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A resource capture efficiency index to compare differences in early growth of four tree species in northern England

Andrew D Leslie (1), Maurizio Mencuccini (2), Mike P Perks (3)

At a trial established in Cumbria, northern England, significant differences in growth rate between tree species were apparent, with cider gum (Eucalyptus gunnii) and alder (Alnus glutinosa) exhibiting most rapid volume and biomass accumulation. Estimations were made of leaf area, specific leaf area, leaf area ratio (based on stem mass not whole tree mass) and length of growing season. These measurements were undertaken to explain tree growth difference and developing a growth potential index based on growing season length and leaf area. The high leaf area of cider gum and alder explained some of their superior growth, while alder also had the longest period in leaf, compared with ash (Fraxinus excelsior) and sycamore (Acer pseudoplatanus). The slow growth of ash can be explained by the short period in leaf and also the relatively low leaf area ratio. Leaf area to stem weight also differed between species with that of ash being relatively low. Specific leaf area was also low for ash, a trait shared with cider gum, which suggests that these species invest highly in each unit of leaf area. Of the tree species assessed, the length of the growing season was longest for alder, enabling it to maintain growth for a longer period. By multiplying growing season by leaf area a resource capture index was calculated and this explained 56% of the variation in stem dry weight between trees. The potential and limitations for using this index are discussed.

Keywords: Eucalyptus gunnii, Fraxinus excelsior, Acer pseudoplatanus, Alnus glutinosa, Resource Capture Efficiency

Introduction
This paper compares the early growth at a trial in northern England of four broad-leaved tree species identified as having potential for short rotation forestry (Hardcastle 2006). Short rotation forestry for bioenergy was identified as a cost-effective and rapid means of reducing greenhouse gases (Matthews & Broadmeadow 2009), yet there is very limited experience of such systems in the UK. While quantifying yields from tree species in short rotation forestry systems is crucial, understanding the underlying factors contributing to their productivity is also important. Yield varies considerably between tree species and on a specific site is dependent on their resource capture efficiency and resource use efficiency (Stape et al. 2004). Resource capture efficiency represents how efficiently a tree is able to allocate its resources to harvesting light for photosynthesis. There are two components: leaf mass fraction (LMF) and specific leaf area (SLA – Poorter et al. 2012). LMF (the ratio of leaf dry mass to total plant dry mass) reflects the priority of allocation of photosynthate to the leaves. Differences in LMF exist among tree species, with higher LMF being an attribute of faster growing trees (Poorter et al. 2012) and also shade bearing trees (Valladares & Niinemets 2008). LMF is higher in evergreen than deciduous trees but this is partly because evergreen trees retain leaves for two or more years (Poorter et al. 2012). This higher LMF in evergreens may therefore be largely because of the lifespan of the leaf rather than higher partitioning of annual photosynthate to leaves (Poorter et al. 2012).

SLA reflects the amount of resources allocated to each unit of leaf area and is the ratio of leaf area to leaf dry mass. SLA is generally higher in conifers, compared with broadleaves and higher in fast growing trees that those that are slow growing. A meta-analysis undertaken by Poorter et al. (2009 in Poorter et al. 2012) found differences in SLA between types of trees were greater than for LMF. High SLA is a characteristic of plants that have a high relative growth rate (RGR), small seed mass and both RGR and SLA were good predictors of a plant’s potential invasiveness. Leaf area ratio (LAR) is a variable that combines LMF and SLA, being the ratio between leaf area and total tree weight and strongly influences RGR, particularly on nutrient rich sites (Poorter & Remkes 1990).

Growth of a tree is also influenced by the duration of its growing season. The length of growing season has a strong influence on a tree’s productivity and differences exist among species, origins and individual trees in terms of their period of dormancy. The dormancy in pioneer trees is largely determined by temperature, rather than photoperiod. In contrast, late successional trees follow a more conservative ap-
Results are compared between the tree species. A re
growth were quantified, and these were
species with enhanced access to nutrients,
origins from long distances away from
the planting site (slightly southern/eastern
locations seems to give more rapid growth)

At this trial, growth was measured but
accumulated temperature above 5 °C;

The hypotheses tested were that: (i)
there were differences in volume and bio-
mass growth, SLA and LAR between the
tree species at the trial; (ii) growth of stem
volume was positively related to leaf area
and growing season; (iii) the differences in
growth between individuals and species
can be explained by their resource capture
efficiency and other aspects of their ecol-
yogy.

Materials and methods

A one hectare trial was established at
Newton Rigg, Cumbria, England (55° 40' 56" N, 2° 47' 22" W) at an elevation of 160
m above sea level. Ash (Fraxinus excelsior),
sycamore (Acer pseudoplatanus) and alder
(Alnus glutinosa) were planted in winter
2008 and cider gum (Eucalyptus gunnii) and
shining gum (Eucalyptus nitens) in April
2009. Excluding the eucalypts, species
selected for the trial were all classified by
EMIS (Perks et al. 2006) as being “suit-
able”, rather than “very suitable” or “un-
suitable” for the site. The transplants were
cell grown 20-40 cm plants raised by Alba
Trees in the Scottish borders and origins
are described in Tab. 1, along with recom-
manded origins for the species.

Aspects of the climate at the trial were
obtained from the weather station at the
Newton Rigg campus and from the Estab-
lishment Management Information System
(EMIS – Perks et al. 2006) and are shown in
Tab. 2.

The trial site was originally grass pasture,
the soil being a slightly acid (pH 6.0) clay
loam brown earth. Soil bulk density was
0.76 at 0 cm to 15 cm depth and 1.07 at
15 cm to 30 cm depth, while the soil nitrogen
concentration was 0.36 g cm⁻³ and 0.29 g
cm⁻³ at 0 cm to 15 cm and 15 cm to 30 cm
depth, respectively (Centre for Ecology and
Hydrology 2015). Soil depth was not mea-
sured but was sufficiently deep to avoid li-
mitations to early tree growth.

The site use was previously improved pas-
ture, which was sprayed before planting with
Propazymide (3.75 litres ha⁻¹) to kill the
sward. The transplants were planted
manually using a “T” notch and protected in
60 cm tubes. Planting was at 2.5 m spac-
ing between rows and 1.5 m spacing within
rows giving a stocking rate of 2667 stems ha⁻¹. Routine spraying of weeds was under-
taken twice during each growing season
using glyphosate (5 litres ha⁻¹). The design
adopted for the trial was a randomised
complete block design, which is the most
commonly used design in forest experi-
ments (Wright & Andrew 1976) and large
10×8 tree plots were adopted.

Measurements and overview of analysis

Measurements taken in the studies are
described in the four sections below. For
the measurements two trees of each of the
four species were selected randomly from
each of the six replicates in the trial. Shin-
ging gum had died in its first winter and is
not included as part of this study.

Stem volume and biomass

Height and root collar diameter were
measured for the twelve trees of each
species in November 2010 (after two grow-
ing seasons) and November 2011 (after
three growing seasons). Between Novem-
ber 2010 and 2011 all the cider gum had
died and so the later measurements were
not possible for this species. Height was
measured using a height rod, while the
root collar diameter was measured to the
nearest 0.1 mm using a digital vernier
gauge and taking the mean of two mea-
surements taken at 90° to one another.

Stem volumes were calculated using height
(h) and diameter (d) and assuming that the
tree stems were conical in shape. To enable
stem weights for the trees to be esti-

ted, wood samples were taken from a
different sample of five trees of each spe-
cies and sections were cut from the base,
middle and top of their stems. Volumes of
these stem samples were measured by a
water displacement method using OHAUS
analytical standard scales to measure
weight which was converted to a volume
using a water density of 1 g cm⁻³. Stem
samples were oven dried at a temperature of
80 °C for 3 days, until no further loss in
weight was observed and then weighed
again to obtain dry weight. Specific gravity
(SG) was then calculated for the water
samples and SG (g cm⁻³) and V (cm³) were
multiplied together to estimate whole-
stem dry weight of the study trees.

Leaf area

In September 2010 after two growing seasons, the crowns of the twelve alder,
ash and sycamore trees measured for stem
volume were wrapped in plastic bird net-

Tab. 1 - Origins of trees used in the trial and recommendations for the origins.

<table>
<thead>
<tr>
<th>Species</th>
<th>Origin</th>
<th>Recommendations</th>
</tr>
</thead>
<tbody>
<tr>
<td>Alder</td>
<td>Zone 108, South west Scotland</td>
<td>Use British provenances¹</td>
</tr>
<tr>
<td>Ash</td>
<td>Zone 108, South west Scotland</td>
<td>Seed stand material or material slightly to the south of planting site²</td>
</tr>
<tr>
<td>Birch</td>
<td>Zone 202, central to north east Scotland</td>
<td>Avoid origins from long distances away from the planting site (slightly southern/eastern locations seems to give more rapid growth)²</td>
</tr>
<tr>
<td>Cider gum</td>
<td>Likely to be from a seed stand at Dipton, New Zealand¹</td>
<td>Origins from Lake McKenzie and Mount Cattley, Tasmania perform particularly well³⁵</td>
</tr>
<tr>
<td>Shining gum</td>
<td>Likely to be from a seed stand at Dipton, New Zealand¹</td>
<td>Victoria provenances are most frost hardy⁴</td>
</tr>
<tr>
<td>Sycamore</td>
<td>Zone 403, Midlands, England</td>
<td>Most British provenances grow well at most sites. May increase productivity by using origins from sites slightly to the south of the planting site²</td>
</tr>
</tbody>
</table>

Tab. 2 - Climate at the trial from: (1) the Establishment Management Information System (EMIS); and (2) from 1971 to 2000 average data from the Newton Rigg weather station (Met Office 2014a, except for minimum temperature, which is from Met Office 2014b). (AT5): accumulated temperature above 5 °C; (CT): continentality; (DAMS): detailed aspect method of scoring; (MD): moisture deficit. A detailed description of these variables is found in Pyatt et al. (2001). Annual rainfall = summer rainfall + winter rainfall.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Value</th>
</tr>
</thead>
<tbody>
<tr>
<td>AT5 (degrees yr⁻¹)</td>
<td>1503.4</td>
</tr>
<tr>
<td>CT (°C)</td>
<td>6.3</td>
</tr>
<tr>
<td>DAMS (mm)</td>
<td>14</td>
</tr>
<tr>
<td>MD (mm)</td>
<td>148.2</td>
</tr>
<tr>
<td>Summer Rainfall (mm)</td>
<td>386.4</td>
</tr>
<tr>
<td>Winter Rainfall (mm)</td>
<td>396.2</td>
</tr>
<tr>
<td>Mean Min Temp (°C)</td>
<td>0.4 (Jan)</td>
</tr>
<tr>
<td>Min Temp (°C)²</td>
<td>-14°C</td>
</tr>
<tr>
<td>Frost days</td>
<td>57.6</td>
</tr>
<tr>
<td>Mean Max Temp (°C)</td>
<td>19.4 (Jul)</td>
</tr>
</tbody>
</table>
tting to trap leaves as they fell. For sym-camore the collections of leaves in late Octo-
bber was straightforward as most of the leaves had already been shed, but for
alder, many leaves had to be carefully re-
moved from the crowns of the sample
trees. For trees with less than fifty leaves
all leaves were measured and for those
with more than 50 leaves, all leaves were
counted and a systematic sample of 50 was
taken. For each leaf, length (L) along the
mid rib and width (W) at the widest point of
the lamina and petiole length (P) was meas-
ured to the nearest millimetre. The
use of netting to capture leaves proved to be
unsuitable for trapping leaves of ash as
their compound leaves disintegrated and
some of the small leaflets fell out of the
bird netting. As such, the leaf length and
width could not be measured but the leaf
stalk (S) without the leaflets, which re-
mained trapped in the netting was mea-
sured for each leaf. For elder gum, the
evergreen species, the method of trapping
fallen autumn leaves was not appropriate.
For each of the twelve trees, all the leaves
were counted, classified as mature or juve-
nile and 50 leaves were removed from the
trees in a systematic way from the bottom
to top of the trees to ensure a good
spread. Measurements of L, W and P were
taken for each type of leaf.
From the leaves collected, a sample of
forty was taken for each tree species
across the range of sizes. L, W and P was
measured and also S for ash and the leaf
area (LA) was then determined using
Compus Eye software (http://www.ehab.
s.com/CompusEye/LeafSArea) and an Ep-
son Perfection 1240 flatbed scanner.
For elder gum forty juvenile leaves and forty
mature leaves were measured. For all spe-
cies, leaves were then dried for 48 hours at
a temperature of 70 °C and weighed to
obtain an oven-dried weight (M) using
OHAUS analytical standard scales and fol-
lowing the approach adopted by Verwijst &
Wen (1996). As the original ash leaves had
disintegrated new ash leaves were col-
lected at the end of the summer of the fol-
lowing year for leaf area and weight deter-
mination purposes.
The total leaf area for the twelve sample
trees of the four species was calculated
using allometric methods, similar to the ap-
proach adopted in other studies (Wargo
1978, Verwijst & Wen 1996, Serdar & Demir-
sosy 2006, Uges et al. 2008). This involved
the determination of relationships be-
tween measurements of L and W (and S
for ash) to leaf area and leaf weight using
least squares regression. Best fit functions
were selected based on R² and standard
error statistics. Best fit relationships were
used to estimate the leaf area of each leaf
sampled from the twelve trees of each
species. For each tree, a mean leaf area
was calculated and this was multiplied by
the total number of leaves present to
obtain an estimate of total leaf area per
tree. For the twelve trees of each species,
the results from the leaf area measure-
ments and of the stem weights were used
to SLA (leaf area/leaf dry mass) and LAR
(leaf area/stem dry weight) parameters.
LAR was calculated based on stem dry
weight rather than the whole tree weight
as below ground biomass was not as-
essed.
Growing season
The same twelve trees of each species
used in the leaf area study, were assessed
during 2011 to determine the length of the
third growing season of the tree species at
the trial. The method adopted elements
from a study of leaf development in rowan
(Sorbus aucuparia – Forest Research 2010)
and one investigating leaf senescence in birch
(Betula pendula – Worrell 2006). The
development of the bud was scored on a 0–
5 scale with 0 for a dormant bud and 5 for
full leaf expansion (the scale was 1 to 6 in
original study from Forest Research 2010).
The stages in the bud burst scoring were as
follows:
0. bud is closed and in a fully dormant win-
ter state;
1. bud is swollen and the bud scales just
start to open, however the bud is still
vertical;
2. bud scales have separated and the
tightly furled leaves are visible. The bud is
bent sideways and can appear “hooded”;
3. bud scales are completely separated,
leaves are starting to unfurl and separate
but the leaflets (pinnae) on each leaf
remain still furled – the leaves appear
brownish in colour since the underside is
predominantly visible;
4. the leaves are elongated and leaflets
have started to separate as well. The
appearance is now much more green
since the topside of the leaves is now visi-
able;
5. all leaflets have separated on the lowest
two leaves and the shoot is expanding.
The end of the growing season was as-
essed through a five stage leaf retention
score based on a four stage scoring system
originally developed by Worrell (2006 – a
zero was added for no leaves). As the trees
were still relatively small, the assessment
was made by estimating the percentage of
the combined leaf area of the tree crown
which was still green, not yellow or brown
or had lost leaves. This was scored in the
following categories:
0. No leaves present;
1. One leaf present to 20% of crown green;
2. 21-40% of crown green;
3. 41-60% of crown green;
4. 61-80% of crown green;
5. 81-100% of crown green.
For ash, sym-camore and elder the growing
season length was calculated by multiply-
all the bud development score or the leaf
retention score by number of days. This
gave a relative measure of photosynthetic
duration. The growing season for cider
gum, an evergreen tree could not directly
be measured in the same way.
Resource capture efficiency
For each of the twelve ash, elder and sym-
camore trees the influence of growing sea-
son and leaf area on growth was examined
using a resource capture efficiency index
(RCI), calculated by multiplying tree grow-
ning season (collected in 2011) by leaf area
(collected in 2010). The formula and units
of measurement are described below (eqn.
1):
\[ RCI = LA \cdot LR \cdot D \]
where \( LA \) is the leaf area (m²), \( LR \) is the leaf retention score, and \( D \) is the length (in
days) of the growing season. The relation-
ship between stem dry weight in 2010 and
resource capture efficiency was investi-
gated.
Statistical analysis
Statistical tests were conducted using
IBM SPSS Statistics v19. The approaches
used to test variables for significance of
differences between species is described in
Fig. 1.
Regression was used to characterise rela-
tionships between L, W and LA and be-
tween L, W and LDV. In SPSS there were
eleven functions available for regression

<table>
<thead>
<tr>
<th>Variables as measured and transformed (LN transformation)</th>
<th>Are the data normally distributed? (Shapiro-Wilkes test)</th>
<th>Are variances equal? (Levene’s test)</th>
<th>Are the data normally distributed? (Shapiro-Wilkes test)</th>
<th>Are variances equal? (Levene’s test)</th>
<th>ANOVA with post-hoc Tukey’s test</th>
<th>Kruskal Wallis and Mann Whitney tests</th>
</tr>
</thead>
</table>
and the best-fit equation was selected by a combination of the smallest standard error of the estimate (SEE) and the highest $R^2$. The same approach was used to define a relationship between stem dry weight and the resource capture efficiency.

**Results**

Where non-parametric approaches to analysis have been applied the median is shown as a measure of centrality, otherwise the mean for the data is presented.

**Stem volume and biomass**

The stem volumes of the twelve trees for the four tree species were assessed in late 2010 after two growing seasons and for the surviving three species in late 2011 after three growing seasons. The data for height, basal stem diameter and calculated volume are shown in Tab. 3. For the two and three growing seasons height, diameter and stem volume were compared between species and significant differences were found by species (Tab. 3).

Tab. 4 shows the specific gravity and stem dry weights after two growing seasons. Kruskal-Wallis and Mann-Whitney tests were applied to these data and significant differences were found and are also described in Tab. 4. Medians for these data are shown.

**Leaf area**

To determine leaf area, relationships between L, W and LA and between L, W and LDW were investigated. The results from best-fit regressions are described in Tab. 5 and Tab. 6. LA (Tab. 5) and LDW (Tab. 6) were estimated for the twelve trees of each species by applying the regression models to the L × W measurements for all but ash, where they were estimated from leaf stalk length. Kruskal-Wallis test and Mann-Whitney tests showed highly significant differences in leaf number, LA and LDW between species. The LA of alder and sycamore were not significantly different, but all others were significantly different.

The LDW of cider gum was different from all others, but differences between the other species were not significant. In terms of leaf number, differences between ash and sycamore were not significant but were significantly different from other species as well as alder and cider gum. LAR and SLA was calculated for the four tree species and the median values are shown in Fig. 2. Statistically significant differences in LAR and SLA were found between species.

Kruskal-Wallis and Mann-Whitney tests were applied to the LAR data and ash LAR was found to be significantly different from the other three species. Kruskal-Wallis and Mann-Whitney tests demonstrated that the SLA of all species were significantly different from each another, except for ash and cider gum. P values were significant for SLA and very highly significant for LAR.

**Growing season**

The period of bud burst and senescence for ash, sycamore and alder for 2011 are shown in Fig. 3. Alder had a longer growing season than the other two species, with an earlier and more rapid bud burst and a later and longer period leading up to complete leaf drop. Ash and sycamore showed a similar response, with sycamore having more rapid bud burst and being slower to drop its leaves.

Cumulative growing season index data was not normally distributed and a Kruskal-Wallis test showed that differences in growing season between species were highly significant, while Mann-Whitney tests showed that there were very highly

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**Tab. 3** - Height, stem diameter and volume for each species after two and three growing seasons. (1) ANOVA and Tukey’s test (mean shown); (2) Kruskal-Wallis and Mann-Whitney U test (median shown); (3) natural logarithm transformed then ANOVA and Tukey’s test (mean shown). The same lower case letter (a, b or c) denotes no significant difference between species.

<table>
<thead>
<tr>
<th>Species</th>
<th>2 growing seasons</th>
<th>3 growing seasons</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Height (cm)</td>
<td>Diameter (mm)</td>
</tr>
<tr>
<td>Alder</td>
<td>155.5 a</td>
<td>28.7 a</td>
</tr>
<tr>
<td>Ash</td>
<td>119.0 b</td>
<td>20.7 b</td>
</tr>
<tr>
<td>Cider gum</td>
<td>199.5 c</td>
<td>35.7 c</td>
</tr>
<tr>
<td>Sycamore</td>
<td>134.0 ab</td>
<td>14.3 b</td>
</tr>
</tbody>
</table>

**Tab. 4** - Specific gravity (SG) and calculated stem dry weight (M) after two growing seasons from 12 randomly selected trees of each species. Kruskal-Wallis and Mann-Whitney U test applied to specific gravity and stem dry weight (medians shown). The same lower case letter (a, b or c) denotes no significant difference between species.

<table>
<thead>
<tr>
<th>Species</th>
<th>Specific gravity (g cm⁻³ Mg m⁻³)</th>
<th>Stem dry weight (g)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Alder</td>
<td>0.391 a</td>
<td>3.759 a</td>
</tr>
<tr>
<td>Ash</td>
<td>0.563 b</td>
<td>3.539 ab</td>
</tr>
<tr>
<td>Cider gum</td>
<td>0.553 c</td>
<td>9.896 c</td>
</tr>
<tr>
<td>Sycamore</td>
<td>0.497 c</td>
<td>2.390 c</td>
</tr>
</tbody>
</table>

**Tab. 5** - Description of the models predicting leaf area, where $y$ is mean area of one leaf (LA) in cm² and $x$ is L (cm) × W (cm) of the leaf, except for ash where $x$ is leaf stalk length and median leaf area by species. Total tree LA was calculated by multiplying number of leaves by the mean area of one leaf and converted in m².

<table>
<thead>
<tr>
<th>Species</th>
<th>Number leaves</th>
<th>Regression model</th>
<th>$R^2$</th>
<th>SEE</th>
<th>Median tree LA (m²)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Alder</td>
<td>202 a</td>
<td>$y = 0.325 x^{0.022}$</td>
<td>0.941</td>
<td>0.202</td>
<td>0.1919 a</td>
</tr>
<tr>
<td>Ash</td>
<td>22 b</td>
<td>$y = 0.1201 x^{2.203}$</td>
<td>0.707</td>
<td>0.524</td>
<td>0.0627 a</td>
</tr>
<tr>
<td>Sycamore</td>
<td>25 b</td>
<td>$y = 0.532 x^{0.021}$</td>
<td>0.964</td>
<td>0.197</td>
<td>0.1856 a</td>
</tr>
<tr>
<td>E. gunii (mature)</td>
<td>657 c</td>
<td>$y = 0.052 x^{0.448} x+1.032$</td>
<td>0.967</td>
<td>0.947</td>
<td>0.4999 a</td>
</tr>
<tr>
<td>E. gunii (juvenile)</td>
<td>657 c</td>
<td>$y = 0.7714 x^{0.581}$</td>
<td>0.881</td>
<td>0.216</td>
<td>0.3599 a</td>
</tr>
</tbody>
</table>

**Tab. 6** - Description of the models predicting leaf area where $y$ is LDW of a leaf in grammes and $x$ is L (cm) × W (cm) of the leaf, except for ash where $x$ is leaf stalk length. Whole tree LDW was calculated by multiplying number of leaves by the mean dry weight of a leaf.

<table>
<thead>
<tr>
<th>Species</th>
<th>Regression model</th>
<th>$R^2$</th>
<th>SEE</th>
<th>Median tree LDW (g)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Alder</td>
<td>$y = 0.054 + 0.001 x + 0.0000751 x^2 - 0.000000292 y^3$</td>
<td>0.967</td>
<td>0.041</td>
<td>21.75 a</td>
</tr>
<tr>
<td>Ash</td>
<td>$y = 0.004 x^2 + 0.005 y - 0.029$</td>
<td>0.853</td>
<td>0.187</td>
<td>12.44 a</td>
</tr>
<tr>
<td>Sycamore</td>
<td>$y = 0.007 - 0.20 x$</td>
<td>0.970</td>
<td>0.099</td>
<td>23.63 a</td>
</tr>
<tr>
<td>E. gunii (mature)</td>
<td>$y = 0.010 x + 0.001 x^2 + 0.029$</td>
<td>0.981</td>
<td>0.017</td>
<td>100.98 b</td>
</tr>
<tr>
<td>E. gunii (juvenile)</td>
<td>$y = 0.012 x + 0.021$</td>
<td>0.932</td>
<td>0.300</td>
<td>100.98 b</td>
</tr>
</tbody>
</table>
significant differences between sycamore and alder, and ash and alder.

**Characterising resource capture efficiency**

A correlation was performed of resource capture index against stem dry weight, which gave an $R$ of 0.729 and was very highly significant ($p<0.0001$). A regression was conducted and the best fitting function was quadratic ($R^2 = 0.557$, SEE = 1.233, $y = -0.17x^2 + 0.683x + 2.267$ – Fig. 4).

As a comparison correlations were separately performed for the two components (growing season index and LA) of the resource capture index against stem dry weight. For growing season index, the correlation with stem dry weight was relatively weak, with an $R$ of 0.444 and a high significance ($p<0.01$). In contrast, the correlation between dry weight and LA was stronger, with an $R$ of 0.733 and was very highly significant ($p<0.0001$). A regression showed the best fitting function to be

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**Fig. 2** - Leaf Area Ratios (LAR) and Specific Leaf Areas (SLA) for the four tree species. Different letters above the bars indicates a significant difference. Confidence intervals are not given because of lack of normality.

**Fig. 3** - Bud burst and leaf retention of ash, sycamore and alder over the growing season of 2011.

**Fig. 4** – Relationship between stem dry weight and resource capture efficiency.
partly explain the fast growth of this species and oaks can be as long as 180 days (Prior & Kendon 1995) and the UK experienced the coldest December in 100 years (Anonymous 2011). This was followed by another severe winter, which apart from that of 2009-2010, was the coldest since the winter of 1985-1986 (Prior & Kendon 2011). The native and naturalised broad-leaves were able to cope with these conditions, but the eucalypts fared badly, particularly the less cold-tolerant shining gum which exhibited complete mortality over each of the two severe winters. An analysis of the cold damage at the trial is described in Leslie et al. (2014). Eucalypts have been planted on a limited extent in the UK; between 2011 and 2016 nurseries sold 220,000 transplants (Purse & Leslie 2016b) and this scale represented trial rather than commercial planting. However, the limited information on suitable origins for cider gum (Cope et al. 2008) and shining gum (Evans 1986) suggests that the origins used in this trial were not particularly well adapted. Furthermore, it is accepted that shining gum is one of the least hardy eucalypts planted in the UK and it is recommended that it be planted only within 20 km of the coast in southern England and closer to the coast elsewhere in the UK (Purse & Leslie 2016a). The severely cold conditions and the origins planted explain some of the eucalypts poor performance.

Of the tree species that survived the first winter, the largest stem volumes were achieved by cider gum and alder, with the eucalypt producing nearly twice the volume of alder (Tab. 3). Cider gum had accumulated the largest leaf area, which would partly explain the fast growth of this species (Tab. 5). The median leaf area of trees of alder (0.1919 m²) was significantly different from ash (0.0627 m²) and cider gum (0.4999 m²), while that of sycamore (0.1856 m²) was significantly different from cider gum. While ash had the lowest leaf area, it attained nearly the same stem volume as sycamore suggesting that it exhibits greater photosynthetic efficiency. Also, the leaf area of alder was not significantly different from sycamore yet it attained a significantly larger stem volume. These observations suggest sycamore has low photosynthetic efficiency. By the end of the third growing season cider gum had died in the winter of 2010-2011 and the relative ranking of the remaining species in terms of stem volume remained the same.

The leaf area of the trees was measured at the end of the growing season and this may not have fully captured the leaf area over the whole season, as it does not incorporate leaf turnover. There are considerable differences in leaf longevity between temperate tree species; mean leaf lifespan of alder is 90 days and in maples and oaks can be as long as 180 days (Kikuzawa 1995). Leaf longevity may explain some of the differences found between species in SLA. The SLA of alder and sycamore was relatively high and cider gum and ash was relatively low (with no significant difference between the two). This suggests a greater allocation of resources per unit leaf area in cider gum and ash and less resources per unit leaf area in sycamore and alder. Generally, there is a positive relationship between leaf mass, leaf area and the longevity of the leaves (Wright & Westoby 2002). Thus some trees invest relatively little in each metre of leaf area, allowing rapid build up of canopy, fast cycling of leaves and high initial growth. In contrast, other trees invest more heavily in each square metre of leaf area but retain these leaves for longer, resulting in a longer period of return from those leaves (Wright & Westoby 2002).

In terms of SLA, this would suggest that trees which retain their leaves for longer periods will have a lower SLA and those with short leaf longevity have a high SLA. Alder leaves are retained by the tree for a relatively short period (Kikuzawa 1995) and so, as found in this study (Fig. 2) exhibit a relatively high SLA of (8.8 m² kg⁻¹) which would support such a strategy, each leaf being allocated a relatively low investment of resources. There are no studies of the leaf longevity of cider gum, but Whitehead & Beadle (2004) note that in general eucalypt leaves are thick, tough and long-lived, a reflection of their evergreen habit and their association with sites of low soil nutrients and mild winters. A study in Australia found Eucalyptus paniculata leaf lifespan to be 1.09 years and that of Eucalyptus umbra to be 2.06 years (Wright & Westoby 2002), but Laclau et al. (2006) studying Eucalyptus grandis in Brazil found unfertilised trees in plantation retained their leaves for 111 days. The relatively low SLA (4.9 m² kg⁻¹) of cider gum (Fig. 2) suggests a relatively long leaf lifespan. Ash also exhibited a low SLA and a study by Alberti et al. (2005) of older trees also found a low SLA for ash, compared with Wych elm (Ulmus glabra). Another characteristic of trees with high SLA, such as the alder and sycamore in this study, is that they tend to exhibit high photosynthetic nitrogen use efficiencies, whereas trees with a low SLA adopt a different strategy, absorbing a greater proportion of the light available through a higher chlorophyll content in the leaves (Poorter & Evans 1998).

Statistically significant differences in specific gravity were found between species, with alder having a particularly low density (Tab. 4), also being lower than the 0.540 Mg m⁻³ cited by Claessen (2005 in Claessen et al. 2010), perhaps due to the young age of the trees. The specific gravity of ash was similar (0.550 as opposed to 0.560 Mg m⁻³) to that found in larger trees from Italy (Alberti et al. 2005) and that of cider gum was similar (0.548 as opposed to 0.500 Mg m⁻³) to that found in French plantations (AFOCEL 2003). The specific gravity was multiplied by stem volume enabling LAR (using stem weight rather than the conventional whole tree weight) to be calculated. This was compared by species and very highly significant differences were found between ash and all other species. Therefore, ash supports a smaller leaf area per unit stem weight than sycamore, alder and cider gum (Fig. 2). A shortcoming of this experiment was not to estimate branch and root weight of the trees, as this would have enabled a true LAR to be calculated and a better understanding of the relative allocation of resources between different parts of these trees. There are known to be differences in the allocation of resources between stem and leaves and roots between tree species (Poorter et al. 2012).
the trial differences were observed; some individuals of shining gum exhibited insta-

dility due to excessive above ground growth, and had fallen over, despite being

upported by a tree shelter and bamboo cane. The other species showed good sta-

ility.

Phenology of temperate trees is deter-

mined by temperature and photoperiod,

with the importance of each of these fac-

tors varying with tree species (Basler &

Korner 2012, Vitasse et al. 2012). This study

used visual assessment of budburst, which is the traditional method used in field dor-

mancy studies (Cooke et al. 2012). The

pattern of bud burst and leaf fall between ash,

alder and sycamore is illustrated in Fig. 3.

This shows that alder begins to come into

leaf earlier than the other two species and

also retains its foliage for longer into au-

tumn, and that ash flushes later and loses

leaves earlier in autumn than the other two

tree species. Basler & Korner (2012) found

that there was no effect of photoperiod on

bud burst of ash or sycamore, while a

study (Vitasse et al. 2012) on the effect of

temperature on budburst in seven temper-

ate trees showed that of those planted at

this trial, ash had the highest sensitivity to

temperature, with sycamore being in the

middle of the ranking. Spring 2011, when

the assessment was made was particularly

warm, being the warmest across the UK

since 1910 (Met Office 2014c). It is likely

that the growing season for 2011 was abnormally long for these species.

The phenology data for ash, sycamore

and alder were based on monitoring the
development and senescence of leaves on

the terminal bud, but development of leaf

area in trees is complex. Focusing on the

terminal bud does not allow the pattern of

whole tree leaf area to be examined and

pioneer trees tend to adopt a different

approach compared to climax species. Cli-

max or forest tree species show a flushing

habit of leaf development, whereas pio-

neers show a successive pattern of leaf

development (Kikuzawa 1995). The pat-

terns of flushing between alder, ash and

sycamore showed differences (Fig. 3). The

progression of leaf unfolding started ear-

lier in alder but was also more gradual in

alder than in the other two species, which

exhibited rapid flushing over a relatively

short period.

Combining leaf area measurements from

2010 with growing season data from 2011
to create a resource capture index ex-

plained 56% of the differences in 2010 stem
dry weight of the trees (Fig. 4). The best

fitting relationship in terms of R² was a

curve, but a linear relationship also pro-

vided a good fit (R²=0.548). The nature of

the relationship is difficult to identify pre-

cisely because of the lack of data at the

higher end of the combined leaf area and

growing season index. A possible explana-
tion for a curved relationship between

growth potential index and stem dry weight is that light interception by ca-

nopies is not linearly related to leaf area

index, but follows a similar curved relation-

ship due to mutual shading of leaves (Can-
nell et al. 1989). This is supported by the

curvilinear relationship between leaf area

and stem dry weight (Fig. 5). Using leaf

area alone explained 54% of the variation in

stem dry weight, only marginally poorer

than combining leaf area and growing sea-

son. This can be explained by the relatively

small differences in growing period be-

tween the tree species. Had the origins

been collected across a wider range of lati-

ditudes it is likely that variation in growing

season between species would have been

greater.

Growth is related to three variables: the

site resources, the resource capture effi-
ciency and the resource use efficiency (Sta-

pe et al. 2004). Multiplying leaf area by

growing season provided a measure of the

resource capture efficiency of the tree spe-
cies at this trial. A combination of greater

leaf area and longer period of growth has

enabled alder to accumulate stem dry

weight more rapidly than ash and sycam-

ore (Fig. 4). The rate of photosynthesis in

trees is strongly linked to the nitrogen content of leaves due to large

amount of leaf nitrogen devoted to chloro-

plasts (Poorter & Evans 1998) and alder,

being a nitrogen fixing tree is likely to be

able to devote larger concentrations of ni-

trogen to its leaves than the other species.

This study also showed that alder exhibited

a high SLA (Fig. 2), allocating relatively little

biomass for every square metre of leaf

area. Trees with high SLA are known to

exhibit high photosynthetic nitrogen use

efficiency (Poorter & Evans 1998) and in
general high relative growth rates (Antinez

et al. 2001). The higher leaf nitrogen con-

centration and this higher photosynthetic

nitrogen efficiency may partly explain why

alder has been able to build up leaf area

rapidly and also use this leaf area effi-
ciently. A further strength of alder is its rel-

cative long growing season (Fig. 3) and this

longer growing season has

enabled alder to accumulate stem dry

weight more rapidly than ash and poten-

tially due to higher leaf nitrogen content,

allowing higher rates of photosynthesis

(Koike & Sanada 1989). Ash was the slow-
est growing species, and had the lowest

leaf area (Tab. 5) and the shortest growing

period of the four tree species (Fig. 3).

Another factor may be low rate of photo-
synthesis in ash; a study by Koike & Sanada

(1989) found that ash (Fraxinus man-
dshurica) had a relatively low rate of photo-
synthesis across soils with a range of levels

of soil nitrogen, when compared with alder

(Alnus hirsuta) and birch (Betula maxmow-

cziana). There were several limitations to this

study. The method used to harvest leaves

at the end of the growing season was un-

suitable for ash and measuring leaf area at

one point in time ignored potential turn-

over of leaves during the growing season.

The approach used to measure growing se-

ason did not allow the estimation of grow-
ing season for cider gum, an ever-

green tree. This prevented a comprehen-

sive comparison of the trees surviving the

first winter. If the study was repeated

the root and branch biomass would also be

estimated to enable calculation of the LAR.

Furthermore, growing season and leaf area

was assessed in two different years and it

would have been more consistent to mea-

sure these in the same year.

Conclusion

It is clear that there are significant differ-

ences in growth between the tree species
tested at this trial. By the end of the sec-

ond growing season all shining gum, the

fastest growing species had been killed by

the cold winter of 2009-2010. Of the surviv-

ing three species, the species with greatest

stem volume after two growing seasons

was cider gum followed by alder (Tab. 3).

After three growing seasons none of the

original eucalypts survived and alder exhib-

ited the largest stem volume, although the

specific gravity of the wood was less than

the other species (Tab. 4). Cider gum had

developed a particularly high LA after two

growing seasons, with alder and sycamore

growing with LA that were not signifi-

cantly different (Tab. 5). However, alder

had grown much more quickly and its

longer growing season (Fig. 3) may contrib-

ute to this higher growth rate. LAR (stem

weight) was particularly low for ash (Fig.

2), indicating that ash allocates less relative

resources to leaves than to its stem. SLA

was also low for ash, as well as cider gum

indicating that these species invest rela-

tively high resources in each unit area of

leaf area, relative to alder and sycamore

(Fig. 2). The strong influence of LA and
growing season on productivity was shown

by creating a resource capture efficiency by

multiplying growing season by LA, and

this explained 56% of the variation in stem
dry weight between trees (Fig. 4). How-

ever, this was only marginally better than
LA alone (Fig. 5). It is likely that growing season would have a greater influence on growth if origins had been selected from a wider range of latitudes.

The results show that for biomass production on similar sites, alder would be a good candidate, being capable of rapidly accumulating LA and exhibiting a long growing season, resulting in high productivity. However, studies have shown that stands of alder emit NOx, which may possibly make it less attractive as a candidate tree for sequestration of greenhouse gases (Arnold et al. 2005, Mander et al. 2008).

**List of abbreviations**
The following abbreviations have been used throughout the text:
- L: length of leaf
- LA: leaf area
- LAR: leaf area ratio
- LMF: leaf mass fraction
- LDW: leaf dry weight
- M: oven dry weight of stem
- RGR: relative growth rate
- S: length of petiole and main midrib in ash
- SG: specific gravity
- SLA: specific leaf area
- V: stem volume
- W: maximum width of leaf

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