Weeds on granite outcrops in temperate Australia, South Africa and the USA

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Summary Granite is a ubiquitous igneous rock that outcrops on 15% of the earth's surface. Recent syntheses of information on the biodiversity of granite outcrops have revealed significant regional differences in the distribution and abundance of weeds on granite outcrops. This paper compares the weed floras on granite outcrops across temperate Australia, South Africa and the USA, with special focus on southern Western Australia where granite outcrops are especially common on one of earth's oldest landscapes. The patterns revealed might be explicable in terms of the regional disturbance history of the lands on which granite outcrops are found. Regions of eastern Australia, South Africa and the USA where glacial activity, orogeny, marine inundation or prolonged soil disturbance by animals have occurred have resilient native floras able to compete under ongoing soil disturbance regimes with exotics. In contrast, native plants on the ancient Australian landscapes unaffected by glacial, eustatic, orogenic or extensive soil disturbance by animals, such as southern WA or Eyre Peninsula, are much less resilient to weed invasion, particularly where contemporary disturbance coincides with elevated soil fertility.

Keywords Temperate weeds, granite, Australia, South Africa, USA, disturbance history, soil fertility.

INTRODUCTION

Outcrops of granite occupy 15% of the earth's surface (Twidale 1982), occurring on every continent and many islands, embedded in a diversity of landscapes, climates and vegetation types. They assume various forms, including flatrocks, boulders, domed bornhardts, inselbergs and mountain ranges with soaring steep-walled peaks. Because granite tends to fracture in exfoliated sheets parallel to the soil surface, it often forms rounded massive exposures of rock with pockets of shallow soil or small pools (gnammas).

Climatic and diurnal extremes are accentuated on granite outcrops compared with surrounding vegetation on deeper soils, and microhabitats ranging from waterlogged shaded clefts to exposed rapidly drying shallow soils occur intermixed in close proximity. The open nature of granite outcrops provides access to high light intensities for those plants able to cope with these often extreme habitats. Disturbance may be common through sheet flooding and associated scouring of shallow soils, windthrow of shallow-rooted trees, fire, drought deaths, extreme cold, and diverse human activities. This mixture of high light intensities and regular disturbance creates habitat suited to many weeds of agricultural or pastoral landscapes.

Granite outcrops have become important sites for comparative biogeographical and ecological studies at a global level (Withers and Hopper 1997, 2000, Porembski and Barthlott 2000). Recent syntheses of information on the biodiversity of granite outcrops have revealed significant regional differences in the distribution and abundance of weeds on granite outcrops. For example, outcrops in forested landscapes appear to be sources of indigenous weeds when adjacent forest is destroyed for agricultural purposes. Wyatt (1997) suggested that such common plants of the south-east USA coastal plain as *Rumex hastulatus*, *Linaria canadensis* and *Crotonopsis elliptica* may have originated from granite outcrops of the adjacent piedmont of the Appalachians. Similarly, in West Africa, Porembski (2000) cited *Cyanotis lanata*, *Sporobolus* spp. and *Fimbristylis* spp. as inselberg escapees along road verges through tropical forest.

Conversely, while no invasive exotic weeds of significance are recorded on the south-east USA granite outcrops, tropical African outcrops are sometimes invaded by South American grasses such as *Axonopus compressus* and *Panicum laxum*, as well as the pineapple *Ananas comosus*. In Madagascar, the neotropical *Agave sisalana* is a serious inselberg weed, while granite outcrops on the Seychelles are occasionally colonised by *Cinnamomum verum* and *Alstonia macrophylla*. The biodiverse inselbergs of south-east Brazil have been invaded by African grasses such as *Melinis repens*, *M. minutiflora* and *Panicum maximum*. Also invasions of African or Madagascan leaf succulents (*Kalanchoe* and *Aloe* spp.) have been recorded (Porembski 2000). On north Queensland granite outcrops, *Melinis repens* and *M. minutiflora* are invasive, together with *Hyptis suaveolens*, *Bidens bipinnata*, *Stylosanthes guianensis*, *Euphorbia hirta*, *Lantana camara* and *Praxelis clematidea* (Clarkson and Hopper, unpublished).

Many granite outcrop systems in temperate parts of the world have yet to be investigated floristically. More general surveys, such as those for Mediterranean climate ecosystems, have enabled regional overviews

of weed floras that may or may not apply to granite outcrops. For example, Groves (1991) and Groves and Kilby (1993) considered the introduced floras of California, South Australia, Chile and South Africa, noting close to an order of magnitude more weed species recorded for the former two regions compared with those recorded for the latter two. No explanatory hypothesis for this striking difference in invasive floras was offered. However, it was noted for all four Mediterranean climate regions, that the majority of weed species had European origins, were either grasses or composites, were annuals or biennials and had been introduced deliberately as ornamental plants. Preadaptation to fire, low nutrients and grazing were suggested as attributes favouring establishment of weeds in the four regions. Of these factors, low nutrients is a hallmark of South African fynbos and South Australian mallee-heath weathered soils, but the younger soils of California and Chile are much richer.

Clearly, some interesting regional patterns in weed floras exist for temperate countries, but knowledge of correlates and causes of these patterns is limited. One way of better understanding these patterns is to exclude a level of variation by focusing on geologically matched sites such as granite outcrops.

Recent work has shown that weeds are most diverse globally on granite outcrops in south-western Australia, where up to 24% of individual outcrop floras may be exotic, set against a background level of 9% weeds for the flora as a whole (Ornduff 1987, Keighery 1995, Hopper *et al*. 1997, Pigott 2000, Hussey *et al*. 1997). Particularly pernicious are annual grasses from the Mediterranean (e.g. *Briza maxima*, *Avena fatua*) or South Africa (e.g. *Ehrharta longifolia*).

Hopper (1997) hypothesised that the high invasibility of disturbed Western Australian plant communities was due to the absence of glacial soil stripping as an evolutionary force acting on the flora. Native species were unable to compete against weeds from regions where soil disturbance is a regular perturbation. This hypothesis could be tested by examining granite outcrop floras from other regions where major soil disturbance has or has not been a significant evolutionary force.

In the present paper, I compare the weed floras on granite outcrops across temperate Australia, South Africa and the USA, with special focus on southern Western Australia where granite outcrops are especially common on one of the earth's oldest landscapes. I examine new regions where glacial soil disturbance and recent mountain building have been absent (Eyre Peninsula, South Africa) or present (Tasmania, New England Tableland, California). It was predicted that weed invasion would be greater in the former stable, unglaciated regions rather than in the latter orogenically active and recently glaciated regions.

MATERIALS AND METHODS

Comprehensive field herbaria were compiled for more than 200 granite outcrops in south-western Australia over the period 1986–2002, for seven outcrops on Eyre Peninsula, South Australia in 2001, for five in north-eastern Tasmania in 1996, for six on the New England Tableland, northern New South Wales in 1998, for seven on the Appalachian Piedmont in Georgia and North Carolina in 1990, for five in the Sierra Nevada of California in 1990, and for eight along the west coast of South Africa's Cape Region and Namaqualand in 1998, 2000 and 2001. Bornhardts or inselbergs sampled were from a few hectares to a few square kilometres in area. Plant collections were made on random walks of one hour to two days duration, depending on outcrop size, and stratified by microhabitat, so that rare sites such as gnammas or deep clefts were deliberately searched for while randomly walking over common habitats such as sheet rock and shallow-soil herbfields. Only steep or dangerous slopes requiring access by rope were omitted from the surveys. A fragment sufficient for identification of each species encountered, native and exotic, was placed under extra-wide clear adhesive tape in a field notebook. Identifications were made through the assistance of experienced local botanists and/or available published floras and field guides, sometimes supplemented by comparison with herbarium specimens. For each outcrop, the percentage of exotic weeds in the total flora was calculated. Only a summary of results is presented here as it is intended to publish comprehensive accounts of the surveys elsewhere.

RESULTS

In south-western Australia 40–200 species of vascular plants may occur on individual outcrops. The percentage of weed species varies from 0–41%. Outcrops with the highest proportion of weeds are either inner urban, exposed to high levels of disturbance and dumping of garden refuse (e.g. Mt. Melville, Albany, whose outcrops have 35–41% weeds), or on sites of elevated soil fertility and high disturbance (e.g. Waterwheel Rock, Cape Leeuwin – 34%). Outcrops throughout the wheatbelt and along the south coast typically have 10–20% weeds, while those included within large reserves or in the extensive semi-arid goldfield woodlands usually have less than 10%. Inselbergs on Eyre Peninsula in South Australia have lower total species numbers (45–103) and the highest proportion of weeds recorded on Earth, ranging from 35–60%. In stark contrast, granite outcrops on the New England

Tableland of New South Wales have only 0–7% weeds in floras comprising 35–57 vascular species. Outcrops in north-eastern Tasmania have 8–13% weeds in floras of 31–87 species. In South Africa's west coast and Namaqualand regions, most outcrops have no weeds, or, at most, one or two species. The same applies to outcrops in Georgia and California, where a maximum of 8% weeds has been recorded.

DISCUSSION

Except for the anomaly of South Africa, the hypothesis that invasive exotic weeds are most common in landscapes where glacial soil stripping and recent mountain building have not been active is supported by these data. Granite outcrops on Eyre Peninsula in South Australia have the highest proportion of invasive weeds in their flora. These outcrops sit on a stable granitic craton last glaciated in the Permian, with little orogeny since (Twidale 1982).

The same applies for granite outcrops in south-western Australia (Hopper *et al*. 1996), which are second highest in abundance of weed species, especially on outcrops that are regularly disturbed and/or have elevated soil fertility. The latter factor may explain why the Eyre Peninsula outcrops are so weedy, as the region is known to be covered in sand dunes blown in from nutrient-enriched west coastal areas through the Quaternary.

In contrast to these two geologically stable ancient landscapes, the younger post-glacial actively orogenous landscapes of north-eastern Tasmania, Georgia and California are all noteworthy in the paucity of invasive exotic weeds comprising their granite outcrop floras. The same applies to those of the New England Tableland on the slopes of the Great Dividing Range (Hunter and Clarke 1998). Outcrops in all these regions sit embedded in landscapes fragmented by agricultural clearing and human transport infrastructure, so the opportunities for exotic weed invasion are assumed to be much the same as those seen on Eyre Peninsula and in south-western Australia. In this context, the paucity of weeds is striking, and suggests that the native floras of these outcrops are much more competitive and resilient to invasion than those of the ancient Australian granite cratons.

South Africa, although mountainous, has old weathered mountain ranges with little active orogeny and no glaciation since the Permian (Goldblatt 1997). It should, therefore, display low resilience to weed invasion according to the hypothesis under test here. Yet this is patently not so for the granite outcrops surveyed, which had few if any exotic weeds in their floras. (Other habitats in South Africa do display extensive weed invasion – van Wilgen *et al*. 2001.)

This might be explained by a third evolutionary force in terms of regular soil disturbance – that due to animals. The sandy soils of the Cape Region and Namaqualand experience remarkable levels of soil disturbance due to the activities of fossorial mammals, porcupines, primates and birds that feed on bulbs of the remarkably rich geophyte flora of the region. Indeed, many rare geophytes are confined to tight crevices on granite and sandstone outcrops where their bulbs are secure from predation. None of the other regions included in this survey have such a rich nor active bulb-eating fauna.

Consequently, the hypothesis needs to be rephrased as follows: *regional weed invasion will be greatest in ancient weathered nutrient-deficient landscapes where regular soil disturbance is least through evolutionary time*. Causes of such soil disturbance include glaciation, mountain building, erosion by water, marine inundation or animal activity.

It is important to note that this study is correlational and descriptive. While it takes advantage of grand natural experiments, the study nevertheless lacks the controls of rigorous experimentation. Such experimentation is now required to establish causation by, for example, disturbing granite outcrop soils and documenting weed invasion in climatically matched sites with similar adjacent weed sources on landscapes of contrasting disturbance histories.

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