Experimental studies on the drought, waterlogging, and frost tolerance of *Ascarina lucida* Hook. f (Chloranthaceae) seedlings

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Abstract: *Ascarina lucida* Hook.f. (Chloranthaceae) is a small tree species endemic to New Zealand. The distribution of *A. lucida* suggests an inability to survive severe frosts or droughts. Therefore, peaks in the abundance of *A. lucida* in pollen records have usually been interpreted as indicating periods of mild, moist climates. The environmental tolerance of *A. lucida* seedlings to climatic extremes was experimentally tested by exposing seedlings to frost, drought, and waterlogged soil conditions. This research confirms the sensitivity of *A. lucida* to climatic extremes. *Ascarina lucida* has a similar drought tolerance to *Coprosma grandifolia*, a species known to be drought intolerant; seedlings had considerable tolerance of waterlogged soils, but exhibited reduced root weights when severely waterlogged; and a frost of -2°C resulted in complete mortality for seedlings sourced from lowland and submontane populations. Peaks in the abundance of *A. lucida* can be attributed, at least in part, to periods of warm, wet climate. However, the early successional nature of this species also suggests that disturbance regime plays an important role in regulating its distribution and abundance.

Keywords: *Ascarina lucida*; Chloranthaceae; *Coprosma grandifolia*; frost; drought; waterlogging; climate change

Introduction

Ascarina lucida Hook.f. (Chloranthaceae) is a small tree species endemic to New Zealand. The species is regarded as rare in the North Island, occurring as small, scattered populations, and is only common on the western coast of South Island (McGlone and Moar, 1977). *Ascarina lucida* is a species of lowland and montane distribution (Sakai and Wardle, 1978) and attains its greatest abundance where the forest has been disturbed (Bartlett, 1984; Burrows, 1996).

Peaks in the abundance of *Ascarina lucida* in Holocene pollen records have usually been interpreted as an indication of mild, moist climates (Newnham *et al.* 1989; Elliot, 1998; Horrocks *et al*., 2002). McGlone and Moar (1977) suggested that drought and heavy frost are the two most important factors limiting the distribution of this species, and noted its restriction to regions where rainfall exceeds 1500 mm per annum. Lees (1986) stated that *A. lucida* is drought tender, and Stevens *et al.* (1988) and Clarkson (1986) claimed that the species favours areas with mild, moist conditions. Experimental work on frost tolerance (McGlone and Moar, 1977; Sakai and Wardle, 1978) indicates that the species is relatively frost tender: in a survey of forty-one native species, only *Metrosideros excelsa* and *Avicennia resinifera*, two coastal species naturally restricted to latitudes north of 39°S, were found to be less frost tolerant.

Pollen records indicate *A. lucida* was common in the early Holocene and began a long, fluctuating decline ca. 7000 years ago (McGlone and Moar, 1977). Correct interpretation of "the *Ascarina* decline" with regard to climate change is dependant on a thorough understanding of the ecology of *A. lucida*. This paper presents results of experiments on the drought, waterlogging and frost tolerance of *A. lucida*, and discusses them in the context of the ecology of the species and palynological interpretation.

Materials and methods

Drought tolerance

The drought tolerance of *A. lucida* was experimentally compared to that of *Coprosma grandifolia*. *Coprosma grandifolia* was selected as the most appropriate species to compare to *A. lucida* as it is commonly found in association with it (Martin, 2001) and is known to be susceptible to drought (Bannister, 1986).

Ascarina lucida seeds were collected from the Hunua Range, Auckland, and sown into flats in July 1999. Seedlings were individually planted into pots 5 cm wide by 5 cm long by 8 cm deep in January 2000 and grown in an outside propagation area until September 2000. Thirty *C. grandifolia* seedlings approximately 1 year old were purchased from a commercial nursery. The seedlings were well established in 7 cm wide by 7 cm long by 8 cm deep pots. In September 2000, 30 *C. grandifolia* and 30 *A. lucida* seedlings were individually planted into PB3 sized planter bags containing standard potting mix, placed in an outside propagation area to establish, and watered nightly by overhead irrigation.

In November 2000, seedlings of each species were randomly assigned to ten blocks, until each block had three seedlings of each species. Each seedling was then randomly assigned to a treatment and position within block. Within each block, a seedling of each species was subjected to one of the following treatments: Treatment 1, watered daily by dripper irrigation for four weeks (control); Treatment 2, water withheld for two weeks, watered to saturation, then water withheld for a further two weeks (moderate drought); Treatment 3, water withheld for four weeks (severe drought). Initial seedling heights were 26.7±0.8 cm and 43.2 ±1.1 cm (mean ± standard error) for *A. lucida* and *C. grandifolia* seedlings respectively.

Each plant was weighed at field capacity prior to the experiment, to enable the assessment of soil water loss for each treatment. We defined field capacity as the weight of the plant and soil 48 hours after being watered to saturation. To reduce the change in field capacity due to evaporation from the soil surface, tinfoil was used to cover the soil surface of each bag while it drained to field capacity. After 48 hours the tinfoil was removed and the mass of each plant/bag combination was weighed to the nearest 0.1 g using a Metler AT460 DeltaRange® balance, and the height of each plant measured from the soil surface to the uppermost node.

At the end of the four week treatment period each plant/bag combination was reweighed and measured as outlined above. Drought damage was assessed as follows: damage rating 0, no visible signs of damage; damage rating 1, leaves wilted; damage rating 2, leaves and stem wilted; damage rating 3, leaves and stem wilted, some permanent leaf damage; damage rating 4, leaves and stem wilted, all leaves suffering permanent damage.

Growth and drought damage were assessed in relation to soil weight loss. A scatter graph with trend lines was constructed showing percentage height growth and damage, in relation to soil weight loss as a percentage of weight at field capacity. The difference in the decline of growth rates between the two species was analysed using a Student's *t*-test.

Temperature extremes were monitored with three maximum/minimum thermometers and during the course of the experiment ranged from 12.0 ±0.6 to 32.3 ±0.7°C (mean ± standard error).

Waterlogging tolerance

Twenty-seven *A. lucida* seedlings were grown from seed collected from Puhipuhi, Eastern Northland in February 1999. The seedlings were transplanted into pots 5 cm wide by 5 cm long by 8 cm deep containing standard potting mix, and grown in a glasshouse. In May 2000 the height for each seedling from soil level to uppermost node was recorded. Nine plants were randomly assigned to each of the following treatments: free draining (control); water level 60 mm below soil surface (Treatment 1); and water level 30 mm below soil surface (Treatment 2). Water level was controlled by placing each plant in a plastic container with holes cut at different heights in the sides. To reduce the effect of unknown environmental gradients on any particular treatment, the plants were arranged in a series of Latin squares. The experiment was conducted in an outside propagation area and water levels were maintained by nightly overhead watering. Temperature extremes were monitored with a maximum/minimum thermometer and ranged between 5 and 25°C for the course of the experiment.

Final seedling height was measured in October 2003. The seedlings were then removed from their pots and carefully washed to remove all potting mix. Excess water from the washing process was removed by allowing the seedlings to dry overnight at room temperature. The seedlings were then separated into roots and shoots and dried (105°C for 24 h) and weighed to the nearest 0.01 g.

The mean dry weight for plant roots and shoots was calculated for each treatment. Single factor ANOVAs were performed to test for differences between the control and treatment groups.

Frost tolerance (Experiment 1)

In November 1999 *A. lucida* seedlings germinated from leaf litter and soil samples that were collected from four different populations: Puhipuhi, Northland (220 m altitude); southern Coromandel Range (470 m altitude); Kohukohunui, Hunua Range (688 m altitude); and northern Coromandel Range (750 m altitude). In February 2000, nine seedlings of each provenance were transplanted into individual pots 5 cm wide by 5 cm long by 8 cm deep containing standard potting mix. The seedlings were grown in a glasshouse until transferred to an outside propagation area in mid April. Between mid-April and early June, the minimum and maximum temperatures recorded were 5 and 23°C respectively.

The site chosen for frost exposure was a low lying grass covered slope in Bethells' Valley, north west of Auckland (grid reference NZMS 260 Q11 438804). The site is commonly subject to low temperatures during the winter months due to cold air drainage from the surrounding hills.

In early June 2000 the plants were arranged in a Latin square design (nine blocks of four) with one plant per provenance within each block. Within blocks seedlings were placed 30 cm apart, and each block of four was placed 90 cm apart from adjacent blocks. The seedlings were placed in the ground so the top of each pot was flush with ground level. A maximum/minimum thermometer was positioned on a pole 1.4 m above ground level in the centre of the experimental area.

Frost damage was assessed visually 14 days after the first frost. Leaf damage was rated on a scale based on the method used by Sun and Sweet (1996); 0 = no leaf damage, 1 = approx. 10% of leaf area damaged (1-19%), 2 = approx. 30% of leaf area damaged (20-39%), 3 = approx. 50% of leaf area damaged (40-59%), 4 = approx. 80% of leaf area damaged (60-89%), 5 = approx. 100% of leaf area damaged (90-100%). Seedling survival was assessed on 26 September, 10 weeks after the first frost.

Frost tolerance (Experiment 2)

The experiment was repeated in a modified form using 30 seedlings from Puhipuhi and Kohukohunui populations only. Ten seedlings 8-months-old from each population, and ten seedlings 12-months-old from Kohukohunui, were grown in the same substrate and pot size as previously outlined. The 12-month-old seedlings were transferred to the outside area in January 2000 and the 8-month-old seedlings in mid April. By the time of planting all seedlings had been exposed to a minimum temperature of 5°C.

Two frost exposure areas were chosen at the Bethells Valley site, one upper slope, where frosts were likely to be less severe, and one lower slope. Five seedlings from each of the three treatments above were randomly assigned to each site. On 25 July 2000 the seedlings were arranged in a Latin square design, and planted in the ground so that the top of each pot was flush with ground level. A maximum/minimum thermometer was placed in a horizontal position 5 cm above ground level in the centre of each experimental area.

Frost damage was assessed as previously outlined. In addition stem tissue damage was also assessed, with the degree of stem tissue damage for each seedling being classified as 0%, 25%, 50%, 75%, or 100% stem tissue damage. Stem tissue damage was defined as stem that had lost all structural support and was limp. Seedling survival was assessed seven weeks after the first frost on 26 September.

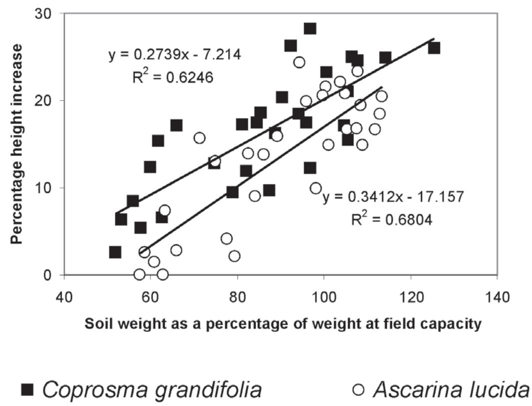

Figure 1. Relationship between soil water loss and percentage height increase for *A. lucida* and *C. grandifolia* seedlings.

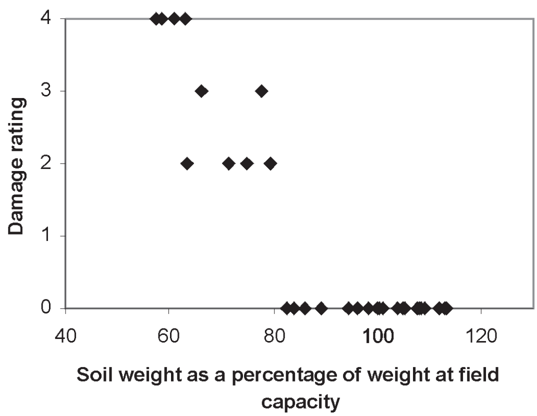

Figure 2. Relationship between soil water loss and damage rating for *A. lucida* seedlings.

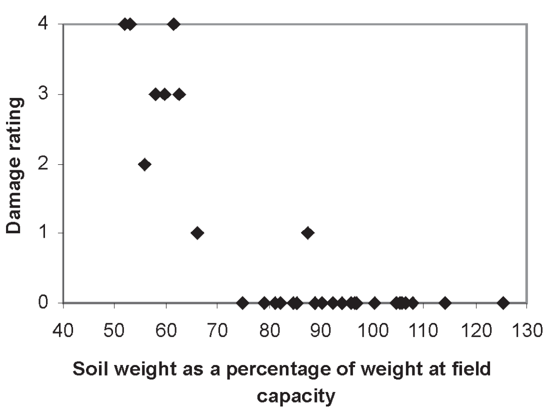

Figure 3. Relationship between soil water loss and damage rating for *C. grandifolia* seedlings.

Results

Drought tolerance

Height growth increased similarly for both *A. lucida* and *C. grandifolia* (Fig. 1, the difference between slopes was not significant, d.f. = 56, t = 0.2525, P >0.10). The majority of *A. lucida* and *C. grandifolia* seedlings remained undamaged when soil weight exceeded 80% of soil weight at field capacity (Fig. 2 and 3). Soil weight below 80% of weight at field capacity resulted in a damage rating of 2 (leaves and stems wilted) or higher for *A. lucida*, and plants subjected to soil weights below 60% were classified as damage rating 4 (two plants with stem and leaf wilt, and permanent leaf damage). In contrast, *C. grandifolia* seedlings were classified as damage rating 2 or higher only when soil weights fell below 65% of weight at field capacity, and plants subjected to soil weights below 60% were classified as damage rating 2 (one plant), 3 (three plants) or 4 (two plants).

Waterlogging tolerance

All seedlings in each treatment exhibited leaf yellowing and abscission, but no mortality occurred. Mean height increase was greatest for the free draining treatment, and decreased with an increasingly waterlogged substrate (Table 1). Surface roots were produced by three plants in the free draining treatment, four plants in Treatment 1 (water level 60 mm below soil surface), and nine plants in Treatment 2 (water level 30 mm below soil surface). Statistical analysis revealed a significant difference at 5% between root weights in each treatment (P = 0.04) but no significant difference between shoot weights (P = 0.34). All other differences were statistically insignificant.

Table 1. The effect of waterlogging on growth of *A. lucida* seedlings (mean ± s. e.).

	Height increase (cm)	Dry root weight (g)	Dry shoot weight (g)
Control	1.7 ± 0.90	0.52 ± 0.04[1]	0.52 ± 0.07
Treatment 1[2]	1.1 ± 0.15	0.42 ± 0.04	0.64 ± 0.06
Treatment 2[3]	0.8 ± 0.20	0.33 ± 0.05[1]	0.48 ± 0.08

[1]significantly different Kolmogorov–Smirnov test (P = 0.04)
[2]waterlevel 60 mm below soil surface
[3]waterlevel 30 mm below soil surface

Table 2. Number of *A. lucida* seedlings from the Puhipuhi and Kohukohunui provenances in each leaf damage class when exposed to frost

			Leaf damage class (%)					
Provenance	Age (months)	Frost	0	10	30	50	80	100
Puhipuhi	8	-2°C	0	0	0	0	2	3
Kohukohunui	8	-2°C	0	0	0	0	2	3
Kohukohunui	12	-2°C	0	0	1	0	3	1
Puhipuhi	8	-4°C	0	0	0	0	2	3
Kohukohunui	8	-4°C	0	0	0	0	2	3
Kohukohunui	12	-4°C	0	0	0	2	3	0

Table 3. Number of *A. lucida* seedlings from the Puhipuhi and Kohukohunui provenances in each stem damage class when exposed to frost

			Stem damage class (%)				
Provenance	Age (months)	Frost	0	25	50	75	100
Puhipuhi	8	-2°C	1	1	3	0	0
Kohukohunui	8	-2°C	2	1	2	0	0
Kohukohunui	12	-2°C	5	0	0	0	0
Puhipuhi	8	-4°C	1	2	1	1	0
Kohukohunui	8	-4°C	1	2	2	0	0
Kohukohunui	12	-4°C	5	0	0	0	0

Frost tolerance (Experiment 1)

Frost occurred on 11 and 12 July 2000, with a minimum temperature of -1°C at 1.4 m above ground level. Expected temperature at seedling height would have been less than -1°C due to radiation frosts increasing in severity towards ground level. Frost damage was assessed on the 25th of July. All seedlings, regardless of provenance, were severely damaged. In September, the only surviving seedling was from the northern Coromandel Range provenance.

Frost tolerance (Experiment 2)

Frosts occurred on 5 and 6 August 2000. The minimum temperature for the frost was -2°C for the upper slope site and -4°C for the lower slope site. Frosts resulted in 80–100% leaf damage, and significant stem damage, to the 8-month-old seedlings from both provenances (Table 2 and 3). The 12-month-old seedlings from the Kohukohunui provenance exhibited no signs of stem tissue damage at either site (10 out of 10 rated as 0% stem tissue damage).

The frosts on 5 and 6 of August were the lowest recorded temperatures at this site during the winter of 2000. By late September no seedlings of any provenance or age had survived.

Discussion

The similarity in growth rate decline for *A. lucida* and *C. grandifolia* when exposed to drought conditions suggests the two species have similar drought tolerance. The damage rating results indicate that *A. lucida* suffers leaf and stem wilt at higher soil moisture levels than *C. grandifolia*, but the significance of this is difficult to assess from the available data set. The relative drought tolerance of the two species could be further investigated by repeating the experiment in a modified form, with treatments subjecting 30 seedlings of each species to soil moisture levels between 60 and 80% of weight at field capacity. This may further differentiate the soil moisture thresholds at which damage occurs.

The survival of all seedlings in each of the waterlogged soil treatments indicates that *A. lucida* seedlings are tolerant of waterlogged soils. This is supported by the occurrence of *A. lucida* in areas of swamp forest (Martin, 2001) and the observed survival of seedlings at Puhipuhi, eastern Northland, after several days of complete submergence. The seedlings in the waterlogged treatments exhibited increased production of adventitious roots above the level of soil saturation (pers. obs. T. Martin), likely allowing the plants to compensate for the loss of oxygen uptake by the submerged portion of the root system (Crawley 1997). This suggests that *A. lucida* can react adaptively to waterlogged soil conditions.

The reduced height growth and root weight of seedlings in the waterlogged treatments compared to the free draining treatment, suggests that while the species can survive waterlogging, free draining soils are optimal for growth. The experiment did not investigate the effect of water levels above the soil surface on seedling growth and survival. However, seedlings of similar size and age to those in the above experiment were dead after total submergence for ten weeks, and seedlings submerged to 2 cm above soil level for the same duration survived, but suffered major leaf loss. Thus *A. lucida* seedlings tolerate waterlogging and temporary submergence, and on flood prone sites are likely to survive periodic inundation. However the 'wetland' niche of *A. lucida* is limited due to its reduced growth rates when waterlogged and its inability to survive prolonged submergence. At sites where these conditions are commonplace *A. lucida* is likely to be out-competed by plants that thrive on wet soils, even if seedlings are able to establish. The preference of *A. lucida* for moist but not waterlogged soils has possibly been detected in a pollen record. Horrocks *et al*., (1999) attributed an increase in *A. lucida* pollen to a lowering of the water table in swamp forest on Great Barrier Island *ca*. 2500 yr B.P.

In comparison with other New Zealand tree species *A. lucida* appears to be frost tender (Sakai and Wardle, 1978). Air temperatures of -4°C caused severe damage to small plants (c. 1 m tall) at Lincoln in October 1976 (McGlone and Moar,1977; Matt McGlone, Landcare Research, Lincoln, N.Z., personal communication). Sakai and Wardle (1978) tested the freezing resistance of excised *A. lucida* shoots collected from 50 m altitude in Westland, and found that the lowest temperature at which little or no injury occurred was -3°C for leaves and -5°C for xylem.

Frost resistance within a species often differs according to provenance. Sakai and Wardle (1978) demonstrated that *Weinmannia racemosa* sourced from a montane population had greater frost resistance than lowland plants, and that the hardiness of *Nothofagus solandri* increased along an altitudinal gradient. An investigation of the frost tolerance of *Nothofagus solandri* var. *cliffortioides* and *Nothofagus menziesii* by Sun and Sweet (1996) showed that for both species, severity of frost damage was significantly influenced by provenance. The known altitudinal range of *A. lucida* in the North Island is from 20 m at Awana, Great Barrier Island, to 860 m on the Moehau Range, Coromandel (Martin, 2001). Thus, with an altitudinal range of over 800 m, the species must experience a wide range of temperature regimes. This may result in significant ecotypic variation between lowland and montane provenances. A literature search found no previous studies that investigated ecotypic variation between *A. lucida* provenances.

The *A. lucida* seedlings were severely damaged at temperatures similar to those described by McGlone and Moar (1977). The testing of leaves from adult plants, and the southerly provenance of the material, may explain the greater frost resistance described by Sakai and Wardle (1978). The greater resistance of xylem than leaves to low temperatures also noted by Sakai and Wardle may explain the initial lack of visible damage to the stems of seedlings exposed to frost. Less severe frosts than those that occurred during the experiments may have resulted in leaf damage only.

The only seedling that survived the frosts, having been exposed to temperatures as low as -4°C, was from a high altitude provenance (750 m, Coromandel Range). The significance of this is hard to assess due to the small sample size. The production of new shoots from the base of this seedling in the spring, suggests that *A. lucida* can resprout after frost has killed all parts of the plant above the ground.

A survey of North Island *A. lucida* populations indicated that high altitude populations were found at sites where frost risk is reduced, due to a combination of topographical and vegetation characteristics (Martin, 2001). No high altitude populations were found in gullies or frost hollows, but plants were present on slopes or ridges where frost risk was lowered. All high altitude populations were found in areas with good soil drainage. In submontane areas *A. lucida* may be restricted to more free draining sites, due to the increased risk of frost damage to plants growing on waterlogged soils (Davidson and Reid, 1987).

The experiments confirm the sensitivity of *A. lucida* to climatic extremes, and frost and drought severity are likely to be major factors controlling its distribution. A third factor influencing the distribution and abundance of *A. lucida* appears to be the disturbance regime. *A. lucida* is commonly found in early successional communities in association with species such as manuka (*Leptospermum scoparium*) (Martin, 2001; 2002); and the seed ecology of *A. lucida* suggests the species is adapted to disturbed environments (Martin and Ogden, 2002). Fluctuations in the abundance of *A. lucida* in the pollen record need to be interpreted with regard to both climate change and changes in disturbance regime.

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