Influence of nutrition and stress on sugar maple at a regional scale

Richard A. Hallett, Scott W. Bailey, Stephen B. Horsley, and Robert P. Long

Abstract: Sugar maple (*Acer saccharum* Marsh.) decline disease on the Allegheny Plateau (region 1) resulted in high levels of mortality during the 1990s. Sugar maple was predisposed to decline because of an imbalance in Mg, Ca, and Mn nutrition and incited to decline by repeated defoliation. We sampled 33 stands in New York, Vermont, and New Hampshire (region 2) to determine if this model of sugar maple decline applies to a broader region. Low Ca and Mg and higher Mn levels were correlated with poorer tree health in both regions, but region 2 stands had little defoliation and few dead trees, suggesting that both unbalanced nutrition and stress are required for mortality to occur. We predict that stands with low foliar Ca and Mg and high Mn levels would incur increased mortality if stressed. In region 2, relationships between Ca, Mg, and Mn levels and dieback suggested that impacts on sugar maple may be caused by nutritional imbalance alone. Partial correlation analysis suggests that antagonism between Mg and Mn is the most important nutritional factor in region 1, while Mn supply is most important in region 2. We suggest that more research is needed on the interacting roles played by Ca, Mg, Al, and Mn in sugar maple performance.

Résumé : Le dépérissement de l'érable à sucre (*Acer saccharum* Marsh.) sur le plateau des Appalaches (région 1) a causé beaucoup de mortalité durant les années 1990. L'érable à sucre était prédisposé au dépérissement à cause d'un déséquilibre nutritionnel impliquant Mg, Ca et Mn et le dépérissement a été déclenché par des défoliations répétées. Dans cette étude, nous avons échantillonné 33 peuplements dans les États de New York, du Vermont et du New Hampshire (région 2) pour déterminer si ce modèle de dépérissement de l'érable à sucre pouvait être appliqué à une région plus vaste. Une concentration faible de Ca et de Mg et élevée de Mn était corrélée avec le mauvais état de santé des arbres dans les deux régions mais il y avait peu de défoliation et d'arbres morts dans les peuplements de la région 2, ce qui indique que le déséquilibre nutritionnel et le stress sont tous les deux nécessaires pour qu'il y ait de la mortalité. Nous prédisons que la mortalité augmentera dans les peuplements dont la concentration foliaire de Ca et Mg est faible et celle de Mn est élevée s'ils subissent un stress. Dans la région 2, les relations entre Ca, Mg et Mn et le dépérissement indiquaient que les impacts sur l'érable à sucre pourraient être causés par le déséquilibre nutritionnel seul. L'analyse de corrélation partielle indique que l'antagonisme entre Mg et Mn est le facteur nutritionnel le plus important dans la région 1 tandis que l'apport de Mn est plus important dans la région 2. Nous croyons qu'il faudrait plus de recherches sur les interactions entre Ca, Mg, Al et Mn et sur leur rôle dans la performance de l'érable à sucre.

[Traduit par la Rédaction]

Introduction

Decline diseases of trees are thought to be the result of interactions among abiotic and biotic factors, in contrast to tree dieback or mortality events that are attributable to single abiotic or biotic factors (Manion and Lachance 1992). Declines are ephemeral events that typically result in a gradual loss in tree vigor, which often ends in tree mortality. Manion (1991) defined decline as "an interaction of interchangeable, specifically ordered abiotic and biotic factors to produce a gradual general deterioration, often ending in death of trees". Manion categorized these factors as predisposing, inciting (or triggering), and contributing, to describe the way each factor might participate in the tree-decline process.

Houston (1992) developed a similar concept of tree decline from studies on Wisconsin sugar maple (*Acer saccharum* Marsh.) blight during the late 1950s and subsequent physiological and biochemical studies (Houston 1999). Houston (1992) proposed that "disease manifestation (progressive crown dieback sometimes leading to continued tree decline and death) results when one or more predisposing (*sensu stricto*) stress factors reduces resistance to invasion by opportunistic, secondary-action organisms that result in death of tissues — sometimes of trees". The scientific team investigating the Wisconsin sugar maple blight episode documented the decline scenario as 10 months of drought (Skilling 1964) followed closely by a complex of three insect species (the leaf rollers *Sparganothus acerivorana* and *Acleris chalybeana* and the maple webworm, *Tetralopha asperatella*) defoliating the trees at different times of the

Received 21 September 2005 Accepted 19 April 2006. Published on the NRC Research Press Web site at http://cjfr.nrc.ca on 7 September 2006.

R.A. Hallett.[1] USDA Forest Service, Northeastern Research Station, 271 Mast Road, Durham, NH 03824, USA.
S.W. Bailey. USDA Forest Service, Northeastern Research Station, Hubbard Brook Experimental Forest, 234 Mirror Lake Road, Campton, NH 03223, USA.
S.B. Horsley. S.B. Horsley. USDA Forest Service, Northeastern Research

 doi:10.1139/X06-120

growing season (Giese et al. 1964), and finally attack by the opportunistic fungus *Armillaria mellea* (Houston and Kuntz 1964). Defoliation and mortality occurred for 2 years, then began to subside with the collapse of the defoliator population. Houston’s (1992) model suggests that drought and defoliation stress predisposed trees to decline by altering the resistance of sugar maple tissue to invasion by *Armillaria* spp., which subsequently triggered decline. Houston and others subsequently clarified that stress from an abiotic factor such as drought and a biotic factor such as defoliation lowered tree resistance by altering carbohydrate, nitrogen, and phenolic defense chemistry, making root tissue susceptible to invasion by *Armillaria* spp. (Houston 1992).

More recently, well-documented episodes of sugar maple decline occurred in Massachusetts in the 1960s (Mader and Thompson 1969), in Ontario in the 1970s (Hendershot and Jones 1989; Gross 1991), in Quebec, New York, and Vermont in the 1980s (Bernier and Brazeau 1988; Kelley 1988; Allen et al. 1992*b*; Ouimet and Camiré 1995), and in Pennsylvania in the 1980s and 1990s (Kolb and McCormick 1993; Long et al. 1997; Horsley et al. 2000). Decline events were usually characterized by a loss of crown vigor, including increased foliage transparency, fine-twig dieback, and loss of major branches, and by increased whole-tree mortality.

Stress events including defoliations, droughts, and extreme weather events (late spring frosts, midwinter thaw/freeze cycles) were common themes in all of these declines. However, foliage and soil sampling in the more recent sugar maple declines suggests that deficiency of the base cations Ca, Mg, and K and (or) excesses of the potentially toxic cations Al and Mn may have been a predisposing factor in sugar maple decline (Bernier and Brazeau 1988; Côté et al. 1995; Wilmot et al. 1995).

The goal in our initial work was to develop a broadly ap-

	Region 1 (n = 43)			Region 2 (n = 33)	
Variable	Mean	Range	p	Mean	Range
Stand characteristic					
Basal area ($m^2 \cdot ha^{-1}$)	30 (0.97)	15–45	**0.01**	34 (1.00)	24–47
Percent sugar maple basal area	59 (0.03)	23–95	0.10	67 (0.04)	25–99
Elevation (m a.s.l.)	570 (12)	386–767	0.07	511 (30.00)	71–885
DSI 10	2.7 (0.4)	0–8	**<0.001**	0.06 (0.06)	0–2
Foliar nutrition					
Calcium concn. ($mg \cdot kg^{-1}$)	8062 (519)	3146–17399	0.16	9539 (894)	3161–24106
Magnesium concn. ($mg \cdot kg^{-1}$)	1100 (52)	499–1781	0.37	1200 (100)	457–2867
Manganese concn. ($mg \cdot kg^{-1}$)	1686 (112)	718–3738	**<0.001**	1011 (115)	179–3113
Phosphorus concn. ($mg \cdot kg^{-1}$)	1314 (41)	953–2073	0.54	1357 (59)	926–2448
Potassium concn. ($mg \cdot kg^{-1}$)	7993 (185)	5693–11154	0.87	8046 (280)	5187–11420
Ca:Mn molar ratio	9 (1)	2–27	**0.004**	25-(5)	2–103
Mg:Mn molar ratio	2 (0.2)	0.4-4	**0.005**	5 (1)	0.5–26

Note:

be explained by soil properties emphasizing the chemistry of the B horizon (Leaf 1973; Morrison 1985; Bailey et al. 2004).

Evaluation of stand health

Stand health was evaluated in mid to late July in 1996 and 1997 (region 1) or 1998 and 1999 (region 2) using North American Maple Project protocols (Cooke et al. 1996), following the modifications made by Horsley et al. (2000). Note that no stands that were impacted by the January 1998 ice storm were included in this study. Within each stand, three 400 m^2 circular plots were established to evaluate stand and site characteristics. Within each of the three 400 m^2 circular plots, all standing live and dead trees ≥10 cm in diameter at a height of 1.4 m (diameter at breast height (DBH)) were evaluated by species, DBH, and crown class (dominant, codominant, intermediate, suppressed).

We used three variables that integrate sugar maple health over varying lengths of time: percent dead sugar maple basal area (PDEADSM), crown-vigor index (SMVIG), and percent fine-twig dieback (PSMDIE). PDEADSM integrates tree health over a relatively long period of time. Dead trees were included as long as they were standing and had a measurable DBH (1.4 m). The measure may not be useful for distinguishing stands in which sugar maple is healthy or declining during the early stages of decline where minimal tree mortality has occurred. However, where enough time has elapsed for dead trees to accumulate, PDEADSM is a discriminating measure; in our work it had the highest *F* value in a cluster analysis to determine healthy and unhealthy stands in region 1 (Horsley et al. 2000). SMVIG integrates crown health over a relatively long period of time. The measure includes dead trees and, depending upon the stage of decline, may include trees with crowns that are continuing to deteriorate, as well as those that are recovering or have recovered. PSMDIE integrates health over a somewhat shorter period of time. The measure includes only living trees and integrates health conditions as long as fine twigs (<2.5 cm diameter) remain attached and visible (2–5 years). Consequently, PSMDIE is a useful indicator of incipient decline, but is of lesser value where dead trees are abundant and recovering live trees have few visible dead fine twigs. Measures of health were estimated for each tree.

PDEADSM was calculated as the proportion of the total stand basal area of sugar maple that is dead (SMVIG = 5).

SMVIG increases as crown health decreases. Values were estimated according to Cooke et al. (1996): 1, healthy (no major branch mortality); 2, light decline (10%–25% of the crown damaged); 3, moderate decline (26%–50% of the crown damaged); 4, severe decline (>50% of the crown dam efficients (r) with Bonferroni-adjusted probabilities were used to measure the strength of association between foliar element concentrations and the health measures used in this study. Partial correlation analysis was conducted on only those elements that had statistically significant Pearson's correlation coefficients ($\alpha \leq 0.05$) with health measures in both regions. Partial correlation analysis was conducted because the foliar elements with the strongest relationship to health (Ca, Mg, Mn) were highly correlated with each other (Ca, Mg: $r = 0.86$; Ca, Mn: $r = -0.51$; Mg, Mn: $r = -0.55$). This allowed us to examine correlations between health variables and foliar element concentrations without the confounding effects of the strong correlations between the foliar elements themselves. Analysis of variance was used to test for differences among the four categories of foliar concentration × defoliation stress (DSI 10) in region 1 — (1) high concentration, low stress; (2) high concentration, high stress; (3) low concentration low stress; and (4) low concentration, high stress — and the two foliar concentrations at low defoliation stress in region 2 (the same as categories 1 and 3 in region 1). Single degree of freedom polynomial contrasts were used to separate the means of categories 4 vs. 1, 2, and 3; the mean of categories 1 vs. 2, and the mean of categories 1 vs. 3 in region 1. Thresholds of high versus low foliar concentration and high versus low defoliation stress were those empirically determined for region 1 by Horsley et al. (2000): Mg: 700 $mg \cdot kg^{-1}$; Ca, 5500 $mg \cdot kg^{-1}$; Mn, 1900 $mg \cdot kg^{-1}$; DSI 10 = 4. An α value of 0.05 was the nominal indicator of statistical significance for all tests. Statistical tests were conducted using SYSTAT® version 10.2 (Wilkinson 2002).

Results

Stand characteristics

Study stands were relatively mature northern hardwoods. Mean basal area was 32 $m^2 \cdot ha^{-1}$ for all study stands regionwide and region 2 had a slightly higher mean basal area than region 1 (Table 1). PDEADSM ranged from 23% to 99% of total stand basal area and values were similar within each region (Tables 1 and 2,). In addition to sugar maple, species that commonly occurred in the study stands included black cherry (*Prunus serotina* Ehrh.) and white ash (*Fraxinus americana* L.) in region 1 and American beech (*Fagus grandifolia* Ehrh.), red maple (*Acer rubrum* L.), and yellow birch (*Betula alleghaniensis* Britt.) in region 2 (Table 2). The range of elevations at which sugar maple stands were located was marginally greater (both higher and lower) in region 2 than in region 1 (Table 1). The incidence of defoliation was significantly greater in region 1 than in region 2. Over the past decade the stands in region 1were defoliated an average of 2.7 times versus an average of 0.06 defoliations for the stands in region 2 (Table 1). Of the region 2 stands sampled, 1 stand was defoliated once in the past decade, 1 stand was defoliated once in the past two decades, and 11 stands were defoliated once or twice in the past 30 years. None of the stands in region 2 approached the number and severity of defoliations associated with declining stands in region 1.

Foliar nutrients

The mean and range for all nutrients were similar in regions 1 and 2 (Table 1). There were no significant differences between the regions except that foliar Mn concentration and the molar ratios of Ca and Mg with Mn were higher in region 1.

Sugar maple health

PDEADSM ranged from 0 to 56 in region 1 and fell between 0 and 15 in region 2. SMVIG values ranged from 1 to 3.7 for all study plots. PSMDIE values were between 3.8 and 17.7 regionwide.

Correlations between foliar nutrients and health

Region 1

Correlations between health measures and concentrations of foliar nutrients in region 1 stands are listed in Table 3. Ca and Mg showed a strong relationship with tree health as indicated by the relatively high negative correlations with PDEADSM, SMVIG, and PSMDIE. Manganese had a relatively high positive correlation with PDEADSM and SMVIG; the relationship with PSMDIE was marginal. P and K were not related to any of the health measures.

Region 2

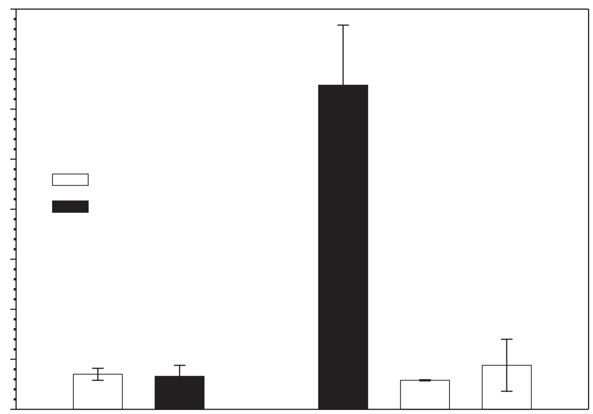
PDEADSM was not significantly related to concentrations of any of the foliar elements measured (Table 3). However, Ca and Mg were negatively correlated with SMVIG and PSMDIE. Mn showed a strong positive correlation with PSMDIE. Again, P and K were unrelated to health measures.

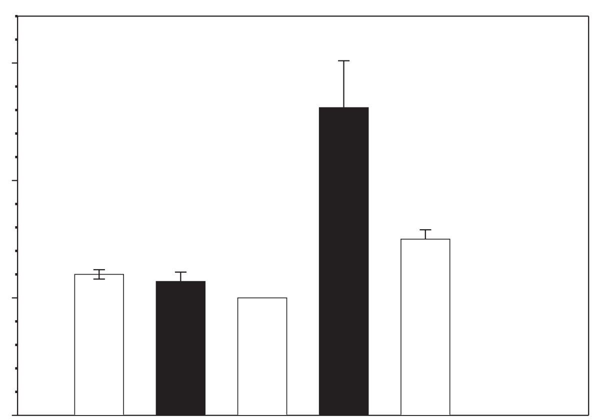
Foliar nutrient ratios in regions 1 and 2

Correlations of Ca:Mn and Mg:Mn molar ratios with health variables were generally weaker than those for Ca,

(PDEADSM). In region 2, where defoliation stress was absent, slightly poorer crown health (SMVIG, PSMDIE) was found in stands with imbalanced Ca, Mg, and Mn nutrition but did not result in increased sugar maple mortality. Stands with low Ca or Mg and high Mn concentrations and low defoliation-stress levels in region 1 did not have poorer crown health as in region 2. In region 1, all stands with imbalance in nutrition and low stress levels were defoliated once in the preceding 10 years. Some fine-twig dieback may have occurred for a few years following defoliation. However, there is an abundance of evidence that once stress, e.g., insect defoliation, abates, crown vigor and growth of surviving trees improve, often returning to predecline levels (Giese et al. 1964; Houston and Kuntz 1964; Hendershot and Jones 1989; Gross 1991; Allen et al. 1992*a*; Houston 1992; Payette et al. 1996; Long et al. 1999). By the time of our crown-health evaluations, many of the dead twigs had fallen from the trees and were no longer observable. Thus, as pointed out earlier, PSMDIE may not reflect stand health as well as PDEADSM or SMVIG does in situations where decline has been occurring for a long period of time and both recovering and dying trees may be present. Overall, we conclude that imbalance in Ca, Mg, and Mn nutrition alone is not sufficient to increase sugar maple mortality; an inciting stress factor also is required.

However, imbalance imDEADSMimDErequired.





Mn functions in plant metabolism in several important ways: in photosynthesis, particularly electron transport in photosystem II, photodestruction of chlorophyll and chloroplast structure; in N metabolism, particularly the sequential reduction of nitrate; in aromatic ring compounds as precursors for aromatic amino acids, hormones (auxins), phenols, and lignins (Campbell and Nable 1988). In excess, Mn has been associated with reduced leaf chlorophyll, net photosynthesis, and leaf carbohydrates (Hecht-Buchholz et al. 1987; Nable et al. 1988; Marschner 1995; St. Clair et al. 2005; Kitao et al. 1997). The negative effect of high Mn concentration on sugar maple health is supported by McQuattie and

Schier (2000), who conducted a dose–response study on sugar maple seedlings and found that increased Mn levels reduced concentrations of all foliar nutrients except P. Moreover, on three of our region 1 sites with low sugar maple foliar Ca and Mg and high foliar Mn concentrations, St. Clair et al. (2005) found a strong relationship between impaired photosynthesis and high late-season antioxidant enzyme activity in the foliage of dominant and codominant trees. The impact of low Ca and Mg supply and Mn toxicity on photosynthesis leads to a direct effect on levels of carbohydrate and energy that are available to build new tissues and repair damaged tissues. Using electron microscopy and energy-dispersive X-ray microanalysis, McQuattie et al. (1999) have demonstrated dense Mn-containing material in sugar maple leaf chloroplasts and delayed transport of starch out of chloroplasts to roots and other carbohydrate-storage locations. Applications of dolomitic limestone to stands containing sugar maple (Long et al. 1997) that increased soil pH and foliar and soil Ca and Mg concentrations and decreased foliar and soil Al and Mn concentrations resulted in an increase in crown vigor and root starch content (Wargo et al. 2002).

Defoliation stress creates a massive demand for carbohydrates to repair the damaged crown (Wargo 1972; Wargo 1981*a*, 1981*b*; Gregory and Wargo 1986; Renaud and Mauffette 1991; Wargo and Harrington 1991; Kolb and McCormick 1993; Wargo 1999). Starch reserves at the end of the growing season may be unaffected by defoliations that occur very early in the growing season, but defoliations that are followed by refoliation during the same growing season or multiple defoliations in the same or subsequent years can reduce carbohydrate reserves to the point where they are inadequate to support over-winter respiratory demands, result-trees, followed by inciting or triggering events that result in dieback and mortality. Furthermore, the results of this study suggest that foliar nutrient (Ca, Mg, and Mn) thresholds could provide land managers with a diagnostic tool to help determine which sugar maple stands are “at risk” of experiencing an increase in mortality in the face of excessive stress, such as deep soil freezing, drought, and (or) insect defoliations.

The results of our study suggest that sugar maple is predisposed to decline by imbalance in Ca, Mg, Mn (and Al) and incited to decline by excessive stress, particularly from defoliation. Increased effort to study the interacting roles of Ca, Mg, Mn, and Al in the physiology, health, and growth of sugar maple is warranted.

Acknowledgements

We thank Ernie Wiltsie, Ralph Perron, and Jen Pontius for their assistance in the field and laboratory. Steve Fay of the USDA Forest Service, White Mountain National Forest, provided knowledge and assistance in stand location, foliar sampling, and stand history. Bob Cooke of the USDA Forest Service, Northeastern Area, State and Private Forestry, trained field crews in health-rating techniques and assisted with rating study stands. Tom Luther and John Omer of the USDA Forest Service, Northeastern Area, State and Private Forestry, provided digitized defoliation sketch maps of study areas and assistance with ArcView®. We also thank Tom Kolb and Dave Houston for their comments on an earlier

piled by A.G. Raske. State University of New York, Syracuse, N.Y. p. 47.

Kitao, M., Lei, T.T., and Koike, T. 1997. Effects of manganese toxicity on photosynthesis of white birch (*Betula platyphylla* var. *japonica*) seedlings. Physiol. Plant. **101**: 249–256.

Kolb, T.E., and McCormick, L.H. 1993. Etiology of sugar maple decline in four Pennsylvania stands. Can. J. For. Res. **23**: 2395–2402.

Leaf, A.L. 1973. Plant analysis as an aid in fertilizing forest. *In* Soil testing and plant analysis. *Edited by* L.M. Walsh and J.D. Beaton. Soil Science Society of America, Madison, Wis. pp. 427–454.

Long, R.P., Horsley, S.B., and Lilja, P.R. 1997. Impact of forest liming on growth and crown vigor of sugar maple and associated hardwoods. Can. J. For. Res. **27**: 1560–1573.

Long, R.P., Horsley, S.B., and Lilja, P.R. 1999. Impact of forest liming on growth, vigor, and reproduction of sugar maple and associated hardwoods. USDA For. Serv. Gen. Tech. Rep. NE-261. pp. 55–58.

Lynch, J.A., Grimm, J.W., and Horner, K.S. 1999. Atmospheric deposition: spatial and temporal variations in Pennsylvania 1998. Environmental Resource Research Institute, Pennsylvania State University, University Park, Pa.

Mader, D.L., and Thompson, B.W. 1969. Foliar and soil nutrients in relation to sugar maple decline. Soil Sci. Soc. Am. Proc. **33**: 794–800.

Manion, P.D. 1991. Tree disease concepts. Prentice Hall, Englewood Cliffs, N.J.

Manion, P.D., and Lachance, D. 1992. Forest decline concepts. APS Press, St. Paul, Minn.

Marcais, D., and Wargo, P.M. 2000. Impact of liming on the abundance and vigor of *Armillaria* rhizomorphs in Allegheny hardwoods stands. Can. J. For. Res. **30**: 1847–1857.

Marschner, H. 1995. Mineral nutrition of higher plants. Academic Press, Orlando, Fla.

McQuattie, C.J., and Schier, G.A. 2000. Response of sugar maple (*Acer saccharum*) seedlings to manganese. Can. J. For. Res. **30**: 456–467.

McQuattie, C.J., Long, R.P., and Hall, T. 1999. Sugar maple seedling anatomy and element localization at forest sites with different nutrient levels. USDA For. Serv. Gen. Tech. Rep. NE 261. pp. 59.

Morrison, I.K. 1985. Effect of crown position on foliar concentrations of 11 elements in *Acer saccharum* and *Betula alleghaniensis* trees on a till soil. Can. J. For. Res. **15**: 179–183.

Nable, R.O., Houtz, R.L., and Chenial, G.M. 1988. Early inhibition of photosynthesis during development of Mn toxicity in tobacco. Plant Physiol. **86**: 1136–1142.

National Atmospheric Deposition Program. 2002. National Atmospheric Deposition Program 2001 annual summary. National Atmospheric Deposition Program, Champaign, Ill.

Ouimet, R., and Camiré, C. 1995. Foliar deficiencies of sugar maple stands associated with soil cation imbalances in the Quebec Appalachians. Can. J. Soil Sci. **75**: 169–175.

Parker, J., and Houston, D.R. 1971. Effects of repeated defoliation on root and root collar extractives of sugar maple treess. For. Sci. **17**: 91–95.

Payette, S., Fortin, M.J., and Morneau, C. 1996. The recent sugar maple decline in southern Quebec: probable caused deduced from tree rings. Can. J. For. Res. **26**: 1069–1078.

Reisenauer, H.M. 1988. Determination of plant-available soil Mn. *In* Manganese in soils and plants. *Edited by* R.D. Graham, R.J. Hannam, and N.C. Uren. Kluwer Academic Publishers, Dordrecht, the Netherlands. pp. 87–98.

p

.