to investigate these changes in several soil properties (nutrients, pH and biomass) as well as foliar nutrient change during the 500 year chronosequences on Etna.

4.2. Methods

4.2.1. Soil sampling and preparation

From each of the 35 sample sites located on Mt.Etna (for site selection see section 2.2.3 – 2.2.7) samples of the top 5cm of soil (to represent the most recent products of the lava flow and hence its nutrient cycling ability) were taken. On the early lava flows this soil was scraped from between the cracks and crevices of the lava. On the later flows where a clear soil profile had formed the overlying leaf litter (L horizon) was removed and the sample taken from directly underneath. These samples were stored in a fridge at 5°C until required for analysis. Before chemical analysis each sample was air dried for three days and sieved to < 2mm particle size (except in the case of the nitrate analysis which was carried out on fresh material two days after returning from Etna). A small sub-sample (5g) was oven dried at 70°C for two days to determine total water content.

4.2.2. Soil pH

Three 5g sub-samples of the air-dried soils from each of the sites visited were taken and placed in 100ml beakers. These samples were mixed with distilled water to a depth twice that of the soil, as outlined in Allen (1989). The samples were stirred and then allowed to stand for ten minutes before being analysed by immersing a pH probe on a pH meter with a temperature probe to correct for variation in ambient temperature. The three samples were combined and an average and standard deviation obtained.

4.2.3. Soil organic matter by loss on ignition

Three replicates of the air dried / sieved to < 2mm particle size soils were taken for organic material content analysis. Each sub-sample of approximately 1g was weighed precisely to three decimal places and placed in a Carbolite CSF 1200 oven. The temperature was then gradually raised to 600°C (as suggested in Allen 1989). The samples were left at this temperature for eight hours to ignite all organics present. Then the temperature was lowered gradually to 150°C at which point the samples were removed from the oven and placed in a desiccator (to prevent water absorption by the samples) until cool enough for re-weighing. Percentage organic matter was then calculated from the following equation:

$$\mathbf{\%\ Organic\ matter = ((W1 - W2)/\ W1) \times 100}$$

Where: W1 = Initial weight of soil; W2 = Weight of soil after 8hrs at 600°C

4.2.4. Soil nitrate analysis of the north and south chronosequences

The amount of free nitrate in the soil samples of the north and south chronosequences was determined using the Ion-selective electrode method outlined in Allen (1989). In this method 5g of fresh (analysed within two days and stored in a coolant bag during transport) soil material was weighed precisely to four decimal places. The soil was then mixed with 50ml of distilled water for ten minutes on a rotary shaker and then filtered. 25ml of the resulting supernatant was then combined with 10ml of a buffer solution to remove chloride, carbonate and bicarbonate ions, which would affect the ion electrode. The buffer solution consisted of 17.32g Aluminium Sulphate ($Al_2(SO_4).18H_2O$). 3.43g Silver Sulphate (AG_2SO_4), 1.28g Borax (H_3BO_3) and 2.52g Sulphamic acid (H_2NSO_3H).

This was made up to 800ml and adjusted to pH 3.0 by adding NaOH. Then made up to 1L.

The solution was then analysed by immersing the nitrate electrode of a Jenway 3040 Ion analyser, into the solution whilst continuously stirring with a magnetic stirrer and reading of the result in mV. This value was then converted into parts per million (PPM) of nitrate by comparing to a calibration curve determined using a KNO_3 standard plotted on semi-logarithmic paper with concentration (1-100ppm) on the log axis and instrument reading on the linear axis (as in Allen 1989 – p132).

Finally, the extractable nitrate in the soils was determined using the following equation:

$$\textbf{Extractable } \mathbf{NO_3^- - N} \textbf{ (mg 100g-1)} = \frac{\textbf{C (ppm) x soln vol (ml)}}{\textbf{10 x sample weight (g)}}$$

Where C = ppm NO_3^- - N obtained from the calibration graph.

4.2.5. Soil total organic nitrogen analysis

Three replicates of the air-dried and sieved < 2mm particle size soil samples were analysed for total soil Nitrogen. From each site three replicates of 1g sub-samples were taken. Total soil nitrogen was analysed using a variation of the Kjeldahl method outlined in Allen (1989). Using this method organic-N is converted to NH_3 by boiling with H_2SO_4. Ammonia is then liberated from the sulphate by distillation with NaOH and determined by titration with HCl. The exact procedure used was as follows: -

1g of soil was weighed out to an accuracy of four decimal places and placed in a kjeldahl flask. 10ml of catalyst containing Sodium Sulphate, Copper Sulphate and Selenium mixed to give proportions of 20: 1 : 0.1 (mixed from a ready made tablet produced by B.D.H. Ltd.) was added to the flask and then left to stand for 30 mins. At this time 7.5ml of H_2SO_4 was pipetted into the flask. The flask was then placed in a digestion rack and heated slowly to a temperature of 150°C. Once the initial vigorous reaction had subsided and the liquid stopped refluxing up the side of the tube the temperature was gradually increased to 400°C. After several hours the liquid became colourless and as this occurred it was necessary to tilt the flask gently, in order to agitate those particles of soil that had moved up the side of the flask, during the earlier vigorous stage, back down into the acid. This was to make sure all the soil particles had been digested.

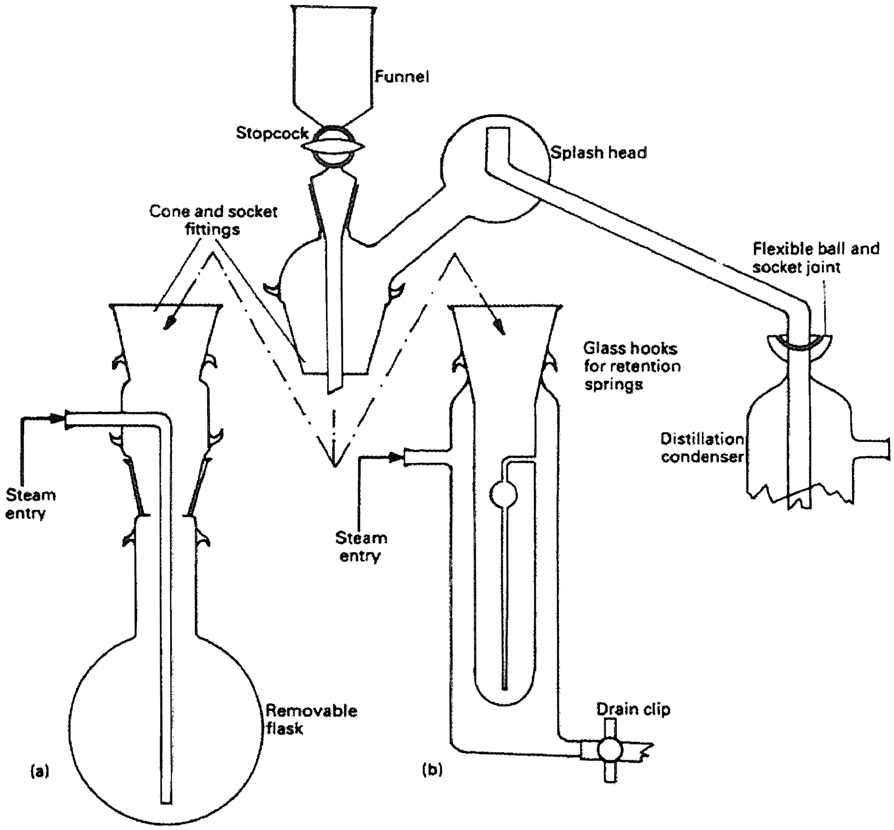


Figure 4.2. Distillation apparatus (taken from Allen 1989). The semi-micro b) apparatus was used in this experiment.

On completion of the digestion the sample was allowed to cool until just warm and then diluted with distilled water. The sample was then filtered into a distillation flask (Fig 4.2). 40ml of sodium hydroxide was then carefully added to the sample and steam allowed into the tube. 30ml of distillate was then collected in a beaker containing 50ml of Boric acid and indicator solution. The distillate was then titratated with 0.05 molar HCl until the liquid changes from light blue to a pale neutral colour. A standard plant reference material was also run concurrently with the soil / plant samples to test the accuracy of the method along with acid digest blanks and titrate / distilled water blanks to determine % nitrogen content.

Total Soil nitrogen was determined using the following equation: -

$$\% \mathbf{N} = (\mathbf{T} - \mathbf{B}) \times \mathbf{N} \times 1.4 / \mathbf{S}$$

Where: T = Sample titration ml HCl, B = Blank titration ml HCl, N = Normality of HCl and S = Soil weight (g).

4.2.6. Soil cations (Calcium, Magnesium and Potassium)

The total Calcium (Ca^{2+}), Magnesium (Mg^{2+}) and Potassium (K^{+}) in the Etna soils was determined using a Perkin Elmer plasma 40 Emission spectrometer which is an Inductively Coupled Plasma Emitter (ICP), using the method outlined in Wray (1998). The samples were first acid digested in a sample of Aqua Regia (ratio of 3:1 Hydrochloric : Nitric acid). A sample of 0.5g of the dried soil material (dried overnight at 70°C to completely desiccate the sample) was weighed precisely to 4 d.p. This sample was placed in a sterile volumetric flask with 10ml of Aqua Regia, and left overnight to passively react. The sample was then heated for 4 hours at 130-150° to completely digest the soil material (NB this required the occasional addition of distilled water to prevent it from boiling dry). Once digestion was complete all that remained was a totally clear liquid with possibly a small quantity of colourless waste. This liquid was then filtered through filter paper and thoroughly rinsed through with distilled water to draw out all the supernatant. The resultant sample was returned to a volumetric flask and made up to 100ml.

These samples were then analysed using the ICP with an Argon carrier gas. The readings were auto calibrated by the ICP using pre-prepared standards in the 0-100ppm range prepared using a separate standard for each element sought.

Total soil cations was determined using the equation:

$$\text{Total element (g / kg)} = \frac{\text{Concentration (PPM)} \times \text{volume} \times \text{dilution factor}}{\text{Weight of sample}}$$

4.2.7. Foliar total nitrogen

Samples of five primary colonising plant species were taken from each of the sites located on the slopes of Mt.Etna. These species were selected for their long-term presence on many of the lava flows over a long age sequence and their abundance on the earliest lava flows. The species sampled were: *Centranthus ruber, Rumex scutatus*, *Genista aetnensis*, *Helichrysum italicum*, *Senecio bicolor*. Sampling consisted of taking the youngest leaves from the top of the plants. In the case of *G.aetnensis*, which has only a very few, tiny leaves, sections of photosynthetic stems were taken instead. The stems taken were the youngest (at the tip of the branches) and from the highest level. Similarly in the case of *H.italicum,* stems were taken which were covered in the tiny spine like leaves. These leaves were later removed in the laboratory in Luton for analysis. All the samples were taken from the field and weighed to determine water content. These samples were then transferred to large paper envelopes and hung outside to dry in order to prevent decomposition. Upon return to the laboratory the semi-dry samples were then completely dried in the oven at 70°C for two days. These samples were then re-weighed to determine total water content. Once dry, the leaf samples were ground to a fine powder using a coffee grinder and stored in standard plastic sampling bags until needed for analysis. This material was then used in each of the following foliar nutrient experiments.

The total foliar nitrogen was determined using the same method outlined in 4.2.5 but with the following adjustments. In this case, three replicates of 0.1g of finely ground samples of the commonest plant species *(C.ruber, R.scutatus, H.italicum, S.bicolor* and *G.aetnensis*) were used for analysis. These samples were acid digested, distilled and titrated as in Allen (1989). These samples were then compared to a standard reference material to determine the accuracy of the method.

4.2.8. Foliar cations (Calcium, Magnesium and Potassium)

Sub-samples of the vegetation (for sampling method and preparation see 4.2.7) were analysed for foliar concentrations of Ca^{2+}, Mg^{2+}, and K^{+}. This method was the same as that outlined in 4.2.6, with the exception that only 0.1g of leaf material was required per replicate.

4.3. Results

4.3.1. Soil pH

Soil pH on the four aspects of the volcano varied considerably both with the age of flow and with aspect. By looking at the data in tabular form it is clear that when averaged there is little variation between the north, south and west aspects of the volcano (all around 6.5 – see Table 4.2). However, when looking at the east aspect there is a clear drop in soil pH, to below pH of 6 (Fig 4.3). The relatively high 1992 value of 7.16 is a measurement of the pH of a pocket of tephra ejected by the volcano just prior to sampling and can be excluded as it is atypical.

Soil pH readings							
South aspect		North aspect		East Aspect		West Aspect	
Lava Flow	pH	Lava Flow	pH	Lava Flow	pH	Lava Flow	pH
1910	5.9	1981	6.54	1992	7.16	1651	6.52
1892	6.77	1947	6.73	1928	5.71	1843	6.44
1780	6.79	1923	6.00	1865	5.72		
1766	6.50	1879	6.85	1792	6.24		
1634	5.86	1809	6.08	1689	5.72		
1537	6.21	1646	6.41				
1536	6.45	1614	6.51				
1444	6.06	1536	7.17				
1334	7.08	Ancient	6.06				
812	6.87						

Table 4.2 Soil pH readings on the four aspects of the volcano.

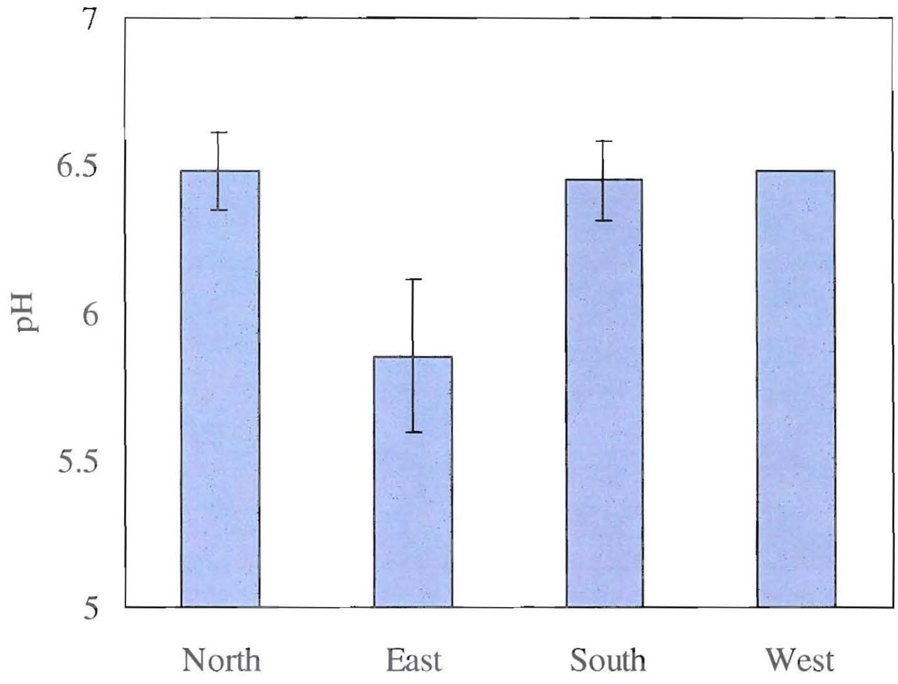


Figure 4.3. Average soil pH on the four aspects of the volcano.

In contrast, a closer look at what actually happens over the southern chronosequence shows us that there appears to be a pattern of pH change over time. There is an early peak of pH of around 6.7 (1892 and 1780 lava flows) followed by a decline to a level of 5.8 (1634 flow) before rising again in the latest stage flows of the sequence (Fig 4.4 a).

A similar pattern is discernible on the northern chronosequence as well with the early peak in pH (6.7 on the 1947 flow) which then declines during the mid age range flows (1809 flow = pH 6.1) before gradually increasing again to a level of 7.2 (Fig 4.4 b).

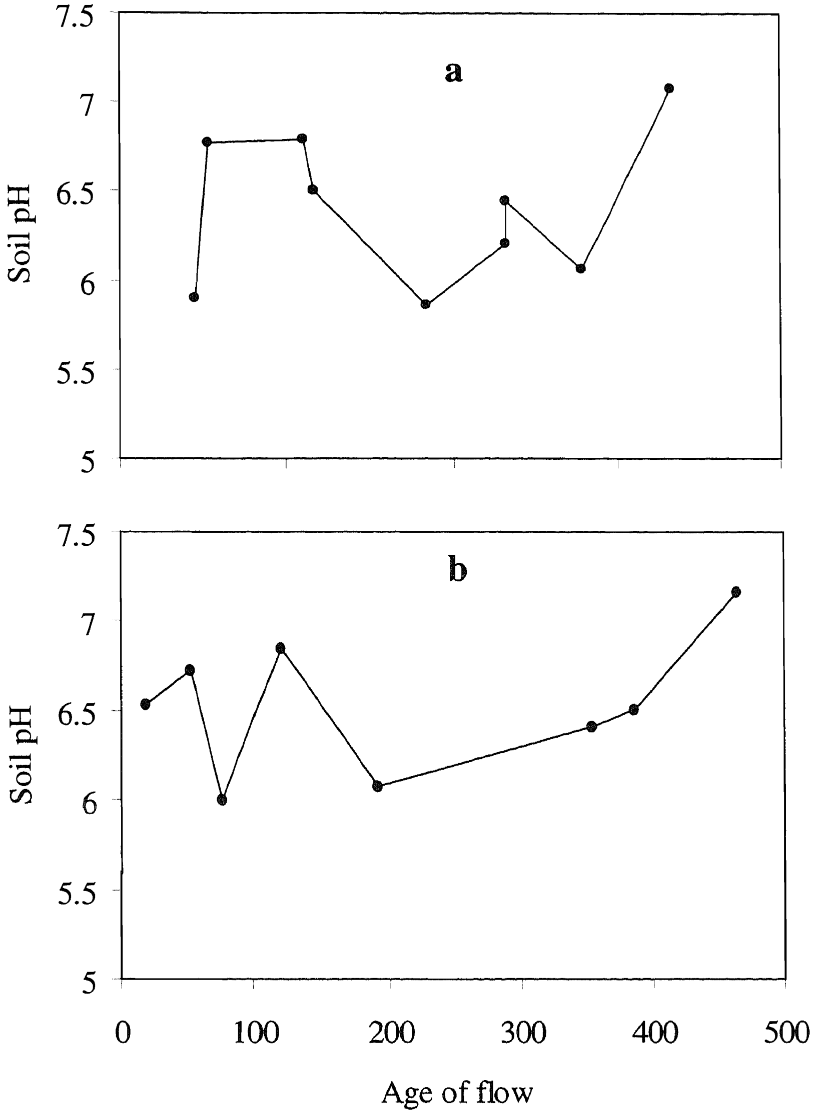


Figure 4.4. Soil pH change on the southern (**a**) and northern (**b**) chronosequences on Mt.Etna.

However, over a range of different altitudes there is a linear relationship – with a decline in soil pH with increasing altitude (Fig 4.5). In addition, the strength of that change appears to vary with age of lava flow. The younger lava flows (1910 and 1892, Fig 4.5 **a** & **b**) show the greatest change (from pH 5.5 – 7.5) and hence have steeper gradients on their trend lines. In contrast, the older flows (1780 **c** and 1634 **d**) show much less variation of pH with altitude (from 5.5 – 6.4 and 5.8 - 6.8 respectively).

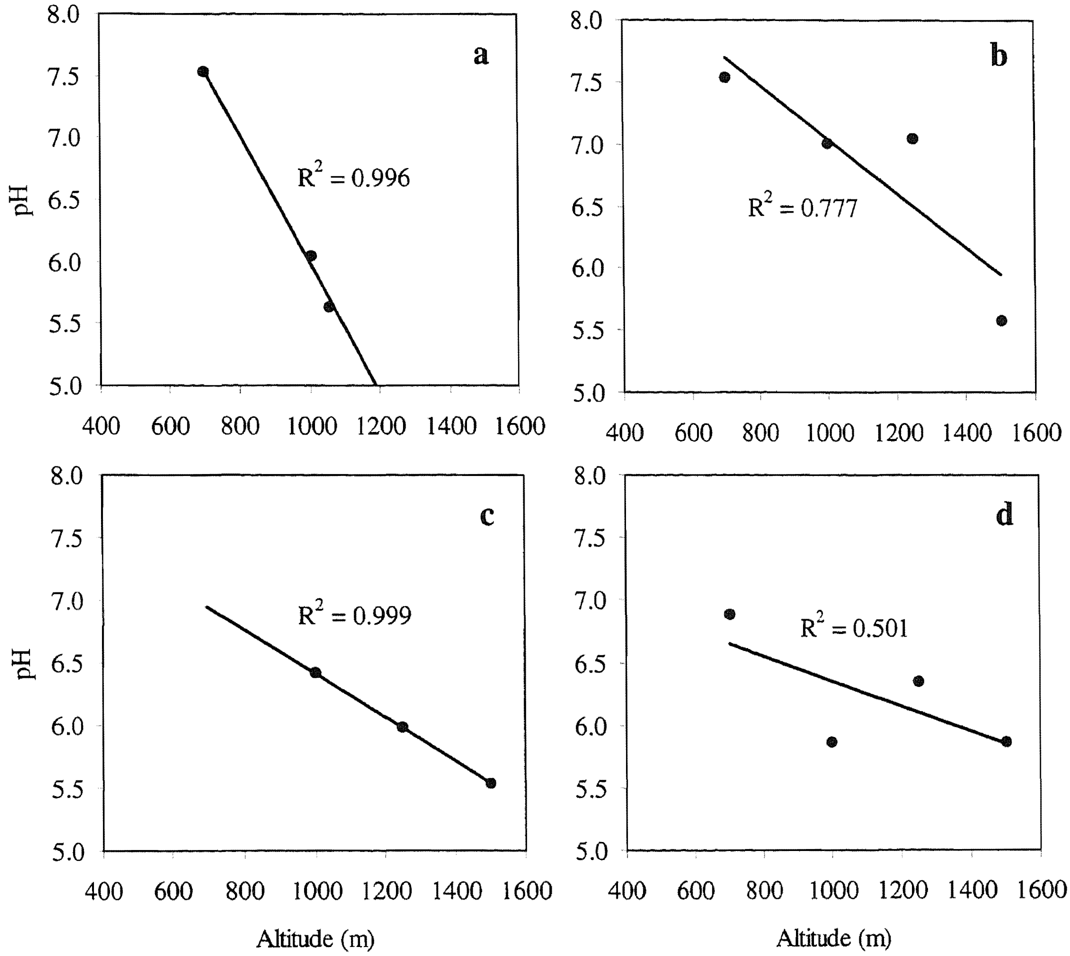


Figure 4.5. pH of the soil on 4 lava flows over a range of altitudes. Where **a** is a 1910 flow, **b** is 1882, **c** is 1780 and **d** is a 1634 lava flow.

4.3.2. Soil organic matter by loss on ignition

There is a clear linear relationship between the percentage of organic material in the soil and the age of the flow (Fig 4.6). All three chronosequences show a statistically significant increase in soil organics as the age of the flow increases. The southern chronosequence (Fig 4.6.a) has an r^2 value of 0.93 very significant. The northern chronosequence (Fig 4.6.b) has an r^2 value of 0.72 (partially significant) and the eastern chronosequence (Fig 4.6.c) which is very significant ($r^2 = 0.92$). The use of r^2 values was employed as the sample number was low (<3) for this experiment (p values require a sample number of 4 or more). r^2 values will show a trend in the data only.

Organic matter content on the three lava flows all show a peak at an altitude of 1250m (Fig 4.7) with the eldest flow (1634 flow, 365 years old) showing the highest (14%). As altitude increases to 1500m all three flows then show a decline in their organic matter content. All three flows also clearly show that as age of the lava increases so too does the organic matter content.

Organic matter content in a comparison of the four aspects on two age matched lava flows (Fig 4.8) clearly shows that in each case there is a larger organic matter content on the older lava flow (e.g. north has 14% on the 1646 lava flow whereas the 1879 has only 5.5%). The lowest recorded organic matter was measured on the west aspect (1843 flow) with less than 2% content.

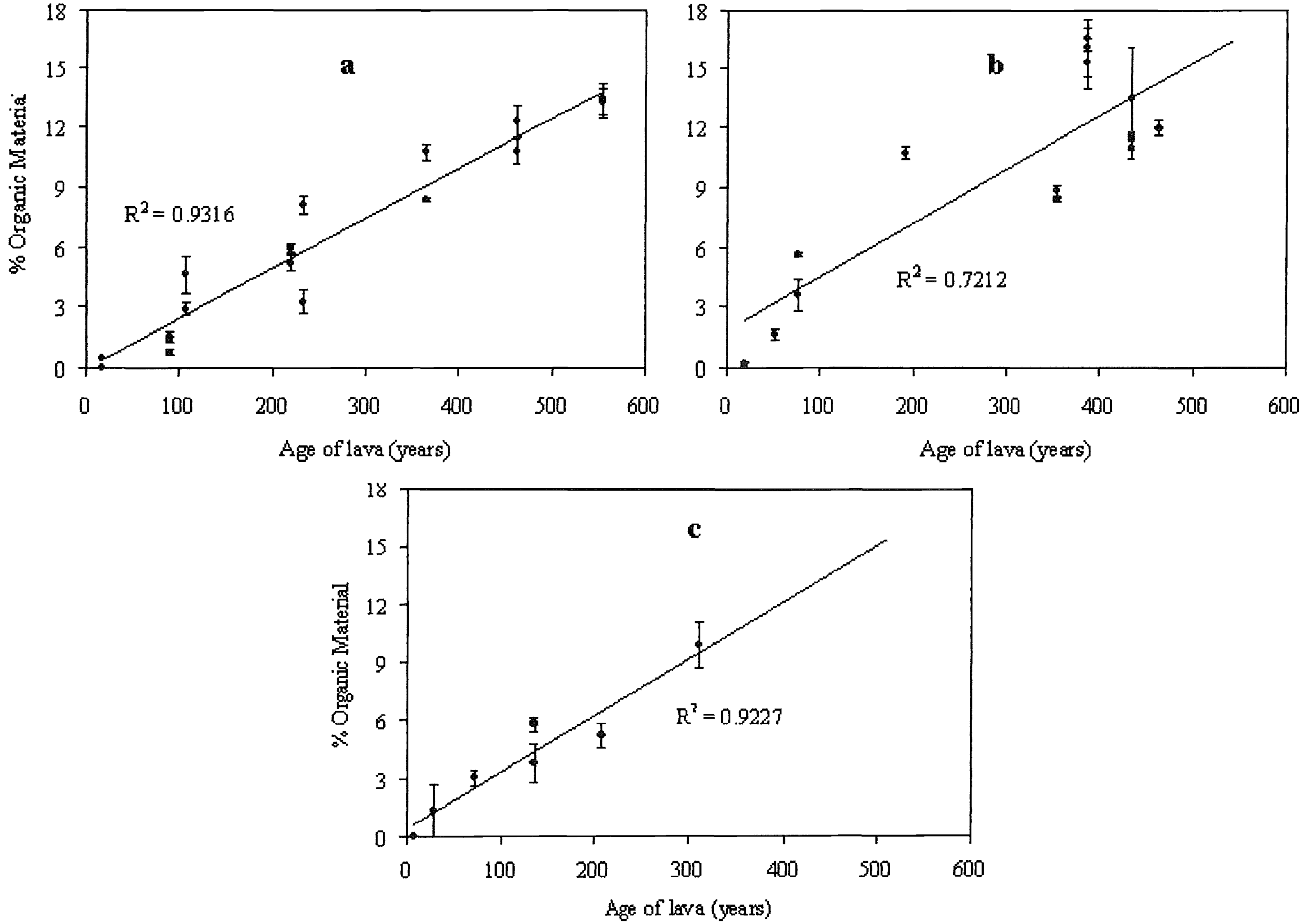


Figure 4.6. Percentage soil organic material over the southern (a), northern (b) and eastern (c) chronosequences on Mt.Etna (where n=5, +/- S.E.).

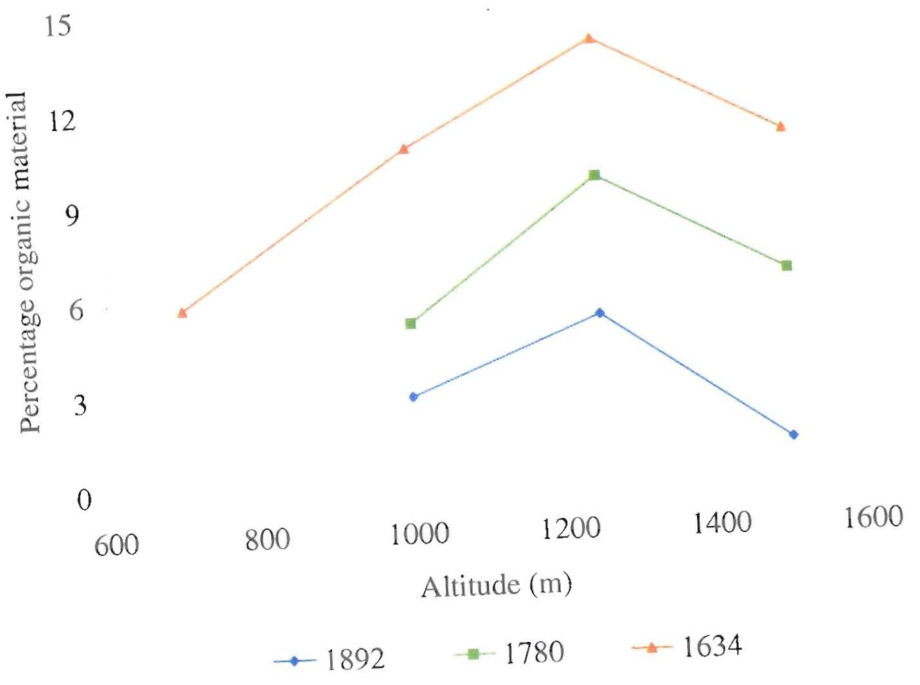


Figure 4.7. Percentage organic matter in the soil over a range of altitudes on three lava flows on the southern aspect (where n=5, +/- S.E.).

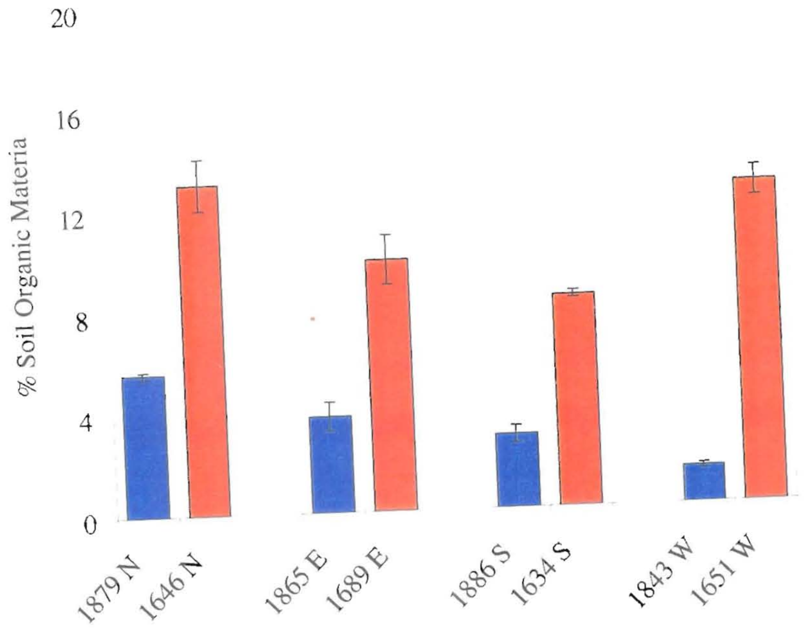


Figure 4.8. Percentage organic matter in the soil on the four aspects of Mt.Etna on two age ranges (where n=5, +/- S.E.).

4.3.3. Soil nitrate analysis

Both the south and north chronosequences show a trend for a increasing extractable soil nitrate with increasing age of the site (Fig 4.9). On the south flow the nitrate rises from a low level of 2mg/100g to a level of over 5mg /100g (r^2 = 0.71). The north rises from a level of 0.5 mg/100g to 2.5mg (r^2 = 0.70).

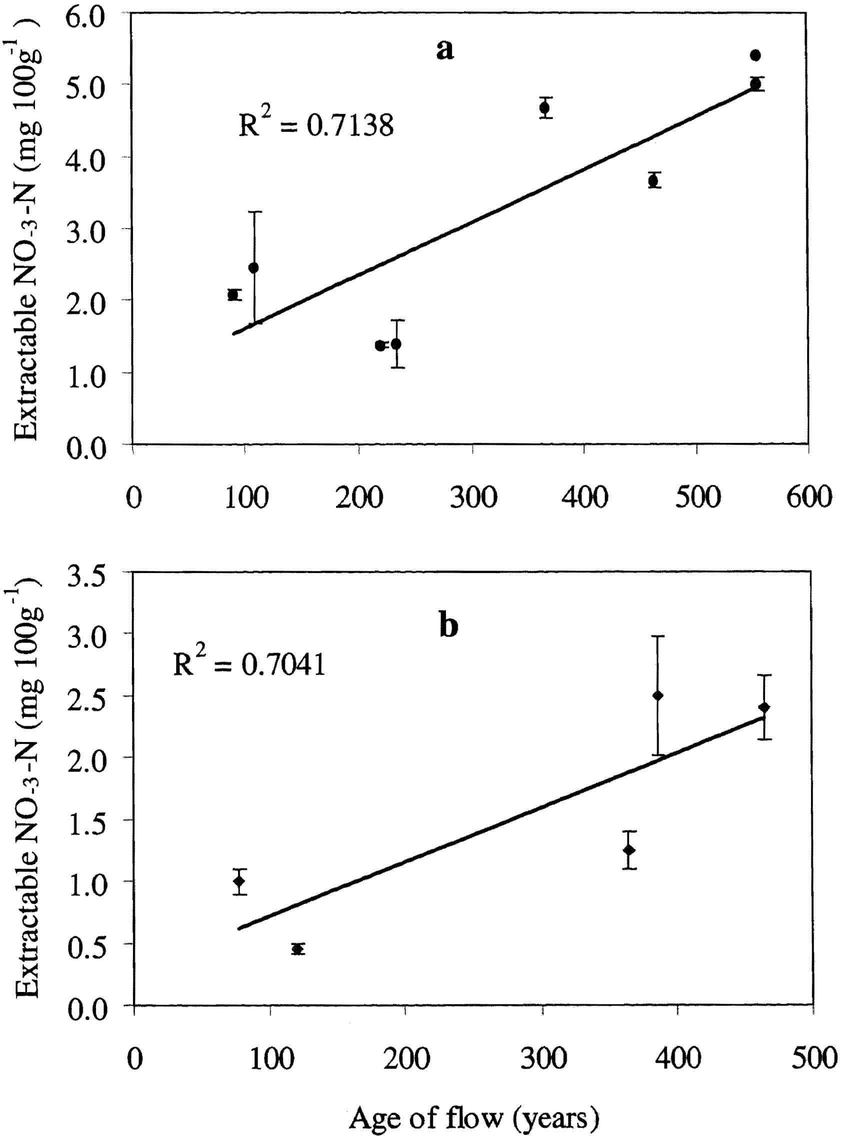


Figure 4.9. Extractable Nitrate from the soil of the south (**a**) and north (**b**) chronosequences (N=3, +/- S.D).

4.3.4. Soil total nitrogen analysis

All three chronosequences on the south (Fig 4.10a), north (Fig 4.10b) and east (Fig 4.10c) aspects of Etna show an increasing soil total nitrogen with age of the site. Each chronosequence shows an increase in from 0.1 to 0.6 %, however while there is very little difference between the south and north chronosequences (Fig 4.10a and b) the east chronosequence is increasing faster. On this east chronosequence the 1792 lava flow (208 years old) has reached a level of 0.7%, far higher than either of the other chronosequences during this period

There is a trend for decreasing soil nitrogen content with increasing altitude on the south aspect of Etna (Fig 4.11). The youngest flow (1892) has a peak of 1% at an altitude of 750m but this quickly drops to 0.1% by 1000m (fig 4.11 blue line). The total nitrogen on the 1780 flow remains constant (green line) while the 1634 flow also shows a drop with increasing altitude (red line)

On the four aspects of Etna on the two age matched lava flows there is a clear trend for higher total nitrogen on the older seventeenth century flows on all four aspects. For example the south has more than 0.4% nitrogen on the 1634 flow in comparison to the 1892 flow which has less than 0.1% (Fig 4.12). Between aspects, there is no difference between the north and east sites (both have 0.2% on the nineteenth century flows and 0.3% on the seventeenth). However the south and west nineteenth century flows have a very low nitrogen content (>0.1%). In contrast, the western 1651 flow (seventeenth century) has the highest nitrogen content at 0.55% (Fig 4.12).

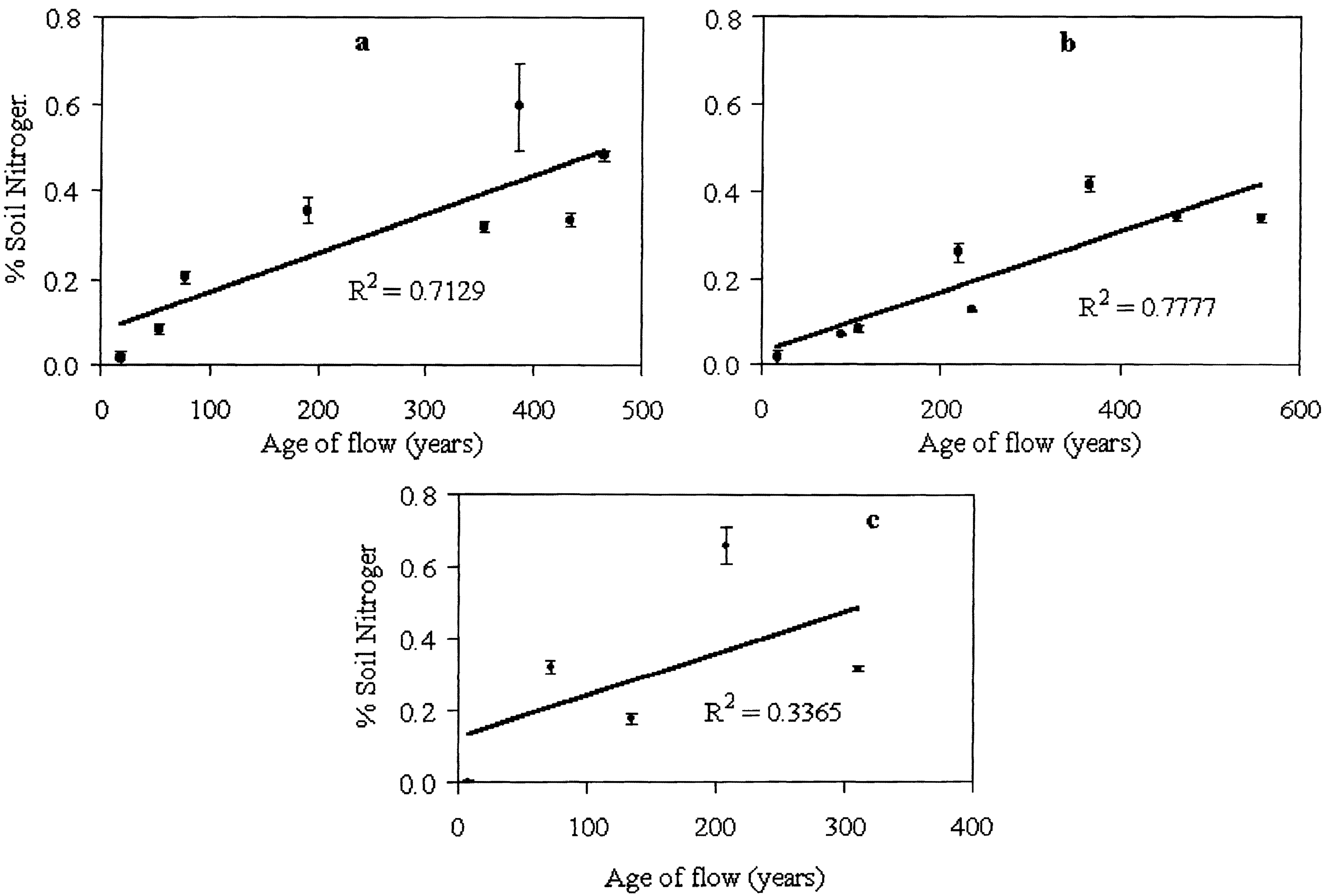


Figure 4.10. Percentage total nitrogen in the soil of the southern (a) northern (b) and eastern (c) chronosequences. (N=3, +/- S.D). Note the different age scales on the graphs.

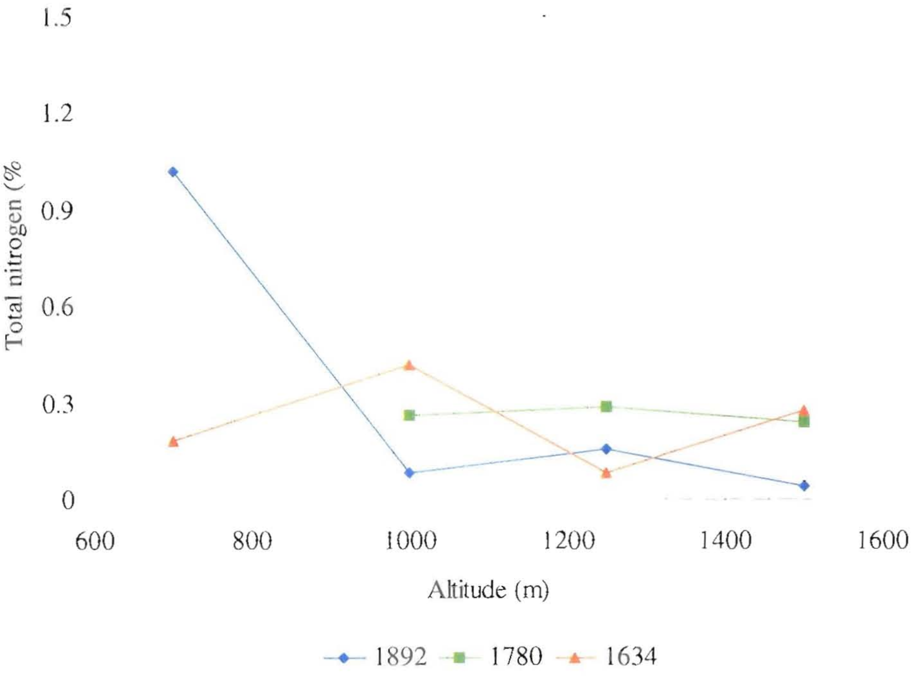


Figure 4.11. Total Nitrogen in the soil over three altitudes (where n=3).

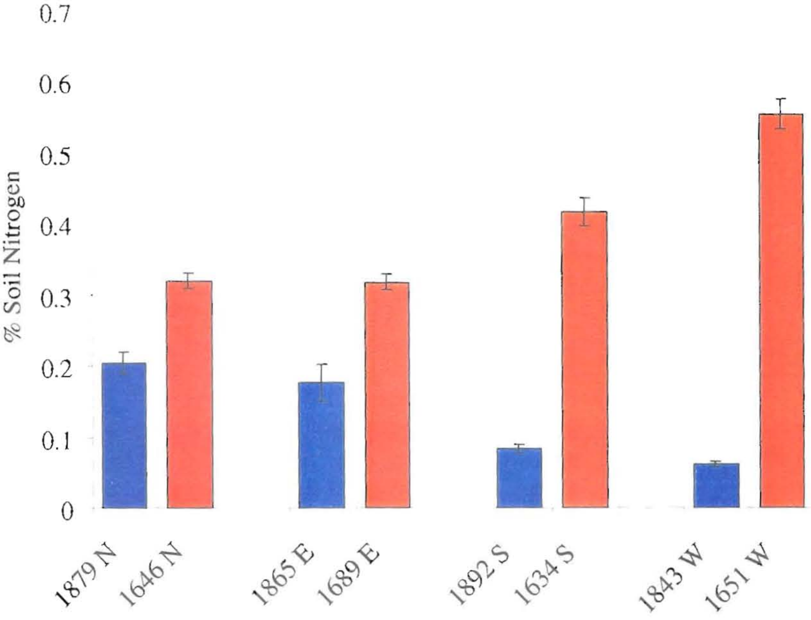


Figure 4.12. Percentage total nitrogen on the four aspects of Mt.Etna.
(n=3, +/-S.E).

4.3.5. Soil Cations (Calcium, Magnesium and Potassium)

For each of the three cations examined there was a larger concentration found in the soils of the northern chronosequence compared with the south (Fig 4.13).

Magnesium

On the south chronosequence magnesium in the soil shows a slight increase from 6g/kg on the 90 year old site to just over 8g/kg on the 464 year old site (Fig 4.13). In contrast, the north shows a slight decline in magnesium from 14g/kg at 53 year old site to 8g/kg on the 464 year old site.

Calcium

Calcium in the soil on the southern chronosequence shows an increasing concentration over time (from 4g/kg on the youngest 90 year old flow to 16 on the 556 year old flow). In contrast the north chronosequence remains constant at approximately 25 g/kg.

Potassium

This element remains constant on both the north and south chronosequences on Etna. The south at a level of 3g/kg and the north at a level of approximately 4g/kg (Fig 4.13).

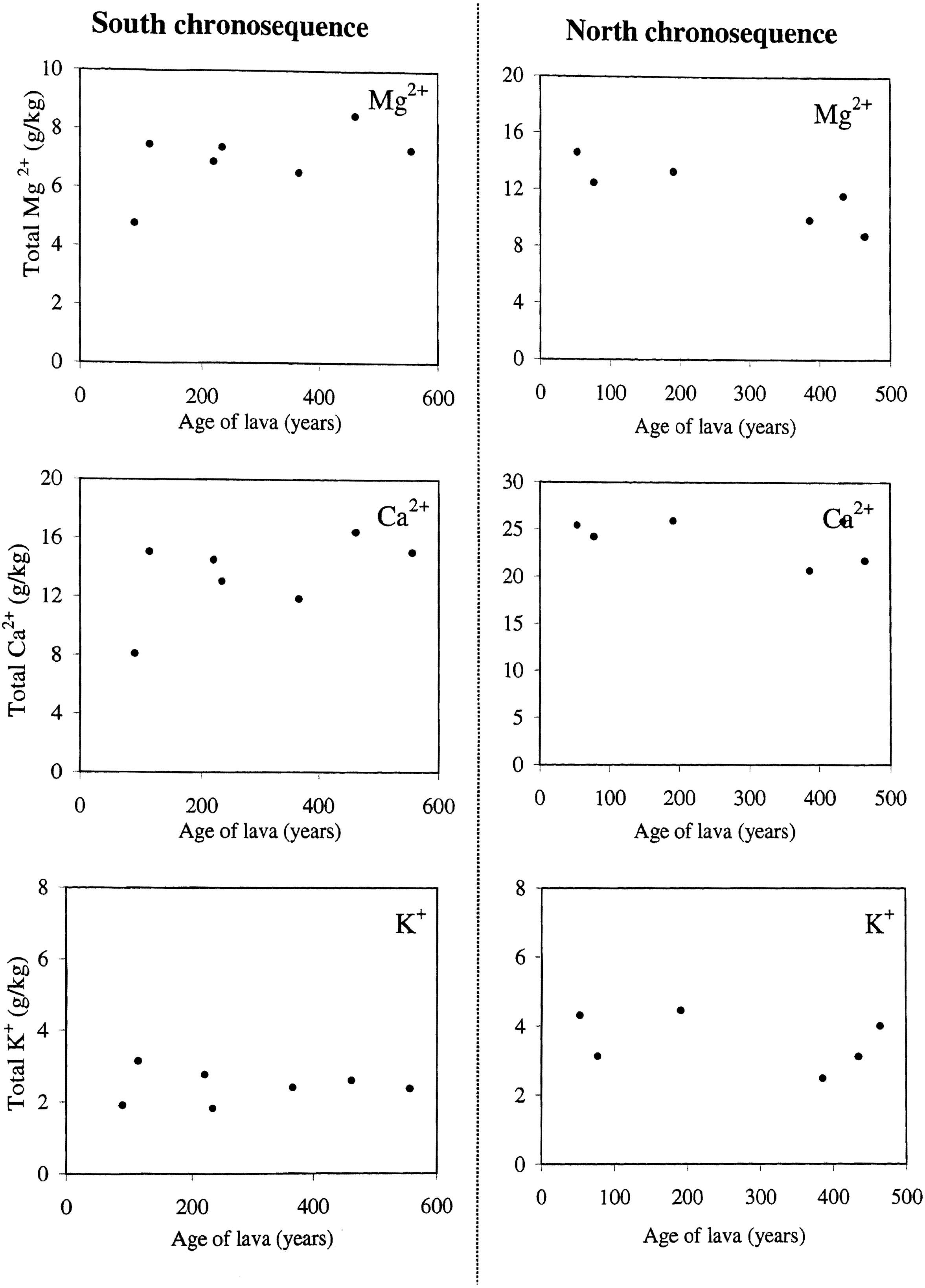


Figure 4.13. A comparison between three essential nutrients Magnesium (Mg^{2+}), Calcium (Ca^{2+}) and Potassium (K^+) in the soil in the south and north and south chronosequences

4.3.6. Foliar total nitrogen

C.ruber

The foliar percentage nitrogen in the leaves of *C.ruber* remains constant at about 2.8% on sites of increasing age (Fig 4.14a).

R.scutatus

The foliar percentage nitrogen in the leaves of *R.scutatus* remains constant at about 4% on sites of increasing age (Fig 4.14b).

G.aetnensis

The foliar percentage nitrogen in the leaves of *G.aetnensis* remains constant at about 2% on sites of increasing age (Fig 4.14c).

S.bicolor

There is a slight trend for increasing foliar nitrogen over time from 1.8 to 2.2 % over the time period of the chronosequence (Fig 4.14d)

H.italicum

This species shows an increase in foliar nitrogen over the chronosequence (Fig 4.14e) with a starting amount at 1.5% after 90 years (1910 flow) rising to 3.5% after 144 years (1766 flow)

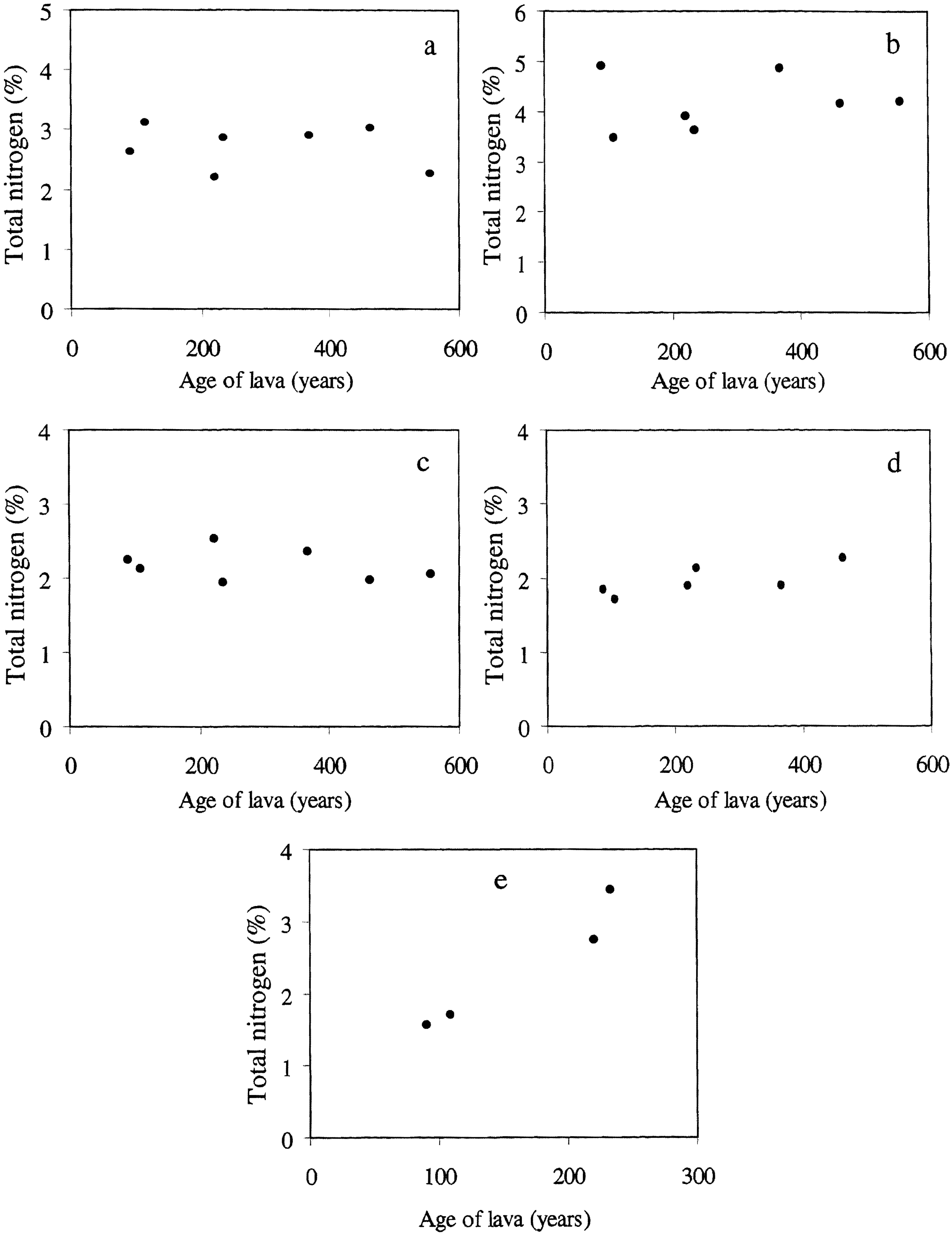


Figure 4.14. Total foliar nitrogen in the leaves of *C.ruber* (a) *R.scutatus* (b) *G.aetnensis* (c) *S.bicolor* (d) and *H.italicum* (e) on the south chronosequence.

Fig 4.15 demonstrates a trend for increasing total foliar nitrogen in the leaves of *R.scutatus* on the southern aspect of Etna as altitude increases, from 3.3% at 450m to 5% at 1500m.

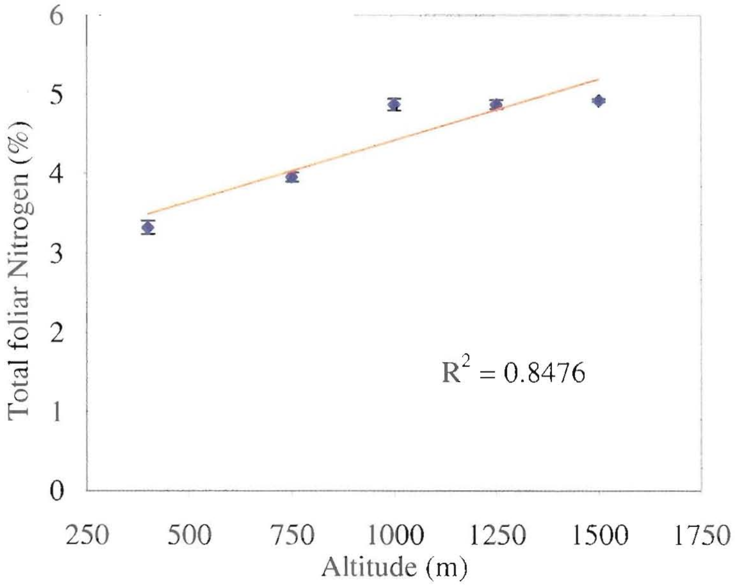


Figure 4.15. Total foliar nitrogen of *R.scutatus* over increasing altitude on the 1634 lava flow on the southern aspect of Etna

4.3.7. Foliar cations (Calcium, Magnesium and Potassium)

For each of the three cations *R.scutatus* has consistently higher levels in its leaves than *C.ruber* (Fig 4.16).

Magnesium

R.scutatus varies from 6g/kg to 12g/kg over the time of the chronosequence but there is no discernible trend over time. However, *C.ruber* maintains a foliar magnesium level of 3g/kg.

Calcium

R.scutatus shows a declining trend in the total calcium content in the leaves from approximately 35g/kg down to 12g/kg on the oldest 566 year old flow. *C.ruber* shows a similar trend from 14g/kg down to approximately 10g/kg.

Potassium

Both *R.scutatus* and *C.ruber* vary widely in their foliar potassium levels but neither show a trend with increasing age of the flow.

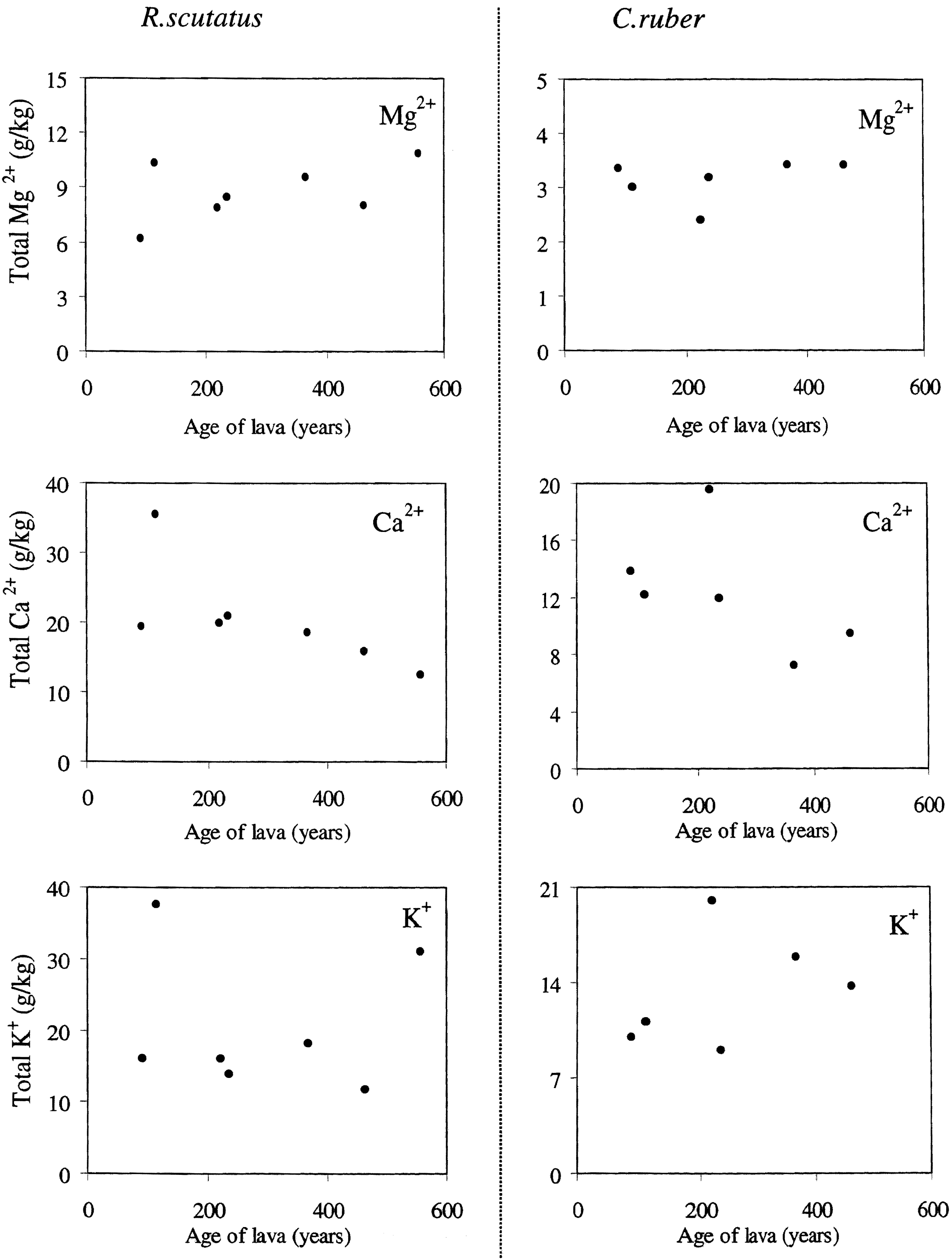


Figure 4.16. A comparison between three foliar nutrients Magnesium, Calcium and Potassium in the leaves of *R.scutatus* and *C.ruber.*

4.4. Discussion

4.4.1. Soil pH

The first thing that is obvious about the soil pH readings is that the east aspect of the volcano has a lower soil pH than that of all the other aspects. This is probably due to two factors acting on the soil. 1) The prevailing wind across the volcano blows to the east carrying volcanic gases towards the east aspect (see climate maps in chapter 1) and 2) the later stages of the eastern chronosequence is dominated by oak woodland.

The prevailing wind will affect the soil pH by causing the east aspect to get a disproportionately larger share of the volcanic gases that are continually being produced by Etna. This has been demonstrated (Davies and Notcutt 1988; Notcutt and Davies 1989) with volcanic fluorides where there is a demonstrably larger deposition on the east side of the volcano. As such it is no surprise that the sulphides and other pollutants produced by the volcano would be affecting the soil pH. This prevailing wind theory is further supported when it is noted that the 1792 flow which has a higher pH than the other eastern sites is located at the southernmost tip of the chronosequence and is probably escaping the worst of the volcanic deposition. Finally the increased precipitation on the east aspect of Etna (see climate map Fig 1.8) will increase the leaching of bases from the lava. The oak dominance on the 1689 lava flow causes the build up of decaying oak leaf litter which invariably lowers the soil pH (Campbell 1993) i.e. oaks thrive in mildly acidic conditions which then helps to continue the acidification of the soil. However this effect will only occur on the well developed oak woodlands of Etna, of which only the 1689 site was investigated here.

Variation in pH over the chronosequences and with changing altitudes (Figs 4.4 and 4.5) reflects changing bases in the soil during the ecosystem development. The variation may be due to the increased weathering activity of the lichens in the early (50-150 year) lava flows. Soil pH clearly declines with altitude on the slopes of Etna (Fig 4.5). Again this may be due to the increasing proximity to the volcanic crater. However, as the age of the flow increases this decline is ameliorated (as shown, the trend line becomes less steep) probably by the developing soil and vegetation.

4.4.2. Soil organic matter content

The clear trend of increasing soil organic matter content with age of site on the three aspects of Etna can be directly linked to the increasing biomass of vegetation growing on the lava flows and to the concurrent increase in species diversity as outlined in chapter two. Similarly, the increasing organic matter content with altitude is related to the increasing precipitation over the same change in altitude, which is similar to the findings of Vitousek *et al* (1992) on Hawaii. In this case the higher water content of the soils aids decomposition and the incorporation of the organics into the soil. The drop in organics, which occurs above 1250m, is almost certainly related to the temperature drop above this altitude – this is probable as it occurs on all three ages of lava flows, at the same altitude (1250m) indicating that age is not a factor. This drop in temperature reduces the growth period and bacterial activity on the higher altitude sites and so the higher altitude soils are generally less fertile/favourable for plant growth.

4.4.3. Soil nitrogen

Over time nitrogen fixation and atmospheric deposition increase the quantity and biological availability of nitrogen in the system as a whole and this is reflected in the trends for increasing nitrogen both as available nitrate (Fig 4.9) and as total nitrogen (Fig 4.10). This is similar to the results found by Stevens and Walker (1970) and Vitousek and Farrington (1997) who showed that nitrogen is a limiting factor in the early stages of primary succession. The faster trend for nitrogen accumulation on the eastern chronosequence is probably related to the much faster soil development (and vegetation diversity and size), caused by the higher precipitation in this region. This results in a higher nitrogen fixing potential in the soil as microorganisms and nitrogen fixing plants grow.

4.4.4. Soil cations

Most of the soil cations in the very early soils of the Etnean lava flows are derived by weathering of the lava surface – both abiotically and biotically by lichen activity. Abiotic disintegration will directly release available cations. However, biotic weathering will increase over an initial colonising period as the weathering action is enhanced by the increasing plant and lichen biomass. Over time this will stabilise as the primary surface of the lava is depleted in these elements and there is a steadier long-term release of elements from further inside the rock. In addition the elements mobilised by the weathering process will be incorporated into the plants growing on the lava flows and this may influence overall cation availability. Ca and Mg are abundant in the lava (Chester *et al* 1985; Giammanco *et al* 1996). However, the available fraction of cations is largely exchangeable and can be adsorbed on well decomposed organic matter – humus. Thus, as humus content increases in the topsoil, the cation exchange capacity and potential adsorbing power of these nutrients increases.

4.4.5. Foliar nitrogen

Although total nitrogen on the flows is increasing with the age of the flow, the nitrogen in the leaves of only two the plant species reflects this increase (*S.bicolor* and *H.italicum*). The three remaining species show no trend for changing levels of nitrogen – it is possible that these plants have mechanisms which keep an optimum level of nitrogen within all the leaves. For example, if a plant grows in a nutrient poor area it will simply grow fewer leaves (as these are small plants with a limited number of leaves this is possible). Most studies on foliar nutrients have been conducted on tree species (Vitousek *et al* 1988; 1989) so the larger plant size will reflect if nitrogen is limited (e.g. thousands of leaves so if nitrogen is low this will be spread very thinly between many leaves).

4.4.6. Foliar cations

Foliar cations in both species on Etna show a similar trend in both *C.ruber* and *R.scutatus*. Both show increasing magnesium concentration over time; decreasing calcium and no trend (but considerable variation) in the potassium. Magnesium is increasing in the soil on the south chronosequence and this is reflected in the foliar content. However, in contrast while the soil calcium levels increase, the foliar content decreases. This could be due to increased competition for this element between species or the calcium could be in plant unavailable forms. Potassium shows no change in the soil – and a great deal of variation in the foliar samples. This may relate to general soil formation – humus production, nutrient cycling and weathering.

4.4.7. Summation

This work contributed to a larger study into the soils of Etna being led by Peter James at Liverpool University (James *et al* unpublished data). However the experimental planning and execution was conducted independently. All the soil data in this thesis was gained by the author alone and was later passed on to form part of the larger study. These data demonstrate that nitrogen is limited in the soils of the early primary succession on Etna. This coupled with the small size of the early soil matrix (as the initial samples were merely scrapings in rock hollows) will limit the ability of plants to colonise the flows.

Chapter 5: *Stereocaulon vesuvianum*: Biomass change over time, evidence for pedogenesis and distribution

5.1. Introduction

5.1.1 Main characteristics of lichens

Lichens are symbiotic organisms composed of a fungal partner (the mycobiont) and one or more photosynthetic partners, (the photobiont) that may be either a green algae or a cyanobacterium (Smith 1962; Smith and Douglas 1987; Hawksworth and Hill 1996; Nash 1996). Most species of mycobiont are ascomycetes, (in a few cases a basidiomycete or deuteromycete; Chen 2000) and do not occur in a non-lichenised state. In comparison, several photobiont members of the chlorophyta and cyanobacteria, can occur in a free-living form (Adamo and Violante 2000). The occurrence of lichens may date from the early Devonian, 400 million years ago (Taylor *et al* 1995). However, the sheer diversity of the lichenised fungi and the occurrence of many classes of fungi in the lichens has led to the assumption that the evolution of the lichen form has occurred several times (Nash 1996).

Lichens are the earliest colonisers of terrestrial habitats. This, coupled with their resilience in surviving extreme environmental conditions in both polar and tropical systems – especially the xerophytic conditions found on bare lavas, has resulted in them becoming an extremely successful group, covering an estimated 8% (Chen 2000) of the terrestrial surface on the Earth. In many polar and sub-polar ecosystems lichens are the dominant autotrophs, forming the basis of many food chains. For example, in the arctic tundra herds of caribou and reindeer graze on carpets of 'reindeer lichen' during times of the year when other foods are unavailable (Campbell 1993). This success has led to an estimated worldwide species total of around 17,000 (Hale 1974).

The lichen symbiosis involves a close physiological integration of the mycobiont and the photobiont. The dominant mycobiont is a heterotrophic organism that derives its carbon nutrition from the photobiont. This movement of carbohydrates as polyols in the case of green algal lichens and glucose in the case of cyanolichens has been well-established (Drew and Smith 1967; Hale 1974; Smith and Douglas 1987). Investigations have shown that radioactive ^{14}C which is taken up during photosynthesis by the algal cells, very quickly appears in the fungal hyphae (Richardson 1973). This is facilitated by fungal structures called haustoria, which surround and penetrate the photobiont. In addition, the photobiont cell walls are more permeable to carbohydrate loss in the lichenised than in the non-lichenised state (Nash 1996). This process is of great benefit to the mycobiont. However, no comparable flux of nutrients from the mycobiont to the photobiont has been proved (Nash 1996). It is suspected that the fungus serves as a reservoir for inorganic nutrients - as other fungi facilitate nutrient uptake in other symbiotic relationships such as mycorrhizae. In addition, the fungus enhances water uptake and retention due to its low water potential, as well as reducing light intensity on the photobiont and hence allowing growth in high light intensity environments where it would otherwise not survive. Therefore, as a result of symbiosis, both mycobiont and photobiont can expand into habitats where separately they would be rare or non-existent. For example, most algae or cyanobacteria require an aquatic or moist environment to survive – but as part of a lichen they can survive dry habitats as well (Nash 1996).

Lichens have long been used as bioindicators of pollution (both natural and man-made). Studies have shown that many volcanic products build up in the vegetative material and can be used to see where the volcanic products are concentrated (e.g. by prevailing wind). These include studies on volcanoes by Davies and Notcutt (1988); Nottcutt and Davies (1989); Barghigiani *et al* (1990); Grasso *et al* (1999); Loppi and Bonini (2000).

5.1.2. Lichen structure.

In all lichens, the two bionts form a heterogeneous structure called the thallus or lichenised stroma. This structure can be stratified into several distinct layers (see Fig 5.1). A cortical layer (absent from some species) is formed by closely meshed, heavily gelatinised hyphae firmly cemented together (Hale 1974) and always covers the upper-side of the thallus. The photobionts are usually restricted to a particular algal layer on the top of the medulla (the central section) which consists of loosely interwoven hyphae forming a cottony layer with a very large internal air space (Budel and Scheidegger 1996).

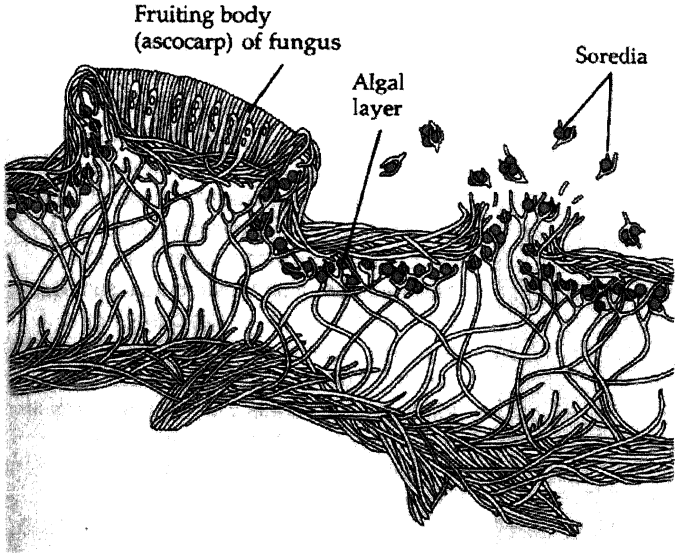


Figure 5.1. Typical lichen structure (from Campbell 1993).

The hyphal cell walls of the medullary and photobiont layers are often encrusted with crystalline secondary products. These crystals make the medullary hyphae hydrophobic which keeps the medullary and photobiotic layers air filled during wet periods, and hence optimum for air flow and photosynthesis. Water transport to the photobiont appears to be limited to the mycobiont cell walls (Budel and Scheidegger 1996). Typical foliose lichens like the Parmeliaceae have a well-developed lower cortex, but unlike the upper surface it is often strongly pigmented. The ability of this lower cortex to absorb water directly is well-documented (Budel and Scheidegger 1996).

Lichen reproduction is extremely complex given that there is a necessity for the fungal spores to meet the proper photosynthetic partner for establishment of symbiosis. The mycobiont symbiote can produce fungal spores from an ascocarp or fruiting body, which can vary greatly in size and structure between groups and species within that group. However, the photobiont reproduction mode is reduced in the lichenised state (Budel and Scheidegger 1996). As such, many fruticose lichens reproduce vegetatively by broken fragments reattaching to the substrate and growing into a new lichen. For instance sections of *Ramalina* species can be torn off and dispersed by strong winds. However the most important methods of vegetative reproduction are isidia and soredia. Isidia are scattered across the thallus surface and range from 30μm to 1 mm. Often cylindrical, these structures serve the dual purpose of reproductive propagules once detached from the surface and also help to increase the surface area of the thallus while still attached – increasing the photosynthetic area and enhancing interaction with the atmosphere (trace gas emission). The most well known method of vegetative reproduction is via soredia. These consist of a few photobiont cells enveloped by a loose spherical mantle of hyphae. Ranging from 20-50μm in diameter, soredia form by proliferation of the algal and medullary layers, often in specially delineated areas called soralia, (Budel and Scheidegger 1996). Once separated from the lichen body both isidia and soredia can form a new lichen.

These different methods of propagation allow lichens to spread very rapidly when a new primary substrate (e.g. lava flow) is produced. The high fecundity of the lichen *Stereocaulon vesuvianum* on Etna and *Stereocaulon vulcani* on Hawaii allows these species to colonise the newly produced lava surface almost as soon as it has cooled.

5.1.3. Lichens as nitrogen fixers

Although the dual nature of lichens is widely recognised, it is less commonly known that some lichens are symbioses involving three or more partners, from each of the three kingdoms of fungi, green algae and cyanobacteria. In this case, a secondary photobiont may form a second layer underneath the green algal layer (as in *Solorina*), or more usually it is restricted to minute to several millimeters wide structures called cephalodia which vary widely in morphology (from warty, glabose or shrubby) and are often characteristic of individual species (Budel and Scheidegger 1996). An example of this can be seen in *Stereocaulon ramulosum,* (Fig 5.2) which incorporates a *pseudochlorella* species as the green algal photobiont and a *scytonema* sp. of heterocystous cyanobacterium as a nitrogen fixer (Nash 1996).

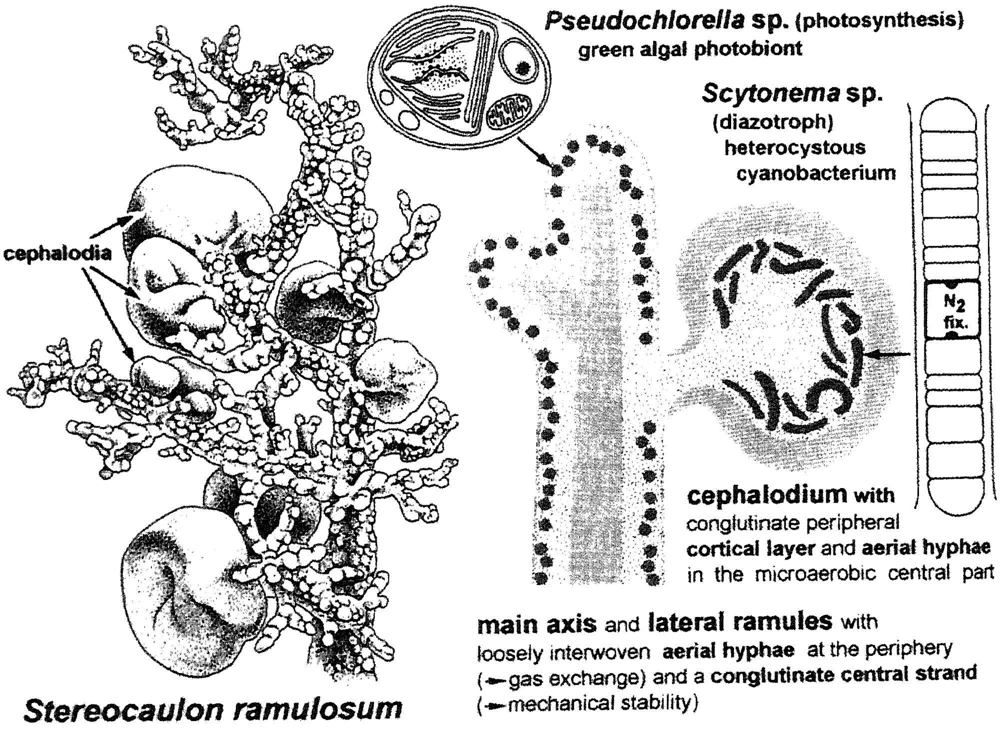


Figure 5.2. The tri-partate structure of *Stereocaulon ramulosum* (taken from Nash 1996) showing the cephalodium filled with nitrogen fixing bacteria

Nitrogen fixation can be an important input of nitrogen into the young lava flows ecosystems. This has been shown by Kurina and Vitousek (2001) who found that showed that *Stereocaulon vulcani* fixes between 0.2 and 0.45 kg N ha^{-1} yr^{-1} at an altitude of 1500m on Hawaii. Nitrogen fixation on the tropical volcano La Soufriere has also been shown by Fritz-Sherridan (1987); Fritz-Sherriden and Coxson (1988).

5.1.4. *Stereocaulon vesuvianum*

Stereocaulon vesuvianum Pers. is a fruticose lichen. It is a widespread, more or less boreal-montane, bipolar species, which occurs on different types of silicate rocks. It is common in upland areas of southern Europe, especially on the volcanic substrates of Etna and Vesuvius (Grillo 1988; Nimis 1993).

Figure 5.3. *Stereocaulon vesuvianum* Pers. Growing on clinker on the 1910 aa lava flow on Mt.Etna (picture by M.Carpenter).

One of the first colonisers of new lava substrate (in most cases it is *the* first), this species dominates the early stages of primary succession on Etna (Fig.5.3 where the lichen can be see to cover almost the entire surface of the rocks). It may very well be the lynchpin on which the later succession stages depend, as it allows the colonisation of pioneer vascular species by nutrient accumulation (Cooper and Rudolph 1953; Knops *et al* 1991 and Kurina 1998). In addition, its contribution to the organic content of the developing soil, as evidenced by the presence of lichen structures in the soil in samples from successional stages where it is absent on the rock surface (450+ years), may be of equal importance.

5.2. Methods

5.2.1. *S.vesuvianum* biomass change over time

S.vesuvianum biomass change over time was measured using a variation of the method developed by Kurina and Vitousek (1999). On each of the north, south and east aspects of the volcano a chronosequence of lava flows was selected. These consisted of a sequence of the 1947,1923, 1879, 1646 and 1566 lava flows in the north (Fig 2.3), the 1910, 1892, 1780, 1766, 1634, 1537 and 1444 lava flows in the south (Fig 2.4), and the 1992, 1971, 1928, 1865, 1792 1689 and 1651 were selected from the east aspect (Fig 2.5). No western chronosequence was possible due to the absence of a spread of suitable lavas at this altitude.

Figure 5.4. Sampling area for lichen biomass. A 3x4m quadrat laid out on the lava. Samples taken from 100cm^2 quadrats at 1m increments in a grid pattern to give a total of 20 samples (1947 north sample site, picture by M.Carpenter).

Each site was located at an altitude of *ca*1000m, using the same parameters of topography, distance from the edge of flow and lava morphology as outlined in 2.2.1. At each sampling site, an area was selected that was both open and flat for lichen biomass estimation. A measuring tape was laid out into a grid measuring 3m x 4m (Fig 5.4). At 1m intervals along the grid a 10x10cm ($100cm^2$) quadrat was positioned over the rock surface and all the lichen present within the quadrat was removed (Fig 5.5) and placed in a sealed bag until returned to the laboratory. The variable surface area of the lava presents a problem in this regard as a number of small lava blocks in the $100cm^2$ quadrat have a correspondingly large surface area for lichens, whereas few large blocks have a small surface area (Fig 5.6). This is difficult to control as a factor and so an optimum number of samples was determined (Fig 5.7).

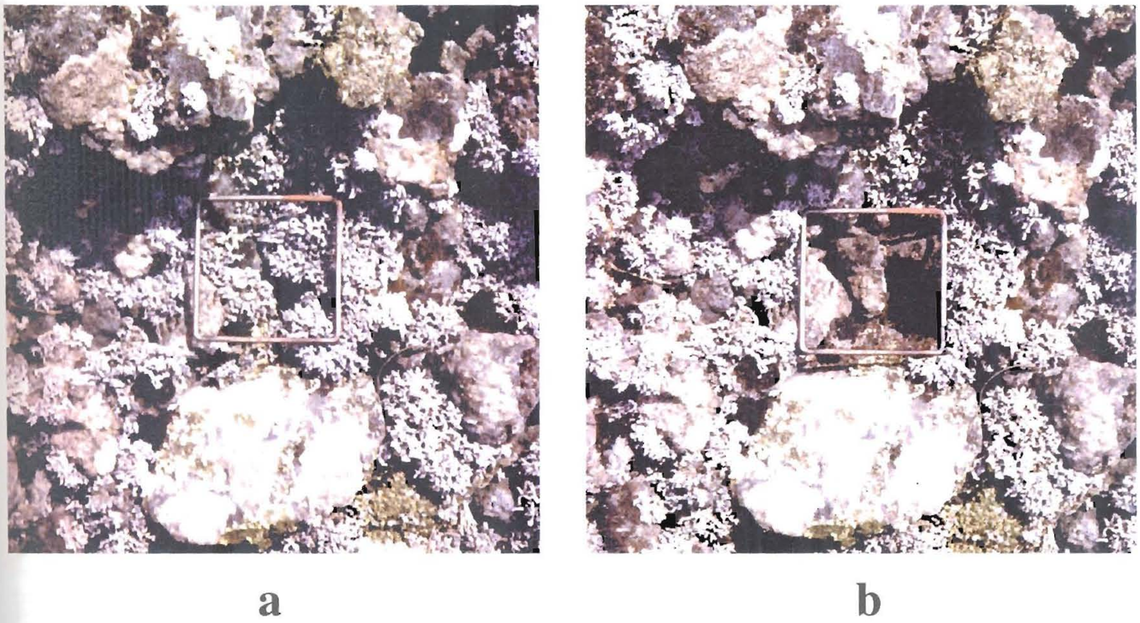


Figure 5.5. Samples of lichen biomass were removed from the rock from $100cm^2$ quadrats, as can be seen here. **a** is pre-sampling and **b** is sampled (pictures by M.Carpenter).

A total of 20 samples were taken per site. In those samples where the quadrat contained no lichen, this point was taken as a zero value. Once in the laboratory, the sample was carefully sorted by hand to remove all other plant species (e.g. mosses and other lichens) as well as particles of soil and other debris, which had accumulated around the base of the lichen thallus. After sorting, the lichen was placed in an oven at 70°C for three days to dry out completely and then weighed. Average biomass per site was then calculated by averaging the 20 samples and converting to g/m^2.

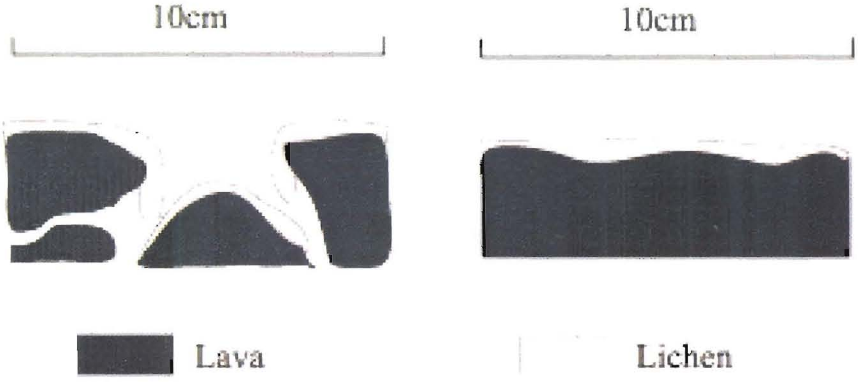


Figure 5.6. Changes in the lava surface area can cause great differences in lichen biomass, as cracks between the blocks allow the lichen to penetrate deeper.

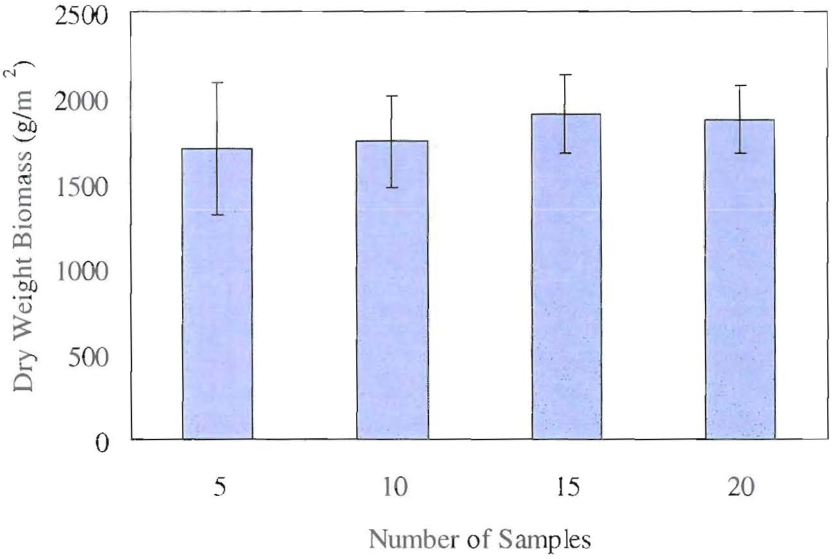


Figure 5.7. Average dry mass of lichen biomass with a cumulatively increasing sample size (1892 south lava flow). As sample size increases the average settles and the standard-error bars decline in size. From this a sample size of 20 was determined as most appropriate without using a prohibitively large number of samples.

5.2.2. *S.vesuvianum* biomass change with altitude

The method of sampling and analysis of samples is the same as that outlined in 5.2.1. Sites were selected on three lava flows on the south aspect of the volcano at 250m increments of altitude variation. These were the 1892, 1780 and 1634 flows (Fig 2.7). Altitudes measured were 1500m, 1250m, 1000m for all three lavas. Additional sites at 850m on the 1892 flow (the furthest extent of this flow) and 750m on the 1634 flow were also taken (the 1780 flow has been extensively modified by human activity below 1000m and hence not sampled). At each site 20 samples of $100cm^2$ quadrats were taken for analysis.

5.2.3. *S.vesuvianum* biomass variation with aspect

The method of sampling and analysis of samples is the same as that outlined in 5.2.1. Samples were taken from sites at an altitude of 1000m on all four aspects of the volcano on two chronologically similar lava flows (one site from a 17th and another from a 19th Century flow). These were the 1892 and 1634 lava flows on the south. The 1865 and 1689 on the east. The 1843 and 1651 on the west, and the 1879 and 1646 on the north aspect (Fig 2.6). At each site 20 samples of $100cm^2$ quadrats were taken for analysis.

5.2.4. Evidence of *S.vesuvianum* as a source of organic matter in pedogenesis

The role of *S.vesuvianum* as a component of soil development on the lava flows was investigated by scanning electron microscopy (SEM). Soil cores from 1566 north and 1536 south sites (where *S.vesuvianum* is extremely rare- and hence its presence in the soil is likely to be from a previous successional stage) were taken to the depth of the underlying bed-rock (approx. 10cm). These samples were dried in the oven at 70°C for three days to remove all moisture.

Once dry, small sub-samples of soil were then taken from the end of the cores (greatest depth). These were then mounted on an Aluminium stub, coated in a thin layer of gold and examined using an ISA-100A scanning electron microscope. These samples were compared to samples of living *S.vesuvianum* structures to look for any identifying structures. This method has to be by visual identification as a search for fungi would not work as mycorrhizae and other soil fungi would also be detected.

5.2.5. *S.vesuvianum* distribution and percentage cover on the rock surfaces

The factors affecting lichen distribution on the rock surfaces were estimated by measuring the percentage cover of *S.vesuvianum* present on the lava flows over a range of different aspects and slopes located on and around the largest lava blocks. This micro-scale approach allows study of minor variations in temperature, and light interception over very small areas on the lava flows. A series of 10-25 quadrats of $100cm^2$ were placed on aa chronosequencs of lavas at 1000m. Large boulders were selected to reduce the effects of competition from vascular plants and allow continuity in method for the later flows (smaller lava blocks are covered by soil/plants in later stages of succession). On the oldest sites rock outcrops were selected for analysis.

Topographical measurements for each quadrat (the aspect on the rock and the slope) were taken. In addition, measurements of relative humidity, light and temperature were also taken. These measurements allowed comparison in physical conditions between the quadrats – but not between sites, as variation in the time of sampling would vary enormously (e.g. comparing early morning and noon).

5.3. Results

5.3.1. *S.vesuvianum* biomass change over time

The *S.vesuvianum* biomass on the three chronosequences shows a consistent pattern of a skewed distribution on the south and north aspects of the volcano (Figs 5.8 and 5.9). In each case the biomass rapidly increased over time to a maximum level after approximately 100 years (of 1870 g/m^2 in the south and 1780g/m^2 in the north). After this point, there is a gradual decline in biomass until the lichen disappeared after about 500 years.

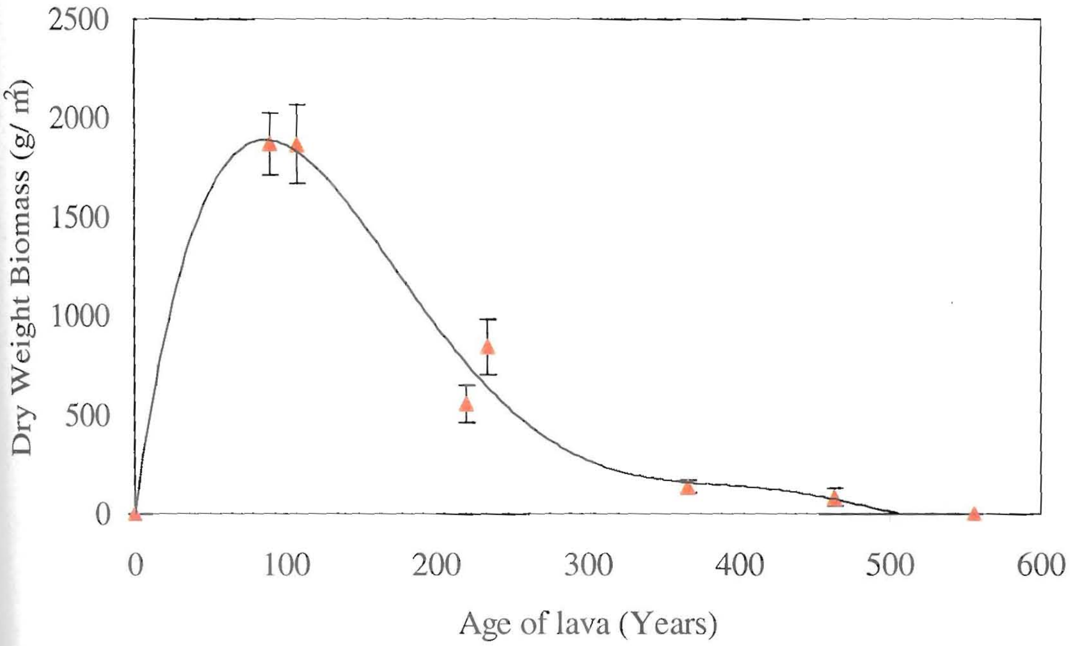


Figure 5.8. *S.vesuvianum* biomass on the south chronosequence of Mt.Etna. (n=20 +/-SE).

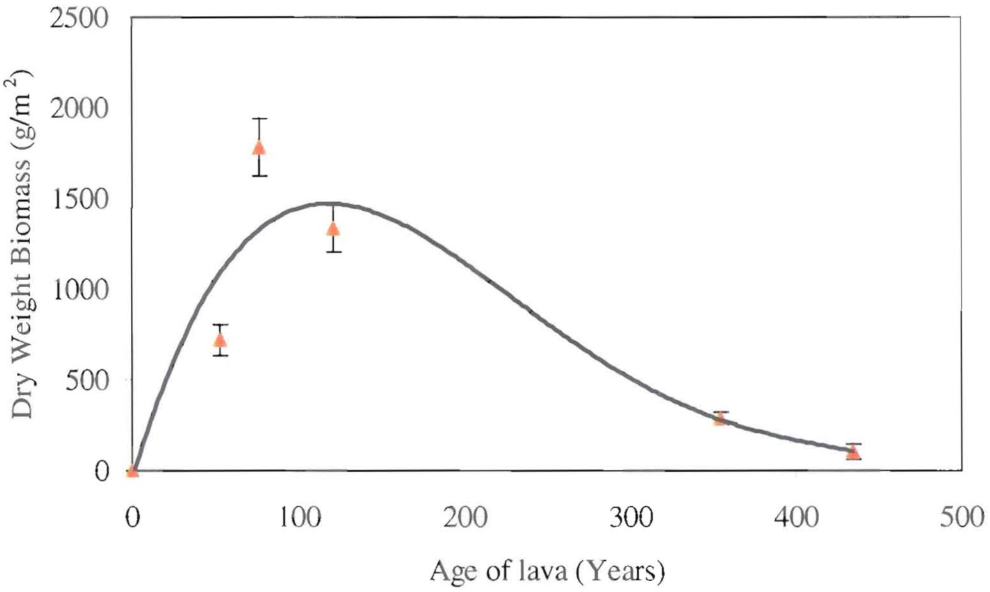


Figure 5.9. *S.vesuvianum* biomass on the north chronosequence of Mt.Etna. (n=20 +/-SE)

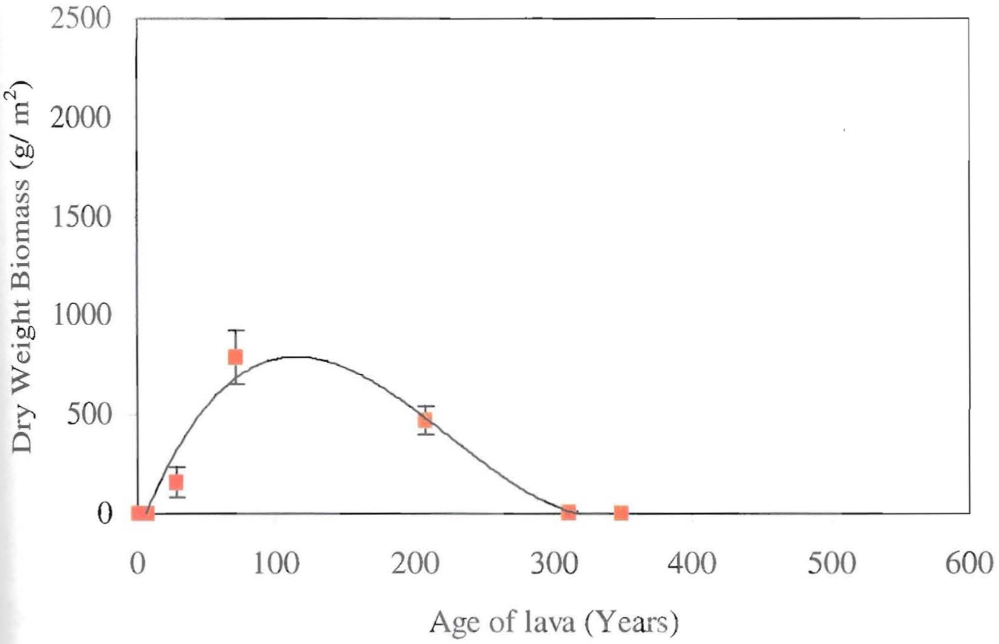


Figure 5.10. *S.vesuvianum* biomass on the east chronosequence of Mt.Etna. (n=20 +/-SE)

In contrast the third chronosequence on the east aspect of Mt.Etna (Fig 5.10) did not reach the high levels of biomass of the north and south aspects. This chronosequence showed a much lower maximum level of about 800g/m^2 on the 1928 lava flow. In addition, the lichen had completely disappeared from the sequence after only 300 years.

5.3.2. *S.vesuvianum* biomass change with altitude

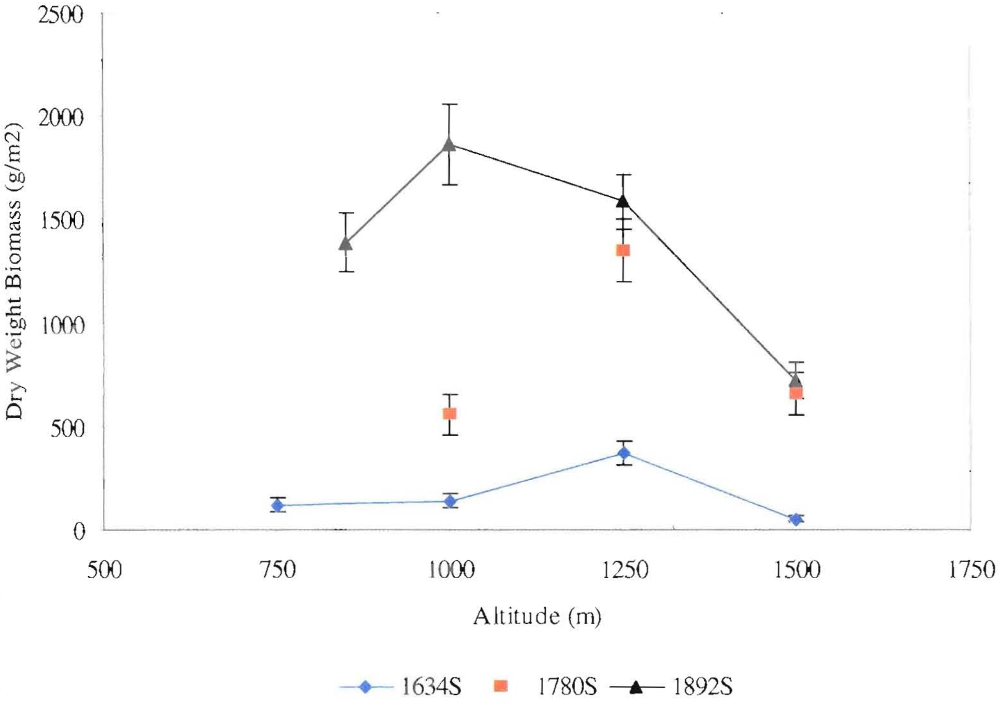


Figure 5.11. *S.vesuvianum* biomass change on three lava flows over increasing altitude. n=20 +/-SE.

S.vesuvianum biomass change with altitude varies with the age of the lava flow upon which it is growing (Fig 5.11). The youngest lava flow (1892) shows a peak of lichen abundance at 1000m (1870g/m^2) after which it declines steadily. However, the 1780 and 1634 flows both show a peak in biomass at 1250m (1350g/m^2 and 370g/m^2 respectively). These data, re-plotted into chronosequences at the three altitudes (Fig 5.12) show a peak biomass at 1000m at ≈100 years, which then declines rapidly. However the 1250m sequence has a peak at ≈150years and a much steadier decline. The 1500m sequence peak is also at ≈150years but is far lower than that found on either the 1000m or 1250m chronosequences.

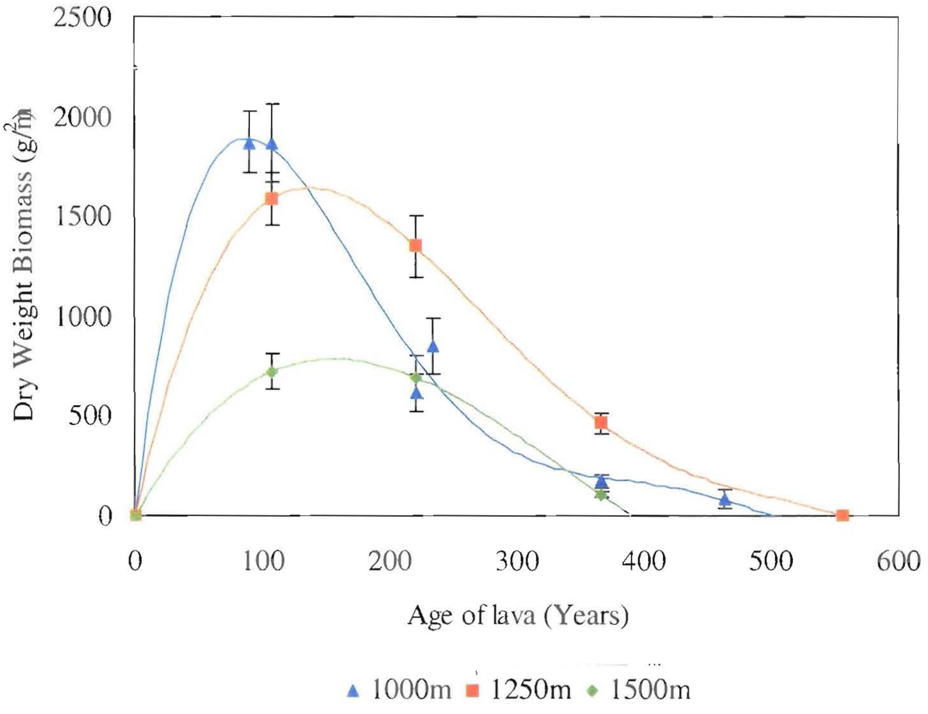


Figure 5.12. *S.vesuvianum* biomass on three chronosequences of lavas at three altitudes. 1000m (blue) 1250m (red) and 1500m (green). n=20 +/-SE.

5.3.3. *S.vesuvianum* biomass variation with aspect

Lichen biomass on each of the four aspects of Mt.Etna clearly shows a decline over time from the 19th century flows to the 17th century. For example the south aspect shows a decline from 1868g/m^2 to 138g/m^2 and the west from 993g/m^2 to 217g/m^2 confirming the results of the three chronosequences. However, there is considerable variation between samples taken from each of the four aspects around the volcano. By comparing all four together (Fig 5.13) it is clear that the east aspect does not favour lichen growth compared to the other three aspects. On the 19th century flows, where the south has a biomass of 1868 g/m^2 the east has 113g/m^2 (less than 10%) and there is almost no *S.vesuvianum* on the eastern 17th century flow (7g/m^2)

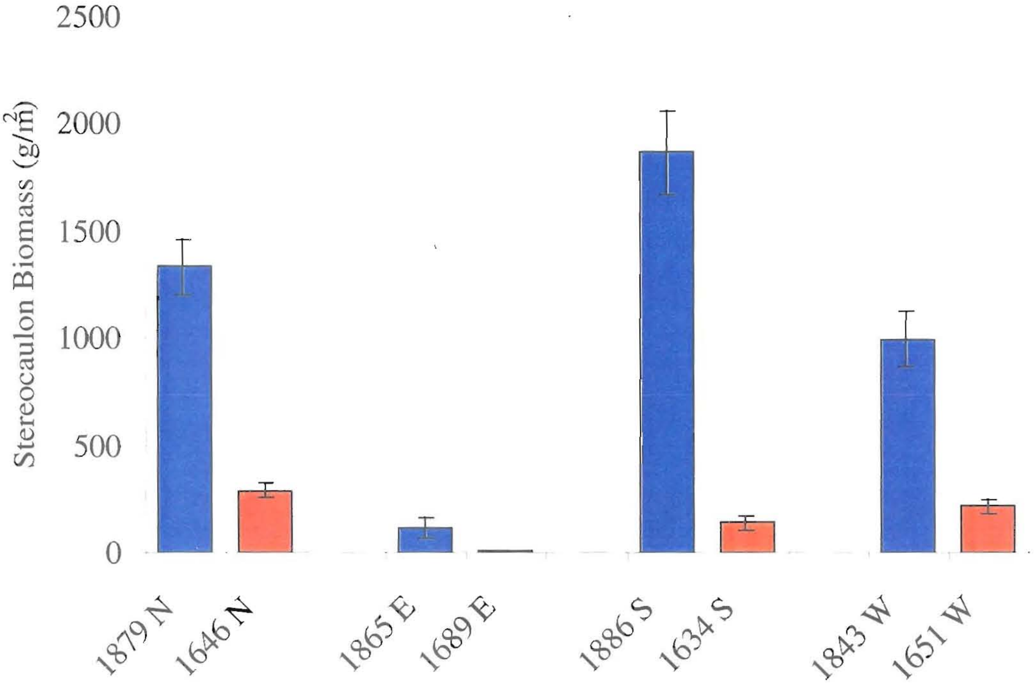


Figure 5.13. *S.vesuvianum* biomass on the two aged matched lava flows on each of the four aspects of Mt.Etna.

5.3.4. Evidence of *S.vesuvianum* as a source of organic matter in pedogenesis

Visual examination of the soil under the electron microscope shows a large number of degraded structures (Figs 5.14 and 5.15) clearly analogous to those of the living *S.vesuvianum* (Figs 5.16 - 5.18). This proves that this lichen is contributing to the biomass of the developing soil on Etnean lava flows. However, this material is impossible to quantify due to the degraded nature of the structures, as a consequence much of the unrecognisable material may also be lichen in origin.

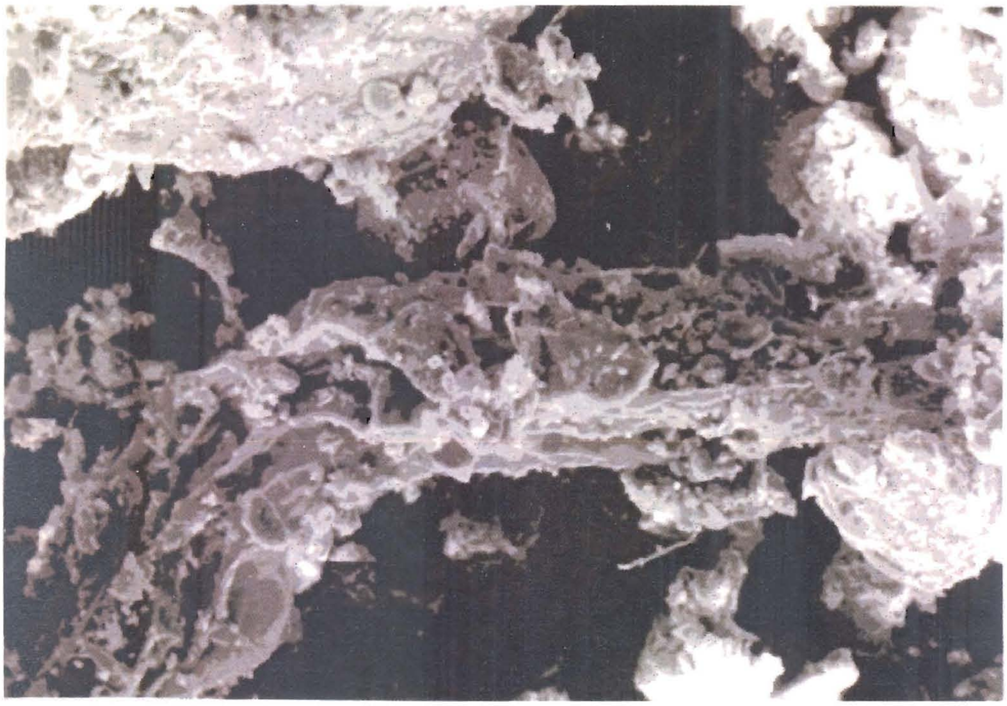


Figure 5.14. Lichen structure in the soil of the 1566 south lava flow. This long thin structure is typical of the hyphae of *S.vesuvianum*. (x500).

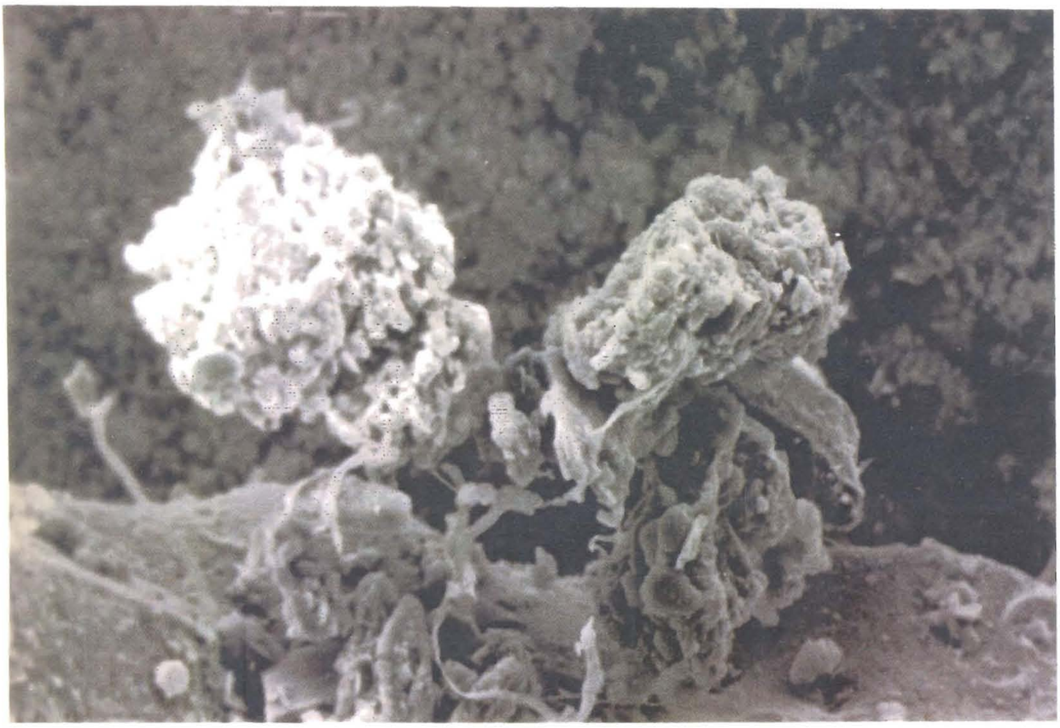


Figure 5.15. Lichen thallus fragment from the soil of the 1566 south lava flow. Clearly visible is a branching of the thallus, which has then been sheared off to display the lichen hyphae (on the left). The right side of the lichen is a mostly intact fruiting body. (x580).

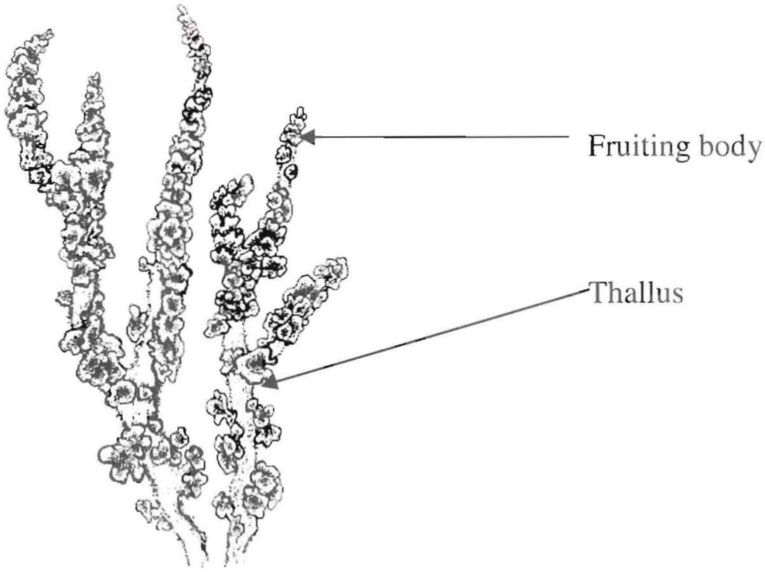


Figure 5.16. *S.vesuvianum.* This diagram displays the major morphology of the lichen with a central thallus and fruiting bodies. (Picture taken from the internet and adjusted by the author).

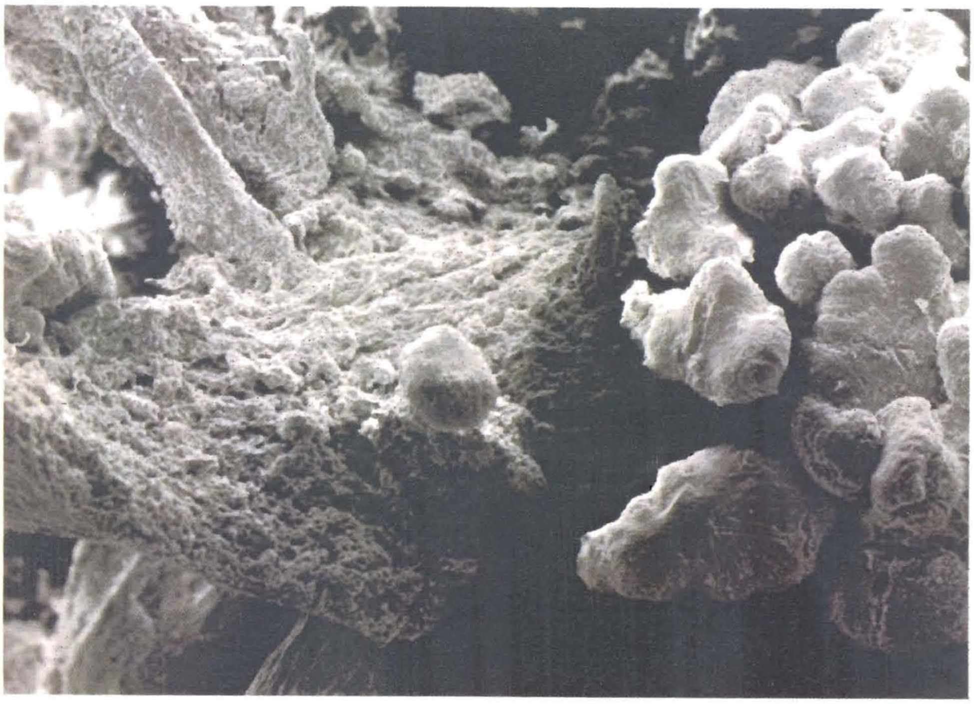


Figure 5.17. Intact living *S.vesuvianum*, showing the various structures, with the thallus in the middle, and the fruiting bodies on the right (x60)

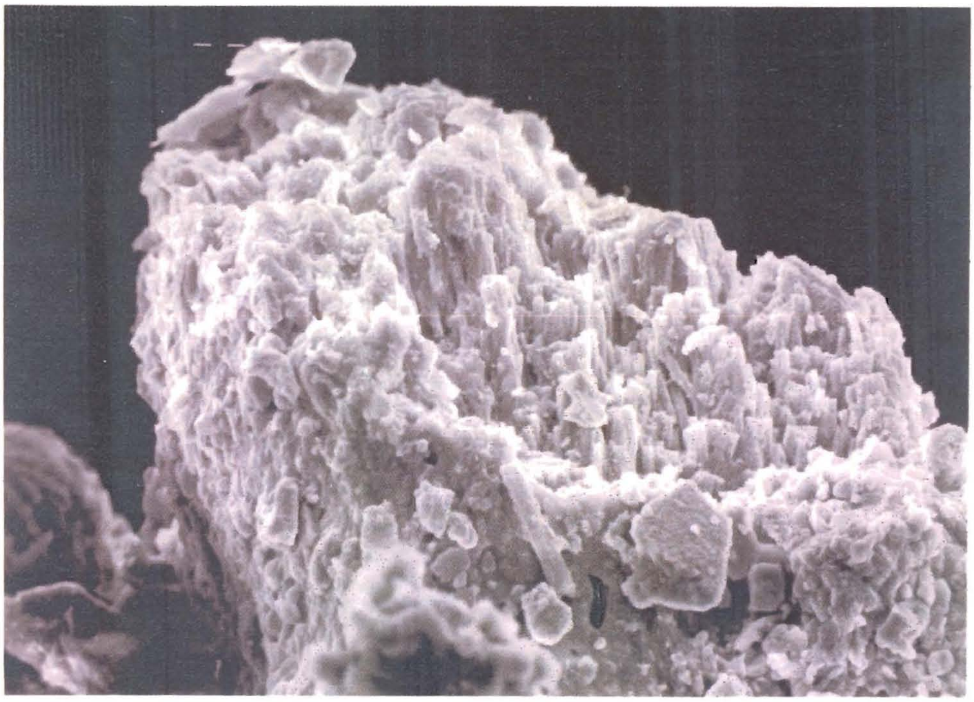


Figure 5.18. Broken off cross-section of the lichen thallus of a living *S.vesuvianum* (x650). This clearly shows the lichen hyphae within the thallus and is very similar to that found in Fig 5.14. in a soil sample.

5.3.5. *S.vesuvianum* distribution on different rock aspect surfaces

There is a significant variation in the surface distribution of lichens on different aspects of the lava surface. This is demonstrated in Table 5.1 which shows the distribution and percentage cover of *S.vesuvianum* on found within a $100cm^2$ quadrat on a range of aspects on boulders located on the 1981 lava flow. Clearly *S.vesuvianum* favours the north aspect of the rocks at this stage of the succession. For example its cover on a north aspect is 90% (quadrat 2) in contrast its cover on a south aspect is a negligible 5% (quadrat 3). The progressive growth of this lichen and interaction with other species can be seen in further tables of percentage cover in the appendix.

	Quadrat				
1981	1	2	3	4	5
Stereocaulon vesuvianum	65%	90%	5%	75%	7%
Temperature	19.9°	21.1°	23.9°	22.5°	22.2°
Relative humidity	22.7	23.7	19.2	23.3	21.5
Slope	35.0°	60.0°	50.0°	32.0°	47.0°
Aspect	N40°W	N75°W	S	N10°W	N120°W
Light	458	146.5	1285	342	1460

	Quadrat				
1981	6	7	8	9	10
Stereocaulon vesuvianum	5%	25%	70%	60%	10%
Temperature	24.3°	24.0°	22.5°	22.3°	23.4°
Relative humidity	19.3	21.3	23	22.3	23.2
Slope	34.0°	45.0°	33.0°	57.0°	85.0°
Aspect	S	N60°W	N10°E	N30°E	S15°E
Light	1358	846	137	105	1247

Table 5.1. Examples of how the percentage cover of *S.vesuvianum* in $100cm^2$ quadrats changes with aspect and other environmental conditions located on different large lava blocks on the 1981 south lava flow.

5.4 Discussion

5.4.1 *S.vesuvianum* biomass change

The lichen *S.vesuvianum* clearly shows a distinct pattern of biomass distribution on each of the three chronosequences on Etna (Figs 5.8 – 5.10). The lichen biomass increases to a maximum level (usually around 100 years) which then declines over time (almost certainly due to competition and shading from vascular plants arriving later in the succession). This is similar to the findings of Kurina and Vitousek (1999) who suggested that lichen decline is linked to shading by colonising vascular plants. However, on Etna, there is considerable variation between the three aspects of the volcano, with the north and south aspects producing a far larger biomass than the east. Several factors could explain this variation. The higher rainfall in the east (Fig 1.7 and 1.8) speeds up the colonisation of vascular plants, which then shade out the lichens at an earlier age of lava flow than in the north and south. This is coupled with large, regular deposits of tephra in the east, which occasionally cover the lichen, killing off those living in the cracks in the rock (which in-fill with this material). Such large tephra deposits like those seen in 2000 and 2001 on the east slopes of Etna, would severely curtail lichen growth, killing off the lichen on almost the entire lava surface and forcing re-colonisation. This new growth could never attain the biomass of that in undisturbed areas, as vascular plants are not as affected by tephra deposits and would continue to grow relatively normally (Kent *et al* 2001). Many such disturbance events have occurred in Etna's history. Finally, fine tephra deposits speeds soil-forming processes by increasing soil water holding capacity and providing a substrate for plant roots, this leads to faster vascular plant succession.

The effect of altitude on lichen biomass is not at first clear (Fig 5.11) until the data are formed into a separate chronosequence at the different altitudes (Fig

5.12). This factor is complicated by the fact that the lichen at a higher altitude, although following the same pattern of distribution over time, has a different maximal biomass due to the changing climatic conditions as altitude increases. Clearly the lichen colonises the lower slopes of the volcano and quickly accumulates a high biomass (maximum of ≈2000g/m^2 at ca1000m). In contrast at higher altitudes the lichen growth is slower and does not achieve the high biomass at lower levels (maximum of ≈400g/m^2 at ca1500m) – but it does however persist as the dominant species for a longer period of time. This shows a strong link between *S.vesuvianum* biomass and the prevalent climatic conditions of rainfall and temperature. This agrees with the findings of Kurina and Vitousek (1999) who found that rates of *Stereocaulon vulcani* colonisation and accumulation on Hawaii, were greatest at low elevation where conditions are warm and wet but that the lichens persisted longest in the colder, drier, higher elevation sites where vascular plant colonisation was inhibited.

It is also probable that pollution in the form of sulphides and fluorides from the volcanic vents is also retarding lichen growth at higher altitudes. The lower slopes receive fewer sulfides from the volcanic plume, this can be inferred as other pollutants like fluoride are more prevalent in lichens nearer the vents especially those located on the east aspect (Davies and Notcutt 1988; Notcutt and Davies, 1989) which is where the prevailing wind carries the products of the plume.

Since *S.vesuvianum* growth is tied to climatic conditions it is possible to speculate that further down-slope on the lava flows (<1000m) the lichen is also producing the same pattern of biomass distribution, but the maximum biomass probably declines again as the drier, hotter conditions do not favour lichen growth. Unfortunately, it is difficult to investigate this relationship below 1000m given that only a few lava flows have extended this far from the vents in the last 500 years and where these do occur (e.g. 1928 east) these flows have been extensively modified by quarrying, building, agriculture and other human activity. (which is why it was not possible to sample the 1780 lava flow lower than

1000m). These gaps in the data however do not stop us from seeing the general patterns of biomass change over time and extrapolating further.

5.4.2. Lichen biomass in the formation of a precursor soil

The measurement of the *S.vesuvianum* biomass on the younger (0-100 year old) lava flows of Etna shows that a huge quantity of organic material is being produced. This biomass formation is in a period when the other sources of organic material are few and also much more random in their distribution (e.g. spreading centres of organics around the few early vascular colonisers; wind blown aeolian material). It is therefore highly likely that this lichen forms a large proportion of the precursor soil on Etnean lava flows. The discovery of lichen structures deeply buried in the soil of older lavas supports this finding. The relatively high resistance of the lichen to decomposition would also be useful in the developing soil as lichens ability to retain water would probably likewise be retained for a long period.

5.4.3. *S.vesuvianum* distribution

There is clearly a link between surface morphology and the distribution of lichen on the lava surface (Table 5.1). Minor changes in surface structure lead to changes in the ambient environmental conditions and the formation of several microclimates within a relatively small area. Moreover, these microclimates shift during the course of the day, as the sun changes position and heats different areas of the rock as well as causing different areas to move into shade. This will clearly have an impact on lichen colonisation patterns as the longer the conditions are good the faster the lichens will grow – as opposed to the exposed drier harsher conditions where *S.vesuvianum* growth will be retarded. This leads to differences in the initial colonisation patterns and is amply demonstrated on the younger lava flows where the lichen covers one side of the rocks and simply by turning around to face the another direction the rocks appear to change colour due to the absence of the lichens. As the colonisation progresses over time the increasing lichen biomass itself provides shade and water allowing the colonisation to spread to all sides of the lava blocks until all are covered.

Chapter 6: *Stereocaulon vesuvianum*: weathering of the lava surface

6.1. Introduction

6.1.1. Weathering processes

Weathering processes can have a significant effect on the texture and morphology of rock surfaces over time. This can have severe implications for cryptogamic species living on the rock surface. In addition, the breakdown of the surface into smaller particles and the attendant mobilisation of elements locked in the rock structure, contributes to pedogenic processes occurring during primary succession. This weathering activity will occur in many different forms by the action of abiotic and biotic factors. Abiotic weathering occurs in the absence of direct or indirect effects of living organisms. This incorporates elements of geochemical (e.g. acidic effects of rainwater) and mechanical (e.g. erosion and frost/thaw cycles) weathering to break down the rock substrate into smaller particles and to release elements important for pedogenesis. In contrast, biotic weathering is by definition the weathering of the substrate in association with organic agencies. This particular study is to assess the impact of biotic weathering on the early stages of primary succession on Etna's basaltic lava. A comparison between abiotic and biotic weathering on Hawaiian lava will be shown later in chapter 8.

6.1.2. Biotic weathering

This is an extremely broad area encompassing the effects of animals, plants and microorganisms (Schwartzman and Volk 1989). Animal activity may include the physical break up of rock from burrowing animals or passage through the guts of worms or other species (Ollier 1984). For example, Shachak *et al*

(1987) showed that the grazing activity of two snail species feeding on endolithic lichens (lichens occurring under the rock surface) in the Negev desert had a major impact on weathering on the desert, of 0.7-1.1 metric tons per hectare per year. This is about the same as the amount of wind borne dust deposition in arid areas, which is widely recognised as a major physical factor in soil formation. However, the main contribution of animals to weathering is by mixing of the soil materials, thus bringing fresh material into exposure to weathering agents and increasing contact between mineral particles with air and water (Ollier 1984).

A far greater role in weathering processes is played by the vascular plants. This is a major process affecting global levels of CO_2 by accelerating the release of Ca^{2+} and Mg^{2+} which are then carried in solution to the oceans where they are precipitated out as carbonates (Berner 1997). The vascular plants affect weathering in a number of ways, both physically and chemically. Cracks may be widened by root pressure, breaking up the rock structure. In addition, larger plants create distinct microclimates at the ground level and affect soil gas composition by root respiration and as a route of gas exchange via the vascular system and stomata. Increased CO_2 in the soil from root respiration can be a significant feature in chemical weathering (Ollier 1984). Cochran and Berner (1996) found that the rate of weathering of Hawaiian basalts by plants was of an order of magnitude higher than that seen by cryptogams and microorganisms alone. They hypothesised that since the density of rhizospheric microflora is always higher around plant roots, that these associated fungi and bacteria would produce a number of organic acids (including chelating agents) which would promote chemical weathering. Decaying organic matter also produces organic acids and carbonic acid, providing additional acids for the breakdown of minerals (Moulton and Berner 1998). The addition of the decaying vegetative matter (humus) would increase the moisture holding capacity of the soil, in turn favouring the weathering process. Finally, transpiration in the plant would draw up solutions from the substrate through the plant and into the atmosphere. In doing so, it would draw out the water from the micropores in the substrate before those waters could become super-saturated with ions and silica from mineral dissolution. If this super-saturation occurred it would cause retardation of the chemical weathering (Cochran and Berner 1996). However, as rainfall constantly replenishes these solutions with fresh water, enriched on its passage through the soil with the chelating agents produced by the microflora, chemical weathering can proceed at a much faster rate. This is supported by the study of Gislason *et al* (1996) which found that fluxes of Mg, Ca and Sr increase with increasing vegetative cover. However, fluxes of Na and K decline (possibly due to their being retained by the plants).

6.1.3. Weathering by lichen activity

It has been accepted for some time that lichens weather the substrates upon which they grow – both organic and inorganic. This has been supported by many studies including: Jackson (1969); Jackson and Keller (1970); Syers and Iskandar (1973); Ascaso *et al* (1976); Jones and Wilson (1985); Cooks and Otto (1990); Adamo and Violante (1991); McCarroll and Viles (1995). The destructive effects of this weathering have been recognised on many of the oldest buildings and monuments. It has even resulted in the practice in some orchards in Europe of destroying lichen growth on fruit trees for fear of the damage they can do to the outer layers of the trees - cork, cortex, bast and cambium (Hale 1974).

However, when it comes to the activity of lichens on lava flows, a more beneficial effect can be observed. As has already been seen in chapter 5, a large biomass of lichens quickly colonises the newly formed lava surface. Once there, the ability of these lichens to weather the lava surface will ultimately contribute to the development of a precursor soil by introducing small fragments, biomass and freeing trace elements from within the lava for use by vascular plants. In the short term it will also alter the very surface of the rock allowing greater water retention and the formation of micro-sites where microorganisms, mosses and small vascular species can gain a foothold. The purpose of this study is to establish the weathering activities of lichens on the lava flows of Mt.Etna and hence gain an insight into their effect on the early stages of primary succession by observing and attempting to quantify the changes in surface texture.

6.1.4. Mechanical weathering by lichens

All lichens are firmly attached to the substrate by the hyphae in an intimate association, but this varies in structure and form between the three main groups of lichens. *Crustose* lichens are fixed to the substrate by the hyphae of the medulla. The thallus of *foliose* lichens adheres by bundles of tendentially parallel aligned hyphae called rhizomes or rhizoidal hyphae (Adamo and Violante 2000). In this group either the whole lower surface is in contact with the substrate or the margin of the lobes becomes free and bends upwards. *Fruticose* lichens, which are strap-shaped or threadlike in structure, are attached by the base to the substrate. The fruticose stalk is called the podetium or pseudopodetium when formed from the generative or vegetative primary thallus tissue, respectively. However, these differences in morphology do not necessarily imply differences in weathering ability, which are more likely to be due to physiological differences among species, e.g. greater water holding capacity (Adamo and Violante 2000).

The close and intimate association of the lichen lower cortex and the underlying substrate, suggests that the physical weathering abilities of the lichen thallus is essentially due to the actions of the mycobiont (Wilson and Jones 1983). This is demonstrable as the phycobiont algal cells are usually found in the sections of the lichen furthest from the substrate. The lichen exerts its mechanical action on the substrate in two ways; by rhizome and rhizoid penetration, exploration and adhesion or more generally fungal penetration and thallus expansion and contraction. This expansion and contraction is usually brought about by wetting / drying of the thallus. The lichen medulla is well known for its water holding qualities and is capable of holding up to 300% of the dry weight in moisture, when water is available (Chen *et al* 2000). With the ability to produce such an appreciable change in mass (and hence volume) it is unsurprising that where alternate wetting / drying is frequent, considerable physical weathering of the substrate rocks can take place in a relatively short period of time (Chen *et al* 2000). This is demonstrated further by observations of rock fragments embedded in the underlying surface of a lichen which has been subjected to repeated drying / wetting (Moses and Smith 1993), in such cases the fragments have been literally torn from the substrate surface.

So regardless of morphology, the lichen thallus exerts a mechanical action on the rock, producing extensive dis-aggregation and fragmentation of the lithic surface immediately below the lichen. The extent of the disintegration will be a result of both the physico-chemical properties of the rock (compactness, hardness, lamination or pre-existing surface alteration) and the nature of the lichen thallus (Adamo and Violante 2000). For example, the presence of many vesicles and less coherent areas allows easier penetration of the lichen, *S.vesuvianum*, into the lava substrate. As such its pseudopodetium has been observed to penetrate down to 30mm into the rock (Adamo *et al* 1997).

6.1.5. Chemical weathering by lichens

Lichens produce many organic compounds formed by the fungal symbiote. These have many functions including: toxins and antibiotic compounds (e.g. phenolics), metal-chelating compounds (e.g. organic acids like oxalic acid), coloured pigments (for light protection), dark pigments (to increase heat absorption) and hydrophobic compounds to prevent water loss (Nash 1996). It is partly the production of oxalic acids and their subsequent actions in substrate weathering which is the focus of this study.

The chemical decomposition of rocks almost certainly proceeds hand in hand with the physical disintegration. Mechanical fragmentation increases the surface area of the mineral or rock upon which chemical action can occur (Adamo and Violante 2000). One of the first studies to provide direct evidence of the role of lichen acids in rock weathering was that of Ascaso *et al* (1976) working on the pedogenic effects of three lichen species on granite, gneiss and various primary rock forming minerals. Using techniques such as transmission electron microscopy and spectrophotometric chemical analysis they identified several key features of lichenised rock; 1) the mineralogy of the rock at the interface varied from that found in fresh rock, 2) that pure lichen acids incubated with various types of feldspars and mica to form metal complexes and 3) that lichen fragments incubated with these minerals to form similar metal complexes and underwent mineral alteration.

Syers and Iskander (1973) suggested that the main chemical processes by which lichens solubilise minerals are: (1) the production of respiratory CO_2, (2) the excretion of oxalic acid, and (3) the production of biochemical compounds with complexing ability. The dissolution of respiratory CO_2 in water held by lichen thalli results in the generation of carbonic acid, which advances solubilisation processes by lowering the local pH values of the thallus and the related microenvironment (Chen *et al* 2000).

6.1.6. Lichen weathering of basaltic lava

Brady *et al* (1999) found that weathering intensity under the lichen *Stereocaulon vulcani* on the basalt lava of Hawaii is routinely 2-18 times greater than that found under abiotic conditions. This agrees broadly with the findings of Jackson and Keller (1970) on lichen covered Hawaiian basalts who estimated weathering was enhanced by 12-72 times, and McCarroll and Viles (1995) on lichen covered gabbros on the foreland of Storbreen (southern Norway). On the Hawaiian basalts, three major factors controlling weathering have been discovered (Brady *et al* 1999): 1) both plagioclase and olivine (important constituents of basalt lava) weather faster when lichens are present and become increasingly porous, 2) weathering increases with rainfall and 3) weathering increases with temperature. However, *S.vulcani* has a greater effect than rainfall, which in turn is more important than temperature.

S.vesuvianum which grows commonly on lava flows of Mt.Etna and Mt.Vesuvius (Nimis 1993), has also been proved to weather the rocks of Mt.Vesuvius (Adamo and Violante, 1991) resulting in the formation of iron oxides in the lichen / rock interface (Adamo *et al* 1997). In addition, Stretch and Viles (2002) observed *S.vesuvianum* growing on basaltic lava in Lanzarote where they estimated that the weathering rate was 16 times that of bare surfaces by comparing the thickness of the weathering rinds. This study looks at the weathering effects of S.vesuvianum on the recent (0-500yr old) lavas of Mt.Etna.

6.1.7. Etna lava petrographic texture

The lava flows of Mt.Etna are porphyritic in texture. Basaltic lavas of the alkalic series contain three main phenocryst minerals; plagioclase ($NaAlSi_3O_8$-$CaAl_2Si_2O_8$), clinopyroxenes, variety augite, ($(CaMgFe)_2Si_2O_6$) and olivine ($(MgFe)_2SiO_4$) see Fig 6.1. The proportion of these three phenocrysts in the lavas varies across the alkalic series, giving rise to the different classifications of alkalic lavas (Fig 6.2). Most of the recent lava flows on Mt.Etna are Hawaiites (Chester *et al* 1985). The fact that the recent lava flows of Etna are so consistent in composition, is very important for this study, as variation in the initial substrate elemental chemistry can impact on the rate of weathering.

As the lichen weathers the rock surface those elements which are easily released are quickly depleted leaving the tougher minerals intact. As a result this uneven weathering produces a ‘lattice’ of tougher material which can be readily broken apart at weak points into flakes of rock by the mechanical activity of the lichens. This is aided by the vesicular nature of the lava, which is filled, with small air bubbles (vesicles) formed during the cooling process. In so doing, in the most rapid phases of weathering a clearly defined ‘weathering rind’ (a band on the outer layer of the rock which is visibly different from the inside) develops. This rind is formed partly of the lichen weathered material and partly by the oxidation of minerals near the surface.

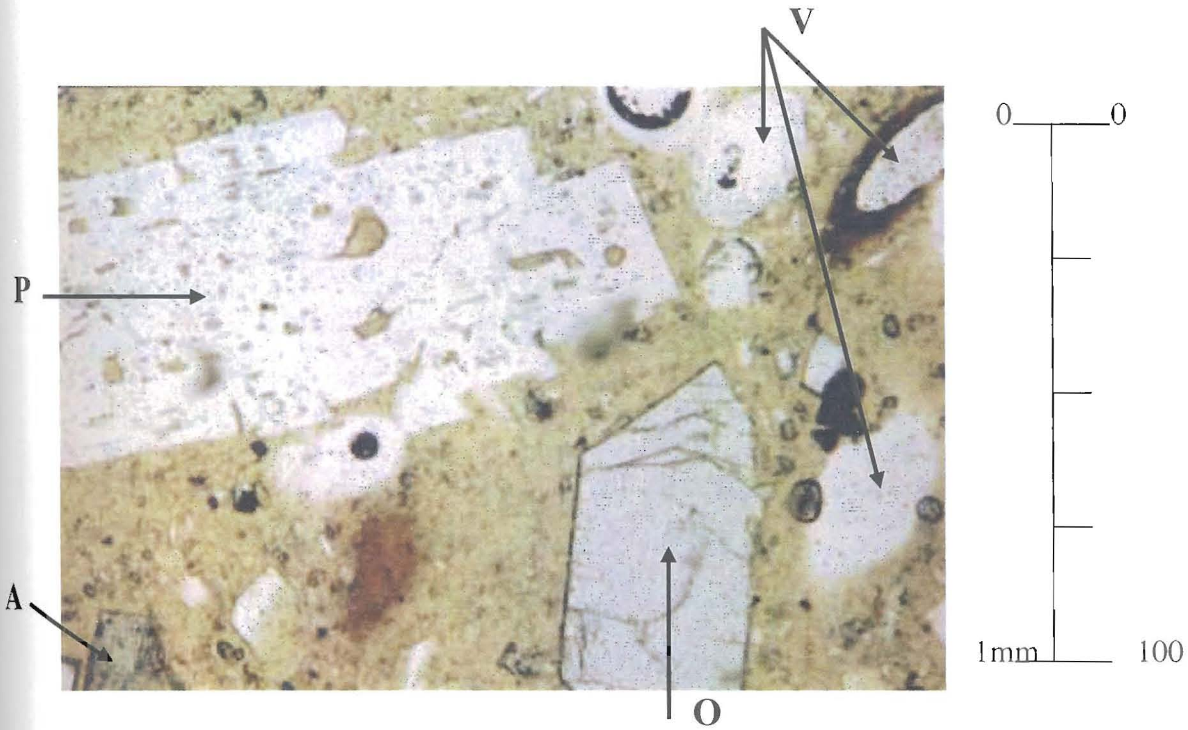


Figure 6.1. Thin section of rapidly cooled Hawaiite lava (1983) showing the three different forms of Phenocryst: plagioclase (P), augite (A) and olivine (O). Vesicles (V) or gas bubbles in the lava are also visible. (Picture by M.Carpenter)

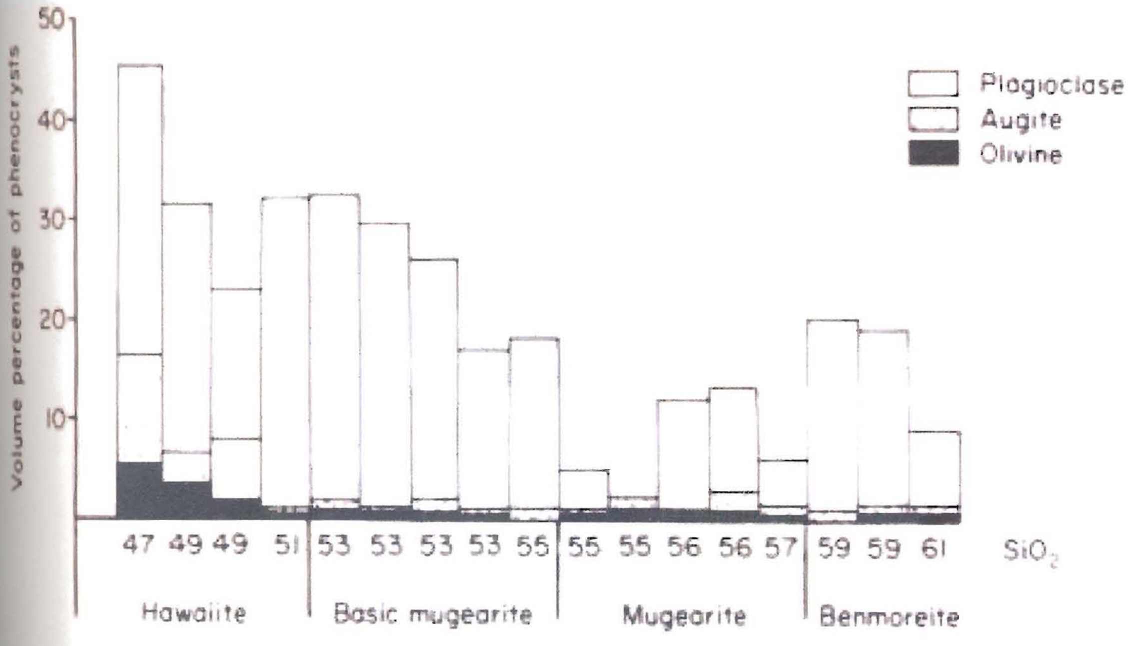


Figure 6.2. Modal analyses of phenocryst content of lavas of the alkalic series from Adrano area (Chester *et al* 1985).

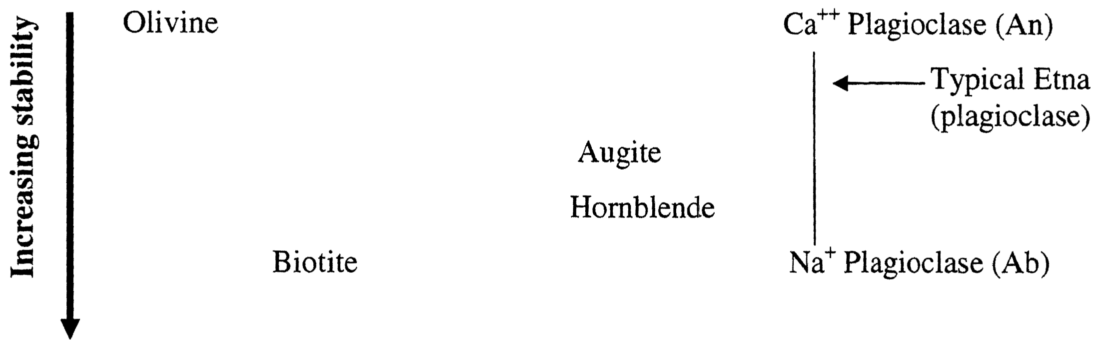


Figure 6.3. Weathering sequence for the common rock forming minerals (Gerrard 1988). Plagioclase feldspars show a continuous compositional range from Anthorite (An) to Albite (Ab).

The relative mobilities of common elements in order of decreasing mobility are :

Ca, Mg, Na, K, Fe, Si, Ti, Al

Augite breaks down to clay minerals with 'etch' pits developing along pre-existing cleavages rather than a general surface attack. Of all the minerals, quartz is the hardest to weather but it is broken down most rapidly in the presence of organic acids. However, quartz is not present in basaltic lavas. Olivine often possesses many irregular cracks and is one of the first minerals to weather (Gerrard 1988).

6.1.8. Weathering and Primary succession

The importance of cryptogam weathering was summed up in four statements by Walton (1993):

1) Biophysical attack at and just below the rock surface, and biochemical attack of particles incorporated within a lichen or algal thallus comminutes the parent

rock to provide an increased surface area for further disintegration by environmental processes.

2) Penetration by rhizines, hyphae and rhizomes almost certainly assists in micro-fracturing of the rock, expanding access channels for other organisms (bacteria, fungi and algae) to colonise and provide increased protective niches.
3) Biogeochemical weathering both releases biologically useful trace elements from the rock which, when leached, are available in other parts of the ecosystem and provides new secondary mineral substrates for attack.
4) Lichens, mosses and algae establishing on rock surfaces or on unstable soil act as foci for the development of more complex miniature ecosystems.

Following on from these four points, observing and quantifying weathering processes over a chronosequence of lava flows is essential in assessing the impact of these early cryptogams in the first stages of primary succession. The contributions of this weathering to the developing soil and the introduction of trace elements to the developing ecosystem could be essential to the future stages of colonisation.

6.1.9. Aims and objectives of the study

To this end three methods were employed to observe the changes occurring on the surface and just under the surface:

1) Visual observation of the changing surface morphology of the lava by scanning electron microscopy.
2) Petrographic analysis of thin sections to observe the interface between the lichen / rock boundary and determine the extent of lichen penetration and the physical and mineralogical changes occurring over time (alteration in the phenocryst structures).
3) An attempt to quantify the rate of lichen weathering of the lava using intelligent machine vision sensing (this will be discussed in full in the results section as it is a method for interpreting the SEM pictures).

6.2. Method

6.2.1. Sample collection

A minimum of four samples of lichen encrusted lava were taken from sites along three chronosequences and on the four aspects at two age groups (19th century and 17th century) on Mt.Etna. These samples were taken from the lava flows erupted in the following years:

East chronosequence: 1992, 1971, 1928, 1865, 1792, 1689.
North chronosequence: 1981, 1947, 1923, 1879, 1809, 1646, 1614, 1566, 1536.
South chronosequence: 1983, 1910, 1892, 1780, 1634, 1537.
Aspects: 1865 & 1689 East; 1879 & 1646 North; 1892 & 1634 South; 1843 & 1651 West.

These samples were taken from the same sites, using the same selection criteria as shown in section 2.2.1. Map grid references to the location of these sites can be seen in the appendix.

Each lava sample was taken as a sub-sample from a much larger rock or boulder (by geological hammer), to reduce the possibility that the rock may have been disturbed / turned over during the time elapsed since the lava cooled, altering the surface being weathered. Each boulder was located in an open flat area to maximise optimum growth conditions of the lichens, minimise the effects of other weathering processes (e.g. surface runoff) and also minimise variation in conditions between sites. Areas of recent tephra fall were also avoided. A control (year 0), unweathered specimen was obtained from a freshly cooled 1999 lava for comparison.

6.2.2. Observations of weathering by Scanning Electron Microscopy

The samples were removed to the laboratory where each was broken up into smaller samples of approximately 1 cm^3 and the lichen carefully removed by hand, taking care not to damage the underlying surface. Each sample was mounted on an Aluminium stub, coated in a thin layer of gold and examined under an ISA-100A Scanning Electron Microscope (SEM). This follows the methods of Viles (1987); Adamo and Violante (1991) and Jones *et al* (1981). A minimum of 15 black and white photographs were taken of each sample at a magnification of x200. These pictures were then compared and the key differences / similarities between the year groups noted by direct observation.

6.2.3. Observations of lichen penetration of lava by petrographic analysis

Thin sections of a from the north Mt.Etna chronosequence of three lava flows (1981, 1879, 1646) were cut taking care not to remove the lichen from the rock surface. In addition, a section of unweathered 1999 rock was sectioned for comparison. These thin-sections were examined under a petrological microscope and compared to observe how the lichen attached to the rock, how far the lichen rhizome had penetrated and interactions between the lichen and the rock interface. In addition, observations of physical changes in the phenocryst minerals (olivine, plagioclase and pyroxene) were made to see how they weathered over time. These were then photographed in thin section.

6.3 Results

6.3.1. Direct observation of the lichen weathered surface

Direct observation of the lava surface directly under the lichen structure revealed varying degrees of weathering. This can be demonstrated by looking at the eastern chronosequence shown in Figs 6.4.a and 6.4.b. This shows a range of representative lavas taken from the eastern aspect of Mt.Etna at an altitude of 1000m. There is a clear progression from a smooth / glassy surface in the earliest flows of 1999 and 1992 (Fig 6.4.a. **a** and 6.4.a.**b** respectively), to an increasingly etched, pitted and roughened surface 1983 and 1892 (Fig 6.4.a. **c** and **d**). This weathering continues with the formation of large hollows and extensive disintegration of the rock surface (Fig 6.4.b **f** and **g**). This same pattern of lichen weathering is also clearly shown on the northern (Fig 6.5) and southern (Fig 6.6) chronosequences. However, on these last two chronosequences a final phase of rock weathering can be seen, as the rock surface begins to crack and break up into small flakes. This forms an 'aggregate' like structure formed of broken up particles (descriptive terms based on Heiken and Wohletz 1985).

From the three chronosequences it is also clear that the rate of weathering around the volcano is not constant but varies considerably with aspect. The east chronosequence initially shows the most rapid weathering. In contrast, the north and south chronosequences are initially slower to weather. This can be by comparing samples from each of the four aspects of Etna (Figs 6.7 and 6.8, which include the two western sites). The east 19th century sample shows the most extensive disintegration of the lava surface in comparison with the other aspects (Fig 6.7). However, on the 17th century flows it is more difficult to discern differences between weathering rates as there is greater surface heterogeneity between the samples (the four shown in Fig 6.8 are representative only).

In order to quantify the weathering activity between these later stage samples a new method was conceived using a computer intelligent machine vision system (Clark 2003), the method for this analysis is described in 6.3.5.

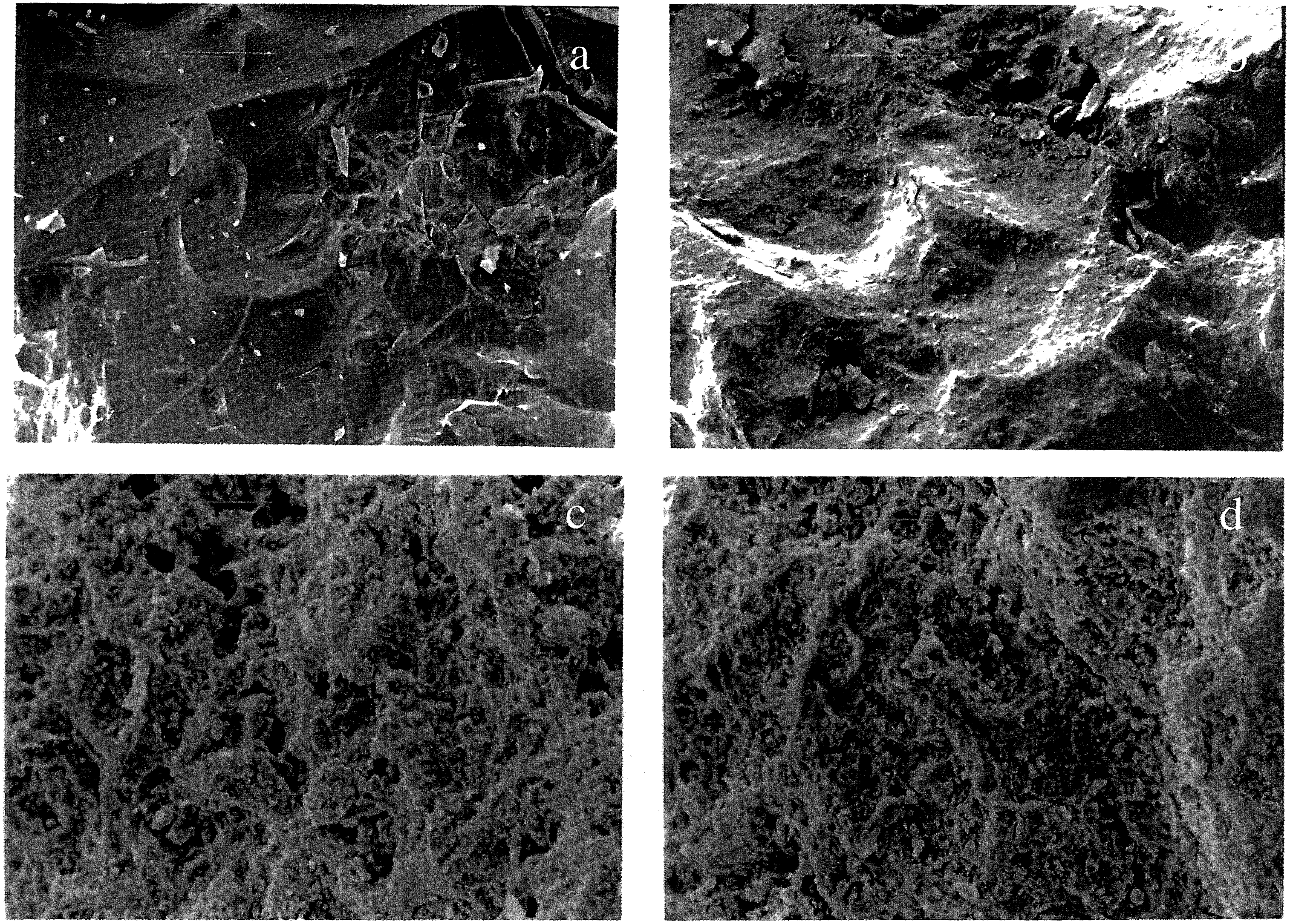


Figure 6.4.a. SEM pictures of lichen weathering along the eastern chronosequence of Mt.Etna. Where **a** is the unweathered 1999 flow (0 years old), **b** is 1992 flow (8 years old); **c** is 1971 flow (29 years old); **d** is 1928 flow (72 years old). Magnification x200

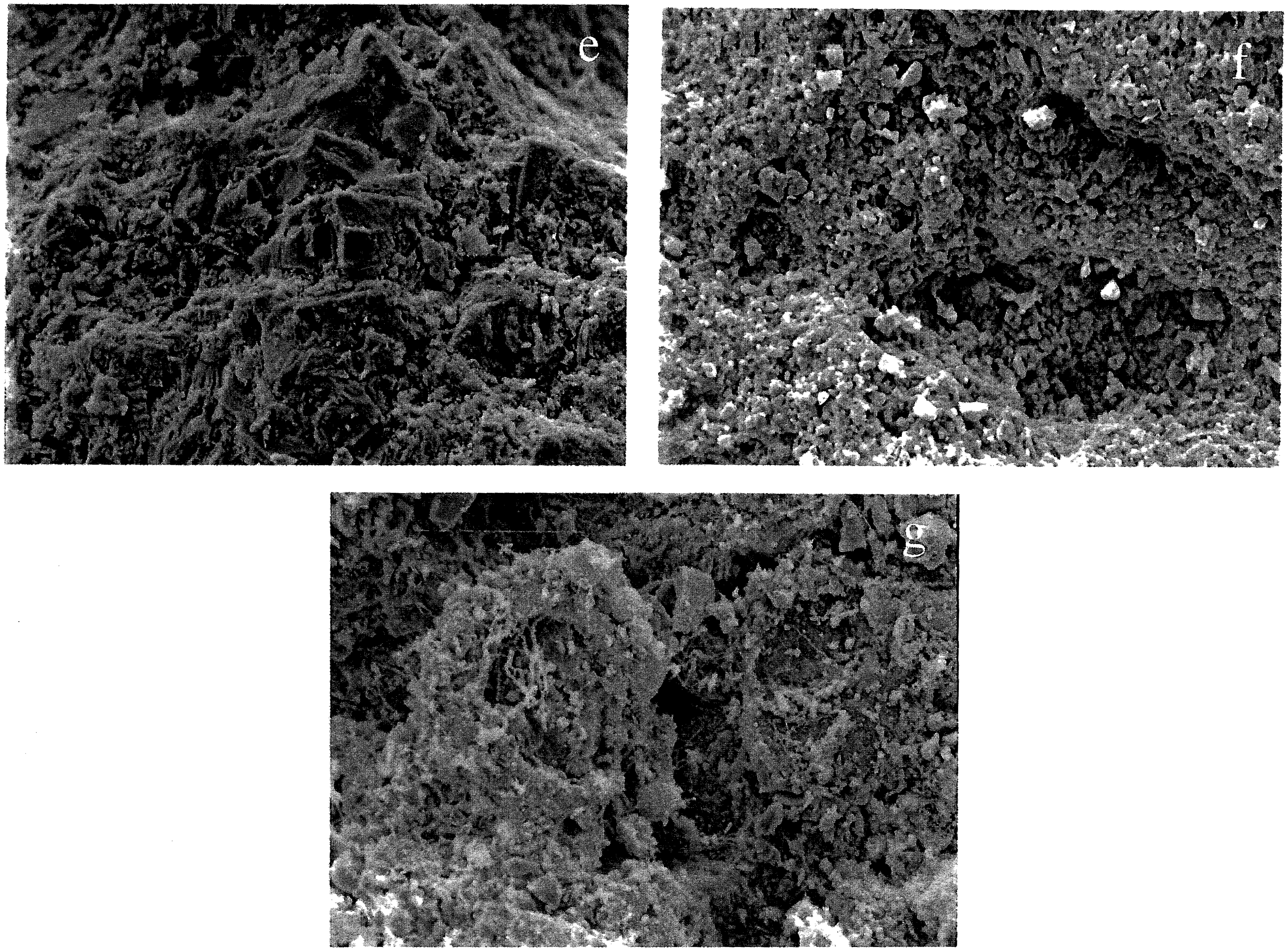


Figure 6.4.b Continuation of Lichen weathering along the eastern chronosequence of Mt.Etna. Where **e** is the 1865 flow (135 years old), **f** is 1792 flow (208 years old); **g** is 1689 flow (311 years old);. Magnification x200

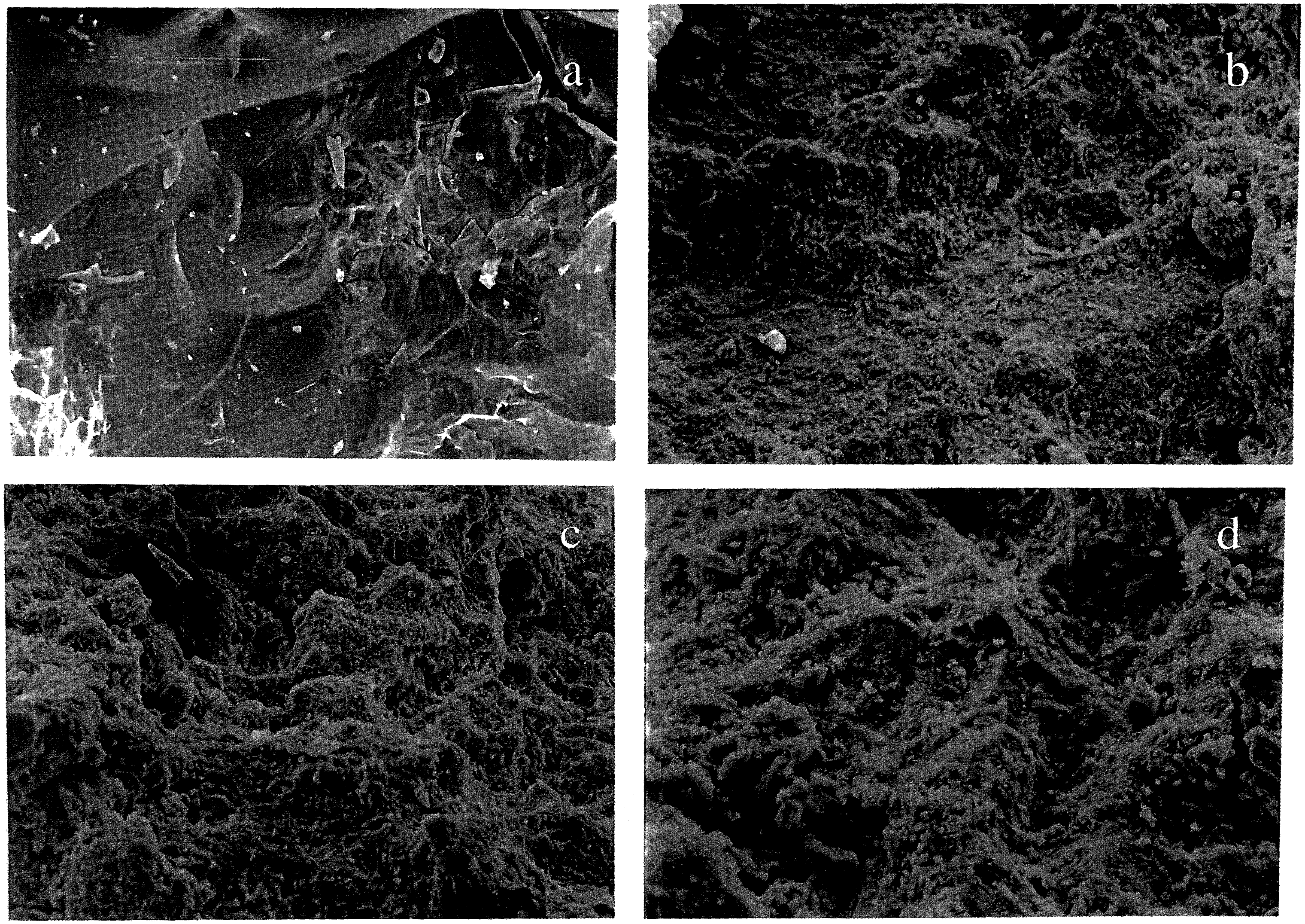


Figure 6.5.a. SEM pictures of lichen weathering along the northern chronosequence of Mt.Etna. Where **a** is the unweathered 1999 flow (0 years old), **b** is 1981 flow (18 years old); **c** is 1947 flow (52 years old) **d** is 1923 flow (76 years old). Magnification x200

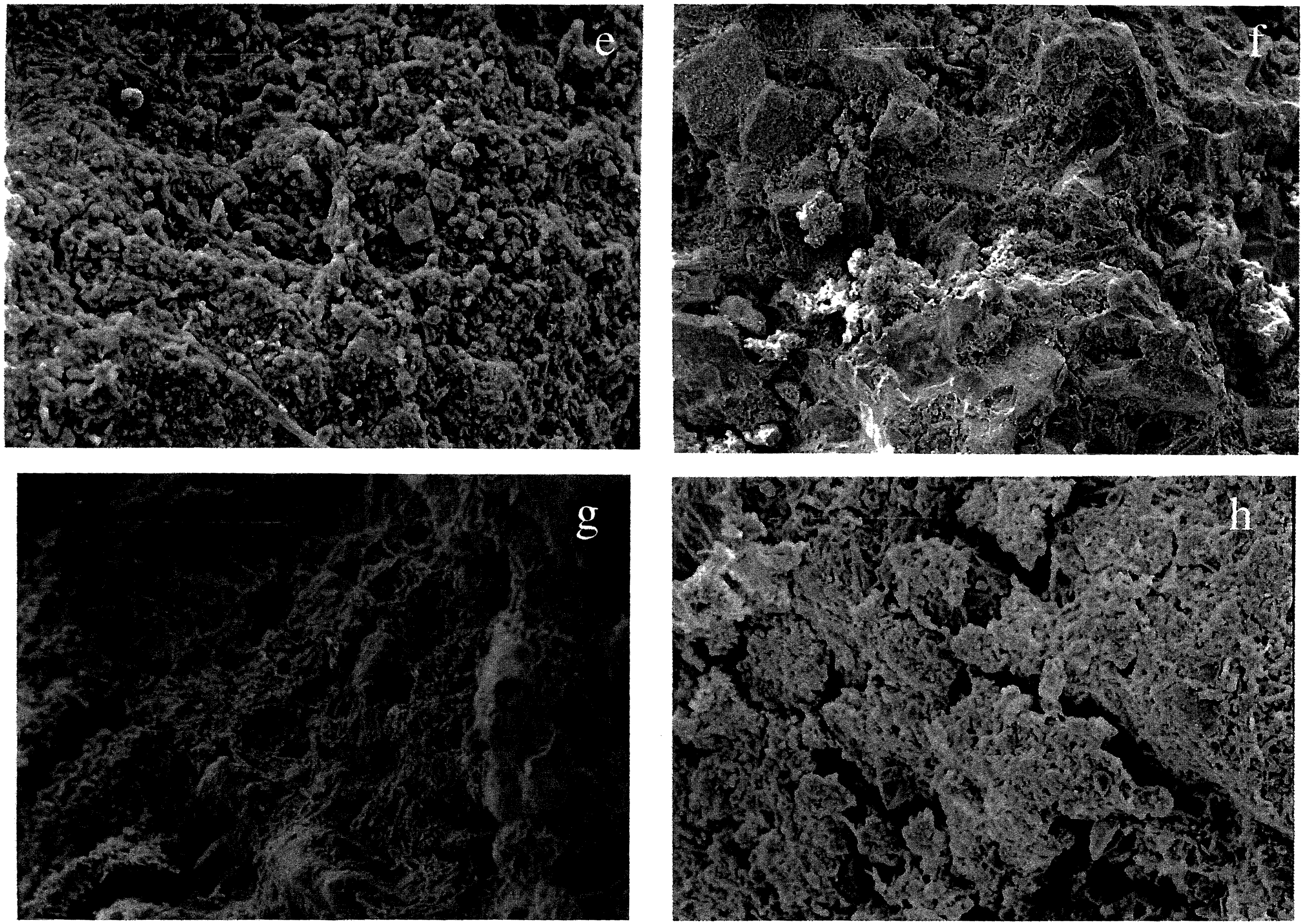


Figure 6.5.b Continuation of Lichen weathering along the northern chronosequence of Mt.Etna. Where **e** is the 1879 flow (120 years old), **f** is 1809 flow (190 years old); **g** is 1646 flow (353 years old);. **h** is 1614-24 (386-376 years old). Magnification x200

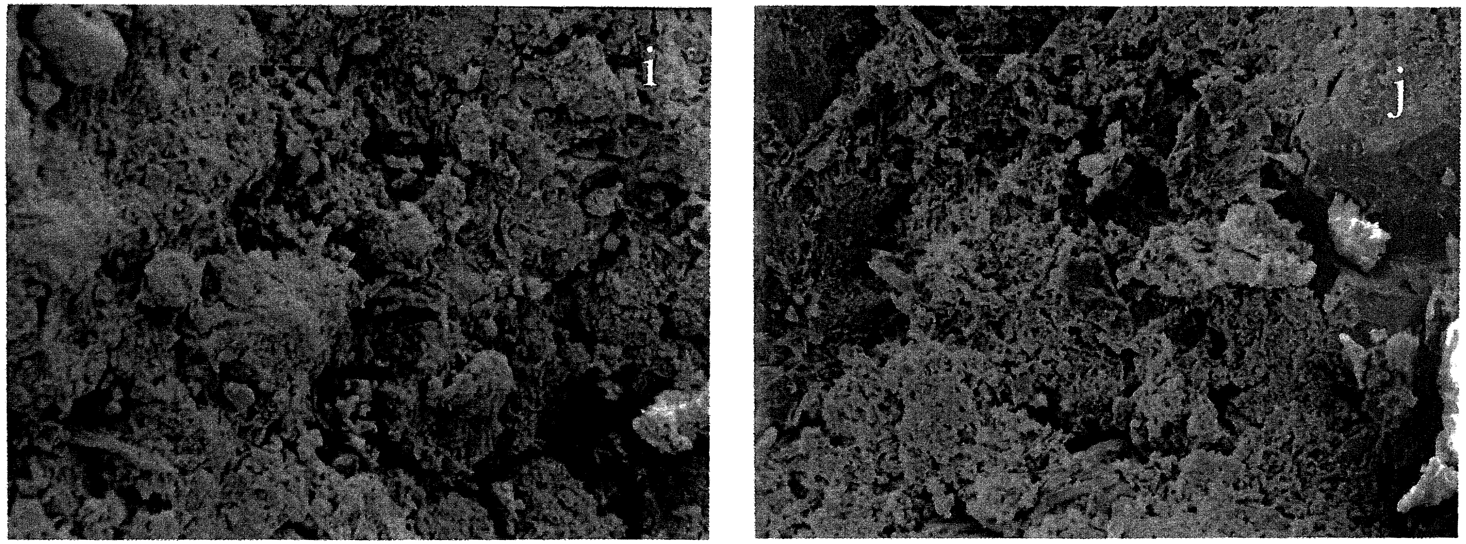


Figure 6.5.c Continuation of Lichen weathering along the northern chronosequence of Mt.Etna. Where **i** is the 1566 flow (433 years old), **j** is 1536 flow (463 years old). Magnification x200

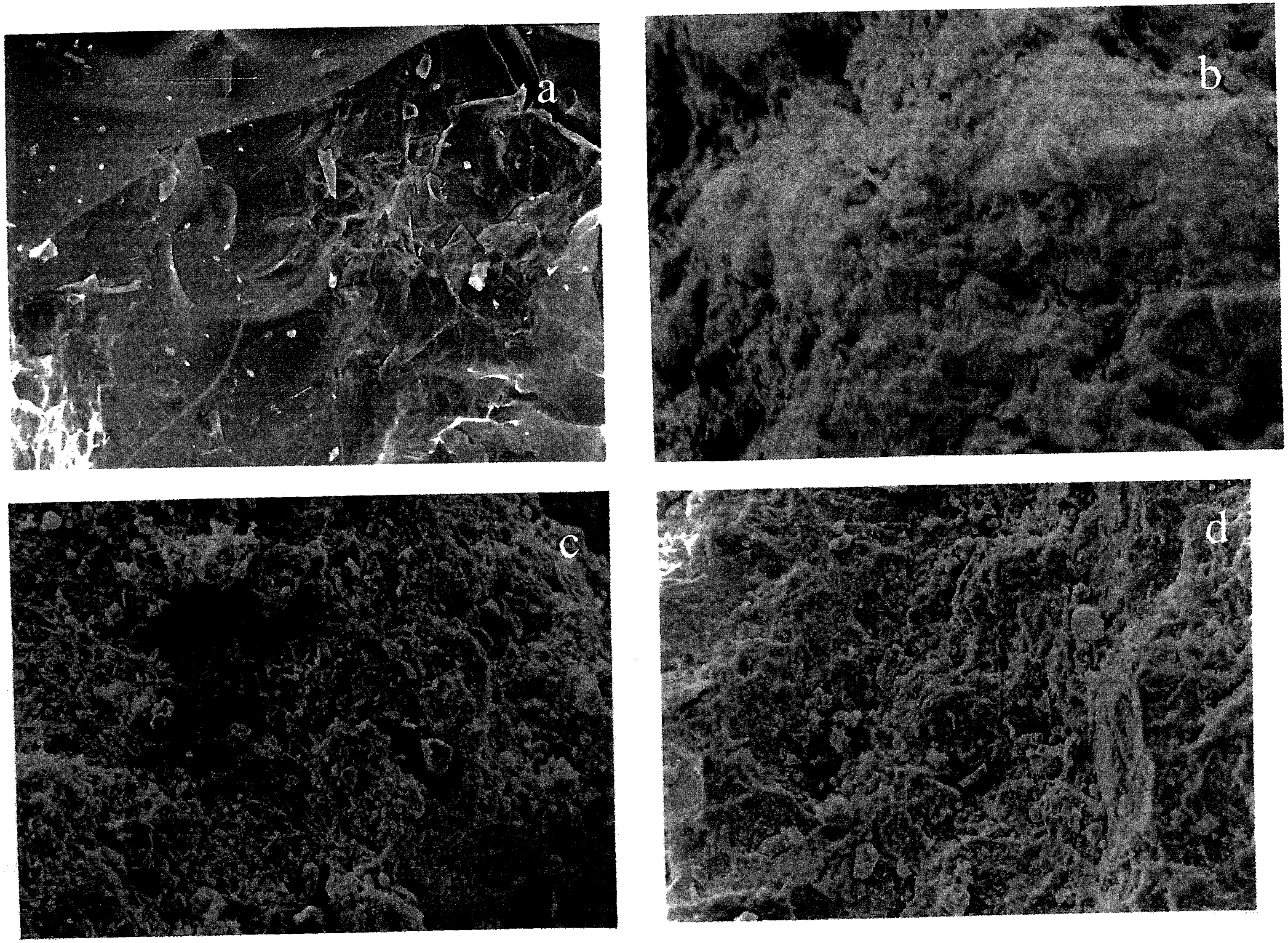


Figure 6.6.a. SEM pictures of lichen weathering along the southern chronosequence of Mt.Etna. Where **a** is the unweathered 1999 flow (0 years old) **b** is 1981 flow (18 years old) **c** is 1910 flow (89 years old) **d** is 1892 flow (107 years old). Magnification x200

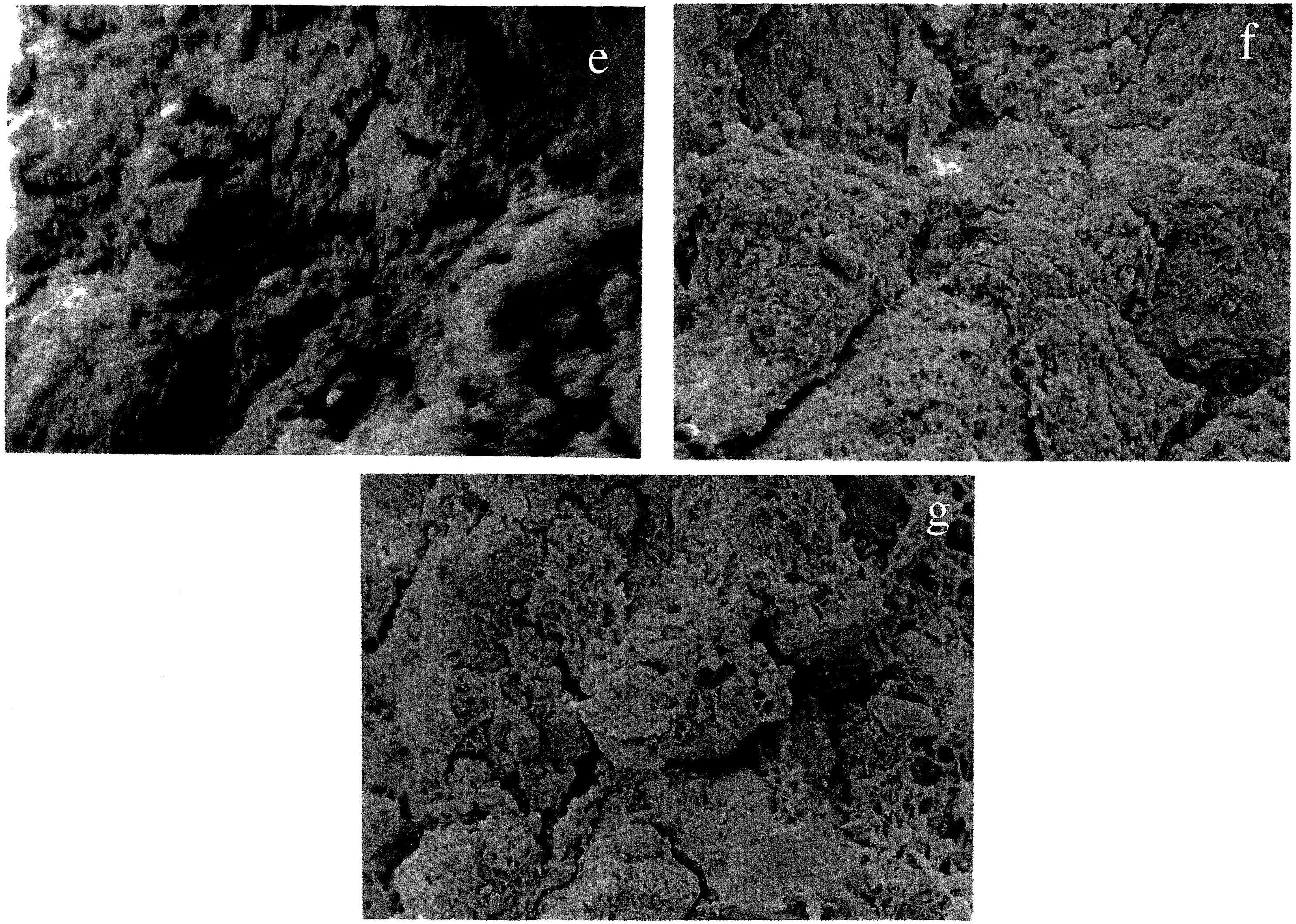


Figure 6.6.b. Continuation of lichen weathering along the southern chronosequence of Mt.Etna. Where **e** is the 1780 flow (219 years old), **f** is 1634 flow (365 years old); **g** is 1537 flow (89 years old);

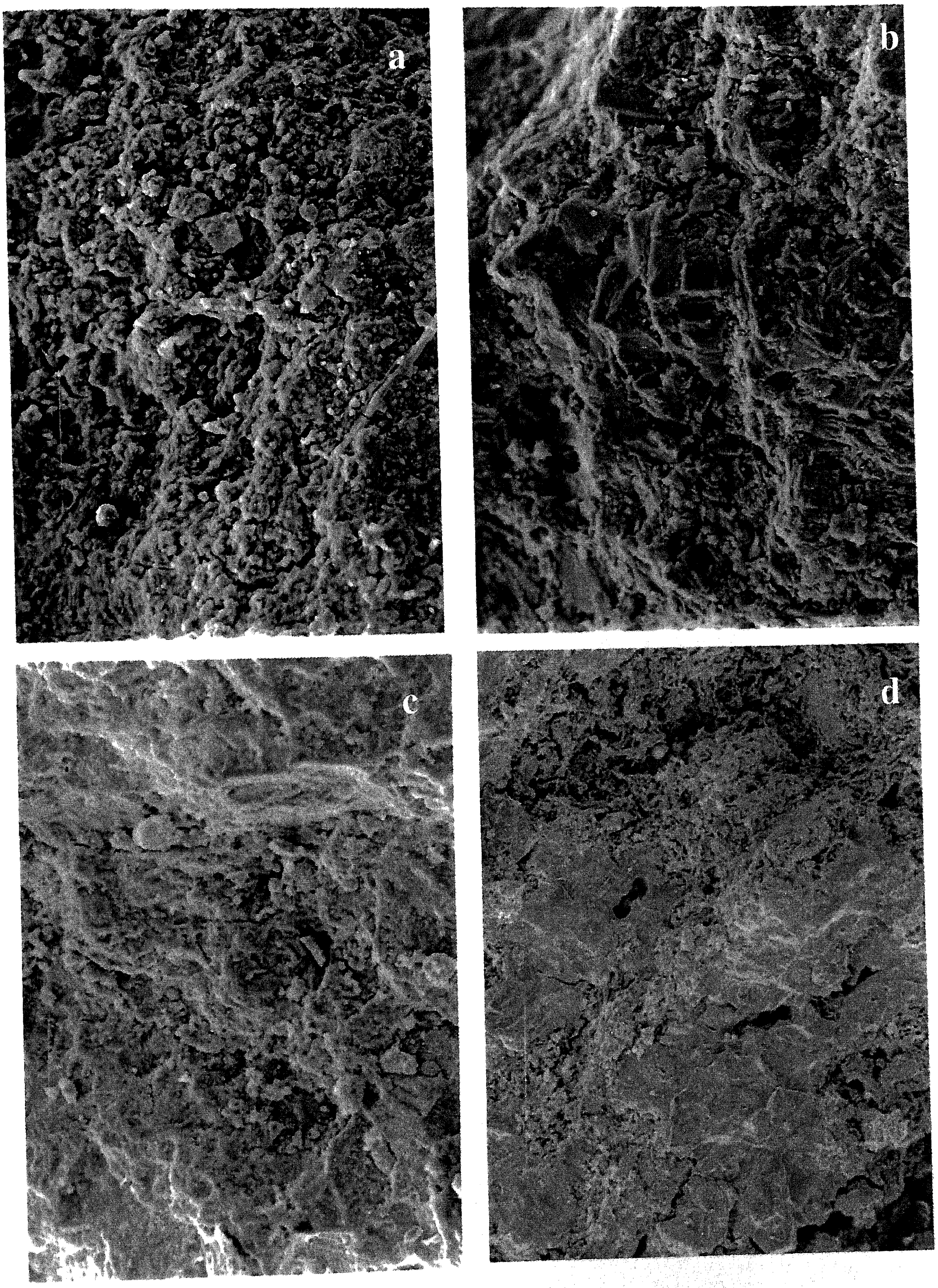


Figure 6.7. Typical lichen weathering of the lava surface on the 4 aspects of Etna on a 19th Century flow: 1879 north **a**; 1865 east **b**; 1843 west **c**; 1892 south **d**. All are x200.

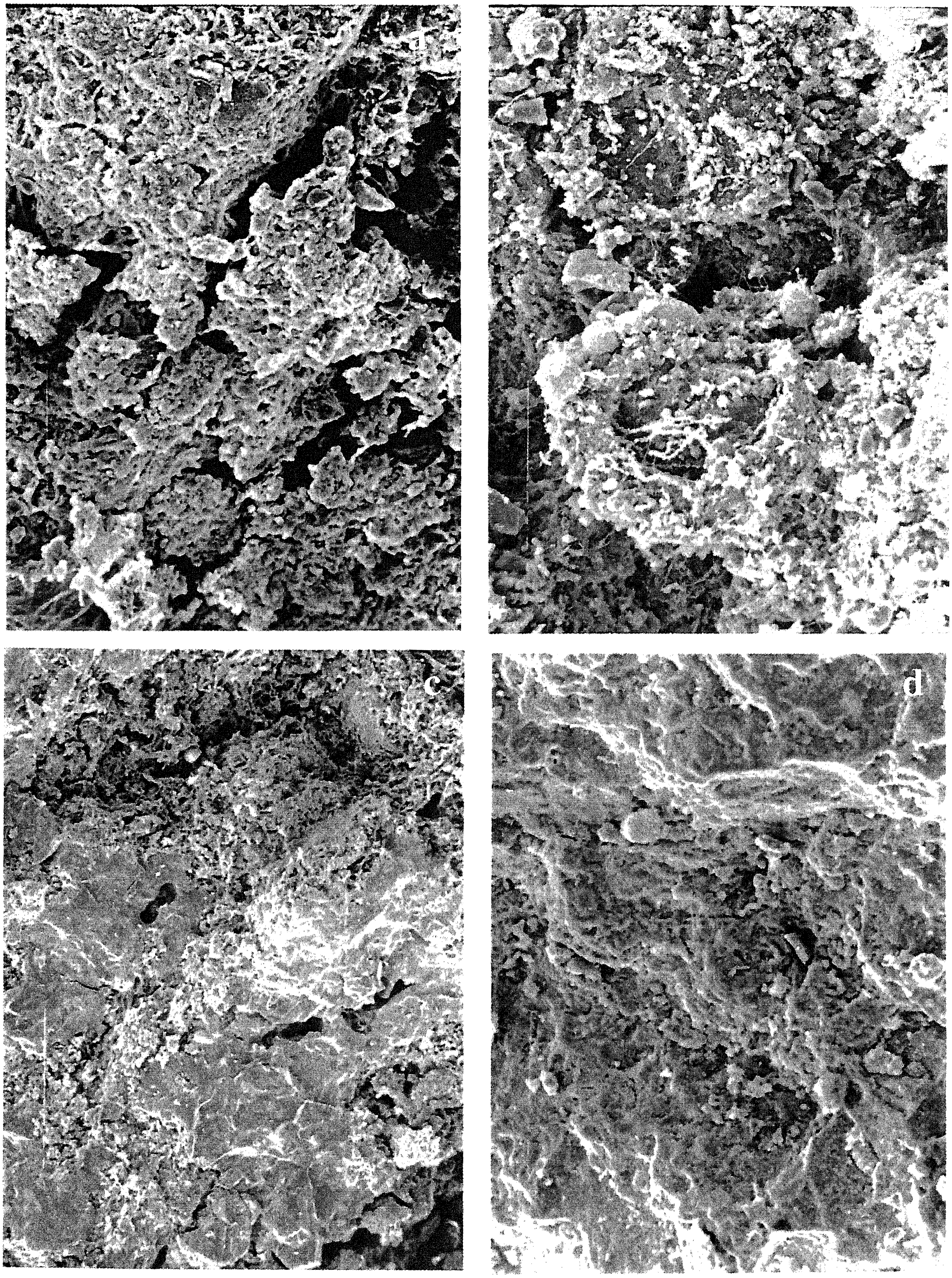


Figure 6.8. Typical lichen weathering of the lava surface on the 4 aspects of Etna on a 17th Century flow: 1614 north **a**; 1689 east **b**; 1651 west **c**; 1634 south **d**. All are x200.

6.3.2. Petrographic analysis of the lava

Figs 6.9 and 6.10 clearly show the interface between the lichen *S.vesuvianum* and the underlying lava on a relatively young sample (year 1981: 19 years old). The lichen binds to the lava surface and penetrates the surface with the thallus.

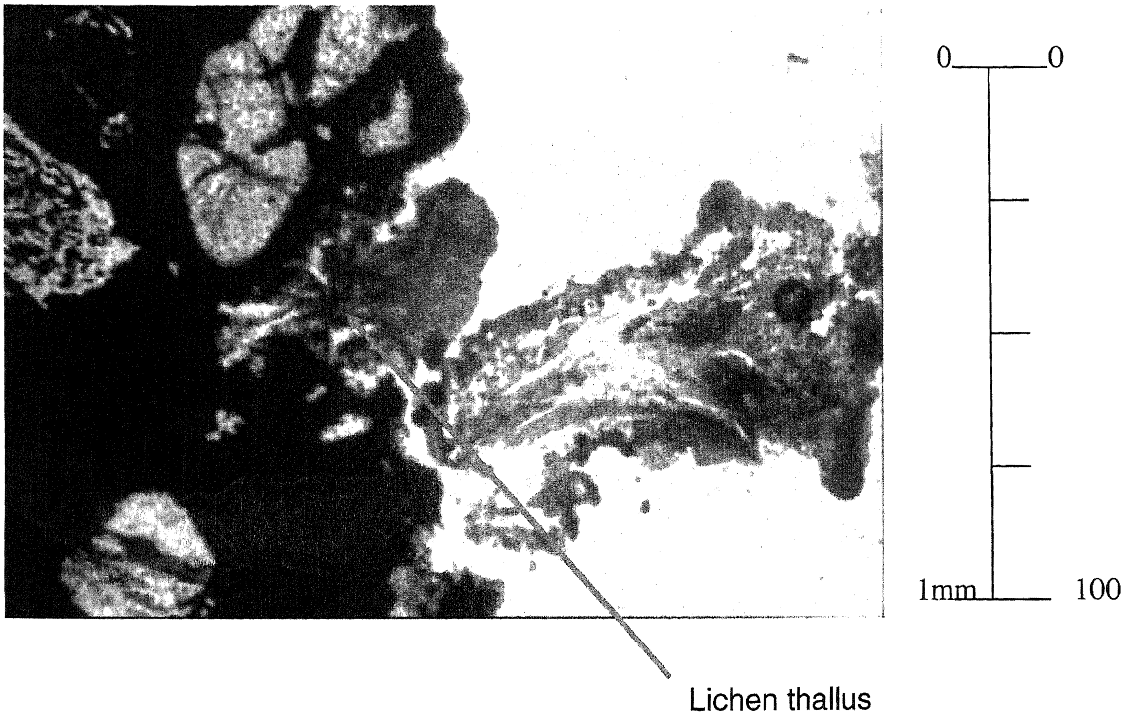


Figure 6.9. Thin section of the interface between the lichen *S.vesuvianum* and lava. The lichen thallus has penetrated approximately 0.5mm (50μm) into the lava.

The large lichen thallus (on the right of the picture) and the smaller thallus which has penetrated further into the lava (marked with red arrow) can clearly be seen on Fig 6.9. This has been magnified further on Fig 6.10.

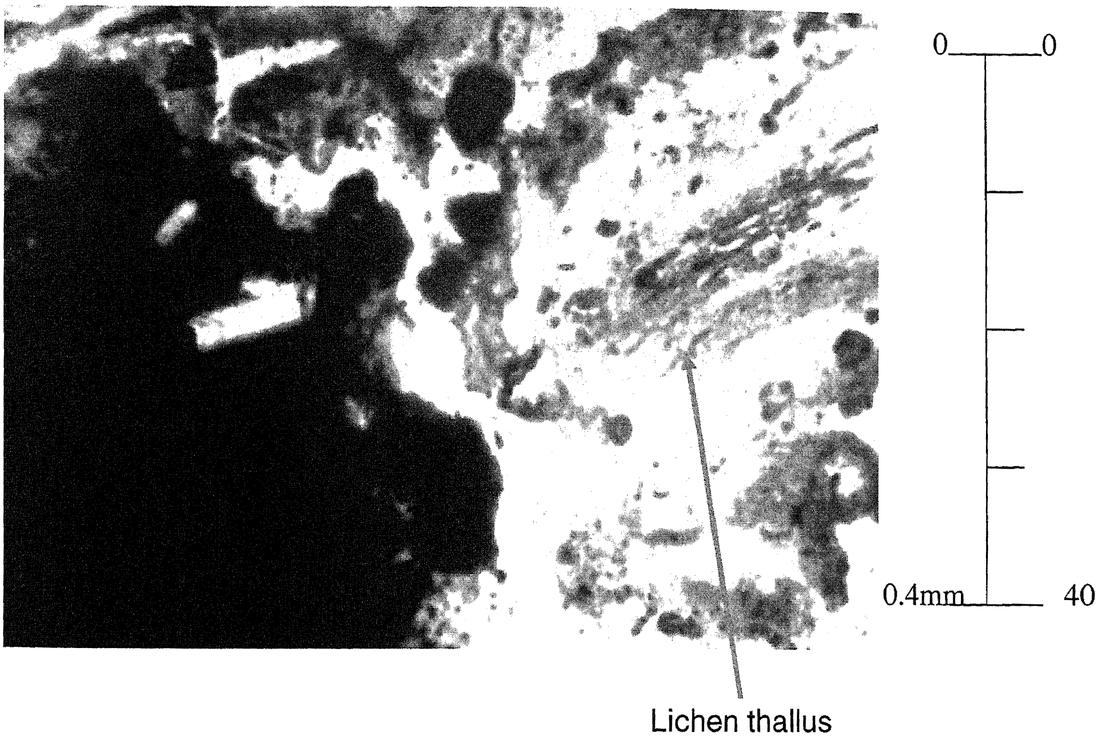


Figure 6.10. Lichen thallus interface with the rock surface on 1981 lava flow.

Over time the weathering rind formed around the outside of the rock surface gradually deepens as the organic and inorganic weathering processes occur. This leads to a clear zonation of the rock with the outer weathering rind (Fig 6.11) being much paler on thin section than the un-weathered interior (Fig 6.12). This is due to fragmentation and dis-aggregation of the glassy matrix around the phenocryst particles. It appears that these phenocrysts are relatively unaffected by the weathering process – with only olivine showing a noticeable change over time. Olivine shows visible alteration to iddingsite around the margins and within cracks (Fig 6.13) on the older samples of lava. In addition, it is worth noting that a piece of olivine that is near the root of a lichen thallus on the young 1981 sample (Fig 6.14) also shows this alteration to iddingsite, which does not occur anywhere else on the sample. This leads to the hypothesis that it is its proximity to the lichen, which is causing this effect.

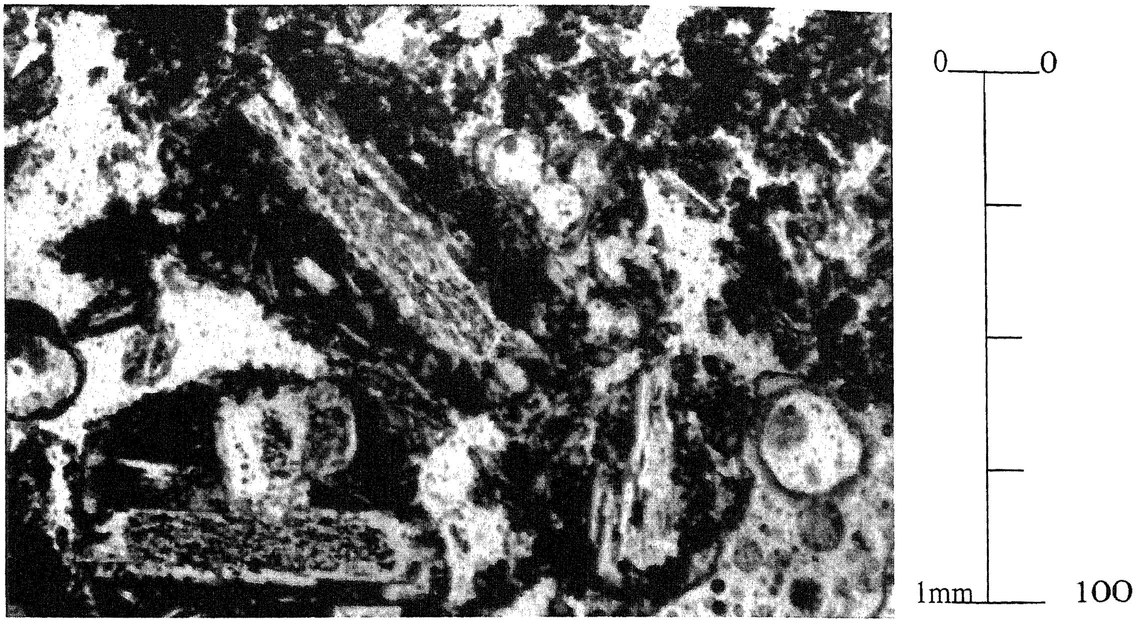


Figure 6.11. Thin section of the outer weathering rind on the 1879 lava flow (depth of 3mm). The glassy matrix of the lava is dis-agreggated and the section is relatively clear.

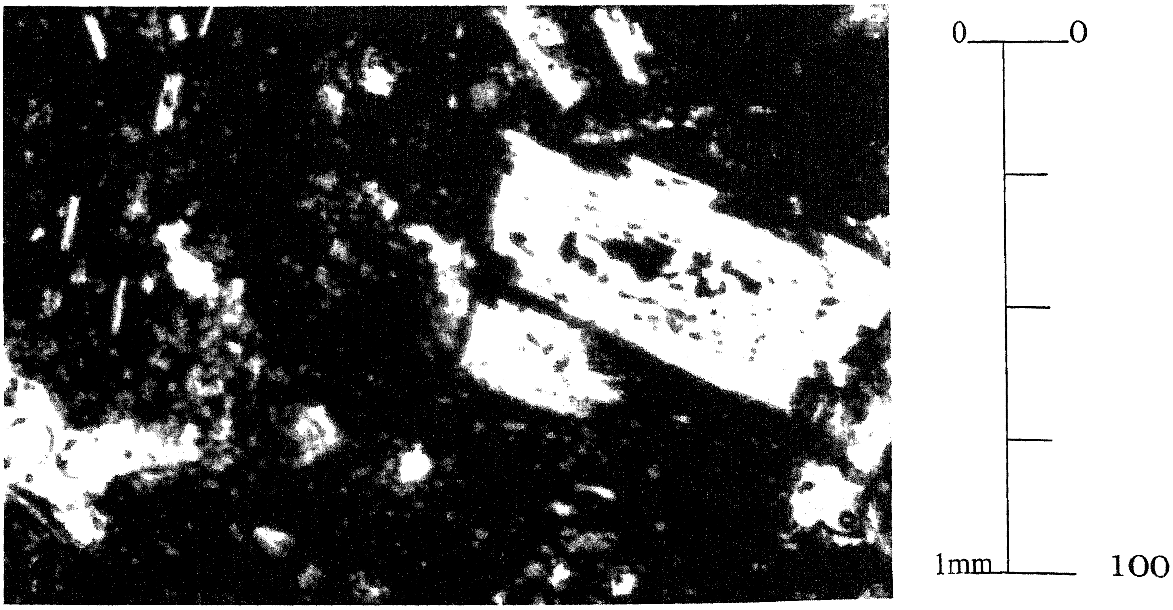


Figure 6.12. Thin section of the unweathered 1879 lava flow (section taken from 1cm inside the rock, past the weathering rind). The glassy matrix is solid and the phenocryst particles are solidly held.

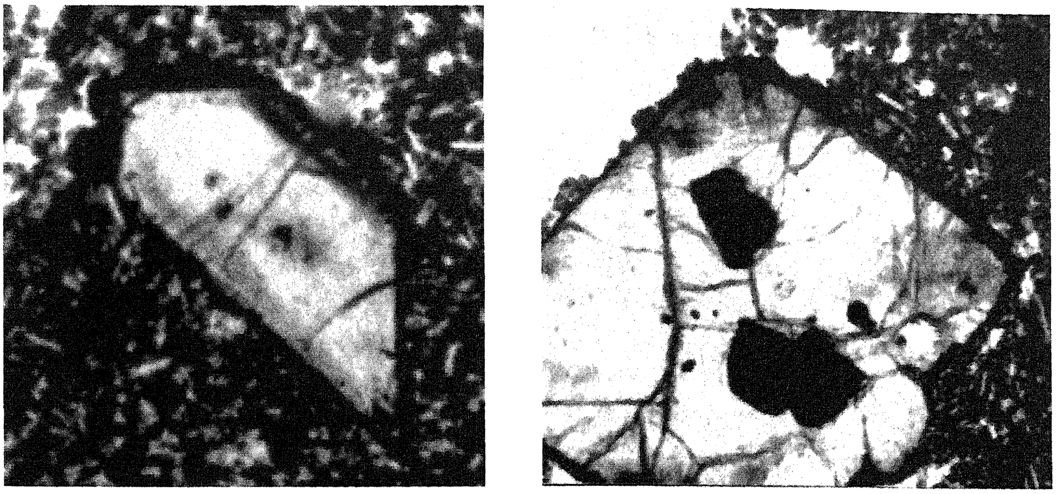


Figure 6.13. Olivine phenocrysts on the 1646 lava sample showing an alteration to iddingsite around the edges and in cracks caused by weathering.

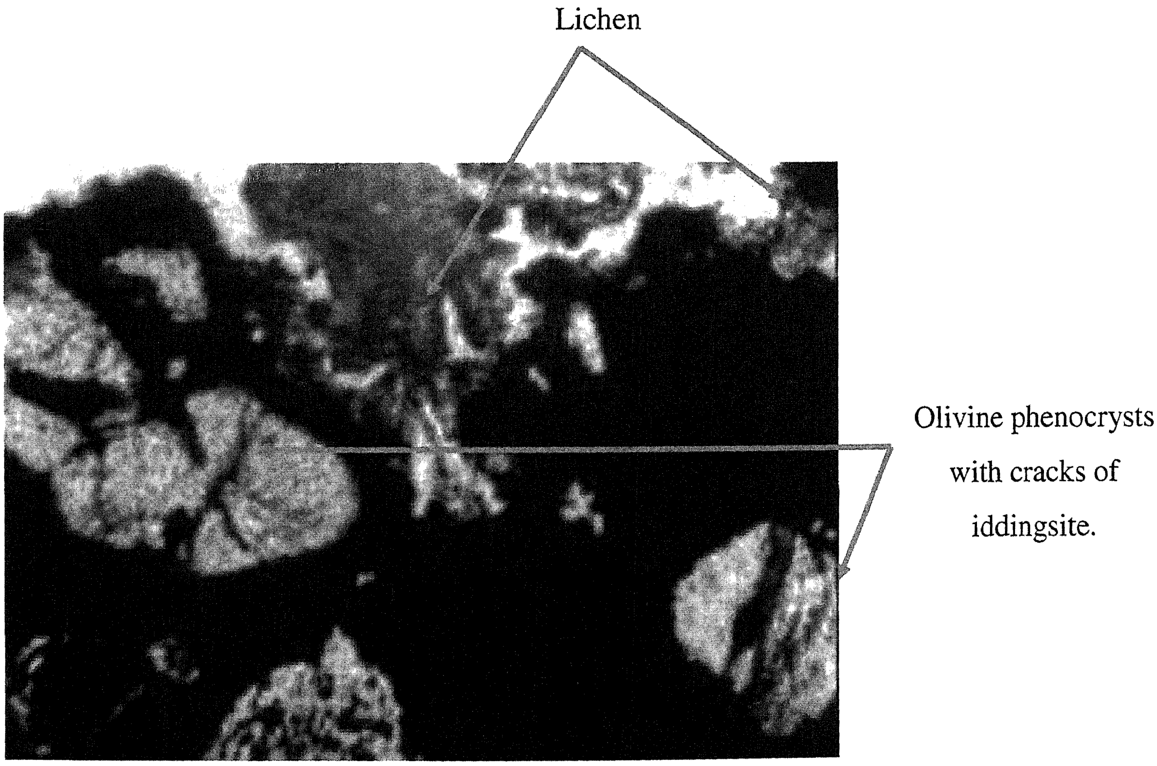


Figure 6.14. Alteration of the olivine to iddingsite on the 1981 sample around the lichen structures.

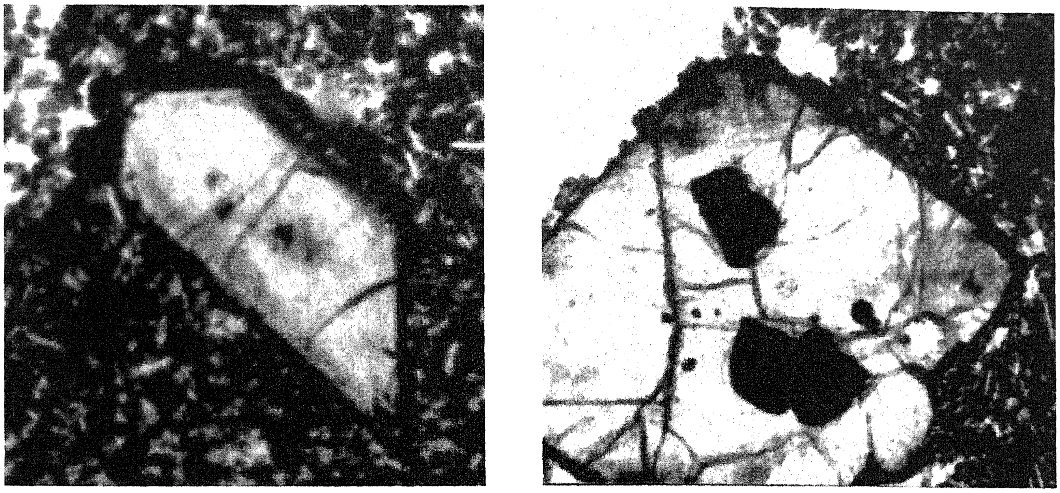


Figure 6.13. Olivine phenocrysts on the 1646 lava sample showing an alteration to iddingsite around the edges and in cracks caused by weathering.

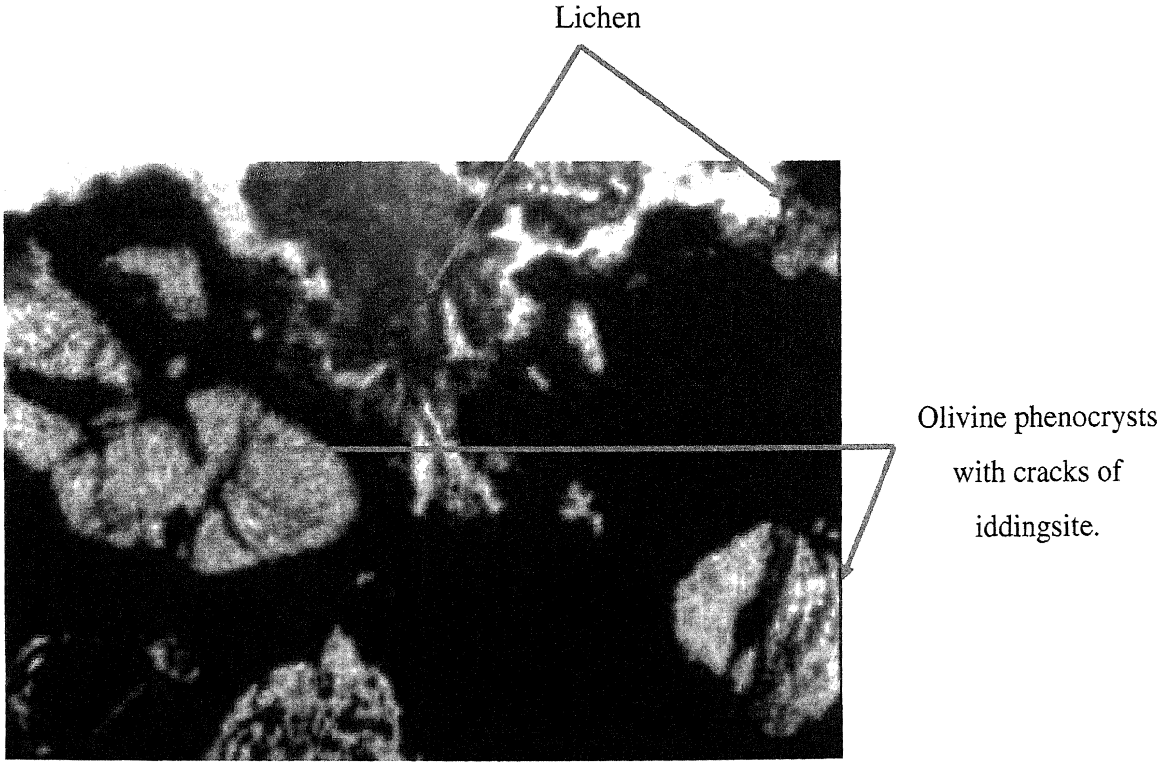


Figure 6.14. Alteration of the olivine to iddingsite on the 1981 sample around the lichen structures.

6.3.3. Quantifying the weathering by image analysis

A great many papers have been published demonstrating the ability of lichens to weather rocks over time – usually by observing surface etching and associated mobilisation of elements (e.g. Iron in Adamo *et al* 1997). However there has been no attempt made to quantify the rate of this weathering in a testable and quantitative manner. By determining the rate of weathering of lava, using chronosequence theory over a variety of environmental conditions, an understanding can be gained, of the effect of lichens in the early stages of primary colonisation. The impact that this weathering has on the mobilisation of elements and the rock surface area (which has water retention repercussions) can be observed. In addition, changing rates of weathering over time could indicate changing environmental conditions such as rainfall and temperature.

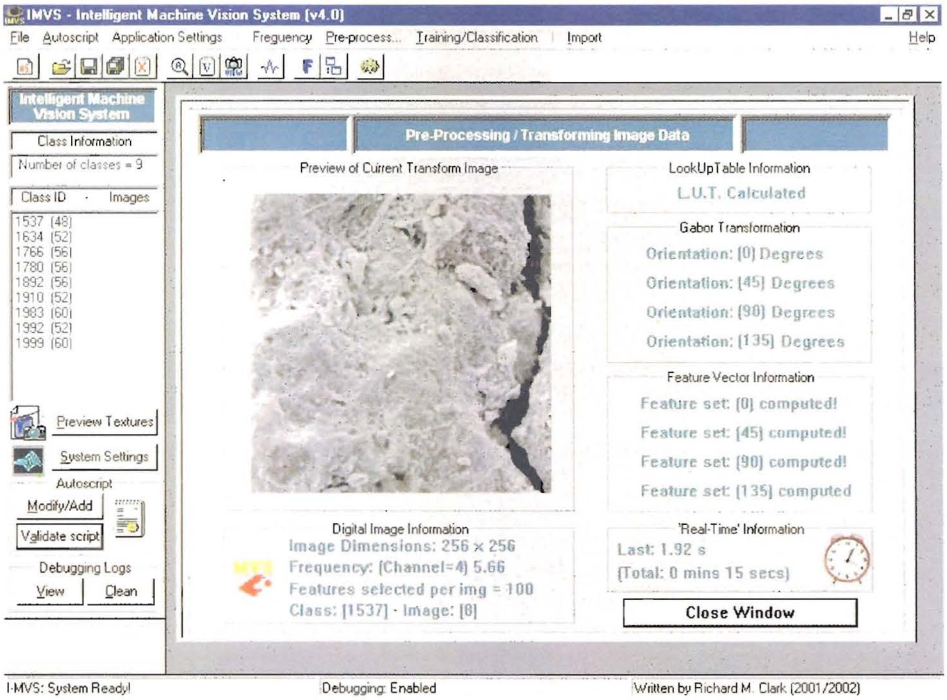
6.3.4. Intelligent machine vision system

Machine vision tools are being increasingly used for a wide variety of medical, scientific and industrial applications. However, many of these systems require a large database of images to classify textures and can be prohibitively expensive to maintain efficiently. A new and less complex system, developed at the University of Luton (Clark *et al* 2000; Clark 2003), offers a more efficient and novel method of interpreting weathering of the basaltic lava from Etna. In addition, it allows for the quantitative variation in the extent of weathering over time sought by the chronosequence theory. This system uses an 'intelligent machine vision system' (IMVS) to classify textures in a systematic way. The intelligence feature allows for incremental learning by the program based on features extracted from Gabor space. Therefore, by training the program using a large database of images of a known age/aspect from a particular chronosequence the program could then learn to distinguish between each 'set' (in this case a lava of different age class). Therefore, by using this method it is hoped that the system can quantify the changes in surface textures over time over a chronosequence. This sequence can then be compared to the other aspects and their associated environmental conditions prevalent on the volcano, to discover the relative weathering rates around the volcano.

6.3.5. Quantitative analysis of the lava using Intelligent machine vision system: Method

The SEM pictures obtained from each of the lava flows making up the south chronosequence were split into two sets; one set for training the program and the second to calculate the recognition rate. This chronosequence has the most complete data set that had a representative lava flow in a consistent time pattern over the 500 years of the study. The lava flows sampled were the: 1983, 1910, 1892, 1780, 1766, 1634, 1537. In addition, the east facing lava of 1992, and a fresh sample of lava from a 1999 flow were added to the data set as the most recent lavas in order to include unweathered samples. Each picture was scanned by the IMVS and the features on the lava surface noted. The program then scans in the surface features again at an angle of 45°, 90° and 135° to determine the surface features of the surface along the vertical (0°) Horizontal (90°) and two diagonal planes (45° and 135°) and completely map the surface (Fig 6.15).

The aim of the training exercise was to run different combinations of images using the program to look at different numbers of feature points (vector size) extracted from each image and then calculate the recognition rate using the second data set. So for each sample site a large number of images was scanned (see examples in Figs 6.16 and 6.17). By running many combinations of age groups (Fig 6.18) and using different numbers of feature points the program was gradually trained to give a recognition rate of 95% accuracy (Fig 6.19). In doing so the optimum number of vectors and feature points required to accurately analyse the sample area was determined. This was a time consuming exercise but once achieved could then be used on all the sites sampled on the other chronosequences.



Number of classes = 9

1537 (48)
1634 (52)
1766 (56)
1780 (56)
1892 (56)
1910 (52)
1983 (60)
1992 (52)
1999 (60)

L.U.T. Calculated

Orientation: (0) Degrees
Orientation: (45) Degrees
Orientation: (90) Degrees
Orientation: (135) Degrees

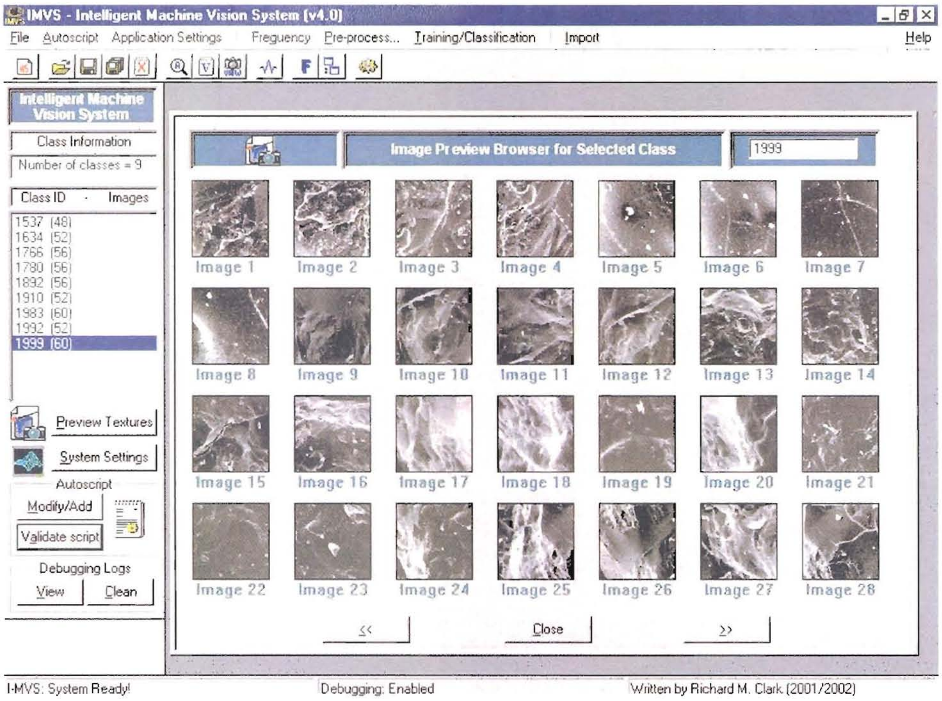
Feature set: (0) computed!
Feature set: (45) computed!
Feature set: (90) computed!
Feature set: (135) computed

Image Dimensions: 256 x 256
Frequency: (Channel=4) 5.66
Features selected per img = 100
Class: (1537) - Image: (8)

Last: 1.92 s
(Total: 0 mins 15 secs)

I-MVS: System Ready! Debugging: Enabled Written by Richard M. Clark (2001/2002)

Figure 6.15. Screen shot from the IMV system. Scanning the SEM photograph and observing the surface features over different orientations of 45°.



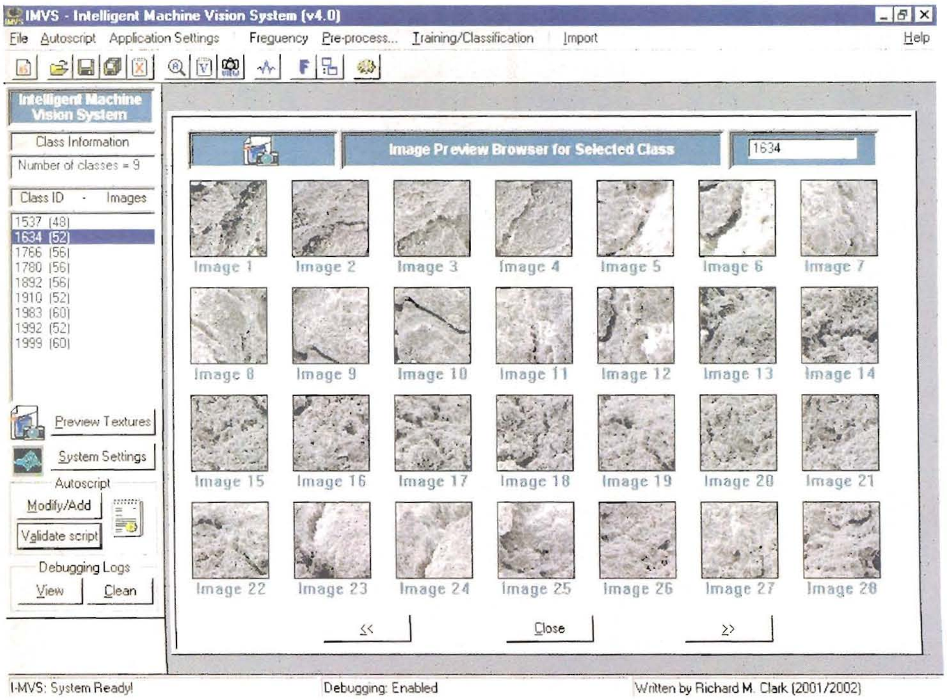
Number of classes = 9

1537 (48)
1634 (52)
1766 (56)
1780 (56)
1892 (56)
1910 (52)
1983 (60)
1992 (52)
1999 (60)

1999

I-MVS: System Ready! Debugging: Enabled Written by Richard M. Clark (2001/2002)

Figure 6.16. Screen shot from the IMV system. The 1999 Age class of representative samples.



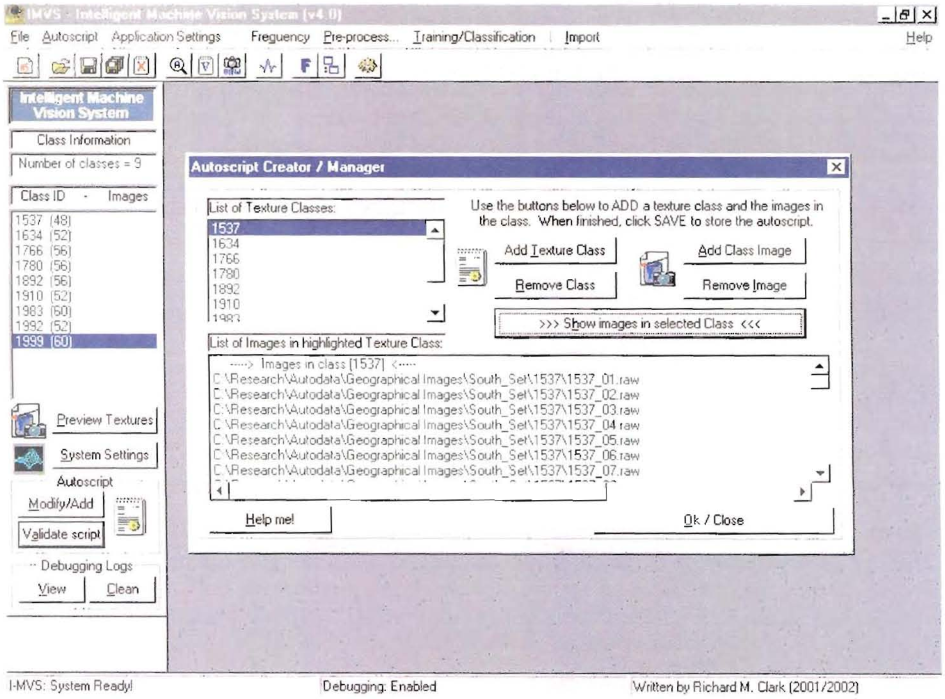
Number of classes = 9

1634

Class ID	Images
1537	(48)
1634	(52)
1766	(56)
1780	(56)
1892	(56)
1910	(52)
1983	(60)
1992	(52)
1999	(60)

I-MVS: System Ready! Debugging: Enabled Written by Richard M. Clark (2001/2002)

Figure 6.17. Screen shot from the IMV system. The 1634 Age class of representative samples.



Number of classes = 9

Class ID	Images
1537	(48)
1634	(52)
1766	(56)
1780	(56)
1892	(56)
1910	(52)
1983	(60)
1992	(52)
1999	(60)

Use the buttons below to ADD a texture class and the images in the class. When finished, click SAVE to store the autoscript.

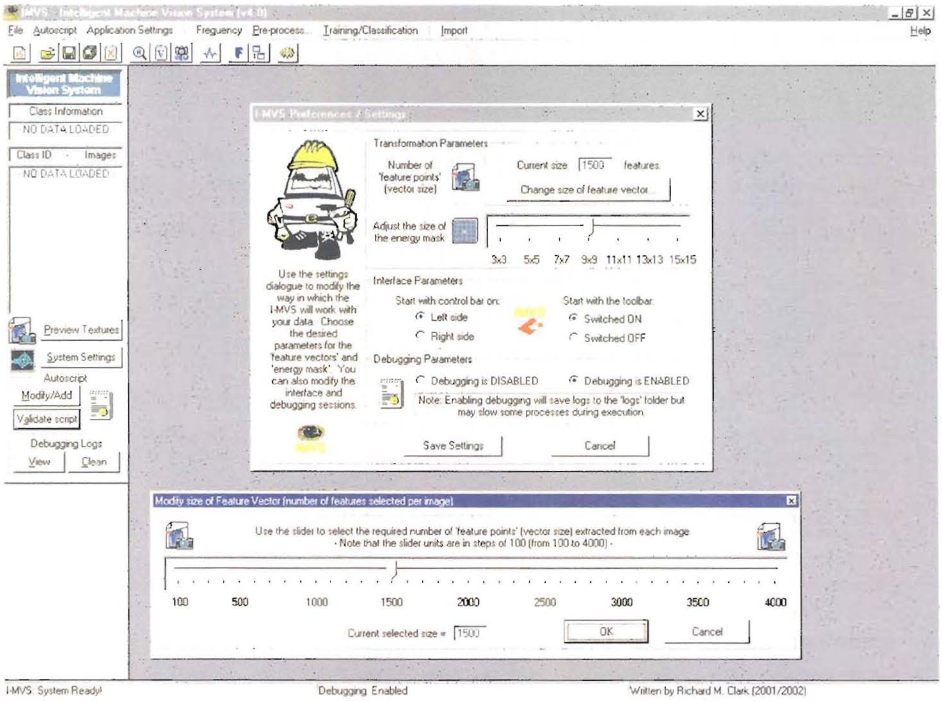
List of Texture Classes:
1537
1634
1766
1780
1892
1910

List of Images in highlighted Texture Class:

```
    -----> Images in class [1537] <-----
C:\Research\Autodata\Geographical Images\South_Set\1537\1537_01.raw
C:\Research\Autodata\Geographical Images\South_Set\1537\1537_02.raw
C:\Research\Autodata\Geographical Images\South_Set\1537\1537_03.raw
C:\Research\Autodata\Geographical Images\South_Set\1537\1537_04.raw
C:\Research\Autodata\Geographical Images\South_Set\1537\1537_05.raw
C:\Research\Autodata\Geographical Images\South_Set\1537\1537_06.raw
C:\Research\Autodata\Geographical Images\South_Set\1537\1537_07.raw
```

I-MVS: System Ready! Debugging: Enabled Written by Richard M. Clark (2001/2002)

Figure 6.18. Screen shot from the IMV system. Setting the age classes.



NO DATA LOADED

NO DATA LOADED

Use the settings dialogue to modify the way in which the I-MVS will work with your data. Choose the desired parameters for the 'feature vectors' and 'energy mask'. You can also modify the interface and debugging sessions.

Number of 'feature points' (vector size) — Current size 1500 features

Adjust the size of the energy mask

Start with control bar on: ● Left side ○ Right side

Start with the toolbar: ● Switched ON ○ Switched OFF

○ Debugging is DISABLED ● Debugging is ENABLED

Note: Enabling debugging will save logs to the 'logs' folder but may slow some processes during execution.

Use the slider to select the required number of 'feature points' (vector size) extracted from each image
- Note that the slider units are in steps of 100 (from 100 to 4000) -

Current selected size = 1500

I-MVS: System Ready!

Debugging Enabled

Written by Richard M. Clark (2001/2002)

Figure 6.19. Screen shot from the IMV system. Training of the Machine vision system by varying the number of feature points selected from each image to gain the best recognition rate.

6.3.6. Intelligent machine vision imaging comparing the south and north chronosequences

The results from the machine vision analysis indicate a similarity between the weathering rates on the north and south two chronosequences (Table 6.1). There is a very close match between the early lava flows (1981 north has an 84% match to 1983 south; 1923 north has a 77% match to 1910 south). However, as the age of the lava flow increases the weathering rates gradually differentiate, with a slightly slower weathering rate becoming apparent in the north (1646 N has a 60% match to 1766 south and a 40% match to 1892 south; 1536 north has a 75% match to 1766 south).

Both the 1566 and 1536 north samples appear to have greatest similarity with the 1766 South samples – and so have clearly weathered more slowly than their southern contemporaries (e.g. 1536 north has only a 6% match to 1537 south).

Sample	Intelligent Machine vision match	Weathering rate (= / + / -)
1981 North	84.78% match to 1983 South 10.78% match to 1910 South 4.35% match to 1992 South	Equal
1947 North	73.08% match to 1983 South 25.00% match to 1910 South 1.92 match to 1892 South	Equal
1923 North	77.09% match to 1910 South 22.91% match to 1983 South	Equal
1879 North	65.22% match to 1910 South 23.91% match to 1983 South 10.87% match to 1892 South	Slightly slower
1809 North	81.29% match to 1892 South 10.41% match to 1910 South 8.30% match to 1766 South	Slightly slower
1646 North	59.10% match to 1766 South 40.09% match to 1634 South	Slightly slower
1614-24 North	76.8% match to 1766 South 8.92% match to 1780 South 7.14% match to 1892 South 7.14% match to 1634 South	Slower
1566 North	78.86% match to 1766 South 17.30% match to 1634 South 3.84% match to 1780 South	Slower
1536 North	75.00% match to 1766 South 18.75% match to 1634 South 6.25% match to 1537 South	Slower

Table 6.1. Weathering rate comparison between the 'fixed baseline' south chronosequence and the north chronosequence.

6.3.7. Intelligent machine vision imaging comparison of the south and east chronosequences

These two chronosequences show a marked difference in their weathering rates with only the youngest sample showing a good match of ages to weathering (1983 south has a 88% correlation to the 1971 east). As the age of the lava flow on the east aspect increases, the difference becomes more pronounced (1928 east matches 87% to 1983 south). The final measurement which shows that the extent of weathering on 1689 lava flow on the east side most closely matches a sample from an 1892 south sample. This indicates that the weathering rate on the east aspect of the volcano is actually slower than that found on the south aspect.

Sample	Intelligent Machine vision match	Weathering rate (=/+/-)
1971 East	87.50% match to 1983 South 12.50% match to 1910 South	Equal
1928 East	87.00% match to 1983 South 10.00% match to 1910 South 1.70 match to 1992 South 1.70% match to 1892 South	Slower
1865 East	79.00% match to 1910 South 21.00% match to 1892 South	Slower
1792 East	73.00% match to 1910 South 27.00% match to 1983 South	Slower
1689	71.00% match to 1892 South 29.00% match to 1766 South	Slower

Table 6.2. Weathering rate comparison between the 'fixed baseline' south chronosequence and the east chronosequence.

6.4. Discussion

It is clear from each of these three chronosequences that the surface of the lava weathers over time through the action of the lichens in a very distinct pattern. The lichen begins to weather the rock almost immediately upon deposition. This agrees with the work of Jackson (1969); Jackson and Keller (1970) (working on Hawaiian basalts) and Stretch and Viles (2002) working on the lava flows of Lanzarote. The initially smooth almost glassy surface (e.g. Fig 6.4.a **a** 1999 east unweathered fresh lava) is gradually pitted by the small lichen colonisers, which in turn allows further colonisation as the surface becomes easier to cling onto, as well as increasing the surface area for water retention. This continues until the pitting results in a rougher surface as the lichen 'burrows' into some areas of the rock forming large hollows in the surface (Fig 6.4.b. **e** and **f**; 135 and 210 year old respectively). Over time these hollows increase in volume as the lichens grow, forming large cracks in the surface (6.5.b **f** and **g**). Eventually these cracks so weaken the rock as to break it off into flakes of lava (no doubt assisted by the lichen hyphae penetrating under the flakes). These flakes are initially held onto the lava by the lichen itself and can become stuck to the base of the lichen hyphae. These flakes are then broken apart still further and when the lichen breaks off the rock will be carried away to form an inorganic component of the precursor soil. This initial soil is formed of lichen debris and aeolian material as discussed in chapter 4.

It is clear that the fastest lava weathering occurs on the southern chronosequence, which also sustains the highest lichen biomass (see Fig 5.8). The southern chronosequence is very similar to its northern counterpart (so similar as to be indistinguishable under the naked eye). However, the IMV results indicate that the northern weathering rate is slower than that found in the south (Table 6.1). Once again this correlates to the lower lichen biomass found on the northern chronosequence.

The surprising result on the north IMVS data (Table 6.1) where the 1614-24 flow shows a 76.8% correlation with the 1766 lava flow – but only an 8.92% match to the 1780 flow, indicates that the IMVS requires further testing. This discrepancy may be caused by problems with the IMVS reading of several of the 1780 pictures which were blurred around the edges. Alternately, this may be a morphological feature of the two sample sites which were several km apart.

Surprisingly, given the prevalent climatic conditions on the eastern chronosequence, this is where the weathering rate was lowest (although in the youngest flows there is no difference). However, given that the lichen biomass in the east is low (Fig 5.10) and also quickly replaced early in the succession by vascular plants this would explain the discrepancy. The weathering caused by *S.vesuvianum* is higher than the climate or vascular plant activity can produce in these early stages of colonisation/succession (Wasklewicz 1994).

From these results the following three conclusions can be drawn:

1) *S.vesuvianum* weathers the lava surface as soon as it finds purchase on the rock. The lichen first etches and pits the surface and then gradually the extent of weathering increases until flakes of rock break off due to the mechanical action of the thallus (and penetration into the rock increases). This weathering occurs primarily on the early (0-200 year old) lavas on Etna, but where the lichen persists longest the extent of weathering is increased.
2) The higher the biomass of *S.vesuvianum* the greater the extent of weathering.
3) The longer the period of *S.vesuvianum* being present the greater the weathering and hence the greater the amount of weathered material that must be entering the ecosystem.

It is possible that on the older lava flows where the lichen remains dominant a state of equilibrium is reached in the weathering, as the surface cannot become further roughened due to particles of lava being lost but the lichen continues to gradually erode the rock surface. The alteration of olivine to iddingsite noticed by petrographic analysis is similar to the findings of Waskelwicz (1994) on Hawaiian basalts, who showed that lichen acids caused the dissolution of olivine to be much faster than is normal in the absence of lichens.

All this results in an ongoing process of weathering on the lava surface under the lichens. This is largely controlled by the climatic conditions prevalent on the site as this will control the growth of a sufficient lichen biomass. Warm wet conditions encourage lichen growth (Kurina and Vitousek 1999, Kurina *et al* In press). The lichen weathering is aided by abiotic weathering of freeze thaw cycles, which weaken the rock still further. Undoubtedly, other lichens species growing Etna are also weathering the lava surface and also contributing to the mobilisation of elements which will be incorporated into the developing ecosystem. However, given the high biomass and percentage cover of *S.vesuvianum* (up to 100% cover in some areas) on these young (0-500 year old) lava flows the bulk of lichen weathering is being produced by this particular species.

Chapter 7: Nitrogen availability and nitrate reductase activity on recent Hawaiian lava flows.

7.1. Introduction

7.1.1. Purpose of the experiment

The aim of the final section of the project was to take the results gained on Etna and to investigate to what extent these are applicable to another basaltic volcano – taking into account the differences in climate and flora. In order to discover if the basic processes observed on Etna also hold true on another volcano and find out if there is a basic pattern to primary succession on lava regardless of local species. As a result another volcano was needed for study, which would have similar properties to Etna in terms of lava morphology, composition and situation. In order to reduce the number of factors affecting the succession, the underlying substrate should match Etna as closely as possible to enable a good comparison.

The following selection criteria were employed when choosing the volcano to be studied:

1) A good selection of recent lava flows in the 0-1000 year range.
2) The lavas to cover a range of altitudes with particular emphasis at 1000m for direct comparison with Etna.
3) Available data on climate (allows comparison between sites and with Etna).
4) Similar basaltic composition of the lava with that of Etna (as a different elemental composition of the lava would weather differently to Etna creating different nutrient availability and potentially change the rate and possible outcome of succession).
5) Easy access to a range of sites.

6) Similar lava morphology to Mt.Etna.

After considering various volcanoes (e.g. Arenal in Costa Rica and Vesuvius in Italy) Mauna Loa on the Big Island of Hawaii, U.S.A was chosen. This volcano addressed all of the criteria required since it has a wide range of recent basaltic lava flows in several climatic zones ranging from dry temperate to tropical rainforest. In addition, this volcano boasts a permanent team of researchers from Stanford University (under Prof. P.Vitousek) and the University of Hawaii, with extensive field knowledge of many of the proposed sites and plant species. These researchers agreed to provide logistical support (transport and laboratory equipment) during the project.

Many studies have been conducted on the volcanic ecosystems of Hawaii in terms of nutrient change where there is an exceptionally long chronosequence of 4 million years (Chadwick *et al* 1999) and long term studies of species succession (Smathers and Mueller-Dombois 1974). However, there has been no investigation into nutrient availability and change over the initial (0-500year) period of chronosequence, or any work on nitrate reductase activity of native Hawaiian species.

The purpose of this study was to measure nitrate reductase activity and total foliar nitrogen and to compare the results to those found on Etna.

7.1.2. The Hawaiian Islands

The Hawaiian Island volcanic chain (Fig 7.1) has been formed over many millions of years by periodic eruptions from a convective plume (hotspot) that generates magma in the upper mantle. The islands have been created as the mantle plume rises (possibly from the core / mantle boundary) to impinge on the base of the Pacific oceanic lithosphere which glides slowly over it. Magma erupted from the hotspot forms a volcanic construct, which eventually grows above sea level to form a sub-aerial shield volcano. Over time, the volcano drifts northwest as the pacific lithospheric plate moves over the centre of the 'hotspot' (Fig 7.2). This plate moves at a rate of about 10cm per year (Hazlett and Hyndman 1996). Once the island has shifted sufficiently away from the magma source the old volcano becomes extinct and a new volcano forms over the hotspot. This has resulted in a number of islands of increasing age gradually moving north west of the hotspot. This allows and unparalleled investigation of chronosequences of hundreds of thousands to millions of years old (Chadwick *et al* 1999).

This process has created an island and sea mount chain extending northwest-ward from the big island to just past Kure Atoll, then north to the Aleutian Islands. The big island of Hawaii lies mostly over the hot spot. This largest and youngest island is made up of five volcanoes; Kohala, Mauna Kea, Hualalai, Mauna Loa and Kilauea (Fig 7.3). A sixth volcano, Loihi, lies just off the south east coast and has yet to reach sea level. Large areas of the big island are covered in recent lava flows. Most of these recent lava flows have been erupted by Mauna Loa and Kilauea. Mauna Loa last erupted in 1984 sending a large lava flow eastwards before stopping approximately 10km from the outskirts of the town Hilo. Kilauea has been continuously erupting since 1983 with lava entering the Pacific Ocean and forming new land on the south east of the island.

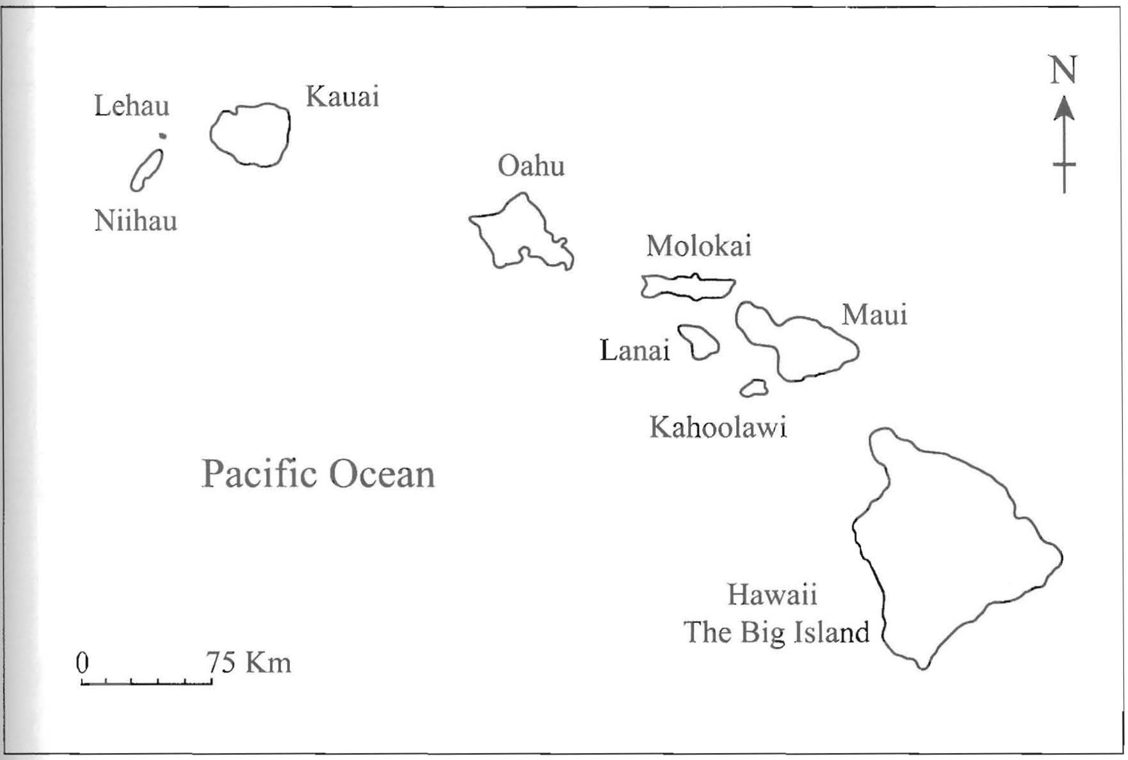


Figure 7.1. The Hawaiian Island chain.

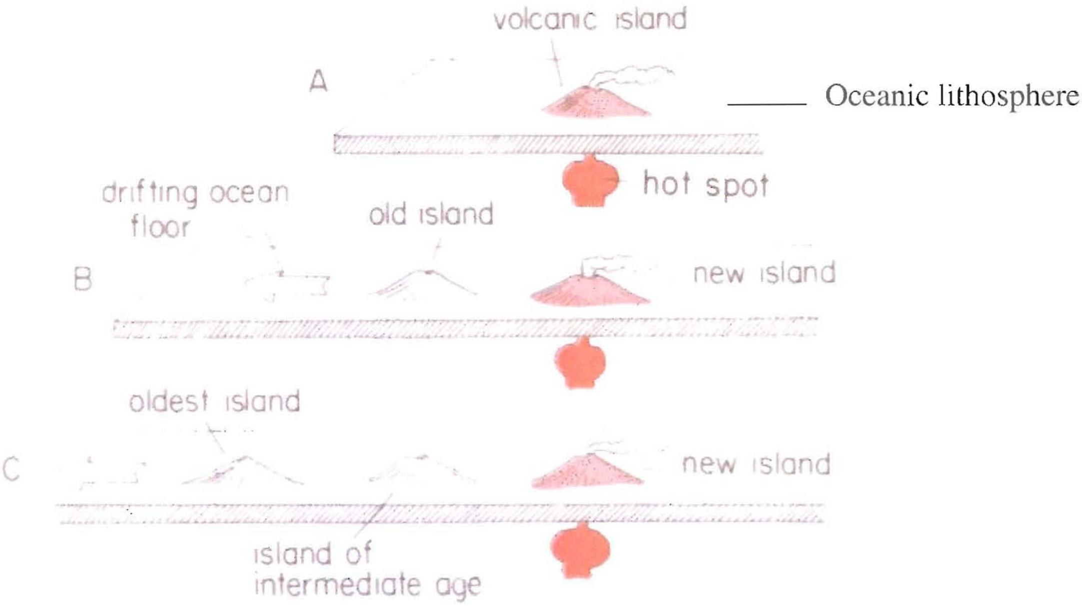


Figure 7.2. Each of the Hawaiian Islands was formed over the hot spot and was then carried to the northwest by the shifting pacific plate. (Taken from Hazlett and Hyndman 1996).

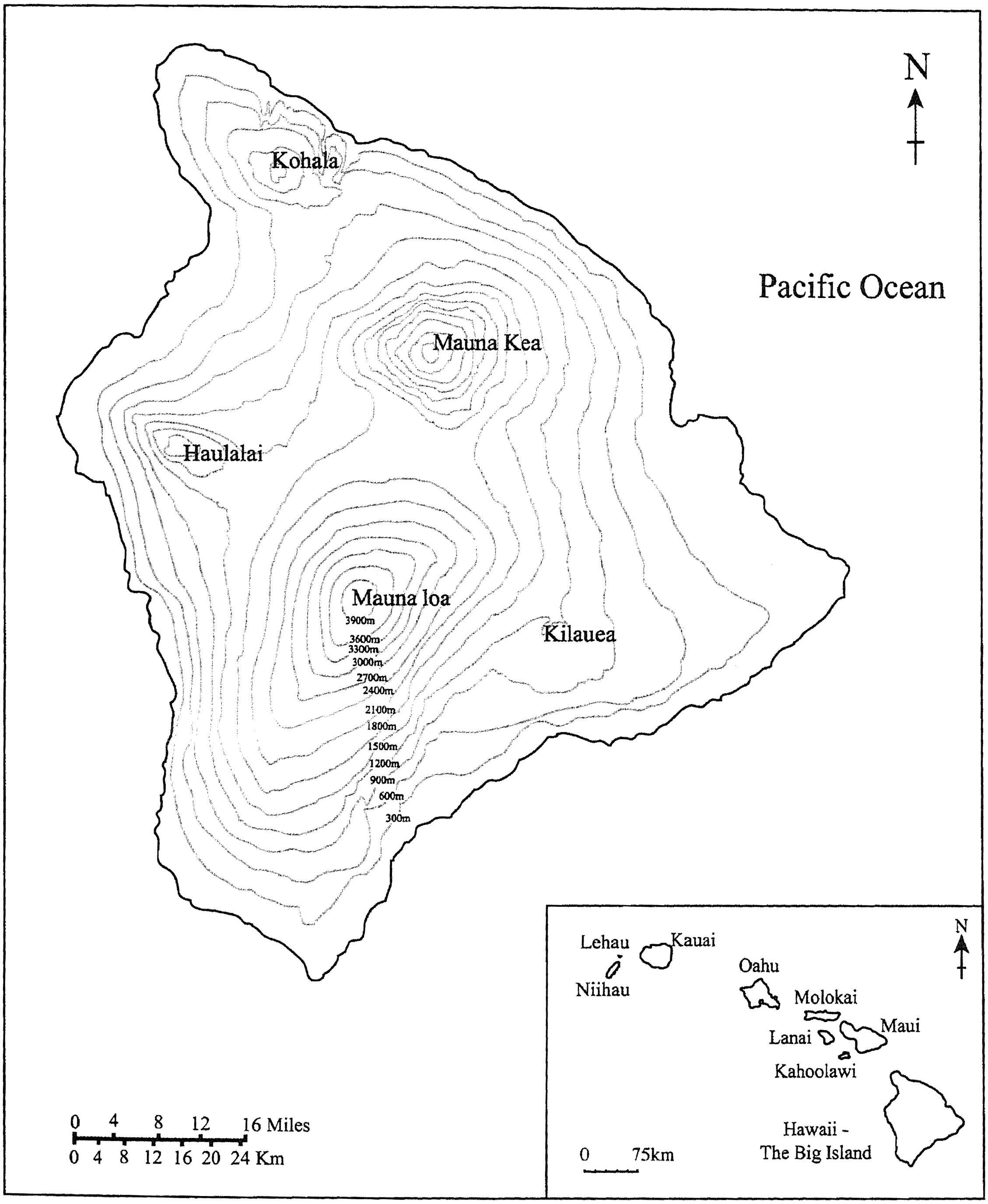


Figure 7.3. The Big island of Hawaii. Showing the five volcanoes that make up the island.

7.1.3. Climatic conditions

Climatic conditions vary greatly across the big island. Both rainfall and temperature change with altitude and aspect in a complex manner related to the position of the volcanoes (Fig 7.4). Rainfall varies tremendously with areas of the Kona coast receiving less than 500mm a year on the west coast, whereas some areas on the east of the island receive 6000mm of rain (Fig 7.4). The reason that the Kona coast is so dry is that it lies on the leeward side of the volcanoes Mauna Loa and Hualalai (Fig 7.4). The saddle between Mauna Loa and Mauna Kea is 2000m at its centre, and thus Kona is cut off from the trade winds, which bring rain to the east of Hawaii. However, Kona does receive some rainfall, due to the size of these two volcanoes. They present a large expanse of land, which absorbs heat, creating updrafts leading up toward the summit (Carlquist 1980). During the afternoon, air surrounding the mountains is rapidly drawn upward and the moisture it carries forms rain. This is the source of the annual rainfall of 1000mm down near the west coast. However, as noted before, this is far less than the 6000mm of the east side of the island.

The climatic pattern on Hawaii is made even more complex by the formation of localised climatic zones in many areas around the volcanoes (in areas so small they are not placed on the climate map). For example, by travelling on the crater rim road around the caldera of Kilauea it is possible to move from areas of dense rainforest, scrubland and through to desert in the space of a few kilometres. Although there are no rainfall data for the Kau desert (by which the barren desert area is known) it is thought that a decrease in rainfall and a more porous substrate coupled with greater surface evaporation (due to the lack of plant cover) causes the drier conditions (Carlquist 1980).

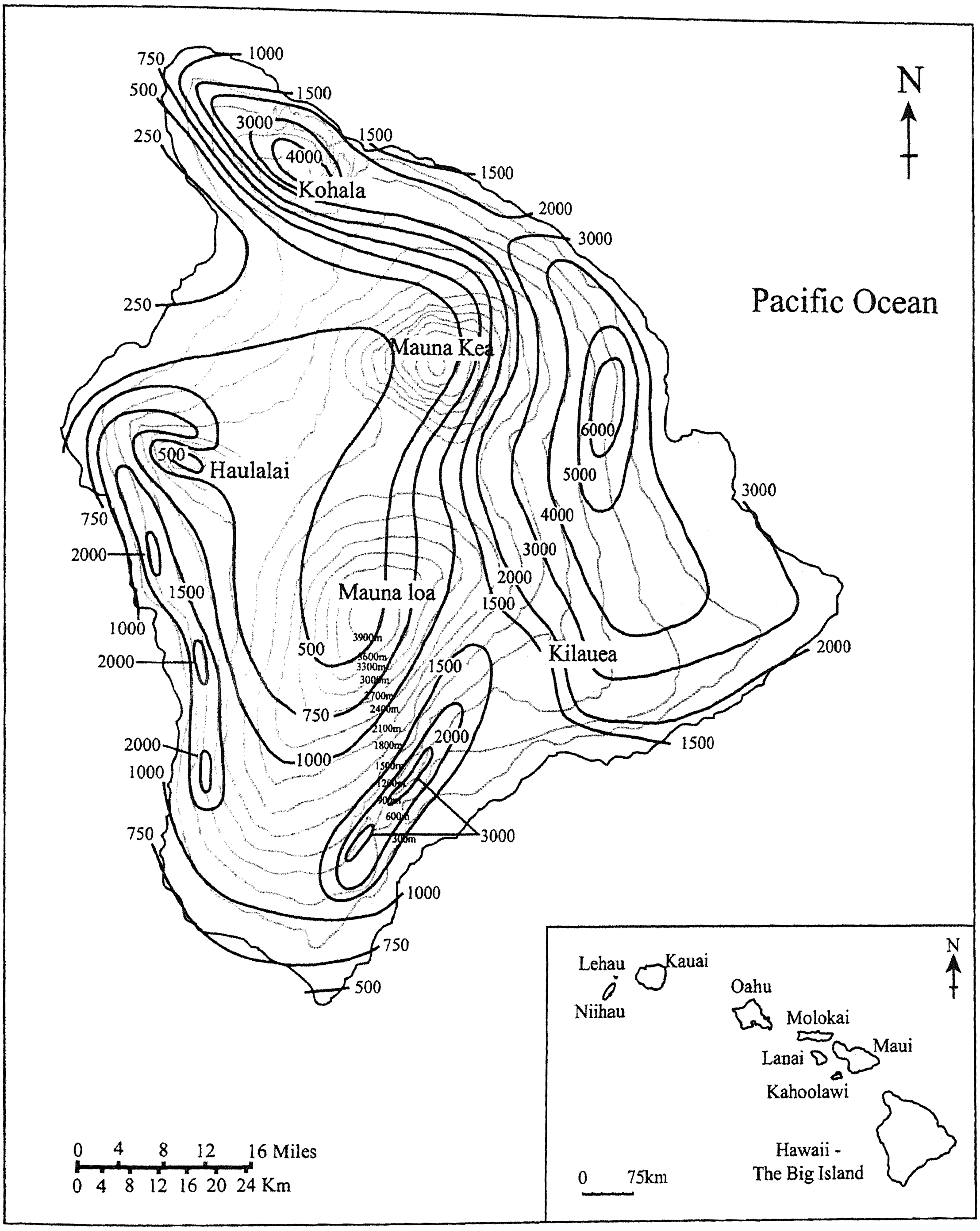


Figure 7.4. Average annual rainfall (black contour lines measured in mm) on the Big Island of Hawaii. Precipitation contours from Giambelluca *et al* 1986.

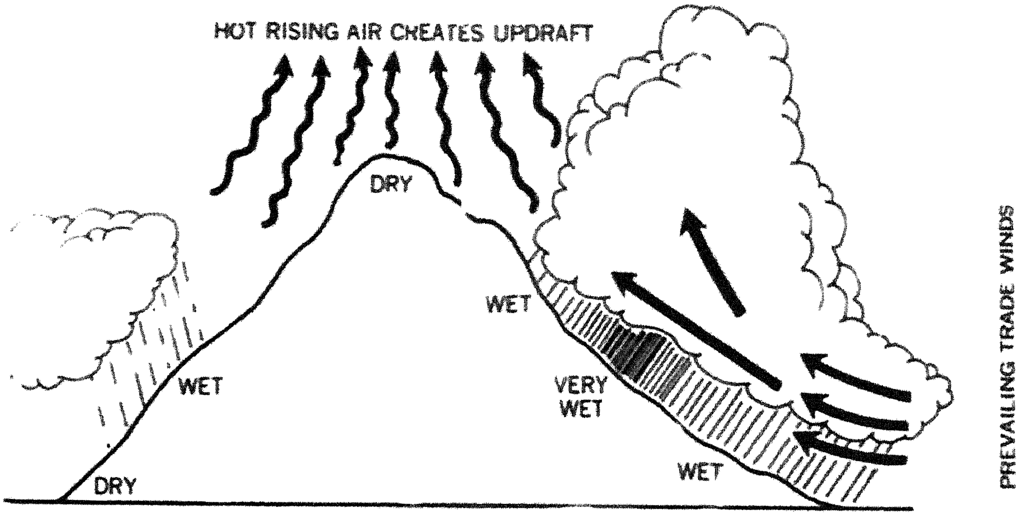


Figure 7.5. Climate system for Hawaii (the Big Island). Taken from Carlquist (1980).

7.1.4. The Hawaiian islands as indicators of successional change

Many studies have been conducted on the volcanic ecosystems of Hawaii in terms of nutrient change (Vitousek *et al* 1983; Drake and Mueller-Dombois 1993; Vitousek *et al* 1995; Raich *et al* 2000). Studies have also analysed changes in the ecosystem by variations with altitude (Kitayama and Mueller-Dombois 1994; Raich 1997; Austin and Vitousek 1998). In addition, there have been long term studies of species succession (Smathers and Mueller-Dombois 1974).

7.1.5. Nutrient change on the Hawaiian Islands

Nutrient availability and change over the period of long term chronosequences has been extensively studied on Hawaii by many authors (Vitousek 1982; 1997; Vitousek *et al* 1987; 1992; 1995; Riley and Vitousek 1995; Kennedy 1998; Chadwick *et al* 1999). These authors have found that nutrient availability varies greatly with age of flow, altitude and the resident climatic conditions. This is similar to the pattern observed on Mt.Etna.

Since the nutrient availability has already been investigated in detail (Vitousek *et al* 1983; 1993; 1995), this study only looks at leaf nitrogen availability in terms of the total foliar nitrogen and nitrate reductase activity. This will directly compare with the results from the chronosequences on Mt.Etna.

7.2. Methods

7.2.1. Species selection and sampling

To compare the Nitrate reductase activity and foliar nitrogen content with that found on Etna, five early colonising species on Hawaii were investigated. These five species were; *Metrosideros polymorpha, Myrsine lessertiana, Vaccinium reticulatum, Coprosma ochracea, Hedyotis centranthoides* (identified using Lamoureux (1976); Kepler (1997) and Pratt (1998)). These species were the commonest consistently occurring species (over the chronosequence) and a full description of each can be seen in the appendix. *M.polymorpha* was the chief subject for investigation, due to its wide abundance throughout Hawaii and its presence as one of the earliest colonisers of new lava flows. From each site small branches/leaves were taken from the topmost level of the canopy. The branches were collected either by hand (on the younger sites where the plants were still small) or by use of a shotgun to bring down leaves from the tops of trees on the older lava flows (Vitousek *et al* 1995). The youngest sun leaves from each branch were then selected and homogenised together for analysis.

7.2.2. Nitrate reductase activity in the leaves of plants along a chronosequence at two elevations (1800m and 1000m)

Sites were selected along two chronosequences of lava flows on the wet east aspect of Mauna Loa during the summer of 2001. Each chronosequence was located at a different altitude (one at approximately 1000m and another at 1800m). Sites were selected using the same criteria as that used on Mt.Etna (topography, distance from the edge of flow and lava morphology) as outlined in 2.2.1. Sites selected at 1000m were the: 1984 (17 year old), 1942 (59 year old), 1852 (149 year old), 400 year old and 3,000 years old lava flows (Fig 7.6). Map grid references for the location of all the sites can be seen in the appendix. The older 3,000 site was added to compare the differences between the younger flows and a fully developed system. Sites on the 1800m chronosequence were the: 1984 (17 year old), 1852 (149 year old), 400 years old, 3,000 year old and a 5,000 year old lava. These sites were identified using the geological maps of Hawaii (Wolfe and Morris 1996). These sites have been used consistently as part of research relating to the development of a chronosequence of the Hawaiian ecosystems (Vitousek *et al* 1992; Vitousek *et al* 1995; Kitayama and Mueller-Dombois 1994; Kitayama and Mueller-Dombois 1995; Kitayama *et al* 1995; Raich *et al* 1996 and 1997; Kurina 1998; Kurina and Vitousek 1999; Raich *et al* 2000; Kurina and Vitousek 2001).

On each site the five target species were sampled wherever possible (some species were not present on all sites). Nitrate reductase activity in the leaves and roots was determined using the same analytical method outlined in section 3.2.3. The concentration of the total nutrients for each altitude was analysed using an ANOVA on SPSS 10.0.

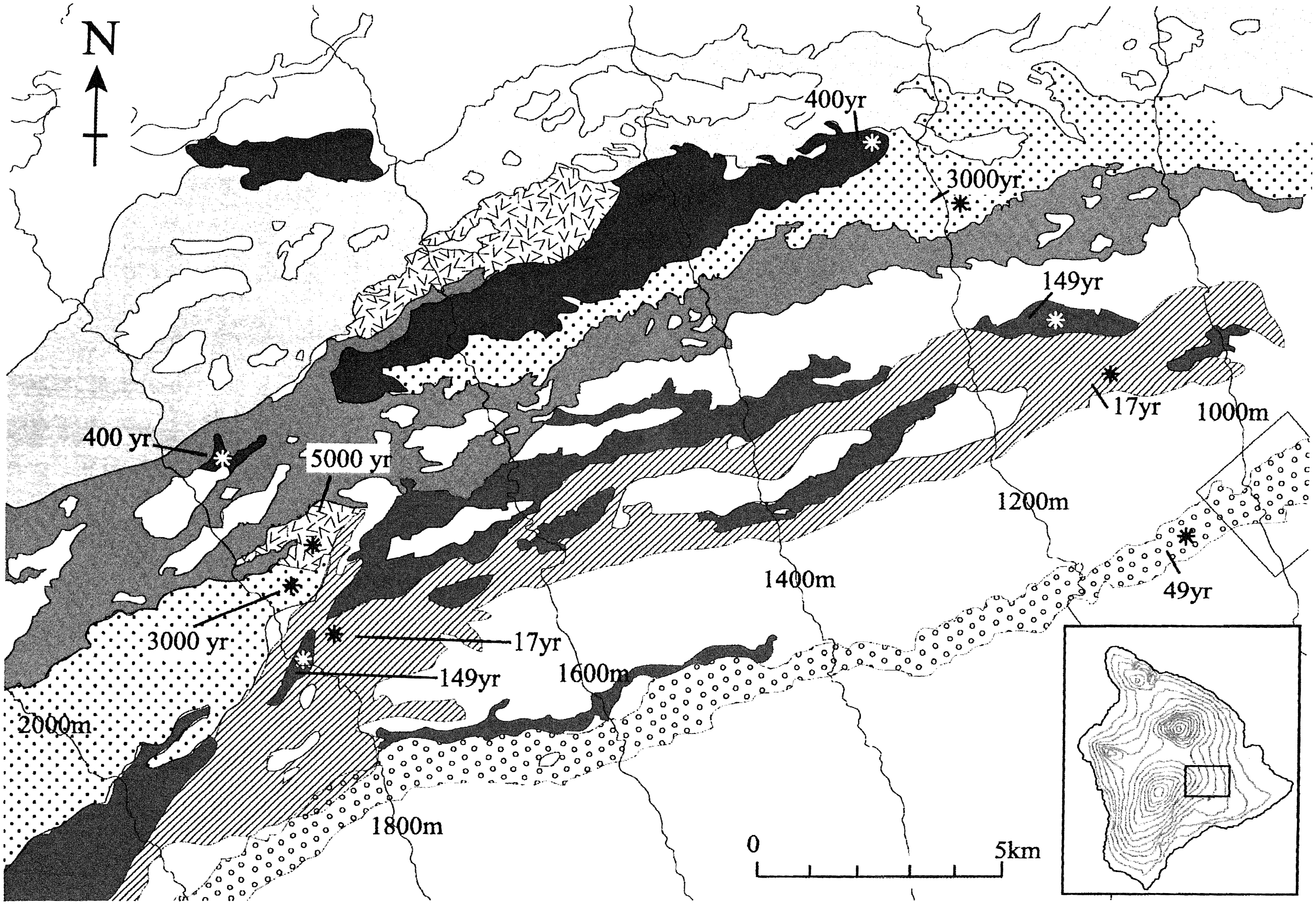


Figure 7.6 site map of the two chronosequences on the east aspect of Mauna Loa.

7.2.3. Foliar Nitrogen in plant species along a chronosequence at two elevations (1800m and 1000m).

A large subsample of the leaf material gathered from each of the sites (Fig 7.6) during the nitrate reductase experiment (Section 7.2.2), was oven dried at 70°C for three days and then ground down to a fine powder. Total foliar nitrogen was determined using the same method outlined in section 4.2.8. Three replicates of 0.1g of finely ground samples of the commonest plant species *(M.polymorpha, C.ochracea, V.reticulatum, M.lessertiana and H.centranthoides*) were taken to Liverpool University for analysis. These samples were acid digested, distilled and titrated as described by Allen (1989). These samples were then compared to a standard reference material to determine the accuracy of the method. Variation between sites was then determined using an ANOVA on SPSS 10.0.

7.2.4. Nitrate reductase activity in the leaves of plants under different nutrient regimes

The Nitrate reductase activity in the leaves and roots of the dominant plant species present on a site subjected to fertilisation experiments, (Vitousek *et al* 1993), was determined to contrast nitrate reductase activity under different nutrient regimes. The fertilisation experiment begun in 1985 by Vitousek *et al* (1993) established a complete factorial fertilisation experiment on several sites over a chronosequence of lava flows in order to test how limiting nitrogen, phosphorous and all other essential nutrients (in a combined fertilisation treatment) are during primary succession on Hawaii. They found the most limiting factor to plant growth was nitrogen as significant growth was observed in plants on the youngest N fertilised plots. However this growth declined on the older flows, an indication that N becomes less limited on the older flows. As a result a comparison of the nitrate reductase activity in leaves on different experimental plots will test how the plants nitrate reductase activity reacts to the increased nutrient availability.

The site is located at an altitude of 1190m, near the Thurston lava tube on the edge of the Kilauea Iki crater (Fig 7.7). An explosive eruption of Kilauea Iki in the year 1790 deposited a 30-40cm layer of coarse tephra overlying a several hundred year old pahoehoe flow. The site has an annual precipitation of 2500mm (Giambelluca *et al* 1986) and is dominated by 14-16m tall forest of *M.polymorpha*, with an understory dominated by the tree fern *Cibotium glaucum* and wild ginger (*Zingiber zerumbet*).

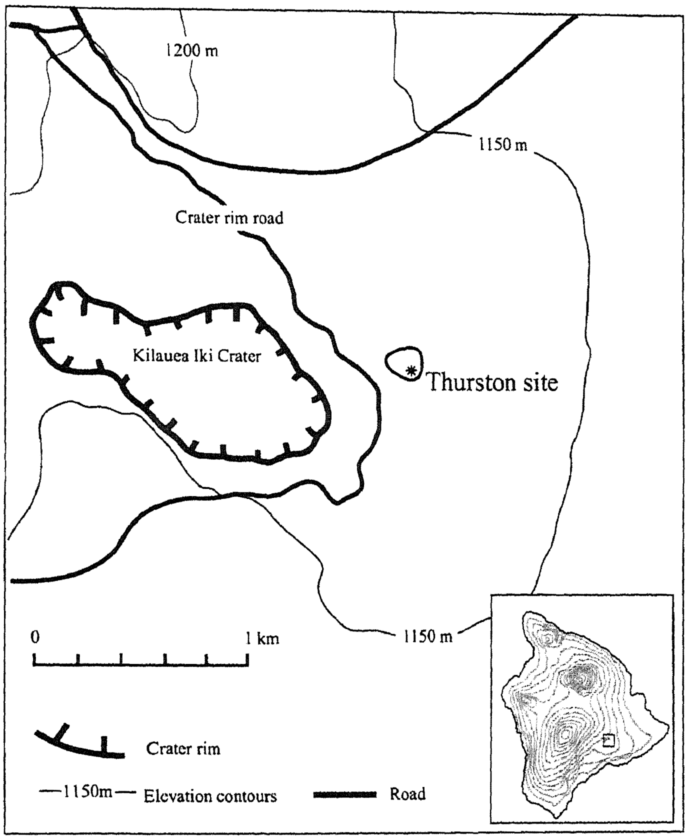


Figure 7.7. Site map for the Thurston nitrate reductase experiment.

For the purposes of this experiment samples were taken from the control and nitrogen treatments only – as nitrogen is the nutrient most likely to affect NR activity. The treatments were nitrogen (initial application 10.0g/m^2 as nitrogen, half as urea and half as $(NH_4)_2SO_4$, (Vitousek *et al* 1993). Treatments consisting of 25% of the initial applications were repeated at six month intervals.

Small branches were randomly collected from the top of two trees in each of the four experimental plots. Branches from the taller trees were brought down using a 12 bore shotgun (as used in Vitousek *et al* 1995). The youngest sun leaves from each branch were then selected and all four plots (eight trees) homogenised together for analysis. Nitrate reductase activity in the leaves and roots of *M.polymorpha*, *C.ochracea*, and *M.lessertiana* was determined using the same analytical method outlined in chapter 3.2.3. The NR activity between treatments was statistically analysed with an ANOVA using SPSS 10.0.

7.3. Results

7.3.1. Nitrate reductase activity in the leaves of plants along a chronosequence at two elevations (1800m and 1000m)

In each of the five species measured for nitrate reductase activity on the slopes of Hawaii there was a low measurement of nitrate reductase activity. However, each species did produce significantly more nitrite than that detected in a blank sample showing that nitrate assimilation was occurring. There was some variation between species with *C.ochracea* and *M.lessertiana* producing the highest readings of around 20 nmol / GFW / hr, whereas *M.polymorpha, H.centranthoides* and *V.reticulatum* all produced less than 10 nmol / GFW / hr. As the readings and the variance for each of these species is so small (e.g. *M.polymorpha* with a variance between 5 and 8 nmol / GFW / hr, compared to *R.scutatus* on Etna which varied between 250 and 500 nmol / GFW / hr) the variation between sites and samples is insignificant. All the data is included here in graphical form but it would be difficult to try and draw any conclusions from such low readings and variation except that nitrogen is limited on all sites investigated.

This method was thoroughly tested in the laboratory in Hawaii against a sample of a *Buddlea* sp. (this genus is a known large NR producer) which detected a large amount of activity (over 500 nmol / GFW / hr). This proved that that the methodology and chemical reagents were functioning as normal but the low readings were consistent from the Hawaiian species and sites examined. This low reading was discovered in all the Hawaiian plants tested on the recent (0-500year old) lava flows.

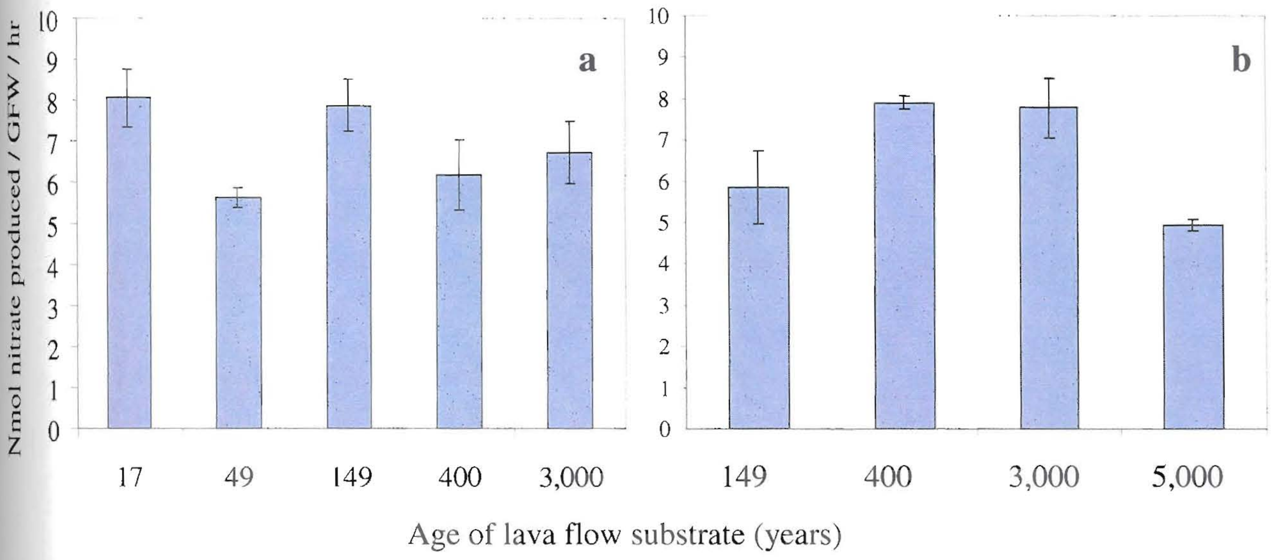


Figure 7.8. Nitrate reductase activity in the leaves of *Metrosideros polymorpha* on sites of increasing age at two altitudes where **a** is 1000m and **b** is 1800m

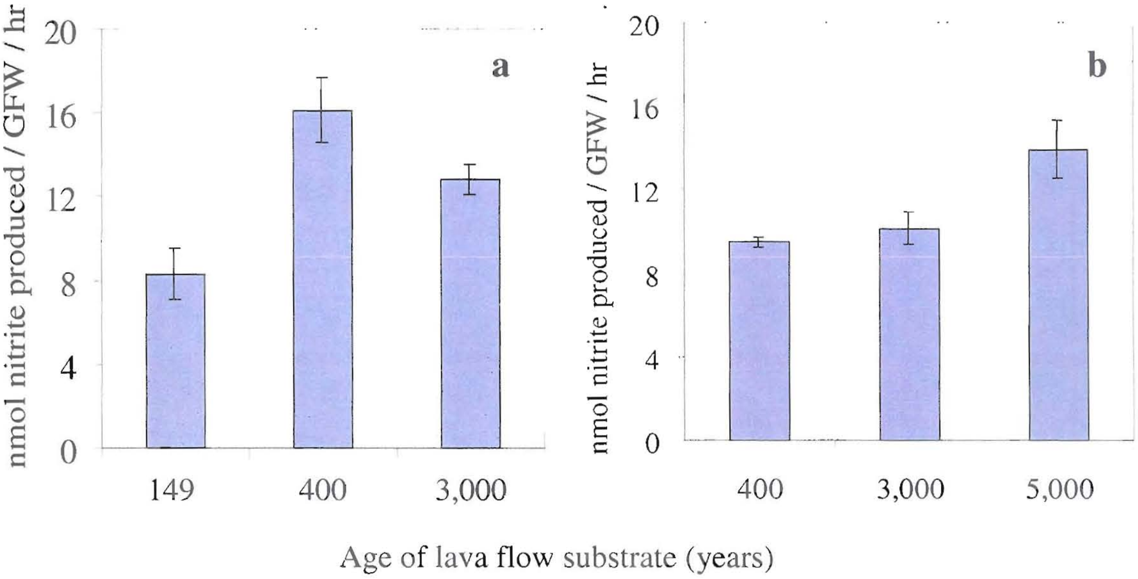


Figure 7.9. Nitrate reductase activity in the leaves of *Coprosma ochracea* on sites of increasing age at two altitudes where **a** is 1000m and **b** is 1800m

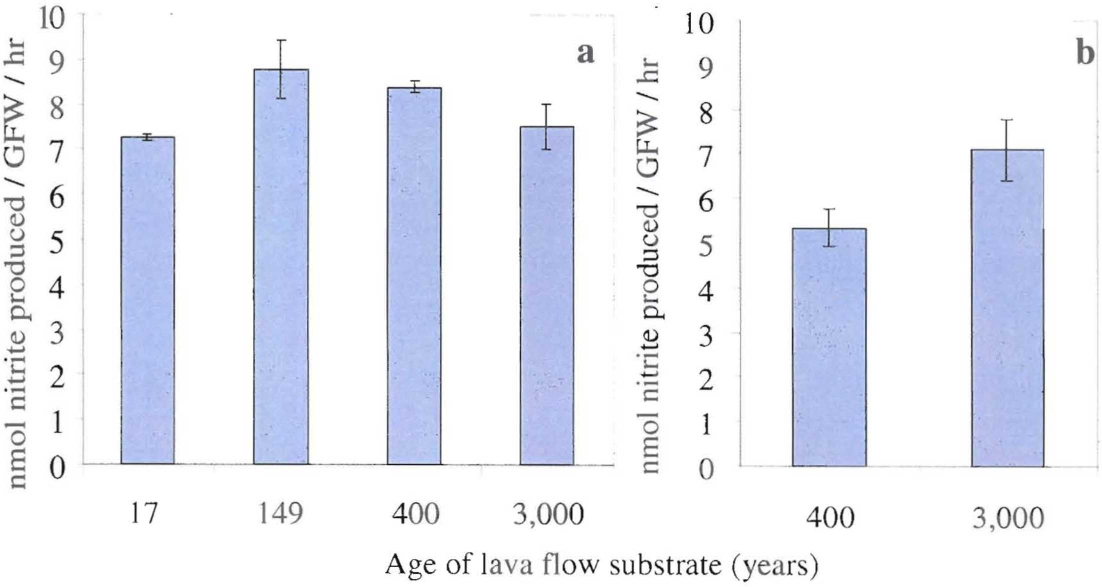


Figure 7.10. Nitrate reductase activity in the leaves of *Vaccinium reticulatum* on sites of increasing age at two altitudes where **a** is 1000m and **b** is 1800m

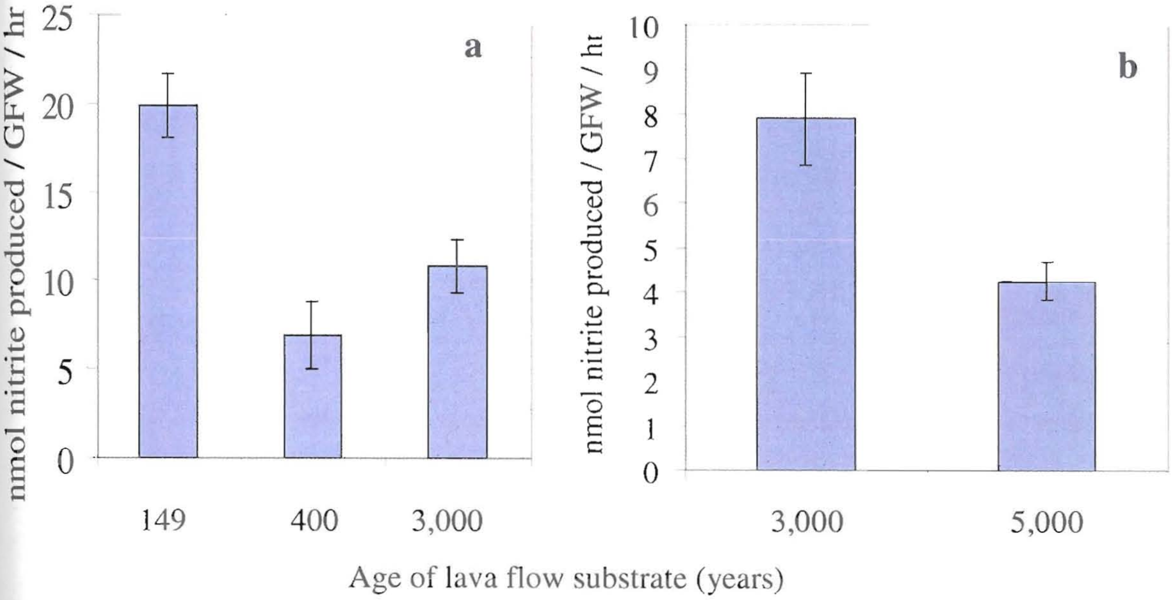


Figure 7.11. Nitrate reductase activity in the leaves of *Myrsine lessertiana* on sites of increasing age at two altitudes where **a** is 1000m and **b** is 1800m

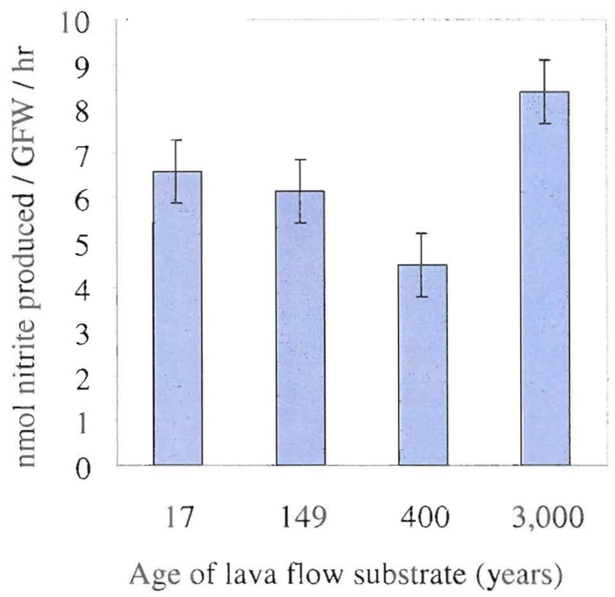


Figure 7.12. Nitrate reductase activity in the leaves of *Hedyotis centranthoides* on sites of increasing age at an altitude of 1000m.

7.3.2. Foliar Nitrogen in plant species along a chronosequence at two elevations (1800m and 1000m)

Metrosideros polymorpha:

There was little variation between the readings on the five sites on the 1000m chronosequence for this species. There was a small decrease in nitrogen on the 68 and 148 year old flows (0.5%) Fig 7.13a. However, there was considerable difference between the three sites at 1800m with the highest reading on a 3000 year old flow (0.9 %) and the lowest on the 1852 flow (0.2 %) see Fig 7.13b.

Coprosma ochracea:

The foliar nitrogen in *C.ochracea* was highest in the 148 year old 1000m site leaves (1.3%) and then decreased on the 400 rear old flow to 0.9% (Fig 7.14a). There a small increase in the nitrogen in the leaves on the 1800m flows with a reading of 0.9 (400 yrs, 1000m) and 1.4 % (400m 1800m); 1.0% (3,000 yrs, 1000m) and 1.2% at 1800m (Fig 7.14b).

Vaccinium reticulatum:

This species shows an opposite to *C.ochracea* with a lower level of nitrogen found in the leaves at the higher altitude (1.2% at 400yrs 1000m; 0.6% at 400yrs 1800m) and 1.2% at 3,000yrs 1000m; 0.6% at 3,000yrs 1800m) see Fig 7.15.

Myrsine lessertiana:

At 1000m these appears to be a slow increase in foliar nitrogen in *M.lessertiana* with age (Fig 7.16a). As this is a much rarer tree species it could be argued that as this is an old growth species it is better at competing in the fully developed (3,000 yr. old) forests rather than in the primary (1-100 yrs old). There is no significant difference between the two altitude readings (only on the 3,000 yr. old flow) which are both at about 0.9 %

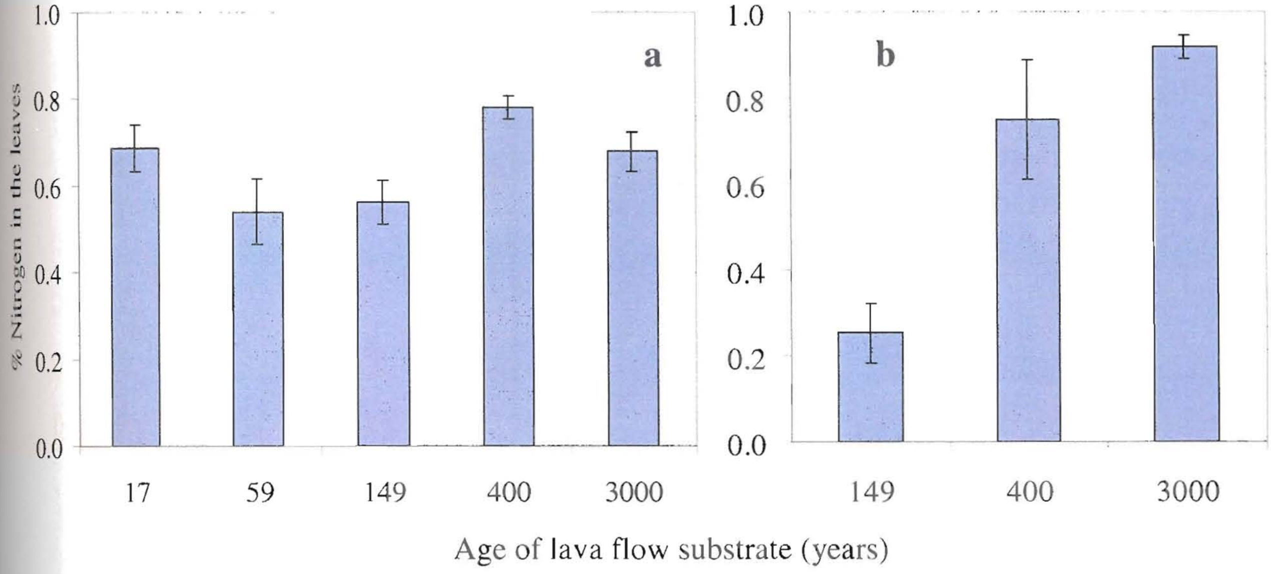


Figure 7.13. Total foliar nitrogen in *Metrosideros polymorpha* on sites of increasing age at two altitudes where **a** is 1000m and **b** is 1800m

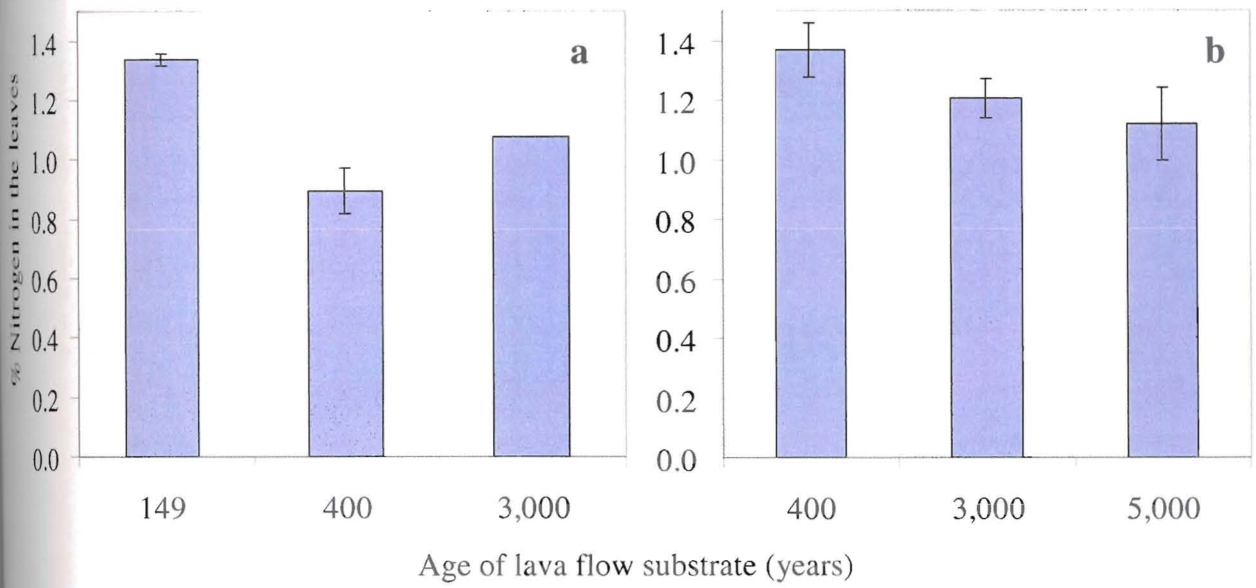


Figure 7.14. Total foliar nitrogen in *Coprosma ochracea* on sites of increasing age at two altitudes where **a** is 1000m and **b** is 1800m

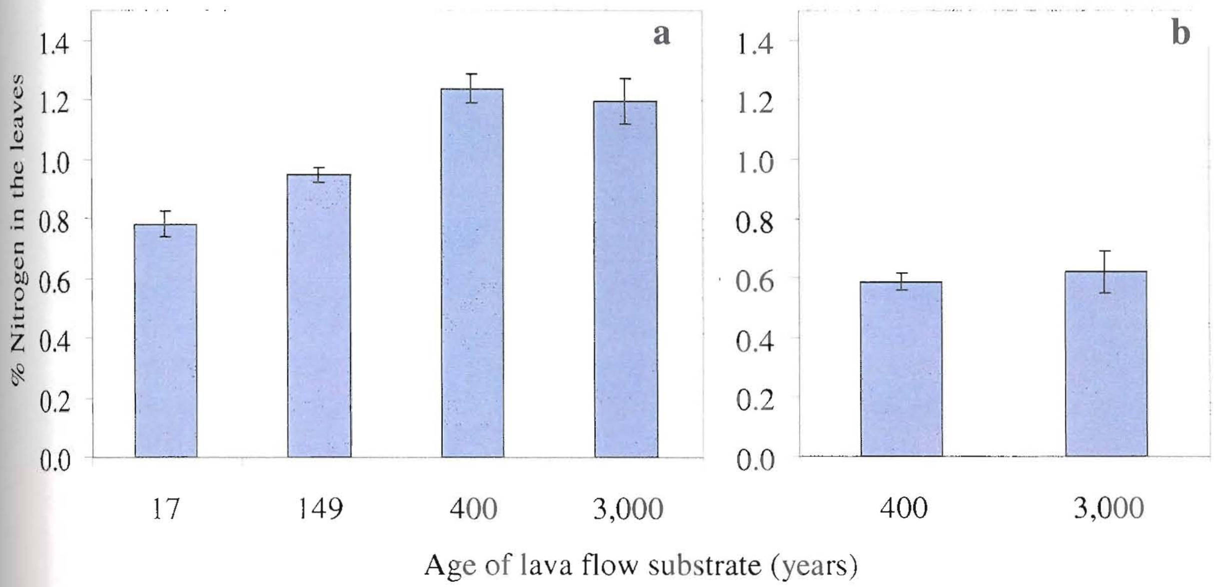


Figure 7.15. Total foliar nitrogen in *Vaccinium reticulatum* on sites of increasing age at two altitudes where **a** is 1000m and **b** is 1800m

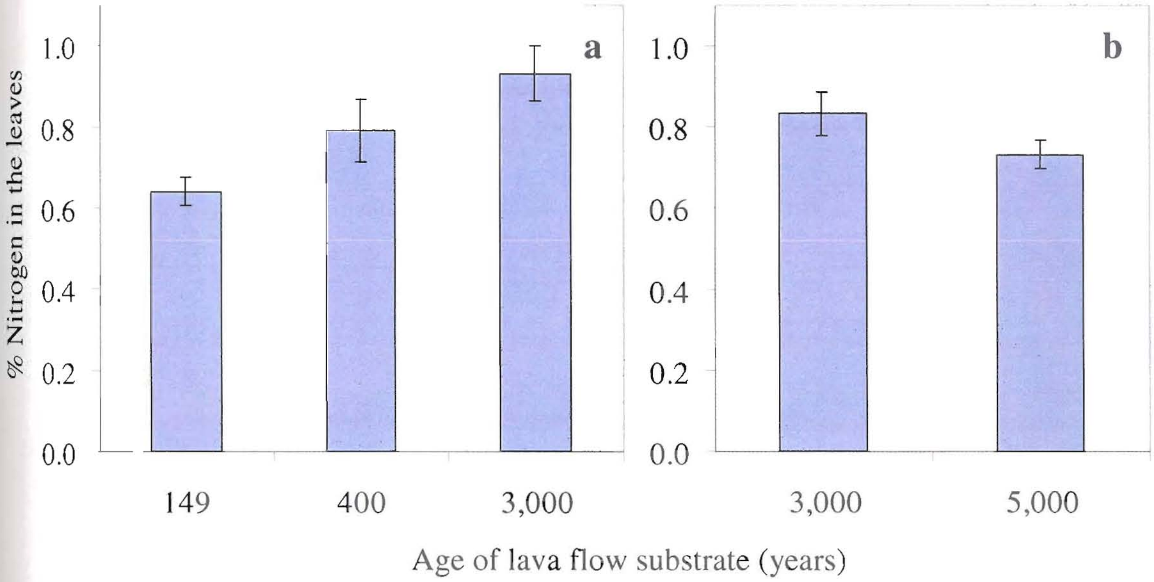


Figure 7.16. Total foliar nitrogen in *Myrsine lessertiana* on sites of increasing age at two altitudes where **a** is 1000m and **b** is 1800m

Hedyotis centranthoides:

H.centranthoides is a much rarer understory plant which showed a significant rise in foliar nitrogen between the 2 younger flows (1.2% at 16 and 148 yrs old) and 1.8 on the 400 year old flow. This species was not found on the higher altitude sites (Fig 7.17).

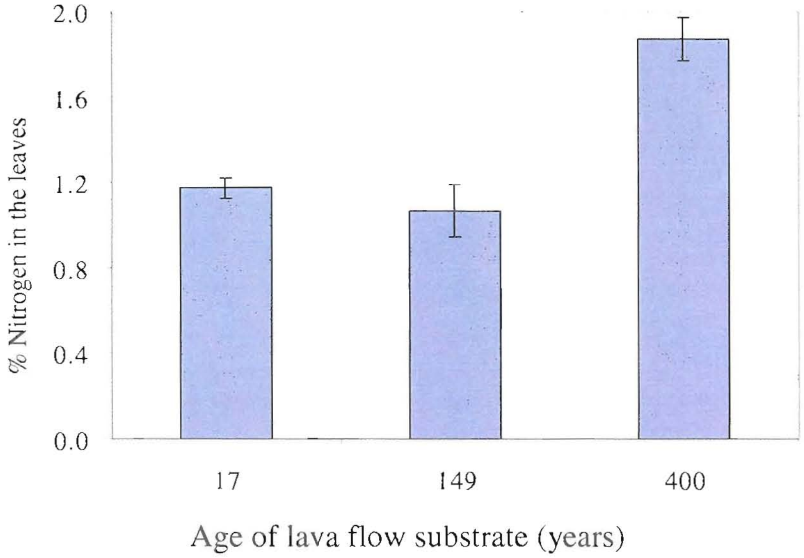


Figure 7.17. Total foliar nitrogen in *Hedyotis centranthoides* on sites of increasing age at an altitude of 1000m

7.3.3. Nitrate reductase activity in the leaves and roots of plants under different nutrient regimes

In a comparison of the leaves and roots of plants growing on the Thurston site there was no difference for *M.polymorpha* (Fig 7.18a) However, both *C.ochracea* and *M.lessertiana* produced more nitrite in the leaves than in the roots (Fig 7.18b and c). There was no difference between the two nutrient regimes.

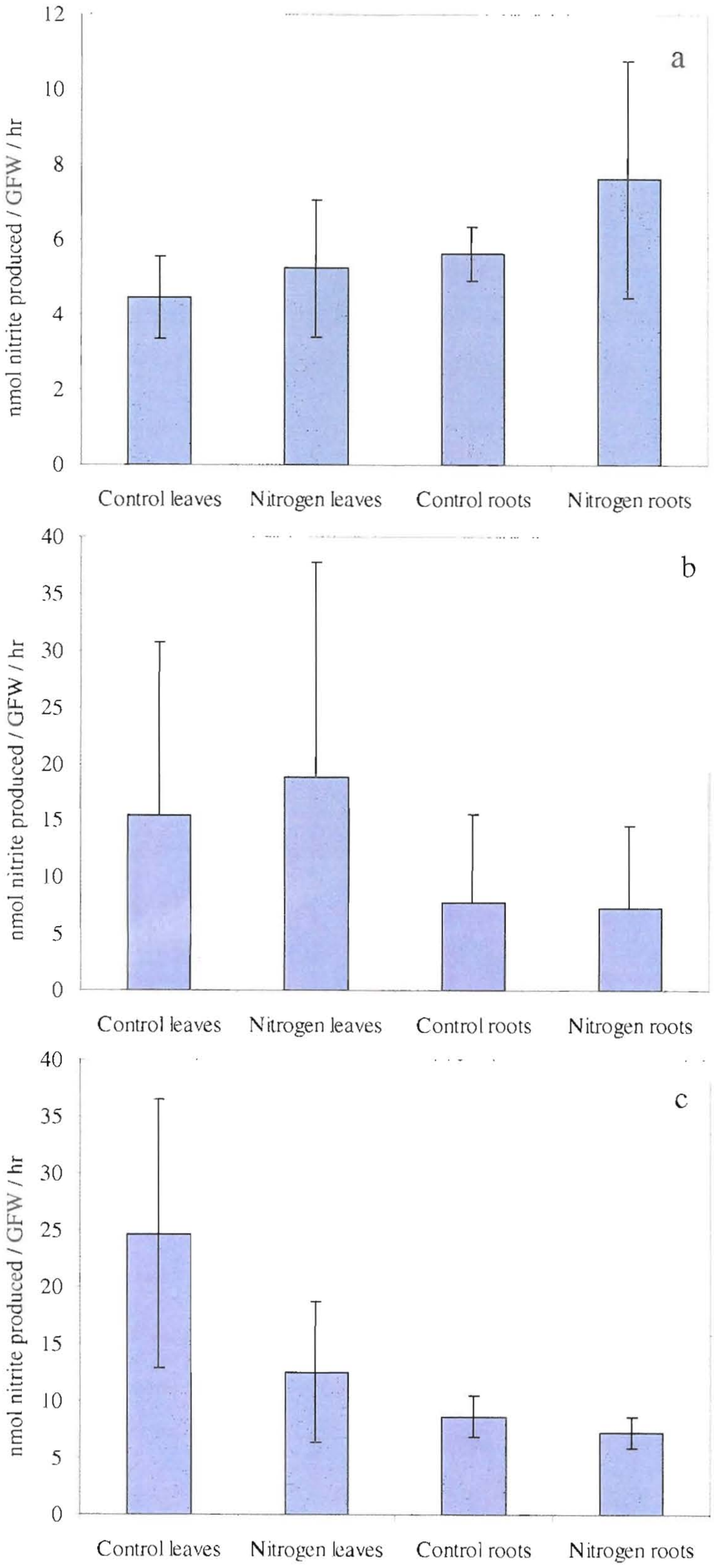


Figure 7.18. Comparison of the Nitrate reductase activity in the leaves and roots of three plant species on two nutrient regimes on Thurston site. **a** *Metrosideros polymorpha*, **b** *Coprosma ochracea*, **c** *Myrsine lessertiana.*

7.4. Discussion

The surprising low nitrate reductase activity in the leaves of native plant species on Hawaii makes it difficult to draw any firm conclusions about nitrogen assimilation on the slopes of Hawaii. However, as the low readings were discovered in all the Hawaiian plants tested this indicates that nitrogen is very limited on the recent lava flows of Hawaii. The relatively low variance between sites for the total nitrogen in the leaves suggests that even on the older (400 and 3,000 year old) sites the plants are competing for a relatively small supply of nitrogen. It is likely that although the nitrogen in the system has increased over this period, the greater competition due to the larger diversity and mass of plants makes nitrogen very limited on an individual plant basis. This is supported by Chadwick *et al* (1999) which shows a slow increase in total nitrogen over the time of their chronosequence (many thousands of years). However, the sites included in this study in the 0-500 year range (even including the additional 3,000 year old samples) are clearly still so nitrogen limited that there is very little variation between the plants found on these chronosequences.

This low nitrogen availability is a common occurrence in tropical ecosystems where most of the available nutrients in the system are bound up in the plant biomass and nutrient cycling processes or leached out by the high rainfall (Vitousek 1982; Austin and Vitousek 2000). This low nitrogen availability on the recent lava flows of Hawaii has been shown many times in numerous studies (Vitousek 1994; Kitayama 1996).

One possible explanation for the low nitrate reductase readings is that as nitrogen is so limited on these flows that nitrate reductase in the leaves may be reduced to a low level in each species leaves. All the plants will be 'primed' with the same low level of nitrate reductase. This enzyme is metabolically expensive to construct and hence on the limited nitrogen flows all the plants will have reduced levels of NR in their leaves. The different levels of nitrate reductase activity between the species would support this argument, as each has a different 'minimum level' of nitrate reductase. This could be tested by examining leaves from plants grown on much older nutrient rich sites or from plants grown in the laboratory under different nutrient regimes.

The lack of response between the samples from the different nutrient plots on the Thurston site, is most likely a factor of the time lapse since the last nutrient treatment. As stated in Vitousek *et al* (1993) there was an initial treatment of nutrients followed by repeated additions at further 6 monthly intervals. However, when this experiment was conducted it was just coming up to the time for the next treatment – so it had been nearly six months since the last application of nitrogen. As a result all the applied nitrogen has probably already been bound up into the biomass of the plants existing on the site and is therefore equally limited on both experimental plots. This experiment should be repeated shortly after the next application of nutrients to determine if there is a nitrate reductase response to the addition of nutrients.

The lack of a detectable variation in the nitrate reductase activity on Hawaii is not reflected in the foliar nitrogen experiments. *V.reticulatum*, *M.lessertiana* and *H.centranthoides* all show a small increase in foliar nitrogen over time on the chronosequence at an altitude of 1000m. In addition, the foliar nitrogen in *M.polymorpha* (Fig 7.13a) shows a higher level of nitrogen on the 17 year old flow followed by a drop in nitrogen which then increases steadily. This is similar to the early nitrogen input observed on the Etna lava flows in Fig 3.2. After this early peak there is a decline in foliar nitrogen followed by another gradual rise with increasing age of the flow. Foliar nitrogen measurement, is a much less temporally variable measurement of nitrogen than using nitrate reductase. This gradual increase in nitrogen is similar to that found in Vitousek *et al* (1983); Vitousek *et al* (1989); Vitousek (1999); Crews *et al* (1995).

Chapter 8: Lichen weathering rates on lava flows of Hawaii. With further comparison of weathering rates with Mt.Etna

8.1. Introduction

8.1.1. Purpose of the experiment

Lichen weathering of the lava surface on Mt.Etna was studied in chapter 6 and was found to cause extensive micro-morphological changes in surface texture and surface area which aided further colonisation by increasing water retention, and creating cracks and crevices for further plant colonisation. In addition, the weathering of the lava releases valuable trace elements, which aid further colonisation. The purpose of this experiment was to demonstrate that the same processes of lichen weathering during primary succession are also occurring on Hawaii. This study primarily looks at the differences between two different chronosequences on the big island of Hawaii, which are located in two distinct climate zones, one extremely wet (east aspect) and one dry (south-west aspect) Fig 8.1. By comparing the differences between the weathering of these chronosequences and then further comparing these Hawaiian chronosequences with those found on Mt.Etna an understanding will be gained of the role of lichen weathering in early basaltic lava succession and how this is influenced by the prevalent climate.

In order to compare the two volcanic ecosystems the lichen *Stereocaulon vulcani* was selected for study on the lava flows of Hawaii. This species is common on the recent lava flows of Mauna Loa and is very similar to *S.vesuvianum* on Etna, filling the same ecological niche.

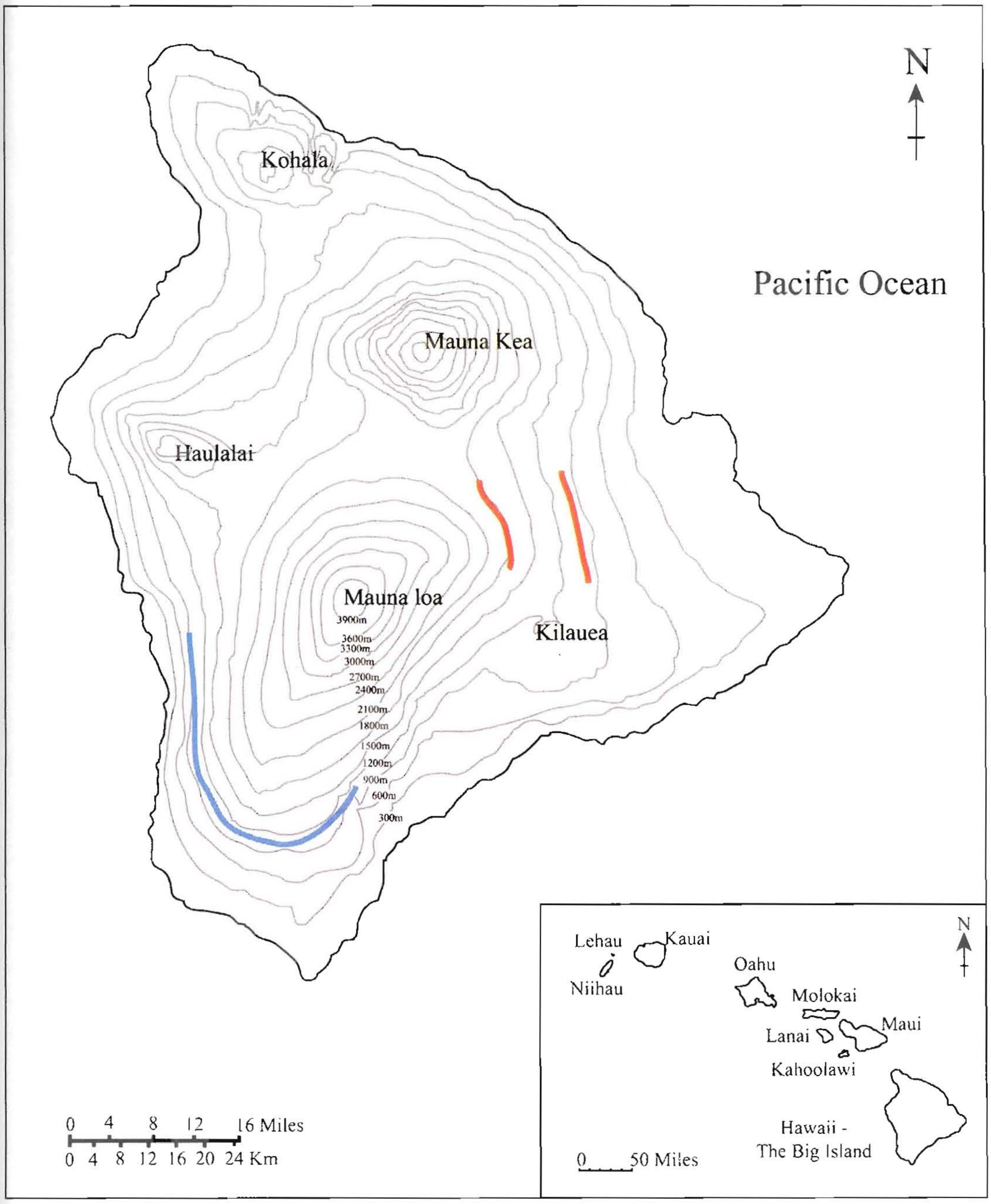


Figure 8.1. Location of the chronosequences on Hawaii. The wet eastern sites at 1000m and 1800m (red lines) and the dry south western sites at 600m (blue).

8.1.2. Stereocaulon vulcani

One of the commonest occurring lichen species on Hawaii, *S.vulcani* (Fig 8.2) is very similar in structure and habitat to *S.vesuvianum* on Etna. *S.vulcani* is common on the young aa lava flows (Uhe 1988). It is a tripartite symbiont involving the fungus *Stereocaulon vulcani*, the green algae *Trebouxia irregularis* and a cyanobacterium in the genus *Stigonema* (Kurina and Vitousek 1999). Investigations into the biomass of this lichen have shown that its abundance is linked to precipitation on the lava flows of the east side of Mauna Loa (Kurina 1998; Kurina and Vitousek 1999). This species is a demonstrated nitrogen fixer (Kurina and Vitousek 2001).

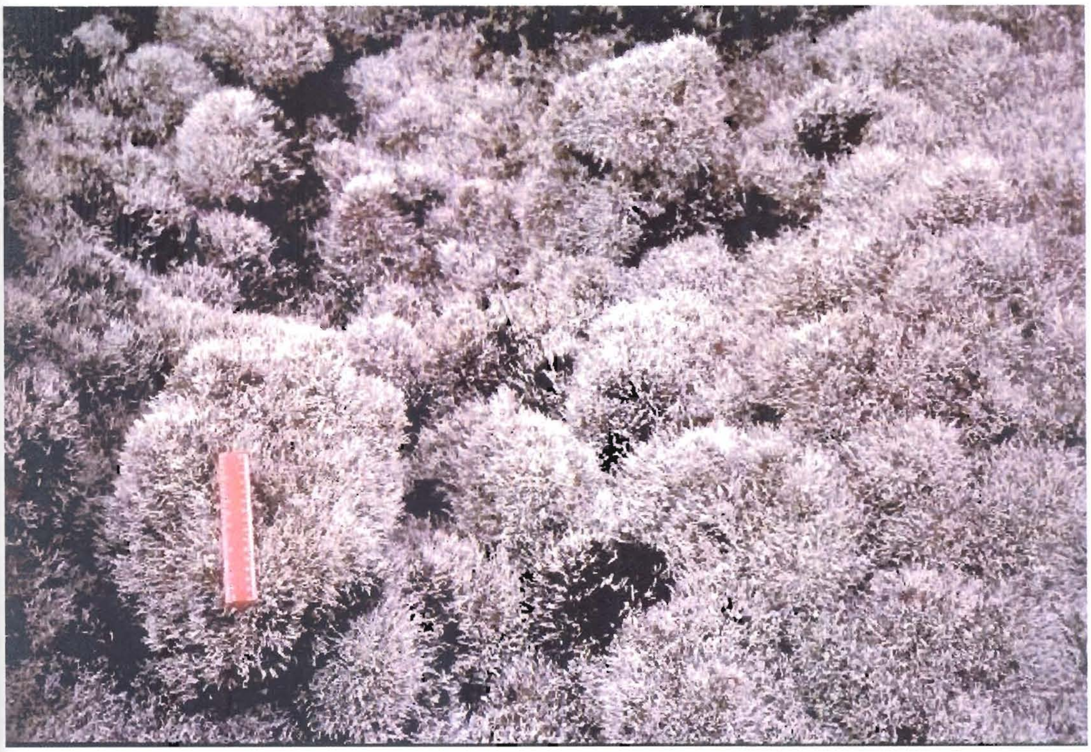


Figure 8.2 *Stereocaulon vulcani* growing on the 1984 Mauna Loa lava flow at an altitude of 1000m (Picture taken by M.Carpenter)

8.2. Methods

8.2.1. Lichen weathering of the eastern wet chronosequence

Samples of lava were taken from five sites of aa lava on the eastern wet side of Mauna Loa located at two different altitudes. Sites sampled were:

1000m : 1984 (17 year old), 1942 (59 year old) and 1852 (149 year old).
1800m : 1984 (17 year old) and 1852 (149 year old). See Fig 7.6 for site map

Each site was sampled using the same methodology for site selection as used on Mt.Etna (topography, distance from the edge of flow and lava morphology) as outlined in 2.2.1 and 6.2.1. These samples were then photographed under a Scanning electron microscope at x200 magnification as outlined in 6.2.2. All the samples for the project were taken from lava covered in *S.vulcani.*

8.2.2. Lichen weathering of the western dry chronosequence

Samples of lava were taken from eight sites of aa lava on the dry east, and southeast coast of Hawaii. All sites were located at the same altitude of approximately 600m. Lava flows sampled were:- 1974 (27 year old), 1950 (51 year old), 1926 (75 year old), 1919 (82 year old), 1907 (94 year old), 1868 flow (133 years old), 200 year old and 750-1500 year old lava (Fig 8.3). Each site was sampled using the same methodology as those taken from Mt.Etna (topography, distance from the edge of flow and lava morphology) as outlined in 2.2.1 and 6.2.1. These samples were then photographed under a Scanning electron microscope at x200 magnification as outlined in 6.2.2.

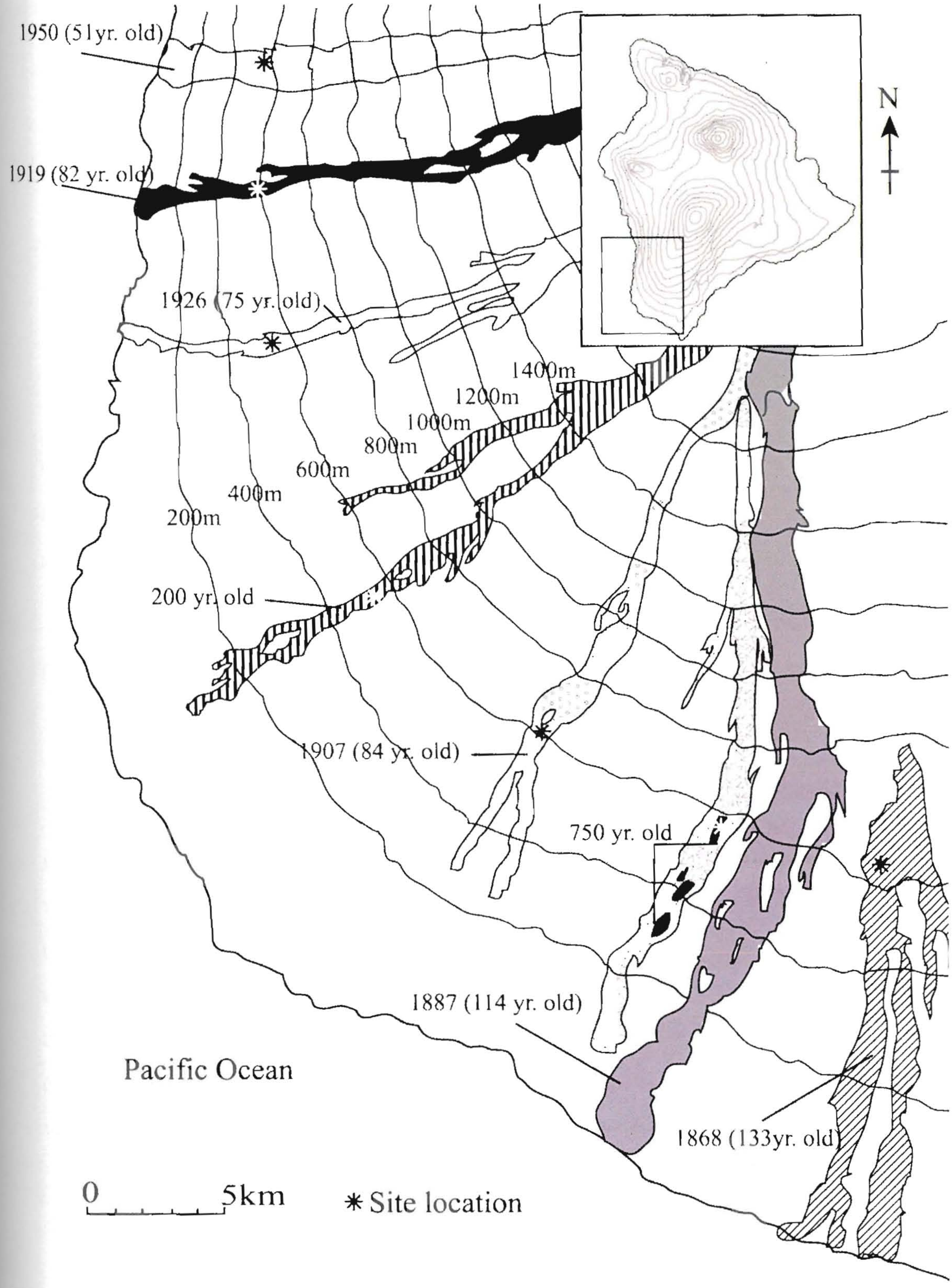


Figure 8.3. Site map for the dry west chronosequence

8.2.3. Comparison of weathering between lichen weathered and non-lichen weathered rocks

On the west 1950 (51 year old) lava flow there was a very clear zonation of the lichen on many of the larger boulders. The lichen mainly grew well on the sheltered east facing side of the lava, but gradually declined in abundance on the other aspects of the rocks until the west facing side was totally barren. This resulted in a good opportunity to compare the effects of lichen weathering of lava with that of un-lichenised rock. Samples of lava from the different aspects, were taken from boulders on the 1950 east lava flow using the same methodology as those taken from Mt.Etna (6.2.1). These samples were then photographed under a scanning electron microscope at x200 magnification as outlined in 6.2.2.

8.2.4 Machine vision comparison of the weathering of lava by *S.vulcani* on Hawaii with the south chronosequence of Etna

Samples taken from three of the sites on the eastern chronosequence of Hawaii were compared using the intelligent machine vision system with the weathered samples of lava taken from the south chronosequence of Mt.Etna as used in 6.3.5. This will confirm if *S.vulcani* weathers the lava in a similar fashion to *S.vesuvianum* (on Etna). In addition it will measure the extent of weathering on the Hawaiian lavas in comparison with the weathering rate of the southern chronosequence of Etna – directly comparing the weathering rates of the two volcanoes

8.3. Results

8.3.1. Lichen weathering of the eastern wet chronosequence

The three sites on the 1000m chronosequence (Fig 8.4) show a clear progression of rock weathering from a relatively smooth unweathered surface (1984) through an initial cracking and further disintegration as the lava surface is split into fine flakes of rock giving a more ‘aggregate’ structure. The two samples at 1800m show a similar trend with the smooth ‘blocky’ 1984 (Fig 8.5a 17 year old) surface structure being replaced by the cracked and pitted 1852 surface (Fig 8.5b) the descriptive terms are based on Heikens and Wohlentz (1985).

A comparison of the two 1984 flow samples at the two altitudes show greater weathering on the 1000m flow (Fig 8.4a) than on the 1800m altitude (Fig 8.5a). The higher 1800m flow shows a relatively smooth surface, whereas the 1000m sample shows a much finer etching of the lava surface. Similarly, a comparison of the two 1852 lava flow samples (149 years old) at the two altitudes show a greater extent of weathering at the 1000m (Fig 8.4c) altitude than at the higher 1800m (Fig 8.5b)

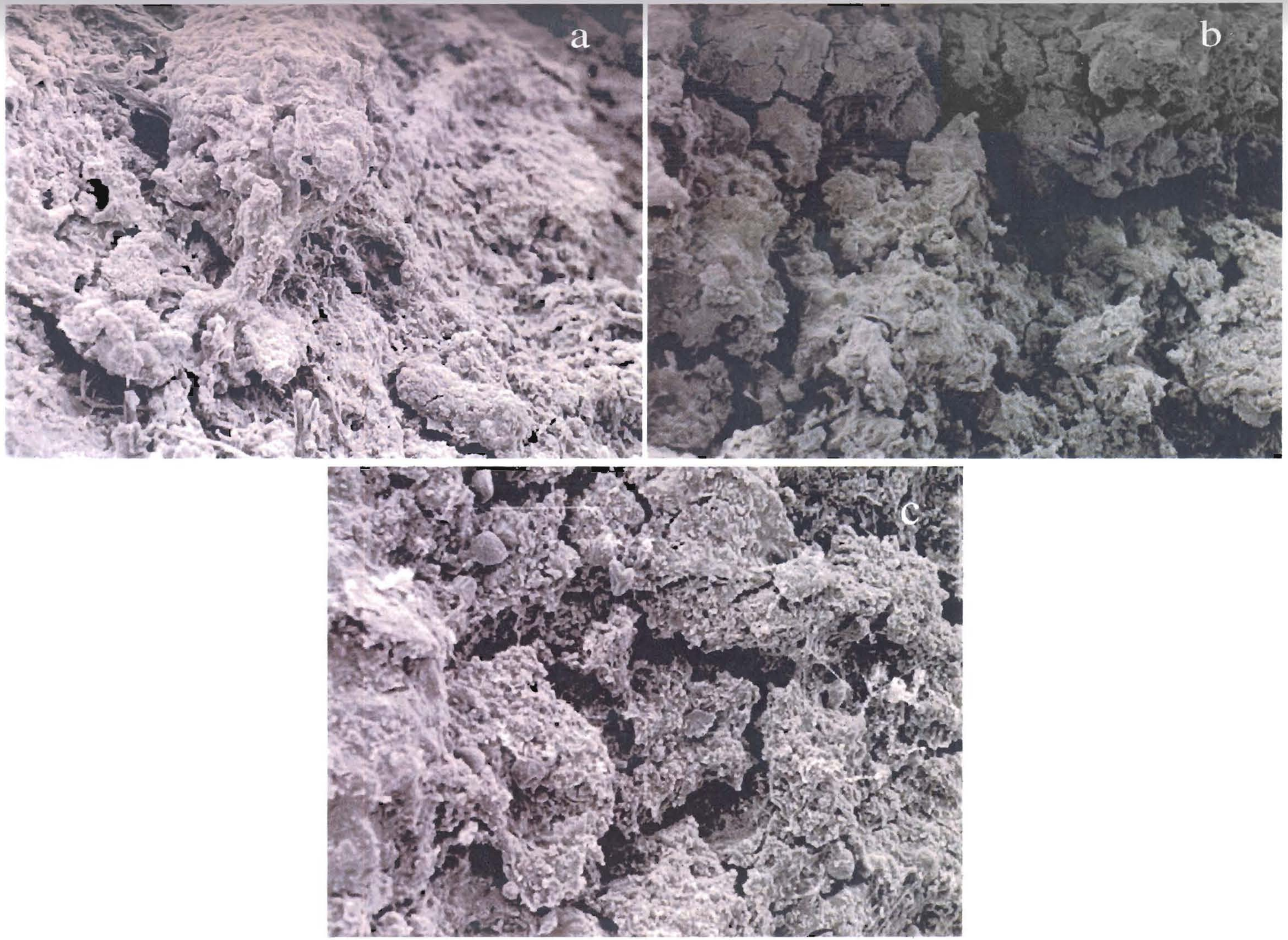


Figure 8.4. Lichen weathering along the eastern chronosequence of Hawaii at an altitude of 1000m Where **a** is the 1984 flow (17 years old), **b** is the 1942 flow (59 years old); **c** is 1852 flow (149 years old). Magnification x200

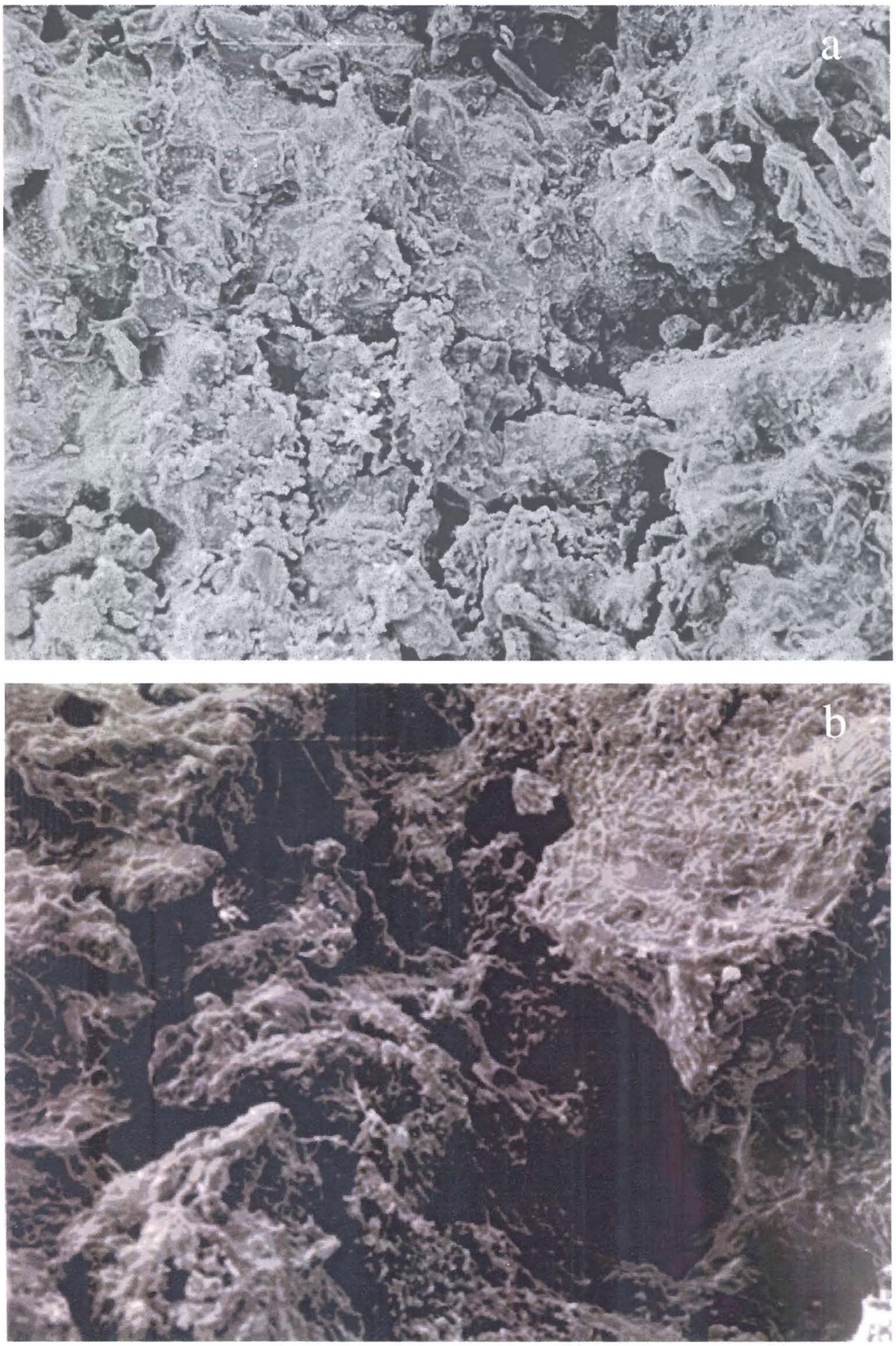


Figure 8.5. Lichen weathered samples from the 1800m chronosequence on the east side of Hawaii. Where **a** is the 1984 flow (17 years old) and **b** is the 1852 flow (149 years old). Magnification x200.

8.3.2. Lichen Weathering of the western dry chronosequence

There is a very clear progression in the weathering by lichen activity on the western chronosequence. This can be seen in Figs 8.6a - 8.6h, where there is an initial slow period of weathering from the initial glassy surface (Fig 8.6a) through minor surface weathering (Fig 8.6c etched surface) which increases as the lichen becomes more dominant on the 1919, 1926 and 1950 flows. After this period the lichen abundance is slowly declining (although it persists for longer than on the east chronosequence where the *S.vulcani* disappears after 100 years). Many patches on these later sites remain surprisingly bare of vascular plants (due to the low rainfall) but weathering continues as demonstrated in the 200 and 750 year old flows.

The extent of weathering on this eastern chronosequence does not achieve the 'aggregate' like fine flake structure found on the 1852 flow on the east 1000m flow.

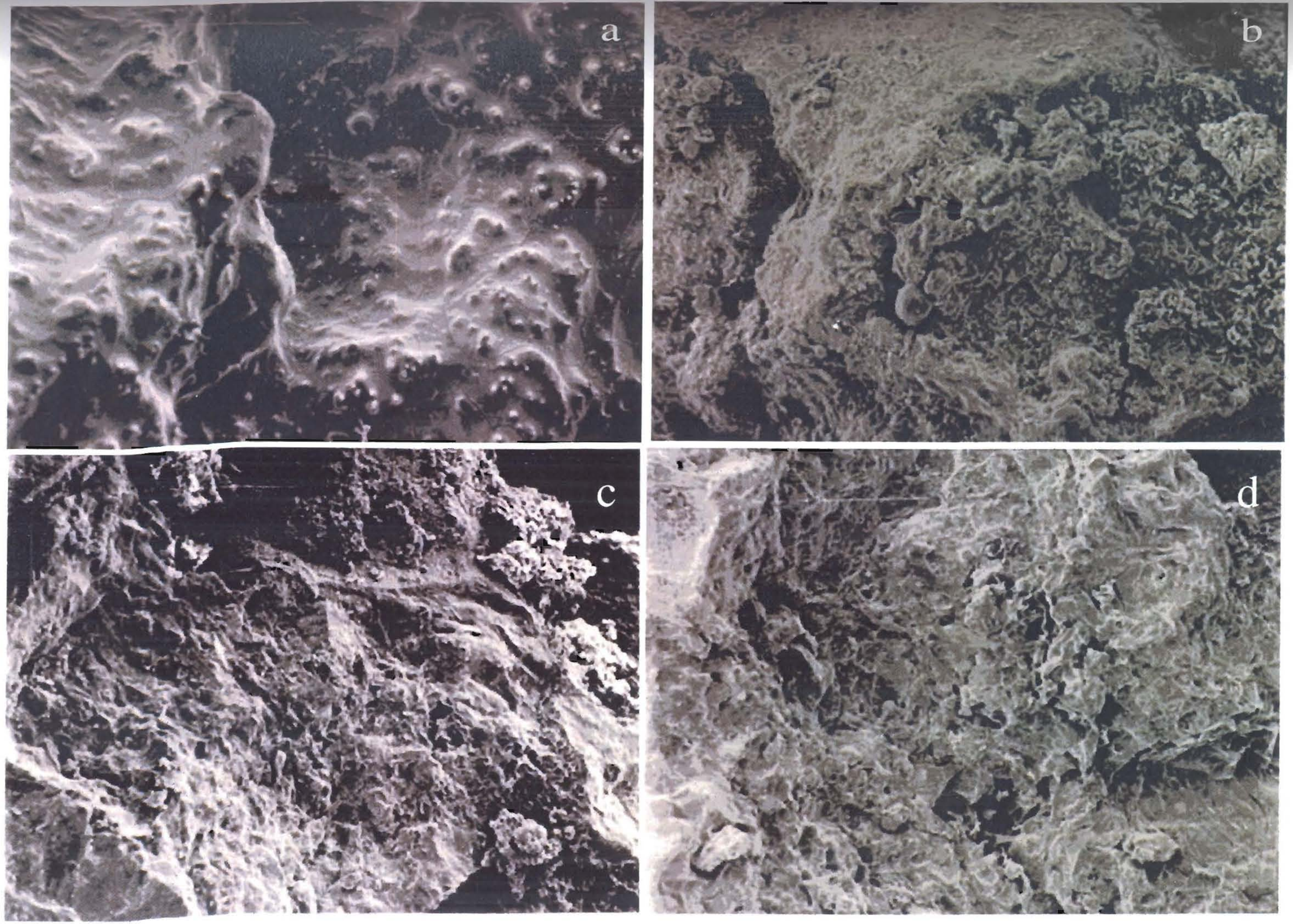


Figure 8.6. Lichen weathering along the south western chronosequence of Hawaii. Where **a** is the 1974 flow (27 years old), **b** is the 1950 flow (51 years old); **c** is 1926 flow (75 years old) and **d** is 1919 flow (82 years old). Magnification x200

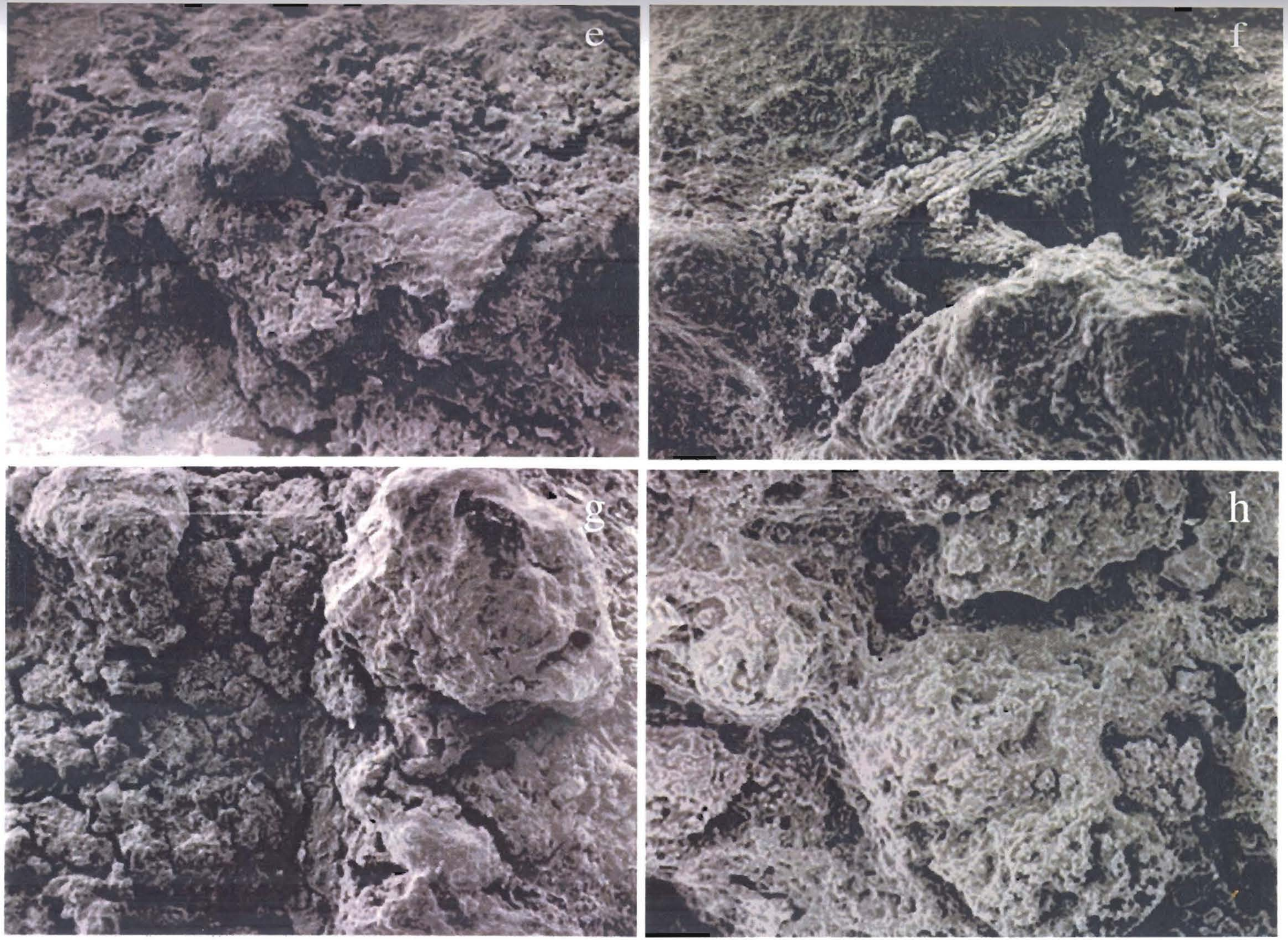


Figure 8.6.continued Lichen weathering along the south western chronosequence of Hawaii. Where **e** is the 1907 flow (94 years old), **f** is 1868 flow (133 years old); **g** is an estimated 200 year old flow and **h** is an estimated 750-1500 year old. Magnification x200

8.3.3. Comparison of weathering between lichen weathered and non-lichen weathered rock

There is a clear difference between samples taken from two different aspects of a large lava boulder on the 1950 east lava flow. The lichenised rock surface shows the distinctive pitting and surface cracks associated with lichen weathered rock (Fig 8.7.a). Whereas the un-lichenised rock surface was much smoother with only a little pitting and no cracking or flaking of the surface (Fig 8.7.b). This proves that the lichen is weathering the rock surface faster abiotic factors alone.

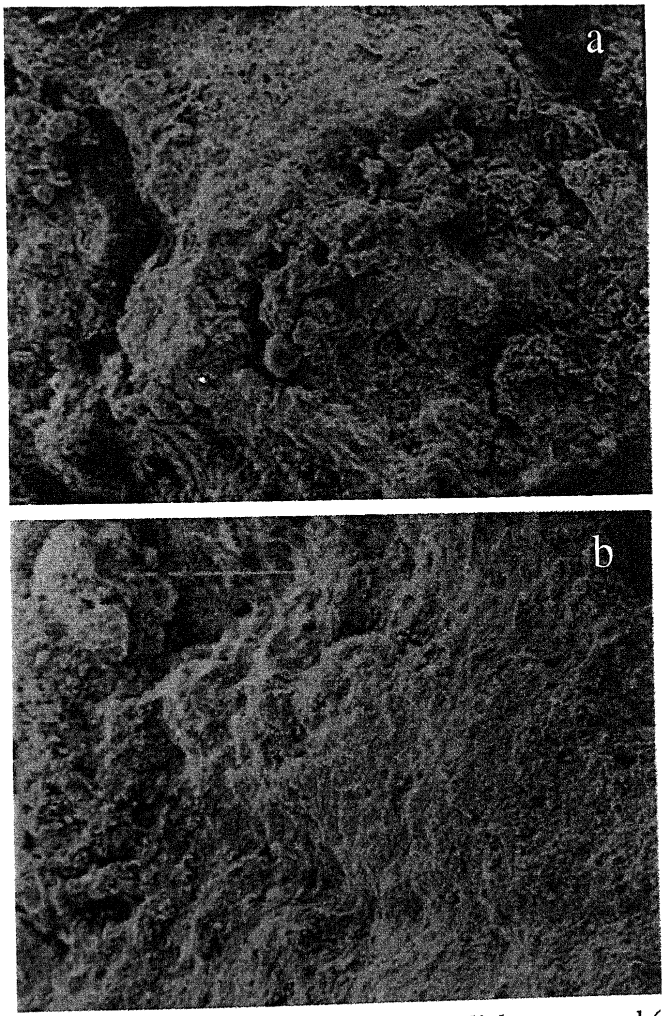


Figure 8.7. A comparison of weathering between a lichen covered (**a**) and a non-lichen covered (**b**) sample taken from the 1950 east lava flow. x200

8.3.4. Machine vision comparison of the weathering of lava by *S.vulcani* on Hawaii with the south chronosequence of Etna

The pattern and morphology of the weathering of the lava by *S.vulcani* on the lava of Hawaii was practically identical to that caused by *S.vesuvianum* on Etna. Three samples from the east wet chronosequences were compared to the Etna south chronosequence baseline as used in 6.3.9. These samples were chosen as they were dominated by the lichen *S.vulcani* and were very similar to the Etna flows of roughly the same age. These flows also covered two different rainfall regimes on Hawaii, (4000mm at 1000m and 2000mm at an altitude of 1800m see Fig 7.4). The results matched the three Hawaiian samples with the closest matching weathered lava from the southern chronosequence of Etna.

The 1984 (1800m) sample from Hawaii was a very good match to the 1983 (1000m) lava flow on Mt.Etna (93.76%). The weathering rates of these two sites was identical (Table 8.1). However, the weathering rate of the same lava flow (1984) at the lower altitude of 1000m was a close match to the 1892 lava of Etna – indicating a much faster rate of weathering than that seen on Etna (it took only 17 years to weather the rock to the same degree as 108 years on Etna). The sample from the 1852 lava flow on Hawaii was a close match (95.52%) to the 1892 sample from Etna, showing that the rate of weathering had slowed and was now roughly equal to the rate of weathering on Etna

These weathering data can be compared to the variables of *Stereocaulon* biomass and annual precipitation rates for the sites (Table 8.1). *S.vesuvianum* biomass data has been transformed (Logged) in order to be comparable to the data of Kurina and Vitousek (1999). The data from Kurina and Vitousek (1999) was taken 7 years before this study and so is a rough guide only to the biomass on the 1984 lava flow (which would have increased). However, there would be little change on the 1852 flow – based on the rapid increase followed by slow decline pattern that is typical of *Stereocaulon* (Fig 5.8).

Hawaiian Sample	Intelligent Machine vision match to Etna samples	Weathering rate	Lichen biomass (Log (g/m^2))		Annual precipitation (mm)	
			Etna	Hawaii	Etna	Hawaii
1984 (1000m) east	91.6% match to 1892 South 5.4% match to 1780 South 3% match to 1634 South	Faster than Etna	1892 flow = 3.3 1780 flow = 2.7 1634 flow = 2.1	2.55	1200mm	4600mm
1984 (1800m) east	93.76% match to 1983 South 5.72% match to 1999 South 0.52% match to 1766 South	Equal to Etna	1983 flow = 0 1999 flow = 0 1766 flow = 2.9	0	1200mm	2000mm
1852 (1000m) east	95.52% match to 1892 South 4.48% match to 1634 South	Roughly equal to Etna	1892 flow = 3.3 1634 flow = 2.1 1634 flow = 2.1	0	1200mm	4600mm

Table 8.1. Intelligent machine vision comparison of weathering between the 'fixed baseline' south chronosequence of Etna and three eastern Hawaii samples with comparisons of lichen biomass (Hawaii biomass from Kurina and Vitousek 1999) and annual precipitation (Etna rainfall from Durbin and Henderson-Sellars 1981; Hawaii rainfall taken from Giambelluca *et al* 1986)

From table 8.1, it can be seen that the 1984 1000m lava flow on Hawaii has a biomass of 2.55 (Log g/m^2) (based on 7 year old data which will have increased by the time of this study). This has a 91% match to the 1892 1000m lava flow of Mt.Etna. In essence, the Hawaiian flow at this altitude has produced a biomass comparable to the 1892 lava flow on Etna during only 17 years. This is probably due to the far greater precipitation on this site, which favours the rapid growth of lichens. This difference in biomass can be seen clearly by comparing photographs of two similar aged lava flows: Fig 8.2 shows that *S.vulcani* completely covers the surface of the 1984 Mauna Loa lava at 1000m. In comparison, the 1981 Etna lava flow (Fig 1.2) has little *S.vesuvianum* cover.

When the precipitation is reduced higher up the slope of Mauna Loa (1984, 1800m data) the lichen biomass is also reduced, to a level comparable to the 1983 Etna flow (both reading 0 Log g/m^2). As a result the extent of weathering is also reduced giving an age match to the 1983 lava flow on Etna.

Finally, on the 1852 Hawaiian lava flow the weathering rates match for the 1892 Etna flow. In this case while lichen biomass has declined on Hawaii, it has increased on Etna – in a sense the extent of weathering on Etna has ‘caught up’ with the weathering on Hawaii.

8.4. Discussion

Lichen weathering of the lava of Hawaii by *S.vulcani* shows a similar pattern to that found on Mt.Etna by *S.vesuvianum.* Both species of lichen quickly colonise the rock surface and begin etching / pitting the surface almost immediately. This pattern can clearly be seen by comparing the electron microscope pictures of a chronosequence on Etna (Fig 6.4) with those of Hawaii (Fig 8.4). This close similarity is further confirmed by the results of the computer machine vision analysis. This identified the lichen weathering on Hawaii and grouped it to its nearest match on the Etna baseline chronosequence.

This weathering takes the form of pitting, cracking and eventually flaking of small chunks of the lava to form an 'aggregate' like structure on the surface of the rock (Heiken and Wohletz 1985). This is produced as the lichen penetrates the lava surface by means of organic acids and by physical pressures exerted by the thallus. However, there are clear differences between the weathering rates on the two climatic chronosequences on Mauna Loa. The weathering is fastest on the east facing slopes of Mauna Loa. This is linked to the wet humid climatic conditions in the east which favour the growth of a large *S.vulcani* biomass as opposed to the dry southwest chronosequence where lichen growth is much slower (Kurina 1998). Weathering is linked to the lichen biomass on the rock and the amount of time that the lichen is present on the rock. This in turn is related to the climatic conditions of the site as it effects the lichen growth (Kurina 1999).

The comparison between the similarly aged lava flows of Etna and Mauna Loa clearly shows that weathering is occurring in the same way on both volcanoes but at a greatly accelerated rate on the east Hawaii sites. The 1984 1000m Mauna Loa site has weathered to the same extent as the 1892 1000m site on Etna. (91.6% match). There is a very high similarity (94% match) in the extent of weathering on the Hawaiian 1984 flow (at an altitude of 1800m) and the Etna south 1983 flow (at an altitude of 1000m). This would indicate that the weathering rates of these two sites is almost exactly alike at this stage of ecosystem development, and the similar biomass on these sites explains the matching weathering rates. The 1852 1000m lava flow on Hawaii shows a good weathering match to the 1892 1000m Etna lava flow. At the same time there is a reduction in lichen biomass on Hawaii and an increase on Etna. This shows that the weathering on Etna has ‘caught up’ with the extent of weathering on Hawaii.

Chapter 9: Primary succession on volcanic ecosystems. Discussion and conclusions

9.1. Introduction

From this study it is clear that the processes controlling colonisation and primary succession that occur after a volcanic eruption has produced a new lava substrate are complex and inter-related. Changes in vegetation type, nutrient availability and the gradual processes of soil formation are all evident during the 500 year period investigated during this project. Each of these processes is affected by the climatic and environmental conditions prevalent on each site. These processes have been examined individually through the experimental chapters of this thesis. However, these different processes interact increasing the complexity of the system. The multidisciplinary nature of this research project allows many of the links between certain inter-related factors to be explored.

The frequent volcanic eruptions of Etna and Hawaii create new lava substrates creating ecosystems at different stages of chronological successional development. This produces a great deal of ecosystem heterogeneity. As a result the overall diversity of these regions is increased and many communities of plants can live in a small geographical area (Motzkin *et al* 1999) due to these disturbance events.

This project has contributed to the research into primary succession by using chronosequence theory on the lava flows of Mt.Etna, which has not been attempted before. These flows are a perfect research area for looking at species change and the attendant nutrient change during long periods of time. In addition, it has expanded the knowledge of the Hawaiian ecosystems as it investigated the early (0-500 year) period of primary colonisation. Previous research on Hawaii (the many papers by Vitousek and Kitayama) has looked at specific changes of a long-term chronosequence of thousands to millions of years of change on the old Hawaiian volcanoes, which make up the islands.

9.2. Vegetation changes

Over the 500 years time interval investigated in this project the lava flows of Etna show a considerable change in vegetation – both in terms of species present but also in the more fundamental terms of growth form (from cryptogam to trees). The initial stage is characterised by cryptogams, especially the lichen *S.vesuvianum*. This species has a considerable impact on the developing lava flow as shown in the many experiments to measure its changing biomass and contribution to weathering. This early lichen phase gradually gives way to the domination by vascular plants (although several species including *R.scutatus* and *C.ruber* do occur in the very early lichen phase). This study of vegetation change on Etna using chronosequence theory has not been done before as other studies on Etna (Poli and Grillo 1972; 1975; Grillo and Caniglia 1988 Poli *et al* 1995) have concentrated on the vegetation heterogeneity located on specific lava flows due to differences in surface morphology and altitude.

Species succession occurs fastest on the east chronosequence as demonstrated by the smaller lichen dominant phase and the attendant decrease in *S.vesuvianum* biomass. In addition, the faster colonisation of the later stage species like *S.junceum* (Fig 2.22), and the growth of an oak woodland of *Q.pubescens* (Fig 2.26) which dominates after only 300 years of succession support this conclusion. This can be linked to the climatic conditions prevalent on this aspect of the volcano as the increased rainfall and humid conditions support the faster growth of vascular plants. This is also seen on areas of Hawaii where the increased rainfall on the east side of the Kilauea caldera supports a large biomass and plant diversity in comparison with the drier Kau desert in the west (Smathers and Mueller-Dombois 1974; Carlquist 1980). On Mt.Etna there may also be an impact from the tephra fall which predominantly falls on the east aspect of the volcano. This speeds colonisation by contributing to the precursor soil in terms of a fine material and enriching the soil with nutrients.

The harsh environment initially present on the open lava fields leads to a successional system quite similar to the older theories of Clements (1916) with a slow but guided change in species over time with a very similar outcome in most of the lava flows (eg from lichen to shub to trees). In the newly formed lava only the cryptogams can survive which starts the succession. It is only later in the succession when the conditions can support a much wider range of species that the more random elements and discontinuities of Gleason (1964) are introduced. This may lead to different dominance by tree species in an area. For example this may explain the separation of the two oak species on Etna where *Q.pubescens* is dominant on the east and *Q.ilex* on the south aspect.

The general changes that occur during a typical chronosequence on Mt.Etna can be shown in a series of stages on Figs 9.1-6.

Figure 9.1. Stage 1: Year 0. The initial bare aa lava.

At this stage the lava is bare and formed from many irregular, loose basaltic blocks. The smaller rocks constantly shift and fall into cracks between larger blocks forming an unstable substrate. This is an extremely harsh and nutrient poor environment.

Figure 9.2. Stage 2: 0-20 Years. First lichen colonisation

The first lichens colonise and grow on the most sheltered / wettest areas on the lava surface. The lava is still unstable and nutrient poor.

Figure 9.3. Stage 3: 20-50 years. Lichen and moss biomass growth

The lichen biomass has now increased to cover almost all of the uppermost areas of the lava, forming a 'blanket' over the rocks under which a continual 'rain' of weathered rock debris and broken off lichen material drops between the cracks to form the precursor soil. This material starts to bind the rocks together and prevents shifting.

Figure 9.4. Stage 4: 50-150 years. Vascular plant colonisation

Lichens still dominate the rock surface but in soil pockets and cracks in the lava, vascular plants have begun to colonise. This increases the organic matter production, which in turn supplies the soil with further nutrients to drive the succession. In addition, nutrient cycling and accumulation by plants (nitrogen fixation) continues to enrich the soil.

Figure 9.5. Stage 5: 150 –250 years. Vascular plant dominance.

At this stage the lichens are restricted to large boulders and open areas of the lava flow. Woody scrub plants and small trees (especially *G.aetnensis*) are scattered randomly throughout the flow. These form spreading centres of high vegetation diversity and biomass due to the associated organic debris, shade and water retention. These in turn allow the seeds of more species to gain a foothold on the lava. There are very few gaps left in the lava, most having been filled with soil and debris.

Figure 9.6. Stage 6 : 250-450 years. Succession.

In this final stage of the chronosequence lichens have almost completely disappeared from the lava flow (restricted to under-story and epiphytic species). Most of the surface is now covered in vascular plants and the trees are becoming dominant. The soil has thickened and has become richer in nutrients. Continuing processes of nutrient cycling and nitrogen fixation gradually build up available nutrients. In addition, environmental conditions have been ameliorated by the growth of the ecosystem (e.g. water retention). Over this period, the processes of succession and species replacement occur, increasing vascular diversity

These general changes in vegetation follow a similar trend on both Mt.Etna and Hawaii. However, on Hawaii the lichen phase (stages 1-4) is of a much shorter duration on the eastern chronosequence as characterised by *S.vulcani* which shows peak biomass on the 1984 and 1942 lava flows (Kurina 1998; Kurina and Vitousek 1999). This is linked to the increased precipitation on this aspect of Mauna Loa which speeds both the growth of the lichen and the following vascular plant colonisation and growth (which rapidly out-shade and supplant *S.vulcani*).

9.3. Nutrient cycling, the changing sources of Nitrogen

At the end of chapter 3 the behaviour of nitrate reductase in the leaves of plants on Mt.Etna showed two peaks of nitrogen entering the system during the 0-500 years of the chronosequence. There was an early peak at the 70-120 year mark, followed by a decline during the 200–300 year period before once again increasing rapidly (Fig 3.2 repeated below). However, the soil nitrogen over the same period on the lava flows is increasing in a nearly linear fashion (Fig 4.10.a. repeated below). This strongly indicates that there is another source of nitrogen entering the ecosystem and supplying the plants on these early lava flows. Not only this, but the limited time frame of this source (70-120-year mark) indicates a specific nitrogen source. Atmospheric and volcanogenic deposition of nitrogen are unlikely sources of this peak as these would be acting on all the sites on each chronosequence (although these will vary between chronosequences on the different aspects of the volcano).

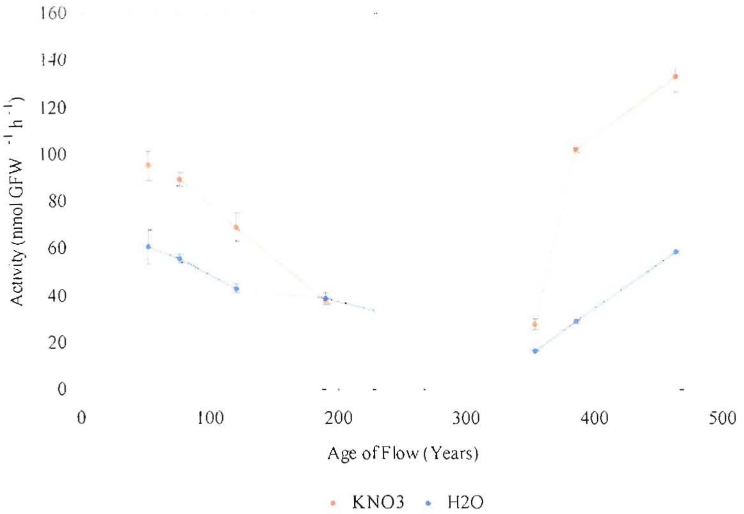


Figure 3.2. Nitrate reductase activity in the leaves of *C. ruber* on the northern chronosequence, in both nitrate treated plants and water treated plants (n=4,+/- S.E.).

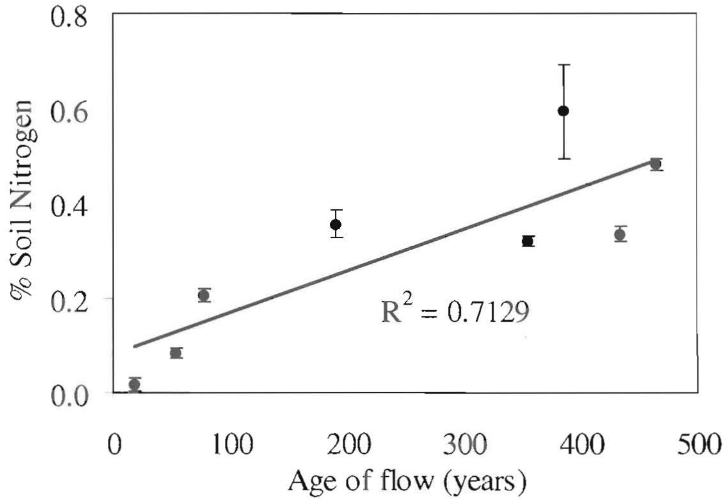


Figure 4.10.a. Percentage total nitrogen in the soil of the north chronosequence. (N=3, +/- S.D).

As has already been shown, lichens of the genus *Stereocaulon* are nitrogen fixers (section 5.1.3) . This, coupled with the large biomass of lichens on Etna, would indicate this lichen is fixing a large quantity of nitrogen. The peak in lichen biomass occurs at the same time as the early nitrogen peak (Fig 5.9). Therefore, it is likely that some of the nitrogen produced by the lichens is leaching out into the ecosystem and is the source of the early peak in nitrogen found in the plants.

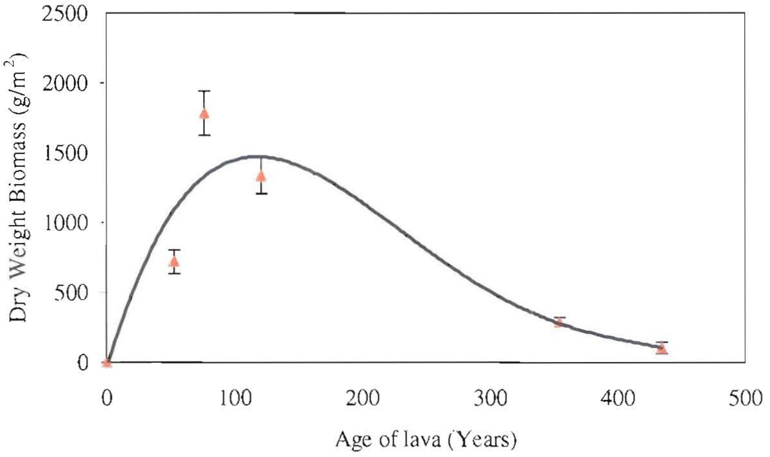


Figure 5.9. *S.vesuvianum* biomass on the north chronosequence of Mt.Etna. (N=20 +/-SE).

The leaching of nitrogen from lichens has been noted before and has been measured in epiphytic lichens growing in oak woodlands (Knops and Tilman 2000; Knops *et al* 1991). These epiphytic lichens fix 2.85 kg N $ha^{-1}yr^{-1}$ in this oak woodland (Knops 1994). An additional study by Kurina and Vitousek (2001) showed that *Stereocaulon vulcani* fixes between 0.2 and 0.45 kg N ha^{-1} yr^{-1} at an altitude of 1500m on the lava flows of Hawaii. Using this nitrogen leaching from the lichen as a basis it can be seen how a combined model of nitrogen sources on the lava flows may work (Fig 9.7).

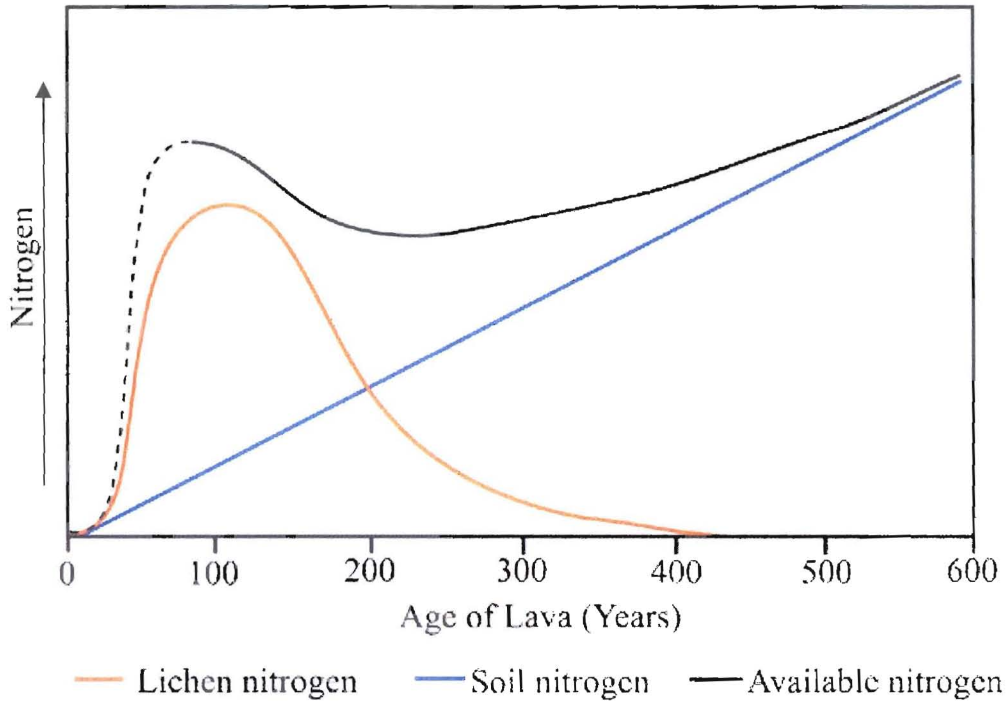


Figure 9.7. A model of the main nitrogen inputs on the early volcanic ecosystems on Etna. The available nitrogen shows an early peak as shown by the nitrate reductase activity results (dashed part of the line is the theoretical rise from 0)

This graph of available nitrogen (broadly based on the nitrate reductase results on Fig 3.2) is a combination of the soil nitrogen (4.10a) and the lichen biomass (Fig 5.9). This model fits much of the available data found on Etna and a similar process may be occurring on Hawaii. The graph of *M.polymorpha* (Fig 7.13a) shows a similar trend for a higher reading of foliar nitrogen in the leaves when *S.vulcani* is dominant (17years old).

The newly produced substrate is limited in nitrogen and other essential nutrients and it is only when a sufficiency of these nutrients has been produced by the autotrophs (lichens) or blown in as wind borne organic material that other species can colonise the rock.

One of the most important findings of this project is the importance of lichens in the successional sequence. Clements (1916) stated that lichens were a very important life stage in early colonisation patterns. This has been clearly shown on the recent (0-200 year old) lava flows of Etna where lichens dominate the lava surface and make an important contribution to the developing ecosystem. This project demonstrates that lichens facilitate succession by harvesting nitrogen from the atmosphere and enhance the further colonisation and growth of vascular plants. In addition, *Stereocaulon* introduces a large biomass to the initially nutrient poor lava ecosystems. This agrees with other studies conducted by Cooper and Rudolph (1953); Knops *et al* (1991) and Kurina (1998).

9.4. Weathering by the lichens *S.vesuvianum* and *S. vulcani*

This study has shown how the lava surface changes over the time period of a chronosequence under the weathering action of *Stereocaulon* (by visual observation of the changing surface). These data adds to the debate as to the nature and extent of lichen weathering on lava. Several authors attribute the breakdown of the lava substrate and the formation of secondary products as well as etching and pitting of the surface to lichen activity (Jackson 1969; Jackson and Keller 1970; Adamo and Violante 1991; Stretch and Viles 2002). For example, Stretch and Viles (2002) showed that weathering on Lanzarote is high even in the arid areas (x16 higher than bare surface weathering). However, Cochran and Berner (1993 and 1996) working over a longer chronosequence attribute more importance to the vascular plant and soil weathering, and dismissing the lichen contribution. They reinterpreted Jackson and Keller's (1970) work as evidence of aeolian material thus reducing the importance of lichen weathering. In a further paper the same authors (Berner and Cochran 1998) showed that plant weathering on the older flows can penetrate to depths of thousands of micrometers (in comparison to *S.vulcani,* which they estimate penetrates to 50-100μm). However the results of this project support the earlier premise of lichens being a significant weathering agent on the early (0-300 year old) lava flows of Etna and Hawaii. Moreover the introduction of this new data from Mt.Etna (where no previous work on lichen weathering of this nature has been done before) on three chronosequences clearly demonstrates that lichens weather the lava in a predictable manner.

This project has taken forward the methods of image analysis of weathering by using the computer machine vision system to quantify minor changes in the lava surface using a large database of images. This allowed comparison of weathering rates of sites under different climatic and environmental conditions as seen on Etna. This was then studied further by the comparison with sites on Hawaii, which expanded the model of lichen weathering under different climatic conditions. The two studies on Etna and Mauna Loa show that the weathering action and rate of the two lichens *S.vesuvianum* and *S.vulcani* is similar and occurs in a predictable and quantifiable manner. Both of these lichens are very similar in structure and growth form. The weathering rate of these lichens is controlled by the extent of lichen biomass on the rocks. This occurs in two ways: 1) the more lichen present the greater the mechanical action on the rock surface and 2) the greater the lichen biomass the more organic acids produced and hence more chemical weathering can occur. As a result the weathering rates are closely linked to the factors which affect the lichen development on the rock surface. These have been identified as climate (warm humid conditions promote growth) and a gradually increasing effect of competition and shading by vascular plants (which reduce lichen growth on older flows).

The intelligent machine vision analysis allows comparison of the weathering rates of the two Hawaiian chronosequences and correlation of these weathering rates to the Etna baseline. The three sample results shown (Table 8.1) clearly indicate that weathering of the lava by the two *Stereocaulon* species is comparable and suggest that the extent of weathering is closely linked to the lichen biomass on the rock surface. The Etna data shows that weathering is related to the climatic conditions controlling lichen growth (primarily precipitation).

9.5. The inter-relatedness of the processes on lava ecosystems.

Most of the works by other authors, which have been discussed in this thesis, have been focused on one particular facet of primary succession (e.g. vegetation change by Smathers and Mueller-Dombois 1974). However this multi-disciplinary study has a quite different holistic approach. As a result, the investigations of this project into many different aspects of primary colonisation on lava, show that the processes of primary succession are all inter-related. For example the process of weathering (by lichens) speeds soil formation which in turn aids plant succession which then out-competes and shades the lichens. This chain of events is based on the initial colonisation of the lichens – which leads to faster colonisation of vascular plants on the lava. Similarly the production of lichen organic matter also aids vascular colonisation. In essence the lichens initiate colonisation of the bare surface. This then changes the ecological conditions enough to support a large vascular biomass, which in turn impedes further lichen growth. This is supported by Kurina (1998), as well as Kurina and Vitousek (1999) who showed that lichen biomass decline is linked to increased shading by vascular plants.

Another similar linkage can be seen when the initial lichen and vascular plant biomass initiates nutrient accumulation and cycling leading to soil development. This soil can in turn support a higher diversity of plant species leading to competition between species and further succession. The wide scope of the study on Etna and its further expansion by research of specific areas on Hawaii (NR and *S.vulcani* weathering) has shown many such links between the ecological processes and the vegetation during the primary succession. A simplistic web diagram of these interrelated processes and their effect on succession can be seen in Fig 9.8. These processes, inputs and vegetation changes, apply to both volcanic systems investigated. However, on Hawaii the lichen stage is reduced on the east chronosequences as the wet tropical climate in many areas allows several vascular species (e.g. *M.polymorpha*) to colonise the bare lava directly.

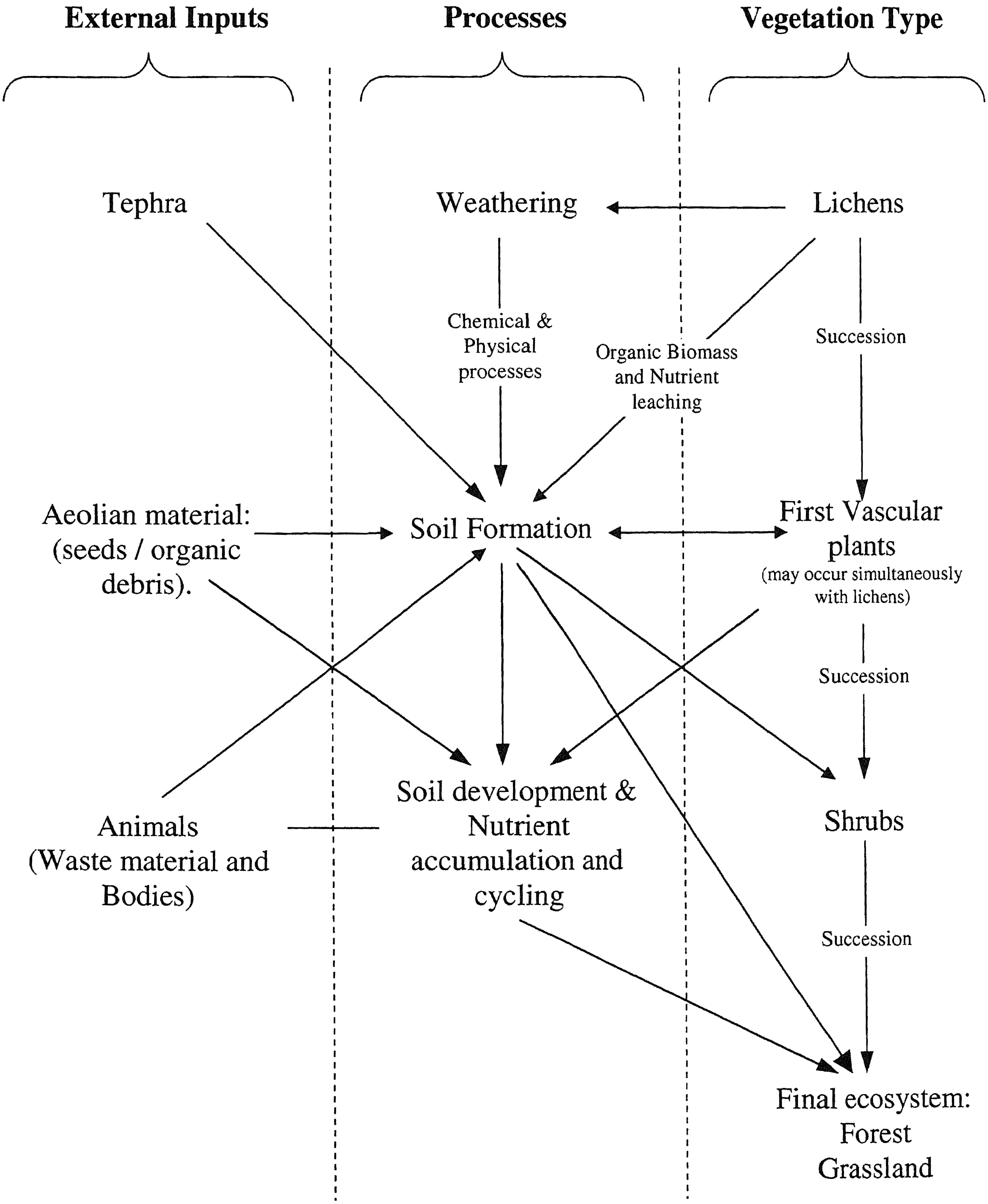


Figure 9.8. Simplistic web diagram of the major inputs, processes and vegetation changes that occur over a chronosequence on a lava flow. Where vegetation change can be linked to the many different processes and vice-versa.

9.6. Final conclusions.

The final conclusions of this project work can be summed up in the following sections:

1) Succession of vegetation on fresh lava is related to the substrate, climate and distance from a source of propagules. All the species present on the flows are effected both temporally (due to changing nutrient availability) and geographically (by aspect / climate). In addition, seed/spore dispersal mechanisms of the plant species also influences the colonisation process – with some species colonising the whole flow simultaneously (e.g. *S.vesuvianum*) and others encroaching gradually from the edges (e.g. *Q.ilex*). Each species investigated has different environmental and nutritional requirements and hence occupies a different niche (and time period) on the chronosequence. This forms a heterogeneous complex of species present over the lava flows.

2) Nitrate reductase has been shown to be a good indicator of nitrogen availability in temperate primary successional ecosystems. It is a good field experiment to measure available nitrogen in indicator plant species over successional time as it measures nitrogen within the leaves of the plants. By doing so it allows the perception of pulses of nitrogen present on the lava flows from sources other than the soil. This was shown on the lava flows of Etna where an early input of nitrogen was detected. On Hawaii the nitrate reductase activity was very low in all species studied indicating that nitrogen is limited on the early (0-500 year old) lava flows.

3) Nitrogen and many other nutrients are limited on the early primary ecosystems and this is a major barrier to plant colonisation of the lava. The slow increase in available nutrients allows the slow colonisation of further species. However, the results from this project show that lichens of the genus *Stereocaulon* are introducing a large pulse of nitrogen onto the lava flows

when they are dominant on the ecosystem (approximately 0-200 years on Etna and 0-100 on the Hawaii east chronosequences). This aids the colonisation and growth of vascular plants.

4) Lichens of the genus *Stereocaulon* introduce a huge biomass into the system during early successional stages on both volcanic systems. This biomass forms a suitable precursor to the soil allowing further colonisation by vascular plants and also contributes a large amount of nitrogen during a period when this would otherwise be limited. The growth of the biomass is controlled by the climate. The lichen grows fastest in warm wet conditions (Etna and Hawaii east sites) however it is also replaced faster by vascular plant species. The lichens persist longest in the drier areas where vascular plants take longer to colonise and become dominant.

5) The two species of *Stereocaulon* investigated on the two volcanic ecosystems (Etna and Hawaii) weather the lava in a distinct and predictable manner. This will introduce valuable trace elements to the developing soil (as shown by the disintegration of the lava surface and the breakdown of minerals like olivine). In addition, weathering alters the surface morphology of the lava on a micro-scale allowing greater water retention and the formation of suitable sites for vascular colonisation. The rate of lava weathering is related to the ambient climate (both temperature and precipitation) as this influences the biomass of the lichen on the rock. Weathering is fastest in areas of high lichen biomass over long periods of time.

6) The same processes of weathering, nutrient cycling and plant colonisation occur on both lava ecosystems investigated. However, the major differences between the sites investigated are caused by the different climatic conditions – primarily precipitation. Primary succession is slowest on the dry temperate sites of Mt.Etna and the dry west of Hawaii. In contrast, the wet humid conditions of the east aspects of both Mt.Etna and Mauna Loa show the fastest colonisation and succession. On the east of Etna this leads to the formation of

oak woodland within 300 years, whereas on east Mauna Loa a dominant *M.polymorpha* rainforest forms within 150 years. However, the nutrient availability (especially nitrogen) within the rainforest is still limited as nutrient cycling binds up nutrients within the rainforest biomass.

Appendix

I. Comparison of the composition of typical lavas of Etna and Hawaii.

Element	Etna lavas (year erupted)				Hawaiian lavas (year erupted			
	1947	1923	1809	1614-24	1950	1926	1907	1868
SiO_2	47.77	46.33	48.30	48.86	50.54	52.29	52.12	47.68
Al_2O_3	17.84	17.84	17.35	18.94	12.92	13.64	13.74	8.95
Fe_2O_3	5.48	5.69	7.06	6.03	2.86	2.43	2.80	3.67
FeO	5.82	5.24	3.95	3.01	8.26	8.74	8.38	7.90
MnO	0.18	0.15	0.16	0.16	0.18	0.17	0.17	0.16
MgO	4.44	5.85	5.14	5.24	8.99	7.90	7.23	21.02
CaO	9.82	10.37	10.79	9.53	9.85	10.61	10.65	6.99
Na_2O	4.40	3.70	3.32	4.16	2.29	2.28	2.30	1.48
K_2O	1.76	1.52	1.50	1.74	0.35	0.37	0.36	0.27
TiO_2	1.56	1.55	1.80	1.55	1.92	2.06	2.11	1.40
P_2O_5	0.62	0.51	0.47	0.69	0.22	0.24	0.23	0.17
H_2O	0.17	0.09	0.07	0.04	-	0.24	0.23	0.28
L.O.I.		0.58	0.43	0.34	ND	ND	ND	ND
CO_2	ND	ND	ND	ND	-	0.08	0.13	0.06
Totals	99.86	99.42	100.34	100.29	98.38	101.05	100.45	100.03

A comparison of the composition of 4 typical Etnean and 4 Hawaiian historic lava flows. Data for Etna lavas taken from Romano and Guest (1979) and the Hawaiian lavas from the Basaltic Volcanism Study Project (1981). L.O.I is the 'Loss On Ignition'. ND is 'Not Determined'. Etnean hawaiite lavas are porphytitic with up to 45% phenocrysts comprising plagioglase, clinopyroxene and olivine (typically in that order of abundance) set in a matrix of microlites and glass with scattered granules of titanomagnetite (Chester *et al* 1985).

Hawaiian lavas are less porphyritic than Etna. Phenocrysts typically make up less than 1% and consist of olivine, plagioclase and pyroxene largely restricted to ground mass (microlites and glass). In terms of major element chemistry the Hawaiian lavas are slightly richer in SiO_2 and MgO and slightly poorer in Al_2O, Na_2O and K_2O.

II. Mt.Etna site locations

North chronosequence (1000m)

Sample site	Site location (map grid reference)
1981 lava flow (year old)	896, 979
1947 lava flow (53 year old)	894, 021
1923 lava flow (77 year old)	884,082
1879 lava flow (121 year old)	893, 033
1809 lava flow (191 year old)	886, 079
1646 lava flow (354 year old)	892, 041
1614-24 lava flow (376 year old)	894, 001
1566 lava flow (436 year old)	875, 091
1536 lava flow (464 year old)	887, 924

East chronosequence (1000m)

Sample site	Site location (map grid reference)
1992 lava flow (year old)	723, 080
1971 lava flow (53 year old)	777, 091
1928 lava flow (77 year old)	811, 099
1865 lava flow (121 year old)	820, 115
1792 lava flow (191 year old)	720, 073
1689 lava flow (354 year old)	768, 093

South chronosequence (1000m)

Sample site	Site location (map grid reference)
1983 lava flow (17 year old)	680, 982
1910 lava flow (90 year old)	667, 997
1886 / 1892 lava flow (108 year old)	668, 003
1780 lava flow (220 year old)	669, 972
1766 lava flow (234 year old)	670,019
1634 lava flow (366 year old)	672, 025
1537 lava flow (463 year old)	673, 012
1536 lava flow (464 year old)	677, 982
1444 lava flow (556 year old)	664, 020
812-1169 lava flow (1000 year old)	674, 985

West sites (1000m)

Sample site	Site location (map grid reference)
1843 lava flow (157 year old)	796, 874
1651 lava flow (349 year old)	804, 873

South altitude sites

Sample site	Site location (map grid reference)
1892 1500m lava flow	712, 025
1892 1250m lava flow	693, 017
1892 850m lava flow	648, 013
1780 1250m lava flow	702, 952
1780 1500m lava flow	712, 962
1634 1500m lava flow	710, 028
1634 1250m lava flow	692, 022
1669 650m lava flow	624, 008
1669 400m lava flow	577, 010
1910 750m lava flow	635, 995

III. The nine plant species studied on Etna

Rumex scutatus var aetnensis (Shield Dock).

Rumex scutatus var. aetnensis. (Picture taken by M.Carpenter).

This species, also known as shield dock or French Sorrel is very common on the slopes of Mt.Etna. It is a woody-based many branched perennial, which grows to a size of 25-50cm in height (Polunin 1969) and has very characteristic leaves – 3-4 cm long which are about as long as broad. The morphology of these leaves does vary widely with some almost round whilst others become elongated to become arrow shaped. In addition, the pigmentation of these leaves also varies considerably, with the common dark green variety being replaced with a grey leafed variety in some areas (Luciani et al 1977a and 1977b). The flowers are unisexual but located on the same plant, reddish in lax branched clusters.

Centranthus ruber

Centranthus ruber – Red Valerian. (Picture taken by M.Carpenter).

Centranthus ruber is also extremely common on the lava flows of Mt.Etna. It is an erect somewhat glaucus, hairless perennial growing from 30-100cm in height. It has numerous red, pink or rarely white flowers in a rather dense oval or branched pyramidal cluster. Each flower has a corolla tube which is slender and 8-10mm long, (Polunin, 1969).

Both this species and *Rumex aetnensis* are the first colonisers of aa lava in any great abundance. These species commonly co-occur in clumps on the lava – although it is unknown if this is due to a scarcity of sites for colonisation or due to a symbiotic relationship. It may well be a combination of both, since there does not appear to be any competition between the species with both members in a clump growing extremely vigorously.

Isatis tinctora – Woad.

Isatis tinctora. (Drawing from Blamey and Grey–Wilson 1993; picture taken by M.Carpenter).

Early coloniser of the lava – one of the first to arrive and abundant on the open areas of the bare lava (after 50-100years). Medium to tall, mostly hairless biennial species. Leaves form a basal rosette in the first year. Stem leaves arrow shaped, clasping the stem. 3-4 mm yellow flowers in much branched racemes. Fruit is oblong, flattened

Genista aetnensis Mt.Etna broom

Genista aetnensis. (Drawing from Blamey and Grey–Wilson 1993; picture taken by M.Carpenter).

This large shrub (or small tree) grows up to 5m high forming a substantial trunk up to 30cm in diameter. The young stems are slender and greatly branched. The leaves are simple and elliptical. Yellow flowers 9-13 mm long borne in lax racemes. Has an oval pod, which is flattened 6-10mm long. Grows very well on the relatively young lava flows of Etna. This species has been linked to colonisation processes on lava as it creates shade and ameliorates the environmental conditions so that other species can colonise the lava (Certini *et al* 2001).

Helichrysum italicum

Helicrysum italicum. (Drawing from Blamey and Grey–Wilson 1993; picture taken by M.Carpenter).

A distinctly aromatic species of small shrub, which grows to height of approximately 50cm. Grey felted when the stems are young. Leaves are greenish with revolute margins, becoming hairless above. Flow heads are yellow in clusters 15-80mm across. This species is also an early coloniser to the lava flows – but its abundance is low.

Senecio bicolor Cineraria

Senecio bicolor. (Drawing from Blamey and Grey–Wilson 1993; picture taken by M.Carpenter)

A white felted dwarf shrub which is abundant on the early lava flows of Etna – usually in the same clumps as *R.scutatus* and *C.ruber.* Grows up to 50cm high and is much branched at the base of the flowering shoots. Leaves oval to lanceolate, toothed to pinnately lobed with rather narrow segments, white beneath the upper surface of the leaf can be white, grey or green. Flower heads are yellow 12-15mm long and borne in dense terminal clusters.

Quercus ilex Holm oak

Quercus ilex. (Drawing from Blamey and Grey–Wilson 1993; picture taken by M.Carpenter).

Large evergreen tree which grows up to 25 m with downy twigs and grey bark with fine fissures. The leaves are leathery, oblong to lanceolate and can be toothed or un-toothed. The leaves are downy beneath when mature. The oak cup is distinctive with scales closely pressed together and downy. Acorn 1.5-2 cm long. Common on the southern aspect of Etna.

Quercus pubescens Downy oak

Quercus pubescens (Drawing from Blamey and Grey–Wilson 1993; picture taken by M.Carpenter).

Deciduous tree (in contrast to *Q.ilex* which is evergreen). This tree grows up to 25m tall and has densely downy twigs. Its bark is dark grey and finely cracked into scales. The leaves are grey/ green oblong and lanceolate. Bluntly lobed and 6-12cm long,.the leaves are densely downy beneath (especially when young). Acorn cup has narrow closely pressed hairy scales. The acorns are short stalked. This species dominates the older lava flows on the east aspect of Etna.

Spartium junceum Spanish broom.

Spartium junceum (Drawing from Blamey and Grey–Wilson 1993; picture taken by M.Carpenter).

A large spineless shrub which grows up to 3m in height (occasionally more). Has numerous cylindrical bluish green rush like stems. The leaves are sparse, linear oblong and soon falling. Flowers are large, bright yellow 20-25mm long, each usually solitary but borne in profusion (see pic) sweetly scented. Pod is flattened 50-80mm long.

IV. Species abundance and percentage cover from Etna

	Date of flow								
Primary Colonising species	**1910**	**1886**	**1780**	**1766**	**1634**	**1537**	**1536**	**1444**	**812-1169**
Centranthus ruber – Red Valerian	C	C	C	C	C	C	C	C	C
Echium vulgarae pustulatum – Vipers Bugloss		O	P		C	C		C	C
Genista aetnensis – Mt. Etna Broom.	C	C	C	C	C	C	C	C	C
Helichrysum italicum italicum –	C	C	C						
Isatis tinctoria – Woad.	P	O	P	C		P	P	C	P
Linaria purpurea – Purple Toadflax.	C	P	C						C
Rumex scutulatus aetnensis – Etna type French Sorrel.	C	C	P	C	C	P	P		
Senecio bicolor (S.cineraria) – Cineraria.	C	C					P		
Spartium junceum – Spanish Broom.				C (Dom.)		C			
Stereocaulon vesuvianum	V.C	V.C	P	C	C	P	O		
Other									
Achillea millefolium – Yarrow, Milfoil.	P							P	
Achillea ligustica – Sneezewort.		P				P			C
Agrostis tenuifolium – Bent.									
Aira caryophylla									
Allium neapolitanum – Naples garlic.									
Anthemis chia – *Chamomile.*									
Anthoxanthum odoratum – Sweet Vernal Grass.									
Arum sp.									
Asphodelus microcarpus – Common Asphodel.			P				P		C
Asplenium trichomanes – Maidenhair Spleenwort.	P		P		P		P	P	P
Atractylis humilis									
Ballota pseudodictamnus –									
Brassica sp. -									
Briza maxima – Large Quaking Grass		P							
Bromus tectorum . – Drooping Brome		P							P
Calycotome villosa – Hairy Spiny Broom.									
Castenia satvia – Sweet Chestnut.						P	P		
Centauria cyanus - Cornflower									
Ceterach officinarum – Rustyback fern	P	P			P		P	P	P
Cirsium creticum –									
Crepis leontodontoides – Hawksbeard.	P	P			P	P	P	P	
Crocus longiflorus			P						
Crupina crupinastrum-									
Dactylis glomerata - Cocksfoot.									
Dasypyrum villosum									
Daucus carota – Wild Carrot									
Dorycnium hursutum – Hairy Dorycnium.									
Dryopteris villarii –									
Elymus repens – Common Couch grass.									
Erodium cicutarium – Common Storks Bill.			P						
Euphorbia characias - Large Mediterranean Spurge.			C						
Euphorbia rigida – Broad-Leaved glaucous spurge.						C	O		
Ferula communis – Giant Fennel			C		P	P	P	P	P
Festuca rubra – Creeping fescue.									
Foeniculum vulgare - Fennel									
Galium aparine – Goose Grass.									
Geranium dissectum – Cut Leaved Cranes Bill.									
Geranium robertianum – Herb Robert.								P	P
Hedera helix – Ivy.			P				C		

Species abundance on the south chronosequence

	Date of flow								
Primary Colonising species	**1910**	**1886**	**1780**	**1766**	**1634**	**1537**	**1536**	**1444**	**812-1169**
Heiracium crinitum – Hawkweed.									
Hyacinthus orientalis - Hyacinth									
Hypericum perforatum – Common St.John's Wort.									
Hypochoeris maculata								P	
Jasione corymbosa – Corymbose Sheeps bit.									
Lagurus ovatus – Hares tail.		P							P
Linaria arvensis –									
Linaria vulgaris - Common Toadflax.	P								
Linum bienne – Pale Flax.									
Lotus sp. –									
Lygeum spartum –									
Mentha suaveoleus – Apple Mint.									
Narcissus sp. . –									
Orobanche rapum – Greater Broom Rape.									
Papaver rhoeas – Common Poppy									
Parentucellia viscosa – Yellow Bartsia.									
Phycotis saxifraga –									
Phyllitis sagittata – Hearts-Tongue Fern.									
Pinus nigra -									
Polypodium cambricum -	P								
Poterium verrucosum – Mediterranean Salad Burnet.									
Ptychotis saxifraga - Ptychotis									
Quercus ilex – Holm Oak.			C	P	C	C	C	C	C
Quercus hirsutium – Downy Oak.									
Quercus pubescens – Downy Oak, White Oak.			C		C	C	C	C	C
Reseda alba – White Mignonette, Upright Mignonette.									
Rhinanthus minor – Yellow Rattle.									
Rosa canina - Wild Rose.									
Rubus sanctos – Blackberry/Bramble.					C	C		C	
Satureja calamintha – Summer Savory.			P			P	C		C
Satureja fruticosa						P			
Satureja hortensis – Summer Savory.									
Scilla peruviana – Peruvian Bluebell.									
Scrophularia canina – French Figwort.									
Sedum reflexum – Rock Stonecrop						P			
Sedum tenuifolium – Stonecrop							P		P
Silene vulgaris – Bladder Campion.		P		P	P			P	
Sonchus oleraceus – Common Sow Thistle.			P			C	P	C	C
Stippa sp.									
Taraxacum laevigatum – Dandylion sp.									
Thymus vulgaris – Thyme.									
Tragopogon pratensis – Goatsbeard.									
Trifolium incarnatum – Crimson clover						C			
Trifolium repens - white clover								P	
Umbilicus rupestris – Navelwort.	P	P	P				O		
Urtica dioica – Stinging Nettle.									
Umbellifia sp. .									
Verbascum thapsus – Great Mullein, Aarons rod.			O					P	P
Vicia villosa – Fodder Vetch, Shaggy vetch.					P	P		P	P
Volutaria lippii -									
	Common -c	Occasional - o		Present - p		Absent-a			

Species abundance on the south chronosequence continued

	Date of flow								
Primary Colonising species	**1910**	**1886**	**1780**	**1766**	**1634**	**1537**	**1536**	**1444**	**812-1169**
Centranthus ruber – Red Valerian	10%	15-20%	5%	10%	5%	5-10%	2%	5%	5%
Echium vulgarae pustulatum – Vipers Bugloss	0%	2%	1%		1%	3%		1%	< 1%
Genista aetnensis – Mt. Etna Broom.	15%	20%	25%	15%	15%	30%	10%	15%	5%
Helichrysum italicum italicum –	5%	4%	5%					0%	0%
Isatis tinctoria – Woad.	1%	2%	< 1%	< 1%		< 1%	< 1%	1%	< 1%
Linaria purpurea – Purple Toadflax.	1%	1%	< 1%						< 1%
Rumex scutulatus aetnensis – Etna type French Sorrel.	7	5%	< 1%	5%	1%	1%	< 1%		
Senecio bicolor (S.cineraria) – Cineraria.	3	5%					< 1%		
Spartium junceum – Spanish Broom.	0%	0%		30%		3%			
Stereocaulon vesuvianum	85%	75%	3%	50%	10%	2%	1%	0%	0%
Other									
Achillea millefolium – Yarrow, Milfoil.	< 1%							< 1%	
Achillea ligustica – Sneezewort.		< 1%				< 1%			< 1%
Agrostis tenuifolium – Bent.									
Aira caryophylla									
Allium neapolitanum – Naples garlic.									
Anthemis chia – Chamomile.									
Anthoxanthum odoratum – Sweet Vernal Grass.									
Arum sp.									
Asphodelus microcarpus – Common Asphodel.			1%				< 1%		1%
Asplenium trichomanes – Maidenhair Spleenwort.	< 1%		1%		< 1%		< 1%	1%	< 1%
Atractylis humilis									
Ballota pseudodictamnus –									
Brassica sp. –									
Briza maxima – Large Quaking Grass		< 1%							
Bromus tectorum . – Drooping Brome		< 1%							< 1%
Calycotome villosa – Hairy Spiny Broom.									
Castenia satvia – Sweet Chestnut.						5%	1%		
Centauria cyanus - Cornflower									
Ceterach officinarum – Rustyback fern	< 1%	< 1%			< 1%		< 1%	1%	< 1%
Cirsium creticum –									
Crepis leontodontoides – Hawksbeard.	< 1%	< 1%			< 1%	< 1%	< 1%	1%	
Crocus longiflorus			< 1%						
Crupina crupinastrum-									
Dactylis glomerata - Cocksfoot.									
Dasypyrum villosum									
Daucus carota – Wild Carrot									
Dorycnium hursutum – Hairy Dorycnium.									
Dryopteris villarii –									
Elymus repens – Common Couch grass.									
Erodium cicutarium – Common Storks Bill.			< 1%						
Euphorbia characias - Large Mediterranean Spurge.			2%						
Euphorbia rigida – Broad-Leaved glaucous spurge.						5%	1%		
Ferula communis – Giant Fennel			2%		2%	1%	< 1%	1%	< 1%
Festuca rubra – Creeping fescue.									
Foeniculum vulgare - Fennel									
Galium aparine – Goose Grass.									
Geranium dissectum – Cut Leaved Cranes Bill.									
Geranium robertianum – Herb Robert.								< 1%	< 1%
Hedera helix – Ivy.			< 1%				3%		

Species percentage cover on the south chronosequence

	Date of flow								
Primary Colonising species	**1910**	**1886**	**1780**	**1766**	**1634**	**1537**	**1536**	**1444**	**812-1169**
Heiracium crinitum – Hawkweed.									
Hyacinthus orientalis - Hyacinth									
Hypericum perforatum – Common St.John's Wort.									
Hypochoeris maculata								<1%	
Jasione corymbosa – Corymbose Sheeps bit.									
Lagurus ovatus – Hares tail.		<1%							<1%
Linaria arvensis –									
Linaria vulgaris - Common Toadflax.	<1%								
Linum bienne – Pale Flax.									
Lotus sp. –									
Lygeum spartum –									
Mentha suaveoleus – Apple Mint.									
Narcissus sp. .–									
Orobanche rapum – Greater Broom Rape.									
Papaver rhoeas – Common Poppy									
Parentucellia viscosa – Yellow Bartsia.									
Phycotis saxifraga –									
Phyllitis sagittata – Hearts-Tongue Fern.									
Pinus nigra -									
Polypodium cambricum -	<1%								
Poterium verrucosum – Mediterranean Salad Burnet.									
Ptychotis saxifraga - Ptychotis									
Quercus ilex – Holm Oak.			5%	5%	15%	20%	20%	20%	5%
Quercus hirsutium – Downy Oak.									
Quercus pubescens – Downy Oak, White Oak.			10%		10%	5%	30%	40%	5%
Reseda alba – White Mignonette, Upright Mignonette.									
Rhinanthus minor – Yellow Rattle.									
Rosa canina - Wild Rose.									
Rubus sanctos – Blackberry/Bramble.					3%	3%		15%	
Satureja calamintha – Summer Savory.			<1%			<1%	<1%		1%
Satureja fruiticosa						<1%			
Satureja hortensis – Summer Savory.									
Scilla peruviana – Peruvian Bluebell.									
Scrophularia canina – French Figwort.									
Sedum reflexum – Rock Stonecrop						<1%			
Sedum tenuifolium – Stonecrop							<1%		<1%
Silene vulgaris – Bladder Campion.		<1%		<1%	<1%			1%	
Sonchus oleraceus – Common Sow Thistle.			<1%			2%	<1%	1%	<1%
Stippa sp.									
Taraxacum laevigatum – Dandylion sp.									
Thymus vulgaris – Thyme.									
Tragopogon pratensis – Goatsbeard.									
Trifolium incarnatum – Crimson clover						5%			
Trifolium repens - white clover								1%	
Umbilicus rupestris – Navelwort.	<1%	<1%	1%				<1%		
Urtica dioica – Stinging Nettle.									
Umbellifa sp.									
Verbascum thapsus – Great Mullein, Aarons rod.			3%					1%	<1%
Vicia villosa – Fodder Vetch, Shaggy vetch.					<1%	<1%		<1%	<1%
Volutaria lippii -									

Species percentage cover on the south chronosequence continued

	Year of lava flow								
Primary Colonising species	**1981**	**1947**	**1923**	**1879**	**1809**	**1646**	**1614-1624**	**1566**	**1536**
Centranthus ruber – Red Valerian	P	C	P	C	C	O	C	O	C
Echium vulgarae pustulatum – Vipers Bugloss			P	O	P	O	O	P	C
Genista aetnensis – Mt. Etna Broom.		C	P	C	C	C	O	O	
Helichrysum italicum italicum –		C	P	C	C	P			C
Isatis tinctoria – Woad.		P	P	P	P	O		O	
Linaria purpurea – Purple Toadflax.		P		P					P
Rumex scutulatus aetnensis – Etna type French Sorrel.	P	C	P	C	C	C	C	C	C
Senecio bicolor (S.cineraria) – Cineraria.		P			P				
Spartium junceum – Spanish Broom.		C	P	C	C	C	C	P	C
Stereocaulon vesuvianum	C (V.Small)	C	P	C	C	P	C	C	P
Other									
Achillea millefolium – Yarrow, Milfoil.		P						P	
Achillea ligustica – Sneezewort.			P						
Agrostis tenuifolium – Bent.		P		P		P		O	
Aira caryophylla			C						
Allium neapolitanum – Naples garlic.								P	P
Anthemis chia – *Chamomile.*							P		
Anthoxanthum odoratum – Sweet Vernal Grass.							v.c	C	P
Arum sp.									
Asphodelus microcarpus – Common Asphodel.						P		C	P
Asplenium trichomanes – Maidenhair Spleenwort.			P		P	P	P	P	
Atractylis humilis			P	P		O	O	P	
Ballota pseudodictamnus –				P					
Brassica sp. -							P		P
Briza maxima – Large Quaking Grass			P	C	C	O	O	O	C
Bromus tectorum . – Drooping Brome					C				
Calycotome villosa – Hairy Spiny Broom.								P	
Castenia satvia – Sweet Chestnut.									
Centauria cyanus - Cornflower				P					
Ceterach officinarum – Rustyback fern			P		P		P	P	
Cirsium creticum –									O
Crepis leontodontoides – Hawksbeard.					P	P		O	
Crocus longiflorus									
Crupina crupinastrum-						P	P		
Dactylis glomerata - Cocksfoot.						P		C	C
Daucus carota – Wild Carrot								P	
Dorycnium hursutum – Hairy Dorycnium.									P
Dasypyrum villosum			P			P	P	C	
Dryopteris villarii –			P	P			P		
Elymus repens – Common Couch grass.								P	
Erodium cicutarium – Common Storks Bill.								P	
Euphorbia characias - Large Mediterranean Spurge.							C		C
Euphorbia rigida – Broad-Leaved glaucous spurge.				C		C	C		C
Ferula communis – Giant Fennel		P		P	P	P	C	O	P
Festuca rubra – Creeping fescue.									
Foeniculum vulgare - Fennel									
Galium aparine – Goose Grass.						P			
Geranium dissectum – Cut Leaved Cranes Bill.			P						
Geranium robertianum – Herb Robert.		P		O	P	P	P	P	

Species abundance on the north chronosequence

	Year of lava flow								
Primary Colonising species	**1981**	**1947**	**1923**	**1879**	**1809**	**1646**	**1614-1624**	**1566**	**1536**
Hedera helix – Ivy.									
Heiracium crinitum – Hawkweed.		P		P	P	P			
Hyacinthus orientalis - Hyacinth						P			
Hypericum perforatum – Common St.John's Wort.								P	C
Hypochoeris maculata???									
Jasione corymbosa – Corymbose Sheeps bit.					P	P	P		P
Lagurus ovatus – Hares tail.		P	P	C	O	O	C	C	C
Linaria arvensis –									P
Linaria vulgaris - Common Toadflax.									P
Linum bienne – Pale Flax.								P	
Lotus sp. –									
Lygeum spartum –		P	P	O	C	O		C	P
Mentha suaveoleus – Apple Mint.						C	O	C	
Narcissus sp. –									
Orobanche rapum – Greater Broom Rape.					P				
Papaver rhoeas – Common Poppy									P
Parentucellia viscosa – Yellow Bartsia.						P		P	
Phycotis saxifraga –									
Phyllitis sagittata – Hearts-Tongue Fern.									
Pinus nigra -		P							
Polypodium cambricum -								P	
Poterium verrucosum – Mediterranean Salad Burnet.									P
Ptychotis saxifraga - Ptychotis						P			
Quercus ilex – Holm Oak.									
Quercus hirsutium – Downy Oak.					P				
Quercus pubescens – Downy Oak, White Oak.								P	
Reseda alba – White Mignonette, Upright Mignonette.						P			
Rhinanthus minor – Yellow Rattle.							P		P
Rosa canina - Wild Rose.							P		
Rubus sanctos – Blackberry/Bramble.		P		P		O		C	C
Satureja calamintha – Summer Savory.									
Satureja fruiticosa									
Satureja hortensis – Summer Savory.						P		P	
Scilla peruviana – Peruvian Bluebell.						P		P	
Scrophularia canina – French Figwort.				P		P			
Sedum reflexum – Rock Stonecrop					P				
Sedum tenuifolium – Stonecrop			P	O	O		P	P	
Silene vulgaris – Bladder Campion.						P	O		C
Sonchus oleraceus – Common Sow Thistle.									P
Stippa sp.							P		C
Taraxacum laevigatum – Dandylion sp.									P
Thymus vulgaris – Thyme.									
Tragopogon pratensis – Goatsbeard.						P			P
Trifolium incarnatum – Crimson clover								O	
Trifolium repens - white clover									
Umbilicus rupestris – Navelwort.		P	P			P	O	P	
Urtica dioica – Stinging Nettle.									P
Umbellifera sp.								O	C
Verbascum thapsus – Great Mullein, Aarons rod.						P			P
Vicia villosa – Fodder Vetch, Shaggy vetch.			P			P			
Volutaria lippii -									

Species abundance on the north chronosequence continued

	Year of lava flow								
Primary Colonising species	**1981**	**1947**	**1923**	**1879**	**1809**	**1646**	**1614-1624**	**1566**	**1536**
Centranthus ruber – Red Valerian	0%	3%	8%	2%	5%	1%	3%	2%	2%
Echium vulgarae pustulatum – Vipers Bugloss	0%			1%	<1%	<1%	1%	<1%	2%
Genista aetnensis – Mt. Etna Broom.	0%	10%	15%	25%	35%	35%	5%	4%	
Helichrysum italicum italicum –	0%	2%	5%	3%	2%	1%			30%
Isatis tinctoria – Woad.	0%	<1%		<1%	<1%	2%		1%	
Linaria purpurea – Purple Toadflax.	0%	<1%		<1%					1%
Rumex scutulatus aetnensis – Etna type French Sorrel.	0%	2-4%		2%	5%	2%	3%	2%	1%
Senecio bicolor (S.cineraria) – Cineraria.	0%	1%			<1%				
Spartium junceum – Spanish Broom.	0%	15%	2%	35%	20%	25%	80%	2%	10%
Stereocaulon vesuvianum	50%	80%	90%	15%	70%	1%	5%	3%	2%
Other									
Achillea millefolium – Yarrow, Milfoil.		<1%						<1%	
Achillea ligustica – Sneezewort.									
Agrostis tenuifolium – Bent.		<1%		<1%		<1%		4%	
Aira caryophylla			1%						
Allium neapolitanum – Naples garlic.								<1%	<1%
Anthemis chia – Chamomile.							<1%		
Anthoxanthum odoratum – Sweet Vernal Grass.							3%	2%	<1%
Arum sp.									
Asphodelus microcarpus – Common Asphodel.						1%		2%	<1%
Asplenium trichomanes – Maidenhair Spleenwort.					<1%	<1%	<1%	<1%	
Atractylis humilis			<1%	<1%		1%	<1%	1%	
Ballota pseudodictamnus –				<!%					
Brassica sp. -							<1%		<1%
Briza maxima – Large Quaking Grass				2%	3%	1%	2%	2%	2%
Bromus tectorum . – Drooping Brome					2%				
Calycotome villosa – Hairy Spiny Broom.								3%	
Castenia satvia – Sweet Chestnut.									
Centauria cyanus - Cornflower				<1%					
Ceterach officinarum – Rustyback fern					<1%		<1%	<1%	
Cirsium creticum –									1%
Crepis leontodontoides – Hawksbeard.					<1%	1%		1%	
Crocus longiflorus									
Crupina crupinastrum-						1%	1%		
Dactylis glomerata - Cocksfoot.						1%		1%	1%
Daucus carota – Wild Carrot								<1%	
Dorycnium hursutum – Hairy Dorycenium.									<1%
Dasypyrum villosum						<1%	<1%	12%	
Dryopteris villarii –				<1%			<1%		
Elymus repens – Common Couch grass.								3%	
Erodium cicutarium – Common Storks Bill.								<1%	
Euphorbia characias - Large Mediterranean Spurge.							3%		5%
Euphorbia rigida – Broad-Leaved glaucous spurge.				4%		10%	2%		25%
Ferula communis – Giant Fennel		1%		1%	1%	<1%	1%	1%	1%
Festuca rubra – Creeping fescue.									
Foeniculum vulgare - Fennel									
Galium aparine – Goose Grass.						<1%			
Geranium dissectum – Cut Leaved Cranes Bill.									
Geranium robertianum – Herb Robert.		<1%		1%	<1%	1%	1%	<1%	

Species percentage cover on the north chronosequence

	Year of lava flow								
Primary Colonising species	**1981**	**1947**	**1923**	**1879**	**1809**	**1646**	**1614-1624**	**1566**	**1536**
Hedera helix - Ivy.									
Heiracium crinitum - Hawkweed.		<1%		<1%	<1%	<1%			
Hyacinthus orientalis - Hyacinth						<1%			
Hypericum perforatum - Common St.John's Wort.								1%	1%
Hypochoeris maculata???									
Jasione corymbosa - Corymbose Sheeps bit.					<1%	<1%	1%		<1%
Lagurus ovatus - Hares tail.		<1%		2%	2%	<1%	2%	2%	1%
Linaria arvensis -									<1%
Linaria vulgaris - Common Toadflax.									1%
Linum bienne - Pale Flax.								1%	
Lotus sp. -									
Lygeum spartum -		<1%		<1%	7%	<1%		5%	<1%
Mentha suaveoleus - Apple Mint.						2%	2%	2%	
Narcissus sp. -									
Orobanche rapum - Greater Broom Rape.					<1%				
Papaver rhoeas - Common Poppy									<1%
Parentucellia viscosa - Yellow Bartsia.						<1%		<1%	
Phycotis saxifraga -									
Phyllitis sagittata - Hearts-Tongue Fern.									
Pinus nigra -		2%							
Polypodium cambricum -								<1%	
Poterium verrucosum - Mediterranean Salad Burnet.									<1%
Ptychotis saxifraga - Ptychotis						<1%			
Quercus ilex - Holm Oak.									
Quercus hirsutium - Downy Oak.					5%				
Quercus pubescens - Downy Oak, White Oak.								5%	
Reseda alba - White Mignonette, Upright Mignonette.						<1%			
Rhinanthus minor - Yellow Rattle.							<1%		<1%
Rosa canina - Wild Rose.							3%		
Rubus sanctos - Blackberry/Bramble.		2%		2%		2%		4%	10%
Satureja calamintha - Summer Savory.									
Satureja fruiticosa									
Satureja hortensis - Summer Savory.						<1%		1%	
Scilla peruviana - Peruvian Bluebell.						<1%		<1%	
Scrophularia canina - French Figwort.				<1%		1%			
Sedum reflexum - Rock Stonecrop					<1%				
Sedum tenuifolium - Stonecrop				2%	1%		<1%	<1%	
Silene vulgaris - Bladder Campion.						1%	1%		1%
Sonchus oleraceus - Common Sow Thistle.									<1%
Stippa sp.							<1%		1%
Taraxacum laevigatum - Dandylion sp.									<1%
Thymus vulgaris - Thyme.									
Tragopogon pratensis - Goatsbeard.						<1%			<1%
Trifolium incarnatum - Crimson clover								3%	
Trifolium repens - white clover									
Umbilicus rupestris - Navelwort.		<1%				<1%	<1%	<1%	
Urtica dioica - Stinging Nettle.									1%
Umbellifa sp.									
Verbascum thapsus - Great Mullein, Aarons rod.								2%	<1%
Vicia villosa - Fodder Vetch, Shaggy vetch.						<1%			<1%
Volutaria lippii -						<1%			

Species percentage cover on the north chronosequence continued

V. Statistical correlation's between the nine species on Etna and Environmental data

The following tables show statistical correlations of the nine species investigated on Mt.Etna and environmental data such as rainfall, age of site, aspect and organic matter in the soil (OM). The first set of tables show the percentage cover and abundance of the species analysed using a parametric pearsons correlation. The second set analyses the same data using a spearmans non-parametric correlation. A significant correlation is denoted by **.

		AGE	ALTITUDE	ASPECT	RAINFALL	OM	CENT	RUMEX	HELICHRY	Q.ILEX
AGE	Pearson Correlation	1	.017	.247**	.108	.571**	.025	.308**	.011	.530**
	Sig. (2-tailed)		.833	.002	.180	.000	.759	.000	.888	.000
	N	155	155	155	155	145	155	155	155	155
ALTITUDE	Pearson Correlation	.017	1	.106	.188*	.118	.028	.048	.545**	.128
	Sig. (2-tailed)	.833		.187	.019	.158	.731	.547	.000	.117
	N	155	155	155	155	145	155	155	155	155
ASPECT	Pearson Correlation	.247**	.106	1	.493**	.163	.140	.041	.030	.111
	Sig. (2-tailed)	.002	.187		.000	.050	.082	.610	.715	.171
	N	155	155	155	155	145	155	155	155	155
RAINFALL	Pearson Correlation	.108	.188*	.493**	1	.131	.177*	.085	.018	.059
	Sig. (2-tailed)	.180	.019	.000		.110	.028	.295	.821	.464
	N	155	155	155	155	145	155	155	155	155
OM	Pearson Correlation	.571**	.118	.163	.131	1	.086	.364**	.000	.413**
	Sig. (2-tailed)	.000	.158	.050	.110		.308	.000	.996	.000
	N	145	145	145	145	145	145	145	145	145
CENT	Pearson Correlation	-.025	-.028	.140	-.177*	.086	1	-.264**	-.263**	.148
	Sig. (2-tailed)	.759	.731	.082	.028	.308		.000	.001	.070
	N	155	155	155	155	145	155	155	155	155
RUMEX	Pearson Correlation	.308**	.048	.041	-.085	.364**	-.264**	1	.098	.114
	Sig. (2-tailed)	.000	.547	.610	.295	.000	.000		.225	.155
	N	155	155	155	155	145	155	155	155	155
HELICHRY	Pearson Correlation	.011	.545**	.030	.018	.000	-.263**	.098	1	-.156
	Sig. (2-tailed)	.888	.000	.715	.821	.996	.001	.225		.053
	N	155	155	155	155	145	155	155	155	155
Q.ILEX	Pearson Correlation	.530**	.128	.111	.059	.413**	.148	.114	-.156	1
	Sig. (2-tailed)	.000	.117	.171	.464	.000	.070	.155	.053	
	N	155	155	155	155	145	155	155	155	155
Q.PUR	Pearson Correlation	.237**	.148	-.111	.252**	.235**	.112	-.194*	.161*	.128
	Sig. (2-tailed)	.003	.066	.168	.002	.005	.165	.017	.044	.121
	N	155	155	155	155	145	155	155	155	155
ISATIS	Pearson Correlation	.120	.341**	-.076	.181*	.123	.229**	.220**	.410**	.001
	Sig. (2-tailed)	.148	.000	.345	.022	.141	.004	.006	.000	.989
	N	155	155	155	155	145	155	155	155	155
GENISTA	Pearson Correlation	.325**	.404**	.131	.230**	.386**	.239**	.135	.612**	.016
	Sig. (2-tailed)	.000	.000	.105	.004	.000	.003	.094	.000	.848
	N	155	155	155	155	145	155	155	155	155
SPARTIUM	Pearson Correlation	.278**	-.338**	.121	.046	.094	.063	.157	-.123	.072
	Sig. (2-tailed)	.001	.000	.133	.573	.262	.436	.051	.127	.371
	N	155	155	155	155	145	155	155	155	155
SENECIO	Pearson Correlation	.086	-.029	.312**	.205*	-.039	.440**	.427**	.071	.127
	Sig. (2-tailed)	.285	.724	.000	.010	.639	.000	.000	.380	.117
	N	155	155	155	155	145	155	155	155	155

Pearsons correlations between the nine plant species abundance, and the environmental variables of: age, altitude, aspect, rainfall and organic matter in the soil on Mt.Etna.

		Q_PUB	ISATIS	GENISTA	SPARTIUM	SENECIO
AGE	Pearson Correlation	.237**	.120	.304**	[illegible]	.086
	Sig. (2-tailed)	.003	.138	.000	.001	.286
	N	155	155	155	155	155
ALTITUDE	Pearson Correlation	.148	[illegible]	.404**	[illegible]	.034
	Sig. (2-tailed)	.066	.000	.000	.000	[illegible]
	N	155	155	155	155	155
ASPECT	Pearson Correlation	.111	.076	.131	[illegible]	.310**
	Sig. (2-tailed)	.168	.345	.103	[illegible]	.000
	N	155	155	155	155	155
RAINFALL	Pearson Correlation	.252**	.183*	.230**	.048	.206*
	Sig. (2-tailed)	.002	.022	.004	.573	.010
	N	155	155	155	155	155
OM	Pearson Correlation	.236**	.125	.396**	.044	.039
	Sig. (2-tailed)	.004	.133	.000	.592	.640
	N	145	145	145	145	145
CENT	Pearson Correlation	.112	.229**	.236**	.061	.580**
	Sig. (2-tailed)	.165	.004	.003	.436	.000
	N	155	155	155	155	155
RUMEX	Pearson Correlation	.158*	.220**	.138	.157	.477**
	Sig. (2-tailed)	.037	.006	.086	.051	.000
	N	155	155	155	155	155
HELICHR	Pearson Correlation	.182*	.510**	.612**	.127	.071
	Sig. (2-tailed)	.044	.000	.000	.127	.380
	N	155	155	155	155	155
Q ILEX	Pearson Correlation	.125	.003	.018	.072	.121
	Sig. (2-tailed)	.121	.969	.548	.371	.133
	N	155	155	155	155	155
Q PUB	Pearson Correlation	1	.067	.062	.134	.146
	Sig. (2-tailed)		.407	.444	.096	.070
	N	155	155	155	155	155
ISATIS	Pearson Correlation	.067	1	.588**	.119	.086
	Sig. (2-tailed)	.407		.000	.136	.285
	N	155	155	155	155	155
GENISTA	Pearson Correlation	.062	.588**	1	.051	.058
	Sig. (2-tailed)	.444	.000		.531	.472
	N	155	155	155	155	155
SPARTIUM	Pearson Correlation	.134	.119	.051	1	.154
	Sig. (2-tailed)	.096	.136	.531		.055
	N	155	155	155	155	155
SENECIO	Pearson Correlation	.146	.086	.058	.154	1
	Sig. (2-tailed)	.070	.285	.472	.055	
	N	155	155	155	155	155

**. Correlation is significant at the 0.01 level (2-tailed).

*. Correlation is significant at the 0.05 level (2-tailed).

Pearsons correlations between the nine plant species abundance, and the environmental variables of: age, altitude, aspect, rainfall and organic matter in the soil on Mt.Etna. Continued…

		AGE	ALTITUDE	ASPECT	RAINFALL	OM	CENT	RUMEX	HELCHRY	Q ILEX
AGE	Pearson Correlation	1	.017	.247**	.106	.511**	.062	.238**	.071	.314**
	Sig. (2-tailed)		.833	.002	.190	.000	.441	.003	.379	.000
	N	155	155	155	155	145	155	155	155	155
ALTITUDE	Pearson Correlation	.017	1	.106	.188*	.118	.054	.074	.389**	.119
	Sig. (2-tailed)	.833		.187	.019	.158	.508	.361	.000	.140
	N	155	155	155	155	145	155	155	155	155
ASPECT	Pearson Correlation	.247**	.106	1	.483**	.163	.044	.028	.037	.120
	Sig. (2-tailed)	.002	.187		.000	.050	.590	.731	.651	.136
	N	155	155	155	155	145	155	155	155	155
RAINFALL	Pearson Correlation	.106	.188*	.483**	1	.133	-.211**	.151	-.135	.033
	Sig. (2-tailed)	.190	.019	.000		.110	.008	.061	.093	.680
	N	155	155	155	155	145	155	155	155	155
OM	Pearson Correlation	.511**	.118	.163	.133	1	.022	.238**	.133	.441**
	Sig. (2-tailed)	.000	.158	.050	.110		.792	.004	.110	.000
	N	145	145	145	145	145	145	145	145	145
CENT	Pearson Correlation	.062	.054	.044	-.211**	.022	1	.664**	.340**	.171*
	Sig. (2-tailed)	.441	.508	.590	.008	.792		.000	.000	.034
	N	155	155	155	155	145	155	155	155	155
RUMEX	Pearson Correlation	.238**	.074	.028	.151	.238**	.664**	1	.222**	.211**
	Sig. (2-tailed)	.003	.361	.731	.061	.004	.000		.006	.008
	N	155	155	155	155	145	155	155	155	155
HELCHRY	Pearson Correlation	.071	.389**	.037	-.135	.133	.340**	.222**	1	.196*
	Sig. (2-tailed)	.379	.000	.651	.093	.110	.000	.006		.015
	N	155	155	155	155	145	155	155	155	155
Q ILEX	Pearson Correlation	.314**	.119	.120	.033	.441**	.171*	.211**	.196*	1
	Sig. (2-tailed)	.000	.140	.136	.680	.000	.034	.008	.015	
	N	155	155	155	155	145	155	155	155	155
Q PUB	Pearson Correlation	.236**	.182*	.108	.239**	.271**	.181*	.156*	.164*	.075
	Sig. (2-tailed)	.003	.024	.182	.003	.001	.024	[illegible]	.041	.351
	N	155	155	155	155	145	155	155	155	155
SATIA	Pearson Correlation	.190*	-.230**	.032	.041	.187*	.206**	.217**	.263**	-.047
	Sig. (2-tailed)	.018	.004	.695	.612	.024	.010	.006	.001	.560
	N	155	155	155	155	145	155	155	155	155
GENISTA	Pearson Correlation	.194*	.243**	.216**	.155	.343**	.300**	.162*	.306**	.127
	Sig. (2-tailed)	.016	.002	.007	.055	.000	.000	.044	.000	.119
	N	155	155	155	155	145	155	155	155	155
SPARTIUM	Pearson Correlation	[illegible]	.291**	.158	.060	.061	.014	[illegible]	[illegible]	.081
	Sig. (2-tailed)	.001	.000	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
	N	155	155	155	155	145	155	155	155	155
SENECIO	Pearson Correlation	.054	.006	.347**	.211**	.042	[illegible]	.346**	.145	-.152
	Sig. (2-tailed)	.504	.938	.000	.008	[illegible]	.000	.000	[illegible]	.060
	N	155	155	155	155	145	155	155	155	155

Pearsons correlations between the nine plant species percentage cover, and the environmental variables of: age, altitude, aspect, rainfall and organic matter in the soil on Mt.Etna.

		Q_PUB	ISATIS	GENISTA	SPARTIUM	SENECIO
AGE	Pearson Correlation	.238**	.180*	.194*	.308**	.054
	Sig. (2-tailed)	.003	.025	.016	.001	.508
	N	155	155	155	155	155
ALTITUDE	Pearson Correlation	.162*	.230**	.243**	-.291**	.006
	Sig. (2-tailed)	.044	.004	.002	.000	.938
	N	155	155	155	155	155
ASPECT	Pearson Correlation	.108	.032	.218**	.158	.347**
	Sig. (2-tailed)	.182	.696	.007	.050	.000
	N	155	155	155	155	155
RAINFALL	Pearson Correlation	.239**	.041	.155	.069	.211**
	Sig. (2-tailed)	.003	.612	.055	.395	.008
	N	155	155	155	155	155
OM	Pearson Correlation	.241**	.187*	.263**	.091	.042
	Sig. (2-tailed)	.004	.024	.001	.275	.613
	N	146	146	146	146	146
CENT	Pearson Correlation	.181*	.206**	.300**	.054	.270**
	Sig. (2-tailed)	.024	.010	.000	.505	.001
	N	155	155	155	155	155
RUMEX	Pearson Correlation	.186*	.353**	.162*	.120	.349**
	Sig. (2-tailed)	.021	.000	.044	.137	.000
	N	155	155	155	155	155
HELICHRY	Pearson Correlation	.164*	.263**	.335**	.102	.145
	Sig. (2-tailed)	.041	.001	.000	.207	.072
	N	155	155	155	155	155
Q_ILEX	Pearson Correlation	.074	.047	.071	.041	.112
	Sig. (2-tailed)	.361	.564	.379	.613	.165
	N	155	155	155	155	155
Q_PUB	Pearson Correlation	1	.089	.018	.122	.169*
	Sig. (2-tailed)	.	.270	.821	.130	.035
	N	155	155	155	155	155
ISATIS	Pearson Correlation	.089	1	.345**	.151	.070
	Sig. (2-tailed)	.270	.	.000	.060	.387
	N	155	155	155	155	155
GENISTA	Pearson Correlation	.018	.345**	1	.072	.022
	Sig. (2-tailed)	.821	.000	.	.369	.784
	N	155	155	155	155	155
SPARTIUM	Pearson Correlation	.122	.151	.072	1	.179*
	Sig. (2-tailed)	.130	.060	.369	.	.026
	N	155	155	155	155	155
SENECIO	Pearson Correlation	.169*	.070	.022	.179*	1
	Sig. (2-tailed)	.035	.387	.784	.026	.
	N	155	155	155	155	155

**. Correlation is significant at the 0.01 level (2-tailed).

*. Correlation is significant at the 0.05 level (2-tailed).

Pearsons correlations between the nine plant species percentage cover, and the environmental variables of: age, altitude, aspect, rainfall and organic matter in the soil on Mt.Etna continued…

			AGE	ALTITUDE	ASPECT	RAINFALL	OM	CENT	RUMEX	HELICHRY
Spearman's rho	AGE	Correlation Coefficient	1.000	.061	.178*	.168*	.892**	.118	.159*	.010
		Sig. (2-tailed)		.449	.026	.037	.000	.144	.048	.906
		N	156	156	156	156	145	156	156	155
	ALTITUDE	Correlation Coefficient	.061	1.000	.041	.290**	.143	.001	.073	.174**
		Sig. (2-tailed)	.449		.611	.000	.086	.990	.366	.000
		N	156	156	156	156	145	156	156	155
	ASPECT	Correlation Coefficient	.178*	.041	1.000	.451**	.081	.091	.041	-.039
		Sig. (2-tailed)	.026	.611		.000	.120	.260	.611	.651
		N	156	156	156	156	145	156	156	155
	RAINFALL	Correlation Coefficient	.168*	.290**	.451**	1.000	.148	.227**	.143	.086
		Sig. (2-tailed)	.037	.000	.000		.076	.004	.076	[illegible]
		N	156	156	156	156	145	156	156	155
	OM	Correlation Coefficient	.892**	.143	.081	.148	1.000	.129	.132	.111
		Sig. (2-tailed)	.000	.086	.120	.076		.123	.114	.177
		N	145	145	145	145	145	145	145	145
	CENT	Correlation Coefficient	.118	.001	.091	.227**	.129	1.000	.651**	.472**
		Sig. (2-tailed)	.144	.990	.260	.004	.123		.000	.000
		N	156	156	156	156	145	156	156	155
	RUMEX	Correlation Coefficient	.159*	.073	.041	.143	.132	.651**	1.000	.567**
		Sig. (2-tailed)	.048	.366	.611	.076	.114	.000		.000
		N	156	156	156	156	145	156	156	155
	HELICHRY	Correlation Coefficient	.010	.174**	-.039	.086	.111	.472**	.567**	1.000
		Sig. (2-tailed)	.906	.000	.651	[illegible]	.177	.000	.000	
		N	155	155	155	155	145	155	155	155
	Q.ILEX	Correlation Coefficient	.508**	.131	.138	.020	.447**	.061	.062	.190*
		Sig. (2-tailed)	.000	.105	.086	.802	.000	[illegible]	.443	.018
		N	156	156	156	156	145	156	156	155
	Q.PUB	Correlation Coefficient	.492**	-.234**	.042	.136	.463**	-.126	-.114	.172*
		Sig. (2-tailed)	.000	.003	.602	.092	.000	.119	.156	.032
		N	156	156	156	156	145	156	156	155
	ISATIS	Correlation Coefficient	.211**	.227**	-.108	.034	.200*	.476**	.476**	.292**
		Sig. (2-tailed)	.007	.005	.183	.674	.016	.000	.000	.000
		N	156	156	156	156	145	156	156	155
	GENISTA	Correlation Coefficient	.338**	.110	.403**	.114	.472**	.356**	.141	.322**
		Sig. (2-tailed)	.000	.171	.000	.386	.000	.000	.081	.000
		N	156	156	156	156	145	156	156	155
	SPARTIUM	Correlation Coefficient	.302**	-.329**	-.210**	.107	.204*	.109	-.143	-.091
		Sig. (2-tailed)	.000	.000	.009	.186	.014	.184	.144	.258
		N	156	156	156	156	145	156	156	155
	SENECIO	Correlation Coefficient	-.030	.120	.409**	.229**	.139	.492**	.531**	.312**
		Sig. (2-tailed)	.710	.138	.000	.004	.094	.000	.000	.000
		N	156	156	156	156	145	156	156	155

Spearmans correlations between the nine plant species abundance, and the environmental variables of: age, altitude, aspect, rainfall and organic matter in the soil on Mt.Etna.

			Q_ILEX	Q_PUB	ISATIS	GENISTA	SPARTIUM	SENECIO
Spearman's rho	AGE	Correlation Coefficient	.408**	.482**	.217**	[illegible]	.302**	.030
		Sig. (2-tailed)	.000	.000	.007	.000	.000	.712
		N	155	155	155	155	155	155
	ALTITUDE	Correlation Coefficient	-.131	.234**	.217**	.110	.329**	.120
		Sig. (2-tailed)	.105	.003	.007	[illegible]	.000	.138
		N	155	155	155	155	155	155
	ASPECT	Correlation Coefficient	.138	.242	.104	.407**	.270**	.408**
		Sig. (2-tailed)	.088	.002	.191	.000	.001	.000
		N	155	155	155	155	155	155
	RAINFALL	Correlation Coefficient	.072	.136	.034	.134	.101	.230**
		Sig. (2-tailed)	.402	.092	.679	.096	.196	.004
		N	155	155	155	155	155	155
	OM	Correlation Coefficient	.447**	.381**	.200*	[illegible]	.204*	.039
		Sig. (2-tailed)	.000	.000	.015	.000	.014	.641
		N	148	148	148	148	148	148
	CENT	Correlation Coefficient	.097	-.029	.410**	.358**	.139	.382**
		Sig. (2-tailed)	.232	.719	.000	.000	.084	.000
		N	155	155	155	155	155	155
	RUMEX	Correlation Coefficient	-.062	.134	.419**	.144	.043	.317**
		Sig. (2-tailed)	.441	.096	.000	.071	.594	.000
		N	155	155	155	155	155	155
	HELICHRY	Correlation Coefficient	.190*	.177*	.362**	.271**	.091	.312**
		Sig. (2-tailed)	.018	.028	.000	.000	.258	.000
		N	155	155	155	155	155	155
	Q_ILEX	Correlation Coefficient	1.000	.432**	.268**	.240**	.151	.047
		Sig. (2-tailed)		.000	.001	.003	.061	.561
		N	155	155	155	155	155	155
	Q_PUB	Correlation Coefficient	.432**	1.000	.102	.240**	.394**	.237**
		Sig. (2-tailed)	.000		.206	.003	.000	.003
		N	155	155	155	155	155	155
	ISATIS	Correlation Coefficient	.268**	.102	1.000	.511**	.198*	.112
		Sig. (2-tailed)	.001	.206		.000	.013	.166
		N	155	155	155	155	155	155
	GENISTA	Correlation Coefficient	.240**	.240**	.511**	1.000	.327**	.004
		Sig. (2-tailed)	.003	.003	.000		.000	.959
		N	155	155	155	155	155	155
	SPARTIUM	Correlation Coefficient	.151	.394**	.198*	.327**	1.000	.260**
		Sig. (2-tailed)	.061	.000	.013	.000		.001
		N	155	155	155	155	155	155
	SENECIO	Correlation Coefficient	.047	.237**	.112	.004	.260**	1.000
		Sig. (2-tailed)	.561	.003	.166	.959	.001	
		N	155	155	155	155	155	155

* Correlation is significant at the .05 level (2-tailed).

** Correlation is significant at the .01 level (2-tailed).

Spearmans correlations between the nine plant species abundance, and the environmental variables of: age, altitude, aspect, rainfall and organic matter in the soil on Mt.Etna continued.

			AGE	ALTITUDE	ASPECT	RAINFALL	OM	CENT	RUMEX	HELICHRY
Spearman's rho	AGE	Correlation Coefficient	1.000	.061	.178*	.168*	.392**	.080	.134	.008
		Sig. (2-tailed)		.449	.028	.037	.000	.324	.097	.919
		N	156	156	156	156	145	155	155	155
	ALTITUDE	Correlation Coefficient	.061	1.000	.041	.290**	.141	.024	.000	.345**
		Sig. (2-tailed)	.449		.615	.000	.088	.768	.998	.000
		N	156	156	156	156	145	155	155	155
	ASPECT	Correlation Coefficient	.178*	.041	1.000	.451**	.051	.014	.027	.121
		Sig. (2-tailed)	.028	.615		.000	.540	.871	.738	.140
		N	156	156	156	156	145	155	155	155
	RAINFALL	Correlation Coefficient	.168*	.290**	.451**	1.000	.148	.278**	.228**	-.080
		Sig. (2-tailed)	.037	.000	.000		.076	.001	.004	.319
		N	156	156	156	156	145	155	155	155
	OM	Correlation Coefficient	.392**	.141	.051	.148	1.000	.102	.126	.122
		Sig. (2-tailed)	.000	.088	.540	.076		.220	.130	.142
		N	145	145	145	145	145	145	145	145
	CENT	Correlation Coefficient	.080	.024	.014	.278**	.102	1.000	.724**	.417**
		Sig. (2-tailed)	.324	.768	.871	.001	.220		.000	.000
		N	155	155	155	155	145	155	155	155
	RUMEX	Correlation Coefficient	.134	.000	.027	.228**	.126	.724**	1.000	.352**
		Sig. (2-tailed)	.097	.998	.738	.004	.130	.000		.000
		N	155	155	155	155	145	155	155	155
	HELICHRY	Correlation Coefficient	.008	.345**	.121	-.080	.122	.417**	.352**	1.000
		Sig. (2-tailed)	.919	.000	.140	.319	.142	.000	.000	
		N	155	155	155	155	145	155	155	155
	Q_ILEX	Correlation Coefficient	.529**	.132	.159*	.040	.465**	.217	.119	.229**
		Sig. (2-tailed)	.000	.101	.048	.614	.000	.649	.144	.004
		N	156	156	155	155	145	155	155	155
	Q_PUB	Correlation Coefficient	.497**	.260**	.024	.094	.386**	.135	-.175*	.179*
		Sig. (2-tailed)	.000	.001	.767	.247	.000	.094	.029	.026
		N	155	155	155	155	145	155	155	155
	ISATIS	Correlation Coefficient	.269**	.130	-.048	.097	.357**	.407**	.444**	.348**
		Sig. (2-tailed)	.001	.108	.551	.199	.000	.000	.000	.000
		N	155	155	155	155	145	155	155	155
	GENISTA	Correlation Coefficient	.284**	.052	.380**	.034	.394**	.430**	.391**	.390**
		Sig. (2-tailed)	.000	.541	.000	.678	.000	.000	.000	.000
		N	155	155	155	155	145	155	155	155
	SPARTIUM	Correlation Coefficient	.409**	.323**	.212**	.136	.188*	.065	.051	.068
		Sig. (2-tailed)	.000	.000	.008	.091	.024	.411	[illegible]	.419
		N	155	155	155	155	145	155	155	155
	SENECIO	Correlation Coefficient	-.211	.077	.397**	-.212**	.059	.468**	.410**	.283**
		Sig. (2-tailed)	.007	.343	.000	.008	.481	.000	.000	.000
		N	156	156	156	155	145	155	155	155

Spearmans correlations between the nine plant species percentage cover, and the environmental variables of: age, altitude, aspect, rainfall and organic matter in the soil on Mt.Etna.

			[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
Spearman's rho	AGE	Correlation Coefficient	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
		Sig. (2-tailed)	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
		N	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
	ALTITUDE	Correlation Coefficient	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
		Sig. (2-tailed)	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
		N	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
	ASPECT	Correlation Coefficient	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
		Sig. (2-tailed)	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
		N	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
	RAINFALL	Correlation Coefficient	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
		Sig. (2-tailed)	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
		N	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
	[illegible]	Correlation Coefficient	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
		Sig. (2-tailed)	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
		N	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
	[illegible]	Correlation Coefficient	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
		Sig. (2-tailed)	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
		N	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
	[illegible]	Correlation Coefficient	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
		Sig. (2-tailed)	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
		N	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
	[illegible]	Correlation Coefficient	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
		Sig. (2-tailed)	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
		N	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
	[illegible]	Correlation Coefficient	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
		Sig. (2-tailed)	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
		N	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
	[illegible]	Correlation Coefficient	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
		Sig. (2-tailed)	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
		N	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
	[illegible]	Correlation Coefficient	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
		Sig. (2-tailed)	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
		N	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
	[illegible]	Correlation Coefficient	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
		Sig. (2-tailed)	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
		N	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
	[illegible]	Correlation Coefficient	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
		Sig. (2-tailed)	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
		N	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
	[illegible]	Correlation Coefficient	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
		Sig. (2-tailed)	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
		N	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]

*. Correlation is significant at the .05 level (2-tailed).

**. Correlation is significant at the .01 level (2-tailed).

Spearmans correlations between the nine plant species percentage cover, and the environmental variables of: age, altitude, aspect, rainfall and organic matter in the soil on Mt.Etna.

VI. *Stereocaulon vesuvianum* distribution on rock surfaces

The following six tables show lichen percentage cover on lava surfaces on a range of aspects and slopes on large lava blocks on Mt.Etna. The cover changes with time (age of the flow). The lichen shows a clear preference for the north aspects of the rocks as it is here that the first growth is observed and the lichen then spreads across the whole lava rock surface.

1992	Quadrat 1	2	3	4	5	6	7	8	9	10	11	12	13
Stereocaulon vesuvianum	<1%	5%	50%	15%	50%	7%	10%	20%	45%	20%	<1%	20%	<1%
Ocrolechia	0%	0%	0%	15%	5%	8%	0%	20%	35%	30%	0%	10%	3%
Temperature (°C)	25.2°	25.9°	26.0°	26.8°	26.0°	24.5°	23.9°	26.9°	25.3°	23.9°	27.4°	27.4°	26.0°
Relative humidity (%)	39.9	35	38.2	32.6	37.4	42.6	36.2	33.5	35.2	38.7	29.1	30.9	34.1
Slope	50.0°	45.0°	65.0°	30.0°	55.0°	65.0°	25.0°	55.0°	35.0°	12.0°	50.0°	45.0°	55.0°
Aspect	S30°E	S25°W	N10°W	N	N5°E	N25°E	S25°E	N25°E	N5°W	N80°E	S40°E	N	N120°W
Light	1280	1195	121	213	192	142	1095	205	183	968	1245	135	1172

1992	Quadrat 14	15	16	17	18	19	20	21	22	23	24	25
Stereocaulon vesuvianum	20%	15%	3%	60%	40%	1%	7%	<1%	0%	15%	10%	20%
Ocrolechia	0%	5%	10%	20%	20%	<1%	3%	<1%	0%	0%	0%	3%
Temperature (°C)	29.9°	30.2°	25.2°	29.5°	28.9°	30.6°	26.6°	25.2°	25.1°	25.6°	25.0°	26.0°
Relative humidity (%)	25.3	27.2	35.2	28.2	30	25.2	30.3	35.7	35.3	34.5	34.5	38.1
Slope	35.0°	50.0°	33.0°	45.0°	32.0°	22.0°	68.0°	43.0°	63.0°	70.0°	50.0°	47.0°
Aspect	N60°E	N	N85°W	N30°W	N20°W	S20°E	N80°W	S40°W	S40°W	N25°E	N40°E	N40°E
Light	425	265	558	229	350	1548	129	1335	860	149	201	182

Stereocaulon vesuvianum percentage cover distribution on 25 Quadrats located on large lava blocks on the 1992 east lava flow over a range of different slopes and aspects.

	Quadrat												
1983	1	2	3	4	5	6	7	8	9	10	11	12	13
Stereocaulon vesuvianum	15%	1%	20%	40%	25%	4%	5%	5%	15%	5%	7%	2%	1%
Caloplaca	1%	1%	2%	0%	0%	2%	1%	1%	0%	15%	1%	0%	0%
Ocrolechia	25%	0%	20%	15%	15%	5%	5%	8%	5%	15%	70%	1%	5%
Temperature (°C)	18.2°	18.4°	24.5°	19.8°	20.7°	21.5°	18.2°	24.5°	23.3°	24.1°	22.1°	25.8°	27.5°
Relative humidity (%)	55.3	53	46.5	52.4	47.7	45.6	52.2	41.7	45.2	46.3	47.1	37.3	33.8
Slope	20.0°	50°	26°	52.0°	41.0°	34.0°	horiz	46.0°	23.0°	34.0°	15.0°	35.0°	42.0°
Aspect	S	S10°E	N100°W	N80°W	N15°E	N90°E	horiz	S25E	N10°W	N60°W	N20°E	N65°E	N43°E
Light	1153	1645	402	93	56.6	1406	1014	1125	442	433	1227	830	84

1983	14	15	16	17	18	19	20	21	22	23	24	25
Stereocaulon vesuvianum	25%	<1%	10%	40%	60%	70%	2%	55%	5%	5%	5%	2%
Caloplaca	<1%	2%	2%	<1%	0%	1%	<1%	3%	4%	<1%	4%	<1%
Ocrolechia	4%	<1%	2%	0%	0%	0%	2%	5%	5%	0%	7%	0%
Temperature (°C)	26.1°	24.2°	20.7°	19.9°	18.3°	19.8°	20.1°	19.8°	20.8°	21.7°	19.7°	18.8°
Relative humidity (%)	36.8	37.5	42.9	46.1	48.6	49.3	46.5	46.1	45.8	43.9	44.6	46.8
Slope	32.0°	60.0°	30.0°	35.0°	35.0°	45.0°	43.0°	horiz	24.0°	60.0°	23.0°	60.0°
Aspect	N3°W	S	N25°E	N5°E	N25°W	N60°W	W	horiz	N40°E	N140E	N60E	S
Light	123	1768	395	88	382	535	1215	1035	633	1152	843	1796

Stereocaulon vesuvianum percentage cover distribution on 25 Quadrats located on large lava blocks on the 1983 south lava flow over a range of different slopes and aspects.

	quadrat									
1981	1	2	3	4	5	6	7	8	9	10
Stereocaulon vesuvianum	65%	90%	5%	75%	7%	5%	25%	70%	60%	10%
Temperature	19.9°	21.1°	23.9°	22.5°	22.2°	24.3°	24.0°	22.5°	22.3°	23.4°
Relative humidity	22.7	23.7	19.2	23.3	21.5	19.3	21.3	23	22.3	23.2
Slope	35.0°	60.0°	50.0°	32.0°	47.0°	34.0°	45.0°	33.0°	57.0°	85.0°
Aspect	N40°W	N75°W	S	N10°W	N120°W	S	N60°W	N10°E	N30°E	S15°E
Light	458	146.5	1285	342	1460	1358	846	137	105	1247

Stereocaulon vesuvianum percentage cover distribution on 10 Quadrats located on large lava blocks on the 1981 north lava flow over a range of different slopes and aspects.

	Quadrat												
1910	1	2	3	4	5	6	7	8	9	10	11	12	13
Stereocaulon vesuvianum	0%	0%	0%	0%	0%	0%	0%	<1%	5%	0%	50%	0%	0%
Rhyzocarpum geographicum	2%	5%	2%	0%	3%	3%	1%	8%	0%	4%	0%	0%	1%
Caloplaca atrina	1%	0%	3%	2%	5%	0%	2%	4%	8%	0%	3%	1%	0%
Ocrolechia parella	50%	20%	60%	35%	25%	20%	25%	25%	20%	15%	30%	30%	30%
Parmelia glabrotula	7%	0%	0%	0%	0%	50%	0%	10%	0%	0%	3%	0%	20%
Lecanora rupicola	0%	40%	0%	0%	0%	0%	0%	0%	40%	0%	0%	20%	15%
Buellia canesci	0%	0%	0%	5%	0%	0%	0%	0%	10%	0%	0%	10%	0%
Temperature (°C)	17.5°	17.4°	17.4°	17.1°	16.8°	16.5°	17.0°	17.1°	17.2°	16.9°	16.7°	17.4°	17.4°
Relative humidity (%)	33.5	54.6	54.8	56.6	56.9	57.5	56.2	56.9	55.4	57.5	59.1	55.9	56.2
Slope	27.0°	15.0°	10.0°	35.0°	54.0°	15.0°	40.0°	8.0°	54.0°	35.0°	70.0°	40.0°	53.0°
Aspect	N40°E	N50°W	N140°E	N20°W	S60°W	N	N70°W	N10°W	S40°W	W	N20°E	N120°W	N65°W
Light	205	237	160	155	245	188	296	233	337	837	113	779	555

1910	14	15	16	17	18	19	20	21	22	23	24	25
Stereocaulon vesuvianum	0%	0%	30%	0%	0%	0%	0%	0%	0%	35%	0%	50%
Rhyzocarpum geographicum	4%	4%	1%	4%	5%	0%	2%	1%	0%	0%	3%	1%
Caloplaca atrina	2%	4%	1%	<1%	3%	0%	1%	0%	<1%	0%	1%	0%
Ocrolechia parella	20%	15%	0%	40%	20%	15%	20%	15%	25%	0%	40%	0%
Parmelia glabrotula	0%	0%	0%	20%	12%	55%	0%	0%	0%	0%	5%	0%
Lecanora rupicola	5%	40%	20%	3%	0%	0%	25%	80%	25%	25%	20%	10%
Buellia canesci	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	2%
Temperature (°C)	16.8°	17.0°	16.5°	16.7°	16.7°	16.7°	16.3°	16.4°	16.7°	16.2°	15.9°	15.6°
Relative humidity (%)	56.8	56.2	57.4	57	57.6	56.2	58.2	57.4	56.2	57.3	59	60.3
Slope	47.0°	30.0°	52.0°	20.0°	20.0°	Horiz.	37.0°	45.0°	55.0°	50.0°	35.0°	43.0°
Aspect	S20°E	S20°E	N20°W	N20°E	N40°W	Horiz.	S	N25°E	N60°W	N20°W	N20°W	N
Light	755	442	51	123	275	225	396	41	286	34	56	27

Stereocaulon vesuvianum percentage cover distribution on 25 Quadrats located on large lava blocks on the 1910 south lava flow over a range of different slopes and aspects.

	Quadrat												
1843	1	2	3	4	5	6	7	8	9	10	11	12	13
Stereocaulon vesuvianum	0	25	75	1	45	0	0	0	75	20	0	20	70
Rhyzocarpum geographicum	30	15	1	10	0	5	3	5	5	7	1	5	4
Caloplaca atrina	0	0	0	0	0	<1%	<1%	0	0	0	0	0	0
Ocrolechia parella	25	15	20	5	10	10	10	10	0	50	7	20	0
Parmelia glabrotula	0	0	0	0	0	0	7	35	0	0	3	0	0
Lecanora rupicola	30	25	0	25	0	15	15	30	0	10	30	12	15
Parmelia ceperabi	0	2	0	0	0	0	0	0	0	0	0	0	0
Buellia canesci	0	10	0	40	7	0	0	0	15	10	5	1	0
Temperature (°C)	22.1°	23.0°	23.3°	23.1°	22.4°	21.8°	22.4°	21.4°	21.9°	22.3°	22.1°	20.6°	21.6°
Relative humidity (%)	19.5	19.1	18.9	18.4	19.4	19.8	19.4	21.6	20.5	19.9	20.1	21.9	21.2
Slope	23.0°	50.0°	55.0°	55.0°	60.0°	30.0°	28.0°	18.0°	70.0°	63.0°	20.0°	28.0°	45.0°
Aspect	N20°W	N50°W	N	N50°W	N40°W	S40°E	S20°E	E	N40°E	N20°W	W	N20°W	W
Light	219	174	101	102	119	172	106	154	104	121	169	186	133

1843	14	15	16	17	18	19	20	21	22	23	24	25
Stereocaulon vesuvianum	5	0	0	12	0	60	55	4	0	65	0	60
Rhyzocarpum geographicum	10	1	4	0	8	5	5	10	2	2	3	0
Caloplaca atrina	0	0	0	2	1	1	0	1	<1%	0	0	1
Ocrolechia parella	10	10	5	20	10	10	15	0	5	20	3	0
Parmelia glabrotula	5	0	20	0	0	0	0	20	0	0	0	0
Lecanora rupicola	40	20	5	20	30	5	5	30	40	0	40	0
Parmelia ceperabi	0	0	0	0	0	0	0	0	0	2	0	3
Buellia canesci	5	0	0	8	5	0	15	7	0	5	0	20
Temperature (°C)	24.5°	21.1°	21.7°	21.7°	20.7°	20.8°	20.5°	20.3°	20.3°	20.6°	20.1°	19.9°
Relative humidity (%)	17.2	22.8	21.9	22.6	20.7	21.3	23.8	23.4	23.2	24.4	25.3	25.5
Slope	55.0°	15.0°	36.0°	58.0°	Horiz	30.0°	60.0°	35.0°	15.0°	40.0°	45.0°	50.0°
Aspect	S40°W	N110°E	N40°W	N5°E	Horiz	N35°W	N	N100°W	E	N40°W	S	N10°W
Light	110	139	156	138	235	211	129	152	173	135	135	91

Stereocaulon vesuvianum percentage cover distribution on 25 Quadrats located on large lava blocks on the 1843 west lava flow over a range of different slopes and aspects.

	Quadrat												
1536	1	2	3	4	5	6	7	8	9	10	11	12	13
Stereocaulon vesuvianum	25%	10%	7%	5%	0%	40%	25%	0%	0%	45%	0%	8%	0%
Rhyzocarpum geographicum	15%	10%	30%	3%	5%	3%	15%	0%	0%	10%	0%	40%	0%
Caloplaca	3%	0%	2%	25%	8%	0%	0%	2%	60%	0%	30%	0%	60%
Ocrolechia	7%	40%	30%	15%	45%	10%	15%	0%	15%	5%	25%	10%	20%
Parmelia glabrotula	10%	10%	0%	0%	0%	0%	0%	0%	0%	16%	20%	7%	0%
Lecanora rupicola	10%	8%	2%	0%	0%	6%	0%	0%	0%	4%	0%	0%	0%
Rhyzocarpum sp	0%	0%	0%	15%	0%	0%	0%	0%	0%	0%	0%	0%	15%
Parmelia ceperabi	0%	0%	0%	0%	5%	0%	0%	80%	0%	0%	10%	0%	0%
Buellia canesci	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	15%	0%
Ramalina fastigiala	0%	0%	0%	1%	1%	0%	0%	1%	25%	0%	0%	0%	0%
Temperature (°C)	20.1°	20.3°	18.3°	17.8°	16.5°	15.7°	16.9°	18.1°					
Relative humidity (%)	45.5	48.6	49.8	50.7	55.1	56.6	52.5	51.6					
Slope	66.0°	15°	28°	50.0°	64.0°	45.0°	12.0°	57.0°	70.0°	22.0°	60.0°	55.0°	55.0°
Aspect	N100°W	S5°E	S20°E	N60°W	N145E	N20°W	S20°E	N20°W	S20°E	S45°E	S40°W	S40W	S80°W
Light	878	411	232	388	420	106.6	445	55					

1536	14	15
Stereocaulon vesuvianum	8%	60%
Rhyzocarpum geographicum	5%	3%
Caloplaca	5%	0%
Ocrolechia	60%	15%
Parmelia glabrotula	9%	0%
Lecanora rupicola	0%	0%
Rhyzocarpum sp	0%	0%
Parmelia ceperabi	0%	0%
Buellia canesci	0%	0%
Ramalina fastigiala	0%	0%
Temperature (°C)		
Relative humidity (%)		
Slope	45.0°	33.0°
Aspect	N60°E	N40°W
Light		

Stereocaulon vesuvianum percentage cover distribution on 15 Quadrats located on large lava blocks on the 1536 south lava flow over a range of different slopes and aspects.

VII. Plant species studied on Hawaii

Metrosideros polymorpha

Metrosideros polymorpha (picture taken by M.Carpenter)

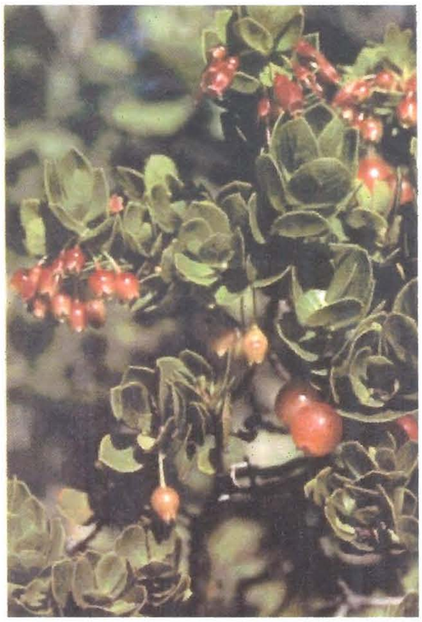
This very adaptable tree occurs in almost every habitat available on Hawaii. As its name polymorpha suggests it comes in a huge range of phenotypical types. It can be a pioneer on a new lava flow, a low shrub of montane bogs or a tall rainforest tree (Pratt 1998). In most areas this tree is the dominant canopy tree, only in certain low precipitation areas at the top of the tree line is it replaced by the Koa (*Acacia Koa*).

Myrsine lessertiana

Myrsine lessertiana (picture taken from Lamoureux 1976).

A Hawaiian endemic species where it is a common tree growing up to 30-40 feet tall in the tropical forests. The young leaves are sometimes pale green but more often pink. Mature leaves are green and leathery. Small green flowers occur among the leaves. Ripe fruits are purple to black berries.

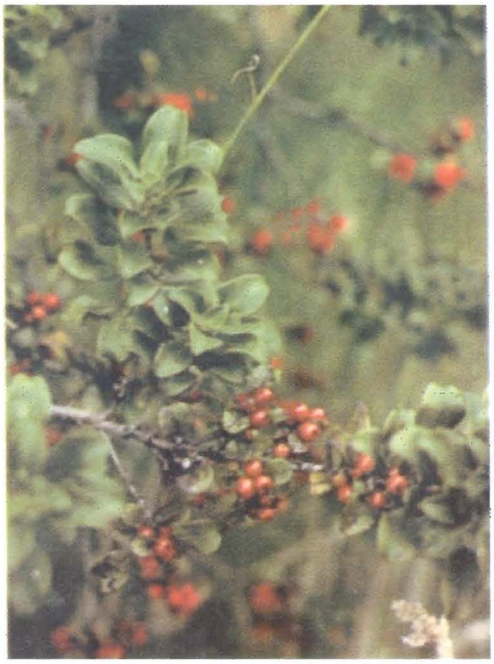
Vaccinium reticulatum



Vaccinium reticulatum (picture taken from Lamoureux 1976).

A shrub about two feet high, which is especially common in Kilauea crater. Leaves are oblong to nearly circular in shape, about one inch long and often bluish or grey-green in colour. Flowers are usually red, orange or yellow berries one forth to one inch in diameter.

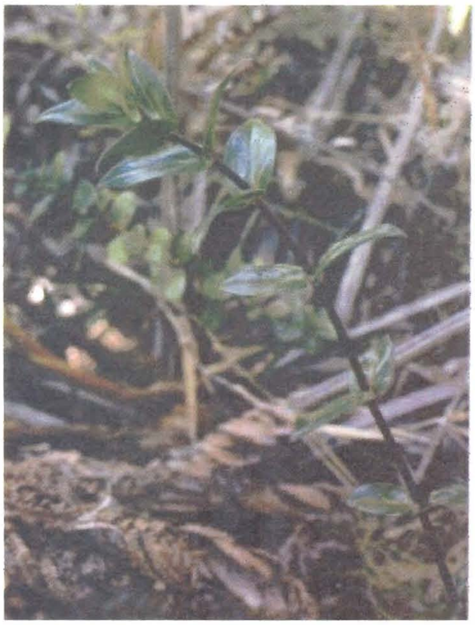
Coprosma ochracea



Coprosma ochracea (picture taken from Lamoureux 1976).

Six species of *Coprosma* grow on the lava fields of Hawaii. *C.ochracea* is a tree which grows commonly in the tropical forests. It has thin oval leaves about 1in wide. Bares red or dark orange egg shaped fruits about ¼ inch long.

Hedyotis centranthoides



Hedyotis centranthoides (picture taken from Lamoureux 1976).

H.centranthoides is an endemic shrub with weak sprawling almost vine like branches which is common on both the wet forest sites and the recent open lava flows. Pairs of oval leaves two to three inches long are widely scattered on the stem. Tiny yellow green flowers grow in several clusters arising from the bases of the uppermost leaves and develop into seed pods about one inch long.

VIII. Hawaii - Site locations

East chronosequence (1000m)

Sample site	Site location (map reference)
1984 lava flow (17 year old)	19° 39' 01'' N 155° 15' 58'' W
1942 lava flow (49 year old)	19° 37' 46'' N 155° 15' 08'' W
1852 lava flow (149 year old)	19° 38' 57'' N 155° 16' 21'' W
3000 year old lava flow	19° 40' 43'' N 155° 16' 59'' W
4000 year old lava flow	19° 41' 18'' N 155° 17' 28'' W

East chronosequence (1800m)

Sample site	Site location (map reference)
1984 lava flow (17 year old)	19° 36' 45'' N 155° 21' 32'' W
1852 lava flow (149 year old)	19° 37' 07'' N 155° 21' 38'' W
400 year old lava flow	19° 38' 40'' N 155° 21' 46'' W
3,000 year old lava flow	19° 37' 30'' N 155° 22' 44'' W
4,000 year old lava flow	19° 37' 53'' N 155° 22' 02'' W

South west chronosequence

Sample site	Site location (map reference)
1950 lava flow (51 year old)	19° 19' 18'' N 155° 52' 26'' W
1926 lava flow (75 year old)	19° 11' 34'' N 155° 51' 47'' W
1919 lava flow (82 year old)	19° 13' 55'' N 155° 52' 30'' W
1907 lava flow (94 year old)	19° 05' 37'' N 155° 46' 28'' W
1868 lava flow (133 year old)	19° 03' 57'' N 155° 41' 53'' W
200 year old lava flow	19° 06' 47'' N 155° 49' 33'' W
750-1500 51 year old lava flow	19° 05' 34'' N 155° 44' 27'' W

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