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

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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 photosynthesize 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 photosynthesize 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-
**Tab. 1 - Origins of trees used in the trial and recommendations for the origins.** A map of regions of provenance (Zones for Great Britain is available in Forestry Commission (2016). Recommendations from: (1) Worrell (1992); (2) Hubert & Cundall (2006); (3) J. Purse, pers. comm.; (4) Evans (1986); (5) Cope et al. (2008).

<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 provenances</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 site</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 seem to give more rapid growth)</td>
</tr>
<tr>
<td>Cider gum</td>
<td>Likely to be from a seed stand at Dipton, New Zealand</td>
<td>Origins from Lake McKenzie and Mount Cattley, Tasmania perform particularly well</td>
</tr>
<tr>
<td>Shining gum</td>
<td>Likely to be from a seed stand at Dipton, New Zealand</td>
<td>Victoria provenances are most frost hardy</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 site</td>
</tr>
</tbody>
</table>

The site was previously improved pasture, 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 spacing between rows and 1.5 m spacing within rows giving a stocking rate of 2667 stems ha⁻¹. Routine spraying of weeds was undertaken 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 experiments (Wright & Andrew 1976) and large 10×8 tree plots were adopted.

**Measurements and overview of analysis for each study**

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. Shining 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 growing seasons) and November 2011 (after three growing seasons). Between November 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 measurements 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 estimated, wood samples were taken from a different sample of five trees of each species 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 wood 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 netting.
ting to trap leaves as they fell. For sycamore the collections of leaves in late October was straightforward as most of the leaves had already been shed, but for alder, many leaves had to be carefully removed 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 midrib and width (W) at the widest point of the lamina and petiole length (P) were measured 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 remained trapped in the netting was measured for each leaf. For sycamore and alder, 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 juvenile 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 Comp Eye software (http://www.ehab.com/CompEye/LeafSArea) and an Epson Perfection 1240 flatbed scanner. For cider gum, forty juvenile leaves and forty mature leaves were measured. For all species, 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 following the approach adopted by Verwijst & Wen (1996). As the original ash leaves had disintegrated new ash leaves were collected at the end of the summer of the following year for leaf area and weight determination purposes.

The total leaf area for the twelve sample trees of the four species was calculated using allometric methods, similar to the approach adopted in other studies (Wargo 1978, Verwijst & Wen 1996, Serdar & Demirsoy 2006, Ugese et al. 2008). This involved the determination of relationships between 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 measurements 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 assessed.

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 winter state;
1. bud is swollen and the bud scales just started 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 visible;
5. all leaflets have separated on the lowest two leaves and the shoot is expanding.

The end of the growing season was assessed 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, sycamore and alder the growing season length was calculated by multiplying 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, alder and sycamore trees the influence of growing season and leaf area on growth was examined using a resource capture efficiency index (RCI), calculated by multiplying tree growing season length (collected in 2011) by leaf area (collected in 2010). The formula and units of measurement are described below (eqn. 1):

\[
\text{RCI} = \text{LA} \times \text{LR} \times D
\]

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 relationship between stem dry weight in 2010 and resource capture efficiency was investigated.

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 relationships between L, W and LA and between L, W and LDV. IN SPSS there were eleven functions available for regression
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 LA, 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 LA × W measurements for all but ash, where they were estimated from leaf stalk length. Kruskal-Wallis 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 were 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. 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</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 of leaves</th>
<th>Regression model</th>
<th>R²</th>
<th>SEE</th>
<th>Median tree LA (m²)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Alder</td>
<td>202 a</td>
<td>$y = 0.325 x^{0.102}$</td>
<td>0.941</td>
<td>0.202</td>
<td>0.1919 a</td>
</tr>
<tr>
<td>Ash</td>
<td>22 b</td>
<td>$y = 0.1201 x^{2.188}$</td>
<td>0.707</td>
<td>0.524</td>
<td>0.0627 b</td>
</tr>
<tr>
<td>Sycamore</td>
<td>25 a</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. gunnii (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. gunnii (juvenile)</td>
<td></td>
<td>$y = 0.7714 x^{0.84}$</td>
<td>0.881</td>
<td>0.216</td>
<td></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>R²</th>
<th>SEE</th>
<th>Median tree LDW (g)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Alder</td>
<td>$y = 0.054 + 0.001 x + 0.0000075 x^2 - 0.000000029 x^3$</td>
<td>0.967</td>
<td>0.041</td>
<td>21.75 a</td>
</tr>
<tr>
<td>Ash</td>
<td>$y = 0.004 x^2 + 0.005 x - 0.029$</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. gunnii (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. gunnii (juvenile)</td>
<td>$y = 0.012 x + 0.021$</td>
<td>0.932</td>
<td>0.300</td>
<td></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
The winter of 2009-2010 was the coldest in the UK since 1978-1979 and the UK experienced the coldest December in 100 years (Prior & Kendon 2011). This was followed by another severe winter, which apart from that of 2009-2010, was the coldest since the winter of 1985-1986 (Anonymous 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 Claessens (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 (AFOCHEL 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). At
the trial differences were observed; some individuals of shining gum exhibited insta-
dibility due to excessive above ground growth, and had fallen over, despite being
supported by a tree shelter and bamboo cane. The other species showed good sta-
bility.

Phenology of temperate trees is deter-
mained 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 usual 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
therefore 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 ap-
proach compared to climax species. Cli-
max or forest tree species show a flushing
habit of leaf development, whereas pio-
nears 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-
dlier 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-
tudes 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 sycama-
more (Fig. 4). The rate of photosynthesis in
a tree species 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-
atively long growing season compared with
sycamore and ash (Fig. 3). Alder, is also
known to have a short leaf longevity (Koike
& Sanada 1989, Kikuzawa 1995), enabling it
to replace damaged leaves rap-
Idly.

The most rapid growing species, cider
gum was able to develop the highest leaf
area of any of the species over two grow-
ing seasons (Tab. 5), a contributory factor
being that it retains leaves for more than
one growing season. Other factors con-
tributing to the high productivity are the
long period of photosynthetic activity and
the high photosynthetic efficiency known
of eucalypts, particularly under conditions
of high stomatal conductance (Whitehead
& Beadle 2004). Furthermore, the oppor-
tunistic nature of eucalypt growth is likely
to have enabled cinder gum to exhibit a
longer growing season than alder.

The leaf area of alder and sycamore were
not significantly different (Tab. 5) and they
both exhibit high SLA, yet alder had accu-
mulated a greater stem dry weight (Tab.
4), due to a longer period in leaf 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). An-
other factor may be low rate of photo-
synthesis in ash; a study by Koike & Sanada
(1989) found that ash (Fraxinus mand-
shurica) 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 maximow-
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
season did not allow the estimation of
growing season for cinder 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 cinder 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
showing 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 con-
tribute 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 cinder 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
Resource capture efficiency of tree species in England


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