Chapter 6. Soil moisture depletion in spring – a possible mechanism for *N. neesiana* impact

“Phenological complementarity promotes coexistence in ... plant communities”.

Cleland *et al.* 2006 p. 13742.

Summary

Soil moisture content under swards of *N. neesiana* and *Themeda triandra* was measured at points spaced 0.1 m or 1 m apart along 6 transects with a total length of 69.9 m, with repeated measurement along two transects (37.9 m) at Yarramundi Reach Grassland in spring. All transects showed markedly lower sub-surface soil water content under *N. neesiana* than under *T. triandra*. The difference was highly significant. This was the case whether the *T. triandra* was senescent or healthy and when both species were either unmown or mown short, and appeared to be independent of micro-topographic position, surface soil features and time of day. Soil drying in spring probably contributes to ongoing losses of native vascular plants in areas invaded by *N. neesiana*, potentially consolidating the occupation of sites by *N. neesiana*, and may drive patch expansion by disadvantaging immediately adjacent native C_4 grasses. At a landscape scale, widespread replacement of native C_4 grasses by *N. neesiana* is likely to reduce runoff and increase deep drainage, resulting in increased salinity, soil acidification, and eutrophication downstream in the catchment. If these effects were happening, *Nassella neesiana* would have the potential to affect biodiversity far beyond the areas infested.

Introduction

Invasive plants can severely modify hydrological cycles (Vidler 2004). Competition for soil water may be a widespread mechanism by which invasive plants cause biodiversity impact, but few studies have provided firm demonstrations of this (Levine *et al.* 2003). Athel pine *Tamarix aphylla* (L.) H. Karst. (Tamaricaceae) in inland Australia lowers the water table, alters stream flow and flooding regimes and ultimately affects salinity levels (Griffen *et al.* 1989). Markedly increased rates of soil drying by high densities of the invasive annual *Bromus tectorum* L. have been found to adversely affect seedlings of a native perennial grass when the two were germinated simultaneously (Evans & Young 1972). Extending this work, Melgoza *et al.* (1990) demonstrated that *B. tectorum* significantly decreased the productivity of the co-occurring native grass *Heterostipa comata* (Trin. & Rupr.) Barkworth by reducing soil water content and the internal water potential of the grass. In contrast the C_4 grass *Andropogon virginicus* L., a native of the southern USA, is invasive in Hawaiian rainforest where it develops a high biomass of dead shoots that reduce evaporation rates from the soil, and also passes through an inactive senescent phase during which transpiration is reduced, resulting in excess water in the soil, increased runoff and accelerated erosion (Mueller-Dombois 1973).

Nassella neesiana is a C_3 or cool season grass that produces most of its vegetative growth from autumn to spring (April to October) and flowers mainly during spring and early summer (September to December) in south-eastern Australia (Snell *et al.* 2007). It produces substantial green biomass in winter but very little in summer (McLaren *et al.* 1998) when tussocks usually bear large numbers of persistent dead culms and leaves (Gardener *et al.* 2005).

Themeda triandra, the most important dominant native grass in the higher rainfall temperate lowland grasslands in the region, is a C_4 grass of the NADP-ME type (Hattersley 1986) that flowers and undertakes most of its growth from the middle of spring into summer (Groves and Whalley 2002). The optimum temperatures for *T. triandra* growth are in the range 25-35ºC (Wijesuriya and Hocking 1999). Below a threshold of 15°C the sward 'hays off' and the grass is dormant in winter and spring in southern Australia (Dunin 1999).

The phenology of *T. triandra* and the extent to which its growth is concentrated in summer is dependent to some extent on particular seasonal and site conditions. In the NSW Riverina *T. triandra* "commences new season's growth in late spring ... puts out new leaves until the soil moisture is depleted" and ceases growth "before the onset of heavy frosts" (Leigh and Mulham 1965 p. 30). In southern Victoria rapid growth commences in October, optimum growth rates occur in late spring and early summer if there is adequate soil moisture, growth continues in summer if soil moisture is not limiting, flowering and seed shed occurs mainly in mid-summer (January-February), and growth continues in autumn until constrained by cooler temperatures (Groves 1965, Morgan 1994, Lunt and Morgan 2002). Groves (1965) recorded inflorescences from early November to early December over two years in one Melbourne grassland. On the New England Tablelands (1060 m altitude) Trémont (1994) recorded flowering occurring in 'mid season' (any two months from November to February of December-January only) in grazed areas and late season (January to April) in ungrazed areas. Chan (1980) studied the phenology of *T. triandra* at Yarramundi Reach over the period of 9 months from September 1973: floral initiation was calculated to commence when day length reached 12 hr 33 min (36 minutes longer than for *Austrostipa bigeniculata* and *Austrodanthonia* spp.), head emergence commenced in mid October, anthesis occurred from c. 12 November to 9 January, and seed fall occurred over a period of c. 3 weeks to the end of

January. Leaf biomass production increased rapidly in early November, fell during December due to low rainfall and continued at levels of c. 30-40 g m^{-2} (dry weight) through until the end of April. Production of new reproductive stems reached a strong peak during mid November and monthly stem biomass production continued at high levels from January to April. Similar biomass production patterns were observed by Groves (1965) in southern Victoria. However McDougall (1989) reported flowering mainly in mid-spring corresponding with the period of highest productivity in Melbourne region grasslands, with seed shed between November and February, usually peaking in early January, but with an additional later peak if there was early summer rain. On the southern tablelands of NSW growth is limited by low temperatures between May and October and potentially by inadequate soil moisture when temperatures are favourable during the remainder of the year (Dunin and Reyenga 1978).

C_3 species as a general rule have lower water use efficiencies than C_4 species, that is they use more water per unit of carbon dioxide fixed (Radosevich and Holt 1984, Ghannoum 2009). C_4 grasses have greater stomatal resistance and greater stomatal control of transpiration than C_3 species (Dunin and Reyenga 1978) and are able to use greater amounts of water when vapour pressure deficits are high (i.e. in dry summer conditions) (Singh *et al.* 2003). Australian C_4 species use, on average, five times more soil water in summer than in winter, and have a summer water use efficiency twice that in winter (Singh *et al.* 2003). But the C_4 photosynthetic pathway is highly sensitive to water stress, equally or more so than the C_3 pathway (Ghannoum 2009).

Use of soil water by *T. triandra* is directly linked with its seasonal growth pattern, and reaches a maximum coincident with production of new leaf growth in summer (Dunin 1999). Swards of *T. triandra* are able to more effectively trap rainfall, reduce runoff and increase evaporation than swards of C_3 grasses (Singh *et al.* 2003). Dunin and Reyenga (1978) found that on an annual basis, 20% of water loss from a *T. triandra* grassland was by evaporation of dew and intercepted rainfall and 80% by evaporation from soil water and transpiration, and that plant control of evaporation was greater during the period of dormancy than during the growing period. During the dormancy period the standing dead biomass of *T. triandra* in ungrazed swards restricts evaporation to less than 50% of that in grazed swards, so conserving soil moisture prior to the growing period (Dunin 1999). McDougall (1989) found that total standing biomass (including substantial proportions of unattached litter) remained constant or fell slightly from the end of one growing period to the start of the next, although the proportion of green foliage declined from a mid spring peak of c. 85% to a June low of c. 35%. Conservative use of water by *T. triandra* during winter and early spring enables carry-over of soil moisture into its growing period, and this strategy is one factor that has enabled the species to be successful in temperate zones with unreliable summer rainfall (Dunin and Reyenga 1978). When the growth period commences again in summer, the conserved moisture is used, and soil moisture is depleted to a very low level by the end of the growing period (Dunin 1999). McDougall (1989) recorded soil moisture values ranging between c. 10 and 27% between September and January, and falls to c. 3-6% in February in burnt and unburnt swards at Laverton North Grassland.

Bolger *et al.* (2005) compared the drought tolerance of a range of native and exotic grasses widely present in south-eastern Australia in pot experiments. *Themeda triandra* had neither high nor low drought tolerance, having good dehydration tolerance and avoidance as the soil dries, but poor dehydration avoidance (high epidermal conductance) when transpiration reaches minimum levels. *Themeda triandra* folds its leaves to reduce dehydration. These findings may be misleading because there is some evidence that unlike the other native species tested, *T. triandra* may avoid dehydration by being deep rooted, and typically has good survival in a dormant condition during drought in south-eastern Australia (Bolger *et al.* 2005). Such experimental evidence also ignores other drought avoidance strategies such as litter accumulation.

Themeda triandra is phenologically complementary to the bulk of the native grassland flora, so largely avoids direct competition for resources with these other plants. *Themeda triandra* has a predominantly summer growing season, offset from the spring growing season characteristic of most of the native grasses and forbs (Patton 1935, Willis 1964, Groves 1965, Lunt *et al.* 1998, Groves and Whalley 2002). The major flowering period of the native grassland flora corresponds with the time that evaporation begins to exceed precipitation (Patton 1935, Willis 1964). As moisture levels decline, the flowering period rapidly ends and "most of the vegetation passes into a resting stage until the following autumn" (Patton 1935 p. 172), being practically dormant from December to April (Willis 1964). Chan (1980) recorded the flowering periods of 61 native species at Yarramundi Reach and found that 33 flowered in September, 51 in October, 49 in November, 32 in December, 28 in January and 7 or fewer species in every other month. Exotic species also showed a marked flowering peak in October and November. However particular conditions may alter this pattern: Davies (1997) found that some native perennials grow actively in summer if rainfall is significant, while Trémont (1994) recorded the peak flowering period was around one month later in ungrazed areas than in grazed areas, and considered native perennials to typically flower both in spring and autumn.

When *T. triandra* is replaced as the dominant grass by *N. neesiana* the phenological complementarity of soil water utilisation with the much of the native flora is presumably reduced: the spring growing and flowering *N. neesiana* would be expected to compete more strongly for soil resources with most of the native grasses and forbs during this critical period. Depletion of soil moisture during spring is one potential mechanism by which *N. neesiana* could have ongoing deleterious impacts on native plant diversity, including the exclusion of *T. triandra* and other native grasses from sites that it occupies. For example, continued soil moisture depletion during successive springs could result in lower fecundity and recruitment of native species in *N. neesiana* patches as patch size or patch age increases.

Depletion of soil moisture by *N. neesiana* prior to the growing period of *T. triandra* would also presumably have a negative impact on subsequent growth of *T. triandra* in areas close to or within *N. neesiana* infestations. Robertson (1985) argued that *T. triandra* was replaced by other grasses as a result of competition for water and McDougall (1989) concurred with this possibility, finding that *Austrostipa* and *Austrodanthonia* species took its place in 'tree halo' areas, where competition for water in the deeper layers of soil is presumably also important. Possibly *T. triandra* is most affected by this competition when the conditions it requires for growth are at their most marginal – for example when plants are in senescence, or subjected to shading.

To investigate these propositions, a series of simple measurements of soil moisture content near the surface were taken to determine whether soil moisture differences existed between areas where *N. neesiana* was the dominant grass and where *T. triandra* was dominant.

Methods

Soil moisture measurement

Soil moisture readings were taken with an MP406 moisture probe (ICT International Pty Ltd, no date). The probe is a battery powered, hand held device that measures the dielectric constant of the soil, giving values as direct volumetric soil water, from 0 to 100%. Measurement is based on the principle that the dielectric constant of water is approximately equal to 80, whereas that of soil is c. 3 or 4 and that of air is 1, so any change in the dielectric value of the soil matrix directly indicates a changed water content. The device uses high frequency radio techniques to measure soil capacitance. The probe consists of three stainless steel needles 60 mm long and 14 mm apart, that are pushed into the soil surface. It thus measures the capacitance of the volume of soil probed by the needles, from the surface to 60 mm depth.

Differences between laboratory-measured volumetric soil water content and the measurements obtained with the device are expected to be ±2-5% (ICT International Pty Ltd no date). However, in the work reported here, the absolute calibration of the device is unimportant, since the purpose was to determine relative differences between soils under *N. neesiana* and those under *T. triandra*. Nevertheless the absolute differences are useful, within the limits of measurement of the instrument, and the actual moisture values are valuable as data in their own right.

Sampling

Only near-surface soil moisture measurements were taken, i.e. at probe depth, without supplementary augering to greater depths. The probe was pushed into the soil until the needles were inserted for their full 60 mm length. This is likely to be in the broad vicinity of the primary root zone of the grasses under consideration. When present, litter mats or other objects were removed from the ground surface immediately before taking readings. Measurements were taken along straight line transects through the boundaries of *N. neesiana* patches, at intervals of 1 m in dense mature grassland, or at intervals of 0.1 m in short mown grassland where small tussocks provided less impediment to probe entry to the soil (Table 6.1). The short distances between probe readings also enabled better qualitative evaluation of the spatial variation of soil moisture levels. The cover and condition (*vis a vis* degree of senescence) of the *T. triandra* swards were subjectively assessed and the micro topographic positions of the grasses along the transect were recorded. Measurements were taken along transects through swards with different characteristics. Two transects (‘D’ and ‘mown zone’) were repeated a few days apart. The sampling was restricted to a relatively discrete portion of the grassland at intermediate topographic positions. Transects were deliberately located to avoid areas where there were indications of possible soil differences under the two vegetation types, such as hard pans, dumped soil or textural contrasts.

Transects were undertaken in six different areas and were repeated in two separate sections of Yarramundi Grassland Reserve, giving a total of eight sets of measurements (Table 6.1). Total lengths of transects was 69.9 m, or 107.8 m if the repeat sampling is included.

Table 6.1. Soil moisture transect samples at Yarramundi Reach grassland, October 2008.

Transect	Date	Time	Sampling interval (m)	Transect length (m)	Sward characteristics
Patch E transect 1	17/10/2008	5.15 pm	1	7	*N. neesiana* mature, dense 60-80% cover; *T. triandra* senescent, close to 100% cover
Patch E transect 2	17/10/2008	5.30 pm	1	8	
Patch B, centre	17/10/2008	5.45 pm	1	11	*T. triandra* variably senescent with cover of 100 or 90%
Patch B, west	17/10/2008	5.55 pm	1	6	*T. triandra* area mixed sward with *N. neesiana* 5 or 10%
Transect D	17/10/2008	6.20 pm	1	31	*T. triandra* mainly dense, senescent 90-100% cover
Transect D	22/10/2008	10.55 am	1	31	
Mown zone	19/10/2008	7:00 pm	0.1	6.9	Infrequently mown area, short turf with more diverse forb flora.
Mown zone	22/10/2008	12.30 pm	0.1	6.9	

Rainfall

Rainfall at the nearest measuring station, at the Australian National Botanic Gardens, c. 2.6 km north-east of the study area was below the long term average during the preceding two months, and during the month when soil moisture measurements were made was less than half the average (Table 6.2).

Table 6.2. Rainfall (mm) at the Australian National Botanic Gardens, Canberra, August to October 2008 and 1968-2010 averages (Source: Bureau of Meteorology, Australian Government).

	August	**September**	**October**	
Average 1968-2010	55.7	62.6	67.6	
Monthly totals 2008	24.4	48.0	33.4	
Daily totals 2008			9.4	4 October
			2.4	5 October
			9.0	7 October
			12.2	14 October
			0.4	22 October

Analysis

Sample soil moisture transects are presented as simple linear plots. For statistical analysis, means were calculated for moisture readings under areas dominated by either *T. triandra* or *N. neesiana*. Data points where neither grass was clearly dominant were excluded. For the purposes of significance testing, the data for the two Patch E transects and the two Patch B transects were combined, and the later sample for both Transect D and the mown zone were not considered independent from the earlier samples and were excluded. Data was analysed using general analysis of variance (ANOVA, F test). Means were $\log_{10}$ transformed.

Results

Samples of transect date are provided in Figures 6.1 and 6.2. Areas dominated by *T. triandra* consistently showed higher soil water contents than areas dominated by *N. neesiana* at Yarramundi Reach in October 2008 (Table 6.3).

For the selected and combined transects, the soil moisture difference under the two dominant grasses was highly significant (Table 6.4), and the overall ratio of soil moisture under *T. triandra* to that under *N. neesiana* was 4.7 (95% confidence interval = 3.0, 7.3). On average, *N. neesiana* depleted soil moisture to 27% of that under *T. triandra*.

Time of day did not appear to alter these relationships (e.g. Fig. 6.1), nor did upslope or downslope position appear to have much influence (Fig. 6.2). Within stands of *T. triandra*, measured soil moisture levels varied by large factors, sometimes 2-4 times.

Table 6.3. Mean soil moisture (%) under *N. neesiana* and *T. triandra* along transects at Yarramundi Reach grassland, October 2008.

Transect	**Date**	**Time**	**No. of soil moisture readings**		**Mean soil moisture (%)**		**Ratio of mean soil moisture *N.n.* : *T.t.***
			Nassella neesiana	***Themeda triandra***	***Nassella neesiana***	***Themeda triandra***	
Patch E transect 1	17/10/2008	5.15 pm	3	3	3.97	26.20	0.15
Patch E transect 2	17/10/2008	5.30 pm	3	3	5.43	26.53	0.20
Patch B, centre	17/10/2008	5.45 pm	4	8	4.25	13.18	0.32
Patch B, west	17/10/2008	5.55 pm	2	3	6.35	22.23	0.29
Transect D	17/10/2008	6.20 pm	12	19	4.84	19.84	0.24
Transect D	22/10/2008	10.55 am	12	19	0.61	12.66	0.05
Mown zone	19/10/2008	7:00 pm	33	29	0.41	2.55	0.16
Mown zone	22/10/2008	12.30 pm	33	29	0.11	1.09	0.10
Total			102	113			
Grand mean					**1.38**	**9.32**	**0.15**

Table 6.4. Significance testing of mean near-surface soil moisture under *N. neesiana* and *T. triandra* along selected transects at Yarramundi Reach grassland, October 2008.

	Log transformed mean	**SE**	**F pr**	**Back transformed mean (%)**
N. neesiana	0.424	0.0617	**0.0017**	2.65
T. triandra	1.093			12.39

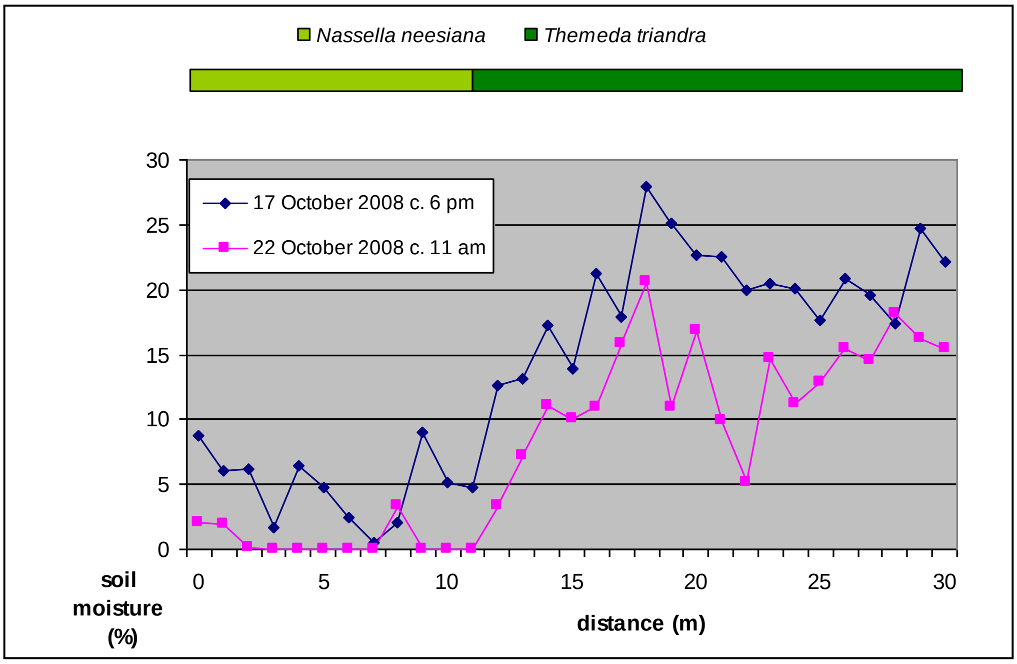

Figure 6.1. Near-surface soil moisture transect from *N. neesiana* into senescent *T. triandra*, Yarramundi Reach, ACT, 17 and 22 October 2008, Transect D. Despite light rain (1-2 mm) in the late evening of 21 October, the soils were drier during the late morning on 22 October than they were during the late afternoon of 17 October.

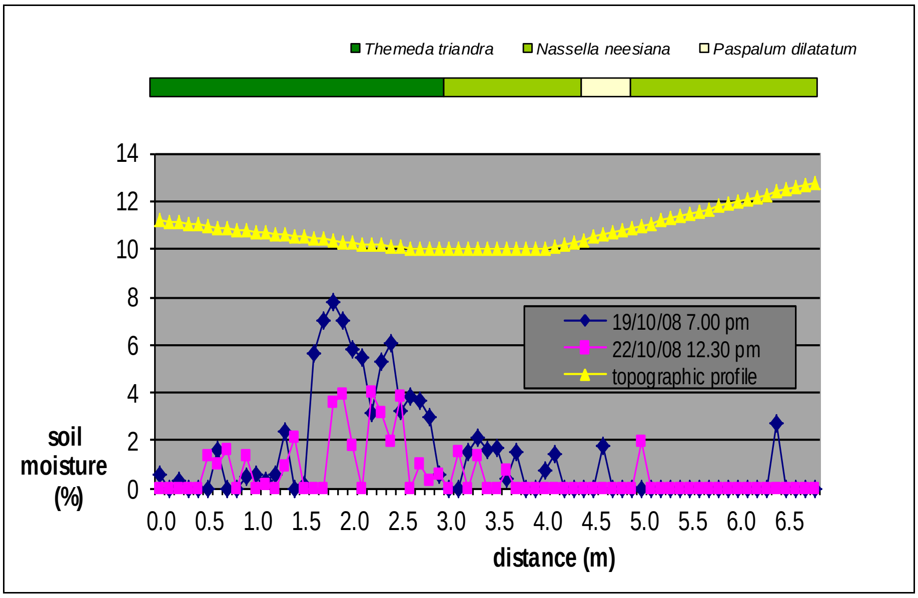

Figure 6.2. Near-surface soil moisture transect in a mown zone from *T. triandra* grassland into an *N. neesiana* patch at Yarramundi Reach, ACT, 19 and 22 October 2008. The “topographic profile” approximately illustrates the relative slopes and elevations along the transect.

Discussion

The data presented here are limited to a single grassland and a short period in October during a single year, but consistently shows that the near surface soil moisture levels under *N. neesiana* were markedly lower than those under *T. triandra*. The difference in soil moisture under the two grass types appeared to be independent of micro topographic position, aspect and time of day. There was no indication of soil differences along any of the short transects, and significant soil differences are unlikely to occur at the scale of investigation. *Nassella. neesiana* significantly depleted surface soil moisture in spring, often to very low levels, compared to the dominant native grass in the areas sampled.

Little information appears to be able available on the depth distribution of roots of *N. neesiana* and *T. triandra*. Groves (1965) found that only a small fraction by weight of roots penetrated below 15 cm in a *T. triandra* grassland at St Albans, Victoria. Dunin and Reyenga (1978) inferred that there was little root extraction of soil water at a depth of 78 cm in *T. triandra* grassland at Krawarree, New South Wales. Perennial grasses can extract soil moisture from depths below 1 m, but on basalt soils roots occur mostly in the top 80 cm of soil (Singh *et al.* 2003). Nie *et al.* (2008) found that the root “density” (roots per m^2) of a range of perennial grasses in the top 10 cm of soil was 2-4 times that in the 10-110 cm zone and that the deepest roots were usually not below 1.5 m, on a range of soil texture types.

Most of the root mass of *N. neesiana* and *T. triandra* is probably in the top 10 cm of soil, so measurements of soil moisture in the top 6 cm are likely to be a reasonable indicator of water content over the whole rooting profile.

Information is not available on the field capacities and wilting points of soils at Yarramundi Reach but values of volumetric soil water content close to zero suggest that soil water deficits under *N. neesiana* were common. Such conditions would create stress for co-occurring plants and impact upon their growth.

McDougall (1989) reported soil moisture values (at unstated depths) of c. 20-27% under *T. triandra* at Laverton North in October 1987. Many of the values reported here are within this range. The results are consistent with the findings of Dunin and Reyenga (1978) that conservative water use by *T. triandra* during its dormancy period results in higher soil water content under *T. triandra* swards than under C_3 dominated pasture in late spring. The results are also consistent with known characteristics of C_3 pasture grasses: they use soil water inefficiently, increase their water use in spring at the time when evaporation is increasing, and thus limit their own growth and that of summer growing species (Johnston *et al.* 1999). By depleting soil water in spring, *N. neesiana* could be controlling the resource available for the later-growing *T. triandra* and thereby disrupting one of the most fundamental hydrological patterns of the ecosystem.

It can be deduced that this pre-emption of soil water use by *N. neesiana* will impact on later growing *T. triandra* and may contribute to its replacement, or ongoing exclusion once *N. neesiana* has occupied previously disturbed sites. Competitive displacements of native grasses by exotic African grasses resulting from differential competitive responses to water stress have been found in Venezuelan savannahs by Baruch and Fernández (1993).

What has not been demonstrated is whether the soil moisture pattern reverses in summer when *N. neesiana* is dormant and *T. triandra* has entered its main phase of growth, as would be expected. Demonstration of this corollary should be one aim of a more thorough investigation of the significance of soil moisture depletion as a possible mechanism by which *N. neesiana* causes a biodiversity impact.

Impact on native plant diversity

The grasslands of temperate south-eastern Australia regularly suffer summer and early autumn droughts (Leeper 1964) and the early-mid spring growth peak of *N. neesiana* would appear to much better coincide with the usual periods of high precipitation than the late-spring and summer growing period of *T. triandra*. Under these conditions *N. neesiana* would *prime facie* appear to have superior competitive abilities to *T. triandra*. In years when rainfall is limiting to native grassland growth, and that may be most years, established *N. neesiana* presumably uses soil moisture reserves that would otherwise be available to the predominantly spring-growing native forbs, and sabotages the growth strategy of the later-growing *T. triandra* by limiting soil moisture accumulation during the period when rainfall is more reliable. A similar process has been recorded where annual pasture replaced an *Austrodanthonia*-dominated understorey in *Eucalyptus camaldulensis* Dehnh. woodland in the South-East of South Australia (Specht 2000). The seasonal growth pattern of the exotic Poaceae, *Trifolium* spp. and Asteraceae that dominated the pasture resulted in depleted surface soil water before the summer growth period of the native understorey species, and they used soil water at a greater rate than the native grasses. The increased evapotranspiration reduced the growth of the summer-growing native perennial grasses, and eventually led to their disappearance, along with native perennial herbs. These competitive advantages of exotic C_3 grasses, resulting from a phenology that enables maximum growth during cool-season wet periods, have been implicated in the major historical declines of *T. triandra* in Australian temperate grasslands (Mack 1989).

Soil moisture depletion in spring by *N. neesiana* impacts during the main growth and flowering period of the native grassland flora and therefore must detrimentally affect the productivity and fecundity of this flora. Depletion of spring moisture restricts the opportunities for establishment of spring germinating species (Johnston *et al.* 1999).

Since *N. neesiana* patches consist of proportionally more biomass generated from spring growth and spring soil moisture than areas dominated by *T. triandra*, these infestations must also deplete soil moisture prior to the main growing period of *T. triandra*, placing this dominant species under additional stress when summer rains are poor. The effect on existing plants would be expected to be greatest on remnant tussocks within *N. neesiana* patches and on plants close to patch edges. Similar effects would occur where *N. neesiana* was invading into disturbed areas within *T. triandra* dominated grasslands, reducing *T. triandra* opportunities for recruitment. The availability of seed and the presence of sufficient soil moisture are the major factors affecting seedling recruitment of *T. triandra* (O’Connor 1996). Reduced soil moisture reduces new growth and thus could be expected to reduce seed production and recruitment. Seeding is reportedly not prolific in dry summers (Leigh and Mulham 1965). *T. triandra* seeds usually germinate in spring in the Melbourne region (McDougall 1989, McDougall and Morgan 2005), and Stafford (1991) reported germination under experimental conditions in October in South Australia, while seedlings generally establish in spring and summer in temperate Australia when soils are moist (Virtue and Melland 2003). Soil moisture depletion by *N. neesiana* is thus likely to negatively affect both fecundity and recruitment of *T. triandra*.

Nassella neesiana tussocks have a centrifugal growth form, continually expanding their size, and growing outward. Experiments with *Bouteloua gracilis* (Willd. ex Kunth) Lag. ex

Griffiths have demonstrated that such directional growth results in higher water use in the direction of expansion than in the trailing direction (Lauenroth and Aguilera 1998). Differential depletion of soil water at the edge of expanding *N. neesiana* fronts can thus be a mechanism driving further infestation expansion, and establishment and occupation in areas where *T. triandra* is dying away due to senescence, or has been removed by other disturbance mechanisms.

In south-eastern Australian natural grasslands where *T. triandra* is the dominant grass, the above scenario suggests that any negative impact on *T. triandra* growth and reproduction is effectively a positive feedback for *N. neesiana*, which may be partially propelling its own invasion through patch expansion via spring soil moisture depletion, or at least enable it to maintain occupation of sites it has invaded against re-establishment by *T. triandra*. Thus, increased early summer aridity created by C_3 grass water use has been cited as a likely cause of widespread decline of summer-active grasses throughout the region (Johnston *et al.* 1999). The effect is better characterised as phenological displacement (Cleland et al. 2006) than as competitive superiority.

Effects at the landscape scale

Dunin and Reyenga (1978) and Dunin *et al.* (1978) presented evidence that *T. triandra* grassland uses less water than sown pastures of exotic C_3 grasses, and has a water use pattern that results in greater runoff. Soil water under *T. triandra* is close to field capacity in late winter and spring is wholly depleted by the end of summer, and the soil remains dry longer into the autumn. Excess rainfall in *T. triandra* grasslands largely results in stream flow, whereas in areas dominated by C_3 species the excess results in deep drainage (recharge), particularly in winter (Dunin 1999, Johnston *et al.* 1999). A similar pattern was apparent in pastures dominated by the small- statured native C_4 *Bothriochloa macra* (Steud.) S.T. Blake compared to the large introduced C_3 *Phalaris aquatica* L. near Wagga Wagga, NSW (Johnston *et al.* 2003): the C_4 catchment produced 10 times more runoff than the C_3 pasture, dried the subsoil more frequently and more completely by greater water use from November to March, and probably prevented groundwater recharge (Johnston *et al.* 2003). Reduction of deep drainage requires increasing the soil water deficit before autumn rains (Singh *et al.* 2003). Replacement of C_4 dominant grasslands by summer dormant C_3 grasslands in south-eastern Australia has thus contributed to dryland salinity across large areas, by raising water tables and mobilising salts stored in the subsoil (Johnston *et al.* 1999, Singh *et al.* 2003, Reseigh *et al.* 2008).

When summer growing grasses are absent from temperate Australian grasslands the use of nitrogen mineralised from organic matter (nitrate and ammonium) in summer is reduced, which enhances its leaching in autumn and results in increased rates of soil acidification

(Johnston *et al.* 1999) and presumably of eutrophication at lower elevations in the catchment. Johnston et al. (2003) found that a C_3 pasture they studied at Wagga had higher nutrient (N and P) wash off risk than a matched C_4 *Bothriochloa macra* pasture.

The replacement of summer growing grasses by winter annuals and summer dormant perennials has already had major hydrological implications in the Murray Darling catchment (Johnston *et al.* 1999 2003) and the continued replacement of *T. triandra* by *N. neesiana* will add to these effects.

Conclusions

Surface soil moisture levels under *N. neesiana* swards in spring were consistently found to be significantly lower than under immediately contiguous swards of *T. triandra* in an ACT grassland, whatever the condition of the swards. Increased drying of the soil in spring may be one mechanism by which *N. neesiana* causes ongoing losses of native plant species once it is established, an effect likely to operate because a high proportion of the natives grow and flower during this period. Soil water depletion in spring probably disadvantages the later growing *T. triandra*, creating a positive feedback cycle for *N. neesiana* that may enable continued occupation of a site after the disappearance of *T. triandra*, and help propel invasion outward from infestation edges.

At a landscape scale, widespread replacement of summer growing native grasses by *N. neesiana* is likely to result in declines in runoff and stream flow and increased recharge, contributing to increased salinity, soil acidification and eutrophication at lower elevations in the catchment. *Nassella neesiana* populations may therefore impact on biodiversity far beyond the areas immediately invaded.

Further research

The review by Görgens and van Wilgen (2004) enables insight into necessary steps beyond the finding reported in this chapter of a difference in water use between an invasive species and indigenous vegetation in a single location and season. How does the effect vary under different rainfall regimes, and are effects measurable in runoff at the small catchment scale or in the groundwater via boreholes? What happens to water use at the plant community level when the alien is controlled or replaced, and are there demonstrable economic benefits in investment in weed management to deliver improved water supplies? Such questions should be addressed by further research.